QK
981
C85
1918a

ALBERT R. MANN
LIBRARY
AT
CORNELL UNIVERSITY

CORNELL UNIVERSITY LIBRARY

3 1924 074 276 571

DATE DUE

GAYLORD			PRINTED IN U.S.A.

The original of this book is in
the Cornell University Library.

There are no known copyright restrictions in
the United States on the use of the text.

http://www.archive.org/details/cu31924074276571

Production Note

Cornell University Library produced this volume to replace the irreparably deteriorated original. It was scanned at 600 dots per inch resolution and compressed prior to storage using CCITT/ITU Group 4 compression. The digital data were used to create Cornell's replacement volume on paper that meets the ANSI Standard Z39.48-1992. The production of this volume was supported by the United States Department of Education, Higher Education Act, Title II-C.

Scanned as part of the A. R. Mann Library project to preserve and enhance access to the Core Historical Literature of the Agricultural Sciences. Titles included in this collection are listed in the volumes published by the Cornell University Press in the series *The Literature of the Agricultural Sciences*, 1991-1996, Wallace C. Olsen, series editor.

PLANT GENETICS

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO, ILLINOIS

THE BAKER & TAYLOR COMPANY
NEW YORK

THE CAMBRIDGE UNIVERSITY PRESS
LONDON AND EDINBURGH

THE MARUZEN-KABUSHIKI-KAISHA
TOKYO, OSAKA, KYOTO, FUKUOKA, SENDAI

THE MISSION BOOK COMPANY
SHANGHAI

PLANT GENETICS

BY

JOHN M. COULTER

Head of the Department of Botany
in the University of Chicago

AND

MERLE C. COULTER

Instructor in Plant Genetics
in the University of Chicago

THE UNIVERSITY OF CHICAGO PRESS
CHICAGO, ILLINOIS

1918

QK
981
C85
1918a

312201

COPYRIGHT 1918 BY
THE UNIVERSITY OF CHICAGO

All Rights Reserved

Published July 1918

Composed and Printed By
The University of Chicago Press
Chicago, Illinois, U.S.A.

PREFACE

There is developing an increasing demand for courses in genetics adapted to the needs of botanical students, and teachers of botany have asked repeatedly for a suitable text. A number of texts on heredity and evolution have appeared, but these have contained far too little genetics. On the other hand, there are several very thorough texts on certain phases of genetics, but these have been more in the nature of monographs than texts. They have focused on too limited a field to give the reader any general appreciation of genetics as a whole and frequently have been too difficult for the uninitiated to appreciate at all. WALTER'S *Genetics* is an admirable elementary text, but is not exactly adapted to the needs of the young botanist. All texts, in fact, have emphasized animal genetics more strongly than the student of botany needs, except certain books on plant breeding, which, however, are general in nature and give little attention to theoretical genetics. In short, the subject has been changing so rapidly that no one has ventured to write a general authoritative text.[1]

The group that the present book is intended to serve primarily comprises those who intend to make botany their profession and who, although not as yet specialists,

[1] After the manuscript of this text had gone to the printer, there appeared a book by BABCOCK and CLAUSEN, entitled *Genetics in relation to agriculture*. This is "a general authoritative text," for it contains a treatment of both plant and animal genetics, well suited to a thorough year's course in genetics.

have had general training in the fundamentals of botany. Such students, for example, are commonly found in the last undergraduate year or first graduate year of their work with no distinct purpose to become geneticists, but wishing to be able to appreciate the important current work in plant genetics.

Such a group of young botanists became evident at the University of Chicago. In their attack upon current botanical literature they frequently encountered papers dealing with plant genetics, but through lack of preparation were unable to grasp their significance. This type of literature seemed too important to be relegated entirely to the specialist, and therefore the authors of the present text organized a course of lectures to meet the need. The purpose of the lectures was not to develop professional geneticists, but merely to initiate students of botany into the point of view of working geneticists, so that they could appreciate an important phase of botanical literature. With such a purpose there was no attempt to give a complete presentation of modern genetics, but rather to introduce the student to genetics in the simplest way. As a consequence, for pedagogical reasons, certain perplexing facts were omitted, while others were slightly adjusted so as to convey the fundamental ideas without confusion. The result of the course was so successful as to suggest the desirability of putting the lectures into text form for the benefit of teachers who wish to profit by this experience. As a reference book it is entirely inadequate, much representative material having been omitted and only enough bibliography given to put the student upon the trail. As a textbook also it has two disadvantages: (1) it

is avowedly not exact in some of the details; (2) it is adapted definitely to young botanists with fairly thorough elementary training. The excuse for the inexactness of certain details is the pedagogical necessity. The preparation of a text for the students referred to is explained by the fact that it represents a very important group which has not been provided for. In brief, the book is neither a technical presentation of genetics nor a general text, but a course of general lectures adapted to a special purpose.

In connection with the laboratory phase of this course the authors wish to make grateful acknowledgment to E. M. East, Albert Blakeslee, R. A. Emerson, and G. H. Shull for very useful illustrative material.

J. M. C.
M. C. C.

CONTENTS

CHAPTER		PAGE
I.	INTRODUCTION	1
II.	EARLIER THEORIES OF HEREDITY	4
III.	THE INHERITANCE OF ACQUIRED CHARACTERS	16
IV.	MENDEL'S LAW	28
V.	NEO-MENDELISM	40
VI.	NEO-MENDELISM (*Continued*)	52
VII.	NEO-MENDELISM (*Continued*)	63
VIII.	NEO-MENDELISM (*Continued*)	76
IX.	NEO-MENDELISM (*Concluded*)	86
X.	NON-MENDELIAN INHERITANCE	97
XI.	MODIFICATION OF UNIT CHARACTERS	104
XII.	PARTHENOGENESIS AND VEGETATIVE APOGAMY	115
XIII.	INHERITANCE IN GAMETOPHYTES	123
XIV.	SELF-STERILITY	133
XV.	THE ENDOSPERM IN INHERITANCE	144
XVI.	HYBRID VIGOR	158
XVII.	SEX DETERMINATION	177
XVIII.	THE BEARERS OF HEREDITARY CHARACTERS	198
	INDEX	209

CHAPTER I

INTRODUCTION

It should be realized that genetics is a natural outgrowth from the study of organic evolution. The conception of evolution began as a speculation, but became scientific in connection with the work of LAMARCK and DARWIN. In such work the method used was that of observation and inference. Facts were observed and an explanation was devised that would relate them. Resemblances and differences among species were noted, and it was inferred that these indicated degrees of relationship. It was assumed that closely related species must have had a comparatively recent common ancestry and that more distantly related species must have had a more remote common ancestry. Through comparisons of structure and of geographical distribution systems of phylogeny have been inferred, and an outline of the evolution of the plant and animal kingdoms has been the result. All of these conclusions are based upon comparison and inference.

This method reached its extreme application in the work of DARWIN, whose observations included a range of forms and an extent of time unequaled by any preceding student of evolution. It may be said that in DARWIN'S work the method of comparison and inference reached the limit of its possibilities. The students of evolution were chiefly concerned with explaining the changes that resulted in phylogeny. In other words,

by comparison and inference they related certain forms and then tried to explain why these forms had become different. For example, LAMARCK'S explanation of the changes was that they are the results of "use and disuse"; DARWIN'S explanation was that they are due to "natural selection."

It was in 1900 that a new method for the study of evolution was announced with the appearance of *The mutation theory* by DE VRIES. The new method was experimentation. Instead of comparing two species and inferring that one of them had produced the other, species were bred through successive generations, under rigid control, and were observed to produce new species. The old method inferred that a certain thing occurred; the new method saw it actually occurring.

In developing this experimental method the facts of inheritance began to accumulate. Presently the facts accumulated sufficiently to be organized into theories of inheritance, and the special field of genetics was the result. In brief, therefore, genetics is the experimental study of inheritance. Aside from the interest of genetics itself, its possible applications are even more important. For example, it will probably eventually explain organic evolution; and, most important of all considerations, it will probably enable us to control plant and animal breeding in a way that will be of the greatest practical importance in agriculture.

It should be realized that, in so complex a subject as heredity, increasing experimental work must greatly increase the range of known facts and make explanations increasingly difficult. The facts of inheritance obtained from experimental work with a few simple forms

may permit satisfactory conclusions; but when greater numbers and more complex forms are included, conclusions become not only difficult but sometimes impossible. It is necessary, however, to organize facts, as they are obtained, into some consistent theory that will relate them to one another and that may be the basis of further investigation. Progress in any complex subject is marked by a series of explanations, each in turn proving inadequate as facts multiply, but each in turn helping to further progress. It should be understood, therefore, that in the subsequent chapters the theories presented are not to be regarded as final, but rather as suggested explanations of the known facts. It is certain that new facts will continue to be discovered and that explanations will have to be modified to fit them; but the present explanations are necessary for coordinating the facts we have. In other words, a sharp distinction must be drawn between established facts and proposed explanations. The former are permanent, the latter are temporary.

CHAPTER II

EARLIER THEORIES OF HEREDITY

It is probable that men have thought of heredity from the earliest times, but so far as is known there was no formulation of any definite theory of heredity before the time of ARISTOTLE. Since that time there are records of numerous theories of inheritance that may well be regarded as wild speculations. They were evolved with little or no basis of fact and of course are not to be regarded as scientific. Some of these early theories are interesting but not profitable for our purpose. They developed from superstition rather than from observation.

It is evident also that inheritance in man first attracted attention; later, animals were taken into consideration. The study of inheritance in plants is of comparatively recent development, due chiefly to the fact that sex was not observed in plants until late in the seventeenth century, and heredity was thought of only in connection with sex. Even after sex in plants was announced by CAMERARIUS in 1694 there was no general belief in the claim until much later. For this reason plant inheritance became a subject of observation and theory, and the history of plant genetics began long after the discovery of sex in plants.

The earliest distinct theory of heredity which falls within the period of modern biology was formulated by DARWIN (1). This was published in 1868 in his

book entitled *Animals and plants under domestication* and was called *pangenesis*. In a certain sense DARWIN apologized for pangenesis, realizing that knowledge had not advanced far enough for the construction of any adequate theory. The theory of pangenesis, therefore, is to be regarded more as a suggestion than as a formulation of belief.

The theory may be summarized as involving two theses which should be kept distinct. The first thesis, in DARWIN'S words, is as follows: "The individual cells and organs of the whole organism are represented in every germ cell and bud by definite material particles. These multiply by division, and at cell division pass on from the mother cells to the daughter cells." This is the essential feature of pangenesis; that is, every germ cell (egg or sperm) contains dividing particles that in cell division pass on to every cell produced. This statement agrees in general with the facts recognized today under a somewhat different terminology, it being only necessary to call these particles chromosomes. This is remarkable when it is remembered that the statement was made fifty years ago.

The second thesis is as follows: "All the cells of the body throw off particles at various periods of their development. These reach the germ cells and hand over to them any characters of the organism which they may lack." This is known as the *transportation hypothesis* and was an attempt to account for certain facts which seemed to indicate the inheritance of acquired characters. It is somewhat surprising to find DARWIN explaining heredity on the basis of the inheritance of acquired characters, for his theory of the origin of

species by natural selection does not call for the inheritance of acquired characters.

The theory of pangenesis proper is quite in keeping with the present point of view; but the weakness of the transportation hypothesis was so evident that it was soon set aside by biologists. In discarding the transportation hypothesis, however, biologists in general rejected also the doctrine of pangenesis, a common result when a truth is found in combination with the obviously false.

The theory of heredity which was chiefly responsible for replacing pangenesis was proposed by WEISMANN (3), whose publications appeared during the decade 1880–1890. WEISMANN developed two companion theories: one called *germinal continuity*, which has to do with heredity; and the other called *germinal selection*, which is a very imaginative explanation of individual variation. Our concern is chiefly with the theory of germinal continuity.

According to DARWIN'S transportation hypothesis, any change arising in the organism at any time during its life would become represented by *gemmules* in the reproductive cells. In this way it would be possible for acquired characters to be inherited. WEISMANN could discover no mechanism in plants or animals which could justify such a conception.

It had been known for some time that germ cells and body cells in animals remain separate during their later development, but WEISMANN seems to have been the first to point out the significance of this fact. He makes the following statement: "The difficulty or the impossibility of rendering the transmission of acquired char-

acters intelligible by an appeal to any known force has often been felt, but no one has hitherto cast doubt upon the very existence of such a form of heredity." The general belief of the time that the inheritance of acquired characters was a fact came from two sources: (1) many examples of the inheritance of acquired characters were being reported; and (2) inheritance of acquired characters was thought necessary to explain evolution. WEISMANN therefore faced two problems: (1) to explain away the reported cases of the inheritance of acquired characters; and (2) to provide a theory which would make evolution possible without the inheritance of acquired characters.

He took up individually the many reported cases of such inheritance and discredited them one after another, showing convincingly how they could be explained in some other way. He also cited from his own experience numerous cases in which the inheritance of acquired characters was distinctly absent. As a result of his investigation of these cases, he developed his theory of germinal continuity, commonly spoken of as *continuity of the germ plasm*, a theory which is in good standing today. In the attempt to provide a theory which would make evolution possible without the inheritance of acquired characters WEISMANN distinctly failed. To explain variation, which is the basis of evolution, he proposed the theory of germinal selection, which is even more imaginative than DARWIN'S transportation hypothesis. As a consequence WEISMANN'S experience was much like that of DARWIN. His theory of germinal continuity has fairly well stood the test of later investigation and is still current among

biologists, while his theory of germinal selection has been practically discarded. A brief explanation of these two theses is as follows.

GERMINAL CONTINUITY.—A statement of this theory in the words of the author is as follows:

> I believe that heredity depends upon the fact that a small portion of the effective substance of the germ plasm remains unchanged during the development of the egg into an organism, and that this part of the germ plasm serves as a foundation from which the germ cells of the new organism are produced. There is a continuity of germ plasm from one generation to another . . . hence it follows that the transmission of acquired characters is an impossibility, for if the germ plasm is not formed anew in each individual, but is derived from that which preceded it, its structure, and above all its molecular constitution, cannot depend upon the individual in which it happens to occur; but such an individual only forms as it were the nutritive soil, at the expense of which the germ plasm grows, while the latter possessed its characteristic structure from the beginning, namely, before the commencement of growth, but the tendencies of heredity, of which the germ plasm is the bearer, depend upon its molecular structure, and hence only those characters can be transmitted through successive generations which have previously been inherited, namely, those characters which were potentially contained in the structure of the germ plasm. It also follows that those other characters which have been acquired by the influence of special external conditions during the lifetime of the parent cannot be transmitted at all.

This is the theory of germinal continuity and it is in general agreement with the results of biological work today (see fig. 1).

GERMINAL SELECTION.—The purpose of the conception of germinal selection was to construct a theory of variation, and therefore of evolution, which does not involve the inheritance of acquired characters. When

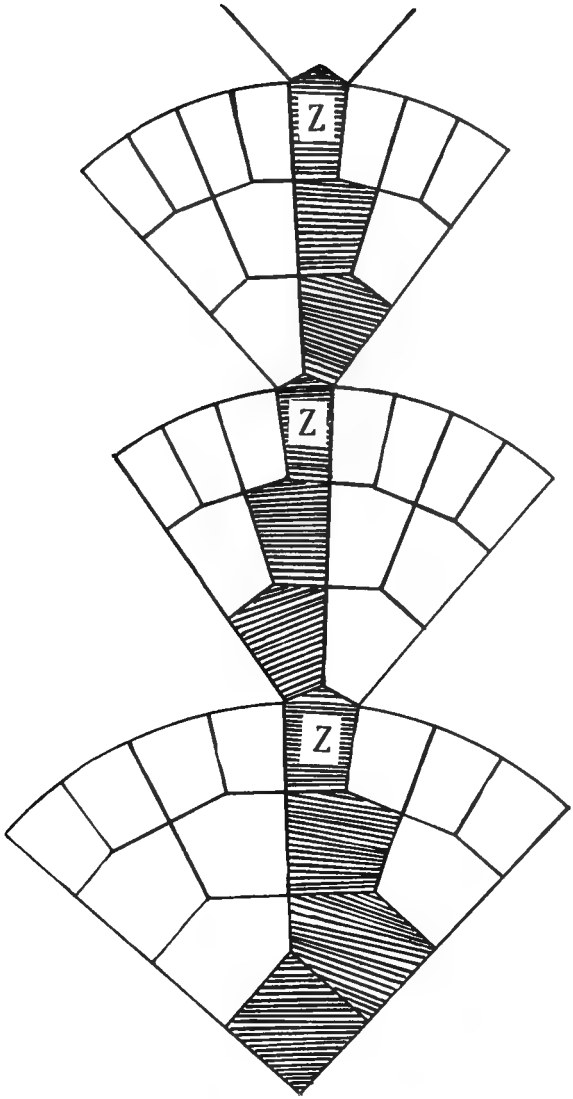


FIG. 1.—Diagram illustrating WEISMANN'S theory of germinal continuity. Three generations are represented, with cells of germ plasm shaded, and those of body plasm unshaded; germ plasm continuous from generation to generation, carried over from parent to offspring by zygote (*Z*); impossible for body plasm to perpetuate itself into a second generation.

the theory was being constructed the theory of natural selection was widely accepted. It should be understood that WEISMANN did not criticize natural selection, but he did not believe that the individual variations upon which natural selection was based were to be explained as the inheritance of acquired characters. The theory of germinal selection, therefore, was intended to explain the origin of individual variations in some other way. The explanation of the theory begins as follows:

> I believe that it is possible to suggest that the origin of hereditary individual characters takes place in a manner quite different from any which has as yet been brought forward. . . . . In the first place, it may be argued that external influences may not only act on the mature individual, or during its development, but that they may also act at a still earlier period upon the germ cell from which it arises. It may be imagined that such influence of different kinds might produce corresponding minute alterations in the molecular structure of the germ plasm; and as the latter is, according to our supposition, transmitted from one generation to another, it follows that such changes would be hereditary. . . . . Without altogether denying that such influences may directly modify the germ cells, I nevertheless believe that they have no share in the production of hereditary individual characters. . . . . Hereditary individual differences must therefore be derived from some other source. I believe that such a source is to be looked for in the form of reproduction by which the great majority of existing organisms are propagated, sexual reproduction. . . . . The object of sexual reproduction is to create those individual differences which form the material out of which natural selection produces new species.

WEISMANN forestalls a criticism which was sure to come by saying that the opinion has already been expressed that deviations from the specific type are rapidly destroyed by the operation of sexual reproduc-

tion. Such an opinion may be true with regard to specific characters, because deviations from the specific type occur in such rare cases that they cannot hold their ground against the large number of normal individuals, but the case is different, as he claims, with those minute differences which are characteristic of individuals, because every individual possesses them, although of different kind and degree. He states that cross-breeding between all the individuals of a species is impossible, hence the obliterating of individual differences is impossible.

According to WEISMANN, therefore, individual variations, and therefore the possibility of natural selection, originate in the sex process. Sex reproduction originates no absolutely new characters, but merely makes possible innumerable combinations of characters. It is evident that the pairing individuals must differ to some extent, if the result is to be a new combination of characters.

This raises the question of the origin of differences in the first sexual individuals. Sexual reproduction was derived from asexual reproduction, and, according to the theory, must have begun with variable material. How did these individual differences arise? WEISMANN offers the following explanation. He had stated that environment has no modifying influence upon the germ plasm in general, but says that "in the lowest one-celled organisms the case is entirely different." In this case, as he puts it, "parent and offspring are in a certain sense one and the same thing," and germ plasm and body plasm have not been differentiated. In this case, therefore, variations induced by external conditions are hereditary because the germ plasm is the body plasm.

In this way individual differences arose in one-celled organisms; and when the sexual method appeared it found varying individuals ready to work upon. The mission of sex, therefore, according to WEISMANN, was to lay hold of these variations and multiply their combinations, thus providing a wider range of choice for natural selection. In this way he explains the origin of individual variation without the inheritance of acquired characters.

WEISMANN also devised a mechanism by which sexual reproduction results in multiplying combinations of individual differences. This mechanism is the basis of his theory of germinal selection and is as follows.

In WEISMANN'S time chromosomes as such had not been recognized, but they were represented in his terminology by the term *idants*. He conceived of each idant as composed of one or more units called *ids*. An id stood for a complete individual, each id being able to control the complete development of an individual. A child received both paternal and maternal ids in equal numbers; that is, father and mother were each represented by a 50 per cent influence on the offspring; each grandparent would be represented by 25 per cent of the ids in an individual; and so on, indefinitely. As a consequence, all existing individuals must now contain as many different kinds of ancestral ids as they are capable of containing. Sooner or later, owing to the accumulation of ids, "sex reproduction can proceed only by reduction in the number of ancestral ids, a reduction which is represented in every generation."

This is WEISMANN'S explanation of the grosser mechanism of heredity, but it was only preliminary to

the theory of germinal selection. In the first place he imagined that each id is composed of *determinants*, which are ultra-microscopic, each of them representing, not the whole body structure as does an id, but all the characters that belong to a particular kind of cell. Each determinant in turn was conceived of as composed of still smaller units called *biophores*, each of which represented a single character of a cell. Biophores have the capacity to assimilate food, to grow, and to reproduce themselves in the germ plasm. This imaginary structure of the cell is spoken of as WEISMANN'S *cell architecture*, in which biophores are built into determinants, determinants into ids, ids into idants. In fact, this is a remarkable theoretical analysis of the structure of a chromosome.

Selection is conceived of as occurring in the following way. After fertilization the biophores are too numerous for all of them to obtain expression, and the result is a struggle for existence, a sort of ultra-microscopical warfare. As a consequence some biophores perish and others survive and are perpetuated. This struggle of the biophores for nutrition, and the almost infinite combinations that might enter into the structure of the resulting determinants, would open up a wide field for variation. This is the theory of germinal selection, a struggle and a survival of fortunate biophores, and it may well be regarded as fantastic. It has been discarded, not only because it is without foundation in fact, but chiefly because it is beyond the reach of experimental testing.

What is called Weismannism had a very wide influence for a number of years, and the continuity of the

germ plasm, with its result on the doctrine of the inheritance of acquired characters, is still current. The first result of Weismannism was to overshadow DARWIN'S theory of pangenesis, which had unjustly shared the deserved fate of its companion theory, the transportation hypothesis. DE VRIES (2) was the first to recognize this injustice, and in 1889 published his *Intracellular pangenesis*. Without attempting to defend the transportation hypothesis, DE VRIES showed the real value of the doctrine of pangenesis. He claimed that his theory of intracellular pangenesis is little more than a restatement of the fundamental ideas of DARWIN'S pangenesis, but in fact it contains enough new material to justify a definition.

The material particles which DE VRIES conceived of as the carriers of heredity he called *pangens*, the equivalent of DARWIN'S gemmules. He claims that in the nucleus every kind of pangen of the individual is represented, while the cytoplasm in each cell contains only those pangens that become active in the cell. He concludes that, with the exception of the pangens concerned in nuclear activities, such as nuclear division, all pangens have to leave the nucleus in order to become active. But most of the pangens of almost every kind are represented in the nucleus, where they multiply, partly for the purpose of nuclear division, partly to pass into the cytoplasm to engage in other activities. These pangens not only pass out into the adjacent cytoplasm, but are also carried by the protoplasmic currents into the various organs of the protoplast, where they multiply and become active. All protoplasm consists of such pangens derived at different times from the nucleus,

together with their descendants. Hence the theory is called *intracellular* pangenesis, as contrasted with DARWIN'S *body* pangenesis, that is, distribution of the heredity particles in the cell as contrasted with distribution through the body as a whole.

DE VRIES formulated this theory before he had conducted the breeding experiments that led to his theory of mutation, and afterward he applied the theory to his experimental results in breeding.

1. DARWIN, CHARLES, The variation of animals and plants under domestication. London. 1890.
2. DE VRIES, HUGO, Intracellular pangenesis. Chicago. 1910.
3. POULTON, SHÖNLAND, SHIPLEY, WEISMANN, on heredity. Clarendon Press. 1891.

CHAPTER III

THE INHERITANCE OF ACQUIRED CHARACTERS

The inheritance of acquired characters has been mentioned in its relation to WEISMANN'S theory of germinal continuity, but it deserves a somewhat fuller consideration. The idea was first developed by LAMARCK in connection with his theory of evolution, the so-called theory of *appetency*, or the effect of use and disuse. FRANCIS GALTON, in 1875, was one of the first to express skepticism in regard to such inheritance, but it was WEISMANN who was most influential in combating the idea. After WEISMANN'S presentation of the situation, biologists were divided into two camps in reference to the inheritance of acquired characters: (1) neo-Lamarckians, who affirm belief in the inheritance of acquired characters, and (2) neo-Darwinians, who deny it. Geneticists and embryologists, however, whose work brings them most in contact with the problem, seem to be fairly well agreed that acquired characters are not inherited.

Much of the lack of agreement in this controversy is due to the definition of an acquired character. It should be kept in mind that actual characters are not inherited, but only the determiners, which regulate the way in which the organism reacts to its environment. For example, when it is said that a child inherits its father's nose, the statement is not meant to be literally true; it is meant that just as there was something in

the body of the father that was responsible for the development of a particular type of nose, so there was a similar something in the child's body that produced a similar result. It is merely a matter of convenience to speak of the inheritance of characters.

WEISMANN defined an acquired character as "any somatic modification that does not have its origin in the germ plasm." This definition is not always easy to apply. Examples of acquired characters in the Weismann sense are mutilations, effects of environment, results of function (as in the use or disuse of certain organs), and many diseases that affect the bodily mechanism. WEISMANN gave three reasons for rejecting the belief in the inheritance of such characters: (1) there is no known mechanism by which somatic characters may be transferred to the germ plasm; (2) the evidence that such a transfer does occur is inconclusive and unsatisfactory; and (3) the theory of the continuity of the germ plasm is sufficient to account for the facts of heredity. This last reason has been discussed, but the other two should be considered.

When WEISMANN says that there is no known mechanism by which somatic characters can be transferred to the germ plasm, to him it is equivalent to saying that it is hard to see how the water that has gone over the dam can return and affect the flow of the water upstream. He assumes, of course, that the germ plasm is isolated from the somatoplasm very early in the development of the fertilized egg into an individual, and that when it is isolated it takes no active part in the history of the body (see fig. 1). The somatoplasm is thus merely a carrier of the germ plasm and is unable to affect the

character of it any more than a rubber hot-water bag, although capable of assuming a variety of shapes, can affect the character of the water it contains (WALTER 6).

Opponents of WEISMANN object to any such view of the complete isolation of germ plasm. Studies of cell lineage in animals have shown that germ cells are set apart very early in the development of the individual, and that they certainly are not derived from distinctly somatic cells. No such statement, however, can be made in reference to plants. Germ cells in plants are derived from epidermal or hypodermal cells, which previously were distinctly somatic; and furthermore germ cells have been induced by experiment to form from almost any living tissue which is as distinctly somatic as any plant tissue can be.

Another objection to WEISMANN'S view is that every organism is a physiological as well as a morphological unity, and that cells completely insulated in such a unity would be impossible. Cytologists also have come to believe that there are protoplasmic connections between adjacent cells in practically all plant tissues, and in general physiology tends to confirm this. All of this means a growing belief that the somatoplasm can affect the germ plasm.

The reply of the Weismannians is that even though somatoplasm can affect germ plasm in this general physiological way, this is a very different thing from the ininheritance of some definite acquired character. To be inherited such a character would have to be exactly redeveloped in the germ plasm, and the influence referred to cannot be so specific as that. This of course is a theoretical answer and the question can only be decided

by experimental work. A theoretical rejoinder to this answer may be suggested. It is like the voice in a telephone transmitter, which starts vibrations that make the receiver repeat the voice.

WEISMANN'S disposition of the claimed cases of the inheritance of acquired characters should be considered. The supposed evidence for such characters falls chiefly into four categories.

1. MUTILATIONS.—Most of the evidence under this head is in relation to animals. It must be the common experience that mutilations are not inherited in man and the domesticated animals. A few quotations from WALTER (**6**) suggest the situation:

> It is fortunate that the sons of warriors do not inherit their fathers' honorable scars of battle, else we would now be a race of cripples. . . . . The feet of Chinese women of certain classes have for centuries been mutilated into deformity by bandages without the mutilation in any way becoming an inherited character. . . . . The progressive degeneration or crippling of the little toe in man has been explained as the inheritance of the cramping effect of shoes upon generations of shoe-wearers; but WIEDERSHEIM has pointed out that Egyptian mummies show the same crippling of the little toe, and no ancient Egyptian could be accused of wearing shoes, or of having had shoe-wearing ancestors.

Sheep and horses with docked tails, as well as dogs with cropped ears, never produce young having the parental deformity. WEISMANN'S experiments with mice, later verified by other investigators, give additional evidence that mutilations are not inherited. He bred mice whose tails had been cut off short at birth, and continued this performance through twenty-two generations, with absolutely no effect on tail length.

Mutilations in plants have received no serious consideration; in fact, no one seems to have considered the possibility of such inheritance. Cuttings for propagation, for example, are usually trimmed to prevent excessive transpiration, but no one ever expects to find this mutilation perpetuated, even in the plant developed from the cutting, much less in the next generation developed from seed. In fact, since we have begun to learn of the remarkable powers of regeneration possessed by plants and animals, we would not expect the inheritance of mutilations.

2. EFFECTS OF ENVIRONMENT.—This has long been a topic in botany. Trees deformed by prevailing winds, like the willows that line the canals in Belgium and Holland, or storm-crippled trees along exposed seacoasts, are not known to produce progeny showing these characters when the adverse environmental conditions are removed. ZEDERBAUER, on the other hand, found that *Capsella*, which in the course of many years had gradually crept along the roadside up into an alpine habitat and there acquired alpine characters, retained these characters when transplanted to the lowlands. This has been accepted as an authentic instance of the inheritance of acquired characters; but it is possible that this conquest of an alpine habitat by *Capsella* can better be explained by the gradual natural selection of just those germinal variations that best fitted individuals to cope with alpine conditions. This would result in the gradual establishment of a strain of germ plasm that would produce body structures fitted to alpine conditions. In other words, this is just the way in which natural selection would develop a new elementary species

from the original type. If such a type were established, of course its germ plasm would produce alpine plants, even in lowland conditions. They might not survive long and natural selection might eliminate them, but their structure would be due, not to the inheritance of somatic structures, but to the inheritance of an alpine germ plasm.

If corn is planted in poor soil weak individuals result. Seed from these weak individuals, when planted in good soil, will develop again somewhat weakened individuals, and this suggests the inheritance of acquired characters. In fact, however, it is merely the direct effect of environment continuing through the second generation. The weak individuals in the poor soil develop small seeds with low nutritive capacity, and plants developed from abnormally small seeds are always weak, whether the individual that produced the seed grew in poor soil or not.

In 1909 MAYR (4) wrote a notable work on silviculture in which he claimed that only species characters are inherited in trees, and that the effects of climate are not inherited, and therefore that the source of the seed makes no difference. In other words, seeds of Scotch pine would always produce Scotch pine progeny, no matter at what latitude or altitude the ancestors had been growing. According to MAYR, therefore, there is no inheritance of acquired characters in trees.

In 1912, however, the United States Committee on Breeding Nut and Forest Trees (5) came to the conclusion that the source of seed is of great importance. This conclusion was based chiefly upon the testimony

of numerous nurserymen, the only significant experimental work being that of ENGLER of Zurich. ENGLER (3) found that in the seedlings in his nursery growth in height distinctly decreased as the altitude or latitude from which the seed came increased. He also found that seeds from pines which had been crippled by growing in poor soil conditions gave rise to crippled plants when grown in good soil. In many cases trees of the third generation still showed the habit "acquired" by their grandparents in different habitats.

These are striking results, but they may be explained in either of the two ways mentioned. ENGLER might have been dealing with slightly different strains of trees, differing in germinal constitution; or it may have been another case of the "false inheritance of acquired characters" that was explained in connection with corn. Seeds from higher latitudes and altitudes might well have been smaller, so that we should have expected smaller progeny, even when grown in the lowlands.

A completely satisfactory investigation of the inheritance of acquired characters in plants still remains to be made. Seed from a single parent from a pure strain should be planted in diverse conditions and the various responses noted. Seed of the second and later generations of each lot should then be planted back in the original conditions. If there should appear in this generation even slight deviations from the original type it would be significant, provided the deviations are similar to those shown by the immediate parents in each case and characteristic of the conditions under which the parents grew. The peculiarities of progeny due to light-weight seed should be tested by controls

and eliminated from consideration. Certain parts of this investigation have been carried on frequently and satisfactorily and the whole investigation has been tried, but under poorly controlled conditions. It remains, therefore, to conduct the entire investigation under proper conditions before one can reach any reliable conclusion in reference to the inheritance of acquired characters by plants.

Another possible illustration of the inheritance of responses to environmental conditions may be obtained from the work of BOLLEY (1) on flax. The resistance of a plant to a given disease is regarded as a character peculiar to certain strains and transmitted as a very definite factor in Mendelian inheritance. BOLLEY claims that he can get a resistant strain of flax from almost any known variety. According to him the resisting ability increases from generation to generation, if the crop is constantly subjected to disease attack. He took a pure-pedigreed strain of flax which had come originally from a single non-resisting seed. This was planted in slightly "sick" soil, that is, soil infected with the wilt-producing organism. Most of the individuals died, but "a few scrubs" survived. He then planted seeds from these in slightly "sicker" soil than before, and thus, by gradually working his crop into sicker and sicker soil in the later generations, he finally obtained a fully resistant strain from the pure non-resistant strain with which he started. Such a strain he says will not lose its resistance if planted progressively in more infected soils.

BOLLEY also found that if he added to the soil manure, alkalies, etc., known to increase the disease by stimulating the fungus, he obtained a very few poorly developed

resisting plants, whose seeds, however, the next year developed a race with enormous resistance. He gives the following theoretical explanation of his results:

> Either (1) the so-called unit character of resistance was present in undeveloped form and becomes stronger from year to year under conditions of disease; or (2) there never was any character present which is entitled to be called a unit character, but it began to develop the first year the parent plant came in contact with the disease, and the protoplasmic nature of the ancestors of the plants which we now have has been such that they accumulated more and more the resisting power from year to year, just as they had opportunity to develop resistance against a constantly acting factor of disease, which, when too powerful, acts as an eliminating factor.

BOLLEY inclines to the second alternative. This general conception seems to explain why homegrown seed is regularly more resistant than seed from the same variety which has had a vacation away from home for several years. It has kept in training like a football player. BOLLEY says that if these conclusions are correct there are probably no unit characters which are not fluctuating and there are no fluctuating characters which may not readily be fixed.

These results are striking enough, but their significance depends entirely upon the purity of the strains which were used originally and also upon the preservation of purity during the experiment. BOLLEY'S phrase "elimination factor," which he uses repeatedly, suggests selection from an impure strain. If his conception is true it could be demonstrated by developing a large majority of resistant individuals among the non-resistant plants which were first subjected to disease attack, rather than merely "a few scrubs." In other words, the

whole result resembles the selection of a few resistant individuals from an impure strain.

3. EFFECT OF USE AND DISUSE.—WEISMANN discredited this belief, which was the foundation of LAMARCK'S theory of evolution. He was successful in practically all the cases that had been presented for animals. In plants, of course, it would be hard to find anything exactly analogous to the use and disuse of parts in animals. One fact, however, may be mentioned which is a common experience of botanists. Functionless organs gradually become aborted, becoming mere vestiges, or even suppressed. A study of the organogeny of a flower shows that when a floral member is belated in its development it is destined sooner or later not to appear at all. The Weismannian explanation of this situation would probably be as follows. A given species has given a nutritive capacity; the less it draws upon its nutritive capital for the development of one organ the more it can afford to expend upon the development of other organs. When an organ becomes functionless it no longer has any survival value; survival is then dependent upon the relative development of the other organs. Certain variations develop the functionless organ less than usual and therefore develop the other organs more than usual, and under the new conditions these variations will survive and the others be eliminated.

This is a description of natural selection by which functionless organs become more and more aborted and vigorous organs survive, but such an explanation is rather imaginative.

4. DISEASE TRANSMISSION.—Roughly speaking this may be grouped as (1) infection by bacteria or fungi, and

(2) some inherent organic weakness. Since the latter condition is chiefly serious only in inviting attacks by bacteria or fungi, we are concerned chiefly with diseases caused by these pathological forms. Realizing this, true inheritance of disease seems to be an impossibility, for if the parasite enters the germ cell it is practically sure to destroy it, and there will be no progeny. In many cases, however, progeny are born diseased, but this is due to reinfection of the young embryo from the body of the mother. This is not an inheritance but a reinfection. In smuts, for example, there is much reinfection by means of the transmission of spores upon seeds. This can in no sense be spoken of as inheritance.

In one respect, however, one may speak of disease inheritance. Breeding experiments have shown that predisposition to disease and disease resistance, commonly called susceptibility and immunity, are inherited. This means that it is of germinal origin, so that it does not involve the inheritance of an acquired character. On the other hand, as was stated, BOLLEY maintains that disease resistance is built up under the influence of disease attack, increasing gradually through the generations. This would make it an acquired character and one that is inherited.

These are a few of the examples of so-called acquired characters and the claims for and against them. Investigation is not yet in a position to come to any definite conclusion in reference to them. The bulk of available evidence, however, seems to be against the inheritance of acquired characters; but there are a number of biological facts that seem difficult to explain in any other way. In animals the mechanism may seem to make the

inheritance of acquired characters impossible; but the situation in plants is distinctly different.

In closing, we quote the opinion of EAST (2):

> My confession of faith is, the environment has been an immense factor in organic evolution, but its effects are shown either so infrequently or after the elapse of so great a time, that for the practical purposes of plant breeding we can neglect it as we would neglect an infinitesimal in a calculation.

1. BOLLEY, H. L., The importance of maintaining a constant elimination factor in plant breeding. Ann. Rep. Amer. Breeders Assoc. 8:508–514. 1912.
2. EAST, E. M., The bearing of some general biological facts on bud-variation. Amer. Nat. 51:129–143. 1917.
3. ENGLER, ARNOLD, Influence of source of seed. Jour. Heredity 5:185–186. 1914.
4. MAYR, H., Waldbau auf naturgesetzlicher Grundlage. Berlin. 1909.
5. SUDWORTH, GEO. B., Report of committee on breeding nut and forest trees. Ann. Rep. Amer. Breeders Assoc. 8:515–522. 1912.
6. WALTER, HERBERT E., Genetics. New York. 1913.

CHAPTER IV

MENDEL'S LAW

Mendel's law is the basis of all work in genetics and should be understood from its original statement to its somewhat complex development. Before passing to the more complex features it is well to recall the points of the original thesis.

In 1865 GREGOR MENDEL (2) published in the proceedings of a local scientific society the result of eight years of breeding experiments. The publication was so obscure that scientific men in general did not see it, and, in addition to this, Darwinism was at that time absorbing the attention of biologists. For these two reasons MENDEL'S work remained unnoticed, and of course unappreciated, until it was discovered in 1900 and became the great classic of genetics. Its influence, therefore, dates from 1900 rather than from the year of its publication.

The substance of MENDEL'S experiments is as follows. Wishing to discover the contributions of each parent to the make-up of their progeny he chose for his work the simple garden pea, which would breed rapidly, and exhibited well marked varieties. To magnify his results he secured hybrids by crossing distinctly different types of peas, and to avoid confusion he considered only one character in each experiment. For example, he crossed peas which contrasted in character of height, of flower color, and of seeds. In every case he obtained

the same result, so that a single example will suffice. Furthermore, he discovered that it made no difference whether the staminate parent was a dwarf and the pistillate tall, or vice versa, and so for all the characters used. In other words, what are called *reciprocal crosses* gave the same results.

The progeny of a tall parent and a dwarf parent were all tall. This generation is known as the first hybrid generation or the F_1 generation. When this generation was inbred the progeny was made up of tall and dwarf individuals in a ratio of 3:1. This generation is known as the second hybrid generation, or the F_2 generation. The dwarf forms of the F_2 generation subsequently bred true, producing only dwarfs. Of the tall forms one-third bred true and two-thirds split up in just such a 3:1 ratio as did their immediate parents of the F_1 generation. This may be expressed diagrammatically (fig. 2).

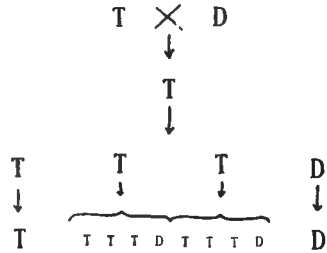


FIG. 2.—Diagram illustrating visible results of MENDEL'S experiments. Cross between tall parent (*T*) and dwarf parent (*D*) gives hybrid progeny, which are all tall; hybrid progeny inbred gives 3:1 ratio in second hybrid generation; inbreeding each of these four individuals separately gives for third hybrid generation results indicated in bottom line.

MENDEL'S explanation of this behavior involved three theses which at that time were new to biology. These theses must be kept distinct from one another.

1. INDEPENDENT UNIT CHARACTERS.—This means that an organism, although representing a morphological

and physiological unity, from the standpoint of heredity is a complex of a large number of independent heritable units. Thus if one pea plant is tall and another one is dwarf the behavior of the hybrid produced from them with reference to this character will be the same, no matter what other characters the parent plants may have had. In other words, the characters are *independent units*, unaffected by other characters or units. The character of tallness from a tall plant with wrinkled seeds or purple flowers will act just the same as from a tall plant with smooth seeds or white flowers. Tallness is a unit and its behavior in inheritance is independent of all other units.

2. DOMINANCE.—In the germ plasm there are certain determiners of unit characters which dominate during the development of the body, causing these characters to dominate over others and thus become visible. The characters dominated over and thus not allowed to express themselves are called *recessive* characters. These recessive characters are present in the germ plasm, but cannot express themselves and become visible as long as the *dominant* characters are present. When a dominant character is absent, however, its recessive alternate is free to express itself and become visible.

For example, in the case of tall and dwarf peas, tallness is a dominant character and dwarfness is its alternative recessive. When a dwarf appears, therefore, there is present no dominant tallness to suppress it. In the F_1 generation all the individuals were tall because, although they had all received the recessive character of dwarfness from one of the parents, they had received the dominant character of tallness from the other parent,

and so dwarfness did not appear in any of them. Such pairs of alternative characters are now commonly called *allelomorphs*. Thus tallness and dwarfness are allelomorphs in the pea, one dominant over the other, which is therefore recessive.

3. PURITY OF GAMETES.—A gamete can contain only one of two alternative characters. For example, it may contain the character for tallness or for dwarfness, but not both. In other words, allelomorphs cannot be represented in the same gamete. If the gamete having the character for tallness unites with one having the character for dwarfness, the resulting zygote will contain both, but will produce a tall individual because tallness is dominant over dwarfness. When this tall hybrid produces gametes, however, one-half of them will contain the character for tallness and one-half of them the character for dwarfness. Thus the alternative characters are "segregated" in gamete formation and no gamete will have both characters.

These three theses, independent unit characters, dominance, and purity of gametes (better called segregation), make up the theoretical explanation of Mendel's law. Independent unit characters was of course a necessary conception. It was original with MENDEL, and has also been original with other investigators, but this conception does not represent the essential feature of Mendel's law. The idea of dominance had been somewhat vaguely proposed before MENDEL'S time. In the old literature on animal breeding one meets theories of *prepotency*, which were proposed again and again before the discovery of MENDEL'S work in 1900. In any event MENDEL was the first to formulate definitely

the theory of dominance among unit characters. It should be realized also that dominance is not an essential feature of MENDEL'S theory. Many cases are known in which dominance fails, but in other regards the Mendelian inheritance is strictly followed.

The essential feature of MENDEL'S theory is his conception of the *purity of gametes*, brought about by the segregation of alternative characters. The striking fact is that this conception, purely theoretical with MENDEL, has since been confirmed by cytology. In the mechanism of cell division each chromosome is divided into two equal parts and each daughter-cell receives one of these parts. It is a reasonable inference that chromosomes are bearers of hereditary characters. In the production of gametes the number of chromosomes characteristic of the organism is reduced one-half. As a consequence each gamete carries only one-half the characters of the individual that produced it. An application of these statements to an explanation of MENDEL'S 3:1 ratio will illustrate the situation.

For convenience we will assume that the nuclei of MENDEL'S peas have four chromosomes each (fig. 3). In the case of a tall plant two of the four chromosomes carry the character for tallness, that is, something that determines the production of the tall character in the somatoplasm, which is practically the *body builder*. This unknown something is called by various names in the literature of genetics, the commonest one being *determiner*. In our illustration, therefore, two of the four chromosomes carry the determiner for tallness (p. 33). At this point two questions may be asked.

1. Why do just two of the four chromosomes carry the determiner for tallness rather than all of them or only one of them? Just here it would be difficult to explain why no more than two of the four chromosomes are represented as carrying the same determiner. This will be explained later. It is easy to answer, however, why the determiner is being carried by more than one chromosome. When gametes are formed the chromo-

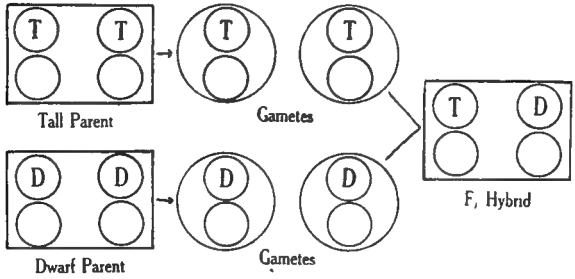


FIG. 3.—Diagram illustrating behavior of chromosomes in MENDEL'S cross of tall and dwarf peas. Large rectangular figures, nuclei of zygotes or mature individuals; large circles, gametes; small circles within zygotes and gametes, chromosomes; letters on chromosomes, determiners (*T*, tallness; *D*, dwarfness).

some number is reduced one-half. Since every gamete from a pure tall plant carries the determiner for tallness there must have been at least two chromosomes carrying the determiner before the gametes were formed.

2. Do these two chromosomes carry any other determiner than that for tallness? In a tentative way this question may be answered in the affirmative, but a fuller discussion of the situation must be deferred. There is much experimental evidence that indicates that more than one determiner is carried on a single

chromosome. In some cases also there are more Mendelian determiners than there are chromosomes.

The situation is represented in fig. 3. This shows a somatic cell with the diploid or $2x$ number of chromosomes. In the formation of gametes this number is reduced to the haploid, or x number, which in this case is two. The diagram shows that the reduction separates (segregates) the two chromosomes carrying the character for tallness, so that each gamete contains one. This occurs for the other characters as well as for that of tallness. From the tall plant, therefore, all the gametes will contain the character for tallness, and from a dwarf plant all of the gametes would contain the character for dwarfness. When these two individuals are crossed the zygote will contain both characters, and these two characters will be transmitted together in the succeeding cell generations. The individual from such a zygote of course would be tall, but at the same time it would be carrying a recessive determiner for dwarfness, and this fact would be shown by its behavior in breeding. The result of inbreeding such hybrids is indicated in the accompanying diagram (fig. 4), which represents the chance matings of two kinds of gametes. The obvious results are three tall individuals and one dwarf. This is the so-called *monohybrid ratio*, which means the ratio when a single pair of allelomorphs is considered.

Before discussing the further development of Mendel's law it will be necessary to explain some of the terminology of genetics. When each gamete carries the same kind of determiner the zygote is said to receive a *double dose;* when a zygote receives only a single such determiner it is said to receive a *single dose.*

In fig. 4 one zygote receives a double dose of tallness and two others a single dose. These phrases are more or less common in the literature of the subject, but the more frequent terminology is as follows. When two similar gametes unite to form a zygote it is called a *homozygote;* when the two pairing gametes are different the zygote is called a *heterozygote.* Using this terminology

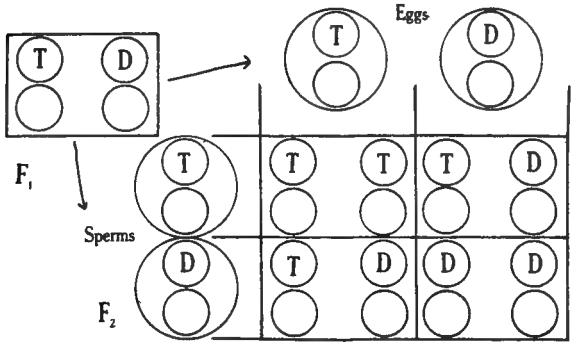


FIG. 4.—Diagram illustrating behavior of first hybrid generation (F_1) when inbred. Illustrates meaning of "segregation" and "purity of gametes," and how chance matings of F_1 gametes result in 3:1 ratio in F_2 generation; dwarf individual produced only by zygote in lower right-hand corner.

it is evident that the 3:1 ratio of the F_2 generation is really a 1:2:1 ratio, as follows: 1 homozygote for the dominant character, 2 heterozygotes, and 1 homozygote for the recessive character. The 1:2:1 ratio therefore is the significant one and appears as a 3:1 ratio only because of dominance.

In the experiment represented in fig. 4 three tall individuals appear in the F_2 generation. Superficially the individuals look alike, but it is realized that 1 differs

from the other 2 in germinal constitution, for 1 will produce only one kind of gamete, while the other 2 will produce two kinds. To indicate this situation JOHANNSEN (1) has introduced some appropriate terminology. Organisms which seem to be alike, regardless of their germinal constitution, are said to be *phenotypically* alike, or to belong to the same *phenotype*. On the other hand, organisms having identical germinal constitution are said to be *genotypically* alike, or to belong to the same *genotype*. From the standpoint of phenotypes only, MENDEL'S F_2 generation shows the 3:1 ratio; but if genotypes are considered, it shows the 1:2:1 ratio. In other words, this group of forms contains two phenotypes but three genotypes.

Referring again to fig. 4 several things may be inferred. It can be seen what will happen in the F_3 generation when the F_2 individuals are inbred. The dominant homozygote will produce only dominant homozygotes in the F_3 generation and will continue to produce them as long as it is inbred. The two heterozygotes will split up in the F_3 generation in the same 1:2:1 ratio as did their hybrid parents of the F_1 generation. The recessive homozygote will produce only recessive homozygotes as long as it is kept pure by being inbred.

It is interesting to consider what will happen if a heterozygote form is crossed with a homozygous recessive. It should be obvious that one-half of the progeny would be pure recessives, while the other half would be heterozygotes, that is, there would be a 1:1 ratio. A similar result would be obtained by crossing a heterozygote with a dominant homozygote, although all the

immediate progeny would show the dominant character. The real situation would be revealed, however, when this progeny was inbred, for one-half would be homozygous (pure breeders) and the other half would be heterozygous (hybrid breeders).

Thus far we have considered only what is called the monohybrid ratio, that is, the ratio obtained from one pair of contrasting characters, such as tallness and dwarfness. The next step is to consider the dihybrid ratio. MENDEL also used contrasting seed characters, finding, for example, that smoothness in seeds is dominant to a wrinkled condition. Introducing this pair of contrasting characters into the situation we have been considering, the dihybrid ratio will be the result. Crossing a tall, smooth-seeded individual with a dwarf, wrinkled-seeded individual it is evident that all of the F_1 or first hybrid generation will be tall, smooth-seeded individuals, since both of these characters are dominant. In the F_2 generation, however, the following ratio will appear: 9 tall smooth, 3 dwarf smooth, 3 tall wrinkled, 1 dwarf wrinkled; which is a 9:3:3:1 ratio. This is the dihybrid ratio, the explanation of which may be indicated in fig. 5. The question may be raised why the characters for tallness and smoothness are not represented on the same chromosome. If they were, the result would be a simple monohybrid ratio, except that the tall individuals would always be smooth-seeded as well, and dwarfs would be always wrinkled-seeded. The possibility of one chromosome carrying two different determiners will be considered later, but at present we shall assume that these determiners are on different chromosomes.

Fig. 5 shows that we are dealing with two homozygotes, each producing only one kind of gamete, so that all the hybrid progeny will be similar, both geno-

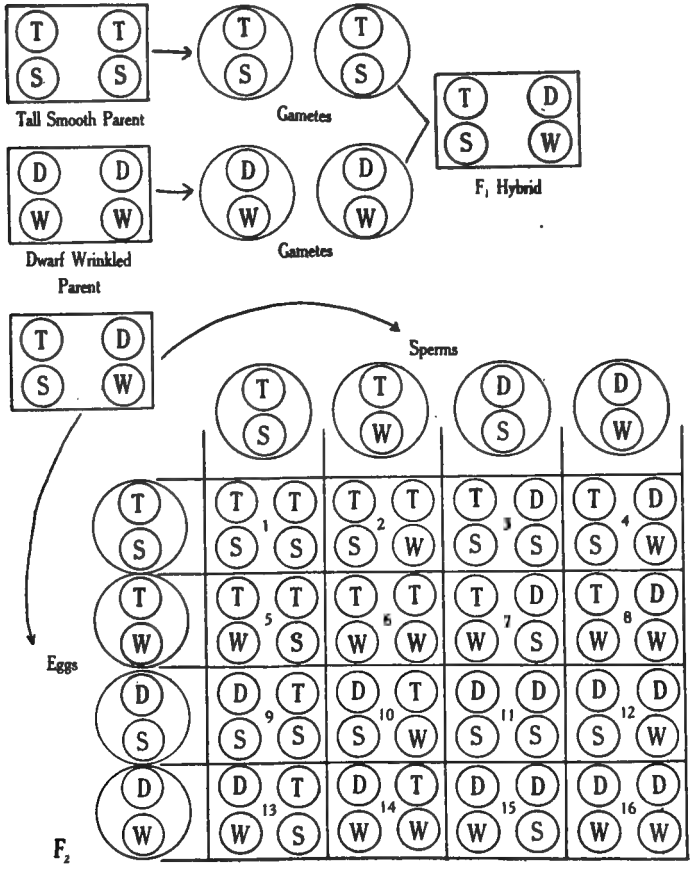


FIG. 5.—Diagram illustrating dihybrid ratio. Upper part shows how original parents were crossed to give F_1 hybrid; lower part shows F_1 hybrid producing four kinds of gametes; chance matings among these gametes, when F_1 is inbred, results as indicated in the large set of squares and explains the 9:3:3:1 ratio in the F_2 generation.

typically and phenotypically, that is, with the same germinal constitution and the same appearance. By inbreeding these F_1 individuals, it will be seen that four kinds of gametes are involved. Crossing these four kinds of gametes the resulting combinations are indicated in fig. 5. The result is four phenotypes, as follows: nos. 1, 2, 3, 4, 5, 7, 9, 10, 13 are tall smooth individuals; 11, 12, 15 are dwarf smooth; nos. 6, 8, 14 are tall wrinkled; no. 16 is dwarf wrinkled. This is the 9:3:3:1 ratio.

It will be noticed that nos. 1, 6, 11, 16 are homozygotes and therefore will breed true; but the rest are heterozygotes, either for one pair of characters or for both, and these would split into various types upon further breeding.

The next step is the trihybrid ratio. MENDEL found yellow seeds dominant over green seeds, and if this pair of characters is included with those used above the trihybrid result can be observed. The experiment would consist in crossing tall, smooth, yellow individuals with dwarf, wrinkled, green individuals; and it is obvious that the hybrid progeny would all be tall, smooth, yellow, since these three characters are dominant. Inbreeding the hybrids gives the following result in the F_2 generation: 27 tall smooth yellow, 9 tall smooth green, 9 tall wrinkled yellow, 9 dwarf smooth yellow, 3 tall wrinkled green, 3 dwarf smooth green, 3 dwarf wrinkled yellow, 1 dwarf wrinkled green. The trihybrid ratio therefore is 27:9:9:9:3:3:3:1. This involves 64 individuals and 8 phenotypes.

1. JOHANNSEN, W., Elemente der exakten Erblichkeitslehre. Jena. 1909.
2. MENDEL, G., Versuche über Pflanzen-Hybriden. Verh. Naturf. Vereins in Brünn 4:1865.

CHAPTER V

NEO-MENDELISM

Thus far we have been considering Mendel's law in its simple form and have enlarged but little upon MENDEL'S original statement. The value of the law is apparent. Upon its republication in 1900 it was taken up by biologists and numerous breeders set to work to test it. As a consequence data for and against it began to accumulate. As might be expected, there was much apparent evidence against the law, but as geneticists developed a better conception of the mechanism the contradictory evidence was explained away. Almost every type of inheritance has now been explained according to Mendel's law. Some of the explanations are very complicated and cannot be included in this presentation. A few of the more important cases, however, will be presented.

I. PRESENCE AND ABSENCE HYPOTHESIS

This may be regarded as a new method of Mendelian thought. It was first suggested by CORRENS (3), but later was worked out in detail by other geneticists, especially HURST, BATESON, SHULL, and EAST. It is merely a modification of the mechanism involved. For example, in the case of a hybrid obtained by crossing tall and dwarf parents the result had been explained as due to the fact that one chromosome bears a determiner for tallness and the other one of the pair carries the deter-

miner for dwarfness. In other words, each one of a pair of allelomorphs is represented by a determiner, two determiners thus being present. Dwarfness in this case would be the result of the interaction of that determiner and its environment during the development of the body; and the same for tallness. When both were present, however, the conception of the situation was as follows. The determiner for dwarfness, setting up its usual series of reactions, early became paralyzed by the determiner for tallness or its products. This result was called the dominance of the character for tallness. It was as if the determiner for tallness completely prevented the activity of the determiner for dwarfness. This conception was apparently borne out by the facts and was the explanation of the mechanism generally accepted.

According to the presence and absence hypothesis, however, the situation is looked at from an entirely different point of view. Tallness is the result of a determiner, but dwarfness is merely the result of the absence of the determiner for tallness. The dominant character is produced by an inheritable determiner, but the recessive character appears only when the dominant determiner is lacking. This conception has some evident advantages and may modify the previous Mendelian diagram, as shown in fig. 6. This appears to be a simpler mechanism to account for the phenomenon called dominance. In the case of the dwarf form there is a normal course of development; in the case of the tall parent or hybrid, however, an additional determiner stimulates cell growth, or cell division, or both. It is a simpler and more useful conception, so long as it fits the facts. Some

investigators, however, claim that it cannot be applied to all the situations that have been discovered.

This hypothesis introduces some additional terminology suggested by BATESON. In our illustration the tall parent has two determiners for tallness and therefore BATESON calls it *duplex*, having a double dose. For the same reason the F_1 individuals, having only one determiner for tallness, he calls *simplex*. According to the

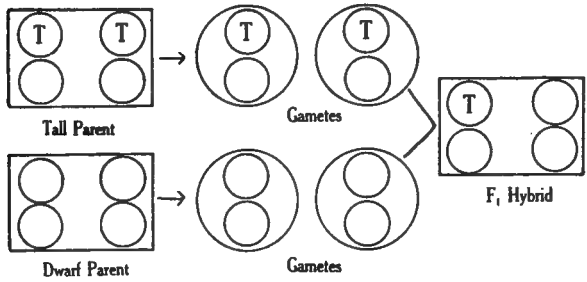


FIG. 6.—Diagram showing how the original scheme must be modified to satisfy the presence and absence hypothesis.

same terminology the dwarf parent is *nulliplex* with respect to its character of tallness.

Additional advantages of the presence and absence hypothesis will appear in connection with a consideration of blending inheritance and of cumulative factors in inheritance. Attention, however, should be called to the fact that those who accept the presence and absence hypothesis do not use the form of notation thus far used in explaining Mendelian inheritance. Assume that T is used to express the determiner for tallness, the same letter (t) is used to express its absence. For example, instead of using D for dwarfness, t is used for "lack

of tallness" (fig. 7). It is a matter of convenience to have a symbol to represent the recessive, the absence of something that is present in another individual.

In summary, the essential difference between the presence and absence hypothesis and that of dominant and recessive is that in the former case the recessive

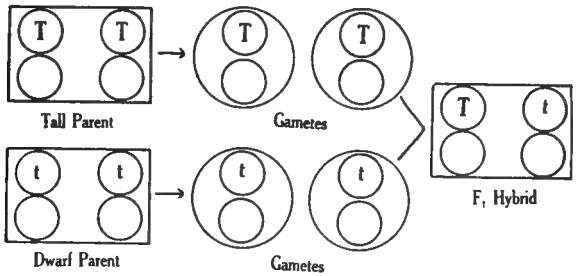


FIG. 7.—Diagram showing how presence and absence scheme is actually used, with small letter representing "absence."

determiner has no existence at all, while in the latter case it exists, but is in a latent condition when associated with the dominant.

II. BLENDS

This type of inheritance when first discovered was thought to be in direct conflict with Mendel's law. It is a case in which dominance seems to fail, for the two alternative characters both express themselves and the result is an average between them. It is easy to explain this situation in accordance with the presence and absence hypothesis without any violation of Mendel's law.

The classic example of blending inheritance was presented by CORRENS (3) in breeding work upon

Mirabilis Jalapa, the common four-o'clock. CORRENS crossed red and white varieties, and all the hybrid progeny had rose pink flowers. This was a color blend, distinctly intermediate between the colors of the two parents. The F_1 generation, therefore, seemed to contradict Mendel's law in that one color character was not completely dominant over the other. The real situation, however, appeared in the F_2 generation obtained by

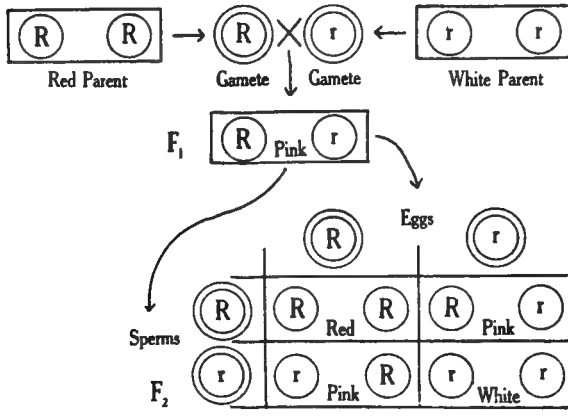


FIG. 8.—Diagram illustrating blending inheritance, discovered by CORRENS in *Mirabilis Jalapa*.

inbreeding individuals of the F_1 generation which showed the blend. By inbreeding the pink hybrids CORRENS obtained the perfect 1:2:1 ratio, that is, 1 red like one grandparent, 2 pink like the hybrid parent, and 1 white like the other grandparent. Segregation was evidently taking place, the only unusual thing being the *appearance* of the F_1 individuals, and that was explained immediately as failure of dominance (see fig. 8).

The question this introduces, therefore, is that of a mechanism which could account for such a result. The easiest explanation offered is that the red parent was a homozygote for redness (double dose) and the hybrid a heterozygote (single dose); the inference is that a single dose produces pink while a double dose produces red. A theoretical explanation of this occasional difference in the result of double and single doses is as follows. Imagine that the body cells of a plant have a certain capacity for expressing hereditary characters. In such a case, just as a given quantity of solvent can dissolve only a given amount of solute, so the body cells can express hereditary characters only to a definite limited extent. In the four-o'clock a single dose of redness may be thought of as half saturating the body cells, while a double dose completely saturates them. In cases showing complete dominance, however, a single dose completely saturates the cells and a double dose can do nothing more. This analogy assists in visualizing on the one hand the necessary mechanism of blends (apparent failure of dominance) and on the other hand that for cases of complete dominance.

Another example of simple blending inheritance is the case of Adzuki beans, described by BLAKESLEE (1). In this bean the mottling of the seed coat is dominant to the lack of mottling. In the hybrid condition, however, the mottling is lighter than in the pure or homozygous condition. Heterozygous plants, therefore, can be easily distinguished from homozygous plants, so that the 1:2:1 ratio is evident on external inspection rather than the usual 3:1 ratio.

These two cases are illustrations of what may be called simple blending inheritance. There are other cases of blending which are more complex and cannot be explained so easily.

EAST (4), in crossing starchy and sweet corn, obtained all starchy in the F_1 generation, followed by the usual 3:1 ratio in the F_2. He says that starchiness is due to the presence of a determiner which enables the corn to mature starch grains. When this determiner is absent starch grains cannot be formed, so that the carbohydrates of the endosperm are left in the condition of sugar, and the result is a sweet corn. This is a simple case of presence and absence, usually accompanied by complete dominance. Occasionally, however, the cross between pure sweet and pure starchy races gave semi-starchy progeny. The hybrid therefore was intermediate in this regard and would seem to represent a case of blending inheritance, which of course means incomplete dominance. This case, however, cannot be explained easily by the presence and absence hypothesis or any other hypothesis. The difficulty is that inheritance, which usually shows complete dominance, occasionally gives way to blending inheritance. The blend in the four-o'clock was a constant behavior; in this corn case it is the occasional behavior; so that the mechanism proposed to explain the four-o'clock blend cannot explain this inconsistent behavior of corn. The best that can be said, apparently, is that something is interfering with the mechanism; and this is about all that EAST concludes; he says "something is interfering with dominance; it is only partial."

There are two other types of blending inheritance that may be mentioned, the mechanism involved in which will be discussed in another connection.

After the first announcement by CORRENS of simple blending inheritance further investigation revealed many similar cases; in fact it was soon regarded to be a common phenomenon that the F_1 should be an intermediate. At the same time it was fully expected in such cases that the hybrid would split in the F_2 generation in a 1:2:1 ratio. Practical breeders were advised that Mendel's law was invariable; that a hybrid must split; and therefore that the only way to preserve a valuable hybrid was by vegetative propagation. Many breeders realized the value of this advice, but some reported certain surprising results. They claimed that they had made numerous crosses and that in many cases the intermediate F_1 individuals continued to breed true to the intermediate hybrid characters, even when propagated from seed. Gardeners today continue to tell of certain *Begonia* hybrids that continue to breed true from seed in intermediate condition. BURBANK (2) claims many such cases, in which hybrid blends breed true to seed, as did their parents. All such claims contradicted the experience of scientific breeders and seem to destroy their theories. Accordingly, the Mendelians sought to explain these claims of pure-breeding hybrids and succeeded in doing so remarkably soon. There has been much discussion of this situation and there is no need to go into the details of it. It will be sufficient to mention briefly the principal methods by which pure-breeding hybrids have been explained as not contradicting Mendel's law.

In the first place botanists suggested parthenogenesis or vegetative apogamy in the F_1, which of course would mean vegetative propagation and would not involve the segregation of characters and recombinations in fertilization. In such a case, of course, the hybrid characters would be continued. This is true, but why should the F_1 generation exhibit apogamy any more than any other generation? An ingenious theoretical answer to this pertinent question has been suggested by EAST (5) as follows. "May not the difficulty of maturing sexual cells in a *wide cross* sometimes cause apogamous development, and therefore a continued propagation of a constant and uniform race?" This suggestion seems reasonable, for it conforms to two other recognized phenomena.

JEFFREY (7) and his followers have shown that in wide crosses the resulting hybrid produces more or less sterile pollen. An investigation of wild plants has indicated that much hybridizing occurs in nature, especially in certain families, as indicated by the amount of sterile pollen, which is sometimes as much as 100 per cent. Such plants, which reveal their hybrid character only by the presence of sterile pollen, are called by JEFFREY "crypthybrids." This fact has also been brought out by many experimental breeders.

A second significant fact in this connection was announced by EAST, who says "apogamy is evidently induced by the extraordinary irritation of foreign pollen." The mechanism involved should be considered. A study of the development of the ovule and female gametophyte shows that stages are passed through before pollination, bringing the ovule to a certain stage of

maturity. At that point, however, it was claimed that development would stop were it not for the stimulus of pollination and pollen tube development. This stimulus apparently causes the female gametophyte to continue its development to the final stage of preparation for the reception of the sperm. Sterile pollen might furnish this stimulus as well as fertile. If then pollination by sterile pollen has taken place and the female gametophyte has been stimulated to its complete ante-fertilization development, this development may continue in spite of the failure of an effective sperm to arrive, and the result might be an apogamous embryo. In some such way the relation of apogamy to sterile pollen, resulting from wide crosses, might be explained.

This conception meets with many objections, so many that they cannot all be discussed. The chief difficulty, however, may be stated as follows. Is there any mechanism for the transmission of a pollen stimulus to the developing female gametophyte? We know of none, but neither can we explain the mechanism of the sensitive plant in which there is obviously the transmission of a stimulus. Furthermore we know from facts in connection with parthenocarpy that pollination stimulates development as deep within the tissue as the ovule itself, and it would be easy to extend this to the development of the female gametophyte as well.

All this is still a field of speculation, but in any event the reason for EAST'S contention that wide crosses may give hybrids that reproduce apogamously is evident. Wide crosses give sterile pollen; sterile pollen stimulates the development of the female gametophyte but cannot effect fertilization; the result is apogamy,

so that the hybrid breeds true to its intermediate character.

Another explanation of pure-breeding hybrids develops from the mathematical possibilities of chance mating when the character in question is due to numerous separate factors. Without going into the details it may be said that in such a case the conclusion is reached that the intermediate hybrids must of mathematical necessity go on producing intermediates with but a remote chance of giving back either of the extreme parent types.

In these various ways the Mendelians explain away pure-breeding hybrids. In doing so they discard a great deal of recorded data which seem to them unsubstantiated. A definite statement of the situation may be obtained from a paper by EAST (5), published in 1910.

> It is believed by many that there are kinds of inheritances other than Mendelian; that is, inheritance in which no segregation occurs. Far be it from me to deny this. *I simply state the fact that there are no exact data extant proving other kinds of inheritance.* Such data may be found, but it is useless to speculate upon other laws without such evidence. There are several cases in which either *new* characters that breed true or *blended* characters that breed true appear to have been formed, but they have not been studied with sufficient care for analysis of their mode of inheritance to be accurate and final.

In 1913 EMERSON and EAST (6), in a joint paper, stated that there are on record only two indisputable cases of non-Mendelian characters. These will be considered later in their proper connection. Neither of them, however, is a case of pure-breeding intermediate hybrids.

Before leaving the general topic of blending inheritance a statement should be made concerning "particulate inheritance," which means that in certain crosses something happens causing unblended fragments of both parental characters to appear in the hybrid progeny, resulting in that patchwork of parental characters called a "mosaic." This is not true blending inheritance, but has been named by GALTON "particulate inheritance." A common illustration is that of a variegated *Amaranthus*, whose leaves show an irregular mosaic of white and green. This is produced by crossing pure white and pure green strains of *Amaranthus*.

1. BLAKESLEE, A. F., and AVERY, B. T., Adzuki beans and Jimson weeds. Jour. Heredity 8:125–131. *figs. 5.* 1917.
2. BURBANK, LUTHER, Another mode of species forming. Ann. Report Amer. Breeders Assoc. 5:40–43. 1909.
3. CORRENS, C., Die neuen Vererbungsgesetze. Berlin. 1912.
4. COULTER, CASTLE, DAVENPORT, EAST, and TOWER, Heredity and Eugenics. Chicago. 1912.
5. EAST, E. M., The rôle of hybridization in plant breeding. Pop. Sci. Monthly 77:342–355. *figs. 12.* 1910.
6. EMERSON, R. A., and EAST, E. M., Inheritance of quantitative characters in maize. Bull. Agric. Exper. Sta. Nebr. no. 2. pp. 120. *figs. 21.* 1913.
7. JEFFREY, E. C., Spore conditions in hybrids and the mutation hypothesis of DE VRIES. Bot. Gaz. 58:322–336. *pls. 22–25.* 1914.

CHAPTER VI

NEO-MENDELISM (*Continued*)

III. THE FACTOR HYPOTHESIS

MENDEL concluded that each plant character depends upon a single determiner. Inheritance, however, has proved to be a much more complex phenomenon than indicated by MENDEL'S peas. Ratios have appeared that were puzzling, and geneticists were forced to the conclusion that there may be a compound determiner for a single character. This conception is called the *factor hypothesis*, and the growing complexity of genetics has developed in connection with this hypothesis. With the consideration of *factors* instead of *determiners* one passes from elementary to advanced genetics. Previously we have used the word determiner, implying MENDEL'S idea that a single determiner is responsible for the development of a plant character, and this has been true of the examples of inheritance previously considered. It is understood now, however, that a character is frequently determined by the interaction of two or more separately heritable factors, and hence the factor hypothesis. The distinction between factors and determiners should be made clear. In case only one factor is involved in determining a character, there is no distinction between factor and determiner; and in such a case the term factor should not be used.

1. COMPLEMENTARY FACTORS.—This is the simplest expression of the factor hypothesis and it may be illustrated by some of EAST'S work. Crossing red-

grained and white-grained corn he obtained all red in the F_1 generation. This would suggest that the F_2 generation would show 3 red to 1 white; but it showed 9 reds to 7 whites, which did not suggest Mendelian inheritance. It is in accord with Mendel's law, however, if we consider that two complementary factors are necessary to produce the red character, and that each of these factors is inherited separately. Such a situation would give a dihybrid ratio, as indicated in fig. 9. It will be seen that out of 16 progeny 9 will be red, for they alone contain the complementary factors; the other 7 will be white. The situation is thus explained by the dihybrid ratio, but although only one character is involved that character depends upon two complementary factors.

Another situation is worth noting. No. 6 of the diagram is white because it contains only one of the necessary factors; no. 11 is white for the same reason, but its germinal constitution is just the opposite. What would happen if these two are crossed? There is only one possibility, since each is a homozygote producing only one kind of gamete. The result would be red, and thus a cross between two whites would produce only reds. What would happen from crossing nos. 6 and 15, the former being a homozygote and the latter a heterozygote? It is obvious that the resulting progeny would be one-half white and one-half red, although both parents are white. The same result would be secured in crossing nos. 11 and 14. A cross between nos. 14 and 15, both of which are heterozygotes, would result in 3 whites and 1 red, the ordinary 3:1 ratio. These illustrations show how differently the same phenotype may behave in inheritance. In each case two whites were

crossed, that is, the same phenotypes, but three different ratios were obtained because the genotypes were different.

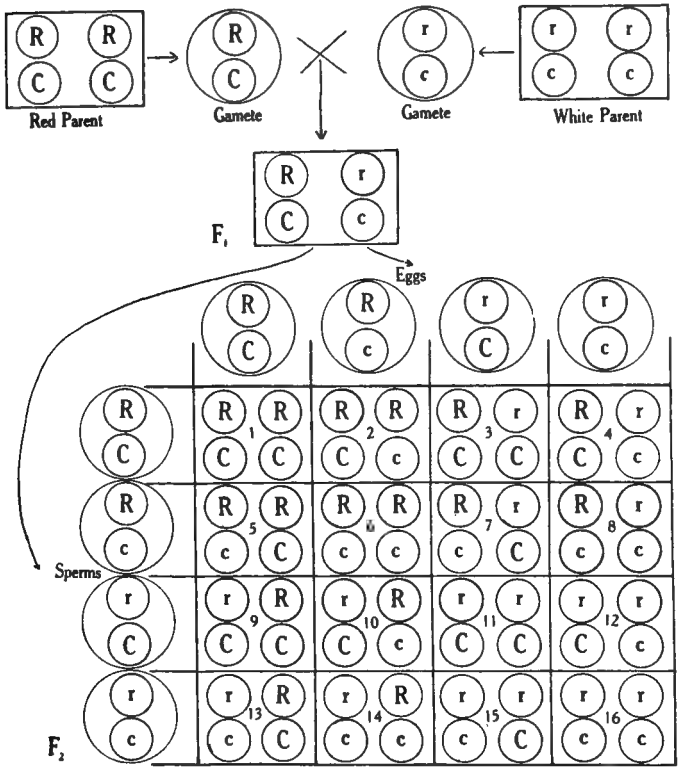


FIG. 9.—Diagram illustrating behavior of complementary factors in cross between red-grained and white-grained corn. *R* and *C* must both be present to produce red-grained corn.

The striking feature of this situation is that one can cross two whites and get a red. This gives an insight into the so-called phenomenon of *reversion*. For ex-

ample, in the course of numerous breeding experiments BATESON (1) obtained two strains of white sweet peas, each of which when normally "selfed" bred true to the white color; but when these two were artificially crossed all the progeny had purple flowers, like the wild Sicilian ancestors of all cultivated varieties of the sweet pea. This appeared to be a typical case of reversion. Further breeding, however, showed that this was just such a case of complementary factors as we have been considering. One of BATESON'S white strains had one of the factors for purple and the other strain had the other factor.

Complementary factors have been defined and the method of their inheritance described, but is there any mechanism to explain the situation? A suggestion may be obtained from plant chemistry (2). The most prominent group of pigments in plants is the group of anthocyanins, which are produced as follows. Plants contain compounds called chromogens, which are colorless themselves but which produce pigments when acted upon by certain oxidizing enzymes or oxidases. This is a sufficient mechanism for the behavior of complementary factors. If one of EAST'S white strains of corn contained a chromogen capable of producing red but lacked the necessary oxidase it would remain colorless. If the other white strain contained the oxidase but no chromogen it would remain colorless. In crossing them, however, chromogen and oxidase would be brought together and a red-grained hybrid would be the result. Inbreeding such red-grained individuals of course would give red and white progeny in a ratio of 9:7, as explained in connection with EAST'S corn. This seems to be the

explanation of the behavior of complementary factors in many cases of color inheritance.

Where other characters are involved the mechanism must be somewhat different. In some cases the two factors may be the enzyme and the compound the enzyme attacks, as in the oxidase and chromogen situation just described. On the other hand, we might be dealing with two chemical compounds that are inert when occurring separately but active when brought together, active in such a way as to produce a distinctly new character. Also two active substances might neutralize one another when brought together in a hybrid, and the failure in their activity might result either in a new character or the failure of some parental character to develop. Such are some of the possible mechanisms to explain the behavior of complementary factors.

Hybridizing, therefore, is much like mixing chemicals in a test tube. We know that very wide crosses cannot be made successfully; but the surprising thing is that certain very close crosses are constantly unsuccessful, even though both parents may cross freely with closely related types. We obtain a glimpse of the possibility of such apparently inconsistent behavior when we consider the chemical possibilities suggested by the behavior of complementary factors.

The origin of complementary factors is an interesting field of speculation. Did they originate together or separately? A natural inference would be that they originated together, for neither would be of any use without the other. It should be remembered, however, that the idea of use as explaining the occurrence of everything in a plant is being abandoned; one must think

rather of a plant as a complex physico-chemical laboratory. No one claims that all chemical reactions are useful; they are simply inevitable; and plant characters are the result of chemical reactions and physical necessities. Even though we assume the simultaneous origin of two complementary factors, they would have to be put on separate chromosomes, for the factors are separately inherited.

The other alternative is to suppose that these factors originated independently in the history of a plant. In this case, of course, the first one to be produced would remain functionless until finally its complement came into existence. This might be an explanation of what are called latent characters. Also they might have not only originated independently but in different varieties or species. In this case if natural hybridizing should bring them together the result would be the appearance of a new character, and this may have been a very important factor in the origin of species.

This may serve as an introduction to the factor hypothesis, with complementary factors as an illustation, simply because it is the simplest situation. There are many other kinds of factors recognized, but we shall not attempt to list all of the proposed types. A simple illustration of the better known types is as follows:

a) A *complementary* factor is added to a dissimilar factor to produce a particular character.

b) An *inhibitory* factor prevents the action of some other factor.

c) A *supplementary* factor is added to a dissimilar factor with the result that the character is modified in some way.

d) A *cumulative* factor, when added to another similar factor, affects the degree of development of the character.

Some examples of these types will make them clear, those for complementary factors having been given previously.

2. INHIBITORY FACTORS.—Recalling EAST'S experiment with red-grained corn it will be remembered that when both factors for red were present the grain was red, but when either factor was absent the grain was white. Later he crossed these strains with a new white strain, and the result was surprising (3). The pure red strain produced gametes carrying both the red factors, and it would be expected that whatever such a gamete mated with would result in red progeny; but when this pure red was crossed with the new strain of white the progeny were all white, although the hybrids certainly contained both factors for red. The explanation which first occurred to EAST, and which later experiments confirmed, was that the new white strain contained an inhibitory factor, which prevented the development of red even though both the complementary factors for red were present. Fig. 10 illustrates the situation and shows why all the individuals of the F_1 generation are white. It is interesting to note further the possibilities of white and red in the F_2 generation. They would be numerous, since we are dealing with trihybrid ratios (see fig. 11). This does not exhaust the possibilities, for the cases given were homozygotes, each producing a single kind of gamete. There remains for consideration the heterozygote situation (see fig. 12).

The possible mechanism of the inhibitory factor is as follows. We have assumed that red is produced

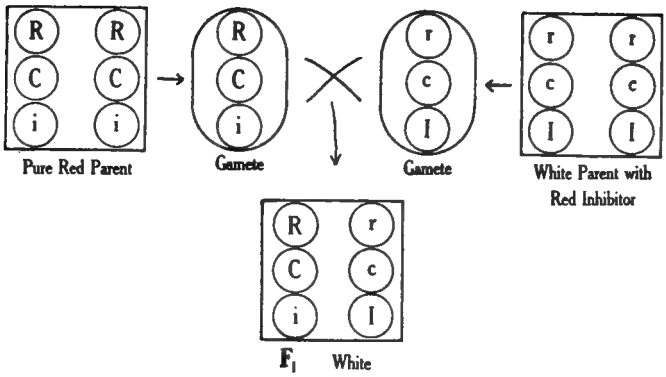


FIG. 10.—Diagram illustrating behavior of inhibitory factor

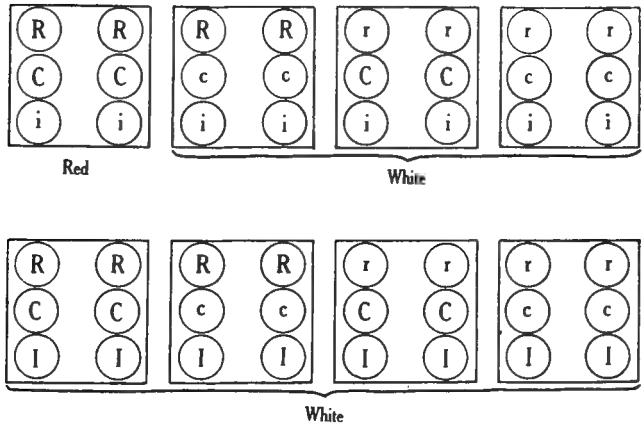


FIG. 11.—Diagram showing some possible combinations in F_2 when F_1 of fig. 10 is inbred. Individual on left end of upper set red-grained, because *R* and *C* both present and *I* absent; other individuals in upper set white, because lacking *C* or *R* or both; individuals in lower set with inhibitory factor and therefore white, whatever other combinations of factors they may contain.

only when the enzyme is present to oxidize the chromogen. Enzymes are very sensitive; their activities may be affected or completely checked by various agents. Suppose that *I* of the diagram be such an agent and the necessary mechanism is apparent. When *I* is present *R* is paralyzed, so that it cannot oxidize *C*.

3. SUPPLEMENTARY FACTORS.—A supplementary factor is one that is added to a dissimilar factor, with the result that a character is modified in some way.

In his work upon red-grained races of corn EAST found occasionally a few purple grains. His conception of the situation is as follows (3). The pure red plant contains two complementary factors, one (*C*) a chromogen, and the other (*R*) an enzyme, which when brought together produced the red color. The purple grains, however, must be explained by the presence of still another factor (*P*), the resulting situation being represented in fig. 13. Of course when *C* is absent no pigment whatsoever can be produced. As a consequence we will assume that the presence of *C* is constant, and that *P* and *R* are variables. For a similar reason we will assume that the absence of *I* is constant. The figure shows three possibilities, from which the following conclusions may be drawn: (1) when *P* and *R* are both present the result is purple grains; (2) red appears only in the absence of *P;* (3) *P* although present will not develop any color in the absence of *R*.

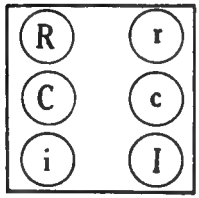


FIG. 12

This is a typical case of a supplementary factor, that is, one which is added to a dissimilar factor, with the

result that the color character is modified. The mechanism of this situation will make clearer the behavior of the supplementary factor. If *C* is the chromogen and *R* the enzyme, what is *P?* The suggested answer can be obtained from plant chemistry. It is found that the purple pigment is produced by the same substance as the red, but represents a higher state of oxidation. The conclusion is obvious. *C* is oxidized by *R* up to a certain point, where red is produced; but if *P*

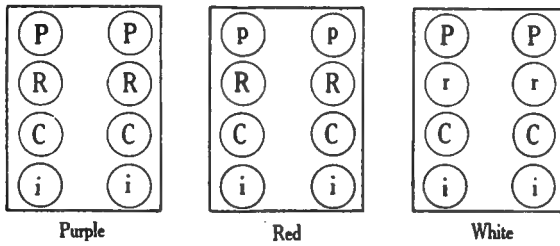


FIG. 13.—Diagram illustrating action of supplementary factor

is also present it represents an additional enzyme, which attacks the red pigment and oxidizes it still further into purple. *P* is incapable of attacking the original chromogen, but when *R* carries the attack to a certain point, *P* can function and carry the oxidation further. As a consequence *P* without *R* gives white grains, while *R* gives red grains only in the absence of *P*

4. CUMULATIVE FACTORS.—These will be considered under the next heading, "Inheritance of quantitative characters."

In addition to the four types of factors given, the literature of genetics also contains discussions on

intensifying factors, diluting factors, distribution factors, etc. These, however, do not introduce any new mechanisms.

1. BATESON, W., Mendel's laws of heredity. Cambridge. 1909.
2. CZAPEK, P. and M. E., Biochemie der Pflanzen. Jena. 1913.
3. EAST, E. M., and HAYES, H. K., Inheritance in maize. Conn. Agric. Exper. Sta. Bull. no. 167. pp. 142. *pls. 25.* 1911.

CHAPTER VII

NEO-MENDELISM (*Continued*)

5. INHERITANCE OF QUANTITATIVE CHARACTERS.—This phase of the factor hypothesis, if true, is of fundamental importance not only to genetics but to general biology. It is based upon the conception of cumulative factors, and as it is presented it will be realized that it throws light not only upon numerous breeding experiments but also upon variation in general, which means evolution also. A cumulative factor was defined as one which, when added to another similar factor, affects the degree of development of the character.

It will be recalled that CORRENS crossed red and white strains of *Mirabilis* and obtained pink hybrids. The suggested explanation of this result was that a single dose of the red determiner gives pink while a double dose gives red. When CORRENS inbred these pink hybrids, he obtained the result presented in fig. 8, that is, 1 red, 2 pink, 1 white. This result is obvious and the mechanism is plain.

With this diagram in mind we shall consider some of the experiments of NILSSON-EHLE (2) at the Swedish Experiment Station. He crossed two strains of wheat with red and white kernels. The F_1 individuals had light red kernels, which of course suggests a repetition of the situation shown by *Mirabilis* in the experiment of CORRENS. The F_2 generation, however, showed a very different result. The reds and whites appeared in the

ratio of 15:1; but in addition to this, among the 15 reds there could be distinguished varying degrees of redness. NILSSON-EHLE suspected that 15:1 meant a dihybrid

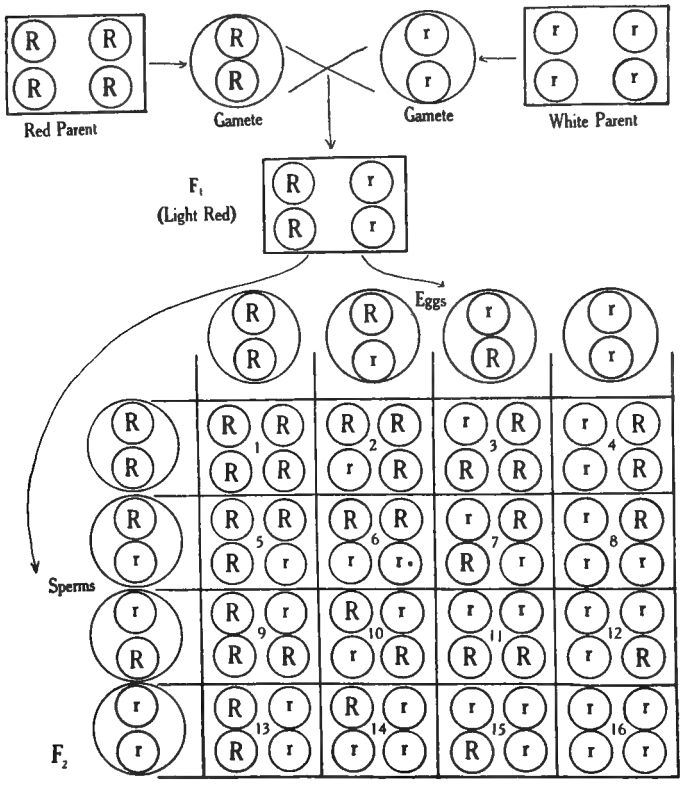


FIG. 14.—Diagram illustrating NILSSON-EHLE'S explanation of 15:1 ratio obtained in F_2 generation from cross between red-grained and white-grained wheat.

ratio, 16 individuals being necessary to give the ratio, so that he constructed the tentative scheme shown in fig. 14.

This shows a regular dihybrid ratio, except that the two factors involved are similar. Applying the single dose and double dose conception, as used in the case of CORREN'S pink *Mirabilis*, we reach the following conclusions: no. 1 only has four doses and therefore it only is deep red; nos. 2, 3, 5, 9 have three doses and are somewhat lighter red; nos. 4, 6, 7, 10, 11, 13 have two doses and are still lighter red; nos. 8, 12, 14, 15 have one dose and are very light red; while no. 16 alone has no dose and is the only pure white. This accounts for the 15:1 ratio, and the different shades of red. This is entirely in accord with the conceptions that have been presented, and only two assumptions are necessary: (1) that dominance is absent, and two doses have twice the effect of one; (2) that the independent similar factors are cumulative in their operation, and are paired with their absence in the hybrid. This was NILSSON-EHLE'S conception, and of course he tested it by further experimental work, the results consistently confirming the conception.

Since it is important to fix this conception clearly in mind, another type of diagram may represent the facts even more clearly. The proportion of individuals showing the various degrees of redness in the F_2 is graphically recorded in fig. 15, each dot representing one dose of the factors in question.

Continuing these investigations, NILSSON-EHLE next discovered a new strain of red-grained wheat, which, when crossed with the pure white strain, yielded F_1 hybrids of intermediate intensity of red as before. The F_2 generation, however, showed a different situation. Reds and whites were obtained in the proportion of

63:1; the 63 reds as before falling naturally into different groups on the basis of degree of redness. Applying the same conception as before NILSSON-EHLE discovered that in this case he was dealing with a trihybrid situation.

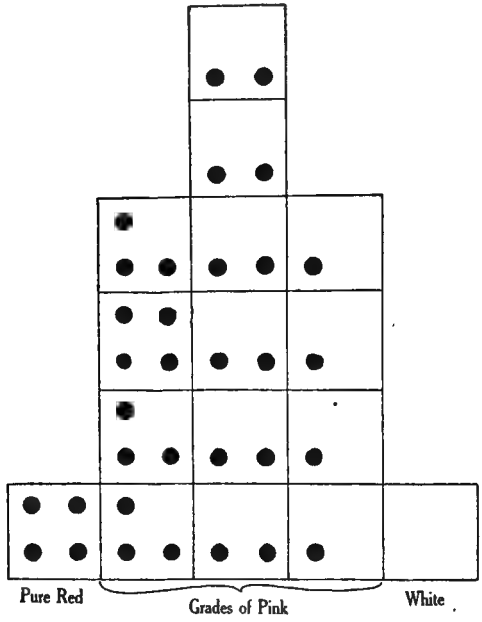


FIG. 15.—Another method of visualizing NILSSON-EHLE'S 15:1 ratio (see fig. 14).

Without constructing the usual Mendelian diagram, which would have to be extensive enough for 64 individuals, the situation as it appeared in the F_2 generation may be represented by fig. 16. If the graph is surmounted by a curve we recognize the regular "probability curve," exactly the kind of curve biometricians

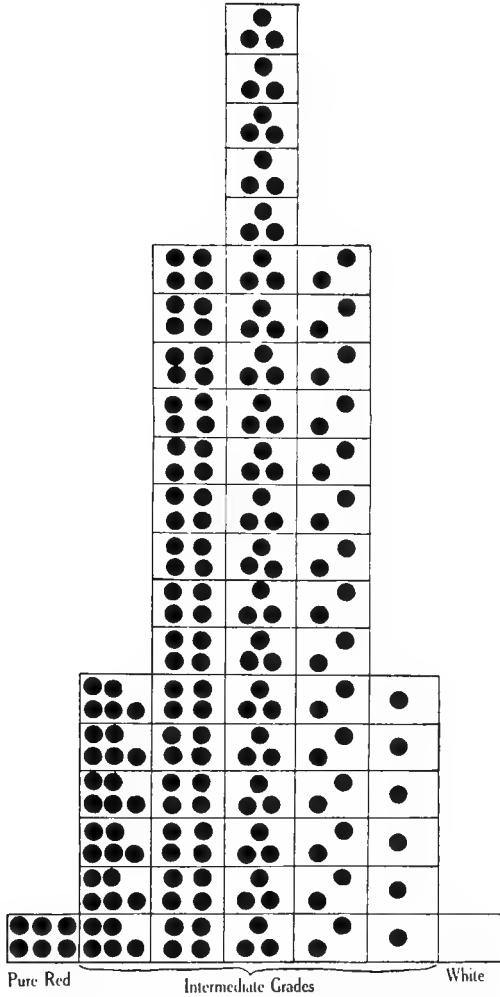


FIG. 16.—Diagram illustrating NILSSON-EHLE'S 63:1 ratio

use to represent the fluctuating individuals about a specific type.

This conception of cumulative factors, therefore, has far-reaching significance. For a long time biologists have recognized individual variation within the species. DARWIN depended upon it as the basis of his theory of natural selection as the origin of species; in fact, ever since DARWIN'S *Origin of species*, individual variation has been fundamental in our conceptions. To account for this universally recognized phenomenon, DARWIN proposed his *transportation hypothesis* as a possible explanation, which, as will be recalled, did not long survive. WEISMANN offered in explanation his *germinal selection*, which was soon discarded because it was beyond the possibility of experimental testing. Aside from these two attempts to explain individual variation no other comprehensive scheme had been presented. Biologists had simply recognized the fact of individual variation without any conception of the mechanism. They knew that individual variation existed but had even stopped asking why it existed.

The importance of this new theory, therefore, is obvious. It is an ingenious explanation of the inheritance of quantitative characters and of the existence of individual variations. Furthermore, the theory has not been developed through meditation, but has its basis in scientific experiments. It is imaginative to a certain extent, of course, as is every other valuable theory, but unlike most such theories it has a substantial foundation, namely, Mendel's law.

The importance of the possible rôle of cumulative factors in explaining individual variation, which in

turn is the basis of evolution, has been emphasized because its importance has perhaps not yet been sufficiently appreciated. It promises to be one of the most important theories of biology, which of course must be tested by future investigation.

The doctrine of cumulative factors was further developed by EAST (1) in his work with corn. He was able to explain some of the ratios obtained by assuming three or four separately inherited cumulative factors, just as NILSSON-EHLE had done. He obtained other ratios, however, which required more independent cumulative factors to explain. Some idea of the extent of these investigations by EAST and his associates may be obtained by noting the list of the plant characters whose inheritance they explained on the basis of cumulative factors: number of rows, length of ear, diameter of ear, weight of seed, breadth of seed, height of plant, number of stalks per plant, earliness of flowering. In all of these cases breeding gave the same characteristic results. A cross between extreme parents gave hybrid progeny intermediate as to the character in question; and in the F_2 generation the two extremes reappeared, along with all gradations of intermediates.

NILSSON-EHLE had been able to put his F_2 intermediates into definite classes, corresponding to the number of doses of the determiner each had received. EAST, however, could not do this with such exactness. His results showed all gradations, but he could not distinguish any definite groups; that is, gradation was continuous and complete. In other words, he could not tell with certainty from outward appearance just how many doses of a given determiner an individual

contained. His results, therefore, do not seem so clear and striking as those of NILSSON-EHLE, but they are by no means vague and uncertain. For example, even if he could not say definitely that a certain individual had exactly three doses, he could always say approximately how many doses it had; and the breeding results always confirmed the idea of a number of cumulative factors at work. For example, a plant with three doses may vary with respect to the character in question. It may approach the condition of the plant with four doses or it may vary toward the two-dose condition. Such variation may be explained by outside influences. Any classification of the F_2 individuals on the basis of the number of doses is more or less obscured by the influence of outside factors which are uncontrollable, or at least uncontrolled as yet in breeding work.

EAST has visualized these outside factors and discussed them. In order to explain this discussion, however, we must recall a feature of genetics which has previously been mentioned. Plant variations in the largest sense fall under two categories, due to (1) differences in gametic constitution, and (2) responses to environment. The first category is the basis of all Mendelian conceptions, while the second category includes such variations as are usually thought not to be inherited, being acquired characters. This category is now commonly called fluctuating variations.

An illustration will make these two categories clear. Assume that a plant with a determiner for tallness usually becomes 6 feet, while one without this determiner becomes 3 feet. The 6-foot plant, however, grown in good soil becomes 6.5 feet, while in poor soil it is 5.5

feet. In inheritance of course the 6.5- and 5.5-foot plants behave exactly alike; the same is true of 6-foot plants. It must be evident, therefore, that a classification of F_2 individuals on the basis of the number of doses might well be slightly obscured. If outside influences were lacking, the F_2 situation could be represented

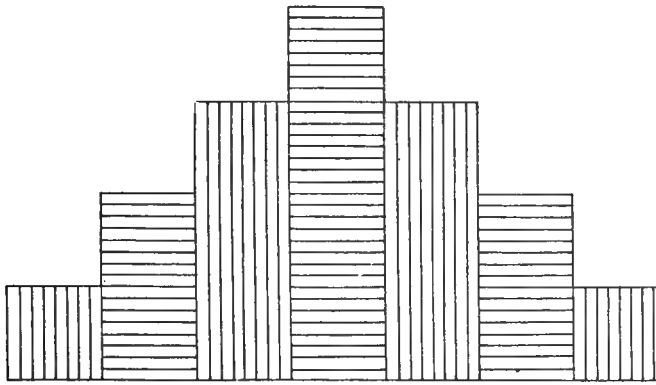


FIG. 17.—Diagram illustrating distribution of phenotype classes in an F_2 population from cross involving cumulative factors. Practically same diagram as fig. 16, and interpreted in same way; short rectangle at left indicates that very few plants of population contain maximum number of doses; short rectangle at right indicates that very few plants contain minimum number of doses; plants with intermediate number of doses most numerous, as indicated by tall rectangle in middle (see also fig. 18).

by fig. 17, or better, fig. 18; but when outside influences are active, it may be represented by fig. 19. It will be seen from this last diagram that not all individuals belonging to a particular size class may have the same number of doses; that is, conditions for a smaller-dosed individual may be so much better than those for a larger-dosed individual that they may exchange size classes in

the result. In this way the results of germinal constitution may be somewhat obscured by the varying external conditions of growth.

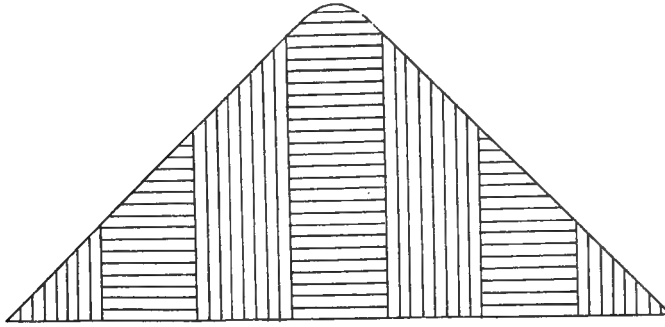


FIG. 18.—Graphic illustration of situation represented in fig. 17. In both diagrams it is evident that two plants appearing in same quantitative class must have same number of doses; this should always occur if environmental influences did not obscure the result.

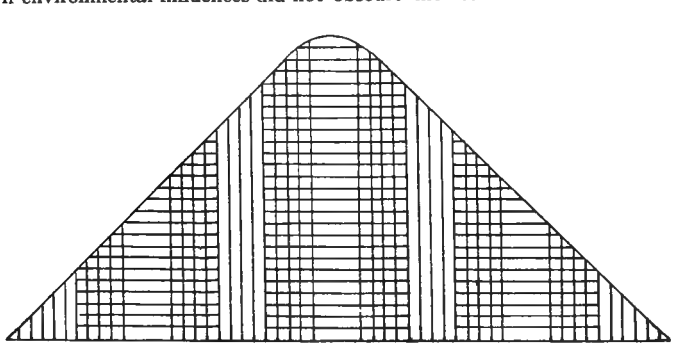


FIG. 19.—Diagram illustrating how environmental influences may obscure phenotype classes of F_2. Overlapping of phenotype classes makes possible that two apparently identical plants might actually have a different number of doses; diagram also shows that while breeder could not recognize whether a plant had two or three doses, he could distinguish between plants of two and four doses, etc.; thus intelligent selection could be effective.

Another factor that may obscure these results is what is called physical correlation. For example, a corn plant of small size but with the hereditary capacity for producing large ears could not fully express this capacity. It could not produce as large ears as if it had been a large-sized plant.

Still another factor that might obscure the result may be called gametic correlation, which is a conception presented by EAST. The idea is that factors which are inherited quite independently and which affect different plant characters might still be conceived of as having an influence upon one another. As EAST puts it, "A gamete may be a mosaic of independent factors, but the plant (produced from the gametes) will not be a mosaic of all the characters and factors produced, for these factors act and react upon one another in complex ways during their development."

Such are some of the conditions or factors that tend to obscure results in the F_2 generation and give rise to ratios hard to interpret. The weaker the influence of these factors the more clearly do the phenomena of cumulative factors come out. The total result of this phase of EAST'S work, in spite of obscuring conditions that have arisen, has been to strengthen greatly the conception of cumulative factors. A summary of his conclusions may be stated as follows:

> When one is dealing with quantitative characters, that is, those produced by cumulative factors, he is confronted by exactly the same principles of Mendelian inheritance as have long been known to apply to qualitative characters. With quantitative characters, however, the problem is more complex, due chiefly to two things: (1) we are usually dealing with more factors, and

factors cumulative in their operation; (2) the significance of the breeding results is usually somewhat obscured by the natural fluctuations due to response to uncontrollable factors in the environment.

Others have investigated the problem of cumulative factors, and many of the results are favorable to the conception; but much more investigation should be made, for the conception deals with exceedingly fundamental situations. If it is true it is extremely important; if it is not true a knowledge of this fact is just as important. It is like a fork of the roads in our biological progress; it is important to know which is the right road for future progress.

In concluding the general topic of cumulative factors a modifying statement should be made as to the mechanism involved. Heretofore it has been assumed that we were dealing with numerous, separately inherited factors, absolutely identical in their nature, cumulative in their effect. No doubt one might regard with suspicion such a seemingly artificial mechanism. Probably it would be easier to believe if it were modified in the following manner. Instead of assuming numerous factors, identical in function, we may assume that each of these factors has its own peculiar function, but that that function plays a part, directly or indirectly, in developing the quantitative character in question. For example, suppose height is the character. One of the factors determines the development of long internodes; another results in numerous nodes; another increases the amount of chlorophyll; another determines the size and vigor of the root system; another brings early germination and long growing season. Such factors, then, although

not identical, will be cumulative in increasing the height of the plant. Of course a single dose of one type of factor will not bring the same increase in height as would a single dose of one of the other types, and therefore the mathematics of the situation would be slightly modified. The fundamental mathematical system, however, would remain the same, and we would have the satisfaction of dealing with a natural mechanism rather than an artificial one.

1. EMERSON, R. A., and EAST, E. M., The inheritance of quantitative characters in maize. Bull. Agric. Exper. Sta. Nebr. no. 2. pp. 120. *figs. 21.* 1913.
2. NILSSON-EHLE, H., Einige Ergebnisse von Kreuzunger bei Hafer und Weizen. Bot. Notiser 1908: 257–294.
———, Kreuzungsuntersuchungen an Hafer und Weizen. Lunds Univ. Arsskr. N.S. II. 5:1–122. 1909.

CHAPTER VIII

NEO-MENDELISM (*Continued*)

6. TRUE-BREEDING HYBRIDS.—This situation was referred to in chapter v, but comes up again in the present context. The statement was made that a number of practical breeders had reported that by crossing distinct races they had not only obtained hybrids intermediate with regard to one or more characters, but also that these hybrids when inbred continued to breed true to their intermediate condition and that the original parent races never reappeared.

One explanation of this situation offered by geneticists was that where a great many factors are involved it is practically a mathematical impossibility for either of the parent races to reappear, for the chances would be overwhelmingly against the exact coming together of the exact combination of factors. This explanation should be considered a little more fully in the light of what has been stated concerning cumulative factors.

Suppose that CORRENS in crossing the red and white races of *Mirabilis* had been dealing, not with one factor determining redness, but with six, the red color being determined by six different factors, cumulative in their effect but separately inherited. With only two cumulative factors the F_2 situation is represented by fig. 15, where it is evident that one individual of each parent type appears in 16 of the F_2 individuals. This ratio

may be referred to as 1:4:6:4:1. When three cumulative factors are considered the F_2 ratio would become 1:6:15:20:15:6:1 (see fig. 16), that is, one of each of the original parents out of 64 individuals. In the same way the six cumulative factors assumed, which is really a conservative number, would give the following F_2 ratio: 1:12:66:220:495:792:924:792:495:220:66:12:1, that is, one of each of the original parent types out of 4096 individuals of the F_2 generation.

With these facts it is easy to explain the experience of breeders and horticulturists. In the first place, practical breeders are not as carefully discriminating as are geneticists, so that they would put their individuals of *Mirabilis* into three classes, that is, red, pink, and white, without considering the various degrees of redness or pinkness. Therefore if they were dealing with six cumulative factors and grew less than 4096 individuals of the F_2 generation, the chances are that they would obtain no individuals representing either the red parent or the white parent. Naturally they would conclude that the original cross produced an intermediate hybrid, which when inbred without exception bred true to the intermediate hybrid character. The question might be raised in reference to the later generations. Would not the original parent type reappear in some generation later than F_2? The mathematics of the situation is too complex for presentation, but the result can be visualized in a less exact way. It has been seen that the vast majority of the F_2 are intermediates of varying degrees, that is, when the F_1 intermediates were inbred the resulting F_2 was made up of practically all intermediates and no extremes. Inbreeding F_2, therefore, would continue

the same situation, so that the chances of a reappearance of the original parent types would be very slight, so slight that if they did appear they would be described as "reversions." In this way many of the cases of true-breeding hybrids can be explained. Of course we have been dealing only with intermediate hybrids which are intermediate quantitatively, due to the action of cumulative factors. The gardeners and horticulturists might claim that their hybrid is not merely different in degree from either parent but that it is different also in kind; that it exhibits an entirely new character, that is, it differs qualitatively. If this is true of course the explanation suggested does not apply. The explanation can be modified, however, leaving the mathematical possibilities the same. Suppose the original parent strains differed, not by six cumulative factors, but by six factors of different kinds. Under these conditions it would be possible to bring together in a cross an entirely new combination of factors which might result in characters that would seem entirely new. If we are dealing with complementary or supplementary factors we might get a character in a hybrid that is entirely new. If these factors were sufficiently numerous, the chances of separating them again and recombining them exactly as in the original parents would be exceedingly slight.

These possibilities have been presented for two reasons: (1) as explanations of true-breeding hybrids, whether quantitatively or qualitatively different from their parents; (2) to illustrate the method of using the conceptions of the factor hypothesis.

7. A PRACTICAL ASPECT OF THE CUMULATIVE FACTOR HYPOTHESIS.—Assume that a practical breeder crosses

two extreme parent types in the hope of obtaining a hybrid combining the desirable characters of the two parents. If the material is corn, he might use one parent with large grains but few in number, while the other parent has many grains but small ones. Such quantitative characters as these would be determined by cumulative factors, and the hybrid would be intermediate in respect to both of these characters, that is, the grains would be of medium size and medium number. No matter how many crosses he made, he would always get this result and not the desired combination of large grains and many of them.

Suppose now that these intermediate hybrids are inbred in the hope of obtaining the desired combination in the F_2 generation. It will be realized that the chances of obtaining a plant combining the two extreme characters of large grains and numerous grains would depend upon the number of factors that enter into the make-up of these quantitative characters. Assume that there are five factors in each case. The mathematics of the situation would show that in order to get the desired pure type from a cross between two parents, each having their desirable character determined by five cumulative factors, it would require 100 acres of corn to have an even chance of getting one such individual in the F_2 generation. It is altogether unlikely that any farmer would use 100 acres and a corresponding amount of labor on such an extreme chance. Even if he did, it would be very problematical whether he would be able to select the proper solitary individual on his 100 acres. Even an agricultural experiment station would not feel justified in conducting such an experiment.

The question arises whether there is any way of avoiding this impossible situation. The escape is suggested by the fact that time can take the place of numbers. EAST (2) has shown that by growing 1000 individuals in the F_2 generation, 100 in the F_3, and 50 in the F_4, one stands as much chance of getting the desired combination as by growing 250,000 in the F_2, provided an intelligent selection is made in each generation. In other words, one who understands the mechanism of the inheritance of quantitative characters will grow only 1000 individuals in his F_2 generation and will select for seed only those individuals with the right number of factors. In this way, by intelligent selection, factors are piled up in the right direction from year to year. In a few years the desired result will be reached without the necessity of growing a very large number of individuals. Such work is practicable at experiment stations, and it is the kind of work that a number of them have been doing recently. Even the ordinary farmer should be able to do such work. Although his selection of individuals should not be quite as intelligent as that of a scientific breeder, he would probably be selecting in the right direction and making some advance. A little more time and a little more acreage would bring him to the desired result.

A further application of the factor hypothesis may be considered. The practice we have been discussing under the name of the *inheritance of quantitative characters* seems to be little more than what has already been called artificial selection, which is the oldest of all methods of plant breeding. It is a method that was thought to be discredited entirely by the work of DE VRIES (1),

JOHANNSEN, and others when they discovered what they called elementary species or pure lines and demonstrated that artificial selection could never result in any large or permanent improvement. In consequence of this, artificial selection, as the most important method of securing desirable races, gave place to pedigree culture at the most important experiment stations. It was not abandoned, for it had its uses, but it seemed to many to be a mediaeval method of breeding. The artificial selection, however, which we have been describing is different from that so long practiced. In brief statement the difference is as follows.

In the first place, the selection proposed is preceded by an intelligent hybridizing, and after that genotypes rather than phenotypes are selected; that is, the selection is made on the basis of germ plasm rather than of body plasm. This would be a sufficient reason for the superiority of the new method of artificial selection as compared with the old. A little further analysis, however, will make the difference clearer.

In the old method of artificial selection the breeder, in the first place, is dealing with such germinal variations as happen to appear in his crop; and in the second place he is dealing with those fluctuations which appear as responses to the environment. When he selects a large plant to use for seed that plant may be large on account of its germinal constitution; but on the other hand it may be large because it is growing in a less crowded place or is more heavily fertilized than the others. In that case the large plant might not furnish good seed. The plant breeder of the old method undoubtedly made such unfortunate selections frequently; that is, he selected

on the basis of external appearance, and external appearance is often a very poor index of hereditary capacity. Intelligent selection is based on germinal constitution only, and therefore its results are quicker and surer.

Another phase of the subject should be considered. When a plant breeder is trying to improve his crops by selection for quantitative characters, although he uses the old method of selection, he is likely to be making some gain, as the experience of hundreds of years has shown. The germinal constitution of his crop plants is masked by fluctuations of course, but this mask is not complete. Most of the plants he selects are bound to possess high numbers of factors of the right kind, and he probably rejects most of the plants with few factors. In any event, he has generally succeeded in the long run in getting a somewhat improved race.

A summarized statement of this situation may be helpful. Our recently developed knowledge of the inheritance of quantitative characters seems to justify artificial selection, but it does not justify the old blind method of selection. It emphasizes the need of intelligent, trained selection and shows how such selection can be made. In order to do this one must understand the mechanism of the inheritance involved and must understand the make-up (race or pedigree) of the plants dealt with, being sure that they are of pure race or strain, for selection from the ordinary mixed races of crop plants is not only tedious at best but often leads to chaotic results.

The situations just considered enable one to understand two phenomena which have been baffling scientific

plant breeders for some years. The races of plants improved by artificial selection have usually reverted to type when selection ceases. This fact was recognized for a long time, but was first pointed out clearly by DE VRIES (1). Since then we have always expected this result, that no improvement will maintain itself but will run back unless the selection is continuous. When a practical breeder announces that he has developed by selection a new race which continues to breed true without further selection we are inclined to disbelieve him, for we know that only elementary species breed true. We explain that the practical breeder bases his selection on fluctuations, and therefore his new race is bound to revert to type. It is obvious now that there is a flaw in this argument. The practical breeder may be basing his selection on fluctuations, but at the same time he may be piling up cumulative factors in the right direction. Thus he might eventually secure a race containing all the cumulative factors. Such a race would be a homozygote and could not help breeding true. Most of the claims of artificially improved races that breed true may be false, but it should be remembered that such a thing is possible and may be stumbled upon accidentally, even with unscientific breeding.

There is another phenomenon which has been much discussed, and which can now be explained in the same way. This is the so-called *fixation of hybrids*. For years breeders have made promiscuous crosses and then begun artificial selection with the F_2 generation. Eventually they have secured a pure-breeding hybrid. It will be remembered that it was in this way EAST

worked with the quantitative characters in corn, and the explanation is the same.

In addition to the practical value of the conception of cumulative factors, the theoretical value is worth considering, for it explains things which have been very vaguely understood. The understanding of the fixation of hybrids just mentioned, and races produced by artificial selection, clears up our practical breeding methods, and this is valuable information; but the conception also shows that the origin of species by natural selection as announced by DARWIN is possible, a method which for some time has been thought to be impossible.

Of course natural selection in a certain sense has always been accepted, almost as generally as the fact of evolution. The point in dispute is as follows: DARWIN used as the basis of natural selection those small individual variations which we have come to call fluctuations, the same kind of variations the old plant breeder used in his artificial selection. DARWIN claimed that such variations could be piled up until the result would be a new species. It was in 1900 that DE VRIES (1) showed in a convincing way that this kind of variation never resulted in a new species; at best it could only develop a race which approached the boundary of the species and never crossed it. Moreover, such a race would revert to type rapidly as soon as some slight change in conditions set up a new standard for selection. This argument, confirmed by experiment, has been generally accepted.

We now know that individual variations are not always mere fluctuations or responses, but may be due to varying doses of cumulative factors. A selection on

this basis may well result in a new race that breeds true; and a race that breeds true is DE VRIES' definition of a new species. To reestablish DARWIN'S theory of natural selection is certainly an important consideration, and the situation illustrates how genetics and evolution are tied up together, so that neither one of them can be appreciated fully without some knowledge of the other.

A few words may be said in reference to the reversion of an old race to its original specific type. DE VRIES outlined the situation clearly, and his conclusions are generally accepted. It is doubtful, however, whether it has ever been understood, since no one has ever devised a reasonable mechanism for such a reversion. The conception of cumulative factors, however, supplies this mechanism. A new race, developed by natural or artificial selection among individual differences, means the piling up of cumulative factors in a given direction. Stop the selection and the old plants with the small number of factors are allowed to survive; reproduce, cross with the new race, and eventually bring back the old species to the original average condition.

1. DE VRIES, H., Species and varieties, their origin by mutation. Chicago. 1905.
2. EMERSON, R. A., and EAST, E. M., The inheritance of quantitative characters in maize. Bull. Agric. Exper. Sta. Nebr. no. 2. pp. 120. *figs. 21.* 1913.

CHAPTER IX

NEO-MENDELISM (*Concluded*)

Thus far we have based our considerations on the rather simple theoretical mechanism of inheritance which was explained in connection with Mendel's law. We shall now consider some well established facts of inheritance which will oblige us to enlarge somewhat our theoretical mechanism.

8. COUPLED AND ANTAGONISTIC CHARACTERS.—The classic illustration of coupled characters was brought to light by EMERSON (1) during breeding experiments with corn. His material included a strain with red grains and red cob. This strain, when crossed with another having white grains and white cob, gave an F_1 generation with red grains and red cob. This indicated that red was dominant over white in both grain and cob; and since the F_2 generation gave the orthodox 3:1 ratio (3 reds and 1 white) the obvious conclusion was that redness in both grain and cob is due to a single determiner.

Other breeding experiments, however, gave a different aspect to the situation. It was found that there are races of corn with red grains and white cobs, and others with white grains and red cobs. It is evident, therefore, that redness in grain and cob is due to two separate determiners.

Let us consider a possible theoretical explanation of these two apparently contradictory situations. The red

grain and red cob of the first mentioned experiment were not produced by a single determiner, but by two determiners coupled together in inheritance. It is as if the two chromosomes concerned had a bond between them which kept them together during the reduction division, and made them pass side by side into the same gamete. A diagram will illustrate this situation (fig. 20). The only unusual thing in this diagram is the bond which holds together the chromosome carrying

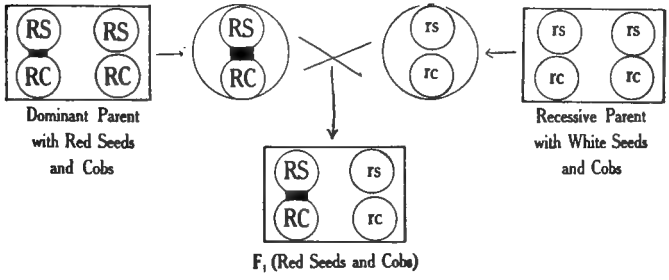


FIG. 20.—Diagram representing, in a somewhat obvious way, how the behavior of "coupled characters" might be visualized.

the determiner for red seeds and the chromosome carrying the determiner for red cob. A peculiar function of the bond, however, appears in the reduction division in connection with gamete formation by the F_1 generation.

In the case of a dihybrid in which two characters are involved the situation developed by the reduction division will be recalled (fig. 21). It will be noted that there are four chances of pairing off by the four scattered chromosomes. The chances of getting a gamete with the two determiners is no greater than

getting one with only one of the determiners. There would be just 25 per cent of each of the type represented in the diagram, the resulting ratio in the F_2 being 9:3:3:1.

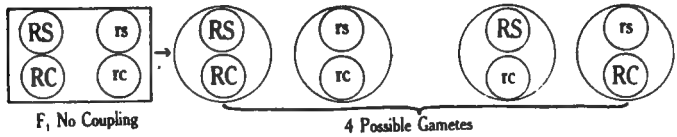


FIG. 21.—Diagram showing how normal dihybrid segregation, in absence of coupling, produces four different gametes.

In the case we are considering, however, the mechanism is different. At the reduction division of the F_1 generation two chromosomes with the dominant determiners are linked together by a bond. In consequence of this there are only two types of gamete

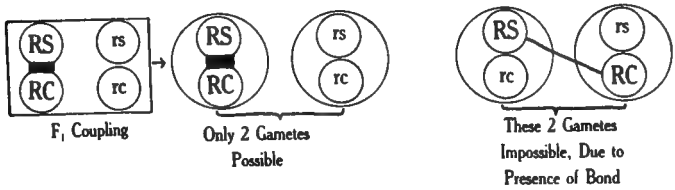


FIG. 22.—Diagram showing how coupling would limit possible kinds of gametes.

possible, as indicated in the diagram (fig. 22). In the terminology of cytology the two chromosomes with the determiners are held so firmly together that they pass to the same pole of the spindle. This is the phenomenon of coupled inheritance and a theoretical mechanism that was devised to explain it.

EMERSON then crossed strains having red grains and white cob with strains having white grains and red cob. The F_1 generation showed all red grains and cobs, as would be expected; but in the F_2 generation three different types of individuals appeared as follows: 1 with red grains and white cob; 2 with red grains and red cob; 1 with white grains and red cob. This result in the F_2 generation differs from any that has been cited, and EMERSON explains it as follows. In this case the two determiners are not coupled; in fact they are antagonistic, so that no true-breeding types are produced having red grains and red cobs. It is as if the two chromosomes carrying the determiners are mutually repulsive, so that they always pass to different poles of the spindle at the reduction division. EMERSON interprets the results of these experiments, therefore, as due to the existence of two coupled chromosomes in the first case and two antagonistic chromosomes in the second case.

But is there not another way of looking at this situation? Granted that there is such a phenomenon as the coupling of chromosomes, the question arises why the second situation may not also be explained by coupling, the difference being that in this case the coupling is between different chromosomes. According to this suggestion the two situations would be represented by the diagram given in fig. 23. Such a scheme explains both cases by using the same kind of force, that is, coupling, and does not call for attraction to explain one situation and repulsion to explain the other.

This last conception, however, raises the question, why should a chromosome which in some strains of corn

is coupled with a similar one, in other strains become coupled with its opposite (its allelomorph)? This is a theoretical difficulty which will be cleared up when we consider the next topic. It will be realized that genetics as yet represents an accumulating mass of data in

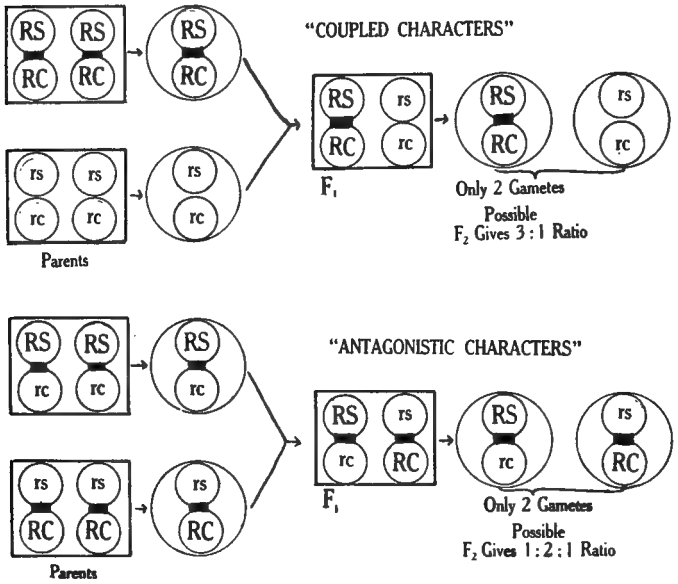


FIG. 23.—Diagram showing how coupled and antagonistic characters might be explained by the same mechanism.

reference to the facts of inheritance, and also an accumulating mass of speculations as to the explanations of the facts. The facts are undoubted, while the speculations suggest further experimental work.

9. LINKAGE AND CROSSING OVER.—EMERSON concluded his original work on coupled and antagonistic

characters with the following statement: "This is an example of a feature which is probably very widespread in the plant world, but of which at present we know little." Long before any further important work was done along this line in the plant world, however, MORGAN (2) published the results of his very careful and intensive breeding experiments with the fruit fly. His ideas have had a very profound influence upon subsequent work in genetics. He has given us a more accurate picture of the hereditary mechanism and one that fits the facts better than any previously proposed. In simplest terms the picture is this. Each chromosome is a rodlike structure and numerous determiners are arranged in a line along this rod.

We cannot discuss here the many ways in which this fundamental conception has cast light upon work in genetics. Suffice it to say that it has resulted in a new "school" of geneticists whose experiments have been more intensive, more exact, and perhaps more "fundamental" than those of any other school. The work so far has been done mainly with the fruit fly and is of a rather complicated nature. We will present here some of the simplest underlying ideas merely to show the nature of MORGAN'S hereditary mechanism. It will be seen how such a mechanism may explain such phenomena as the coupled and antagonistic characters in corn. This general situation, however, will now be referred to by the term *linkage*, which is in more common use.

When first considering Mendel's law the statement was made that more than one determiner might be located on a given chromosome. As yet we have

considered no such case, but linkage involves this situation. In connection with some of MENDEL'S original crosses fig. 24 will be recalled. In this case a double dominant mates with a double recessive, and the result is a dihybrid ratio in the F_2 generation. Suppose, however, that determiner *T* and determiner *S* are on the same chromosome, the situation would be as represented

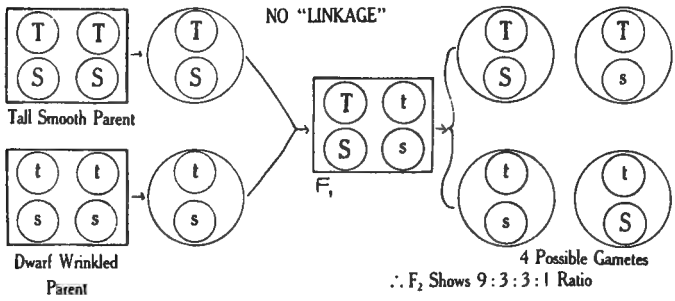


FIG. 24.—Diagram showing normal dihybrid behavior when no linkage is involved.

in fig. 25. This is linkage; that is, with two determiners a monohybrid ratio instead of a dihybrid ratio is obtained. MORGAN'S definition is as follows: "When factors lie in different chromosomes they give the Mendelian expectations; but when factors lie in the same chromosome they may be said to be linked, and they give departures from the Mendelian ratios." It will be noted that this conception rests upon the belief that the chromosome is the indivisible unit in inheritance, a conception that seems to have been justified by most of the breeding results and which conforms to Mendelian inheritance.

On the other hand, facts have begun to appear which seem contrary to this view. When the idea of linkage began to be developed the breeding expectations were modified in accordance with it. For example, when it is discovered that tall individuals always have smooth seeds this fact is explained as linkage. The inference is that there never can appear a tall plant with wrinkled

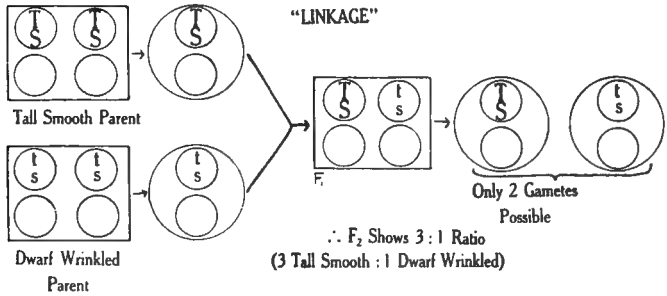


FIG. 25.—Diagram showing how linkage would limit the possible kinds of gametes. This mechanism will explain simply and accurately the "coupling" and "antagonism" of the previous diagrams; this mental picture of chromosomes, suggested by EMERSON and developed fully by MORGAN, is now generally accepted by geneticists.

seeds or a dwarf plant with smooth seeds, for if there is linkage and the chromosome is the indivisible unit of inheritance it would be impossible for tallness and smoothness to become separated.

This was the situation a few years ago, when suddenly there appeared what corresponds to tall individuals with wrinkled seeds and dwarf individuals with smooth seeds. These unusual types appear rather rarely as a general rule, although in a few special cases they have appeared as frequently as 20 in 100. The work was done with *Drosophila* (the fruit fly) under such conditions

of control that there could have been no experimental error. This new fact demanded explanation, for with such chromosomes as *TS* and *ts* it would be impossible to obtain a tall wrinkled individual as long as the individuality of the chromosome is maintained. When chromosomes were examined with the modern lenses they were found to show all kinds of tangled contortions during reduction division, and accordingly the scheme shown in fig. 26 was devised. These five stages represent phases that allelomorph chromosomes may go through during reduction division. Two allelomorph chromosomes, which normally would be side by side (1) may at times come to lie across one another (2). In this position the middle regions of the chromosomes are in contact and are conceived of as fusing (3). The spindle fibers from each pole then lay hold of this compound chromosome and the pull comes in the direction of the arrows shown in the figure. This results in the break indicated in 4. Finally, two new chromosomes separate from the old compound chromosome, as indicated in 5. Thus *T* is linked with *s*, and later, when two such chromosomes are brought together in crossing, the result is a tall wrinkled individual. In the same way dwarf smooth individuals may appear.

This is known as *crossing over*, and the literature in reference to it is extensive. It is on the basis of this conception that certain geneticists claim to be able not only to locate given determiners on their proper chromosomes, but also to tell exactly on what parts of the chromosomes these determiners are located.

This mechanism readily explains the phenomenon of coupled and antagonistic characters without involving

such clumsy bonds and repulsions between the chromosomes as were presented in the previous scheme.

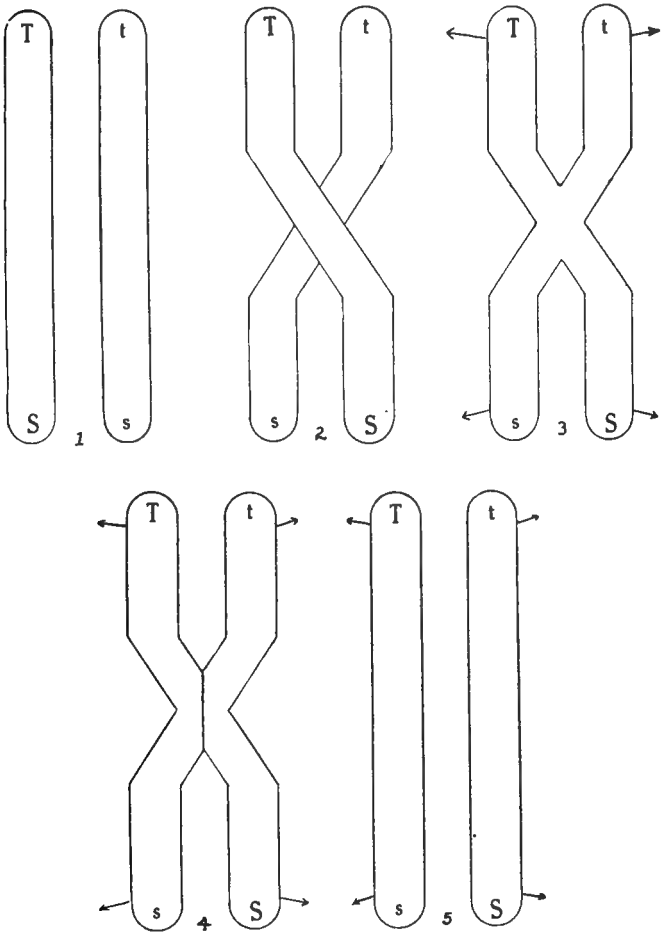


FIG. 26.—Illustrating how crossing over may occur

As stated before, most of the work on linkage and crossing over has been done with the fruit fly. The same technique, however, is now being applied among plants. In a recent article WHITE (3) discusses four linkage groups in *Pisum*, and considerable data on linkage and crossing over in corn are now being assembled at Cornell under the able direction of EMERSON.

Perhaps a warning is needed as to the term *correlation* in this connection. Coupling and linkage are phenomena of inheritance, involving the reduction division, the gametes, and the zygote. Correlation is a physiological phenomenon that appears in the developing plant. A tall corn plant may produce large ears merely because the plant is tall and regardless of the determiners for ear size. This is correlation, and it appeared, not in the gametes and zygote, but in the physiology of the individual after it started to develop. A correlation, therefore, may sometimes deceive as to inheritance.

1. EMERSON, R. A., see Heredity and eugenics (COULTER, CASTLE, DAVENPORT, EAST, and TOWER). Chicago. 1912 (pp. 101–104).
2. MORGAN, T. H., Heredity and sex. New York. 1914.
3. WHITE, ORLAND E., Inheritance studies in *Pisum*. IV. Interrelation of the genetic factors in *Pisum*. Jour. Agric. Research 11:167–190. 1917.

CHAPTER X

NON-MENDELIAN INHERITANCE

Up to this point Mendelism and its various modifications have been considered, and the impression to be gained thus far is as follows. Mendel's law as originally stated is clear, reasonable, and well established. There have appeared certain types of inheritance which have seemed at first sight to contradict Mendel's law; but practically all of these later have been shown to be consistent with that law. The conclusion, therefore, may be that Mendel's law is firmly established but that its expression is not always so simple as was once supposed. Illustrations have been given showing how Mendelian explanations must be based frequently upon numerous factors of various types. The impression, therefore, may be that Mendelism is so established and its application so universal that it explains every type of inheritance that is known or that ever will be known. It is true that Mendel's law is dominant with most geneticists as explaining most of the known facts of inheritance, although there are certain types of inheritance that have not been explained as yet quite satisfactorily in this way. As a consequence, a number of prominent geneticists protest against the universality of the law. These unexplained phenomena must now be considered under what may be called non-Mendelian inheritance. It will be recalled that EMERSON and EAST stated that only two indisputable cases of non-

Mendelizing characters are known, and these cases may be used as illustrations of non-Mendelian inheritance.

In connection with his work on *Mirabilis* CORRENS (2) uncovered the following situation. The ordinary race of *Mirabilis* has pure green leaves, but one was discovered with variegated leaves. The leaves were green for the most part but showed irregular white patches, an examination showing that in the white areas the chloroplasts were more or less bleached out. CORRENS named this race the *albomaculata* type, a name which appears frequently in the literature of genetics.

The behavior in this type of inheritance was as follows. When self-fertilized it bred true, but the *pollen* from albomaculata, when used in crosses, behaved as if it had come from normal green plants. For example, CORRENS took pollen from an albomaculata plant and used it to pollinate a normal green plant. The individuals of the F_1 generation were all normal green, and the natural Mendelian conclusion would be that albomaculata is a recessive condition appearing when the determiner for normal green leaves is lacking. But when the F_1 generation was inbred the progeny continued to be normal green generation after generation. If albomaculata pollen had introduced a recessive character into the hybrid, this would have reappeared in the later generations, but it did not reappear. The obvious conclusion was that albomaculata pollen is just like the pollen of the normal green plants and that all pollen carried the determiner for the development of normal green plants.

This raised the question as to the result from using pollen of normal green plants to pollinate albomaculata.

It is obvious that the F_1 generation should all be normal green and albomaculata would appear only in later generations. CORRENS made this cross, using normal green pollen and albomaculata ovules, and secured results that seemed startling. All of the individuals of the F_1 generation were albomaculata and all the later hybrid generations were albomaculata. To CORRENS there seemed to be only one conclusion possible, and that was that the pollen did not affect anything one way or the other, and that inheritance was all on the maternal side. When a possible mechanism to explain such a phenomenon is considered it is obvious that the situation cannot be explained on the basis of Mendel's law. The explanation suggested by CORRENS is ingenious and seems fairly reasonable.

He suggests that the albomaculata character is due to a disease of the cytoplasm which does not affect the nucleus. The nuclei in these albomaculata plants are supposed to carry factors for chlorophyll formation, just like those of the normal green plants, but the cytoplasm about the nucleus is diseased. Thus the disease is passed on at cell division simply because the cytoplasm is divided and passed on. In fertilization, however, no cytoplasm enters the egg with the male gamete, but only a nucleus; therefore it would be impossible for the disease to be transmitted by the pollen, and an albomaculata pollen would have no effect in inheritance. The only chance to transmit the disease would be through an egg with diseased cytoplasm. In inheritance, therefore, the albomaculata character is handed down only by the female parent, and this is *maternal inheritance.*

This would explain the peculiar breeding results obtained by CORRENS. If this explanation is true Mendel's law is not contradicted, for such a phenomenon is entirely outside the field of that law. In fact, this should perhaps not be regarded as inheritance at all but as a case of reinfection. The albomaculata condition is not a true plant character; it is a pathological state, not inherited as such, but the bacteria in the cytoplasm of the egg reinfect the next generation.

The conclusion therefore is that Mendel's law is not contradicted by this phenomenon, but it introduces entirely new possibilities of inheritance quite outside the scope of Mendel's law. This conclusion is reached if one accepts CORRENS' explanation, but this might well be doubted. To state that albomaculata cytoplasm is always infected and that the nuclei are always immune is a bold assumption. If we assume, with some cytologists, that the nucleus consists entirely of chromatin and that chromatin is immune to this disease this would furnish the proper mechanism, but this is questionable. Again, when it is claimed that no bacteria could enter the egg with the male nucleus another rash assumption is made. After all, the case of albomaculata may still be regarded as a genuine case of non-Mendelian inheritance of the type known as maternal inheritance.

The other example of non-Mendelian inheritance to which EMERSON and EAST referred is much more serious, introducing *somatic segregation*, which is a very far-reaching topic. When EMERSON and EAST made their statement somatic segregation had been rarely observed, there being really only one authentic case on record, that is, the case of the common geranium (*Pelargonium*

zonale) described by BAUER (1). Since that time, however, many more cases have been discovered, and the fact of somatic segregation has become fairly well established.

An illustration of the situation may be given as follows. If a white-leaved plant and a normal green-leaved plant are crossed the resulting hybrid illustrates what has been mentioned as "particulate inheritance," that is, the hybrid is variegated, showing irregular patches of white and green. If one of these white patches completely includes a bud there will probably be produced by that bud a completely white branch. The flowers of this branch, when self-fertilized, give rise through their seeds to white individuals only and would evidently continue to breed true to the white condition if white individuals could be matured. In like manner the variegated hybrid may give rise to a pure green branch, which would start a line of pure green individuals.

This is an illustration of what is called "somatic segregation." Ordinarily, of course, factors are segregated only at the reduction division, and only in that division does the proper cytological mechanism for segregation exist. Somatic segregation, however, means that segregation takes place in the somatic tissue, quite apart from the usual reduction division. Cytologists assure us that cell divisions in the somatic tissue are not reduction divisions, in this tissue chromosomes being regularly reproduced in equal numbers. Each chromosome divides to form two chromosomes, and these two are similar to the mother and to one another; therefore they carry exactly the same quota of determiners, that is,

there is no segregation of determiners. This situation is not merely shown by cytology, but is also in accord with most of our breeding results.

In the case of somatic segregation, therefore, there seems to be only one possible conclusion, and that is that sometimes reduction division occurs in the somatic tissue, at least so far as certain chromosomes are concerned. Such a conclusion is not unreasonable. Crosses of certain factors might cause a very unstable condition in certain chromosomes, so that they might not conform to the ordinary mechanism of cell division. Certain chromosomes, or certain determiners on the chromosomes, instead of dividing normally might pass undivided to one pole of the spindle at cell division and be entirely lacking at the other pole.

The only other alternative would be to discard the old ideas of the mechanism of cell division and inheritance, and this we are hardly ready to do. In any event the phenomenon of somatic segregation opens an important field for some critical cytological research.

It will be realized that somatic segregation is a much more fundamental situation to explain than maternal inheritance. There is no reason to suppose, however, that it contradicts Mendelian inheritance seriously; perhaps it enlarges the scope of Mendelism. Mendel's law is violated only in the fact that segregation occurs at an unusual place; and that is no reason for discarding Mendelism. It complicates the situation somewhat because the ordinary reduction division furnishes such a complete mechanism for segregation; but MENDEL formulated his law before the reduction division was discovered in plants. Somatic segrega-

tion may lead to the discovery of an occasional unusual kind of reduction division in the somatic tissue.

1. BAUER, ERWIN, Das Wesen und die Erblichkeitsverhältnisse der "Varietates almomarginatae hort." Von *Pelargonium zonale.* Zeitschr. Ind. Abstamm. Vererb. **1**:330. 1909.
2. CORRENS, CARL E., Über Bastardierungsversuche mit *Mirabilis*-Sippen. Ber. Deutsch. Bot. Gesell. **20**:594. 1902; *ibid.*, Vererbungsversuche mit blass (gelb) grünen und bluntblatterigen Sippen bei *Mirabilis jalapa*, *Urtica pilulifera*, u. *Lunaria annua*, Zeitschr. Ind. Abstamm. Vererb. **1**:291. 1909.

CHAPTER XI

MODIFICATION OF UNIT CHARACTERS

The severest blow at Mendelism is the modification of unit characters. The three theses involved in Mendel's law are unit characters, dominance, and segregation. It has been seen how dominance may fail without affecting the essential feature of Mendel's law. We have just considered how segregation might occur elsewhere than at the reduction division and yet not interfere seriously with Mendel's law. Unit characters, however, cannot be treated in this way, for they are the very foundation of Mendel's law. In the very nature of things they remain as units, separate in inheritance; if they are observed splitting up or varying in any way they would no longer be units, and the foundation of Mendelism would be weakened.

Before taking up the real cases of modification of unit characters, another unusual phenomenon concerning unit characters may be considered first, a phenomenon which is quite in accord with Mendelism as explained today. It is introduced here because at first thought it might seem to strike at the essential nature of unit characters; in fact, it has been so used.

CASTLE (1), working with fancy mice, found that on rare occasions a unit character might disappear completely in cross-breeding. It might be claimed that this result is due to the introduction of an inhibiting factor, or to the separation of complementary factors. CASTLE

realized these possibilities and tested them. Of course if it was a case of complementary factors which had become separated he would have been able to recombine them in later generations by the proper crosses. Recognizing the significant crosses and making them he obtained no result; the character did not reappear. In the same way breeding tests for an inhibiting factor which could be separated out in later generations yielded no results. The unit character was gone beyond recovery; it had simply dropped out and was lost.

Such an occurrence may seem surprising at first, but it is what should be expected as an occasional occurrence. Mendel's law was republished along with DE VRIES' mutation theory, and as a consequence scientific breeders, interested in Mendel's law, were also on the watch for mutations. DE VRIES had shown that mutations might involve either the appearance of an entirely new character or the dropping out of an old character. It is this situation, therefore, that appeared in CASTLE'S experiments with mice, namely, the abrupt disappearance of a unit character is simply the result of mutation, and this involves no violation of Mendel's law.

The real attack upon Mendelism involves a different kind of behavior on the part of unit characters. The notable example of this unexpected behavior of unit characters was discovered in connection with CASTLE'S work on hooded rats (2).

He isolated from his rat populations a certain strain which showed a particular black and white coat pattern. This type was then inbred for a number of generations to insure that it bred true. This fact having been established it was next determined that this black and

white coat pattern behaved as a simple unit character in inheritance. Then, starting with a single pair of rats of this new pure strain, the following breeding experiments were performed. For twelve generations selections were made from this new strain without a single outcross, that is, every generation was inbred, thus insuring the constant purity of the stock. In one series selection was made for an increase in the extent of the pigmented areas; in the other series selection was made for a decrease in the extent of these areas. The result was that the areas in the one series steadily increased while in the other they steadily decreased. Thus far nothing very unusual is involved. CASTLE points out, however, the following important facts which were developed: (1) with each selection the amount of regression ("running back") grew less; that is, the effects of selection became more permanent; in other words, in each succeeding generation there was a decreasing tendency to revert to the original average type; (2) advance in the upper limit of variation was attended by a like advance of the lower limit. The total range of variation, therefore, was not materially changed, but there was a progressive change in the point about which the variation occurred. In other words, it is like a progressive shifting of the center of a circle; the diameter of the circle does not change but the position of the circle, determined of course by its center, is gradually changing. These were the two important facts which CASTLE brought out and they have been stated approximately in CASTLE'S words.

Fig. 27 will help to make the situation plain. The average amount of variation in any one generation of

the pure stock (the diameter of the circle referred to) is indicated by $\overset{A}{\longleftrightarrow}$. Of course, even "pure stock" varies somewhat, since no two individuals are

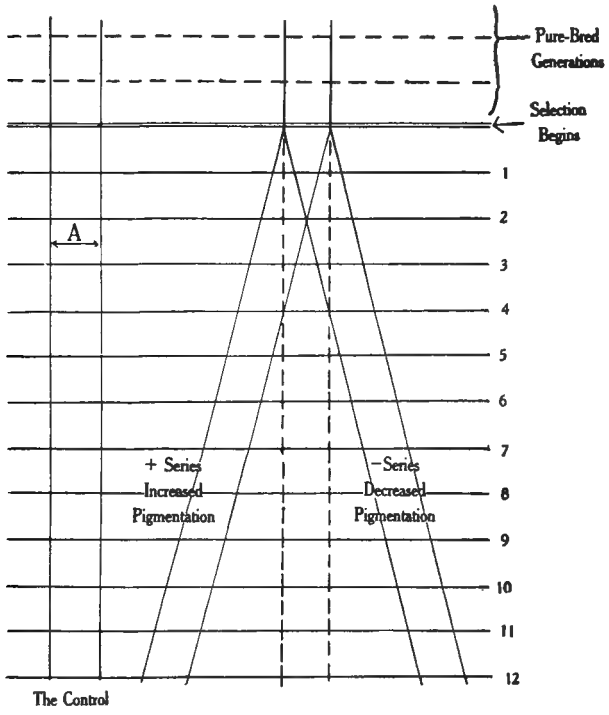


FIG. 27.—Diagram illustrating CASTLE'S selection experiment with hooded rats.

exactly alike, biology recognizing what is called "individuality." The point, however, is that the comparatively small variation in a pure stock is not due to germinal differences but to responses called out by varying external conditions, such as nutrition, light, etc.

These response variations, usually called fluctuations, vary with different individuals, but the hereditary capacity of all of them remains the same. A selection on the basis of fluctuations within a pure line, therefore, should not result in any permanent improvement; in fact, it has been demonstrated many times that no such improvement can be effected in this way. When selection is made, however, among varying doses of cumulative factors, an entirely different situation is faced, for in such a case we are not dealing with a pure line.

The significance, therefore, of CASTLE'S results may be realized. He bred his original pure line for many generations and found that it varied only within very narrow limits; and these slight variations therefore he regarded as mere fluctuations. Furthermore, he found that the character of his pure line developed in crossing as a simple unit character and that no complex factors were involved. With this evidence he should not have been able to effect any permanent changes by selection; but this is exactly what he did. Selecting in opposite directions he developed two new strains, the boundaries of the new strains being distinct from one another and distinct from the boundaries of the original strain, that is, the non-selected pure type.

CASTLE'S next step was significant. He crossed each of his new strains with the same wild race, the result being that each of his new strains behaved as a simple recessive unit, giving a 3:1 ratio among the grandchildren.

The logical conclusion from this series of experiments may be given in CASTLE'S words, as follows: "The conclusion seems to me unavoidable that in this case

selection has modified steadily and permanently a character unmistakably behaving as a simple Mendelian unit." The importance of this conclusion is evident. Mendelism has been based upon the conception that unit characters cannot be modified. Mendelians have granted only two possible methods for the origin of new races: (1) by recombinations of existing characters by hybridizing; (2) by the sudden and complete dropping out of an existing unit or the equally sudden addition of a new unit, both of which possibilities may arise from mutation. No Mendelians will grant, however, the possibility of modifying an existing unit character, the thing which CASTLE claims to have done, and bases his claim upon well controlled experimental breeding. If CASTLE'S contention is true it must result in the fundamental modification of Mendel's law. The whole mechanism will have to be modified or new fields of variation not known to exist will have to be taken into account.

The statements of the Mendelians in reference to this situation should be considered. Their explanation is based in effect upon the situation we have already developed in connection with cumulative factors. The claim is made that CASTLE started with a peculiar character which fluctuates continually and has never been brought to as small a variability as have most other characters. The question is raised whether CASTLE'S assumption that this variability is merely due to fluctuation is altogether justified. May not the variability be due to varying doses of cumulative factors? Suppose for the moment that this were the case; it would not be surprising that CASTLE could

develop two diverse strains by selection, for selection would result in piling up the cumulative factors in one direction or another. CASTLE'S rejoinder would be that if this is a cumulative factor situation why do none of the extremes appear in the non-selected stock, which instead breeds approximately true within very narrow limits of variability? The answer is made that the extremes do not appear in the pure-bred stock merely because of mathematical possibility. If we are dealing with six cumulative factors, and the so-called pure stock has an intermediate number of doses, there could not be much chance of getting out the extremes in later generations. It will be remembered that it would be necessary to secure over 4000 progeny to have an even chance of getting one such extreme; or at least 50 progeny to get anything that would visibly approach the extreme. It would seem, therefore, that CASTLE'S chances to determine this would be very small. Rats certainly do not produce 4000 progeny in a single generation; in fact, they produce much less than 50; therefore CASTLE'S pure stock goes on in the intermediate condition, and only by selection can he pile up the factors and reach either extreme.

Thus far the explanation seems satisfactory. CASTLE showed, however, that the coat pattern condition behaved in crosses as a simple Mendelian unit; that is, it did not split up into complex ratios, but came out as a recessive in a regularly 3:1 ratio. This really involves no difficulty. Suppose CASTLE crosses one of his pure strain rats having the pattern character with another strain having an inhibitory factor for the pattern or some other character that conceals the pattern. Since the

inhibiting factor is simple, the resulting ratio may be a monohybrid ratio; that is, in the F_2 generation from such a cross the ratio of pattern to non-pattern will be 1:3, and this is exactly what CASTLE got and what would be expected. At the same time the amount of pigmentation, determined by numerous cumulative factors, goes on in the same intermediate condition, unaffected by the cross. The relation of pattern to non-pattern is merely a simple monohybrid system temporarily superimposed upon the other more complex system without permanently affecting it, any more than any inhibitory factor permanently affects the factors it inhibits, or a dominant permanently affects a recessive.

It is in this way that Mendelians can explain away CASTLE'S results. CASTLE does not admit the justice of the explanation, but continues to maintain that he has modified a unit character by selection, and some geneticists agree with him. Whether CASTLE is dealing with cumulative factors or not can never be settled by exact demonstration, since the progeny of rats is too small. It is rather significant, however, that in plants, where larger progenies are involved, the cumulative factor hypothesis is well established, and no one claims to have modified a Mendelian unit in plants. The best that can be said concerning CASTLE'S claim is that it cannot be proved false, but that it is possible to explain his results by the cumulative factor hypothesis.

The question might be raised, however, why cling so strongly to the cumulative factor hypothesis and force CASTLE'S results into this conception? Is there anything sacred about a unit character that it should not be modified just as complex chemical molecules may

be modified in certain reactions? Why not admit that Mendelian factors may be modified, and explain CASTLE'S results in this way? The reason is that when we begin to admit that unit characters and single Mendelian factors may be modified, the whole conception of inheritance becomes chaos. The great advantage of the factor hypothesis is that it furnishes the clearest method of describing breeding results. A statement by EAST (3) on this point is pertinent.

> Taking into consideration all the facts, no one can well deny that they are well described by terminology which requires hypothetical segregating units, as represented by the term "factors." What then is the object of having the units vary at will? There is then no value to the unit, the unit itself being only an assumption. It is the expressed character that is seen to vary; and if one can describe these facts by the use of hypothetical units, theoretically fixed, but influenced by the environment and by other units, simplicity of description is gained. If, however, one creates a hypothetical unit by which to describe phenomena, and this unit varies, he really has no basis for description.

In other words, this statement means that the great value of the factor hypothesis is to supply a terminology for describing the facts of inheritance rather than a means of explaining these facts. According to this, therefore, it may be seen that although CASTLE claims to have modified a unit character by selection, his results can come under the factor hypothesis, and thus our descriptions may be kept clear and uniform.

There is another piece of work, however, that certainly cannot be explained (that is, described) in terms of the factor hypothesis; on the contrary, it almost forces one to admit that unit characters, even though hypothetical, may vary. This is the work of JENNINGS (4)

on Protozoa. JENNINGS, for example, takes a single rhizopod (*Difflugia*) and uses it as the basis of a new strain. Every member of this new strain has come from this original individual by cell division. In this case sex is not involved, and the possibility of new combinations of factors is eliminated. It is obvious that such a strain should breed perfectly true, but JENNINGS shows that it does not. Changes of two kinds occur, namely, mutations, which of course are a part of the Mendelian program, but according to JENNINGS "the overwhelming majority of hereditary variations are minute gradations. Variation is as continuous as can be detected." He gradually piles up these minute variations by selection and finally develops a new species. There can be no claim of piling up cumulative factors here, for no sex is involved nor can these gradual changes be mutations. Mutations of course can be minute, but they are not continuous and in the same direction; mutations are jumps, even if the jumps are small, and they occur in every direction.

The only other possibility is as follows. It will be remembered that WEISSMAN claimed that environment may directly affect the germ plasm in the simplest microorganisms, just such organisms as JENNINGS deals with; but JENNINGS claims that the characters of his rhizopods are not modified by environment. How he is assured of this is a question, for the factors of environment are very numerous and complex and organisms are probably very sensitive. So far as circumstances permit, the conditions of environment were kept constant, but whether they really were constant or not is another matter. Leaving out of consideration this question of

environment, it must be admitted that JENNINGS' work proves that unit characters may be modified by selection.

The evidence just given as to the modification of unit characters seems rather conflicting. It will be realized, however, that there are at present two leading schools of geneticists, one believing that unit characters may be modified by selection, and the other believing that unit characters are invariable. This latter school we have been referring to as Mendelians, but this is hardly an accurate designation, since both schools are really Mendelians. They are usually distinguished as follows: "mutationists," who believe in the introduction of new hereditary units by mutation alone and believe that unit characters cannot be modified by selection; and "selectionists," who believe that unit characters may be modified by selection. In the previous discussions the views of the mutationists have been emphasized for two reasons: (1) mutationists are in the majority at present; (2) their hypothesis gives a comprehensive and systematic basis for describing the facts of inheritance. JENNINGS has recently tried to reconcile the two schools by showing that their claims amount to the same thing. Such a reconciliation is hopeful but it may prove to be impossible.

1. CASTLE, W. E., Heredity in relation to evolution and animal breeding. New York. 1911.
2. ———, The inconstancy of unit characters. Amer. Nat. 46:352–362. 1912.
3. EAST, E. M., The Mendelian notation as descriptive of physiological facts. Amer. Nat. 46:633–655. 1912.
4. JENNINGS, H. S., Observed changes in hereditary characters in relation to evolution. Jour. Wash. Acad. Sci. 7:281–301. 1917.

CHAPTER XII

PARTHENOGENESIS AND VEGETATIVE APOGAMY

Parthenogenesis and vegetative apogamy are very important to keep in mind in connection with work in genetics. Geneticists have paid too little attention to these phenomena, and as a consequence their data are not always reliable. The distinction between the two terms is as follows. Parthenogenesis is the development of an embryo by an unfertilized egg, while vegetative apogamy is the development of an embryo by another cell of the female gametophyte. The term "apogamy" includes both, meaning the production of a sporophyte by a gametophyte without involving an act of fertilization. Parthenogenesis is not peculiar to any region of the plant kingdom, and a few illustrations will be sufficient.

In water molds (*Saprolegnia*) parthenogenesis is very common. All stages in the abortion of the male organ (antheridium) are found and still eggs apparently germinate as freely as if fertilized. In fact, in many species of *Saprolegnia* it is a question whether fertilization ever occurs.

Ferns are notably apogamous, any cell of the gametophyte (including unfertilized eggs) producing an embryo under certain conditions. This miscellaneous production of embryos by the gametophyte is an impressive illustration of the fact that any vigorous protoplast, under appropriate conditions, can produce

a new individual. This behavior of ferns is particularly interesting on account of the chromosome situation involved. Since the gametophyte is an x structure and the sporophyte a $2x$ structure, when apogamy was first discovered it was taken for granted that in some way nuclear fusion had occurred and the $2x$ number obtained. More recent work, however, notably that of YAMANOUCHI (2), showed that the apogamous sporophyte is an x structure, and such a sporophyte produces spores without the reduction division.

Ferns are also aposporous, which means the formation of gametophytes by vegetative cells of the sporophyte, the gametophyte in such a case being a $2x$ structure. With the phenomena of apogamy and apospory established, the question naturally rises as to their bearing upon the machinery of Mendelism, involving the reduction division and the segregation of hereditary factors.

Seed plants, however, are of particular interest, since they have furnished the chief material for work in genetics. Many cases of parthenogenesis and vegetative apogamy in seed plants have come to light. It is an interesting fact that, although these cases are well distributed throughout the groups of seed plants, they seem to be especially numerous among the Compositae. In many cases, therefore, the embryos of seed plants are produced by unfertilized eggs or other cells, as in *Antennaria*, *Hieracium*, *Taraxacum*, *Thalictrum*, etc. Some of the best known cases were subjected to cytological investigation, and it was found that in most cases the parthenogenetic egg is diploid ($2x$), thus containing the sporophyte rather than the gametophyte number of

chromosomes. It is evident that for some reason the reduction division had failed in connection with spore formation, so that the spores were diploid, resulting naturally in a diploid gametophyte. In these cases it was found that no reduction division occurred during the life-history, the diploid number continuing through both sporophyte and gametophyte. The interesting observation was made also that parthenogenetic eggs are slower in starting to germinate than those normally fertilized.

Polyembryony is also common among seed plants, and this involves apogamy. Mention has been made of the case of an onion seed containing five embryos, only one of which could have come from a fertilized egg. The four possible sources of embryos are found to be the fertilized egg, the unfertilized egg, gametophyte cells, and sporophyte cells.

Another interesting fact concerning parthenogenesis in seed plants has been added comparatively recently (1). A plant known to be parthenogenetic was shown to have $2x$ eggs, but it was also known to be pollinated and its sperms were seen discharged into the embryo sac. These sperms were apparently functional in every particular, and with the x number of chromosomes, and yet, although a sperm came into contact with an egg, there was no fusion. The inference has been that a diploid egg may be incapable of fertilization and is parthenogenetic if it functions at all. It does not follow that only diploid eggs are parthenogenetic, for parthenogenesis in ferns contradicts this conclusion.

The bearing of these facts upon genetics should be considered. Plant geneticists have been using the most

complex material. Results have been given in experimental work with peas, four-o'clocks, wheat, and, most of all, corn, all of them seed plants. This selection of material was natural, for such plants represent the region of the plant kingdom in which practical breeding occurs. It was natural to make practical breeding scientific.

Not only have geneticists used the most complex material but they have selected sexual reproduction as the method of reproduction to be investigated, which is the most complicated kind of reproduction. This selection was also natural, for Mendel's law is based upon sexual reproduction, and it is this law that geneticists have been testing.

The further difficulties of the situation should also be considered in order that one may be in a position to estimate the value of results. Students of morphology are familiar with the fact that the sexual structures of seed plants are peculiarly involved with other structures. They do not stand out distinctly, as in the algae, for example. Not only are the sexual structures (eggs and sperms) beyond the reach of observation, and therefore of experimental control, but there is the alternation of generations to consider, inheritance being carried through one generation to express itself in the next. A sporophyte does not beget a sporophyte but a gametophyte, and this in turn begets the embryo sporophyte.

Add to this complex situation the possibility of parthenogenesis and vegetative apogamy and it is obvious that the origin of embryos found in seeds is not assured. If two embryos appear it is evident that at least one of them holds no relation to the pollen parent;

and even when only one appears, as is usually the case, how can it be certain that it has arisen from an act of fertilization? One can assume for the most part that embryos are the result of fertilization, but the increasing number of cases of apogamy introduces a serious element of uncertainty. If two individuals have been crossed, and the expected results in the F_1 or F_2 generations do not appear, how can it be told whether the pollen parent has entered into the result at all? Doubtless puzzling results in genetics have arisen more than once through apogamy; the crossing has been controlled, but the results are taking place out of sight and of course out of control. The crossing is only the gross part of the performance. If instead of applying pollen to stigma one could apply sperm to egg, there would be far more control. The program of events between pollination and fertilization should be kept in mind, and also the program between fertilization and the escape of the embryo from the seed. Not a single stage of these performances is under observation, much less under control. Pollination is effected, and then the plant emerging from the seed is observed. One must take for granted that all of the numerous events that lie between have been completely orthodox. Usually they are, but sometimes they are not; and then the unexpected result is forced into the orthodox program.

It is really surprising, with so much of our experimental work out of sight and beyond control, that so many constant results are obtained. It is an impressive lesson as to the wonderful uniformity of conditions between pollination and fertilization, and then between fertilization and embryo escape. This gives assurance

that, in spite of the complexity of material and in spite of lack of control, the facts of inheritance are being uncovered when the consistent results are considered. It also assures us that an unexpected result may occur now and then and that it is not necessary to explain it by trying to make it consistent with other results. A single illustration will make this clear. Suppose that a species is persistently parthenogenetic, as some are known to be, and still there is pollination. If one were conducting breeding experiments with such a plant he would discover that inheritance was of a sort called maternal inheritance, that is, inheritance determined by the ovule parent and not affected by the pollen parent. In explaining this situation it would not be necessary to have recourse to CORRENS' idea of diseased cytoplasm; one would suspect parthenogenesis and then look for it.

Self-sterility, which is an important and growing subject, to be developed later, is related in one way or another to apogamy. Mention has been made of the stimulating effect of the mere presence of a pollen tube in inducing an unfertilized egg to germinate without sperms being discharged or even formed. An increasing number of plants are found to behave in this way, especially in certain families. Notably in some cultivated races of apples and grapes self-sterility has been developed, that is, the pollen grains are impotent upon their own stigmas. In such cases the fruit develops just as if fertilization had taken place; in many cases seeds develop within the fruit and even embryos in the seeds. Strangely enough if "foreign" pollen is used it may not be impotent but results in fertilization. All

of this indicates that the origin of embryos cannot always be assured, and apogamy is a factor that may at any time upset any expectation based on Mendel's law without violating that law. If Mendel's law is based on the act of fertilization, and that act does not occur, the result has nothing to do with the law.

In view of what has been said, the recent movement of some plant geneticists to include the lower plants in their work will be understood. This results in the following opportunities. In the study of sexual reproduction the simpler plants (such as algae) have sexual structures that are not involved with other structures, and the whole performance of fertilization and embryo development is in sight and capable of control. The difference between a sex act and embryo development under cover and in the open, when observation and control are desired, is obvious. Furthermore, back of inheritance through the sex act is inheritance through spores. Such inheritance needs investigation in connection with inheritance through sex. There are certain things that all forms of inheritance have in common, and these things should be kept distinct from those which are peculiar to sex inheritance. Only in this way can any knowledge be reached of the special rôle of sex in inheritance and the peculiar features it has added.

A practical plant breeder may be interested only in the fact that he can obtain a new individual from a seed the pedigree of whose embryo in the nature of things cannot be demonstrated; but a scientific plant breeder, that is, a geneticist, must be interested in the conditions that determine inheritance, and these will be discovered

by investigating and controlling all kinds of inheritance. No more favorable material for determining the fundamental facts of inheritance can be found among plants than the spores of the simpler forms. They are accessible and therefore capable of control; a succession of spore-produced individuals represents a line whose purity cannot be questioned; the so-called "modification of the germ plasm" can be accomplished with a precision that is impossible in the case of an egg nucleus within an ovule and an ovary. In short, free from all the entanglements of sex, the possibilities of variations in pure lines can be determined and the possibilities of inheritance of such variations. Such observations will establish the facts common to all inheritance and will enable us to recognize the contribution of sex to inheritance.

This is no criticism of the work that has been done with seed plants. That work was the natural beginning and the results have been remarkable. It is simply calling attention to the necessary limitations of experimental work in genetics with seed plants and the desirability of extending the field of genetics so as to include the lower forms that will permit certain desirable things to be done with greater exactness.

1. PACE, LULA, Apogamy in *Atamosco*. Bot. Gaz. **56**:376–394. *pls. 13, 14.* 1913.
2. YAMANOUCHI, SHIGÉO, Apogamy in *Nephrodium*. Bot. Gaz. **45**:289–318. *pls. 9, 10.* 1908.

CHAPTER XIII

INHERITANCE IN GAMETOPHYTES

Thus far the discussions have dealt with inheritance in sporophytes; in fact, genetics practically never considers gametophytes, through which inheritance must pass from one sporophyte to the next. The reasons for this neglect are obvious. Practically all of our land vegetation is made up of sporophytes and therefore practically all of our experimental material has been sporophytes. Furthermore, gametophytes are inconspicuous (out of sight in seed plants), hard to get at, hard to work with, and apparently of no economic importance. Besides, in animals, as is well known, the generation equivalent to the gametophyte of plants is represented only by a few cell divisions in the maturation of gametes. In other words, the gametophyte has no significance in the animal kingdom; and since inheritance in plants is of interest to most investigators chiefly because it throws some light upon inheritance in animals, there has been no demand for any knowledge of inheritance in gametophytes.

This means that this subject has not been studied, but it may be considered here briefly. It may be admitted that our ideas of genetics have been fairly well developed without including the gametophyte in inheritance, but the question is whether they cannot be developed better and perhaps more quickly by including the gametophyte. There are two reasons that may be suggested:

(1) Such a study will test the theories of inheritance derived from the study of the sporophyte; (2) it deals with less confusing material.

In the first place, the genetics of gametophytes may furnish a good test of the theories of inheritance derived from the study of sporophytes. The chromosome equipment of a gametophyte is exactly the same as the chromosome equipment of a gamete, in both cases the chromosome number being haploid. This results from the fact that in plants the reduction division occurs in connection with spore formation; it is only rarely that it occurs in connection with gamete formation, as in animals, and then only when spores are cut out of the life-history. Fig. 28 represents the typical life-history of one of the higher plants, so far as the chromosome situation is concerned. At the reduction division, whose Mendelian significance has been considered, the chromosome number is reduced from 8 to 4; and as a result the spore, the gametophyte, and the gamete all contain 4 chromosomes. At fertilization two sets of 4 chromosomes are brought together by the male and female gametes, and therefore the zygote contains 8, and the resulting sporophyte continues the 8 chromosomes. At a certain season or, better, under certain conditions cells of the sporophyte are set apart to produce spores (spore mother-cells, each with 8 chromosomes), and the reduction division follows, each spore receiving 4 chromosomes. This familiar picture of the life-cycle may now be applied to genetics.

The fact that the chromosomes are reduced in number from 8 to 4 is not the significant fact; the significant fact is how this reduction takes place, that is, not the

superficial result but the process. The process may be recalled for a moment. Suppose that each of the 8 chromosomes in a spore mother-cell contains a single determiner; in such a case a nucleus can be represented

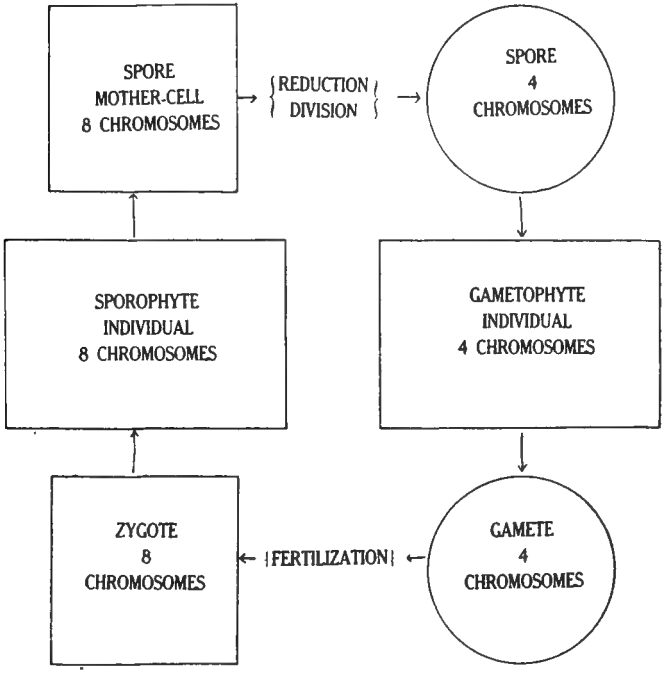


FIG. 28.—Diagram representing life-history of a higher plant as regards chromosome number.

by fig. 29. When the reduction division occurs it means that 4 of these chromosomes will go to each of the two resulting nuclei. When this happens, are the chromosomes chosen indiscriminately? It has been learned that there is a certain limitation in the choice,

a limitation expressed by the statement that at the reduction division allelomorphs never go to the same nucleus, that is, the reduction division would never produce a spore whose nucleus would contain both *A* and *a*, for *A* and *a* are allelomorphs. All of this is evident in connection with the Mendelian diagrams. It should be remembered, however, that when it is said that a spore or a gamete contains only half as many chromosomes as does a sporophyte the whole truth has not been stated. In fact, such a statement does not include the most significant fact from the Mendelian point of view; that is, that a spore or a gamete never contains both of a pair of allelomorphs in the nucleus. It should be realized that 4 and 8 chromosomes are used only as convenient representative numbers, for in plants there is a wide variation as to these numbers, and in the vast majority of cases the sporophyte number is considerably more than 8. In angiosperms, for example, the haploid number ranges from 3 in *Crepis* to 45 in *Chrysanthemum*. The statement that the essential feature of the reduction division is to separate allelomorphs into different nuclei is simply a statement of the theory of segregation, which is the fundamental feature of Mendel's law. If this statement is not true Mendel's law is not true, and all of our ideas of inheritance will have to be reconstructed.

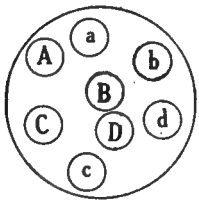


FIG. 29

With this in mind, it may be considered how a knowledge of inheritance in gametophytes may be of service. For convenience we will consider first a single pair of

allelomorphs (*A* and *a*). It will be recalled that such a pair of allelomorphs may behave in two different ways in hybrid sporophytes. In case of complete dominance, *A* alone will be expressed in the hybrid *Aa*. In case of lack of dominance or of only partial dominance, the hybrid *Aa* will partake of the nature of both *A* and *a*; or, in other words, it will be a blend, intermediate between the two pure parents *AA* and *aa*.

A similar situation may be considered in the gametophyte generation. In a gametophyte, *A* can be present or *a*, but not both. Here at least is a case of presence and absence about which there is no doubt. In this case there would be invariably pure dominance, or what corresponds to it, but there could not be a blend. It is interesting to consider the results of this situation. If in a study of inheritance in gametophytes cases of pure dominance only are discovered the result is quite consistent with our theories. If, on the other hand, cases of blending inheritance are discovered what are to be the conclusions? The only possible conclusion would be that our theoretical mechanism is wrong; that chromosomes are not the bearers of hereditary characters, or at least not the only bearers; or else that the behavior of the chromosomes at the reduction division is different from that which cytologists and breeders have long supposed. In other words, we have here a chance to test the doctrine of segregation through the reduction division.

The case of complementary factors may also be considered. Recalling the behavior of complementary factors in the sporophyte generation the question arises about their behavior in the gametophyte generation.

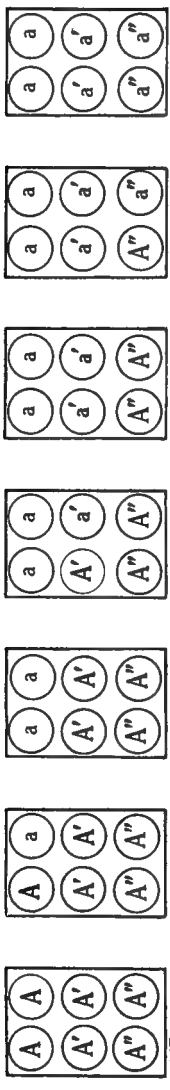


FIG. 30.—Diagram showing how cumulative factors, located on three different chromosomes, may produce seven different quantitative classes in sporophyte generation.

Of course complementary factors can exist together in a gametophyte. A gametophyte could not contain *Aa* (allelomorphs), but it could contain both *A* and *B*, which may be complementary factors.

It is evident also that supplementary and inhibitory factors are also possible in gametophytes, just as are complementary factors, for they are not segregated by the reduction division. Of course a gametophyte showing an entirely new character produced by the interaction of two complementary factors would have to be a gametophyte grown from a hybrid sporophyte in which these two factors had been brought together; and the same is true in reference to supplementary and inhibitory factors. With these facts in mind the validity of our theoretical mechanism could be tested.

Finally, the case of cumulative factors could be

considered. These could also coexist in a gametophyte but not to the same degree as in a sporophyte. If three cumulative factors were active in a sporophyte, it is evident that there could be gradations as indicated by fig. 30. If, on the other hand, three cumulative factors were active in a gametophyte there could only be the gradations indicated by fig. 31. Thus the behavior of cumulative factors in sporophytes and gametophytes would differ quantitatively; there would

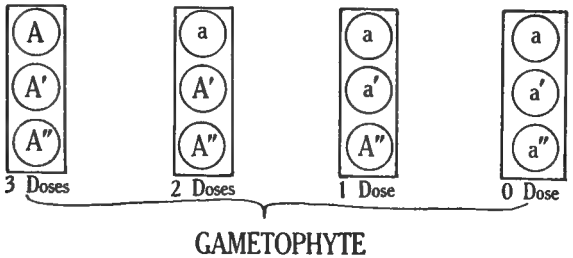


FIG. 31.—Diagram showing how the cumulative factors of fig. 30 could produce only four different quantitative classes in the gametophyte generation.

not be so many gradations in gametophytes for the same number of factors involved.

As a general conclusion, therefore, it may be said that a knowledge of inheritance in gametophytes would test our theoretical mechanism for inheritance in sporophytes.

There is another important value to be secured from a knowledge of genetics in gametophytes. In the study of genetics in the sporophytes of the higher plants we are dealing with very complex organisms. Attention has been called to the possibilities of parthenogenesis

and vegetative apogamy, and to the fact that in such a case any theoretical scheme of factors constructed to explain breeding results would be without any significance.

Again, in such a complex organism as the sporophyte it is hard to say at all times just what things are being inherited and what things are merely responses. Finally, there always remains the confusing problem connected with germ plasm and body plasm. Are these two plasms as distinct in the higher plants as they seem to be in animals? In any event, can the body plasm affect the germ plasm in any significant way, and is there any mechanism to justify the inheritance of acquired characters? These questions are simply samples of the many complexities that confront us when dealing with such organisms as the higher plants. The suggestion has been made already that simpler plants be studied which show fewer complexities. Algae, and even bryophytes, have much to teach in the field of genetics, for in such plants germ plasm and body plasm are not clearly differentiated; frequently they are almost one and the same thing. Also such a phenomenon as parthenogenesis is more easily studied in such plants, for the structures involved are superficial and therefore easily observed and controlled. This suggests another advantage, therefore, in the study of inheritance in gametophytes, for in algae practically everything is gametophyte, while in bryophytes the gametophyte generation is the dominant one and therefore the one providing the best experimental material.

There is one disadvantage in breeding work among these lower forms that should be realized, and that is

the question of technique. It might be asked how one could breed such a form as *Ulothrix*, in which the productive cells are microscopic and are practically impossible to identify or even to isolate successfully. One could begin with such a form as *Spirogyra*, however, in which the zygotes are rather large cells, so large that they can easily be detected without a microscope. Two biologists, BARBER (1) and KITE (3), by using fine pipettes, have been able to isolate bacteria successfully and even to drag individual chromosomes out of nuclei. It would be far simpler to isolate the zygotes of *Spirogyra*. Incidentally, it may be mentioned that the zygotes of *Spirogyra* are sometimes produced by the union of three sexual cells instead of two, and breeding results in such a case should be very interesting.

For the following two reasons, therefore, a study of inheritance in gametophytes is demanded and should be undertaken: (1) to test our hypothetical mechanism with its segregation of many kinds of factors; (2) to study the lower plants where breeding phenomena are not obscured by so many complexities.

In a secondary way, also, the gametophyte generation becomes significant in genetics. Under the topics of self-sterility, xenia, and hybrid vigor, inheritance in gametophytes will be touched upon again. The preceding discussion has been merely a suggestion of the perspective of an entirely new territory for exploration, a territory which should be made a part of that which is already occupied.

In conclusion, the following quotation from EAST (2) is pertinent: "Modern discoveries tend more and more to show that the sole function of the gametophyte of

the angiosperms is to produce sporophytes. The characters which they carry appear to be wholly sporophytic, the factors which they carry functioning only *after* fertilization." This is a logical inference from most of the data on genetics. It does not mean, however, that we should leave all gametophytes out of consideration, for active investigation of their behavior in inheritance should reveal facts of considerable theoretical value.

1. BARBER, M. A., Univ. of Kansas Sci. Bull. no. 4. 1907 (p. 3).
2. EAST, E. M., and PARK, J. B., Studies on self-sterility. I. The behavior of self-sterile plants. Genetics 2:505–609. 1917.
3. KITE, G. S., The physical properties of the protoplasm of certain animal and plant cells. Am. Jour. Physiol. 22:146–173. 1913.

CHAPTER XIV

SELF-STERILITY

It has been discovered that many of the races of cultivated plants, notably apples, do not develop viable seed when self-pollinated. The practice adopted by horticulturists, therefore, to meet this situation is to make mixed plantings of several races. In this way foreign pollen is always present, and this results in viable seed where "own" pollen fails. This phenomenon is known as self-sterility and seems to be well established in many cases.

In connection with this phenomenon the following problem confronts us. Is self-sterility of any advantage to plants in nature, or is it merely a necessary evil that has arisen as a result of culture; or is it merely mechanical or chemical necessity that has arisen in response to certain conditions and is of no significance one way or the other in the economy of plants? Opinion is divided on this point. Most biologists, however, claim that self-sterility is of some advantage to the plant. This opinion is related of course to belief in the Darwinian doctrine of the survival of the fittest, survival being a proof of usefulness. For this reason it has become customary to regard a plant character as useful until the contrary is proved. This point of view has been of service in the past and is still useful, subject to certain limitations.

If self-sterility is useful to the plant the nature of its usefulness should be considered. The situation may be outlined as follows. The first plants used only asexual reproduction, and this has proved to be a very simple and effective method. Why then was sex ever developed? It will be remembered that WEISMANN was the first to answer this question clearly, claiming that sex was developed to secure greater variation. Greater variation is desirable of course to secure adaptations to diverse conditions of living. It is well known that asexual reproduction is the surest way to duplicate the parent form and would result in uniform plants generation after generation. If a species remains uniform within certain narrow limits it will be impossible to meet changing conditions. This will result in two evils: (1) if conditions are changed where the uniform species is growing the species will be exterminated; (2) even if the local conditions remain the same the species will be unable to spread into new localities where the conditions are different. If, on the other hand, a species shows wider variations, certain of these might fit the new conditions. Such variations will survive when conditions change and would always solve the problem of migrating into new habitats. For these reasons variation is necessary to the general success of the species.

This increase in the range of variations, therefore, is the significance of the introduction of sex, for the fusion of two germ plasms in the sex act greatly increases chances for variation. WEISMANN thought that sex secured the small individual variations which are so common in any species, but now most such variations

are regarded merely as fluctuations or responses. Such variations are not inherited, and therefore can be of no phylogenetic significance; that is, of no value to the future of the species. Our recent knowledge of the factor hypothesis, however, indicates that many of these variations are more than fluctuations. They may represent germinal differences, such as varying "doses," and such differences are inherited and may be of some value therefore in the future of the species.

It will be realized, however, that it is possible to have a homozygous race. If a race were strictly homozygous in respect to every heritable factor the sex act would result in no more variation than would asexual reproduction, provided of course our ideas of the mechanism of inheritance in sexual plants are correct. The fact is that a perfectly homozygous plant is probably rare. Supposing, however, that it were common, we would have to resort to some other mechanism than the sex act to secure the desirable variation. If sex does not secure variation what can?

The answer is cross-pollination. Although races were all homozygous, cross-pollination would make possible the crossing of different races, which would inevitably result in great variation in the progeny. Even if homozygous races are few it is certainly true that in any event cross-pollination results in greater variation than self-pollination. This is the biological basis of the many devices in plants to secure cross-pollination; in fact, this is carried to such an extreme in many cases that self-pollination is absolutely prevented. Stamens and carpels may mature at different times; and the great number of dioecious plants must all be

cross-pollinated. DARWIN uncovered this situation and concluded that there is a general tendency among plants to secure cross-pollination. The significance of this universal tendency seems to be to secure variation.

Some ascribe another value to cross-pollination. Hybrid vigor is a well established phenomenon, which will be discussed later. Continued inbreeding frequently results in degeneracy, such inbreeding races being spoken of as "running out." It is a well known fact that to cross an inbred race with some other race results in a kind of rejuvenescence, a regaining of the original vigor that was present before inbreeding began. Even in the case of two normally vigorous races a cross will often produce a hybrid more vigorous than either parent. Of course, one might regard hybrid vigor itself as a device to secure crossing.

In any event, it seems to be safe to conclude that cross-pollination is of advantage to plants, and of all mechanisms to secure cross-pollination, self-sterility may be regarded as the culmination. If "own" pollen cannot produce viable seed in a plant cross-pollination becomes a necessity. Inbreeding cannot continue in a race that has become or is becoming self-sterile.

This raises the question why is "own" pollen not effective where foreign pollen is? There are well known cases in which pollen is not effective on stigmas of the same race but quite effective on those of another race. Although the biological advantage of such behavior is evident, this does not explain the mechanism involved.

The theories offered in the explanation of self-sterility are very numerous. Some years ago an attempt was

made to explain self-sterility as a response. It was demonstrated that when a race of plants was grown under conditions of unusually high humidity its pollen grains would burst before they had a chance to function. This explanation was obviously true in a few simple cases, but the phenomenon of self-sterility usually involves something much more perplexing than merely the non-functioning of pollen. The real problem is to explain why pollen will not function on "own" stigmas and will function on the stigmas of other closely related races, while it requires foreign pollen to function on "own" stigmas. Such a complex situation could hardly be explained as a response; more probably it is involved with inheritance. Morphologists, cytologists, ecologists, physiologists, and practical horticulturists have all contributed explanations; in fact, it is not assured as yet to which of these fields the phenomenon belongs. In the meantime, what concerns us is whether self-sterility can be explained by the principles of genetics.

Such a theory has been proposed. Several investigators have suggested that there is a heritable factor for self-sterility, and some investigations of this possibility have been undertaken, but as yet most of the results have been negative. It must be realized, however, that if self-sterility is ever to be explained on the basis of hereditary factors the mechanism involved will be rather unusual. Although most of the explanations proposed by geneticists have proved inadequate there is at least one that deserves consideration. It is a typical Mendelian explanation and very ingenious. It fitted the facts perfectly when first proposed and, still better, it has continued to fit the facts that have been uncovered

by subsequent breeding work. Furthermore, it is the first true Mendelian explanation that has been based on the germinal constitution in the gametophyte as a deciding factor.

In 1914 BELLING (1) published a paper entitled "A study of semi-sterility." Apparently this is not true self-sterility, but it is a closely related phenomenon and may be considered in this connection. BELLING was conducting breeding experiments with two races of beans, both of which were completely fertile. When he crossed them, however, the resulting hybrids were semi-sterile. Uniformly just one-half of the pollen grains appeared empty and collapsed, while one-half of the ovules had no embryo sacs. The sterile pollen and ovules appeared in random distribution with the fertile.

Inbreeding the semi-sterile hybrids, BELLING obtained an F_2 generation which showed the following features: one-half the plants had perfect pollen, the other one-half had a mixture of equal numbers of good and bad pollen grains in all their flowers. The plants which had perfect pollen also had perfect ovules, while the plants with 50 per cent sterile pollen also had 50 per cent sterile ovules. In the F_3 generation all the descendants from the fertile plants had perfectly good pollen and ovules; but the progeny of the semi-sterile plants again split up into two classes (fertile and semi-sterile) as before.

BELLING states his general conclusion as follows: "The explanation of the random abortion of one-half of the pollen and one-half of the embryo sacs must apparently be by the segregation of Mendelian factors

among pollen grains and embryo sacs individually, and not by the action of these factors on the zygotes."

To make this suggestive situation clear the diagram (fig. 32) may be considered. It enlarges a little upon BELLING'S original ideas as he stated them, and emphasizes the sporophyte-gametophyte relationship. Pollen grains and embryo sacs are gametophytes in the sense that they inclose the male and female gametophytes, so that when the diagram shows sterile gametophytes it is the same as saying that both pollen grains and embryo sacs are sterile. This of course is just what BELLING found; whenever one-half the pollen grains in random distribution were sterile one-half the embryo sacs in random distribution were also sterile.

It should be remembered that BELLING started with two completely fertile races. Suppose that the parent race A had a factor (X) whose absence brought sterility in the gametophytes (pollen grains or embryo sacs). Species B has a different factor (Y), with a similar effect, but inherited independently. When BELLING crossed these races, all of the resulting F_1 hybrids were semi-sterile. In other words, in every F_1 plant one-half the gametophytes were sterile. It is easy to see why XO and OY are fertile, also why OO is sterile (lacking both factors); but why should XY be sterile when it has both factors? BELLING explains it by saying that gametophytes are unlike sporophytes in that normally they have single factors instead of double factors. The germinal capacity of a gametophyte is just one-half that of a sporophyte. It is as if a gametophyte were "supersaturated" by a double factor. Such a situation is abnormal for a gametophyte

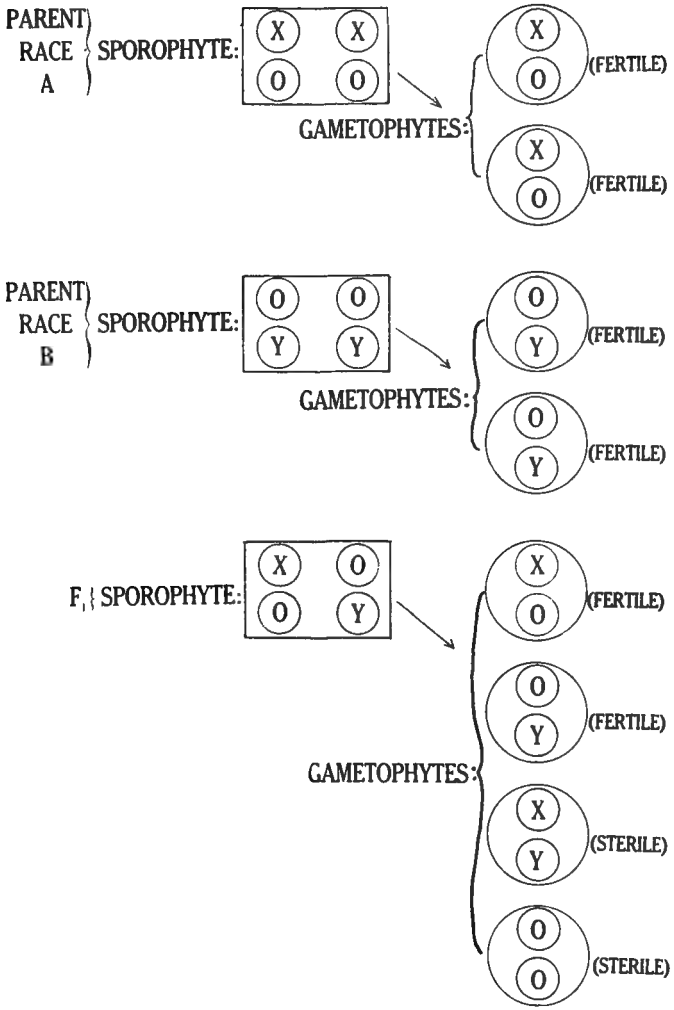
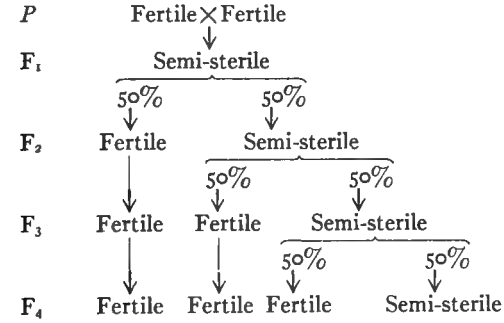


FIG. 32.—Diagram illustrating Belling's explanation of semi-sterility.

and brings abnormal results. Therefore the gametophyte having the abnormal double dose (XY) is just as sterile as the gametophyte with no dose (OO).

In developing the F_2 ratios of course only the fertile gametophytes function. XY and OO are eliminated, so far as posterity is concerned, so that we have to deal only with the chance matings among the fertile gametophytes (XO and OY). According to mathematics there are four possible matings between these two gametophytes (fig. 33). Out of these four resulting F_2 sporophytes two would evidently produce only fertile gametophytes and would remain fertile as long as they are inbred. The other two are exactly like the original F_1 hybrid and therefore semi-sterile, giving one-half sterile gametophytes. The whole dynasty may be represented as follows:



This is a very ingenious scheme and, like others, should be tested by further experiments. To a certain extent it has already met this test, for BELLING (2) has subsequently reported a few more generations in which the breeding results were entirely consistent

with those of the earlier generations. Also he has discovered two new pure races of beans which give similar results. It remains to be seen whether this explanation will fit other cases of semi-sterility.

This theory of semi-sterility of course may have some value in throwing light upon the problem of complete self-sterility. It seems to be of greater theoretical interest, however, in being the first attempt to include inheritance in gametophytes in an explanation of Mendelian results. BELLING himself does not stress this gametophyte relationship; in fact, he does not use the word "gametophyte"; and yet it is probably this gametophyte relationship that represents the most significant feature of his work and will prove to be the most suggestive feature in future investigations.

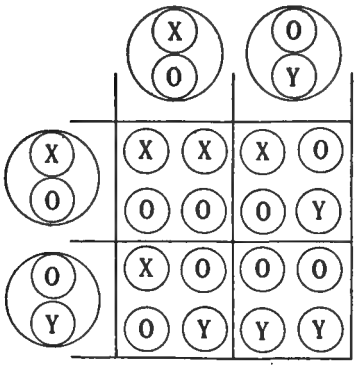


FIG. 33.—Diagram showing how the F_2 would be produced according to BELLING'S idea of semi-sterility.

Attractive as this explanation may be, we must realize, however, that as yet it merely explains semi-sterility and does not clear up the fundamental complexity of the more general topic of self-sterility, that is, why pollen fails on "own" stigmas and functions on foreign stigmas.

Very recently an explanation of the more general problem of self-sterility has been proposed by EAST

and PARK (3). This explanation seems to fit the facts correctly but has certain theoretical disadvantages. In any event it involves such complex Mendelian conceptions that we shall not try to explain it here. One statement, however, which was considered in the previous chapter again commands our attention. EAST and PARK state "that modern discoveries tend more and more to show that the sole function of the gametophytes of the angiosperms is to produce sporophytes. The characters which they possess appear to be wholly sporophytic, the factors which they carry functioning only *after* fertilization." This statement would seem to throw out of court all consideration of the gametophyte generation and would regard as impossible BELLING'S theory, which is based on the direct influence of the germinal equipment of gametophytes upon gametophytes themselves. We will not enter into any general discussion of this point, but merely suggest that the self-sterility in the two cases might have been involved with distinctly different phenomena, since BELLING'S material showed degeneration and sometimes complete abortion in pollen and embryo sacs, while the material (*Nicotiana* spp.) of EAST and PARK was self-sterile merely because of the failure of pollen tubes. The hereditary mechanism of the two cases must be quite different.

1. BELLING, JOHN, A study of semi-sterility. Jour. Heredity 5:65–75. *figs.* 7. 1914.
2. ———, A hypothesis of semi-sterility confirmed. Jour. Heredity 7:552. 1916.
3. EAST, E. M., and PARK, J. B., Studies on self-sterility. I. The behavior of self-sterile plants. Genetics 2:405–609. 1917.

CHAPTER XV

THE ENDOSPERM IN INHERITANCE

We have dealt chiefly with inheritance in the sporophyte, in connection with which most work in plant genetics has been done. Brief mention has been made of inheritance in the gametophyte, in connection with which there has been very little work. It is natural now to consider inheritance in the endosperm. This classification raises the question as to the nature of the endosperm. In general it has been regarded as belonging to the gametophyte generation, but since the discovery of "double fertilization" in 1898 some have claimed that it belongs to the sporophyte generation. On the basis of chromosome numbers it is neither, so that there is also the claim that the endosperm is neither sporophyte nor gametophyte; at least we are justified in considering inheritance in endosperm as a separate topic. As might be inferred, endosperm shows some features characteristic of a gametophyte, others characteristic of a sporophyte, and still others peculiar to itself. Judgment as to its nature, therefore, will depend upon which of these features are emphasized.

It is generally believed that angiosperms have been derived from gymnosperms, and it is natural therefore to explain angiosperm structures by the corresponding structures of gymnosperms. The gymnosperm and angiosperm ovules are contrasted in fig. 34, which will assist in the following discussion. In gymnosperms the

situation is clear. After the germination of the megaspore, everything within the old megaspore wall is

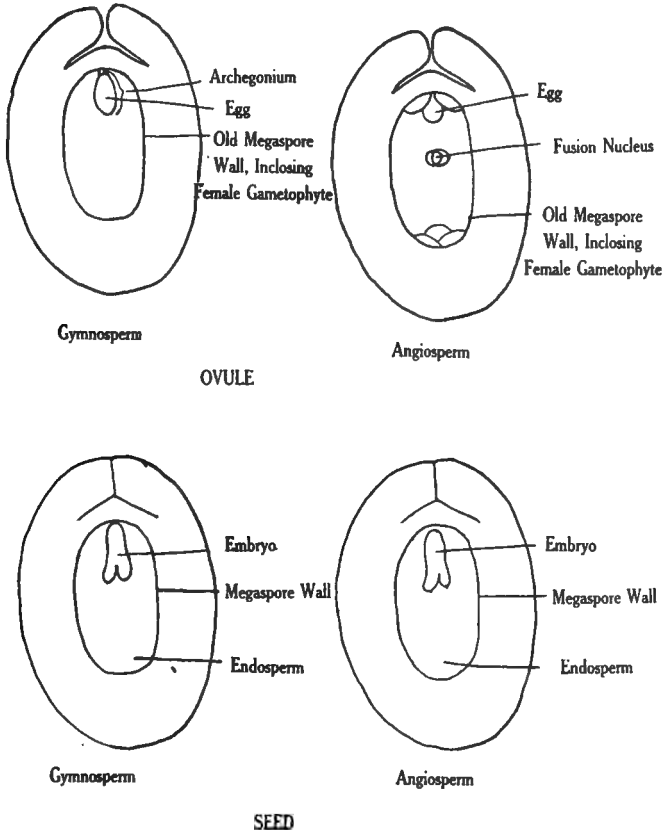


FIG. 34.—Diagrams contrasting young ovules and mature seeds of gymnosperms and angiosperms.

gametophyte tissue; fertilization affects the egg only, resulting in a sporophyte embryo. In the seed, therefore, the embryo is imbedded in nutritive tissue which is

evidently the vegetative body of the female gametophyte, and this tissue is called the endosperm.

In angiosperms, however, a new situation introduces doubt. It can be said as before that after the germination of the megaspore everything within the megaspore wall is a female gametophyte tissue, but it cannot be said that fertilization affects the egg only, for one of the sperms fuses as regularly with the fusion nucleus as does the other sperm with the egg. It will be remembered that the fusion nucleus is formed by two nuclei, which have migrated from each end of the sac, so that when the sperm enters into the fusion there is a triple fusion. After fertilization the fertilized egg of course forms the embryo sporophyte, but usually every nucleus of the old gametophyte disappears except the fertilized fusion nucleus, which then forms the endosperm in which the young sporophyte is imbedded. For this reason the fertilized fusion nucleus is usually called the endosperm nucleus.

A comparison of angiosperm and gymnosperm seeds reveals the following contrast (see fig. 34). In the appearance of their essential structures they are exactly alike, and for this reason some botanists claim that the endosperm of angiosperms is the same as that of gymnosperms, that is, gametophyte tissue. The opposing claim is that, although the gymnosperm endosperm is gametophyte tissue, the situation in angiosperms is essentially different. In angiosperms the endosperm does not arise from morphologically unmodified gametophyte tissue, as in gymnosperms, but entirely from the endosperm nucleus, and this nucleus is clearly the product of the fusion of male and female nuclei. With such an origin the endo-

sperm nucleus is comparable with the zygote, and the endosperm tissue is sister to the embryo sporophyte. In other words, in angiosperms, embryo and endosperm are twins. This means that the endosperm of angiosperms belongs to the sporophyte generation, although of course it is a distinct individual which produces no progeny. The embryo sporophyte is a parasite upon its twin and destroys it.

It will be recognized that there is some reason for each of these claims. Is there any way of testing the claims, that is, of distinguishing between sporophyte and gametophyte tissue? The cytological distinction is that the sporophyte is $2x$ tissue and the gametophyte x tissue. Applying this test it is found that endosperm tissue is neither x nor $2x$, but $3x$, as might be expected from the triple fusion. The conclusion involves several possibilities, as follows: $3x$ is evidently nearer $2x$ than x, and therefore endosperm tissue is more like sporophyte tissue than gametophyte tissue; but on the other hand two of the x's have come from the female gametophyte, and therefore two-thirds of the endosperm nucleus is female gametophyte tissue. On the basis of predominance, therefore, endosperm tissue is more like female gametophyte tissue than anything else. Finally, there is a third alternative, and that is that the $3x$ condition deserves to be set apart in a category by itself, which would mean that the endosperm is neither gametophyte nor sporophyte.

These are the claims and the evidence as to the nature of angiosperm endosperm. Opinion is not settled, but the facts are clear. This prepares for a consideration of the bearing of this situation upon genetics.

The geneticist is not much concerned about the exact morphological or cytological nature of endosperm, but he is much concerned about its behavior in inheritance, and perhaps the phenomena of endosperm inheritance may help to decide whether endosperm is gametophyte or sporophyte or neither.

Certain races of corn have yellow endosperm, while in other races it is white (colorless). If a cross is made with pollen from the yellow endosperm race on the silks of the white endosperm race, what would the inference be as to the result? We could assume that yellow is dominant over white, since yellow is probably due to the presence of a factor which is lacking in the white. In making such a cross, therefore, we would expect a hybrid embryo to be formed which would show the dominant character of yellow endosperm when this embryo becomes a plant bearing ears the next season. On the contrary, we find that the dominant yellow character appears, but it appears that same year. The cross of course puts the yellow endosperm factor in the young hybrid embryo, but we cannot imagine that this embryo passed the character out into the endosperm that surrounds it. The real mechanism is as follows.

Some time after this phenomenon was discovered in 1872, it was named *xenia* (in 1881), the definition of the term being the direct effect of foreign pollen upon the endosperm. At the time of its discovery the mechanism involved in xenia was not understood. Later, double fertilization was discovered, and this furnished a complete mechanism. A pollen grain from the yellow endosperm race contains two male gametes, and each gamete contains the factor for yellow endosperm. One of the

gametes fertilizes the egg and produces a hybrid embryo, which, in the next generation, behaves as a heterozygote for yellow endosperm. The other male gamete fertilizes the fusion nucleus and produces the endosperm nucleus, which therefore contains the factor for yellow endosperm, the result being that the endosperm is yellow, although the ovule belongs to the white race. Xenia means, therefore, that the endosperm is a hybrid as well as the embryo, and "triple fusion" involves the transmission of hereditary characters. Fertilization of the fusion nucleus is just as essential as fertilization of the egg, and so far as inheritance is concerned the endosperm and embryo are sister sporophytes.

Xenia has caused much discussion in genetics. It throws light upon the nature of endosperm and suggests that it belongs to the sporophyte generation because it is a product of an act of fertilization. Because of its behavior in inheritance geneticists would naturally regard the endosperm as a sporophyte, an abnormal sister to the embryo.

Cases of xenia are not limited to yellow endosperm. Xenia appears also in the crosses between sweet and starchy corn. Crosses of red corn and purple corn also show xenia, but in this case additional details appear. A section of a grain of corn is shown in fig. 35. There is first the pericarp or "seed coat," which is the ovary wall, belonging to the old sporophyte, and therefore does not concern us. Within this is a thin aleurone layer, which is the outer layer of endosperm, while the bulk of the seed consists of the starchy endosperm. Since aleurone is endosperm, colors peculiar to it would show xenia in inheritance. This was shown in the case

of EAST's red and purple corn, the colors being located in the aleurone.

There is another phase of this situation to which attention should be called. By pollinating the silks of a white-grained individual with pollen from a red-grained individual xenia is secured, the resulting grains being red like those of the pollen parent. In the reciprocal cross, however, that is, pollinating silks on a red-grained individual with pollen from a white-grained individual, a different result is obtained. The resulting grains are not white like those of the pollen parent, but red like those of the ovule parent. There is no xenia, therefore, for the pollen has no immediate effect upon the developing endosperm. This seeming difficulty, however, is easily explained. When the pollen parent is white and the ovule parent is red, the endosperm gets its characters from both parents, and since red is dominant over white the resulting endosperm will be red because the female nuclei that entered into the triple fusion carried the factor for red endosperm; and therefore the pollen from the white parent seemed to have no effect. The mechanism works in all cases, but owing to dominance, xenia appears only in certain cases. There is no need to discuss all of the Mendelian situations in which xenia may occur. An understanding of the

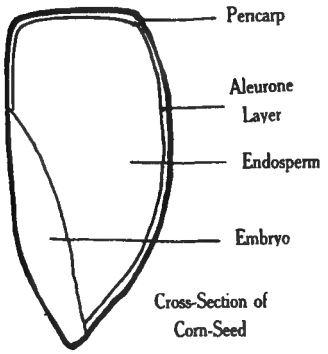


FIG. 35.—Diagram of corn seed

fundamental situation as described should enable us to analyze such cases and reach a conclusion as to the expected results.

A law which EAST (1) has formulated in reference to xenia is pertinent: "When two races differ in a single visible endosperm character, in which dominance is complete, xenia occurs only when the dominant parent is male (pollen parent). When the two races differ in a single endosperm character, in which dominance is incomplete, or when they differ in two characters, both of which are necessary for the development of the visible differences, in both of these cases xenia occurs when either parent is male." This may be called "normal" xenia. What may be called "abnormal" xenia must now be considered.

WEBBER (3) in 1900, in experimenting upon xenia in corn, uncovered some interesting abnormalities. Pollen from a red-grained race, applied to silks of a white-grained race, should result in solid red grains if xenia is normal. In most cases WEBBER obtained this result; but sometimes there appeared grains which showed blotches of red and white in a kind of irregular mosaic. For these cases he constructed an ingenious and reasonable explanation.

Normally the second male nucleus fuses with the fusion nucleus, and the result is a solid red grain. In some cases, however, the second male nucleus does not join with the two other nuclei, but all three divide separately without having fused, and in such a case the mature grain is white with red streaks. In still other cases the two polar nuclei fuse, but the second male nucleus does not enter into the complex, and in this case

the fusion nucleus and male nucleus divide separately to form endosperm. WEBBER concludes that in this last case there will be very much white and very little red in the mature grain; for the fusion of the polars to form the fusion nucleus has resulted in the usual growth stimulus that is evident in all fusions. In the previous case in which all three divided separately, if more white than red develops, it is simply because there are two female polars (white-producing) to one male gamete (red-producing). In the latter case, however, the fusion of the two female polars stimulates them to more rapid division, so that they greatly preponderate over the single unstimulated male gamete, the result being that much white and little red appears in the mature grain.

The appearance of red and white blotches rather than a more regular distribution of colors is explained by the usual method of endosperm formation. Endosperm formation begins with free nuclear division, the resulting nuclei being free in the cytoplasm of the sac. The cell walls, which limit them, are not formed for some time; sometimes not until all the nuclei have been formed. Before a large number of free nuclei have appeared they move from the central region of the sac and usually become placed near the wall, where free nuclear division continues. When walls begin to appear, separating the nuclei, wall formation begins at the periphery of the sac and extends toward the center, in what is called centripetal growth. This program, which is common in seed plants and is known to occur in wheat, is doubtless the program in corn. If then the second male gamete fails to unite with the fusion nucleus

and each divides separately, when their progeny nuclei move out to the periphery of the sac the nuclei of male and female origin doubtless become more or less interspersed. In their further division there would be groups of cells of male origin interspersed among groups of female origin. The result would be red and white areas on the mature grain, intermingled as irregular blotches.

Later, EAST (1) met the same phenomenon in his experiments. He found, however, that sometimes half the grain was red and half white, with a definite boundary line between the two areas. Such a situation evidently did not agree altogether with WEBBER'S conception of the mechanism; in fact, WEBBER himself found similar cases and explains them as follows. When the migration of the nuclei from the center of the embryo sac to the periphery occurs, if the nuclei from the male gamete have remained grouped together, as might well occur, and the nuclei from the fusion nucleus have remained grouped, it is probable that in their migration to the periphery those of one group would come to occupy one portion of the periphery and those of the other group the other portion. In other words, the two groups would migrate *en bloc* to different regions of the sac wall. This would lead to the production of grains in which approximately half the endosperm would resemble one parent and the other half the other parent.

We have called these cases abnormal xenia. The explanation is ingenious, based upon facts known to be true in other seed plants. Whether these phenomena occur in corn or not remains to be proved, but the angiosperm embryo sac program is so uniform that we can hardly doubt it. Inasmuch as corn is probably

the most important material in plant genetics today it is very desirable that the histology of the sac should be investigated in detail. It will be realized that xenia supplies a very convenient index for breeders. Corn breeders especially must realize fully the fact of xenia, and they are able to work more intelligently if they understand the mechanism, since the principal work in corn breeding has to do with the character of the endosperm.

Having introduced the phenomenon of double fertilization in connection with xenia, its use in explaining other things than the mere fact of xenia may be considered. It will be recalled that EAST (2) has done a large amount of experimental work with sweet and starchy corn. Careful examination enabled him to distinguish two distinct races of starchy corn. Both races of course had starchy grains, but the starch seemed to be laid down in different ways in the two races. In one race the starch occurred in a loose powdery or floury condition, while in the other race it was compacted into a hard, flinty, or so-called corneous condition. The two races, therefore, may be spoken of as floury and corneous races of starchy corn.

EAST made various crosses between these two races to discover the method of inheritance of the two endosperm characters. Naturally such characters would be expected to show xenia. In the following description, therefore, when the F_1 generation is referred to, both the hybrid embryo and the hybrid endosperm surrounding it will be included.

When EAST used the floury race as the pollen parent and the corneous race as the ovule parent, the F_1 generation was all corneous. When he made the reciprocal

cross (corneous pollen and floury ovule), the F_1 generation was all floury. This result certainly suggests maternal inheritance, for in both cases it is the character of the ovule parent that is transmitted, while the pollen parent seems to have no effect. If it is assumed that this is a case of maternal inheritance, similar to the four-o'clocks of CORRENS, with their diseased cytoplasm, two problems are encountered: (1) to prove that this behavior is not due merely to parthenogenesis; (2) to discover the mechanism to explain maternal inheritance in this case.

In the first place EAST established the fact that there was no possibility of parthenogenesis. Continuing his investigation he inbred the F_1 generation in each case and examined the F_2 progeny. If we are dealing with a case of maternal inheritance, what should the F_2 generation show? It should be exactly the same as the F_1 generation, for in true maternal inheritance a race will go on forever breeding true to the maternal character, whether it is self-pollinated or cross-pollinated. If this had been a case of true maternal inheritance EAST should have obtained the following situation:

	Floury × Corneous	Corneous × Floury
	↓	↓
F_1	Corneous	Floury
	↓	↓
F_2	Corneous	Floury
	↓	↓
	etc.	etc.

Actually, however, he obtained the following result:

	Floury × Corneous	Corneous × Floury
	↓	↓
F_1	Corneous	Floury
F_2	$\frac{1}{2}$ Floury $\frac{1}{2}$ Corneous	$\frac{1}{2}$ Corneous $\frac{1}{2}$ Floury

The conclusion is therefore that this is not a true case of maternal inheritance. EAST offers a very reasonable explanation of these results, based upon double fertilization plus the cumulative factor idea. These characters appear superficially to be maternal for the following reasons. The endosperm nuclei are $3x$, $2x$ from the female and $1x$ from the male. In the characters under discussion the presence of two factors always dominates the presence of one factor; thus corneous female crossed with floury male produces progeny which are all phenotypically (in appearance) corneous, while floury female crossed with corneous male for the same reason produces progeny which are all phenotypically floury. The cumulative factor idea will be recognized. The mother always determines the character of the hybrid endosperm because there are always two female nuclei to predominate over the single male nucleus. In the embryo, however, this predominance does not occur, for there only a single female nucleus has fused with a single male nucleus. When this hybrid embryo matures, therefore, it is evident that it will produce gametes of two sorts, 50 per cent corneous and 50 per cent floury. It is evident that the female is really the only decisive factor, so far as the appearance of endosperm is concerned, so that the ratios appearing among the female gametes in the F_1 generation will be the ratios that will appear also in the F_2 endosperms. In other words, 50 per cent of the F_2 endosperms will be corneous and 50 per cent floury, no matter what may be the source of the pollen. It is obvious that the explanation of this peculiar form of apparently maternal inheritance depends entirely upon a clear conception of

the phenomenon of triple fusion. On the other hand, this type of inheritance indicates that the triple fusion, so far from being an unimportant cytological process, is really significant.

It may be questioned why the other endosperm characters are not inherited in this way, as for example aleurone colors, just as well as floury and corneous characters. The question cannot be answered satisfactorily, any more than it can be explained why sometimes there is complete dominance and sometimes only partial dominance. All that can be said is that corneous and floury characters appear to be inherited in a different way from endosperm colors, where the presence of one color factor is sufficient to cause the complete determination of color.

1. EAST, E. M., and HAYES, H. K., Inheritance in maize. Conn. Agric. Exper. Sta. Bull. no. 167. pp. 142. *pls. 25.* 1911.
2. HAYES, H. K., and EAST, E. M., Further experiments on inheritance in maize. Conn. Agric. Exper. Sta. Bull. no. 188. pp. 31. *pls. 7.* 1915.
3. WEBBER, HERBERT J., Xenia, or the immediate effect of pollen in maize. U.S. Dept. Agric. Bull. no. 22. pp. 44. *pls. 4.* 1900.

CHAPTER XVI

HYBRID VIGOR

The phenomenon of hybrid vigor has been mentioned in a general way, but its relation to genetics remains to be considered. Geneticists have proposed various explanations of hybrid vigor, and some of these will be presented.

The first record of observations on hybrid vigor is that of KÖLREUTER in 1776, who states that crossing results in an increase in general vegetative luxuriance and an increase in the facility of vegetative propagation and viability. Later GÄRTNER discussed the same phenomenon but gave no important new ideas. Finally, hybrid vigor attracted the attention of DARWIN, who states that crossing hastens the time of flowering and maturing and increases the size of the individual. He adds the very important fact that it is not mere crossing that gives the stimulus, but crossing forms that differ in the constitution of their sex elements; in other words, crossing between individual flowers on the same plant gives no advantage. It is DARWIN who is responsible for bringing hybrid vigor to the attention of botanists, although the modern popular impression would be that BURBANK deserves this credit because of his experience in producing some remarkably fast growing, large, and vigorous hybrids. Among the modern investigators of hybrid vigor, the work of SHULL and EAST will be considered, both of whom have worked upon the subject during the last ten years.

SHULL'S (6) conclusions up to the year 1910 may be summarized as follows. His work was entirely with corn, and the conclusions contained some very significant points.

1. "The progeny of every self-fertilized corn plant is of inferior size, vigor, and productiveness, as compared with the progeny of a normally cross-bred plant derived from the same source." In general this conclusion would be admitted by everyone, but it raised one question. It was known that when two races have been inbred for many generations they frequently "run out," gradually losing their vigor. In such a case a cross between the two races tends to restore the original vigor. The remaining question, however, is whether the same thing may be effected by a cross between two inbred races which have not run out but remain in normal vigor. SHULL answers that hybrid vigor is exhibited when both parents are above the average condition as well as when they are below it.

2. Another question which naturally arises is as follows. When these crosses are made it is of course the F_1 generation that shows the hybrid vigor. If the F_1 generation is inbred, what is the status of the F_2 generation with reference to vigor? SHULL answers this question in the following general way. "The decrease in size and vigor which accompanies self-fertilization is greatest in the first generation, and becomes less and less in each succeeding generation, until a condition is reached in which there is (presumably) no more loss of vigor." The facts involved in this statement may be represented in fig. 36. In this figure it can be seen clearly how the great loss of vigor comes immediately after self-

fertilization again begins. After that self-fertilization brings additional loss in vigor, but this loss is less with each succeeding generation. It is as though a very definite limit were being approached and each generation goes down one-half of the remaining distance toward that limit. Just why and in what way this limit is approached will be considered later in connection with the work of EAST.

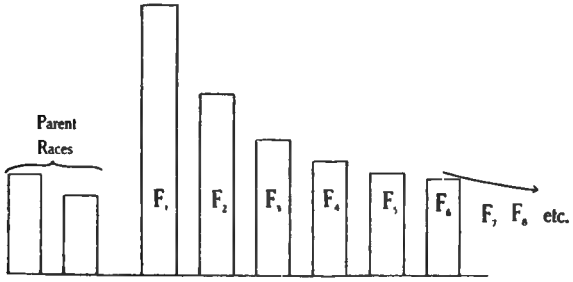


FIG. 36.—Illustrating status of hybrid vigor in F_1 and later generations. Vigor represented by height of rectangles.

3. "A cross between sibs (sister and brother) within a self-fertilized family shows little or no improvement over self-fertilization in the same family." This, it will be noticed, is simply carrying a little farther the point that DARWIN originally discovered. DARWIN found that crosses between flowers on the same plant did not result in hybrid vigor. SHULL now finds that crosses between different individual plants in the same race is of no effect. We realize that an inbred race should be homozygous; therefore all the individuals involved would have the same germinal constitution. A cross between any two such individuals certainly could not

produce a hybrid in any sense, so that it would not be surprising that such a cross fails to bring hybrid vigor.

4. "A cross between plants belonging to two self-fertilized families results in a progeny of as great vigor, size, and productiveness as are possessed by families which have never been self-fertilized." The conclusion from this is that inbreeding results in no permanent loss of vigor. A race may "run out" if inbred continuously, but when crossed with another race it immediately seems to regain all the original vigor. It is as though all germ plasm contains the potentiality of developing vigorous individuals. This potentiality, however, cannot express itself until the proper combination of conditions arises, and this proper combination seems to be connected in some way with hybridizing.

5. "Reciprocal crosses between two distinct self-fertilized families are equal" in producing hybrid vigor. When reciprocal crosses are equal it immediately suggests Mendelian segregation. Is it possible that hybrid vigor may be explained in terms of Mendelism? These are the five "laws" of hybrid vigor developed by SHULL in 1910. It should be noted that they are not hypotheses but observed facts. The hypotheses were developed later when more of the facts were in.

A practical suggestion made by SHULL in connection with hybrid vigor is of interest. Granted that hybrid vigor is an established fact, the question of its practical use in connection with crop plants should be taken into account. If a farmer after years of work has finally developed a desirable new strain of corn by selection, or isolation, or both, he is not likely to favor hybridizing with some other strain in any wholesale way. He must

preserve his pure strain at all costs. SHULL has suggested the following solution of this practical problem, as indicated in fig. 37. Two desirable strains (A and B) are developed. One small plot (I) is planted entirely with A, and at some distance another small plot (II) is planted with A and B in alternating rows. Plot I is used only to perpetuate strain A in pure condition. In plot II all the A plants are detasseled. The silks of these A plants, therefore, are pollinated by B pollen only,

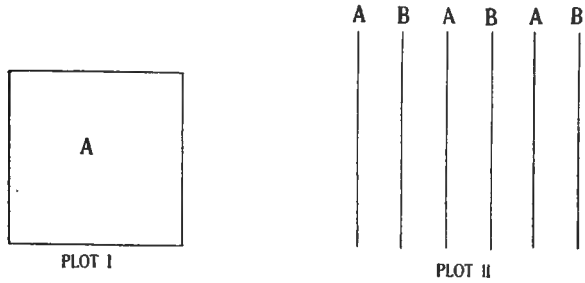


FIG. 37.—SHULL'S scheme of planting for making practical use of hybrid vigor in corn.

and the resulting grains in the A rows are all bound to be hybrids. Using these grains as seed for the crop, hybrid vigor will be obtained. At the same time both A and B are perpetuated in the pure condition, since the B rows in plot II are always self-pollinated, as there is no other pollen in that neighborhood. This is a very simple solution of the problem, without necessitating laborious hand-pollination.

The investigations and conclusions of EAST (2) may next be considered. SHULL did his work entirely with corn, but EAST investigated the problem in a more wholesale way. After assembling an extensive collec-

tion of data, he gives the summarizing statement that 59 out of 85 angiosperm crosses showed a noticeable increase in vigor. EAST of course did not continue to investigate all of these 85 types, but concentrated upon two representatives chiefly. Corn was selected as representing species normally cross-fertilized in nature, while tobacco was used as representing those species generally self-fertilized in nature. EAST'S results with corn need not be discussed, for they confirmed in every point SHULL'S results. One very valuable addition, however, was made; namely, that some crosses resulted in relatively less hybrid vigor than others. For this result EAST developed a very significant explanation, which has revolutionized ideas on hybrid vigor, and that is that hybrid vigor is proportional to the number of factors in which parents differ. This situation may be visualized from the diagram, in connection with which certain situations may be developed.

Parents		F_1
AABBCCDD × AABBCCdd	= AABBCC<u>Dd</u>	= little hybrid vigor
AABBCCDD × AABBccdd	= AABB<u>Cc</u><u>Dd</u>	= more hybrid vigor
AABBCCDD × AAbbccdd	= AA<u>Bb</u><u>Cc</u><u>Dd</u>	= still more hybrid vigor
AABBCCDD × aabbccdd	= <u>AaBbCcDd</u>	= most hybrid vigor

It is the F_1 generation of course that shows the vigor, but what index can be obtained from the germinal formula of the F_1 generation as to the amount of hybrid vigor that it will show? It is evident that the index is that hybrid vigor is proportional to the number of factors in the F_1 generation in the heterozygous condition. Thus in the first case shown in the diagram there is only a single heterozygous set (Dd), and the

result is little hybrid vigor. Following down the diagram it will be noted that 2, 3, and 4 of these heterozygous sets show an increasing amount of hybrid vigor. These are the facts which lie at the basis of EAST's theory which he calls *heterozygosis*. This term should not be confused with "heterosis," which is commonly used to express merely the fact of hybrid vigor.

We shall now consider how this conception of heterozygosis explained the phenomena that SHULL had previously discovered in reference to hybrid vigor.

1. The fact of hybrid vigor.—Heterozygosis claims that hybrids are vigorous because of the heterozygous sets.

2. The decrease in vigor after self-fertilization begins again.—The greatest loss in vigor comes between the F_1 and the F_2 generations. Thereafter the loss becomes gradually less each generation, approaching a definite limit when no more loss in vigor occurs. Heterozygosis explains this as follows:

AABBCCDD × aabbccdd
↓
AaBbCcDd

In this case the F_1 generation is 100 per cent heterozygous, all four sets being heterozygous, and therefore it is very vigorous. In later generations, as is well known, more or less homozygous sets will be split off. Introducing homozygous sets into some individuals will reduce the aggregate heterozygous condition of the whole crop to something less than 100 per cent; there will therefore be a corresponding loss in vigor. Mathematics will show why this loss is greatest between the F_1 and the F_2 generations. Thereafter the loss gradually approaches

the limit when the perfectly homozygous condition is reached for the whole population, and then there can be no more loss of vigor.

3. A cross between sister and brother effects nothing. —This is evident, for it introduces no heterozygosity.

4. "A cross between plants belonging to two self-fertilized families results in a progeny of as great vigor, size, and productiveness as are possessed by families which have never been self-fertilized."—Heterozygosis explains this by showing that a cross between two pure lines may bring into the hybrid a maximum number of heterozygous sets, quite as many as are normally present in normally cross-fertilized families.

5. Reciprocal crosses are equivalent.—This obviously follows from the theory of heterozygosis.

In connection with this work EAST was undertaking to discover the nature of hybrid vigor. In what respects are such hybrids vigorous? In reply to this question EAST offers the following analysis of hybrid vigor.

Primarily it is an increase and acceleration of cell division; in other words an increase in the power of assimilation. One can early observe a slight increase in the size of the cotyledons. The more rapid growth and earlier maturity of the seedlings is quite noticeable. Then one sees a distinct increase in the size of the roots. In the stem there is no increase in the number of nodes, but the internodal development is striking. Usually the stem growth is greater than the leaf growth, but the increase of the latter can be definitely traced. The size of the flower is usually not affected, nor is there any change in the size of small fruits, such as tobacco. In

fleshy fruits, such as tomato and eggplant, there is a marked increase. On the individual plant there are distinctly more flowers and fruits, and in some cases separate inflorescences are longer, such as the ears of corn.

EAST next studied tobacco as representing those species which are generally self-fertilized in nature. It is the common impression that tobacco is a striking exception in the matter of hybrid vigor. In tobacco crosses the hybrid progeny, instead of being more vigorous, are frequently less vigorous than either parent. EAST admits that there are certain cases of this kind, but points out a number of other cases which are quite normal. As yet there is no very satisfactory explanation of the tobacco situation, and we must be satisfied at present with the tentative conclusion that in tobacco there appear certain unknown limitations to hybrid vigor. In general it may be said that hybrid vigor appears prominently in species normally cross-pollinated in nature and less prominently in species generally self-fertilized in nature.

In this connection it should be stated that hybrid vigor is also manifested in some regions of the animal kingdom. It seems, however, that it is not so general a phenomenon among animals as among plants. In fact, many zoologists refuse to recognize in hybrid vigor any general law, pointing out the many cases among animals in which hybridizing apparently results in loss of vigor. It should be noted, therefore, that the present discussion of hybrid vigor applies primarily to plants and should not be extended in any general way to the animal kingdom.

Having considered the salient facts of heterozygosis, a statement by EAST on the "value of heterozygosis in evolution" is pertinent.

> It can hardly be doubted that heterozygosis does aid in the development of the mechanisms whereby flowers are cross-fertilized. Variations must have appeared that favored cross-fertilization. Those plants producing a cross-fertilized progeny would have had more vigor than their self-fertilized relatives. The crossing mechanism could then have become homozygous and fixed, while the advantage due to cross-fertilization continued. But was this new mechanism an advantage? It must have been often an advantage to the species as a whole. In competition with other species the general vigor of those which were cross-fertilized would aid in their survival. But the mechanism may not have been useful in evolving real vigor in the species, because of the survival of weak strains in combination. In self-fertilized species, new characters that weakened the individual would have been immediately eliminated. Only strains that stood by themselves, that survived on their own merits, would have been retained. On the other hand, weak genotypes in cross-fertilized species were retained through the vigor that they exhibited when crossed with other genotypes. The result is, therefore, that self-fertilized strains that have survived competition are inherently stronger than cross-fertilized strains. On this account weak genotypes may often be isolated from a cross-fertilized species that as a whole is strong and hardy.

Some recent investigations have furnished striking confirmation of the theory of heterozygosis. The work was done originally by COLLINS and KEMPTON (1), and later confirmed and extended by JONES (3). In brief it is as follows. If corn sporophytes exhibit heterozygosis, will the endosperm also show the same phenomenon? Endosperms, as has been stated, are genetically equivalent to sporophytes in several ways. If crossing increases

vigor and size of sporophytes, therefore, it might be expected to increase the size of endosperms also. Furthermore, endosperms have considerable advantage over sporophytes as material for such investigation. We say that hybrid sporophytes are more vigorous than pure-bred sporophytes, but just how much more vigorous cannot be stated with exactness. In order to demonstrate this clearly it would be necessary to have the hybrid and the pure-bred stock growing side by side in exactly the same conditions, but such conditions cannot be controlled with exactness. The environmental factors affecting the size and vigor of a corn plant are numerous, complex, and to a large extent uncontrollable. Thus two different plants, growing side by side, might be in a distinctly different environment without the fact being recognized. It cannot be said, therefore, with much certainty that one plant shows hybrid vigor and one does not when there are so many other unknown factors that might affect size and vigor. On the other hand, if it is claimed that the endosperm of one grain shows hybrid vigor while the endosperm of the grain next to it upon the same ear does not, the statement would be more exact, for the two endosperms have developed under conditions which are unquestionably much more constant than the conditions surrounding the different sporophytes in a cornfield.

JONES selected a plant with white endosperm and pollinated it with a mixture of its own pollen and pollen from a yellow endosperm race. In the mature ear, therefore, he had a mixture of yellow endosperm grains and white endosperm grains. The former grains of

course were hybrid, since the yellow factor was introduced by the foreign pollen, while the white endosperm grains must have resulted from "own" pollen and were homozygous. In this way JONES obtained side by side in the same ear endosperms obviously hybrid and endosperms obviously homozygous. When he weighed these two types he found that the hybrids exceeded the homozygotes in weight by from 5 to 35 per cent, or an average of 20 per cent.

He then made the reciprocal cross, using a similar mixture of yellow and white pollen on silks of the yellow race. Of course all the resulting endosperms were yellow, but the hybrids which had the yellow factor only from the female side were distinctly lighter yellow than the homozygotes which had the yellow factor from both male and female sides. Weighing these two types JONES obtained the same results as before, the hybrids exceeding the others in weight by an average of 20 per cent. This is the clearest demonstration of heterozygosis that has yet been given, for the conditions of the experiment were ideally constant.

The theory of heterozygosis accounting for the phenomenon of hybrid vigor is the one most generally accepted. Its claim is that hybrid vigor appears in proportion to the number of factors in which the parents of the cross differed.

This claim may be considered briefly. Is heterozygosis really an explanation of the phenomenon of hybrid vigor? It seems obvious that it is not. It was known that hybrids are vigorous because they are hybrids. Heterozygosis states that hybrids are vigorous to the degree that their parents differed in hereditary

factors; in other words, this is merely a statement that hybrids are vigorous because they are hybrids, with the addition that the more hybrid a hybrid is the more vigorous it is. It follows therefore that heterozygosis is not an explanation of hybrid vigor, but merely a restatement of the phenomenon in Mendelian terms, with the additional idea that there may be various degrees of hybrid vigor. It is not the intention to discredit heterozygosis as a valuable conception, but merely to point out that it is not a real explanation, merely a more intelligent statement of the facts. Restatements should not be confused with explanations.

A suggested explanation may be considered. In nature a "struggle for existence" occurs among species and individuals. There occurs also a struggle for existence among unit characters. If a unit character is undesirable it is eliminated, for the individual or species that carries it is eliminated. The unit characters, therefore, that have survived and appear in the plants of today are for the most part desirable ones, although some undesirable ones also may have survived, having been carried through in association with the desirable characters. The majority of unit characters today, however, may certainly be regarded as desirable ones, and a majority is sufficient for our present consideration.

The question may be raised as to what constitutes a desirable character. It may be any one of a number of things, but is there not some feature common to all desirable characters? The common feature of all desirable characters would seem to be vigor. Each desirable character must add somewhat to the vigor of

the plant that contains it, and if vigor is increased such things as size and productiveness will also be increased. Those plants, therefore, will be most vigorous which have in combination the greatest number of desirable characters, and it is obvious that the plants which have the greatest combination of such characters are hybrids.

A diagram similar to that which was used to explain heterozygosis may be considered:

P_1	P_2	F_1	
AABBCCDD ×	AABBCCdd	= AABBCCDd	= little hybrid vigor
AABBCCDD ×	AAbbccdd	= AABbCcDd	= still more hybrid vigor

In that explanation it was stated that the first case showed little hybrid vigor because it had only one heterozygous set (Dd), while the other case showed more hybrid vigor because it had three such heterozygous sets. Hybrid vigor, therefore, appeared in proportion to the number of heterozygous sets in the hybrid. This diagram served the purpose in explaining heterozygosis, but it will now be discarded because it does not represent the most important result when two races are crossed. The important result is represented in the following diagram:

	F_1	
P_1 – AABBCCddeeff P_2 – aabbccDDEEFF	AaBbCcDdEeFf	= more hybrid vigor
P_1 – AABBccddeeff P_2 – aabbCCDDeeff	AaBbCcDdeeff	= less hybrid vigor

The thought is that in each of these two cases the hybrid is more vigorous than either parent, not because it contains more heterozygous sets but because *it contains more positive, dominant factors*. For example,

in the first case each parent contains three factors, the small letters representing merely the absence of factors. The F_1 generation, therefore, contains six factors, and for this reason is more vigorous than either parent. It is stated in the diagram that in the first case there is "more hybrid vigor" and in the second case "less hybrid vigor," simply because hybrid vigor is a relative term. It represents merely how much more vigorous the hybrid is than either parent. In the first case the parents have three factors and the hybrid six, and the increase is three, which measures the amount of hybrid vigor. In the second case each parent has two and the hybrid four; the increase therefore is only two, and for this reason there is less hybrid vigor in the second case than in the first.

Assuming that the majority of factors are desirable, and the desirable factors make for general vigor, it would follow that the most vigorous plant will be the one containing the greatest number of positive factors. It has been shown that plants that contain the greatest number of factors are hybrids, and for this reason hybrids are more vigorous.

The following question may be raised. If it is granted that all desirable factors tend somewhat to increase the general vigor, do they all do this to the same degree? The obvious answer is in the negative, and this has no bearing upon the validity of the explanation. On the other hand, if heterozygosis be accepted for an explanation the question would present a difficulty. Heterozygosis would claim that Aa induces vigor, not because of any particular factor that it represents, but because it is a heterozygous set. It seems to

be more reasonable and accurate to suppose that certain factors induce more vigor than others. EAST recognizes this in the following statement: "This stimulus to development is cumulative up to a limiting point, and varies directly with the number of heterozygous factors in the organism, although some factors may have more powerful action than others."

It is obvious that the suggestion made above is that of a real explanation of hybrid vigor and not merely a restatement. It is rather an obvious explanation that has probably occurred to a number of geneticists. KEEBLE and PELLEW (5) suggested it in 1910, and since that time it has been somewhat discussed in the literature, being referred to as "the hypothesis of dominance (accounting for hybrid vigor)." At first statement the theory seems sound, but actually it does not fit the facts. The two chief objections to this theory of dominance may be found in the publications of SHULL, EMERSON, and EAST (2).

1. If hybrid vigor were due to dominance it would be possible in generations subsequent to the F_2 to recombine in one race all of the dominant factors. Thus there could be isolated a race that was "100 per cent vigorous," and since it would be homozygous its vigor would not be lost by inbreeding. Actually, though, hybrid vigor cannot be fixed in this way; "all maize varieties lose vigor when inbred."

2. Experience assures us that the distribution of individuals in the F_2 generation with reference to hybrid vigor is represented graphically by a symmetrical curve, similar to the normal probabilities curve; the class containing the greatest number of individuals is that

which shows the medium amount of hybrid vigor, while on either side of this class the fall in the curve is regular, reaching its lowest points in the two small extreme classes which show respectively greatest hybrid vigor and least hybrid vigor. According to the dominance hypothesis the largest class of the F_2 individuals would be that showing greatest hybrid vigor, while the smallest class would be that showing least hybrid vigor. The curve representing such a situation would be unsymmetrical and strikingly different from that which actually occurs.

For these two reasons the dominance hypothesis seems to have been discarded. Although it is theoretically attractive its failure to satisfy these two important details of the hybrid vigor situation has condemned it.

Very recently JONES (4) has ingeniously modified the dominance hypothesis so as to avoid these difficulties. At first consideration his theory seems to be clearly the most reasonable explanation of hybrid vigor that has yet been presented, although in time it may suffer from destructive criticism. The argument is essentially the same as that for the old dominance hypothesis, with the following important modification. Under the old hypothesis it was stated that in the cross AAbb × aaBB = AaBb the hybrid showed vigor because it combined the two dominant determiners AB. This met with the practical objections mentioned above. JONES visualizes the situation as represented in fig. 38. In this case it is a question of linkage. The vigor of one parent is due to the two dominant determiners A and D, while that of the other parent is due to the two dominant determiners C and B. The hybrid is more vigorous than

either because it combines all four dominant determiners. The attractiveness of this scheme is that it escapes the objections that were made to the older dominance hypothesis.

1. The fact that 100 per cent hybrid vigor cannot be fixed is quite in accordance with JONES'S scheme, for it is obviously impossible to isolate a homozygous race with all four factors A, B, C, and D.

2. A simple mathematical demonstration will show that the distribution of F_2 individuals is quite what it

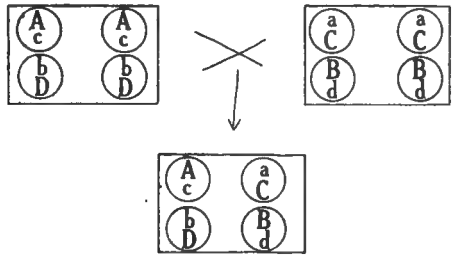


FIG. 38.—Diagram to aid in visualizing JONES'S explanation of hybrid vigor by dominance of linked factors.

should be, represented by a symmetrical curve similar to the curve of probabilities.

In fact this new theory, "the dominance of linked factors," seems altogether sound. We should reasonably expect that each chromosome would contain one or more dominant determiners (conducive to vigor) linked with one or more recessives.

The discussion has left the impression that hybrid vigor is to be explained by dominance (and linkage). In this day of factors and determiners such a hypothesis is quite appropriate. It may be, however, that in the

future such a phenomenon as hybrid vigor may be explained in terms of the stabilities and reactivities of the constituents of specific protoplasts.

In conclusion, attention should be called to the danger of confusing phenomena of hybrid vigor with those of cumulative factors. The two situations are somewhat similar, but careful consideration will discover distinct differences. It is perhaps unsatisfactory to assume absolute lack of dominance in the case of cumulative factors and the essential presence of dominance (partial at least) in explaining hybrid vigor. Such assumptions, however, are not necessarily contradictory. The two things should be recognized as distinct phenomena, although they are at work simultaneously and probably interact to give complex results.

1. COLLINS, G. N., and KEMPTON, J. H., Effects of cross-pollination on the size of seed in maize. U.S. Dept. Agric. Circular 124. 1913.
2. EAST, E. M., and HAYES, H. K., Heterozygosis in evolution and in plant breeding. U.S. Dept. Agric., Bur. Pl. Ind. Bull. 243. pp. 68. *pls. 8.* 1912.
3. JONES, D. F., Bearing of heterosis upon double fertilization. Bot. Gaz. 65:324–333. *figs. 3.* 1918.
4. ———, Dominance of linked factors as a means of accounting for heterosis. Genetics 2:466–479. 1917.
5. KEEBLE, F., and PELLEW, C., The mode of inheritance of stature and of time of flowering in peas (*Pisum sativum*). Genetics 1:47–56. 1910.
6. SHULL, G. H., Hybridization methods in corn breeding. Amer. Breeders Mag. 1:98–107. 1910.

CHAPTER XVII

SEX DETERMINATION

The subject of sex determination must be included in any consideration of genetics, but it is extensive enough as measured by the amount of investigation to form the subject of a book. In consequence in this connection it can only be given brief consideration. The current theories of sex determination fall naturally into two general categories:

1. Many biologists believe that sex is predetermined by the chromosome equipment that enters into the zygote.

2. Other biologists believe that sex may be determined otherwise than by chromosomes; that it may be determined at fertilization, or before, or even afterward; in any event, that it is not the chromosomes that determine sex but some general physiological condition.

These are the two schools in regard to sex determination; in fact, each school includes a number of theories, but the fundamental idea in each group is the same. These two general views will be referred to as the chromosome theories and the physiological theories. Representative examples of each will be given first, and since sex determination has been investigated more thoroughly and for a much longer time in animals than in plants the illustrations will be taken from animals.

CHROMOSOME THEORIES.—A classic example of the simplest kind is found in the nematode worms. Fig. 39 will indicate how sex is determined in this case. The mechanism is obvious. Both male and female have ten

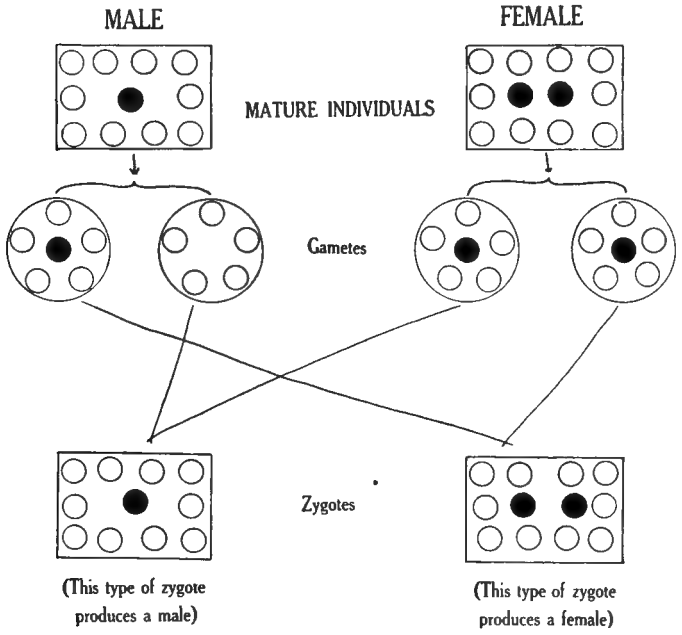


FIG. 39.—Illustrating behavior of sex chromosomes

chromosomes to determine most of their somatic characters; but in addition there are extra chromosomes that determine sex, known variously as *sex chromosomes*, *x chromosomes*, and *heterochromosomes*. In this case the male contains only one sex chromosome while the female contains two. At the reduction division, connected with gamete formation, the chromosome equipment

is reduced one-half. It is obvious that in the female each egg receives one sex chromosome, and therefore all eggs are alike in this feature. In the male, however, with one sex chromosome, at the reduction division the solitary sex chromosome goes to one pole, leaving the other pole without such a chromosome. As a result there are two kinds of sperms, one half containing a sex chromosome, the other half containing none. At fertilization, if an egg mates with a sperm having a sex chromosome the zygote contains two, and this results obviously in a female, for females are characterized by two sex chromosomes. With a sperm of the other type, the zygote receives only one sex chromosome and must produce a male individual. As a result males and females are produced in equal numbers, and sex is determined by the type of sperm that enters into the sex fusion.

In such cases females are homozygous for sex and males are heterozygous, for in the male the sex chromosome is paired with its absence. This is the commonest situation, although it would be theoretically possible to have females heterozygous for sex, having the single chromosome, while the male had a pair. In this case sex would be determined by the type of egg that entered into the sex fusion. In addition, there are cases where one sex has one sex chromosome and the other sex has none. Finally, there are cases in which one sex has a pair of large chromosomes, while the other sex has one large and one small sex chromosome. In all of these cases, however, the fundamental mechanism is the same. Either male or female (commonly the former) is heterozygous for sex, producing two kinds of gametes, as

shown by the chromosome situation. Sex, therefore, is predetermined by the kind of gamete that enters into the sex fusion.

This statement represents the chromosome theories of sex determination, according to which it seems evident that sex is absolutely predetermined. Outside conditions can effect no change, and therefore sex cannot be controlled. It results, therefore, with mathematical precision in 50 per cent males and 50 per cent females, just as a Mendelian ratio comes out 3:1.

PHYSIOLOGICAL THEORIES.—In 1906 RICHARD HERTWEG (5) performed some sex determination experiments with frogs. The eggs are laid free in the water before fertilization, so that they furnish unusually good material for such experiments. Normally the eggs are fertilized very soon after they are laid, with the result that the progeny consists of approximately 50 per cent males and 50 per cent females. HERTWEG took some of these eggs and allowed them to overripen before fertilization took place; that is, he put aside some eggs as soon as they were laid and allowed them to remain unfertilized for an unusually long period. While these eggs were standing in the water he found that they absorbed an unusual amount of water, and the obvious conclusion was that very ripe eggs show high water content. He then allowed these overripe eggs to be fertilized, and the resulting progeny were 100 per cent males. His conclusion was that sex was not determined by the chromosome equipment, but by the physiological conditions in the egg, high water content resulting in males.

This theory was confirmed in a striking way in 1912 by Miss KING (7), who performed the converse of

HERTWEG's experiments, using toads' eggs. Taking some newly laid eggs she withdrew water from them, then allowed them to be fertilized, and the resulting progeny were 90 per cent females. The obvious conclusion is that eggs with low water content produce females.

Finally, there is the remarkable work of RIDDLE (11) with pigeons. HERTWEG and Miss KING had found that sex is determined by the physiological factor of water content. RIDDLE has investigated a little more critically, analyzing the physiological conditions of both male and female, and gives the following contrast:

Male	Female
High percentage of water	Low percentage of water
Low percentage of fat	High percentage of fat
Low percentage of phosphorus	High percentage of phosphorus
High metabolism	Low metabolism

It appears from this that high water, low fat, and low phosphorus are male attributes or conditions, while the female attributes are the reverse. The main feature of difference, however, to which the other contrasting conditions are subordinate is that the male shows high metabolism and the female low metabolism. The idea is that any physiological conditions that affect water content or fat content or phosphorous content in the egg will affect the sex in the resulting progeny.

Following these ideas, RIDDLE was able to control sex by various means; furthermore, he makes the somewhat startling statement that sex is a quantitative phenomenon; that is, the difference between male and female is a difference in degree only. A diagram (fig. 40) will illustrate the situation. It represents a

graduated scale based on relative water, fat, and phosphorous content. The egg may be at any point on the scale, and the sex of the individual produced by the egg will depend upon its position on the scale. An egg in any position to the left of the middle results in a male and to the right in a female. It should be noted, however, that if the egg is near one of the extremes the progeny will be either a very masculine male or a very feminine female; while if the egg lies near the middle point, on one side or the other, the progeny will be a

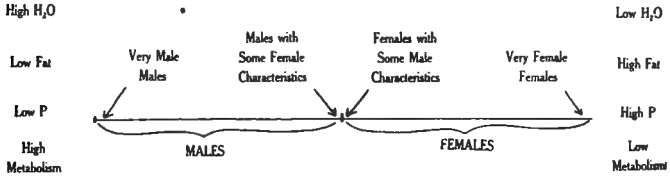


FIG. 40.—Illustrating RIDDLE'S idea of sex. Sexes differ only quantitatively, and it is possible to find various degrees of maleness and femaleness at different points along the scale.

male with some female characteristics or a female with some male characteristics; in other words, a feminine male or a masculine female. In fact, RIDDLE is actually able to bring this about, obtaining at will males with all degrees of maleness, etc. He even suggested at one time that when we learn more about this method of sex control we might be able to eliminate from human society such undesirables as the effeminate man or the masculine woman.

There are three possible conclusions in reference to these contradictory theories: (1) an acceptance of the one and rejection of the other; (2) the claim that both amount to the same thing, that is, that they express the

same fundamental facts in different terms or by the use of different indices; (3) the claim that both are true but cover different territories; that one of them explains certain types of cases and the other explains other types of cases. At present the third alternative seems to be the most reasonable and least difficult of explanation.

In view of the evidence on both sides one can hardly say that either the chromosome theory or the physiological theory is absolutely wrong. Again, to interpret either theory in terms of the other is theoretically very difficult. The cytologists certainly present a striking demonstration of the chromosome theory, showing the sex chromosomes and the constant occurrence of the proper numbers in a given sex. They also show the machine at work with its inevitable sex product of 50–50; and of course they are logical in concluding that sex cannot be controlled.

On the other hand, the physiologists show just as clearly that sex can be controlled artificially; by changing the chemistry or physics of the situation they change the sex. This of course is cytologically unorthodox; and as a consequence some cytologists have attempted to clear up the situation by the following claim. Granted that certain chemical changes may change the sex, the result is due to the fact that the mitotic figures are disturbed and the sex chromosome situation changed. It is always the sex chromosomes that determine sex, but they may rearrange themselves in consequence of abnormal chemical stimuli. Such an explanation seems like the last resort. One might imagine that the nucleus might cast out a sex chromosome and thus change an expected female into a male; but to make the change in

the other direction the nucleus would have to manufacture an additional sex chromosome, which is difficult to imagine. It seems safe to conclude, therefore, that physiological conditions determine sex in some cases and sex chromosomes determine sex in other cases.

With this background we will consider briefly such work as has been done with plants. In the first place, the sex chromosome has not been established for plants. SYKES, DARLING, STRASBURGER, and others have searched for it diligently but with negative results. It is true that certain forms show odd chromosomes, such as *Ginkgo*, *Galtonia*, *Melandrium*, *Fagopyrum*, and *Houstonia*, but they have never been satisfactorily connected with sex. The most hopeful work has been done by ALLEN (1) with *Sphaerocarpus*, which will be mentioned later. It must not be concluded, however, that the chromosome theory of sex determination does not hold for plants. Many cytologists fully expect sex chromosomes to be demonstrated in plants, and at present they point out certain indirect indications of the chromosome situation, such as the even separation of sexes at the reduction division. The theory therefore is firmly believed by many plant cytologists, even though the sex chromosome situation has been established in no plant. Attention may be called to the fact, however, that plants differ from animals in ways that present obstacles to the chromosome theories of sex. Without discussing these obstacles fully attention may be called to two of them.

In the first place, hermaphroditism is very common in plants, and this is difficult to explain in terms of the sex chromosome theory. In the second place, all the

higher plants exhibit alternation of generations, a phenomenon practically unrepresented in animals. In attempting to apply the sex chromosome theory through the life-history of such a plant, with its alternation of generations and heterospory, great theoretical difficulties are encountered. In general, therefore, we reach the conclusion that the sex chromosome theory has not been established in plants and that certain obstacles seem to stand in the way of its establishment.

On the other hand, no very general physiological theory has been established; in short, sex determination in plants is not yet well understood. A few suggestive facts are known, however, and when more facts are available some general theories doubtless will be developed. A general survey of the plant kingdom will show the suggestive facts that are available.

ALGAE.—No conclusive work has been done with this group, but some of the experimental work of KLEBS (8) suggests that sex may be controlled in algae.

FUNGI.—Mention will be made only of the work of BLAKESLEE and BURGEFF. In his experimental work with *Mucor*, BLAKESLEE (2) found in general three different sexual types of mycelia, two of which he called plus and minus strains. Although they looked alike in every particular, he concluded that they were sexually different for the following reason. Neither strain by itself is capable of producing zygotes, but when plus and minus strains are brought together sexual branches from the one meet sexual branches from the other and produce abundant zygotes. The natural conclusion is that BLAKESLEE'S plus and minus strains represent the male and female conditions, although the

sex cannot be distinguished. The third type of mycelium he called the neutral strain. Although this cannot produce zygotes by itself it does produce them when mated with either a plus or minus strain. Evidently, therefore, the sex branches from the neutral strain contain both male and female potentialities.

The answer to the question as to where and how sex is determined in these forms involves a number of possibilities. When a zygote germinates, one or more sporangia are produced very early, and this raises the question as to the sexes developed. In *Mucor* itself the segregation of sex is evidently completed before the formation of the spores in the sporangium, for all the spores in a given sporangium are of a given strain, producing either male or female mycelia. The sporangium as a whole, therefore, is either male or female. In *Phycomyces*, however, a different behavior is regular. The zygote produces a sporangium, but the sporangium is not completely of one sex. It produces three types of spores: spores producing the plus strain, spores producing the minus strain, and spores producing the neutral strain. The plus strain then perpetuates only plus strains through its spores, which means that the sex is fixed in this case. The minus strain behaves in the same way. The neutral strain, however, produces spores of all three types, an interesting situation, for it suggests the Mendelian segregation. The *Mucor* group deserves to be studied further for suggestions as to sex determination.

The work of BURGEFF (3) is brief but striking. He took BLAKESLEE'S plus and minus strains and found that they always bred true to their plus and minus

conditions. Then by using some remarkable technique he grafted parts of one strain on to the other, and the result was a neutral strain. This seems surprising for the moment, but when it is remembered that *Mucor* is coenocytic the result is what might be expected, for the two sets of nuclei can mingle freely.

LIVERWORTS.—A great deal of experimental work has been done with this group, but only one conclusive result has been obtained. In dioecious liverworts, as *Marchantia*, the sexes appear in about equal numbers. It is natural for cytologists to conclude from this that sex is determined at the reduction division in the formation of spores. Thus when a mother-cell produces a tetrad, two of the spores would produce male gametophytes and the other two female gametophytes. This of course was an assumption, for no sex chromosome was discovered, nor was it known that the spores of a tetrad always divide in this 50–50 way as to sex.

The assumption was strengthened by some work by NOLL (10). He found that gemmae from male gametophytes always produce male gametophytes, while gemmae from female gametophytes always produce females. This established the fact that in the mature gametophyte sex has been fixed, but it did not indicate where it had been fixed.

It remained for STRASBURGER (13) to answer this question. He selected *Sphaerocarpus*, which is peculiarly favorable material for such work. It is dioecious, like many liverworts, but a remarkable feature is that the spores hang together in the tetrad. Ordinarily when spores are mature the tetrads are no longer distinguishable. Sowing such free spores one may get the

50–50 ratio of males and females, but it cannot be inferred that the sexes are evenly divided in every tetrad; it may have been only an equal division in the capsule as a whole. If, for example, the upper half of a capsule produced all females and the lower half all males, sex would not have been determined at the reduction division, where, according to the sex chromosome theory, it is determined. *Sphaerocarpus*, therefore, gave STRASBURGER an opportunity to determine this situation, for he was able to isolate mature individual tetrads, the four spores hanging together. He sowed these tetrads in separate pots, obtaining four gametophytes in each case. The experiment was conducted upon rather a large scale, and the results were strikingly constant. Two male and two female gametophytes were always produced from a tetrad. This certainly established the fact that in this case sexes were evenly separated at the reduction division, and indicated strongly that the sex-chromosome theory applies in this group. What these facts established for *Sphaerocarpus* has been taken for granted for the other dioecious liverworts.

Recently ALLEN (1) has claimed to have demonstrated the *x* chromosome in *Sphaerocarpus*. He says that one large chromosome, exceeding in length and thickness the other chromosomes, characterizes the cells of the female gametophyte, while the cells of the male gametophyte are characterized by one very small chromosome. His investigation seemed to show that in spore formation two of the spores of the tetrad receive the large chromosome, and the other two the small chromosome. These chromosomes have not been defi-

nitely connected with sex determination, but the situation is most suggestive.

The sex chromosome theory cannot apply, of course, to the monoecious liverworts, where the sexes must be separated at a much later period than the reduction division. In these cases obviously every spore contains the potentialities for both sexes, and the two are separated in connection with some of the vegetative divisions of the bisexual gametophyte. In some species of *Riccia* we know that a developing gametophyte produces only antheridia for a time and at a later period produces archegonia only. The structural basis of this change is not known nor the exact point at which it occurs.

MOSSES.—A single very significant piece of work by MARCHAL (9) will be mentioned. *Funaria* is a dioecious moss, and hence it may be assumed that the sexes are separated at the reduction division in the formation of spores. Each spore carries the potentialities for one sex only; but of course the sporophyte as a whole before the reduction division must carry the potentialities for both sexes. MARCHAL, by a peculiar technique of his own, clipped a fragment from a young sporophyte and induced it to reproduce aposporously; that is, the sporophyte fragment produced a gametophyte directly. The fragment must have contained the potentialities for both sexes, since it consisted of tissue in which reduction division had not yet occurred. Logically the gametophyte should be bisexual, producing both antheridia and archegonia, and this was the result obtained. It is quite in accord with the sex chromosome theory and is a striking confirmation of it.

PTERIDOPHYTES.—In this group we are confronted by a new complexity. In the preceding groups it was necessary to consider separately monoecious and dioecious forms, assuming that in the latter the sexes are separated at the reduction division. In the higher Pteridophytes, however, heterospory appears, and establishes once for all the dioecious condition in the gametophyte generation. In heterosporous forms therefore the gametophytes are always dioecious, but it cannot be said that the sexes are separated at the reduction division. Obviously no such claim can be made, for it would have to assume that each tetrad consists of two megaspores and two microspores, a thing which probably never occurs, unless possibly in *Equisetum*, which should be investigated. It is safe to conclude therefore that sex in heterosporous forms is differentiated before the reduction division. A megasporangium produces only megaspores, although in doing so the reduction division occurs. In *Selaginella*, which is perhaps the best example, one can distinguish a megasporangium from a microsporangium as soon as the mother-cells are formed. Clearly the sexes are separated before the reduction division. In attempting to explain this situation cytologists claim that the sexes are separated at one of the vegetative divisions of the sporophyte previous to the formation of mother-cells. This is merely an assumption and an extremely unsatisfactory one, for only in connection with the reduction division is there a proper mechanism for the separation of sexes according to the sex chromosome theory. Furthermore, at present there is just as good reason to believe that sex in *Selaginella* is determined by physiological conditions.

Before leaving Pteridophytes the homosporous forms, notably the true ferns, should be considered briefly. In the ordinary bisexual fern prothallium, antheridia and archegonia appear, as was described for *Riccia*. A young prothallium can produce antheridia only, while a mature prothallium produces archegonia only. These facts are interpreted in two ways. From the physiological standpoint it is claimed that more nutrition is required for the production of archegonia and eggs than for the production of antheridia and sperms. Young prothallia, therefore, have not the nutritive capacity to produce archegonia and can produce antheridia only. Mature prothallia, of course, have a greater nutritive capacity and can produce archegonia. This nutrition theory has now considerable vogue and is applied not only to ferns but also to other plant groups.

Another interpretation is given by cytologists. They claim that the sexes are separated by some sex chromosome mechanism at some one of the vegetative divisions midway in the life of the prothallium. This claim is difficult to accept on account of what it involves. In accordance with this view a cell division occurs, so that thereafter only archegonia will be produced; while before this division only antheridia were produced. It is hard to understand how a cell division can affect the sex of its ancestors, the cells that came before. This difficulty is avoided by saying that a sex chromosome whose presence determines maleness drops out of existence at this intermediate cell division, so that only archegonia could be produced thereafter. The physiological claim certainly seems to be the more reasonable one in this instance.

There is an apparently easy experiment which should test these claims and decide between them, but as yet it has not been performed. Fern prothallia are known at times to produce proliferations which reproduce the parent prothallium vegetatively. If a proliferation could be produced on the archegonium-bearing region of a mature prothallium its sexual behavior should throw much light upon this problem. According to the physiological claim, this proliferation should first produce antheridia, for it will pass through a young stage of low nutritive capacity. According to the cytological claim the cells from which the proliferation arose have female potentialities only, and therefore the proliferation should never produce antheridia but only archegonia.

SEED PLANTS.—Most of the work on sex determination has been carried on with seed plants. Experiments have been performed to show the effect of manuring, light, temperature, and other environmental factors on the sex ratio. The results have been both positive and negative. Some conclude that sex is rigidly predetermined in the seed, while others claim that it is determined by the later environmental conditions. The general results are not conclusive, so that they may be passed by with this brief statement.

There are certain theories of sex determination, however, with which every botanist should be familiar, for they are an important part of botanical literature. They may be stated briefly.

CORRENS (4) thought that sex was determined at the reduction division of the pollen mother-cell. Two pollen grains are produced having female tendencies and two having male tendencies. The sex of the progeny,

therefore, depends upon which kind of pollen grain functions. Such an idea, of course, would be quite in keeping with a sex chromosome theory, where the male is the heterozygote for sex.

STRASBURGER (13) took exception to this view. He thought that the phylogenetic development of the seed plants had completely separated the male and female tendencies through heterospory. As a consequence, he would regard CORRENS' idea that half the pollen grains have female tendencies as impossible. STRASBURGER'S idea is that the pollen mother-cell develops pollen grains with stronger and weaker male tendencies, while the megaspore mother-cell develops eggs with stronger and weaker female tendencies. It is therefore the algebraic sum of the two as they meet in fertilization that determines the sex of the progeny. If a pollen grain with strong male tendencies fuses with an egg with weak female tendencies the progeny will be male, and similarly for the other combination. This flavors of RIDDLE'S work. Just what would happen if two strong male and female tendencies should meet would be interesting.

STRASBURGER'S strongest evidence for this theory is his classic experiment with *Mercurialis annua*, with which every botanist should be familiar. *Mercurialis* may be called imperfectly dioecious. Certain plants are prevailingly female but bear a few weak male flowers. It would seem as though the female tendencies of such a plant are stronger than the male. When such a plant is inbred, using pollen from the weak male flowers on the stigmas of the strong female flowers, the resulting progeny is 100 per cent female, which is in accordance

with the theory. Other plants are prevailingly male but bear a few weak female flowers, and inbreeding in this case results in 100 per cent males. Finally, there are occasional plants which are evenly monoecious; that is, half of their flowers are strong males and the other half strong females. From inbreeding such a plant, the resulting progeny is 50 per cent male and 50 per cent female. It is obvious that from such results STRASBURGER would be convinced of his theory of male and female tendencies.

Such a theory involves too much of RIDDLE's quantitative idea to be acceptable to cytologists. They seem confident that sex determiners will be demonstrated eventually as distinct physical entities and that such phrases as "male and female tendencies" will disappear.

It will be interesting to apply STRASBURGER's theory to cases of parthenogenesis and vegetative apogamy and discover the difficulties encountered. In the first place, in monoecious forms it is found that a parthenogenetic egg produces a monoecious plant. Should it not produce a strictly female plant, because eggs contain only female tendencies? STRASBURGER avoids this difficulty by saying that these parthenogenetic eggs are diploid; hence they are not truly eggs but merely sporophyte cells. The process of producing the new plant, therefore, is merely vegetative multiplication, which would naturally perpetuate the tendencies of the parent body. The parent was monoecious, and quite properly the progeny of a diploid egg should be monoecious.

STRASBURGER used this same situation to confirm his theory. In dioecious forms parthenogenetic eggs should produce only female plants. As a matter of fact this is true, as STRASBURGER shows by a number of

examples. The dioecious *Thalictrum*, however, behaves differently in cases of parthenogenesis. The progeny are sometimes female, but just as often they are male. This situation deserves further investigation. There is no question but that STRASBURGER'S theory is ingenious, reasonable, and promising.

A striking bit of work on sex determination was done by CIESIELSKY (14) of Lemberg, who worked with *Cannabis sativa*, the Indian hemp. When he used pollen fresh from the anthers the progeny were 85 per cent males. When he took pollen from the anthers and allowed it to stand for twelve hours or more before using it the resulting progeny were 92 per cent females. The conclusion is obvious that fresh pollen results in males and stale pollen results in females. This can be combined with STRASBURGER'S idea, for one might expect fresh pollen to show stronger male tendencies than stale pollen. CIESIELSKY'S work deserves to be repeated upon a more extensive scale.

Probably the most unorthodox behavior of sex is that which was rather recently described in the Papaya (6). A few cases were described in which male Papaya trees had been cut back. The whole head of the tree had been cut off, eliminating all of the male flowers. When new branches put up from the cut trunk they bore in some cases hermaphrodite and in other cases prevailingly female flowers. That sex could be so completely changed by such an operation was incredible. Further examination showed that this result was not always obtained and that in fact there were only a few such cases on record. Most botanists today doubt the validity of this reported behavior.

We have a suggestion of the same sort of behavior in the case of begonias. Gardeners claim that in *Begonia* one can secure female flowers by pinching off the male inflorescences, female inflorescences developing later in the same place. One gardener, at least, has been practicing this remarkable process for some years.

In concluding this brief survey of sex determination in plants it is obvious that some of the evidence points to the sex chromosome theory, while other evidence points to some physiological theory. It is perhaps best at this time to conclude that one theory holds for certain cases and the other theory for other cases.

This topic should not be left without mention of the classic experiments of CORRENS and SHULL. CORRENS (4) crossed the dioecious *Bryonia dioica* with the hermaphroditic *B. alba*, while SHULL (12) crossed *Lychnis dioica* with hermaphroditic mutants from the same. The sexual behavior of the progenies in the two cases was not identical, but both suggested a sex chromosome theory, with the male heterozygous for sex. The theoretical explanations are so complex and dubious that they cannot be conveniently discussed here; but the experiments themselves represent a very significant type of work.

1. ALLEN, CHARLES E., A chromosome difference correlated with sex differences. Science **46**:466–467. 1917.
2. BLAKESLEE, A. F., Sexual reproduction in the Mucorineae. Proc. Amer. Acad. **40**:205–319. 1904.
———, Differentiation of sex in thallus gametophyte and sporophyte. Bot. Gaz. **42**:161–178. 1906.
3. BURGEFF, H., Über Sexualität, Variabilität, und Verebung bei *Phycomyces nitens*. Ber. Deutsch. Bot. Gesell. **30**:679–685. 1912.

4. CORRENS, C., and GOLDSCHMIDT, R., Die Verebung u. Bestimmung des Geschlechts. Berlin. 1913.
5. HERTWEG, R., Verhandl. Deutsch. Zoöl. Gesell. 1906; see also Biol. Centralbl. **32**:1. 1912.
6. HIGGINS, J. E., Growing melons on trees. Jour. Heredity **7**: 208–220. *figs.* 7. 1916.
7. KING, H. D., Jour. Exp. Zoöl. **12**:19. 1912.
8. KLEBS, G., Über Probleme der Entwicklung. Biol. Centralbl. **24**:8–9, 14–15, 257–267, 289–305, 444–614. 1904.
9. MARCHAL, EL. et EM., Aposporie et sexualite chez les Mousses. I, II, III. Bull. Acad. Roy. Belgique. Cl. Sci. 1907. 765–789; 1909. 1249–1288; 1911. 750–778.
10. NOLL, FR., Vorläufiger Abschluss der Versuche über die Bestimmung des Geschlechts bei diöcischen Pflanzen. Sitzungsber. Niederrh. Gesell. Bonn. Naturwiss. Abt. 1907. S. 68.
11. RIDDLE, OSCAR, The control of the sex ratio. Jour. Wash. Acad. Sci. **7**:319–356. 1917.
12. SHULL, G. H., Reversible sex mutants in *Lychnis dioica*. Bot. Gaz. **52**:329–368. 1911.
13. STRASBURGER, E., Versuche mit diöcischen Pflanzen in Rüchsicht auf Geschlechtsverteilung. Biol. Centralbl. **20**: 657. 1900.
———, Über geschlechtbestimmende Ursachem. Jahrb. Wiss. Bot. **48**:427–520. 1910.
14. WESTER, P. J., The determination of sex. Jour. Heredity **5**:207–208. 1914.

CHAPTER XVIII

THE BEARERS OF HEREDITARY CHARACTERS

The conclusion reached in the preceding chapter was that sex may be determined by chromosomes, but that it also may be determined by physiological conditions. To the geneticists this suggests the following question: If the sex character may be determined by physiological conditions, why may not other plant characters be determined in the same way? In other words, this opens up the general question of the chromosome hypothesis in reference to inheritance. It has been taken for granted in the preceding discussion that chromosomes are the bearers of hereditary characters, but is this position altogether justifiable? It will be well to consider some of the arguments for and against the claim that chromosomes are the bearers of what are called hereditary characters.

ARGUMENTS IN FAVOR OF THE CHROMOSOME HYPOTHESIS

This evidence will be considered under two heads, namely, that from cytology and that from breeding.

CYTOLOGY.—(1) The program involved in the ordinary mitotic division is very suggestive evidence. We discover a very exact mechanism worked out, the result of which is to divide the chromosomes evenly, so that each daughter-nucleus receives an exactly similar set of chromosomes, a set exactly similar to the original one in the mother-nucleus. These chromosomes are

thus carefully divided and evidently perpetuated without alteration. Furthermore, nothing else can be discovered in the cell which is so carefully divided and perpetuated without alteration. It is natural to conclude, therefore, that chromosomes are the bearers of hereditary characters, for if these bearers were anything that is not so carefully divided inheritance would be chaos instead of the remarkable cosmos it is.

(2) The behavior of chromosomes in the reduction division is a remarkable piece of evidence. The fundamental features of this division are so familiar that they need not be repeated. It is sufficient to say that reduction division supplies a remarkable mechanism which explains perfectly MENDEL'S theory of segregation. This remarkable coincidence of the observed cytological facts with the preconceived theoretical explanation of inheritance is probably the strongest argument in favor of the chromosome hypothesis.

(3) An argument may also be obtained from the cytology of fertilization. In the higher plants the contributions of male and female to the structure of the zygote are as follows. The egg contributes a nucleus plus a portion of the cytoplasm in the embryo sac, which may well contain many types of cell constituents. The male, however, contributes only the nucleus stripped of its cytoplasm. It is safe to infer that the male contributes quite as much to the offspring as the female, at least in the matter of hereditary characters, so that the conclusion may be that hereditary characters are carried entirely in the nucleus. Many cytologists claim that the nucleus is entirely made up of chromatin, and since chromatin is the material of

which chromosomes are composed the male contributes only chromosomes to the progeny, and judging from breeding results the female contributes nothing more. Thus by elimination the conclusion is reached that chromosomes are the bearers of hereditary characters.

(4) In addition to the foregoing arguments there are some minor cytological evidences that confirm the chromosome theory. Tetraploid sporophytes, that is, sporophytes with twice the normal number of chromosomes, have appeared as mutants, as in *Oenothera*, or in apospory, as in MARCHAL'S mosses; such sporophytes are distinctly larger and more vigorous than their normal ancestors. This is indirect confirmation of the chromosome hypothesis. Many hybrids are sterile, and in some cases cytology shows that this sterility is the result of, or at least associated with, a chaotic condition of the chromosomes in the germinal tissue of the hybrid, while everything else in the hybrid seems normal.

BREEDING.—(1) MENDEL'S theory of segregation, which must be regarded as well established, requires that the bearers of hereditary characters must behave in a certain particular way at maturation of the gametes. This necessary behavior is found to occur quite regularly among the chromosomes at the reduction division, and nothing but chromosomes can be shown to behave in this way.

(2) Mention has been made of MORGAN'S unique work on linkage and crossing over. It is only necessary to say that his unusual results are associated with observed irregularities in the behavior of chromosomes, and furnish strong confirmation of the chromosome hypothesis.

(3) If chromosomes bear hereditary characters, and there are only two pairs of chromosomes in a plant, the result would obviously be nothing above the dihybrid ratio. Although the plant might show many more than two Mendelian characters these characters should be linked into two groups and dihybrid ratios result. If trihybrid ratios were obtained, one should have to conclude that something else than two pairs of chromosomes was involved. It is a mechanical necessity that *the ratios should not exceed the number of chromosomes.* For example, do we ever have pentahybrid ratios in a plant with four pairs of chromosomes? This question cannot be answered fully for plants, because all the plants used in experiments have an ample number of chromosomes to account for the highest ratios discovered. In MORGAN'S fruit fly, however, there are actually only four pairs of chromosomes, and in all the great mass of data collected on inheritance in the fruit fly tetrahybrid ratios occur regularly, but pentahybrid ratios never.

(4) Finally, the fact that the chromosome hypothesis is coming into more and more use in plant-breeding is a general evidence in its favor. The plant breeder does not usually question whether the theory of inheritance he uses is true or false, but merely whether it is useful or barren in leading to new results or connecting up known facts. On this basis the chromosome hypothesis is proving very useful.

ARGUMENTS AGAINST THE CHROMOSOME HYPOTHESIS

(1) Without going into details the general fact may be stated that the chromosome hypothesis does not

appeal to many of the most prominent physiologists and physiological chemists.

(2) Physiological chemists claim that chromosomes in all plants are chemically identical. If chromosomes differ so much in the factors they carry, one should expect them to show some chemical differences in the various races of plants, but they show no such differences. On the other hand, there are other plant constituents that show a remarkable chemical specificity. Plant proteins, for example, are chemically different in about every plant species. Plant starches, also, have been shown to be peculiar in their chemical constitution to the race of plants in which they occur. It is natural to ask why are not these proteins and starches, with their remarkable specificity, more like what the carriers of hereditary characters ought to be than the chromosomes which are chemically the same throughout the plant kingdom.

(3) Such work as that of RIDDLE is directly against the chromosome hypothesis. If it is found that characters which were supposed to be determined by chromosomes can be controlled artificially by regulating the physiological conditions, it makes one conclude that chromosomes are not of controlling importance in inheritance.

(4) Finally, there is the growing impression that chromosomes are consequences instead of causes. Instead of actually determining hereditary characters, chromosomes may well be merely a rather useful superficial index of the hereditary situation. It may be that this is all the claim made for the chromosome hypothesis by many cytologists. In this connection we may

quote from WILSON (3): "For the present, at least, all the requirements of investigation are met if we think of the chromosomes, or that which they carry, only as *differential factors* in heredity, not as primary or exclusive 'determiners.'" It is a very dominant conception in biology today that all plant and animal phenomena are to be explained ultimately on a physico-chemical basis. Cytology, therefore, should not be satisfied with observing and recording the peculiar contortions of chromosomes in their different phases. Such a study is justified only in so far as it furnishes some useful working hypotheses. The ultimate thing to be striven for is to be able to control plants and animals artificially, and this can be done only by understanding the physics and chemistry that underlie the chromosomes as well as all other life-phenomena.

With this presentation of the arguments for and against the chromosome hypothesis of inheritance, a conclusion seems to be difficult, but a suggestion may be made that seems reasonable and may be useful. That chromosomes are the visible bearers of hereditary characters is probably true, at least in most cases upon which there are data. Chromosomes, however, are not the ultimate things; behind lies the physico-chemical background, and it is this which is the ultimate aim of biology to understand.

Such a statement may seem unsatisfactory. It has been said that chromosomes determine sex in some cases and that physiological conditions determine sex in other cases; then it was inferred that the same may be true of other plant characters as well. Can we not unify these two alternative conclusions in some single theoretical

scheme? Two attempts to devise such a unifying conception will be presented briefly for what they are worth. Both are highly theoretical.

The first of these theories is rather simple, sketching a picture which is easy to visualize as a whole but is inexact in its detail. Sex determination may be taken as an example of the more general situation. The determination of sex may be likened to a pair of balances. If one side goes down a male is the result; if the other side goes down a female is the result. What are the weights that operate the balance? They are of two kinds; one is represented by the sex chromosomes, the other by the physiological conditions. The sex chromosomes are very heavy weights, so that if they are put on one side of the balance, it would require a great many physiological weights on the other side to counterbalance them. Nevertheless, this can be done. With the heavy chromosome weights all on one side they can still be overbalanced by piling all of the physiological weights on the other. In the organisms in which the sex chromosome theory seems rigidly established, it means that the chromosome weights are relatively heavy and cannot be counterbalanced by all of the physiological weights on the other side; or it may merely mean that all of the physiological weights have not yet been discovered. In other forms the chromosome weights are not so heavy, and can be overbalanced by the known physiological weights.[1]

It may be asked why the chromosome weights are imagined to be so much heavier in some forms than in others. The explanation may be that where the chromo-

[1] This analogy of weights has been suggested by DONCASTER (1).

some weights are heaviest there is rigidity in inheritance, but where the physiological weights are more prominent there is plasticity in inheritance. Speaking in terms of ontogeny, all embryo tissues are plastic and mature tissues are rigid. Applying this thought to phylogeny it may be assumed that young unit characters are plastic and may be modified by physiological conditions; while old unit characters are fixed, rigid, and determined by chromosomes, against which the influence of physiological conditions is feeble and avails little or nothing.

The second theory contains more physiological complexities, sketching a picture which is harder to visualize as a whole but is more exact in its details. As previously mentioned, the physiologist would like to believe that the protoplasts of each variety of plant show a certain specificity in their chemical make-up. The physiologist finds that the cytoplasm is the seat of the most important physiological activities, and consequently expects to find that the cytoplasm is also in some way the bearer of hereditary characters. He does not readily agree with the cytologist that hereditary characters are limited entirely to the chromosomes. He cannot, however, controvert the great bulk of data, collected by cytologists and Mendelians, indicating that chromosomes are the bearers of hereditary characters. He must reconcile his views with these undeniable facts. Perhaps he may be able to do this in the following manner.

In the first place how must he visualize the so-called "determiners"? Physiologically they seem to behave more like enzymes than anything else that we can think of. If, then, these enzymes are transmitted

from generation to generation in the orderly manner that the Mendelian data indicate, can we conceive of their being located in the cytoplasm? Enzymes diffuse rather readily through the cytoplasm; but if each determiner were represented by an enzyme, what a chaotic mixture this cytoplasm would be, with the numerous determiner-enzymes intermingling, interacting, and probably losing their specificity. This is not the orderly picture required to account for the orderly Mendelian results actually obtained.

If, however, we conceive of these determiner-enzymes inclosed in a linear arrangement along the chromosomes we can paint a much more orderly picture. The chromosome itself is not an active substance chemically; it is merely a framework, an "apartment house" for determiner-enzymes, having, however, the power of reproduction. Each determiner-enzyme is contained (and "nourished") within its own compartment. When the chromosome reproduces, each determiner-enzyme reproduces within the chromosome and is passed on, at all times, however, being well bound in by the walls of its compartment and thus kept from reacting in the cytoplasmic medium which surrounds the chromosomes. Sooner or later, as the automatic and inevitable result of a natural series of physiological changes that has taken place in the cell dynasty of the individual plant, certain physiological conditions appear in the cytoplasm which bring about the "release" of certain of these determiner-enzymes, which then react in the cytoplasm to produce the specific plant characters of which they are the determiners. If all these determiner-enzymes had been released at once, or if they had never been con-

fined, chaos rather than cosmos would have resulted. Actually we know that cosmos exists, and our highly theoretical scheme at least can account for that. After all, what is this scheme but the "intracellular pangenesis" of DE VRIES (see chapter xiv)?

Applying the scheme still further, we may make two assumptions: (1) certain unusual physiological conditions are capable of "releasing" determiner-enzymes earlier than they would naturally be released. Thus they are free to react in an unusual medium, or to interact with other determiner-enzymes which they would not have met in the natural course of events. In either event the reaction is an unusual one, and the final result may be the appearance of an unusual plant character. (2) Unusual physiological conditions may per se bring about unusual reactions and result in unusual plant characters. The determiner-enzymes would not be involved in this.

These two possibilities would account for some of the unusual (hereditary) responses that have appeared as the result of unusual physiological conditions, as, for example, the mutants obtained by MACDOUGAL (2) when he injected the ovaries of *Onagra* with various chemicals. In short, such a theory may help to reconcile some of the apparently contradictory data of the physiological school and the cytological school.

To apply this theory to the matter of sex determination would involve certain difficulties, since sex is a unique character and is inherited in a unique way. It is quite possible, however, to overcome these theoretical difficulties and to make our scheme reconcile the two conflicting views even on the matter of sex determination;

but it would not be appropriate to enter into the theoretical complications any further. In this connection, however, we may recall the work of CIESIELSKY (see page 195), in which it is claimed that staleness of pollen affects sex. Staleness probably means an unusual amount of oxidation and would be a typical instance of "unusual physiological conditions." One might predict that staling of pollen might be found to affect other plant characters as well as sex. This suggests a new field of investigation. The male gamete of angiosperms, however, is pretty well insulated within the pollen coat. If work of this kind is to be done, the algae and fungi would furnish much more favorable material (see page 130).

These are two theoretical pictures in which both chromosomes and physiological conditions may play their rôles. The latter is more complex, but at the same time more exact and more suggestive of further investigation. Both are highly theoretical and should not be confused for a moment with any of the actual known facts of inheritance. At best either one of them may help to unify the situation that has been discussed, and unless some such scheme is constructed it will be found difficult to keep one's bearings among conflicting theories based upon apparently conflicting facts.

1. DONCASTER, L., The determination of sex. Cambridge Univ. Press. 1914.
2. MACDOUGAL, D. T., see Heredity and eugenics (CASTLE, COULTER, DAVENPORT, EAST, TOWER). Chicago. 1912 (p. 205).
3. WILSON, E. B., Heredity and microscopical research. Science N.S. 37:814–826. 1913.

INDEX

INDEX

Acquired characters, inheritance of, 6, 16
Adzuki beans, inheritance in, 45
Albomaculata type of Mirabilis, 98
Aleurone layer, inheritance of color in, 149
Algae: inheritance in, 121, 130; sex determination in, 185; sexual structures of, 118
Allelomorphs, 31
Allen, C. E., 184, 187
Antagonistic characters, 86, 91
Antennaria, parthenogenesis in, 116
Anthocyanins in inheritance, 55
Apogamy: and true-breeding hybrids, 48; vegetative, 115
Apospory, 116, 189
Appetency, 16
Artificial selection, effect of, 80

Babcock, E. B., v
Bacteria, isolation of, 131
Barber, M. A., 131
Bateson, W., 40, 42, 55
Begonia: hybrids, 47; sex in, 196
Belling, John, 138
Biophores, 13
Blakeslee, A. E., 45, 185
Blends, 43, 127
Bolley, H. L., 23, 26
Bryonia, sex determination in, 196
Bryophytes, inheritance in, 130
Burbank, Luther, 47, 158
Burgeff, H., 186

Camerarius, discovery of sex in plants, 4
Cannabis, work on, 195
Capsella and alpine characters, 20
Castle, W. E., 104, 105
Cell architecture of Weismann, 13
Chlorophyll inheritance, 98, 101
Chromogens in inheritance, 55
Chromosomes: numbers in plants, 126; as bearers of hereditary characters, 198; as differential factors in heredity, 203; isolation of, 131; theories of sex determination, 178
Chrysanthemum, chromosomes in, 126
Ciesielsky, T., 195, 208
Clausen, R. E., v
Collins, G. N., 167
Complementary factors, 52, 57, 78, 127
Compositae, parthenogenesis in, 116
Continuity of germ plasm, 7
Continuous variations, 113
Corneous endosperm, inheritance of, 154
Correlation, 96; physical and gametic, 73
Correns, C., 40, 43, 98, 192, 196
Coupled characters, 86, 91
Crepis, chromosomes in, 126
Crossing over, 90
Cross-pollination, significance of, 135
Crypthybrids, 48
Cumulative factors, 58, 61, 76, 78, 109, 128
Czapek, P. and M. E., 55

Darling, C. A., 184
Darwin, Charles, 1, 4, 14, 68, 84, 136, 158
Determinants, 13
Determiner, 32, 52
De Vries, Hugo, 2, 14, 80, 84, 207
Dihybrid ratio, 37
Disease transmission, 26
Dominance, 30, 156; failure of, 45; and hybrid vigor, 170
Doncaster, L., 204
Dose, double and single, 34
Double fertilization, 144
Drosophila, work on, 93
Duplex, 42

East, E. M., 27, 40, 46, 48, 50, 52, 69, 80, 112, 131, 142, 151, 153, 154, 162, 173
Elimination factor, 24
Embryo, sources of, 117
Emerson, R. A., 50, 86, 173
Endosperm, inheritance in, 144
Engler, Arnold, 22
Environment, effects of, 20
Enzymes in inheritance, 55, 205
Equisetum, sex in, 190

Factor hypothesis, 52
Fagopyrum, heterochromosomes in, 184
Failure of dominance, 45
Ferns: apogamy in, 116; sex determination in, 191
Fixation of hybrids, 83
Floury endosperm, inheritance of, 154
Fluctuating variations, 70
Four-o'clock, inheritance in, 44
Fruit fly, inheritance in, 93
Funaria, sex determination in, 189
Functionless organs and inheritance, 25
Fungi, sex determination in, 185
Fusion nucleus, 146

Gärtner, J., 158
Galton, Francis, 16, 51
Galtonia, heterochromosomes in, 184
Gametes, purity of, 31
Gametic correlation, 73
Gametophytes, inheritance in, 123, 138
Gemmules, 6
Genotype, 36
Geranium, work on, 100
Germ cells, origin of, 18
Germinal continuity, 6, 8; selection, 6, 9, 68
Ginkgo, heterochromosomes in, 184

Hemp, sex in, 195
Hertweg, Richard, 180
Heterochromosomes, 178
Heterosis, 164
Heterozygosis and hybrid vigor, 164, 169
Heterozygote, 35
Hieracium, parthenogenesis in, 116
Higgins, J. E., 195
Homozygote, 35
Houstonia, heterochromosomes in, 184
Hurst, C. C., 40
Hybrid vigor, 158

Idants, 12
Ids, 12
Indian hemp, sex in, 195
Inheritance: of acquired characters, 6, 16; in endosperm, 144; in gametophytes, 138
Inhibitory factors, 57, 58, 110, 128
Intermediate hybrids, 43

Intracellular pangenesis, 14
Isolation of bacteria and chromosomes, 131

Jeffrey, E. C., 48
Jennings, H. S., 112
Johannsen, W., 36, 81
Jones, D. F., 167, 174

Keeble, F., 173
Kempton, J. H., 167
King, Miss H. D., 180
Kite, G. S., 131
Klebs, G., 185
Kölreuter, J. G., 158

Lamarck, J., 2, 16
Light seed, effect of, 21
Linkage, 90
Liverworts, sex determination in, 187
Lychnis, sex determination in, 196

Macdougal, D. T., 207
Marchal, El. and Em., 189, 200
Marchantia, sex in, 187
Maternal inheritance, 99, 155
Mayr, H., 21
Melandrium, heterochromosomes in, 184
Mendel, Gregor, 28
Mendel's law, 28
Mendelian segregation, essential features of, 126
Mercurialis, sex in, 193
Mirabilis, inheritance in, 44, 98
Modification of unit characters, 104
Monohybrid ratio, 34
Morgan, T. H., 91, 200, 201
Mosaic inheritance, 51
Mosses: sex determination in, 189; tetraploidy in, 200
Mucor, sex determination in, 185
Mutation, 105, 113
Mutationists, school of, 114
Mutilations, inheritance of, 19

Neo-Darwinians, 16
Neo-Lamarckians, 16
Neo-Mendelism, 40
Nicotiana, hybrid vigor in, 166; self-sterility in, 143
Nilsson-Ehle, H., 63
Noll, Fr., 187
Non-Mendelian inheritance, 97
Nulliplex, 42

Oenothera, tetraploidy in, 200
Onagra, experiments on, 207
Onion, polyembryony in, 117
Oxidases in inheritance, 55
Oxidizing enzymes in inheritance, 55

Pace, Lula, 117
Pangenes, 14
Pangenesis, 4, 14; intracellular, 14
Papaya, sex in, 195
Park, J. B., 131, 142
Parthenocarpy, 49
Parthenogenesis, 115; and true-breeding hybrids, 48
Particulate inheritance, 51, 101
Pelargonium, inheritance in, 100
Pellew, C., 173
Phenotype, 36
Phycomyces, sex determination in, 186
Physical correlation, 73
Physiological theories of sex determination, 180
Pigments in inheritance, 55
Polyembryony, 117
Predominance, 156
Prepotency, 31

Presence and absence hypothesis, 40
Protoplasmic connections, 18
Protozoa, inheritance in, 113
Pteridophytes, sex determination in, 190
Pure-breeding hybrids, 47, 76
Purity of gametes, 31

Quantitative characters, inheritance of, 63, 79

Reciprocal crosses, 29
Reinfection and inheritance, 25, 100
Responses, 70
Reversion, 54, 83
Riccia, sex in, 189
Riddle, Oscar, 181, 194, 202
Running out, 159

Saprolegnia, parthenogenesis in, 115
Segregation, 31; essential feature of, 125; somatic, 100
Selaginella, sex in, 190
Selection, effect of, 80, 106
Selectionists, work of, 114
Self-sterility, 133; and apogamy, 120
Semi-sterility, 138
Sex chromosomes, 178
Sex determination, 117
Sex: discovery of, in plants, 4; significance of, 10, 134
Shull, G. H., 40, 159, 173, 196
Sibs, 160
Simplex, 42
Single dose, 34
Somatic segregation, 101
Sphaerocarpus, sex determination in, 184, 187
Spirogyra, inheritance in, 131
Spores, inheritance by, 121
Staleness of pollen and sex, 208
Sterile pollen in crypthybrids, 48
Strasburger, E., 184, 187, 193
Supplementary factors, 57, 60, 78, 128
Sykes, M. G., 184

Taraxacum, parthenogenesis in, 116
Tetraploidy in mosses and Oenothera, 200
Thalictrum: parthenogenesis in, 116; sex in, 195
Tobacco: hybrid vigor in, 166; self-sterility in, 143
Transportation hypothesis, 5, 68
Trihybrid ratio, 39
Triple fusion, 146, 149
True-breeding hybrids, 76

Unit characters, 29; modification of, 104
United States Committee on Breeding Nut and Forest Trees, report of, 21
Use and disuse, effect of, 25

Vegetative apogamy, 115; and true-breeding hybrids, 48
Vigor, hybrid, 158

Walter, H. E., v, 19
Water molds, parthenogenesis in, 115
Webber, H. J., 151
Weismann, August, 6, 13, 17, 25, 68, 113, 134
White, Orland E., 96
Wiedersheim, W., 19
Wilson, E. B., 203

X-chromosomes, 178
Xenia, 148; abnormal, 151

Yamanouchi, Shigéo, 116

Zederbauer, E., 20