UNIVERSAL
LIBRARY
OU_162818
UNIVERSAL
LIBRARY

OSMANIA UNIVERSITY LIBRARY

Call No. 575/C 89 G Accession No. 32553

Author Crane. M. B. & Lawrence, W. J. C.

Title Genetics of garden plants. 1951

This book should be returned on or before the date last marked below.

THE GENETICS OF GARDEN PLANTS

THE GENETICS OF GARDEN PLANTS

BY

M. B. CRANE

F.R.S., A.L.S., V.M.H.
HEAD OF THE DEPARTMENT OF POMOLOGY

AND

W. J. C. LAWRENCE, V.M.H.

HEAD OF THE GARDEN RESEARCH DEPARTMENT
THE JOHN INNES HORTICULTURAL INSTITUTION, BAYFORDBURY

WITH A FOREWORD BY THE LATE

SIR DANIEL HALL

K.C.B., LL.D., D.Sc., F.R.S.
LATE DIRECTOR, THE JOHN INNES HORTICULTURAL INSTITUTION

FOURTH EDITION

LONDON
MACMILLAN & CO. LTD
1952

This book is copyright in all countries which are signatories to the Berne Convention

—

First Edition 1934
Second Edition 1938
Third Edition 1947
Fourth Edition 1952

PRINTED IN GREAT BRITAIN

TO

THE MEMORY OF

WILLIAM BATESON

1861-1926

FOREWORD TO THE FIRST EDITION

DARWIN changed the whole course of thought on the evolution of animals and plants by turning to the breeders and fanciers of our garden crops and domesticated animals in order to obtain a clue which would lead to an understanding of the mechanism of variation and inheritance. Before Darwin, Thomas Andrew Knight's work with fruit and other horticultural plants had provided some of the earliest examples of controlled breeding ; just as Goss's and Laxton's experimental breeding of the garden pea foreshadowed a method of investigation of problems of inheritance, and yielded results which did not receive their full explanation until the present century. It was by experiments with garden crops again that Mendel laid the foundations of the science of genetics, which deals with the heredity principle invoked by Darwin in his evolutionary theories. The geneticist is not concerned with evolution, though he is always providing material which the student of evolution must take into account, and indeed himself can hardly avoid speculating about evolution. But primarily he is concerned with a more limited field in which exact knowledge is growing from year to year. On the one hand, genetics is extending its range in the way it is linking up with other pure sciences ; on the other, it is offering greater potentialities to the practical plant-breeder.

During the present century we have learnt to regard the chromosomes as made up of the unit bearers of heredity, and on that view have arrived at a much more constructive basis for investigation of the laws of inheritance. Most of the early investigations by which the main principles of mendelian inheritance have been demonstrated have been concerned with plants of a comparatively simple constitution in which the characters are the expression of a single pair of genes. There has been some disappointment that experimenters with many of our garden plants did not find them behave in the simple way that they had been led to expect from mendelian theory. Inheritance there clearly was, but often it seemed to be in the nature of the gradual building-up or intensification of a character instead of the clear-cut

presence or absence expected on mendelian principles. Elucidation of this point came with the discovery that many of our cultivated plants—for example, wheat and oats, the potato, the dahlia, the apple and the strawberry, are polyploids in which the genes governing any character may be repeated many times over.

It follows that the genetic analysis of such plants is a long and complex process, to complete which is very often impracticable, though enough can be done to demonstrate that inheritance is proceeding upon orderly lines in accordance with expectation. It is very necessary, therefore, for the practical plant-breeder to become acquainted with this new knowledge and the lines of work it dictates, sometimes by way of guidance along a tangled path, sometimes as a warning against a blind alley.

But as the work dealing with such plants as are of interest to horticulturists and fruit-growers is scattered through many journals, English and foreign, it is not easy for the plant-breeder, busy with practice, to keep track of all that has been published on his subject. The authors of this book therefore, Mr. Crane and Mr. Lawrence, have endeavoured to bring together under one cover an account of investigations dealing with the plants of the garden and the orchard that have a bearing on the practice of the plant-breeder who is aiming at results of economic value. Both the authors come to their subject with an exceptional foundation of practical experience and are familiar with the practical man's point of view. Singly or jointly they are the authors of some of the most illuminating investigations on the constitution and breeding of certain of our fruits and garden plants. Thus they are fitted, as few other men are, to be guides to the practical plant-breeder in this important field. They learned their science from our great English pioneer in genetics, William Bateson ; they have worked for years under the favourable conditions afforded by the John Innes Horticultural Institution. They speak with authority, and I count myself favoured in that I have in some degree been associated with their work.

A. D. HALL

MERTON
August 1934

PREFACE

THE aim of this book is twofold: first, to give an introduction to the essential principles of genetics and cytology; and secondly, to give an account of recent results in relation to horticulture.

The cytologist studying the life-history of the cell and the intricate processes of germ-cell formation, and the geneticist who is concerned with the consequences of these processes, have in recent years elucidated a number of problems which directly concern the horticulturist. To those engaged in the breeding and raising of productive forms of commercial value, the chromosomes, the principal vehicles of heredity, are of first importance. Not only are they concerned with the identity of the individual, but they also decide whether the resulting offspring will be fertile and productive, or highly sterile and of no commercial value. A knowledge of chromosome numbers and relationships therefore can be of great assistance when considering the practical possibilities of obtaining improvements through the inter-crossing of distinct forms.

The science of genetics has a wide horticultural application; it is of value to the plant-breeder, seedsman and gardener in providing a detailed knowledge of variation and heredity, and guidance in the maintenance of purity in their stocks. Genetics may also be of value to the nurseryman whose business lies in the vegetative reproduction of plants. Many of them are of a peculiar chimerical constitution, and their behaviour both in sexual and asexual reproduction is of practical importance. Again, since effective pollination is a first essential for the formation of fruit, to obtain the best result the fruit grower must interplant varieties which are mutually compatible.

Our knowledge of the genetics of polyploids has been largely developed from investigations with horticultural plants, hence the genetics of garden plants is of direct interest to the student of genetics as well as of use to the plant-breeder and horticulturist.

The literature reporting the results of genetic and cytological

investigations is very considerable and often difficult of access, and friends and correspondents have often expressed to us the need for a book which will bring together recent results and provide an account of modern genetics in relation to orchard and garden plants. With this object in view we have prepared the text which follows.

Our plan has been to describe principles as simply as the technicalities of our subject will allow, illustrating them with typical examples from a range of flowers, fruits and vegetables, and to give references to the original sources of information which may be of interest to the specialist or student. The book will, we hope, serve as an introduction to the science of genetics, and particularly in its application to horticulture.

This edition has been emended and revised in accordance with recent research. The brief account of Heterosis formerly in Chapter VI has been revised and enlarged in a new chapter, number VIII, pages 168, 169 and 169A to 169H. In other chapters additions and occasional rewriting have been necessary to bring the book up to date. Among major additions are the inheritance of flower colour in *Nemesia strumosa*, pages 61-62; the genetics and chemistry of flower colour in the carnation *Dianthus caryophyllus*, pages 82-84; and an account of the genetics of *Brassica oleracea*, pages 108-110.

M. B. C.
W. J. C. L.

BAYFORDBURY
January 1951

CONTENTS

CHAPTER I

PAGE

THE GENETICS OF DIPLOID PLANTS 1

Reproduction—Genetics—Cytology—Heredity—The Gene—Dominance—Segregation—Pure Lines Incomplete Dominance—Mendelian Ratios—Complementary Genes Interaction of Genes—Lethal Genes—Multiple Allelomorphs—Linkage Qualitative and Quantitative Characters—Extra-nuclear Inheritance.

CHAPTER II

THE CYTOLOGY OF DIPLOID PLANTS 16

The Chromosomes—Mitosis—Meiosis—Germ-cell Formation and Fertilisation The Genes—Linkage Crossing-over—Linkage in *Zea Mays*—Chromosome Rearrangement.

CHAPTER III

THE CYTOLOGY AND GENETICS OF POLYPLOIDS . . . 31

Anouploids—The Origin of Polyploids—The Auto-polyploid—The Allo-polyploid—Secondary Polyploids—Secondary Association—Polyploids and Segregation—Chromatid Segregation—Multiple Genes—Hybridisation and Polyploidy—Asexual Reproduction—Apomixis—Parthenogenesis—Vivipary.

CHAPTER IV

FLOWERING AND ORNAMENTAL PLANTS 44

The History and Genetics of the Sweet Pea, the Garden Stock, *Primula sinensis*, the Diploid and Tetraploid Forms—*Nemesia strumosa*—Herbaceous Plants—Inter-specific Hybrids—*Delphinium*—*Iris*.

CHAPTER V

THE CHEMICAL AND GENETICAL BASIS OF FLOWER COLOUR . 70

Anthocyanins—Anthoxanthins—Plastid Pigments—The Chemistry and Genetics of Flower Colour in *Streptocarpus*, *Callistephus*, *Dianthus caryophyllus*, *Dahlia* and *Papaver*.

CHAPTER VI

PAGE

VEGETABLE AND SALAD PLANTS 91

The History and Genetics of the Tomato — The Induction and Genetics of Tetraploid Tomatoes—The History of the Garden Pea—Mendel's Investigations—The Genetics of the Garden Pea; Radish; Lettuce; Onion; Beetroot; Cucumber—Melon—Cabbage—The History and Genetics of the Potato.

CHAPTER VII

FRUITS 127

The Genetics of Peaches and Nectarines—Correlations and Disease Resistance—The Inheritance of Colour and Sex in Raspberries—*Rubus chamaemorus* — Gooseberries — Currants — Cherries — Grapes — The Origin and Development of the Garden Strawberry—The Cherry Plum—*Prunus domestica*—Pears—Apples, Diploid and Triploid Forms.

CHAPTER VIII

HETEROSIS 168

Theory of heterosis—Linkage—Heterosis in maize, in asexual reproduced plants, *Sorghum*, egg plant, tomato, onion—Male sterility and heterosis.

CHAPTER IX

BUD-SPORTS, VARIATIONS AND FLUCTUATIONS . . . 170

Bud-sports—Graft Chimaeras, Method of Production—*Solanum* Chimaeras—*Cytisus Adami*, *Crataegomespilus*, Apple Graft Chimaeras—Autogenous Chimaeras, *Bouvardia*, *Pelargonium*, Apple, *Citrus*, Plum, Pear, Potato, *Coleus*, Rose—Infectious Transmission—Somatic Variations and Plant-breeding — Variegated Plants — Fluctuations — Environment.

CHAPTER X

INCOMPATIBILITY 185

Self and Cross-pollination—Pollen Tube Growth—The Inheritance and Behaviour of Incompatibility—Self- and Cross-incompatibility in *Nicotiana* — *Veronica* — *Verbascum* — Cherries — Plums — Polyploidy and Incompatibility—Apples and Pears—Economic Aspects—Heterostylism.

CHAPTER XI

PAGE

STERILITY 210

Generational Sterility—The Germ-cells and Sterility—Sterility and Chromosome Number — *Rubus* — *Prunus* — *Fragaria* — *Vaccinium* —Apples and Pears—Triploidy and Sterility—Inter-specific Sterility—Relationship of Chromosomes and Fertility—Chromosome Doubling—Morphological Sterility—Strawberries.

CHAPTER XII

XENIA 225

The Action of Foreign Pollen—On the Developing Zygote—The Endosperm—On Maternal Tissue.

CHAPTER XIII

THE ORIGIN OF NEW AND IMPROVED FORMS . . . 233

Gene Mutations—Cultivation—Auto-polyploids—Inter-specific Hybrids —Allo-polyploids—The Origin of *Dahlia variabilis*, *Prunus domestica*, *Aesculus carnea*, *Rubus loganobaccus*, *Primula kewensis*, etc.—Constant Hybrids—The Induction of Mutation and Polyploids—Polyploidy, Fertility and Variation—The Cumulative Effects of Genes—Breeding for Specific Purposes: Hardiness, Resistance to Disease, etc.—Hybrid Vigour—The Processes of Evolution.

APPENDICES—

I. CHROMOSOME NUMBERS OF CULTIVATED PLANTS . . 263

II. GLOSSARY 270

III. BIBLIOGRAPHY 275

INDEX 295

LIST OF ILLUSTRATIONS

FIG.		PAGE
1.	Scheme for Inheritance of Hairy and Glabrous Fruits in *Prunus persica*	5
2.	Foliar Glands of Peaches	7
3.	Diagram illustrating a 9 : 3 : 3 : 1 Ratio in Peaches	8
4.	Diagram illustrating a 9 : 7 Ratio in Sweet Peas (Complementary Genes)	10
5.	Diagram illustrating a 9 : 3 : 4 Ratio in Raspberries (Interaction of Genes)	10
6.	Flower Colour Patterns in *Primula sinensis* (Multiple Allelomorphs)	12
7.	Mitosis : Photograph of a Section through a Root Tip of *Crepis dioscoridis*	16
8.	Chromosome Complements of some Cultivated Plants	17
9.	Diagram of Mitosis	18
10.	Pollen Grains of *Kniphofia corallina*, *Leucojum aestivum* and Hyacinth	19
11.	Drawing of Prophase Chromosomes in *Lilium pardalinum* and *Fritillaria lanceolata*	20
12.	Diagram of Meiosis	22
13.	Diagram illustrating the Cytological Basis of Linkage	25
14.	Map of the chromosomes of Maize	26
15.	Diagram illustrating Types of Chromosome Rearrangement	28
16.	Chromosome Rings in *Campanula persicifolia*	29
17.	Chromosome Complements of Diploid and Polyploid *Rubi*	31
18.	Diagram of Chromosome Constitution of Auto- and Allo-Tetraploids	32
19.	Chromosomes of Apple and *Dahlia* showing Secondary Association	36
20.	Map of the chromosomes of *Lathyrus odoratus*	49
21.	Diagram illustrating the Inheritance of Double Flowers in the Garden Stock	52
22.	*Campanula persicifolia*, Diploid and Tetraploid Forms	64
23.	Diagram illustrating the chemical structure of the basic anthocyanins	72
24.	Diagram illustrating the methylation of anthocyanidins leading to a decrease in blueness of flower colour	73
25.	Diagram illustrating the chemical structure of flavones and flavonols	75

FIG. PAGE

26. Diagram illustrating the chemical structure of the anthocyanins of *Verbena* 78
27. Diagram illustrating the chemical structure of the anthocyanins of *Streptocarpus* 81
28. Diagram illustrating the Origin and Constitution of the Garden Dahlia 90A
29. F_1 Generation from Single-crossed Double Flowers in *Dahlia variabilis* 90C
30. Map of the Chromosomes of the Tomato 94
31. Diagram illustrating the Production of Tetraploid Tomatoes . 95
32. Figure illustrating the Inheritance of Root Shape in Radishes . 104
33. Chromosomes of the Potato, *Solanum tuberosum*, illustrating Secondary Association 121
34. A, polar view, B, side view of meiosis in the potato, showing primary and secondary association of the chromosomes . 123
35. Suggested origin of the cultivated potato 124
36. Branches of Peach Trees, illustrating Correlation between Physiological and Morphological Characters, i.e. Foliar Glands and Resistance to Mildew 128
37. Raspberries: illustrating Correlation between Leaf-shape and Sex 129
38. Graph illustrating Inheritance of Fruit Size in Plums . . 149
39. Graph illustrating Inheritance of Fruit Shape in Plums . . 151
40. Graphs illustrating Inheritance of Fruit Size in Apples . . 155
41. Graphs illustrating Inheritance of Fruit Shape in Apples . 157
42. Chromosome Complements of "Diploid" and "Triploid" Apples 161
43. Three-year-old Seedling Apples from Diploid and Triploid Parents 163
43A. Heterosis in Maize 169D
43B, 43C. Yield of parental varieties and F_1 lines of tomatoes . 169F
44. Diagram illustrating Cross-section of Grafted Stock . . 171
45. Diagrams illustrating different Types of Chimaeras . . 171
46. Periclinal *Solanum* Chimaera produced from Grafting . . 172
47. *Crataegus monogyna*, *Mespilus germanica* and the Periclinal Graft-chimaera *Crataegomespilus Asnieresii* . . . 173
48. Diploid and tetraploid fruits of the pear variety Fertility . 178
49. Potato Golden Wonder; illustrating its chimerical constitution . 179
50. Diagram illustrating Pollen-tube Growth in Compatible and Incompatible Pollinations 187
51. Cherry Variety Early Rivers, Group I, illustrating the Results of Compatible and Self- and Cross-incompatible Pollinations . 188
52. Cherry Variety Bigarreau Napoleon, Group II, illustrating Compatible and Incompatible Pollinations . . . 189
53. Plum Variety Coe's Violet, illustrating Compatible and Incompatible Pollinations, and the Primary Development of the Fruits 198

FIG. PAGE
54. Plum Variety Coe's Violet, illustrating the Final Results of Compatible and Incompatible Pollinations . . . 199
55. Plum Variety Victoria, illustrating Self-compatibility . . 200
56. *Rubus* Hybrids. Triploid and Tetraploid Forms illustrating Sterility and Fertility 211
57. Graphs illustrating Inter-specific Fertility in Cherries . . 221
58. Pollination and Xenia 231
59. Leaves of *Rubus idaeus*, *Rubus rusticanus* and Veitchberry . 242
60. Showing the origin of the Swede 243
61. A, untreated and B, colchicine-treated apple seedlings . . 248
62. Chromosomes of *Rubus* Species and Hybrids . . . 250
63. *Rubus* Hybrids, Sterile and Fertile Forms 251
64. *Rubus rusticanus inermis*, illustrating Diploid and Tetraploid Forms 256
65. *Rubus* Merton Thornless 257
66. Apple Seedlings illustrating Susceptibility and Immunity to Woolly Aphis (*Eriosoma lanigerum*) 258
67. *Solanum pòlyadenium*. A, normal diploid 2n = 24. B, tetraploid 2n = 48 obtained by treatment with colchicine . . 262

CHAPTER I

THE GENETICS OF DIPLOID PLANTS

SINCE individual plants all grow old and die, one of the main objects of the horticulturist is the production of new individuals to perpetuate their kind.

This may be achieved by *asexual* (vegetative) propagation, e.g., by means of cuttings, grafting, division of the rootstock, etc., or by *sexual* reproduction as in the normal method of raising plants from seed. Vegetative propagation is particularly useful when a large number of individuals is required identical in their main characteristics, such as flower colour, height and habit. On the other hand although many plants may be reproduced from seed with considerable uniformity, sexual reproduction is of the greatest importance in giving rise to variety of form from which new and improved selections may be made. Vegetative propagation is usually adopted when a plant is sterile, does not breed true or is more quickly raised to maturity by vegetative means than from seed.

GENETICS

The study of uniformity and variation, of resemblances and differences between plants and the frequency in which the characters constituting these resemblances and differences appear from generation to generation, is the business of the geneticist, whose work therefore is of immediate importance to the raiser of plants.

CYTOLOGY

Ultimately all individuals owe their identity to certain materials received from their parents. In all plants and animals this material is present in every cell, but its transmission from one generation to another depends upon the production of specialised

cells, in plants the pollen and egg-cells—the male and female germ-cells respectively. It is by the fusion of these specialised cells in fertilisation that the parental characters are combined. Therefore it is to a study of the cell that we must turn for a knowledge of the *mechanism* of heredity, by which the characters of the parents are transmitted to their offspring. The study of the cell, its constituents, mode of multiplication and function in the alternation of generations is the business of the cytologist. A knowledge of cytology is fundamental to an understanding of the processes and principles of heredity and evolution which, in turn, are the result of the interaction of the cell with its environment.

Heredity

When we compare the characters and qualities by which we identify the individual plant, we find that, in many ways, offspring resemble one or both of their parents. In other ways they may differ from both parents. Closer comparison frequently shows that various characters are alternative and sharply discontinuous, e.g., white or coloured flowers, red or yellow fruits, annual or biennial habit, single or double flowers, etc., etc. Often a given individual shows one or other of the alternative characters seen in its parents, but not infrequently a third intermediate condition is found. Occasionally an entirely new character may appear suddenly in an individual and be transmitted to its progeny. That these phenomena are not fortuitous is now clearly recognised, and by suitable methods of study under controlled conditions the laws of inheritance have been developed and a knowledge of the mechanism of heredity obtained.

In general the higher plant arises from the union of two germ-cells—the pollen and ovules[1]; in the act of fertilisation, therefore, the units of inheritance must be carried by each of these cells. But examination of the microscopic germ-cells is a tedious process, and so we turn to the *expression* of the units of heredity as manifested in the growing or mature plant for an easier way of approach to the study of inheritance.

In *Prunus persica*, there are varieties with downy skins to the fruit (peaches) and others with smooth-skinned fruits (nectarines). Downy skin and smooth skin constitute a pair of alternative

[1] The ovules are the bodies which contain the female germ-cells.

characters between which there is no intermediate form. If we cross a true-breeding peach with a nectarine, the first generation (F_1) are all peaches. So far there is no evidence that the smooth-fruit character has been passed on to the progeny; but if any of the F_1 now be self-pollinated or crossed together, in the next generation (F_2) nectarines reappear in a proportion of about one-quarter of the total progeny.

From this it is evident that the F_1 plants must have carried something which determined the smooth-skinned character in the following generation, although they themselves were peaches. Similarly, since all the F_1 plants had downy skins, something determining this character must have been passed on to them from their peach parent. This something is called a *factor* or *gene.*

The Gene

The gene is the unit of reproduction in the hereditary material; and a character the end result of a long and complex chain of reactions which, initiated in the genes, cause the production of the character under favourable environmental conditions. For example, it would be said that the downy-skinned character was the end result of the action of a particular gene (or genes) and that this gene had the property of causing hairs of a certain kind to form at a particular period of the plant's development and upon a certain portion of the plant. In the case of the nectarine we should say that the character distinguishing it from the peach was determined by a gene for smooth skin. The fact that a gene (which we may denote by the letter **D**) causes hairs to form on the fruits of the peach must not be taken to mean that this is the only function of **D**, or that **D** independently is able to cause hairs to develop. What it does mean, however, is that the gene **D** is identified by its most conspicuous effect and that if **D** is absent the effect will not be produced. Thus peaches breed true to downy skin not merely because they contain the gene **D** but because their germ-cells contain all the genes necessary for the development of the peach character.

A given character may be the expression of one or many genes, and depend not only on the specific action of one or more genes, but also upon the interaction of all the other genes and of the genes with the environment. Furthermore, the effect of a gene

may be expressed in more than one character. Thus a character may vary in its expression (1) according to the genetic "background" (i.e. the influence of the other genes present), (2) according to the environment.

The precise nature of the gene is at present unknown but it seems probable that it is a highly complex chemical molecule or group of molecules with the characteristic power of self-reproduction. From a genetic point of view it is therefore evident that a plant is a double structure derived from the union of two cells carrying similar or dissimilar genes, the identification of which depends upon the study of differences (e.g., downy *v.* smooth skin).

Dominance

We saw that the F_1 plants from peach × nectarine were all peaches. Since nectarines appeared in the F_2 it is clear that the F_1 plants must have carried the gene for smooth fruit though they themselves were peaches. When one of a pair of alternative characters dominates the other in the development of the individual it is said to be a *dominant* character, whilst the other is said to be *recessive.*

Segregation

If F_3 generations are raised by self-pollinating *individual* F_2 peaches and nectarines, we find that all the nectarines breed true. The peaches, however, are of two kinds; some breed true whilst others behave like the F_1 plants, giving approximately three peaches to every nectarine. As Gregor Mendel showed in his classic experiments on the edible pea, results such as these can be interpreted on simple fundamental laws which are practically universal in application.

Mendel studied pairs of alternative characters (e.g., round and wrinkled seeds, tall and dwarf habit, etc.) and as a result of his investigations he enunciated three principles of heredity, (1) dominance, (2) unit characters and (3) segregation. Mendel's experimental methods and his discoveries were a great advance on previous work and for the first time provided a satisfactory basis for the study of heredity. Since his day, however, a greater knowledge of the mechanism of heredity has been obtained and his laws have been more accurately defined. In consequence the

necessary modifications have been made in the examples which follow. Thus, referring to our peach-nectarine example the results can be interpreted on the assumption that there is a gene (**D**) for downy skin, and another (alternative) gene (**d**) for smooth skin; and that these genes occur in equal numbers in the germ-cells or *gametes* [1] of hybrid (cross-bred) plants. That is to say, at gamete formation there is an orderly distribution or *segregation* of the genes to separate gametes, so that a gamete may carry either of the genes **D** and **d**, but not both. This is Mendel's law of segregation, which, though it must be qualified for complex cases, holds for all plants (and animals) of simple constitution. The result of crossing peaches and nectarines can be represented by the following diagrammatic scheme (Fig. 1).

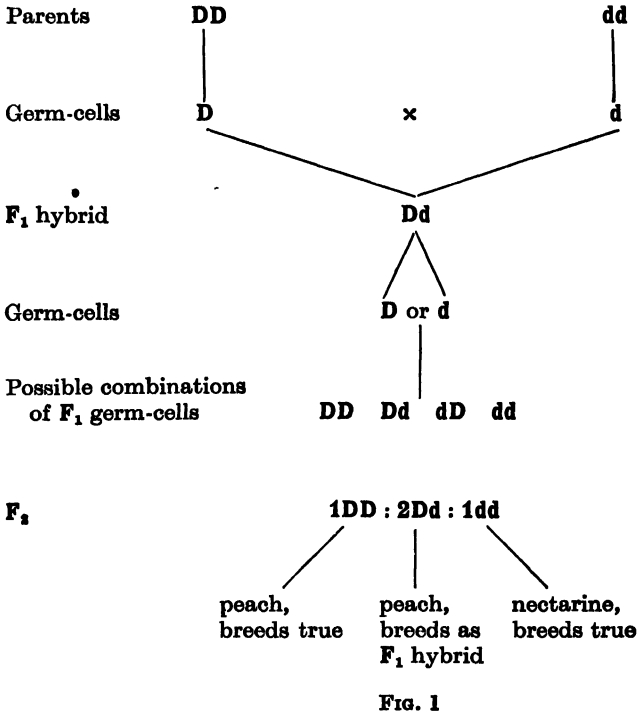


FIG. 1

Since the pollen and ovules of the F_1 plants carry **D** and **d** in equal numbers, a moment's consideration will show that when

[1] Gamete = marrying cell.

union of the gametes occurs in fertilisation to form a new individual or *zygote* [1] there are three possible combinations of the genes, viz. **DD**, **Dd** and **dd**, and of these the **Dd** class will be twice as large as the others. Because of the dominance of **D** the **Dd** class cannot be distinguished from the **DD** class, so that we have three peaches to every nectarine. The *homozygous* classes **DD** and **dd** breed true because their germ-cells carry only **D** and **d** genes respectively, but the *heterozygous* **Dd** class will continue to segregate peaches and nectarines in the proportion 3 : 1. Alternative genes such as **D** and **d** are called *allelomorphs*.

If we back-cross any $\mathbf{F_1}$ individual (**Dd**) with the nectarine (**dd**) parent, i.e. the recessive parent, equal numbers of peaches and nectarines will be obtained. In the hybrid the gametes are produced in equal numbers, 1**D** : 1**d**, which uniting with the **d** gametes of the recessive nectarine give **Dd** and **dd** plants in the proportion 1 : 1. This back-cross ratio directly shows all the different kinds of gametes and the proportions in which they occur, i.e. the *gametic series* of the $\mathbf{F_1}$ plant. For this reason the back-cross to the recessive parent is an invaluable method of analysing the genetic constitution of a hybrid individual.

Pure Lines

The progeny of homozygous plants constitute a *pure line* the individuals of which, as shown by Johannsen (1911) in his classical experiments with beans, may fluctuate slightly in regard to the characters concerned owing to nutritional, environmental or other non-heritable causes, but breed true within the limits of fluctuations.

By self-fertilising a number of plants of the Princess bean and growing their progenies separately, Johannsen was able to establish a number of strains whose seeds exhibited a characteristic mean weight. Within any one of these strains seed size varied considerably, but no matter whether large or small seeds were selected for planting, the progeny had the same average weight of seed. Thus Johannsen was able to show that differences in seed size in such a strain were not heritable differences but arose from nutritional, environmental and other non-heritable causes. Johannsen called such progeny and their descendants a pure line.

[1] A zygote is the individua larising from the fusion of two gametes.

Incomplete Dominance

In certain cases the F_1 hybrids may be more or less intermediate in character between the parents. For example, some varieties of peaches and nectarines have large reniform glands on the base or petioles of the leaves. Some have small round glands, and others again have no glands (Fig. 2). Upon breeding these forms the results show that a gene which we may call **G** governs the

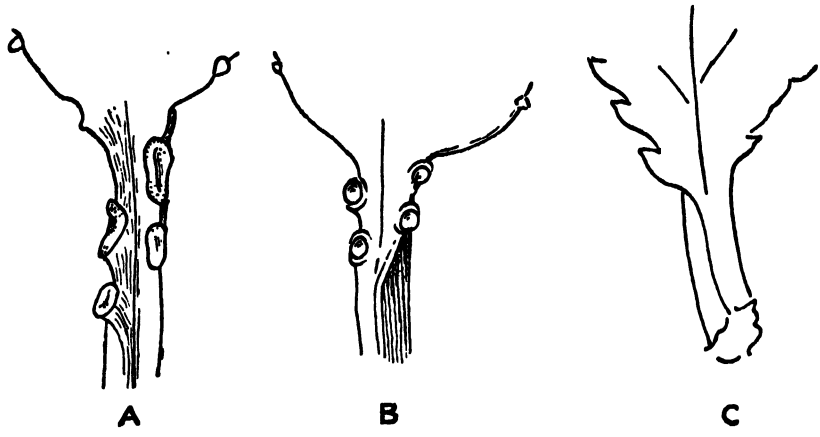


Fig. 2.—Foliar Glands of Peaches.
A, reniform glands. B, round glands. C, eglandular.

development of reniform glands, no glands being formed when **G** is absent. On crossing reniform glands (**GG**) with no glands (**gg**) the F_1 plants are all intermediate in character with small round glands. In such a case neither **G** nor **g** can be said to be dominant. However, in instances where the F_1 approaches one parent more than the other, the character borne by this parent is said to be *incompletely dominant.*

Mendelian Ratios

The application and extension of Mendel's laws to combinations of two or more independent pairs of genes is readily made if we remember that alternative genes are distributed among the gametes independently and in equal numbers. In other words,

the total number of different germ-cells is the number of possible combinations of the particular genes involved. This is the gametic series, from which the F_2 may be calculated. Thus, referring to our example from the peach and nectarine, upon *selfing* (self-pollinating) an individual heterozygous for both pairs of genes **DdGg**, the gametic series will comprise four types in equal numbers, viz. **DG, Dg, dG** and **dg**. Therefore the zygotic series is given by $(DG + Dg + dG + dg)^2$, since any ovule stands an equal chance of being fertilised by any pollen grain, as shown in Fig. 3.

Parents DDGG × ddgg

germ-cells DG, dg

F_1 DdGg

F_1 germ-cells (gametic series) DG, Dg, dG, dg

F_2

	DG	Dg	dG	dg
DG	DDGG	DDGg	DdGG	DdGg
Dg	DDGg	DDgg	DdGg	Ddgg
dG	DdGG	DdGg	ddGG	ddGg
dg	DdGg	Ddgg	ddGg	ddgg

F_2 (zygotic series) = 9 peaches with glands (DG)
3 peaches without glands (Dg)
3 nectarines with glands (dG)
1 nectarine without glands (dg)

FIG. 3

Now in the " Chequer board " square of Fig. 3 all individuals with a **D** gene will be peaches and any with **G** will have glands. Thus the F_2 will comprise nine peaches with glands, three without, three nectarines with glands and one without glands, or the result from (3D + 1d) (3G + 1g). This 9 : 3 : 3 : 1 ratio is the one obtained when any individual heterozygous for two dominant factors is

selfed. In our example, since **G** is not dominant to **g**, the **GG** and **Gg** classes will be distinguishable by their reniform and round glands respectively. Thus the total number and proportions of the *different* forms in F_2 (the zygotic series) will be

$$\begin{array}{ll} 9 & \begin{cases} 3 \text{ peaches with reniform glands} \\ 6 \quad ,, \quad ,, \text{ round} \quad ,, \end{cases} \\ & 3 \quad ,, \quad \text{without} \quad ,, \\ 3 & \begin{cases} 1 \text{ nectarine with reniform glands} \\ 2 \text{ nectarines} \quad ,, \text{ round} \quad ,, \end{cases} \\ & 1 \text{ nectarine without} \quad ,, \end{array}$$

The ratios for any number of factors may be obtained in the same way by multiplying together the gametic series of the male and female parents (Table I). It is apparent that when we are dealing with many factors we should require larger and larger numbers in order to obtain all possible combinations, including the " bottom " recessive or mainly recessive classes. For this reason it is far easier to consider the inheritance of one or two pairs of allelomorphs at a time, and even then to back-cross the F_1 or any heterozygous plant to an individual for those characters.

TABLE I

Parents	Gametes (always in Equal Numbers)	Zygotes	Dominants to Recessive
Aa	**A, a**	**3A, 1a**	**3 : 1**
AaBb	**AB, Ab, aB, ab**	**9AB, 3Ab, 3aB, 1ab**	**15 : 1**
AaBbCc	**ABC, ABc, AbC, aBC, Abc, aBc, abC, abc**	**27ABC, 9(ABc, AbC, aBC) 3(Abc, aBc, abC), 1abc**	**63 : 1**

Ratios of gametic and zygotic series from selfing individuals heterozygous for one to three pairs of factors respectively (with complete dominance). The gametic series are identical with the zygotic series from back-crossing to the bottom recessive form.

Complementary Genes

In the examples we have so far considered, each gene produces by itself a definite effect. Exceptions to this are sometimes found. In the Sweet Pea, *Lathyrus odoratus*, *two* genes **C** and **R** are necessary for the production of anthocyanin in the flowers. Individuals with **C** or **R** alone have white flowers, but when crossed together give an F_1 with purple flowers. The F_2 from selfing the F_1 comprises nine coloured to seven whites, i.e. only those

individuals with both **C** and **R** have coloured flowers (Fig. 4). Genes such as these are known as *complementary* genes.

Interaction of Genes

Typical mendelian ratios are often modified in this way by the interaction of genes. For example, in the Raspberry (*Rubus idaeus*) spine colour is governed by two genes **T** and **P**. **T** produces

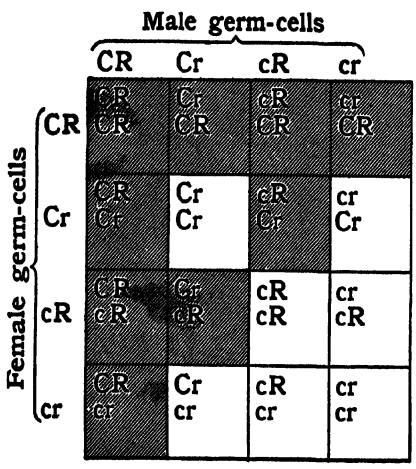


Fig. 4

Showing: 1, The complementary effect of the flower colour genes **C** and **R** in Sweet Pea; 2, the constitution of the nine coloured and seven white offspring in F_2 from the cross **Cr** (white) × **cR** (white).

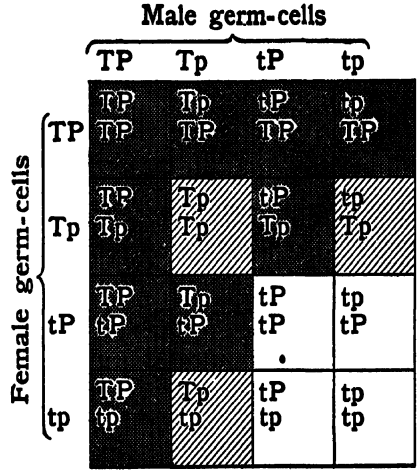


Fig. 5

Showing: 1, Interaction of the genes **T** and **P** in Raspberry; 2, the constitution of the nine purplish, three tinged and four green-spined individuals in F_2 from the cross **Tp** (tinged) × **tP** (green).

anthocyanin tingeing and **P**, which has no effect by itself, deepens the spine colour to reddish purple. Thus **TP** forms have purplish spines, **Tp** tinged, **tP** and **tp** green, and on selfing the double heterozygote, **TtPp**, a ratio of 9 purplish : 3 tinged : 4 green is obtained (Fig. 5).

Intensifying, diluting and inhibiting genes are commonly found to modify the expression of genes for flower colour. Not infrequently the expression of a given gene may be acted upon by another gene governing a different character. In the simplest case one gene masks the expression of another and it is then said to be *epistatic* to the other *hypostatic* gene. For example, a gene **I** produces ivory colour in dahlia flowers, and another

independent gene **Y** produces yellow colour; **yI** is ivory, **Yi** is yellow and so also is **YI**, as the yellow pigment completely masks the less intense ivory. **Y** is therefore epistatic and **I** hypostatic.

A more complicated case is found in *Primula sinensis*, in which a gene **A′** suppresses the yellow eye of the flower and **S** shortens the style and lengthens the stamens. **aass** plants, however, have short styles and stamens, and the stigma is usually pointed as a result of the interaction of genes **a** and **s**. It is probable that most genes affect more than one morphological character or physiological process in the plant, and that only the most prominent difference is accredited to the action of a given gene, which is thus identified by its most conspicuous effect.

Lethal Genes

Genes which, at some point or other in the life of the plant, so modify its development as to result in premature death are called lethal genes. Actually no sharp distinction can be drawn between lethal and other genes, since many recessive genes, when homozygous, have a harmful effect, rendering the individual less viable, especially under unfavourable conditions. Lethal genes are very common, and usually exhibit their effect when in the homozygous recessive condition. They may affect the gamete (Beadle 1933, Fabergé 1937) as well as the zygote. A typical case of zygotic lethals is in *Antirrhinum*, where the genes **Y** for yellow and **g** for albinotic are lethal when homozygous. Thus on selfing the double heterozygote **YyGg**, the only viable zygotes are the types **YyGg, YyGG, yyGG** and **yyGg**. Normally, this would result in a ratio of eight yellow to three green, but since **Y** and **G** are linked with an average cross-over value of 10 per cent, the ratio is modified to about nine yellow to one green. This is an example of the way ratios may be modified by the action of lethal genes.

Multiple Allelomorphs

Finally, we must refer to the case of *multiple allelomorphs*, where, instead of one pair of alternative genes, we have two, three, or more genes all affecting the same character and whose action usually differs only in degree. Thus referring again to *Primula sinensis*, **A′** suppresses the yellow eye of the flowers while **A**

merely restricts it. Both these genes are dominant to a third, **a** (Fig. 6).

In the cherry (*Prunus avium*) a multiple-allelomorphic series of at least thirteen genes is responsible for pollen-tube growth (see Chapter IX). Such multiple series are found in widely separated

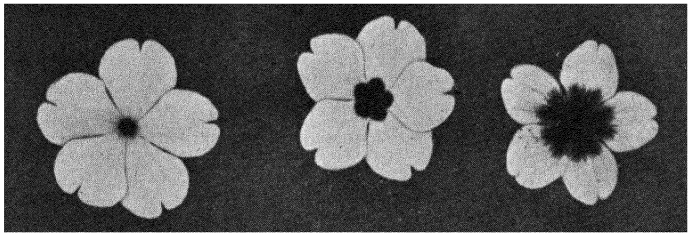


FIG. 6

Showing the effect of the multiple allelomorphs **A′**, **A** and **a** respectively in diploid *Primula sinensis*.

plants, and in each case any two genes in a series behave towards each other and the remaining genes in their series according to mendelian law.

LINKAGE

So far we have dealt with examples of the independent inheritance of genes only. When, however, the inheritance of a sufficient number of characters is studied in a given plant, it is common to find that certain characters either appear together (1) more frequently or (2) less frequently than is expected from the law of independent inheritance. Moreover, it is always those genes which are contributed by the same parent which tend to be inherited together. Conversely, those genes which seem to repel one another in inheritance are always found to have come from opposite parents. These two phenomena are known as "coupling" and "repulsion" and together they constitute "linkage".

Examples of coupling and repulsion are given below. When a number of genes exhibit a tendency to be inherited together they are said to form a *linkage group*. Since the basis of linkage is a cytological one, the explanation of it is deferred to the next chapter.

TABLE II

SHOWING IN THE SWEET PEA LINKAGE OF THE TWO PAIRS OF ALTERNATIVE CHARACTERS DARK LEAF AXIL–LIGHT LEAF AXIL AND FERTILE ANTHERS–STERILE ANTHERS

	Dark Axil, Fertile Anthers.	Dark Axil, Sterile Anthers.	Light Axil, Fertile Anthers.	Light Axil, Sterile Anthers.
Coupling: observed . .	1560	38	49	500
Calculated on independent inheritance . . .	1207·7	402·6	402·6	134·2
Calculated on 4·12 per cent crossing-over . . .	1565·0	43·5	43·5	495·0
Repulsion: observed . .	1723	817	877	4
Calculated on independent inheritance . . .	1924·3	641·4	641·4	213·9
Calculated on 4·12 per cent crossing-over . . .	*ca.* 1712·0	853·5	853·5	1·4

QUALITATIVE CHARACTERS

The characters in plants which we have so far considered are definite and comparatively easy to recognise. Those, for example, described in the fruits of peaches and raspberries and flowers of sweet peas show alternative inheritance and are easily distinguished by contrast with their opposites. The interaction of genes, complementary effects, linkage and other causes may give rise to complications in inheritance, but an analysis of segregating families and of the ratios obtained is in general an easy task. Such characters involve differences in some quality of the individual, such as the colour of the fruit or flower, form of gland, or nature of the surface of the fruit, and for this reason they are generally referred to as *qualitative characters*.

QUANTITATIVE CHARACTERS

Variation in the characters of plants, however, is not always sharply discontinuous. That is to say, the characters are not always clearly divided from one another like smooth from hairy, large from small or red from white, but they intergrade and range from one extreme to the other. For example, in the tomato the colour of the skin and flesh of the fruit show alternative

inheritance, but size of fruit intergrades. Characters of this kind involve differences in degree or quantity, hence they are commonly referred to as *quantitative characters*. It must, however, be pointed out that there is no wide difference between quantitative and qualitative characters. Colour, shape and size, which in many plants show alternative inheritance, may in others give a series which show slight differences in quantity and which grade almost imperceptibly into each other. The analysis of quantitative inheritance is generally complicated owing to the absence of clearly marked characters, and it almost always depends on several factors or genes acting together and affecting the same character. Quantitative variation has been shown to be due to systems of genes, the members having small effects similar to one another and supplementing one another. Such *polygenic systems*, as shown by Mather (1943), have certain special properties, one of which is the storage of variability by the actions of plus or minus allelomorphs of different genes balancing one another in the genotype. Recombination frees the variability by upsetting this balance. Polygenes working in the same direction are thereby brought together and the action of selection is facilitated. Examples of quantitative inheritance are given in subsequent chapters. It occurs in both diploid and polyploid plants, but is more common in polyploids, as described in Chapter III.

Extra-nuclear Inheritance

As we shall see later, the units of inheritance are almost entirely contained within the nucleus of the plant-cell, and are carried over from one generation to another in the nuclei of the germ-cells and in normal crossing it does not matter which is the female parent, the results are the same. The cytoplasm and its inclusions, which comprise the remainder of the cell contents, seem to play no very conspicuous part in inheritance. Exceptions to this are known, however, and in certain cases the cytoplasm itself may transmit a definite character or profoundly modify the action of the genes. Thus, there is a yellow-leaved (chlorotic) form of *Primula sinensis* which when pollinated by green-leaved forms gives only yellow-leaved progeny in the first and all subsequent generations. When the reciprocal cross is made the progeny are all green. Thus the chlorotic character is maternally

inherited and is only transmitted when brought in from the female side. Such a result can be explained by the assumptions that (1) the normal green-colouring bodies carried in the cytoplasm of the cells of the chlorotic primula are defective and do not produce chlorophyll, and (2) the cytoplasm is transmitted through the female germ-cells only. This indeed appears to be the case, and it is thought that the cytoplasm is inherited maternally and not from both sides in the majority of plants. If this is true, it is obvious that in a cross between two different plants a gene may, in $\mathbf{F_1}$, be combined with the cytoplasm of the one or the other according to which is used as the female parent. Differences in reciprocal crosses of this kind have been observed in a number of plants and are often associated with variegation.

In other cases a gene, or group of genes, behave differently according as they are associated with cytoplasm from one plant or another. For example, in a cross between procumbent and tall forms of flax (*Linum usitatissimum*) a gene, or genes, associated with the cytoplasm from the tall parent give *hermaphrodite* plants (having both male and female organs in the same flower) whereas the same gene, or genes, associated with cytoplasm from the procumbent parent gives female forms. Similar examples of extra-nuclear inheritance have been reported in the Broad Bean (*Vicia Faba*), Evening Primrose (*Oenothera*) and Maize (*Zea*).

Phenomena such as these are most commonly found in reciprocal hybrids between species.

Most of the principles enunciated in this chapter have been inferred from investigations on plants of comparatively simple constitution, whereas many of our important cultivated flowers, fruits and vegetables are complex individuals having more than two genes of each kind. As a result of this complexity, genetical analysis in cultivated plants is often a slow and difficult matter; yet even in these, when clearly defined characters are studied, the same principles of inheritance are found to apply as in simple plants, and inheritance can be seen to be an orderly phenomenon.

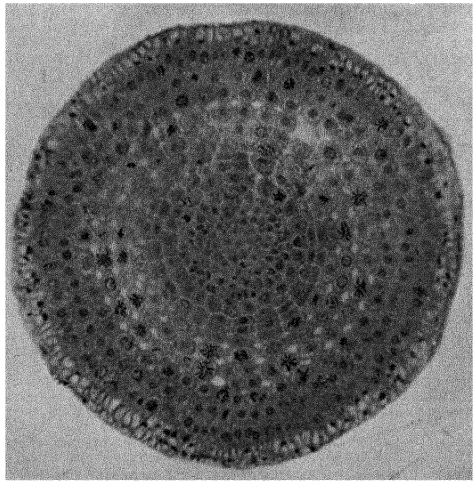
A great deal of light has been thrown on the genetical constitution and behaviour of the complex cultivated plants by the findings of cytology. Indeed, it is now true to say that cytological investigation is a necessary prerequisite to any comprehensive genetical study. It is also necessary for a proper understanding of heredity and for this reason we shall now proceed to consider the elements of cytology.

CHAPTER II

THE CYTOLOGY OF DIPLOID PLANTS

We have already pointed out that, compared with the simple nature of the methods employed in the study of genetics, examination of the microscopic germ-cells requires elaborate measures. In recent years, however, the cytologists's technique has been developed so successfully that a very considerable advance has been made in our knowledge of the cell and the intricate processes of germ-cell formation and reproduction.

When Mendel put forward his laws of segregation and independent inheritance they were hypotheses without any physical basis. Since then, detailed studies on the nature and behaviour of the cell and its contents have clearly indicated the structures which are the chief vehicles of heredity.



With acknowledgments to Dr. M. S. Navashin.

FIG. 7

Photomicrograph of a section through a root tip of *Crepis dioscoridis* showing the complement of eight somatic chromosomes.

THE CHROMOSOMES

If a living cell from the *somatic* (body) tissue of a plant is examined, it will be seen to contain a spherical body called the nucleus. By staining with suitable dyes, the nucleus at certain stages is seen to be a composite structure consisting, in the main, of a number of deep-staining elongated bodies called *chromosomes* (Fig. 7). The number, size and shape of the chromosomes are the same in all the

somatic cells of a given plant and indeed (with rare exceptions) throughout the whole of the particular species. Thus the raspberry has fourteen chromosomes, the apple thirty-four, the radish eighteen, the potato forty-eight, the snapdragon sixteen, the

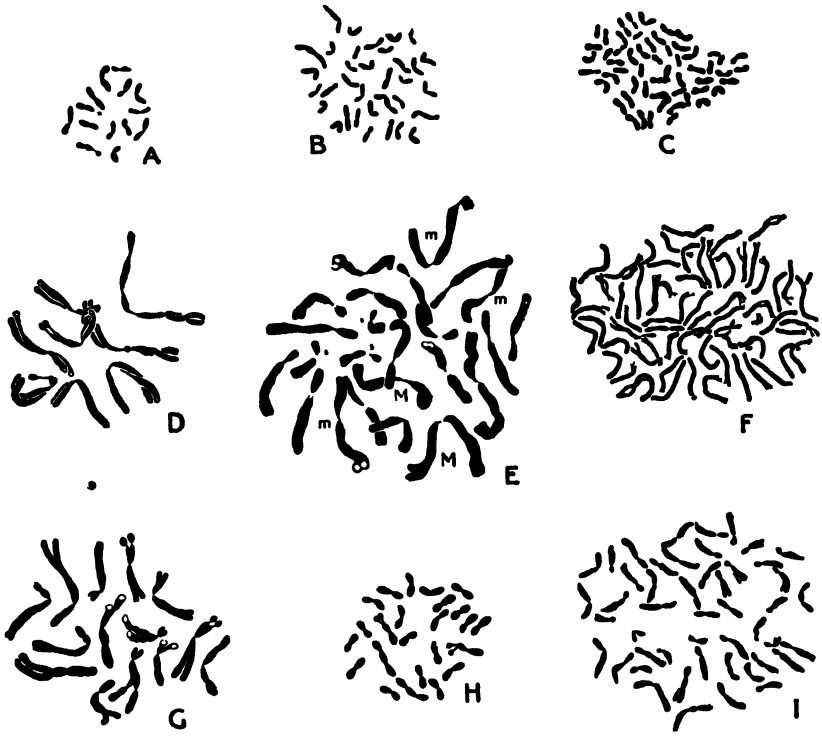


FIG. 8

The somatic chromosome complements of some cultivated plants: A, raspberry var. Superlative (diploid 2x = 14). B, apple var. Worcester Pearmain (secondary polyploid 2x = 34). C, strawberry var. Keen's Seedling (octoploid 8x = 56). D, *Crocus vernus* (diploid 2x = 8). E, *Aconitum Napellus*, Spark's var. (triploid 3x = 24). F, *Dahlia variabilis* (octoploid 8x = 64). G, Garden pea (diploid 2x = 14). H, tomato (diploid 2x = 24). I, potato var. Sharp's Express (tetraploid 2x = 48). All × 2350.

lilies twenty-four, the dahlia sixty-four, etc. See also Fig. 8. In the simplest species the chromosomes can be seen to occur in morphologically identical pairs which differ among themselves in length, size and the position of their constrictions, and in other ways. The members of each pair are derived, one from the male and the other from the female parent. The raspberry, for example, has seven pairs of chromosomes, i.e. two sets of seven

chromosomes each. A single set of chromosomes is known as the haploid (n) and the normal somatic number as the diploid (2n) chromosome complement.

Mitosis

The plant grows by the process of cell division. In between successive cell divisions (the resting stage) the chromosomes are not easily discerned, but when division is about to begin (prophase) they can be seen as twining, attenuated bodies which are "split" longitudinally (Fig. 9A). The chromosomes contract until they assume a rod-like appearance and at the end of this contraction they move to the equator of the cell, where they align themselves more or less at random in the equatorial plane (Fig. 9B). This stage is known as metaphase. The half-chromosomes, or *chromatids*, formed by the splitting of the chromosomes next begin to move towards the opposite ends of the cell (anaphase, Fig. 9C), as if each pair of chromatids were strongly repulsed. This repulsion begins first and is most evident at the *centromere* or "attachment constriction", so-called because it was thought to be the point where each chromosome was "attached" to the spindle-like striations seen in the cytoplasm

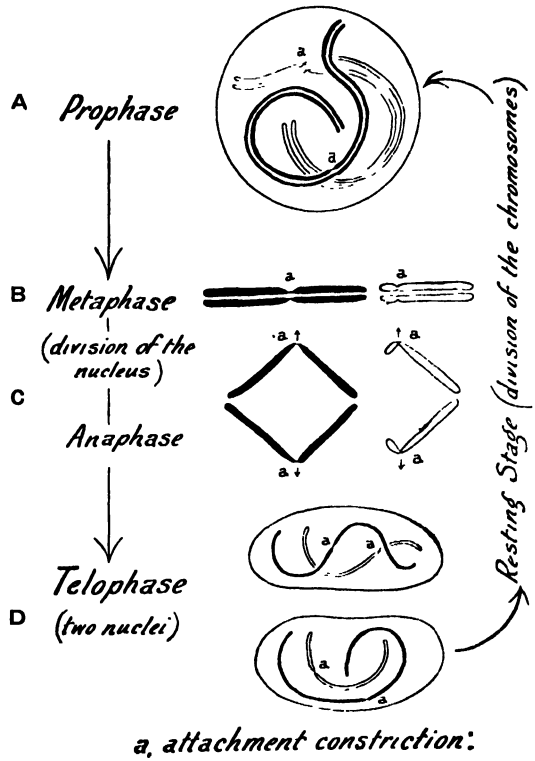


FIG. 9

Diagram showing the changes undergone by two chromosomes in the course of mitosis. (After Darlington.)

at this stage. The point of attachment may vary in position along the chromosome from one type to another, and the separating chromatids form characteristic configurations at anaphase according to the position of their points of attachment.

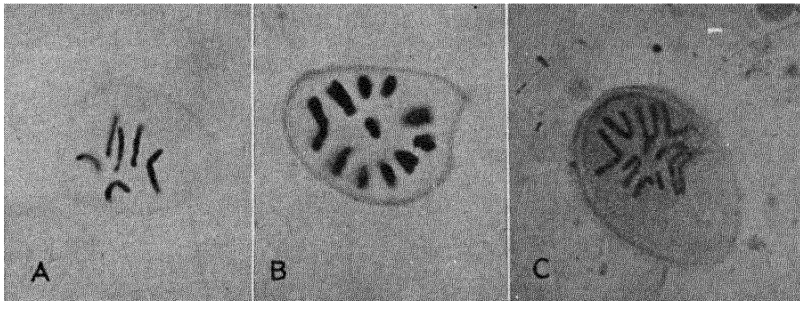
When the half-chromosomes arrive at the poles of the cell they again pass into the resting stage, and a new cell wall is formed between these daughter nuclei, each of which contains precisely the same number of chromosomes as the parent cell and of identical form (Fig. 9D). During the resting stage the chromosomes enlarge to their normal size, again split longitudinally and are then ready for the next division and the formation of further cells.

This behaviour of the somatic cells in division is known as *mitosis*. It is important to notice that the chromosomes are permanent throughout the life of the plant, since the nuclear complement of every cell is identical. Thus, though the individual plant may change greatly in regard to form and function as it develops from seed to maturity, the chromosomes remain unchanged. Mitosis therefore is a mechanism which secures genetic continuity through the vegetative life of the individual.

We have now to see the mechanism by which this genetic material is transmitted from generation to generation.

Meiosis

Most higher plants arise by the division and multiplication of an original cell (the zygote) formed by the union, in fertilisation,



With acknowledgments to Dr. C. D. Darlington and Mr. L. La Cour.

Fig. 10

Germ-cells (pollen grains) showing the haploid (n) or reduced number of chromosomes: A, *Kniphofia corallina* (n = 6); B, *Leucojum aestivum* (n = 11); C, Hyacinth (n = 12).

of the germ-cells borne by the pollen and ovules of the respective male and female parents. It is obvious that, if each germ-cell had *all* the chromosomes found in a somatic cell, the number of chromosomes would be doubled in each generation. Since a given species or variety continues from generation to generation to possess the same number of chromosomes, it follows that some means must exist whereby the number of chromosomes is reduced by one half (Fig. 10) before the cells of the new generation are formed.

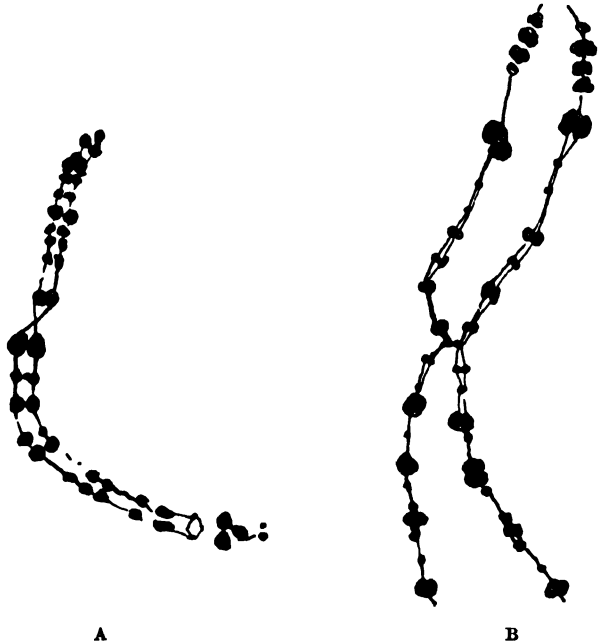


FIG. 11

Camera lucida drawings of prophase chromosomes in A, *Lilium pardalinum*; B, *Fritillaria lanceolata*. Note the correspondence between the size and sequence of the particles of the pairing chromosomes. In B the four strands (chromatids) are clearly seen. There is one chiasma in each figure. (After Belling, 1931.)

This reduction is brought about in the formation of the germ-cells by a special kind of mitosis in which *two* divisions of the nucleus occur in rapid succession, while the chromosomes divide only *once*. This special behaviour is called *meiosis* and the division is known as the *reduction division*. It precedes the formation of the germ-cells. Meiosis differs from mitosis in that

at prophase the attenuated chromosomes are not already split longitudinally (Fig. 12*a*), but are single particulate (beaded) structures, the particles being unequally spaced and unequal in size. These single threads are attracted to one another in pairs, particle by particle, along their lengths, and as they come together the pairing chromosomes are seen to be linearly identical in the sequence and size of their particles (Fig. 11A). The chromosomes comprising each pair are known to be constituted by the corresponding types from each parent. When pairing is complete (Fig. 12*b*) each member of the pair splits longitudinally as in mitosis, with the result that four chromatids are found in close association (Fig. 12*c*). Almost immediately, however, the chromatids fall apart in pairs, which are now seen to be physically connected at certain points (Figs. 11B and 12*d*).

The origin of the physical connections is believed to be as follows. During the close pairing of the four chromatids it often happens that transverse breaks occur amongst them. If two chromatids break at the same point and different ends join up, then each new chromatid will consist of segments of the two old ones (Fig. 12*c*). In other words, the chromatids will have " crossed over " at this point, which is known as a *chiasma* from the cross-like appearance at the point of interchange (Figs. 11B and 12*d*). These chiasmata arise with a frequency and distribution along the chromosomes which is characteristic of a particular plant or species, and one or more chiasmata may occur between each pair of chromosomes. From this we see that chromosomes derived from opposite parents must always come out of this stage interchanged for a part or parts of their length—according to the number of cross-overs which have occurred (Fig. 12*c-h*). Thus recombination of *parts* of similar chromosomes is an essential feature of normal meiosis and, as we shall see later, is of great importance to the geneticist and the plant breeder.

Following this stage the paired chromosomes contract further, and at metaphase, when they are orientated at random on the equatorial plate, they have a characteristic sausage-shaped appearance, each member of the pair being attached to the other by the interchanges between chromatids (Fig. 12*e*). Thus when anaphase begins it is the members of each *pair of chromosomes* which are distributed independently to the opposite poles, and not half-chromosomes as in mitosis (Fig. 12*f*). Since the orientation of each pair of chromosomes at metaphase is at random in regard

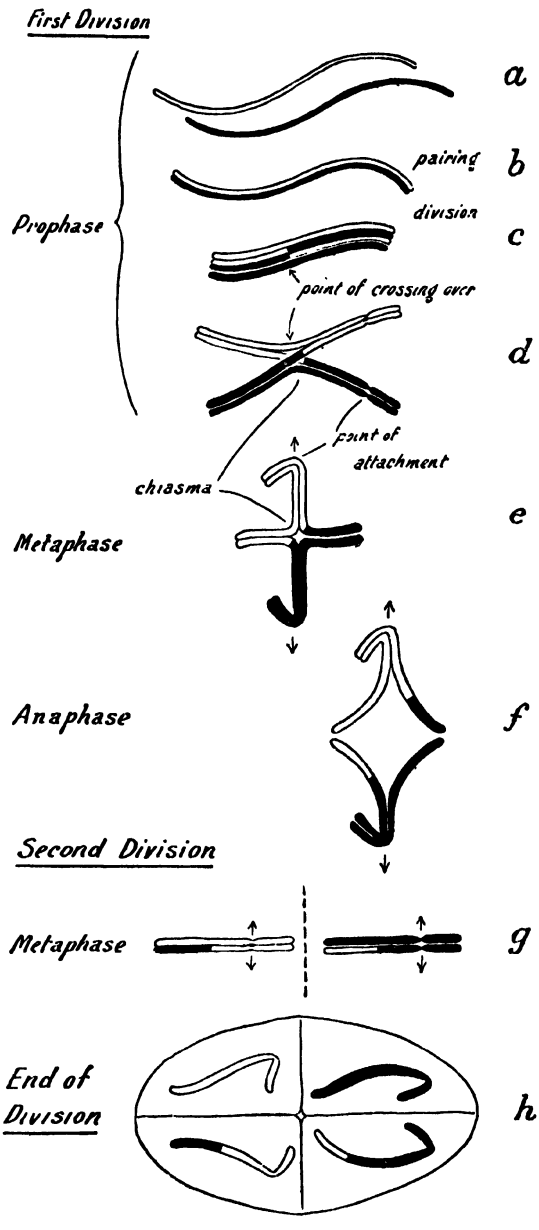


FIG. 12

Diagram of meiosis showing the reduction of chromosomes in germ-cell formation. (After Darlington, 1932.)

to the poles, anaphase of this reduction division results in the segregation and recombination of the chromosomes derived from the respective parents, in addition to halving the total number of chromosomes in each of the daughter nuclei.

The chromosomes disjoin by the unravelling and separation of the chromatids involved in the chiasmata and, arriving at the poles, pass through a very short resting stage. The second division follows quickly and is in all respects a typical mitosis, in which the chromosomes divide longitudinally and pass to the opposite poles, and hence to different germ-cells (Fig. 12*g*). Thus by these two successive divisions, four daughter nuclei are formed, each of which has half the number of chromosomes found in the somatic cells (Fig. 12*h*). On the fusion of the male and female germ-cells to form a new individual the somatic chromosome number is again restored.

From the foregoing brief account we may summarise the most important features of meiosis, as follows :

(*a*) At prophase the chromosomes associate in pairs, and split longitudinally to give four chromatids in close association.

(*b*) During this pairing there is a recombination of parts of the chromosomes contributed by the respective parents.

(*c*) At metaphase the pairs are orientated on the equatorial plate ready for distribution to the poles of the cell. The orientation of each pair is at random in regard to the pole.

(*d*) At anaphase the members of the respective pairs are distributed independently to the daughter nuclei, which, therefore, have half the normal chromosome complement.

As we saw in the first chapter, the laws of heredity, as derived from a study of the way in which particular characters are passed on from parents to progeny, demand a mechanism whereby the units of heredity are (1) permanent in both somatic and germ-cells and (2) distributed independently and at random among the gametes of the parents. Now these two requirements are precisely satisfied by the behaviour of the chromosomes in mitosis and meiosis. If we suppose the genes to be arranged in linear order along the chromosomes, then the longitudinal separation of each chromosome to give identical halves ensures the permanence of every gene. Further, meiosis provides a mechanism whereby members of each pair of chromosomes are distributed independently to the different germ-cells.

Thus at germ-cell formation a segregation and recombination

of the units determining parental identity occurs, and in fertilisation the products of this segregation and recombination within the parent plants are brought together and combined in the progeny.

Linkage

The phenomenon of linkage, however, is not explained by the random distribution of the chromosomes at meiosis. For example, it is obvious that there could not be more factors than chromosomes if the chromosomes themselves were the ultimate units of heredity, whereas a number of plants and animals are known in which the number of factors studied is greatly in excess of the total number of chromosomes. Thus in maize (*Zea*), which has ten pairs of chromosomes, about 400 genes have been identified. In maize and all other cases investigated, the number of linkage groups never exceeds the number of chromosome pairs. From this we might assume that the chromosomes were compound bodies composed of or carrying a number of genes, and indeed the results of many investigations have amply confirmed this view.

The genes are supposed to be arranged along the chromosomes in a definite linear sequence, like beads on a string. Allelomorphs occupy corresponding positions in the chromosomes comprising a pair, e.g. the dominant gene on one chromosome and the recessive in a similar position on the other (Fig. 13*a*).

Now it will be remembered that when the chromosomes are pairing in meiosis, breaks may occur in the chromatids followed by the rejoining of the same or different ends, i.e. the chromosomes " cross-over " at certain points so that portions are interchanged (Fig. 12). Let us consider the result of this crossing-over on the segregation and inheritance of three pairs of allelomorphs **Aa, Bb** and **Cc** situated on the same chromosome, **Aa** and **Bb** being very close together while **Cc** is distant. The dominant genes **A, B** and **C** have been contributed by one parent, and the recessive genes **a, b** and **c** by the other (Fig. 13). Since crossing-over occurs more or less at random along the length of the chromosomes it is obvious that it will hardly ever occur between **Aa** and **Bb** since their loci are so close, whereas it will frequently occur between **Aa** and **Cc** since they are separated by a large portion of the length of the chromosome. Genes **A, B** and **a, b** will therefore almost always pass to the germ-cells borne on the same chromosomes or segments of chromosomes as contributed by the parents (Fig. 13*e*) with the

result that the progeny from selfing F_1 will tend to resemble one parent or the other in regard to **AB** and **ab** characters, i.e. **A** and **B** (or **a** and **b**) will appear to be linked in inheritance.

In the case of **Bb** and **Cc**, however, crossing-over may frequently occur between them. On the occasions when it does not

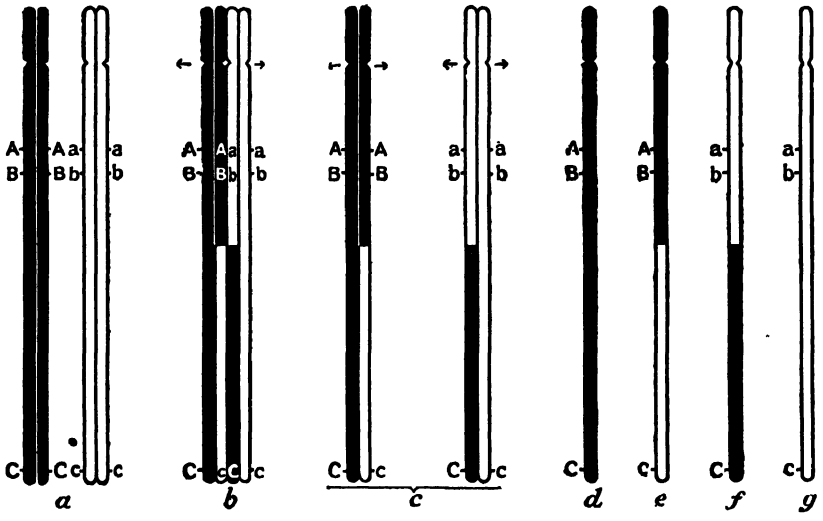


FIG. 13

The cytological basis of linkage (diagrammatic): *a*, Two somatic chromosomes carrying the genes **A, B, C** and **a, b, c** respectively; each chromosome consists of two chromatids. *b*, During the close pairing of the chromosomes in meiosis, breaks occur in the chromatids, which join up with different partners, i.e. segments of the chromatids become interchanged. *c*, At anaphase of the first division the two chromosomes with their interchanged segments are distributed to different nuclei and at anaphase of the second division each of the four daughter chromosomes (*d–g*) is distributed to a germ-cell. *d* and *g* are non-cross-over and *e* and *f* cross-over types. The zygotes from combinations of four such germ-cells will show independent inheritance for the gene **C** and linkage between **A** and **B**.

occur, the daughter-chromosomes and germ-cells will carry the genes **ABC** or **abc** (Fig. 13*g*). When crossing-over does occur between **Bb** and **Cc** the daughter chromosomes and germ-cells will carry the genes **ABC, ABc, abC** and **abc** respectively (Fig. 13*d-g*), **ABc** and **abC** being the cross-over types, the proportion of which depends upon the frequency with which crossing-over occurs between **Bb** and **Cc**. If the locus of **C** is far enough removed from **B** so that 50 per cent or more of crossing-over occurs between them, the inheritance of **B** and **C** will be independent and conform

to Mendel's law, though they are actually carried on the same chromosome. At any distance less than this a proportional amount of linkage will be observed and the closer together the gene pairs are, the more frequently will those genes be inherited together—each chromosome comprising a linkage group. The

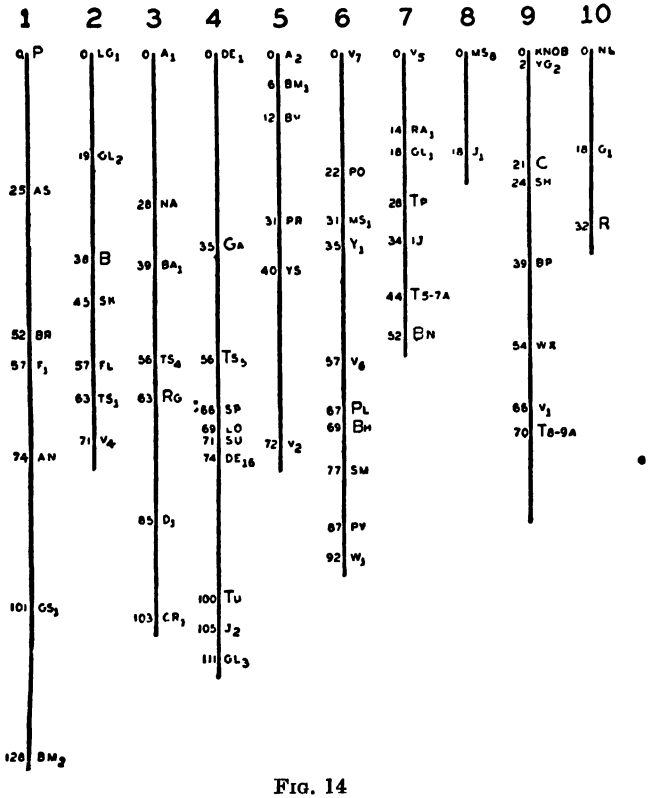


FIG. 14

The ten linkage groups in maize with the map distances (cross-over values) between the different linked genes. The genes comprising linkage group I are carried in chromosome I, those in group II in chromosome II, etc. Only those genes whose loci are known with approximate certainty are shown in the map (after Rhoades and McClintock).

degree of linkage (expressed as " percentage crossing-over ") and the relative positions of linked genes (the chromosome-map distance) are calculated from the proportion of the cross-overs. It will be noticed in our example that, had the genes brought in by different parents been **Ab** and **aB**, then **A** and **B** would appear to be " repulsed " in inheritance, instead of " coupled ".

The mechanism of crossing-over therefore is one which results in new combinations and frequent recombination of the individual genes, i.e. crossing-over leads to greater variability of the species, from which nature or man may make selection.

The linear order of the genes is well illustrated in the genetic map of *Zea Mays* (Fig. 14). As previously mentioned, the number of known genes in maize is about four hundred. The somatic number of chromosomes is twenty, and the gametic number ten. All of these chromosomes are morphologically distinguishable. As there are ten members of the gametic chromosome complement, it is to be expected that the genes in maize would fall into ten linkage groups. This has been found to be the case, and the genetic map shows the linkage groups with the distance (i.e. cross-over value) between the different linked genes. Only those genes whose approximate location is known are given. Not only has it been found that the genetic characters in maize fall into ten linkage groups, but it has been possible to relate each linkage group with a specific chromosome.

Chromosome Rearrangement

Chromosome behaviour in mitosis and meiosis is a singularly exact and orderly process. Were it not so, there could be no genetic continuity or any fixed type of individual or inheritance. We have seen that the processes of cell-division and gamete formation perpetuate the units of inheritance and at the same time constitute a mechanism whereby the genes are combined and recombined in many ways. In this manner there arise varieties of a given species.

The mechanism as described, however, does not allow for any differentiation in the structure of the chromosomes, which are often to be recognised by differences of form and size. Neither does it explain how the two genes comprising an allelomorphic pair have differentiated.

Occasionally a new character arises suddenly in a species which has never shown it before, and the character or *mutation* is found to behave as a simple dominant or recessive to the type; e.g. the appearance of the waved flower ("Spencer") in the sweet pea. In such a case it is probable that the change has arisen in, and is confined to, a single gene, presumably by some modification of its molecular structure.

Though gene mutation is fundamental to all variation and evolution, results of consequence have arisen through alteration of the gross structure of the chromosomes. For example fragmentation, duplication and translocation of parts of the chromosome are known to occur, although comparatively rarely. A portion of a chromosome may become inverted, attached to another chromosome, or deleted altogether (Fig. 15). In such ways the chromosome complement may be reorganised without

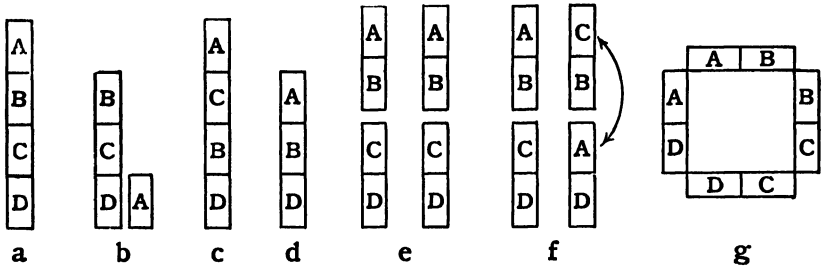


FIG. 15

Diagram illustrating types of chromosome rearrangement. The letters indicate successive segments of the chromosomes. a, Normal chromosome; b, fragmentation; c, inversion; d, deletion; e, two pairs of normal chromosomes; f, reciprocal translocation of segments **C** and **A** resulting in g, " ring " formation at meiosis.

any addition to or loss from the total complement of genes; or the genetic constitution may be vitally changed with profound consequences.

Important examples of reorganisation of the chromosome complement are found in *Pisum*, *Oenothera* and other genera. In *Pisum sativum* varieties occur in which segments of non-homologous chromosomes have become interchanged. Since homologous but interchanged parts may pair with each other although included in different chromosomes, the result of this interchange is that rings of four chromosomes are formed at meiosis when the interchanged parts are terminally located (see Fig. 16). Pairing is usually restricted to the homologous ends of the chromosomes, since the middle portions (differential segments) are not homologous with any part of either of the adjacent chromosomes. For example, let us take a variety of *Pisum* with one ring of four and five pairs of chromosomes. The bivalents disjoin normally. The ring of four (Fig. 15*g*) may disjoin in two ways,

If adjacent chromosomes go to the same pole the gametes will be **AB.BC** and **CD.DA** or **BC.CD** and **DA.AB.** In every case there is reduplication of one segment and absence of another, with the result that these gametes are inviable. When alternate chromosomes go to the same pole two types of gametes are formed, **AB.CD** and **BC.DA.** As both of these gametes have one each of the four segments **A, B, C, D** they are viable. Thus in ring-forming structural hybrids half the pollen and ovules are

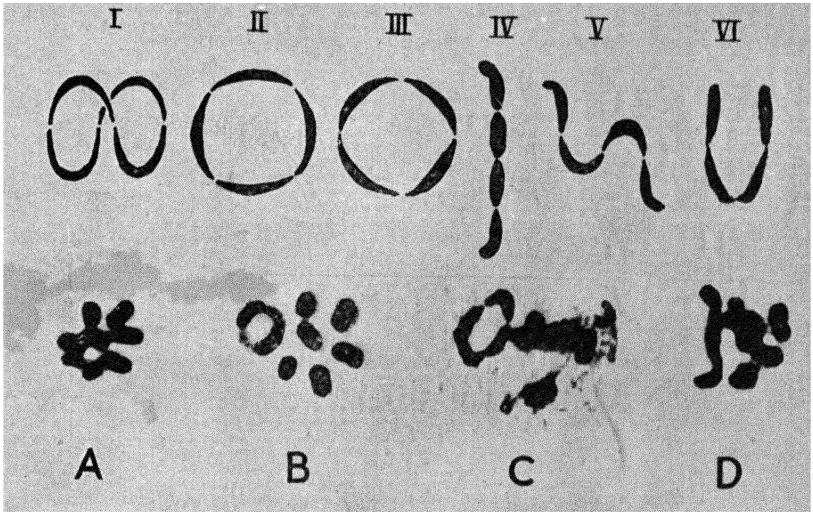


FIG. 16.—RINGS OF FOUR IN A DIPLOID PLANT

I-VI. Diagram showing different arrangements of four chromosomes in a ring or chain at meiosis in the diploid *Campanula persicifolia* giving regular segregation in I and V only. A-D, photomicrographs. A, normal plant with eight pairs of chromosomes. B-D, a plant with four chromosomes associated. (After Gairdner and Darlington, 1930, *Nature*, 125.)

abortive. The semi-sterility associated with ring formation is therefore due to non-disjunction in the ring. It should be noted that apart from crossing-over in the middle or differential segments or further structural changes, so far as the ring is concerned the plant must breed true if self-fertilised. Thus if all the chromosomes of a plant form a ring (e.g. *Oenothera muricata*) then such an individual must breed true even though it is intrinsically heterozygous in respect of the genes carried by the differential segments. The " linkage " of two or more chromosomes to form

rings in interchange hybrids may give rise to apparent genetic linkage, with the paradoxical result that a gene may appear to be independent in one strain and linked in another (as in *Pisum*).

Ring-formation in diploids is seen, *par excellence*, in *Oenothera* ($n = 7$), in various forms of which rings of four, six, eight, ten, twelve and fourteen chromosomes have been found. Many of these evening primroses are complex hybrids and yet, owing to their chromosome structure and behaviour, they breed practically true. Summaries of the investigations on ring-formation will be found in Darlington (1937) and Sansome and Philp (1939).

CHAPTER III

THE CYTOLOGY AND GENETICS OF POLYPLOIDS

In the previous chapter we considered the cytology of individuals in which the somatic cells carry only two, and the germ-cells only one of each chromosome type.

Among our cultivated plants, however, numerous examples are found in which each chromosome type (and therefore each chromosome set) is represented a number of times. For example,

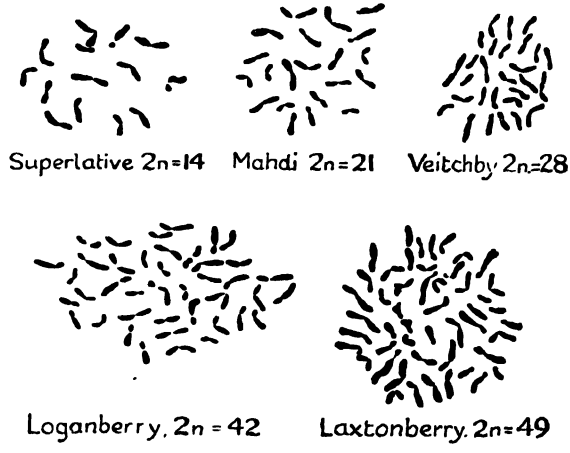


FIG. 17

The somatic complements of diploid and polyploid *Rubi*.
(After Crane and Darlington, 1927.)

in the raspberry, with fourteen chromosomes, there are two sets of seven different chromosomes. Among other cultivated Rubi the "Mahdi" has three sets of seven, the veitchberry four sets, the loganberry six and the laxtonberry seven sets—each species or hybrid having some multiple of the basic number of seven *types* of chromosomes (Fig. 17). The various multiples are conveniently designated triploid (3x), tetraploid (4x), pentaploid (5x), hexaploid

(6x), etc., according to the number of chromosome sets. Polyploids with chromosome numbers which are not a multiple of the basic number, e.g. 4x + 2, 6x – 1, etc., are called *aneuploids*.

Polyploids may originate in two ways : (1) By doubling of the chromosome number in a somatic cell and its descendants. (2) By the formation of germ-cells containing (*a*) the unreduced number of chromosomes or (*b*) more than the haploid chromosome number.

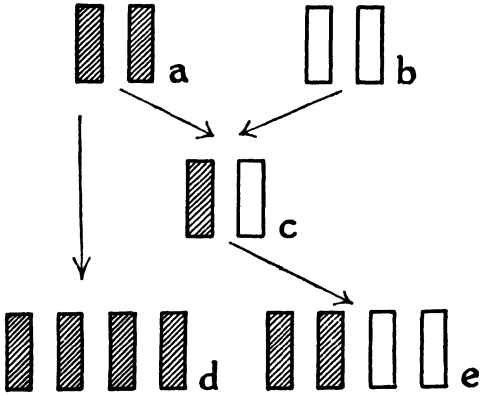


FIG. 18

Diagram showing the origin and constitution of the chromosome complements of auto- and allo-tetraploids. a and b, Diploid species; c, diploid hybrid from a × b; d, auto-tetraploid derived from doubling of the chromosome sets in a; e, allo-tetraploid derived from the doubling of the chromosome sets in c.

In the first case the only difference in the chromosome complement of the doubled individual is a quantitative one, i.e. it has twice the number of chromosomes and genes as the original form. Similarly if two unreduced gametes with identical chromosome sets unite to form a new individual it will only differ from the parents cytologically in having twice as many chromosomes. But if two unreduced gametes having chromosome sets which are *not* identical in regard to their allelomorphs unite, the chromosome complement of the resulting polyploid will be qualitatively as well as quantitatively different. In other words, the first kind of polyploid is a variety of the original form, whereas the second kind is a true hybrid.

Polyploids are conveniently described according to their origin as (1) simple or *auto-polyploids*, (2) hybrid or *allo-polyploids*. In the auto-polyploid the chromosome sets are practically identical with one another, e.g., the auto-tetraploid tomato (see page 95). In the allo-polyploid the sets, though similar to a certain extent, are not all alike since they have come from different lines of descent, e.g., *Primula kewensis* (*P. floribunda* × *P. verticillata*). For example, in a homozygous auto-tetraploid each chromosome or gene is represented four times (Fig. 18*d*), whereas in the simple

allo-tetraploid two sets of chromosomes have come from one species and two from the other (Fig. 18*e*), and the corresponding allelomorphs borne on the two different chromosome sets may be different or alike. Both types of polyploids occur naturally, but by far the greater number of wild and cultivated polyploids are either allo-polyploid or partly allo- and partly auto-polyploid.

Somatic doubling of the chromosome number arises through the failure of cell-wall growth between daughter nuclei, while unreduced gametes may also arise from failure of chromosome separation. Failure or abnormalities of reduction is particularly common at meiosis of species hybrids.

The Auto-polyploid

As we saw earlier, in meiosis of diploid plants the chromosomes come together in pairs (bivalents), the members of which then separate and pass to the daughter nuclei. In the auto-polyploid, however, there are three or more chromosomes of each type and these tend to associate in threes (trivalents), fours (quadrivalents), etc., according to whether the plant is a triploid, tetraploid, etc. For example, if chromosome pairing were ideal we might expect the chromosomes of an auto-tetraploid always to conjugate in fours, e.g. an individual with twenty-four chromosomes forming six quadrivalents. Actually this is rarely the case, since competition in the pairing of four identical chromosomes reduces the frequency of chiasma formation between any two of the four and thus often leads to one or more of them remaining unpaired, giving 1 trivalent + 1 univalent, 1 bivalent + 2 univalents, or 2 bivalents.

Further, should multivalent formation occur, the arrangement and orientation of the multivalents at metaphase may be of such a kind as to result in irregular distribution of the chromosomes to the daughter nuclei. Thus four chromosomes connected end to end to form a ring will probably divide into 2 and 2 whatever their orientation may be at metaphase. In contrast a chain of four may divide into 2 + 2 or 3 + 1 or all four pass to one pole.

We see, therefore, that (1) competition in pairing at prophase of meiosis in an auto-polyploid may give rise to univalent (unpaired) chromosomes which do not follow the orderly behaviour of the bivalents and are only included by chance in the daughter nuclei of the reduction division; and (2) the distribution of the multi-

valent chromosomes may be numerically unequal. In each case irregular distribution of the chromosomes occurs, so that some of the gametes come to have more or less than the haploid number of chromosomes. Such gametes are usually sterile and unable to function, and a certain amount of gametic or *generational* sterility is always found in true auto-polyploids.

The Allo-polyploid

In true allo-polyploids chromosome pairing may be as regular as in diploid plants. The reason is clear to see. Taking an allo-tetraploid, for example, of the constitution **AAA'A'** the **A** chromosomes pair with **A** and **A'** with **A'**, so that bivalents only are formed, as in diploid plants, and meiosis is regular in every respect. The true allo-polyploid therefore is potentially as fertile as the diploid individual. Comparing the auto-polyploid and allo-polyploid we may say that multivalent chromosome conjugation in the former leads to meiotic irregularities and a percentage of sterility, whereas the differentiation of the chromosome sets in the allo-polyploid permits of greater regularity in meiosis and a higher percentage of fertility. The allo-polyploid is therefore better fitted to survive under natural conditions, and natural selection tends to work away from auto-polyploidy to allo-polyploidy.

Many forms occur which are intermediate between allo- and auto-polyploids. Thus an individual may have one or more chromosome types virtually identical (**AAAA**) and other types differentiated (**BBB'B'**) and every degree of such genic and structural variation may occur. Also a plant may combine both auto- and allo-polyploid conditions within itself, as in the case of the garden dahlia, which is a double auto-tetraploid or allo-octoploid (see p. 86).

Finally, species are known in which the chromosome types are not equally represented in regard to number, there being, as for example in the apple, three out of the basic number of seven chromosome types represented six times while the other four types are represented only four times. Such forms are known as *secondary polyploids*. The relation of chromosome sets of various polyploids is given in Table III.

TABLE III

Showing the Number and Homology of the Chromosome Types (A to F) in the Various Types of Polyploids

Haploid x	Diploid 2x	Auto-tetraploid 4x	Allo-tetra-ploid 4x	Partly auto-partly allo-hexa-ploid 6x	Aneuploid 4x − 1 4x + 1 etc.	Secondary Polyploid 4x + 2 + 2 + 2.
A	AA	AAAA	AA A′A′	AAAA A′A′	AAA′ or AAAA	AA A′A′ A″A″
B	BB	BBBB	BB B′B′	BBBB B′B′	BBB′B′ BBBBB	BB B′B′ B″B″
C	CC	CCCC	CC C′C′	CCCC C′C′	CCC′C′ CCCC	CC C′C′ C″C″
D	DD	DDDD	DD D′D′	DDDD D′D′	DDD′D′ DDDD	DD D′D′
E	EE	EEEE	EE E′E′	EEEE E′E′	EEE′E′ EEEE	EE E′E′
F	FF	FFFF	FF F′F′	FFFF F′F′	FFF′F′ FFFF	FF F′F′
Normal gamete	Normal zygote; unreduced gamete				etc.	

Changes in Basic Chromosome Number

As we have previously shown, the basic chromosome number in a particular species, with rare exceptions, is constant. But if we compare the chromosome numbers of related species and genera we find considerable variation (see Darlington and Janaki, (1946)). For example, in the genus *Brassica* basic chromosome numbers of 9, 10, 11 and 12 are known, while in the *Rosaceae* we find primary basic numbers of 7, 8 and 9. In other words, differentiation into species and genera from common prototypes over a long period of time has involved a change in the basic number. These changes are brought about by gene rearrangement and by unequal chromosome separation. They can occur more readily in polyploids, where an initial chromosome unbalance is less deleterious than in diploids. In this way *secondary polyploids* are produced. On cytological grounds there is reason to believe that apples and pears are secondary polyploids of the constitution shown in Table III.

In certain plants with small chromosomes such as *Dahlia*, *Cicer*, *Brassica*, *Pyrus* and *Solanum* there is a tendency for bivalents to be arranged in groups at meiosis. This secondary association, as it is frequently termed, begins after the homologus chromosomes have paired by specific gene-to-gene attraction. It is due to fusion between special regions (termed heterochromatic) on chromosomes which are relatively non-homologous.

Recent work has shown that this secondary grouping can be regarded as a measure of homology in polyploids. This is because an attempt to form multivalents brings these regions close together. This, therefore, confers a degree of apparent specificity, but inherently the attraction is non-specific. Secondary association does not generally affect segregation or the normal process of germ-cell formation, but it may be of value to the cytologist in determining the homology of the chromosome sets in polyploids. Thus, in an allo-tetraploid in which **A** always pairs with **A** and **A′** with **A′**, the degree of affinity between **A** and **A′**

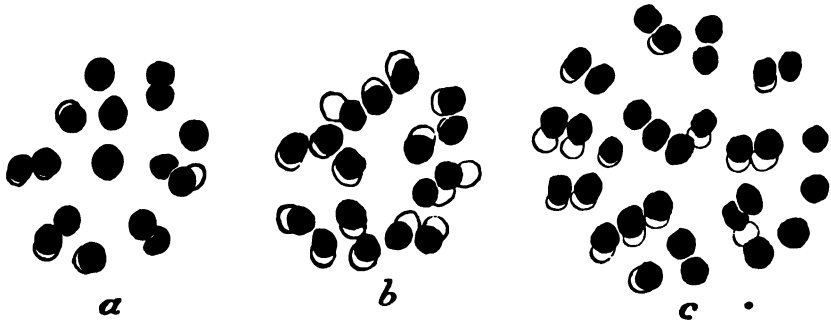


FIG. 19

Secondary association of the chromosomes in *a*, *Dahlia coronata*, allo-tetraploid (x = 8, n = 16); *b*, Apple var. Northern Spy, partly hexaploid (x = 7, n = 17), partly tetraploid; *c*, *Dahlia variabilis*, allo-octoploid (x = 8, n = 32), showing groups of 2, 2 and 3 and 2, 3 and 4 bivalents respectively. (Polar views metaphase I, meiosis.)

is revealed by secondary association, which therefore becomes a valuable criterion of homologies more remote than those expressed in normal chromosome pairing. For example, the lowest haploid chromosome number found in the genus *Dahlia* is sixteen, and although no quadrivalents are ever formed, the secondary groups of four chromosomes each (Fig. 19*a*) show that the n = 16 species are in reality allo-tetraploids whose basic chromosome number is eight. In this way analysis of primary and secondary association in meiosis of polyploids and comparison with related diploid and polyploid species may be of considerable value, either supplementing genetic studies or throwing light on the constitution of plants which are difficult to analyse genetically.

Following this brief outline of polyploid cytology we have now to consider the effect of increase in chromosome number upon inheritance.

In the auto-polyploid there will be more than two allelomorphs of each kind, and segregation will have to be traced for three or more allelomorphic genes. For example where reduction is regular each gamete in an auto-tetraploid will now receive, not one, but two allelomorphic genes, as shown in Table IV.

TABLE IV

Parents	**AAAA**			**aaaa**
Germ-cells	**AA**		×	**aa**
F_1 hybrid		**AAaa**		
Germ-cells (gametic series)		**AA**	**4Aa**	**aa**

F_2 (zygotic series) $(AA + 4Aa + aa)^2$
$= 1AAAA, 8AAAa, 18AAaa, 8Aaaa, 1aaaa$
or $35A : 1a$.

Thus instead of the gametic series being **1A : 1a** as in the comparable diploid plant, there are now three types of gametes in the proportions **1AA : 4Aa : 1aa**, and the zygotic series (F_2) will consist of three different heterozygotes in addition to the top dominant **AAAA** and bottom recessive **aaaa** forms. These five types are conventionally described as quadriplex (**AAAA**), triplex (**AAAa**), duplex (**AAaa**), simplex (**Aaaa**) and nulliplex (**aaaa**) according to the number of dominant genes present.

Back-crossed to the bottom recessive **aaaa** form, the ratios of **A : a** forms obtained when **A** is completely dominant are

	A		**a**
AAAA × aaaa	all		none
AAAa × aaaa	all		none
AAaa × aaaa	5	:	1
Aaaa × aaaa	1	:	1
aaaa × aaaa	none		all

Other characteristic ratios are 3 : 1 from **Aaaa × Aaaa**, 11 : 1 from **AAaa × Aaaa** and 35 : 1 from **AAaa × AAaa**. All other combinations give dominants only.

A further possibility is introduced when tetraploid segregations are being considered. In the diploid each gamete contains only one of the two chromatids derived from a given chromosome type. In the tetraploid, however, a gamete will contain two chromatids from each chromosome type. These are derived, as far as regions close to the centromere are concerned, from different chromosomes, but owing to crossing over on either side of the centromere the two chromatids may be derived from the same chromosome in

parts remote from the centromere. Thus **AAAa** genotypes can give not only four gametes **AA, AA, Aa, Aa** but also, occasionally, **AA, AA, AA, aa** for genes distant from the centromere. In the diploid, chromatid segregation does not affect the calculated ratios but in polyploids its consequence is to increase the number of recessives. Thus with random chromosome segregation in an auto-tetraploid the ratio from selfing the duplex form **AAaa** is **35A : 1a,** whereas the ratio expected from random segregation of the *chromatids* (in the parts furthest from the centromere) is 21 : 1.

An example of chromatid segregation is seen in the F_2 from the blackberry " John Innes " (4x) which was raised from crossing a prickled with a prickle-less blackberry. The observed and calculated figures are given below.

	Prickles	No Prickles
Selfed (**AAaa** × **AAaa**)		
Observed (872 plants) . . .	835	37
Chromatid expectation . . .	832·0 ± 6·2*	40 ± 6·2
Chromosome expectation . . .	847·8 ± 4·9	24·2 ± 4·9
Back-crossed (**AAaa** × **aaaa**)		
Observed (43 plants) . . .	33	10
Chromatid expectation . . .	33·8 ± 2·7	9·2 ± 2·7
Chromosome expectation . . .	35·8 ± 2·4	7·2 ± 2·4

* Standard error $\sigma = \sqrt{p(1-p)n}$.

It will be clear from these figures that although the autotetraploid differs from the diploid in the number of its chromosome sets only, yet there is a profound difference in its genetics, the number of genotypes (**AAaa, Aaaa,** etc.) being increased and the recessive form segregating much more rarely. Inheritance of two or more different (non-allelomorphic) genes is correspondingly intricate, large numbers of individuals being required to obtain segregation of all possible genotypes. It will be seen that in polyploids complementary genes, interaction of genes and multiple allelomorphism, etc., introduce extensive possibilities of variation. In particular, incomplete dominance has important results, since the expression of simplex, duplex, triplex and quadriplex forms may be cumulative in effect, each gene supplementing the action of the other. Thus instead of alternative characters arising from the expression of genes **A** and **a,** incomplete dominance in the

auto-polyploid may give rise to several intermediate forms differing in degree, and character-expression will be less discontinuous as compared with that of diploid forms. This is especially true of high polyploids.

Owing to the occurrence of two or more genes affecting the same character, quantitative inheritance is common in polyploids. Such genes often have an additive effect and hence they are commonly referred to as *multiple genes*. One of the earliest experiments which demonstrated the occurrence and effects of multiple genes was made on hexaploid wheat by Nilsson-Ehle (1908). Nilsson-Ehle found that the red colour of the grain in wheat was dominant to white, but that the reds could throw whites in different proportions. Analysis of numerous families showed that they fell into three groups, in which the proportion of reds to whites was 3 : 1, 15 : 1 and 63 : 1 respectively. It is therefore evident that there are three independent genes, each of which can produce the red effect. If we call them **A, B** and **C** the reds which give a 3 : 1 ratio on selfing can be expressed either as **Aa bb cc, aa Bb cc** or **aa bb Cc** ; those which give a 15 : 1 ratio as **Aa Bb cc, aa Bb Cc** or **Aa bb Cc** ; and the reds which give 63 red to 1 white as **Aa Bb Cc.** A white-grained plant can only arise from the union of two **abc** germ-cells. Though a plant with all three dominant genes may be deeper red than one in which but a single gene occurs, the differences in intensity of colour are not sufficiently well marked to allow of a colour classification of the reds in terms of their genetic constitution. Nilsson-Ehle's elucidation of the inheritance of colour in wheat placed the conception of multiple genes on a firm basis, and since then it has been applied to numerous cases where a series of intergrading forms occurs. In the hexaploid wheats duplicate and triplicate genes govern the inheritance of certain other characters, and the frequency of these multiple genes suggests that the hexaploid wheats are allopolyploids which have arisen from the hybridisation of different species carrying similar genes affecting these characters. Duplicate genes may arise in a diploid by parallel gene mutations or duplication of parts of chromosomes, but the explanation that the similar genes have been brought into hexaploid wheat by hybridisation is more probable in this case.

Inheritance in the allo-polyploid may be of various degrees of complexity, depending largely on the age of the species. The simple allo-tetraploid with four chromosome sets well differentiated

in pairs is virtually a double diploid, and segregation in certain combinations resembles that of a typical diploid plant, giving 1 : 1, 3 : 1 and 15 : 1 ratios when dominance is complete. Unlike the diploid, however, there may be more than two grades of dominance in regard to the expression of any one kind of gene. In relatively new allo-polyploids inheritance may assume a very complex character, especially if a high degree of polyploidy also obtains, the segregation of similar (but differing) genes affecting the same character differentially; this results in numerous genotypes, and consequently in very fine degrees of expression. (Cf. Apple, Chapter VII.)

As we have seen, the allo-polyploid is intrinsically hybrid, since it combines the differences between two or more species, but owing to the characteristic pairing of its chromosomes it will breed true if the parent species are true-breeding.

Hybridisation and Polyploidy

The main course of evolution appears to have proceeded by changes in the nature and action of the gene, natural selection preserving those changes which have a positive survival value. In the passage of time a given species may come to be different in its genetic constitution owing to the accumulation of mutations. Thus variation within a given species may eventually give rise to two or more specific forms which, when crossed, give only sterile offspring, owing to the differentiation of the chromosome sets and consequent failure of pairing in the hybrid. Thus, representing the chromosome types of one species as **A, B, C, D** and of the other as **A′, B′, C′, D′**, although **A** and **A′**, **B** and **B′**, etc., have descended from a common ancestor and still carry many identical or similar genes, they are too different to pair, meiosis is a failure and the germ-cells sterile.

But they can survive sexually if doubling of the chromosome number occurs, for then each of the respective chromosomes has an identical mate—**AA, A′A′, BB, B′B′, CC, C′C′, DD, D′D′**—pairing proceeds normally and fertile germ-cells are formed. A case of this kind is *Primula kewensis*, the diploid form of which is highly sterile, but the tetraploid form is fertile (see page 66).

Polyploidy therefore is of great importance in that it (1) increases the effective range of hybridisation, (2) combines the products of specific differentiation within a single (new) species and

(3) increases the potential range of species variation.

Union of an unreduced (diploid) gamete from a diploid plant with a normal haploid gamete, or the crossing of a diploid with a tetraploid, may give rise to a sterile triploid, which by doubling of the chromosome number becomes a fertile hexaploid. From the hexaploid × diploid, tetraploid forms may arise, and by a similar process other polyploid forms. Numerous genera are known in which the evolution of the species has followed some such course.

Before proceeding to give details of practical breeding experiments with plants it is necessary to describe some unusual forms of reproduction.

Asexual Reproduction

Numerous horticultural plants have for centuries been reproduced by asexual means. Such plants, although widely distributed throughout the world, are all parts of one individual and are collectively known as " clones ". In horticulture clonal reproduction takes a prominent place, and owing to heterozygosity and sterility it is often the only means of perpetuating an important variety.

Although several methods of asexual reproduction occur, we can provisionally divide them into two classes: (1) artificial asexual reproduction as is widely practised in horticulture by such operations as budding, grafting, layering, cuttings, etc., and (2) natural asexual reproduction, by means of bulbs, corms, tubers and other methods.

Apomixis [1]

Some plants, whilst appearing to form seed sexually, reproduce themselves vegetatively without the process of fertilisation being involved. This form of reproduction is called apomixis, and it is characteristic of many plants of hybrid origin which rarely or never set true seed, i.e. seed formed by the fusion of male and female germ-cells.

In apomixis a frequent course of development is that the tissue surrounding the embryo-sac produces buds from which seed-like

[1] The term apomixis is here used in its widest sense. Some authors use the term in a more restricted way.

structures develop, resembling the normal seeds produced from fertilisation. The process is equivalent to clonal reproduction, and a seed produced in this way gives rise to a new plant identical with its mother irrespective of its genetic constitution, just like a plant raised from a graft, cutting or other vegetative method. This form of reproduction has been reported in *Rubus*, *Rosa*, *Hieracium*, *Citrus* and other plants.

Haploid Parthenogenesis

Another exceptional form of reproduction where fusion of the male pollen nucleus and the female egg-cell nucleus does not take place occasionally occurs in plants. In these cases a haploid nucleus develops into a new embryo which gives rise to a haploid plant with only one set of chromosomes. This abnormal mode of reproduction called " parthenogenesis " has been described in *Datura*, *Solanum*, *Campanula*, *Oenothera* and several other plants. Haploid plants are much smaller than their diploid parents and are generally sterile.

The above are examples of female parthenogenesis ; a few cases of male parthenogenesis have also been recorded. In these cases the nucleus of the male parent develops into an embryo within the ostensible female parent, without fertilisation or fusion with the female nucleus. It has been reported in the strawberry, *Nicotiana*, *Vicia sativa* and *Euchlaena mexicana*. In *Nicotiana* the offspring had the reduced (n) chromosome number of the male parent, but in the strawberry, *Vicia* and *Euchlaena* the offspring had the 2n number of the male parent, presumably as a result of subsequent chromosome doubling, or the functioning of an unreduced germ-cell. Thus Ichijima (1928), from crossing *Fragaria vesca* (2n = 14) with *Fragaria virginiana* (2n = 56), obtained a plant with fifty-six chromosomes. Bleier (1929), from crosses between *Lens esculenta* (2n = 14) and *Vicia sativa* (2n = 12), found a proportion of the offspring to be *Vicia sativa* with twelve chromosomes, and apparently this frequently happens in *Vicia* following natural cross-fertilisation.

Diploid Parthenogenesis

In this form of reproduction the mother-cell develops into the embryo-sac, sometimes directly and sometimes after division. In

this way diploid plants arise without the intervention of the male nucleus. This mode of reproduction has been reported in *Erigeron*, *Hieracium*, *Artemisia*, *Taraxacum* and several other plants.

Viviparv

Certain grasses and some species of *Allium* form buds in the place of flowers which, like seeds, fall to the ground and perpetuate the plant. These species when they are incapable of setting normal seeds by sexual means, are also clones. The phenomenon is known as viviparous reproduction.

CHAPTER IV

FLOWERING AND ORNAMENTAL PLANTS

For centuries selection was the only method practised for the improvement of plants, and the natural seedlings of selected plants were the only material from which a choice was possible. Selection thus operated on the maternal side only, the pollen was derived by chance from other individuals and there was no selection of the paternal parent.

The discovery of sex in plants in the eighteenth century and the recognition of the importance of the male parent gave a great impetus to the breeding of improved forms, but it was only after the discovery of the laws of inheritance by Mendel that the possibilities of plant-breeding were realised. In more recent years the knowledge attendant upon the concept of the gene and the identification of the chromosomes as the vehicles of inheritance has very considerably enlarged our understanding of the potentialities of plant-breeding. Indeed, it is probably true to say that we are now able to visualise for the first time, not only the possibilities of controlling the production of desirable forms, but the methods by which this will be achieved.

From this point of view the chapters which follow present accounts of what is largely pioneer work in experimental plant-breeding. Our procedure therefore has been to deal most fully with those plants which have been intensively investigated, and then, from plant experiment generally, to give examples which demonstrate particular points or have some bearing on future development.

Sweet Pea, *Lathyrus odoratus* (diploid, 2n = 14)

The sweet pea provides an excellent illustration of how, first by gene mutation and then by hybridisation, numerous varieties may arise from a single wild species.

This species was first introduced into England in 1699, when

seeds were received by a Dr. Uvedale of Enfield from the Sicilian monk Franciscus Cupani. In habit it was similar to the tall sweet pea, but it had relatively small flowers borne in pairs on short stems. The flowers had reddish-purple standards with light bluish-purple wings. All the " sports " which subsequently appeared were apparently due to gene mutation from the dominant to the recessive condition. A chronological list of some of the mutant characters and the names of the varieties first showing the new characters, together with the genes (see Table V) determining the respective characters, is given below.

TABLE V

Character	Gene	Date of First Appearance	Original Mutant Variety or Source of Origin
Wild sweet pea	..	Intro. 1699	..
White flowers	g_1 and/or f_1	1718	..
Red flowers	a_1	1731 (? 37)	Painted Lady
" Black "	..	1793	..
" Scarlet "	..	1793	..
Picotee	d_5	1860	..
Hooded	a_3	1886	Waverley
Dilute	g_3	1890	Countess of Radnor
Cupid	e	1893	*Ex* Emily Henderson
Dull	d_2	1899	Navy Blue
Round pollen	a_2	Before 1900 ?	Emily Henderson
Open keel	h	1900	Spencer
Sterile anthers	b_2	1903	*Ex* Emily Henderson × Lady Penzance
Copper	g_2	1905	Cambridge
Marbled	F_1'	1905	Helen Pierce
Bush	f_2	Before 1905	..
Crotin	b_3	1907	Cambridge
Acacia	d_1	1908	Mr. W. J. Unwin
Smooth	d_4	1912	Mr. T. A. Dipnall

Owing to the structure of the flower the sweet pea, in England, is naturally self-pollinated, pollination occurring before the flower opens. Hybridisation of the sweet pea was not practised until 1880 and onwards.

Breeding investigations were begun by Bateson, Saunders and Punnett (1905, 1911) at the commencement of the present century, and have been carried on chiefly by Punnett (1927, 1932, 1936). In Table VI nineteen pairs of characters are given, with the

symbols used by Punnett to identify them. The characters grouped under the same letter show linkage towards one another and are presumably controlled by genes located in the same chromosome. The dominant character is given first in each case.

TABLE VI

Gene	Character-pair	
	Dominant	Recessive
A_1	Purple	Red flower colour
A_2	Long	Round pollen
A_3	Erect	Hooded flower shape
B_1	Dark	Light leaf axil
B_2	Fertile	Sterile anthers
B_3	Normal	Cretin flower
B_4	Purple	Maroon
D_1	Tendril	Acacia leaf
D_2	Bright	Dull flower colour
D_3	Dark Flake	Light Flake
D_4	Hairy	Smooth
D_5	Deep	Picotee flower shade
E	Tall	Cupid
F_1, F_1'	Colour	Marbled—white
F_2	Procumbent	Bush (erect) habit
G_1, G_1'	Colour	Flaked—white
G_2	Purple	Copper flower colour
G_3	Full	Dilute (mauve) flower shade
H	Clamped	Open keel (= normal – Spencer flower)

Several of these genes exhibit secondary effects. Thus, in **ee** forms the plants are not only dwarf but have foliage of a deeper green; g_2g_2 plants are smaller, and deeper green than the dominant G_2G_2 forms and suffused with anthocyanin; the "Spencer" (**hh**) form of flower has wavy petals in addition to an open keel, and is usually not so highly scented as the type; Cupids (**e**) are comparatively lacking in scent as compared with tall (**E**) plants. With the three exceptions of marbled plants (F_1') which are heterozygous for C-white, and flaked plants which are heterozygous for R-white and the allelomorphs normal-acacia (D_1–d_1) the genes in Table VI are all completely dominant. Thus plants heterozygous (**Ee**) for the tall habit give a 3 : 1 ratio of talls and Cupids (dwarfs), the heterozygotes being indistinguishable from

the true-breeding talls. Similarly the typical 9 : 3 : 3 : 1 ratio is obtained from plants segregating for any two of the gene pairs (excepting multiple allelomorphs and linked genes), e.g. plants heterozygous for both tallness and the procumbent habit ($\mathbf{EeF_2f_2}$) give, on selfing, nine tall procumbent : three tall erect (bush) : three Cupid procumbent : one Cupid erect. The first class is the normal type of tall sweet pea which, though trained upright on sticks or wires, is really of a sprawling, procumbent habit. The tall-erect and Cupid-erect types attain heights of $3\frac{1}{2}$-4 ft. and under 1 ft. respectively and are distinguished from the well-known tall and Cupid procumbent forms of the garden by the non-divergent growth of the stems, which all grow up side by side, giving the appearance of a compact bush. The main difference between the tall and Cupid habits is really one of internode length, the internodes being very short in the Cupid plant.

Of great horticultural importance was the sudden appearance of the " Spencer " type of sweet pea in 1900. Prior to this time, the most advanced forms of sweet pea were the improved " grandiflora " types with moderate-sized flowers and plain standards without any trace of waving. The modern type of large flower with a waved standard appears to have arisen in several localities simultaneously. Mr. Silas Cole of Althorpe Gardens, Northampton, was the first to introduce it under the name Countess Spencer. In a letter to Mr. W. Cuthbertson (1912) he states that in 1898 he crossed the variety " Lovely " with " Triumph " and in the following year crossed two or three of the best seedlings with " Prima Donna ". The next season (1900) one of the seedlings was much stronger and later-flowering than the others, and this proved to be the original Countess Spencer. It bred true from the beginning.

The Spencer sweet pea also arose with Mr. E. Viner of Frome, who, late in the season of 1901, in a row of Prima Donna " noticed a spray of two blooms at the extremity of a shoot with a peculiar crimped character. I marked them and allowed them to seed (no other flowers appeared), and I obtained seven good seeds." The following year (1902) these seeds produced five plants of the waved and two of the Prima Donna type. The waved blooms were exhibited at the Bath Show in July under the name " Nellie Viner ". The stock was eventually sold to Mr. Eckford, but since Mr. Coles' variety had been put on the market first, the name

Nellie Viner was not retained, the stock being sent out as Eckford's superior stock [1] of "Countess Spencer".

The waved type also appeared in two other localities, Mr. Eckford finding it in a row of Prima Donna at Wem, and Mr. W. J. Unwin in a row of Prima Donna at Histon. Mr. Unwin's variety was saved and introduced under the name of "Gladys Unwin", but as it was less wavy and not so large as the Spencer types it was eventually superseded. It appears, therefore, that the waved forms appeared about the same time in four different localities, and that these plants comprised three slightly different grades of Spencer, Unwin's being the least waved, and Cole's original Countess Spencer being intermediate. Moreover *Prima Donna was involved in each of the four cases*, although Unwin states that it had bred true for colour and type for at least eight years before the advent of the waved form, and did not give it again.

As Punnett and his colleagues have shown, the waved character is determined by a recessive gene (**h**) which must have arisen as a mutation from the dominant normal form. In a very short time the new character was combined with numerous other flower colours by hybridisation, and where due precautions were taken to avoid cross-pollination, these new waved varieties were quickly fixed, since only two generations are actually necessary to raise plants homozygous for a character which is a simple recessive such as the Spencer flower.

The most probable explanation of the simultaneous appearance of these waved forms in different localities is that the original mutation occurred in one of the chromosomes of a homozygous (**HH**) Prima Donna plant, and that a few heterozygous (**Hh**) seeds giving plants indistinguishable from Prima Donna were distributed under that name. The fact that the Spencer mutation involved both size and waviness of the standard and that degrees of size and waviness occurred among the original plants suggests that Prima Donna was heterozygous for one or more modifying genes acting only on the recessive (**hh**) forms, thus giving rise to degrees of size and waviness.

It is interesting to note that the Cupid form which first arose in California in 1893 also appeared in England, France and Germany between 1893 and 1895 and prior to its distribution by Burpee in 1895. Here again it seems probable that the mutation occurred in a homozygous tall plant (Emily Henderson) and a few

[1] Owing to their finer form.

heterozygous seeds were distributed, which ultimately gave rise to the recessive Cupid forms. "Emily Henderson" was distributed by Henderson's of America in 1892.

It was in the sweet pea that the explanation of the phenomenon of reversion on crossing was first given, and linkage discovered and worked out. The case of "reversion" to the purple type following the crossing of two white-flowered forms has been given on page 9. The original instance of linkage was between purple-red flower colour (A_1-a_1) and long-round pollen (A_2-a_2) and it was pointed out that the ratios obtained in the subsequent generations were explicable on the assumption that the four types of gamete were produced, not equally, 1**AB** : 1**Ab** : 1**aB** : 1**ab**, but in the proportions 7**AB** : 1**Ab** : 1**aB** : 7**ab** ("coupling"). Subsequently, the chromosome theory provided an explanation of these unusual gametic series (see page 25). As will be seen from Table VI, there are five linkage groups and two independent genes, hence the number of linkage groups and independent genes does not exceed seven, the haploid number of chromosomes in *L. odoratus*.

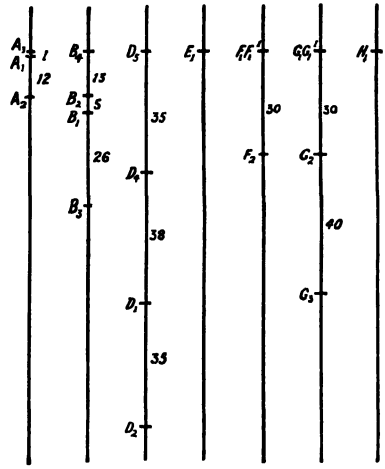


FIG. 20

Provisional map of the chromosomes of *Lathyrus odoratus*. (After Punnett—modified.) The approximate cross-over values are shown at the right of the line.

The strength of linkage varies considerably among the different pairs of genes. It is strongest between A_1 and A_3 with 1 per cent of cross-overs, and weakest between D_2 and D_4 with about 48-49 per cent cross-overs. Chromosome "maps" giving the approximate positions of the genes which show linkage towards one another are given in Fig. 20.

A consequence of a high degree of linkage is that the "cross-over" forms appear very rarely, the strain breeding practically true. Thus in a cross between purple-hooded (A_1a_3) and red-erect (a_1A_3), of the four types of gamete produced, two, viz. purple-erect (A_1A_3) and red-hooded (a_1a_3), occur in only about 1 per cent of the total gametes, i.e. the great majority of the gametes are of the

parental types, namely purple-hooded or red-erect. Hence the F_2 generation consists of purple-hooded, purple-erect and red-erect in the proportions 1 : 2 : 1, the purple-hooded and red-erect breeding true, but the purple-erect continually giving three forms again. The chance of a true-breeding purple-erect appearing is the same as that for a red-hooded, being in either case less than 1 in 50,000. In recording the above facts Punnett indicates the possibility that this may explain the case of certain forms of sweet pea, which cannot be got to breed true, e.g. "Audrey Crier", which habitually gives "Helen Lewis" and "Princess Victoria", in addition to plants like itself.

The Garden Stock, *Matthiola incana* (diploid 2n = 14)

The garden stock has been grown in the gardens of England and on the Continent from early times and is still found wild in the Isle of Wight.

The following brief history of its development under cultivation is taken from the excellent account given by Miss Saunders (1928), whose breeding investigations contributed largely to our knowledge of the genetics of the stock. The type, *Matthiola incana*, is a hoary biennial of bushy habit with purple flowers and blackish green seeds.

Earliest Record	Character	Mutant Genes
1536	Only two forms described, purple and white	**cR** or **Cr** (white)
1542	Red flowers	**b**
1563–68	Double flowers	**s**
1588	Shades of purple	..
1629	Yellow plastids	**w**
1660	Unbranched, single-spiked biennial (English Brompton stock)	..
1762	Half-hoary	..
1861	Glabrous	..

The actual dates of origin of most of the above mutations are unknown; the year given is for the first record of the respective characters. Each of the new characters arose apparently by gene mutation. Although one and the same species, the summer-flowering ten-week stock is sometimes referred to as *Matthiola annua*, as distinct from the biennial Brompton stock.

Breeding investigations were begun by Correns (1900), followed by Tschermak (1912), Saunders (1928) and Lesley and Frost (1927). The results of these workers' experiments, together with the chief characters studied, are as follows. The genes **C** and **R** are both necessary for the production of anthocyanin in the flower. **B** converts red anthocyanin colour into blue. **V** is a gene causing the difference between pure, **V**, and impure, **v**, colour. The colours arising from the combination of these four genes may be represented thus :

CRBV . . .	Purple
CRBv . . .	Plum
CRbV . . .	Red
CRbv . . .	Copper
All other genotypes .	White

In addition to these genes there are others which dilute flower colour, e.g. the dilute colours rose, pale marine, azure and flesh are dominant respectively to the deep colours carmine, marine, purple and terra-cotta. On the other hand, certain pale colours are recessive to deep ones, e.g. rose is dominant to pale lilac, suggesting that there are different diluting genes with specific actions. In addition to these main colour genes Saunders has shown that two others, **A** and **A′**, are also necessary for the production of anthocyanin even though **C** and **R** are present.

In the absence of anthocyanin three colour forms may be distinguished, namely white, sulphur-white and cream, the last two deriving their yellowish colour from the plastids. These colours are due to a single gene difference, white (**W**) being dominant to cream (**w**). Since **W** is not completely dominant the heterozygote is intermediate (sulphur-white) in colour.

Hoariness of the foliage is governed by three pairs of genes, **Cc, Rr** and **Kk,** and three multiple allelomorphs, **H, H_1** and **h.** Any combination involving **C, R, K** and **H** (or **H_1**) is hoary, all others being glabrous. Degrees of hoariness occur, e.g. **H_1H_1KK** is half-hoary, **H_1H_1Kk** is mid-hoary (i.e. less than half-hoary) and **H_1hKK** quarter-hoary, less hoary still.

A unique instance of a cytological character controlled by a single gene has been investigated by Lesley and Frost (1927). They found that a certain variety " Snowflake " had chromosomes which were distinctly longer than normal. Crossed with races with short chromosomes, the **F_1**'s were all found to have short chromosomes, but on selfing, a ratio of three short to one long

was obtained. This case is of considerable importance since it shows that the chromosomes themselves are subject to genetic control in the same way as other structures, internal and external, of the organism.

The inheritance of single and double flowers in the stock is of outstanding and traditional interest. As early as 1629 it was known that there were two kinds of single-flowered races. Both

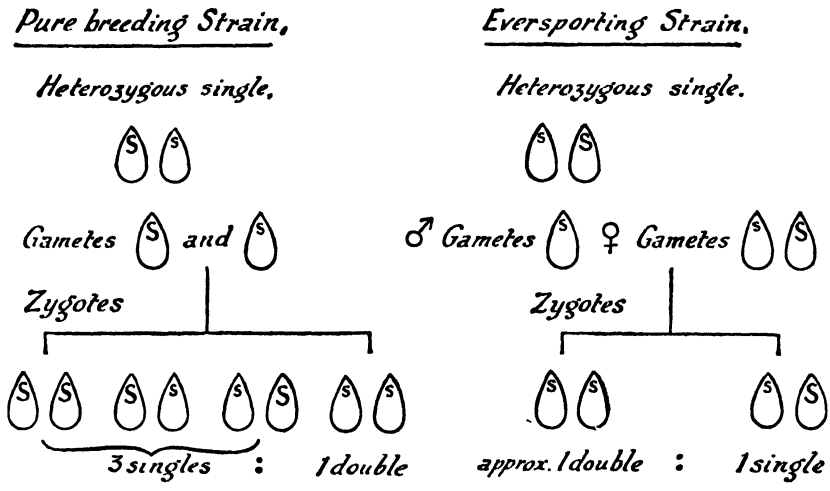


FIG. 21

Diagram showing the inheritance of double flowers in the Stock (see text).

have the normal number of chromosomes (Allen, 1924). Inheritance of singleness or doubleness in the first or pure breeding race is strictly mendelian, the homozygous singles breeding true and the heterozygous ones giving three singles to one double. In the second strain the singles are always ever-sporting and upon selfing give singles and doubles in approximately equal numbers, instead of the normal 3 : 1.

In both pure-breeding and ever-sporting races the genes **S** and **s** differentiate singleness from doubleness, i.e. **SS** and **Ss** forms are single and **ss** is double. All double stocks are completely sterile, having neither pistils nor stamens. Breeding results show that the pollen of the ever-sporting singles transmits the double character only, and pollen tests of the two kinds of single support the view that a pollen lethal occurs in the ever-sporting race, the female germ-cells of which are normal and carry both singleness and doubleness (Waddington, 1929).

Philp and Huskins (1931) made cytological studies on stocks and stated that in the ever-sporting singles, one of the chromosomes carrying the genes for singleness and doubleness (the A chromosome) lacked a trabant, i.e. a small terminal portion of chromatin, which was present in the pure singles. According to them, it is this chromosome lacking the trabant that carries the gene **S** for singleness, the recessive gene **s** being borne on the normal chromosome. The locus of this gene is so close to the trabant that crossing-over practically never occurs between them ; the result is that the chromosome lacking the trabant almost always carries the gene **S** for singleness, i.e. the trabant and **s** are very closely linked. On the male side pollen without the trabant (and therefore carrying the gene for singleness) is lethal and incapable of effecting fertilisation. Westergaard (1936) and Kuhn (1938), however, deny that the ever-sporting race of stocks lacks a trabant, and Kuhn is doubtful whether chromosome A bears the genes concerned. Both authors point out that the lethal effect may be seen in the rarity of metaphases and the different quality of fixation in plants carrying the lethal form from those without it. The result of selfing a heterozygous single is very similar to that from back-crossing a normal heterozygote to a pure recessive, e.g. 1**S** : 1**s** × **s** giving 1**Ss** : 1**ss**.

Although the proportion of doubles is strictly determined in the seed, the proportion of doubles actually grown and flowering may be increased by discarding the weakest seedlings at an early stage, since the singles are apparently on the average a little smaller than the doubles. Again, seed giving single plants is said to be a little less viable than double seed, in which case old seed may give a higher percentage of doubles.

As Frost (1928) has shown, however, the proportion of doubles actually flowered may be increased definitely and considerably in another way. A certain form of the ever-sporting single " Snowflake ", characterised by slender leaves, has a chromosome fragment over and above the normal chromosome number (i.e. 14 + 1), this fragment being the part which also carries the **S-s** genes. About 37 per cent of the progeny from selfing this slender form are found to be slender also and of no horticultural importance, since they lack vigour and decorative value. The remaining normal plants, however, include nearly 90 per cent of doubles. In other words, if the slender type of plant is discarded in the seedling stage a large proportion of the single-flowered plants

is also discarded—the slender character behaving as if closely linked with singleness. The reason for this unusual segregation lies in the fact that most slender plants carry one gene for singleness and two for doubleness, the **SSs** progeny, like the **Ss** pollen, being unable to survive. In order to obtain this high proportion of double-flowering plants, seed must, of course, be saved from the slender types in each generation and not from the normal singles, which should be discarded.

We see, therefore, that in the case of the ever-sporting single slender types we have two instances in which characters of horticultural importance are associated with definite cytological phenomena, the origin of slender indeed being the product of an attempt by cytological and genetical investigators in an American research station to obtain the complete range of trisomic stocks, these being required to elucidate a theoretical study.

The inheritance of other characters investigated in the stock is as follows, the dominant character being given first in each case :

Tall	Dwarf habit
Branched . . .	Unbranched habit
Glandless . . .	Glands on leaves
Blue embryo colour .	Yellow embryo colour
Brown seed coat colour .	Light yellow seed coat colour

The blue embryo colour is associated with coloured flowers, the yellow with white or cream flowers. In the absence of **B,** which changes purple flower colour to red, the embryo colour is brown instead of blue.

Chinese Primrose, *Primula sinensis* (diploid, 2n = 24)

Among the numerous flowers which have been the subject of genetic study, the investigations on the Chinese primrose take a foremost place. Breeding experiments with this plant were begun early in the present century by Bateson and Gregory (1905 and 1911), and have been continued by de Winton (1923), de Winton and Haldane (1933), Sverdrup (1930) and others. References to a number of important publications by these investigators are given in the accompanying bibliography.

There are two forms of *Primula sinensis* in cultivation at the present time, diploids with twenty-four and tetraploids with forty-eight chromosomes. The tetraploids arose from the diploids spontaneously under cultivation.

Primula sinensis was first successfully introduced into England about 1820, and early descriptions show that the first plants raised were pin- or thrum-eyed, sinensis or stellata in habit of growth, but in other respects they were uniform. All of the other numerous varieties which exist at the present time have arisen in cultivation, and, as far as is known, they have all resulted from gene mutation.

The history of the Chinese primrose following its introduction to Europe is not easy to trace in regard to the appearance of definite mutations. Certain gene mutations appear to have occurred more than once, e.g., **g, y, f**^{s} and probably **o** and **m.** In Britain only a limited number of varieties seem to have been cultivated until about 1860, but from this date the development of *P. sinensis* began to grow apace, the subsequent twenty-five years seeing the production of numerous varieties.

The principal developments since the introduction of the Chinese primrose are given in Table VII. The dates in a few cases are approximate only.

TABLE VII

History of Primula sinensis (*mainly in England*)

1819	Seeds and plant sent from Canton, China. Died.	
ca. 1820	Plant brought from China and flowered. Sinensis type, magenta flowers, thrum ?	
1821–26	Seeds arrived from Mr. Potts, China. Sinensis and stellata forms. Chief source of cultivated varieties	**ch**
1824	First record of pin stylo	**s**
	First record of purplish-crimson flowers =red stigma	**g**
1827	First whites recorded	**D**
1838	Fertile double magentas and whites offered by Anderson, London	**m**
1837–42	Nine varieties offered by Bosse, Germany, including a double white.	
1846–48	Crimson and " Sirdar " forms figured	**b** and **j**
1850	Sterile doubles grown before this date	**x**
1854	Bosse had a fern-leaved form ? Not preserved	**y**
1861–65	Fertile double—deep magenta, carmine, red, pink, bluish and white varieties listed.	
1862	Flaked forms figured. Fertile doubles received from Continent. Twelve well-marked varieties in cultivation in England	**e**
1863	Fern leaf arose before this date	**y**
	Leafy calyx	**n**
	Duchess types recorded.	

TABLE VII—*continued*

1864	Large eyes recorded	a
1866	Large and *medium* eyes figured (also white and green foliage. v, j ?)	A
1869	Fifteen to twenty sorts grown at Glen Eyre.	
ca. 1880	" Reading Pink "	v
1884	" Reading Blue "	r
1884	" Snowdrift "	vj
1887	Crimped leaf	f^s
1902	White eye	A′
1905	Purplish stems and leaves	l
1906	Coral flowers	k
1907	Ivy leaf	iv
1909	Tetraploids.	
1913	Lee's crimp leaf	f^1
1919	Harlequin flowers	h
1922	Peculiar eye	p
1925	Feeble-minded habit	w
1928	Umbellated habit	u
1929	Maple leaf	mp
1930	Cup leaf	c
1930	Ghost eye	sp
1931	Claw leaf	z
1933	" Dazzler "	dz

De Winton and Haldane (1933) have described the action and interaction of twenty-five pairs of allelomorphic genes and two sets of three multiple allelomorphic genes in the diploid *P. sinensis*. Of these genes two or three are dominant to the original type, the remainder recessive. Eleven of the genes affect anthocyanin, four affect the plastids of the flower, three of them also having structural effects. The remainder have purely structural effects, four acting mainly on flower structure and one mainly on bract structure. In addition one extra-nuclear factor governs the colour of leaf chloroplasts. The genes and their action are given in Table VIII. The genes **Ch, D** and **A′** which are italicised are dominants over the wild type. The remaining mutant types are recessive, but **Jj** plants are intermediate in some respects.

De Winton and Haldane have provisionally divided the genes into groups according to their most conspicuous effects, as follows :

Genes intensifying anthocyanin . . .	**V J K E H**
Genes inhibiting anthocyanin . . .	**G D I L B**
Gene altering anthocyanin . . .	**R**

Genes inhibiting flower plastids and flattening edge of leaves and petals	**F** (three allelomorphs) **A** (three allelomorphs) **P**
Genes affecting flower structure . . .	**S X M Ch N**
Genes affecting leaf structure . . .	**Y O T Mp C Z**
Genes affecting both flower and leaf structure	**W Iv**
Gene affecting habit	**Q**

TABLE VIII

Linkage Group	Gene	Action of Gene	Appearance of Mutant
I	**S**	Shortens style, lengthens anthers	"Pin", long style, short anthers (probably present in nature)
	B	Blues anthocyanin, increases flavone	Red flowers
	X	Converts extra petals into stamens, etc.	Sterile double flowers
	G	Suppresses anthocyanin in flower centre	Red stigma, dark centre to flowers
	L	Partly suppresses anthocyanin in stem and leaf	Dark purple stems and leaves
II	**P**	Restricts eye, flattens petals	"Peculiar" large eye, rolled petals
	F	Suppresses growth of leaf edge	.. ..
	f^s	.. ..	"Sutton's" moderately crimped leaf, normal eye
	f^l	.. ..	"Lee's" intensely crimped leaf, large eye
	Ch	Increases flower growth, shortens stem	"Sinensis", fringed petals, ten calyx teeth
III	*D*	Suppresses anthocyanin in flowers, especially at edge	White flowers
	E	Spreads anthocyanin over petals	Flaked petals
IV	**M**	Suppresses extra whorl of petals	Fertile double flowers
	Y	Shortens leaves	"Fern" leaf
	H	Makes petal colour and size uniform	"Harlequin" flowers
	K	Oxidises pink anthocyanin to darker type	"Coral" stems, pale or white flowers
V	**O**	Joins leaflets	"Oak" incised leaves
	Mp	Lengthens hairs, alters leaf edge	"Maple" leaf, semi-glabrous

TABLE VIII—*continued*

Linkage Group	Gene	Action of Gene	Appearance of Mutant
VI	R	Acidifies petal sap	Blue flowers
	N	Inhibits overgrowth of calyx and bracts	Leafy bracts and large calyces
	V	Makes anthocyanin	Green stems, white—pale pink flowers
	J	Makes anthocyanin	Green stems, "Sirdar" flowers
	I	Slightly dilutes anthocyanin	Deeply coloured flowers
	A'	Suppresses plastids of eye	"Alexandra" white eye in flower
	A	Restricts plastids of eye	.. ..
	a	.. ..	Large "Primrose Queen" eye, very short style
	Sp ?	Intensifies plastids of eye	"Ghost" eye
	Ep ?	Restricts petal number	Extra petals
	T	Makes leaves rounder, and incises them	"Tongue" triangular leaves
	C ?	Increases vigour of plant	"Cup" leaves, small unhealthy plants
	Z	Expands leaf, suppresses dorsal comb, etc.	"Claw" leaves, rolled up
	Iv	Makes leaf margins crenate	"Ivy" leaf, reduced flowers
	W	Increases vigour of plant	"Feeble-minded", stunted plants
	Q	Causes open growth	Rosetted habit
	U ?	Reduces leaf number and stem size	Umbellated, often fasciated habit

As will be seen from Table VIII, a number of these genes have effects secondary to the major ones by which they are usually identified. Moreover, a large number of interaction effects arise from the many gene combinations possible and result in unforeseen character modifications. Thus plants lacking the anthocyanin modifiers **V** and **L** are also female sterile, the ovules failing to develop. Crimping of the leaf is much greater when combined with sinensis flowers than with stellata, and crimped leaves combined with large yellow eye results in very small flowers which drop easily.

The genes **A'**—**A**—**a** provide a good example of the action of multiple allelomorphs. **A'** gives a white ("Alexandra") eye, **A** the normal (medium) yellow eye, and **a** a large yellow ("Primrose

Queen ") eye. The **A** factors thus cumulatively inhibit the production of yellow plastid pigment.

As will be seen from Table VIII, the factors **S, B, X, G** and **L** are all borne on one chromosome and constitute the first linkage group in *P. sinensis*. In **gg** plants the gynaecium, and especially the stigmatic surface, is coloured red, flower colour usually only reaching full development when **G** is absent. The combination of these full-coloured flowers with the purplish leaves found in *ll* plants was a notable example (the first) of the practical application of the theory of linkage. **G** and **l** and **g** and **L** are situated close together on the first chromosome and are therefore tightly linked. Actually the cross-over form **GL** was expected only once in 6500 [1] plants of the F_2, and it was not found until over 6000 plants of the F_2 were actually raised. Among the progeny, however, a plant was noticed to have red stigmas combined with leaves slightly darker in colour than the normal. Although heterozygotes cannot usually be distinguished, this plant was suspected of being heterozygous for **L**, a suspicion which was proved correct when, on selfing, the new combination of dark flowers and foliage was obtained. These plants were later distributed by Messrs. Sutton & Sons under the name " Etna ".

Linkage in the diploid *P. sinensis* varies from about 2·5 per cent between **G** and **L** to over 40 per cent between **S** and **L**.

The genetic constitutions of some of the varieties in commerce to-day have been given by de Winton and Haldane (1933) and are reproduced below.

Sutton's Royal White	**ss DD ChCh**
,, Double-white Purity	**ss BB vv ii mm ChCh**
,, White Star	**ss DD A'A' ll**
,, Queen of the Pinks	**ss bb vv mm ChCh**
,, Coral Pink	**ss kk gg bb ii ChCh**
,, Coral Pink Star	**ss kk gg bb ii**
,, Crimson King	**ss KK gg bb ii ChCh**
,, Etna	**ss bb gg ll ii ChCh**
,, Vesuvius Star	**ss bb gg ii Chch**
,, Czar	**ss gg rr ii ChCh**
,, Reading Blue	**ss rr ii ChCh**
,, Duchess	**ss bb gg DD ChCh**

[1] In a similar and strictly comparable case one cross-over was obtained in 6843 plants.

Primula sinensis (tetraploid, 2n = 48).

All forms of tetraploid *Primula sinensis* have arisen from the diploid race and are therefore auto-tetraploids. Their fertility is lower than that of the diploids, but high enough to enable seeds to be obtained fairly readily.

The cross tetraploid × diploid occasionally gives seedlings, the majority highly sterile triploids with thirty-six chromosomes, and a few fertile tetraploids arising apparently from the functioning of unreduced pollen grains with twenty-four chromosomes. The reciprocal cross, diploid × tetraploid, has only once given a seed.

Twelve or thirteen of the genes studied in the diploid are found in the tetraploid, viz. **s, b, g, l, f^{l}, Ch, D, y, v, A′, a** and **ep,** while **x** was formerly found in it. Since in the tetraploid there are four chromosomes of each type as compared with two in the diploid, each of the genes may occur from one to four times, the possibilities therefore being much greater than in the diploid. For example, instead of only **SS, Ss** and **ss** plants we may have five different genotypes **SSSS, SSSs, SSss, Ssss** and **ssss**, and, if dominance is not complete, cumulative effects will be obtained.

Of the dozen or so genes studied, **S** and **V** appear to be completely dominant, i.e. even **Ssss** cannot be distinguished from **SSSS**. **G** is almost completely dominant. The different dosages of **B** can be distinguished in certain combinations. **Y** and **A** can always be recognised in the simplex form. **Ch** is less dominant than in the diploid, while all four types of **D** are readily distinguished in the presence of **g,** but less readily when **G** is present, since **D$_3$G** may also be white. Similarly, all forms of **F** show some degree of crimping. Thus **F** is not dominant at all in tetraploid *P. sinensis*, and **D** is greatly affected by the interaction of other genes. Results such as these clearly demonstrate that not only is the ratio of dominant to recessive genes of critical value in the character expression of polyploids, but a change in number, though not in proportion, of the genes may also alter the phenotypic expression.

We see, therefore, that the cumulative action of identical genes in polyploids may not only considerably increase the range of variation but in high polyploids give rise to imperceptible gradations, as described subsequently. When a number of similar genes govern the same character the expression of dominance is

essentially more variable. Indeed certain balances may suggest that a character is recessive whereas others may point to dominance.

The deliberate transference of a mutant gene from the diploid to the tetraploid race of *P. sinensis* is a laborious task, only accomplished by the crossing of a tetraploid plant with a diploid homozygous for the desired gene. For example, in 1927 de Winton crossed a tetraploid (**LLLL**) primula with pollen of the purple-leaved diploid variety " Etna " (**ll**). From this cross a tetraploid was obtained, apparently from the functioning of an unreduced **ll** gamete from Etna. By selfing and crossing the progeny of this plant, the tetraploid form of Etna (**llll**) was eventually obtained in 1934, thus making many new combinations possible in the giant race. Recently two other genes have been transferred to the tetraploid strain in the same way.

It is therefore evident that the accident of the unreduced gamete may be of considerable importance to the plant breeder, in the first place because it is the commonest way in which polyploids arise, and secondly because it is the means whereby selected genes may be transferred from the diploid to the tetraploid condition.

Nemesia strumosa (diploid 2n = 18)

Nemesia strumosa has been in cultivation since the last part of the nineteenth century.

The inheritance of flower colour in *N. strumosa* has been studied by Riley (1945, 1948, 1949). The corolla consists of a short tube which bears a short spur or pouch. The limb of the corolla is two-lipped, an upper and a lower lip. The inside of the corolla limb may be white, orange, yellow, or several shades of red and purple ; there may be a blue margin on the upper lip, or it may be streaked with red. The lower part of the tube may be orange or straw colour and may have a few or many dots of very deep purple. The upper part of the tube is generally colourless, but above the stamens there frequently is formed a large spot of very deep purple, the " eyebrow ". Apparently all these colours exist in wild plants, and a very large number of interacting genes seem to be present. The species is self-incompatible.

Six genes for yellow or orange flowers have been found in *N. strumosa*. **O** produces a deep yellow or orange colour, usually

Cadmium Yellow [1] or Light Cadmium, on both the upper and lower lips of the corolla. Plants with the **O** gene may have the colour diluted by two other genes, **bu** and **p**: **bu** changes the upper lip to Sulphur Yellow and the lower lip to Buff Yellow, while **p** lightens the upper lip to approximately Apricot Yellow. **o** is epistatic to **p** and **bu** which are therefore expressed only in the presence of **O**. **bu** is epistatic to **p**, so that **O-ppbubu** and **O-P-bubu** plants are indistinguishable. **bu** is linked with the self-incompatibility alleles. All **O-P-Bu** plants are orange.

Three genes produce some yellow in **oo** plants but apparently do not express themselves in the presence of **O**. **y**, yellow, produces yellow-coloured flowers and is recessive to **Y**, non-yellow. **gl**, glass-green, produces flowers in which the corolla limb is Glass Green or Seafoam Yellow, and is recessive to **Gl**, non glass-green. **ys**, yellow-spot, produces a yellow spot with yellow lines radiating from it on the lower lip of the corolla near the throat. Yellow appears to be epistatic to glass-green and possibly yellow-spot. **Y-Gl-Ys** plants are white.

C is a basic anthocyanin gene. Anthocyanin on a yellow background gives Carmine, Bordeaux, Ox-blood Red, or some other reddish colour. On a "white" background the colours are Pomegranate Purple, Amaranth Purple, Tyrian Rose, or some other bluish colour.

Blue and blue-margin seem to form a series of multiple alleles with orange and white with orange the top dominant, white dominant to blue types, blue-margin dominant to blue, and blue recessive to the other three types. The genes are designated, respectively, **O**, **o**, o^{bm}, and o^{bl}. A recessive gene for blue-margin reducer, **br**, reduces the width of the margin in blue-margin, eyebrow plants.

C is epistatic to **E-e**, eyebrow and its allele: all **C** plants have the eyebrow character regardless of their eyebrow genotypes.

Antirrhinum (diploid 2n = 16)

Baur and his co-workers have raised very large numbers of these plants, including a number of species and species hybrids. In all about 200 genes have been studied, the great majority of which are recessive mutations causing minor changes in the phenotype. Among the more important characters investigated

[1] Ridgeway Colour Standards.

are habit of plant, flower form, colour and pattern, leaf shapes, chlorophyll deficiencies and pollen incompatibility genes. Of considerable interest are Baur's experiments on the rate of mutation in *Antirrhinum*. As shown in the histories of *Primula sinensis* and the sweet pea, gene mutation has, under cultivation, given rise to new forms from time to time. From these and other records the frequency of mutation appears to be low, but Baur found that when large numbers of F_2 and F_3 generations are grown the frequency may be as high as from 1·3 to 7 per cent. Practically all of the mutations are recessive, the heterozygous being indistinguishable from the dominant homozygous forms—hence the necessity of raising F_2 generations to reveal the mutations. The rate of mutation has been very considerably accelerated by the use of X-rays, chemicals, heat and other means, as many mutations being found in the year following X-ray treatment as had occurred in the whole of the previous twelve years.

Rudbeckia hirta (2n = 38)

The typical colour of the discs in the flowers of this species is purple. Blakeslee (1921) found two genetically different races with yellow discs, one giving a black reaction with potassium hydroxide and the other a reddish colour. These two yellows were recessive to the purple colour, and, crossed together, give a purple F_1 and a dihybrid ratio of nine purple : four red-yellow : three black-yellow in F_2.

Among the many other plants which have been studied genetically the following examples are of particular interest.

In *Tropaeolum majus* (2n = 28) forms with variegated leaves commonly occur, the variegation resembling an irregular marbling of green and yellowish white. In the great majority of cases variegation mosaic in appearance is due either to a virus which may be transmitted by contact or inoculation, or the variegation has an extra-nuclear origin and is transmitted maternally, through the cytoplasm. In *Tropaeolum*, however, the variegation is inherited as a simple recessive character, green leaf being completely dominant (Correns, 1920; Warren, 1919). A similar example is reported by Correns in *Ipomoea imperialis*.

Campanula persicifolia, which normally grows two to three feet high, sometimes gives dwarf forms about 8 inches high with intense dark green leaves. This dwarf form is so strikingly

different from the normal that it is known among horticulturists as *C. nitida*. Nevertheless Bateson (1920) has shown that *nitida*

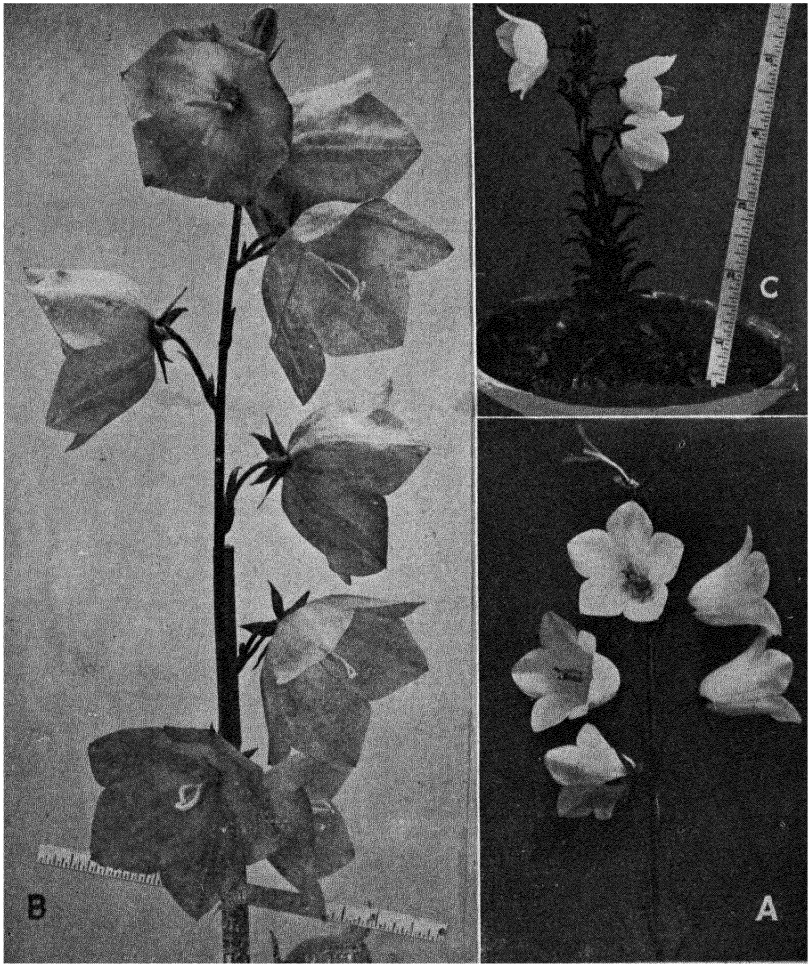


FIG. 22

A, *Campanula persicifolia*, diploid with sixteen somatic chromosomes; B, "Telham Beauty", a tetraploid with thirty-two chromosomes which arose from the diploid species; C, *C. persicifolia*, var. *nitida* (2n = 16), a dwarf recessive of *C. persicifolia*. (After Gairdner, 1926.)

is a variety of *C. persicifolia* from which it differs by one gene only, i.e. it is a simple recessive, the tall habit of *C. persicifolia* being completely dominant. *C. persicifolia* and *C. nitida* are

both diploid forms (2n = 16). A giant form, " Telham Beauty ", which arose from the diploid *C. persicifolia*, is a tetraploid with thirty-two chromosomes (Fig. 22).

In contrast to the simple inheritance of the rather striking characters just mentioned is that shown by the velvety-black viola, *Viola tricolor nigra* (2n = 26). Clausen (1930) has shown that this darkest of all colours in *Viola* is an extremely recessive condition in which five genes, $\mathbf{M_1}$–$\mathbf{M_5}$, suppressing the black colour, are all in the recessive condition, while three dominant polymeric genes necessary for the production of anthocyanin colour (violet or reddish) must be present. Thus the constitution of the flower colour of *Viola tricolor nigra* may be written

$$\mathbf{m_1m_1\ m_2m_2\ m_3m_3\ m_4m_4\ m_5m_5\ A_1A_1\ A_2A_2\ A_3A_3}$$

Inter-specific Hybrids

So far, the examples we have given in this chapter have dealt with variation within established species. Many of our most valued decorative plants, however, are interspecific hybrids of more recent origin, and the phenomena associated with their origin and behaviour will now be considered.

Generally speaking, the behaviour of inter-specific hybrids, both in regard to fertility and segregation, is largely correlated with the affinity of their parents. Species which are very closely related and have the same chromosome number usually give fertile offspring whenever the cross is made, e.g. *Antirrhinum majus* × *A. Linkianum* and *Lycopersicum esculentum* × *L. racemigerum*.

A typical example of inheritance in fertile species hybrids is seen in the inter-specific crosses made by Chittenden (1928) in the Vernales section of *Primula*. Crosses were made mainly between *P. Juliae*, *P. acaulis* and *P. elatior* but also with *P. officinalis* and various polyanthus types. The following is a brief summary of the breeding results.

Flower colour.—The $\mathbf{F_1}$ between *elatior* (deep yellow) and *Juliae* (magenta) usually had yellow flowers. Some plants of *elatior*, however, gave, when crossed with *Juliae*, an $\mathbf{F_1}$ consisting of yellow-flowered and coloured (anthocyanin) plants in approximately equal numbers.

The $\mathbf{F_1}$ between *acaulis* (pale yellow) and *Juliae* (magenta) had

flowers pigmented with anthocyanin, two shades occurring. In the F_2 at least six shades of colour were detected, in addition to yellows and whites.

Chittenden interprets the results as follows :—*Juliae* carries two genes affecting anthocyanin colour, a colour gene **R** and an intensifier **D** ; *elatior* carries an inhibitor of anthocyanin, **I**, which is effective against **D** and **R** in the heterozygous as well as in the homozygous condition. Most of the *elatior* plants used were homozygous for **I**. A few were heterozygous and gave equal numbers of coloured and yellow flowers in the F_1 *elatior* × *Juliae* mentioned above.

Pin and Thrum.—The segregation obtained was sharp in both intra- and inter-specific crosses, thrum being clearly dominant. The difference between pin and thrum styles is apparently governed by a single gene.

Hairiness.—*Juliae* is semi-glabrous ; *acaulis* and *elatior* are very hairy. The F_1 in each case resembled *Juliae*. The results suggested that *acaulis* (and probably *elatior* also) carry two genes for hairiness, while *Juliae* contributes an inhibitor.

Peduncle elatior (umbellate inflorescence) × *Juliae* (solitary flowers) gave an F_1 all with pedunculate inflorescences. In crosses between pedunculate and non-pedunculate species the difference between these characters appears to be due to a single gene.

Eye Colour.—Both *acaulis* and *Juliae* have a yellow eye ; in *elatior* the eye colour is orange. In the F_1's from *elatior* × *Juliae* and *elatior* × *acaulis* all the individuals had orange eyes, the evidence from the F_2's and back-crosses suggesting that eye-colour also is the expression of a single gene difference.

Other observations made were : Deep flower colour is almost invariably associated with the semi-glabrous condition seen in *Juliae*. *Juliae* eye was never seen on a white or yellow flower. Deep flower colours or *Juliae* eye rarely if ever occur on an *acaulis* leaf type. As Chittenden suggests, many genes in many different chromosomes are probably necessary, for example, to give *acaulis* leaf shape, so that in plants having this leaf shape the chromosome complex is predominantly *acaulis*. A similar argument may be used to explain the other cases.

It should be noted, however, that with continued breeding and selection it is probable that forms would be obtained combining the contrasting characters of the parent species, e.g. *acaulis* leaf

with the deep flower colour of *Juliae*, as the result of selection of cross-over types.

In a number of other species-crosses in *Godetia*, *Nemophila* and *Phacelia* Chittenden was able to show that the relation of the characters he studied was the same in inter-specific crosses irrespective of whether a pair of characters (1) was common to both parent species, (2) occurred in one species only or (3) occurred in distinctly different sections of the genus.

Ranging from fertile hybrids such as those mentioned above, examples are known in which the degree of fertility of the hybrids grades from high fertility to almost complete sterility, the degree of fertility being proportional to the regularity of pairing between the parental chromosome complements.

Complete sterility of the hybrid ensues when the chromosomes are too differentiated to pair regularly. Among bulbs, herbaceous plants and shrubs, many sterile but highly decorative plants have been obtained from inter-specific crosses, and since they are maintained and multiplied by asexual means their sterility is of no immediate consequence to the horticulturist. The genus *Cytisus* affords several examples, *C. kewensis* (*C. Ardoini* × *C. albus*), and *C. Beani*, which is presumably derived from *C. Ardoini* × *C. purgans*.

Occasionally sterile hybrids such as these may suddenly become fertile, as in the case of *Primula kewensis* (*P. floribunda*, n = 9, × *P. verticillata*, n = 9), the original form of which was for many years completely sterile, Newton and Pellew (1929). Later a fertile inflorescence gave seed, which was the source of the giant fertile strain of *kewensis* with eighteen pairs of chromosomes. Apparently a cell-wall had failed to develop in a somatic division of the chromosomes, thus giving rise to tissue with double the number of chromosomes.

An increasing number of cases is known where chromosome doubling has occurred in sterile species hybrids, and in each case fertility is seen to be restored. Each chromosome has an identical partner, and pairing, disjunction and germ-cell formation are in consequence quite regular. The tetraploid *P. kewensis* breeds practically true, since *verticillata* rarely pair with *floribunda* chromosomes, so that there is little or no segregation of specific characters ; and in addition the parent species must have been largely homozygous, since little segregation occurs within the respective genetic complements.

Where one or both of the parents of species hybrids are heterozygous then segregation may occur at once and give rise to a number of forms. In this respect the origin and behaviour of certain garden forms of *Delphinium* are of special interest. The hybrid *D. belladonna* has been grown in gardens for many years and no record exists of its first appearance. It is well known, however, that for a long period it was sterile, until in 1902–3 Mr. G. Gibson of Leeming Bar obtained three seed pods, from which the fertile race of *belladonna* originated. Now *D. belladonna* is exceptional in that it is the only hexaploid *Delphinium* species (2n = 48) so far known, a fact that suggests it arose as a sterile triploid from the crossing of diploid (2n = 16) and tetraploid (2n = 32) forms, the latter of which include the tall growing garden hybrids known as *grandiflorum*, *hybridum*, etc. The accident of somatic chromosome doubling in a flowering shoot would then give rise to more or less fertile flowers as found by Mr. Gibson, whose note that only three fertile seed pods were found suggests that chromosome doubling was confined to a small part of the inflorescence.

More recently an exceptionally interesting case has been reported by the Dutch nurseryman Mr. B. Ruys (1931). For many years Ruys had attempted to cross the red-flowered, dwarf, early flowering species *D. nudicaule* with the tall blue species *D. elatum*, for the express purpose of obtaining a red border delphinium. His deliberate crosses did not succeed, but in the summer of 1929 a plant with a stem 4½ feet high bearing dull purplish flowers appeared in a batch of *nudicaule* seedlings. This natural seedling proved to be intermediate between *nudicaule* and *elatum* in every respect. It was fully fertile, and the next generation gave the desired forms with red flowers.

The cytology of the species involved gives the clue to the origin of the red-flowered race. *D. nudicaule* is a diploid with sixteen chromosomes and *D. elatum* is a tetraploid with thirty-two. Since the hybrid was found in a batch of *nudicaule* seedlings it is highly probable that it arose from the meeting of an unreduced *nudicaule* egg-cell with a normal *elatum* pollen-grain, thus giving the fertile hybrid. The new red-flowered strain *D. Ruysii* therefore should be tetraploid (2n = 32) and an examination we have made of the root tips of the original plant shows this to be the case. From a preliminary examination of meiosis it is also apparent that multivalent association occurs, i.e. crossing-over

must take place between some of the *nudicaule* and *elatum* chromosomes, thus giving rise to certain of the new colour combinations obtained by Ruys in later generations (Lawrence, 1936). It is also probable that the original parents were heterozygotes, segregation occurring in F_2 and subsequent generations.

It is noteworthy that not only have the desired red-flowered tall forms been obtained, but all colours between white, yellow, pink, red, purple to deep violet, some dwarf, others up to 5 feet in height. (The average height is 3–4 feet.) The new strain flowers early in May and has a longer flowering season than either parent.

Thus two-colour series, viz. red and yellow from *D. nudicaule* and blue and white from *D. elatum*, have been combined in Ruys' new strain—which is virtually a new species—and in addition the range of variation in regard to habit and flowering season have been considerably extended (cf. Dahlia).

Longley (1928), Simonet (1929–32) and Randolph (1934) have studied cytologically many species and varieties of Iris. Randolph and his collaborators have also published an informative summary of the history, origin and breeding of the Iris (Pridham *et al.*, 1935. The European species *Iris pallida* and *I. variegata* and their derivatives are diploids with twenty-four, or approximately twenty-four, somatic chromosomes. The Asiatic species *I. cypriana*, *I. mesopotamica*, *I. macrantha* and *I. trojana* are tetraploids with forty-eight chromosomes, and their derivatives, which comprise the majority of the tall bearded irises, are also tetraploid or approximately tetraploid. Among the latter, varieties occur with numbers slightly above or below the tetraploid number, ranging from forty-six to fifty-one chromosomes. Hybrids between the diploid and tetraploid species would be expected to be triploid, and a number of varieties with thirty-six chromosomes are known. Breeders of Iris commonly experience difficulty in crossing diploids such as *pallida* and *variegata* types with the large-flowered tetraploid forms, and the triploid hybrids obtained from such crosses frequently have a pronounced infertility and usually their offspring lack vigour. This is also characteristic of the hybrids obtained from inter-crossing the dwarf and tall bearded varieties, which have different chromosome numbers.

I. chamaeiris, *I. olbiensis* and other dwarf forms have forty chromosomes. Exceptions are *I. pumila* with thirty-two and the dwarf variety *azurea* which has thirty-six chromosomes. The

varieties of hybrid origin obtained by intercrossing the dwarf and tall bearded forms are intermediate in height, blooming period and also chromosome number (forty-four). *I. germanica*, *I. Kochii* and *I. albicans* also have forty-four chromosomes, and, Randolph states, this suggests a similar hybrid origin for these species. Randolph also discusses the possibility of polyploid forms arising from the functioning of unreduced germ-cells, an explanation also advanced by Simonet (1932) to account for the origin of the tetraploid variety Ambassadeur from the diploid variety Liberia, and the pentaploid variety Magnifica from the triploid Isoline.

In the genus Iris, as in many other horticultural plants, vegetative reproduction allows forms to be perpetuated which could not be maintained by sexual means, and consequently the breeder may often use forms which are exceedingly complex genetically. Certain characters in Iris appear to have a relatively simple mode of inheritance. In many characters, however, such as height of flower stem, shape of flower and to a large extent flower colour, there is a wide diversity of forms. Sharp discontinuity and complete dominance of characters do not occur, and it is probable that much of the difficulty experienced in interpreting breeding results on a genetic basis is due to the hybrid origin and polyploid constitution of many members of the genus.

From these examples the importance of the unreduced gamete is clearly evident. In crosses between diploid varieties it may give rise to tetraploid forms, and, as we have seen in the tetraploid *Primula sinensis*, by its aid genes may be transferred from the diploid to the tetraploid strain.

In species-crossing the chance occurrence of unreduced gametes makes it possible to get fertile species hybrids where, normally, sterile and useless plants would be obtained, or no seed at all. It is possible that recognition of the great possibilities associated with the functioning of the unreduced gamete will, in the future, lead to the deliberate crossing of species and varieties which, because of differences of chromosome number and constitution, normally fail to give any results of practical importance upon crossing. From both the academic and the practical point of view any method which stimulates the production of unreduced gametes will be of great value, since polyploidy, in addition to being frequently associated with increase in size, may also be accompanied by increase in the range of variation with the consequent emergence

CHAPTER V

THE CHEMICAL AND GENETICAL BASIS OF FLOWER COLOUR

FLOWERS may be conveniently divided into three colour classes, (i) white, (ii) yellow and (iii) red and blue. Variation within these classes comprises intensification, dilution, increase in redness or increase in blueness of tone, and in the past the geneticist when analysing the inheritance of flower colour has classified the differences observed in terms of these four variables.

In recent years, however, collaboration between geneticists and biochemists has yielded accurate information concerning the chemical basis of floral pigmentation and the part played by genes in determining the nature and relative amounts of the substances responsible.

The great majority of such substances are either anthocyanins, anthoxanthins or plastid pigments.

ANTHOCYANINS

The anthocyanins are outstanding, since they are responsible for the scarlet, red and blue shades which predominate among ornamental flowers. They occur in the plant as sap-soluble glycosides, that is, they are compound molecules formed by the union of the true colouring matter with one or more molecules of a sugar. The colour-producing part of the anthocyanin molecule, known as the anthocyanidin, may be derived from one of three basic structures, pelargonidin, cyanidin or delphinidin, which differ only in the number of substituent hydroxyl (– OH) groups in the phenyl ring (A, see Fig. 23). As the formulae show, pelargonidin has one hydroxyl group at position 4′, cyanidin has two at 3′ and 4′, while in delphinidin positions 3′, 4′ and 5′ are all substituted. In other words, cyanidin has one and delphinidin two more oxygen atoms in the molecule than pelargonidin. These differences represent one of the principal factors upon which

variation in flower colour depends, since an increase in the number of oxygen atoms (in the form of hydroxyl groups) results in a marked increase in blueness of tone. Thus, cyanidin is bluer than pelargonidin and delphinidin is bluer than cyanidin, and subject to certain other conditions which will be discussed shortly, one can with reasonable accuracy diagnose scarlet flowers as being pigmented by pelargonidin derivatives, red and magenta by cyanidin derivatives and mauve, purple and blue by delphinidin derivatives. (Examples: pelargonidin in the scarlet pelargonium, cyanidin in the red rose and delphinidin in the blue delphinium.)

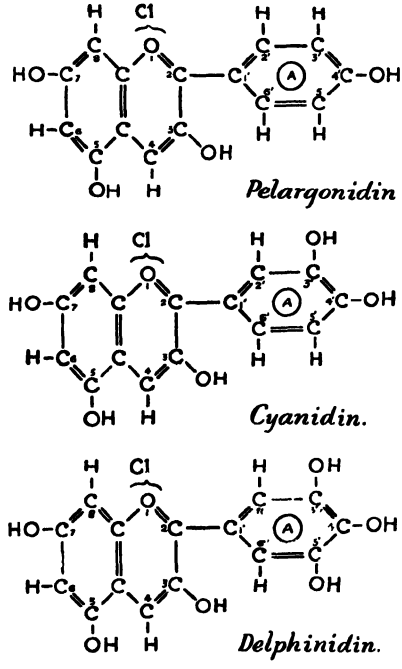


FIG. 23
The structure of three basic anthocyanidins, pelargonidin, cyanidin, delphinidin.

As mentioned above, the anthocyanins occur as compounds involving one or more molecules of a sugar. Of these sugar molecules one is always attached at the 3 position; if there is a second sugar molecule it may be attached either directly to the first one or it may unite with the anthocyanidin in quite a different position, at 5. Hence there are two classes of glycosides, (*a*) those with one or two sugar molecules attached at position 3, and (*b*) those with sugar molecules at both 3 and 5. These two classes are visibly different in colour and constitute another important factor in flower colour variation, the 3 : 5-diglycosides being always bluer than the corresponding 3-type. (Example : purple verbenas contain delphinidin 3 : 5-diglycoside, maroon verbenas contain delphinidin 3-monoglycoside. See Fig. 26, page 77.)

A third variable involving structural differences in the anthocyanins themselves is the existence or otherwise of " methylated " anthocyanins. Methylation consists in replacing the hydrogen atom of a hydroxyl group by a $-CH_3$ or methyl radical, and this

produces a lessening of the blue tone, i.e. an increase in redness. So if a change involving an increase in the number of hydroxyl groups is accompanied by methylation, the increased blueness of tone will only be slight, whereas we have already shown that increase in the number of hydroxyl groups alone produces a marked blueing effect. This can best be shown by means of a diagram (Fig. 24).

In general the only hydroxyl groups which are methylated are those at 3′ and 5′; that at 4′ is never methylated. Thus ignoring sugar types there is only one kind of pelargonidin (having

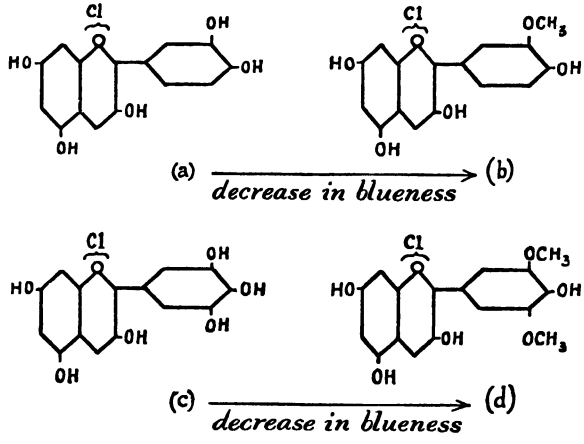


FIG. 24

(*a*) Cyanidin
(*b*) Peonidin (3′-O-methyl cyanidin)
(*c*) Delphinidin
(*d*) Malvidin (3′ : 5′-O-dimethyl delphinidin)

no hydroxyl groups at 3′ and 5′ it cannot be methylated), but there are two kinds of cyanidin (cyanidin and 3′-O-methyl cyanidin) and three of delphinidin (delphinidin, 3′-O-methyl delphinidin and 3′-5′-O-dimethyl delphinidin). Each of these will have sugar molecules attached either at position 3 or at both 3 and 5, giving rise to twelve anthocyanins, all of slightly different colours and covering a wide range from scarlet to purple.

So far we have dealt with three factors influencing the colour of anthocyanins, namely:

(*a*) The number of hydroxyl groups present.
(*b*) The position of attachment of the sugar molecules.
(*c*) The methylation of hydroxyl groups.

These factors are all dependent upon structural changes in the anthocyanin molecule, that is, the differences are internal. We shall now see how conditions external to the molecule can affect the colour of anthocyanins in the plant. If a solution of carbonate of soda is added slowly to an extract of the petals of a red rose (cyanidin 3 : 5 diglucoside) in dilute hydrochloric acid the colour changes from bluish red, becoming gradually redder, as the hydrochloric acid is neutralised. As more carbonate of soda is added the solution becomes alkaline and the colour changes from red to red-violet, violet and blue-violet and at last to a pure blue. This simple experiment illustrates the effect of one external condition upon the colour exhibited by an anthocyanin, namely the *p*H, i.e. the degree of acidity or alkalinity of the liquid in which it is dissolved. It is obvious, then, that flower colour will depend upon the *p*H of the cell-sap, and variation in this constitutes another factor to be added to our list. In the plant the limits of variation are considerably less than in the experiment described above, and actual measurements show that the sap in most flowers is slightly acid, the *p*H varying between the limits 3·0–7·0.

There are two other ways in which the colour due to an anthocyanin may be altered without change in the chemical structure. The first of these is a phenomenon known as co-pigmentation, which will be discussed in connection with the anthoxanthins. The second is one about which very little is known; it may, in fact, be due to more than one cause. In the majority of flowers the anthocyanin is in solution in the cell-sap, but where differences occur which are inexplicable on other grounds, it has been suggested that the anthocyanin may either be in a colloidal condition or may be in the solid state adsorbed by tannins. For example, an artificial preparation of colloidal cyanin appears much bluer than a true solution.

Anthoxanthins

The substances included under this heading are closely related chemically to the anthocyanins, but differ in colour, ranging from pale ivory to deep yellow. Like the anthocyanins, they are sap soluble and usually occur as glycosides. Structural variation is greater than in the case of the anthocyanidins, but the majority are analogous and fall into two classes, the flavones and flavonols, which differ in that the flavones have no hydroxyl group at

position 3. The formulae of representative members of each class are appended and it will be seen that in so far as the side ring is concerned, apigenin corresponds to pelargonidin and quercetin to cyanidin. See Fig. 25.

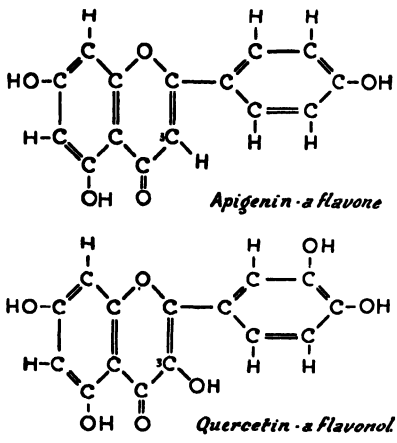


FIG. 25

Representatives of the two anthoxanthin types, flavone and flavonol.

Increase in the number of hydroxyl groups present in an anthocyanidin molecule results in increased blueness. This effect is manifest in the flavones and flavonols, which become more yellow. Apigenin, for example, is ivory, whereas quercetin is pale yellow, and the delphinidin analogues are a deeper yellow. There are four ways in which the anthoxanthins are concerned in flower colour :

(*a*) In flowers which have no anthocyanin they may be directly responsible for some or all of the colour.

(*b*) If a yellow anthoxanthin occurs together with an anthocyanin, the resultant colour is a blend of the two, in the same way that orange is obtained by mixing red and yellow paints. This is strictly true only where the two substances are present in the same cell, and if, as sometimes happens, they are in different cell-layers, the result is not a blending but a background effect, visually much the same.

(*c*) In the presence of anthocyanins, ivory anthoxanthins, as would be expected, do not contribute directly to the colour ; nevertheless, they are of great importance on account of their " co-pigmenting " action. This phenomenon is as important to the plant-breeder as a change from one anthocyanin to another. Certain anthoxanthins (usually ivory) when present in the same solution as an anthocyanin, combine loosely, in some way as yet unknown, with the anthocyanin, so as to give a much bluer colour. The effect is very marked, and in many cases flowers pigmented with a cyanidin derivative appear bluer than those containing an uncopigmented delphinidin glycoside. It is probably not an exaggeration to say that upwards of 70 per cent of garden flowers are co-pigmented, to some extent at least. The degree

of co-pigmentation varies with the nature of the anthocyanin —delphinidin derivatives being most readily co-pigmented and pelargonidin derivatives least. It also varies with the nature of the flavone or flavonol. There is no exact information on this point, but observations have shown that the yellow anthoxanthins do not generally behave as co-pigments. The great majority of blue, mauve and magenta flowers owe their blueness partially to co-pigmentation, in the absence of which the flower colour is redder. Thus in *Streptocarpus* the loss of an ivory anthoxanthin results in purple instead of blue; in the garden dahlia, chocolate instead of magenta; in freesia, crimson instead of mauve, and so on.

It should be noted that tannins sometimes share this property with the anthoxanthins; this is the only respect in which they merit special mention.

(*d*) It has been pointed out that there is a near relationship between the anthocyanins and anthoxanthins, as is shown by inspection of their respective chemical formulae. Therefore it might be expected that their syntheses in the plant would follow along similar lines. Evidence that this is so has been advanced (Lawrence and Scott-Moncrieff, 1935) and it has incidentally thrown further light on the problem of flower colour variation. Not only are the anthocyanins and anthoxanthins formed in much the same way, but they are formed from the same starting material which may be limited in quantity. This results in competition between the two, and if most of the source is utilised in the synthesis of one pigment, then of necessity less of the other is produced. So in garden dahlias we find that there is competition between the anthocyanins and anthoxanthins, and certain flowers containing both types of pigments have less of either than a corresponding flower with only one type. For example, the presence of much yellow anthoxanthin [1] may lead to almost complete suppression of anthocyanin, giving rise to delicately flushed " apricot " tints.

Plastid Pigments

The plastid colouring matters comprise a number of yellow or orange substances such as xanthophyll or carotene, which are insoluble in the cell-sap. Structurally they are so different from the anthocyanins and anthoxanthins that there can be no question

[1] See note on page 90n

of parallel syntheses. Hence interaction between the plastid and sap-soluble pigments does not occur.

On account of their insolubility, co-pigmentation by them (if it were possible) is excluded, and they are unaffected by changes in *p*H. In the absence of anthocyanins they are either solely responsible for flower colour or are supplementary to yellow anthoxanthins. In the presence of anthocyanins their effect is purely that of a background, since there is no possibility of blending as with yellow anthoxanthins. Thus in the tulip the introduction of a yellow plastid pigment produces such a background effect, the colour changing from pink, crimson or purple to orange, scarlet or brown.

To summarise the position, variation in flower colour is brought about by one or more of the following factors. In the table, changes are shown in one direction only; the reverse may be inferred.

ANTHOCYANINS	I.	Increase in number of hydroxyl groups	Increased blueness
	II.	Alteration from 3- to 3 : 5-sugar types	,, ,,
	III.	Methylation of one or more hydroxyl groups	Decreased ,,
	IV.	Increase in *p*H	Increased ,,
	V.	Co-pigmentation	,, ,,
	VI.	Colloidal condition	,, ,,
ANTHOXANTHINS	VII.	Increase in number of hydroxyl groups	Increased yellowness. Alteration of background. Change in co-pigment effect
	VIII.	Interaction of anthocyanins and anthoxanthins	Partial suppression of one or both types
PLASTIDS	IX.	Presence of plastid colour	White becomes yellow or orange. Alteration of background
	X.	Alteration in nature of plastid pigment	Yellow becomes orange. Alteration of background

The majority of these factors are known to be controlled by genes, whose action is highly specific. Thus a single gene may determine the presence or absence of an anthocyanin, a second may bring about a change in the nature of the anthocyanidin, a third may change the sugar type and a fourth control the production of a co-pigmenting flavone. For example, purple and maroon Verbenas differ in that the purple contain delphinidin

3 : 5-diglycoside and the maroon delphinidin 3-monoglycoside. This is a single gene difference, and when an F_1 plant containing the 3 : 5-diglycoside is self-pollinated, purple and maroon segregate in the ratio of 3 : 1.

Primula sinensis provides numerous examples of other types

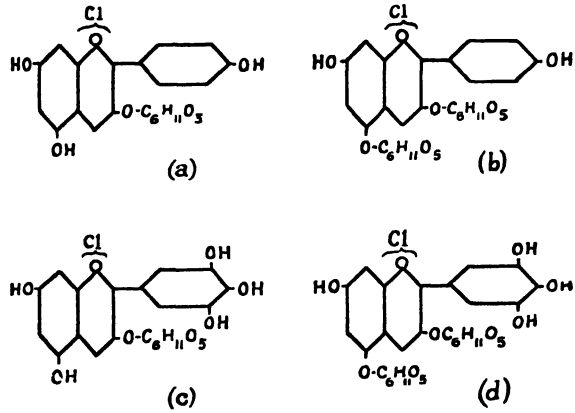


FIG. 26

(*a*) Pelargonidin 3-monoside—scarlet
(*b*) Pelargonidin 3 : 5-dimonoside—scarlet-magenta
(*c*) Delphinidin 3-monoside—maroon
(*d*) Delphinidin 3 : 5-dimonoside—purple

Verbena colour types
(Scott-Moncrieff and Beale unpublished.)

of variation; the change from red to blue can be brought about in stages, thus :

bR	plants	have	red flowers
br	,,	,,	slaty flowers
BR	,,	,,	magenta flowers
Br	,,	,,	blue flowers

where **B** and **R** are genes governing the production of a co-pigmenting ivory flavone and more acid cell sap respectively. The anthocyanin in these cases is malvidin 3-monoglycoside, controlled by the gene **K**; the recessive mutant **k** producing pelargonidin 3-monoside. All these genes show normal mendelian segregation.

Streptocarpus, *Callistephus chinensis* and *Dahlia* have been the subject of special investigations on the genetics and chemistry of flower colour, and will therefore serve to illustrate the general account previously given.

Streptocarpus

The great majority of *Streptocarpus* species come from Africa. Taxonomically they comprise two distinct groups : the caulescent and acaulescent species. The caulescent forms are mainly found in Central Africa and the four in cultivation all have thirty rather small chromosomes. The acaulescent species come from South Africa and sixteen in cultivation have thirty-two chromosomes, rather larger than those of the caulescent section. All species show a moderate amount of secondary association of the bivalents in pairs, and this fact, taken into consideration with the rather high chromosome numbers, suggests that the species are probably ancient allo-tetraploids. Within each of the two sections many of the species hybridise freely ; they give progeny which vary from completely sterile to highly fertile.

The history of the origin of the garden forms of *Streptocarpus* is fully recorded. Until the year 1884 there were only five species in cultivation, namely *S. Rexii*, introduced in 1826, with bluish flowers ; *S. polyanthus*, *ca.* 1855, bluish ; *S. Gardeni*, 1855, bluish ; *S. Saundersii*, 1860, bluish ; and *S. parviflorus*, 1882, white. In 1884 seeds of *S. Dunnii*, with flowers of a bright brick-red colour, were sent to Kew from the Transvaal. It flowered in 1886 and was crossed with the bluish-flowered species *S. Rexii* and the white-flowered species *S. parviflorus*. The hybrids flowered in 1887 and were intercrossed and backcrossed in all possible combinations. Later, one or two other species were crossed into the garden strain, but these all had bluish flowers. *Dunnii* is still the only species with red flowers.

Seven blue-flowered species have been examined and their anthocyanin pigment has in all cases proved to be malvidin (3′-5′-**0**-dimethyl delphinidin) 3-5-diglycoside. *Dunnii* is pigmented with cyanidin 3-pentoseglycoside. It appears, therefore, that in so far as flower pigments are concerned, the contribution of any of the blue-flowered species which have been crossed into the garden strain would be practically identical, and the garden strain has arisen essentially from the crossing of forms pigmented with malvidin 3-5-diglycoside and cyanidin 3-pentoseglycoside.

Breeding work on the genetics of flower colour in *Streptocarpus* has given results which are consistent throughout the genus (Lawrence *et al.*, 1939).

In the first place the garden hybrids fall into seven natural

groups for flower colour, viz. ivory, salmon, pink, rose magenta, mauve and blues. These colour classes correspond to certain genotypes as follows:

Ivory	All **a** forms
Salmon	**Arod**
Pink	**AroD**
Rose	**ARod**
Magenta	**ARoD**
Mauve	**AROd**
Blue	**AROD**

A is necessary for the production of anthocyanin (pelargonidin); when **R** is present the anthocyanin is peonidin (3′-**O**-methyl cyanidin) while malvidin is produced in the presence of **O**. The action of **D** is to attach a sugar residue at position 5 of the anthocyanin molecule in addition to the sugar at position 3.

From chemical and genetical comparisons of the garden hybrids with the species, it is clear that flower colour is due to various combinations of the two anthocyanidins and the types of sugar residue found in the species, the intermediate colours (mauve and magenta) resulting from recombination of the pigments of the parent species. Finally, segregation of the gene **r** (which is hypostatic in *Rexii*) gave rise, about 1912, to the new salmon and pink forms. The scheme for *Streptocarpus* is shown in Fig. 27.

As mentioned on page 72 pelargonidin is never methylated even though a gene for methylation be present. Bearing this in mind it would seem that a gene (or genes) for methylation is dominant throughout the hybrids examined. This gene must have been contributed by the *Rexii* parent, since the cyanidin of *Dunnii* is unmethylated. Should this gene be identified, then the full range of major structural changes in the anthocyanidin molecule which control anthocyanin flower colour will be demonstrated in *Streptocarpus*.

Callistephus chinensis

The china aster grows wild in the rocky hills of Northern China. In habit it is an annual, growing 2–3 feet high with a rather thin rosette of spreading branches; the flowers are made up of violet-blue female ray florets and yellow hermaphrodite disc florets. Seeds were first sent to Europe from China in 1728, and yielded violet, red and white varieties. By the end of the eighteenth century, double and quilled flowers had appeared and

the new colours rose, lilac, blue and purple. The first dwarf aster appeared about 1834 and the pyramidal habit about 1840. Sub-

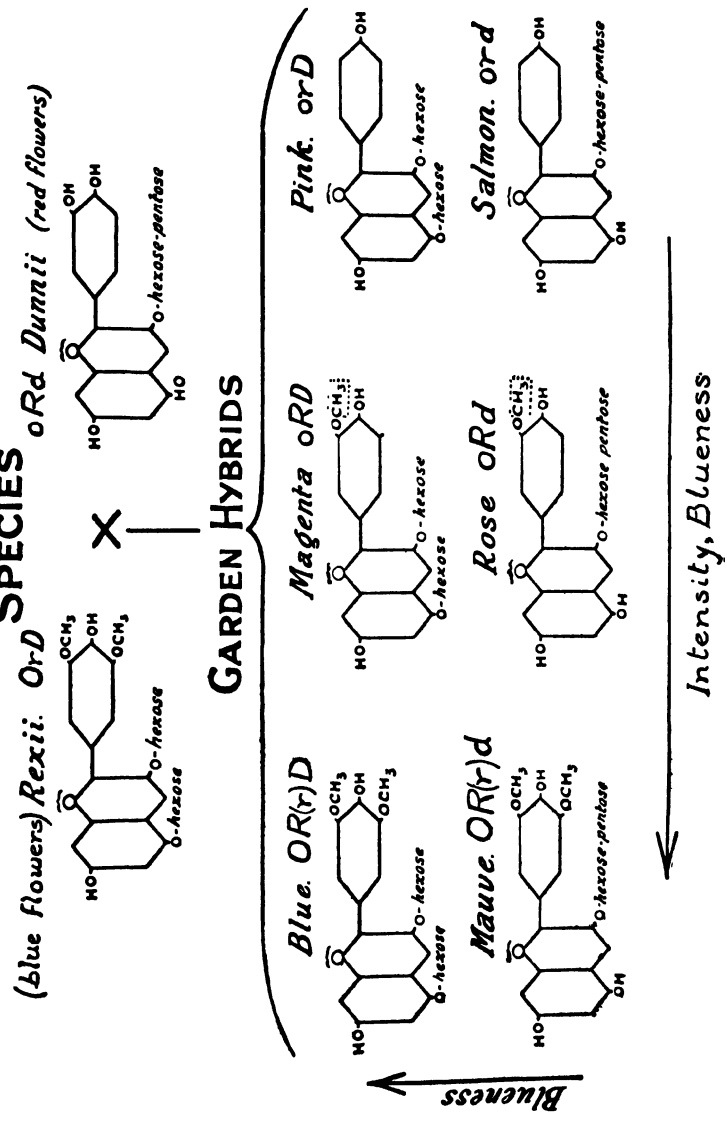


FIG. 27

The inheritance of anthocyanin variation in *Streptocarpus*.
(After Scott-Moncrieff and Lawrence.)

sequent variations and improvements have mainly concerned the form, size and colour of the flower. A true yellow form is said to have appeared in recent years.

The colour of the ray florets depends upon the presence of anthocyanin and anthoxanthin pigments, but only the first of these has been studied (Wit, 1936). The flower colours may be divided into three classes, the blue, purple and red shades, which are controlled by a series of three multiple allelomorphs, **R, r′** and **r,** producing delphinidin, cyanidin and pelargonidin respectively. **M** determines the glycosidic type of the anthocyanin. In all **M** genotypes there are two sugar residues attached to the anthocyanin molecule ; in **mm** plants there is only one.

In the presence of **I** not only are the colours more intense but in **r** types cyanidin is produced in addition to pelargonidin and in the **r′** forms delphinidin apparently in addition to cyanidin. Two other gene pairs affect intensity. **S** dilutes the anthocyanin and increases its susceptibility to the bleaching effect of sunlight, while **s** intensifies the colour and confers resistance to bleaching. **Pa** also intensifies flower colour.

Other characters which have been studied in the chinese aster are as follows :

Spreading—pyramidal habit . .	**P—p**
Tall—dwarf	**N—n**
Loose—compact	**C—c**
Single—double flowers . . .	**D—d**
Quilled—normal	**T—t**
Plumed—normal flowers . .	**O—o**
Normal—tubular ray florets . .	**R—r**

CARNATION. *Dianthus caryophyllus* (diploid 2n = 30).

Dianthus caryophyllus was in cultivation as early as 300 B.C. In British gardens, a wide range of colours, also double forms, were listed as being grown in the sixteenth century. The perpetual flowering carnation seems to have been developed in Europe before 1750 and is reported to be a hybrid between *D. caryphyllus* (2n = 30) and *D. chinensis* (2n = 30, 60). Norton (1907) and later Stuart (1912) found that crosses between single carnations and super-doubles (bullheads) gave commercial doubles (which are really semi-doubles), and these crossed together gave about 3 doubles to 1 single. On this basis, the commercial double of the florist is an unfixed hybrid from single crossed with super-double, doubleness being incompletely dominant.

The genetics and chemistry of flower colour in carnation have been studied by Mehlquist and Geismann (1947 *a* and *b*). Their findings may be summarised as follows :

The colours fall into three main groups : (1) the acyanic group, composed of whites and yellows ; (2) the " transition " group in which the colour is due to a small amount of pale anthocyanin on yellow background ; and (3) the cyanic group in which full anthocyanin colours from salmon to magenta occur. Six main genes govern colour variation. The acyanic group comprises all forms recessive for **a.** In this group, all **Yu** and **yu** forms are yellow and pale yellow respectively and all **I** forms white, i.e. **I** is apistatic to **Y.** The transition group is **YiA** and the cyanic group **YIA.** In the two latter groups, gene pairs **S-s, R-r,** and **M-m** modify the shade and intensity of the colours. In general, **S** intensifies anthocyanin colour, while **R** and **M** make it bluer. A summary of genotypes and phenotypes for self-coloured carnations is given below.

Genotypes	*Phenotypes*
yia - - -	= Pale yellow
yiA - - -	= Pale yellow
Yia - - -[1]	= Yellow
YiAsrm	= Salmon-yellow
YiAsrM	= Salmon-yellow
YiAsRm	= Pale maroon
YiASrm	= Orange
YiAsRM	= Pale maroon
YiASrM	= Orange
YiASRm	= Maroon
YiASRM	= Maroon
yIa - - -	= Pure white petals, white anthers and stigmas
YIa - - -	= Pure white petals, white anthers and stigmas
yIA - - -[1]	= White petals, anthocyanin-coloured anthers and stigmas [2]
YIAsrm	= Salmon
YIAsrM	= Light pink

[*contd. overleaf*

[1] Any allele of **SRM** may be substituted for **- - -** without change in appearance.

[2] Under favourable conditions the petals also may be faintly flushed with anthocyanin. The kind of anthocyanin will depend on the specific genotype but only the pink-red series with **r** and the crimson-magenta series with **R** can be recognised by inspection. Whether the plants have **m** or **M** cannot be determined with certainty by inspection.

Genotypes	*Phenotypes*
YIAsRm	= Lavender [1]
YIASrm	= Scarlet, red
YIAsRM	= Lavender
YIASrM	= Deep pink
YIASRm	= Crimson
YIASRM	= Magenta-purple

The chemistry of the flower colours is as follows. **rr** whites contain the flavone kampferol and no other flavone or flavonol was found in them. A yellow form also contained kampferol. It is not known whether **S-s, R-r,** and **M-m** affect the constitution of the flavone in whites and yellows, but a crimson **Rr** form was found to contain the flavone quercetin in much larger amounts than kampferol, so it is possible that **R** acyanics also may contain quercetin.

In the cyanic forms, **rr** genotypes are pigmented by pelargonidin and **R** genotypes by cyanidin. In **mm** cyanic forms, the anthocyanins are monosides and in **M** forms, diglycosides.

Mehlquist (1940) also studied the inheritance of nine abnormal types of carnation. Each type differs from the normal by a single recessive factor. The recessive genes and their action are as follows :

alb albino seedling, lethal.
yel yellow seedling, lethal.
lut lutescent seedling, lethal.
cb clubneck, nearly always lethal.
vir " virescent ", a chlorophyll deficient type, sub-lethal.
laz " lazy virescent ", a weak deficient type, sub-lethal.
dw " dwarf ", extremely short plant, less viable than the normal type, highly sterile.
sto " stocky ", short and stocky plant, somewhat less viable than the normal type, highly sterile.
th " thin ", an annual type, less hardy than the normal type but fully as fertile.

As Mehlquist points out, none of these abnormal types is of economic importance in itself, but their elimination from commercial breeding stock is desirable, since obviously their presence materially increases the numbers of seedlings required to provide a reasonable chance for the occurrence of a desirable type.

[1] This lavender cannot be distinguished from **M** lavender except by breeding tests. The same is true for maroon, pale maroon, and orange.

POPPY. *Papaver Rhoeas* (2n = 14) ; *Papaver nudicaule* (2n = 14)

Newton (1929) and Philp (1933) have elucidated the constitution of *P. Rhoeas* (Shirley Poppy, etc.) with regard to flower colour and other factors. Wild *P. Rhoeas* has scarlet petals with a black petal blotch, black filaments, anthers and stigmatic rays and may be represented factorially by **CCPPBBTTwaFfIIEE.**

c dilutes and localises the petal colour
p produces claret petal colour
b dilutes the petal colour and produces a white petal blotch and tinged filaments, with which are associated yellow anthers and white stigmatic rays
t converts the petal colour to crimson magenta
W produces a white petal edge
F intensifies the petal colour in **bt** and **et** plants and also localises the petal colour in **bti** and **eti** plants
i produces ivory flavone ; makes anthocyanin bluer
e in a **t** plant dilutes and alters the petal colour and produces a brown petal blotch, brown filaments, yellow anthers and brown stigmatic rays.

Another factor, **m**, is concerned with the elimination of the white margin to the black petal blotch. Doubleness is probably incompletely recessive to singleness. Self-incompatibility is common in *P. Rhoeas.*

The genetics of the garden forms of *P. nudicaule* (Yellow Iceland Poppy) has been investigated by Fabergé (1942). Those factors of most interest to horticulturists are as follows :

C produces white flowers
d produces buff flower colour
o produces orange flowers
r produces buff flowers (the pigment is different from that of **d** flowers)
db produces double flowers
mp produces narrow petaloid petals and stamens.

The garden Iceland Poppy is self-incompatible and has a system of oppositional factors as in *Nicotiana.* Self-fertility due probably to an S_F allele has also been found.

THE GARDEN DAHLIA, *Dahlia variabilis* (octoploid, 2n = 64)

A large number of our most important cultivated plants are polyploids, some indeed being exceedingly complex in their constitution. Genetic investigation of such plants is likely to be a long and intricate process, owing to the intergrading of the characters, and the consequent difficulties of interpretation of results. In a simple diploid, cytological and genetical studies, if reasonably extensive, usually give a fairly clear picture of the disomic character of the individual (cf. sweet pea). Similarly, in the auto-tetraploid, although the results are more complex, a comprehensive study will usually lead to definite results of a kind recognised as characteristic for auto-tetraploids. Although a number of allo- and auto-tetraploids have been studied genetically very few higher polyploids have been investigated intensively and even in these the evidence is largely fragmentary and the analysis incomplete. In this respect the combined morphological, cytological, genetical and chemical investigations on dahlia (Lawrence, 1929, 1931; Lawrence and Scott-Moncrieff, 1934) provide a clue to the origin, constitution and behaviour of the complex polyploid individuals, and may be taken as representative of a number of our cultivated plants which are themselves less amenable to investigation.

The natural habitat of dahlia is in the Mexican region of Central America. The garden dahlia was first introduced into Europe in 1789, when two plants were sent from Mexico, one with purple and the other with rose-coloured flowers (Table IX). Little variation occurred until 1804, when seeds were sent from Mexico by Humboldt, but from about this time a phenomenal change took place in the development of the dahlia. Numerous variations of form and colour arose; and at a rate probably without parallel in the history of domesticated plants. In a little over twelve years practically every colour we know to-day had appeared.

At the present time only six species are in cultivation, but if the botanical descriptions of all the species recorded are examined we find that, with the exception of the garden dahlia, the genus may be divided into two groups for flower colour, (1) pale to deep magenta with ivory white varieties, (2) orange to scarlet with yellow varieties. The colours in Group 1 are due to two soluble sap pigments, ivory flavone which forms the ground colour, and pale anthocyanin, which mixed with the ivory flavone gives the

magenta colours. The colour in Group 2 is also due to two sap pigments, yellow flavone forming the ground upon which deep anthocyanin gives the orange or scarlet colours.

Examination of the great array of colours in the garden dahlia shows that this wide range is due solely to the mixture, in varying proportions and degrees of intensity, of the two flavone colours and pale and deep anthocyanin. Thus magenta and purple result from pale and deep anthocyanin respectively on ivory grounds, and similarly apricot and scarlet result from pale and deep anthocyanin on yellow grounds. If the ground colour is intermediate (cream or primrose), then when anthocyanin is present the flower colour is intermediate, e.g. pale or deep crimson according to the depth of the anthocyanin pigmentation. In the absence of both flavones and anthocyanins the colour is white.

In other words, the great variety of colour in the garden dahlia is mainly due to the combination of the colours found separately in the two flower-colour groups into which the other species fall.

TABLE IX

History of Dahlia variabilis *in Europe*

1789 Introduced into Europe (Madrid) from Mexico. Two plants—purple semi-double and single rose.
1798 Introduced into England (Kew) from Madrid. Plants died.
1802–5 Distributed to France and Germany.
1804 Seeds sent from Madrid to England.
Seeds sent from Mexico to Paris and Berlin by Humboldt.
1804–6 First extensive increase in variety.
1806 Berlin Botanic Gardens had 55 single and semi-double varieties.
1808 First perfect double raised by Hartweg, Karlsruhe.
1809 First white (single).
1818 Practically all colours obtained. Numerous colour patterns; red-ringed discs; dark eyes, etc. Eighteen doubles and 100–150 singles and semi-double varieties offered in English catalogues.
1821 First double pure white "Waverley".
1828 Early flowering dwarf plants twelve inches high raised by Douckelaar, Liége.
1830 Anemone-flowered type.
1831 Swiss amateur grows 1500 varieties.
1841 Harrison grew 1200 double varieties.
1845–50 Pompom type developed.
1872 Cactus type tubers introduced from Mexico.*
1900 Collarettes developed in France.
1900–3 Paeony and decorative types developed.

* But Bailey says 1864.

Cytological examination next showed that, with the exception of the garden dahlia, four of the five species in cultivation had thirty-two chromosomes and the fifth thirty-six (Lawrence, 1929, 1931). Three of these species belonged to Group 1, and the other two to Group 2. The garden dahlia has sixty-four chromosomes.

The fact that *D. variabilis* alone combined the colours of the two groups, suggested that it might be a hybrid between them, a view that was strengthened by the fact that it also had twice as many chromosomes, a not infrequent occurrence in fertile species hybrids.

Breeding experiments were begun on the inheritance of the clearest character in dahlia, the flower colour, but before any results were to hand it was discovered that although the garden dahlia had twice as many chromosomes as the other species examined, it was not tetraploid but octoploid. The evidence for this came from examination of meiosis in both the species and garden forms (Lawrence, 1929, 1931). In the species with thirty-two chromosomes the bivalents tend to associate secondarily in pairs, a phenomenon which seems to indicate homology of the secondarily associated types (see page 36). The species with thirty-six chromosomes (*D. Merckii*) also shows secondary association, but two of the chromosome groups consist of three bivalents each, thus indicating that the two extra pairs ($16^{II} + 1^{II} + 1^{II}$) are homologous with two other pairs. No multivalent association whatever was found in the above five species. Briefly, the cytological evidence showed that these five species were ancient allo-tetraploids (i.e. hybrid tetraploids) in which secondary association alone indicated the true chromosome constitution.

In *D. variabilis* secondary association is particularly evident, groups of two, three and four bivalents occurring. In addition quadrivalents frequently and sexivalents occasionally are found. Primary and secondary association together show that *D. variabilis* is a hybrid octoploid (i.e. a double auto-tetraploid) of more recent origin than the tetraploid species.

When breeding was commenced it was discovered that all dahlias were self-sterile (self-incompatible). Because of this it was possible to make crosses in spite of the composite nature of the "flower" (*capitulum*) which makes emasculation impracticable, and thus accomplish with ease what would otherwise have been a prolonged and unsatisfactory experiment. It was found that there were four main genes for flower colour, **Y** for yellow and

I for ivory flavone, and **A** for pale and **B** for deep anthocyanin. The inheritance of **Y, A** and **B** is tetrasomic, giving the characteristic tetrasomic ratios of 5 : 1, 11 : 1 or 35 : 1 in the appropriate crosses. The inheritance of **I** is also tetrasomic but modified owing to the simplex as well as the nulliplex forms being without pigment.

Though all the genes are tetrasomic their expression varies. **Y** and **B** are completely dominant in the simplex condition, simplex, duplex, triplex and quadriplex being indistinguishable phenotypically. **A** is cumulative from simplex to quadriplex, **AAaa** being deeper than **Aaaa, AAAa** than **AAaa** and **AAAA** than **AAAa**. **iiii** is without pigment, **Iiii** is practically devoid of pigment and **IIii, IIIi** and **IIII** fully pigmented. In addition to these, a tetrasomic inhibitor **H** of the yellow flavone progressively inhibits the production of this pigment, giving the cream and primrose shades. An inhibitor of ivory also seems to occur. The main genotypes and their colours are shown in Table X.

TABLE X

Showing the Main Genotypes for Flower Colour in Dahlia variabilis

Flavone :	**I** produces ivory flavone	
	Y „ yellow flavone	
Anthocyanins :	**A** „ pale anthocyanin	
	B „ deep „	
Inhibitor :	**H** cumulatively inhibits yellow chalkone	
iyab = white	**iYabh** } = yellow	
Iyab = ivory	**IYabh*** }	
iyAb = rosy-magenta	**iYabH** = cream to primrose	
IyAb = bluish-magenta	**iYAbh** = apricot	
iyaB = rosy-purple	**iYaBh** = scarlet	
IyaB = bluish-purple	**iYaBH** = crimson	

* Y is epistatic to I.

Two kinds of anthocyanin are found in the garden dahlia, namely cyanidin and pelargonidin diglycosides. They must not be confused with the pale and deep pigmentation, which may involve either anthocyanin. The anthocyanin may be produced in the presence of ivory or yellow flavone and in the absence of flavone. The anthocyanins in Group 1 of the species are cyanidin types and the flavone apigenin. The anthocyanins in Group 2 are pelargonidin types.

It has been found that pronounced interaction occurs in the

production of the pigments (Lawrence and Scott-Moncrieff, 1934). Thus when yellow flavone is produced in quantity, ivory flavone is more or less suppressed. Similarly the flavones and anthocyanins compete with one another, the flavones having the greater effect, even to the complete suppression of the anthocyanin in certain genotypes—the precise degree of interaction depending upon the total number and proportion of all the flower colour genes present.

Further, the chemical investigations on the flower pigments of the garden dahlia led to the remarkable discovery that the nature of the anthocyanin produced in the presence of **A** or **B** is not due to the action of a specific gene or genes for cyanidin or pelargonidin but depends entirely upon the total number and proportion of all the flower colour pigment genes. This differs from the other cases mentioned. Thus all **A** and **AI** forms produce cyanin, all **AY** and **BY** forms pelargonin, whereas **B** or **BI** may produce either cyanin or pelargonin, depending on the aggregate of the potential unit values of **A, I, B** and **Y,** which are $\frac{1}{2}$, 1, 6 and 9 + respectively. An aggregate of more than eight results in the production of pelargonin instead of cyanin. For example, all anthocyanin forms with **Y** produce pelargonin; **A** and **AI** produce cyanin only; **BbbbIIii** produces cyanin and **BbbbIIIi** pelargonin, and so on.

In addition to interaction resulting in alteration in the nature and amount of specific pigments, the ivory flavone has a strong co-pigmenting effect upon cyanin, pelargonin being less affected.

The experiments show that although only four main colour genes and two flavone inhibitors control the production of two anthocyanins and two flavones, yet the action and interaction of these genes is complex in the extreme.

It is now apparent why the garden dahlia was, and is, so variable. In the first place the introductions from Mexico were but forms of a species already widely varying, e.g. double forms were known in Mexico as early as 1575, where the dahlia seems to have been cultivated by the natives for a number of centuries. Secondly *D. variabilis* is a high polyploid and a hybrid between hybrids. Thus each of the eight types of chromosomes (Fig. 19) is not composed of eight identical chromosomes but consists of two half-sets, which, because of their different descents, have become more or less differentiated. Thus comparing the genes carried by the respective half-sets we should expect to find that

some were identical or very much alike (e.g. **A** and **B** both produce anthocyanin but **B** produces a greater amount than **A**, a quantitative difference), while other genes would be rather more different (e.g. **I** and **Y**, which produce flavones that are qualitatively

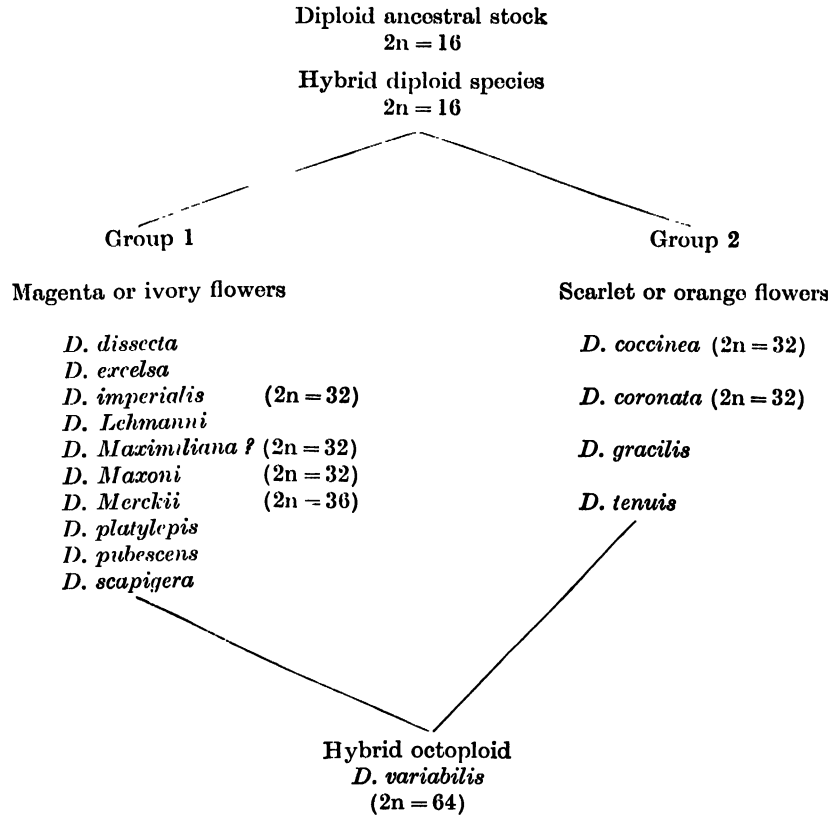


FIG. 28

Showing the origin and constitution of the garden dahlia *Dahlia variabilis*.

different). In brief, in *D. variabilis* the gene types are either in duplicate (identical) or differ somewhat, though generally similar, each gene being at least tetrasomic, thus permitting of a very large number of possible combinations. The number of phenotypes is still further increased owing to the differential expression of the similar genes and their pronounced interaction effects. Finally the self-incompatibility of *Dahlia* enforces out-crossing, thereby maintaining the species in a highly complex heterozygous condition.

Summarising the results of the experiments, the evidence strongly suggests that the tetraploid *Dahlia* species have descended from a diploid ancestral stock unknown and presumably now extinct. In their descent differentiation has occurred, giving rise, among other differences, to the two flower-colour groups; *D. variabilis*, therefore, combines the products of specific differentiation with a high degree of polyploidy. Fig. 28 presents the scheme for the origin of the garden dahlia.

We have seen that flower colour in the garden dahlia depends ultimately on an intricate action and interaction of a number of genes. Other examples of this extremely complex action and interaction are seen in the great variation not only in colour, but also in pattern, size and shape of flower, leaf shape, habit, etc., found in the " garden " dahlia. Some of the characters are not so well defined as flower colour, being almost continuous in their variation. For example, a cross between a perfect single with eight petals and a perfect double with 160–170 petals gave immediately in the F_1 a continuous range of forms in regard to doubleness, though neither parental form was recovered in a total of forty-eight plants (Fig. 29). Evidently a number of genes determine doubleness in dahlia, and even perfectly double or single plants may be distinctly heterozygous for these genes. Size of " flower ", breadth of petal, height and habit of plant are characters showing almost continuous variation, which are probably controlled by one or more tetrasomic, hexasomic or octosomic genes, or sets of genes slightly differentiated, and often cumulative in their expression. Characters such as the above, which are the expression of a number of differentiated polymetric genes (cf. the Apple, Chapter VII) cannot be precisely described as dominant or recessive, as in the case of characters governed by single or duplicate dominant genes.

It is noteworthy that there is no record of a new character

appearing in *D. variabilis* at a single step (cf. Spencer Sweet Pea). The characters have always appeared in a mongrel condition,

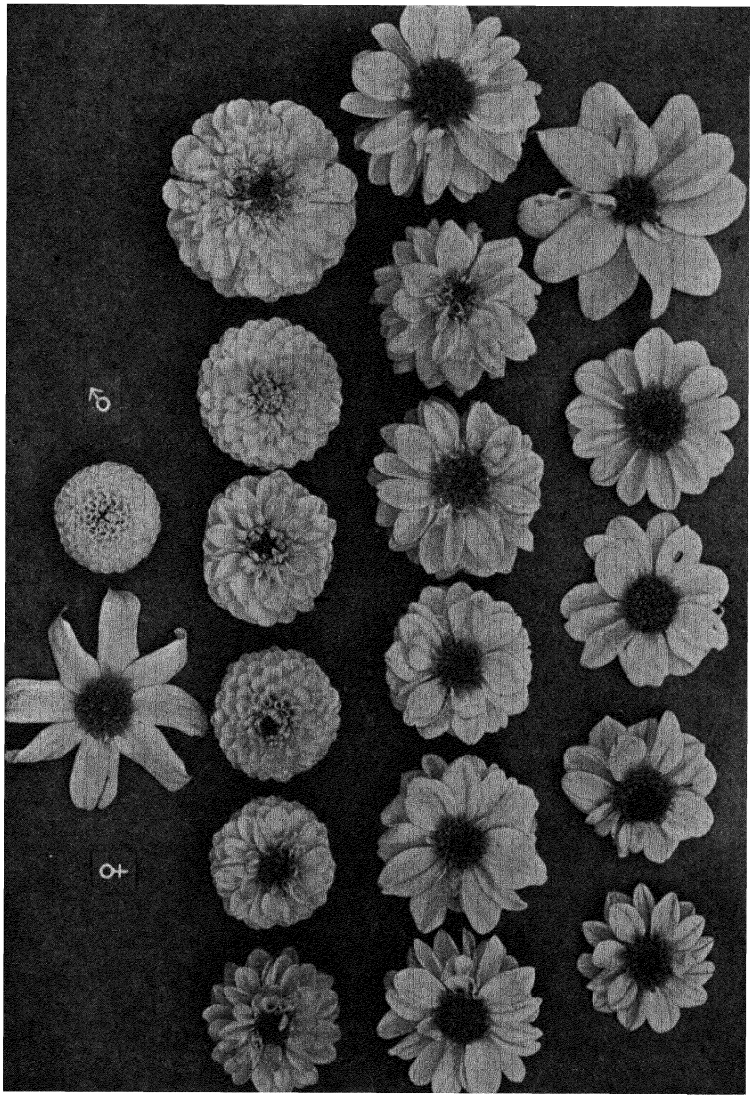


FIG. 29
Inheritance of doubleness of the flowers in *Dahlia variabilis* showing the parents and range of variation in F_1.

plants having to be selected from generation to generation before the character is relatively homozygous and well expressed. There is little doubt that many of the references in horticultural literature

to the time required for " fixing " a new character in some well-known cultivated plant all unconsciously refer to polyploid species like the dahlia, whose history reveals many examples of this kind. Hence in high polyploids comparatively slight but unusual variations may be well worth treasuring, for continued selection may improve and establish them as attractive or useful novelties.

Note.—Since the last paper on the genetics of *Dahlia* was published, Price (1939) has identified the yellow pigment, originally thought to be a flavone, as the chalkone, butein. We thus have the interesting situation where three related substances, anthocyanin, flavone and butein, are produced from a common intermediate, for which the three lines of synthesis compete.

CHAPTER VI

VEGETABLE AND SALAD PLANTS

TOMATO, *Lycopersicum esculentum* (diploid, 2n = 24)

THE tomato is a native of South America, from whence it was early introduced into the southern parts of Europe. Dodoens (1582) describes it as grown at that time in continental gardens, and says that its fruits were eaten as a salad, being dressed with pepper, salt and oil. Gerarde (1597) and Parkinson (1656) describe it as grown in England for ornament and curiosity only, although they were aware that its fruits were eaten on the continent of Europe. Sabine (1819) states " the great use which has been made of the tomato of late years for culinary purposes has occasioned it not only to be regularly grown in private gardens, but has also rendered it an object of cultivation for the market of the metropolis". Sabine also records that " the varieties of tomato with red fruit, which are at present (i.e. 1819) known in the gardens of Europe, are four, viz. the Large Love Apple, or Tomate Grosse of the French ; the Small Love Apple, or Tomate Petite ; the Pear-Shaped Love Apple, or Tomate en Poire ; and the Cherry Love Apple, or Tomate Cerise". Sabine also describes two varieties with yellow fruits ; the Large Yellow Love Apple which was similar in all characters except colour to the Large Red Love Apple, and the Small or Cherry Love Apple which was raised from seeds obtained from France, where it was called Tomate Petite Jaune. Early in the seventeenth century a variety with white fruits was mentioned by Besler (1613), but Sabine states that it appeared to have been lost to cultivation at the time of his paper mentioned above.

In the tomato two pairs of genes govern the colour of the fruit, one pair the colour of the flesh, and the other pair the colour of the skin. Thus **R** gives red flesh, **r** yellow flesh, **Y** gives an opaque deep yellow skin, and **y** a transparent almost colourless skin. The combination of red flesh and yellow skin (**RY**) gives a bright red fruit, the common tomato of commerce. Red flesh and transparent skin (**Ry**) give a dull red fruit. Yellow flesh and

yellow skin (**rY**) give a deep golden yellow fruit, and yellow flesh and transparent skin (**ry**) give a pale yellow, almost cream fruit, which is probably the genetic constitution of the white tomato mentioned by Besler.

During the present century the tomato has been the subject of intensive investigation. Hurst (1906), Hedrick and Booth (1907), Price and Drinkard (1908), Crane (1915), Lindstrom (1924–32), MacArthur (1926–38), Yeager (1937) and others have carried out genetic experiments with this plant.

TABLE XI

Characters	Genes	Dominant	Recessive
Anthocyanin pigmentation of stems and leaf veins	A_1–a_1	Purple stem	Green stem
	A_2–a_2	,, ,,	Purple stem becoming green
Stature	D_1–d_1	Tall	Dwarf
,,	D_2 d_2	Ordinary dwarf	Accentuated dwarf
Leaf shape	C c	Normal cut leaf	Potato leaf
,, ,,	W–w	,, ,,	Wiry foliage
,, colour	L–l	Green	Yellow or lutescent
Hairiness	H–h	Smooth, lacking long hairs and large glands	Normal hairy condition
Habit	B_r–b_r	Tall	Brachytic stem with short internodes
Inflorescence	S–s	Normal, simple inflorescence	Compound, much branched inflorescence
,,	S_p–s_p	Normal, simple inflorescence	Self-pruning, more or less determinate growth
,,	L_f–l_f	Normal, simple inflorescence	Leafy inflorescence
Foliage	W_i–w_i	Normal	Wilty foliage
Fruit	P p	Smooth	Hairy
,,	U–u	Dark base when unripe	Uniformly coloured
,,	F–f	Shape regular	Shape fasciated
,,	O or P_r–o or p_r	,, short	,, elongated
,,	N–n	,, normal	Nipple tipped
,,	R–r	Red flesh	Yellow flesh
,,	T–t	,, ,,	Tangerine orange
,,	Y–y	Yellow skin	Clear skin

MacArthur (1931, 1934) describes the results he obtained in his investigations involving twenty-one genes. These genes and their characters are detailed in Table XI.

In the course of his detailed investigations MacArthur has grown over 48,000 plants, and he states that monofactorial inheritance of most of the characters has been definitely proved. Dominance is usually complete or nearly so, but the hairy heterozygote **Hh** is intermediate and segregates a typical 1 : 2 : 1 ratio. The gene interactions of the two types of dwarfness lead to 12 : 3 : 1 ratios in F_2, and those between the two forms of green stem produce 9 : 3 : 4 ratios. In both cases the appropriate crosses give the normal tall and normal anthocyanin pigmented stems in F_1.

In Table XII are shown some of MacArthur's results, and the close approximation to the theoretical 3 : 1 and 1 : 1 ratios he obtained from F_2 and back-cross families respectively.

TABLE XII

Characters	Genes	F_2 Families. Observed Ratios (3 : 1 *ratios*)		Back-crossed Families. Observed Ratios (1 : 1 *ratios*)	
		Dominant	Recessive	Dominant	Recessive
Purple-green stem .	A–a	3084	1093	482	526
		3132·75	*1044·25*	*504*	*504*
Normal-potato leaf .	C–c	5473	1874	694	619
		5510·25	*1836·75*	*656·5*	*656·5*
Tall-dwarf stature .	D–d	5283	1753	560	538
		5277	*1759*	*549*	*549*
Green-yellow foliage	L–l	5392	1772	671	569
		5373	*1791*	*620*	*620*
Simple-compound inflor. . .	S–s	752	213	458	444
		723·75	*241·25*	*451*	*451*
Smooth-fasciated fruit . . .	F–f	2655	893	442	426
		2661	*887*	*434*	*434*
Short-elongate fruit	O–o	1919	637	521	525
		1917	*639*	*523*	*523*
Red-yellow flesh .	R–r	3629	1176	541	553
		3603·75	*1201·25*	*547*	*547*
Yellow-transparent skin . . .	Y–y	4443	1408	351	296
		4388·25	*1462·75*	*323·5*	*323·5*

MacArthur states that the discrepancies between the observed and expected ratios in the above table are either small or not significant, or are reasonably explained, and there seems no reason

to doubt the simple monofactorial nature of any of these characters. In the case of yellow foliage the discrepancy appears to result from a lower viability in the recessive class, and disturbing effects of *certation* phenomena are suspected in the case of the **Y–y** genes.

In the tomato, several examples of linkage occur, and six linkage groups involving sixteen genes have been established.

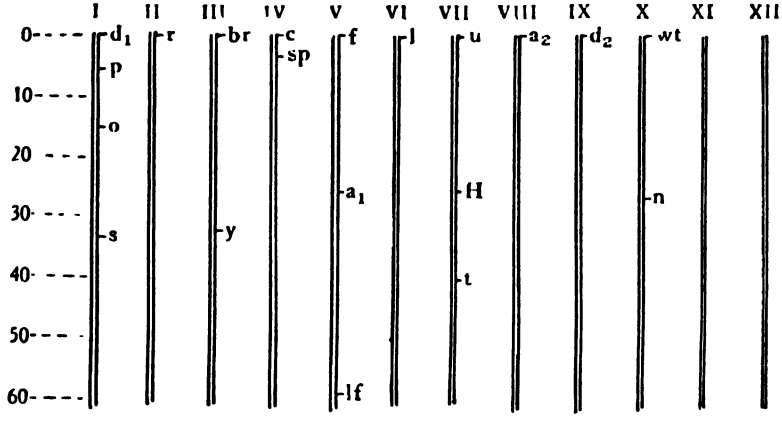


FIG. 30

Chromosome maps for the tomato, giving the approximate location of twenty genes in ten of the twelve pairs as determined by the linkage method. (After MacArthur.)

These are : one group of four genes **d–p–o–s,** two groups of three genes each, **f–a_1–l_f** and **u–H–t,** and three groups of two genes each, **b_r–y, c–s_p** and **w_t–n.** These genes and their approximate location in the chromosomes as given by MacArthur are shown in Fig. 30.

Hackbarth, Hasenbusch and Sengbusch (1933) have carried out a series of breeding experiments with the object of obtaining earlier maturing tomatoes. They found that the small fruited *Lycopersicum racemigerum* ripened eight to fourteen days earlier than cultivated varieties of *Lycopersicum esculentum.* In the F_2 from inter-crossing varieties of these species a number of early maturing plants appeared, but only a few with good-sized fruits, and the authors inferred that large size of fruit was governed by multiple factors. A correlation was found between early flowering and early maturity, and the results indicate that earlier maturing forms of tomatoes may be obtained from the inter-crossing of *L. racemigerum* and *L. esculentum.*

TETRAPLOID TOMATOES (2n = 48)

The normal tomato is a diploid plant with 24 somatic chromosomes. It has, however, been shown by Winkler (1916), Jørgensen (1928) and Sansome (1930) that by the simple process of decapitating young diploid plants of vigorous growth, adventitious shoots may be induced to arise, a proportion of which are tetraploids with forty-eight somatic chromosomes. The somatic

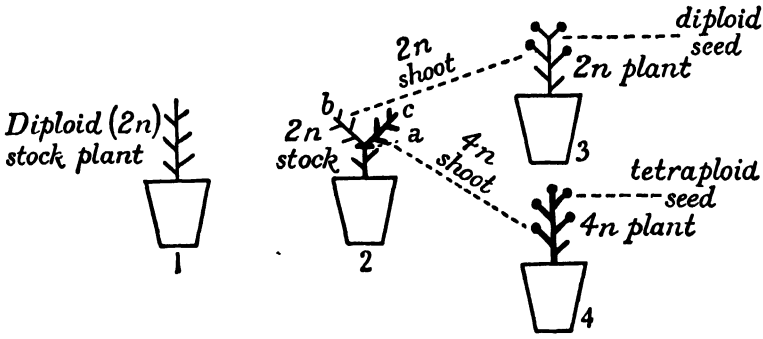


FIG. 31.—THE PRODUCTION OF TETRAPLOID TOMATOES

1, Normal diploid tomato (2n = 24); 2, diploid cut back at *a* giving rise to shoot *b* (diploid) and shoot *c* (tetraploid); 3, diploid plant raised vegetatively from shoot *b* of 2; 4, tetraploid plant raised vegetatively from shoot *c* of 2. (After Sansome and Zilva.)

production of such tetraploids is diagrammatically presented in Fig. 31.

The doubling of the chromosome number, by this method, in the somatic tissue, is of considerable value in genetic experiments. Tetraploid plants can readily be obtained, and since their genetical constitution is under the control of the investigator, inasmuch as he can get comparable diploid and tetraploid plants, they provide valuable material for approaching some of the problems which arise in plants which have more than two sets of homologous chromosomes.

The tetraploid shoots which arise from the callus formed on the decapitated surface are readily recognised by the fact that the stems are stouter, the leaves broader, less dissected, thicker and generally of a darker green than those of the diploid. Both the tetraploid and diploid shoots are easily propagated vegetatively.

Sansome (1933) gave a detailed account of a series of experi-

ments he carried out with such induced tetraploid tomatoes. He began his investigations with lines of diploid plants pure for one or more of the following genes: **d**–dwarf, **s**–compound inflorescence, **o**–oval fruit, **p**–smooth fruit, **r**–yellow flesh, **y**–clear skin, and $\mathbf{a}_1$ and $\mathbf{a}_2$–lack of anthocyanin. These genes have been widely investigated in the diploid tomato and their hereditary behaviour determined.

The experiments with the tetraploids, allowing strict comparison with diploids, show many interesting features. The range of variation in the tetraploids is considerably greater than that in the diploids, e.g. Sansome states that there are nine possible colours of fruit in the tetraploid, of which five are not found in the diploid. Several of these have been identified. Thus the simplex condition of **R** (**Rrrr**) gives rise to an orange-coloured fruit, while further doses of **R** in the tetraploid and **RR** and **Rr** in the diploid give red fruit. Plants simplex for **Y** (**Yyyy**) are also distinguishable from plants with higher proportions of **Y**. In plants with a colour gene in the simplex condition other genes such as **p** also affect the expression of that gene, and the genes for fruit shape exhibit so many effects that it has not been possible, so far, to identify some of the types with certainty.

Sansome and Zilva (1933), found the Vitamin C content and weight of dry matter in certain comparable diploid and tetraploid tomatoes to be almost twice as great in the tetraploids as in the diploids. In other tetraploids this was not the case. The juices from the fruits of the tetraploid forms contain considerably more dry matter than those from the diploid forms.

The fertility of the tetraploid tomato is less than that of the diploids. Thus Sansome found that the tetraploid portions of diploid plants gave an average of 21 seeds per fruit, while the diploid portions of the same plants gave an average of 115 seeds per fruit. The germination was 35 and 64 per cent respectively. As described in a later chapter, the fertility of auto-polyploids is invariably lower than that of corresponding diploids.

Lindstrom (1932) has described a tetraploid form of *Lycopersicum pimpinellifolium* which, in contrast to *Lycopersicum esculentum* tetraploids, is highly fertile. There appears, however, to be some suspicion that this tetraploid may have been derived from both *pimpinellifolium* and *esculentum*, and its high fertility suggests that it is an allo-tetraploid rather than an auto-tetraploid.

The segregation of certain of the genes studied by Sansome

in the tetraploid tomatoes are given in Table XIII. It will be seen that in some cases segregation approximates to expectation from random chromatid segregation, some to chromosome segregation, while other cases are intermediate between the two. Thus Sansome states that it is probable that random chromatid segregation is shown by **d, p** and **s,** while **y** shows chromosome segregation, the segregation of **r** being intermediate.

TABLE XIII

TETRAPLOID SEGREGATION IN THE TOMATO
(After Sansome)

		Observed	Expected on Chromosome Segregation	Expected on Random Chromatid Segregation
Duplex plants selfed .	S	787	805	790
	s	39	23	38
" " "	D	995	1019	990
	d	43	28	48
" " "	P	988	1010	990
	p	50	28	48
" " "	R	647	655	639
	r	26	18	31
" " "	Y	554	556	545
	y	17	15	26
" " "	A_1	172	170	169
	a_1	4	4·8	7·6
" " "	A_2	207	210	206
	a_2	8	5·9	9·9
Simplex plants selfed	D	611	591	565
	d	178	197	224
" " "	S	136	132	128
	s	41	44	49
" " "	P	519	465	442
	p	103	155	180

THE GARDEN PEA (diploid, 2n = 14)

The cultivated varieties of pea are included in the Linnean species *Pisum sativum* along with a sub-species *arvense* which is indigenous to Persia. Remains of the garden pea have been found in the Stone Age and in the Swiss lake-dwellings of the Bronze Age. Whether it was cultivated in these times is unknown, but it is undoubtedly one of the oldest of cultivated plants. As a

result of his extensive researches Vavilov (1929) concluded that *Pisum* has been distributed from two primary centres, one in the Mediterranean region from which came predominantly the large types with large fruits and seeds, and the other in Asia giving rise to small types with small fruits and seeds. Thus no large-seeded peas are found in Persia, India or China.

The history of the pea in this country since mediaeval times has been followed up by Sherwood (1898). From the names of varieties and from the records it is known that exchanges between France, Holland, Spain and England were very frequent. In England it is probable that peas were cultivated before the Norman Conquest. Gerarde's (1597) and Parkinson's (1629) descriptions of garden peas show that already in the first quarter of the seventeenth century there were variations in height and habit, in time of flowering, in texture and shape of pod and in quality of seed. With the possible exception of dwarfness no important new character appeared until the end of the eighteenth century. Knight (1822) says that the sweet flavoured wrinkled pea was common in the shops of London in 1813, and he appears to have been the first to develop it by hybridisation, having combined its valuable seed qualities with other characters before 1799 (e.g. British Queen, Knight's green and white wrinkled marrow peas and Knight's Superb). Besides Knight, two other English plant-breeders, Alexander Seton and John Goss, made hybridisation experiments on peas in the early part of the nineteenth century. Their results (*Trans. Hort. Soc.* 1824) are of especial interest, for their work was carried on to the second generation, so that the facts on which Mendel was to base his great discovery of segregation some fifty years later had already been observed in this country. Goss (1822) found in a cross between peas with blue and yellowish white seeds that the first generation were all white like the male parent. He then states : " Towards the end of the summer I was equally surprised to find that these white seeds had produced some pods with all blue, some with all white, and many with both blue and white peas in the same pod. Last spring, I separated all the blue peas from the white, and sowed each colour in separate rows ; and I now find that the blue produce only blue, while the white seeds yield some pods with all white, and some with both blue and white peas intermixed."

The blue seeds would now be called recessives, and the white seeds dominants, and Goss's experiments provide a typical example

of dominance and segregation from heterozygous dominants, but without statistical data.

Mendel began his historic experiments, which were to lay the foundations of genetical science, in 1856. The characters he studied comprised tall and dwarf habits; axial or terminal inflorescences; light green, dark green or yellow unripe pods; round, smooth, angular and wrinkled forms of ripe seeds; pale yellow, bright yellow, orange or green endosperm colour; white, grey, grey-brown, leather-brown seed-coats, with or without violet spotting. He realised the necessity of studying the inheritance of particular well-contrasted characters through several generations, and thus was able to elucidate the principles of heredity where others had failed. His results, which were communicated to the Natural History Society of Brünn in 1865, were published in the records of the Society. Although the account of Mendel's work was distributed to the chief libraries of Europe, no appreciation or understanding was forthcoming from his contemporaries, and it was not until the rediscovery of his work by Correns, de Vries and Tschermak in 1900, sixteen years after his death, that it was accepted as one of the most fundamental and important discoveries made in biology.

Since 1900, a large number of workers have investigated inheritance in the pea. Wellensiek in his monograph (1925) has references to all papers up to that time. More recent work includes that of Sverdrup (1927), Rasmusson (1927), Håkansson (1929), De Haan (1931), Pellew and Sansome (1931), Sansome (1932) and Winge (1936).

The chief conclusions by different workers on peas may be summarised as follows:

(1) The number of independent factors and groups of factors exceeds the number of chromosomes (n = 7).

(2) The linkage value for given genes may vary considerably.

(3) More than 50 per cent crossing-over may occur.

(4) Single-factor gametic ratios often show striking deviations from equality.

In the cases of (1) and (2) it is probable that these anomalous conditions are due to segmental interchange leading to "ring" and other multiple chromosome associations (see page 28). Eight different strains of peas are known, each with seven pairs of chromosomes, which upon crossing to normal types give a proportion of half-sterile plants with multiple chromosome association.

The occurrence of more than 50 per cent crossing-over probably results from the preponderance of a certain type of chiasma formation, while the deviations found in respect of single-factor ratios arise, at least in some cases, from differential pollen-tube growth.

A list of the characters which have been most studied together with the linkage groups is given in Table XIV. Eight linkage groups are indicated, but it is possible that Group IV belongs to Group III.

TABLE XIV

LIST OF GENES IN PEAS

(This list is not complete; it includes only those genes which have been the subject of many experiments)

Dominant	Recessive	Genes	Remarks
I. *Anthocyanin factors*			
1. Coloured flowers .	White flowers	A–a	Fundamental gene for colour
2. Purple flowers .	Violet flowers	A_r–a_r	2-5 affect the shade of pigmentation in flowers, axils, testa, etc.
3. ,, ,, .	Salmon-pink flowers	B–b	
4. ,, ,, .	Apple-blossom-pink flowers	A_p–a_p	
5. ,, ,, .	Pinkish white flowers	A_m–a_m	
6. Pigmented axils, single ring	No pigment in axils	D_a–d_a	6-10 affect the distribution of pigment in the plant
7. Pigment in axils broken, a double ring	Single ring in axil	D_b–d_b	
8. } Pod purple .	Pod green if 8 or 9 or both are absent	P_1–p_1	Both dominants necessary to make pod purple
9. }		P_2 p_2	
10. Testa uniformly pigmented	Testa spotted or without pigment	W–w	Many other genes influence the distribution of the anthocyanin in the testa
II. *Chlorophyll factors*			
11. Cotyledons yellow	Cotyledons green	I–i	The colour of the cotyledons is affected by O–o

TABLE XIV—*continued*

Dominant	Recessive	Genes	Remarks
12. Pods green . Stem green .	Pods creamy yellow Stem pale	O–o	Full green cotyledons are not found on oo plants if the seeds are wrinkled
13. Pods green . Stem green .	Pods yellow	G_p–g_p	
14. Green foliage .	White foliage	W_b–w_b	The white plants die in the seedling stage
III. *Morphological factors*			
15. Long internodes, tall plants	Short internodes, dwarf	L_e–l_e	Talls may be $L_eL_aL_b$ or $L_eL_al_b$ or $L_el_aL_b$
16 and 17. Short internodes, dwarf	Very long internodes, "slender" peas, if both 16 and 17 are absent	L_a–l_a L_b l_b	"Slender" peas are taller than "tall" peas. Their internodes may be 15 cm. long
18. Tendrils normal .	Leaves in place of tendrils, = acacia pea	T_1–t_1	Dominance incomplete
19. Leaves and tendrils normal	No tendrils, only one leaf, "unifoliate"	U_{nl}–u_{nl}	
20. Stipules normal .	Stipules much reduced in size	S_t–s_t	
21. Wings normal .	Wings abnormal, keel-like structures	K–k	
22 and 23. Blunt-ended pods when 22 and 23 are present, "stumpy"	Pointed pods if 22 or 23 or both are absent	B_t^b–b_t^b B_t^a–b_t^a	Both dominants are necessary to make the pod stumpy
24 and 25. Stems normal when 24 or 25 or both are present	Organs ("emergences") on the stem corresponding to tendrils, when 24 and 25 are absent	E_m^1–e_m^1 E_m^2–e_m^2	Both recessives necessary to make "emergences"
26. Stem normal .	Stem fasciated	F_a–f_a	
27. Pods straight .	Pods curved	C_p–c_p	Dominance incomplete

TABLE XIV—*continued*

Dominant	Recessive	Genes	Remarks
28 and 29. Pods hard when 28 and 29 are present	Pods soft, "sugar" pods when 28 or 29 is absent	**P**-**p** **V**–**v**	Both dominants required to make hard pods. **Pv** gives a thin membrane lining the pod. **pV** and **pv** are without a membrane inside the pod
30. First flower high on stem, = late flowering	First flower low, = early	L_l–l	Dominance incomplete. Several other genes influence this character
31. Normal habit .	Foliage narrow pointed, elongated, small	**N** n	Small plants, fertility reduced
32. Normal pods and habit, fertile	Carpels split along suture (posterior), completely sterile as female. Leaves elongated, flower abnormal	F_e–f_e	
IV. *Other factors*			
33. Hilum black .	Hilum not pigmented	P_1–p_1	The chemical nature of the pigment in the hilum is not known
34. "Round" seeds, with starch in cotyledons simple	Wrinkled seeds, the starch compound	**R**–**r**	Dominance incomplete
35. Testa with brown marbling "Maple" or "Partridge" peas	Testa without brown marbling	**M**–**m**	The brown marbling is faintly developed in some white-flowered varieties. Its chemical nature is not known
36. Seeds free in the pods	Seeds adhere, = "brochette" peas	**S**–**s**	In absence of **A** (=I) the seeds are free or almost free
37 and 38. Bloom on stem, leaves and pods and "glaucous", when 37 and 38 both present	No bloom present or very little	G_1^a–g_1^a G_1^b–g_1^b	Either recessive gives emerald. Several other genes for emerald are known to exist

LINKAGE GROUPS

I.	Genes	34, 18, 23
II.	,,	11, 12
III.	,,	3, 20, 8
IV.	,,	19, 35
V.	,,	38, 21
VI.	,,	1, 30, 31
VII.	,,	15, 29 and ? 28
VIII.	,,	13, 27

RADISH, *Raphanus sativus* (diploid, 2n = 18)

Genetical experiments with radishes have been carried out by several investigators. Uphof (1924) investigated the inheritance of root-shape, colour and various other characteristics of the radish. In crosses between yellow-rooted and white-rooted forms a 3 : 1 segregation was obtained in F_2, yellow being dominant. Crosses between varieties with red and varieties with white roots, such as Long Red and Icicle (white), Early White and Early Red, and Long Red and Early White, gave purple in F_1 and approximately one red : two purple : one white in the second generation. Icicle (white) crossed French Breakfast (red), however, gave a small proportion of pink-rooted plants in F_2, in addition to the expected parental types and purples, and the purples were greatly in excess of expectation. The red striping of the variety Triumph proved to be dominant over white, but in the second generation the ratio of red-striped to white approximated 1 : 1 instead of 3 : 1, which Uphof suggests may be due to the action of a gametic lethal.

In the variety Long White, Uphof found, from an examination of very young plants, two distinct types ; some of the seedlings had red primary-cortex cells while others had white. This difference is only observable in the seedling stage, since as the roots become fleshy the red colour disappears. Some of these red seedlings bred true, others gave ratios of three red to one white, and others fifteen red to one white, indicating that the pigment is due to the occurrence of two duplicate genes.

In all his crosses, where a difference in root shape was concerned, Uphof obtained simple mendelian results, and in all cases the F_1 was intermediate between the two homozygous parents and an approximation to a 1 : 2 : 1 ratio was always obtained in F_2. Thus Triumph (round) crossed Icicle (long) and Early White

(round) crossed Long Red gave an intermediate F_1, and one round, two intermediate and one long in F_2 (see Fig. 32). Malinowski

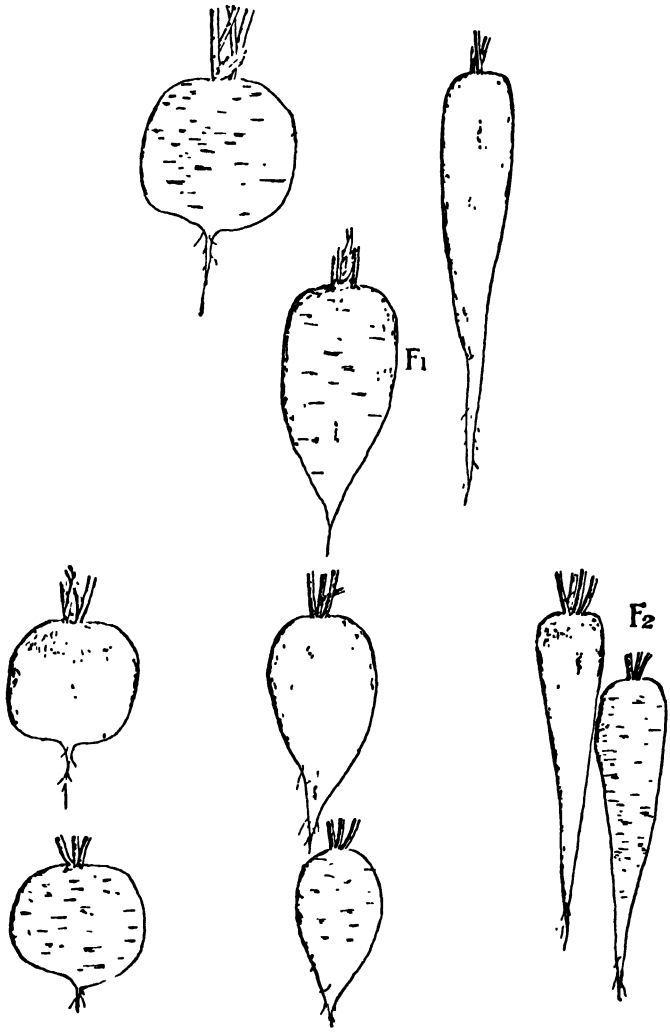


FIG. 32

The inheritance of root shape in the radish. Showing parents, F_1 and F_2. (After Uphof.)

(1916), however, from a cross between Eiszapfen (long) and Vienna (round), found that the long shape was determined by several partially dominant genes, as L_1, L_2, etc. Uphof made crosses

between black winter radishes, which are characterised by the presence of a corky tissue around the periphery of the roots, and the ordinary summer varieties. The corky character proved to be dominant in all cases, and the black colour dominant or epistatic over the other colours. Crosses between round and conical black winter radishes gave intermediates in F_1 and thirty-eight round, seventy-two intermediates and twenty-seven conical in F_2.

In the summer radishes differences in the length and vigour of the foliage were found to be due to a single pair of genes.

LETTUCE, *Lactuca sativa* (diploid, 2n = 18)

Durst (1929) investigated the inheritance of certain characters in the cultivated lettuce. In crosses between varieties such as Big Boston and May King which have anthocyanin pigment in their leaves and stems, and Grand Rapids and Paris White which are unpigmented, the coloured character proved to be a simple dominant. Crosses were made between black and white seeded varieties and black was found to be a simple dominant in all cases. Differences in length, width and area of leaf, plant length and rosette habit, and the time required to produce flowers, were found to be inherited in a quantitative manner.

Durst also made crosses between cultivated varieties of lettuce and forms of the wild *Lactuca scariola*. In crosses between Big Boston and May King, varieties with unlobed leaves, and *L. scariola*, with lobed leaves, the latter proved to be dominant, but apparently two complementary genes were involved. In crosses between lobed and unlobed wild forms only one pair of genes was involved. The anthocyanin pigment of the wild forms was dominant to unpigmented cultivated varieties. Crosses between cultivated varieties and prickly wild forms were made, and the prickly condition was dominant ; but in some cases, in following generations, the ratios deviated significantly from the expected proportions.

Durst states that " cultivated varieties apparently possess genetic qualities which respond more favourably to moist weather conditions than those of wild forms ".

In an investigation relating to the inheritance of immunity to mildew (*Bremia lactucae*) in lettuce, Jagger (1924) found that immunity behaved as a simple dominant to susceptibility to mildew. Jagger tested a large number of varieties of lettuce and

found eight varieties which appeared to be entirely immune to mildew in both California and Florida. These were crossed with the popular variety Los Angeles Market or New York, which is very susceptible to mildew. All the first generation plants were immune, and the second generation gave ratios which approximate to three immune to one susceptible. From these experiments it was expected to obtain immune forms of the New York and other popular varieties.

ONION, *Allium cepa* (diploid, 2n = 16)

Tschermak (1916) and Meunissier (1918), working on the cultivated onion, both report a complex inheritance for bulb colour. Tschermak found dark yellow and red to be dominant to white in F_1, with a complex segregation in F_2. In F_3 some white individuals gave coloured and white. Meunissier found that yellow normally behaved as a dominant over red, although a recessive yellow also occurs.

More recently Rieman (1931) has investigated the inheritance of bulb colour in the onion, with special reference to disease resistance. The pigments are formed in the outer scales of the bulb. Five genes governing bulb pigmentation are postulated as follows :

W, a gene for red pigment (anthocyanin)
W^y, ,, ,, yellow pigment (flavone)
w, ,, ,, white (no pigments)
I, ,, ,, incomplete inhibition of colour (anthocyanin and flavone)
i, ,, ,, allowing expression of colour (anthocyanin and flavone)

W, **W^y** and **w** are considered to be multiple allelomorphs, **W** being dominant to **W^y** and **W^y** to **w**. **I** is incompletely dominant over **i** and inhibits both red and yellow. The four bulb-colour classes studied are given the following formulae :

Red = **Wi**
Red neck = **WIi**
Yellow = **W^{y}i**
White = **WII**, **wI**, **wi**

It is of particular interest that red and yellow onions were found to be highly resistant to the smudge fungus *Colletotrichum circinans*. Red and yellow bulbs grown in the field and sprayed with spore suspensions of the smudge organism were highly immune, whereas white bulbs showed typical smudge lesions. In general red-necked bulbs showed intermediate resistance.

Laboratory tests were made by placing pieces of dry outer scales into drops of spore suspension of *Colletotrichum circinans*. In the presence of red or yellow scales distinctly abnormal germination occurred, whereas germination was normal in the presence of white scales. On the basis of these spore germination tests, the bulbs were divided into three classes, resistant, intermediate resistant and susceptible according to the amount of toxic materials indicated. Most of the white bulbs were found to be extremely susceptible whereas a high correlation was evident between the heterozygous red-neck character and intermediate toxicity. White bulbs of the constitution **WWIi** and **WwIi** showed partial resistance to the disease. The toxic substance, protocatechuic acid, is formed in the outer scales of resistant onions. Reiman points out that although the pigmented condition in the onion is closely correlated with resistance, the toxic substance which has been isolated is colourless. Thus although the genes **W** and $\mathbf{W}^{y}$ are responsible for the production of red and yellow pigments respectively and for the production of the colourless protocatechuic acid, there is the possibility that toxins may be formed without the development of red or yellow pigments and that resistant white onions may be obtained.

BEETROOT, *Beta vulgaris* (2n = 18)

Extensive experiments on root colour in the garden beet have been made by Kajanus (1917). Kajanus distinguishes four classes for root colour: dark red, pale red, white with green top and yellow. Anthocyanin is present in the red forms and absent in the white and yellow roots. The scheme for the inheritance of these characters is as follows: **GR** plants have red roots, **Gr** yellow, **gR** and **gr** white.

CUCUMBER, *Cucumis sativus* (diploid, 2n = 14)

Wellington (1913) studied the inheritance of the following

characters in the cucumber : colour, size, number of spines, smooth or rough skin ; and obtained ratios approximating to disomic segregation. Smooth skin and small spines few in number appeared to be linked.

The English forcing cucumbers are parthenocarpic and develop fruits freely without pollination. In most of the American varieties pollination is necessary to secure a satisfactory crop. Wellington and Hawthorn (1928) investigated the inheritance of these characters and found that the parthenocarpic character is almost completely dominant to non-parthenocarpy. Strong (1921) from crosses between English and American types of cucumbers found the presence of spines on the fruits to be dominant to spinelessness, and black spines to be dominant over white. In melons, *Cucumis melo* (2n = 24), Lumsden (1914) found that yellow skin colour was dominant to white, round fruit to elliptical, large fruit to small fruit and large seeds to small seeds. In F_2 a close approximation to a 3 : 1 ratio was obtained in respect of all these characters. Other characters investigated were netting and ribbing of the fruit. The inheritance of these characters was more complex. The variety Sutton's Superlative, which has pronounced netting on the surface of the fruit but no ribbing, was crossed with Delices de la Table, which has deep ribbing but no netting. The F_1 fruit was ribbed and netted, but in F_2 wide variation occurred with respect to each character.

Amongst many other vegetables investigated, the following may be mentioned. In the carrot *Daucus carota sativa* the white skin colour is dominant to the yellowish-red colour, and the large root form of the giant carrots is dominant to the shorter, thick form of the garden carrot. The cabbage *Brassica oleracea* and other species in the genus *Brassica*, and the garden beans *Phaseolus vulgaris*, *Phaseolus multiflorus* and *Vicia Faba* have been widely investigated. In beans, numerous genes governing colour of seeds and flowers, size, height and habit of growth have been elucidated. In the turnip *Brassica rapa* the deep violet-red colour of the root appears to be dominant or epistatic to the pale violet-red, and yellow recessive to white.

Cabbage, etc., *Brassica oleracea* (diploid, 2n = 18)

The cabbage is one of the oldest of cultivated plants and was used extensively by the ancient Greeks and Romans. It is supposed to have had its origin either on the chalk cliffs near Dover,

or on the Mediterranean coast of France. Primitive forms of cabbage may still be found in these areas; they are leafy non-hearting forms. From such wild ancestors it is generally agreed that the entire cabbage tribe has originated, which includes the different varieties of cabbage, brussels sprouts, cauliflower, broccoli, savoy, kohlrabi and kale. Variation within *B. oleracea* therefore is very wide.

The work of many investigators show that the genetics of the cabbage and related forms is complex, and their conclusions are not in all respects in full agreement. This to some extent may be due to different varieties or strains being used in their experiments. Kristofferson (1924) reported on the inheritance of leaf-colour in various forms and assumed the interaction of five genes, each with the following effect. **A** is normal green and produces no colour, but with **B** it produces a dark-red midrib; **B** gives a light-red midrib; **C** a faint pink colour, but with **A** it gives the dark-violet midrib found in kale. **D** gives the general dark red colour of red cabbage; **E** is concerned with the distribution of the dark red colour. In a later paper Kristofferson (1927) states that the gene **D** only has an effect when both the genes **A** and **C** are present.

Other investigators report a single gene difference between red-purple and green foliage. Pease (1927) concludes that two complementary genes are concerned in the inheritance of colour in purple Kohlrabi × green Savoy. In the F_2 he obtained 9 purples : 7 greens.

In an F_1 between broad-leaf (cabbage) × narrow-leaf (kohlrabi) Pease (1926) states the plants approached more closely the broad type, and in the F_2 about 25 per cent of the plants were of the narrow type. Kristofferson, however, in a cross between broad-leaf (cabbage) and narrow-leaf (kale) found that the F_1 resembled kale and most of the F_2 plants had more or less intermediate leaves, but both parental types were also obtained. A type of leaf having supernumerary outgrowth leaflets called "asparagodes" which occur along the midrib and large leaf veins, was found by Pease to be dominant to normal leaf and due to a single gene. Detjen and McCue (1933) report a similar character but in their material they believe its expression to be due to multiple genes.

The curliness of the leaves of kale appears to depend on the action of several genes. The F_1 of cabbage × kale is intermediate in curliness and the F_2 gives continuous variation between the parental types. Malinowski (1929) states that three genes are concerned, and Pease and Detjen an indeterminate number.

Tallness of plants is dominant to dwarfness, and according to Pease and Malinowski, is due to a single gene. Kristofferson, however, found continuous variation in plant height between parental types in the F_2 and both he and Detjen conclude that multiple genes are concerned with height.

In the F_1 from crosses between the typical hearting or heading cabbage and non-hearting forms of *B. oleracea* most investigators report a slight degree of hearting, the F_2 giving continuous variation with a recovery of both types, full heading being in a minority. Malinowski considers that hearting depends on three pairs of genes, and Pease attributes it to duplicate genes. Detjen working with related hearting and non-hearting types of cabbage found hearting to be fully dominant among related plants, or else that the hearting gene in non-hearting forms is prevented by one or more genes from fully manifesting itself. In crosses between inbred lines Pearson (1932) concludes that the shape of the heart is controlled by many genes. Crosses between long and flat headed strains showed an intermediate shape. Detjen studied season of maturity and concluded that hearting is governed by multiple genes for season of maturity and that this explains the many seasonal strains of cabbage. Rasmusson (1932) in crosses between early and late maturing varieties found the F_1 to be only a little later than the earliest parent.

Crosses between brussels sprouts and cabbage, give F_1's that closely resemble the brussels sprouts but have a heart at the top. In the F_2 there is continuous variation in the firmness of sprouts (the axillary buds), most of the plants having loose axillary buds. Kristofferson believes the formation of axillary buds is governed by a number of genes that are independent of genes for the formation of the terminal head or heart.

Pease (1927) investigated the inheritance of the swollen stem or bulb of kohlrabi and found it to be incompletely dominant to the unswollen stem as in cabbage. He concludes that three genes are concerned, B_1, B_2, and B_3, of which the first two are major genes and the third a modifying gene. In the homozygous condition both B_1 and B_2 result in a bulb, and when either or both are in heterozygous condition, B_3 converts the stalk into a semi-bulbous condition.

POTATO, *Solanum tuberosum* (tetraploid, 2n = 48)

The potato was introduced into Europe from the New World near the end of the sixteenth century, but like so many other

of our cultivated vegetables, its origin is lost in antiquity. Apparently it was cultivated thousands of years before the discovery of America, especially in Chile and the Peru-Bolivian plateau. It has been concluded (Juzepezuk and Bukasov, 1929) that Chile and the neighbouring islands off the coast of Chile were the chief centres from which the cultivated *S. tuberosum* was derived.

The first mention of the introduction of the potato into Europe is by Clusius in 1587, who received indirectly some tubers from Spain. A year later Gerarde obtained tubers from (? via) Virginia.

The history of the cultivated potato has recently been reviewed by Salaman (1946). He discusses *S. andigenum* and *S. tuberosum* and concludes that *tuberosum* is a variety of *andigenum*. But whatever their relationship may have been, it seems safe to conclude that selection has operated over a long period and that *tuberosum* is by now sufficiently differentiated from *andigenum* to be regarded as a distinct species. We therefore adhere to the cultivated potato as *S. tuberosum*.

Among those characters of the potato which have been studied genetically, the following are included in Salaman's (1926) description of the two original introductions :

	Clusius' Potato	Gerarde's Potato
Habit . .	Upright, spreading	Spreading
Stem colour .	Bronzed	Red in midrib
Flower ,, .	Dark heliotrope on upper surface	Pale heliotrope
Tubers, skin .	Beetroot-red, smooth	White, smooth
,, shape .	Cylindrical, irregular	Round to oval, very irregular
,, eyes .	Very deep	Deep
,, flesh .	White	? Pale yellow
Maturity . .	Very late	Maincrop

There is little doubt but what these two introductions were the source of all the potatoes cultivated in Europe, at least until 1851. Both were heterozygous in a number of characters and variations must have occurred as soon as ever plants were raised sexually from seed. There are no records of the origin of any new character by mutation under cultivation, and practically all of the large number of new forms which had been raised before

1785 appear to have arisen by segregation from heterozygotes. By the end of the eighteenth century varieties with white, pale red, parti-coloured, dark red and black-skinned tubers were known, as well as forms with white or yellow flesh. Round, oval kidney and long finger-shaped tubers with deep, medium or shallow eyes ; colourless and coloured eyes ; early and late maturing, and dwarf and tall stocks, all abounded.

In 1851 a new cultivated potato was obtained by Goodrich from Chile. It was named " Rough Purple Chile " and from it in later generations were raised Early Rose and Beauty of Hebron, both of which were used as parents by English breeders. About the beginning of the twentieth century other species, e.g. *S. Commersonii*, *S. edinense*, were introduced and attempts made to hybridise them with domestic varieties, and still more recently extensive collections of wild forms have been made by the U.S.S.R. So far as is known, however, interspecific hybridisation has played little or no part in the development of the cultivated European varieties, all of which, apparently, are forms of *S. tuberosum*.

Breeding : (i) Anthocyanin Inheritance

Extensive experiments have been made, particularly by Salaman, Sirks and Black, on the inheritance of anthocyanin. The following is an attempt to summarise and co-ordinate the various hypotheses.

(*a*) *Tuber Skin Colour*

Tubers may be divided into two classes for skin colour, viz. " white " and coloured. The " white " class varies from whitish to yellow or brown according to the amount of cork in the periderm. The coloured class has anthocyanin in the periderm cells, and may be further divided into forms with (*a*) red anthocyanin, (*b*) blue or purple anthocyanin. In both (*a*) and (*b*) the intensity may vary from very faint to deep. Anthocyanin may be distributed (1) evenly over the whole surface of the tuber (e.g. Kerr's Pink), (2) confined to an area involving the eye (e.g. King Edward), or (3) confined to areas between the eyes (e.g. Leinster Wonder). The distribution of pigment may vary somewhat from tuber to tuber, especially in faintly pigmented varieties.

Salaman states that flavone is present in the flowers of all varieties.

The results of various investigations on tuber skin colour are given by Black (1933), who has summarised the several factorial hypotheses. These, with his own scheme, are presented in Table XV. Comparison of the several schemes shows that there is substantial agreement in regard to there being three main genes for pigmentation, namely:

D, a basic gene,
R, a red-colour producing gene,
P, a blue-colour producing gene.

TABLE XV

GENES FOR TUBER SKIN COLOUR SUGGESTED BY VARIOUS AUTHORS

Author	Basic Gene 1	Basic Gene 2	Red-producing 1	Red-producing 2	Blue producing	Diluting	Restricting	Eye Colour	Intensifying	Inhibiting
Salaman (1910, 1926)	D	..	R	..	P	..	..	..	..	..
Müller (1923)	G	..	H	..	..	..	..	..	..	Y
Kelly (1924)	B	..	..	..	..	D	M	..	..	..
Kranz (1925)	D	..	R	A	..	..	..	..	..	..
Asseyeva (1926, 1930)	D	..	R	R	P	..	..	A	..	..
Köhler (1927)	D	..	R	..	..	..	..	..	..	..
Sirks (1929)	D	S	R	..	P	..	..	..	..	..
Lunden (1929, 1932)	B	..	..	..	P	..	..	..	A	..
Huber (1930)	D	..	R	..	..	..	..	..	..	..
Black (1933)	D	..	R	..	P, B	..	..	..	..	H
Carson and Howard (1945)	..	..	K		..	..	..	..	..	..

Salaman, Asseyeva and Black found **D** and **R** to be complementary, neither producing colour in the absence of the other. **P**, which is epistatic to **R**, was necessary in addition for the development of blue pigment. On the other hand, Sirks maintained that blue pigment could be produced by **P** and **D** in the absence of **R**. Sirks assumes a second basic gene, Kranz and Asseyeva a second red-producing gene, and Black a second blue-producing gene. Both Müller and Black assume a gene which inhibits anthocyanin colour.

There is somewhat less agreement in regard to the genetic

constitution of the parti-coloured varieties. Collins (1924), working with King Edward, considered that a dominant gene governed parti-coloured, and that uniformly coloured, parti-coloured and white might form a multiple allelomorphic series. Salaman supports this view, and suggests that a fourth gene may give " picked " (coloured) eye pattern. Kelly (1924) who worked with the variety Red McCormick in which the colour (as in King Edward) is restricted to the region of the eyes, assumed three genes, viz. **B**, a basic gene, **D**, a diluting gene, and **M**, which along with **D** gives the Red McCormick pattern. Thus **MBD** = parti-coloured, **(M)Bd** = dark, uniformly coloured, **mBD** = light self-coloured, all combinations lacking **B** being cream-coloured. Kranz, using the red-skinned varieties Triumph and Red McCormick, assumed parti-colour to be produced by the interaction of the genes **D** and **R**, uniform-coloured tubers containing a third gene in addition. Asseyeva considered eye pigmentation to be governed by a gene **A** which is only active in the presence of **D**, and when absent results in eyes of light colour or no colour. Hence **ARD** = uniform-coloured and **ArD** = parti-coloured. **A** and **R** are linked. On the other hand Sirks concluded that three genes **P**, **R** and **S**, were involved in the production of eye colour, as follows : **P(R)S** = blue eyes, **pRS** = red eyes, all other combinations having white eyes.

Carson and Howard (1945) using tetrasomic nomenclature state that the varieties King Edward and Gladstone are simplex for the gene **K**, which produces areas of pink pigment in the periderm, and nulliplex for the gene **R**. Secondly, the variety Flourball is nulliplex for **K** and simplex for **R**, which produces pink pigment in the outer layer of the cortex of the tubers.

(*b*) *Seedling, Sprout, Stem and Foliage Colours*

Müller (1923) assumed that the formation of anthocyanin in seedlings (the colour of which is associated with that of young sprouts from the tubers) was due to triplicate genes $\mathbf{A_1}$, $\mathbf{B_1}$ and $\mathbf{C_1}$. He also assumed three genes, **B**, **D** and **E**, for stem colour, while a fourth, **X**, inhibited it. Since seedling colour was always associated with colour in the flowers, stem and flesh of the tubers, Müller concluded that the $\mathbf{A_1}$, $\mathbf{B_1}$ and $\mathbf{C_1}$ genes were either identical or closely linked with his **A**, **B** and **C** genes for flower, stem and flesh colour respectively.

Sirks investigated the inheritance of anthocyanin in various parts of the plant, his scheme including the four genes **D**, **R**, **P** and **S** and a multiple allelomorphic series **B**, **C** and **b**. The chief effects of these genes are given as follows : **P** and **R** produce blue and red anthocyanin respectively in old internodes, but not in young internodes unless **D** is present. In the presence of **S**, **P** produces blue and **R** red eye colour in the tubers, whereas **D** also is necessary for the production of either blue or red skin colour. **P** is epistatic to **R** in all cases. **B** and **C** when homozygous produce blue and red pigments respectively in the seedlings, axil and sprouts. When **B** or **C** is heterozygous the axils only are coloured. **b** is the common recessive gene in this series of triple allelomorphs. On the other hand **DP**, and **DR** also produce colour in seedlings, axils and sprouts, but in contrast to **B** and **C**, the heterozygous forms have colour in seedlings and sprouts as well as in the axils and cannot be distinguished from the homozygotes by absence of pigment in those parts. The **DP**, **DR** series is epistatic to the **B, C, b** series.

The interrelations of the anthocyanin colours in various parts of the plant ascertained by Sirks are given below :

Colours of tuber skins governed by	.	**R, S, D** and **P**
,, eyes governed by	. .	**R, S** and **P**
,, young internodes governed by		**R, D** and **P**
,, old internodes governed by	.	**R** and **P**
,, seedlings, sprouts and axils	.	**B, C, R, D** and **P**

(c) *Tuber Flesh Colour*

The flesh colour of the tubers may be yellow or white, and in addition coloured purple by anthocyanin. White is usually recessive to yellow, though Heribert-Nilsson (1913) obtained some white in the cross true-breeding yellow × white. He also found yellow-fleshed forms which bred true, as well as others which gave yellows and whites in the ratio 15 : 1. Krantz (1922) on selfing the purple-fleshed variety Congo Black found purple colour to be due to a single gene difference. Müller (1923), on the other hand, described a coloured-flesh variety which, on selfing, gave a ratio of nine coloured to seven white. Crossed with a pure-breeding white variety it gave white-fleshed plants only in F_1. Müller suggested therefore that the formation of anthocyanin in the flesh is governed by the interaction of two genes, **C** and **I** ; and that the white-

fleshed parent was homozygous for an inhibitory gene **Z**. Salaman[1] states that there is a definite linkage between the absence of anthocyanin in the flesh and a diluted purple skin colour.

(*d*) *Flower Colour*

According to Lunden (1932), flower colours in the potato fall into two groups, coloured and white. The coloured varieties may again be divided into (*a*) red and reddish purple and (*b*) blue and bluish purple. Both the coloured groups range in colour intensity from a very pale to a very deep coloration. The tips of the petals may also be more or less white. The colour is confined to the upper epidermis of the petals. Salaman (1926) and Black (1930), however, have reported that certain of the white-flowered class possess a small amount of pigment, usually confined to the lower epidermis (cf. *S. etuberosum* with colour in lower epidermis only, and *S. verrucosum* with both surfaces coloured).

A number of workers have shown that white flower colour is recessive to coloured. On the other hand white × white may give coloured forms. It has been concluded that various genetically different white-flowered varieties exist.

Salaman (1912, 1926) interpreted his results on the following scheme : **D** is a basic gene which, alone, produces no colour in the flowers ; **R** in the presence of **D** gives red, while a third gene **P** is required for purple. Thus :

PRD = purple,
pRD = red (heliotrope),
PRd = tinged white.
Other combinations = white.

From the analysis of his results Salaman states further that other colour genes must be concerned.

Lunden (1932) assumes two complementary genes for flower colour, **A** and **B**. Neither of these genes produces flower colour alone, and each governs pigmentation in other parts, e.g. **B** produces a faint reddish tuber colour and faint tinging in some portions of the stem and leaves. **A** produces some pigmentation in the inflorescences, and acts as an intensifier of **B** in tuber and stem. Lunden also found it necessary to postulate other genes, namely **A′** with a similar effect to **A** ; **F** and **G** complementary

[1] *Vide* Matsuura, 1933.

to **A** (**F** only affecting flower colour); two complementary genes **P**, **P'** giving purple flowers but not alone or with **A** or **A'**. Lunden's data were obtained from various crosses, therefore the precise relationship and action of the above genes is uncertain.

Reviewing the foregoing experiments on the inheritance of anthocyanin in various parts of the plant it is clear that pigmentation is governed by three main types of gene: (1) a basic gene, (2) a red-producing and (3) a blue-producing gene. To these may be added a fourth type, namely the anthocyanin inhibitor. Distribution of pigment, including coloration of the eyes, is also closely connected with the occurrence and functions of the main gene types. It is especially noteworthy that there is strong evidence of a number of duplicate (identical) or similar genes controlling pigmentation, e.g. two basic, two red-producing and two blue-producing genes (Krantz, Asseyeva, Sirks, Black); Sirks' duplicate series **D**, **P** and **R** and **B**, **C**, **b**; Lunden's **AA'**, **F** and **G**, etc. Certain of these genes are not identical, though closely similar in their effects, e.g. Salaman, Asseyeva and Black found **P** was ineffective unless both **D** and **R** were present, whereas Sirks found **P** produced colour in the presence of **D**: **DP** and **DR** produce similar effects to **B** and **C**, but whereas **D**, **P** and **R** are independent genes, **B** and **C** (and **b**) are allelomorphs. The **DPR** series is epistatic to the **B**, **C**, **b** series, and the heterozygotes in the respective series express themselves differently (Sirks). It is, indeed, highly probable that a given gene (e.g. **P**) studied by one worker may not be the same **P** gene studied by another, and that failure to obtain similar results from apparently identical material may be attributed to the occurrence of these closely similar yet nevertheless different genes.

The significance of the unquestionable occurrence of this complex of duplicate and similar genes is of considerable interest and will be dealt with in the discussion on the cytology of the potato, which follows.

(ii) Tuber Shape

Experiments by Salaman showed that varieties with round tubers breed more or less true. Oval tubers give long, oval and round tubers from selfing. The difference between long and round tuber shape is considered to be due to a single gene which is incompletely dominant. Salaman concludes that modifying genes

are involved in tuber shape. Results obtained by East, Fruwirth and Krantz support this view. Heribert-Nilsson (1913), however, found a round variety which did not breed true.

(iii) Depth and Size of Eye

Salaman and Heribert-Nilsson consider that plants with deep eyes breed true and the $\mathbf{F}_1$ from deep crossed shallow eyes are more or less intermediate. On the other hand East's results indicated that shallow eye was dominant. Heribert-Nilsson found large broad eyes were dominant to small round eyes.

(iv) Disease Resistance

Several workers have made investigations on the inheritance of resistance and susceptibility to potato wart disease (*Synchytrium endobioticum*). Heribert-Nilsson obtained in $\mathbf{F}_1$ 29 per cent of resistant plants from the cross Jaune d'Or (very susceptible) × Up to Date (slightly resistant). Collins (1921) from the results of his investigations concluded that susceptibility was dominant. Orton and Weiss (1921) and Salaman and Lesley (1923) made more extensive experiments and concluded that there were at least four kinds of immunes : viz. (1) immunes breeding true, (2) those which, on selfing, give fifteen immunes to one susceptible, (3) those which give three immunes to one susceptible, and (4) those which give nine immunes to seven susceptible. Three genes were assumed, **X** or **Y** conferring immunity in the presence of a complementary gene **Z**. Thus **XYZ**, **XyZ** and **xYZ** are immune types and all others susceptible. Evidences were found, however, of inhibitors of the immunity genes, e.g. President and Myatt's Ashleaf (susceptible) give rise to a large percentage of immune plants when selfed or crossed. Various degrees of susceptibility occur, though little variation is found in the degree of immunity.

The recent work of Black (1947) on resistance to potato blight *Phytophthora infestans* has shown that the inheritance of resistance to blight is complicated owing to the different strains of this parasite which exist. The common strain **A**, and two new strains **B** and **C**, were used by Black in testing potato seedlings for resistance to the disease. These seedlings were bred from the blight-immune species *Solanum demissum* and they were found to consist of five different phenotypes, viz. :

(1) Plants immune to strains **A, B** and **C.**
(2) Plants immune to **A** and **B** but susceptible to **C.**
(3) Plants immune to **A** and **C** but susceptible to **B.**
(4) Plants immune to **A** but susceptible to **B** and **C.**
(5) Plants susceptible to **A, B** and **C.**

Thus all plants possessing immunity to the **B** or **C** strains are also immune to **A.** As far as these strains are concerned, Black found that blight resistance is a heritable character, behaving in a dominant fashion, and it appears to be controlled by four major genes as follows :

Ra—confers immunity to strain **A**
Rb—confers immunity to strains **A** and **B**
Rc—confers immunity to strains **A** and **C**
Rbc—confers immunity to strains **A, B** and **C**

In addition, minor genes appear to be present which determine the degree of susceptibility in susceptible varieties and act as modifiers in resistants.

Krantz, Becker and Fineman (1934) investigating pollen sterility in the potato, and Stevenson, Schultz and Clark (1939) investigating immunity to virus infection, explained the segregations they obtained on a tetraploid basis. In both cases, however, the number of plants and progenies they dealt with were small, and additional data are needed to substantiate the hypotheses put forward. Cadman (1942) produced evidence in his work on resistance to virus that the resistance is inherited tetrasomically.

Among other characters investigated Salaman and Heribert-Nilsson found male-sterility to be dominant to fertility, several genes probably being involved. The variety Edzell Blue, with normal pollen, was found to be heterozygous on its female side for male sterility. Krantz, Müller and Krantz, and Hutchins studied the time of maturity of the tubers and again the results indicated that this character was governed by a number of genes. Salaman says that the early maturing character is recessive and breeds true. Salaman also investigated the degree of cropping expressed as the ratio of the tuber mass to above-ground haulm. He found higher cropping to be dominant, and two or more genes were involved. Long stolons were found to be dominant to short.

The Russian workers have noted a number of periclinal and other chimaeras in their investigations upon the potato, and Asseyeva (1927) in particular has dealt with the problems they

raise. It should be pointed out here that it is possible that the failure of workers to obtain similar results in their studies of certain characters (i.e. colour, disease resistance, etc.), might be due to the chimerical nature of the material used (see Chapter VIII).

Cytology

Cytological studies of potato varieties and species have been made by a number of workers, chief of whom are Smith (1927), Vilmorin and Simonet (1927, 1928), Lewitsky (1927), Longley and Clark (1930), Rybin (1930), Meurman and Rancken (1932) and Müntzing (1933). As in the great majority of the Solanaceae, the basic number in potato is found to be n = 12 and polyploidy is common. A list of the species examined and their chromosome numbers is given below (Table XVI):

TABLE XVI

Solanum (*Potato*) *Species*

Diploids (2n = 24): S. aracpapa, S. Bukasovii, S. Caldasii, S. chacoense, S. Jamesii, S. lanciforme, S. muricatum, S. polyadenium, S. ruderale, S. Rybinii.

Triploids (2n = 36): S. cardiophyllum, S. Commersonii, S. coyoacanum, S. medians.

Tetraploids (2n = 48): S. acaule, S. ajuscoense, S. Antipovichi, S. colombianum, S. Fendleri, S. palustre.

Pentaploid (2n = 60): S. edinense.

Hexaploid (2n = 72): S. demissum.

Also S. tuberosum varieties 2n = 24, 36 and 48.

Numerous varieties of the cultivated potato grown in Europe and the United States have been found to be tetraploids (2n = 48).

A great deal of light has been thrown on the constitution of the potato by the detailed analysis of Müntzing (1933) who examined diploid, triploid and tetraploid native cultivated varieties of *S. tuberosum* received from Bolivia. The chromosomes were studied during meiosis, and in each of the diploid, triploid and tetraploid varieties examined a conspicuous grouping of the chromosomes was observed at metaphase of both first and second divisions (Fig. 33). In the diploid forms this grouping proved to be secondary association. No multivalents occurred and meiosis was quite regular. In the triploid and tetraploid forms primary (normal) and secondary chromosome association were found side by side and meiotic irregularities were more abundant. In the

triploid forms the frequency of trivalent formation was definitely high, thus indicating that these forms were auto-triploids. Meiosis in the tetraploid variety was fairly regular, though other workers (e.g. Longley and Clark) have found all grades of irregularity in tetraploid forms, pollen sterility being closely correlated with this meiotic irregularity. Müntzing found that seven diploid plants had an average of 75 per cent good pollen, the extremes being 63-94 ; thirteen triploids had an average of 25 per cent (extremes 13-37) ; while the tetraploid varieties grown under the same conditions as the others had a variable pollen fertility ranging from 4 to 86 per cent good pollen.

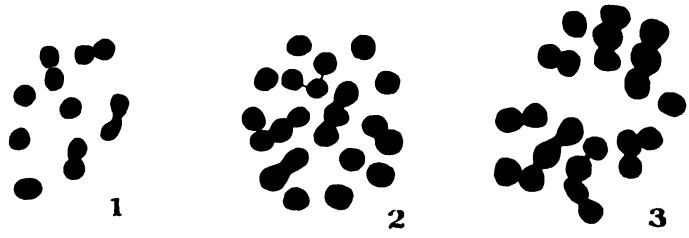


FIG. 33

Polar views of metaphase second division in *Solanum tuberosum*. Showing groups of 2, 2 and 3, and 2, 3 and 4 chromosomes respectively, in (1) diploid, (2) triploid and (3) tetraploid forms of this species. (After Müntzing.)

The rather wide variation in fertility encountered in cultivated varieties is probably an expression of genetic variation in regard to those factors influencing chromosome pairing and the meiotic processes, e.g. temperature, which is known to have a very considerable influence upon pollen fertility in the potato.

Müntzing's statistical analysis of secondary association is of great interest. Observations were made on first and second metaphases in the diploid forms and on second metaphases (where only secondary association occurs) in the triploid and tetraploid varieties (Fig. 33). The results are given below (Table XVII).

Müntzing did not observe the kind or frequency of multivalent associations at meiosis of the tetraploid variety he examined. Meurman and Rancken (1932), however, describe the occurrence not only of univalents, bivalents, trivalents and quadrivalents but also of quinquevalents and sexivalents. The occurrence of these last two multivalent types is normally unexpected on the basis that the potatoes with forty-eight chromosomes are tetraploids.

Meurman and Rancken conclude that the quinquevalents and sexivalents indicate, and arise from, segmental interchange. Somatic metaphases from root-tips of two different varieties showed a pair of chromosomes with trabants—suggesting an allo-tetraploid constitution for the potato.

From his observations that in the diploid varieties half of the twelve bivalents tended to form secondary groups of two bivalents

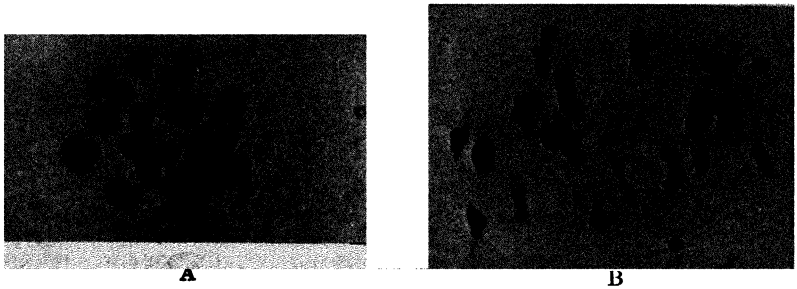
TABLE XVII

Chromosome Number	No of Plates examined (Second Metaphase)	Chromosomes in Groups of							
		1	2	3	4	5	6	7	8
Diploid (2n = 24)	46	303	212	24	8	5	..	..	..
		55%	38%		7%				
Triploid (2n = 36)	40	338	186	147	20	5	..	..	..
		49%	27%	21%	4%				
Tetraploid (2n = 48)	25	187	118	90	76	15	24	14	24
		34%	21%	16%	14%	14%			

each, Müntzing concluded that the so-called diploid potato varieties are really ancient allo-tetraploids whose basic number is n = 6. Secondary groups with proportionately higher numbers of chromosomes which he found in triploid and tetraploid forms are in agreement with this suggestion. On the other hand, Longley and Clark, and Rybin, are of the opinion that the triploid species *S. Commersonii*, *S. medians* and *S. coyoacanum* are all hybrids. Rybin, who examined the extensive material collected by Bukasov and Juzepezuk in South America, concluded that the cultivated potato had a polyphyletic origin. Further, these workers state that " the different forms of the collective *S. tuberosum* differ from each other and from some wild growing tuberiferous species of *Solanum*, considered by some writers as independent species, by sharper and more important characters than those which constitute the difference between these species " (*vide* Rybin, 1929).

Recent cytological observations have helped to explain some of the divergent views discussed as to the origin and constitution

of the cultivated potato. Thus, Thomas (1946) studied and compared the types of chromosome configurations in an induced tetraploid *S. polyadenium* with those found in the cultivated potato, and he concluded that in the potato there is an average of less than two true quadrivalents, which represents only a third of the total number of multiple configurations (see Fig. 34). He



A B

FIG. 34

A, polar view, B, side view of meiosis in the potato, showing primary and secondary association of the chromosomes, *i.e.* bivalents, trivalents and quadrivalents and secondarily associated configurations. (After Thomas.)

also studied the following related *Solanum* hybrids supplied by Dr. W. Black:

S. demissum × *S. Rybinii*			Hybrid
(2n = 72)	(2n = 24)		(2n = 48)
(*S. demissum* × *S. Rybinii*)		× *S. tuberosum*	Hybrid
(2n = 48)		(2n = 48)	(2n = 48)

Thomas found that chromosome differentiation between these related species is not sufficient to affect pairing to any extent, and from these combined results he concluded that the cultivated potato is an allotetraploid hybrid between related species whose chromosomes are structurally similar. Therefore, while the potato appears to have originated as a hybrid, as Rybin and others have suggested, the chromosomes of the parents are so similar that the potato itself can to some extent behave as an autopolyploid. Indeed the common occurrence of duplicate or similar genes, whose inheritance is disomic, is symptomatic of the allopolyploid. The similarity of the chromosomes, however, allows for some degree of tetrasomic inheritance, as is suggested by the results obtained by Cadman and others.

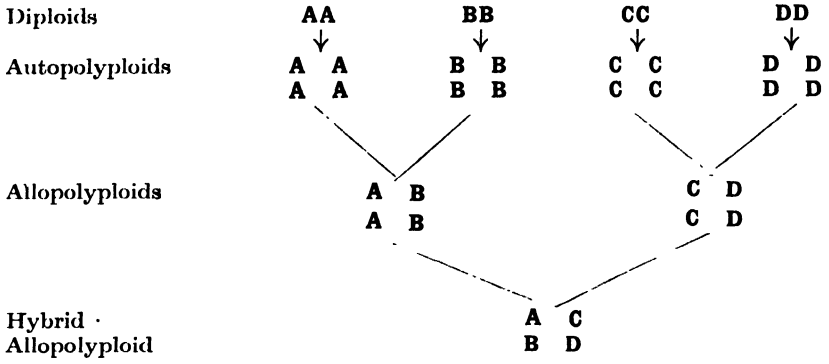


FIG. 35

Suggested origin of the cultivated potato.

As shown above, the cultivated potato may be a hybrid between two allopolyploids, behaving like an autopolyploid in chromosome pairing but with higher segregation and lower fertility.

The problem of the origin and constitution of the cultivated potato and the elucidation of the mode of inheritance is not only a peculiarly interesting problem, but is also a typical example of the sort of investigation where the collaboration of the taxonomist, cytologist and geneticist is essential to a satisfactory solution.

CHAPTER VII

FRUITS

ALTHOUGH breeding experiments with our edible fruits have been very considerable, they have been mainly conducted in the search for new forms of commercial value, rather than for the purpose of detailed genetic studies. Consequently, although in a general way much knowledge is available, in many cases genetic analysis cannot be so precise as the information derived from the more detailed investigations carried out with many flowers and vegetables allows. Our tree fruits especially do not provide favourable material for genetic studies. The length of time which elapses from seed to maturity, the space the seedlings occupy, the cost of maintenance, etc., all militate against large-scale investigations unless exceptional facilities are available, whereas for the purpose of genetical analysis their involved polyploidy and complex heterozygous constitution make large families especially desirable.

PEACHES AND NECTARINES, *Prunus persica* (diploid, 2n = 16)

In an earlier chapter the mode of inheritance of the hairy character of the fruits and of the foliar glands of the peach was described. Among other characters in this fruit which have been investigated are size of flowers, colour of foliage, size of fruit, the condition of the stone whether free or adhering to the flesh, colour and texture of flesh and habit of growth. Our knowledge of the genetics of the peach is mainly derived from the investigations of Rivers (1906), Connors (1919, 1921, 1922), Crane (1921), and Bailey and French (1931). In some cases the investigations have not been sufficient to afford conclusive results, but most of the characters studied conform to simple mendelian rules. Some characters, however, such as the condition of the stone, the texture of the flesh and the season of ripening are not so sharply discontinuous in variation or in inheritance. Complete dominance

only occurs in two of the characters studied, namely the white colour of the flesh and the hairy surface of the fruits. The F_1 from crosses between other allelomorphic characters studied are more or less intermediate, as shown in the following table :

	Characters	F_1
Fruit surface .	Hairy or smooth	Hairy
Flesh colour .	White or yellow	White
Foliar glands .	Reniform or eglandular	Globose (intermediate)
Flower size .	Large or small	Medium (intermediate)
Habit of growth	Upright or spreading	Upright-spreading (intermediate)
Foliage colour .	Deep red or green	Medium red (intermediate)

Connors states that the tough-flesh texture is recessive to soft texture, and that the evidence points to the free condition of the stone being dominant to the clinging condition, but intermediates where the stone partially adheres to the flesh also occur. The information regarding the inheritance of the time of flowering, and the time of ripening and size of the fruits indicates that probably more than one pair of genes are involved in the expression of these characters. According to Connors (1922), the inheritance both of the time of flowering and time of ripening most often follows that of the parents, although in some families the offspring exceeds the limits of the parents, both earlier and later ripening individuals occurring. There is some evidence that male sterility, such as occurs in the variety J. H. Hale, is a recessive character in peaches.

Correlations

Several important correlations have been noted in the characters of the peach. Hedrick (1913) drew attention to a correlation between the coloration of the inside of the calyx cup and the colour of the flesh. When the calyx cup is green the colour of the flesh is white, and when the calyx cup is orange the flesh is yellow. Connors (1922) as a result of further observations states that a green, white or pale cream calyx indicates a homozygous white-fleshed fruit, yellow-cream to yellow-buff calyx cup indicates a heterozygous white-fleshed fruit, and deep orange colour indicates a yellow-fleshed fruit. Connors also suggests that a correlation may exist between the pigment in the twigs, the midrib and petiole

of the leaves and the red colour of the flesh. If this correlation was established it would be of value to those engaged in breeding varieties for canning, as for this purpose red flesh is undesirable.

It has long been noted that the glandless varieties of peaches and nectarines are highly susceptible to mildew, whilst varieties with glands are at least considerably resistant. Hedrick (1911) states that the correlation between glandlessness and mildew may account for the fact that peaches with glandless leaves are rapidly disappearing from American peach lists. In this country we have commonly observed the effect of this correlation both in established varieties and seedlings. In Fig. 36 are shown two seedlings from two families we raised from selfing the peach Royal George, a variety with eglandular leaves, and the nectarine Lord Napier, a variety with reniform glands. The families were homozygous for eglandular leaves and reniform glands respectively. The eglandular Royal George seedling is on the left-hand side, the reniform gland Lord Napier seedling on the right-hand side of the photograph. The Royal George family were all badly affected with mildew, and eventually they all died owing to the severity of the attack. In contrast, the majority of the Lord Napier family were entirely free from mildew, although many branches of the two families, which were grown side by side, were interlaced. There were twenty-eight individuals in this family and only on two was mildew observed, the attack being very slight and confined to a few young terminal leaves towards the end of the growing season.

The eglandular peaches and nectarines have a serrate leaf margin, whereas the glandular forms have a shallow crenate margin. Peaches can be distinguished from nectarines at the flowering time by their respectively hairy or smooth ovaries.

RASPBERRIES, *Rubus idaeus* (diploid, 2n = 14)

Investigations we have carried out with raspberries (Crane and Lawrence, 1931 and unpublished) have shown that in raspberries, as in most domestic fruits, our cultivated varieties are invariably heterozygous in many respects. For example, such red-fruited varieties as Lloyd George, Superlative, Norwich Wonder, Pyne's Royal and Red Cross are heterozygous for yellow fruit. Norwich Wonder and Lloyd George have hairy growth and green leaves, and give a proportion of glabrous and yellow-leaved seedlings



FIG 36.

Correlation between physiological and morphological characters in *Prunus persica*. Seedling 616 eglandular and highly susceptible. Seedling 1139 glandular and highly resistant to mildew.

when selfed. Superlative, Norwich Wonder, Red Cross and many other varieties which have hermaphrodite flowers when selfed or intercrossed give forms which are hermaphrodite, male, female or neuter (Fig. 37).

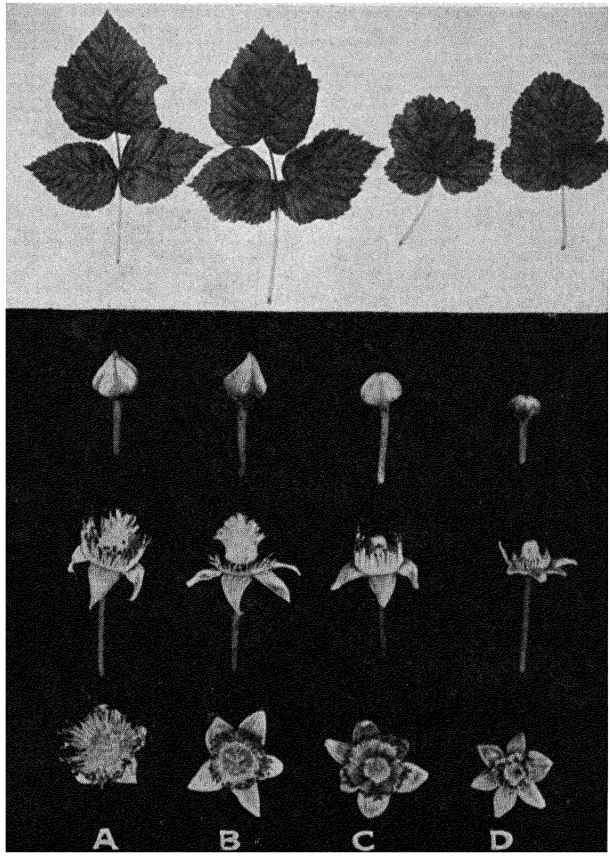


FIG. 37

Flowers, flower buds and leaves of raspberries: A, hermaphrodite; B, female; C, male; D, neuter. Showing correlation between leaf-shape and sex. (After Crane and Lawrence, 1931.)

As far as our investigations have gone, we have isolated three pairs of genes concerned with colour, two with sex, and one with each of the following characters: spines, hairiness, the development of wax or bloom on the growth, colour of leaves and pigmentation

of the hypocotyl. **T** is a gene which produces anthocyanin in spines and fruits. **P** intensifies the colour of the spines. **MF** individuals are hermaphrodite; **Mf**, male; **mF**, female, and **mf** neuter. In **Mf** and **mF** plants the female and male organs respectively are suppressed. **S** determines spines or prickles, **H** hairiness, **B** bloom or wax, **R** red coloration of the hypocotyl and **G** green leaves. The phenotypes therefore are as follows:

PT	Fruits red, spines red
T	Fruits red, spines tinged
P	Fruits apricot,* spines green
pt	Fruits yellow, spines green
FM	Flowers hermaphrodite
F	Flowers female
M	Flowers male
fm	Flowers neuter
S	Growth with spines
s	Growth without spines
H	Growth hairy
h	Growth sub-glabrous
B	Growth with bloom or wax
b	Growth green
R	Hypocotyl red †
r	Hypocotyl green
C	Growth pigmented
c	Growth green
G	Leaves green
g	Leaves yellow

* The apricot fruits are yellow with a slight tinge of red.
† Pigment of the hypocotyl is only observable in the seedling stage; as the plants develop the red colour disapp ars.

Linkage between the genes **B** and **T** has been found, with a cross-over value of 28 per cent. **T** and **G** are also linked. Dr. D. Lewis (1932) has continued these experiments and we are indebted to him for details of unpublished results.

The characters and genetic constitution of some of the varieties we have used, and seedlings raised from them, are presented in Table XVIII. From selfed and crossed families raised for the purpose of determining the mode of inheritance of the various characters detailed, a close approximation to the expected ratios was obtained.

The male plants which have appeared in these experiments approximate to *Rubus idaeus obtusifolius* Willd. (2n = 14). They have very distinct *obtuse* downfolded and undivided leaves on

the two-year-old flowering canes, and on the young one-year-old canes the leaves have only three lobes, and very short petioles. The leaves of the neuters are similarly obtuse, and are quite distinct from the normal lobed and spaced leaves of the hermaphrodite and female plants. The female plants fruit freely when growing near and pollinated by hermaphrodite or male plants, but the males and neuters never bear fruits. The secondary sexual characters of the leaves of the male and neuter plants would enable them, in any economic breeding work, to be distinguished and discarded early in the seedling stage. Varieties which are heterozygous for sex appear to be characterised by curled and rugose foliage, whereas in varieties homozygous for sex the surface of the leaves is flat. For example, compare the curled foliage of such heterozygous varieties as Superlative, Norwich Wonder and Pyne's Royal, with Lloyd George which has flat leaves and is homozygous for sex.

It will also be seen from Table XVIII that there is a correlation in raspberries between the colour of the spines and the colour of the fruit. The red and tinged forms always have red, and the green-spined forms apricot or yellow fruits. Hence plants with apricot and yellow fruits may be separated from those with red fruits at an early stage. In our experience, yellow fruit colour, although often associated with the finest flavour and good size, is invariably associated with a soft flesh. Large size of fruit appears to be a recessive character, but the results indicate that several factors are concerned in the determination of the size and also of the shape of the fruit.

The results relating to sex show that in the raspberry we have the genetic basis of a sex mechanism. If the hermaphrodite type were eliminated, the species would only be able to continue through differentiated male and female forms, and it would be possible for these to develop alternative sex chromosome types such as occur in *Rumex* (Kihara and Ono, 1925) and other genera. Such a visible chromosome difference would not, however, be the cause of sex but the result of it.

In *Rubus chamaemorus* the sexes are more completely differentiated than in *R. idaeus*. In *R. chamaemorus*, although occasional intersex flowers occur, male and female forms are the rule. Rozanova (1928) has reported that the male plants of this species have obtuse leaves, but those of the female are incised and the apices more acute. These secondary sexual characters

TABLE XVIII

Variety	Leaves	Growth	Spines	Flowers	Fruit	Genetic Constitution
Superlative (Type) .	Normal, Curled, Rugose	Sub-glabrous	Red	Hermaphrodite	Red	PpTt MmFf hh
Superlative (Rogue A) .	,, Nearly Flat	,, ,,	,,	,,	,,	PpTt MMFF hh
Norwich Wonder (Type).	,, Curled	Hairy	,,	,,	,,	PpTt MMFf Hh
Norwich Wonder (Rogue)	,, Nearly F.	,,	,,	,,	,,	P-TT MMFF Hh
Lloyd George . .	,, Flat	,,	,,	,,	,,	PPTt MMFF Hh
Pyne's Royal . .	,, Curled, Rugose	Sub-glabrous	,,	,,	,,	PPTt -MFF hh
Red Cross . . .	,, Rugose	Hairy	Tinged	,,	,,	-Tt MMFf Hh
Seedling 8/31, 1743 .	Obtuse, Curled, Rugose	Sub-glabrous	Green	Male	..	pptt Mmff hh
,, ,, 1824 .	,, Curled, Rugose	Hairy	Red	,,	..	P-T- MMff H-
,, ,, 1742 .	Normal, Nearly Flat	Sub-glabrous	Green	Female	Yellow	pptt mmFF hh
,, ,, 1819 .	,, Nearly Flat	Hairy	Red	,,	Red	PPTt mmFf H-
,, ,, 1838 .	Obtuse, Curled, Rugose	Sub-glabrous	Green	Neuter	..	pptt mmff hh
,, 13/31, 2630 .	Normal, Flat	Hairy	,,	Hermaphrodite	Apricot	Ptt MMFF H-
,, 13/31, 2635 .	,, Flat	Sub-glabrous	,,	,,	,,	PPtt MMFF hh

of the leaves of *R. chamaemorus* are morphologically analogous to those of *R. idaeus*. Rozanova further reports that environmental conditions influence the leaf shape in minor degree, but the mature leaves of the two sex forms in *R. chamaemorus* are always distinct. The factors which we have detected as differentiating sex forms in *R. idaeus* are evidently homologous with those determining sex dimorphism in *R. chamaemorus*. It is, therefore, probable that the sexual dimorphism in *R. chamaemorus* has a factorial basis.

Wellington (1913) and Anthony and Hedrick (1916), in a series of breeding investigations with American varieties of raspberries, *Rubus neglectus*, which appears to have been derived from the species *R. strigosus* × *R. occidentalis*, found that dwarfness, which is characterised by short internodes, is recessive to long internodes and greater height. Purple appears to be epistatic to other colours, and red is dominant to yellow. The Columbian variety possesses glaucous and purple canes, and when selfed gave twenty-nine purple, nineteen brownish and two green. Evidently green is a recessive character. With regard to the glaucous character, ten were glaucous, twenty-six intermediate and fourteen non-glaucous. The rough condition of the bark of the canes was found to be dominant to smooth bark, and few spines recessive to many spines.

GOOSEBERRIES, *Ribes grossularia* (diploid, 2n = 16)

A series of breeding experiments with gooseberries was begun at Merton by Mr. W. O. Backhouse and Mr. M. A. Bailey in 1911, and some of the characters they studied are still under investigation. The results so far obtained are insufficient to enable a detailed genetic analysis to be attempted, but the following is a brief summary of some of the characters they studied.

In the following table are given the results with respect to the inheritance of fruit colour obtained from selfing a number of varieties (Table XIX).

The red varieties all proved to be heterozygous, and gave a proportion of seedlings with non-red fruits. Omitting the family obtained from selfing the variety Ostrich, the red varieties, out of a total of 226 plants, gave 164 with red and 62 non-red, the latter being either yellow or green. Red is dominant to non-red, but it is probable that more than one pair of genes govern this character. The non-reds in the selfed Golden Drop family were all yellow, and

the offspring from the dark-green varieties were all green, but they varied from dark to light green. The pale-green varieties gave pale greens, yellow greens and yellows. The behaviour of the red variety Ostrich in giving all green-fruited seedlings when

TABLE XIX

Parents		Selfed Derivatives	
Variety	Colour of Fruit	Colour of Fruit	
Echo	Red	Red, 19 :	No Red, 9
May Duke	,,	,, 46 :	,, 6
Lion's Provider	,,	,, 16 :	,, 8
Ostrich	,,	,, 0 :	,, 23
Whinham's Industry	,,	,, 52 :	,, 22
Crown Bob	,,	,, 23 :	,, 6
Champagne Red	,,	,, 8 :	,, 11
Golden Drop	Yellow	,, 4 :	,, 12
Pitmaston Greengage	Green	,, 1 :	,, 58
Early Green Hairy	,,	,, 0 :	,, 45
Whitesmith	Pale Green	,, 0 :	,, 83
Langley Gage	,, ,,	,, 0 :	,, 70

selfed, is at present obscure, but the results suggest that the variety may be a one-layered periclinal chimaera. The appearance of red-fruited seedlings in the proportion of 3 yellow : 1 red in the selfed family from Golden Drop suggests that this variety carries red, but has, in addition, a gene which inhibits red. Assuming such a gene to be heterozygous (**Ii**), three yellows to one red would be expected.

In gooseberries certain forms exist which develop very few prickles, those which do occur being greatly reduced. Such forms are Belle de Meaux, Souvenir de Billard, Edouard Lefort and *Ribes grossularia inermis*. All these four forms are characterised by comparatively weak growth and make small bushes. Belle de Meaux selfed gave a family of forty-nine plants very similar to the parent in habit and all had few and reduced prickles, and small selfed families raised from Edouard Lefort and *inermis* were also similar to their parents in these respects. Crosses between Edouard Lefort and *inermis*, and forms such as Crown Bob, Whinham's Industry, etc., which have numerous large prickles, gave $\mathbf{F}_1$ families all possessing numerous large prickles.

Some varieties of gooseberries have a very pronounced upright

habit of growth ; others are definitely spreading or sprawling, and between these extremes varieties occur with an intermediate habit. The following results were obtained by Backhouse and Bailey with respect to the inheritance of these characters (Table XX).

TABLE XX

Parents		Selfed Derivatives		
Variety	Habit	Upright	Intermediate	Spreading
Rumbullion . .	Upright	61	1	0
May Duke . .	Spreading-upright (intermediate)	0	16	70
Pitmaston Greengage	Spreading-upright (intermediate)	0	83	47
Early Green Hairy .	Upright	70	0	0
Echo . . .	Spreading	0	0	78
		Derivatives on Crossing		
Echo × Early Green Hairy, and reciprocal		0	0	152

All the individuals raised from selfing the variety Echo had a pronounced spreading habit like their parent, and the selfed individuals from Early Green Hairy, which has an upright habit, were all definitely upright. Individuals from reciprocal crosses between these two varieties all had a pronounced spreading habit. This indicates that Echo and Early Green Hairy respectively are homozygous for spreading and upright and that spreading is dominant, but among the spreading individuals raised from selfing Pitmaston Greengage some were more spreading than others, and the occurrence of forms with intermediate habit suggests that more than one pair of genes are concerned with the determination of these characters.

Apparently all English varieties of gooseberries in general cultivation are susceptible to the gooseberry mildew, *Sphaerotheca mors-uvae*, and as a control for this disease sulphur washes are used. Some varieties, however, are sensitive to sulphur, and after the application of a sulphur spray serious leaf-fall occurs. Among the numerous seedlings of the European gooseberry he raised, Bailey found striking differences in sensitiveness. The plants sensitive to sulphur injury dropped their leaves about five days after spraying, and some of the results he obtained are given in the following summary (Table XXI).

The varieties Whinham's Industry and May Duke are resistant to sulphur injury, and that their offspring were all non-leaf-droppers

TABLE XXI

Parents	Selfed Derivatives	
	Non-leaf-droppers	Leaf-droppers
Whinham's Industry .	98	0
May Duke . .	92	0
Early Green Hairy .	56	14
Pitmaston Greengage	95	36
Ostrich . . .	115	60
Langley Gage . .	80	42
Golden Drop . .	23	2

is of considerable interest. The proportion of non-droppers to droppers in the selfed Pitmaston Greengage family approximates to a 3 : 1 ratio, but in Langley Gage and Ostrich families it approximates to 2 : 1.

RED AND WHITE CURRANTS, *Ribes rubrum* (diploid, 2n = 16)

The following results were obtained by Bailey, and they indicate that the red currant Fay's Prolific is a homozygous red, and from analogy with other fruits one would presume that the red colour of the fruit is dominant to white.

Parents		Selfed Derivatives	
Variety	Colour of Fruit	Red	White
Fay's Prolific .	Red (selfed)	10	0
Versaillaise .	White (selfed)	5	9
Versaillaise × Fay's Prolific .		2	1

Presumably the white currant Versaillaise is a heterozygous dominant white, the red colour being suppressed by an inhibiting gene as described in the case of the gooseberry Golden Drop.

BLACK CURRANTS, *Ribes nigrum* (diploid, 2n = 16)

In breeding experiments with black currants Tydeman (1930)

found that the varieties French Black, Seabrook's Black and Siberian were heterozygous for leaf shape. Tydeman states that the selfed seedlings from French Black were of two kinds : (1) The majority, which resembled the parents very closely in leaf shape, having the flat leaf sinus and characteristic marginal serrations of the parent ; (2) the remainder, approximately 25 per cent of the whole, had leaves which were more attenuated and in which the marginal serrations were markedly more acute. Seabrook's Black, a variety similar to French Black, gave four leaf types when selfed : (1) A leaf type similar to the parent ; (2) a type similar to the segregates obtained from French Black ; (3) a rounded leaf type in which the terminal and lateral lobes were much suppressed ; and (4) a type which in shape bore no resemblance to the normal black currant leaf. In their extremest form the leaves of this type were almost round, and were adherent along their lower margins round the petiole. The variety Siberian gave a selfed family with four similar types of leaves. Tydeman concluded that two genes govern the leaf characters and he designated them as follows : Type 1 (**SR**), type 2 (**Sr**), type 3 (**sR**), type 4 (**sr**). The following summarises Tydeman's results. The actual figures for the French Black segregates were not given, but he states that about one-fourth were of the **S** type. In addition to the results from selfing the varieties French Black, Seabrook's Black and Siberian, the table (XXII) includes results obtained from **SR** and **Sr** derivatives of Seabrook's Black.

TABLE XXII

Parents	Selfed Derivatives			
	Leaf Types			
	SR	S	R	sr
French Black **SSRr** approx.	75%	25%	0	0
Seabrook's Black **SsRr** Fam. No. 1	54	18	23	
„ „ „ „ 2	65	17	17	3
Ex „ „ „ „ 3	164	48	54	
Total	283	83	97	
Expectation 9 : 3 : 4	*260·3*	*86·7*	*115·6*	
Ex „ „ **Ssrr**		155	39	
Expectation 3 : 1		*146*	*48*	
Siberian **SsRr**	49	9	17	3
Expectation 9 : 3 : 3 : 1	*43·8*	*14·6*	*14·6*	*4·8*

Tydeman made considerable observations on the length of the raceme and found that the average length of the racemes of the **SR** and **S** leaf types was appreciably greater than were those of the **sR** and **sr** types. The results of this investigation are given in Table XXIII.

TABLE XXIII

Parents	Leaf Type	No. of Seedlings	Average length of Raceme	Longest	Shortest
Seabrook's Black Selfed	SR	63	39·0 mm.	53·0 mm.	25·0 mm.
	S	16	40·5 mm.	57·0 mm.	28·5 mm.
	R	15	34·0 mm.	43·0 mm.	22·0 mm.
	sr				
Seedlings *Ex* Seabrook's Black Selfed	SR	53	38·6 mm.	52·0 mm.	21·0 mm.
	S	7	36·8 mm.	45·0 mm.	27·0 mm.
	R	12	33·7 mm.	52·5 mm.	19·0 mm.
	sr	2	30·5 mm.	35·0 mm.	26·0 mm.
Siberian Selfed	SR	49	37·0 mm.	54·0 mm.	20·0 mm.
	S	9	40·9 mm.	49·5 mm.	34·0 mm.
	R	16	34·3 mm.	46·5 mm.	16·0 mm.
	sr	1	24·0 mm.	..	..

The origin of French Black and Seabrook's Black is obscure, but both have been in cultivation for a long time. According to Bunyard (1925) the variety Siberian was found by the late Mr. J. H. Elwes on the Altai Mountains in a wild state. It is therefore interesting as a wild variety which is heterozygous for leaf shape and length of raceme.

CHERRIES, *Prunus avium* (diploid, 2n = 16)

Provisionally the sweet cherries can be divided into two classes according to the colour of the fruit—the so-called blacks and whites. Both the skin and the flesh of the blacks are intensely coloured, but they vary from reddish purple to almost black. The so-called whites have a cream or yellow flesh, and the ground-colour of the skin is also cream or yellow, but a flush or flecks of red may occur, and in some cases the flush covers the major part of the fruit. The two classes are, however, readily distinguished.

In Table XXIV we have provisionally summarised the

results we have so far obtained relating to the inheritance of fruit colour.

The results show that white is recessive to black. White crossed white gives white only, and white crossed black and the reciprocal give either all black or both black and white. Bigarreau de Schrecken is evidently homozygous for black, since wherever used as a parent the offspring are all black. Other black varieties

TABLE XXIV

INHERITANCE OF FRUIT COLOUR IN THE SWEET CHERRY

Parents	Offspring		
	Black	:	White
White × White			
Big. Frogmore × Belle d'Orléans . .	..	:	9
Governor Wood × Belle d'Orléans . .	..	:	12
Black × White			
Big. de Schrecken × Belle d'Orléans . .	11	:	..
,, ,, × Governor Wood . .	17	:	..
,, ,, × Elton . . .	12	:	..
Big. Late Black × Governor Wood . .	12	:	9
Early Rivers × Governor Wood . .	2	:	6
White × Black			
Elton × Big. de Schrecken . . .	11	:	..
Big. Napoleon × Big. de Schrecken . .	4	:	..
,, × Black Tartarian "A" .	4	:	6
Emperor Francis × Bedford Prolific . .	16	:	7
Governor Wood × Black Tartarian "B" .	3	:	4
Belle Agathe × Bedford Prolific . .	6		9
Black × Black			
Knight's Early Black × Big. de Schrecken.	9	:	..
Early Rivers × Big. Noir de Schmidt .	6	:	1
Big. Late Black × Big. Noir de Schmidt .	3	:	1

such as Early Rivers, Bedford Prolific, Black Tartarian A and B, Bigarreau Late Black and Bigarreau Noir de Schmidt, are heterozygous for white. When these varieties have been crossed with white varieties, the total proportions of black to white obtained approximate to equality. Although the results are simple, as far as the black and white classes are concerned, the different intensities of colour within the blacks, and the different shades and patterns of red which occur within the whites, show that a number

of genes are involved in fruit colour, although the families are too small to attempt a finer analysis.

The variety Belle Agathe is somewhat exceptional. In general it resembles a white cherry, but the flesh is considerably coloured around the stone. When Emperor Francis (white) was crossed with Belle Agathe eleven blacks and five whites were obtained. This suggests that Belle Agathe is a heterozygous dominant white. Another exceptional result was obtained when we intercrossed the two self-coloured black varieties Bohemian Black and Early Rivers. From this cross only one real black was obtained out of twenty-nine seedlings, the remaining twenty-eight being partially white and partially black. The partially white- and partially black-fruited individuals were peculiar in many respects, e.g. their ground colour was a much deeper yellow than occurs in the white cherries, and the flecks and flushes of anthocyanin were nearer to the colour of the so-called blacks than to the usual red of the whites. The flesh of eighteen of these seedlings was intensely pigmented around the stone.

In a subsequent chapter we show that, in the sweet cherry, the phenotypic and hereditary behaviour of incompatibility has a disomic basis.

Prunus cerasus (tetraploid, 2n = 32)

From selfing Morello, a variety with roundish oblate fruit, occasional long oval fruits occurred. Kentish Red, a variety with bright red roundish oblate fruits, when selfed, gave a family variable in size and shape of fruit. In shape they varied from roundish oblate to oblate. Some were a little deeper in colour than the parent, but all were bright red.

In our experiments the offspring from crosses between the tetraploid sour cherries and diploid sweet cherries have always been highly sterile. A number of such seedlings have been examined and found to have twenty-four chromosomes, and presumably they are all triploids. As described in a later chapter the Duke cherries are tetraploids which have arisen from the diploid sweet cherries *P. avium*, and the tetraploid sour cherries *P. cerasus*. They are themselves productive, but their hybrid constitution is reflected in the common occurrence of defective seeds and in the lack of vigour of their offspring. In our experiments seedlings raised both from selfing and intercrossing Duke

varieties have always been characterised by a high degree of sterility and weak growth, and presumably the majority of the seedlings have an anueploid chromosome constitution.

GRAPES, *Vitis* spp. (? secondary polyploid, 2n = 38)

The investigations of Hedrick and Anthony (1915) show that in regard to the colour of the fruits the majority of coloured grapes are heterozygous, and that white is recessive to both black and red. White crossed white gave all white-fruited offspring. Families which segregated only black and white gave approximately three blacks to one white, and families which segregated only black and red gave results reasonably close to the same ratio.

From biochemical investigations Anderson (1928) and his collaborators have shown that the grape hybrids Siebel and Isabella inherit their fully methylated delphinidin pigment, oenin, from their European parental species *Vitis vinifera*, and not from their America parents *Vitis rupestris* and *V. labrusca* respectively, which latter, like the American hybrids they examined, contained considerable proportions of less methylated delphinidin.

STRAWBERRIES, *Fragaria* spp.

The knowledge relating to the origin and development of the cultivated strawberry is of considerable horticultural and genetical interest. In recent years the history of the strawberry has been extensively dealt with by Bunyard (1913) and by Pearl (1928).

Fragaria vesca (diploid, 2n = 14)

The earliest definite evidence of the cultivation of the strawberry in Europe was in the fourteenth century, when in the Royal Gardens at the Louvre in Paris, considerable numbers of the wild wood strawberry *Fragaria vesca* were grown. For nearly two centuries this was the only strawberry under cultivation. Variations in this species have occurred from time to time both under cultivation and in nature, and they have affected such characters as the colour of the flowers, colour and size of the fruit, the form of the leaves, the runners by which the plants vegetatively reproduce themselves, and the period of flowering and fruiting.

This last variant, known as the Alpine or perpetual strawberry, *Fragaria vesca semperflorens*, produces a crop in the autumn in addition to the usual summer one.

Genetical investigations have shown that most of the variations derived from *Fragaria vesca* are simple mendelian characters. Thus Richardson (1914-23) found that the pink colour of the flowers was dominant to white, and in the second generation he obtained pink, pale pink and white flowered individuals. Later Mangelsdorf and East (1927) showed that the flower colour is governed by one pair of genes. In F_2 they obtained 128 pink and 46 white, a close approximation to a 3 : 1 ratio, and in back-crosses the results also approximated closely to a disomic expectation. The red colour of the fruit is dominant to white. Red is also dominant to dark red and light red. All shades of red are dominant to white. The runnerless forms are recessive to forms with runners, and the trifoliate type of leaf is dominant to the monophylla type with simple leaves.

Of the many variations which have occurred in *Fragaria vesca*, only one proved of any appreciable economic value, the so-called Alpine or perpetual strawberry *Fragaria vesca semperflorens*. This form was not brought into cultivation until a comparatively later period, first appearing in French gardens in the eighteenth century. Later several kinds of Alpine strawberry appeared and improved varieties such as Belle de Meaux and Reine des Quatre Saisons were popular in France even as late as the middle of the nineteenth century. The Alpine strawberries, however, never secured wide popularity in England, and the appreciation they originally held has now been entirely displaced by the modern cultivated varieties.

It is therefore evident that the wood strawberry and its Alpine derivatives fail to provide evidence of the origin of the large-fruited cultivated strawberry. *Fragaria vesca* has only produced forms with comparatively small fruits, distinct in appearance and flavour from the present-day cultivated varieties.

Fragaria elatior (hexaploid, 2n = 42)

The second species of strawberry to be brought into cultivation was the Hautbois strawberry, *Fragaria elatior*. This species is not a native of Britain, but is found sporadically in woods on the continent of Europe, from whence it was brought into cultivation in the sixteenth century. The Hautbois strawberry is easily

distinguished from the wood strawberry by the large size of the plants, and other characteristics. The fruit, however, is small, of a dull purple colour and a distinct musky flavour. In general it is not very productive. The sexes are often separate, making it necessary to grow pollen-producing plants near by to obtain fruit on the female plants. Although its distinctive flavour was much esteemed, the Hautbois strawberry never equalled the Alpine strawberry in popularity, probably owing to its unproductiveness. For a long time it was but little known, and not until the end of the eighteenth century does it appear to have received much attention, and even then its culture was limited. A few varieties were known, such as the Prolific or Royal, the Globe, and later, in the early part of the nineteenth century, the Black Hautbois. At no time have varieties been numerous, and the Hautbois is seldom seen in this country at the present time, although it is stated to be cultivated in parts of Germany where its flavour is still appreciated.

Up to the end of the sixteenth century only the two European species *Fragaria vesca* and *Fragaria elatior* were grown under cultivation. Both are distinct in appearance and flavour, and the small size of their fruits contrasts greatly with the large fruited strawberry grown to-day.

Fragaria virginiana (octoploid, 2n = 56)

The next species to be introduced into European cultivation was the scarlet strawberry, *Fragaria virginiana*, the common woodland and hedgerow strawberry of Eastern North America. The precise date that this species was brought to Europe is not clear. Parkinson refers to the Virginian Strawberry in 1629 in his *Paradisus Terrestris*, but earlier French references occur, and probably it had been introduced to Europe very early in the seventeenth century. Like the species previously detailed, *F. virginiana* produces small fruit, but in many respects it is distinct. The fruits are roundish in shape and scarlet in colour. The flesh is usually pink, juicy and acidulous with a pronounced sweet strawberry scent. The spread of *Fragaria virginiana* was very gradual, and even by the middle of the eighteenth century it was not widely known. Towards the end of the eighteenth century, however, it increased in popularity, and in England during the early part of the nineteenth century between twenty and thirty varieties of the scarlet strawberry were cultivated.

The fruits of these varieties were, however, small and they were soon superseded by the new large-fruited strawberries which then appeared. At the present time one or two varieties still remain in cultivation, and the variety Little Scarlet is grown in considerable quantities by preservers and is much esteemed on account of its delicious flavour, fine scent and retention of shape and colour when cooked.

The introduction and cultivation of the Virginian strawberry had made little progress with strawberry culture at the close of the seventeenth century. Only the wild species *Fragaria vesca*, *F. elatior* and *F. virginiana* and varieties of these which occurred naturally were grown, and at this date no appreciable increase in the size of fruit was evident.

Fragaria chiloensis (octoploid, 2n = 56)

Early in the eighteenth century a fourth species of strawberry, the Chilean or Pine Strawberry, was introduced into Europe. This species is a native of Chile, and is very distinct from the species previously described. The plant is large, and the leaves very thick and dark green. The flowers are big, with six or more large creamy-white petals instead of five as in the other species. The fruit is large and of a dull purplish-pink colour. The flesh is soft, with a flavour resembling pineapple, and the sexes are usually separated in male and female plants.

The Chilean strawberry was brought from South America to France in 1712 by a French officer, Captain Frezier, who was attracted by the large size of the fruit. He had great difficulty in keeping the plants alive on the long sailing-ship voyage, but five plants reached France. Unfortunately all were females, and for a long time no fruit was obtained from them. One of the plants was the beginning of the strawberry industry in the neighbourhood of Brest, where growers interplanted it with other varieties, principally with forms of the Hautbois and Scarlet Strawberry and later with the variety "de Barbier" which, according to Mme de Vilmorin is a cross between the Virginian and Chilean strawberry. In this way provision for pollination was made and satisfactory crops developed.

Although the greatly increased size of the fruit of the Chilean strawberry attracted considerable attention, comparatively little progress followed its introduction during the eighteenth century.

A few varieties arose in cultivation, such as the Ananas, Caroline, Bath and Quoimio, and probably synonymous with one or other of these are the Surinam and *Fragaria grandiflora*. In England at this time the cultivated varieties of the wood strawberry were considered better than all the others. The lack of interest in the original Chilean strawberry was probably due to its several defects. The colour of the fruit and the quality of the flesh were poor, and its unproductiveness recognised. In addition it was not very hardy, which probably accounts for the fact that it was at Brest that it made an outstanding success. Although later varieties to some extent avoided these defects, it is remarkable that, following its introduction, the Chilean strawberry for the best part of a century occupied only a comparatively minor position in strawberry culture.

THE GARDEN STRAWBERRY (octoploid, 2n = 56)

The early part of the nineteenth century saw considerable progress in the development of the garden strawberry, and it was at this date that the English horticulturists took the lead in the raising of new kinds. Varieties were obtained possessing a marked improvement in size, flavour and hardiness. The progress made by the English raisers was due to the fact that they resorted to sexual reproduction, and by this means the number of varieties began to increase rapidly.

Early in the nineteenth century Thomas Andrew Knight, President of the Horticultural Society of London, began extensive cross-breeding experiments with many of our hardy fruits. Knight's success with strawberries was only moderate, but his variety Elton Pine remained in commerce for many years. At about the same time Michael Keens, a market gardener of Isleworth, also began to raise strawberries from seed. In 1806 he raised Keens' Imperial from the seed of White Chile. From Keens' Imperial he raised Keens' Seedling in 1821, which in appearance, size and flavour was a great advance on any variety then known. Keens' Seedling still exists, and in some respects is comparable to many of our modern varieties. In 1822 a Mr Wilmot, another market gardener of Isleworth, raised the variety Black Prince from seed of Keens' Imperial, and in the following year he raised Wilmot's Superb from crossing the Chilean with a scarlet strawberry. The variety Hovey was raised in America

in 1834, and was the first notable large-fruited variety raised in that country; from the known details of its origin it appears highly probable that Keens' Seedling was one of its parents.

Later, Mr Myatt of Deptford raised British Queen in 1840, Eleanor in 1847 and Filbert Pine in 1852. Samuel Bradley at Elton Manor Gardens, Nottingham, raised the widely famed Sir Joseph Paxton in 1862, and the highly flavoured Dr Hogg in 1866. The most successful of the English raisers of strawberries, however, was Thomas Laxton, who began extensive and systematic cross-breeding experiments in many cultivated plants in 1858. Laxton raised and introduced the variety Traveller in 1872 and Noble and King of the Earlies in 1884, the merits of which were recognised by the Royal Horticultural Society by the award of first-class certificates. Laxton's most outstanding success was Royal Sovereign, which he raised from intercrossing the varieties Noble and King of the Earlies. This world-famous variety was introduced in 1892; it was an immediate success, and in the opinion of many remains unsurpassed.

In recent years the genus *Fragaria* has been cytologically examined, and the results of the investigations are of considerable interest in relation to the development of the strawberry. Longley (1926) found the basic chromosome complement of the strawberry to be seven. The wild European strawberry *Fragaria vesca* is a diploid species with fourteen chromosomes. The other species we have mentioned and our modern cultivated varieties are found to be polyploids. Thus *F. elatior* is a hexaploid with forty-two, and *F. virginiana* and *F. chiloensis* are both octoploids with fifty-six chromosomes. The investigations of Ichijima (1928), Mangelsdorf and East (1927), Yarnell (1931 *a* and *b*) and Lilienfeld (1933) confirm and extend the findings of Longley. Diploid forms, including *Fragaria vesca*, hybridised freely and gave fertile progeny. Similarly crosses between octoploids gave fertile offspring, but attempts to intercross species with different chromosome numbers, such as *F. vesca* × *F. elatior* or *F. virginiana*, and *F. elatior* with *F. virginiana* or *F. chiloensis*, were abortive or at the most resulted in sterile hybrids. The facts throw direct light upon the development of the strawberry subsequent to the introduction into Europe and cross-breeding of the two octoploid species *F. virginiana* and *F. chiloensis*, which were previously geographically isolated; it is significant that our cultivated strawberries are also octoploids and there is little doubt that these

species were the immediate parents of our modern varieties. We have recently examined Keens' Seedling, King George and other cultivated varieties and they all prove to be octoploids.

During recent years we have raised families from crosses between *F. chiloensis* and *F. virginiana* and between these species and Keens' Seedling and more modern garden forms. Whenever *F. chiloensis* has been used as one of the parents the vigour of the offspring has been outstanding, and, in many individuals resulting from crossing this species with garden varieties, the flavour and size of fruit has been good, and, in particular, plants of this origin have been comparatively free from the serious troubles so often evident in cultivated strawberries at the present time. The form of *F. chiloensis* we used proved to be homozygous for black seeds, and, since this is a dominant character, all the $\mathbf{F}_1$ families raised had black seeds, but it should be possible to eliminate this presumably undesirable character by selection in the second and subsequent generations. Richardson's (1914, 1923) results indicate that in the garden strawberry the inheritance of size, shape and flavour of the fruit is complex and that a number of genes are concerned in the determination of these characters. In high polyploids this behaviour is in accordance with genetic expectation.

For a long time selection in the strawberry appears to have been mainly directed to the characters of the fruit, and other desirable characters such as vigour of growth and general constitution appear to have been neglected. It is possible that this accounts for some of the serious troubles to which many modern varieties are prone. We suggest that breeders should consider using the original species again, in particular crossing *F. chiloensis* with modern varieties and raising $\mathbf{F}_2$ and $\mathbf{F}_3$ generations.

The Cherry Plum, *Prunus divaricata* (diploid, 2n = 16)

The leaves of the cherry plum *Prunus divaricata* are of three kinds, the normal green, the moderately coloured, e.g. *P. divaricata* var. *Pissardi*, and a form with more deeply pigmented leaves known as " Pissardi nigra " or " Pissardi improved ". The forms with green leaves have white flowers, and those with purple leaves have flowers tinged with colour ; the colour also extends to the fruits and wood. In a breeding experiment with these forms we found that only one pair of genes governs the characters and that the green and deeply coloured forms are homozygous, and the

heterozygous F_1 is the intermediate *P. Pissardi*. Thus, green selfed and green crossed green gave all green. Green crossed the deeply coloured form gave all intermediates, and green crossed *P. Pissardi* gave intermediates and greens in the immediate offspring.

Prunus domestica (hexaploid, 2n = 48)

The results of our investigations with plums *Prunus domestica* (Crane, 1921 and unpublished) indicate that the ground colours of the fruit are green and yellow and that the various combinations of yellow and green are usually heterozygous. A genetic analysis of the anthocyanin colours is more difficult to summarise, but in general the purplish-red forms in which red predominates, as in the variety Victoria, appear to be dominant to the reddish purple and purplish blue, as when selfed this variety gave red with purple, red, yellow with red or purple, green with red or purple, yellow and purplish blue. It is evident that the ground colour affects the appearance of the anthocyanin colours, for example, red on yellow is much brighter than red on green. The variety Prince Engelbert which has purplish-blue fruits, when selfed, gives blue purples, red purples, brownish purples and green, which suggests that this variety is homozygous for green ground colour. The variety Pershore which has yellow fruits is homozygous for yellow.

The habit of growth of plums can be provisionally classified as spreading-erect, erect, spreading-drooping and drooping. The latter appears to be a recessive character. Victoria, a spreading-erect variety, when selfed, gave 146 seedlings spreading-erect, 38 erect, 31 spreading-drooping and 2 drooping. Selfed seedlings from Prince Engelbert and Pershore, relatively erect varieties, were in general all erect. Hairiness of the growth of plums varies in degree, but sub-glabrous growth is recessive. From selfing Victoria, Denniston's Superb, Early Transparent and Czar, varieties with hairy growth, we obtained 329 seedlings with hairy and 110 with sub-glabrous growth. Selfed derivatives of sub-glabrous varieties such as Pershore were all sub-glabrous. The freestone character is recessive to cling, but among the latter varying degrees of adherence to the flesh occur.

In Figs. 38 and 39 and Tables XXV and XXVI is shown the range of variation with respect to shape and size of fruit

which we obtained from selfing the varieties Victoria, Early Transparent, Pershore and Prince Engelbert, and from crosses between these and other varieties. The relative shape and size of the parental varieties is shown in the figures. In Fig. 38 and Table XXV the figures denoting fruit size (volume) are an approximation derived from the formula length × breadth, and in Fig. 39 and Table XXVI the figures for fruit shape show the excess length over breadth expressed as a percentage. Thus at 100 the fruits are round, their height and breadth being of equal dimensions, at 82·5 they are oblate, and at the other extreme, 157·5, the fruits are more than half again as long as broad.

The selfed offspring from Early Transparent, which has roundish-oblate fruits and the F_1 from Cambridge Gage × Early Transparent, ranged from oblate to round, and the selfed offspring from Pershore, a variety with pyriform fruits, were all more or less pyriform. These three families were the least variable with respect to fruit shape that we have so far raised. An analysis of our results indicates that in the plum many factors are concerned in the determination

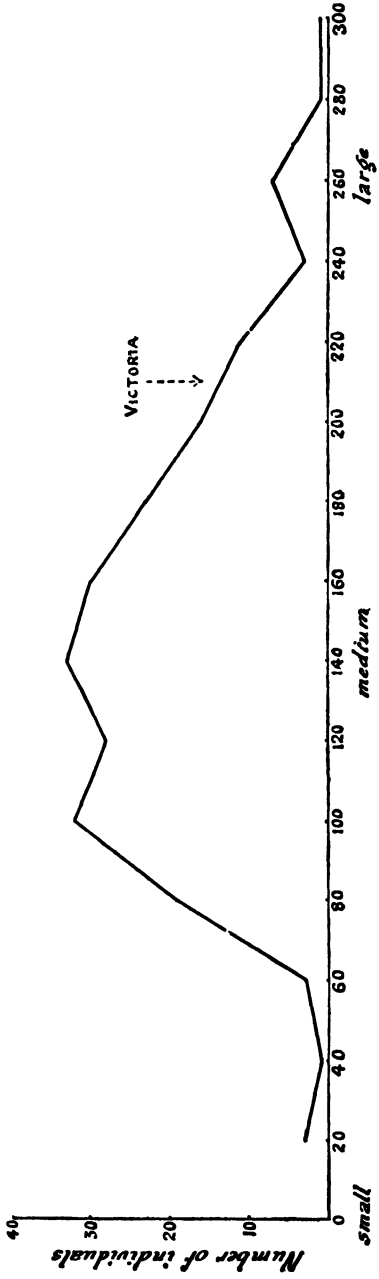


FIG. 38
Showing the range of variation in fruit size from selfing the plum variety Victoria.

TABLE XXV

The Inheritance of Fruit Size in Plums

Parents	Mean Size of Parents	Small				Medium						Large					
		20	40	60	80	100	120	140	160	180	200	220	240	260	280	300	
Late Orleans (160) × Farleigh Damson (28)	94		1	5	5	3											
Late Orleans (160) × King of the Damsons (36)	98		1	2	10	6	2	2	1								
Cambridge Gage (112) × Early Transparent (129)	120·5				2	4	4	3	1								
Early Transparent (129) Selfed	129					3	7	4	6	1	1						
Farleigh Damson (28) × President (260)	144		2	6	4	7	3	1	1								
Pershore (153) Selfed	153							7	4	1							
Prince Engelbert (159) Selfed	159				2	2	5	4	6	1							
Coe's Golden Drop (202) × Denniston's Superb (150)	176					1	4	3	3	6	0	2					
Pond's Seedling (231) × Early Transparent (129)	180					1	1	5	5	2							
Victoria (213) × Pershore (153)	183			1	0	0	1	8	2								
Victoria (213) Selfed	213	3	1	3	19	32	28	33	30	23	16	11	3	7	1	1	

of fruit shape and size, and this, as we show in a later chapter, probably arises from a polyploid constitution and interspecific origin. The smallest and largest plums, though more homozygous than the intermediate sizes, are evidently heterozygous to some extent. In regard to fruit shape whereas the extreme oblate forms are relatively homozygous, the elongated forms are apparently somewhat heterozygous. As is general with most fruits, the inheritance of flavour in plums is difficult to record and summarise.

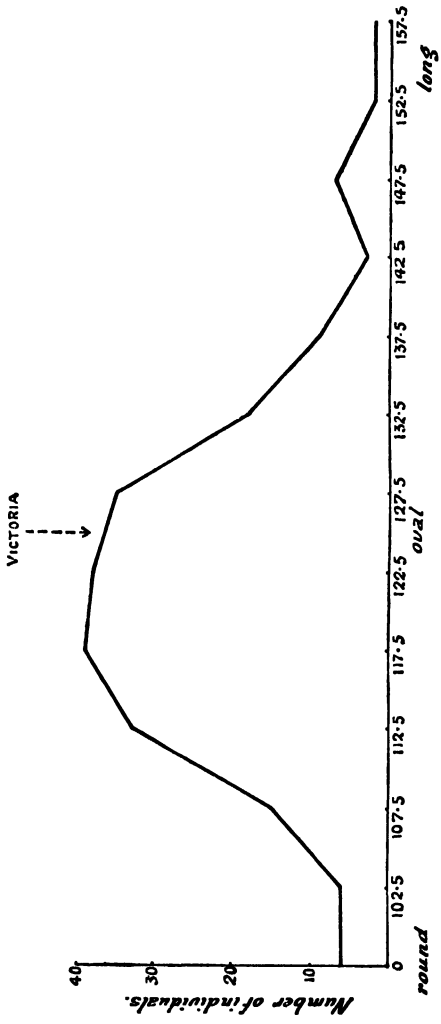


FIG. 39
Showing the range of variation in fruit shape from selfing the plum Victoria.

In some families variation in flavour has been remarkably wide; in others high quality has been evident in the large majority of the individuals raised, while in other families poor quality has prevailed. For example, in the Victoria family the flavour varied from individuals as good as Victoria to individuals with a flavour comparable to a sour astringent damson. In the Early Transparent family the rich flavour of the parent was evident in most of the seedlings. All the seedlings from Pershore had the insipid flavour of the parent. Crosses between such rich-flavoured plums as Cambridge, McLaughlin's Gage, Denniston's Superb and Transparent Gage, gave a high proportion of seedlings with a rich flavour, whereas crosses between plums with

TABLE XXVI

The Inheritance of Fruit Shape in Plums

Percentage of Excess Length over Breadth or Breadth over Length		Oblate								Oval								Long		
Parents	Mean Shape of Parents	82·5	87·5	92·5	97·5	102·5	107·5	112·5	117·5	122·5	127·5	132·5	137·5	142·5	147·5	152·5	157·5	162·5
Early Transparent (92·5) Selfed	92·5	2	4	10	6													
Cambridge Gage (95) × Early Transparent (92·5)	93·75		1	5	4	3	1											
Late Orleans (110) × Farleigh Damson (104)	107				2	1	5	1	2	1	1	0	1					
Late Orleans (110) × King of the Damsons (108)	109				2	4	6	4	2	2	2	1	2					
Pond's Seedling (130) × Early Transparent (92·5)	111·25				1	2	2	4	0	1	2	0	1	1				
Coe's Golden Drop (113) × Denniston's Superb (110)	111·5					4	4	4	1	3	2	1						
Prince Engelbert (116) Selfed	116			1	2	2	5	3	2	1	1	3						
Farleigh Damson (104) × President (130)	117							5	5	7	3	2	1	0	1			
Victoria (125) Selfed	125					6	15	33	39	38	35	18	9	3	7	2	2	
Victoria (125) × Pershore (132)	128·5					1	0	1	1	1	0	1	3	3	0	0	1	
Pershore (132) Selfed	132									1	4	2	2	1	0	0	1	1

a relatively poor flavour such as Pershore, Pond's Seedling and Czar gave a high proportion of poor-flavoured seedlings. The practical conclusions are therefore self-evident; to obtain good flavour the breeder should select good-flavoured varieties as parents, and from them relatively small families may provide new varieties of good flavour. When, however, the breeder desires the combination of other characteristics with flavour, as for example, the resistance to Silver-leaf disease evident in Pershore with the colour and flavour of Victoria, or again the fruit size of Pond's Seedling with the flavour and self-fertility of Denniston's Superb, much larger families are necessary, and probably further generations will have to be raised before the desired combination is obtained.

From the results of his extensive breeding investigations with plums Wellington (1927) came to the following conclusions. In *Prunus domestica* oval fruit shape is dominant to oblate. Thick bloom on the surface of the fruits is dominant to thin bloom. Yellow colour of the fruit is recessive to the red, purples and blacks. The free-stone character appears to be recessive to clingstone; free-stones being obtained from cling and semi-cling parents.

Wellington made many inter-specific crosses in *Prunus*, but apart from crosses between *P. domestica* and *P. insititia*, very few seedlings were obtained. Numerous crosses between *P. domestica* and *P. armeniaca*, *P. americana* and *P. domestica*, *P. cerasifera* and *P. armeniaca*, *P. domestica* and *P. tomentosa*, *P. domestica* and *P. armeniaca* and *P. domestica* and *P. persica* entirely failed.

We have obtained some success in inter-crossing *P. insititia* and *P. spinosa*, and *P. cerasifera* and *P. domestica*. The seedlings raised from these inter-specific crosses are described in a later chapter.

PEARS, *Pyrus* spp. (partly tetraploid, partly hexaploid, 2n = 34, 51)

In the European varieties of pears, *Pyrus communis*, Wellington (1913) found that the green skin of the fruit is dominant to russet-brown skin. Kikuchi (1930) has investigated the inheritance of the fruit skin colour of varieties of the Japanese pear, *Pyrus serotina*, and in contrast with the European pears, he found that in this species the russet skin behaves as a dominant character. This author states that two genes **R** and **I** govern the russet character. **R** gives a russet-brown colour; **r** is green. When **R** is heterozygous **I** partially inhibits cork formation, to which

russetness is due, but the action of **I** is weakened under dry climatic conditions. Kikuchi concludes that the genetic constitution of the phenotypes is as follows :

(*a*) The constant russet-brown : **RRII, RRIi,** and **RRii.**
(*b*) The modifiable russet-brown : **RrIi.**
(*c*) The intermediate : **Rrii.**
(*d*) The pure green : **rrII, rrIi,** and **rrii.**

In **RrII** the inhibiting action of **I** is so strong that the cork layer does not extend over the whole surface of the fruit.

At Merton, Crane and Lewis (1940) have begun a genetical investigation of cultivated pears, and preliminary results of five of the characters studied, namely pigmentation of growth, form of leaf-margin, colour of leaf, hairiness of growth and glandular leaves, can be explained on a simple genetical basis.

(1) **R** = growth red, **r** = growth green or pale yellowish-green. The constitution of twelve diploid varieties for this factor has been established as follows :

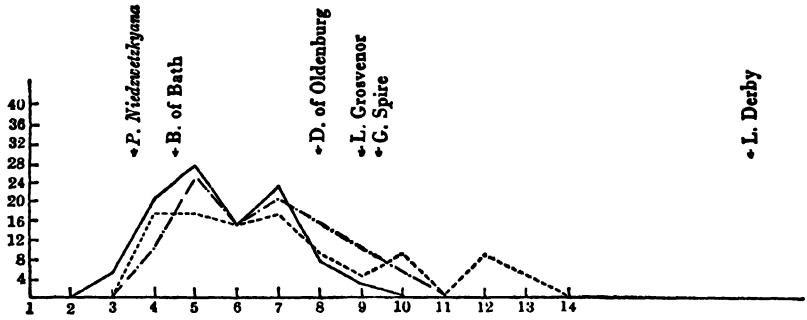
RR	**Rr**	**rr**
Beurré Giffard	Beurré Clairgeau	Conference
Fertility	Beurré Hardy	Laxton's Superb
	Doyenné du Comice	Marguérite Marillat
	Durondeau	Williams Bon Chrétien
	Dr. Jules Guyot	
	Hessle	

(2) **S** = leaf margin serrate or crenate, **s** = leaf margin entire.

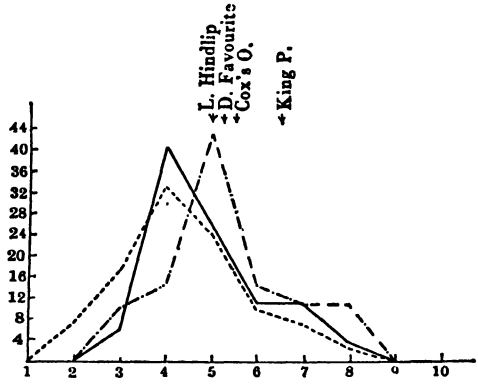
SS	**Ss**	**ss**
Doyenné du Comice	Beurré Hardy	Beurré Giffard
Fertility	Conference **A, A_2**	Conference **A_1, A_3**
	Charles Ernest	
	Dr. Jules Guyot	
	Durondeau	
	Marguérite Marillat	

Except for reciprocal differences in families raised from crosses in which the variety Fertility was one of the parents, a single gene difference fits the breeding data so far available. The anomalous behaviour of Conference is being further investigated. These differences of leaf margin are quite distinct on the leaves of old growth, though not on the current season's growth.

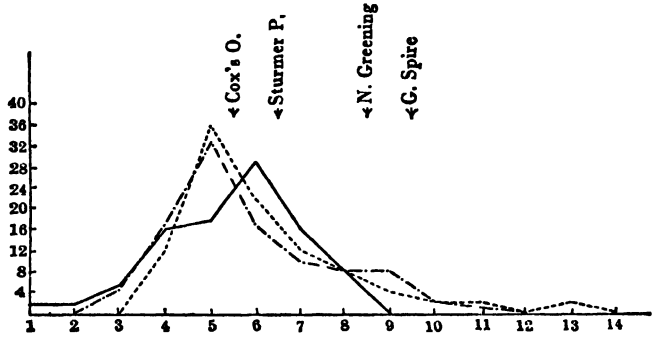
(3) **C** = leaf dark green, **c** = leaf pale green. Pale green is recessive, but this character has not been completely investigated.



— Golden Spire × Beauty of Bath (40). –·– Lord Grosvenor × *P. Niedzwetzkyana* (21). ··· Lord Derby × Duchess of Oldenburg (23)



— Cox's Orange × King of the Pippins (27). –·– Lord Hindlip × Cox's Orange (21). ··· Cox's Orange × Duchess Favourite (41)



— Cox's Orange × Sturmer Pippin (59). –·– Northern Greening × Cox's Orange (48). ··· Golden Spire × Cox's Orange (50)

FIG. 40

Inheritance of size in apples. (After Crane and Lawrence, 1933.)

(4) **H** = stem hairy, **h** = stem glabrous or sub-glabrous. The available data indicate that a single gene governs this character.

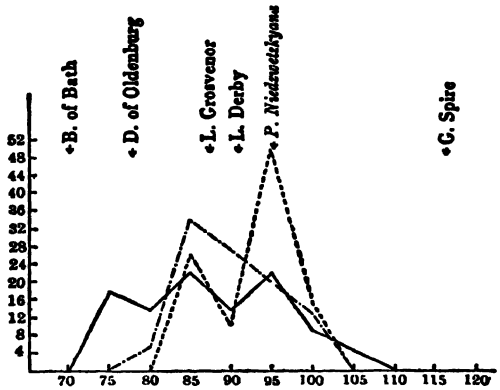
(5) **E** = leaf eglandular, **e** = glands on main venation. From preliminary results it appears that **E** is a dominant gene which suppresses the production of glands on the midrib of the leaf. Further data, however, are required before its genetical behaviour can be confidently established.

APPLES *Malus* spp. (partly tetraploid, partly hexaploid, 2n = 34, 51)

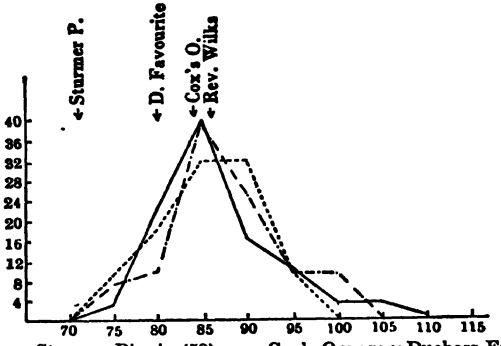
In the apple, variation in almost all characters is exceptionally wide. The ground colour ranges from pale cream through grades of yellow and greenish yellow to green. The red anthocyanin colour may occur as an even flush or in stripes. As a flush it may vary in intensity from pale to deep, may extend over the whole fruit or be confined to the side exposed to the light. Similarly the stripes may occur all over the fruit or be confined to one side ; may vary from pale to deep in intensity and in addition range from a few small flecks through broken stripes of varying dimensions to continuous broad stripes of colour. Both flush and stripes may occur together, independently or not at all. If there is much anthocyanin it is difficult, sometimes impossible, to distinguish ground colours which are closely alike, but when fruits with anthocyanin on contrasting grounds are compared, then the difference in fruit colour is considerable. Thus red on yellow gives a bright red, almost crimson or scarlet apple, e.g. Worcester Pearmain or Lady Sudeley. Red on cream gives a pink colour, e.g. Rev. W. Wilks, and red on yellowish green or green is generally brownish red, as in the varieties Sturmer Pippin and Allen's Everlasting. The flesh colour varies from white through cream to yellow, and may be tinged with green as in Northern Greening or with red as in Beauty of Bath.

Crane and Lawrence (1933) gave a summary of results obtained from breeding experiments carried out with many varieties of apples. These results show that the inheritance of most of the characters studied is complex, and precise analysis difficult owing to the almost continuous variation.

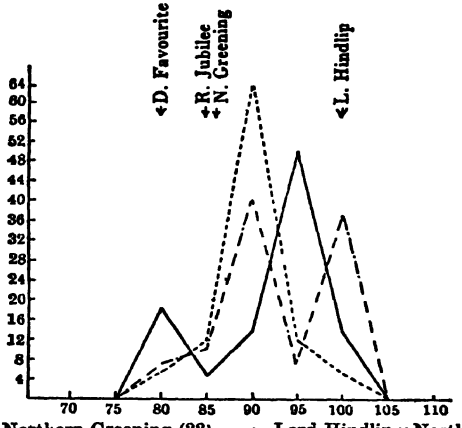
The inheritance and distribution of anthocyanin appears to be controlled by a number of genes. The factors determining its inheritance seem to be dominant, since individuals without



— Lord Derby × Duchess of Oldenburg (23). —— Golden Spire × Beauty of Bath (40).
... Lord Grosvenor × *P. Niedzwetzkyana* (21)



— Cox's Orange × Sturmer Pippin (59). —— Cox's Orange × Duchess Favourite (41).
... Cox's Orange × Rev. W. Wilks (22)



— Royal Jubilee × Northern Greening (22). —— Lord Hindlip × Northern Greening (30).
... Lord Hindlip × Duchess Favourite (17)

FIG. 41

Inheritance of shape in apples. (After Crane and Lawrence, 1933.)

anthocyanin give progeny with very little or no anthocyanin, whereas coloured forms crossed together commonly segregate individuals without anthocyanin. The ground colour appears to be determined by a number of cumulative genes, and yellow ground appears to be partially dominant or epistatic to green ground. Flesh colour also appears to be determined either by cumulative or complementary genes.

In the apple, differences in fruit size are very considerable. The range of variation which occurred in nine families in respect of fruit size is presented in Fig. 40. The approximate size of the parents is also shown in the figures. The figures denoting fruit size (volume) are derived from the formula

$$\frac{\text{Length} \times (\text{radius})^2}{1000}$$

This product, multiplied by 2·7, approximates closely to the actual size of the fruit in cubic centimetres. In all the families we have raised, the mean fruit size of the progeny is smaller than the mean size of their parents, and the results suggest that small size is dominant to large size. The results also indicate that a number of cumulative genes are concerned in the determination of fruit size.

The shape of the fruit varies from a flattened oblate, where the diameter is much greater than the depth, as in Beauty of Bath, to a tall apple where the depth is greater than the breadth, such as the varieties Golden Spire and Smart's Prince Arthur.

The range of variation which occurred in a number of families is presented in Fig. 41, which also gives the approximate shape of the parents. The figures for fruit shape represent the ratio length/breadth expressed as a percentage. At 100 the fruits are practically round, their height and breadth being the same. Above 100 the fruits are long and below 100 flat.

In the inheritance of flavour, there is also an almost insensible gradation from one extreme to the other, and in the time of ripening no sharply discontinuous variation occurs, although when comparatively early ripening varieties have been inter-crossed the time of maturity of the resulting offspring is mainly early. For example, all the seedlings from Golden Spire (October) and Beauty of Bath (August) ripened between August and October. When comparatively late maturing varieties have been inter-crossed the variation, although considerable, is mainly confined to lateness. For example, the offspring from inter-crossing such varieties as

Lord Hindlip and Northern Greening, and Cox's Orange and Sturmer Pippin, ripened from November to March. Where families were raised from comparatively early varieties crossed with late varieties, the variation in the period of ripening occasionally exceeded the extremes of the parents, but usually it was confined to the limits of the parental extremes.

The free formation of root-burrs is characteristic of many of the apple rootstocks propagated by layering. Indeed it appears to be one of the principal characters which separate the Paradise rootstocks from the cultivated apple. In the seedlings we have raised from cultivated varieties, forms with various degrees of burring have occurred. The variation ranged from seedlings which were entirely free from root-burrs to seedlings with numerous pronounced burrs. The results indicate that the genes governing root-burr formation are cumulative, the degree of burring increasing as the completely recessive condition is approached.

From the results of his breeding experiments with apples, Wellington (1924) concluded that such skin characters as oiliness and russeting were recessive to the more general smooth skin. Yellow flesh appears in some cases to be dominant to white, and acidity to sweetness, but it is evident that a number of genes are concerned with these characters. Wellington found the season of ripening more variable, but in general early maturing varieties crossed with early gave mostly early, while late varieties crossed with late gave mostly late maturing seedlings. Wellington, and also Macoun and Davis (1919), comment on the variety McIntosh Red and state that it has proved to be a very suitable parent, as in several crossed families a large proportion of the seedlings possessed many of its desirable characters. Nevertheless, it is evident that McIntosh Red is heterozygous in several respects, though it is probable that for certain desirable characters such as red colour it has a larger number of dominant than of recessive genes. Tydeman (1933), in a detailed report on breeding experiments he has carried out with Paradise apple rootstocks, has shown that discontinuity is exceptional and that a greater or lesser amount of inter-grading occurred between the numerous characters he studied.

The complexity of the hereditary behaviour of the apple is probably due to two causes, namely, hybridity and an intricate polyploid constitution. The ease with which many species of

Malus intercross points to the frequent occurrence of hybridisation both now and in the past. Vavilov (1930) states that the area of the wild apples is very extensive and describes localities in Asia where they are concentrated, and where such species as *Malus pumila* and *M. silvestris* are found. He reports that the fruits of the wild apples of Turkestan are characterised by their comparatively large size. Individual trees bear fruit which in quality is not inferior to that of cultivated forms, and some are of astonishingly large size and exceptional productivity. Vavilov also states that in some localities the whole scale of transition from the typical small, sour apple to the cultivated, perfectly edible forms may be observed.

With the exception of the Pomoideae, the basic chromosome numbers of the genera of the Rosaceae are seven, eight and nine, and of these seven is by far the commonest. In the apple, however, the haploid chromosome number is seventeen and our cultivated varieties are of two kinds, the so-called diploids and triploids with thirty-four and fifty-one chromosomes respectively (see Fig. 42). Darlington and Moffett (1930) have shown that the apple, although functionally a diploid with two sets of chromosomes, is fundamentally a complex polyploid in which there is a repetition of similar chromosomes in each set of seventeen, derived from an original basic number of seven. From the behaviour and association of the chromosomes they have further concluded that the haploid set of seventeen chromosomes is made up of two sets of seven with three of the chromosomes repeated a third time. In other words, the so-called diploid apples with thirty-four chromosomes are partly tetraploid and partly hexaploid, and the triploids with fifty-one chromosomes are partly hexaploid and partly nonaploid, as follows :

Ancestral Complement	Haploid, 2n = 17	Diploid, 2n = 34	Triploid, 2n = 51
A	A_1 A_2 A_3	A_1 A_2 A_3 A_1 A_2 A_3	A_1 A_2 A_3 A_1 A_2 A_3 A_1 A_2 A_3
B	B_1 B_2 B_3	B_1 B_2 B_3 B_1 B_2 B_3	B_1 B_2 B_3 B_1 B_2 B_3 B_1 B_2 B_3
C	C_1 C_2 C_3	C_1 C_2 C_3 C_1 C_2 C_3	C_1 C_2 C_3 C_1 C_2 C_3 C_1 C_2 C_3
D	D_1 D_2	D_1 D_2 D_1 D_2	D_1 D_2 D_1 D_2 D_1 D_2
E	E_1 E_2	E_1 E_2 E_1 E_2	E_1 E_2 E_1 E_2 E_1 E_2
F	F_1 F_2	F_1 F_2 F_1 F_2	F_1 F_2 F_1 F_2 F_1 F_2
G	G_1 G_2	G_1 G_2 G_1 G_2	G_1 G_2 G_1 G_2 G_1 G_2

Moffett (1934) has further shown that our cultivated varieties of

pears consist of similar diploid and triploid forms, and that seventeen is the haploid chromosome number throughout the Pomoideae. The group of species are therefore complex allo-polyploids described as secondary polyploids. A list of diploid and triploid apples and



FIG. 42

The chromosome complements of A, Northern Spy (2n = 34); and B, Bramley's Seedling (2n = 51). 1, The somatic complements; 2 and 3, successive stages in germ-cell formation. (After Darlington and Moffett, 1931.)

pears is given and some of their characteristics described in a subsequent chapter.

Since out of a total of thirty-four chromosomes in the apple there are, according to Darlington and Moffett's conclusions, eighteen chromosomes (6 × 3) any one of which is more or less similar to five others, the chances are slightly more than even that a gene will be

represented six times or have one to five other genes similar but slightly different from itself. For example, if one of the chromosome types which is represented six times be designated by the letter **A**, and this chromosome carries a gene for fruit shape or colour, then each of the other five **A** chromosomes might carry (1) identical genes acting in a cumulative manner, thus giving seven different genotypes, or (2) some identical and some slightly different genes, all of them governing shape or colour but in slightly different ways, and from such a constitution a wide and complex range of variation would be expected. As we have shown in the tetraploid *Primula sinensis* and octoploid *Dahlia*, when a number of cumulative and differential factors govern the same character, the expression of dominance is essentially more variable. Indeed, certain balances may suggest that a character is recessive whereas others may point to dominance. In the apple, difficulty in deciding dominance is frequently encountered, and it is probable that it arises from some such cause.

As we have shown, in several of the characters of cultivated pears, variation is discontinuous. Moffett (1934) cytologically studied many varieties. In diploids no multivalents were observed, and he also found that the degree of secondary pairing was lower in pears than in apples. He concluded that this indicated a greater degree of differentiation of the chromosomes in pears as compared with apples. This may be directly associated with the differences in variation. Also, from what is known of the history of pears, it appears that fewer species are immediately involved in the origin of cultivated forms than is the case in cultivated apples.

The Triploid Varieties of Apples

In a paper published in 1930 we presented some preliminary breeding results with apples, in which attention was drawn to the high degree of generational sterility which occurs among the triploid varieties ; and to the weak and feeble growth invariably evident in families where either one or both parents are triploids (see Fig. 43). These and additional results are detailed in Table XXVII, and they show that comparatively few viable seeds are obtained from triploids and that the resulting offspring are mostly weak.

The occurrence of non-viability of seeds and of wide variation

in the vigour of seedlings in families of apples has been commonly reported upon in pomological literature. Wellington (1924), Crandall (1924), Dahl and Johansson (1924, 1930), Dickson (1928)



FIG. 43.—SEEDLINGS OF APPLES, THREE YEARS OLD

Left, from diploid varieties inter-crossed; Right, from diploid varieties crossed with triploids.

and many other investigators have described the occurrence of such variations. Owing to lack of knowledge of the chromosome complement of the varieties used as parents it is not possible to

TABLE XXVII

Family No.	Parentage	Flowers pollinated	Fruits matured	Apparently good Seeds	Good Seeds per Fruit	No. Seeds germinated	No. Seedlings surviving	Average Height of Seedlings in in.	Total Growth of Family in in.
	Diploid × Diploid								
1/27	Lane's Prince Albert × Cox's Orange	87	10	27	2·7	26	24	60·2	6080
3/27	Cox's Orange × Lane's Prince Albert	110	8	10	1·2	8	7	47·0	1163
9/27	Cox's Orange × Peasgood's Nonsuch	89	10	28	2·8	28	17	46·3	2604
6/27	Charles Ross (selfed)	139	2	1	0·5	1	1	14·2	34
	Diploid × Triploid								
4/27	Cox's Orange × Blenheim Orange	160	12	14	1·1	9	4	26·2	170
5/27	Peasgood's Nonsuch × Blenheim Orange	42	2	4	2·0	2	2	24·5	62
2/27	Lane's Prince Albert × Blenheim Orange	18	3	9	3·0	8	2	14·0	44
	Triploid × Diploid								
11/27	Blenheim Orange × Cox's Orange	60	3	12	4·0	5	1	26·0	99
	Triploid (selfed)								
7/27	Blenheim Orange (selfed)	218	5	11	2·2	3	1	25·5	37
	Diploid × Diploid								
2/28	Jaune de Metz × Northern Spy	..	7	22	3·1	18	16	53·9	2720
3/28	Northern Spy × Old English Broadleaf	117	10	84	8·4	82	76	48·0	9940
1/28	Jaune de Metz × Northern Spy	..	4	8	2·0	7	6	44·1	828
	Diploid × Triploid								
4/28	Cox's Orange × Blenheim Orange	36	3	5	1·6	2	0	..	..
6/28	Lane's Prince Albert × Blenheim Orange	109	4	2	0·5	2	1	12	17
	Diploid × Diploid								
8/29	Lane's Prince Albert × Mother	20	4	13	3·2	13	11	49·2	680
6/29	Lane's Prince Albert × Ellison's Orange	42	1	3	3	3	3	49·0	1423
12/29	Northern Spy × Malling Type VII	29	1	8	8	8	8	48·8	391
1/29	Jaune de Metz × Northern Spy	307	11	13	1·1	12	12	45·0	831
3/29	Lane's Prince Albert × McIntosh Red	23	2	1	0·5	1	1	44·0	44
7/29	Charles Ross × Ellison's Orange	23	3	8	2·6	7	7	41·5	350
9/29	Lane's Prince Albert × Cox's Orange	70	5	20	4·0	18	18	39·3	763

TABLE XXVII (*continued*)

Family No.	Parentage	Flowers pollinated	Fruits matured	Apparently good Seeds	Good Seeds per Fruit	No. Seeds germinated	No. Seedlings surviving	Average Height of Seedlings in in.	Total Growth of Family in in.
	Diploid × Diploid (*continued*)								
11/29	Ellison's Orange × Cox's Orange	121	1	9	9·0	7	6	38·3	259
5/29	Cox's Orange × McIntosh Red	326	21	38	1·8	35	35	38·0	212
4/29	Cox's Orange × Ellison's Orange	336	15	7	0·4	7	7	34·0	335
10/29	Margil × Cox's Orange	50	7	49	7·0	45	44	28·2	1344
	Diploid (selfed)								
13/29	Cox's Orange (selfed)	1616	13	10	0·7	9	9	46·5	495
16/29	Ellison's Orange (selfed)	229	4	9	2·2	8	7	38·5	379
17/29	Mother (selfed)	284	2	5	2·5	4	3	38·0	114
14/29	Lane's Prince Albert (selfed)	475	9	7	0·7	7	7	35·7	250
15/29	Charles Ross (selfed)	35	1	1	1·0	0	0	..	..
	Diploid × Triploid								
22/29	Cox's Orange × Ribston Pippin	124	9	1	0·1	1	1	40·0	52
23/29	Lane's Prince Albert × Crimson Bramley	57	4	10	2·5	6	4	21·0	84
21/29	Cox's Orange × Blenheim Orange	155	8	0	0	0	0	..	..
20/29	Lane's Prince Albert × Blenheim Orange	38	2	0	0	0	0	..	..
	Triploid × Diploid								
25/29	Crimson Bramley × Cox's Orange	10	1	1	1·0	1	1	8·0	8
27/29	Blenheim Orange × McIntosh Red	59	7	15	2·1	13	13	15·1	207
26/29	Blenheim Orange × Cox's Orange	107	8	17	2·1	17	17	14·5	270
28/29	Blenheim Orange × Mother	59	1	4	4·0	4	2	9·5	19
24/29	Blenheim Orange × Ellison's Orange	24	2	1	0·5	1	..	..	..
	Triploid × Triploid								
31/29	Blenheim Orange × Ribston Pippin	35	3	4	1·3	4	2	17·5	35
30/29	Blenheim Orange × Crimson Bramley	72	1	2	2·0	1	1	15·0	15
32/29	Crimson Bramley × Blenheim Orange	51	1	2	2·0	1	1	9·0	9
	Triploid (selfed)								
18/29	Blenheim Orange (selfed)	339	8	12	1·5	3	3	17·3	52
19/29	Ribston Pippin (selfed)	123	8	21	2·5	21	13	9·1	119

consider all the cases to which the above investigators refer, but in many cases it is clear that the lack of vigour and feeble growth they describe is the result of using triploid varieties as parents. For example Wellington (1924) describes the extreme feebleness of the progeny where Baldwin and Gravenstein have been used as parents; both are triploid varieties. Dahl and Johansson found that Belle de Boskoop and Gravenstein varieties, of vigorous growth, in general gave very weak offspring, whereas Ananas and Bismarck, themselves of less vigorous growth than Belle de Boskoop and Gravenstein, gave vigorous seedlings. These authors suggested that there was a correlation between weight of seeds and vigour of seedlings, as the seeds from Belle de Boskoop and Gravenstein were lighter in weight than those of Reinette Ananas and Bismarck. Belle de Boskoop and Gravenstein are triploids, and Reinette Ananas and Bismarck, although not cytologically examined, have all the characters of diploids. Dickson (1928), from the results of his investigations, suggested that " with age of variety, abnormalities occur which cause low seed content, poor germination of seed and lack of vigour in the seedlings ". Among the varieties which Dickson investigated are the triploid varieties Belle de Boskoop, Baldwin, Blenheim, Gravenstein, Ribston and Stayman. It is therefore evident that the correlation between weight of seeds and vigour of seedlings suggested by Dahl and Johansson, and probably that of age and sexual degeneracy suggested by Dickson, are simply the natural consequences which arise from using triploid varieties as parents. The imperfections of the seeds and the lack of vigour of the seedlings result from the irregularities in germ-cell formation in the parents.

The offspring obtained from selfing diploid varieties are often weak, and considerable variation in the viability of the seeds and in the vigour of the seedlings occurs within families raised from diploid parents, but as is shown in Table XXVII the offspring from diploids × diploids are invariably more uniform and vigorous than the offspring from triploids × triploids or diploids × triploids.

Our colleague Dr. A. A. Moffett (1931) has reported upon a number of the seedlings we have raised from crosses between triploids and between diploids and triploids. The somatic chromosome numbers of the seedlings from crosses between triploid varieties ranged from forty-seven to sixty-four, and those from diploids × triploids from thirty-seven to forty-seven. It is therefore evident that the weak and feeble growth characteristic

of the majority of the seedlings raised from triploid parents is associated with an irregular aneuploid chromosome constitution. Possibly an exceptional form may occur as a rarity among such seedlings, but the vigour and productivity of the aneuploids which we have raised at Merton have not so far been sufficiently high to consider their ever becoming widely grown varieties. Therefore, although many varieties of triploid apples are of outstanding merit, the breeder must beware of following the traditional method and using these excellent varieties as parents. As we show in a later chapter, the triploid apples and pears are exceptional among our European fruits in possessing an irregular chromosome complement, and yet being sufficiently productive to be of economic value. Nevertheless, the inevitable irregularity in germ-cell formation makes them practically useless to the plant-breeder.

CHAPTER VIII

HETEROSIS

It is well known that heterozygosity is often accompanied by increased vigour ; and that the seedlings of the F_1 generation are more vigorous than their parents is a common observation. This phenomenon is known as heterosis or hybrid vigour and it is generally assumed to be the result of bringing together the greatest number of favourable growth factors. Jones (1917) explained the phenomenon as being due to a large number of dominant genes, some contributed by one parent and some by the other, which are favourable for growth and development, and held that linkage of genes and the large number involved virtually prevent the perpetuation of hybrid vigour of the same degree in subsequent generations. Jones' theory is generally accepted as providing the underlying mechanism of hybrid vigour. Large numbers of genes are concerned with characters such as height, weight and size which operate to produce hybrid vigour, and as large numbers of genes are probably located in different chromosomes no line is likely to have all the unfavourable or all the favourable genes. Probably most varieties have a moderate proportion of each, and if the majority of more favourable genes have some degree of dominance, even though small, then the F_1 is the only generation with the maximum number of different genes. In any study of hybrid vigour it is important to realise that besides those major characters controlled in simple mendelian fashion, by far the most common genes in a plant are those minor genes determining quantitative characters. The problem of hybrid vigour is therefore complex and consequently in most plants it is not open to a simple explanation.

As Haskell (1949) has pointed out heterosis is the developmental stimulation resulting from the union of different gametes while hybrid vigour is a manifestation of heterosis. Actually there may be + or − heterosis so that the synonymous use of the two terms is not always satisfactory.

Rasmusson (1935) in experiments with peas found that the heterozygous **Aa** plants gave seeds with better germination than the homozygous **AA** plants, and that these were better than **aa.** This was repeated for several generations and gave the same results. He therefore concluded that this is an example of heterosis where heterozygous individuals are better than the best of the homozygous plants, and also that the dominant homozygous plants are better than the recessives. Rasmusson explains the results on the combined dominant gene and linkage theory as follows :

A = red flower colour. **a** = white.
$\mathbf{V_1}$, $\mathbf{V_2}$ are dominant, positive vitality factors.
A is closely linked to $\mathbf{V_1v_2}$ and **a** to $\mathbf{v_1V_2}$.

According to his scheme the parents and the $\mathbf{F_1}$ and $\mathbf{F_2}$ generations are :

Parents	$\mathbf{AAV_1V_1v_2v_2 \times aaV_2V_2v_1v_1}$
$\mathbf{F_1}$	$\mathbf{AaV_1v_1V_2v_2}$
$\mathbf{F_2}$	$\mathbf{1AAV_1V_1v_2v_2 : 2AaV_1v_1V_2v_2 : 1aav_1v_1V_2V_2}$

Therefore plants heterozygous for flower colour **Aa** will always have two dominant vitality factors, whereas no homozygote will have more than one, and the maximum vigour can only be obtained in the heterozygous types.[1] In an earlier publication Rasmusson (1933) discusses various aspects of quantitative inheritance and suggests that the number of genes involved in such characters may be as high as 200-400. East (1936) in a detailed discussion and review of the literature describes numerous examples of heterosis in both diploid and polyploid plants and concludes that heterosis increases with genetic disparity between the parents.

Ashby (1930–33) from experiments with maize and tomatoes concluded that hybrid seeds have a greater initial weight of embryo, and that this gives an advantage which is maintained throughout the period of growth. Passmore (1934), however, found that hybrid plants with small embryos showed a tendency to catch up those with larger embryos, and she points out that in such a study of hybrid vigour, not only the initial size but the duration of the period of growth must be considered.

[1] We are indebted to Dr. E. Akerberg for translating this account from the Swedish text of Rasmusson's publication.

Passmore's experiments were made on varieties of *Cucurbita Pepo*. She made reciprocal crosses between large- and small-seeded varieties, and found that when the large-seeded parent was used as the female, the resulting seeds had much larger embryos than when it was used as male. The hybrids from the large embryos were markedly larger during early development, particularly during the first few weeks, and after nineteen days' growth the differences in leaf number and area were very considerable, but after sixty-four days such differences were not significant. Passmore concludes from this that the ultimate size attained may be the same in the two hybrids from a reciprocal cross, but that the limit is reached first by the one that starts with the largest embryo, the other attaining the limit by virtue of a longer period of growth.

Hybrid vigour is as a rule readily recognised, since its maximum effects are always evident in the generation immediately following a cross. For example, in maize the $\mathbf{F_1}$ hybrids between certain inbred strains show a marked increase in height, have thicker stems, larger leaves and a better root system than their inbred parents, and frequently show an increase of 100 to 200 per cent in yield.

Hybrid vigour is expressed in different plants in different ways and hence it has to be measured differently. Height, for example, is not always an indicator, as hybrid vigour as shown by final plant height has in general a two-fold effect according to whether a plant is of determinate growth habit, like maize, or of indeterminate growth habit like many solanaceous plants. In the first kind vigour is expressed by increased size of the parts already present, for example, maize hybrids have larger leaves, larger root systems and larger seeds on larger ears. In the tomato and the egg-plant, however, heterosis is not expressed so much as an increase in the size of the parts as in an increase in their numbers. As we later show, in these types increased yields are due to a greater number of fruits rather than to larger fruits.

Since heterosis results from the union of unlike gametes it invariably declines in the succeeding generations, particularly where a plant is normally self-fertilised. For example, an individual heterozygous for a single gene **Aa** will produce, following self-fertilisation, offspring of the constitution **AA, Aa** and **aa,** in the proportion of 1 : 2 : 1. On continued selfing the homozygous forms breed true and their number is progressively increased by

segregates from the heterozygotes. Such a reduction in heterozygosity takes place automatically regardless of the number of genes involved, the rate of reduction depending upon the degree of inbreeding. As hybrid vigour is at a maximum in the heterozygous generation it is necessary, in plants raised from seed, to repeat the parental cross for each crop if maximum vigour is to be maintained. In plants where vegetative reproduction occurs by means of bulbs, tubers or corms, or where it is practicable to propagate and increase by cuttings, graftings, etc., hybrid vigour can be maintained by asexual reproduction. Many of our asexually propagated horticultural plants have been selected for vigour of growth, high yield, etc., which are to a large extent the result of heterosis. Among such plants may be mentioned potatoes, apples, pears, strawberries and raspberries. Varieties of these plants invariably lose much of their vigour when inbred. Deterioration of asexually propagated forms does sometimes occur, but this has been demonstrated to be generally due to disease and not to asexual reproduction in itself or to loss of heterosis. For example, in potatoes, strawberries and raspberries deterioration of varieties is commonly due to virus disease, but where the same varieties are free from disease vigour is maintained. Occasionally bud mutations give rise to sub-clones with a decrease in yield and other defects (see Chapter IX), but in general, apart from the effects of disease, our various asexually reproduced fruits, flowers and vegetables retain their vigour over very long periods of time.

The results of numerous experiments indicate that the utilisation of hybrid vigour may be of considerable practical value. Breeding experiments by Stout, McKee and Schreiner (1927) have shown that in forest trees, marked increase of vigour of growth frequently occurs in hybrids. Karper and Quinby (1937), in breeding experiments with *Sorghum*, obtained different degrees of hybrid vigour, and they state: "It follows that the different degrees of vigour obtained represent differences in the number of dominant genes favourable to growth, and that the effect of these genes, though small individually, is cumulative. More specifically, it is apparent that certain genes affect the ability of the plants to tiller, certain others affect the number of nodes, others size of leaf, etc." In crosses between varieties giving the maximum hybrid vigour in *Sorghum*, an increase in the yield of grain approximating to two and a half times that of the higher producing parent was obtained.

In maize the increased yield and other economic advantages associated with hybrid vigour, such as ability to withstand gales and abnormally dry conditions, have been commercially utilised in America, and a number of different hybrids have been introduced for general cultivation both from experimental stations and from commercial seed companies. Most of the hybrid maize strains used for commercial purposes are the result of bringing together four inbred strains, by three separate crossings as shown in Fig. 43A.

One of the advantages of double crossing is that the production of hybrid seed is greater from crosses between F_1 ears, than from crosses between the original inbreds. Also the seed is better developed and more regular in shape, which assists in mechanical planting and hence better stands of maize in the field. This is not so important with sweet corn, the vegetable sugary maize, as the seed of sweet corn is always irregular and invariably hand sown. Double crossing in maize also results in a slight variability in the time of flowering and especially in the time of pollen dispersal. Under adverse conditions this can be of great value, as it enables pollination to be effectively carried out over a longer period.

According to Hainsworth (1949) in pre-war years, up to 1939, the average yield of maize per acre in U.S.A. was 25 bushels, whereas by using hybrid vigour the average yield in 1948 was 42·7 bushels, an increase of over 70·0 per cent; and during the period 1946–48 the U.S.A. produced more than 3,000,000,000 bushels of maize annually. In this enormous increase in yield hybrid vigour has taken a major part and although the old kinds have to be retained for crossings and for providing new inbreds, this type of maize, raised anew each year from controlled crossing, has almost displaced the older standard kinds from cultivation.

Kakizaki (1929) in a series of experiments relating to hybrid vigour and its practical utilisation in the egg plant, *Solanum melongena* ($2n = 24$) found that the plants in the F_1 generation exceeded in yield the better yielding parent by 17 per cent on the average. Crosses between widely different varieties usually gave a greater degree of hybrid vigour than crosses between less diverse varieties, and most of the crosses exhibiting significant increases in yield were between varieties which differed widely from each other in their characters. The cross which gave the highest increase yielded 140·8 per cent more than the better yielding

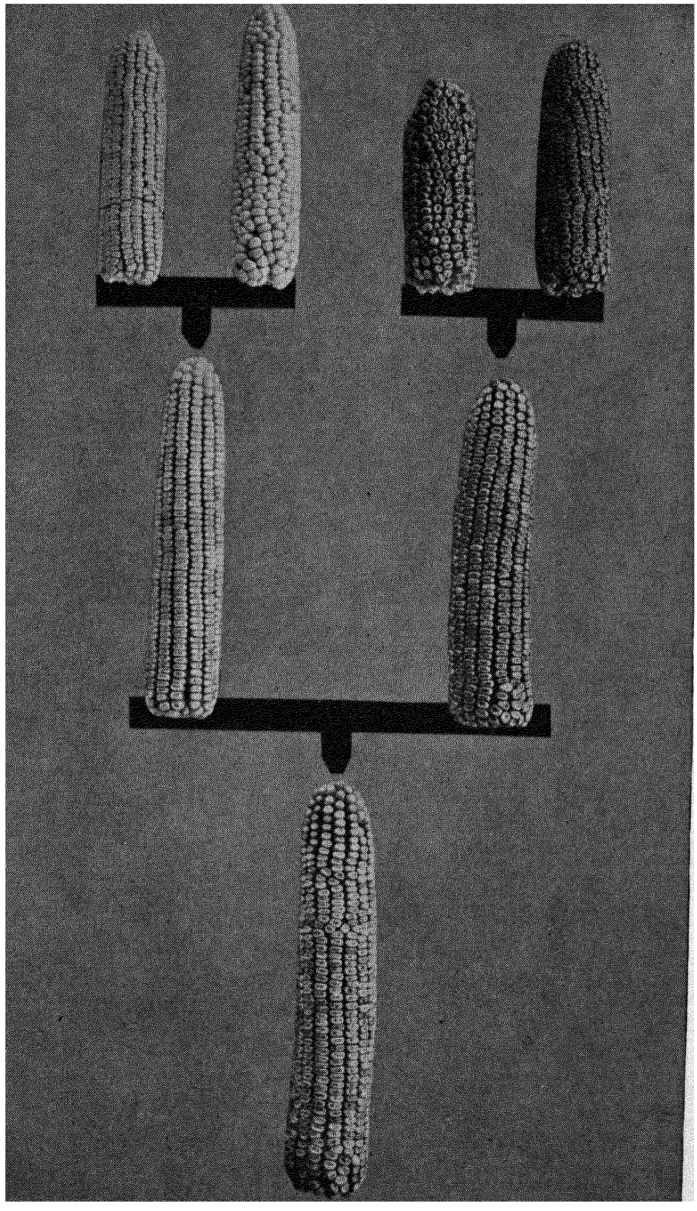


FIG. 43A

Heterosis in maize. The result of bringing together four inbred strains, by three separate crossings.

parent, and Kakizaki states that two heterozygous cross-bred families which were determined as the most superior for practical use have to some extent come to be grown for commercial culture in Japan.

More recently Odland and Noll (1948) report in experiments they have carried out with egg plants that in every case the yield of the hybrid progeny exceeded the mean yield of the parents. The range of increase in yield in the F_1 hybrids was from 11 per cent to 153 per cent and the mean of all hybrids exceeded the mean of all parents by 62 per cent. Yield in egg plants is determined by number and size of fruits and Odland and Noll state that in general the size of the fruit of the F_1 hybrids is approximately the size of the fruits of the respective mean of the parents. It therefore follows that the increase in yield results, not from an increase in size, but from an increase in number of fruits. Thus in the F_1 hybrid " Early Long Purple " × " New Hampshire " the weight per fruit of the parents is 0·7 and 0·9 lb. respectively, while the weight per fruit of the hybrid is 0·88 lb., and in this cross the hybrid out-yielded the average of the parents by 106 per cent. The hybrids were also significantly earlier in maturity, thus giving a desirable early yield.

Kakizaki (1931) reports that in some varieties of the egg plant the yield of seed averages 2,500 seeds per fruit. Therefore the production of hybrid seed in quantity is not difficult as the seed from only a few fruits is sufficient to plant an acre of land.

Wellington (1912) in similar experiments in the tomato reported that in all cases the F_1 showed an increased yield, but in the second and third generations the yield decreased in direct ratio to the decrease in the number of heterozygous plants.

Larson and Currence (1944) studied the extent of hybrid vigour in tomato crosses with special reference to early yield, total yield and fruit size. They found the average increase in early yield of fourteen F_1 generations over parental average, was 47 per cent and for total yield the average increase of the F_1 over the mean of the two parents was 30 per cent. The average fruit size was, however, slightly less than that of the mean of the parents.

At the John Innes Institution we are investigating the possible utilization of hybrid vigour in tomatoes and, as shown in Figs. 43B and 43C in some hybrid lines a considerable increase in yield has been obtained beyond that of either parent, but refinements such as uniformity in size and shape of fruit requires further

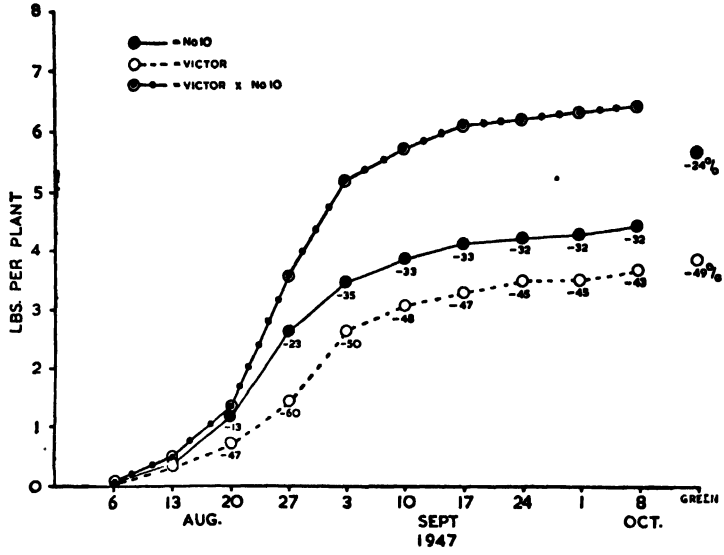


FIG. 43B

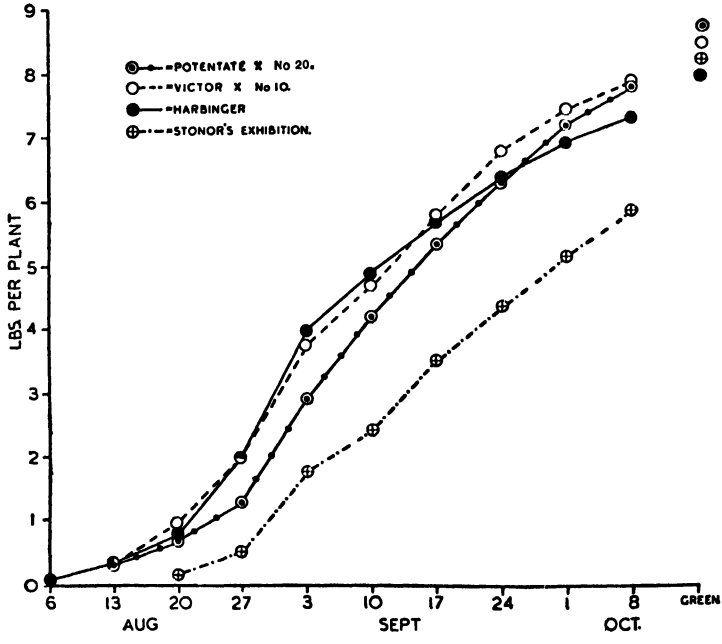


FIG. 43C

FIGS. 43B and 43C

Showing the yield of parental varieties and F_1 lines of tomatoes (see page 169G). The curves = ripe fruit, and circles on right total crop ripe and green fruit.

investigation. In these experiments the tomatoes have been grown out of doors and stopped at the fifth inflorescence ; picking of ripe fruit was begun the first week in August and finished the second week on October. As shown in Fig. 43B by that time the hybrid line had given two lbs. of ripe fruit per plant more than its highest yielding parent. In Fig. 43C the same hybrid line is shown with the varieties " Harbinger " and Stonor's " Exhibition ". In experiments we have carried out with many established varieties " Harbinger " has been outstanding for early ripening and " Exhibition ", though late ripening, has been outstanding for high yield, and we now use them as a measure of earliness and yield respectively. In the F_1 of crosses between certain varieties of cucumbers an increase in yield of over 30 per cent has been reported.

In maize the production of hybrid seed is easily carried out because the male and female inflorescences are borne separately on the same plant and the usual method of emasculation can be avoided by the removal of the male inflorescences before the pollen is dispersed. In the same way in cucumbers and other cucurbits the male flowers can be removed before they shed their pollen. In most species, however, the flowers are hermaphrodite, and unless seed production per flower is very high, as in the egg-plant and tomato, the emasculation of huge quantities of flowers by hand would usually be uneconomic.

Sometimes this difficulty can be overcome. From time to time, abnormal male-sterile forms have appeared in a number of genera, e.g. carrot, onion, sugar beet, tomato, flax, etc. Emasculation is avoided in these male-sterile forms and they can be used as females with pollen from hermaphrodite flowers of normal varieties. Thus, rows of male sterile forms can be alternated with rows of normal varieties, similar to the method adopted for the production of hybrid seed in maize, and in this way mass crossing is made possible by insects or wind as the case may be. The onion provides a good example of the application of this technique. Inbreeding produces a progressive decrease in vigour in onion varieties, particularly in loss of bulb weight. Some inbred lines, however, have been established by Jones and Davis (1944) with certain characters, such as storage quality and uniformity, superior to commercial parental varieties. Crosses between such inbreds usually exhibit increased vigour and greater uniformity in shape and size in the F_1 compared with the parents.

In this work Jones and Emsweller (1936) have used male sterile onions in the commercial production of hybrid seed. They found the mean bulb weight of the hybrids with various inbreds and commercial varieties exceeded that of either parent and increases in yield as large as 50 per cent have been obtained.

Male sterility in the onion, according to Jones and Clarke (1943), is the result of interaction between a recessive nuclear gene **ms** and a cytoplasmic factor **S** showing only maternal inheritance. In other words interaction between the recessive **ms** gene and the **S** cytoplasm results in male sterility. Hence male sterile plants are **S msms** and normal hermaphrodites are **N MsMs**, **Msms**, or **msms**. The study of the inheritance of male sterility in onion has shown that **msms** forms exist in most commercial varieties, and by using male-sterile **S msms** forms as female parents and crossing them with different hermaphrodite varieties of the constitution **N msms,** male-sterile offspring can be obtained carrying the genes which govern the desirable characters of commercial varieties. In this way male-sterility has been introduced into many onion varieties.

In the cases referred to above, heterosis is described in varietal hybrids. It may also be found in species hybrids, which in addition often show increase in size due to chromosome doubling (see Chapter XIII). Such species hybrids, though intrinsically heterozygous, characteristically breed true, as a result of the chromosomes of the same species pairing (see page 40) and any hybrid vigour evident in the hybrid will then be maintained in the second and following generations.

CHAPTER IX

BUD-SPORTS, VARIATIONS AND FLUCTUATIONS

THE occurrence of somatic or vegetative variations in plants has an especial appeal to the horticulturist, as many varieties of flowers, fruit and vegetables have arisen in this way. The apple Crimson Bramley arose as a bud-sport from Bramley's Seedling, the plums Coe's Violet and Crimson Drop from Coe's Golden Drop, the climbing form of the rose Mrs. W. J. Grant arose from the bush form. In chrysanthemums, dahlias and many other flowers colour-sports are frequent.

Among our cultivated plants vegetative differences are common, but it is often a matter of considerable difficulty to determine their nature. In studying these differences, therefore, it is necessary first of all to differentiate genetic variations, which are the result of some inherent change in the plant itself, from differences which are due to the influence of soil, climate and other environmental causes. In general, differences of the latter class are not heritable and are better termed fluctuations. Next we must consider whether the genetic variations are superficial and confined to the epidermis and outer tissues of the plant, or whether all the tissues are involved; that is to say, are the plants what is known as *periclinal*, *mericlinal* or *sectorial* chimaeras? Thirdly we have to consider the cause of the change, whether due to the loss, gain, mutation of a gene or a number of genes, to the loss of a whole or part of a chromosome, reduplication, or other nuclear or cytoplasmic aberrations. The above questions give rise to many points of practical importance; particularly when it is desired to perpetuate " bud-sports " by sexual or asexual means.

Before discussing in detail examples of somatic variations in plants, a brief description will be given of the investigations of Winkler (1907–14), who was the first deliberately to produce chimaeras. These researches have materially assisted in the elucidation of the peculiar structure of many of our cultivated plants.

GRAFT-CHIMAERAS

Winkler exchanged the main shoots of young plants of different species of *Solanum* by grafting, and after the grafts had united, the plants were cut across at the point of union, as shown in Fig. 44 (the white area representing the stock, and the black area part of the scion). From callus tissue formed on the surface young shoots differentiated. Most of these consisted of uniform tissue of one or other of the species used, but from parts of the surface where the two tissues united, shoots occasionally arose in the formation of which both species—the stock and the scion—had taken part. The chimaeras formed were of different kinds, being either periclinal or sectorial as described by Baur (1908) or mericlinal (Jørgensen and Crane, 1927).

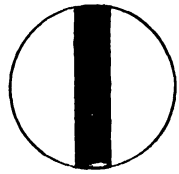


FIG. 44
Cross-section of grafted stock.

A periclinal plant has its interior completely covered by a skin of another type, just as a glove covers a hand. Such an external covering may be one or more cell-layers thick. Fig. 45*a* diagrammatically represents a cross-section of a stem of such a plant. In plants which are entirely periclinal the leaves and fruits are all alike, and when well-marked differences in leaf- or fruit-shape occur, they are to some extent intermediate in shape or colour between those of the two species or varieties of which the plant is composed.

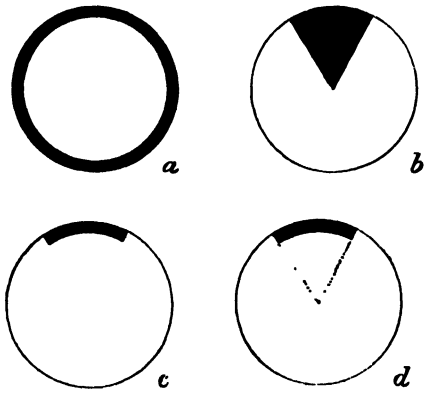


FIG. 45
Cross-sections of different types of chimaeras. *a*, Periclinal; *b*, sectorial; *c* and *d*, mericlinal. (After Jørgensen and Crane, 1927.)

In a sectorial plant a sector or wedge of the stem is composed of tissue of another species or type, see Fig. 45*b*. Such a plant will have three types of leaves and fruits, some of the type of one species, some of the other and a few sectorial. The sectorial leaves and fruits form in the region of the stem where the two tissues meet, the two parts meeting in a longitudinal line. The mericlinal type of chimaera is diagrammatically represented

in Figs. 45*c* and 45*d*. These plants have the external appearance of sectorials and are often confused with sectorials; they are, however, quite distinct and are actually incomplete periclinals. Sectorials in the real sense of the word are of very rare occurrence. The large majority of the variations in plants referred to in the literature as "sectorials" are actually mericlinal variations. Among our cultivated fruits and plants mericlinal variations are quite common. Sometimes the major part of the plant is involved, but often only a shoot or individual flower or fruit, or even a part of a fruit, is concerned. A periclinal chimaera in *Solanum* is shown in Fig. 46.

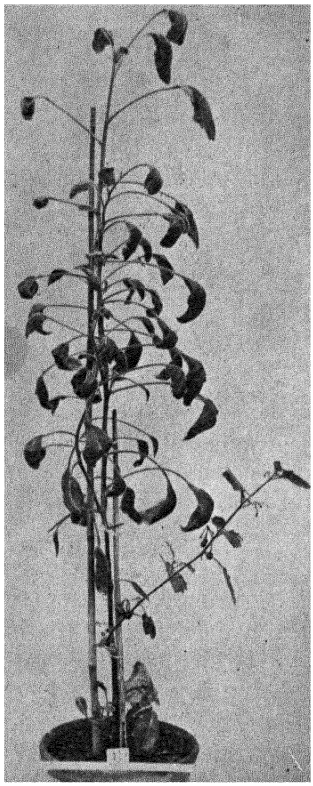
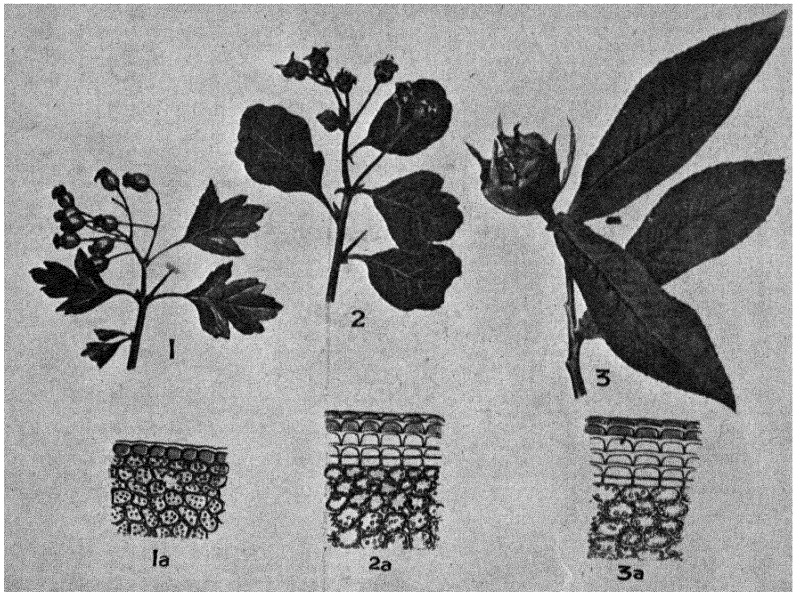


FIG. 46

A periclinal chimaera produced from grafting *Solanum luteum* on the tomato "Sutton's Best of All". The chimaera is composed of two layers of *S. luteum* over a core of tomato. The branch on the bottom right-hand side is pure *S. luteum*. (After Jørgensen and Crane 1927.)

One of the earliest examples of a graft-chimaera is *Cytisus Adami*. According to the records it originated as follows: M. Adam, a nurseryman at Vitry in France, in 1825 bud-grafted the small semi-prostrate *Cytisus purpureus* on to the common Laburnum. From the region of the insertion of the bud a shoot developed which was very different from either *purpureus* or Laburnum. This shoot subsequently produced flowers which in form and colour were intermediate between the two species. The leaves were also intermediate in size. The behaviour of *Cytisus Adami*, in occasionally segregating branches which were entirely Laburnum and others which remain wholly *Cytisus purpureus* for a long period, gave rise to considerable discussion and speculation regarding its origin, and although it was previously suspected by some investigators to be a graft-chimaera it was not until 1910 that Buder

demonstrated that *Cytisus Adami* is a periclinal chimaera with a core of the common Laburnum surrounded by an epidermal layer of *Cytisus purpureus*. Other well-known examples of chimaeras which have resulted from the horticultural practice of grafting are the various combinations of the common Hawthorn and Medlar, the so-called *Crataegomespili*. The best-known forms are *Crataegomespilus Asnieresii* (Fig. 47) and *Crataego-*



1, *Crataegus monogyna*; 2, the periclinal graft-chimaera *Crataegomespilus Asnieresii*; 3, *Mespilus germanica*. (After Baur, 1909.)

mespilus Dardari. These plants are composed of an inner core of the Hawthorn, *Crataegus monogyna*, surrounded by the Medlar, *Mespilus germanica*, and from analogy with other graft-chimaeras, *Asnieresii* appears to have one and *Dardari* two external layers of Medlar.

In the past it has been a matter of considerable debate whether *Cytisus Adami* and the *Crataegomespili* were graft-hybrids in the real sense of the word, resulting from a somatic fusion of the cells of the two components. Some investigators, notably Daniels (1923), still incline to this view. Haberlandt (1926) also originally

considered such a possibility, but following further investigations (1930) he has concluded that *Asnieresii* is a periclinal chimaera, and is prepared to extend this conception to the other forms of *Crataegomespilus*. No graft-chimaera adequately investigated has provided indisputable evidence of nuclear fusion having occurred between the two grafted components.

Among apples a number of graft-chimaeras have been recorded. In the example figured and described by Castle (1914) and composed of the varieties Boston Stripe and Golden Russet, the latter appears unable completely to cover the larger variety Boston Stripe, and in consequence the basal half of the fruits have the character of Golden Russet and the apical half those of Boston Stripe. Other apple graft-chimaeras have been described by Rodway in Tasmania between the varieties Senator and Rome Beauty, and by Stout (1920) in the United States between King and Roxbury Russet. Graft-chimaeras have also been reported in other plants, i.e. pear-quince and rose.

Autogenous Chimaeras

The chimaeras which we have so far discussed have originated from the horticultural practice of grafting, but many of our cultivated plants are chimerical in structure without any process of grafting having been involved. Such *autogenous* chimaeras originate in somatic cells as a result of some natural process by which diverse cells arise and give rise in turn to diverse tissues. Well-known autogenous chimaeras are the albo-marginate forms of *Pelargonium*, which have a green core and white outer layers. Other forms have a white core surrounded by green outer layers. Many plants are amenable to propagation by root-cuttings, and by adopting this method their periclinal structure has been demonstrated. Normally the buds and lateral shoots of plants arise exogenously, consequently asexual propagation of stem or lateral shoots by grafting, budding, layering, cuttings, etc., perpetuates the characters of the variety. In most plants, however, buds from roots which differentiate into shoots to form new plants arise endogenously, i.e. from the internal tissues, therefore, if the interior of a plant differs from the exterior, root-cuttings or any buds or shoots of endogenous origin will give rise to individuals which differ from the type. For example, Bateson (1916–21), experimenting with *Bouvardias*, found that root-cuttings of the pink-

flowered variety Bridesmaid invariably produced the red variety Hogarth. Chittenden (1927) found that plants of endogenous origin raised from the *Pelargonium* Double New Life, a variety with double flowers devoid of anthers, produced plants with single hermaphrodite flowers. Many other plants are known which behave in a similar fashion.

Environmental influences generally affect the whole of the plant, whereas somatic variations when they first appear usually affect a small part only. Asexual reproduction, however, enables even a single bud which differs from the type to give rise rapidly to a plant which differs from the original variety. Somatic differences in the colour of the fruits of apples are common. In the variety Bramley's Seedling two forms occur: (1) the original Bramley's Seedling and (2) Crimson Bramley. In this case the bud-sport, or somatic variant, has received varietal recognition, but between these two forms trees with fruits intermediate in colour intensity commonly occur. The variety Lady Sudeley also has two well-defined forms: (1) the original with a bright yellow ground and almost scarlet stripes, and (2) a paler and slightly russet form. This bud-sport is a sharply discontinuous variation, whereas most colour variations in apples have intermediate forms, or, more correctly speaking, they bear fruits which are only changed in part, the other part corresponding with the original. The variety Gravenstein has given rise to a number of colour variations, viz. Henze's Gravenstein, Koch's Gravenstein, three varieties distinguished respectively as Gravenstein of Palaiser, Hesom and Sabygard, and a Red Gravenstein (Roter Gravenstein). Nebel (1929–30) found all these clonal variations of Gravenstein to have fifty-one chromosomes like the original Gravenstein. In the variety Cox's Orange three colour-forms occur: (1) a yellow ground with the red colour distributed in flecks, which appears to be the original form; (2) a form with the red in stripes; and (3) a form almost entirely red. As far as our observations go, the all-red forms occur only on the red-striped forms, which suggests that the striped condition is an intermediate stage between the two extremes, perhaps of the nature of a mericlinal chimaera. Although they appear to be sectorial chimaeras, the more deeply pigmented sectors occasionally seen on many varieties of apples are doubtless mericlinal variations. They are very common on some varieties, e.g. Gladstone and Feltham Beauty.

The above are clearly examples of somatic variations in apples, and many others could be quoted which involve season, colour, size, shape of fruit, etc. (see for example " Bud Mutations in the Apple ", by Shamel and Pomeroy, 1932, *J. Hered.* 23). In many varieties, however, differences occur which are not so easy to define, but the question may be asked if the wide differences in colour so commonly seen in such varieties as Lane's Prince Albert and Newton Wonder are always due to the influences of soils, root-stocks or other environmental causes. From the nature of the colour differences in these varieties it is highly probable that, in addition to environmental influences, genetic variations are also involved.

A striking variation in the shape of the fruits of apples is described and figured by Carrière (*Revue Horticole*, 1881); it is a normal apple which has a number of pear-shaped fruits. In recent years we have had similar fruits sent to us from a tree in Suffolk, and were informed that the tree invariably carries a number of typically pear-shaped fruits each season. There is but little doubt that by bud selection trees and clones with pear-shaped fruits could be established from this somatic variation. Trees of Blenheim Orange with angular, almost oblong fruits, occur which are widely different in shape from the typical symmetrical fruits of Blenheim Orange. The question may arise as to whether the angular form is a bud-sport from the original Blenheim Orange, or whether it is a different individual, but, with the exception of this difference in fruit shape, the trees are in all details typically Blenheim Orange.

The examples of vegetative variation in apples to which we have so far referred have been concerned with characters which are fairly readily seen, and the question arises as to what extent do apple varieties vary in other respects and in characters not readily discernible to the eye. With respect to the fruits of the variety Gladstone, to which we have previously referred, colour appears to be correlated with a change in flavour. At least we have a decided preference for the fruits with the yellow ground and red flecks, over those of the red somatic variant, both in respect to flavour and texture of the flesh.

It is well known that high- and low-yielding trees frequently occur within one variety, and the possible cause of such differences is often discussed. They have also been the subject of experiment by various investigators. In most cases, as for example in the

experiments carried out by Crandall (1918), Sax (1923) and Rawes (1922), no significant differences in the yield of the clones raised from high- and low-yielding trees occurred. Macoun (1921), however, obtained a significant difference in the average yield, over a period of nine years, of two sets of trees vegetatively raised from the highest and lowest yielding trees in an orchard of the variety Wealthy. In those experiments, where no significant difference in yield occurred, it may be concluded that the differences in the original trees were merely fluctuations due to environmental influences, but Macoun's results at least suggest that a genetic variation affecting the yield of the trees may have been involved. Shamel, Pomeroy and Caryl (1927–29) have shown that unproductive strains of the Washington Navel and Valencia oranges have arisen as bud variations. They state: "The limb and tree variations of the Washington Navel orange that have been strikingly and inherently unproductive have been segregated into three groups: (1) those of very light production, but bearing fruits apparently identical with those of the parent strain; (2) those having a very low production of small, wrinkled fruits; and (3) those bearing somewhat larger crops of rather coarse fruits as compared with the other two groups. These strains are important ones to the Washington Navel orange industry, because the presence of trees of these strains has been proved to be largely responsible for the very low production of several commercial orchards where individual tree studies have been carried on, and it is doubtless the cause of low yields in many other unprofitable orchards." Shamel *et al.* (1933) have also described a low-yielding bud variation in the plum Prune d'Agen, and also bud variations involving differences in the shape, size and time of maturity of the fruit of this variety of plum.

The plums Crimson Drop and Coe's Violet originated as bud-sports from Coe's Golden Drop. Coe's Violet has a pronounced violet line along the suture of the fruit, and Crimson Drop, as its name implies, is crimson and more russet than the type. In Coe's Golden Drop the red colour generally occurs as flecks or spots on the exposed side, and as is common in apples, the bud-sports have an increased and intensified colour. A similar example is the plum Yellow Magnum Bonum which sported a branch bearing red fruits (Darwin, 1882).

In peaches the hairy condition is dominant over the nectarine's glabrous condition, and several sports of peach to nectarine are

well known. On the other hand, the recessive nectarine has been known to sport the dominant peach (Darwin, 1882).

Among numerous other recorded bud-sports in fruits are red currants giving white currants and, more rarely, white giving red. The red currant has also sported a pink form with fruits intermediate in colour between white and red. The peach Grosse Mignonne gave the variety Grosse Mignonne Tardive, which ripens two weeks later. The cherry May Duke has also sported a branch bearing fruit of a more oblong shape, which ripens later

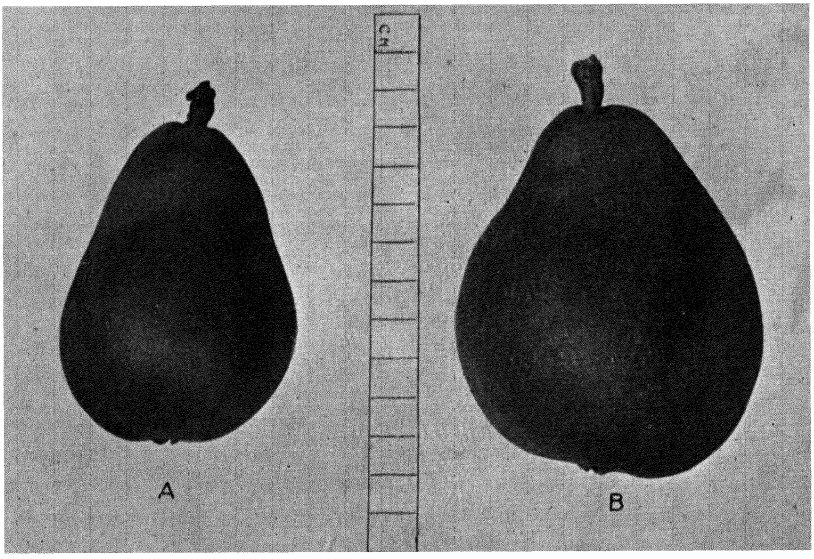
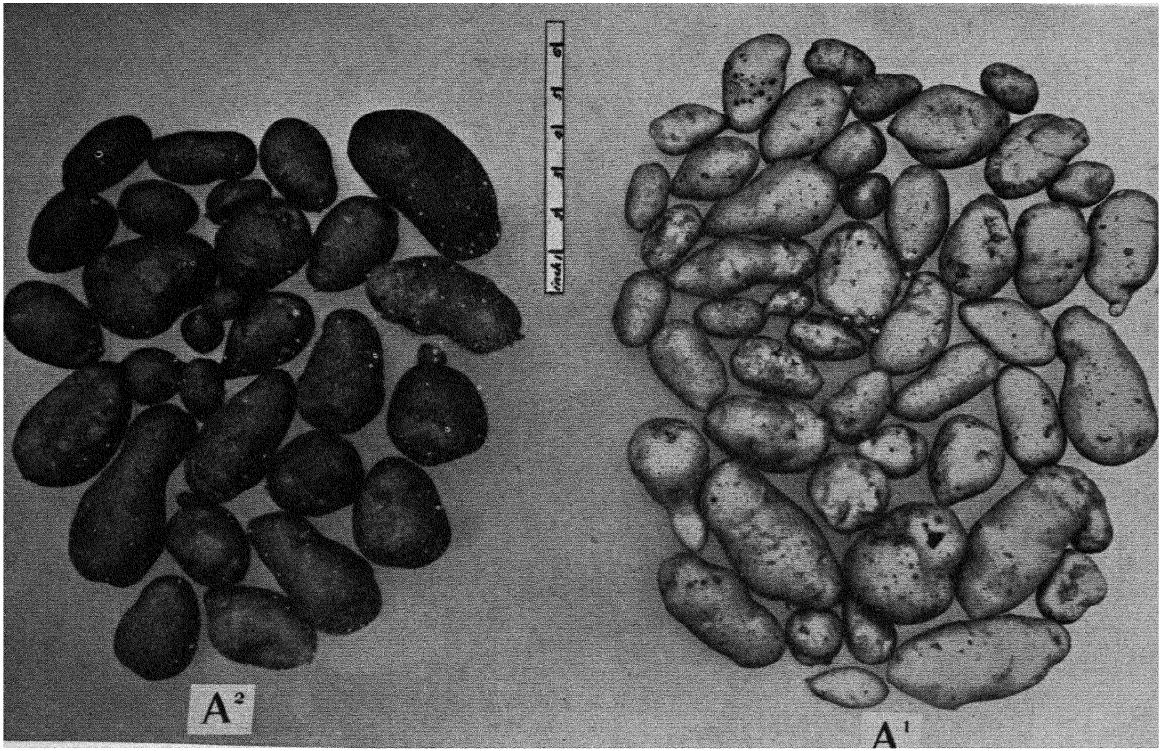


FIG. 48

A = The pear variety Fertility 2n = 34, and " B " its tetraploid bud-sport 2n = 68.

than May Duke. We have also observed striking colour-sports in Late Duke and Archduke. Mr. W. P. Seabrook has recently sent us fruits and flowers of a bud-sport of the pear Fertility which occurred on his nurseries at Boreham, Essex. This sport has much larger fruits than the original variety (see Fig. 48). Our colleague, Dr. P. T. Thomas, has cytologically examined this new giant form of Fertility and found it to be tetraploid 2n = 68. The original Fertility is diploid 2n = 34. Shamel (1937) describes a bud mutation of the pear Winter Nelis which has much larger fruits than the type. This mutation is presumably the result of



Tubers obtained from two halves of one potato of the variety Golden Wonder. A^2, from the control half tuber. All typically Golden Wonder, thick, brown russet-skinned tubers. A^1, from the treated half, eyes removed. All thin, white, smooth-skinned tubers characteristic of the variety Langworthy (after Crane).

a gene change, as it has the same chromosome number, 2n = 34, as the type. In the same publication Shamel also refers to a large-fruited bud mutation of the pear variety Bartlett, which appears to have resulted from somatic chromosome doubling, the type being diploid and the mutation tetraploid.

In potatoes a number of sports are known (see Salaman, 1930 ; and Asseyeva, 1927) ; the latter has experimentally demonstrated the chimerical composition of several varieties. For example, by removing the eyes of the tubers and causing buds to form from internal tissues, Asseyeva found that the American variety Noroton Beauty, which has mottled tubers, gave the variety Triumph, which has self-coloured red tubers ; and the variety Tchugunka, which has blue flowers and purple tubers, gave L'Institut de Beauvais, which has white flowers and white tubers ; just as Bateson found root-cuttings of the pink-flowered *Bouvardia* Bridesmaid gave the red variety Hogarth. Crane (1936) found that the potato " Golden Wonder ", a variety with tubers having a thick brown russet skin, is a periclinal chimaera with a core of the variety " Langworthy " which has tubers with a thin white smooth skin (see Fig. 49). In addition to the russet character of the tubers, these varieties also appear to differ in certain physiological characters. Langworthy is generally considered to give a higher yield, and to be more floury when cooked than Golden Wonder.

Colour-sports in *Chrysanthemum*, *Tulipa*, *Dahlia*, *Coleus* and many other flowers are common. Lawrence (1931) has suggested that some of the colour-sports in *Dahlia* are the result of a chromosomal change. Stout (1915) has shown that new varieties of *Coleus* can be established by the selection of somatic variations. Sports affecting such widely different characters as dwarf-bush and tall-climbing habit are numerous in roses. The tall-climbing form of the rose Mrs. W. J. Grant invariably gives a proportion of the dwarf-bush form when asexually reproduced by budding. From buds taken from the climbing form of this rose we raised thirty-two plants, of which twenty-six were tall-climbing and six dwarf-bush plants. As we have previously mentioned, the sterile diploid *Primula kewensis* sported a fertile tetraploid branch, and a similar increase in chromosome number is easily induced experimentally in the tomato.

Bud-sports affecting the colour of the flower in roses are also common, especially in varieties of dwarf polyanthus. The variety

" Paul Crampel ", which has scarlet flowers, has sported two forms, one having crimson and the other pink flowers. From a chemical examination of the pigments involved, Scott-Moncrieff (1936) found that the normal scarlet flowers were deeply pigmented with pelargonin and some flavone, whereas in the two sports cyanin took the place of pelargonin. The pale pink flowers had a smaller amount of anthocyanin than either the scarlet or crimson flowers, but a proportional increase in flavone content.

The foregoing account of somatic variation in plants is far from complete. Numerous other differences affecting the size and form of flowers and leaves, habit of growth, season of maturity and other characters have been recorded, and only a comparatively few examples of different types have been selected to indicate the variety of characters and the wide range of plants affected by bud-sports.

From a survey of the occurrence and behaviour of somatic variation in plants it appears possible to make the following generalisations : (1) Heterozygous individuals are more likely to show somatic variations than those which are homozygous. (2) The longer and more widely an individual is grown as a clone the greater will be the opportunity for somatic variations to occur. (3) In addition to obvious morphological and external characters, somatic variations may also affect various physiological processes, resulting in differences in yield, fertility, quality and other characters which are not readily discernible. (4) Somatic variations appear to be more frequent in polyploid than in diploid plants. Hence in such genetically complex and vegetatively reproduced horticultural plants as the apple, dahlia, chrysanthemum, etc., it is evident that conditions are favourable for the occurrence of vegetative variations.

In certain variegated plants such as *Abutilon Thomsonii* the variegation is transmissible by vegetative means. In this and similar cases the variegation appears to result from virus infection, and when a normal green scion is grafted on to a variegated stock the variegation is transmitted to the scion. The phenomenon known as " breaking " in tulips, whereby flowers originally self-coloured suddenly become striped or splashed, is also due to infection by virus. Investigations by Cayley (1928) and M'Kenny Hughes (1930–31) show that breaking in tulips is transmissible both by grafting and by insects.

Somatic Variations and Plant Breeding

The reproductive cells of the flowering plants are generally formed from the sub-epidermal cells, and consequently when periclinal plants are fertile their progeny reproduce only the characters of the species or variety of which the sub-epidermal layer is composed. To demonstrate the significance of this to the plant-breeder reference may be made to an experiment of Clausen and Goodspeed (1923). These investigators crossed two varieties of *Nicotiana Tabacum* ; one, purpurea, with carmine flowers, and the other, Cuba, with white flowers. Colour is dominant to white, and the $\mathbf{F}_2$ generation approximates to the dihybrid expectation : nine carmine : three pink : four white. In the $\mathbf{F}_1$ generation 200 plants were raised, and all had carmine flowers except one. This exceptional plant was divided into two portions, one having carmine flowers, and the other light pink flowers. A genetic analysis of the two portions of the chimaera was made by appropriate breeding investigations, and the following summarises the results obtained (Table XXVIII) :

TABLE XXVIII

Parents	Carmine	Pink	White	Total
Carmine selfed . .	8	13	39	100
Pink selfed . .	56	13	31	100
Expectation 9 : 3 : 4 .	*56·25*	*18·75*	*25*	*100*
Back-crosses :				
White × Carmine .	54	29	64	147
White × Pink . .	40	37	72	149
Expectation 1 : 1 : 2 .	*37*	*37*	*74*	*148*

The above results show that the change resulting in the production of the pink-flowered variation, or bud mutation, did not involve the sub-epidermal layer from which the germ-cells—the ovules and pollen—are derived. Plants were raised from stem-cuttings from both portions of the chimaera, and the two clones raised were uniform for carmine and pink flowers respectively. Plants were also raised from root-cuttings of both the carmine and pink clones, and the plants obtained from all produced only carmine flowers.

The fact that, in breeding, the pink flowers behaved in the same way as the carmine flowers, and that the root-cuttings of the pink-flowered sport all bore carmine flowers, proved that the pink

bud-sport was due to a change in the epidermal layer only. Since such variations do not penetrate as far as the germ track they are entirely dependent upon vegetative reproduction for their continuance.

In the same way self-fertilisation of the white-margined *Pelargonium zonale* and other albo-marginate plants with a white sub-epidermis can only produce white seedlings, and plants raised endogenously from root-cuttings are wholly green. Similarly in the reversed condition, green over white plants give all green seedlings when selfed, and plants raised from root-cuttings are wholly white. Occasionally a variegated or exceptional white seedling occurs, and is attributable to an incomplete periclinal condition of the parent. McIntosh (1927) states that the russet character of the tubers of Golden Wonder and certain other varieties of the potato is not inherited. This behaviour is explicable on the assumption that they are periclinal chimaeras and that the russet character is genetically confined to the outer layer. Breeding results show that the Pink Currant is also a chimaera of this kind, as a family of thirty-six plants which we raised from selfing this variety all had yellowish white fruits similar to certain varieties of the so-called white currant.

In many fruits and flowers bud-sports with an intensification of colour are fairly common. If such an intensity is the result of a change in the epidermal layer only, it would not be inherited and passed on to its offspring. Should, however, the change be associated with the second or sub-epidermal layer it would be inherited.

Fluctuating Characters

As we have already indicated, fluctuations affect many characters, and are often liable to be confused with variations. Investigations have shown that in fruits the rootstock alone markedly influences such widely different characters as colour of fruit, size of tree, habit of growth, season of maturity and period of flowering (Hatton and Grubb, 1926; Rogers, 1927; Hatton, 1930).

The investigations of Kikuchi (1930) on the skin colour of the Japanese pear bear upon the problem to which the occurrence of fluctuating characters gives rise. According to this author, the surface of the fruit of the Japanese pear can be classified into four

groups as follows : (1) the constant russet-brown, (2) modifiable russet-brown, (3) intermediate and (4) pure green. The constant russet-brown varieties always remain russet-brown, but the modifiable varieties fluctuate according to conditions. Under dry conditions of climate the russet character of these latter varieties is less pronounced than it is under moist conditions. Kikuchi found that the russet character in these fruits is determined by two genes which he designated **R** and **I**, and it may be significant that the modifiable forms proved to be the double heterozygous type **RrIi**. The other three forms are not affected by climatic conditions, and are all homozygous for at least one, and some for both pairs of factors.

In many varieties of apples the degree of russetness fluctuates widely, and it may be that such varieties are heterozygous, and that the real russet varieties such as Golden Russet are less heterozygous or even homozygous for the factors concerned. One is further led to reflect on the possibility of a similar heterozygous constitution being involved in other fluctuating characters ; and if so, whether this may not account for the greater response of some varieties to the influence of a certain type of soil or of a particular rootstock than others.

Often the height and habit of plants and the colour of flowers and fruits is influenced by temperature and other climatic conditions. It is a common observation that a cool temperature intensifies colour, whereas in a high temperature the colour of many flowers is lessened. For example, the delicate pink varieties of *Primula sinensis* have moderately deep-pink flowers when grown in a cool greenhouse, but the flowers are much paler when grown in considerable heat.

The normal conditions of soil and climate are more favourable to the growth of certain plants in some localities than in others, and in many cases horticultural operations such as thinning, disbudding, manuring, etc., increase the size of flowers, fruits and vegetables far beyond their normal size. Such enhanced size is, however, entirely dependent upon the continuance of the cultural operations and conditions, and when these are withheld the plants soon revert to their normal size and characteristics.

NOTE.—Recently our colleague, Mr. E. Marks, has found that the tetraploid pears " Fertility " and " Bartlett ", described on page 178, are periclinal chimaeras, the epidermal layer being diploid and the inner tissue tetraploid. Einset *et al.* (1947, *J. Hered.* 38 : 371-376) have examined a number of tetraploid bud-sports in apples and found some were like the above pears with only the epidermal layer diploid and others with two or more outer layers diploid.

CHAPTER X

INCOMPATIBILITY

THE occurrence of sexual incompatibility is widespread throughout the plant kingdom, and is due to the failure of the pollen, although functional, to grow down the style and effect fertilisation. The horticulturist who is concerned with the sexual reproduction of plants, for example the seedsman and plant-breeder, is in some respects more affected by the occurrence of incompatibility than are the nurseryman and fruit-grower, whose interests lie mainly in the asexual reproduction of plants. Nevertheless the frequent occurrence of incompatibility in fruit trees has seriously to be considered by the fruit-grower, for although fruit trees are invariably reproduced by vegetative means, the fruit itself results from the sexual process. Indeed, the practical problems to which incompatibility gives rise are often more acute in plants subjected to wide vegetative reproduction than in those raised sexually. For example, in the sweet cherry self-incompatibility is the rule and cross-incompatibility common. Such widely grown and important commercial cherries as Early Rivers, Black Eagle, Knight's Early Black, Bedford Prolific and Baumann's May are completely self- and cross-incompatible. That is to say, the pollen of any one of these varieties is unable to fertilise its own ovules, or the ovules of any of the varieties mentioned, and since the formation and development of the fruit is dependent upon fertilisation the young unfertilised fruits fall from the trees at a very early stage. A knowledge of suitable varieties to interplant so as to provide for effective cross-pollination is therefore of paramount importance to the practical man.

Self-incompatibility is frequently referred to as self-sterility and cross-incompatibility as cross-sterility. It may be pointed out, however, that when dealing with incompatibility we are not concerned with sterility in the strict sense of the word, as in the former case both the pollen and the ovules—or at least a good proportion of them—are functional. The failure to obtain fruit

or seed from self- or cross-incompatible pollination is due to the arrest of pollen-tube growth in the stylar tissue. Hence the pollen tubes fail to reach the ovary and fertilisation cannot take place. On the other hand, in compatible pollinations, although the same pollen and ovules (in different combinations) may take part, the pollen tubes travel the full length of the style, the male and female nuclei fuse, and the fertilised ovaries develop fruit and seeds.

The terms " self-sterile " and " cross-sterile " are thus better confined to sterility which arises from defective pollen and ovules, and other aberrations as described in a later chapter.

The phenomenon of incompatibility has long attracted the attention of biologists. East (1929) states: " The somewhat cursory examination of the literature that I have made has yielded a list of 176 self-sterile species, representing fifty-five families and including both monocotyledons and dicotyledons ". Correns (1912–13), working with *Cardamine* and *Linaria*, first applied the methods of genetic analysis to the problem. He was followed by a number of investigators, amongst whom East and his collaborators (1925–26) working with *Nicotiana*, Lehmann (1926) with *Veronica*, and Sirks (1926) with *Verbascum*, after many years of extensive experiments arrived independently at conclusions which are fundamentally the same.

The above investigators' experiments have shown that incompatibility is determined by genes, just as are morphological characters, and following East's terminology these genes designated by the letter **S** form a multiple allelomorphic series, $\mathbf{S}_1$, $\mathbf{S}_2$, $\mathbf{S}_3$, etc. As in the case of other allelomorphs, any two of the above may be carried by a given plant. The essential feature of the genetic behaviour of incompatibility is that pollen cannot function in the style of a plant carrying the same incompatibility factors as the pollen. " Like repels like." Self- and cross-pollination between individuals with the same genetic constitution with respect to incompatibility factors fail because either the pollen tubes grow so slowly that in normal cases they are unable to reach the ovules in time to effect fertilisation, or the growth of the pollen tubes is inhibited in the nutrient stylar tissue. Consequently groups of individuals occur within which all cross- and self-pollinations fail. In Fig. 50 we have diagrammatically illustrated the behaviour of incompatibility in diploid plants. Thus an individual of the constitution $\mathbf{S}_1\mathbf{S}_2$ cannot be fertilised by $\mathbf{S}_1$ or $\mathbf{S}_2$ pollen (Fig. 50*a*). On the other hand, in the cross $\mathbf{S}_1\mathbf{S}_2 \times \mathbf{S}_3\mathbf{S}_4$

both S_3 and S_4 pollen can penetrate the style of the mother and effect fertilisation (Fig. 50*c*). The offspring from such a cross will consist of four intra-sterile inter-fertile groups of the constitution S_1S_3, S_1S_4, S_2S_3 and S_2S_4. When a plant carrying S_1S_2 is pollinated with an S_1S_3 individual (Fig. 50*b*), the S_3 pollen alone functions and fertilises the S_1 and S_2 ovules of the female plant, to give rise in the next generation to two intra-sterile inter-fertile groups of plants of the constitution S_1S_3 and S_2S_3. In this cross the S_1 pollen fails to function because the mother plant also carries S_1. The S_1S_3 group will be reciprocally incompatible with the male parent as they are of the same genetic constitution with

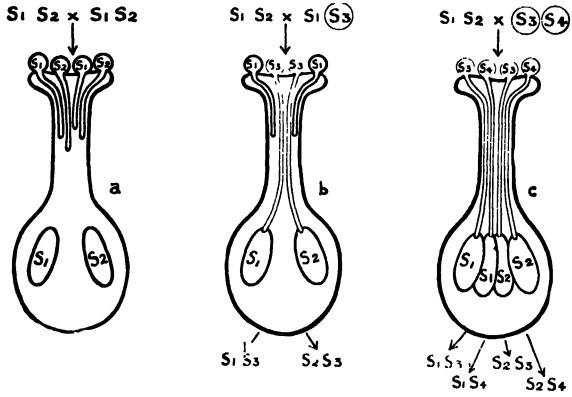


FIG. 50

Diagram of pollen-tube growth in compatible and incompatible pollinations. (After Crane and Lawrence, 1929.)

respect to these physiological incompatibility factors. All other combinations between parents and F_1 will be compatible.

Previous to this genetic interpretation of incompatibility, Prell (1921), in a paper surveying the published work of others, had suggested a solution which closely accorded with the facts, but as a result of their extensive investigations in *Nicotiana* East and his collaborators were the first to provide conclusive evidence and advance a genetic interpretation of incompatibility. Brieger and Mangelsdorf (1926), also investigating *Nicotiana*, found a unique example of linkage between C, a colour factor, and incompatibility factors. Their work substantiates the validity of East's interpretation.

Knowledge of the interrelation of self-compatibility and self-incompatibility is not so extensive, but East and Yarnell (1929-30)

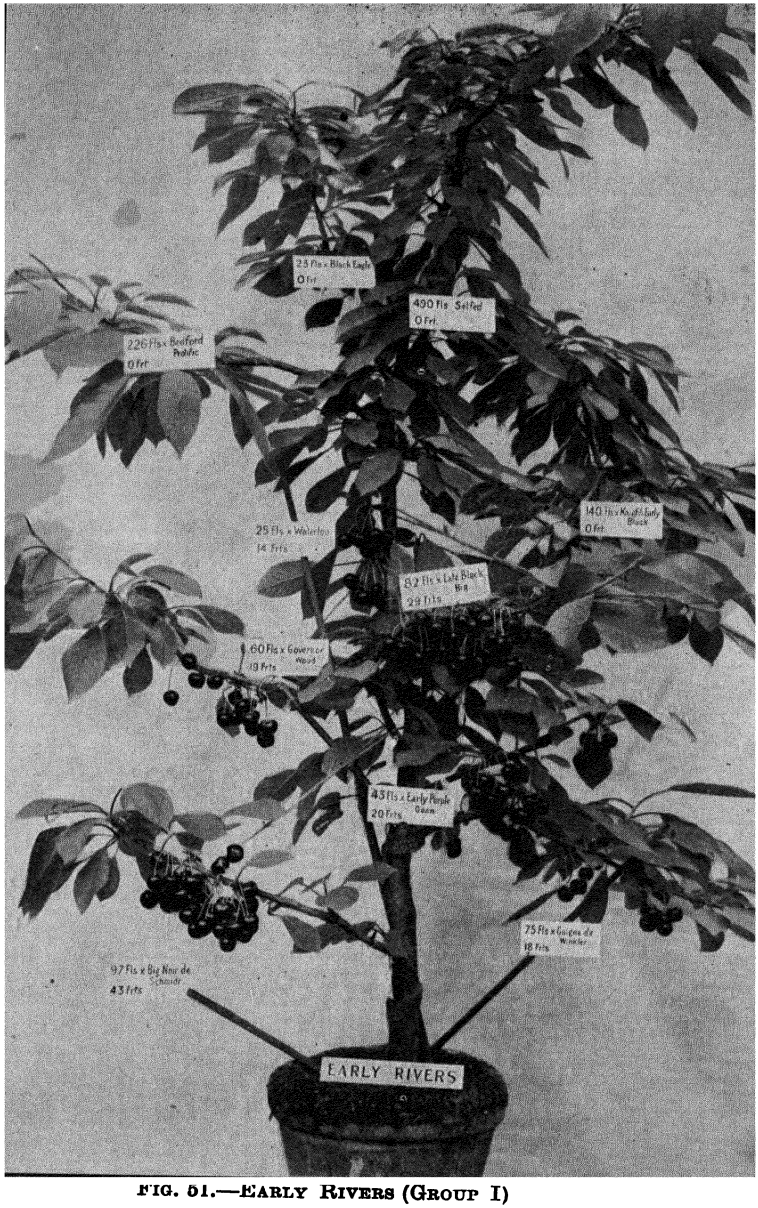


FIG. 51.—EARLY RIVERS (GROUP I)

(At top of tree) 490 flowers self-pollinated, no fruit set. 226 flowers × Bedford Prolific (Group I), no fruit set. 23 flowers × Black Eagle (Group I), no fruit set. 140 flowers × Knight's Early Black (Group I, no fruit set. (Bottom of tree) 82 flowers × Late Black Big., 29 fruits set. 25 flowers × Waterloo, 14 fruits set. 60 flowers × Governor Wood, 19 fruits set. 43 flowers × Early Purple Gean, 20 fruits set. 97 flowers × Big. Noir de Schmidt, 43 fruits set. 75 flowers × Guigne de Winkler, 18 fruits set. A few of the matured fruits had fallen from this tree before it was photographed. (After Crane, 1925.)

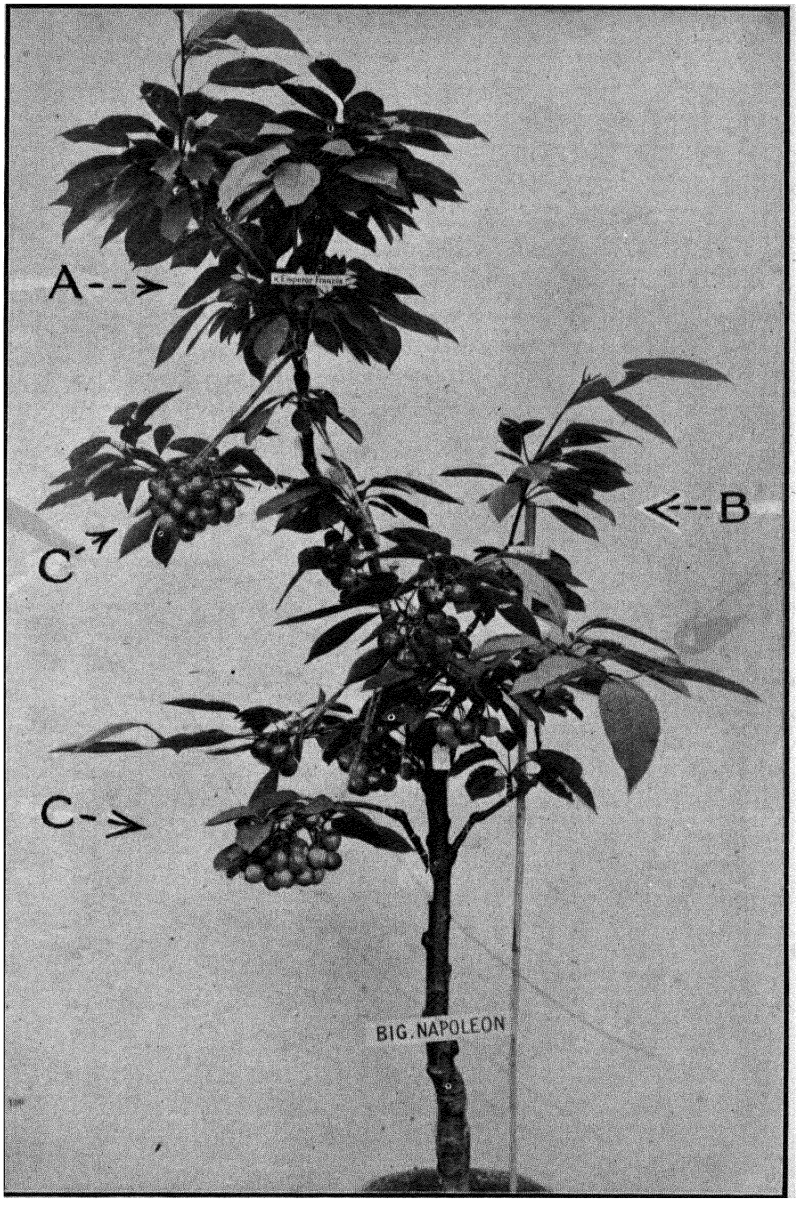


FIG. 52.—BIG. NAPOLEON (GROUP III)

A = 258 flowers pollinated with Emperor Francis, no fruit set. B = 34 flowers self-pollinated, no fruit set. C = compatible pollinations, 154 fruits matured from 273 flowers pollinated, i.e. 86 flowers × Guigne de Winkler, 42 fruits set; 37 flowers × Big. de Schrecken, 19 fruits set; 36 flowers × Roundell, 19 fruits set; 60 flowers × Belle d'Orleans, 41 fruits set; 54 flowers × Early Purple Gean, 33 fruits set. (After Crane, 1926.)

have shown that in *Nicotiana* there is a fertility factor S_f which is a member of the allelomorphic series. Plants having the constitution S_fS_x, where S_x is any other factor of the series, such as S_1, S_2 or S_3, will be self-compatible. Such plants, though heterozygous for incompatibility factors, will on selfing only give self-compatibles of the constitution S_fS_f and S_fS_x; self-incompatibles S_xS_x fail to appear owing to the inhibition of S_x pollen. Following the same scheme self-compatibles crossed with self-incompatibles will give both self-compatibles and self-incompatibles in the proportion of 1 : 1 or 2 : 1 according to the constitution of the self-incompatible plants used. For example, as shown below, $S_fS_1 \times S_2S_3$ would give equality and $S_fS_1 \times S_1S_2$ two self-compatibles to one self-incompatible.

$S_fS_1 \times S_1S_2$

	S_1	S_2
S_f	S_1S_1	S_fS_2
S_1	fails	S_1S_2

$S_fS_1 \times S_2S_3$

	S_2	S_3
S_f	S_fS_2	S_fS_3
S_1	S_1S_2	S_1S_3

Anderson and De Winton (1931), also working with *Nicotiana*, found another allelomorph S_f which is able to inhibit the pollen tubes carrying the S_1 factors. In *Antirrhinum* and *Petunia* there is a dominant self-fertility gene. In *Antirrhinum* it is not allelomorphic with the incompatibility genes of the S series, and in *Petunia* (Tseng, 1938) the present evidence is not sufficient to show whether it is allelomorphic or independent. The physiological action of independent genes often modifies the action of the S genes and gives rise to complications, and in some plants the hereditary behaviour of incompatibility seems not to be subject to simple interpretation. For example in *Brassica oleracea capitata* Kakizaki (1930) concludes that in addition to inhibitory genes of the *Nicotiana* type, genes stimulating pollen-tube growth also occur, and he postulates a theory which involves an allelomorphic series of inhibiting genes S_1, S_2, etc., and another series of stimulating genes T_1, T_2, etc. The S series is epistatic to the T series, but T in double dose is more active than S in single dose. Thus a pollen-tube carrying an S gene which is also present in the style in heterozygous condition, is compatible if it also carries a

T gene for which the style is homozygous. However, in most of the plants so far investigated, self- and cross-incompatibility conform to the oppositional factor hypothesis described in *Nicotiana*, and as we discuss later, certain plants which originally appeared not to be in agreement with the scheme fall into line when their polyploid constitution is considered.

The studies of numerous investigators have shown that the physiological basis of incompatibility in the higher plants is the relation between the male gametophyte and female sporophytic tissue. The precise time at which the incompatibility reaction occurs varies with different species. This is presumably due to the reaction occurring in different parts of the female structure, e.g. stigma, style, integuments. Sears (1936) made the following classification according to when the inhibition of pollen-tube growth or the incompatibility reaction occurs.

Group I. Before the pollen germinates. *Brassica oleracea, Raphanus sativus. Pelargonium hortorum, Secale cereale.*

In these plants the germination of the pollen is suppressed, or a few tubes may be produced but their growth is inhibited soon after they penetrate the style.

Group II. While the pollen is growing in the style. *Petunia violacea, Abutilon hybridum, Nicotiana Sanderae, Linaria reticulata, Nemesia strumosa, Tolmiea Menziesii.*

In these plants the incompatible pollen tubes are arrested in the stylar tissue, some only penetrate a short distance, but others grow nearly to the bottom of the style. In *Nemesia* a few tubes may reach the ovary and their tips protrude into the ovarian cavity. In *Tolmiea*, a few ovules are fertilised, but Sears states that the number fertilised is too small to prevent abscission of the ovary.

Group III. When the pollen-tube reaches the ovary. *Gasteria verrucosa.*

In this plant incompatible tubes grow as fast as compatible tubes and effect fertilisation, but the incompatibly fertilised ovules

degenerate at the same time as unfertilised ovules. According to Sears, self-incompatibility of this type is rare in the plant kingdom. Ledeboer and Rietsema (1937) have described a case of sterility in currants which seems to be very similar to the *Gasteria* type.

Not only does the incompatibility reaction vary with different species but it is greatly affected, within a species, by temperature. Whereas higher temperature increases the growth rate of compatible pollen-tubes, it decreases the growth rate of incompatible tubes (Lewis, 1942; Modlibowska, 1945). This shows that the incompatibility reaction is not merely due to a lack of some growth substance but is due to a positive chemical reaction between the pollen and style. Furthermore the actual place in the style where pollen-tubes stop growing can be shifted by temperature; thus the differences between the three groups given above are probably differences in strength of reaction and not localisation of the reaction to different parts of the style.

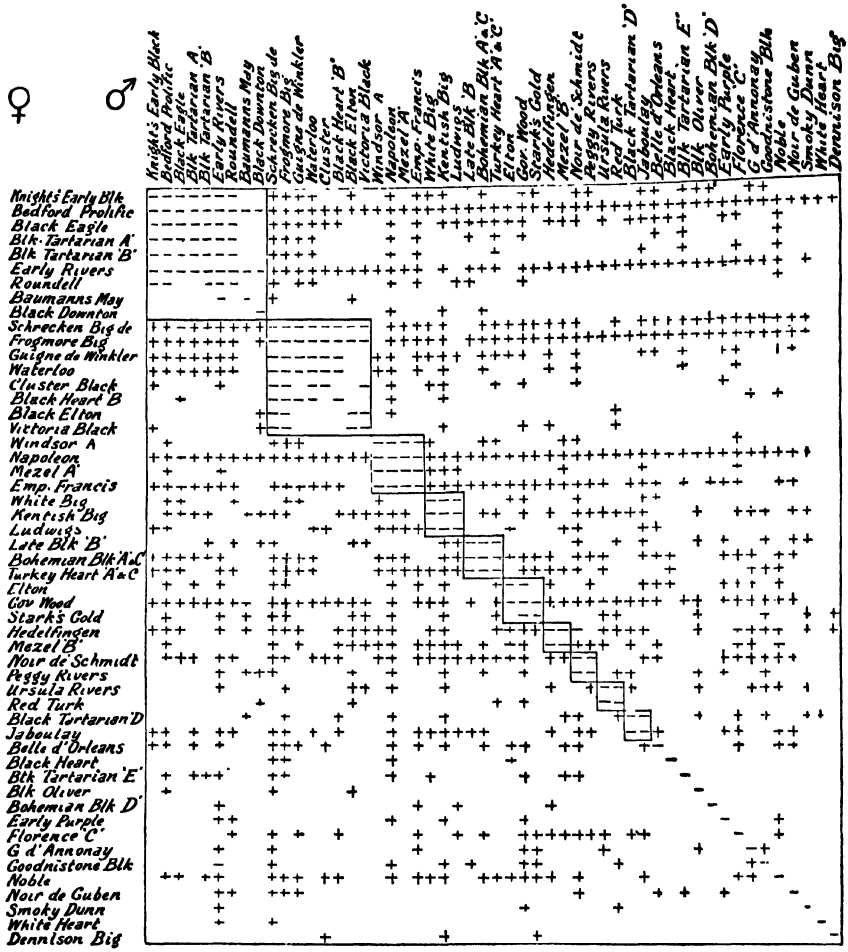
Incompatibility has been the subject of investigation in many horticultural plants. In addition to the plants already mentioned, it has been reported upon, amongst others, by Andersson-Kotto (1931) in *Dianthus*, Lawrence (1931) in *Dahlia*, Kakizaki (1930) in *Brassica*, Compton (1912–13) in *Reseda*, Stout (1918–21) in *Cichorium*, *Lilium* and *Hemerocallis*, Moore (1917) in *Tradescantia*, Terao (1923), Yasuda (1929) in *Petunia*, Tuft and Philps (1922) in almonds, Riley (1935) in *Nemesia*, Schuster (1924) in filberts and by numerous investigators in plums, cherries and apples.

In a series of publications, Crane (1923–25–26–27), Crane and Lawrence (1929–30*a* and *b*, 31*a*), we have reported upon the occurrence and behaviour of incompatibility in cherries, plums and apples. In the sweet cherry, *Prunus avium*, all the varieties we have tested have proved to be self-incompatible, and the majority of our established varieties we have found to belong to groups within which all self- and cross-pollinations fail (see Figs. 51 and 52). The varieties and the incompatible groups to which they belong are detailed in Table XXIX. The positive sign + shows the compatible and the negative sign — the incompatible combinations.

Since Table XXIX was prepared we have carried out further investigations and the following varieties have been added. Group I: Black Circassian, Carnation, Leicester Black and Ronald's Heart. Group II: Merton Bigarreau, Semis de Burr

and Windsor. Group III: Ohio Beauty. Group IV: Late Amber, West Midlands Bigarreau and Yellow Spanish. Group

TABLE XXIX



Self and Cross Incompatibility in Cherries.

+ = Compatible — = Incompatible Pollinations.

VI: Early Amber, Merton Heart and Turkish Black. Group VII: Bradbourne Black and Hooker's Black. Group IX: Red Cluster. Group X: Ramon Oliva. Cryall's Seedling and Guigne d'Annonay are co-incompatibles and belong to a new group, i.e. Group XI.

The gross totals of (*a*) self-pollinations, (*b*) cross-incompatible pollinations and (*c*) cross-compatible pollinations made between the varieties in Table XXIX and the results obtained are summarised on Table XXX.

TABLE XXX

CHERRIES : SUMMARY OF POLLINATIONS

	No. of Flowers pollinated	No. of Fruits set	Percentage set
Self-pollinations . .	34,717	36	0·10
Cross-incompatible pollinations	30,873	48	0·15
Cross-compatible pollinations	96,671	24,977	26·06

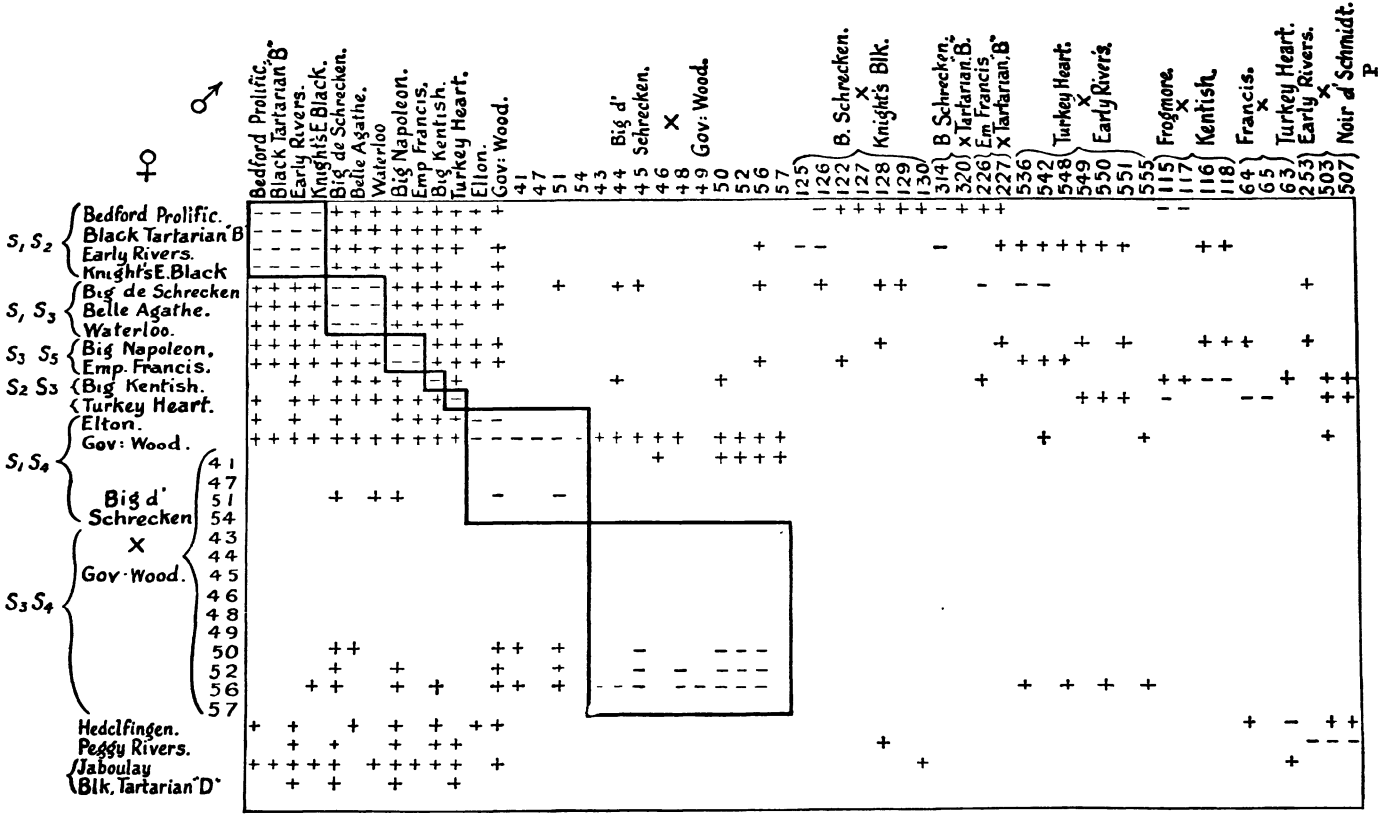
In this and all subsequent summaries " number of fruits set " means the number which reach maturity.

As shown in Table XXX, a few fruits have been obtained both from selfing and from cross-incompatible pollinations. We have evidence that in the incompatible combinations as a rarity a pollen tube travels the full length of the style and effects fertilisation. This would account for the occasional fruits which have been obtained from incompatible combinations.[1]

Breeding results with cherries accrue slowly, but as far as our results go they are in agreement with the genetic interpretation previously detailed. For example, when we crossed two varieties possessing one factor in common, namely Bigarreau de Schrecken (S_1S_3) with Governor Wood (S_1S_4), we found that the immediate offspring consisted of two intra-sterile inter-fertile groups, one of which fails with its male parent, Governor Wood, as shown in Table XXXI. The results obtained both in established varieties and in their offspring indicate that in the sweet cherry incompatibility is an orderly phenomenon, general throughout the species, and always reciprocally expressed ; that is to say if A fails with B, it follows that B will also fail when pollinated with A.

[1] In certain self-incompatible forms of *Nicotiana* East has obtained some seeds from pollinating flowers in the bud stage and also from flowers late in the season of growth, from self-pollinations. Such seeds give rise to plants either of the same genetic constitution as the parent, e.g. S_1 S_2, or homozygous plants, e.g. S_1 S_1 or S_2 S_2. Those of the same constitution reciprocally fail with the parent. The homozygous derivatives are effective when used as females, but fail when used as males in pollinations with the parent. This phenomenon was called " pseudo-fertility " by East and Park (1917) and presumably it occurs as a rarity in the sweet cherry.

TABLE XXXI


♀
♂
Bedford Prolific.
Black Tartarian 'B'
Early Rivers.
Knight's E. Black.
Big de Schrecken.
Belle Agathe.
Waterloo
Big Napoleon.
Emp Francis.
Big Kentish.
Turkey Heart.
Elton.
Gov: Wood.
41
47
51
54
43
44
Big d'
45
Schrecken.
46
×
48
Gov: Wood.
49
50
52
56
57
125
126
B. Schrecken.
122
×
127
Knight's Blk.
128
129
130
B Schrecken.
314
× Tartarian B.
320
Em Francis
226
× Tartarian 'B'
227
536
542
Turkey Heart.
548
×
549
Early Rivers.
550
551
555
Frogmore
115
×
117
Kentish.
116
118
Francis.
64
×
65
Turkey Heart.
63
Early Rivers.
253
×
503
Noir d' Schmidt.
507
P
S1 S2
Bedford Prolific.
Black Tartarian 'B'
Early Rivers.
Knight's E. Black
S1 S3
Big de Schrecken
Belle Agathe.
Waterloo.
S3 S5
Big Napoleon.
Emp. Francis.
S2 S3
Big Kentish.
Turkey Heart.
S1 S4
Elton.
Gov: Wood.
Big d' Schrecken
S3 S4
×
Gov: Wood.
Hedclfingen.
Peggy Rivers.
Jaboulay
Blk. Tartarian 'D'

Plums and Damsons

The results of our investigations at Merton show that we can conveniently classify our varieties of the domestic plum as follows :—

(1) The varieties which are completely self-incompatible and which entirely fail to set fruit with their own pollen, namely :

Allgrove's Superb	Late Orange
Bryanston Gage	Late Orleans
Coe's Golden Drop	Mallard
Coe's Violet	McLaughlin's Gage
Comte d'Althan	Old Greengage
Crimson Drop	Pond's Seedling
Decaisne	President
Early Greengage	Primate
Frogmore Damson	Prune d'Agen
Grand Duke	Transparent Gage
Jefferson	White Damson
Kirke's Blue	Yellow Magnum Bonum

(2) Those varieties which are only partially self-compatible and are incapable of producing a satisfactory crop with their own pollen. In this class there is considerable variation ; some set very few fruits, while others set a moderate crop when selfed, but all produce heavier yields when crossed with compatible varieties. The following are varieties in this class :

Belgian Purple	Early Orleans
Blue Rock	Farleigh Damson
Cambridge Gage	Reine Claude Violette
Cox's Emperor	Rivers' Early Prolific
Early Favourite	Utility

(3) Those varieties which are completely self-fertile and which develop full crops when self-pollinated :

Blaisdon Red	Monarch
Czar	Oullin's Golden Gage
Denniston's Superb	Pershore
Early Mirabelle	Prince of Wales
Early Transparent	Prosperity
Gisborne's	Prune Géante
Golden Transparent	Purple Pershore
Goliath	Reine Claude de Bavay
Guthrie's Late	Victoria
King of the Damsons	White Magnum Bonum
Laxton's Gage	

The following are the only cross-incompatible pollinations we have found in established varieties of plums :

Group I	Group II	Group III
Allgrove's Superb	Late Orange	Blue Rock
Coe's Golden Drop	President	Rivers' Early Prolific
Coe's Violet	Cambridge Gage	
Crimson Drop	Old Greengage	
Jefferson		

The varieties in Group I are completely self- and cross-incompatible. Late Orange and President in Group II are reciprocally incompatible, but they set a full crop when pollinated by Cambridge Gage and Old Greengage. Cambridge Gage and Old Greengage, however, fail when pollinated by President and Late Orange. Rivers' Early Prolific when pollinated by Blue Rock sets a full crop of fruit, but from the reciprocal pollination only a small proportion of fruit is obtained.

The total results we have obtained from pollinations in the above varieties of plums are summarised in Table XXXII, and examples of incompatibility and compatibility are shown in Figs. 53, 54 and 55.

TABLE XXXII

PLUMS : SUMMARY OF POLLINATIONS

	No. of Flowers pollinated	No. of Fruits set	Percentage set
Incompatibles—selfed .	26,169	30	0·1
Incompatibles—crossed .	9,289	34	0·3
Partial compatibles—			
Selfed	45,716	1,072	2·3
Crossed	3,471	84	2·4
Compatibles—selfed . .	39,034	8,360	21·8
Compatibles—crossed . .	60,586	17,415	28·7

It will be observed that, compared with the sweet cherry, not only are the results in plums much more complex, but fewer groups occur, and those found include self-incompatible, self-compatible, partially self- and cross-compatible, cross-compatible, cross-incompatible and reciprocal differences involving both partial and complete incompatibility. The degrees of fertility, reciprocal differences and the complexity of the results in plums are undoubtedly due to their hexaploid constitution and manner of

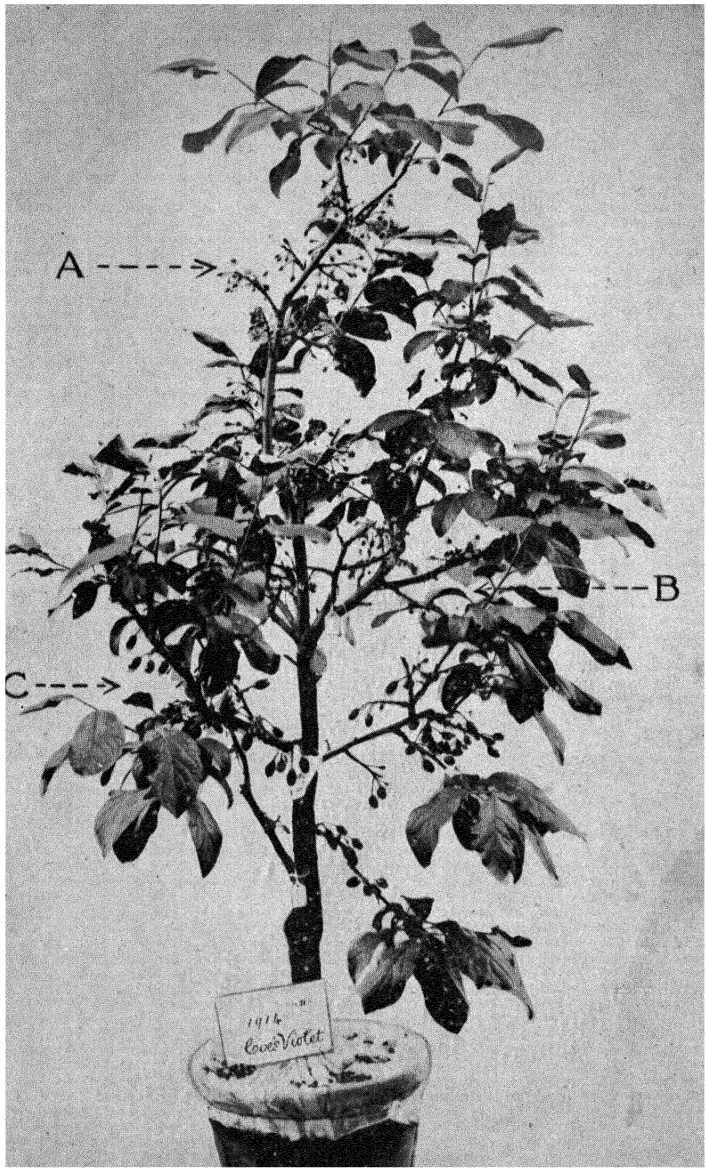


FIG. 53.—COE'S VIOLET

A = pollinated with Jefferson. B = self-pollinated. C = pollinated with Bryanstone Gage. About four weeks after pollination, showing that the fruits pollinated with Bryanstone are larger than the others. Note the primary development of the fruits which were self-pollinated, and cross-pollinated with Jefferson. (After Crane, 1926.)



FIG. 54.—COE'S VIOLET

The same tree as Fig. 52 at a later stage, showing the final result; fruit only on the branches cross-pollinated with Bryanstone Gage. Nothing set with own pollen, nor with the pollen of Jefferson. (After Crane, 1926.)



FIG. 55.—VICTORIA PLUM, SELF-POLLINATED

Number of flowers on tree, 609. Number of fruits set and matured, 196 = 32 per cent. (After Crane and Lawrence, 1929.)

chromosome pairing. In a diploid, such as the sweet cherry, each gamete carries but one incompatibility factor, and no plant produces more than two types of gametes. In a hexaploid, however, each gamete may carry three incompatibility factors, and the number of gametic types will be greatly increased. A greater variability in the behaviour of incompatibility is therefore to be expected in polyploid plants, and the chances of individuals of similar constitution meeting to form incompatible groups is correspondingly lessened. An examination of our results shows that incompatibility is not so common in the hexaploid plums as in the diploid cherries, and even less frequent in the even more complexly polyploid apples.

The different results which occur in certain reciprocal pollinations in plums are undoubtedly directly attributable to their polyploid constitution, and to the multiplicity of the factors concerned. For example, taking plants less complex than plums, namely two tetraploid plants of the constitution $S_1S_1S_2S_3$ and $S_1S_1S_2S_2$, it is probable that they would present different inhibiting effects to S_2S_3 pollen, and it is conceivable that the plant carrying S_3 might be effective when used as male, whereas in the reciprocal cross the gametes of the male, since they do not carry any factors different from those of the female, might be expected to fail.

Apart from these more numerous relationships of the S genes in polyploids than in diploids, some entirely new effects have been found in auto-polyploids. For example, the tetraploid form of the Pear variety Fertility is self-compatible; Fertility $2x \times 4x$ is compatible, while the reciprocal cross is incompatible (Crane and Lewis, 1942). In tetraploid Petunia a similar condition has been found by Stout and Chandler (1942). Tetraploids of *Oenothera organensis* are not completely self-compatible but they have a much weakened incompatibility, as shown by their long pollen tubes. This breakdown of incompatibility has been analysed in these species by Lewis and Modlibowska (1942), Lewis (1943) and has been found to be due to the competitive interaction of two different S alleles in the same pollen-grain. Thus S_1S_2 pollen is compatible, while S_1S_1 and S_2S_2 pollen is incompatible in an $S_1S_1S_2S_2$ style. All pairs of S alleles, however, do not behave in this way. Certain combinations, e.g. S_2S_3, in pollen-grains are not compatible in a style carrying both these alleles, and in these cases one allele may be dominant over the other in such a way

that S_2S_3 pollen is compatible in an $S_1S_1S_3S_3$ style but is incompatible in an $S_1S_1S_2S_2$. Thus in this case the S_2 allele is dominant over the S_1.

Incompatibility in polyploids, already complex as a result of the multiplicity of genes, is complicated still further by these new effects which are peculiar to the diploid pollen-grain.

Verbascum

The work of Sirks (1926) on *Verbascum phoeniceum* may be mentioned here. Sirks' results could not be directly explained by the oppositional-factor hypothesis, so he put forward a modification of the theory whereby S_1 pollen was incompatible with S_1 or S_2 styles but S_2 pollen functioned in S_1 styles. Although Sirks' scheme explained the facts quite well, Lawrence (1930) pointed out that a duplicate factor scheme gave an even better fit. Multiple series of duplicate factors would be expected in an allotetraploid. Comparison between the chromosome numbers of *Verbascum phoeniceum* and twelve other species of *Verbascum* show that *phoeniceum* is a tetraploid; and the behaviour of its chromosomes at meiosis strongly suggests that it is an allotetraploid. With autosyndetic pairing, each gamete would carry two incompatibility genes which may be denoted as **S** and **Z**, and on the assumption that only pollen will function which carries one or two genes unrepresented in the female sporophyte there is a good agreement between theory and results. Thus S_1 fails in an S_1 or Z_1 style but S_2 or Z_2 grows down an S_1 or Z_1 style.

APPLES

We have investigated over fifty varieties of apples, and among them varying degrees of incompatibility occur. The results we have obtained from self-pollinations are detailed in Table XXXIII.

The results we have obtained from a number of cross-pollinations are summarised in Table XXXIV, page 204. Only two varieties have entirely failed upon selfing and four on crossing. The imperceptible gradations of compatibility which occur in apples are at the present time beyond a detailed analysis, but nevertheless the results present features of genetical interest. It may be recalled that recent cytological studies have shown that our cultivated apples and pears have an exceptionally complex

TABLE XXXIII

Apples: Results from Self-Pollinations

Variety	No. of Flowers pollinated	No. of Fruits matured	Percentage matured
Gascoyne's Scarlet	47	0	0
Grimes' Golden	36	0	0
Royal Jubilee	1,017	1	0·09
Brownlees' Russet	618	1	0·16
Northern Greening	940	2	0·21
Margil	1,352	4	0·29
Blue Pearmain	436	3	0·67
Mother	284	2	0·74
Cox's Orange Pippin	12,680	96	0·74
Northern Spy	3,306	25	0·75
Duke of Devonshire	229	2	0·87
Encore	334	3	0·87
Duchess' Favourite	334	3	0·87
Newtown Pippin	211	2	0·94
Lady Sudeley	197	2	1·01
King's Acre Pippin	370	4	1·09
Newton Wonder	454	5	1·1
Ellison's Orange	514	6	1·16
Blenheim Orange	2,110	27	1·27
Worcester Pearmain	858	12	1·3
Egremont Russet	440	6	1·36
Rival	215	3	1·39
McIntosh Red	202	3	1·48
Lane's Prince Albert	3,699	57	1·54
Beauty of Bath	1,795	30	1·6
King of the Pippins	522	10	1·9
Norfolk Beauty	210	4	1·9
Orleans Reinette	1,018	20	1·9
Annie Elizabeth	294	6	2·0
Lord Derby	701	14	2·0
St. Edmunds Russet	1,077	23	2·13
Peasgood's Nonsuch	173	4	2·3
Grenadier	250	6	2·4
Charles Ross	324	8	2·46
Bismarck	180	5	2·7
Golden Spire	2,457	79	3·2
Laxton's Superb	238	9	3·78
St. Everard	481	19	3·9
Crimson Bramley	616	25	4·05
Lord Grosvenor	250	11	4·4
Ribston	559	25	4·47
Rev. W. Wilks	1,528	69	4·51
Gennet-Moyle	64	3	4·6
Bramley's Seedling	1,269	61	4·8
Washington	1,232	63	5·1
Sturmer Pippin	135	7	5·2
Antonowka	388	28	7·2
Baumann's Reinette	226	17	7·5
Stirling Castle	1,631	131	8·0
Cellini Pippin	160	14	8·7
Coronation	143	19	9·6

chromosome constitution, and it is doubtless due to this complexity that we find a corresponding complexity in the behaviour of incompatibility in this group. The rare occurrence of cross-incompatibility in apples is noteworthy. Since incompatibility

TABLE XXXIV

APPLES: RESULTS FROM CROSS-POLLINATIONS

Varieties	No. of Flowers pollinated	No. of Fruits matured	Percentage matured
Beauty of Bath × Golden Spire	157	11	7·0
" " × Norfolk Beauty	106	12	11·3
" " × Rev. W. Wilks	75	9	12 0
Charles Ross × Ellison's Orange	23	3	12·8
Cox's Orange × Antonowka	103	7	6 7
" × Baumann's Reinette	88	4	4·5
" × Coronation	155	9	5 8
" × Charles Ross	18	1	5·5
" × Egremont Russet	67	10	13 4
" × Ellison's Orange	281	15	5·3
" × Golden Spire	97	8	8·2
" × Herring's Pippin	271	14	5 1
" × Lane's Prince Albert	198	20	10 0
" × Laxton's Superb	569	26	4·5
" × Lady Sudeley	425	16	3·7
" × Newton Wonder	303	17	5·6
" × Peasgood's Nonsuch	125	11	8 8
" × Rev. W. Wilks	258	17	6·5
" × St. Everard	160	10	6 2
" × Stirling Castle	45	7	15·5
" × Sturmer Pippin	300	26	8 6
Duchess' Favourite × Cox's Orange	68	4	5·7
Duchess of Oldenburg × Cox's Orange	60	16	26 6
" " × Lord Derby	88	14	15·9
Ellison's Orange × Cox's Orange	366	14	3·8
" " × Laxton's Superb	100	4	4·0
Gascoyne's Scarlet × Cox's Orange	77	14	18·2
" " × Norfolk Beauty	160	10	6 2
Golden Spire × Cox's Orange	70	7	10 0
" " × Beauty of Bath	61	10	16 4
" " × Emneth Early	105	6	5 7
" " × Lane's Prince Albert	24	4	16 6
" " × McIntosh Red	29	7	24·1
Lane's Prince Albert × Cox's Orange	711	41	5·7
" " " × Lord Derby	134	8	6 0
" " " × Encore	90	9	10 0
" " " × Newton Wonder	131	8	6·1
" " " × Lord Grosvenor	210	35	16 6
Laxton's Superb × Cox's Orange	329	13	3·9
" " × Ellison's Orange	228	11	4·8
" " × Rival	61	16	26·2
Lady Sudeley × Cox's Orange	169	23	13·6
Margil × Cox's Orange	50	7	14·0
" × Egremont Russet	186	6	3·2
McIntosh Red × Cox's Orange	137	7	5·2
" " × Ellison's Orange	102	8	7·8
Newton Wonder × Cox's Orange	270	22	8·1
" " × Lane's Prince Albert	115	6	5·2
Northern Greening × Royal Jubilee	126	18	14·3
Peasgood's Nonsuch × Cox's Orange	33	2	6·0
Royal Jubilee × Lane's Prince Albert	62	10	16·1
" × Northern Greening	70	10	14·2
Stirling Castle × Cox's Orange	110	7	6·3
" × Lord Derby	30	10	33·3
St. Everard × Beauty of Bath	37	4	10 8
" × Cox's Orange	90	3	3·3
St. Edmunds Russet × Cox's Orange	180	24	14·4
" " × Egremont Russet	91	10	11·0
" " × Brownlees' Russet	81	10	12·3
Sturmer Pippin × Cox's Orange	234	45	14·9
Worcester Pearmain × Cox's Orange	177	14	7·9

is determined by like factors failing to meet like, it follows that the more complex the polyploidy the less frequently will incompatibility occur, as the chances of individuals of similar constitution meeting to form incompatible groups are considerably reduced. The decreasing frequency of cross-incompatibility in cherries, plums and apples is therefore in accordance with genetic expectation, as shown in Table XXXV, page 206.

Pears

Rawes (1933) carried out experiments with ninety-eight varieties of pears and classified twenty-two as self-compatible, thirty-four partially self-compatible and forty-two self-incompatible. The work of Hooper (1933) has also shown that in pears self-incompatibility both complete and in degree is common.

The following pear varieties fall into a small co-incompatible group in which pollination between any varieties fail to give fruit and seeds :

Belle Lucrative	Louise Bonne of Jersey
Laxton's Superb	Williams' Bon Chrétien
Seckle	

Other examples of cross-incompatibility found in pears are : Fertility Improved (4x) × Fertility (2x) and Beurré d'Amanlis (3x) × Conference (2x). The reciprocals of these crosses are compatible (Crane and Lewis, 1942).

In preliminary investigations at Merton our colleague Dr. A. A. Moffett has found that out of sixteen varieties he has examined five are triploids with fifty-one chromosomes. These are Pitmaston Duchess, Beurré Diel, Beurré d'Amanlis, Uvedale's St. Germain and Catillac. The remaining eleven are diploid kinds, viz. : Conference, Beurré Giffard, Beurré Clairgeau, Durondeau, Dr. Jules Guyot, Fertility, Beurré Superfin, Beurré Hardy, Marguerite Marrilat, Williams' Bon Chrétien, and Doyenné du Comice. Marguérite Marillat appears to be entirely sterile on its male side, at least after repeated examinations we have not found any good pollen on this variety. It is, however, perfectly fertile on its female side, as when pollinated with Conference and Doyenné du Comice it has freely set fruit and seed. Further evidence of the male sterility of Marguérite Marillat is afforded by the results of Rawes (1933), who states : " It is interesting to note

that in one instance, Beurré Bedford pollinated with pollen of Marguérite Marillat, fruit has been set and developed apparently normally until some seven weeks after the time of pollination, but in three successive seasons the fruits formed have failed to mature, while on other branches of the same tree, flowers pollinated with pollen of other varieties have matured good fruits ".

TABLE XXXV

SHOWING INVERSE CORRELATION BETWEEN CHROMOSOME NUMBER AND COMPLEXITY AND THE FREQUENCY OF COMPLETE INCOMPATIBILITY

Chromosome Constitution	Percentage of Varieties completely Self-incompatible	Percentage of Varieties completely Cross-incompatible
Cherries (2n)	100	73
Plums (6n)	40	13·5
Apples—		
Diploid (3 × 6 + 4 × 4) . . .	4·8	4·8
Triploid (3 × 6 + 4 × 4)$\frac{3}{2}$ . . .	0	0

In Table XXXVI are given combinations of pears which have resulted in a high percentage of fruits set and matured. This table comprises Rawes' (1933) results, and a number of our own results hitherto unpublished.

As we have previously shown, many of our cultivated varieties of apples and pears are triploids and characterised by a high degree of sterility. Such varieties are dealt with in the following chapter. Among the diploid cherries, hexaploid plums and diploid forms of apples and pears varying proportions of defective pollen and ovules occur. But the degree of generational sterility in these forms is not sufficiently high to prevent a satisfactory yield.

In concluding this account of the behaviour of incompatibility in plants, it may be emphasised that it is only the likeness of the particular physiological factors which determine pollen-tube growth that constitutes incompatibility, e.g. the cherries Bigarreau de Schrecken, Bigarreau Frogmore, Belle Agathe and Waterloo are all in the same incompatible group, although they differ widely in fruit colour and in many other respects.

In some species of plants where self-incompatibility is the rule, cross-incompatibility has not been found to occur, e.g. *Tolmiea Menziesii* (Correns, 1928).[1]

[1] In recent years our colleague, Mr. L. G. Wigan, has investigated this species and found examples of cross-incompatibility.

TABLE XXXVI

PEARS: EFFECTIVE POLLINATIONS

Variety	Pollinators*
Beurré Bedford	Conference, Dr. Jules Guyot, Laxton's Superb
Beurré Clairgeau	Conference, Fertility
Beurré d'Amanlis	Durondeau, Louise Bonne of Jersey
Beurré Diel	Conference, Durondeau, Beurré Giffard
Beurré Giffard	Durondeau, Williams' Bon Chrétien
Beurré Hardy	Dr. Jules Guyot, Doyenné du Comice, Fertility
Conference	Dr. Jules Guyot, Emile d'Heyst, Laxton's Superb
Dr. Jules Guyot	Conference, Beurré Clairgeau, Fertility
Doyenné du Comice	Beurré Hardy, Glou Morceau, Winter Nélis
Durondeau	Beurré Giffard, Louise Bonne of Jersey, Williams' Bon Chrétien
Emile d'Heyst	Conference, Durondeau, Fertility
Fertility	Beurré Hardy, Conference, Dr. Jules Guyot
Glou Morceau	Beurré Hardy, Dr. Jules Guyot, Doyenné du Comice
Laxton's Superb	Conference, Glou Morceau
Marguérite Marillat	Durondeau, Louise Bonne of Jersey, Williams' Bon Chrétien
Marie Louise	Conference, Doyenné du Comice
Pitmaston Duchess	Beurré Hardy, Conference, Fertility
Souvenir de Congress	Conference, Winter Nélis
Williams' Bon Chrétien	Beurré Giffard, Durondeau
Winter Nélis	Conference, Doyenné du Comice

* The varieties given as pollinators also correspond in their time of flowering.

ECONOMIC ASPECTS OF INCOMPATIBILITY

The occurrence of incompatibility often impedes the progress of the plant breeder, and gives rise to a number of problems, but to the fruit-grower the practical implications are self-evident. It is imperative that he should make adequate provision for efficient pollination by interplanting varieties which flower at the same time and are known to be mutually compatible. In existing plantations where trees, though in a healthy condition and flowering freely, consistently fail to yield satisfactory crops, it is probable that facilities for efficient pollination are inadequate, and where this is suspected, trees of a known compatible variety should be introduced or, where more convenient, a proportion of

the existing trees could be top-grafted with scions of a suitable variety. The present-day practice of planting comparatively few varieties and a large number of each calls for especial care in the selection of suitable varieties, particularly in cherries where cross-incompatibility is common. There is no reason why such highly self-compatible plums as Victoria, Early Transparent, Pershore, etc., should not be planted in large blocks; but it is worthy of note that, as far as we know at present, the pollen of self-compatible kinds is always effective on self-incompatible varieties. Therefore if any self-incompatible varieties are to be grown, self-compatibles might advantageously be interplanted with them.

The almost continuous variation of compatibility in apples makes it difficult to make any precise statement, but the safest plan is to interplant all varieties. In this fruit and in pears a high degree of sterility is characteristic of many varieties, and the practical problems to which its occurrence gives rise are discussed in the following chapter. Most of our fruits are dependent upon insects, notably bees, for efficient pollination and the production of paying crops. It is probable that some plantations are more favoured than others by the visits of wild bees and other pollinating insects. Wild bees are frequently active during inclement weather, but over them we have little control, and unfortunately conditions which are favourable to their welfare are often inconsistent with present-day views of good culture and plant hygiene. Hive bees, however, can be kept in orchards, and since their presence may make all the difference between a light and a heavy crop, any trouble or expense involved in their maintenance is likely to be well repaid, apart from their utility in providing honey. That bees travel a considerable distance is well known, but it should be remembered that they are after pollen and nectar and not primarily concerned with cross-pollination, and if there is a large batch of one variety abundantly supplying their need, there is nothing to induce them to do otherwise than work between the hive and this block. Judicious interplanting is therefore advisable, and large blocks of one variety should be avoided.

Heterostylism

In certain plants the relative length of the styles and stamens is found to vary in different individuals. For example in several

species of *Primula* and *Linum* two kinds of flower occur, the " thrum " and " pin ". In the thrum type the style is short and the stamens long, whereas in the pin type the style is long and the stamens short. This is known as dimorphic heterostylism. In other plants, such as *Lythrum Salicaria* and some species of *Oxalis*, trimorphic types are found, in which there are two whorls of stamens and three variations in the length of the styles and stamens, e.g. long styles with medium and short anthers, medium styles with long and short anthers and short styles with long and medium anthers. In the majority of such species pollination is effective only between styles and stamens of similar length, e.g. long by long is effective but long by medium or short fails, and so on.

The result of this condition is that as a rule self-pollination is impossible and cross-pollination is enforced.

In a recent review, Lewis (1944) has shown that the systems for self-sterility in plants can be summarized as follows:

(i) Heterostyled plants, such as *Primula sinensis* and many other species.
  (*a*) One or two genes with two alleles.
  (*b*) Co-ordinated gene action in pistil and pollen.
  (*c*) Diploid pollen control.
  (*d*) Dominance.

(ii) Non-heterostyled plants, such as *Nicotiana sanderae* and many other species.
  (*a*) One gene with multiple alleles.
  (*b*) Independent gene action in the pistil but not in the pollen.
  (*c*) Haploid pollen control.
  (*d*) No dominance.

More recently a third system has come to light as a result of the work by Hughes and Babcock (1950) on *Crepis*, and by Gerstel (1950) on *Parthenium*. This new system is as follows:

  (*a*) One gene with multiple alleles.
  (*b*) Independent gene action in the pistil.
  (*c*) Diploid pollen control.
  (*d*) Dominance.

The genetical system controlling self-sterility in *Crepis* and *Parthenium* therefore is unique in that it is a combination of features from the two systems of homostyled and heterostyled plants. It has the first two features of the homostyled and the last two features of the heterostyled systems.

CHAPTER XI

STERILITY

ALTHOUGH sterility in plants results from many different causes, we can conveniently analyse and discuss the various forms which occur in our cultivated plants under the following two headings : (1) *Generational Sterility*, due to the failure of any of the processes concerned with the normal alternation of generations, namely, development of pollen, embryo-sac, embryo and endosperm, and the relation of these to one another and to their parents regardless of the cross made. (2) *Morphological Sterility* due to suppression or abortion of the sex organs.

GENERATIONAL STERILITY

Whereas incompatibility is determined by the interaction of particles of the chromosomes, namely the genes, generational sterility is often the result of unbalance in the whole chromosome complement. It occurs in varying degree among our cultivated plants, and is common in hybrids which have resulted from wide crosses.

It may be recalled that from a genetic point of view a plant is a double structure resulting from the fusion of the nuclei of two germ-cells—a pollen grain and an ovule. Hence the somatic or body-cells of a plant result from the addition of the parental germ-cells, and in order for the plant to repeat this process in its own reproduction it is necessary that corresponding elements derived from the parental germ-cells should separate. If the parental germ-cells themselves did not correspond, then this process cannot be carried out in an orderly way and sterility will result.

In diploid plants the body-cell nucleus contains two sets of corresponding chromosomes which divide during the process of reproduction, forming germ-cells—pollen grains and ovules—each with one set of chromosomes. But among our cultivated plants

this process of reduction is often complicated, owing to their hybrid origin and complex polyploid chromosome constitution. Those with an even number of chromosomes, such as tetraploids with four sets, hexaploids with six and octoploids with eight, are usually more productive than those having an odd number of

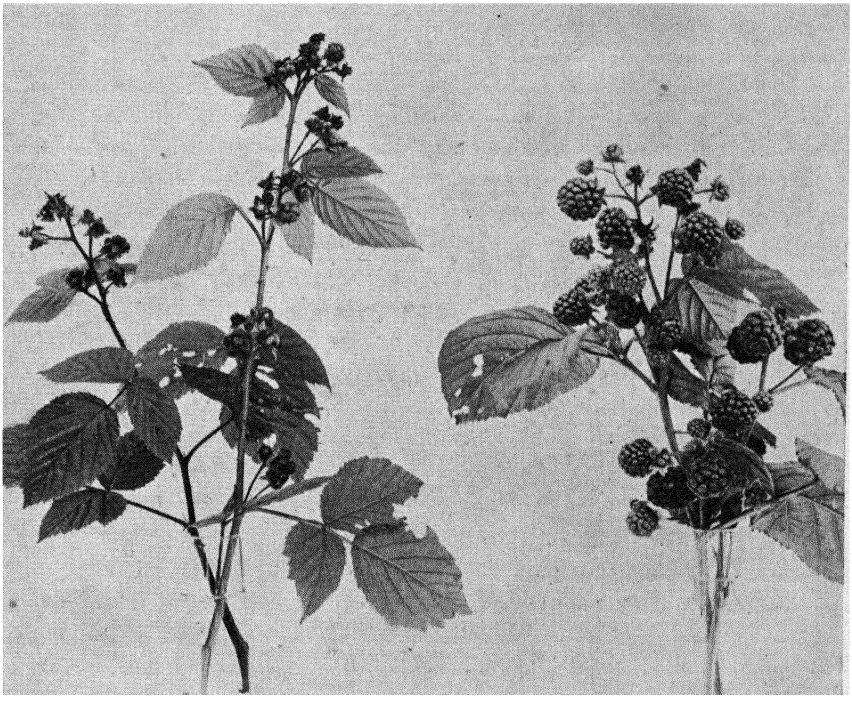


FIG. 56

A, the infertile Mahdiberry, 2n = 21; B, the fertile Veitchberry, 2n = 28.

sets, such as triploids with three, pentaploids with five and heptaploids with seven, etc. Apart from other considerations, it is obvious that an odd number cannot divide evenly, and so irregularities and sterility will inevitably follow.

A brief consideration of some of our cultivated *Rubi*, which have been cytologically studied by our colleague, Dr. C. D. Darlington, will serve to demonstrate the importance of polyploidy in relation to sterility and fruit production. In the genus *Rubus* the basic chromosome number is seven. The raspberry varieties Superlative and Lloyd George have fourteen chromosomes, the

Mahdi twenty-one, the Veitchberry twenty-eight, the Loganberry forty-two, and the Laxtonberry forty-nine, and it is well known that the fertility and fruit production of the odd multiple forms, the triploid Mahdi and heptaploid Laxtonberry, is much below that of the even multiples and balanced chromosome forms, the diploid raspberries, the tetraploid Veitchberry and the hexaploid Loganberry (see Fig. 56). Longley (1926) has studied many of the American horticultural forms of *Rubi*, and has shown that those which possess an odd multiple of seven produce very little good pollen and are highly sterile, but that the even multiples have comparatively little sterile pollen.

In the genus *Prunus* the basic chromosome number is eight (*v.* Ewert, 1922; Knowlton, 1924; Kobel, 1927; Darlington, 1926–28–32; and Moffett, 1930). The somatic number of the commoner species is as follows :—

Prunus divaricata (Myrobolan Plum)	16
„ *spinosa* (Sloe)	32
„ *insititia* (Damson)	48
„ *domestica* (European Plum)	48
„ *mahaleb* (St. Lucie Cherry)	16
„ *avium* (Sweet Cherry)	16
„ *cerasus* (Sour Cherry)	32
„ *cerasus* × *avium* (Duke Cherries)	32
„ *persica* (Peach)	16
„ *armeniaca* (Apricot)	16

The above fertile forms of *Prunus* have a balanced diploid, tetraploid or hexaploid chromosome complement. Hybrids we have raised from *Prunus domestica* (forty-eight) crossed by *P. cerasifera* (sixteen) and *P. insititia* (forty-eight) crossed by *P. spinosa* (thirty-two) have the intermediate chromosome numbers expected, viz. thirty-two and forty. Pollinations we have made between *P. domestica* and *P. insititia*, both hexaploid, have always been completely inter-fertile. But from pollinations between diploid and polyploid and between different polyploid forms, such as *P. domestica* crossed *P. cerasifera* and from *Prunus insititia* crossed *P. spinosa*, fruits with viable seeds are but rarely formed. In the American plums Dorsey (1919) found that the percentage of aborted pollen was higher in hybrids than in species. So far as is known, triploid forms of *Prunus* are only found as ornamental varieties, their degree of sterility being too high to enable them to be grown for their fruits, e.g. *Prunus*

nana and *Prunus Mume* (Darlington, 1928) and many of the Japanese flowering cherries (Okabe, 1928). Since in an ornamental tree fruit is not required, sterility is an asset; no energy is expended in the formation of fruit, consequently the trees flower abundantly year after year. Triploids we have raised from crosses between diploid and tetraploid species, and pentaploids from crosses between tetraploid and hexaploid species, have always been highly sterile.

Longley (1926) found the basic chromosome complement of the strawberry *Fragaria* to be seven. The wild European strawberry (*Fragaria vesca*) has fourteen chromosomes. The other species, including our modern cultivated varieties, are found to be polyploids. Thus *Fragaria elatior* (the Hautbois strawberry) has forty-two, *Fragaria virginiana* fifty-six, and *Fragaria chiloensis* fifty-six. The work of Ichijima (1928) and Mangelsdorf and East (1927) confirms and extends the conclusions of Longley. Five diploid forms, including *Fragaria vesca*, hybridised freely and gave fertile progeny. Similarly crosses between octoploids gave fertile offspring. Attempts to inter-cross species with different chromosome numbers were often abortive or at the most only resulted in sterile hybrids.

In *Ribes* the basic chromosome number is eight, and as far as is known, although many species have been cytologically studied, polyploidy does not occur within the genus (Tischler, 1927–28; Meurman, 1925–28; Darlington, 1927–29).

In grapes Nebel (1929) found that the varieties Muscat Gigas and Sultanina Gigas were tetraploid forms, their somatic chromosome number being seventy-six. Nebel also made the interesting observation that Muscat Gigas (tetraploid) has six chromosomes with satellites, whereas Muscat (diploid) has only three.

Longley (1927) in a cytological study of the Blueberry, *Vaccinium* species and hybrids, found three diploid, six tetraploid, one pentaploid and two hexaploid forms. The basic chromosome number is twelve. Coville (1927) in the same genus found that he could inter-cross species with the same chromosome number, but crosses between forms with a different number of chromosomes failed or produced highly sterile offspring.

In the cultivated fruits so far discussed we have shown that the really productive forms have a balanced chromosome complement, and that those with an odd multiple or unbalanced chromosome constitution are generally unproductive. Although

a certain amount of bad pollen and ovules is evident in the productive varieties, nevertheless they have a sufficient proportion of good pollen and ovules to ensure, under favourable conditions, an abundant yield.

Apples and Pears

In a previous chapter we have shown that our cultivated varieties of apples and pears are of two kinds, the so-called diploids with thirty-four and triploids with fifty-one chromosomes. In Tables XXXVII to XL we have tabulated the chromosome complement of a number of varieties of apples and pears and the percentage of pollen germination as determined by a number of investigators. In Tables XXXVII and XXXIX are triploid, in Tables XXXVIII and XL diploid varieties. Kvaale (1926), Kobel (1927), Miedzyrzecki (1933) and Moffett (1934) gave the actual percentage of pollen which germinated, but Florin (1926) divides his results into three classes: (1) "poor", with average pollen germination not above 30 per cent, (2) "medium", 30 to 70 per cent, and (3) "good", at least 70 per cent. It will be observed that considerable variation in the proportion of good and bad pollen occurs, both among diploids and triploids, but that the proportion of bad pollen is very much higher in the triploids than in the diploids. Thus all the triploid varieties which were used by Florin in his tests are in his "poor" class, with less than 30 per cent good pollen, and those examined by Kobel and Kvaale, Miedzyrzecki and Moffett gave only 4 to 27 per cent good pollen. It is therefore evident that there is a correlation between the proportion of good pollen and chromosome number in apples and pears, and that many of our important varieties such as Bramley's Seedling, Blenheim Orange and Ribston Pippin apples, and Beurré d'Amanlis, Pitmaston Duchess and Catillac pears are triploids and sterile to a high degree.

A comparison of the results in Tables XXXVIII and XL shows that generational sterility occurs to a higher degree among the diploid pears than among the diploid apples. In this connection it is noteworthy that Moffett (1934) has shown that the degree of primary pairing and also the secondary association of the chromosomes is not so great in pears as in apples. These conditions may lead to greater irregularities in germ-cell formation, and hence a greater average degree of sterility in pears.

TABLE XXXVII

Triploid Varieties of Apples

Variety	Somatic Chromosome Numbers					Percentage of Pollen Germination		
	Rybin, 1926	Kobel, 1927	Crane and Lawrence, 1929	Nebel, 1929	Darlington and Moffett, 1930	Kvaale, 1926	Florin, 1926	Kobel, 1927
Arkansas	..	..	..	51	..	11·4	..	..
Baldwin	..	48-49	..	51	51	12·3	0-30	11·0
Belle de Boskoop	..	*ca.* 46	..	51	..	..	0-30	13·0
Blenheim Orange	..	..	51	51	51	..	0-30	..
Bramley's Seedling	..	..	51	..	51	20·9	0-30	..
*Crimson Bramley	..	..	..	..	51	..	..	..
Gennet-Moyle	..	..	51	..	51	..	..	..
*Gravenstein	..	45-46	..	51	..	13·0	0-30	7·0
Gravenstein von Hesam	..	..	..	51	..	..	..	..
Henze's Gravensteiner	..	..	..	51	..	..	..	..
Kock's Gravensteiner	..	..	..	51	..	..	..	..
Gravensteiner von Palaiser	..	..	..	51	..	..	..	..
Gravensteiner von Sabygard	..	..	..	51	..	..	..	..
Roter Gravensteiner	..	..	..	51	..	..	0-30	..
Schleibnitzer Gravensteiner	..	..	..	51	..	..	..	..
Harbert's Reinette	..	45	..	..	..	..	..	16·0
Reinette du Canada	..	38-40	..	51	..	..	0-30	4·0
Rhode Island Greening	..	..	..	51	..	2 ·0	0-30	..
Ribston Pippin	..	42	..	51	51	21·4	0-30	..
Tompkins King	..	..	..	51	..	..	..	..
Warner's King	..	42	..	..	..	14·8	0-30	27·0
Washington	..	..	..	..	51	..	..	..

* Crimson Bramley is a bud-sport from Bramley's Seedling, and the Gravensteins are apparently a group of eight clonal variations.

TABLE XXXVIII

Diploid Varieties of Apples

Variety	Somatic Chromosome Numbers					Percentage of Pollen Germination		
	Kobel, 1927	Crane and Lawrence, 1929	Nebel, 1929	Heilborn, 1928	Darlington and Moffett, 1930	Kvaale, 1926	Florin, 1926	Kobel, 1927
Allington Pippin	..	34	..	..	34	..	..	..
Annie Elizabeth	..	34	..	..	34	76·0	..	..
Beauty of Bath	..	34	..	..	34	..	70-100	..
Ben Davis	..	..	34	..	..	..	..	..
Carlisle Pippin	..	34	..	..	34	..	..	..
Cellini Pippin	34	..	..	..	..	68·1	70-100	82·0
Cox's Orange Pippin	34	34	..	..	34	69·3	70-100	..
Cox's Pomona	..	34	..	..	34	98·0	..	..
Baumann's Reinette	..	..	..	..	34	..	70-100	..
Duchess' Favourite	..	..	..	..	34	..	..	..
Duchess of Oldenburg	..	..	34	..	..	87·3	70-100	..
Early Victoria	..	34	..	..	34	..	70-100	..
Grenadier	..	34	..	..	34	..	..	..
Irish Peach	..	34	..	..	34	..	70-100	..
Kentish Codlin	..	..	..	..	34	..	..	..
Keswick Codlin	..	34	..	..	34	96·5	70-100	..
Lane's Prince Albert	..	34	..	..	34	57·6	70-100	..
Lord Derby	..	34	..	..	34	..	70-100	..
Mank's Codlin	..	..	34	..	..	..	70-100	..
McIntosh Red	..	..	34	..	..	56·9	..	..
Newton Wonder	..	..	34	..	34	52·1	..	..
Northern Spy	..	..	..	..	34	90	30-70	..
Ontario Reinette	34	..	34	..	..	..	30-70	68·0
Red Astrachan	..	..	34	..	..	..	..	..
Reinette Zuccamaglio	..	34	..	..	34	..	70-100	..
Rev. W. Wilks	..	..	..	..	34	..	..	..
Rival	..	34	..	..	34	..	70-100	..
Rome Beauty	..	..	34	..	..	90·5	..	..
Transparente de Croncels	34	..	..	..	..	60·3	30-70	55·0
Wealthy	..	..	..	34	..	85·9	30-70	..
Winter Majetin	..	..	..	34	..	..	..	..
Worcester Pearmain		34	..	..	34	..	70-100	..
Yellow Bellflower	..	..	34	..	..	..	70-100	..
Yellow Newtown	..	..	34	..	..	..	..	..

Nevertheless the average fertility of the diploid pears is much higher than the fertility of the triploid varieties. The diploid variety Marguérite Marillat is exceptional in being almost if not entirely sterile on its male side.

We have previously shown that in most fruiting trees the free production of fruits is associated with an even multiple and balanced chromosome constitution. The condition of our pomiferous fruits is, however, in many ways exceptional; seed fertility is not so closely related to fruit production, and comparatively few fruits are required to give a satisfactory yield.

TABLE XXXIX

TRIPLOID VARIETIES OF PEARS

Variety	Somatic Chromosome Numbers			Percentage of Pollen Germination			
	Kobel, 1927	Miedzyrzecki, 1933–34	Moffett, 1934	Florin, 1926	Kobel, 1927	Miedzyrzecki, 1933–34	Moffett, 1934
Beurré d'Amanlis	..	..	51	0-30	..	..	8·2
Beurré Diel	45	51	51	0-30	6·0	5·0	12·0
Catillac	..	..	51	..	..	..	16·0
Conseiller à la Cour	44-8	..	..	..	13·0	..	..
Bärikerbirne	51	..	..	0-30	11·0	..	..
Pitmaston Duchess	..	..	51	0-30	..	..	10·0
Schweizer Wasserbirne	*ca.* 46	..	..	..	13·0	..	..
Theilersbirne	48	..	..	0-30	22·0	..	..
Vicar of Winkfield	55	..	..	0-30	4·0	..	..
Rateau Gris	..	51	..	..	..	9·0	..
Uvedale's St. Germain	..	..	51	..	..	..	9·0

Often if only 5 per cent of the flowers form fruits which reach maturity it is sufficient. Consequently varieties of apples and pears with an odd-multiple chromosome complement and a high degree of sterility may be sufficiently productive to be of economic importance.

Since the diploid varieties of apples and pears in general have a higher proportion of good pollen than the triploids, it follows that, apart from incompatibility, the diploid varieties are likely to be much more effective as pollinators in the garden and the field than triploid varieties. This knowledge should guide the fruit-grower when considering the interplanting of varieties. Triploid varieties of apples such as Bramley's Seedling and Ribston Pippin, and pears such as Beurré Diel and Pitmaston Duchess, which are characterised by a low proportion of

good pollen, can only be very ineffective pollinisers for other varieties. Consequently, although interplanting with a highly fertile diploid variety like Worcester Pearmain might be effective for Bramley's Seedling, the latter would not be of much use as a pollinator for Worcester Pearmain. In all such cases where triploid varieties are involved it is advisable to add a third

TABLE XL

DIPLOID VARIETIES OF PEARS

Variety	Somatic Chromosome Numbers			Percentage of Pollen Germination			
	Kobel, 1927	Miedzyrzecki, 1933–34	Moffett, 1934	Florin, 1926	Kobel, 1927	Miedzyrzecki, 1933–34	Moffett, 1934
André Desportes	34	..	..	30-70	54	..	..
Belle des Abrés	..	34	..	..	..	66	..
Beurré Bosc	..	..	34	..	..	..	59
Beurré Clairgeau	..	..	34	30-70	..	..	81
Beurré Dumont	..	34	..	..	..	36	..
Beurré Giffard	..	34	34	30-70	..	..	..
Beurré Hardy	34	..	34	30-70	72	..	82
Beurré Naghin	..	34	..	..	..	43	..
Beurré Six	..	..	34	..	..	..	61
Beurré Superfin	..	..	34	70-100	..	..	..
Bon Chrétien d'Hiver	..	34	..	..	..	..	..
Charles Marchal	..	34	..	..	..	..	..
Clapp's Favourite	..	34	..	30-70	..	55	..
Conference	..	..	34	70-100	..	..	72
Doyenné du Comice	..	..	34	30-70	..	..	74
Durondeau	..	..	34	..	..	..	50
Dr. Jules Guyot	..	34	34	30-70	..	54	46
Fertility	..	..	34	..	..	..	69
Hessle	..	..	34	..	..	..	71
Louise Bonne de Jersey	34	..	..	30-70	54	..	..
Marguérite Marrilat	..	..	34	0-30	..	..	2
Marie Louise	..	..	34	..	..	..	57
Olivier des Serres	..	34	..	0-30	..	40	..
Passe Crassane	..	34	..	..	..	56	..
Triomphe de Vienne	..	34	..	30-70	..	46	..
William's Bon Chrétien	34	..	34	30-70	46	..	56

variety, another diploid such as Lord Derby for the pollination of Worcester Pearmain, so as to secure the pollination of the diploids *inter se*, or if these kinds do not meet the grower's requirements, two other diploid varieties.

In apples and pears it does not necessarily follow that the development of a fruit to maturity means that the fruit contains viable seeds, for although in the large majority of varieties pollination and fertilisation are necessary for fruit formation,

a subsequent breakdown in embryonic growth does not always affect the fruit. In the case of such a breakdown, which commonly occurs, the fruit may continue to develop and reach maturity. This arrest and breakdown of the growth of the embryo may be due to various causes and accentuated by others, e.g. disease, nutrition, climatic conditions, etc., but among them cytological and genetical unbalance play a leading part, no matter what may be the prevailing cultural conditions and general health of the trees.

With regard to the so-called "June drop" of apples, which in this country more often occurs in the month of July, there are indications that under unfavourable conditions failure to develop to maturity is most common with those fruits which contain only or mainly imperfect seeds. It is therefore probable that the falling of partially developed fruits known as the "June drop" is in general heavier among those apples which have poorly developed seeds. Some varieties of apples and pears occasionally develop fruits without seeds, and in some varieties the seed content is reflected in the shape of the fruit, those with few seeds often being irregular in shape.

Although certain diploid varieties, such as Cox's Orange Pippin, when pollinated by Lane's Prince Albert, result in a low proportion of good seeds, it may be predicted that in those years when the "June drop" is prevalent it will in general be more acute in plantations where provision for pollination is inadequate, than in those well provided for effective pollination.

Inter-specific Sterility

Among plants derived from the inter-crossing of species all degrees of sterility occur. Sterility of this kind occurs when species with the same chromosome numbers are intercrossed, and also between species with different chromosome numbers. The degree of sterility varies from complete failure to obtain seeds from inter-specific pollinations, to the other extreme where inter-specific hybrids are as fertile as the parental species themselves. Complete fertility in such hybrids is, however, exceptional, and following inter-specific hybridisation some degree of sterility is almost the rule. When high fertility does occur it often results from an unusual form of reproduction. Although many species fail to inter-cross, initial failures should not be too readily accepted

as indicating complete inter-sterility, as repetition may yield a few seeds and give rise to plants of outstanding value.

Results we have obtained from inter-specific pollinations in cherries have varied considerably. Varieties of *Prunus avium* used as female, pollinated by varieties of *P. cerasus* as male, have generally produced and matured fruits freely, but from reciprocal pollinations fruits were less freely formed. The Duke cherries are also less productive when used as females with the sweet cherries than when used as males. The total results of such crosses are summarised in Table XLI.

TABLE XLI

	No. of Flowers pollinated	No. of Fruits set	Percentage set
Sweet Cherries × Sweet Cherries .	96,671	24,977	26·06
,, ,, × Sour ,, .	2,953	703	23·7
Sour ,, × Sweet ,, .	1,144	93	8·1
Sweet ,, × Duke ,, .	4,786	601	12·5
Duke ,, × Sweet ,, .	2,406	129	5·3
Sour ,, × Duke ,, .	353	42	11·8
Duke ,, × Sour ,, .	1,317	45	3·4
Sour ,, × Sour ,, .	489	60	12·2
Duke ,, × Duke ,, .	534	44	8·2

The extent of the trials with the sour (*P. cerasus*) and Duke cherries is comparatively small, and consequently we hesitate to make any general statement with regard to the results they have given. But in the Sweet × Sour and the Sweet × Duke and reciprocal pollinations the number of flowers used is large and the differences in proportion of fruits set in the reciprocal pollinations between these groups are considerable. These reciprocal differences are probably due to hybridity and sterility. The sweet cherry *P. avium* is a diploid species and the Dukes and sour cherries are tetraploids. Consequently, when the Dukes and sour cherries are used as females, the endosperm, which results from a triple fusion in which two maternal nuclei combine with one male nucleus, will be pentaploid or approximately so. When, however, the sweet cherries are used as females the endosperm, following triple fusion, will be tetraploid or approximately so, and it is possible that differences in balance between the chromosome complement of the embryo and endosperm may account for the difference in the proportion of fruit set in the reciprocal pollinations between these groups.

The Duke cherries are tetraploids, which have arisen in an exceptional way from hybridisation between the diploid sweet cherries and the tetraploid sour cherries. Consequently the immediate hybridity of the Dukes is much greater than that of the varieties of *P. avium* and *P. cerasus*—the sweet and sour cherries respectively—and a corresponding difference in sterility may be expected. An examination of the results in Table XLI and their graphical presentation in Fig. 57 substantiates this view, for not only do the sour and sweet varieties show a considerably greater fertility than the Duke varieties, but in reciprocal crosses with sweet varieties a striking parallelism is shown. For example, the difference between the percentage of fruit set in sweet crossed sour and sour crossed sweet, and sweet × Duke and Duke × sweet, is proportional. The results of these experiments show that although fertilisation is essential for fruit development, a subsequent breakdown in embryonic growth frequently occurs. This breakdown may result from several causes, the most probable of which is a discordance (*a*) of the parental chromosome contributions to the nucleus and endosperm of the zygote, or (*b*) between the nucleus and endosperm. The consequence of these inharmonious relations is seen in the degree of development of the embryo and the resulting bad and non-viable seeds. At maturity some fruits contain but shrivelled testas, and others only partially developed embryos. In general the proportion of imperfect seeds is higher in the Dukes than in the sour and sweet cherries.

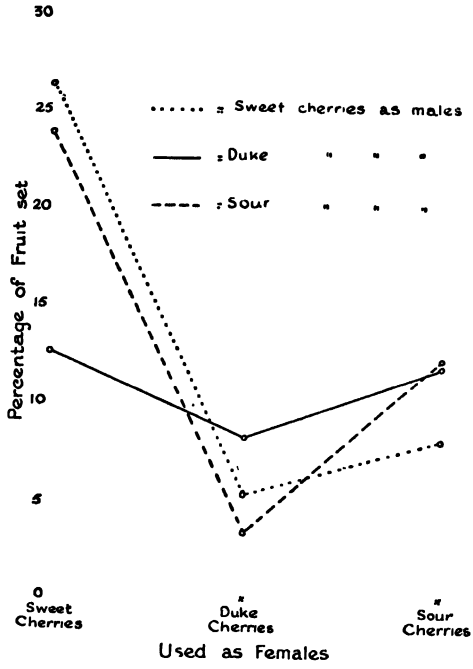


FIG. 57.—INTER-SPECIFIC FERTILITY IN CHERRIES

Showing the percentage of fruit set in pollinations between varieties of *P. avium*, *P. cerasus* and the hybrid Duke Cherries.

Relationship of Chromosomes and Fertility

In addition to numerical differences, too great a dissimilarity or even too great a similarity of the chromosome complement may also lead to reduced fertility or to sterility. Many sterile diploid hybrids have, upon doubling of the chromosome complement, given rise to fertile tetraploid forms. For example, the highly sterile diploid *Primula kewensis* (Newton and Pellew, 1929) has given rise to a tetraploid form which is highly fertile (see Chapter IV, page 66), and similarly the highly sterile diploid Raphanus-Brassica hybrids raised by Karpechenko (1928) gave tetraploids that were highly fertile and in the almost sterile form of the geranium *Pelargonium roseum*, fertility was restored following chromosome duplication. In this case duplication was vegetatively induced (Shchavinskaya, 1937).

On the other hand, reduced fertility sometimes results from chromosome doubling. For example, the tomato of commerce is a highly fertile diploid plant with twenty-four chromosomes. By the simple process of decapitation adventitious shoots may be induced to arise, some of which are tetraploid with forty-eight chromosomes. Compared with that of the diploid forms, the fertility of the tetraploids is greatly reduced. Again in the tetraploid forms of raspberries, such as the varieties Belle de Fontenay and Merveille Rouge, and in the auto-tetraploid forms of *Primula sinensis* fertility and productivity are lower than in the case of the diploid forms. Many other examples of sterile plants giving increased fertility and fertile plants decreased fertility following chromosome doubling could be quoted. Consequently it appears possible to predict that the doubling of the chromosomes of sterile hybrids will lead to increased fertility, but in fertile forms will lead to a reduction of fertility. The reason for this apparent contradiction becomes clear when we consider the nature of the chromosome complement in the two kinds of polyploids. An auto-polyploid may be represented as **AAAA,** derived from doubling in a fertile diploid **AA** ; an allo-polyploid as **AABB,** derived from doubling in a more or less sterile diploid **AB,** itself the result of the cross **AA** × **BB**. In the former case the change from two to four identical groups will set up mechanical difficulties in pairing, owing to excess of choice. In the allo-polyploid the doubling of **AB** to **AABB** will allow identical sets **AA** and **BB** to

pair, giving germ-cells all **AB** and identical ; the plant will function as a diploid and fertility will be restored.

The sterility associated with the offspring of wide crosses, such as that of the plum-crossed peach, the black-currant-crossed gooseberry and many other inter-specific hybrids is well known. It is frequently met with among our ornamental plants which are asexually reproduced, for example in the rose Mermaid, and many shrubs and herbaceous plants. In such extreme crosses the two sets of chromosomes derived from the respective parents work in harmony throughout the somatic life of the hybrid, but are unable to pass successfully through the more intricate processes of germ-cell formation.

A number of cases in which meiosis is affected by a definite gene are known. For example, Beadle (1933) in his experiments on maize found that chromosome pairing (chiasma formation) was greatly reduced by a gene which was inherited as a mendelian recessive. Since meiosis could rarely proceed normally the majority of the germ cells were inviable and a high degree of sterility resulted. Fabergé (1937) has shown that the recessive gene $\mathbf{b}_2$ in the sweet pea (see Table V) disorganises meiosis on the male side and gives rise to contabescent anthers, devoid of pollen.

Chromosome rearrangements, such as ring formation and inversions, illustrated in Fig. 15, commonly lead to partial or more or less complete sterility. When individuals which differ in regard to several inversions, whether they belong to the same species or not, are crossed, they frequently give rise to hybrids whose chromosomes, on account of these differences, are unable to pair at germ-cell formation, or if they pair, crossing-over gives rise to unworkable new structures. Such hybrids are therefore sterile, and the sterility of many inter-specific hybrids, as in *Lilium* (Richardson, 1936) is largely due to this cause.

Morphological Sterility

So far, the form of sterility discussed in this chapter has been due to gametic irregularities—abortive pollen or ovules, or to zygotic degeneration—the breakdown of embryonic growth. Another form of sterility occurs in plants which is due to the suppression or abortion of the sex organs. For example, the anthers of the plum Golden Esperen are contabescent and contain no good pollen. Consequently although the variety is fertile

on its female side and sets fruit when pollinated with other varieties it is useless as a pollinator for other varieties owing to the sterility of its male organs.

In the peach, Connors (1926) has shown that the variety J. H. Hale and others are sterile on their male side, although fully fertile on the female side. Among the many seedlings we have raised at Merton we find male-sterility to be not uncommon. As we have previously shown, in the progenies raised from commercial varieties of raspberries we have obtained four sexually distinct forms, hermaphrodite, male, female and neuter. In the neuters both male and female organs are suppressed. The male forms of course never bear fruits; but the females crop freely when pollinated by other individuals. As we have previously shown, these sex-forms in raspberries are the expression of genetic differentiation, the suppressed forms being recessive, and from crosses between them a close approximation to the expected Mendelian segregation is obtained. Stout (1921), Wellington (1930) and Dorsey (1932) have shown that in the grape aborted and suppressed sex organs commonly occur. Valleau (1918) has described similar conditions in strawberries. More recently Swarbrick and Thompson (1932) have shown that the strawberry variety Tardive de Leopold is male-sterile, possessing only abortive stamens, hence to produce fruit it is essential that this variety should be planted adjacent to other varieties which provide pollen for fertilisation. The variety Oberschlesien also appears to be male-sterile to a considerable extent. Since these varieties are being widely planted commercially, care should be taken that a sufficient number of plants of a free pollen-producing variety is also included in the plantations. Swarbrick and Thompson have shown that plantations consisting of the varieties Tardive de Leopold and Royal Sovereign were almost invariably successful, but that plantations composed of Tardive de Leopold and Oberschlesien were rarely if ever successful, except where one or other of the stocks contained other varieties as rogues, notably Sir Joseph Paxton or Royal Sovereign. In a number of cases where only Tardive de Leopold and Oberschlesien were planted both varieties completely failed to set fruits.

CHAPTER XII

XENIA

THE so-called phenomenon of xenia in plants has for long attracted the attention of the horticulturist. The term xenia was first used by Focke (1881) to denote any deviation from a normal form or colour in any part of the plant through the action of foreign pollen. It appears possible to place the examples which Focke described into three classes : (1) where the developing zygote is affected, (2) where the endosperm is affected and (3) where the effect is on the maternal tissue. In the light of modern genetics two of these three effects are readily explicable. They are the results of the action of paternal genes in heredity. Thus (1) in *Pisum* yellow cotyledons are dominant to green, and if a green variety is pollinated with a yellow variety the cotyledons of the developing zygote will be yellow. (2) The discovery by Navashin in 1898 that the polar nuclei of the endosperm fuse with the second male nucleus provides an explanation of endosperm differences. For example, in white-seeded maize the endosperm is white, **yyy** ; when, however, a white variety is pollinated with a deep yellow variety, **YYY**, the effect of the pollen of the male is expressed directly in the endosperm of the female ; it is pale yellow, **Yyy**, instead of white, **yyy**, owing to the triple fusion whereby two maternal nuclei combine with one male nucleus. A number of other differences in maize behave in a similar fashion. Differences in the size and shape of seeds, due to difference in chromosome number, genetic constitution, heterosis, etc., also commonly occur. Since these effects are now well understood and explained on a simple genetic basis, there is no reason why they should continue to be referred to as xenia.

In the remaining class, (3), where the maternal tissue is affected, we have not such a precise or simple explanation of the cause of the effect, but many examples as described in Table XLII have been reported upon in recent times. Swingle (1926) found that the time of maturity of dates could be made to

vary according to the pollen used in fertilisation. Nixon (1928–1936), also working with dates, found that most pollinations which gave smaller seeds also gave earlier ripening fruits. This appears to be true throughout the pollinations made within the species *Phoenix dactylifera*, but in some interspecific pollinations, especially where the pollen of *Phoenix canariensis* was applied to *Phoenix dactylifera*, small seeds gave late ripening fruits. In all cases, both in varietal and interspecific pollinations, small seeds and small fruits go together. In melons, Rosa (1926) found that fruits with a larger number of seeds were heavier than those with a smaller number. In chestnuts, McKay and Crane (1939) found that some pollinations gave larger nuts than others; in cotton, Harrison (1931), and in oaks, Schreiner and Duffield (1942), found some pollinations gave heavier seeds than others. Harrison (1931) has also reported that in certain varieties of cotton the length of the lint differs in different pollinations.

Swingle (1928) has suggested that the developing embryo and endosperm secrete hormones, or analogous substances, which exert a specific effect on the maternal tissues, the effect varying according to the particular male parent used. The work of Gustafson, later referred to, possibly supports the above view.

Swingle (1926) introduced the term *metaxenia* to describe the differences he observed in the time of maturity of dates. The title of his paper explains his usage of the term: "Metaxenia or the influence of the male parent on the tissues of the mother plant outside of the embryo and endosperm, especially as exemplified in the date palm". Since Focke's original description of xenia covered effects on any part of the plant, whether embryonic or maternal, and especially since classes (1) and (2) are readily explicable on a simple genetic basis, it is a pity that the effect on the maternal tissue (class 3), which is the only one to which the term xenia can be properly applied, has been unnecessarily described as metaxenia. It is, however, becoming the fashion to describe any effect, associated with foreign pollen, on the maternal tissue under this name.

In addition to the publications cited in Table XLII, many papers have been published dealing with closely related phenomena. In Gustafson's experiments (1936–40), where in many species of plants he obtained parthenocarpic fruits (*a*) by growth-promoting chemicals and (*b*) by pollen extracts, the induced

TABLE XLII

Female	Pollinated by	Effect on Fruit	Effect on Seed	Author
Castania crenata var.	*C. crenata* var.	—	Size	McKay & Crane (1939)
C. crenata var.	*C. mollissima* var.	—	Size	McKay & Crane (1939)
C. mollissima var.	*C. mollissima* var.	—	Size	McKay & Crane (1939)
C. mollissima var.	*C. crenata* var.	—	Size	McKay & Crane (1939)
C. sativa var.	*C. mollissima* var.	—	Size	McKay & Crane (1939)
Chamaerops humulis	*Phoenix dactylifera*	Size	—	Jambert, *vide* Rosa (1926)
Cucumis melo var.	*C. melo* var.	Size	Increase in number	Rosa (1926)
Diospyros kaki var.	*D. kaki* var.	Flavour, time of maturity, flesh colour	Development	Hume (1913)
D. kaki var.	*D. kaki* var.	Flavour, shape	—	Noguchi (1934)
Gossypium barbadense var.	*G. hopi* var.	—	Size, lint length, fuzziness	Harrison (1931)
G. barbadense var.	*G. hirsutum* var.	Boll period	Lint length, fuzziness	Harrison (1931)
G. hirsutum var.	*G. barbadense* var.	Boll period	Size, lint length	Harrison (1931)
G. hirsutum var.	*G. hopi* var.	Boll period	Lint length	Harrison (1931)
Morus alba var.	*M. alba* var.	Size	—	Emme & Schablovskaja (1933)
Phoenix dactylifera var.	*P. dactylifera* var.	Size, time of maturity	Size, development	Swingle (1926, 1928)
P. dactylifera var.	*P. canariensis*	Size, time of maturity	Size, shape, development	Nixon (1928, 1935, 1936)
P. dactylifera var.	*R. reclinata*	Size, time of maturity	Size, shape, development	Nixon (1928, 1935, 1936)
P. dactylifera var.	*P. rupicola*	Size, time of maturity	Size, shape, development	Nixon (1928, 1935, 1936)
P. dactylifera var.	*P. roebelenii*	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
P. dactylifera var.	*P. sylvestris*	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
P. rupicola × *P. reclinata*	*P. dactylifera* var.	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)
P. rupicola × *P. reclinata*	*P. reclinata*	Size, time of maturity	Size, development	Nixon (1928, 1935, 1936)

TABLE XLII (*continued*)

Female	Pollinated by	Effect on Fruit	Effect on Seed	Author
P. dactylifera var.	*P. dactylifera* var.	Size, time of maturity	Size, development	Crawford (1936)
P. dactylifera var.	*P. reclinata*	Size, time of maturity	Size, development	Crawford (1936)
Pistacia vera	*P. atlantica*	Length, time of maturity	Development	Peebles & Hope (1937)
P. vera	*P. chinensis*	Length, splitting	Development	Peebles & Hope (1937)
Prunus divaricata var.	*P. domestica* var.	Size, time of maturity	Development	Crane & Brown (1942)
P. divaricata var.	*P. spinosa*	Time of maturity	Development	Crane & Brown (1942)
Pyrus communis var.	*P. communis* var.	Misshapen	—	Crane & Lewis (1942)
P. malus var.	*P. malus* var.	Shape, colour	—	Close (1907)
P. malus var.	*P. malus* var.	Size, colour	—	Lewis & Vincent (1909)
P. malus var.	*P. malus* var.	Size, shape	—	Crow (1913)
P. malus var.	*P. malus* var.	Shape	—	Petrov (1929)
P. malus var.	*P. malus* var.	Size, shape	—	Zederbaur (1926)
P. malus var.	*P. malus* var.	Shape, colour	—	Bach (1928)
P. malus var.	*P. malus* var.	Size, shape, colour, keeping quality, specific gravity, chemical composition	—	Roh (1929)
P. malus var.	*P. malus* var.	Size, shape, colour	Length	Nebel (1930, 1932, 1936)
P. malus var.	*P. malus* var.	Chemical composition, acidity, keeping quality	—	Nebel & Trump (1932)
P. malus var.	*P. baccata*	Size, acidity	Length	Nebel & Kertesz (1934)
P. malus var.	*P. atrosanguinea*	Size, acidity	Length	Nebel & Kertesz (1934)
P. malus var.	*P. malus* var.	Size	Size	Krumbholz (1932)
P. malus var.	*P. malus* var.	Size	—	Hibbard (1934)
Quercus alba	*Q. robor*	Size, time of maturity	Size	Schreiner & Duffield (1942)
Solanum citrullifolium	*S. delilei*	Size, colour	Development	Yasuda & Kitamaru (1930)
S. citrullifolium	*S. aggregatum*	Size, colour	Development	Yasuda & Kitamaru (1930)

parthenocarpic fruits were invariably smaller than the normally developed seeded fruits.

The question is sometimes raised whether the character of the fruit — its shape, colour or flavour — is influenced by the kind of pollen by which it has been fertilised ; whether, for example, Cox's Orange apples will be different according as they have been fertilised by the pollen of a red apple like Worcester Pearmain or a green variety like Lord Derby. In our pollination experiments we have never observed any difference in the colour of fruits which could be attributable to the direct effects of the pollen used in fertilisation. Nebel (1930–32) has, however, reported that he has detected such differences in apples.

Differences in the shape of fruits, however, are often associated with the number and condition of the seeds which develop within the fruit. For example, the apple Golden Spire when self-pollinated often develops parthenocarpic fruits, and the height of such seedless fruits is usually greater than the breadth ; they are also ribbed towards the apex and around the eye. These characteristics may also appear when only a few seeds develop in a fruit, and, if the seeds have developed in adjacent carpels, the fruit is usually more evenly formed on the side where the seeds have developed. When, however, flowers of this variety are adequately cross-pollinated, the resulting fruits usually develop many seeds and often the full complement of ten. Such fruits are much more symmetrical in shape, their height and breadth being almost equal, and the ribbing is scarcely noticeable.

In interspecific pollinations in plums, Crane and Brown (1942) showed that different pollinations can result in differences in the time of maturity and in the size of the fruits. We found that the pollen influences the development of the fruit inasmuch as defective embryos promote earlier ripening and smaller fruits. Further, the wider the difference between the two parents used in the pollinations the more defective the embryos. Thus in these cases the developmental differences in the fruit were an expression of different degrees of seed growth. The work of Tukey (1936) in *Prunus* is also of interest. In plums, cherries and peaches Tukey found that an asymmetrical shape of the fruit is due to one of the two ovules in the carpel failing to develop, the one which does develop into a seed being attached to the larger and better side of the fruit.

In pears similar differences occur and they are often more

pronounced than in apples. Such differences in the shape of pears resulting from self- and cross-pollinations were observed by Waite as early as 1894, and have been reported subsequently by many investigators. There is also evidence that in some varieties of pears the time of maturity and even the flavour differs according to whether they result from self- or cross-pollinations (*vide* Tufts and Philp, 1923), and it is probable that these differences are also associated with the number, condition and genetic constitution of the seeds developed.

Parthenocarpy may be induced in certain varieties of pears by cold temperature. Thus in our pollination experiments at Merton the variety Fertility has never set seedless fruit when grown in a greenhouse where the temperature is always above freezing-point, but it has freely set seedless fruits out-of-doors following frost damage to the styles (Crane and Lewis, 1942). Lewis (1942) has also obtained seedless fruits of the variety Conference after artificial-cold treatment, the flowers being kept in a temperature of $-9°$ C. for 17 hours.

The pollen of the variety Beurré Bedford also induces the formation of parthenocarpic fruits. This variety, although a diploid, produces pollen varying from haploid to tetraploid, and, when applied to other varieties, the abnormal pollen grains frequently stimulate fruit formation without seed.

In recent publications Nebel (1930, 1932 a, b) states that differences in acidity occur in apples, resulting from different cross-pollinations. In an experiment with regard to the flavour of almonds, we found that when we crossed the sweet almond variety Marie Dupuy with the bitter almond *Amygdalus communis amara*, the resulting seed were decidedly bitter, but here, of course, we are concerned with the actual seeds. Among sweet almonds purchased in the ordinary way occasional bitter almonds occur, and it is possible that their occurrence is due to chance cross-pollination. It therefore seems advisable to ensure that no bitter almonds are allowed to grow in the vicinity of sweet almonds grown as an economic crop. In other nuts, such as the walnut, where wide differences in flavour occur, it is also possible that cross-pollination may affect the flavour.

In many plants seed characters, such as the colour of the endosperm we have described in maize and the cotyledons of peas, are directly affected by the genetic constitution of the pollen used in fertilisation.

Heterosis is frequently discussed in connexion with xenia and the two phenomena often overlap. For example, in a paper describing the results of their work with apples Nebel and Kertesz (1934) state: "Xenia of seed length have been shown to occur. Whether the term heterosis is preferable in this case is a matter of definition or interpretation". As we have seen, xenia sometimes has negative and sometimes positive effects. Thus the decrease

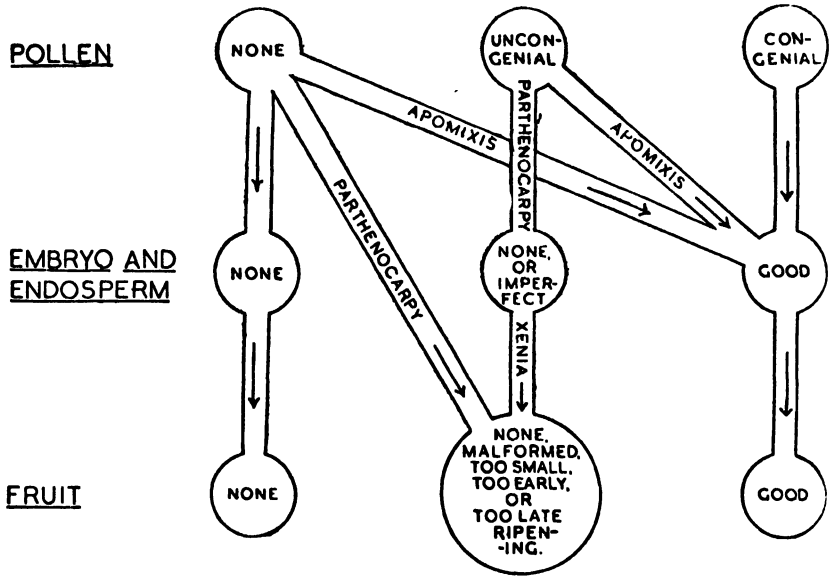


FIG. 58.—Pollination and Xenia. (After Crane and Brown, 1942.)

in size of fruits as occurs in dates and plums can be regarded as negative, and the increased length of lint in cotton as a positive effect. This is similar to the phenomenon of heterosis, where in the next generation the seeds from some pollinations give positive results such as an increase in growth rate, yield, etc., whilst in plants raised from other pollinations no increase and in some cases even a decrease occurs. In the case of xenia the effect is on the maternal tissue of the potential female parent, and in heterosis in the resulting zygote or its offspring. Parthenocarpy and heterosis, indeed all conditions between none and many, bad and good, small and large seeds, may affect the maternal tissue, and such conditions are determined by the absence of or kind of pollen that takes part, or potentially takes part, in fertilisation,

as is diagrammatically shown in Fig. 58. In this figure apomixis is used in a broad sense and includes pseudogamy.

All cases of so-called xenia in which the maternal tissue is affected are doubtless due to differences in the constitution and development of the embryo. That is to say, embryonic differences are transferred to and expressed in the maternal tissues. In most cases no seeds, few seeds or small seeds result in smaller fruits, and often in earlier ripening. In the exceptional cases where late ripening and small seeds go together, it is probably due to a slower rate of embryonic development occurring in the later than in the earlier ripening cases.

CHAPTER XIII

THE ORIGIN OF NEW AND IMPROVED FORMS

In the previous chapters the genetical constitution and behaviour of a range of widely different plants has been described. In this, the concluding chapter, there remain to be discussed in greater detail the different methods and processes by which new forms, varieties and species of plants have originated.

Study of the genetics and cytology of a group of plants is often of the greatest help in elucidating their origin and relationships. Such combined studies have shown that from an evolutionary point of view we can arrange our races of cultivated plants, according to their mode of origin, into four classes, although of course these classes overlap, and selection operates in the majority of cases. These methods by which new varieties and species of plants originate are as follows :

(1) From mutations within a single species.

(2) By simple auto-polyploidy, such as results from the functioning of unreduced germ-cells or from somatic duplication.

(3) By selection from products of inter-specific hybridisation unaccompanied by chromosome duplication or aberration.

(4) By inter-specific hybridisation accompanied by chromosome duplication or nuclear aberration.

Gene Mutations

The part which gene mutations have played in the origin of new and improved plants is well illustrated in the accounts we have given of the sweet pea, the Chinese primrose, the edible pea, the raspberry and other horticultural plants. We have also shown how, by cross-breeding, new characters can as a rule be easily recombined, and further desirable combinations obtained in a relatively short time. In this way the more attractive Spencer type of flower in the sweet pea was rapidly recombined

with other desirable characters and in a short time it completely ousted the typical hooded form from cultivation.

Gene mutations result spontaneously from inherent genetic changes. They are not due to hybridisation, nor, as is sometimes supposed, to the direct effects of cultivation. Indirectly, however, cultivation plays an important part; first on account of the close inbreeding involved, which reveals mutations latent in the stock, secondly on account of selection and vegetative reproduction, which enable mutations to be maintained as distinct strains or varieties, and thirdly on account of the protection which cultivation frequently affords to the less robust forms. Another important result of cultivation is that geographical and ecological barriers are artificially overcome; species distantly separated in nature are commonly brought together in gardens and plantations and this provides opportunities for hybridisation, and, as we show later, has led to very important results.

The Origin of Auto-polyploids

The second way in which new forms of cultivated plants have arisen is by simple auto-polyploidy. In this case the chromosome complement is duplicated, either somatically or as a result of unreduced germ-cells taking part in fertilisation, without hybridisation being involved. The tetraploid forms of raspberries, which include such varieties as Belle de Fontenay, Merveille Rouge, Hailshamberry and Everbearing are auto-polyploids. They appear to have arisen from the diploids in the last eighty years. Raspberries can be grouped into two classes, the (ordinary) summer-fruiting varieties and the autumn-fruiting ones. The former bear their fruits on the previous season's growth, whilst the autumn-fruiting varieties bear on the current season's growth. All the tetraploid, $2n = 28$, varieties are in the autumn-fruiting class, whilst with rare exceptions the diploids, $2n = 14$, are in the summer-fruiting class. The tetraploid, $2n = 48$, race of *Primula sinensis* are giant auto-polyploids. They arose from the diploids, $2n = 24$, spontaneously at the beginning of the present century.

In pears the recent new giant tetraploid forms, $2n = 68$, of the varieties Fertility and Bartlett, arose from their respectively diploid varieties. They appear to be the first tetraploid forms of our European pears, *Pyrus communis*. In grapes the varieties Muscat and Sultanina have thirty-eight chromosomes, whilst their respect-

ive giant forms Muscat gigas and Sultanina gigas have seventy-six.

The above are examples of auto-polyploids which have arisen from a complete duplication of the chromosome complement. Sometimes, as in *Primula*, they have originated through the sexual process, and sometimes, as in pears, vegetatively from somatic duplication. Many new forms have also arisen from unilateral duplication. For example, the triploid varieties of apples and pears apparently arose from the fusion of an unreduced germ-cell, $2n = 34$, with a normal reduced germ-cell, $2n = 17$. Some of the finest varieties of tulip and hyacinth are triploids of a similar origin. In the tulip they include Keizerskroon and Pink Beauty, which are early varieties with exceptionally large flowers, and Massenet, a tallish pink Darwin. The earliest of the triploid varieties to appear was Zomerschoon, which arose in the sixteenth century. The first triploid variety of hyacinth to appear was Grand Maître in 1870. Other triploid varieties are General de Wet, King of the Blues, Lord Balfour and Lord Derby. Triploids are common among plants which are vegetatively reproduced, whether artificially by budding, grafting, cuttings, etc., or naturally by means of bulbs, corms, tubers and other methods, e.g. several of the highly decorative varieties of Japanese cherry are triploids.

Some of the most important varieties of flowers and fruits in the world are triploids. In apples the triploids include the outstanding varieties, Bramley's Seedling, Belle de Boskoop and Baldwin. Bramley's Seedling is probably more widely grown than any other variety of apple in England and is notable for its hardy constitution, admirable cooking qualities and high vitamin C content. Belle de Boskoop, according to a recent questionnaire by Kemmer (1932) is the most popular apple in Germany. Baldwin, according to Hedrick (1922) " is the standard winter apple of eastern America, and is more largely grown than any other variety of this fruit on the Continent ". Ribston Pippin, one of the richest flavoured apples ; Blenheim Orange, one of the best all-round apples in cultivation ; and Gravenstein and Reinette du Canada are other notable triploid varieties. In tulips and hyacinths the giant triploid forms are widely grown and have largely displaced the old diploids from cultivation.

In addition to the auto-triploids which originate in the way described above, triploids also commonly arise from the intercrossing of diploid and tetraploid forms or species. Reference to these will be made later.

Inter-specific Hybrids

The third method by which new plants have arisen is by inter-specific hybridisation between diploid species or between polyploid species, without chromosome duplication or other major cytological aberration being involved. As shown by Bunyard (1917) three species of *Ribes* have entered into the constitution of the garden red currant, namely *Ribes vulgare*, *R. rubrum* and *R. petraeum*. Some of the cultivated varieties strongly favour one or another of these three species, others combine the characters of two, say *rubrum-vulgare* or *petraeum-vulgare*. The three species, and all the varieties examined, are alike in chromosome number, having sixteen chromosomes, two sets of eight.

The account, given in Chapter VII, of the garden strawberries, is an example of the origin of a new race of plants from hybridisation between polyploid species. From all accounts it is clear that the introduction into Europe, and bringing together, of the two octoploid species, *Fragaria virginiana* from eastern North America and *F. chiloensis* from South America, provided the first opportunity of raising the large-sized fruits characteristic of our modern race. The first varieties of this type, combining the large size of *F. chiloensis* with the aromatic qualities of *F. virginiana*, appeared in Europe towards the end of the eighteenth century.

Amongst the many other genera in which species hybridisation, without chromosome doubling, has given rise to new races of cultivated plants may be mentioned *Rubus*, *Streptocarpus*, *Rhododendron*, *Vitis* and *Iris*.

Hybrid or Allo-polyploids

The fourth and most important way in which new forms have arisen is by inter-specific hybridisation in which unreduced germ-cells have taken part, or where somatic duplication of the chromosome complement has subsequently occurred. As before, there is sometimes complete duplication of the complement and sometimes unilateral duplication, i.e. non-reduction of the germ-cell of one parent only. Details are given below of several important races and species of cultivated plants which have originated in this way.

Dahlia variabilis. As shown in Chapter V, the species of

Dahlia excepting *D. variabilis* are tetraploid, 2n = 32, and they can be divided into two classes: (1) where the anthocyanins are cyanidin types and the flowers magenta, and (2) where the anthocyanins are pelargonidin types and the flowers scarlet or orange. The garden dahlia, *D. variabilis*, combines the pigments of the two classes, and it also has twice as many chromosomes, 2n = 64. Combined genetical, cytological and chemical studies (Lawrence and Scott-Moncrieff, 1935) have convincingly led to the conclusion that the octoploid *D. variabilis* with its wide range of colour and form arose in nature from hybridisation between the two types of tetraploid species followed by chromosome duplication. *D. variabilis* was introduced into Europe from Mexico in 1789.

Prunus domestica. Our European plum *P. domestica* has probably arisen on many different occasions in prehistoric and historic times from hybridisation between diploid and tetraploid species, followed by chromosome duplication to give the fertile hexaploid *P. domestica.* Indeed the results of breeding experiments with species and varieties of *Prunus* have led to the conclusion that the diploid species *P. divaricata* and the tetraploid species *P. spinosa* are involved in the origin of *P. domestica* (Crane and Lawrence, 1930). Such a view is supported by a consideration of the variation which occurs within these species; for example, in *P. divaricata* the ground colour of the fruits is yellow and the anthocyanin red. In *P. spinosa* the ground colour is green and the anthocyanin blue, and the range of variation in both species is limited. In *P. domestica*, however, both red and blue colours and also yellow and green grounds occur, and from their various recombinations an infinitely wider range of variation results. The increase in size and wider variation in form and flavour of the fruits of *P. domestica* is also in agreement with the above view. The hypothesis also receives support from recent investigations by Dr. Rybin (1936) in Russia. In correspondence Dr. Rybin informs us that he has raised seedlings from crosses between *P. spinosa* L. and *P. divaricata* Led. (= *P. cerasifera* Ehrl.) One of these seedlings is a hexaploid; it is larger and more robust than the normal triploids of the same origin. Rybin also states: "In the forests of the Maikop district, North Caucasus, both species *P. spinosa* and *P. divaricata* hybridise rather freely. I found many wild-growing hybrids which showed twenty-four chromosomes in the root-tips, and flowered abundantly but were highly sterile. One of these trees bore only six fruits and another

seven. The characters of the branches, leaves, flowers, fruits stones, the colour of the bark and other characters of the hybrid trees showed clearly their close relationship to both parental species. All these facts I think may be regarded as giving strong support to your idea that the European plum *P. domestica* arose by means of hybridisation which took place between the Asiatic species *P. spinosa* L. and *P. divaricata* Led."

Aesculus carnea. Although the precise details are not known, it is generally agreed that the pink-flowered chestnut *A. carnea* arose from hybridisation between two species of distinct sections of the genus, namely the common horse chestnut *A. Hippocastanum* of Europe and Asia, which makes a tree up to 100 feet high, and *A. Pavia* from North America, a comparatively small shrubby species which only attains a height of about 12 feet. Several other well-marked characters separate *A. Hippocastanum* from *A. Pavia.* The fruits of the former are very spiny and the flowers usually have five petals with a patch of colour confined to the base. In *A. Pavia* the fruits are smooth and the flowers only have four petals, which, in contrast to those of *A. Hippocastanum,* are richly coloured and glandular at the margins.

A. carnea is in many respects intermediate between the above two species; it makes a tree 50 to 70 feet high and its fruits are slightly spiny. In habit of growth and foliage it resembles *A. Hippocastanum,* whilst in the colour of its flowers and the glandular edged petals it approaches *A. Pavia.* Although generally accepted as a hybrid, it is usually propagated by sexual means and it has aroused considerable interest both among horticulturists and biologists, first by its fertility and secondly by its behaviour in breeding approximately true from seed. Thus Bean (1914) states: "Plants raised from seed at Kew, about 1896, which are now 20 feet high, have flowered for several years past. They do not differ from ordinary *A. carnea,* or from each other, except in the depth of colour in the flowers. This is rather unusual in the progeny of a hybrid." More recently Hurst (1932) states that of 218 seedlings he raised, only slight variations in the amount of yellow at the base of the flowers and other minor differences were evident. In hybrids from widely distinct parents we are perhaps more familiar with the occurrence of sterility than fertility, and when hybrids are fertile considerable diversity in the progeny and some approach to parental forms is a common expectation. But during the last decade genetical and cyto-

logical research has shown that to expect a distant hybrid always to be infertile or to assume that its parental types will inevitably appear in the second generation is to take too simple a view of the potentialities of inter-specific hybridisation. In this connection cytological studies of *A. carnea* and its parental species have again been of great value in determining the relationships and origin of a new species. Hoar (1927) and Skovsted (1929) found that both *A. Hippocastanum* and *A. Pavia* had twenty pairs of chromosomes whilst *A. carnea* had forty pairs. The chromosomes of *A. carnea* have therefore doubled, and thus given rise to a constant true-breeding new species in which the characters of the two sections of the genus are combined. Thus taxonomic, genetic and cytological studies all confirm the hybrid origin of the species.

Rubus loganobaccus. The loganberry appeared about 1881 in the garden of Judge J. H. Logan, in California, and was originally described as a natural hybrid. The parents were believed to be the Aughinburgh, a form of *Rubus vitifolius*, and a raspberry of the species *R. strigosus*, probably the variety Red Antwerp, since the two were growing close together in the garden when the loganberry appeared. The assumption of its hybrid origin went unchallenged for some years, no doubt on account of the obviously intermediate character of the new form. Subsequently, however, its alleged origin came to be disputed. This disputation arose for various reasons; in the first place, the high fertility of the loganberry seemed inconsistent with the nature of a hybrid derived from such distinct parents. Secondly, its seedlings, although variable, did not show the diversity commonly expected from a distinct cross; that is to say, the supposed parental types of habit and fruit failed to reappear amongst its seedlings. Again, on crossing with blackberries or raspberries, the dominance of many characters of the loganberry seemed essentially like that of a species. Wilson (1906), for example, states that on crossing with the raspberry no true raspberry characters emerge, and in our hybrids with *R. neglectus*, *R. niveus* and other *Rubi*, almost complete dominance of the vegetative characters of the loganberry occurs. For these reasons some authors came to consider the loganberry as a variety of *R. vitifolius* rather than to accept the postulated hybrid origin. However, as we have shown in *Dahlia*, *Aesculus* and *Prunus*, constant and relatively true-breeding hybrids may arise from the hybridisation of very distant species. The loganberry is hexaploid, $2n = 42$, and in his systematic studies

of the genus *Rubus*, Bailey (1923) gave it specific rank as *R. loganobaccus*.

Plants we have raised from seeds of *R. vitifolius* collected in California and kindly sent to us by Dr. H. M. Butterfield proved to be octoploid, 8X = 56. The probable chromosome constitution of the loganberry is therefore: twenty-eight chromosomes derived from *R. vitifolius* and fourteen from the raspberry as the result of the functioning of an unreduced germ-cell. The leaves of *R. vitifolius* are three-lobed, the fruits small, and the sexes borne separately, some plants being male and others female. In the raspberry, both diploid and tetraploid, and in the loganberry, the flowers are hermaphrodite, and the leaves are pinnate, when fully developed bearing five leaflets. In families we have raised from crossing these *Rubi* (Crane and Thomas, 1940) there is a gradation from the three-lobed leaf to the pinnate leaf with five distinct leaflets. This is directly correlated with the proportion of the chromosomes derived from the pinnate-leaved raspberry, as follows :

TABLE XLIII

	Chromosome Number	Proportion derived from Raspberry	Leaves
Raspberry × Raspberry .	2X = 14, 4X = 28	all	Five distinct leaflets
R. vitifolius ♀ × *R. v.* ♂ .	8X = 56	0	Uniformly 3-lobed
R. vitifolius × Loganberry	7X = 49	$\frac{1}{7}$	3-lobed, but more deeply incised than *ursinus*
R. vitifolius × Raspberry (2X)	5X = 35	$\frac{1}{5}$	3-lobed, but more deeply incised than previous family
R. vitifolius × Raspberry (4X)	8X = 56 and 6X = 42	0 $\frac{1}{3}$	3-lobed Five distinct leaflets
Loganberry . .	6X = 42	$\frac{1}{3}$	Five distinct leaflets

The heptaploid and pentaploid families obtained from crossing *R. vitifolius* with the loganberry and the diploid raspberry have 3-lobed leaves and are highly sterile. From crossing with the tetraploid raspberry the plants are of two kinds ; about one-half have fifty-six chromosomes, female flowers and 3-lobed leaves like *R. vitifolius*, and it seems clear that these plants are of an apomictic, non-sexual, origin. The majority of the other plants in the family are hexaploid, 6X = 42, whilst a few are 42 ± 1 or 2, the

latter arising from aneuploid germ-cells of the tetraploid raspberry. The characters of some of these hexaploid seedlings resemble those of the loganberry; they have leaves with five leaflets, hermaphrodite flowers, are very productive and form perfect fruits. The fruits are not quite so large as those of the loganberry, but this may be accounted for by the probability of the named variety of *R. vitifolius*, "The Aughinburgh", having larger fruits than the seedlings of *R. vitifolius* we used in these experiments. In our experiments $\mathbf{F_2}$ families have yet to be raised and studied, but the characters of the 6X seedlings from *R. vitifolius* × tetraploid raspberry, particularly their hermaphrodite flowers and pinnate leaves, strongly support the originally postulated hybrid origin of the loganberry.

The Veitchberry. This hybrid was raised by Messrs. Veitch from crossing the November Abundance raspberry by the hedgerow blackberry, *Rubus rusticanus*. The chromosome complement of the raspberry November Abundance used may have been either diploid or tetraploid. The forms we obtained under this name were triploids; but doubtless these were not the true November Abundance. *R. rusticanus* is a diploid species ($2n = 14$). The veitchberry has twenty-eight chromosomes and is therefore a tetraploid which has arisen by hybridisation and chromosome doubling, either of one or of both parents. The characters of the veitchberry are in several respects interesting, for example, as shown in Fig. 59, the raspberry has pinnate leaves, the blackberry palmate leaves, while the fully developed leaves of the veitchberry are partly pinnate and partly palmate. As in the case of the loganberry, the offspring of the veitchberry vary only in minor respects (Crane, unpublished). Upon selfing there is no approach to either of the parental forms, and upon crossing with other species the behaviour of the veitchberry is typically that of a species. Thus considering the morphological, genetical and cytological results together, it is clear that the veitchberry is a fertile and constant interspecific hybrid.

In a previous chapter we have shown that sterility is a common result of inter-specific hybridisation, but that chromosome doubling invariably restores the fertility of such hybrids. This is due to the identical sets of chromosomes, which arise from the duplication, being able to pair amongst themselves. Thus if we designate the chromosome constitution of the tetraploid veitchberry as **RRBB, RR** representing the raspberry and **BB** the blackberry

complement, and assume that **R** chromosomes pair with **R** and **B** with **B** (autosyndesis), then all the gametes will be of the constitution **RB** and the chromosomes complex of the veitchberry, **RRBB,** will be restored at fertilisation. If, on the other hand, allosyndetic pairing occurred, some of the gametes would be **RR** and others **BB,** and 4n parental types **RRRR** and **BBBB** would reappear in the second generation in addition to **RRBB** types.

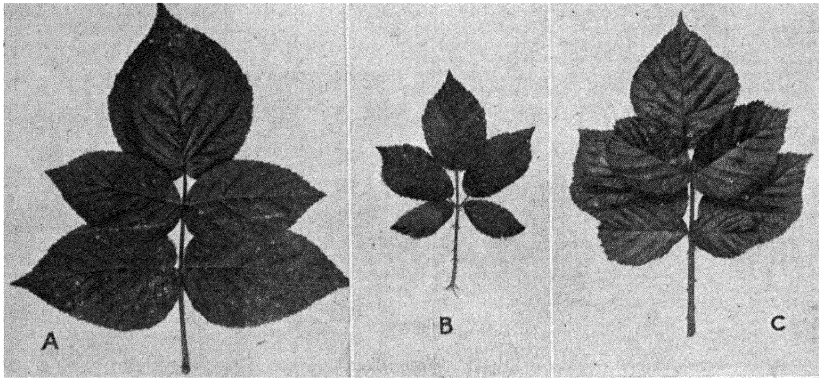


FIG. 59

Leaves of A, Raspberry (pinnate); B, *Rubus rusticanus* (palmate) and C, Veitchberry, partly palmate and partly pinnate.

These forms, however, have not appeared in the progeny of the veitchberry. It breeds practically true, therefore it must be assumed (1) that allosyndesis does not occur or (2) that the only effective gametes are those arising from autosyndesis. Minor variations which occur in the progeny may be attributed to an original heterozygous condition of one or both parents.

The swede *Brassica napus* is another example of a species which has originated from hybridisation and chromosome duplication. As shown in Fig. 60, it appears to have arisen from the cabbage group *Brassica oleracea* (2x = 18) and the turnip group *Brassica rapa* (2x = 20). The swede has 38 chromosomes.

A further example of hybridisation and chromosome duplication giving rise to a new form is afforded by the cytological and genetic studies on strawberries by Ichijima (1926). From intercrossing the two diploid species *Fragaria bracteata* and *F. Helleri* Ichijima obtained a tetraploid plant with twenty-eight chromosomes instead of the expected fourteen. This tetraploid plant

possessed distinct morphological characteristics, and bred true instead of segregating and recombining the characteristics of the parents. The tetraploid plants may be considered therefore to be representatives of a new species—no allo-tetraploid example of *Fragaria* are known to exist in nature.

Brassica napocampestris. From crosses between the turnip, *Brassica campestris* (2n = 20), and the swede, *Brassica napus*

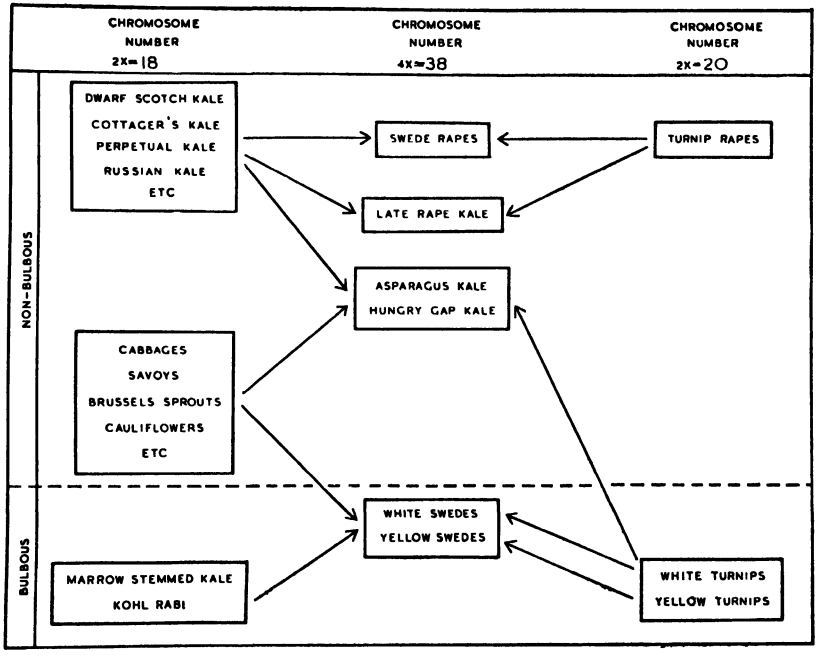


FIG. 60

Showing the origin of the Swede. (After Crane, 1943.)

(2n = 38), Frandsen and Winge (1931) obtained a fertile form. The hybrid *Brassica napocampestris* (2n = 58) is in general intermediate between its parents and is another example of a constant hybrid or new species originating by species crossing and chromosome duplication.

Digitalis mertonensis. The constant hybrid arising from a cross between *Digitalis ambigua* (2n = 56) and *D. purpurea* (2n = 56), described by Buxton and Newton (1928) and Buxton and Darlington (1931), has larger leaves and flowers than either parent. This

new species, *D. mertonensis* (2n = 112), has double the chromosome number of its parents.

Galeopsis Tetrahit. Müntzing (1930–32) crossed *Galeopsis pubescens* (2n = 16) with *G. speciosus* (2n = 16). In the $\mathbf{F}_2$ a triploid plant appeared which to some extent resembled the species *G. Tetrahit.* This triploid was crossed with *G. pubescens* and gave one seedling, a tetraploid (2n = 32). This tetraploid was fertile and in all respects similar to *G. Tetrahit.* The artificially produced *G. Tetrahit* crosses readily with the natural *G. Tetrahit* and gives fertile offspring.

Saxifraga potternensis. Marsden-Jones and Turrill (1930–34) crossed *Saxifraga rosacea* (2n = 64) with *S. granulata* (2n = 48). The $\mathbf{F}_1$ plants were 2n = 56, and in $\mathbf{F}_2$ they obtained a plant 2n = 80. This plant bred approximately true and was named *Saxifraga potternensis.* Philp (1934) from cytological studies concludes that *S. granulata* is hexaploid, *S. rosacea* octoploid, the $\mathbf{F}_1$ heptaploid, and *S. potternensis* decaploid, probably having arisen from unilateral failure of reduction. The origin and genetic behaviour of the new species *S. potternensis* is of interest in view of the possibility of the loganberry also originating from unilateral chromosome duplication, i.e. from non-reduction of its postulated raspberry parent.

Nasturtium officinale. There are two types of cultivated watercress, the so-called summer cress which has green leaves, and the winter cress which has brown to purplish tinged leaves especially when the temperature of the water is low. Recent investigations by Howard and Manton (1946–7) have shown that the chromosome number of the green type is 2n = 32 and the brown type 2n = 48. Until recently watercress was considered as belonging to the single species *N. officinale* (2n = 32), but Howard and Manton have shown that another species which they have named *N. uniseriatum* (2n = 64) is also involved. These two species are distinguishable by their fruits and seeds. The fruits of *N. uniseriatum* are narrow and its seeds are arranged in a single row, whilst those of *N. officinale* are broader and the seeds are arranged in two rows. They have concluded that the green cresses (2n = 32) are varieties of *N. officinale* and the brown cresses (2n = 48) are triploid hybrids between *N. uniseriatum* and *N. officinale.* Like most triploids they are highly sterile, producing seed only occasionally, but since watercress is propagated vegetatively and its commercial product is the leaves and stems

and not the seeds or fruits, its high degree of sterility is an asset rather than a disadvantage.

Howard and Manton have also obtained two new types of watercress which they suggest may be of commercial value: (1) an auto-tetraploid obtained by colchicine treatment from the normal green cress, (2) an allo-tetraploid obtained from crossing this new auto-tetraploid with *N. uniseriatum*.

Delphinium Ruysii. This species arose from hybridisation between *D. nudicaule* (2n = 16), and *D. elatum* (2n = 32). *D. Ruysii* also has thirty-two chromosomes and arose from unilateral duplication on the female side (Lawrence, 1936).

Spartina Townsendii. This species first appeared at the edge of Southampton Water in the year 1870. It was suggested on morphological grounds that it was a hybrid between the local European species *S. stricta* and the American species *S. alterniflora*, which had been introduced from America and was growing side by side with *S. stricta*. *S. alterniflora* was first reported in Europe at Bayonne in 1803 and near Southampton in 1829, and its introduction was attributed by De Candolle (1855) to shipping from America. Huskins (1930) found the somatic chromosome numbers to be *S. alterniflora* (2n = 70), *S. stricta* (2n = 56), *S. Townsendii* (2n = 126). *S. Townsendii* is therefore another example of a new species which has arisen from hybridisation and chromosome duplication. It is fertile and breeds practically true; it has spread with great rapidity and in many places has almost exterminated the original species *S. stricta*. It thus appears to have a higher selective value than its parental species.

Reference to the synthesis of *Galeopsis Tetrahit* and the origin of *Spartina Townsendii* have been made as they directly illustrate how interspecific hybridisation has led to the production of new species in nature, as it does in cultivation. Incidentally the way in which the European and American species of *Spartina* were brought together to give rise to *S. Townsendii* is analogous to the way geographical barriers are overcome in cultivation.

Precise knowledge of the method of origin of particular polyploids is often lacking, but it is clear that the functioning of unreduced germ-cells is a frequent method by which new polyploid forms, varieties and species arise. But the possibility of cells of apomictic origin being fertilised and giving rise to polyploid forms must also be considered. For example, in the genus *Rubus*,

apogamy, resulting in 2n maternal offspring, appears to be frequent. Again, in this genus many cases of new polyploid forms alleged to have arisen from unreduced germ-cells have been recorded. Since, however, apogamy occurs, the question arises as to whether new polyploids always result from unreduced germ-cells, or whether they may not also arise from the union of male germ-cells with 2n maternal apomictic cells.

Somatic doubling of the chromosomes also occurs and the origin of the tetraploid *Primula kewensis* (2n = 36) provides a good example. As reported by Digby (1912), and later by Newton and Pellew (1929), the sterile diploid hybrid between *P. floribunda* (2n = 18) and *P. verticillata* (2n = 18) produced a branch with fertile flowers. Tetraploid offspring (2n = 36) which bred approximately true were obtained from this branch, which had double the chromosome number of the rest of the plant tissue.

In *Streptocarpus* the species *grandis* was crossed with a garden hybrid (Lawrence). The $\mathbf{F}_1$ plants were practically identical in all characters and completely sterile, no seed being obtained after many attempts. Finally a capsule developed from natural pollination. $\mathbf{F}_2$ plants raised from these seeds were identical with the $\mathbf{F}_1$ except that they were larger in all their parts, and fertile. Cytological examination showed that the chromosome number of the two parent forms was 2n = 32, and that of the fertile forms 2n = 64. In this case, therefore, chromosome duplication occurred in the somatic tissue, a phenomenon which has since been twice repeated in this particular sterile hybrid. The strain of fertile tetraploids is highly decorative and has been named Merton Giant. No other tetraploids are known in the genus.

A number of examples of somatic duplication were found by Blakeslee and Belling (1924). On several occasions, mainly after low temperature treatment, they found tetraploid (2n = 48) branches on normal diploid plants of *Datura Stramonium*. These branches gave tetraploid offspring. Branches were also found with an aneuploid chromosome constitution, i.e. $2n \pm 1$. Somatic duplication has also been reported in *Nicotiana* (Clausen and Goodspeed, 1925). *Nicotiana glutinosa* (2n = 24) was crossed with *N. Tabacum* (2n = 48). This cross normally gives triploid hybrids (2n = 36). One $\mathbf{F}_1$ plant, however, was found to be hexaploid (2n = 72) and is believed to have doubled its number of chromosomes after fertilisation. This hexaploid is known as *N. digluta*. The bud-sports of the Fertility and Bartlett varieties of pears,

referred to in Chapter VII, are also examples of somatic doubling, and polyploid somatic cells have frequently been observed in many plants.

During recent years attempts have been made to accelerate mutations and to induce polyploidy by artificial means. Chemicals, extremes of temperature, X-rays and other radiations have all been used to induce or accelerate the rate of mutation. Baur (1931), for example, found in *Antirrhinum* that as many mutations occurred in the year following X-ray treatment as had occurred in the whole of the previous twelve years. Polyploids have also been deliberately produced by decapitation, wounding, etc. In a number of species of *Solanum*, somatic doubling of the chromosomes is found to be readily induced by the decapitation method (Winkler (1916), Jørgensen and Crane (1927) and Jørgensen (1929)). It has also been reported by Shchavenskaya (1937) that by a similar method tetraploids have been obtained in *Brassica* and *Pelargonium*.

In recent years colchicine has been successfully used to induce chromosome duplication, Blakeslee and Avery (1937). By treatment with the same chemical Nebel and Ruttle (1938) have obtained tetraploid forms of Marigold, Tomato, *Dianthus* and other plants. These authors have shown that the action of colchicine is to inhibit spindle formation, thus leading to cells with the doubled chromosome number. *Dianthus* plants were treated in the early cotyledon stage with 0·4 per cent solution for seven hours. Tomatoes were treated with colchicine in aqueous solution and with colchicine in lanolin, and from all treatments tetraploid shoots were obtained. Cuttings of *Tradescantia* were treated with 0·2 per cent for four hours. In the control, untreated cuttings, the number of pairs of chromosomes at metaphase was uniformly six. In most of the treated cuttings cells with twelve pairs of chromosomes occurred, and occasionally cells with twenty-four pairs were found.

For producing polyploid plants, by the use of drugs such as colchicine, treatment of dormant or relatively inactive tissue is least effective. It is probably due to this that, so far, success has been mainly obtained by treating plants with relatively soft tissues which produce new growths freely and rapidly, e.g. annual or herbaceous plants such as antirrhinum, marigold, tomato, tradescantia, etc. The effectiveness of the treatment is directly proportional to the degree of mitotic activity. The aim of the

treatment is to induce chromosome duplication in the cells of the growing point, i.e. those cells which will develop into a new shoot, and the best results are obtained by early treatment such as on germinating seeds or young seedlings or young shoots. The usual method is to soak germinating seeds or young shoots in a weak solution of colchicine or to apply drops to the growing point of a seedling or young branch. Since the drug is only effective when there is active cell division, it is important to encourage rapid growth. Sometimes this can be achieved in plants which are normally slow-growing by removing the seed coat and growing them at higher temperatures. For example, with apples and pears Thomas (1945) obtained the best result by dissecting out the

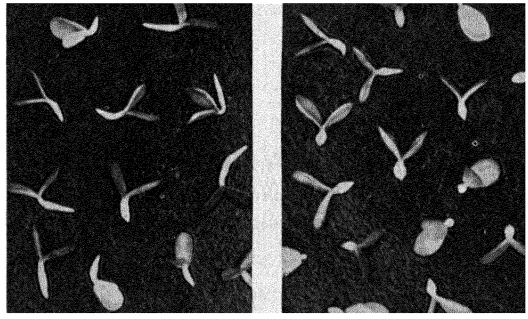


FIG. 61

A, untreated and B, colchicine treated apple seedlings. Note the treated seedlings have bulbous swellings on the roots which indicate successful treatment. (After Thomas.)

embryo of seeds freshly removed from the fruit before treatment. Under these conditions of most rapid growth the most severe treatment can be given. This results in a high proportion of cells in mitosis and the highest proportion in these of regression anaphases, i.e. of new tetraploid nuclei. Where treatment has been effective, growth is often temporarily stopped and the root tips are swollen or bulbous (see Fig. 61); this is mainly due to the polarisation of mitosis being upset. With such material the aim should be to select the most retarded plants and nurse them back to normality by growing them in a moderate high temperature and moderately humid conditions.

It is probable that one of the most valuable uses of colchicine

lies in the restoration of fertility in sterile hybrids by chromosome duplication.

Lewis (1943, unpub.) is using a different and novel method for producing polyploids by the use of heat shocks and by what he calls the incompatibility sieve. The heat shock, 45° C. for 1–2 hours, is given to branches of fruit trees in pre-zygotene or 2nd metaphase of meiosis by means of a thermostatically controlled heating cylinder. This gives rise to a proportion of diploid pollen grains. The resulting mixture of haploid and diploid pollen is then applied to incompatible styles, in which only the diploid pollen functions, thus giving triploid seedlings. Triploid types of apples, Beauty of Bath, Northern Spy and Cox's Orange, and pears, Fertility and Conference, have been produced. An adjunct to the colchicine method for vegetative tissues has also been applied. In some plants X-rays as a cell-killing agent are twice as effective on diploid as on tetraploid cells, and as a result a suitable dose of X-rays given to the chimaerical tissues that frequently result after colchicine treatment kills undesired diploid cells, leaving the tetraploid parts to regenerate into new shoots.

The possibilities of obtaining fertile progeny from cross-breeding in polyploid genera are often limited by the numerical relations of their chromosome complements. For example, the offspring from a diploid crossed with a tetraploid will be triploid, and those from a tetraploid crossed hexaploid will be pentaploid and usually highly sterile, but, as we have already described, exceptional seedlings may occasionally arise from such crosses, and the following are further instances. When we crossed *Rubus rusticanus inermis*, a diploid species with fourteen chromosomes, with *Rubus thyrsiger*, a tetraploid species with twenty-eight, we obtained four seedlings. Three of these were triploids arising from the addition of seven *rusticanus* and fourteen *thyrsiger* chromosomes, the haploid or reduced number for each species, and, as would be expected, these seedlings were highly sterile. The other seedling had twenty-eight chromosomes, and arose from the functioning of an unreduced egg of its mother, whereby the full chromosome complement of *rusticanus* (fourteen) combined with the haploid complement of *thyrsiger* (also fourteen) to give rise to a tetraploid plant with twenty-eight chromosomes (Fig. 62). This tetraploid seedling, named "John Innes", is highly fertile and very productive, and contrasts sharply with

its sister triploid seedlings, which only set occasional drupels (see Fig. 62).

In such cases as the above, where the sexual process is essential for the purpose of obtaining either seed or fruit, fertility is of the first importance. But in ornamental plants which can be readily reproduced asexually, sterility may not necessarily concern the practical grower. Indeed, in some respects it may be rather an asset than otherwise. For example, many of the Japanese cherries which are grown for a display of flowers are triploid and highly sterile. They do not expend energy and exhaust themselves in the production of heavy crops of fruit, and as a result they invariably flower abundantly year after year. The same applies to many other vegetatively propagated ornamental trees, shrubs and herbaceous plants.

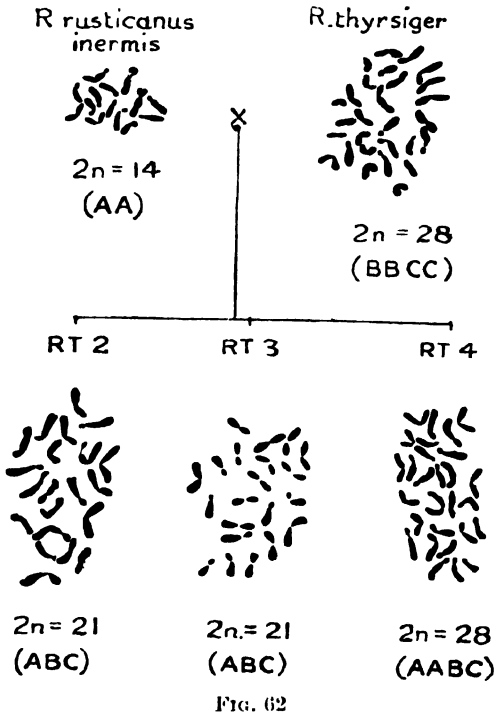


FIG. 62

Showing the origin of the *Rubi* RT 2, RT 3 and RT 4. (After Crane and Darlington, 1927.)

The consequences of the different methods of origin of plants are seen in various ways, and, when we compare the studies of the systematist, the geneticist and the cytologist, a striking parallelism is frequently evident in their results and conclusions. Thus the systematist long ago found that he could satisfactorily classify the variation within *Prunus persica* according to whether individuals had smooth or hairy fruits, eglandular or glandular leaves, small or large flowers and so on. The geneticist found that the mode of inheritance of these characters conformed to the comparatively simple mendelian rules ; and the cytologist found

Prunus persica to be a simple diploid plant with two sets of eight chromosomes. At the other extreme, numerous attempts have been made to provide a really satisfactory classification of apples, *Malus malus*, but systematists continue to find such a classification an involved and difficult task. The geneticist and practical breeder are likewise beset with many problems, and find our cultivated apples difficult to analyse; and, finally, the cytologist

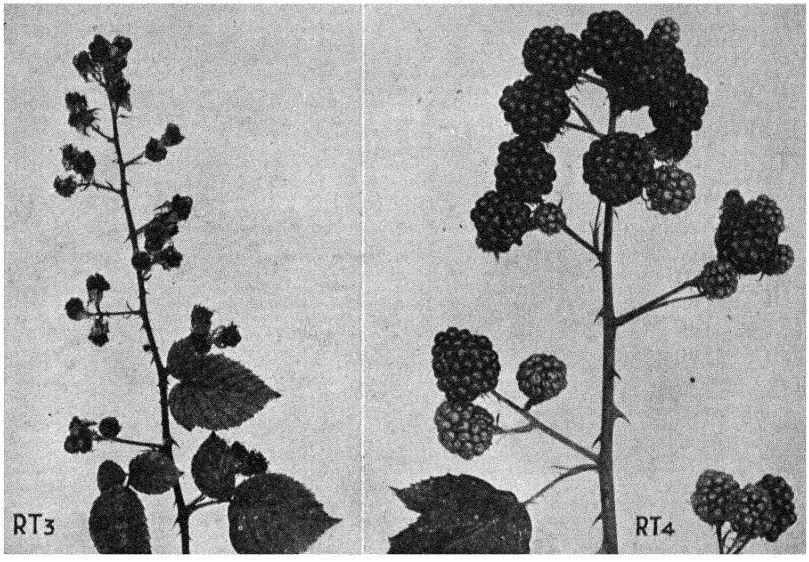


FIG. 63

Sister seedlings, RT3 (2n = 21), RT4 (2n = 28), from the cross *R. rusticanus inermis* (2n = 14) × *R. thyrsiger* (2n = 28). (After Crane and Lawrence, 1931.)

has found them to be secondary polyploids with a complex nuclear constitution.

It is not only in respect to morphological characters that such differences are seen, but also in the chemical and physiological processes of plants. Thus, as we have shown in Chapter IX, sexual incompatibility, both in inheritance and in its phenotypical behaviour, is a comparatively simple phenomenon in the diploid cherry, *Prunus avium*; it is more complex in the hexaploid plum, *Prunus domestica*, and most involved in the secondarily polyploid apple. A comparison of the early seedling growth of diploids and polyploids is again often of interest. In seedlings of diploids such as the sweet cherry, peaches and nectarines there is no period of

juvenile growth comparable to that found in the polyploid plums, apples and pears. The leaves of seedling cherries and peaches are of course smaller during the early weeks of growth, but after a few months their leaves are practically as large as those of established specimens twenty or more years old. In plums, apples and pears, however, there is a prolonged juvenile period of growth, characterised by small leaves and a semi-spinous habit, which seedlings have to grow out of before flowers and fruits are formed. In our experience cherries and peaches come into bearing at an earlier age than plums, and plums usually grow out of the juvenile condition quicker than apples and pears.

Although exceptions occur, it is a commonplace to find a more complex and wider range of variation in polyploid species, and specially in high polyploids than in diploids; compare, for example, the variation within the diploid *Prunus divaricata* and the tetraploid *Prunus spinosa* with that in the hexaploid *Prunus domestica*, also the variation within the tetraploid species of *Dahlia* with that of the octoploid *D. variabilis*. Again, variation is, as a rule, sharply discontinuous in diploid plants, but in polyploids it is often more of a continuous nature, owing to the presence of a greater number of gene differences. As we have shown in previous chapters, where two or more genes govern the expression of the same character, as is common in polyploids, their effect is often cumulative, and consequently a given character may intergrade from one extreme to the other. Although new forms and species which arise from interspecific hybridisation reproduce themselves as new and distinctive types, great variation may occur subsequently as a result of recombination and interaction of the many different genes brought together. These are the kinds of complications which have frequently caused practical breeders of plants to doubt the truth of the mendelian theory of heredity. The simple ratios and simple laws of inheritance they have been led to expect, from the early investigations with such diploid plants as the sweet pea, Chinese primrose, etc., did not seem to apply to such plants as dahlia, chrysanthemum, carnations, plums and apples. The phenomenon of dominant and recessive characters was often obscure, and simple segregation was not always evident. However, as we have previously pointed out, in the case of polyploids where a number of cumulative and differential genes may govern the same character, the expression of dominance is essentially more variable. Indeed, certain balances may suggest that a

character is recessive, whereas others may point to dominance. Since the complexity of the nucleus and the manner of chromosome pairing is reflected in the range and nature of the variation and in the mode of inheritance of characters, the practical breeder must expect to find different degrees of complexity in the hereditary behaviour of plants.

The action and cumulative effects of genes are well illustrated by the investigations of Mangelsdorf and Fraps (1931) relating to the number of genes for pigmentation in the cells of the endosperm and the amount of vitamin A in the seed of maize. As in most of the angiosperms, the endosperm of maize results from a sexual fusion in which two maternal nuclei combine with one male nucleus. The endosperm is therefore triploid in its chromosomal constitution, and this permits of four classes of seed differing in the proportion of dominant and recessive genes. Hence in respect of the factor for yellow pigmentation, the cells of the endosperm may have none, one, two or three genes for yellow pigment with the corresponding constitution **yyy**, **yyY**, **yYY**, **YYY**. These four classes are approximately white, pale yellow, dilute yellow and deep yellow respectively. By making appropriate pollinations these four classes of seeds were obtained, and their vitamin assay determined by feeding to albino rats. The results obtained from experiments carried out in 1928 showed a high degree of association between the number of **Y** genes present in the endosperm and the number of units of vitamin A per gram of the material. The experiments were repeated in 1929 and again an almost complete association was shown. The average results for the two years were as follows:

TABLE XLIV

No. of Genes for yellow	Factorial Composition of Endosperm	Units of Vitamin A per gram		
		1928	1929	Average
0	yyy	0·05	0·05	0·05
1	yyY	2·50	2·00	2·25
2	yYY	5·00	5·00	5·00
3	YYY	7·00	8·00	7·50

These results show, firstly, that a white-seeded variety of maize, the endosperm of which ordinarily has little or no vitamin A, is capable of forming this substance in its seeds if the gene for yellow pigmentation is introduced, the only difference in the seeds

being in the microscopic pollen nuclei which entered to produce the endosperm. Secondly, the results show that there is a direct quantitative relationship between the number of genes for yellow in the cells of the endosperm and the amount of vitamin A in the seed, each gene for yellow inducing approximately 2·5 units of vitamin A per gram of seed.

In the apple there is a considerable variation in the vitamin C content, both among the diploid and triploid varieties, and there is some evidence (Crane and Zilva, 1932) that an association may exist between the chromosome number and the amount of antiscorbutic vitamin present.

When polyploids are compared with diploids, an increase in size is frequently evident. For example, the tetraploid forms of *Primula sinensis*, *Primula kewensis*, *Campanula* Telham Beauty, the triploid tulips and hyacinths, the tetraploid pears, and the octoploid garden strawberries are much larger than the corresponding diploid forms. In the genus Iris, Simonet (1929–32) found a correlation between the size of the flower and the chromosome number. Thus *Iris variegata*, 2n, has a comparatively small flower, whilst in the varieties Isoline, 3n, Altair, 4n and Magnifica, 5n, the flowers are larger as the chromosome number increases. A further example of increase in size accompanying polyploidy occurred when we crossed the small diploid blackberry *Rubus rusticanus inermis* with the tetraploid species *R. thyrsiger*. The exceptional $\mathbf{F}_1$ tetraploid seedling from this cross, to which we have previously referred, gave a proportion of $\mathbf{F}_2$ seedlings without prickles like *R. rusticanus inermis*, and, as shown in Fig. 64, these tetraploid forms without prickles are much larger than the diploid form of inermis in all characters. In the tetraploids a degree of sterility is expressed in slightly imperfect fruits, but with further breeding it should be possible to obtain fully fertile tetraploids without prickles and with perfect fruits. Since the original edition of this book appeared, a further generation of these prickleless tetraploids has been raised (see Fig. 65) and, as predicted, among them are appreciably more fertile forms.

During the past two or three decades considerable progress has been made in the breeding of agricultural crops for specific purposes. A notable achievement was the breeding of bread wheat for resistance to rust. At the present time much breeding work is being done with horticultural crops in an attempt to combine such characters as early maturity, resistance to cold,

drought, disease, etc., with size, quality and other desirable characters. One of the earliest investigations of this kind was begun by the late Dr Saunders in Canada. Saunders' problem, as described in his report (1911), was to combine the desirable characters of cultivated apples, which are too tender to withstand the extreme cold of parts of Canada, with hardiness. He began his experiments in 1887 by obtaining from Russia seeds of the small Siberian crab *Malus baccata*, which flourishes in such extreme temperatures as minus 30° F. The seedlings raised proved to be completely hardy in Canada. In 1894, when the seedlings of *Malus baccata* began to flower, Saunders made crosses between them and many of the cultivated varieties. About 800 of the cross-bred seedlings were raised and the best of them were tested in the cold prairies of the Canadian North-West and proved to be hardy. The fruits of these seedlings, although comparatively small, were from twelve to fourteen times larger than the fruits of *M. baccata*. Saunders back-crossed some of these F_1 seedlings with the large-fruited cultivated varieties and raised several hundred more seedlings. Among these back-crossed families hardy seedlings appeared with fruits of pleasant flavour and a far greater size than those previously raised. It is therefore evident that hardiness in the apple is transmissible, and there is no obvious reason why further breeding experiments, being continued by Saunders' successors, should not give rise to even better hardy varieties of apples.

Experiments we are carrying out in conjunction with the East Malling Research Station have shown that the resistance to the apple woolly aphis, *Eriosoma lanigerum*, possessed by the variety Northern Spy is a heritable character. In families raised from crossing this immune variety with some of the susceptible Paradise root-stocks, both immune and susceptible seedlings occur, as shown in Fig. 66. As a result of these investigations, Crane, Greenslade, Massee and Tydeman (1936) have shown that the hereditary behaviour of immunity to the woolly aphis is complex and in several respects exceptional. Seedlings in the same family grade from high susceptibility to complete immunity as follows :—

Group I. Immune.
„ II. Infections slight, not permanent.
„ III. Attack slight, but small colonies and small glands form.
„ IV. Whole seedling attacked; severe infestation, but late in year.
„ V. Seedlings killed by severity of attack.

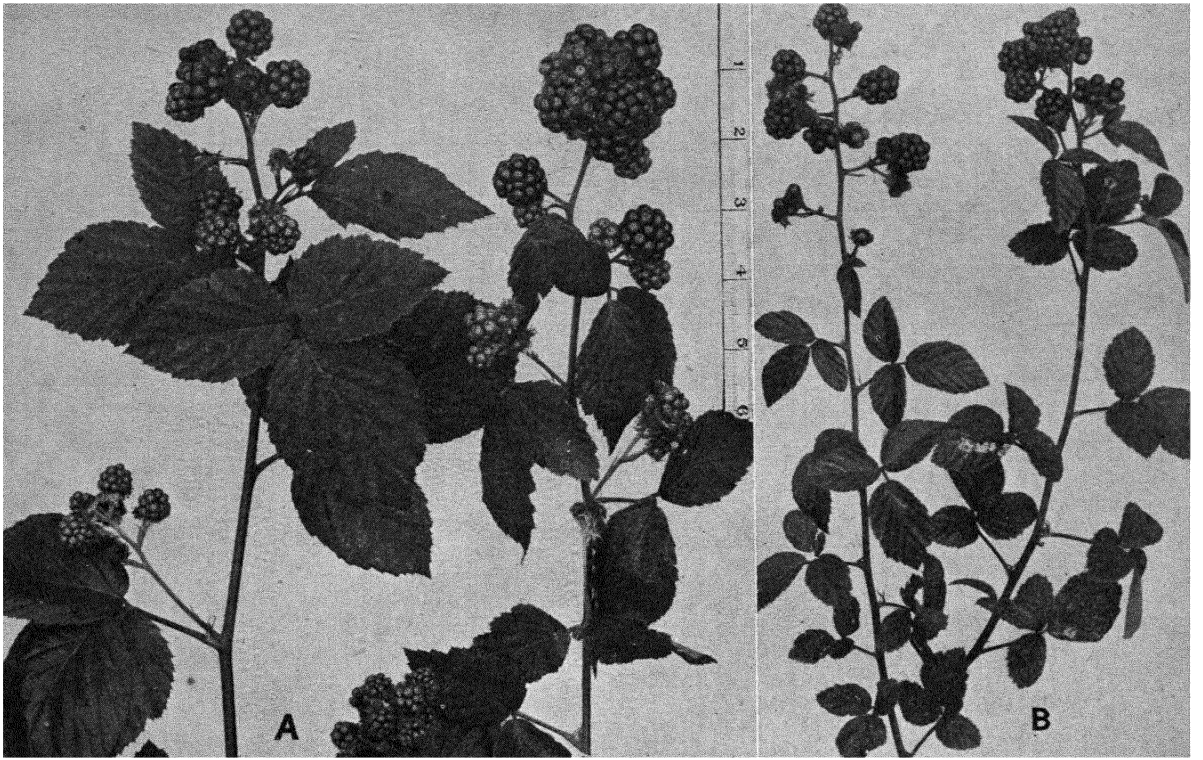


FIG. 64

A, *Rubus* thornless (tetraploid), 2n = 28. B, *Rubus rusticanus inermis* (diploid), 2n = 14. From *R. rusticanus inermis* × *R. thyrsiger*.

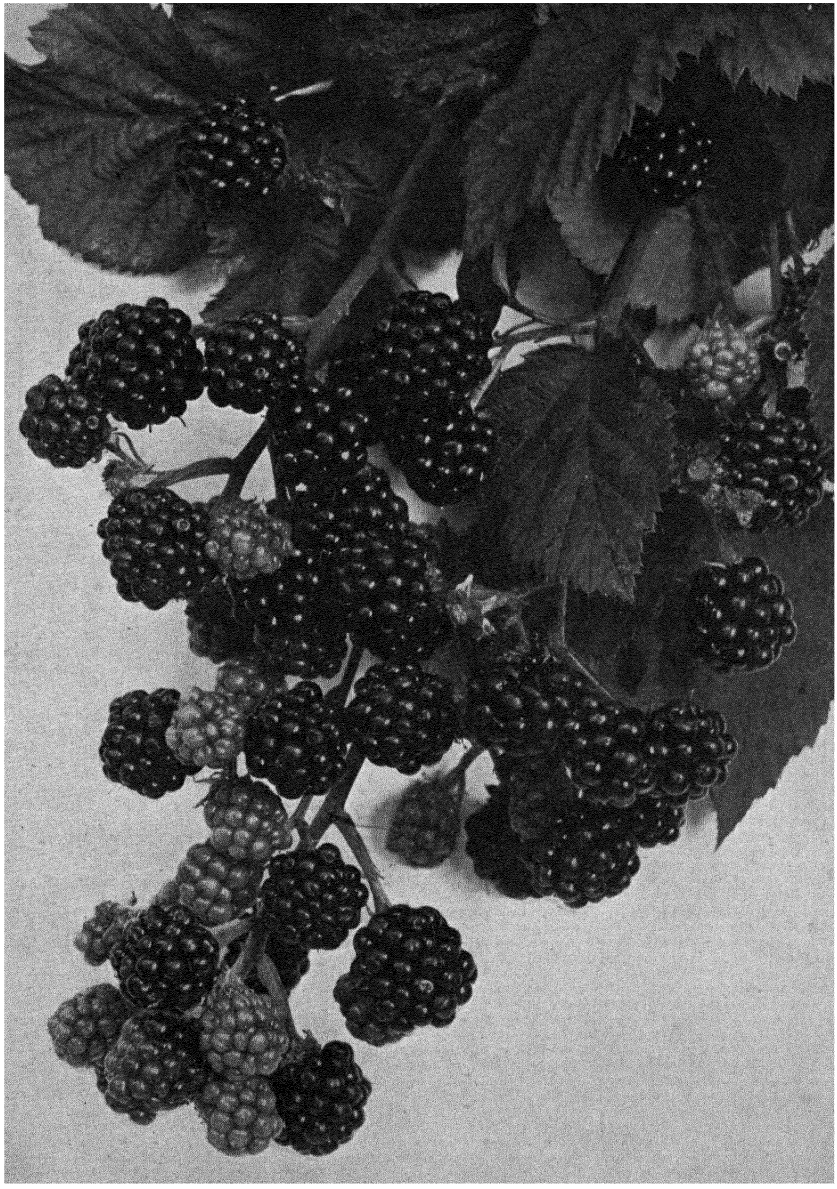


FIG. 55

Rubus Merton Thornless (2n = 28), F_3 from *Rubus rusticanus inermis* (2n = 14), crossed *Rubus thyrsiger* (2n = 28). This character segregates approximately 22 plants with thorns to 1 thornless, see pages 37 and 38.

Some crosses between susceptible and immune gave all susceptible offspring. At the other extreme, the highest proportion of immune seedlings, 47 per cent, was obtained by crossing susceptible with immune, whereas 33 per cent was the highest proportion of immune obtained from crossing immune with immune. An analysis of the results shows that the susceptible forms are genetically of different kinds; some possess factors concerned



With acknowledgments to Mr. A. M. Massee.

FIG. 66

Apple seedlings: A, immune; B, susceptible to Woolly Aphis. Raised from Doucin susceptible, crossed Northern Spy, immune.

From *The Apple*, by Sir Daniel Hall, K.C.B., F.R.S., and M. B. Crane, by courtesy of Messrs. Martin Hopkinson, Ltd.

with immunity, others do not. The immunes are also of different kinds, and, amongst the crosses so far made, the immune variety Northern Spy has a higher value in respect of the hereditary transmission of immunity than any of the other immune varieties used. It is tentatively concluded that the immunity of apples to the attack of the woolly aphis is determined by and dependent upon a certain balance of genetic factors and that it is governed by a number of genes, the action of which is in part complementary and in part cumulative.

The woolly aphis is a stem and root feeder and in some parts

of the world it is particularly difficult to control, owing to the fact that at all times of the year the insect may live both on the branches and on the roots of the trees. Therefore, if the branches are cleaned of the pest by spraying or other means, reinfection is liable to follow from the roots. In this country root infestation is rare, but in some countries, such as Australia, South Africa and parts of the United States, root infestation is often serious. The feeding of the aphides gives rise to galls which may retard or even kill the young growth of trees. They also provide entry for fungi, and render young trees unsaleable. The primary aim of the present experiments is to obtain rootstocks possessing the necessary pomological characters which are also immune to the attacks of the woolly aphis. Since, however, immunity has been shown to be a heritable character, there is no reason why it should not be combined with vigour of growth, fruit colour, size and other characteristics which determine a good cultivated apple.

According to Baur (1931), the profitableness of the grape-growing industry in Germany has been almost wholly destroyed by *Phylloxera* and *Plasmopara*, the vine louse and vine mildew, and the cost of fighting these pests amounts to between thirty and fifty million marks annually. In an attempt to obviate this heavy expenditure Baur initiated large-scale investigations at the plant-breeding station at Müncheberg and the Institute for Phylloxera Research at Naumberg. The object was to breed grapes which combined high quality with resistance to the two pests. In North America varieties of the vine *Vitis rupestris* are resistant both to *Phylloxera* and *Plasmopara*, but the berries are poor in quality. The *rupestris* varieties can, however, be crossed with the high quality varieties of the susceptible European grape vine *Vitis vinifera*. Baur states that the hybrids between these species are perfectly fertile, and that among the numerous types which segregate in the subsequent generations it is expected that some few types will occur representing the ideal combination of absolute resistance to *Phylloxera* and *Plasmopara* on the one hand, and high quality of *vinifera* berries on the other. Baur (1931) stated that in a search for these types about 500,000 seedlings are grown annually at the Müncheberg Institute. In a more recent publication (1933) five to ten millions was stated to be the number of seedlings grown. All the seedlings are artificially infected and tested for *Plasmopara*, and only the few which prove absolutely resistant are retained. These are grown on and

their vigour and fruit qualities determined. Selected seedlings are then passed on to the Phylloxera Research Station to enable them to be tested for resistance to *Phylloxera*. Baur stated that the work was very expensive, but he calculated that in about ten years the desired types would have been found, and the enormous annual expenditure on spraying, etc., rendered unnecessary.

The exhaustive plant-breeding experiments carried ont by Vavilov and his colleagues in the Soviet Union have been reported upon in a joint publication of the Imperial Bureaux of Plant Genetics (1933). Realising the limitations and inadequacy of the material at their disposal, the Soviet breeders have sent expeditions to many parts of the world and have made an unrivalled collection of plant-breeding material. Among the numerous horticultural crops they have under investigation are cabbages, peas, beans, potatoes, artichokes, tomatoes, carrots, beets, onions, melons, strawberries, raspberries, gooseberries, pears, apples, cherries, currants, peaches and grapes. The aims of these exhaustive experiments include breeding for the improvement of quality, early and late maturity, resistance to cold, drought, and disease, and many other purposes. The economic aspects of sterility and incompatibility, the induction of mutations and polyploidy and the practical possibilities of certain forms of plant chimaeras are also being investigated. The report on their investigations is in many ways unique, and, as a result of their systematic study of plants on a world scale, it is clear that many possibilities remain in the field of plant breeding. The following quotation from Vavilov, with reference to the potato, shows the far-reaching possibilities of the material they have collected: "Our ideas of such plants as the potato have been entirely revised, the whole work of breeding and genetics having been formerly based on one Linnean species (*Solanum tuberosum*), whereas the expedition to South America disclosed the existence amongst the cultivated potatoes at its original home of no less than thirteen well-defined Linnean species, many of which are of great practical interest. These species differ from one another in chromosome number, morphological and physiological characters and area of distribution. They contain species and forms extremely resistant to diseases and frost. The potatoes formerly known to geneticists and breeders were only fragments of one species, collected at random by the first travellers, and on these the whole of the breeding and genetic work of the nineteenth

and the beginning of the twentieth century has been based."

An expedition was sent to South America in 1939 by the Imperial Agricultural Bureaux and the numerous indigenous wild and cultivated potatoes they collected have been described by Hawkes (1944). Like Vavilov and his colleagues, they collected species and forms with valuable economic characters. Several of these, such as *S. lanciforme*, which is immune to blight, *Phytophthora infestans*, and *S. polyadenium*, which is aphid-repelling, are diploids. As shown in Fig. 67, with modern technique tetraploid forms of these species can be induced and used for crossing with the tetraploid varieties of *S. tuberosum*.

The improvement of plants by systematic breeding and selection is often a long process, since in the breeding of a new character there are so many others which must not be overlooked. It may be quite possible to breed a plant possessing resistance to a certain disease, but if, in the process, desirable characters are lost or adversely modified, e.g. quality and yield, the new plant may be valueless to the grower, even though it is completely immune to a troublesome disease. Again, a plant may be produced which is eminently suitable for localised areas but unsatisfactory in others. At the present time throughout the world much effort is being concentrated on breeding for disease resistance, and much has been accomplished in breeding plants resistant to drought and extreme cold. In America a profitable investigation has been the breeding of tobacco plants with a very high nicotine content, for use as a source of a valuable insecticide. In Germany, and later in Russia, the breeding of lupins which are free of poisonous alkaloids has provided a new and important forage crop. This achievement is all the more valuable since the lupin thrives on poor, light, sandy soils upon which most crops are unprofitable.

To give an outline of the breeding of plants for economic purposes and the achievements attained would require a large manual to itself, but it will be evident from the few examples given above that even a moderate improvement attained by breeding may run into huge sums in the economy of a nation.

In an earlier chapter we described how the phenomenon of hybrid vigour was being utilised in certain agricultural crops. It is highly probable that the increase in yield and other advantages which are associated with hybrid vigour could be successfully utilised in a number of horticultural plants. Since, however, hybrid vigour is at a maximum in the generation immediately

following a cross, the cost of producing cross-fertilised seed by artificial pollination may in some cases render its use unprofitable. Where, however, the sexes are borne on different plants, or on different flowers, as in the cucumber, crossed seeds are easily obtained. In the tomato, where numerous seeds are obtained from each pollination, the production of crossed seed should not be too costly for it to be practised commercially. The capital outlay and the cost of growing these crops under glass is very



A B

FIG. 67

Solanum polyadenium. A, normal diploid 2n = 24. B, tetraploid 2n = 48 obtained by treatment with colchicine. (After Thomas.)

high, and any appreciable increase in yield would well repay the extra cost of producing cross-fertilised seed.

From the details given in this chapter it is clear that mutation, polyploidy and hybridisation are fundamental to plant improvement. They are the principal causes of variation and the process by which evolution continues, and real progress in plant breeding depends ultimately on the acquisition of knowledge which will lead to the control of these processes.

APPENDIX I

CHROMOSOME NUMBERS OF CULTIVATED PLANTS

In this Appendix are given the chromosome numbers of the species and varieties of plants mentioned in the text. In some cases the numbers of additional related species are given.

As shown in the text, in most genera series of multiples of a common basic number occur as a result of chromosome multiplication. In some genera, such as *Verbena* and *Brassica*, more than one basic number is found. The basic number is denoted by the letter x. The somatic number of the plant is represented by 2n ; thus the germ-cell number, where this is a regular one, will be n. Where 2n is an odd multiple of x, as in triploids, pentaploids, etc., and in aneuploids, no regular value can be given for n, nor, as described in the text, can such forms breed true by sexual reproduction. The possibility of error in recent determinations of chromosome number is slight, and where more than one number has been given for one species or variety this may be due to inaccurate naming of the material, or to the occurrence of two or more chromosome numbers within the species.

For particulars of the material examined, reference must be made to the original papers, or to *The Chromosome Atlas of Cultivated Plants* (1945). In most cases they are referred to in the text and cited in the Bibliography (Appendix III).

	2n		2n
ABUTILON x = 8		*AESCULUS* x = 20	
hybridum	16	*Hippocastanum*	40
striatum		*Pavia*	40
var. Thomsonii	16	× *carnea*	80
ACONITUM x = 8		*ALLIUM* x = 8	
heterophyllum	16	*Cepa* (onion)	16
paniculatum	16	*Porrum* (leek)	32
variegatum	16		
vulparia	16	*ANCHUSA* x = 8	
× *sterile*	24	*Barrelieri*	16
× *Stoerkianum*	24	*capensis*	16
Anthora	32	*hybrida*	16
chinense	32	*officinalis*	16
Napellus	32	*ochroleuca*	24
palmatum	48	*italica*	32
Wilsoni	64	var. Dropmore	32

	2n
ANCHUSA—continued	
italica—continued	
var. Opal	32
Pride of Dover	32
ANTIRRHINUM x = 8	
Linkianum	16
majus	16
APIUM x = 11	
graveolens (celery)	22
ARABIS x = 8	
albida	16
alpina	16
hirsuta	32
BERBERIS x = 14	
Darwinii	28
empetrifolia	28
Veitchii	28
buxifolia	56
BETA x = 9	
maritima	18
vulgaris (Beet)	18
BRASSICA x = 9	
oleracea (cabbage)	18
v. capitata	18
Napus (Swede)	38
x = 10	
campestris	20
Rapa (turnip)	20
× *napo-campestris*	58
CALLISTEPHUS x = 9	
chinensis	18
CAMPANULA x = 8	
nitida	16
persicifolia	16
var. Telham Beauty	32
CHEIRANTHUS x = 7	
Cheiri	14
cinereus	28
Allionii	42

	2n
CHRYSANTHEMUM x = 9	
carinatum	18
coronarium	18
japonicum	18
segetum	18
alpinum	36
indicum	36
Leucanthemum	36
hakusanense	54
morifolium	54
Decaiseneanum	72
arcticum	90
marginatum	90
CICHORIUM x = 9	
Intybus (chicory)	*ca.* 18
CREPIS x = 4	
dioscoridis	8
CROCUS	
vernus	8, 18, 19
CUCUMIS x = 12 and 7	
Melo (melon)	24
sativus (cucumber)	14
CUCURBITA x = 20	
Pepo (marrow)	40
CYDONIA x = 17	
japonica	34
Maulei	34
vulgaris (Quince)	34
CYTISUS x = 12	
Adami	48
purpureus	48
DAHLIA x = 8	
coccinea	32
coronata	32
imperialis	32
Maxoni	32
variabilis	64
Merckii	36

	2n
DATURA x = 12	
Stramonium	24
DAUCUS x = 9	
carota sativa (carrot)	18
DIGITALIS x = 7	
ambigua	56
purpurea	56
mertonensis	112
DELPHINIUM x = 8	
nudicaule	16
elatum	32
hybridum	32
× *Ruysii*	32
belladonna	48
EUCHLAENA x = 10	
mexicana	20
FRAGARIA x = 7	
vesca	14
semperflorens	14
elatior	42
chiloensis	56
virginiana	56
GALEOPSIS x = 8	
pubescens	16
speciosa	16
Tetrahit	32
HYACINTHUS x = 8	
orientalis	
var. Hofdijk	16
Homerus	16
L'Unique	16
Marchioness of Lorne	16
Roi des Belges	16
Spring Glory	16
Yellow Hammer	16
Grand Maître	24
King of the Blues	24
Lady Derby	24

	2n
HYACINTHUS—continued	
orientalis—continued	
var. Lord Balfour	24
Moreno	24
Queen of the Pinks	24
L'Innocence	27
La Grandesse	28
Totula	30
amethystinus x = 12	24
HYDRANGEA x = 18	
arborescens	36
paniculata praecox	72
petiolaris	36
IRIS x = 12	
pallida	24
variegata	24
cypriana	48
macrantha	48
mesopotamica	48
trojana	48
var. azurea	36
Isolino	36
Altair	48
Magnifica	60
x = 10	
chamaeiris	40
olbiensis	40
x = 11	
albicans	44
germanica	44
kochii	44
KNIPHOFIA x = 6	
corallina	12
LACTUCA x = 9	
sativa (lettuce)	18
scariola	18
LATHYRUS x = 7	
odoratus	14
LENS x = 7	
esculenta (lentil)	14

	2n
LEUCOJUM x = 11	
aestivum	22
LILIUM x = 12	
auratum	24
candidum	24
chalcedonicum	24
croceum	24
longiflorum	24
Martagon	24
regale	24
speciosum	24
tigrinum	24, 36
LINARIA x = 6	
reticulata	12
LINUM x = 8, 9, etc.	
grandiflorum	16
perenne	18
usitatissimum	30
LUNARIA x = 15	
annua	30
LYCOPERSICUM x = 12	
esculentum	24
gigas	48
pimpinellifolium	24
racemigerum	24
LYTHRUM x = 5	
salicaria	30, 50
MALUS x = 17	
baccata	34
coronaria	34
var.	68
floribunda	34
malus	34
(see tables, 37, 38)	51
Niedzwetzkyana	34
prunifolia	34
pumila	34
Sargentii	34
var.	68
silvestris	34

	2n
MATTHIOLA x = 7	
incana	14
NARCISSUS x = 7, etc.	
bulbocodium	14, 35
	42
poeticus	14, 21
	28
Pseudonarcissus	14
incomparabilis	14, 21
Jonquilla	14
polyanthus	24
Tazetta	20, 22
	30, 32
NASTURTIUM x = 16	
officinale (watercress)	32
uniseriatum	64
officinale × *uniseriatum*	48
NEMESIA x = 9	
strumosa	18
NICOTIANA x = 12	
glutinosa	24
Tabacum	48
gigas	96
digluta	72
x = 9	
Sanderae	18
OENOTHERA x = 7	
muricata	14
PAEONIA x = 5	
anomala	10
Delavayi	10
suffruticosa	10
Mlokosewitschii	10
obovata japonica	10
albiflora	10
var. The Bride	10
Clairette	10
Whitleyi major	10
Primevere	10
James Kelway	10
Bakeri	20

	2n
PAEONIA—continued	
peregrina	20
officinalis	20
sessiliflora	20
tomentosa	20
Willmottiae	20
PASTINACA x = 11	
sativa (parsnip)	22
PELARGONIUM x = 9	
hortorum	18
zonale	18, 36
roseum	72, 144
PETUNIA x = 7	
violacea	14, 28
nyctaginiflora	14
PHASEOLUS x = 11	
multiflorus (bean)	22
vulgaris	22
PHILADELPHUS x = 13	
coronarius	26
microphyllus	26
PISUM x = 7	
sativum (pea)	14
var. *arvense*	14
PRIMULA x = 9	
floribunda	18
verticillata	18
kewensis	18, 36
x = 11	
acaulis	22
elatior	22
Juliae	22
officinalis	22
x = 12	
sinensis	24, 48
PRUNUS x = 8	
amygdalus	16
armeniaca	16
avium	16
PRUNUS—continued	
divaricata	16
decumana	16
mahaleb	16
persica	16
tomentosa	16
Mume	16, 24
nana	16, 24
cantabrigiensis	32
cerasus	32
avium × *cerasus* (Duke cherries)	32
spinosa	32
domestica	48
insititia	48
PYRUS x = 17	
Calleryana	34
communis	34
(see tables 39, 40)	51, 68
nivalis	34
serotina	34
sinensis	34
RAPHANUS x = 9	
sativus (radish)	18
RESEDA x = 6	
odorata	12
RHODODENDRON x = 13	
all species counted	26
except *calendulaceum*	52
and *canadense*	52
RIBES x = 8	
Grossularia	16
inermis	16
rubrum	16
nigrum	16
ROSA x = 7	
acicularis	14, 42
	56
Banksiae	14
cinnamomea	14

	2n
ROSA—continued	
Davidii	14
Hugonis	14
moschata	14
multiflora	14
polyantha	14
rugosa	14
Wichuriana	14
Willmottiae	14
centifolia	28
grandiflora	28
laxa	28
pimpinellifolia	28
canina	35
rubiginosa	35
Moyesii	42
RUBUS x = 7	
idaeus	14
obtusifolius	14
rusticanus	14
inermis	14
neglectus	14
Mahdi (raspberry × blackberry)	21
laciniatus	28
nitidioides	28
thyrsiger	28
procerus (Himalaya berry)	28
John Innes (*rusticanus inermis* × *thyrsiger*)	28
Veitchberry (raspberry × blackberry)	28
Loganberry	42
Laxtonberry (raspberry × loganberry)	49
chamaemorus	56
vitifolius	56
RUDBECKIA x = 19	
hirta	38
SAXIFRAGA x = 8	
granulata	48
rosacea	64
potternensis	80

	2n
SECALE x = 7	
cereale (rye)	14
SPARTINA x = 7	
stricta	56
alterniflora	70
Townsendii	126
SOLANUM x = 12	
aracpapa	24
Bukasovii	24
Caldasii	24
chacoense	24
Jamesii	24
lanciforme	24
Melongena (aubergine)	24
muricatum	24
polyadenium	24
ruderale	24
Rybinii	24
tuberosum (potato)	24, 36
	48
andigenum	48
cardiophyllum	36
Commersonii	36
coyoacanum	36
medians	36
acaule	36, 48
ajuscoense	48
Antipovichi	48
Fendleri	48
luteum	48
palustre	48
edinense	60
demissum	72
nigrum	72
STREPTOCARPUS x = 15	
caulescens	30
Kirkii	30
Holstii	30
Saxorum	30
x = 16	
Dunnii	32
Gardenii	32
gracilis	32
grandis	32

		2n
STREPTOCARPUS—con.		
Haygarthii		32
polyanthus		32
Rexii		32
Wendlandii		32
garden hybrids		32
Merton Giant		64
TOLMIEA	x = 14	28
Menziesii		
TRITICUM	x = 7	
monococcum		14
durum		28
vulgare		42
TROPAEOLUM	x = 14	
majus		28
TULIPA	x = 12	
australis		24
Batalini		24
biflora		24
Clusiana		24, 48
		60
chrysantha		24, 48
Eichleri		24
Fosteriana		24
Greigii		24
Gesneriana		24, 36
Kaufmanniana		24
linifolia		24
montana		24
violacea		24
stellata		24, 48
saxatilis		36
praecox		36
lanata		36
silvestris		48
turkestanica		48
VACCINIUM	x = 12	
atrococcum		24
canadense		24
vacillans		24
angustifolium		48
corymbosum		48
hirsutum		48
pallidum		72
virgatum		72
VERBASCUM	x = 8	
Blattaria		32
phlomoides		32
phoenicеum		32
Ternacha		48
maurum		64
VERBENA	x = 5	
chamaedrifolia		10
erinoides		10
hybrida		10
radicans		10
teucrioides		10
ambrosifolia		30
canadensis		30
racemosa		30
tenera		30
	x = 7	
hispida		14
officinalis		14
prostrata		14
stricta		14
bonariensis		28
litoralis		28
venosa		42
corymbosa		56
VICIA	x = 6	
Faba (broad bean)		12
sativa		12
VIOLA	x = 13	
tricolor		26
VITIS	x = 19	
labrusca		38
rupestris		38
vinifera		38
gigas		76
ZEA	x = 10	
Mays (maize)		20

APPENDIX II

GLOSSARY

Albinism, absence of chorophyll, producing an albino.
albinotic, affected with albinism.
allelomorph, one of a pair of contrasted characters which are alternative to each other in inheritance and which are governed by genes situated in homologous chromosomes.
allo-polyploid, a polyploid having dissimilar sets of chromosomes usually differentiated in pairs.
allo-syndesis, the pairing in a polyploid of chromosomes derived from opposite parents.
anaphase, the stage at which the chromosomes or daughter chromosomes move apart in nuclear division at meiosis or mitosis respectively.
aneuploid, having more than at least one member of the basic set of chromosomes than of others, as $4n \pm 1$, $5n \pm 1$, etc.
anther, the male organ in a flowering plant, the portion of the stamen which contains the pollen.
apomixis, abnormal budding and reproduction in the reproductive organs without sexual intervention. See Footnote, page 41.
asexual, without sex or functional sexual organs.
auto-polyploid, a polyploid having similar sets of chromosomes.
auto-syndesis, the pairing in a polyploid of chromosomes derived from the same parent.

Back-cross, cross of a hybrid to one of its parents.
basic number, the number of chromosomes found in the gametes of a diploid ancestor of a polyploid.
bivalent. See **univalent.**
bud-sport, a somatic variation.

Cell, the unit of organic structure, usually containing one nucleus.
certation, competition in rate of growth of pollen-tubes of different genetic type.
chiasma, an exchange of partners in a system of paired chromatids. See page 21.
chimaera, a plant composed of tissues of two or more genetically distinct types.
chromatid, the half chromosome (derived from longitudinal fission of a chromosome) found paired with its sister chromatid at the prophase of a division of the nucleus.
chromosomes, rod-like bodies contained in the nucleus, bearers of the hereditary material.
clone, the collective name of all the plants asexually reproduced by division, grafting, etc., from one (seedling) individual.

compatible, capable of fertilisation.
complement, the group of chromosomes, derived from a particular nucleus, composed of one, two or more sets.
crossing-over, the interchange of genes usually linked in inheritance. Probably due to the exchange of corresponding segments between corresponding chromatids of different chromosomes.

Daughter-chromosome. See **chromatid.**
deficiency, / **deletion,** } loss of a segment of a chromosome from the complement
diakinesis, the last stage in the prophase of meiosis.
diploid, an organism with two sets of chromosomes.
disjunction, the separation of the chromosomes at anaphase, particularly of the first meiotic division.
disomic, referring to two homologous chromosomes, or genes.
dominant, a character expressed by one parent which appears in the hybrid to the exclusion of the contrasted (recessive) character from the other parent.
duplex, having two dominant genes.

Emasculation, the removal of the stamens before they burst and shed their pollen.
embryo, the rudimentary plant present in a seed.
endogenous, growing from within ; arising from internal tissues.
endosperm, the substance which surrounds the embryo, as the starchy part of maize. The albumen of seeds.
epidermal, relating to the epidermis.
epidermis, the cellular skin or covering of a plant.
epistatic, dominance of one of a pair of characters which are not allelomorphic.
exogenous, arising from the external tissues.

F_1, the first filial generation, the immediate offspring of a given cross.
F_2, the second filial generation, arising from inter-crossing or self-fertilising the F_1.
factor, the unit of heredity, transmitted in the germ-cells. See **gene, allelomorph.**
fertile, capable of producing fruit, or more strictly, of producing seeds.
fertilisation, the fusion of male and female germ-cells and of their nuclei.
filament, the stalk of an anther.
fluctuation, the response of an individual to its environment. See page 170.

Gametes, cells specialised for fertilisation. A reproductive cell of either sex.
gene, the unit of reproduction and variation in the hereditary material.
genotype, the entire genetic constitution of an organism.
germ-cells. See **gametes.**
gigantism, appearance of giant forms.
graft, a vegetative union of different individuals, the rooted part being termed the *stock,* and the part inserted the *scion.*

graft hybrid, more strictly *graft chimaera,* a plant composed of two distinct types as a result of fusion following grafting.

Haploid, having one set of chromosomes. See **diploid.**
heptaploid, having seven sets of chromosomes.
heterosis, the increased vigour often exhibited in the F_1 generation of a cross.
heterozygote, a zygote derived from the union of gametes of dissimilar genetic constitutions.
hexaploid, having six sets of chromosomes.
homology, the similarity of structures in different organisms derived from the same ancestral structure.
homozygote, a zygote derived from the union of gametes of similar genetic constitution.
hybrid, a heterozygote.
hypostatic, recessive, of non-allelomorphs. See **epistatic.**

Incompatibility, incapable of fertilisation, the condition where the pollen-tubes are arrested in the style, and fail to reach the ovules.
inversion, the reversal of the linear sequence of the genes in a segment of a chromosome.

Lethal factors, genetic factors which render an organism inviable.
linkage, association of genetic factors in inheritance, due to the factors being in the same chromosome.

Meiosis, the process by which the nucleus divides twice and the chromosomes once, giving daughter nuclei each having half the number of chromosomes of the parent nucleus.
periclinal chimaera, a plant composed of genetically diverse tissues, with one partly surrounding the other ; an incomplete periclinal chimaera.
metaphase, the stage of mitosis or meiosis in which the chromosomes lie in a plane at right angles to the axis of the spindle and half way between the poles.
metaxenia, a term erroneously used to denote the influence exerted by foreign pollen on the maternal tissue. See page 226.
mitosis, the nuclear division of the somatic cells, the process by which the chromosomes are separated without change into two groups forming two daughter nuclei.
mutation, a sudden variation in an inherited character.

Nucleus, the most constant constituent of the cell ; contains the chromosomes.
nulliplex, recessive ; used in polyploids when all the genes for a given character are recessive.

Octoploid, having eight sets of chromosomes.
ovary, the part of the flower which contains the ovules ; the immature fruit.
ovule, the body which contains the female germ-cell ; and which, after fertilisation, develops into a seed.

Parthenocarpy, the formation of fruit without fertilisation and without seeds.
parthenogenesis, the development of the female or the male gamete without fertilisation.
pentaploid, having five sets of chromosomes.
periclinal chimaera, a plant composed of genetically diverse tissues, with one completely surrounding the other.
phenotype, the external appearance produced by the reaction of an organism of a given genotype with a given environment.
pistil, the female organ of the flower, consisting, when complete, of ovary, style and stigma.
pollen, the male germ-cells of flowering plants.
pollen-tube, the tube growing out from a germinating pollen-grain and passing down from the stigma to the ovary and ovules.
pollinate, to deposit pollen on the stigma.
polygenes, genes having small, similar and supplementary effects.
polymeric, non-allelomorphic genes affecting the same character and having identical phenotypic results.
polyploid, an organism with more than two sets of chromosomes, hence triploid, tetraploid, hexaploid, etc.
polysomic, relating to a number of homologous chromosomes or genes.
prophase, the stage in mitosis or meiosis from the appearance of the chromosomes to metaphase.

Quadriplex, having four dominant genes.

Recessive. See **dominant.**
reduction, the halving of the chromosome number at meiosis.
reversion, the reappearance of an ancestral character not exhibited by the immediate parents.
rings, chromosomes associated end to end in a ring.

Scion, a young shoot used for grafting.
secondary association, the lying together of bivalent chromosomes at meiosis.
secondary polyploid, an allo-polyploid in which some of the chromosomes in the basic set occur more frequently than others.
sectorial chimaera, a plant with a deeply seated sector of genetically distinct tissue.
segregation, the dissociation of characters from each other in the formation of the gametes (germ-cells).
self-fertilisation, the fertilisation resulting from self-pollination.
self-pollination, pollination between the pollen and stigmas of the same flower or clone.
set of chromosomes, a minimum group of chromosomes derived from the gametic complement of a supposed ancestor.
simplex, having one dominant gene (not used in diploids).
somatic, pertaining to the body.
sport, a mutation.
stamen, the male organ in flowering plants, consisting of anther and filament.

stigma, that part of the pistil or style which receives the pollen; the receptive surface of the style.

Telophase, the last phase of nuclear division.
tetraploid, having four sets of chromosomes.
tetrasomic, relating to four homologous chromosomes, or genes.
trabant, a segment of a chromosome separated from the main body of the chromosome by a long constriction.
translocation, change in position of a segment of a chromosome to another part of the same chromosome, or to a different chromosome.
triplex, having three dominant genes.
triploid, having three sets of chromosomes.
trisomic, an organism with three genes or three chromosomes of one type, as $2x + 1$. See **disomic.**

Univalent, a body at the first meiotic division corresponding to a single chromosome of the complement. Bivalents, trivalents, quadrivalents, multivalents, etc., are associations of chromosomes held together by chiasmata at meiosis.

Variation, the departure in any direction from the characters of the type, resulting from change in the hereditary material, and the process by which evolution continues.
viviparous (in plants), producing asexually separable buds instead of seeds. See page 43.

Xenia, the physiological effects of foreign pollen on the maternal tissue of the fruit.

Zygote, the cell formed by the union of gametes and the individual derived from it. Cf. **heterozygote.**

APPENDIX III

BIBLIOGRAPHY

ALLEN, I. M. 1924. The cytology of *Matthiola incana* with reference to the genetics of certain cultivated varieties. *New Phytol.* **23**: 103-112.

ANDERSON, E., and DE WINTON, D. 1931. The genetic analysis of an unusual relationship between self-sterility and self-fertility in *Nicotiana*. *Ann. Missouri Bot. Gard.* **18**: 97-116.

ANDERSSON-KOTTO, I., and GAIRDNER, A. E. 1931. Interspecific crosses in the genus *Dianthus*. *Genetica* **13**: 77-112.

ANTHONY, R. D., and HEDRICK, U. P. 1916. Some notes on the breeding of raspberries. *N.Y. Agr. Exp. Sta.* (Geneva) *Bull.* **417**: 75-88.

ASHBY, E. 1930. Studies on the inheritance of physiological characters, I. A physiological investigation of the nature of hybrid vigour in maize. *Ann. Bot.* **44**: 457-467.

—— 1932. II. *Ann. Bot.* **46**: 1007-1032.

ASSEYEVA, T. 1927. Bud mutations in the potato and their chimerical nature. *J. Genet.* **19**: 1-26.

BACH, F. 1928.a. Über die künstliche Kreuzung einiger wichtiger Apfelsorten. *Gartenbauwiss.* **1**: 358-374.

—— 1928.b. Kreuzungsversuche mit weissem Winterkalvill. Eine neue Apfelxenie. *Gartenbauwiss.* **1**: 615-618.

BAILEY, J. S., and FRENCH, A. P. 1932. The inheritance of certain characters in the peach. *Proc. Amer. Soc. Hort. Sci.* **29**: 127-130.

BATESON, W. 1902. *Mendel's principles of heredity.* Cambridge.

—— 1916. Root cuttings, chimaeras and sports. *J. Genet.* **6**: 75-80.

—— 1919. Studies in Variegation I. *J. Genet.* **8**: 93-98.

—— 1920. Genetic segregation. *Proc. Roy. Soc.* B **91**: 358-368.

—— 1921. Root cuttings and chimaeras II. *J. Genet.* **11**: 91-97.

—— and GREGORY, R. P. 1905. On the inheritance of heterostylism in *Primula*. *Proc. Roy. Soc.* B **76**: 581-586.

—— and PUNNETT, R. C. 1911. On gametic series involving reduplication of certain terms. *J. Genet.* **1**: 293-302.

——, SAUNDERS, E. R., and PUNNETT, R. C. 1905 *et seq.* Experimental Studies on the Physiology of Heredity. *Reports of the Evolution Committee of the Royal Society.*

BAUR, E. 1909.a. Pfropfbastarde Periclinalchimaeren und Hyperchimaeren. *Ber. Deuts. Bot. Ges.* **27**: 603-605.

—— 1909.b. Das Wesen und die Erblichkeitsverhältnisse der "Varietates albomarginata hort." von *Pelargonium zonale*. *Z.I.A.V.* **1**: 330-351.

BAUR, E. 1931. I.—Evolution. II.—Scope and methods of plant-breeding work at the Kaiser Wilhelm Institut für Züchtungsforschung Müncheberg (Mark). *J.R.H.S.* **56**: 176-190.

—— 1933. Der heutige Stand der Rebenzüchtung in Deutschland. *Züchter* **5**: 73-77.

BEADLE, G. W. 1933. Further studies in asynaptic maize. *Cytologia* **4**: 269-287.

BEAN, W. J. 1914. *Trees and Shrubs Hardy in the British Isles.* London. (Vol. 1, 64.)

BESLER, B. 1613. *Hortus Eystettensis.*

BLACK, W. 1933. Studies in the inheritance of tuber colour in Potatoes. *J. Genet.* **27**: 319-304.

—— 1947. Blight in relation to potato breeding. *Ann. Appl. Biol.* **34**: 613-633.

BLAKESLEE, A. F. 1921. A chemical method of distinguishing genetic types of yellow cones in *Rudbeckia*. *Z.I.A.V.* **25**: 211-221.

—— and AVERY, A. G. 1937. Methods of inducing doubling of chromosomes in plants by treatment with colchicine. *J. Hered.* **28**: 393-412.

—— and BELLING, J. 1924. Chromosomal mutations in the Jimson Weed, *Datura stramonium*. *Heredity* **15**: 195-206.

—— and CARTLEDGE, J. L. 1928. Genetics of Datura. *5th Int. Cong. Genet. Berlin*, 1927, **1**: 117-130.

BLEIER, H. 1928. Karyologische Untersuchungen an Linsen-Vicken Bastarden. *Genetica* **11**: 111-118.

BRIEGER, F. G., and MANGELSDORF, A. J. 1927. Linkage between morphological characters and factors for self-sterility. *Mem. Hort. Soc. N.Y.* **3**: 369-371.

BUDER, J. 1910. Studien an *Laburnum Adami*, I. *Ber. Deuts. Bot. Ges.* **28**: 188-192.

—— 1911. Studien an *Laburnum Adami*, II. *Z.I.A.V.* **5**: 209-284.

BUNYARD, E. A. 1913. The history and development of the strawberry. *J.R.H.S.* **39**: 541-552.

—— 1917. The history and development of the red currant. *J. Roy. Hort. Soc.* **42**: 260-270.

—— 1925. A Handbook of Fruits. *Stone and bush fruits.* (London.)

BUXTON, B. H., and DARLINGTON, C. D. 1932. Behaviour of a new species, *Digitalis mertonensis*. *New Phytol.* **31**: 225-240.

—— and NEWTON, W. C. F. 1928. Hybrids of *Digitalis ambigua* and *Digitalis purpurea*, their fertility and cytology. *J. Genet.* **19**: 269-279.

CADMAN, C. H. 1942. Autotetraploid inheritance in the potato: some new evidence. *J. Genet.* **44**: 33-52.

CARRIÈRE, E. A. 1881. Pommier hétéromorphe. *Rev. Hort.* **54**.

CARSON, G. P., and HOWARD, H. W. 1945. Note on the inheritance of the King Edward type of colour in potatoes. *J. Genet.* **46**: 358-360.

CASTLE, W. E. 1914. An apple chimaera. *J. Hered.* **5**: 200-202.

CAYLEY, D. M. 1928. "Breaking" in tulips. *Ann. Appl. Biol.* **15**: 529-539.

CHITTENDEN, R. J. 1927. Vegetative segregation. *Bibliographia Genet.* **3**: 355-442.

CHITTENDEN, R. J. 1928. Notes on species crosses in *Primula, Godetia, Nemophila* and *Phacelia. J. Genet.* **19**: 285-314.

CLAUSEN, J. 1929-30. Inheritance of variegation and black flower colour in *Viola tricolor* L. *Hereditas* **13**: 342-356.

CLAUSEN, R. E., and GOODSPEED, T. H. 1923. Inheritance in *Nicotiana Tabacum* III. The occurrence of two natural periclinal chimaeras. *Genetics* **8**: 97-105.

—— —— 1925. Interspecific hybridisation in *Nicotiana*, II. A tetraploid *glutinosa-Tabacum* hybrid, an experimental verification of Winge's hypothesis. *Genetics* **10**: 279-284.

CLOSE, C. P. 1907. Immediate effect of cross pollination of apples. *Proc. Amer. Soc. Hort. Sci.* **4**: 47.

COLLINS, E. J. 1921. The problem of inheritance of immunity from wart-disease in potatoes. *Gard. Chron.* **70**: 260, 271, 290, 314, 326.

—— 1924. Inheritance of the colour pattern of King Edward potato. *J. Genet.* **14**: 201-202.

COMPTON, R. H. 1912. Preliminary note on the inheritance of sterility in *Reseda odorata. Proc. Camb. Phil. Soc.* **17**: 7.

—— 1913. Phenomena and problems of self-sterility. *New Phytol.* **13**: 197-206.

CONNORS, C. H. 1919. Some notes on the inheritance of unit characters in the peach. *Proc. Amer. Soc. Hort. Sci.* **16**: 23-35.

—— 1921. Inheritance of foliar glands of the peach. *Proc. Amer. Soc. Hort. Sci.* **18**: 20-26.

—— 1922. Peach Breeding—a summary of results. *Proc. Amer. Soc. Hort. Sci.* **19**: 108-115.

—— 1927. Sterility in peaches. *Mem. Hort. Soc. N.Y.* **3**: 215-222.

CORRENS, C. 1900. Über Levkojenbastarde. Zur Kenntnis der Grenzen der Mendel'schen Regeln. *Bot. Zbl.* **84**: 97-133.

—— 1913. Selbststerilität und Individualstoffe. *Biol. Zbl.* **33**: 389-423.

—— 1920. Vererbungsversuche mit buntblattrigen Sippen. *Sitzber. d. Preuss. Akad. Wiss.* **6**: 212-240.

—— 1928. Neue Untersuchungen an selbststerilen Pflanzen. I. *Tolmiea Menziesii. Biol. Zbl.* **48**: 759-768.

COVILLE, F. V. 1927. Blueberry chromosomes. *Science* **66**: 565-566.

CRANDALL, C. S. 1918. Apple bud selection; apple seedlings from selected trees. *Illinois Agr. Exp. Sta. Bull.* **211**.

—— 1924. Additional records of self-sterility in apples. *Proc. Amer. Soc. Hort. Sci.* **21**: 63-67.

CRANE, M. B. 1915. Heredity of types of inflorescence and fruits in the tomato. *J. Genet.* **5**: 1-11.

—— 1921. Experiments in breeding plums, with a note on peaches. *J. Pomol.* **2**: 137-159.

—— 1923. Report on tests of self-sterility and cross-incompatibility in plums, cherries and apples. *J. Pomol.* **3**: 67-84.

—— 1925. Self- and cross-incompatibility in plums and cherries. *J. Genet.* **15**: 301-322.

CRANE, M. B. 1927. Self- and cross-sterility in fruit trees. A summary of results, 1911-1925. *J. Pomol.* **6**: 157-166.

—— 1927. Studies in relation to sterility in plums, cherries, apples and raspberries. *Mem. Hort. Soc. N.Y.* **3**: 119-134.

—— 1931. Fertility in relation to yield in cultivated fruits. *Bull. Fac. Agr. Univ. Reading* **41**: 119-129.

—— 1934. The origin of cultivated fruits and the raising of new varieties. *R.H.S. Conference on Apples and Pears*, 90-97.

—— 1935.a. The origin of the pink-flowered chestnut, *Aesculus carnea*. *J. Roy. Hort. Soc.* **60**: 171-176.

—— 1935.b. Blackberries, hybrid berries and autumn-fruiting raspberries. *R.H.S. Conference on Cherries and Soft Fruits*, 121-128.

—— 1936. Note on a periclinal chimaera in the potato. *J. Genet.* **32**: 73-77.

—— 1940. Reproduction versatility in *Rubus* I. *J. Genet.* **40**: 109-118.

—— 1940. The origin of new Forms in *Rubus* II. *J. Genet.* **40**: 129-140.

—— 1943. The origin and relationship of the Brassica Crops. *J. Roy. Hort. Soc.* **68**: 172-174.

—— and DARLINGTON, C. D. 1927. The origin of new forms of *Rubus*. *Genetica* **9**: 241-278.

—— and BROWN, A. G. 1937. Incompatibility and sterility in the sweet cherry, *Prunus avium* L. *J. Pomol.* **15**: 86-116.

—— —— 1942. The causal sequence of fruit development. *J. Genet.* **44**: 160-168.

—— GREENSLADE, R. M., MASSEE, A. M., and TYDEMAN, H. M. 1936. Studies on the resistance and immunity of apples to the woolly aphis, *Eriosoma lanigerum*. *J. Pomol.* **14**: 137-163.

— — and LAWRENCE, W. J. C. 1929. Genetical and cytological aspects of incompatibility and sterility in cultivated fruits. *J. Pomol.* **7**: 276-301.

— — —— 1930. Fertility and vigour of apples in relation to chromosome number. *J. Genet.* **22**: 153-163.

—— —— 1931.a. Sterility and incompatibility in diploid and polyploid fruits. *J. Genet.* **24**: 97-107.

—— —— 1931.b. Inheritance of sex, colour and hairiness in the raspberry, *Rubus idaeus* L. *J. Genet.* **24**: 243-255.

—— —— 1931.c. Studies in sterility. *Proc. 9th Int. Hort. Cong.*, London, 1930, 100-116.

—— —— 1933. Genetical studies on cultivated apples. *J. Genet.* **28**: 265-296.

—— and LEWIS, D. 1940. Genetical studies in Pears, II, A classification of cultivated varieties. *J. Pomol. & Hort. Sci.* **18**: 52-60.

—— —— 1942. Genetical studies in Pears, III, Incompatibility and sterility. *J. Genet.* **43**: 31-43.

—— and Thomas, P. T. 1942. Genetic classification of Brassica crops. *Nature*, **150**: 431.

—— and ZILVA, S. S. 1931. The antiscorbutic vitamin in apples, IV. *J. Pomol.* **9**: 228-231.

—— —— 1932. The antiscorbutic potency of apples, V. *Biochem. J.* **26**: 2177-2181.

CRAWFORD, C. L. 1936. Growth rate in Deglet Noore dates in metaxenia. *Proc. Amer. Soc. Hort. Sci.* **33**: 51-54.

CROW, J. W. 1913. The effect of pollen of Wagener and McIntosh on the size and number of seeds in Wealthy apples. *Proc. Amer. Soc. Hort. Sci.* **10**: 153-155.

DAHL, C. G. 1930. Root stocks from seeds of known parents. *Proc. 9th Int. Hort. Cong.* 141-149.

—— and JOHANSSON, E. 1924. Forsok med uppdragning av appelgrundstammergenom ustade av Karnor tillhocande vissa bestamda appelsorter. *Med. Perm. Komm. Frukt.* **2**.

DANIEL, L. 1923. Les hybrides de greffe. Internat. Tuinbouw. Cong. Amsterdam, p. 175-193.

DARLINGTON, C. D. 1927. Reversion in Black Currants. A study of the chromosome complement. *J. Pomol.* **6**: 242.

—— 1928. Studies in Prunus I and II. *J. Genet.* **19**: 213-256.

—— 1930. Studies in Prunus III. *J. Genet.* **22**: 65-93.

—— 1932. *Chromosomes and plant breeding.* London.

—— 1933. Studies in *Prunus*, IV. *J. Genet.* **28**: 327-328.

—— 1937. *Recent advances in cytology.* London.

—— 1938. *The Evolution of Genetic Systems.* Cambridge.

—— and JANAKI AMMAL. 1945. The Chromosome Atlas of Cultivated Plants. London.

—— and MOFFETT, A. A. 1930. Primary and secondary chromosome balance in *Pyrus*. *J. Genet.* **22**: 129-151.

DARROW, G. M., and WALDO, G. F. 1933. Pseudogamy in blackberry crosses. *J. Hered.* **24**: 313-314.

DARWIN, C. 1882. *The variation of animals and plants under domestication.* London.

DETJEN, L. R., and MCCUE, C. A. 1933. Cabbage characters and their heredity. *De. Agr. Expt. Sta. Bull.* **180**: 1-147.

DE WINTON, D., and HALDANE, J. B. S. 1933. The genetics of *Primula sinensis* II. *J. Genet.* **27**: 1-44.

DICKSON, G. H. 1928. Variability of vigour in apple seedlings. *Proc. Amer. Soc. Hort. Sci.* **25**: 165-168.

DIGBY, L. 1912. The cytology of *Primula kewensis* and other related Primula hybrids. *Ann. Bot.* **26**: 357-386.

DODOENS, R. 1582. *Stirpium Historiae.*

DURST, C. E. 1929. Inheritance in lettuce. *Science* **69**: 553-554.

EAST, E. M. 1910. Inheritance in potatoes. *Amer. Nat.* **44**: 424-430.

—— 1929. Self-sterility. *Bibliogr. Genet.* **5**: 331-369.

—— 1937. Heterosis. *Genetics* **21**: 375-397.

—— and PARK, J. B. 1917. The behaviour of self-sterile plants. *Genetics* **2**: 505-609.

—— and JONES, D. F. 1919. *Inbreeding and outbreeding.* Philadelphia.

—— and MANGELSDORF, A. J. 1925. A new interpretation of the hereditary behaviour of self-sterile plants. *Proc. Nat. Acad. Sci.* **11**: 166-171.

EAST, E. M., and MANGELSDORF, A. J. 1927. The genetics and physiology of self-sterility in Nicotiana. *Mem. Hort. Soc. N.Y.* **3**: 321-323.

EMME, H., and SCHLABLOVSKAJA, M. 1933. Beitrag zur Frage der Morus Züchtung. *Züchter*, **5**: 222-225.

FABERGÉ, A. C. 1937. The cytology of the male sterile *Lathyrus odoratus*. *Genetica* **19**: 423-430.

—— 1942. Genetics of the scapiflora section of *Papaver* 1. The Garden Iceland Poppy. *J. Genet.* **44**: 169-193.

FLORIN, R. 1927. Pollen production and incompatibilities in apples and pears. *Mem. Hort. Soc. N.Y.* **3**: 87-118.

FRANDSEN, H. N., and WINGE, O. 1931. *Brassica napocampestris*, a new constant amphidiploid species hybrid. *Hereditas* **16**: 212-218.

FROST, H. B. 1928. Chromosome-mutant types in stocks. *J. Hered.* **19**: 105-111.

FRUWIRTH, C. 1912. Zur Züchtung der Kartoffel. *Deuts. Landw. Presse* **39**: 551-552, 565-567.

GAIRDNER, A. E. 1926. *Campanula persicifolia* and its tetraploid form. "Telham Beauty." *J. Genet.* **16**: 341-351.

GAISER, L. O. 1926. A list of chromosome numbers in Angiosperms. *Genetica* **8**: 401-484.

—— 1930.a. Chromosome numbers in Angiosperms, II. *Bibliogr. Genet.* **6**: 171-466.

—— 1930.b. Chromosome numbers in Angiosperms, III. *Genetica* **12**: 161-260.

—— 1933. Chromosome numbers in Angiosperms, IV. *Bibliogr. Genet.* **10**: 105-250.

GARDNER, V. R. 1913. A preliminary report on the pollination of the sweet cherry. *Bull. Oregon Agric. Coll.* **116**.

GERARDE, J. 1597. *The Herball, or generall Historie of Plantes*. London.

GOSS, J., and SETON, A. 1824. On the variation in the colours of peas. *Trans. Hort. Soc.* **5**: 234-237.

GREGORY, R. P. 1911. Experiments with *Primula sinensis*. *J. Genet.* **1**: 73-132.

——, DE WINTON, D., and BATESON, W. 1923. Genetics of *Primula sinensis*. *J. Genet.* **13**: 219-253.

GUSTAFSON, F. C. 1936. Inducement of fruit development by growth promoting chemicals. *Proc. Nat. Acad. Sci.* **22**: 628-636.

—— 1937. Parthenocarpy induced by pollen extracts. *Amer. J. Bot.* **24**: 102-107.

—— 1940. Parthenocarpic and normal fruits compared as to percentage of setting and size of fruits. *Bot. Gaz.* **102**: 280-286.

HAAN, H. DE. 1931. Contributions to the genetics of *Pisum*. *Genetica* **12**: 321-439.

HABERLANDT, G. 1926. Über den Blattbau der *Crataegomespili* von Bronvaux und ihrer Eltern. *Sitzber. Preuss. Akad. Wiss.* **17**: 170-208.

—— 1927. Sind die *Crataegomespili* von Bronvaux Verschmelzungspfropfbastarde oder Periclinalchimaeren ? *Biol. Zbl.* **47**: 129-151.

—— 1930. Das Wesen der *Crataegomespili*. *Sitzber. Preuss. Akad. Wiss.* **20**: 374-394.

HACKBARTH, J., LOSCHAKOWA-HASENBUSCH, N., and SENGBUSCH, R. v.

1933. Die Züchtung frühreifer Tomaten mittels Kreuzungen zwischen *Solanum Lycopersicum* und *Solanum racemigerum*. *Züchter* **5**: 97-105.

HAINSWORTH, R. G. 1949. *World Agriculture*. U.S.D.A. misc. pub. **705**: 1-51.

HÅKANSSON, A. 1929. Chromosomenringe in *Pisum* und ihre mutmassliche genetische Bedeutung. *Hereditas* **12**: 1-10.

HALDANE, J. B. S. 1930. Theoretical genetics of auto-polyploids. *J. Genet.* **22**: 359-372.

HARRISON, G. J. 1931. Metaxenia in cotton. *J. Agr. Res.* **42**: 521-544.

HASKELL, G. 1949. *Hybrid Corn (Maize) in Theory and Practice*. Pp. 1-23. The Biological Press. London.

HATTON, R. G. 1930. Stock: scion relationships. *J.R.H.S.* **55**: 169-211.

—— and GRUBB, N. H. 1926. Some factors influencing the period of blossoming in apples and plums. *J. Pomol.* **5**: 210-215.

HAWKES, J. G. 1944. Potato collecting expeditions in Mexico and South America. *Imp. Bur. Plt. Brd. & Genet. Tech. Comm.* 1-142.

HEDRICK, U. P. 1917. *The Peaches of New York*. New York Agr. Exp. Sta.

—— 1922. *Cyclopedia of Hardy Fruits*. New York.

—— and ANTHONY, R. D. 1915. Inheritance of certain characters of grapes. *N.Y. Exp. Sta. Bull.* **45**.

—— and BOOTH, N. O. 1907. Mendelian characters in tomatoes. *Proc. Amer. Soc. Hort. Sci.* **5**: 19-24.

HERIBERT-NILSSON, N. 1913. Potatisförädling och potatisbedömning. *W. Weibulls Arsbook* **8**: 4-31.

HIBBARD, A. D. 1934. Metaxenia in apple and squash. *Proc. Amer. Soc. Hort. Sci.* **30**: 140-142.

HOAR, C. S. 1927. Chromosome studies in *Aesculus*. *Bot. Gaz.* **84**: 156-170.

HOOPER, C. H. 1924. Notes on the pollination of cherries. *J. Pomol.* **3**: 185-190.

—— 1933. Results of pear pollination trials at Faversham, Kent, 1932. *Gard. Chron.* **93**: 266.

HOWARD, H. W. 1947. Wild and cultivated watercress types. *Agric.* **53**: 453-456.

—— and MANTON, I. 1946. Autopolyploid and allopolyploid watercress with the description of a new species. *Ann. Bot.* **10**: 1-13.

HUGHES, A. W. MCKENNY. 1930. Aphis as a possible vector of "breaking" in tulip species. *Ann. Appl. Biol.* **17**: 36-42.

—— 1931. Aphides as vectors of "breaking" in tulips. *Ann. Appl. Biol.* **18**: 16-29.

HUME, H. H. 1913. Effect of pollination on the fruits of Diospyros Kaki. *Proc. Amer. Soc. Hort. Sci.* **10**: 88.

HURST, C. C. 1906. Mendelian characters in plants and animals. *Rep. 3rd Int. Conf. Genet.* (R.H.S.): 114-129.

—— 1932. *The Mechanism of Creative Evolution*. Cambridge.

HUSKINS, C. L. 1930. The origin of *Spartina Townsendii*. *Genetica* **12**: 531-538.

ICHIJIMA, K. 1926. Cytological and genetical studies on *Fragaria*. *Genetics* **11**: 590-604.

ICHIJIMA, K. 1930. Studies on the genetics of *Fragaria*. *Z.I.A.V.* **55**: 300-347.

IMPERIAL BUREAUX OF PLANT GENETICS. 1933. *Plant breeding in the Soviet Union*. Cambridge (and Aberystwyth).

JAGGER, I. C. 1924. Immunity to mildew (*Bremia lactucae*) and its inheritance in lettuce. *Phytopathol.* **14**: 122.

JOHANNSEN, W. 1911. The genotype conception of heredity. *Amer. Nat.* **45**: 129-159.

JONES, D. F. 1917. Dominance of linked factors as a means of accounting for heterosis. *Genetics* **2**: 466-470.

—— 1925. *Genetics in plant and animal improvement*. New York.

—— 1937. Somatic segregation and its relation to atypical growth. *Genetics* **22**: 484-522.

JONES, H. A., and EMSWELLER, S. L. 1936. A male-sterile onion. *Proc. Amer. Soc. Hort. Sci.* **34**: 582-585.

—— and CLARKE, A. E. 1943. Inheritance of male sterility in the onion and the production of hybrid seed. *Proc. Amer. Soc. Hort. Sci.* **43**: 189-194.

—— and DAVIS, G. N. 1944. Inbreeding and heterosis and the relations to the development of new varieties of onions. *U.S.D.A. Tech. Bull.* **874**: 1-28.

JØRGENSEN, C. A. 1928. The experimental formation of heteroploid plants in the genus *Solanum*. *J. Genet.* **19**: 133-211.

—— and Crane, M. B. 1927. Formation and morphology of *Solanum* chimaeras. *J. Genet.* **18**: 247-273.

JUZEPEZUK, S. W., and BUKASOV, S. M. 1929. A contribution to the question of the origin of the potato. *Proc. U.S.S.R. Cong. Pl. and Animal Breeding* **3**: 593-611.

KAKIZAKI, Y. 1930. Studies on the genetics and physiology of self- and cross-incompatibility in the common cabbage (*Brassica oleracea* var. *capitata*). *Jap. J. Bot.* **5**: 133-208.

—— 1931. Hybrid vigor in egg-plants and its practical utilisation. *Genetics* **16**: 1-25.

KAPPERT, H. 1924. Über die Zahl der unabhängigen Merkmalsgruppen bei der Erbse. *Z.I.A.V.* **36**: 1-32.

KARPECHENKO, G. D. 1928. Polyploid hybrids of *Raphanus sativus* L. × *Brassica oleracea* L. *Z.I.A.V.* **48**: 1-85.

—— and BOGDANOVA, E. N. 1937. A fertile tetraploid hybrid *Brassica oleracea* L. × *Brassica chinensis* L., experimentally produced. *Bull. Appl. Bot. Genet.* Ser. 2, **7**: 455-464.

KARPER, R. E., and QUINBY, J. R. 1937. Hybrid vigour in *Sorghum*. *J. Hered.* **28**: 83-91.

KEMMER, E. 1932. Welche Apfelsorte halten Sie im Hinblick auf Empfehlung, Verbreitung u. Marktwert für die wichtigste Deutschlands ? *Obst- u. Gemüsebau* **78**: 120.

KIKUCHI, A. 1930. On the skin colour of the Japanese pear, and its inheritance. (In Japanese.) *Cont. Inst. Plant Industry Kyoto Imp. Univ.* **8**: 1-50.

KNIGHT, T. A. 1799. An account of some experiments on the fecundation of vegetables. *Phil. Trans.* **87**: 195-204.

KNIGHT, T. A. 1822. On the prevention of Mildew in particular cases. *Trans. Hort. Soc.* 1822, **2**: 87.

KNOWLTON, H. E. 1924. Pollen abortion in the peach. *Proc. Amer. Soc. Hort. Sci.* **21**: 67-69.

KOBEL, F. 1927. Zytologische Untersuchungen an Prunoideen und Pomoideen. *Arch. Jul. Klaus-Stift.* **3**: 1-84.

KOVALEVSKAJA, M. F. 1933. The wounding method applied to sugar beet for producing mutations. Nauk. Zapiski, *Tsukr. Prom.* **10**: 123-132.

KRANTZ, F. A. 1922. The application of genetic principles to potato breeding. *Proc. Amer. Hort. Sci.* **19**: 124-129.

——, BECKER, C. L., and FINEMAN, Z. M. 1939. Incidence and inheritance of pollen sterility in the potato. *J. Agric. Res.* **58**: 593-602.

KRISTOFFERSON, K. B. 1924–27. Contributions to the genetics of *Brassica oleracea* (I-II). *Hereditas*, **5**: 297-364; **9**: 343-348.

KRUMBHOLZ, G. 1932. Untersuchungen über das Vorkommen von Xenien und Metaxenien bei Apfeln. *Gartenbauwiss.* **6**: 404-424.

KUHN, E. 1938. Über die Trabantenchromosomen bei normalen und immerspaltenden Sippen von *Matthiola incana*. *Z.I.A.V.* **74**: 388-408.

KVAALE, E. 1926. Abortive and sterile apple pollen. *Mem. Hort. Soc. N.Y.* **3**: 399-408.

LANTZ, H. L. 1925. Some observations on the effect of inbreeding on the vigor of apple seedlings. *Proc. Amer. Soc. Hort. Sci.* **22**: 115-123.

—— and EDGECOMBE, S. W. 1930. Apple breeding; some significant differences in the vigor and grade of cross-bred apple seedlings. *Proc. Amer. Soc. Hort. Sci.* **27**: 289-295.

LARSON, E. R., and CURRENCE, T. M. 1944. The extent of hybrid vigor in F_1 and F_2 generations of tomato crosses. *Univ. Minn. Agr. Expt. Sta. Bull.* **164**: 1-32.

LAWRENCE, W. J. C. 1929. The genetics and cytology of *Dahlia* species. *J. Genet.* **21**: 125-159.

—— 1930. Incompatibility in polyploids. *Genetica* **12**: 269-296.

—— 1931. The genetics and cytology of *Dahlia variabilis*. *J. Genet.* **24**: 257-306.

—— 1931. Secondary association in polyploids. *Cytologia* **2**: 252-284.

—— 1932. The chromosome constitution of *Cardamine pratensis* and *Verbascum phoeniceum*. *Genetica* **13**: 183-208.

—— 1936. The origin of new forms in *Delphinium*. *Genetica* **18**: 109-115.

—— 1938. *Streptocarpus* Merton Giant. *Gard. Chron.* **103**: 60.

—— and SCOTT-MONCRIEFF, R. 1935. The genetics and chemistry of flower colour in *Dahlia*; a new theory of specific pigmentation. *J. Genet.* **30**: 155-226.

—— ——, and STURGESS, V. 1939. Studies on Streptocarpus I, Genetics and chemistry of flower colour in the garden strains. *J. Genet.* **38**: 299-306.

LAXTON, T. 1866. Observations on the variations effected by crossing in the colour and character of the seed of peas. *Rep. Int. Hort. Exh. and Bot. Congr.* 156.

LAXTON, T. 1890. On the improvement amongst Peas during the last quarter of a century. *J.R.H.S.* **12**: 29-40.

LEDEBOER, M., and RIETSEMA, I. 1937. A case of unfruitfulness in black currants. *J. Pomol.* **15**: 191-204.

LEHMANN, E. 1926. The heredity of self-sterility in *Veronica syriaca*. *Mem. Hort. Soc. N.Y.* **3**: 313-320.

LESLEY, M. M., and FROST, H. B. 1927. Mendelian inheritance of chromosome shape in *Matthiola*. *Genetics* **12**: 449-460.

LEWIS, C. J., and VINCENT, C. C. 1909. Pollination of the apple. *Bull. Oregon Agric. Exp. Sta.* No. **104**.

LEWIS, D. 1942. Parthenocarpy induced by frost in pears. *J. Pom. & Hort. Sci.* **20**: 40-41.

—— 1942. The physiology of incompatibility in plants, I. The effect of temperature. *Proc. Roy. Soc.* B, **131**: 13-26.

—— 1943. The incompatibility sieve for producing polyploids. *J. Genet.* **45**: 261-264.

—— 1944. Incompatibility in plants, its genetical and physiological synthesis. *Nature*, **153**: 575-582.

—— and MODLIBOWSKA, I. 1942. Genetical studies in Pears, IV, Pollen-tube growth and incompatibility. *J. Genet.* **43**: 211-222.

LEWITSKY, G. A. 1927. On the karyotype of *Solanum tuberosum*. *Bull. Appl. Bot.* **17** (3): 289-303.

LILIENFELD, F. A. 1933. Karyologische und genetische Studien an *Fraguria*. Ein tetraploider fertiler Bastard zwischen *F. nipponica* (n = 7) und *F. elatior* (n = 21). *Jap. J. Bot.* **6**: 425-458.

LINDSTROM, E. W. 1926. Linked inheritance in tomatoes. *Iowa State College J. Sci.* **1**: 3-13.

—— 1928. Linkage of size, shape and colour genes in *Lycopersicum*. *Z.I.A.V.* **2**: 1031-1057.

—— 1932. A fertile tetraploid tomato. *J. Hered.* **23**: 115-121.

LONGLEY, A. E. 1926.a. Chromosomes and their significance in strawberry classification. *J. Agr. Res.* **32**: 559-568.

—— 1926. b. Relationship of polyploidy to pollen sterility in the genera of *Rubus* and *Fragaria*. *Mem. Hort. Soc.* N.Y. **3**: 15-17.

—— 1927. Chromosomes in Vaccinium. *Science* **66**: 566-568.

—— 1928. Chromosomes in Iris species. *Amer. Iris Soc. Bull.* **29**: 43-54.

—— and CLARK, C. F. 1930. Chromosome behaviour and pollen production in the potato. *J. Agr. Res.* **41**: 867-888.

LUMSDEN, D. 1914. Mendelism in melons. *N. Hampshire Agr. Exp. Sta. Bull.* **172**: 3-58.

LUNDEN, A. P. 1932. Inheritance of flower and tuber colour in potato. *J. Genet.* **25**: 339-358.

MACARTHUR, J. W. 1926. Linkage studies with the tomato. *Genetics* **11**: 387-405.

—— 1928. Linkage studies with the tomato. II. *Genetics* **13**: 410-420.

—— 1931. Linkage studies with the tomato. *Trans. Roy. Canad. Inst.* **18**: 1-19.

—— 1934. Linkage groups in the tomato. *J. Genet.* **29**: 124-133.

—— and BUTLER. 1938. Size inheritance and geometric growth processes in the tomato fruit. *Genetics* **23**: 253-268.

MACOUN, W. T. 1921. Individuality in apple trees. *Interim Rep. Domin. Hort.* 11.

—— and DAVIS, M. B. 1919. Progress in apple breeding for the Canadian prairies. *Proc. Amer. Soc. Hort. Sci.* **16**: 13-18.

MALINOWSKI, E. 1916. On the inheritance of some characters in radishes. (English Summary, 770-776.) *C.-R. Soc. Sci. Biol.* **9**: 757-776.

—— 1929. Genetics of *Brassica*. *Biblio. Genetica*, **5**: 1-26.

MANGELSDORF, A. J., and EAST, E. M. 1927. Studies on the genetics of *Fragaria*. *Genetics* **12**: 307-339.

MANGELSDORF, P. C., and FRAPS, G. S. 1931. A direct quantitative relationship between Vitamin A in corn and the number of genes for yellow pigmentation. *Science* **73**: 241.

MARSDEN-JONES, E. M., and TURRILL, W. B. 1930. The history of a tetraploid *Saxifraga*. *J. Genet.* **23**: 83-92.

—— —— 1934. Further breeding experiments with *Saxifraga*. *J. Genet.* **29**: 245-268.

MATHER, K. 1943. Polygenic inheritance and natural selection. *Biol. Revs.* **18**: 32-64.

MATSUURA, H. 1933. *Bibliographical monograph on plant genetics*. 2nd edition. Sapporo, Japan.

MAUDE, P. F. 1939. The Merton Catalogue. *New Phytol.* **38**: 1-31.

MCKAY, J. W., and CRANE, H. L. 1939. The immediate effect of pollen on the fruits of the chestnut. *Proc. Amer. Soc. Hort. Sci.* **36**: 293-298.

MEHLQUIST, G. A. L. 1940. Inheritance in the Carnation. II. Inheritance of nine abnormal types. *Proc. Amer. Soc. Hort. Sci.* **38**: 699-704.

—— and GEISMANN, T. A. 1947.a. Inheritance in the Carnation, *Dianthus caryophyllus*. III. Inheritance of flower colour. *Ann. Missouri Bot. Gard.* **34**: 39-72.

—— —— 1947.b. IV. The chemistry of flower colour variation. *Genetics*, **32**: 410-433.

MENDEL, GREGOR JOHANN. 1865. Versuche über Pflanzen-hybriden. *Verh. naturf. Ver. in Brünn.* **4**: 1. English translation *J.R.H.S.* 1901, **26**: 1-32.

MEUNISSIER, A. 1918. Expériences génétiques faites à Verrières. *Bull. Soc. Nat. Acclimat.* **65**: 1-31.

MEURMAN, O., and RANCKEN, G. 1932. Untersuchungen über die Chromosomenverhältnisse bei kultivierten Kartoffelsorten. *Soc. Scient. Fenn. Comment. Biol.* III, **20**: 1-28.

MIEDZYRZECKI, CH. 1933. Études cytologiques et stérilité du pollen chez le pommier et le poirier. *C.-R. Soc. Biol.* **114**: 1267.

—— 1934. Stérilité du pollen chez les arbres fruitiers. *Cong. Internat. Arb. Frut. Pomol.* 46-56.

MODLIBOWSKA, I. 1945. Pollen tube growth and embryo-sac development in apples and pears. *J. Pom. & Hort. Sci.* **21**: 57-89.

MOFFETT, A. A. 1931. A preliminary account of chromosome behaviour in the Pomoideae. *J. Pomol.* **9**: 100-110.

—— 1931.b. The chromosome constitution of the Pomoideae. *Proc. Roy. Soc.* B **108**: 423-446.

—— 1932. Note on the cytology of *Prunus* root-stocks. *J. Pomol.* **10**: 181-183.

MOORE, C. W. 1917. Self-sterility. *J. Hered.* **8**: 203-207.
MÜLLER, K. O. 1924. Zur Kenntnis der Faktoren der Anthocyanbildung bei der Kartoffel. *Ber. Deuts. Bot. Ges.* **41**: 60-66.
MUNTZING, A. 1932. Cyto-genetic investigations on synthetic *Galeopsis Tetrahit*. *Hereditas* **16**: 105-154.
—— 1933. Studies on meiosis in diploid and triploid *Solanum tuberosum* L. *Hereditas* **17**: 223-245.

NEBEL, B. [R.] 1929. Zur Cytologie von Malus II. *Züchter* **1**: 209-217.
—— 1930. Recent findings in cytology of fruits. (Cytology of Pyrus III.) *Proc. Amer. Soc. Hort. Sci.* **27**: 406-410.
—— 1929. Zur Cytologie von *Malus* und *Vitis*. *Gartenbauwiss.* **1**: 549-592.
—— 1930. Xenia and metaxenia in apples. *N.Y. State Agr. Exp. Bull.* **170**: 1-16.
—— 1932. Metaxenia and xenia in apples. *Proc. 6th Int. Cong. Genet.* **2**: 140-141.
—— 1936.a. Metaxenia in apples. V. *J. Pom. & Hort. Sci.* **14**: 203-204.
—— 1936.b. Metaxenia in apples. *J. Hered.* **27**: 345-349.
—— and KERTESZ, Z. I. 1934. Metaxenia and xenia in apples, IV. *Gartenbauwiss.* **9**: 45-64.
—— and RUTTLE, M. L. 1938. The cytological and genetical significance of colchicine. *J. Hered.* **29**: 3-9.
—— and TRUMP, I. J. 1932. Xenia and metaxenia in apples, II. *Proc. Nat. Acad. Sci.* **18**: 356-359.
NEWTON, W. C. F. 1929. The inheritance of flower colour in *Papaver Rhoeas* and related forms. *J. Genet.* **21**: 389-404.
—— and PELLEW, C. 1929. *Primula kewensis* and its derivatives. *J. Genet.* **20**: 405-467.
NILSSON-EHLE, H. 1908. Einige Ergebnisse von Kreuzungen bei Hafer und Weizen. *Bot. Notiser* **1908**: 257-294.
NIXON, R. W. 1928.a. Immediate influence of pollen in determining the size and time of ripening of the fruit of the date palm. *J. Hered.* **19**: 241-255.
—— 1928.b. The direct effect of pollen on the fruits of the date palm. *J. Agric. Res.* **36**: 97-128.
—— 1935. Metaxenia in dates. *Proc. Amer. Soc. Hort. Sci.* **32**: 221-226
—— 1936. Metaxenia and interspecific pollinations in *Phœnix*. *Proc. Amer. Soc. Hort. Sci.* **33**: 21-26.
NOGUCHI, Y. 1934. Metaxenia in the Japanese persimmon. *Jap. J. Bot.* **7**: 61-71.
NORTON, J B. 1907. Heredity in carnation seedlings. *Amer. Breeders' Assoc.* **3**: 81-82.

ODLAND, M. C., and NOLL, C. J. 1948. Hybrid vigour and combining ability in egg plants. *Proc. Amer. Soc. Hort. Sci.* **51**: 417-422.
OKABE, S. 1928. Zur Zytologie der Gattung *Prunus*. *Sci. Rep. Tohoku Agric. Imp. Univ.* IV. **3**: 733-743.

PARKINSON, J. 1629. *Paradisi in sole Paradisus Terrestris*. London.

PASSMORE, S. F. 1934. Hybrid vigour and reciprocal crosses in *Cucurbita Pepo*. *Ann. Bot.* **48**: 1029-1030.

PEARL, R. T. 1928. The history of the cultivated strawberry. *Bull. S.E. Coll. Wye.*

PEARSON, O. H. 1932. The influence of inbreeding upon the season of maturity of cabbage. *Proc. Amer. Soc. Hort. Sci.* **28**: 359-366.

PEASE, M. S. 1926. Genetic studies in *Brassica oleracea*. *J. Genet.* **16**: 363-385.

—— 1927. Genetic studies in *Brassica oleracea*. II. The Kohlrabi. *J. Genet.* **17**: 253-267.

PEEBLES, R. H., and HOPE, C. 1937. The influence of different pollen on the development of the Pistache nut. *Proc. Amer. Soc. Hort. Sci.* **34**: 29-32.

PELLEW, C., and SANSOME, E. R. 1931. Genetical and cytological studies on the relation between Asiatic and European varieties of *Pisum sativum*. *J. Genet.* **25**: 25-54.

PETROV, A. F. 1929. Experiments on the influence of self-pollination on the forming and variation of the apple fruit. *Bull. Appl. Bot. Leningrad*, **14**: 117-118.

PHILP, J. 1933. The genetics of *Papaver Rhoeas* and related forms. *J. Genet.* **28**: 175-203.

—— 1934. Note on the cytology of *Saxifraga granulata* L. *S. rosacea* Moench and their hybrids. *J. Genet.* **29**: 197-201.

—— and HUSKINS, C. L. 1931. The cytology of *Matthiola incana* R. Br. especially in relation to the inheritance of double flowers. *J. Genet.* **24**: 359-404.

PRELL, H. 1921.a. Das Problem der Unbefruchtbarkeit. *Naturwiss.* **20**: 440-446.

—— 1921.b. Anisogametie, Heterogametie und Äthogametie als biologische Wege zur Förderung der Amphimixis. *Arch. Entwm.* **49**: 463-490.

PRICE, H. L., and DRINKARD, A. W. 1908. Inheritance in tomato hybrids. *Virginia Agric. Exp. Sta. Bull.* **177**.

PRICE, J. R. 1939. The yellow colouring matter of *Dahlia variabilis*. *J. Chem. Soc.* 1017-1018.

PRIDHAM, A. M. S., GUTERMAN, C. E. F., GRISWOLD, G. H., and RANDOLPH, L. F. 1935. The bearded iris. *Cornell Univ. Bull.* **324**: 51.

PUNNETT, R. C. 1925. *Lathyrus odoratus*. *Bibliogr. Genet.* **1**: 69-81.

—— 1927. Linkage groups and chromosome number in *Lathyrus*. *Proc. Roy. Soc.* **102**: 236-238.

RANDOLPH, L. F. 1934. Chromosome numbers in native American species and cultivated varieties of Iris. *Amer. Iris Soc. Bull.* **52**: 61-66.

—— 1935. Iris breeding. *Cornell Univ. Bull.* **324**: 40-51.

RASMUSSON, J. 1927. Genetically changed linkage values in *Pisum*. *Hereditas* **10**: 1-152.

—— 1932. Results from a cross cabbage × Savoy cabbage. *Hereditas*, **16**: 241-248.

—— 1935. Ärftlighetslären som Grundval för Värlförädlingen. Vaxtodling, Svenska, Stockholm.

RAWES, A. N. 1922. Comparative cropping of apple trees propagated from parent trees of good and bad history. *J.R.H.S.* **47**: 163-168.

—— 1933. Pollination in Orchards. (IX.) *J.R.H.S.* **58**: 228-295.

RHOADES, M. M., and MCCLINTOCK, B. 1935. The cytogenetics of maize. *Bot. Rev.* **1**: 292-325.

RICHARDSON, C. W. 1914. A preliminary note on the genetics of *Fragaria*. *J. Genet.* **3**: 171-178.

—— 1918. A further note on the genetics of *Fragaria*. *J. Genet.* **7**: 167-170.

—— 1920. Some notes on *Fragaria*. *J. Genet.* **10**: 39-46.

—— 1923. Notes on *Fragaria*. *J. Genet.* **13**: 147-152.

RICHARDSON, M. M. 1936. Structural hybridity in *Lilium Martagon* × *L. Hansoni*. *J. Genet.* **32**: 411-450.

RIEMAN, G. H. 1931. Genetic factors for pigmentation in the onion and their relation to disease resistance. *J. Agric. Res.* **42**: 251-278.

RILEY, H. P. 1935. Self-sterility and self-fertility in species of the genus *Nemesia*. *Amer. J. Bot.* **22**: 889-894.

—— 1945. Inheritance of orange and yellow flower color in *Nemesia strumosa*. *Bull. Torrey Bot. Club*, **72**: 435-453.

—— 1948. Inheritance of the "Eyebrow" gene in *Nemesia strumosa*. *J. Hered.* **39**: 170-172.

—— 1949. Relationship of blue and orange flower-color types in *Nemesia strumosa*. *Bot. Gaz.* **111**: 43-52.

RIVERS, H. S. 1906. The cross-breeding of peaches and nectarines *Rep. 3rd Int. Conf. Genet.* 463-467.

ROGERS, W. S. 1925. Rootstock effect on colour and size of apples. *East Malling Ann. Rep.* 16-32.

ROH, L. 1929. Zum Stadium der Beeinflussung der Bestäuber auf die Entwicklung der Früchte und Samen bei den bestäubten Sorten. *Bull. Mleev. Hort. Exp. Sta.* No. 23.

ROSA, J. T. 1926. The direct effect of pollen on the fruits and seeds of melons. *Proc. Amer. Soc. Hort. Sci.* **23**: 243-249.

ROZANOVA, M. A. 1928. On the sexual dimorphism in *Rubus chamaemorus* L. *Bull. Appl. Bot.* **19**: (2), 315-324.

RUYS, B. 1931. Red delphiniums. *Gard. Chron.* **90**: 172.

RYBIN, V. A. 1926. Cytological investigations of the genus Malus (preliminary account). *Bull. Appl. Bot. Genet.* **16** (3): 187-200.

—— 1929. Karyological investigation of some wild and indigenous cultivated potatoes of America. *Bull. Appl. Bot. Genet.* **20**: 655-720.

—— 1936. Spontane und experimentall erzeugte Bastarde zwischen Schwarzdorn und Kirschpflaume und das Abstammungsproblem der Kulturpflaume. *Planta* **25**: 22-58.

SABINE, J. 1819. On the love apple or tomato. *Trans. Hort. Soc.* **3**: 342-354.

SALAMAN, R. N. 1912. The hereditary characters in the potato. *J.R.H.S.* **38**: 34-39.

—— 1926. *Potato varieties*. Cambridge.

—— 1930. Somatic mutations in potatoes. *Proc. 9th Int. Hort. Cong.* 117-140.

—— 1946. The early European potato: its character and place of origin. *J. Linn. Soc.* **43**: 1-27.

SANSOME, E. RICHARDSON. 1932. Segmental interchange in *Pisum sativum*. *Cytologia* **3**: 200-219.

SANSOME, F. W. 1930. Graft hybrids and induction of polyploids in *Solanum*. *Proc. 9th Int. Hort. Cong.* 92-99.

—— 1933. Chromatid segregation in *Solanum Lycopersicum*. *J. Genet.* **27**: 105-132.

—— and PHILP, J. 1939. *Recent advances in plant genetics*. London.

—— and ZILVA, S. S. 1933. Polyploidy and Vitamin C. *Biochem. J.* **27**: 1935-1941.

SAUNDERS, E. R. 1928. *Matthiola*. *Bibliogr. Genet.* **4**: 141-170.

SAUNDERS, W. 1911. Progress in the breeding of hardy apples for the Canadian North-West. *Dom. Canad. Dept. Agric. Bull.* **68**.

SAX, KARL. 1923. Bud and root selection in the propagation of the apple. *Proc. Amer. Soc. Hort. Sci.* **20**: 244-250.

—— 1931. The origin and relationship of the Pomoideae. *J. Arnold Arbor.* **12**: 3.

SCHREINER, E. J., and DUFFIELD, J. W. 1942. Metaxenia in an oak species cross. *J. Hered.* **33**: 97-98.

SCHUSTER, C. E. 1924. Filberts, I.—Growing filberts in Oregon. II.—Experimental data on filbert pollination. *Oregon Agr. Exp. Sta. Bull.* **208**.

SCOTT-MONCRIEFF, R. 1936. A biochemical survey of some mendelian factors for flower colour. *J. Genet.* **32**: 117-170.

SEARS, E. R. 1937. Cytological phenomena connected with self-sterility in flowering plants. *Genetics* **22**: 130-181.

SHAMEL, A. D. 1937. A large-fruited bud mutation of the Winter Nelis pear. *J. Hered.* **28**: 350-352.

—— and POMEROY, C. S. 1932. Bud variation in apples. *J. Hered.* **23**: 173.

—— —— and CARYL, R. E. 1927. Bud selection in the Valencia orange; progeny tests of limb variations. *U.S.D. of Agric. Bull.* **1483**.

—— —— —— 1929. Bud selection in the Washington Navel orange; progeny tests of limb variations. *U.S.D. of Agric. Tech. Bull.* **123**.

—— —— —— and HARMON, F. N. 1933. Bud variations in the Agen prune. *J. Hered.* **24**: 289-292.

SHCHAVINSKAYA, S. A. 1937. Octoploid cabbage experimentally obtained. *Bull. Appl. Bot. Genet.* II, **7**: 69-77.

—— 1937. Restoration of fertility in the Geranium (*Pelargonium radula roseum* W.) by doubling the chromosome complex. *Bull. Appl. Bot. Genet.* II, **7**: 101-106.

—— 1937. Tetraploid cabbage obtained by means of regeneration. *Bull. Appl. Bot. Genet.* II, **7**: 13-33.

SHERWOOD, N. N. 1898. Garden Peas. *J.R.H.S.* **22**: 239-260.

SHRINER, R. L., and ANDERSON, R. J. 1928. A contribution to the chemistry of grape pigments. V.—The anthocyans in Ives grapes. *J. Biol. Chem.* **80**: 743.

SIMONET, M. 1929. Le Nombre des chromosomes chez les Iris. *Soc. nat. d'Hort. Bul.* **2**: 88-94.

—— Recherches cytologiques et génétiques chez les Iris. *Bull. biol. France et Belg.* **66**: 416.

SIRKS, M. J. 1927. The genotypical problems of self- and cross-incompatibility. *Mem. Hort. Soc. N.Y.* **3**: 325-343.

SIRKS, M. J. 1929. The interrelation of some anthocyane factors in the potato, *Genetica* **11**: 293-328.

SKOVSTED, A. 1929. Cytological investigations of the genus *Aesculus* L. *Hereditas* **12**: 64-70.

SMITH, F. F. 1927. Chromosome counts in the varieties of *Solanum tuberosum* and allied wild species. *Genetics* **12**: 84-92.

STEVENSON, F. J., SCHULTZ, E. S., and CLARK, C. F. 1939. Inheritance of immunity from virus *X* (latent mosaic) in the potato. *Phytopathology* **29**: 362-365.

STOUT, A. B. 1915. The establishment of varieties in *Coleus* by the selection of somatic variations. *Carneg. Inst. Wash. Pub.* **218**: 1-80.

—— 1918. Fertility in *Cichorium intybus*, self-compatibility and self-incompatibility among the offspring of self-fertile lines of descent. *J. Genet.* **7**: 71-103.

—— 1920. A graft-chimaera in the apple. *J. Hered.* **11**: 233-237.

—— 1921. Sterility and fertility in *Hemerocallis. Torreya* **21**: 57-62.

—— 1921. Types of flowers and intersexes in grapes with reference to the fruit development. *N.Y. Agr. Exp. Sta. Bull.* **82**.

—— 1922. Sterilities in lilies. *J. Hered.* **13**: 369-373.

—— and CHANDLER, C. 1942. Change from self-incompatibility to self-compatibility accompanying change from diploidy to tetraploidy. *Science* **9**: 178.

—— and SUSA, T. 1929. Chromosome irregularities in relation to sterility in *Hemerocallis fulva*, clon Europa. *Ann. N.Y. Acad. Sci.* **31**: 1-30.

—— MCKEE, R. H., and SCHREINER, E. J. 1927. The breeding of forest trees for pulp wood. *J.N.Y. Bot. Gard.* **28**: 49-63.

STRONG, W. J. 1921. Greenhouse cucumber breeding. *Proc. Amer. Soc. Hort. Sci.* **18**: 271-273.

STUART, W. 1912. Mendelian inheritance in the Carnation. *Vt. Agr. Exp. Sta. Bull.* **163**: 49-72.

SVERDRUP, ASLANG. 1927. Linkage and independent inheritance in *Pisum sativum. J. Genet.* **17**: 221-251.

—— 1930. Genetics and cytology of the tetraploid form of *Primula sinensis. J. Genet.* **23**: 447-508.

SWARBRICK, T., and THOMPSON, C. R. 1932. Some observations on the partial self-sterility of the Oberschlesien strawberry and its failure to pollinate Tardive de Leopold. *Long Ashton Res. Sta. Ann. Rep.* 1932: 24-31.

SWINGLE, W. T. 1928. Metaxenia in the date palm. *J. Hered.* **19**: 257-268.

—— 1928. Metaxenia or the influence of the male parent on the tissues of the mother plant outside of the embryo and endosperm, especially as exemplified in the date palm. *Pan-Pacif. Sci. Cong. Tokyo, Proc.* **1**: 1164-1165.

TERAO, H. 1923. On the inheritance of self-sterility. (In Japanese.) *Jap. J. Genet.* **2**: 144-155.

THOMAS, P. T. 1940. Reproduction versatility in *Rubus* II. *J. Genet.* **40**: 119-128.

THOMAS, P. T. 1940. The origin of new forms in *Rubus* III. *J. Genet.* **40**: 141-156.
—— 1945. Supercharging the nucleus. *Discovery* **6**: 376-378.
—— 1946. The study of polyploid hybrids between related species. *J.I.H.I. Ann. Rep.* 1945.
TISCHLER, G. 1927. Pflanzliche Chromosomenzahlen. *Tab. Biol.* **4**: 1-83.
—— 1931. Pflanzliche Chromosomenzahlen. *Tab. Biol.* **7**: 109-226.
—— 1936. Pflanzliche Chromosomenzahlen. *Tab. Biol.* **11**: 281-304; **12**: 1-115.
TSCHERMAK, E. 1911. Examen de la théorie des facteurs par le croisement méthodique des hybrides. *Rep. 4th Int. Conf. Genet.* 91-95.
—— 1912. Bastardierungsversuche an Levkojen, Erbsen und Bohnen mit Rücksicht auf die Faktorenlehre. *Z.I.A.V.* **7**: 81-234.
—— 1916. Über den gegenwärtigen Stand der Gemüsenzuchtung. *Zeits. f. Zücht.* **4**: 65-104.
TSENG, H. P. 1938. Self-sterility in *Antirrhinum* and *Petunia*. *J. Genet.* **36**: 127-138.
TUFTS, W. P., and PHILP, G. L. 1922. Almond pollination. *Agr. Exp. Sta. Berkeley, Bull.* **346.**
—— —— 1923. Pear pollination. *Agr. Exp. Sta. Berkeley, Bull.* **373.**
TUKEY, H. B. 1936. A relation between the seed attachment and carpel symmetry and development in *Prunus*. *Science* **84**: 513-515.
TYDEMAN, H. M. 1930. Some results of experiments in breeding black currants. *J. Pomol.* **8**: 106-128.
—— 1933. Breeding experiments with "paradise" apple rootstocks. *J. Pomol.* **11**: 214-236.

UPCOTT, M. B., and LA COUR, L. 1936. The chromosome structure of Tulipa, I. A genetic survey. *J. Genet.* **33**: 353-372.
UPHOF, J. O. TH. 1924. On mendelian factors in radishes. *Genetics* **9**: 292-304.

VALLEAU, W. D. 1918. Sterility in the strawberry. *J. Agric. Res.* **12**: 613-670.
VAVILOV, N. I. 1926. Studies on the origin of cultivated plants. *Bull. Appl. Bot.* Leningrad **16**: 1-248.
—— 1930. Wild progenitors of the fruit trees of Turkistan and the Caucasus and the problem of the origin of fruit trees. *Proc. 9th Int. Hort. Cong.* 271-286.
—— and BUKINICH, D. D. 1929. Agricultural Afghanistan. *Bull Appl. Bot. Gen. Plt. Brd. Suppl.* **33**: 576-577.
VILMORIN, R. DE, and SIMONET, M. 1928. Recherches sur le nombre des chromosomes chez quelques Solanées. *C. R. Acad. Sci.* **184**: 164-166.

WADDINGTON, C. H. 1929. Pollen germination in stocks and the possibility of applying a lethal factor hypothesis to the interpretation of their breeding. *J. Genet.* **21**: 193-206.
WAITE, M. B. 1894. The pollination of pear flowers. *U.S. Dept. Agric. Bull.* **5.**

WARREN, E. 1919. The pure line hypothesis and the inheritance of small variations. *S. Afric. J. Sci.* **15**: 535-567.

WEBBER, H. J. 1931. The economic importance of apogamy in Citrus and Mangifera. *Proc. Amer. Soc. Hort. Sci.* **28**: 57-61.

WEISS, F. E. 1925. On the leaf-tissues of the graft-hybrids *Crataegomespilus Asnieresii* and *Crataegomespilus Dardari*. *Mem. Manchest. Lit. and Phil. Soc.* **69**: 73-78.

—— 1930. The problem of graft-hybrids and chimaeras. *Biol. Revs.* **5**: 231-271.

—— 1931. Addendum to the Review on Graft-hybrids and Chimaeras. *Biol. Revs.* **6**: 132.

WELLENSIEK, S. J. 1925. Genetic monograph on *Pisum*. *Bibliographia Genet.* **2**: 343-476.

WELLINGTON, R. 1912. Influence of crossing in increasing the yield of the tomato. *N.Y. Agr. Exp. Sta. Bull.* **346**: 57-76.

—— 1913.a. Mendelian inheritance of epidermal characters in the fruits of *Cucumis sativus*. *Science* N.S. **38**: 61.

—— 1913.b. Inheritance of the russet skin in the pear. *Science* N.S. **37**: 156-157.

—— 1913.c. Raspberry breeding. *Proc. Amer. Soc. Hort. Sci.* **10**: 155-159.

—— 1924. An experiment in breeding apples, II. *N.Y. Agr. Exp. Sta. Geneva Tech. Bull.* **106.**

—— 1927. An experiment in breeding plums. *N.Y. State Agr. Exp. Sta. Geneva, Bull.* **127.**

—— 1930. The value of the European grape in breeding grapes for New York State. *Proc. Amer. Soc. Hort. Sci.* **27**: 416-421.

—— and HAWTHORN, L. R. 1928. A parthenocarpic hybrid derived from a cross between an English Forcing cucumber and the Arlington White Spine. *Proc. Amer. Soc. Hort. Sci.* **25**: 97-100.

WESTERGAARD, M. 1936. On the satellites in the ever-sporting *Matthiola* races. *C. R. Trav. Lab. Carls.* **21**: 195-204.

WINGE, O. 1936. Linkage in *Pisum*. *C.R. Lab. Carls.* **21**: 271-343.

WINKLER, H. 1907. Über Pfropfbastarde und pflanzliche Chimären. *Ber. Deuts. Bot. Ges.* **25**: 568-576.

—— 1910. Über die Nachkommenschaft der *Solanum* Pfropfbastarde und die Chromosomenzahlen ihrer Keimzellen. *Zeits. f. Bot.* **2**: 1-38.

—— 1914. Die Chimärenforschung als Methode der experimentellen Biologie. *Sitzber. Phys.-Med. Ges. Wurzburg*, **1**: 95-119.

—— 1916. Über die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. *Zeits. f. Bot.* **8**: 417-531.

WIT, F. 1936. Contributions to the genetics of the China Aster. Groningen. Dissertation (Hague).

YARNELL, S. H. 1931.a. Genetic and cytological studies on *Fragaria*. *Genetics* **16**: 422-454.

—— 1931.b. A study of certain polyploid and aneuploid forms in *Fragaria*. *Genetics* **16**: 455-489.

YASUDA, S. 1929. Physiological researches on the fertility of *Petunia*

violacea. VI.—Growth of the pollen-tubes in the style. *Bot. Mag. Tokyo* **43** : 156-169.

YASUDA, S., and KITAMARU, T. A. 1930. A metaxenia-like phenomenon found in some plants of Solanaceae. *Jap. J. Genet.* **6** : 141-142.

YEAGER, A. F. 1937. Studies on the inheritance and development of fruit size and shape in the tomato. *J. Agric. Res.* **55** : 141-152.

ZEDERBAUR, E. 1926. Apfelxenien. *Fortschr. Landw.* **1** : 8-9.

INDEX

Aberrations, chromosome, 186, 233
Abutilon Thomsonii, 181
Aconitum Napellus, 17
Adventitious shoots, 95
Aesculus carnea, chromosomes of, 239
  origin of, 238
  Hippocastanum, 238
  Pavia, 238
Allelomorph, 6, 24
  multiple, 11, 186
Allium, 43
  Cepa, 106
Allo-polyploid, 32, 34, 236
Allosyndesis, 242
Allo-tetraploid, 32
Almond, 192, 230
Alternative characters, 4
Amygdalus communis amara, 230
Anaphase, 18, 22, 23
Aneuploid, 32, 167
Anthocyanins, 71
Anthoxanthins, 74
Antirrhinum, 11, 62
  Linkianum, 65
  majus, 65
  mutation in, 62
Apigenin, 75
Apomixis, 41, 246
Apple, aneuploid forms, 169
  bud-sports, 170, 175
  chromosome complement, 161
  diploid varieties, 216
  fluctuations, 184
  graft-chimaeras, 174
  immunity to Woolly Aphis, 258
  incompatibility, 202
  inheritance of fruit shape, 157
  inheritance of fruit size, 155
  June-drop, 219
  origin, 162
  parthenocarpy, 230, 231
  root-burrs, 159
  root-stocks, 159, 183
  secondary polyploid, 35
  sterility, 214
  tetraploid, 184
  triploid varieties, 162, 215
    origin of, 235
  xenia, 225
Artemisia, 43
Autogenous chimaeras, 174
Auto-polyploids, 32, 33, 234
Autosyndesis, 242
Auto-tetraploid, 32, 234

Back-cross, 9, 93
Balance of chromosomes, 213
Basic number, 31, 263
Bees, 208
Beetroot, 107
Beta vulgaris, 107
Bivalent, 33
Blackberry "John Innes", 38, 251
  origin of, 249
Black currants, 136
Blueberry, 213
Bouvardia, 174, 175, 180
Brassica campestris, 243
  napocampestris, 243
  napus, 243
  oleracea, 108
  rapa, 108
Bremia lactucae, 105
Broad bean, 15
Bud-sports, 170
  and low production, 177
  in apple, 175, 184
  in citrus, 177
  in *Coleus*, 180
  in currant, 178, 183
  in *Nicotiana*, 182
  in peach, 177
  in pear, 178
  in plum, 170, 177
  in potato, 119, 179, 180
  in rose, 180

Callistephus chinensis, 80
Callus, 171
Campanula persicifolia, 29, 63
  "Telham Beauty", 65
  nitida, 64

Cardamine, 186
Carotene, 76
Carrot, 108
Cell, 1, 16, 19
Cell division, 18, 19
Centromere, 18
Character (genetic), 3
Cherry, Duke, 140, 221
  Japanese, 213
  sour, 140
  sweet, 138
  triploid, 212
Chiasma, 21
Chimaeras, 170
  autogenous, 174
  graft, 171
  mericlinal, 171
  periclinal, 171
  sectorial, 171
Chinese primrose, 55
Chromatid, 18, 25
  segregation, 37
Chromosomes, 5
  aberrations, 186, 233
  and breeding, 249
  and linkage, 24
  pairing, 21, 33
  particulate nature of, 21
  rearrangement, 27
    deletion, 28
    duplication, 28
    fragmentation, 28
    inversion, 28, 223
    rings, 28, 223
    translocation, 28
  secondary association, 35
  segregation, 23, 38
Chrysanthemum, 180
Cichorium, 192
Citrus, 42
Clonal multiplication, 41, 42
  propagation, 181
  selection, 180
  variation, 170, 176
Clone, 41, 43
Colchicine, 247, 248
Coleus, 180
Collections of plant-breeding material, 260
Colletotrichum circinans, 107
Compatibility, 193. *See also* Incompatibility
Complement, chromosome, 18, 31
Complementary genes, 10, 38
Constant hybrids, 239
Constriction, 18
Continuous variations, 39, 90B, 252
Co-pigmentation, 74
Coupling, 13, 26
Crataegomespilus Asnieresii, 173
  Dardari, 173
Crataegus monogyna, 173
Crepis dioscoridis, 16
Crocus vernus, 17
Cross-bred, 5
Cross-over, 24
Crossing-over, 26
Cucumber, 107
  parthenocarpy in, 108
Cucumis Melo, 108
  sativus, 107
Cucurbita Pepo, 169A
Cultivated plants, origin of, 233
Cultivation, effect of, 234
  plant protection and, 234
Cyanidin, 72
Cytisus Adami, 172, 173
  purpureus, 172
Cytoplasm, 14

Dahlia coccinea, 90A
  coronata, 36, 88, 90A
  imperialis, 88, 90A
  Maxoni, 88, 90A
  Merckii, 88, 90A
  variabilis, 36, 86, 236
    chemistry of flower colour, 89
    chromosome complement, 36
    gene interaction, 89
    history, 86
    origin, 90A
Datura, 42, 246
Daucus carota sativa, 108
Delphinidin, 72
Delphinium, 68
  belladonna, 68
  elatum, 69
  nudicaule, 69
  Ruysii, 69, 245
Dianthus, 82, 192
Digitalis ambigua, 243
  mertonensis, 243
  purpurea, 243
Dimorphism, sexual, 133
Diploids, 16, 18, 29, 32
Disease resistance, in grapes, 259
    in lettuce, 105
    in onion, 107
    in potato, 118, 119
Dominance, 4
  in polyploids, 60, 252
Dominant, 4
Double stock, 52
Doubling of chromosome number, 32, 222, 233 *et seq.*
  in *Campanula*, 64

in *Dahlia*, 88
in *Primula*, 60, 246
in *Rubi*, 241
in *Solanum*, 95
Duplex, 38, 97

Egg-cells, 2
Embryo, 210
Embryo-sac, 42, 210
Endogenous growth, 174
Endosperm, 210, 253
Epistatic, 10, 89, 105
Erigeron, 43
Eriosoma lanigerum, 258
Euchlaena mexicana, 42
Evening primrose, 15
Ever-sporting stock, 52
Evolution, 40, 262
Exogenous growth, 174

Factor, mendelian, 3
Female sterility, 132, 224
Fertile hybrids, 222, 236, 249
Fertilisation, 2, 19
absence of, 41
Fertility, chromosomes and, 222, 239, 249
in fruit, 211, 213, 242
of species hybrids, 67, 68, 238
of tetraploids, 67, 222
Fixation of varieties, 48
in diploids, 48
in polyploids, 61
Flavone, 75
Flavonol, 75
Flax, 15
Flower colour, chemistry of, 71
genetics of, 79, 89
Fluctuating characters, 183
Fluctuations, 170
Foliar glands of peaches, 7, 127
Fragaria bracteata, 242
chiloensis, 144, 213
elatior, 142, 213
garden varieties, 145
Helleri, 242
vesca, 141, 213
semperflorens, 144
virginiana, 143, 213
Fragment, 53
Fritillaria lanceolata, 20

Galeopsis Tetrahit, 211
Gametes, 5
Gametic series, 6, 37
Gasteria verrucosa, 191
Gene, 3
mutation, 233
Generational sterility, 34, 210
Genes, alternative, 11
complementary, 9
diluting, 10
inhibiting, 10
intensifying, 10
interaction of, 10
lethal, 11
linear sequence, 24, 27
linkage of, 25, 26
multiple, 39
mutations, 233
nature of, 4
Genotypes, 38
Germ-cells, 2, 5, 19, 37
Germ tract, 183
Giant, 65, 234
Godetia, 67
Gooseberry, 133
susceptibility to sulphur injury, 135
Graft-chimaeras, 171
formation of, 171
Grafting, 1, 171, 179, 181
Grapes, 141, 213, 224, 259

Haploid, 18, 42
Hemerocallis, 192
Heptaploid, 211
Heredity, 2
mechanism of, 2, 23
units of, 2
Hermaphrodite, 15, 129
Heterosis, 168
in cucumber, 169G
in maize, 169, 169C
in peas, 169
in *Solanum melongena*, 169C
in *Sorghum*, 169B
in tomato, 169, 169E
Heterostylism, 208
Heterozygous, 6, 90B, 169H
Hexaploid, 31, 211, 237
Hieracium, 42, 43
Homologous, 28, 36
Homozygous, 6
Hyacinth, 19
triploid varieties, origin of, 235
Hybridisation and polyploidy, 40, 236
Hybrids, 5
interspecific, 32, 65, 236
true breeding, 40, 169H, 239
Hypostatic, 10

Immunity, 118, 255, 258
to cold, 254, 255
to disease, 105, 107, 118, 128, 259
to insects, 255, 258, 259

Incompatibility, 185
and chromosome number, 206
behaviour of, 186
economic aspects of, 207
inheritance of, 187
in apples, 202
in cherries, 193
in *Nicotiana*, 186, 187, 190
in pears, 205
in plums, 196
in *Verbascum*, 186, 202
in *Veronica*, 186
Incomplete dominance, 7, 162
Inheritance, 2
extra-nuclear, 14
maternal, 14
units of, 2
Interchange hybrids, 28
Inversions, 28
and sterility, 223
Ipomoea imperialis, 63
Iris, 70
chamaeiris, 69
cypriana, 69
germanica, 70
Kochii, 70
macrantha, 69
mesopotamica, 69
albiensis, 69
pallida, 69
polyploid varieties, 254
trojana, 69
variegata, 69, 254

Kniphofia corallina, 19

Laburnum, 172
Lactuca sativa, 105
scariola, 105
Lathyrus odoratus, 9, 44
male sterility in, 223
Laxtonberry, 31
Lens esculenta, 42
Lethal, 11
Lettuce, 105
immunity to mildew, 105
Leucojum aestivum, 19
Lilium, 192
hybrids, sterility in, 223
pardalinum, 20
Linaria, 186
Linear arrangement of genes in the chromosome, 24, 27
Linkage, 12, 24, 27
cytological basis of, 25
groups, 12
in *Nicotiana*, 187
in peas, 103
in *Primula*, 57
in sweet peas, 49
in tomato, 94
Linum, 209
usitatissimum, 15
Loganberry, 31
origin of, 239
Lupins, 261
Lycopersicum esculentum, 91
pimpinellifolium, 96
racemigerum, 94
Lythrum Salicaria, 209

Mahdiberry, 31, 211
Maize, 15, 24
chromosome map of, 26
heterosis in, 169c, 169d
linkage in, 27
male sterility in, 223
vitamin content, 253
Male sterility, 169g, 224
in peach, 126
in plum, 223
in raspberry, 129
in *Rubus chamaemorus*, 131
in strawberry, 224
Malus baccata, 255
resistance to cold, 255
malus, 160
pumila, 160
silvestris, 160
Malvidin, 73
Maps, genetical and cytological, 26, 49, 94
Matthiola annua, 50
incana, 50
ever-sporting singles, 52
history of, 50
long and short chromosome strains, 51
Meiosis, 19
Melon, 108
Mendelian ratios, 5, 7
segregation, 5
Mendel's laws, 7
Mespilus germanica, 173
Metaphase, 18, 22
Metaxenia, 226
Methylation, 73
Mitosis, 18
Multiple allelomorphs, 11, 186
Mutation, 27
acceleration of, 247

Natural Selection, 40
Nectarines, 2, 5, 122, 177
Nemesia strumosa, 61
Nemophila, 67

Nicotiana, 186, 187, 188, 190
Tabacum, 182
chimaera, 182
Non-heritable characters, 6, 170
Nucleus, 14, 254
Nulliplex, 37

OENIN, 141
Oenothera, 15, 28
Onion, 106, 169G
immunity to smudge fungus, 107
Ornamental plants, 44
triploid, 235
Ovules, 2, 187
Oxalis, 209

PAIRING, 21
Papaver, 85
Parthenocarpy, 108, 231
Parthenogenesis, 42
diploid, 42
female, 42
haploid, 42
male, 42
Peach, 2, 5, 125, 177, 224
Pear, 153
diploid, 218
russet skin, 153
tetraploid, 178, 184, 234
triploid, 217
origin of, 235
Peas, 97
chromosome rings, 99
genes in, 100-102
history, 98
linkage groups, 103
Pelargonidin, 72
Pelargonium, 174, 175, 183
Pentaploid, 31, 120, 249
Peonidin, 73
Petunia, 190
pH of cell sap, 74
Phacelia, 67
Phylloxera, 259
Pisum arvense, 97
sativum, 97
Plasmopara, 259
Plastid pigments, 76
Plum, 148
inheritance of fruit colour, 148
of fruit shape, 152
of fruit size, 150
Point of attachment, 18, 22
Pollen, 2, 185
germination, 214, 216, 218
grains, 19
tubes, 186
Polygenes, 14
Polyploids, 32
and fertility, 222
and variation, 41, 90C, 162, 252
induction of, 95, 247
Potato, 17, 110, 117, 179
cytology, 120
flower colour, 116
history, 111
immunity to wart disease, 118
secondary association in, 121-122
tuber colour, 112, 115
shape, 117
Primula acaulis, 65
elatior, 65
floribunda, 67
Juliae, 65
kewensis, 32, 40, 67, 222
officinalis, 65
sinensis, 11, 54, 222, 234
diploid, 56
history of, 55
linkage groups, 57-58
list of genes, 57-58
tetraploid, 60
unreduced gametes, 61
verticillata, 67
Propagation, 1, 174
Prophase, 18, 22
Prunus americana, 153
armeniaca, 212
avium, 138, 192, 212, 221
× *cerasus*, 140, 221
cerasifera, 212
Pissardi, 147
cerasus, 140, 212
divaricata, 147, 237
domestica, 148, 212, 237
origin of, 237
insititia, 153, 212
Mume, 213
nana, 212-13
persica, 2, 125, 212
spinosa, 153, 212, 237
Pure lines, 6
Pyrus communis, 153, 229
serotina, 153

QUADRIPLEX, 37
Quadrivalent, 33
Qualitative characters, 13
Quantitative characters, 13
Quercetin, 75

RADISH, 103
root shapes, 104
Raphanus sativus, 103

Raspberry, 10, 17, 31, 127
inheritance of sex, 129
sex correlations, 129
tetraploid varieties, 222, 234
Ratios, mendelian, 7
polyploid, 37, 38
Recessive, 4, 11, 162
Reciprocal differences, 15, 197, 210, 220
Recombination, 21, 23
Red currants, 136, 178
Reduction division, 20
Reproduction, 1
asexual, 1, 41
parthenogenetic, 42
sexual, 1
viviparous, 43
Repulsion, 13, 26
Resting stage, 18
Reversion, 9, 49
Ribes grossularia, 133
inermis, 134
nigrum, 136
rubrum, 136
Rings, chromosome, 28, 29, 99
Root cuttings, 174, 182
Rosa, 42, 180
Rose " Mrs. W. J. Grant ", 180
" Mermaid ", 223
Rubus, apomixis in, 41, 246
chamaemorus, 131
idaeus, 10, 127
obtusifolius, 130
loganobaccus, 239
Merton Thornless, 257
neglectus, 133, 239
niveus, 239
rusticanus, 241
inermis, 249, 256
diploid and tetraploid forms, 256
strigosus, 239
thyrsiger, 249
vitifolius, 239
Rudbeckia hirta, 63
Rumex, 131

Saxifraga granulata, 244
potternensis, 244
rosacea, 244
Scion, 171
Secondary association, 35, 85, 121
polyploids, 34
sexual characters, 131
Segregation, 4, 23
in polyploids, 37, 97
Selection, 40, 44
Self-sterility, 185. *See also* Incompatibility
Simplex, 37
Solanum species, 120
andigenum, 111
Commersonii, 122
coyoacanum, 122
etuberosum, 116
luteum, 172
medians, 122
melongena, 169E
tuberosum, 110
verrucosum, 116
Somatic variations, 170, 182
Spartina alterniflora, 245
stricta, 245
Townsendii, 245
Species, new polyploid, 233, 236, 239
Sphaerotheca mors-uvae, 135
Sterility, 210
and chromosome number, 211
generational, 210
interspecific, 219, 221
morphological, 210, 223
Stock, garden, 50
Strawberry, 141
history, 145
polyploidy, 146
sterility in, 224
Streptocarpus, chemistry of flower colour, 81
Dunnii, 79
garden hybrids, 80
Gardeni, 79
genetics of flower colour, 80
grandis, 246
Merton Giant, 246
Rexii, 79
Sugar molecules, 72, 81
Sweet pea, 44
chromosome map, 49
history, 45
linkage groups, 46, 49
linkage in, 12, 49
list of genes, 46
reversion, 9, 49
Synchytrium endobioticum, 118

Taraxacum, 43
Tetraploid, 31
hybrids, 32
pairing in, 33
Tolmiea Menziesii, 206
Tomato, 17
chromosome map, 94
diploid, 91
heterosis, 169E
history, 91
increased yield in F_1, 169F
induction of tetraploids, 95
linkage groups, 94

list of genes, 92
tetraploid, 95
vitamin content, 96
Trabant, 53
Tradescantia, 192, 247
Triplex, 36
Triploids, 31
in horticulture, 235
Trivalent, 33
Tropaeolum majus, 63
Tulip, " breaking " in, 181
triploid varieties, origin of, 235
Turnip, 108, 243

UNIT-CHARACTERS, 4
Univalent, 33
Unreduced gametes, 32
Utilisation of hybrid vigour, 168, 169c

VACCINIUM, 213
Variation, 1, 38, 252
continuous, 39, 90B, 158
discontinuous, 2
in polyploids, 39, 252
somatic, 170
Variegation, 63, 181
and infectious transmission, 63, 181
extra-nuclear, 63
in *Abutilon*, 181
in *Pelargonium*, 183
in *Tropaeolum*, 63
mendelian, 63
Varieties, 233
and immunity to disease, 128, 259
in lettuce, 105
in onion, 107
in potato, 118
and immunity to insects, 258, 259
origin of, 27, 233
Veitchberry, 31, 211, 241
origin, 241
Verbascum, 186, 202
Verbena, anthocyanins in, 78
Veronica, 186
Vicia Faba, 15, 108
sativa, 42
Vigour in F_1 hybrids, 168
Viola tricolor nigra, 65
Vitamins, 253, 254
Vitis, 141
disease resistance, 259
rupestris, 141, 259
vinifera, 141, 259
Vivipary, 43

WALNUT, 230
Watercress, 244
White currants, 136, 178, 183

X-RAYS, 63
Xanthophyll, 76
Xenia, 225

ZYGOTE, 6, 19
Zygotic series, 8, 37

THE END

PRINTED BY R. & R. CLARK, LTD., EDINBURGH