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The Relation of Certain Biological Principles to Plant Breeding.

BY

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THE RELATION OF CERTAIN BIOLOGICAL PRINCIPLES TO PLANT BREEDING.

By EDWARD M. EAST.

INTRODUCTION

The recent stupendous progress in the experimental study of variation, evolution and heredity has awakened greater interest in the improvement of cultivated crops, for the theory of the two studies must inevitably go together. Since the publication of the Origin of Species in 1859, the questions involved have been much at the mercy of the speculations of theorists; and it was seemingly forgotten that Darwin himself obtained much of his evidence from domestic animals and cultivated plants. The theorists were too busy in their debates to obtain many results of practical value to the plant breeders; and the plant breeders were obtaining so many surprising complications in their experimental work, that the thought of the possibility of classifying their thousands of observations under a few natural laws did not occur to them.

The last decade has brought about a change of heart in the two classes of workers, and a change in method in their work. The student of natural evolution and the follower of changes under domestication have recognized that they stand upon common ground, and as a result, the brilliant researches of a score or more of recent investigators have made the prospects of gain in the practical side almost too alluring.

For the plant breeder who can devote his whole time to the study of his immediate problems, who will prepare himself by a study of former investigations concerning variation and heredity, and who will keep his ideas abreast of modern research, the rewards indicated in some of the current journals are hardly exaggerated. But for the busy farmer who wishes to know the best methods of improving his general farm crops there is need of caution in accepting the promise of results. Popular articles have been written of such roseate hue that large numbers of men are quite ready to spend a portion of their time and money in the improvement of their favorite crop. The general feeling toward plant breeding is good and is certain to be productive of valuable results; but it is not a subject from which to expect great things without the study necessary for a general appreciation of its principles. Most certainly the writer does not wish to discourage an increase in the number already interested in plant breeding, but to encourage a greater study of its underlying principles and to have a rational view taken of our present status of knowledge as to the possibilities which lie within the application of these principles.

The prevalence of inadequate preparation for undertaking special problems of practical plant breeding is partially due to the unavailability of collected information on the subject. Compilation in text-book form has not kept pace with the rapid increase in results of research. There is disagreement as to detail of method in the application of the few principles which have been discovered and it is well that the prospective plant breeder should consider these principles from various points of view and draw his own conclusions.

There will be given in the following pages a short outline of the current belief in the most important theories and principles of variation, evolution and heredity, with their practical application to methods of breeding farm crops, which it is hoped will give the farmer an idea of the scope and present state of the problems. Should the reader be sufficiently interested to pursue the subject further, he should consult the annotated list of supplementary reading given at the end of this paper.

In the preparation of this paper, the writer has made free use of the works of the following writers:—Bailey, Bateson, Biffen, Castle, Correns, Darwin, Davenport, De Vries, Hurst, Johannsen, Lock, Kellogg, Morgan, Pearson, Punnet, Romanes, Saunders, Shirreff, Tschermak, Vernon, Webber, Weismann and others, including our own government and experiment station workers.

I.

The Evolution of Darwin and his Predecessors.

Lamarckism.

The idea of organic evolution had germinated in the minds of a number of deep thinkers from the time of Aristotle, and finally bore fruit in the overwhelming evidence presented by Charles Darwin in 1859. The adoption of the Jewish idea of the separate creation of species by the Christian churches had almost stifled early speculation. However, in the eighteenth and early nineteenth centuries, we find a more or less definite idea of the production of species by the modification of their progenitors, expressed by Erasmus Darwin, De Maillet, Goethe and Treviranus. Lamarck had even developed a well rounded theory of evolution through the inheritance of characters *acquired during the lives of individuals,* a full half century before the time of Darwin.

The underlying thought of Lamarck's theory of the inheritance of the effect of use and disuse may be seen in the example which he himself first proposed in its favor. A bird, driven through hunger to the water for food, will instinctively separate its toes when they strike the water. The skin uniting the bases of its toes will be stretched, in consequence. By the continuation of this process, the descendants of such birds will develop the broad membrane possessed by water birds such as ducks and geese.

Lamarck's arguments may be given in a summary of his own which is often quoted. He gives it as two laws of nature. First law: "In every animal which has not finished its term of development, the frequent and sustained use of any organ strengthens and develops it and increases it in size proportionate to the length of time it has been employed. On the other hand, the continued lack of use of any organ gradually weakens it until at last it disappears." Second law: "Nature preserves everything she has caused the individual to acquire or lose through the influence of the environment to which its race has been for a long time exposed, and hence the predominance or loss of certain organs through use or disuse. She does this by the production of new individuals which are endowed with the newly acquired organs, provided the acquired changes were common to the two sexes of the individuals that produced the new forms."

In other words, Lamarck has explained the diverse instances of the survival of certain characters useful to the organism by the theory that the need of such characters has caused their necessary modification through the inheritance of such characters partially acquired or partially lost during the lifetime of different separate individuals.

Since Darwin's time, the principles of Lamarck, with some modifications, have received warm support by a large following of eminent scholars, the so-called Neo-Lamarckian school, of which Spencer, Cope, Eimer, Hyatt, Cunningham and Osborn are a few of the well known writers who have collected data in its support. It is noticeable that the best evidence has been advanced by paleontologists, who have been deeply impressed by the direct lines of evolution that geological evidence seems to show has taken place. To their minds, the inheritance of acquired characters must have taken place, to give a sufficient explanation of these facts.

We can only say that while many of the facts seem to be reasonably explained by the theory, the crucial point of the whole thing, which is actual permanent inheritance of an acquired character, has not been shown. It is true that this definite question has been attacked by but few experiments, but in such experiments the results have been negative. Successive generations of mutilations, such as docked tails of horses, have never resulted in a single case of undisputed inheritance. The idea that previous fecundations have an effect upon succeeding progeny of a mother has been shown to be without foundation. The allied botanical phenomenon of zenia, as illustrated by the effect during the current season of pollen of a black maize upon the endosperm of a white variety, has been proved to have another and a simple explanation. Thus we may go through the entire list.

The one class of data that comes the nearest toward showing inheritance of body acquirements, is that of the modification of certain characters by the immediate influence of the factors of environment, as food, light, heat, moisture, etc. In many instances, where the environment of plants has been changed, there does indeed seem to be a temporary inheritance of certain modifications. For instance, various grains have been taken from their native plains and transplanted to mountains or high plateaus. Among other minor changes that here have taken place are earlier ripening and dwarfer forms. The complete change of these characters does not take place in one generation, but in the course of three or four generations they reach the limit of their modification. When these grains, after several years cultivation on the mountains, are again resown on the valley soil, they temporarily ripen earlier and remain more dwarfish than their relatives that have been continuously cultivated in the valley. These characters, however, do not remain permanent, but in a few generations the plants go back to their former habits of growth.

Weismann has developed an elaborate theory tending to show from a physiological standpoint that inheritance of acquired characters is impossible. Every higher organism, both animals and plants, is developed from a single cell, the fertilized egg. Under circumstances favorable for growth this cell divides into two equal portions; and studies with the microscope have shown that there is a very complicated mechanism which makes this division exact and equal. By continuous divisions of this sort, the adult body of every organism is formed. Some of the cells which are formed, however, are modified in form and function, and go to make up distinct organs and tissues. But there are cells which appear to have undergone no modification or change whatever; these are the reproductive or germ cells of the body. If we trace back to the original germ cell from which the organism came, we see that each cell of the adult must have had this germ cell for a common ancestor. Then since the reproductive cells of this body are qualified to transmit all of its minute characters, it is probable that they came from the parent egg cell by a continuous careful division; and have received all of its properties. The conclusion is that the inheritance of qualities is transmitted from germ cell to germ cell in every race of organisms and that the body is merely an offshoot,—a house built up out of a part of the substance of the original germ cell to shelter it until it decays, and the germ cell is transmitted to another house.

It is clear then that any inherited variation must be a variation which affects the germ cell, from Weismann's point of view; the use of a particular organ of the body would have no effect upon it. There is no objection, however, to the belief that the general health of the organism would affect the germ cells as well as any other cells of the body. If the environment is excellent for the body development, then the germ cell should be well nourished and able to produce a healthy body in the next generation if it has a fair chance, and *vice versa*. This theory would readily explain the apparent temporary inheritance in the case of the plants transplanted from the plains to the mountains and back.

There are evidently certain characters which are somewhat modified by environment and which temporarily transmit these modifications more or less perfectly; but for a variation to be permanently inherited, it seems probable, from both theory and practice, that *the germ cell must be affected structurally*. It is unlikely that a temporary "fattening" or "starving" of the germ cell due to good or poor nourishment of the body, is sufficient to produce a permanent change.

As a possible inheritance of acquired characters has such a broad bearing upon plant-breeding questions, we must remember when we come to their discussion, that as yet such *permanent* inheritance is decidedly unproved. Moreover, such a conclusion does not commit us to a belief in Weismann's ingenious but unprovable theories. The plant breeder only wishes to know that the relative probability of outside influences affecting the structure of the germ cell and thereby making new characters heritable—is extremely small.

Darwinism.

The great work of Darwin was influenced, if not suggested, by an essay of Malthus on "Population" published in 1798. Its author gave incontrovertible evidence, by data from countries all over the world, that human population tends to increase by geometrical ratio (that is, by multiplication) while food supply tends to increase by arithmetrical ratio (that is, by addition). This means that if human population were not kept down by disease, war, famine and other checks, the increase would soon outrun the food supply. As examples of similar but more rapid increase may be cited many of the lower forms of animals, which produce on the average one hundred eggs and reproduce every week. If the entire progeny of a pair of such animals were preserved living at the end of a year, *their bulk would exceed the limits of the whole known universe.*

This manner of increase is common to a greater or less degree with all living organisms, both animals and plants; and since space and food are not available for such increase, it follows that a very large proportion of all individuals born must perish without producing offspring. Darwin's idea was that out of all the individuals coming into existence, some will show variations or modifications in directions which adapt them better for the environment in which they are placed than do the characters possessed by their less fortunate brethren, and the former will survive at the expense of the latter. This principle he called Natural Selection, though later the more common term was that of Herbert Spencer, the "survival of the fittest." Darwin's own description of the process is this:

"If under changing conditions of life, organic beings present individual differences in almost every part of their structure, and this cannot be disputed; if there be, owing to their geometrical rate of increase, a severe struggle for life at some age, season, or year, and this certainly cannot be disputed; then, considering the infinite complexity of the relations of all organic beings to each other and to their conditions of life, causing an infinite diversity in structure, constitution and habits—to be advantageous to them; it would be a most extraordinary fact if no variations had ever occurred useful to each being's welfare, in the same manner as so many variations have occurred useful to man. But if variations useful to any organic being do occur, assuredly individuals thus characterized will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance, these will tend to produce offspring similarly characterized. This principle of preservation, or survival of the fittest, I have called Natural Selection. It leads to the improvement of each creature in relation to its organic and inorganic conditions of life, and, consequently, in most cases, to what must be regarded as an advance in organization. Nevertheless, low and simple forms will long endure, if well fitted for their simple conditions of life."

The very large amount of data that Darwin brought together in support of his theory, fell naturally under several distinct heads. It was all historical evidence in that it was made up of a large number of facts collected from the different natural sciences, which were most reasonably explained by assuming evolution to be true. It neither satisfactorily explained how evolution took place, that is, how small a variation would be preserved by natural selection, nor did it show experimental evidence of the actual production of natural species. It is difficult to pick out from the mass of facts which Darwin had collected, particular examples which are more illustrative than others, but we will endeavor to give particular cases from each of the different lines.

Organic Relationship. At the lower end of both the animal and vegetable kingdom, we find creatures of a very simple organization. They are living beings composed of one cell, and cannot definitely be said to be either animals or plants. Moreover, these organisms resemble in many ways the egg cell from which all higher animals and plants originate. From these simple organisms, we may follow up the two different and yet in many respects similar lines of organisms which go to make up the animal and vegetable kingdoms, until we reach, on the one hand, man, and on the other, the complex flowering plants. The gradation is noticeable in each line, although there are many large gaps which are not filled by any known organisms. The change in the simplest case is by the addition of some single character, though in most cases a number of characters are different between the two nearest related kinds or species. First, there is the addition of more cells and the single-celled organism becomes (if we may speak with the definite idea of progress) a multicellular organism. The simpler multicellular creatures have all of their cells seemingly alike. Then comes the specializing of different sets of cells to become tissues, and finally a multiplicity of different tissues and organs useful for different needs and performing different functions, form the higher plants and animals with which we are more familiar.

Long before Darwin's time, it had been seen by different naturalists that a study of the known animals and plants from the simpler to the most complex showed related forms. Some were evidently very closely related, that is they differed by very few essential characters; as an eagle and a hawk. Other types were very far apart, as an oyster and a dog; and yet there are a number of similar attributes possessed by both the oyster and the dog. They both digest food, possess voluntary and involuntary muscles and have circulatory systems.

The natural result of such study was to show that the plant and animal kingdoms could be compared to a great tree, which had branched at the root into two large trunks, each of which is divided into many branches. The animal trunk, for instance, has one great branch of fishes and another great branch of birds. From these great branches come smaller branches and twigs of closer and closer relationship as to characters. The whole arrangement seems to show the development of more complex from less complex beings.

Geographical Distribution. In working out this tree of relationships, it has been shown that groups of closely connected creatures are often found living in small districts, and that when a natural barrier, as an ocean or a lofty mountain range, is passed, there is found largely a new fauna and flora. Of course there are types of both animals and plants that exist over large areas, but in most cases they are species able to migrate freely and are adapted to the differences in environment that have been encountered. Some species live in numerous small areas: the mountain hare, for instance, exists from the Arctic regions over the greater part of Europe in the spots where there are mountain ranges or climates cold enough to suit its requirements. It is a natural explanation of these facts to suppose that the mountain hare had a continuous range over Europe during the last glacial epoch when the European climate was much as the present Arctic climate. But when the climate of Europe gradually became temperate, the hare was able to exist only on certain mountain ranges corresponding in climate to the Arctic regions.

The flora of the high mountain ranges also is essentially Arctic in all of its general characters, and yet the species are not the same as those found in the Arctic regions. It is not rational to suppose that new species were separately created upon different mountain ranges after the formation of the present climate in the temperate zone, and yet are so closely allied to Arctic species as to be included in the same germs.

Finally, it has been shown that the number of species indigenous to isolated islands is proportional to their biological isolation from other larger or older islands. By biological isolation is meant not only distance in miles, but also freedom from prevailing winds or ocean currents from other lands. The nearer islands are to continents, the closer related are their fauna and flora. As far as is known there is no exception to this law.

Geological Evidence. When Darwin's theory was first published, there was much criticism concerning the gaps existing in the 'family tree' of the animal and the vegetable kingdom. Especially was there a lack of types possessing structures which would show them to be links between the larger families and orders of animals and plants. It is on this point that modern study of the science of the classification of animal and plant remains found in the different strata of rocks, which we call paleontology, has produced such valuable evidence. These remains of ancient animals or plants which we call fossils have naturally been confined to their hard parts such as bones and teeth, which have been the more easily preserved. However, from such remains as were available, large numbers of these primitive types have been discovered and described. In America has been found a long line of remarkable progenitors of the horse, leading back to an animal the size of a dog, with four separate toes to each fore-leg and three to each hind-leg. More striking still, in the earliest known bird, the Archæopteryx, the similarity to a reptile is easily seen. The tail is very long, with twenty-one separate joints, every joint bearing a feather upon each side. In the modern bird, the tail joints are very much fewer in number, short and enlarged, and bear long tail feathers in a fan shape, forming the so-called tail. This shortening up of the tail did not come at once but is seen in all gradations in fossil birds of later periods.

In point of time the geological evidence is found to be exactly in conformation with the theory. The earlier remains are those of less specialized forms, while the remains found in strata of rocks of later ages are of more specialized or higher forms. The record shows that of the vertebrate animals, the first to appear were fishes, followed successively by amphibians, reptiles, birds and mammals. However, because mammals arose later than birds, we do not need to conclude that mammals arose from birds, or even from our present form of reptiles. Probably there was a diverse evolution from some early amphibians which gave rise to reptiles, birds and mammals.

Geological evidence alone is not necessarily conclusive, for many fossil forms represent the highest development of extinct types, and hence are not progenitors of yet higher types; but as yet there are no data among fossils that is directly against the theory of evolution.

Comparative Structures. The evidence of geology and that of classification is based largely upon the study of comparative structures, for the external appearance of organisms is often deceiving. We must get beyond the superficial points and study the more permanent characters. As an example, the porpoise is a fish-like animal, its teeth being more fish-like than mammal-like; but on the other hand, it suckles its young. Is it then a fish or a mammal? A mammal most assuredly, for teeth are very variable organs, while suckling the young is characteristic of the whole class of mammals and of them alone.

The evidence of comparative structures is divided into two parts, that of the change of organs to become better fitted for different kinds of work, or more useful under different conditions of life, and that of the tenacity with which organs which are now functionless, remain.

Returning to the porpoise and its relative the whale, it must be inferred from the whole structure of these animals that their progenitors were terrestrial quadrupeds of some kind which for some reason became aquatic in their habits. Such a change of life made it desirable for the animals to possess characters more fish-like. Probably such changes first took place in the most variable parts, such as the skin, claws and teeth. Then, as time went on, the modifications extended to more typical structures, until the whole shape of the body was affected by the bones and muscles becoming better adapted for aquatic than for terrestrial locomotion. We see in seals the stage where the hind legs are thrown backward until they are of little use on land, but serve to form a kind of double fish-like tail. In the whale the modification has gone still further: the visible signs of posterior limbs have entirely disappeared, but there still remains within the body the bones of a rudimentary pelvis with indications of bones of the hind limbs. The fore-arm also, which looks externally very like a fin, still retains, in a modified form, all of the mammalian bones of the fore-arm, wrist and hand, so that the general appearance of the skeleton of these parts bears a strong resemblance to that of the fore-arm of man. Moreover, the head, although modified until it resembles that of a fish, still retains all of the bones of the mammalian skull.

Such adaptations to fit conditions of life are very general in both animal and plant life. Plant adaptations are largely modifications to make sure of fertilization and consequently of very definite use to the species in continuing its existence. A common example noticed by everyone is the very great amount of pollen produced by maize, which is wind-pollinated, with necessarily a great loss. Compare this with the small amount of pollen produced by the pea, which by its structure is assured of self-pollination. Moreover, there are thousands of examples of wonderful modifications by which plants secure animal aid in their fertilization,—such as showy blossoms, secretion of nectar, and modified shapes of corollas which assure pollination by the insects that come to the blossoms for nectar.

The amount of evidence showing that once useful but now functionless organs often persist when their existence is not harmful to the organism, is not so large as that of which we have just been speaking. But certain vestigial organs still remain in man which are interesting evidences of his part in the system of evolution, and of his close relation to the animals to which he feels superior. The tenacious grasp of the young infant and the extreme natural inflection of the feet is very reminiscent of the monkey family. The muscles of the external ear which are large and of use in quadrupeds, are still retained by man in a small and functionless condition. The absence of a tail in man is popularly supposed to be a final argument against his quadrumanous descent. But this is exactly what we should expect, for tails have been done away with in man's nearest relatives, the anthropoid apes. Man, however, as well as the apes, retains a few rudimentary caudal vertebrae at the end of his sacrum and even vestigial tail muscles are present in some adults. Finally may be mentioned the vermiform appendix, which in its reduced size is useless to man, and even is harmful in some cases as being the seat of appendicitis. In herbivorous animals the organ is of large size and functions in the process of digestion. Some such heritages are present in all classes of animals and plants and serve as particularly incontrovertible evidence of the relationships of different types.

Embryological Evidence. Embryology is that branch of biology that deals with the formation and early development of organisms. Such great advances in the science have been made since the time of Darwin, that many evolutionists have regarded it as giving the principal evidence to the theory.

Without going into technical detail, the evolutionary proofs of embryology might be largely summed up in the following sentence. The early development of any organism partially recapitulates the embryonic history of its race formation. This does not mean that there are not many gaps in the process; but this expresses the general tendency of development. As an example, young salamanders before birth are found to be furnished with gills; and if they are taken from their mothers shortly before birth, the gills are able to perform their functions, and the young salamanders can respire in water which would drown their own mothers. The complete formation of gills in the embryo salamander is an entire waste of time, as the gills are never of use in the normally developed young. It is clear, then, that one could only expect such a phenomenon to happen from the viewpoint of a previous evolution.

In man himself there are stages in the development of the embryo when it is scarcely distinguishable from the embryos of any of the other vertebrates, such as fish, amphibians, reptiles, birds or lower animals. It early possesses the two-chambered heart of the fish, and gill slits of undeveloped gills. Further on in its development, the embryonic heart has the three chambers characteristic of amphibians and finally the four-chambered heart characteristic of the double circulation of birds and mammals.

Variation under Domestication. In the study of the varied forms of our domestic animals and cultivated plants, Darwin found a great deal of his best data regarding the variability of organisms. He showed that particularly among domestic animals, for example the pigeons, there are varieties descended from a common wild ancestor, which if met with in a state of nature would be classed as different species and possibly as different genera. There is no reason to believe that animals in the wild state are not just as variable as domestic animals, although man undoubtedly selects and perpetuates variations which would not be of sufficient value to the organism to survive by natural selection. However, proof of such variation of characters of specific rank is proof enough that *sometimes* there must occur variations which are sufficiently useful to protect their possessors in the struggle for existence that we saw is continually taking place in nature.

Such in brief were the lines of argument brought together by Darwin in support of his evolution theory; and with such brilliancy and with so many data did he maintain it that before his death practically the whole thinking world was converted from the orthodox Jewish belief in the special creation of every species, to that of the development of all organisms from very primitive types.

To summarize the whole question, we may state just what were the fundamental points which Darwin proved. The overwhelming amount of his historical data, as we have seen, left no reason to doubt that there had been an organic evolution. In order for a natural organic evolution to have taken place there must have been three coöperative factors: first, variability within species; second, a capacity among organisms for transmitting particular characters; and third, a means of selection of variations for perpetuation.

Many examples of sufficient variability were easily found among existing data, though it is true they were generally confined to domestic animals and plants; and there was no reason to doubt that certain variations of sufficient specific character had been inherited under man's selection. As to his natural selection factor, it was unquestionably shown that there was and is a struggle for existence in which the greater part of all organisms coming into being, perish. Variations sufficiently of advantage to their possessors, to make their attaining adult life and reproducing their kind relatively more probable, would obviously survive. These facts will stand forever as a sufficient monument to the memory of Darwin.

The questions to which he did not give a sufficient answer are: first, What is the physiological meaning of the different kinds of variation? second, how great must a variation be to be selected, or how often must it occur to have stability? third, what is the rate of inheritance of different kinds of variation? fourth, what is the mechanism of inheritance? and fifth, must only favorable variations be selected or will variations which are simply non-injurious survive? In other words, Darwin proved the *fact* of evolution and established *one* of its great working principles, but left to the future to largely explain its detailed mechanism.

The criticisms of Darwin's work are many and a large number of them are very just, but they do not affect the truth of general Organic Evolution. Huxley well expressed the facts when he said: "Even if the Darwinian hypothesis were swept away, evolution would still stand where it is." The criticisms that are at all pertinent concern the five questions just given. Other criticisms are largely due to a misunderstanding of Darwin's own work. His work was so broad that he himself fairly stated a large number of the criticisms that were brought to bear upon it. He recognized that the detail of the manner in which evolution took place was yet almost untouched by investigation. Yet in many of these issues the problems were outlined by the hand of a master.

It is odd, at first thought, that all of the important criticisms are of primary and direct importance to plant breeding; yet it really is not odd, for the factors in the improvement of crops are the same as those of a natural evolution. There are the same classes of variations to deal with, the same questions of inheritance of these variations. It is true that artificial selection takes the place of natural selection, but also here it is important to know in each case whether the laws of inheritance are such that a *single useful* variation which has occurred, can be preserved, or if it *must* be lost by intercrossing with individuals not possessing the variation.

In the next chapter, we deal with some of the points of evolutionary criticism which have affected our entire conception of the methods to be used in plant breeding.

II.

Later Evolutionary Theories and Principles.

Criticisms of Darwin's Mechanical Theory.

There are two main classes of variations, both of which Darwin recognized as agents in the work of evolution. The first he called "fortuitous" or chance variations, although he admits that this is an incorrect expression which serves only to plainly acknowledge our ignorance of the exact cause or causes of each particular variation. This is the common type of variation seen in every growing plant and animal. It is now called *fluctuating variation,* and each individual variation a *fluctuation,*—terms which we shall henceforth use. Illustrations of fluctuating variation are found in every character of all living organisms; which is the same as saying that no two plants or animals are *exactly* alike. Take as an example a number of ears of maize. They may be of the same variety, have grown on the same soil, and have had exactly the same treatment during the growing season; nevertheless they differ among themselves in length, in circumference, in weight, in number of rows, in fact in every character we may pick out.

The second class of variations are those which Darwin called "definite" or discontinuous variations. To this kind of variation belong those characters that suddenly appear in their perfection, capable of transmitting the new feature with only the ordinary amount of fluctuating variation. These variations are now called *mutations.* To illustrate our meaning take the peach tree. It is not an uncommon thing for one branch to bear those smooth-skinned fruits called nectarines. This is mutation,* which continues constant from year to year. The nectarines, however, differ among themselves in size, weight, amount of flesh and other characters. In other words, they still have fluctuating variations among themselves. Galton illustrates the point of distinction nicely by use of a polyhedron,—an object with a number of equal sides. Suppose some force rocks the polyhedron as

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* Some writers refuse to recognize bud mutations as real mutations, but as bud mutations are sometimes transmitted by seed, there seems to be no reason for their exclusion until a definite scientific distinction between them and germ mutations is known.

it rests upon one of its faces. It will rock back and forth but always tends to come to rest upon this face. These oscillations represent fluctuating variation. But should a sudden shock rock the object so violently that it finally comes to rest on another of its faces, we might think of it as a mutation.*

Darwin believed that evolution and the changes in domestic animals and plants were very largely the result of the selection of the small individual variations or fluctuations, as the following quotation shows:—

"It may be doubted whether sudden and considerable deviations of structure such as we occasionally see in our domestic productions, more especially with plants, are ever permanently propagated in a state of nature. Almost every part of every organic being is so beautifully related to its complex conditions of life that it seems as improbable that any part should have been suddenly produced perfect, as that a complex machine should have been invented by man in a perfect state. . . . If monstrous forms of this kind ever do appear in a state of nature [he was speaking of a pig which had been born with a short proboscis, E. M. E.] and are capable of reproduction (which is not always the case), as they occur rarely and singly, their preservation would depend on unusually favorable circumstances. They would, also, during the first and succeeding generations, cross with the ordinary form, and thus their abnormal character would almost inevitably be lost."

It is only fair to say that Darwin changed his views slightly in the last edition of his work. So many examples of mutations had come under his notice that he could not disregard them entirely, and he says: "In the earlier editions of this work I underrated, as it now seems probable, the frequency and importance of modifications due to spontaneous [mutations] variability. But it is impossible to attribute to this cause the innumerable structures which are so well adapted to the habits of life of each species."

We shall see later from the work of De Vries that mutations do not necessarily occur singly, and from the work of Mendel, that they would not need to be swamped by intercrossing; but

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* De Vries believes fluctuations are confined to plus or minus variations of the same character; that is, "linear" variations. Mutations, on the other hand, may take place in any direction.

we will now take up some of the earlier criticisms of Darwin's views that are particularly related to the part played by fluctuations and mutations in evolution.

A great obstacle toward explaining all adaptive structures by the use of natural selection is the fact that many structures which are useful in a fully developed state must have been useless in the beginning when rudimentary and undeveloped. This criticism has been made by all opponents of the theory, but was stated with particular force by the Duke of Argyll. He argues that if an organ was developed gradually and very slowly, it follows as a matter of course that every beginning of such an organ must have been functionless at first. "No structure can be selected by utility in the struggle for existence until it has not only been produced, but has been so far perfected as to actually be used." For example, the eye of animals or the wing of birds, he thinks, could not have been of sufficient use to the possessors of their first rudiments to have caused them to have been selected. Romanes, in replying to this criticism, thinks that even if only rudimentary as eye or wing, they may have been useful for other purposes. A nerve ending may have been sensitive in a slight degree to light, and thus have enabled the animal to find more food or to hide itself better from its enemies. Likewise a rudimentary wing might not have been useful for flight but still have served for more rapid locomotion. These explanations, while ingenious, seem to be rather strained and make us feel as if we should rather have some theory which does not put too great a burden on our faith.

Morgan has put forth an objection belonging to this same class which is even more pertinent. Many species of animals have the power to regenerate, or grow again, certain parts of the body, when lost by accident. It is absurd to think of natural selection as preserving an individual which has this power in a very slight and imperfect manner, and by a continued selection of those individuals that can better regenerate lost parts,—finally perfecting this power. It has been shown experimentally that only a small per cent. of the animals of a species possessing this power ever lose a limb or other part. What chance would they have of surviving by natural selection in competition with numerous perfect, healthy specimens? The only possible explanation of the perfecting of such a power by the selection of small fluctuating variations is that they might be dependent upon other variations in structure which were useful when rudimentary. We know that sometimes seemingly independent structures do go together in an unaccountable manner, a phenomenon which is called correlated variation. But here again, such an explanation is as unsatisfactory support as is a straw to a drowning man.

There are at least four important objections among early criticism which cannot admit explanation by the natural selection theory alone:—first, that a large proportion of the characters that distinguish species from each other are seemingly useless and therefore cannot be explained by a use selection; second, the most common of specific characters, sterility between species, Darwin himself showed could not be explained by natural selection; third, the swamping effects of free intercrossing would render impossible by natural selection any evolution of species in divergent lines;* fourth, many characters useless for the preservation of individuals have been developed by only one sex of a given species. In the latter class belong the beautiful plumage developed by many male birds. Darwin has developed a theory supplementary to natural selection, that he calls *sexual selection,* to account for such cases. In brief, it is that higher animals do not mate at random but exercise an instinctive choice in obtaining their nuptial partners. The female cardinal or redbird, for example, has had an instinctive liking for a scarlet color. In the early history of the species, males were accepted as mates by the females only when they possessed certain red markings that had appeared as variations upon the plumage of certain individuals. These particular males were sires of the greater part of the next generation, and thus impressed upon it a large amount of their characteristics. A continuation of this process is thought to have produced the characteristic coat of the male of the species. Why only the males of some species possess certain characters to the exclusion of the females, our present knowledge of heredity offers no explanation. Sexual selection seems a reasonable explanation for the evolution of a few characters belonging to this class, but it, like natural selection, has been given more and broader phenomena to explain than it can possibly cover.

These earlier criticisms conclusively show that the natural selection theory is mainly, as Morgan states, a theory of adaptation

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* See Mendel's work for an explanation of this objection.

to environment. It is a sieve which sifts out variations which have appeared that are of prime utility to the organism or to the species. It is not a cause of evolution itself, but a working agent for destroying organisms less fit for their station in life than some of their relatives or species less fit for existence than others. It is not a selective agency, but a rejective agency. It is plainly evident that it is one of the great factors of evolution, possibly the greatest factor; but it is as plainly evident, even with the added theory of sexual selection, that numerous characters possessed by living organisms must have developed without its agency.

We will next mention the more recent criticisms of Darwin's theory, which have to do with the probability of evolution having taken place through the selection of fluctuating variations. Lord Kelvin has furnished the first telling obstacle by his calculations of the age of the earth. Earlier geologists and biologists, when they had once turned away from the idea that the earth was only about six thousand years old, allowed themselves to suggest millions of millions of years as the amount of time necessary for the geological changes and those of evolution to have taken place. These ideas in turn were forced to give way when Lord Kelvin calculated the earth's age upon definite physical data. His calculations were divided into three sets: first, based upon the rate of the earth's rotation as affected by the retardation of the tides; second, based upon the rate of cooling of the earth, calculated from the rate at which the temperature increases on boring inward toward its centre; third, based upon the rate of cooling of the sun by radiation. There was a noteworthy agreement in these three calculations, all tending to show that less than one hundred million years has elapsed since the earth's surface has been in a condition to support life. These calculations have been somewhat changed since the discovery of the immense amount of energy stored up in radioactive substances, yet it still remains necessary to conclude that life has not flourished on this planet a sufficient length of time to have developed our present fauna and flora solely by the selection of fluctuating variations.

De Vries has attacked the question of the probability of evolution through the selection of fluctuations from another point, that of their inheritance. He believes that fluctuations are a kind of acquired characters; at least that they depend solely upon the effect of food, light, temperature, moisture and other factors of environment. Nevertheless, they are, in a certain degree, inherited. There is nothing unusual in this when we consider that all higher organisms are but collections of cells each with its own purpose to fulfill. Should the environment of an individual be particularly favorable so that its general health is above the average, then might not the reproductive cells be better nourished and they therefore be enabled to produce better organisms, owing to their better start in life? We should expect, however, that such improvement would not be permanent, but would cease if the selection of such individuals was abandoned, and even degenerate to the original type. This is exactly what has been found both in historical cases and in experiments. The improvement of sugar beets in their sugar content has now been in progress for about fifty years, yet the maximum improvement was obtained in a very few years after the start, and now all that continued selection of the highest fluctuations of sugar content can do is to keep the average up to the point to which it had been raised years ago.

As an experiment upon this point, De Vries tried to raise the average number of rows of a variety of maize by selection. This variety had an average of 13 rows per ear. As we know, no ears of maize have an odd number of rows, but the *average* was between 12 and 14 rows per ear. The actual number of rows in individual cases varied between 8 and 22. He planted an ear having 16 rows and in the crop found a new average of 15 rows per ear. From this crop some good ears bearing 20 rows were planted, and this process of selection was continued annually for six seasons. At the end of this time the average of the variety had reached 20 rows. The lowest number on any ear was then 12 and the highest found was 28, a number which he had never seen in the regular variety. There are two points to be considered in this experiment, as De Vries points out. The first is: Could this average of 20 rows have been obtained in one year? On examining the results of the different years it was found that an average increase was obtained equal to two-fifths of the deviation of the parent ear from the average. An average of 20 rows per ear is a deviation of 7 from the average of the original variety of 13 rows per ear. Then if 7 equal two-fifths of the deviation, to obtain an average deviation of 7 in the progeny, we should need a deviation of 17½ rows above the average 13 rows; that is, a selected ear containing 30-32 rows. Two hundred ears had been examined originally and one 22-rowed ear was found. Now by the mathematics of probability, we can predict that by doubling the number of ears examined we would expect to find one ear with one more row, or 23 rows. This means that by the examination of 100,000* ears, he would have had the same likelihood of finding an ear of 32 rows as he had of finding the ear of 22 rows when he examined the two hundred.

The point is this: By examining 100,000 ears he could probably have found and planted an ear containing 32 rows and would have obtained his race of corn averaging 20 rows to the ear in one season. But by taking six years for the selection, he was able to obtain the 20-rowed race by the use of only about 1,000 plants. Hence the gradual change that takes place in the type of a selected fluctuating character is apparent rather than real, and is due to the rejection and non-propagation during the breeding of so many numbers below the selection standard.

The second important point is: Does an average, such as De Vries obtained for his corn after six years selection, remain constant? To test this point De Vries allowed the 20-rowed race to propagate indiscriminately and found that in only three or four years the old type of 13-rowed corn was reached. A number of other instances could be cited that indicate that all races improved by the selection of fluctuating variations are inconstant and tend to return to their original type. This conclusion is perfectly in accord with the conclusion we reached in the last chapter regarding acquired characters.

These conclusions of De Vries regarding the inconstancy of races improved by selection of fluctuations, have in the main been confirmed by an entirely different school of investigators called biometricians. Biometry is the science of applying mathematical methods of dealing with statistics to biological problems. It is not necessary for us to go into their technical methods, but we must give two of their important discoveries, whose derivation it is not necessary to understand to appreciate their value.

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* There is necessarily a physical limit in the production of rows in ears of maize, as in all other natural productions. Above this limit mathematical calculation is valueless.

The first is called Quetelet's law. Quetelet, a Belgian astronomer about the middle of the last century, discovered that the relative frequency of the occurrence of fluctuating variations in living organisms obeys the mathematical theory of probability; that is, it is just what we should expect if the number of causes combining to make fluctuations in nature is infinitely large. For example, we measured the lengths of a hundred and eighty-six ears of a certain variety of corn and found that they fell into classes of one inch in the following manner.

Length in inches	3	4	5	6	7	8	9	10	11	12	13	14
Frequency	0	1	1	5	19	37	58	40	18	6	1	0

Now if we draw a horizontal line and divide it into equal parts marked with these classes of one inch each; then erect perpendiculars at each point proportional in height to the number of ears found in each class; by joining the tops of these perpendiculars we get a close approximation to what the mathematicians call the normal curve. By knowing this fact, we can predict approximately how many ears of a certain length we should find in one thousand ears of this variety.

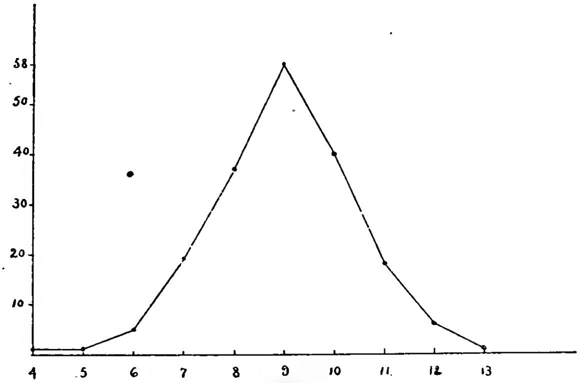

FIG. 1. Frequency polygon or curve of variation in length of maize ears

The second great law of the biometricians is called the law of ancestral heredity. It was enunciated by Galton but received modification and confirmatory data from Pearson. In its present form, it supposes that the average resemblance of this offspring to the two parents is 50 per cent., to the four grandparents 25 per cent., and to the eight great-grandparents 12.5 per cent. and so on.*

Assuming the truth of the law of ancestral heredity, and a perfectly normal distribution of fluctuations, Pearson has shown what could be accomplished by continued selection, provided all biological data followed the laws that he has found in his data from measurements of the human race. The conclusions were derived from measurements of several different characters, but the following will serve as an imaginary example to illustrate his results. If the average height of the population were five feet and six inches, and individuals six feet high were selected as parents, then in the first generation he has found that the average height of the offspring would be five feet six inches plus 62 per cent. of six inches, which is the deviation of the parents from the average. Again selecting six-foot parents, the height of the offspring would be five feet six inches plus 82 per cent. of six inches, and in the third generation five feet six inches plus 89 per cent. of six inches. Selection of six-foot parents for a large number of generations would only bring the average up to five feet six inches plus 92 per cent of six inches. This shows that

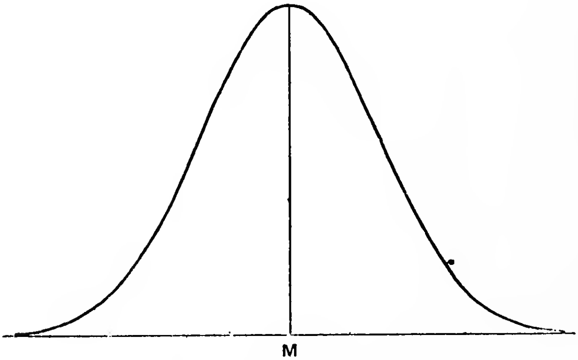

FIG. 2. Normal curve

Compare with Fig. 1.

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* This law has been much misunderstood, and a great deal of criticism of it has arisen through the activities of the Mendelian school of biologists. If we consider a single character possessed by the organism, it may be generally untrue, but if we consider all of the thousands of characters possessed by the organism, it certainly approximates the truth.

in three or four generations the offspring may have an average of 90 per cent. of the selected character, but after this selection has only little effect. Moreover, Pearson showed that if selection was stopped at any time and the offspring allowed to inbreed, they quickly returned toward the average of the selected character in the original race.

Recently some tentative conclusions of Johannsen's, from experiments upon barley and kidney beans, may be interpreted as agreeing with Weismann's theory, and De Vries' and Pearson's conclusions,—that fluctuating characters have almost nothing to do in the permanent improvement of a race. All of his experiments were made upon plants which could be self-fertilized during successive generations. In this way he made the experiment simpler than he could have done if he had used different plants for the two parents. All of the descendants of a single plant, arising by self-fertilization, he speaks of as a 'pure line.' The characters used were typical fluctuating characters such as the weight of the seeds. All members of a pure line showed normal fluctuations around a mean or type value. Moreover, all seeds from plants of the same variety, made up of a number of such pure lines, also showed a normal variability. In the pure lines, some of the mean or type values were very close to the mean of the variety in general, while others were quite different, being both lower and higher than the general mean value. When any individual, differing widely from the mean value of its pure line, was selected for propagation, its offspring showed a regression or tendency to go back toward the type of its particular line; but showed no regression to the mean value of the variety.

It is quite clear if these conclusions are warranted, that the only improvement that selection can effect is towards the isolation of one of these pure lines and must of a necessity come to an end when the pure line is entirely isolated. The difficulty of doing this in practical work is obviously very great because of natural intercrossing. It was the opinion of Darwin that by selection the type of the race would be raised and a new selection possible from the extremes in fluctuation of this new type. This would set no limit to the amount of improvement that could be made. The experiments of De Vries and Pearson, however, and the experience of breeders in general as illustrated by the case of the sugar beet seem to agree with Johannsen's theory, that such is *not* the case. Johannsen's work, however, indicates that the complete isolation of a pure line would give a strain which would not regress to the mean of the original mixed population, but would breed true to its own type. This is contrary to the general belief of breeders, and his further results will be awaited with great interest.

The results of our considerations of the criticism of Darwin's theory, that evolution must take place through natural selection or some kindred eliminating agency as sexual selection of minute fluctuating variations, have led to three general conclusions. First, natural selection will not explain either the evolving of many characters that could not have been useful in a rudimentary state, or the large numbers of characters that appear to be entirely useless to organisms. Second, the age of the earth since the formation of oceans, as calculated by physicists, does not allow sufficient time for the evolution of higher plants and animals by the selection of minute fluctuating variations. Third, experimental evidence from several diverse lines all tends to show that a selection of fluctuating variations can make no permanent improvement, and that there is a narrow limit to the changes that can be made, even with their continuous selection.

The Mutation Theory.

The study of evidence relating to the points that have just been discussed, has resulted in a waning belief in the efficiency of fluctuating variations to explain the facts of evolution, and in a growing belief in the prominent part played by discontinuous variations or mutations. We owe to Hugo De Vries, an eminent Dutch botanist, the largest amount of data regarding mutations, and even the word itself when used in this sense. It is true, other prominent workers were beginning to trace out similar theories, and particularly important experiments had been conducted by the distinguished English zoologist, Bateson; but when De Vries' investigations were published the time was ripe for their general appreciation.

The data from which De Vries evolved his theory is thought to show not only that mutations are a class of variations useful as a factor in evolution, but that they are the only possible way by which evolution could take place. Whether this is true or not is not possible at present to determine; but we can say that the rapidly increasing volume of data points toward this conclusion. Moreover, there is no experimental data at hand to refute this view. The mutation theory certainly does clear up many of the points which did not seem to be clearly explained from Darwin's point of view. We will endeavor to give an outline of the chief points involved.

In the middle of the eighteenth century, Linnaeus, the great Swedish botanist, introduced our present system of classifying plants and animals. He used two names: a species name or name of a group of individuals which were fairly constant and alike in their characters and which differed from other related groups by characters which could be recognized from descriptions; and a generic name which included related groups of these species in a broader class called a genus. He supposed that his species were the units of nature and were created as such in the beginning. He did recognize subdivisions of species which he called varieties but had no very clear ideas concerning them. The object of his work was to bring into some order the plants then known, and not to study lesser divisions.

The classifying of species has since been more or less a series of individual judgments of different botanists; some used more definite characters as distinctions between species, and made a small number of species, while others used fewer or smaller distinctions and described four or five times as many species in the same genus.

More recently Jordan, a French botanist, became satisfied that the only reasonable way to classify species was to grow a large number of individuals and study the characteristic differences between them. When this was done, he found that while some of Linnaeus' species were relatively uniform, others contained many groups of plants which differed from each other by one or more constant characters. Often these differences were in parts of the plant which would remain unnoticed by the untrained eye, but still the differences were there and were transmitted to the succeeding generations.

De Vries has called these groups of plants, "elementary species." His idea is that plants and animals are made up of thousands of large or small, but distinct heritable characters; and that these characters have arisen, one or more at a time, fully formed and able to function, from parents which did not possess the characters.

It is recognized that some plants are much more variable in this respect than others: the common whitlow grass (*Draba verna*) has had several hundred of these elementary species described, while others of Linnaeus' species seem to vary only with the common fluctuating variation. This phenomenon is explained by the hypothesis that there are periods when a species is producing mutations and other periods when mutations very rarely if ever appear. These periods may be hundreds of years apart and thus account for the apparent constancy of some species such as wheat, of which we have a long history under domestication.

In making culture studies of many species of plants, these elementary species have been found very common indeed, but no one had seen a new form originate from an older wild one until De Vries had the good fortune. It is true that many wide mutations, or jumps of a distinct kind, had been isolated among cultivated plants, and were called "sports" by horticulturists. De Vries, however, discovered and propagated a series of interesting mutations from a plant growing wild on some fields near Amsterdam.

The plant which was caught in the act of originating a new species is an American plant of the evening primrose family known as *Œnothera Lamarkiana.* It had been cultivated in Holland many years but had escaped from cultivation and had been growing wild for a long time. On closely examining these plants, De Vries discovered two new and unknown forms that were quite unlike the remainder of the plants which were typical of the species. Each of these types occurred in spots, as if they had arisen as the offspring of a single plant. Fortunately, De Vries was not satisfied with the single observation, but took seed and roots of a number of the plants of each type and grew them in his garden for a number of generations. In all, he cultivated at least 50,000 plants, and among this number about 800 were found which differed distinctly from the parent species, and whose characters were constant when reproduced by self-fertilization. That is, he was able to obtain from one to three per cent. of new and distinct forms which did not tend to go back to the parent form but to remain constant. One of the forms was a giant form with large flowers; one was a dwarf form; in one the ovules were imperfect; and another had defective pollen. The last two forms were evidently less fitted for existence than the parent form and were raised with difficulty, while other forms were able to survive in natural competition with the parent species.

These new forms corresponded to the elementary species that had been observed before in nature, but had never been seen to arise. Each character had the common fluctuating variability which often made the fluctuation of two forms overlap, for instance the longest leaves of the short form being longer than the shortest leaves of the long form. But in each of these cases, when the two forms were cultivated separately, the variability was found to group itself around a typical point and to be distinct in each form.

We cannot go deeply into the numerous questions regarding variability and inheritance upon which these experiments have shown light, but it may be well to sum up some of the chief points.

1. Mutations are not so rare as was formerly supposed. They are found in wild as well as cultivated plants. Their occurrence reasonably accounts for the numerous "elementary species," or subdivisions of Linnaeus' species that are found in nature.

2. Mutations are constant in succeeding generations and thus account for the constancy in nature of these elementary species. The tendency of the progeny of extreme fluctuating variations to return to the original type appears to make continuous evolution impossible, but with mutations which remain constant until succeeded by other mutations, there is no such difficulty.

3. The criticism that imperfect and rudimentary characters would not survive by natural selection, is here valueless, for mutations appear fully formed.

4. Anticipating the text a little, we may state that Mendel's work on heredity has shown that mutations would not necessarily be swamped by intercrossing with the parent kind, even if they occurred singly. It may also be deduced from his work that useless characters may survive.

5. De Vries' work shows that in the working of the principle of natural selection, it is more likely a contest in which the fittest elementary species survives. The contest for survival among individuals due to fluctuating variations has not yet been shown to produce permanent changes. Possibly this would be done, however, if we imagine a gradually but permanently changing environment to which individual organisms adapt themselves in different degrees.

6. By mutations, it is believed that evolution may have been accomplished in the time allotted for its action by the calculations of the physicists and geologists.

From this discussion we can see that whether or not we accept De Vries' theory as proven* in its entirety; nevertheless as a theory it explains reasonably and clearly the majority of the pertinent criticisms of the theory of evolution by the selection of fluctuating variations, which were given at the end of the first chapter.

According to De Vries, there are three classes of mutations, progressive, degressive and retrogressive. If an entirely new character appears in an organism, it is a progressive mutation. It is thought that this class has been the great factor in evolution. The degressive mutations are those which occur when a character appears that has been partially latent† or hidden. A retrogressive mutation is when a character previously active becomes latent, as when a species that has always produced colored flowers suddenly produces a white variety.

A mutation is held to be the appearance or disappearance of a distinct heritable character. De Vries disclaims any idea that these changes must be wide, but they must be distinct in that there in a change of type in the variation which is inherited. The mutation may be within the limits of a fluctuation, but still be a true mutation. To illustrate this, cut-leaved plants of a number of species have appeared as mutations, but there may be individual leaves of the ordinary types which have as deep or deeper incisions through fluctuating variations than have the least incised individuals of the cut-leaved type. It has been customary to regard mutations as sufficiently definite changes in botanical characters that they may be recognized when grown in pedigree

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[*] There are points concerning the germ cell structure of De Vries' primrose mutations, and the fact that certain of these aberrant forms have continued to give off mutations, that make it a question if these cultures were not either hybrid forms, or parthenogenetic forms (forms in which the seeds develop without fertilization). The original wild plant seems to have disappeared in America, hence experiments with it to determine these points cannot be made. Nevertheless, even if the primrose mutations should be otherwise explained, it would not affect the general theory of the discontinuity of heritable characters. Other data presented by Bateson, De Vries and others, are more convincing to my mind, than are the primrose experiments; although the latter have been received with greater popular acclaim.

[†] Latent is a term used to explain the condition of a character that appears to be lost, but is only obscured or hidden.

cultures; that is when isolated and reproduced in pure lines for several generations. Doubtless with sufficiently accurate methods this could always be done. But it does not seem to be a necessary part of the theory to regard mutations as additions or subtractions of what are generally regarded as specific characters. If mutations may appear in any direction, I see no reason why they may not sometimes appear as linear changes (plus or minus) of characters already present. Johannsen's results might then be interpreted as mutations in which the real unit characters are portions or segments of what visibly appears as the character, but differing from fluctuations of the same character by the constancy with which they are reproduced. A perfectly isolated line containing only a definite number of segments of the character in their germ cells, would remain true to its own type in succeeding generations of progeny. The difficulty in isolating a pure line is that the fluctuations of different lines overlap and are indistinguishable in appearance.

If we regard the growing sugar beet as containing a chemical laboratory for the manufacture of sugar, we may imagine changes taking place in the germ cells from which an apparatus and reagents appear by which a higher or lower amount of sugar would normally be produced. But grouped about this normal type would be fluctuating variations due to environment. In other words, there might be germinal or genetic variations of the sugar-producing character, a pure line from which would normally produce beets with 12 per cent. sugar, but with fluctuating variations of from 10 per cent. to 14 per cent. sugar. Another pure line might normally produce 10 per cent. sugar with fluctuations of from 8 per cent. to 12 per cent.

III.

HEREDITY.

Through common usage, the term heredity brings to our minds a more or less definite meaning, but a precise definition is difficult. Suppose we say that it is the tendency of the characters of blood relations toward duplication. Variation, which we have just been discussing, and heredity are in one sense opposite in their meaning. If nothing interfered, and inheritance were perfect, there would be no variation and hence no evolution; differences in species would necessarily be due to direct creation, or spontaneous generation, and each species would be made up of individuals exactly alike. On the other hand, we could hardly imagine the chaos if there were no limits to variation. Heredity and variation have been spoken of as two opposed forces, the first a centripetal force which is striving to keep nature fixed within due bounds, and the second a centrifugal force which is continually striving to overleap these bounds. The continued working of these two forces under laws of which we as yet know little, has built up the organic world which surrounds us.

Blended Inheritance.

Of the mechanism of bisexual inheritance very little is known, but from observation of its results it has been divided into blended, mosaic and alternate inheritance. Blended inheritance is where there is a fusion of two characters, so that a character possessed by an offspring appears to be an average of the two characters as possessed by the parents. The most familiar case of blended inheritance is the mulatto—the result of the union of a white and a black individual of the human race. The mulatto is intermediate between the two colors, and breeds true for generation after generation. If the mulatto is crossed again with white or black stock, the resulting offspring is correspondingly whiter or blacker.

Cases of blended inheritance are found in all sorts of crosses,—those between races, varieties and elementary species. It has been thought to be a characteristic occurrence in hybridization between different Linnean species, but it is now known that even here the other forms of inheritance occur. No general law for the mechanism of blended inheritance has been found, but Galton's law of ancestral inheritances as mentioned in the last chapter gives the expectation of average ancestral resemblance in the different generations. This law is thought to apply especially to blended inheritance, but there is no reason why it could not apply to all forms of inheritance if we consider the total sum of characters of an individual and not a single character.

It is particularly in blended inheritance that the phenomenon of prepotency* has been noticed. This is the tendency of one of the parents of a cross to have more of its characters reproduced than would be normally expected. It is stated that in the production of the mule the characters of the ass are prepotent, while in crosses between the dog and the jackal the latter is prepotent. It is variously stated that in crossing plants, the characters of the older species are prepotent, and that progressive mutations are prepotent. Accepting the mutation theory of evolution as true, these two statements are in direct opposition to each other. We should be cautious about accepting any theories concerning prepotency until we know more about the subject.

Mosaic Inheritance.

The most familiar example of mosaic inheritance is where animals of different coat colors are bred together. We sometimes get an individual that is piebald. The characteristic colors of the two parents are inherited by the offspring in patches on different parts of the body. These spotted races have originated among almost all of our domestic animals and are noticeable in many of our flowering plants. In some cases they may be mutations that breed true, as is believed by Cuénot, but it is most generally thought that this is only a special form of alternate inheritance and that it will be explained later on that basis.

Alternate Inheritance and Mendelism.

It is upon alternate inheritance that results of greatest value have been obtained. By this term are designated numerous cases in which a character of one parent is inherited, apparently to the complete exclusion of any influence of the other parent on this character. Data now being obtained by investigators indicate that this exclusion is sometimes an exclusion of appearance and

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* It may be that prepotency will later be explained as due entirely to dominance of characters. (See Mendelian Inheritance.)

function, and that the alternate character may yet appear in subsequent progeny under certain conditions. The classical example of this type of inheritance is that of eye color in the human race. It is a matter of common observation that the offspring from a union of a brown-eyed parent and a blue-eyed parent is never a mixture or blend of the two; the children are either brown-eyed or blue-eyed like one or the other of the parents. Until 1900 this type of inheritance was thought to be comparatively rare. In that year, however, it was discovered by workers in heredity in three different parts of the world, that two laws of the utmost importance to both science and practice had been buried in the oblivion of an unnoticed journal for a whole generation. These laws are now known as Mendel's laws.

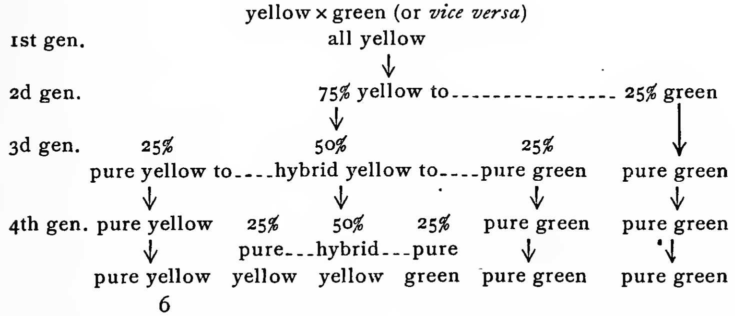
Gregor Johann Mendel was an Austrian priest, a teacher of physics and natural science in the Cloister at Brünn. He was appointed Abbot at Brünn, about 1869, and unfortunately for science he had little time left from his executive duties for the pursuance of his studies. He died in 1884 practically unknown to the world. It was not until sixteen years after his death that it became widely known that in 1865 he had reported a paper giving results of ten years' experiments on inheritance,—results that were fundamental and epoch making.

By a wonderful foresight, he perceived that if progress was to be made in the study of heredity the problem must be simplified as much as possible. It was the simplicity of his experiments that crowned them with success. There were two things especially necessary to be controlled, namely, accidental mixtures due to crossing, and differences in too many characters. The common garden pea fulfilled these demands. It could be self-fertilized generation after generation without deterioration, and varieties were found that differed from each other in but few characters. Mendel selected varieties of the pea which differed from each other in such characters as "round or wrinkled seeds," "yellow or green cotyledons" or seed leaves, and "purple or white flowers." These varieties he found to be true to their characters by inbreeding. He then crossed them once and made careful records of their progeny when inbred for a number of succeeding generations.

He crossed a yellow seeded variety with pollen from a green seeded variety, and again crossed the green seeded variety with pollen from that bearing yellow seeds. It was found that it made no difference which variety was used as the pollen parent and which as the seed parent, the seeds resulting from the cross were in every case *yellow*. He called the yellow color the *dominant* color and the green color the *recessive* because it had receded from sight for a time.

These yellow seeds were planted the next season and the blossoms were allowed to self-fertilize, that is, pollen from the stamens of a flower was allowed to fertilize the pistils of the same flower. It was found that all of the plants bore both yellow and green seeds, frequently both colors being found in the same pod. This proved that although the seeds from the cross were in the first generation all yellow in color, the green color was still there potentially, waiting to appear in the next generation. Continuing the work for the third generation, he found that all of the plants from green seeds, when allowed to self-fertilize, produced green seeds entirely. This was continued for six generations with no reappearance of the yellow character. In other words, the recessive character bred true.

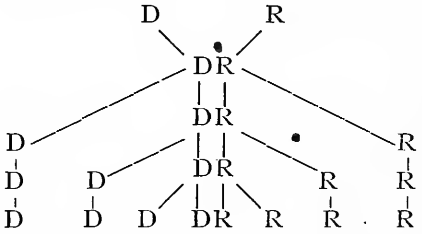
When the same method of inbreeding was used on the yellow seeded progeny of the cross, however, a different result was obtained. Some of the plants were found, when self-fertilized, to produce both yellow and green seeds just as their parents had done, while others bred true in succeeding generations. That is, some of these yellow seeds were "pure" yellow seeds, while others were "hybrid" yellow seeds like the parents. But in the case of the hybrid yellow seeds, the yellow color was still dominant; that is, it was apparent to the eye; while the green color was recessive or hidden. Moreover, long continued experiments showed that there was a constant numerical ratio between the yellow and green seeds, which is illustrated by the following table.



His results may be stated as follows:

If two contrasted characters which have previously bred true are crossed, one only, the dominant character, appears in the hybrid. (The Law of Dominance.)

Second, in succeeding generations, self-fertilized plants grown from seeds of this cross reproduce both characters in the proportion of three of the dominant character to one of the recessive character. Furthermore, the recessive character continues ever after to breed true, while those plants bearing the dominant character are one-third pure dominants which ever after breed true to the dominant character, and two-thirds hybrid dominants which contain the recessive character in a hidden condition. (Mendel's law of inheritance.) Using D to represent the dominant character and R to represent the recessive character, the working of the law may be thus illustrated:



Mendel did not claim that this law of inheritance holds good for all organisms or even for all plants, but it is now being corroborated for an ever increasing number of characters in both plants and animals. Even the results which he obtained did not follow the exact numerical ratio just given but were sufficiently exact for him to formulate a theory to account for the observed facts.

The theory supposes that when a dominant and a recessive character meet in a cross, the germ cells which are produced in the hybrid do not blend these characters but possess either the one or the other; and as the possession of either character is a matter of chance, on the average 50 per cent. of the germ cells will bear the dominant character and 50 per cent. will bear the recessive character. In a plant, for example, 50 per cent. of the pollen cells would bear the dominant and the other 50 per cent. would bear the recessive character. The egg cells would likewise one-half contain the dominant character and one-half the recessive character.

Now if we could pick out at random any one hundred pollen or male cells to fertilize any one hundred egg or female cells, we can see that there are equal chances for four results. A D male cell might meet a D female cell, a D male cell an R female cell, an R male cell a D female cell, and an R male cell an R female cell. In an abbreviated form it amounts to this:

$$\begin{tikzcd}
 & D \arrow[r] & D & \\
\text{Male} & D \arrow[dr] & D & \text{Female} \\
\text{cells} & R \arrow[ur] & R & \text{cells} \\
 & R \arrow[r] & R &
\end{tikzcd}$$

We have (D + D), (D + R), (R + D) and (R + R) formed in equal quantities, but as the two middle terms are the same, we can reduce the formula to one (D + D) to two (D + R) to one (R + R). But wherever there is a D present in the germ cell, the dominant character shows while the recessive character is hidden. The one part or the 25 per cent. of the individuals showing the character (D + D) will appear to be just like the two parts or 50 per cent. of the individuals having the character (D + R). Therefore there will be 75 per cent. of the individuals which will show the dominant or D character while 25 per cent. will show the recessive or R character. These 25 per cent. showing the R character will ever after breed true because they contain nothing but the recessive character, while of the 75 per cent. showing the dominant character, one-third or those having the pure (D + D) character will breed true in succeeding generations while the other two-thirds having the (D + R) or hybrid character will again split in the next generation.

Of course it is only theoretically that these ratios are exact. They increase in accuracy with larger numbers. If one thousand seeds were counted in the second generation, they would come nearer the proportion of three to one (3D to 1R) than if one hundred were counted. As a tangible illustration of what may be expected in practical work, take one hundred black beans and one hundred white beans and shake them up in a hat. Now draw them out in pairs, and see what combinations you get. In an actual count I obtained the following results.

Actual number		Theoretical number
22	2 black	25
55	1 black, 1 white	50
23	2 white	25

This explains why the practical work is not in exact accord with the theory. The actual results approach nearer and nearer to the theory as larger and larger numbers are used.

Mendel was not content with experiments in which only one pair of differentiating characters were concerned. He made crosses in which two and three pairs of characters were associated and found that they *independently* obeyed the same laws. Taking two pairs of characters, he designates the dominant characters as A and B and the recessive characters as a and b. The characters crossed were as follows:

Seed parent AB	A form round B seed-leaf color yellow	Pollen parent ab	a form angular b seed-leaf color green

When these two forms were crossed all of the hybrid seeds appeared round and yellow (AB) like those of the seed parent, that is, the round and yellow forms were dominant.

When these seeds were sown and the plants self-fertilized, four kinds of seeds appeared in the four combinations that were possible; and with the following numbers of each:

AB	round and yellow	315
aB	angular and yellow	101
Ab	round and green	108
ab	angular and green	32

These figures stand approximately in the relation of 9AB to 3Ab to 3aB to 1ab: but these forms which appeared to be of only four classes were found in the next generation to be made up of nine really different classes.

From the round yellow seeds (apparently AB) were obtained:

(1)	AB	round and yellow seeds	38
(2)	ABb	round yellow and green seeds	65
(3)	AaB	round yellow and angular seeds	60
(4)	AaBb	round yellow and green, angular yellow and green seeds	138

From the round and green seeds (apparently Ab) were obtained:

(5)	Ab	round green seeds	35
(6)	Aab	round angular and green seeds	67

From the angular and yellow seeds (apparently aB) were obtained:

(7)	aB	angular and yellow seeds	28
(8)	aBb	angular and yellow green seeds	67

From the angular and green seeds (ab) were obtained:

(9)	ab	angular and green seeds	30

We notice that there were nine classes of individuals produced whose characters had the formulae given above. This was experimentally proved. The forms AB, Ab, aB and ab were found to be true and did not afterwards vary. The hybrid character of the remaining classes was subsequently shown.

The numerical relations found were approximately the following series. AB, Ab, aB, ab, 2ABb, 2aBb, 2Aab, 2AaB and 4AaBb. This is really a combination by multiplication of the two series,—

$$(A + 2Aa + a) \times (B + 2Bb + b) = AB + Ab + aB + ab + 2ABb + 2aBb + 2Aab + 2AaB + 4AaBb.^*$$

The two pairs of characters behave independently of each other and as if chance only governed their combinations. Moreover, three pairs of contrasted characters were found to behave in exactly the same manner, the number of forms found being what would theoretically be expected if the above product were multiplied by another series represented by C + 2Cc + c.

These results can be reduced to still simpler terms, as is shown in the following table. Let n represent the number of pairs of contrasted characters in the parents. When they are crossed, the second generation, when self-fertilized, show visible differences of 2 to the *n*th power. These visibly different classes actually contain 3 to the *n*th power different classes, the phenomenon of dominance obscuring part of them. Finally when crossing to secure combinations of *n* characters, we must have 4 to the *n*th power number of individuals to be theoretically certain of at least one individual in each class.

MENDEL'S LAW OF INHERITANCE OF UNIT CHARACTERS.

No. of pairs of dif. between parents. n	No. of visibly dif. classes each cont. one pure individual. 2^n	No. of actual classes, both pure and hybrid. 3^n	Smallest No. of offspring allowing at least one to a class. 4^n	
1	2	3	4	Experimentally tested by Mendel for peas.
2	4	9	16	
3	8	27	64	
4	16	81	256	Calculated
5	32	243	1024	
6	64	729	4096	

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* Instead of writing AA and aa in the series one of the letters is dropped.

When such a noteworthy set of conclusions as those of Mendel's is announced it is important that they should be confirmed by other investigators. This has been done by investigators in several countries, and in recent years Mendel's laws have been found to hold for a large number of characters in numerous varieties of our domestic plants and animals. Characters in such different subjects as rats, mice, guinea pigs, cats, horses, oxen, poultry and various insects, among animals; and for wheat, oats, maize, peas, beans, etc., among plants have shown Mendelian inheritance in certain characters in hybrids between their varieties. How far these laws will be found to hold, we do not know at present; but the number of cases is being extended daily. It is possible and even probable that a great many cases which are now considered as blended and mosaic inheritance will be found to obey some extension of Mendel's law; when it is better understood, moreover, it is quite likely that many characters that are now regarded as units will be finally divided into several units, and their behavior in different combinations thus accounted for. Bateson has already found that several characters, such as certain colors, which would at first thought be regarded as unit characters, are actually made up of two, three or even a larger number of factors; and such facts make it very difficult to derive conclusions from experimental data on account of their very great complication.

We have treated Mendelism rather more fully than blended or mosaic inheritance because it is the only law of inheritance that has been formulated that will greatly help the plant breeder. Galton's law of ancestral inheritance, even though it should finally be brought into conformity with Mendelian results, will probably never be of great practical use because it will be much more of a law of averages within races than a law of expectation from crosses.* Mendelism has been treated in this chapter just as the author himself left it. In the next chapter some of the more important modern results along Mendelian lines will be described.

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*Galton's law is statistical and deals with averages; Mendel's law is physiological and deals with individuals.

IV.

Methods of Plant Improvement.

We have tried to show that there are three main methods by which the numerous improvements in our cultivated plants and domestic animals have been effected. They are:

1. The continued selection of individuals whose desirable characters have fluctuated above the average of their race.

2. The isolation, from natural mixtures of several elementary species, of those forms which possess the most desirable economic qualities.

3. The combination of desirable qualities possessed by different related forms, by means of hybridization.

The most progressive plant breeders use all three methods; but these methods must be modified to meet the various peculiarities of different kinds of plants. Sometimes free intercrossing or a tendency toward sterility in inbred plants almost prohibits the complete isolation of natural forms. In some cases the common method of propagation is by buds, and fluctuations can be multiplied in a commercial way. In other plants desirable characters are possessed by different types, and hybridization must be used to determine if certain combinations of characters will not produce the desired quality.

We cannot take up any extended history of what has been done in plant breeding, for that would be to give the history of each of the thousands of varieties of our cultivated plants; but we will give a number of typical examples, illustrating what has been accomplished by the use of these three lines of work. The investigations along theoretical lines have shown that there are obstacles and limitations belonging to each class. It is necessary to know how these facts affect practical work.

The Selection of Fluctuations.

We have already mentioned the sugar beet as an example of a crop in which fluctuating variations have been selected for a long term of years. We do not know just how much progress was made, if any, in raising the sugar content of the sugar beet previous to the middle of the nineteenth century. The beginning of its culture for sugar purposes was about the year eighteen hundred. Experiments were carried on in both Germany and France, and even with the very imperfect methods of the time, 6 per cent. of sugar was often obtained. What the fluctuations in sugar content of individual beets were at that time we do not know, for modern and accurate methods of sugar determinations in beets have been in use only for a generation. Previous to the time of Louis Vilmorin, about 1850, there had been some few selections of mother beets for higher sugar content by placing the roots in solutions of different density and selecting those having the highest specific gravity. There was probably little improvement made in this manner, for the frequent formation of hollows in the centre of the root introduces large errors in such determinations. Louis Vilmorin recognized the fault in this method and began the first real selection of mother beets for higher sugar content by pressing out the juice from a section of the beet, making density or specific gravity determinations upon the juice itself and planting the mother beets whose superiority was thus shown.

Later the improvement of chemical methods of analysis, including the use of the polariscope, has made rapid determinations of sugar possible. At present there are German and French seed growers that make as many as 100,000 sugar determinations upon individual beets ever year. Their method is to take a cylindrical piece cut from the beet in a diagonal. In this way a fair sample is taken, for different cross sections of the roots vary in their sugar content. After these cylinders from all of the beets are analyzed, the best are selected and are carefully saved until next season, when they are planted to produce seed for the commercial growers.

As early as 1878, the time of the Paris Exhibition, we have records of varieties that averaged 16 per cent. to 18 per cent. sugar and whose individual beets ran as high as 25 to 28 per cent. Since that time thirty years of continuous selection has made no progress. Our commercial beet races are kept up to about 16 per cent. by annual selections from large numbers of mothers of known composition, but it is impossible to reach a higher average. The fluctuations are practically the same as we find in our earliest records. Apparently no mutations have intervened, and the best strains of beets have been fairly well isolated. Now all that selection is doing is to perpetuate these improved races. Beets are open fertilized, that is, they cross-fertilize naturally in the field, hence the continuous need of careful selection to keep their sugar content up to the standard reached a generation ago. It has been definitely shown that without this continuous selection their constant intercrossing with inferior blood that still remains, will immediately make them regress toward the old average of sugar content of a hundred years past. Possibly there are causes contributory to this regression, but it can hardly be doubted that they would reach this average in a very few years if selection ceased.

Work analogous to raising the sugar content of the sugar beet has been going on in this country for the past ten years. I refer to the work of Hopkins and his associates at the Illinois Agricultural Experiment Station in changing the composition of the maize kernel. With this work the writer had the pleasure to have been connected for five years.

Work was started in 1896 to change the composition of the maize kernel along four different lines, for higher and lower protein, and for higher and lower oil contents. One hundred sixty-three individual ears of Burr's White maize from the 1896 crop were analyzed and the proper selections in each case planted in their respective plots. In each plot from twelve to twenty-four rows were planted and each row contained only the kernels from a single ear. In succeeding years, a hundred or more ears were analyzed from each breeding plot and those ears from the "High Protein Plot" which showed the highest per cent. protein were saved to plant the next year's "High Protein Plot," while those ears from the "Low Protein Plot" which showed the lowest per cent. protein were saved to plant the "Low Protein Plot" of the next season. Like methods were followed in the "High Oil" and "Low Oil" breeding plots.

The results of the "High Protein" and "Low Protein" plots for ten generations are shown in the following table.

We have here a concrete illustration of what was done in ten years; but we must not get from it the idea that this average increase or decrease of protein in a variety of white maize obtained in ten years is a measure of what would be obtained by the selection of any other fluctuation in any other plant. This is

RESULTS OF SELECTION FOR INCREASE AND DECREASE OF PROTEIN IN MAIZE AT THE ILLINOIS AGRICULTURAL EXPERIMENT STATION.*

Year.	High Protein Plot. Average in per cent.		Low Protein Plot Average in per cent.		Difference between the crops, per cent.
	Seed planted.	Crop.	Seed planted.	Crop.	
1896		10.92		10.92	0
1897	12.54	11.10	8.96	10.55	.55
1898	12.49	11.05	9.06	10.55	.50
1899	13.06	11.46	8.45	9.86	1.60
1900	13.74	12.33	8.08	9.34	2.99
1901	14.78	14.12	7.58	10.05	4.07
1902	15.39	12.34	8.15	8.22	4.12
1903	14.30	13.04	6.93	8.62	4.42
1904	15.39	14.98	7.00	9.27	5.71
1905	16.77	14.72	7.09	8.57	6.15
1906	16.30	14.26	7.21	8.64	5.62

what was obtained under the soil and climatic conditions at Urbana, Illinois, during a certain period of ten years, when about (in most cases) one hundred ears were analyzed and, on an average, the proper, best twenty fluctuations planted. The amount of average change that can be made will vary with the *number* of individuals considered and with the strictness of selection. If one thousand ears had been analyzed each year and only five of these planted, the same results would have been obtained in a much shorter time. There are also environmental conditions, such as moisture, light and available plant food of the proper kind, that would undoubtedly influence the results. Moreover, in other characters and in other plants the variability of the variety would affect the progress that could be made.

The next table gives the results that were obtained in the "High Oil" and "Low Oil" plots from the same variety of maize with about the same rigidity of selection.

Here we see an illustration of the point just mentioned: the percentage changes in oil content, when referred to the total oil contents of the crops are much greater than the changes that took place in the proteids in the same amount of time.

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* The figures for the following three tables have been furnished through the courtesy of Dr. L. H. Smith, Assistant Professor of Plant Breeding at the University of Illinois.

RESULTS OF SELECTION FOR INCREASE AND DECREASE OF OIL IN MAIZE AT THE ILLINOIS AGRICULTURAL EXPERIMENT STATION.

Year.	High Oil Plot. Aver. in per cent.		Low Oil Plot. Aver. in per cent.		Differences between the crops, per cent.
	Seed planted.	Crop.	Seed planted.	Crop.	
1896		4.70		4.70	0
1897	5.39	4.73	4.03	4.06	.67
1898	5.20	5.15	3.65	3.99	1.16
1899	6.15	5.64	3.47	3.82	1.82
1900	6.30	6.12	3.33	3.57	2.55
1901	6.77	6.09	2.93	3.43	2.60
1902	6.95	6.41	3.00	3.02	3.39
1903	6.73	6.50	2.62	2.97	3.53
1904	7.16	6.97	2.80	2.89	4.08
1905	7.89	7.29	2.67	2.58	4.71
1906	7.86	7.37	2.20	2.66	4.71

There are given in the next table the extremes of fluctuation in the ears analyzed for protein each season. It is noticeable that several years of selection passed before certain extremes appeared, as, for instance, the high proteid ear containing 15.71 per cent. protein that appeared in the year 1900. It would be easy to calculate the number of ears that must have been analyzed the first year in order to have had the same relative probability of finding an ear containing this amount of protein, as there was of obtaining the ear with 13.87 per cent. protein which was found in that year. Could there have been a sufficient number of ears examined and the proper number planted, there is a great probability that these averages obtained in the crops after ten years' breeding might have been obtained in one or two years. In fact, we may note here that at this station an ear of the Longfellow variety whose ancestry had been unselected was found, in which the protein content was 16.2 per cent., which shows that nature is producing quite high extremes if we can but find them.

But there is a point still more important. We can see in the next table that there is evidently a limit to the fluctuations in protein or oil. The record-breaking ears—those with extremes of composition greater than had been obtained before are fewer in later years and the extreme is not pushed up or down to any considerable extent. It seems evident that the isolation of the extreme lines is fast being accomplished, if indeed it has not already been done. The curve of crop averages given below will

FLUCTUATIONS IN PROTEIN CONTENT OF INDIVIDUAL EARS.

Year.	High Protein Plot.			Low Protein Plot.		
	No. Ears analyzed.	Minimum.	Maximum.	No. Ears analyzed.	Minimum.	Maximum.
1896	163	8.25	13.87	163	8.25	13.87
1897	112	8.34	13.62	48	8.22	13.98
1898	252	7.72	14.92	126	7.50	16.08
1899	216	7.71	14.78	144	6.66	13.06
1900	216	10.31	15.71	144	7.08	12.29
1901	60	8.94	16.12	126	7.54	13.05
1902	90	9.54	15.01	90	6.37	9.69
1903	100	8.47	17.33	100	6.38	10.20
1904	100	10.61	17.79	100	6.13	10.46
1905	120	10.77	17.39	120	6.62	12.14
1906	120	10.46	17.67	120	6.49	10.91

show this much plainer. We see that the separation of the lines, in both the high protein and low protein plots, seems to have reached its limit.

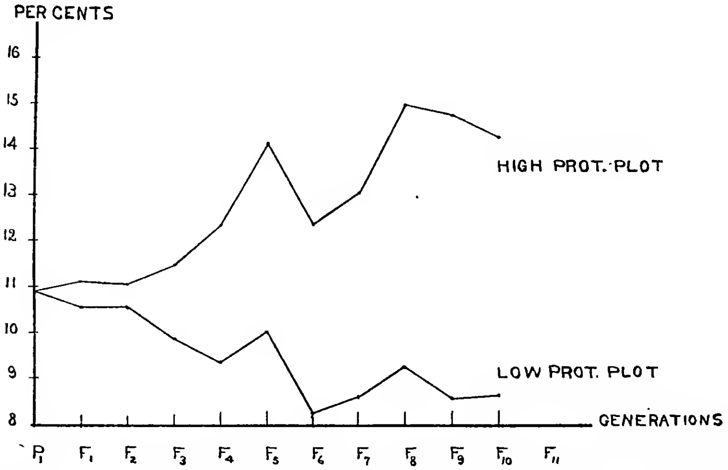

FIG. 3. Crop averages in maize breeding for high and for low protein Notice that the curves are each approaching a limit—the horizontal.

The important experimental data of the constancy of either of these races has not been determined. That is, it is not known what these strains of maize with compositions made different from the average of unselected Burr's white through selection of extremes, would show in their composition after several years cessation of selection. But there is no reason to believe that these races are more stable than other improved races on record, that have been established in the same way.

These two cases of sugar beets and maize are typical of all improved races, whose improvement is due to the selection of fluctuations. General selections to improve the yield and quality of our farm crops, such as oats, rye, potatoes and so on, all come under this head. Much good has been accomplished by Von Lochow and Rimpau in Germany in increasing the yield of rye by the use of this method of selection, but the process has been slow and must still be continued from year to year to keep the strain up to the excellence that has been obtained.

In this country many of the varieties of maize are due to this selection. It is a common thing to hear of these varieties that have been raised to a state of comparative perfection by skillful breeders, "running out" or deteriorating in the hands of others. This "running out of varieties" is largely a regression to their original types by varieties that have been improved through their fluctuations. The grower does not keep up the selection, or the variety is ill-adapted to the soil and climate, and deterioration is almost inevitable. On the other hand there are varieties, as the Longfellow, whose excellence is due to desirable characters that have been found in nature, and have been isolated, and perpetuated. The greater constancy of these varieties is undoubtedly due to mutating characters. Numerous constant hybrid varieties have also been established, by combining the desirable characters in two or more of these varieties.

There are other cases in which extreme fluctuations can be propagated with less likelihood of their deterioration. This is by means of bud propagation. Seedlings of many fruits and of garden plants can be reproduced by grafts or by cuttings, so that their variation is to a great degree lessened. There is variation even among grafted apples and peaches, but in general this variation is too small to affect the qualities of the fruits to a great extent. What is the amount of this kind of fluctuation as compared to that of fluctuation in varieties reproducing by seed, when environments are comparable, is not known. We do know, however, that there is considerable variation in potatoes which are propagated by buds (the tubers). In potatoes, however, each plant has a more or less different environment, and much greater differences are to be expected than with different branches on the same tree. We know that potatoes must be selected within the variety to keep them from deteriorating, but whether improvement can be made by the selection of their fluctuations is yet undetermined.

Isolation of Elementary Species.

The improvement of our valuable field crops by the isolation of the best of their elementary species has only recently attracted attention. For the increasing prominence of this method, Nilsson and De Vries are largely responsible.

De Vries believes Le Couteur, an English breeder on the coast of Jersey, to have been the first to recognize that the cereals as usually grown were full of different types. In a field of his wheat twenty-three distinct types were found. These when grown separately were true to type and remained so generation after generation. Some types were found that were better than the average of the mixtures grown in the fields, and some types were less productive and of inferior quality. A few of the better types were isolated and multiplied as soon as possible, and put on the market. Le Couteur's Bellevue de Talavera wheat is said to be still grown in England and France, and is reported to be a very uniform type.

De Vries also notes that the work of Patrick Shirreff, the Scotch wheat grower, whose cereal breeding has been famous for three-quarters of a century, was the isolation of natural types which struck his eye. In his little book entitled "Shirreff on Cereals" published in 1873, he says:

"My experiences in the improvements of the cereals arose from the following circumstance. When walking over a field of wheat on the farm of Mungoswell, in the county of Haddington, in the spring of 1819, a green spreading plant attracted my notice, the crop then looking miserable from the effects of a severe winter, and the next day measures were taken to invigorate its growth by removing the surrounding vegetation and applying manure to its roots. In the course of summer several stalks were cut down by hares; but notwithstanding this loss to the plant, sixty-three ears were gathered from it at the harvest, yielding 2,473 grains, which were dibbled in the following autumn at wide intervals. For the two succeeding seasons the accumulating produce was sown broadcast, and the fourth harvest of the original plant amounted to about forty-two quarters of grain fit for seed; and proving to be a new variety it was named Mungoswells wheat."

Shirreff's method of improvement was the same as Le Couteur's, and they both possessed the true idea of selecting out elementary species. He says: "New varieties of the cereals can usually be obtained from three sources—from crossing, from natural sports, and from foreign countries." He seems to have had no idea of the use of fluctuations in improving crops. He thought that "sports" or wide variations of note should be separated and multiplied. These he says, "usually breed true," and when those which did breed true were found to be of value he immediately set about raising seed to supply the demand. During the first forty years he found only four plants that attracted his notice, and from them he raised four varieties. After this time he took up more systematic work in breeding and made several valuable crosses among wheats and among oats.

More recently the work which has attracted wide attention throught its intrinsic merit is that of Dr. Hjalmar Nilsson and his associates at the Swedish Agricultural Experiment Station at Svalöf. Here plant breeding by the Darwinian idea of the selection of fluctuations was tried, but was soon discarded because it did not give results. In some cases improvement was made, but even in these instances the amelioration was slow, and was inconstant when obtained. Besides, failures were so numerous through trying to force improvements in characters in which nature furnished insufficient variation, that a surer method was desired.

A closer study of elementary species or types among the mixtures of plants of the cereals, grasses and clovers as originally grown, showed Dr. Nilsson that different types were not rare but very numerous, so numerous in fact, that the present generation would find them entirely adequate for their needs if they could only give them the minute study necessary to find out their differences and inherent qualities. Such studies have been and still are being carried out at the Svalöf station and by their means several new varieties of oats, wheat, rye and other plants have been isolated and introduced to cultivation. In this country the method is being used at several Agricultural Experiment Stations. The Cornell Agricultural Experiment Station is separating the elementary types of timothy; the Minnesota Station has done a large amount of work upon wheat and flax; while at the Connecticut Agricultural Experiment Station the types contained in our common clovers and ryes are being studied.

As an example of what is to be found in the seed ordinarily bought for pure seed of our clovers and grasses, take the medium red clover. The seeds vary in color from white to purple. Some of this variation is due to differences in maturity of the seeds, but only a small portion may be so explained. There are types with different colored stems. In some the leaves have different patterns of white markings; while others have plain leaves with no markings. In some the leaves are very hairy, while others are nearly smooth. Types are found with leaves almost smooth at the edges; others are contrasted with rather deep indentations. Some run to foliage, some are profuse in blossoms, and some produce little besides stems. The flowers are of different sizes and colors, and the head shapes are varied. Nearly every variation needed for commercial uses can be found already produced by nature. The general task before the breeder in a case of this kind is plain. Individual heads from plants of all these types must be grown in separate pedigree cultures. Then the types which are suited to the production of the best quality of clover hay are retained.

At Svalöf it has been found that the various types of the different grains, legumes and grasses are adapted to different uses. Some are resistant to certain fungous diseases, others are able to withstand severe frosts; some are suited to clayey soils and some to loose soils. In fact, the various needs of the different parts of Sweden are fast being suited with particular types of especially adapted plants. This is what the breeders here must strive to do. Connecticut has various types of soil and a great range of climatic conditions and types should be found to suit these conditions.

The questions arise: Are these different types within a supposedly pure species of cereal, grass or legume, old types persistent through a long term of years, are they still arising or are they mostly hybrid forms? The experiences at Svalöf indicate that yes must be answered to all these questions. There are undoubtedly some very old types that have remained unnoticed and therefore unisolated, but, nevertheless, there is absolute evidence that new types are being continually produced in a great number of species. Many of the types are probably natural hybrids, but this does not render them useless. They are found in ever increasing numbers to split up in succeeding generations according to Mendelian laws, and the delay occasioned in making isolations is counterbalanced by the greater number of types from which to select the needed ones.

We will summarize the distinctions between the selection of fluctuations and the isolation of elementary species in the improvement of farm crops. In each case we have a field of plants which are supposedly of a pure and uniform variety. In reality the field is full of elementary species—types which are slightly but distinctly different from each other. Some of these types are valuable, some are worthless. Taken all together they make up the average yield and average quality that the whole field shows. Each of these types when completely isolated from the mixture produces a uniform progeny, with of course the usual fluctuations. But in the field natural crossing obscures many of these types, making the mixture still more heterogeneous.

Suppose we wish to increase the yield of these plants by the Darwinian method of selecting fluctuations. We select out a dozen or more of the best heads,—say of rye. We plant these next year and again select out the best dozen heads. What have we done? We have in all probability selected a mixture of several types which intercross in our breeding plot. These different types have "blood" of types less productive in them. This tends toward keeping up the heterogeneity of types.—good, bad and indifferent. By continuous and very rigid selection we will necessarily reduce the number of types in our selected rye from the number in the original rye with which we started, but we are never certain of reaching our aim, particularly as the process is slow. One important reason for this uncertainty lies in the fact that the soil of a field is never uniform. There are spots which retain moisture a little better, and places that are a little more fertile than others. In these places plants belonging to poorer yielding types will do well and are likely to be selected in place of really better types that have grown on slightly poorer ground.

On the other hand, in the method of isolation of types by pedigree cultures, these objections are in large measure overcome. All of the types that are in the slightest degree different in their botanical characters are grown separately. Some intercrossing between the different types will take place, but it is much rarer than is usually supposed. The types of most of our agricultural plants will remain fairly pure when a reasonable distance intervenes between the plots. (Maize is an exception, however, and will be treated separately.) Some of these types are distinct natural types and others are due to crossing. The natural types will remain distinct and true in subsequent generations, that is, their botanical characters will remain true. Mutations may take place and should immediately be separated and reproduced in pedigree cultures by themselves. The hybrid types will split up into different types and these should always be isolated. We will then have a large number of types whose characters remain distinct but in which the ordinary fluctuating variation will take place due to slight differences in environment. These types will then need to be studied, and the economic qualities of each noted. If a rye is wanted that will grow upon a light soil and produce a large amount of green forage for soiling, then a number of the types should be tested upon that kind of soil and the best selected. If a clover is wanted that is resistant to frost and will not winter-kill, such a type may be found among the large number being tested. In no case are we trying to force a variation along unnatural lines; we take types as nature has produced them, isolate, propagate and use them. In most crops there is no need for selection other than to obtain the necessary purity of type. The variety can then be propagated away from danger of intercrossing and put to commercial use as soon as sufficient seed is obtained. Those crops which possess characters whose high fluctuations it is desirable to perpetuate, can then be subjected to the method of continuous selection.

Judging Plants by their Progeny.—There are two important methods used to obtain results both in this kind of breeding and in the selection of fluctuations. The first is judging the value of a type by the average value of its progeny, and the second, judging economic qualities by correlations with botanical characters.

Judging the value of a plant by its progeny was introduced* independently by Hopkins of the Illinois Agricultural Experiment Station, Hays of the Minnesota Agricultural Experiment Station and Von Lochow of Germany. The principle has since come to be generally used in breeding work. We can grow fifty to one

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*This principle was really discovered by Vilmorin and was used first by him on sugar beets.

hundred seeds from a timothy plant, a wheat plant or an ear of maize and get a much better idea of the qualities of their mother plants than if we grew but one or two seeds from each plant. The seeds must of course be grown in plots by themselves so that they can be known to be the progeny of a single plant. The difficulties of non-uniformity of environmental conditions are thus obviated. It is the average in the long run that counts.

Correlated Characters.—We have all noticed that dark seeds among beans and other crops are associated with dark colored flowers or dark colored stems or both. In some cases berries also show dark colors associated with dark colored flowers. It is clear in these cases that a certain amount of a coloring matter stored up in a seed gives it a dark color which may be increased and transmitted to other portions of the plant which it produces. Such associations of character are called correlations. Many of them have been known for years and their causes are obvious. Varieties of sugar beets whose leaves are in open rosette form contain the highest amount of sugar. This is what should be expected, for with leaves growing in this form the maximum amount of sunlight is possible for the plant, and increased amounts of sunlight make possible increased amounts of sugar. Hopkins of Illinois has shown that in Dent varieties of maize, kernels containing relatively large amounts of the translucent horny starch of the endosperm are comparatively higher in protein. This correlation is explicable from the fact that this part of the kernel contains a much higher per cent. of protein than does the white starch portion. In very few cases, however, are the causes as obvious as in those just given.

De Vries states that in France the common stock is cultivated in double-flowered and single-flowered varieties. As the doubles produce no seed, seed to produce them is saved from the single-flowered specimens of the same variety, since such a variety usually produces half singles and half doubles. Owing to their higher market price it is advantageous to separate the doubles from the singles as soon as possible. This is done by children who are able to pick out the doubles without error when the plants are very small and still without branches or flower buds. De Vries says that these differences in the seedling plants are so small that no botanist has been able to describe them but the slight differences which do occur are sufficient for the experienced eyes of the children. The same writer remarks that hyacinth growers are able to distinguish their varieties in the bulb, by the differences in size, in the number of side bulbs, in form or in color. Such slight markings would mean nothing to the average gardener, but the correlations of these bulbs with the characteristics of their flowers were so familiar to the Dutch hyacinth grower, Voorhelm, that he is said to have been able to distinguish a thousand different varieties of hyacinths solely by examining their bulbs.

Although these correlations are evidently of different kinds and probably of different value to the breeder, but very little work has been done concerning their classification and probable causes. Still the breeder should not delay putting them to use until their precise scientific classification is known, for all classes are undoubtedly of *some* practical value. In biennial and perennial plants where large numbers of seedlings are grown and possibly a number of years must elapse before the economic value of the fruits can be determined, any correlations which will indicate those plants which are absolutely worthless are of immense value to the breeder. These plants can be rejected before a great deal of time has been spent in their care, leaving the ground which they would have occupied free for other plants. Likewise many commercial qualities are difficult to judge, such as the milling qualities of grains, value of plant fibres, etc. If botanical characters can be found which are correlated with these qualities, the problem of the improvement of such plants is greatly simplified.

The idea of the use of correlations has assumed a much greater importance since we are but just now learning the supreme value of the original choice in plant breeding, where the method of breeding is the isolation of elementary species. As these elementary species when separated and found of value are to be immediately multiplied and placed on the market, a mistake in the original selection leaves no room for correction; for a continued selection of fluctuations by which it is expected to breed into a variety qualities which it does not naturally possess, is of no value. The elementary species must first be isolated and then their agricultural qualities tested; and in these tests nothing can be of greater value than the knowledge that a certain agricultural quality is correlated with a definite botanical character. The breeder can then inspect his mixture of elementary species—the commercial variety—and immediately separate the proper elementary type which carries with it the agricultural qualities which he is seeking. At this point, after having obtained an elementary species which naturally possesses a desirable quality as a distinct heritable unit character, there are undoubtedly many cases in which it is commercially profitable to use selection to keep this character up to the highest limit in fluctuation. Note that this is entirely distinct from trying to breed into a variety by selection a heritable character that it does not naturally possess.

It is probable that many of these correlations will be found to hold good only in very narrow "blood lines" of plants, and each breeder of a particular variety of our important agricultural plants should make it his duty to keep a systematic record of all the correlated characters which he finds. Such a study will not only be productive of value to the individual breeder in his own special field, but by the general tabulation of such breeders' records, the knowledge of correlations might finally be brought to such perfection that results in agricultural breeding could be obtained in half the time it requires at present.

The value of correlations has been generally acknowledged in this country and in isolated cases they have been put to use, still they have not been given the amount of study to which their importance entitles them, and we must look to Sweden as the leader in the practical utilization. Nilsson, at the Svalöf station less than a decade ago, recognized that the study of correlations would be of the highest values in the breeding of agricultural crops; and he and his assistants have taken up this work. Each species of agricultural plant is carefully described, noting all the differences that distinguish its elementary species and at the same time all its economic qualities. In this way all possible correlations are recorded and a careful study of these tables has given them a large number of ideas which they have put to practical use.

As an illustration of the results Nilsson has obtained by the scientific study of correlated characters, I will give a description of his production of the "Primus" barley as reported by De Vries. The barley that is cultivated in the central parts of Sweden, although of good yielding qualities, has a great tendency to "lodge," through the weakness of its stalks. Nilsson selected the best yielding variety, the Chevalier barley, for a number of years to try to obtain stronger stems, but his selection of these fluctuating variations brought no results. Other varieties were known with strong sturdy haulms but these were worthless as to their brewing qualities. A careful study of the botanical characters of the barley heads showed that there was a relation between the form of hairiness to their spikelets and scales and the composition of the grain which makes a fine brewer's barley. Long straight scales were correlated with coarse kernels but short crisp wooly scales indicated the barley desired for the brewery. When the fields of the large coarse Imperial barley with the stout haulms were examined, out of many thousands plants about sixty were found with the proper kind of short wooly scales. When these were isolated and grown the next season, certain of them proved to be an elementary species having the strong haulms of the Imperial barley and the fine brewing qualities of the best Chevalier varieties. The new variety was constant and uniform from the beginning and was multiplied and placed upon the market as soon as possible, where it now supplants the older varieties.

Improvement by Hybridization.

This brings us to the consideration of methods of hybridization as a means of animal and plant amelioration. The modern use of the word hybrid is much broader in its meaning than when used by the writers immediately succeeding Darwin. We shall apply the term to all individuals arising from crosses between elementary species, making no distinction as to whether the parents of these individuals belong to different Linnean genera, species or varieties.

The practical application of artificial cross-fertilization to the production of new forms dates from the beginning of the eighteenth century when Thos. Fairchild, an English gardener, crossed the carnation with the sweet william. The hybrid was almost sterile, but proving to be a valuable variety, it was propagated by cuttings for many years. This novelty seemingly aroused little enthusiasm for the scientific study of crosses, and no important generalizations were made until about 1760. At this time Kölreuter began a systematic study of hybrids, and obtained a knowledge of their behavior that was not greatly increased until the last quarter of the nineteenth century.

Kölreuter established upon a firm basis Camerarius' previous discovery of the sexuality of plants. He also found that hybrid plants resembled the pollen (male) parent as closely as they did the seed (female) parent. Further, that in most cases it made very little difference in the final results of a cross, as to which of the two parents was used as the pollen and which as the seed parent. That is, the products of reciprocal crosses are nearly identical and the male parent transmits as many characteristics to the hybrid as the female parent.

Kölreuter, without the apparatus of the modern microscopist, came very near discovering the mechanism of fertilization. We now know that the application of pollen grains to the stigma of the flower's pistils is merely a mechanical act. The pollen grain contains a minute structure called the nucleus, which passes down the style of the pistil through the growing pollen tube, into the ovary, where it unites with a similar nucleus in the ovule (fertilization). From this one cell the embryo in the seed and later the whole plant is formed by exact and equal divisions. Kölreuter believed that fertilization consisted in the mingling together of two vital fluids, one contained in the pollen and one contained in the stigma, and that these passing down the style started the ovule to developing into the seed. He actually determined that about fifty pollen grains were sufficient to mature at least thirty seeds. It is marvelous how near the right path he was, with such limited facilities.

Kölreuter also found that by repeatedly recrossing a hybrid with one of the parent varieties from which it was derived, he could finally obtain individuals that were indistinguishable from that parent species. Furthermore, he found that there were exceptional cases where reciprocal crosses could not be made. *Mirabilis jalapa* (female parent) was easily crossed with *Mirabilis longiflora* (male parent), but with eight years' work he did not succeed in making the reverse cross. We now know that a reciprocal cross is sometimes impossible, because of a seeming mechanical inability of the nucleus of the pollen to break through and gain admission to the nucleus of the ovule. When this difficulty is artificially overcome the fertilization is possible.

In the beginning of the nineteenth century we have the work of Thomas Andrew Knight, an English plant physiologist, who has very justly been called the father of modern plant breeding. Knight was probably the first who really appreciated the immense possibilities of hybridization as a means of improving domestic plants, although it is only fair to state that the principle of selection was known and made use of in improving strains of cultivated plants by Joseph Cooper of New Jersey at a somewhat earlier date. Kölreuter's work was theoretical, while Knight, in addition to his contributions to theory, made definite practical use of his knowledge gained by experiments. The commercial varieties that he obtained through crossing were numerous and important.

Knight's greatest contributions to knowledge will probably always be known from the two following principles that he proclaimed; but science owes him a still greater debt from the fact that he was a pioneer of the type of inductive experiment. He generalized from his experiments instead of making theories to prove by philosophical discussion. Knight's first principle was that modification of the food supply is the leading cause of variation. If we write fluctuating variation instead of variation, the principle is still accepted. He also found that the products of crosses were often more vigorous than the parents of the hybrid; and that a strain of plants that had deteriorated through continued self-fertilization could be renewed in vigor by crossing with another strain. This conclusion has since become known as the Knight-Darwin law. Darwin supplemented Knight's work by many experiments comparing cross-fertilization with self-fertilization and expressed his results in this terse saying: "Nature abhors perpetual self-fertilization." Darwin's results, however, rest on a rather slender basis. He used characters such as heights of plants as a measure of vigor, and these are far from desirable standards. There are also many cases known, such as tobacco and wheat, where self-fertilization is indefinitely continued by nature without evil results; in fact, with them a decrease in vigor seems to be the immediate effect of a cross. The Knight-Darwin law should probably be changed to read: *Nature resists any sudden change in long established conditions.*

During the remainder of the nineteenth century several noted investigators into the phenomena attending hybridization lived and worked. Gærtner, Naudin, Focke, Vilmorin and many others contributed large numbers of important facts, but made no great generalization.

It was found that in general the closer the botanical relations of two plants, the more easily they will cross. Crosses between varieties are generally very easy to make; those between Linnean species have been made in quite a number of instances, while crosses between genera and families are rare, although they have been recorded. Close botanical relationships, however, are not unfailing proofs of the easy production of hybrids; Bailey states that the squash absolutely refuses to cross with its near relative the pumpkin, while on the other hand Focke mentions successful crosses between plants of the lily and amaryllis, and of the figwort and gloxinia families. It was likewise discovered that hybrids arising from widely different parents are usually much more likely to be sterile than are those from nearly related parents. But this rule is by no means without exceptions, for a number of hybrids between different Linnean species are known that are perfectly fertile. Sterility of hybrids among themselves does not always unfit them as prospective commercial varieties, as they are often fertile with one or other of their parents, and the progeny of this cross are fertile among themselves. In other cases infertile hybrids can become of great value through propagation by means of cuttings, grafts, tubers, etc.

It was also early discovered that when two kinds of pollen were placed on the stigma of a plant at the same time, only one kind was effective in the fertilization. This was called prepotency of pollen. It is thought to be due to the greater activity of some kinds of pollen grains, since some send out their pollen tubes faster than others and hence their nuclei reach the ovule first. The pollen of a different variety is often prepotent over pollen from the plant itself. In other cases, as in the potato, the plant's own pollen is prepotent over that of other varieties.

We can see from the above short account that although many experiments of merit were conducted, and quantities of isolated facts were observed and recorded, still no great principle was established until the work of Mendel which was described in the previous chapter.

Later Mendelian Work.—We discussed the work of Mendel practically as he left it. It seems desirable at this point, after having outlined the work that can and has been done concerning fluctuations and mutations, and the early work in hybridization, to give a few short examples of the former puzzles that have been cleared away by extensions of Mendelian principles. Bateson and his co-workers in England, Tschermak in Austria, and Davenport, Castle and others in the United States, are fast building up a firm foundation for the laws of heredity from the impulse of Mendel's work. Experimental biology has had a door of knowledge opened comparable to that which Dalton opened for chemistry with his atomic theory. The work will undoubtedly be slower due to its inherent complexity, but who shall say it will not be accomplished?

Previously we have given explanations of Mendelian phenomena stripped of the technical terms that have grown up with the increase of Mendelian experiments. But in order to prepare the reader who may wish to learn the latest extensions of the theory as they are published from time to time, we will explain such terms as are in constant use.

The cells whose nuclei unite in the process of fertilization are called *gametes* or *germ-cells.* When these cells fuse in the process of fertilization, a *zygote* is formed, and this name has been extended to include the adult organism that is finally formed by the succeeding divisions of this cell. Two characters with contrasting features which give Mendelian ratios upon inter-breeding the product of a cross are called *allelomorphs,* and the pair are an allelomorphic pair. When gametes bearing similar allelomorphs unite to form a zygote, the product is a *homozygote.* For example, the union of two yellow colored peas forms a homozygote in regard to the color character. When contrasting characters of an allelomorphic pair are united in a zygote, it is called a *heterozygote*: that is, the crossing of a yellow and a green pea forms a heterozygote for color.

We remember that in cross breeding Mendel believed that contrasting characters were united in the heterozygote, but that when this zygote produced gametes the two factors were segregated, fifty per cent. of the gametes bearing the character from one grandparent and fifty per cent. from the other grandparent. For example, a pea with yellow cotyledons (Y) crossed with a pea with green cotyledons (G) produces a heterozygote whose germ-cells bear the characters Y and G in equal proportions. Mendel's view was that these unit characters were actual pairs of contrasting characters, of which a germ-cell *could possess* but one. Recently there has been some doubt as to whether this is the correct hypothesis. It has been found that in some cases, the extracted dominants or extracted recessives, which are the names given to the characters which separate out apparently pure from the cross and breed true,—have not entirely lost their possession of the contrasted character but that under certain conditions of crossing, the other character may reappear. It seems that the opposed character may be contained by the germ-cells, although hidden, and may appear again when conditions are right. What these conditions are is not known, but the phenomenon is quite rare, and no fear need be felt that it will vitiate numerical results in practice. Morgan has proposed the hypothesis that both characters are contained in each germ-cell but only one of them shows under ordinary conditions; that is, one character or the other by chance obtains the mastery in the germ-cell and shows in the organism to the exclusion of the other character. It is illustrated as follows:

$$\begin{array}{cc} A(B) & (A)B \\ A(B) & (A)B \\ \hline \multicolumn{2}{c}{1A(B)+2A(B)\ (A)B+1(A)B.} \end{array}$$

Representing by A the dominant character and by B the recessive character, if at some time after making the cross the A character becomes the master of half the germ-cells of both male and female, it may be represented as A(B). In the other half of the germ-cells the B character obtains the mastery and the cell may be represented as (A)B. Separations then take place after crossing as is shown in the formula. In the first and third term, the free characters (the one outside the parenthesis) show, while in the second or hybrid term, the A character shows because it is thought to be dominant when both A and B are "free" characters.

Morgan's proposition is that the characters are not separated in the gametes but that the contrasting characters are *both* present but *one* always in a latent condition which can sometimes be made patent by proper crossing. This view explains some of these exceptional cases but a larger number of others are inexplicable by it. The view which has so far explained by far the largest number of cases is called the presence and absence hypothesis and was propounded by Bateson.

On this hypothesis a yellow pea is based on green; i. e., the yellow color is superimposed upon the green. The yellow pea produces gametes bearing two factors, one for yellowness (Y) and one for greenness (G). When it is self-fertilized or fertilized with another yellow pea a zygote is produced whose gametes have the formula YG but the resulting zygotes always have the yellow color through the presence of the yellow factor.

In the same way the pure green pea produces gametes carrying two factors—one for greenness (G) and one for *absence* of yellowness (y).

In cross breeding the yellow pea producing gametes YG would meet the green pea producing gametes yG and the resulting zygote will be a yellow hybrid whose constitution is YGyG. The hybrid zygote would produce gametes YG and yG in equal quantities, which meeting by chance upon self-fertilization would give the following results:

$$\begin{tikzcd}
 & YG \arrow[r] & YG & \\
\text{pollen} & YG \arrow[dr] & YG & \text{egg} \\
\text{cells} & yG \arrow[ur] & yG & \text{cells} \\
 & yG \arrow[r] & yG &
\end{tikzcd}$$

The results would be numerically and, apparently, the same as those of the Mendelian hypothesis. Those zygotes whose formulae are YGYG would be pure yellow superimposed upon green, those whose formulae are YGyG would be hybrid yellow superimposed upon green, and those whose formulae are yGyG, by the absence of yellow (y), would be green.

We do not know what is the precise nature of the absence factor in the germ-cell. Three hypotheses have been presented: there may be (1) an actual substance representing absence, (2) there may be literally nothing, or (3) there may be presence but in a latent state. The third view is much the same as Morgan's, but it is open to the objection that cases are known in which the "presence" factor is itself latent—cases which Morgan's theory would explain.

Whatever is the explanation, it may very well be that these pairs of unit characters represented by two allelomorphs are really two pairs of characters. Let us recall that two pairs of characters were shown by Mendel to give four classes of zygotes in the F_2* generation in the proportions 9:3:3:1. Now if the two

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* Hybridizers use the letter F_1 (= 1st filial generation) to represent the immediate product of a cross. The succeeding generations arising from the F_1 generation are denoted by the letters F_2, F_3, etc. The parents of the F_1 generation are called P_1 (= 1st parental generation), and the grandparents P_2, and so on.

first classes were indistinguishable for some reason and the two last also alike, we would have the proportion of 12 to 4, or 3 to 1. Hurst has shown this to be actually the case in a large number of experiments on both plants and animals, and has been able to distinguish between the different classes.

On crossing the Fireball tomato (possessing a red flesh showing through a yellow skin) with the Golden Queen (possessing yellow flesh showing through a white skin), he obtained an F_1 generation which was exactly like the Fireball, red being dominant to yellow. Upon self-fertilizing the F_1 generation there was a segregation in the F_2 generation into reds and yellows, with the expected Mendelian ratio of three reds to one yellow. However, there were found to be four distinct types, two reds, and two yellows. These four types occurred in ratio of 9:3:3:1 as follows: nine with red flesh through a yellow skin; three with a red flesh through a white skin; three with yellow flesh through a yellow skin; one with yellow flesh through a white skin. Mr. Hurst thinks that it is quite probable that the two pairs of factors under consideration are (1) presence (R) and absence (r) of red in the flesh, and (2) the presence (Y) and the absence (y) of yellow in the skin; presence being the dominant character in each case. The red is superimposed upon the yellow and when the factor for the presence of red is there the zygote is red; but when the factor for the absence of red is there the zygote is yellow. The point is that while the red and yellow types of tomatoes behave as Mendelian characters with the red dominant, there are really four types which can be isolated and will breed true. The conception of the presence and absence factor may be a little puzzling at first but not more puzzling than the chemists' physical conception of the atom. It is as if dominance were the outcome of the presence of a certain factor, and recessiveness the result of its absence. If we strip off dominance, we have recessiveness.

Masked Characters.—This construction of a presence and absence hypothesis has been the means of clearing up several important cases which at first appeared unconformable to the Mendelian ratio. Hurst found upon crossing a pure bred "Belgian Hare" rabbit with a grey coat, with a pure bred "White Angora" with a white coat that all of the offspring of the F_1 generation were grey. But oddly enough in the F_2 generation there appeared an approximate ratio of nine grey, three black, four white.

This ratio appears to be due to two sets of characters: a color factor C dominant to absence of color c, and greyness G dominant to blackness b. The gametes of the Belgian Hare would have the formulae (C + G), and those of the albino the formula (c + b). The albino actually carries the factor for black (b) but the black color is invisible because of the absence of the color factor (C). When both C and G are present, the animal is grey; when both C and b are present the animal is black. But both G and b may be present without the color factor C and the animal will still be white. Moreover, out of the four albinos produced, three carry the color factor (b) while one is without it. The four albinos are alike in appearance and if bred together will give only albinos. But if they are bred to blacks carrying the color factor, it is found that three of the albinos carry either a pure grey G or a hybrid grey (Gb) factor, while the other carries only a pure black factor. Thus we really have two classes among the albinos with the ratio of 3:1, and instead of the 9:3:4 ratio that appears to have been obtained, we actually have the true Mendelian expectancy for two pairs of characters, 9:3:3:1. These cases, where two classes of individuals appear as one class, are called cases of *masked characters.*

The accompanying diagram will help elucidate the case. If we represent color by C (dominant) and no color by c (recessive) then by crossing the two characters we get an individual with a gametic formula CCcc in the F_1 generation and with self-fertilization the ratio CC + 2Cc + cc in the F_2 generation. We will represent these four individuals by the four large squares in the diagram. If in the other pair of characters greyness G is dominant to blackness b, by crossing and then self-fertilizing the offspring, we get the ratio GG + 2Gb + bb in the F_2 generation. This we represent by subdividing the four large squares, for there is an equal chance that each of the four classes represented by the large squares will fertilize one individual of each of the classes represented by the four small squares. Notice that there are nine squares criss-crossed where C and G both are present; these represent individuals with both color and greyness present and these individuals appear grey. In the three solid squares color C and no grey, or blackness b, are present and the individuals that they represent are black; in the four white squares the color factor C is absent and the individuals that they represent are all albino. However, in three of the albino squares G is present, either pure as GG or hybrid as Gb; these individuals carry the grey color masked and it can be brought out by proper crossing. The other albino carries the black color b which is recessive in grey, also masked, and this too can be brought out by proper crossing.

Reversion.—Another very important phenomenon that has long puzzled hybridists has been found to yield to a simple Mendelian explanation. I refer to the phenomenon of reversion, or appearance of an ancestral character on crossing. It has long been known that by crossing two pure individuals that each breed true to a particular color; individuals would sometimes be found in the F_2 generation that show the color of a bygone ancestor. The phenomenon is known in both animals and plants but is illustrated nicely by the sweet pea.

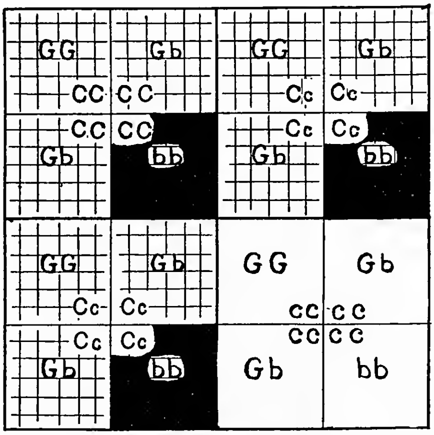

FIG. 4. Masked characters

There are two white varieties of the sweet pea, each of which breeds true to white, but Bateson found that upon crossing, the F_1 generation are all purple. Then upon self-fertilizing or interbreeding the F_1 generation, nine purples and seven whites appear out of every sixteen plants of the F_2 generation. It is clear that each race of whites contains one factor necessary for the production of the old ancestral purple of the sweet pea, but as neither variety contains both factors, each breeds true to white until they are brought together. The two factors are color (C) dominant to absence of color (c) and purple (P) dominant to absence of purple (p); but since one variety has gametes with the formula color plus absence of purple (C + p), it is white, and since the other variety has the gametic formula purple plus absence of color (P + c), it is also white. If we make use of the same style of diagram in this case, using CC + 2Cc + cc to represent the color factor in the large squares, and PP + 2Pp + pp to represent the purple factor in the four small squares of each large square, the matter is entirely clear. Wherever P and C are present in the same square the individual is purple, but where either P or C is absent (represented by p or c) the individual is white. There are nine squares in which the P character brought by one variety is in combination with the C character brought by the other variety and these represent nine purple individuals. Likewise, there are seven squares in which either the P character or the C character, or both, are absent; they therefore represent white individuals. It is simply a case where the ratio of 9:3:3:1 has the last three terms combined and the ratio is 9:7.

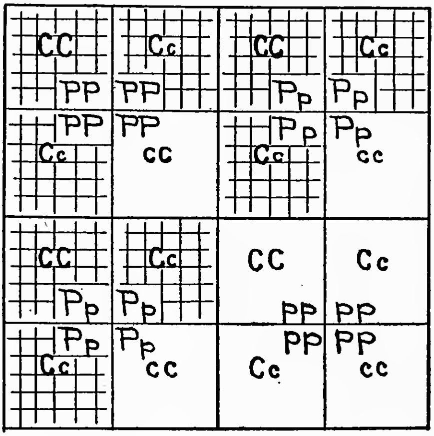

FIG. 5. Reversion

Heterozygotes.—We have already stated that dominance in a complete form is not universal in cases of Mendelian inheritance. In fact in possibly the majority of cases the dominant character appears in a diluted form in the hybrid progeny of a cross. There are other cases where the segregation of the characters takes place according to Mendelian ratios but the appearance of the hybrid is totally different from either of the parent types. This class of hybrids has in the past been a stumbling block to breeders, because they have tried to "fix" this character which they now know is from its very nature an impossibility.

This is the case with the blue Andalusian fowl. No matter how carefully this type is selected and inter-bred, poultry breeders have never been able to get it absolutely true. About half come true to the blue character, while of the remainder one-half are black and the other half white with black splashes. The very fact that these proportions were the Mendelian expectation from a cross—1 part black: 2 parts blue: 1 part splashed white—led Bateson to believe that the blue character was merely the characteristic appearance of the heterozygote due to the crossing of the black and the splashed white. This was found by crossing to be the correct view. Curious and paradoxical as it may seem, by inter-breeding the "pure" blues only one-half of the offspring came blue, but by breeding together the blacks and the splashed whites *all* of the offspring were blue. These, however, split into the three classes, as would be expected, in the next generation. "The riddle of the impossibility of obtaining a pure race of blue Andalusians was thus solved." The very nature of the case showed that the breeders were following a will-o'-the-wisp.

There have already been several valuable practical applications of these laws in problems of breeding. Mr. R. H. Biffen, in England, has found that susceptibility and immunity to rust in wheat are a pair of simple Mendelian characters in which immunity is the recessive. He has by this knowledge been able to produce in only three generations a pure race of rust-resistant wheat. Spillman has shown that the polled character in cattle dominates the horned character, and that by proper crossing a polled race of cattle can be established, with only a single polled mutation as foundation stock. Thus when single characters are of supreme importance, our knowledge of a plan of action is of greatest value. We know that we must avoid trying to obtain in combination both of a pair of contrasted characters. We know that we must breed for one character at a time, for by referring to the table on page 43 we can see that with six pairs of characters we must have 4,096 individuals to obtain one with all six dominant characters combined.

It has been stated that Mendel's work will make the characters of hybrids as easy to predict as are those of chemical compounds. This is taking an extreme view of the case. The production of hybrids is work of great complexity owing to the great number of unit characters that make up the higher plants and animals. What we are coming to know is the *most direct plan of procedure in combining known desirable characters possessed by distinct varieties.* Before predictions concerning the results of hybridizing can be made, it must be known for all of our domestic plants and animals what characters Mendelize and which of each pair is dominant. There is an enormous amount of work yet to be done, before we will be able to refer to a book giving lists of important characters of different plants which will Mendelize together with the characters which they dominate or by which they are dominated. Mendel has originated a new style of experimental work,—the careful observance of individual characters in each of the offspring of a cross. He has brought confirmatory evidence that characters are established fully formed by mutation, and are inherited as such.

In conclusion it may be stated that the general idea has been that it is only hybrids between varieties that follow Mendelian laws, but there are already several records of characters in both elementary* species and Linnean species that obey them, and many more cases will undoubtedly be brought into conformity when a larger number of types have been studied.

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* De Vries distinguishes between elementary species and varieties, in that the elementary species of a Linnean species are of equal rank and usually differ from each other in several characters, while varieties, he says, are derived from elementary species and differ from them in ways which are common in a large number of species. Varieties, he thinks, are less striking in their differences and follow different laws of inheritance when crossed. This appears to the writer to be an arbitrary distinction, and the correctness of his conclusions will remain in doubt until more light is thrown on the question.

V.

Technique in Plant Breeding.

In the subject matter up to this point, special methods for the improvement of particular crops have been purposely omitted. As the work in plant breeding increases in size and scope, methods more or less suited to each important field crop will doubtless be published. Experiments are necessary to determine the proper details for such work. Many mistakes are to be expected, due largely to the complicated data from which conclusions must be drawn. It is hoped that a study of the underlying principles of variation and heredity will reduce the fallacious proceedings of breeders to a minimum and give them ability to criticize the weak points in the methods which have been proposed for their use. The most important contributions to the technique of breeding will probably be made by those who, like the Vilmorins in France, are well abreast with the science of the day, and yet who regard the work from its commercial side. The balance sheet of any business is a great teacher of quick and direct methods.

Although this paper aims only to give a short introduction to the principles of breeding and consequently must necessarily omit the discussion of the improvement of individual crops, still a few examples of technique in breeding will be given in order to make clearer the explanation of the theoretical part. Following a statement of the essential points with which the hybridizer must be familiar, are given (1) the important features of breeding to isolate elementary species, using red clover, *trifolium praetense* L. as a type, and (2) criticisms of the modern method of breeding our most important crop, maize. The latter is an example of a crop where both elementary species and fluctuations are dealt with in practice.

Flowers and their Parts.

A flower is said to be *complete* when it has calyx, corolla, stamens and pistils. Of these the calyx and corolla are called the floral envelopes. The *calyx* is the outer whorl of leaf-like parts of the flower, and is usually green. The showy part of the flower is usually the *corolla*. The different shapes of the floral envelopes in nature show wonderful adaptation to make certain fertilization and hence to assure the production of seed. In artificial pollination we have to do only with the stamens and pistils which are called the *essential* organs of the flower. The important feature of the stamen is the pollen grains. These are borne within the enlarged terminal part of the stamen called the *anther*. When the pollen grains mature the anthers open and the pollen can then be seen as a yellowish or brownish dust. Each of these minute pollen grains contains at least one *nucleus* or essential part of a reproductive cell. The pollen grains are the male reproductive cells of the plant. The *pistil,* whether simple or compound, has three parts when complete. The *stigma* at the upper end is generally rough or flattened or sticky in order to hold the pollen when it is applied. This actual application of pollen to the stigma, whether by insects or wind or by the hand of man, is *pollination.* When pollen grains are applied to the stigma, the sticky substance upon the latter causes them to grow. This growth is called the *pollen tube.* It makes a pathway down through the *style*—the slender part of the pistil—and finally reaches the female or egg-cell in the interior of an ovule in the lower part of the pistil called the *ovary.* The male nucleus passes down this pollen tube and unites with the female nucleus in the ovule; this process is *fertilization.*

Fertilization in plants may bring about a much closer degree of relationship than it may in animals; fertilization may be effected by pollen which was produced upon the same flowers or the same plant upon which the ovules grew. This is *self-fertilization.* Fertilization by the union of pollen and ovules which grew upon different plants of the same "pure line," that is, sister or cousin plants, gives different degrees of *close-fertilization.* Union between plants of different "pure lines," whether of the same or different varieties, is *cross-fertilization.*

Cross-fertilization appears to be important to a large number of plants, for there are many devices in nature by which cross-fertilization is effected. Natural cross-fertilization is effected by water, wind and insects, although the first agency is so rare among cultivated plants that it can be disregarded. Wind-pollinated plants are called *anemophilous* (wind loving), while those pollinated by insects are said to be *entomophilous* (insect loving).

Flowers that contain both stamens and pistils are known as *perfect* or *hermaphrodite* flowers. A very common means of insuring cross-fertilization among these plants is to have the stamens and the pistils mature at different times. When the stamens mature first, as in the hollyhock, the flower is *protandrous;* when the pistils mature first the flower is *proterogynous.* Flowers of either of these kinds are known as *dichogamous.* When flowers lack either pistils or stamens they are said to be *incomplete* or *diclinous,* and are called staminate or pistillate according to which organs are present. When the staminate and pistillate flowers are borne on the same plant, as with chestnuts, walnuts, squashes, maize and others, the plant is *monœcious.* When the different kinds are borne upon separate plants, as willow and hemp, the plant is *diœcious.*

The entomophilous flowers are generally distinguished by irregular corollas which are so adapted that insects visiting them for nectar are almost certain to pollinate them with pollen they have brushed from other flowers. The artificial pollination of this class of flowers is difficult because of the care that must be taken to prevent injury to the essential organs while removing the floral envelopes preliminary to applying the pollen. There is also a class of flowers which pollinate themselves before opening, thus insuring self-fertilization. They are called *cleistogamous* flowers. Examples of this class are rare, and usually the same plant bears flowers of some other class. A careful examination of the common blue violet will show a few inconspicuous cleistogamous flowers down beneath the showy blue ones.

Technique of Hybridizing.

Success from artificial crossing only comes from close study of the difficulties attending the work, in each particular case. There are four points with which the operator must be familiar.

1. *The natural habits of the plant in its fertilization.* It must be known whether the plant is diclinous or complete; and whether the stamens and pistils mature at the same or at different times. These facts will be given in any manual of botany. The hybridizer must find out by experience, however, whether early, medium or late flowers are the best seed producers, and whether care must be taken to pollinate sufficiently at the first application,

or whether several applications can be made to the same flower, before the pistil falls.

2. *The maturity of the pollen.* The pollen is generally ready for use when nature releases it from the anthers. But in different plants flowers of different times of opening produce pollen in different amounts and of different degrees of viability. In some cases the flowers that open first produce but little pollen and this unhealthy. It may be that in other cases the late blossoms should not be used. Healthy pollen has a regular shape, characteristic of the species or variety to which it belongs, but when examined under the microscope it should always be plump. Shriveled, irregular pollen of pure forms should be discarded. It should be recognized, however, that it is characteristic of many hybrids that the ability to form perfect pollen is lessened.

3. *The maturity of the stigma.* The proper time for the application of the pollen to the stigma varies from the time of the opening of the flower in some species until three or four days later in others. An examination of the stigma with a hand lens is of some value; for in some types the stigmas are quite profuse with a gummy exudation at the time the stigma is most receptive. In many types, however, experience alone will show when to make the cross. An absolute record upon this point is very important for every specialist who breeds a particular crop, for Hartley has shown that premature pollination is quite injurious in cases of tobacco, orange, cotton and tomato that he had investigated.

4. *Prevention of pollination other than that which is intended.* Not only must the entrance of foreign pollen be provided against, but in all perfect blossoms, precautions must be taken that self-fertilization is prevented. To prevent self-fertilization the flowers must be emasculated—that is, the anthers must be removed—before the blossom opens. When the blossoms are comparatively large this is easily done by cutting off both the corolla and stamens with a small pair of surgeon's scissors. If it is in the way the calyx also may be removed. In case the flowers to be used are small, a pair of very fine tweezers with the points slightly flattened may be used. When using tweezers the anthers should be removed with considerable care, as they may be opened mechanically, allowing the flower to self-pollinate. When operating upon composites or upon flowers borne in large

numbers upon heads or spikes, most of the flowers and flower buds should be removed, leaving only three or four individual buds somewhat isolated from each other. Each of these should then be emasculated.

In monœcious or diœcious plants, it is of course only necessary to protect against foreign pollen, as is likewise done with complete flowers after their preparation by removing the anthers. Ordinary paper bags such as are used by the grocer serve very well for protection. They should be moistened at the end so they can be tied close to the stem of the emasculated bud. In particularly careful work, we should also bag the pollen parent, but in commercial hybridizing sufficient pollen can usually be obtained by shaking the flowers over a watch glass. There is in this case a possibility of contamination, but the relative probability of it is small. When the stigma is receptive, it should be dipped in the pollen if it is available in sufficient amount; otherwise it can be applied with a small camel's hair brush. After pollination the flower should immediately be rebagged, and labelled with the date and the name of the pollen parent. After several days, when fertilization has taken place, it is better to change the paper bag to a cheese cloth bag, which will serve the purpose of retaining the fruit should it be dropped, and at the same time admit light and air.

In certain cases the stigmas of the plant to be used as the seed parent are not ready for some time after pollen has been obtained. When this happens the pollen should be slowly and carefully dried under glass, then put away in a tightly corked glass vial. If the pollen is dried too fast, rapid evaporation of moisture causes the grains to split, and the pollen is rendered useless; but when dried with care some kinds of pollen—grapes, for instance—will retain their vitality for a whole year.

Technique of Isolating Elementary Species.

In breeding field crops by the isolation of elementary species there are three things to be accomplished: 1. The separation of the elementary species; 2. Comparison of the different types; 3. Rapid propagation of selected types for commercial use. As a typical example of this kind of breeding we will use the experience of others and ourselves in the breeding of our common red clover, *trifolium praetense* L.

The first point to be observed in separating the natural types of any species, is to find out the probability of natural crossing. In maize, where large amounts of pollen are formed and pollination is entirely anemophilous, natural crossing is so great that isolation of pedigree cultures is almost impossible. In the case of smaller plants which commonly cross in nature, a framework covered with very fine cheese cloth is placed over individual plants from which foreign pollen is to be kept. Sometimes a few humble bees are placed in the tent to make pollination more certain. This method is often used with choice plants of the red clover, although it has been recently found that self-pollination is much more common than Darwin supposed. The crop of seed from a field in which humble bees (their chief insect pollinating agent) are common, is much larger than the crop in fields with few of these visitors, but nevertheless the amount of self-pollination is very considerable, and the separation of individual plants by a few feet of space renders their isolation comparatively easy even without cloth screens.

The breeder begins by selecting seed from individual plants growing in a mixed field. He also selects seeds of different sizes, shapes and colors from the commercial product. These seeds are planted in hills about two and one-half feet each way. The seeds of each individual plant are planted in separate plots, making the product of each plot the progeny of a single plant of the year before. Each of these plots and each plant in the plot bears a separate number, which is the means of reference to the description that is always carefully kept of all plants that are to be again propagated. It is only by these minute descriptions of characters that the different types can be separated, for it is impossible for a breeder to keep in mind the exact distinctions between types. When a plant is found in a plot that is different from the others, its flowers are separately bagged and pollinated. If it appears worthy of further consideration its seed is planted in another plot the next year.

The seed from each plot is not mixed for planting the next year's plot. If there are different types in a single plot, they have their seed saved separately and each plant of a slightly different type has a different plot for planting its seed in the succeeding fall. In no case does seed from more than one plant enter a plot. The breeding is distinctly in-and-in breeding, for this is the only way in which we can expect to separate the types.

Of course many of these plants are rejected each year as useless types, otherwise the work would become too unwieldly to conduct with proper economy of time and space. The remainder are gradually separated into distinct types which reproduce their characteristics year after year, and are then selected or rejected as their commercial value or uselessness becomes apparent. Variations that we have noted, that are of agricultural value, include the following:

(a) In vigor: some succumb to frost and their usefulness comes to a natural end; others are resistant and come through the winter in the best of shape;

(b) In stooling: some produce a large number of stalks; others very few;

(c) In leafiness: some produce long, weak stems, with leaves only at wide intervals, while others are remarkable for their leafiness;

(d) In character of bloom: some have numerous heads, others few; some heads are large, others small; some bear large individual flowers, others small;

(e) In habit of growth: some are erect and are easily cut by the mower, while others are recumbent;

(f) In yield: the differences are very marked;

(g) In character of stem: some are hard and woody, others make better hay.

There are many other differences that serve to help distinguish the types, but these differences are in slight physical distinctions that are probably of no agricultural value. It is true that these botanical marks may be found to be correlated with valuable qualities when they can be more closely studied with this idea in view.

Out of all the different types probably but two or three will be found of particular merit. The others must be discarded and the selected strains multiplied for field use, as rapidly as possible. The superior strains are not mixed but each are propagated separately as different varieties.

It is hoped before many years we will have varieties of each of the different forage grasses and legumes, as we now have garden varieties, adapted for special purposes. The important way to obtain valuable improvement of such crops is by *isolation of naturally better strains from their present mixtures.* Hybridization may be necessary later, but at present it is undesirable to complicate the work until we have accomplished what can be done without it.

Technique of Maize Breeding.

The breeding of maize or Indian corn is in many ways quite different from the breeding of our other field crops. Maize is the only one of our cereals that is monœcious. The tassel contains the pollen or male element while the silks are the stigmas of female flowers. In order that the pollination of the silks shall be relatively certain, each tassel produces about thirty million pollen grains; and as the ears average considerably less than five hundred grains apiece, there are about sixty thousand pollen grains produced for each kernel. With such a large waste of pollen floating about in the air, there are a great number of intercrosses between plants of the same variety. This inter-crossing has been an obstacle to the improvement of maize, but it has been offset by the advantage over the other cereals, in the possession of large ears. Since each individual ear must be handled and its characters noted at husking time, it is not strange that ears with desirable variations sufficiently striking to catch the eye of the grower, have become the parents of numerous distinct varieties.

It was early learned that maize varieties inter-crossed freely and the lesson was heeded by the pioneers in maize breeding. By selecting seed ears toward a desired type and by isolation from other varieties, various strains have been produced that are remarkably uniform in characters such as color, that have forcibly attracted the attention of the grower. Nevertheless, even in an isolated maize field grown from seed that comes pretty true to type, such as the Longfellow flint or the Reid's yellow dent, there are many natural types growing side by side. There are stalks which bear their ears high and there are stalks which bear them low; stalks with long ear shanks and stalks with short, stalks with different leaf markings and with notably different tendencies to produce suckers. The silks shade in color from purple to green as do also the tassels. Differences are everywhere present, although those in the ears themselves are the most familiar.

A large number of these differences are due solely to fluctuations, which are more easily noted in the large stalks and ears of maize than they are in the smaller plants of cereals like wheat and rye. The variations due to fluctuations are so large that the natural types are more or less obscured. Furthermore, the natural types are in a very mixed condition due to constant crossing with other types by wind pollination. We have on this account a much harder task than in most plants to separate the naturally productive types. Moreover, after a complete separation of such types there is still the wide and valuable fluctuating variation to consider; for to obtain the best results from breeding with such a large fruited plant as maize, the highest fluctuations in yield must be constantly selected and perpetuated.

To sum the matter up there are these tasks before the breeder:

1. To isolate the best yielding and otherwise desirable natural types of maize from the varieties in which the "blood" of these types is in a chaotic mixture with the "blood" of less desirable types; and to do this in the face of constant chances of further inter-crossing.

2. Constantly to select and propagate the highest fluctuating variations of desirable characters.

To solve these two problems has been the sole aim of maize breeders; and has been the means of building up the various methods of maize breeding now in use in the United States. Each of these methods has its advantages and its disadvantages, which the writer will try to discuss without bias, hoping that the advantages of each may sometime be combined into a more perfect method than there is at present. At least it is the right of the commercial breeder to know just what obstacles are in the way of the highest success; he may then adjust a method to meet his own conditions, without being led away by false hopes of large profit from blindly following the introducer of an imperfect method. We leave out of consideration, because of previous discussion, the fact that there may be definite strong points in two varieties which it may be desirable to combine by hybridization. This of course should be done when it is desirable, but there are probably natural types now being grown that answer all present agricultural purposes could we but get from them their greatest possibilities. Even to secure best results from hybridizing we must start with pure types.

In the primitive method of selecting large ears from the crib, the selections were especially poor in point of germination; for the ears were not properly dried and many of them were partially mouldy. While this is particularly bad for the yield in the succeeding season, it has very little to do with the hereditary characters of maize. The fluctuating variations in the succeeding season would be affected by the weak diseased stalks produced by seed embryos with poor vitality; but there is little probability of the weakness becoming permanent. Indeed, long continued selection of this kind does have quite an effect toward separating a particular natural type because the grower naturally selects those ears that appeared to be nearest in character to his ideal.

The first improvement over this primitive method was selection in the field. The advantage of this method over the crib selection was that the characters of the plant which bore the ear could be taken into consideration as well as the characters of the ear itself. Hence progress in separating natural types was much faster than formerly. It was this method that gave us such varieties as Leaming and Reid's yellow dent and Longfellow flint varieties. These varieties, in the hands of conscientious breeders, have been brought to the most uniform type of any varieties that we possess. Furthermore, when selections were made in the field more care was naturally taken with the selected ears, which ultimately made germination better and hence gave larger total yields. Field selections were made by the most progressive growers as early as the first half of the nineteenth century.

Not much over ten years has elapsed since the next step was taken in maize breeding. This was the introduction of what is now called the row system of breeding made by Hopkins at the Illinois Agricultural Experiment Station. The principle is, that more definite idea of the productive efficiency of an individual ear can be obtained by getting the average record of its progeny. That is, when one hundred or more hills are planted from a single ear and compared at the end of the season with rows of equal lengths from other ears, the weights of the ears produced on each row are a more exact measure of the productive efficiency of the mother ear of that row than are the weights of one or two of its daughter ears, selected at random. The average appearance of the progeny of an ear is a more correct index of the productiveness of a mother ear than is the appearance of the mother ear itself, for slight differences in soil fertility, moisture or sunlight may largely have been the cause of a superior looking ear, and this superiority might not be transmitted to any great degree to succeeding generations. In fact it often happens that in testing two seed ears, practically alike in size and appearance, by this method, that one yields at double the rate of the other. This is a great contribution toward a quicker method of isolating natural types, because a row that is exceedingly uniform in type growing from a single mother ear, shows that it (the mother ear) is less likely to carry the blood of numerous other natural types, than is the ear from which comes a varied progeny. Nevertheless, there is in this method the disadvantage that in planting these rows in the open field, there is a very large chance of inter-crossing between a superior row and an inferior row growing near it. Moreover, it is obviously incorrect to measure the productive capacities of two rows growing at opposite sides of a large field on account of very probable inequalities of soil. The disadvantage of inter-crossing in the row system was to a slight degree overcome by the United States Department of Agriculture, by the introduction of a plot system similar in character to the one previously described for clover. Kernels of single ears planted together in plots have the chances for inter-crossing with other types minimized, at least for the stalks growing toward the centre of each plot. But the advantage of this system is offset by the greater difficulty of planting, harvesting and keeping the records of the progeny of the individual ears, without making mistakes by which mixtures of other types would be introduced.

It has been suggested by the Ohio Agricultural Experiment Station that the error of comparing distant rows with each other can be decreased by the duplication of rows from the same mother ear in different parts of the field; while at the Illinois Agricultural Experiment Station it has been proposed to reach the same end by comparing with each other only ears which grew in one-quarter of the breeding plot. Selections were made of the best rows in each quarter of the breeding plot. Later the Ohio Experiment Station introduced the plan of planting so-called standard rows between every five rows. These standard rows were made by planting in each one a certain number of kernels from the same ears. The rows between two of these standard rows were not compared with each other but with the average product of the two standard rows between which they grew. It is evident that it is not desirable to perpetuate these standard rows made up of composite samples of several ears. To keep from doing this, in the method of continuous selection, it is necessary to detassel all of these standard rows, thus preventing any possibility of pollen which they had produced fertilizing silks of other rows.

About this same time an extended experiment at the Illinois Station showed that there were distinct effects from continuous propagation from very nearly related blood lines such as is ordinarily obtained in a rigidly selected breeding plot. To decrease this fault it was suggested to detassel every alternate row and to select seed for the succeeding season only from the detasseled rows. A plan* of planting was worked out mathematically by which near relatives were separated. A breeding plot of ninety-six rows was grown, and every alternate row detasseled, leaving in all forty-eight rows from which seed might be selected. These forty-eight rows were considered in four quarters and four ears were selected from each of the six best producing rows of each quarter. Of these twenty-four ears selected in each quarter, twelve were grown the next season in that quarter and detasseled; the other twelve were taken to the farthest removed quarter and grown the next season in rows that were not detasseled. In this way the blood lines were continuously kept as far apart as is possible in an open field breeding plot.

It is clear that while this method lessens the evil effect of inbreeding and is easy to manipulate, it nevertheless does very little toward isolating natural types because of the selection each year of so many ears for the next year's breeding plot. On the other hand, the propagation of the highest extremes of fluctuations was brought to a high degree of perfection.

This method, however, does *contribute* toward the *slow* isolation of the best natural high yielding type, for the selection is made each year from high yielding rows, that is, from the progeny of the best mothers, which gradually weeds out the least productive types. The pollen parents are of course unknown although

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* This plan is explained in detail in Bulletin No. 152 of this station, which will be mailed free upon request.

they must be better than the general field average because they come each year from the best yielding rows of the previous season; but there is no way always to guard against the pollination of the best detasseled rows by relatively inferior tasseled rows. The influence of *very* inferior individuals or rows, however, is guarded against by detasseling all weak and barren stalks as well as the regular detasseled rows. Rows that produce a large number of undesirable stalks are entirely detasseled to prevent the inferior blood of the parent ear from being propagated. Another point in which this method is inefficient is that a small number of rows are used in the beginning. If there could be an initial selection of a very large number of ears, there would be a much greater probability of a final isolation of the best types now being naturally produced. The number of ears planted in succeeding years could be materially decreased, for the relative probability of obtaining blood of the best natural types in the first selection is much greater than where small numbers are used; and having partially isolated these types by the first selection, it would not be so necessary or even desirable to continue using large numbers. But even if this were done, there remains an obstacle in the fact that even with a large number of ears selected from the general field for the first breeding plot, there would still be an indefinite number of crosses among these selections; that is, it cannot be known what per cent. of inferior blood there was in the original ears which were selected as appearing to be the best. It may be that from this cause a relatively pure ear of a comparatively ordinary type would show up to better advantage in a breeding plot than an ear of a superior type but with a large admixture of an inferior type. Moreover, when the selection is made at the end of the first season from the best yielding rows, there is nothing to guard against these selected ears having been pollinated from inferior rows in proximity, and at this stage the rows are all from field selections with no previous breeding. Hand pollination is of little practical use, for we could not tell definitely until harvest which rows would prove the best and a large amount of tedious work would have to be done which would ultimately prove useless.

Williams, of the Ohio Agricultural Experiment Station, obviates this deficiency by the method he has originated. He plants twenty-five rows in an ear-to-the-row test plot but uses only one-half of the kernels of each ear. This test plot is treated as an ordinary field plot with no necessity of detasseling or removing suckers. The rows, however, are weighed at the end of the season and compared with a standard row which is made up as described above (page 83) and planted between every five rows. The remnants of the four ears that have been shown to possess the greatest yielding efficiency are planted the succeeding season in two small isolated plots, detasseling all the plants grown from one ear in each plot. By saving the seed only from the detasseled rows, a direct cross is obtained of two of the best ears upon the other two selected ears. In the third season ears from each of these crosses are again crossed by planting in alternate rows and detasseling the even numbered rows. Each year new field selections are grown in test plots and the remnants of the two ears which prove the best are crossed the following season. Finally, these are again crossed with best ears from previous crosses. This is continued indefinitely, as is shown in the following diagram.

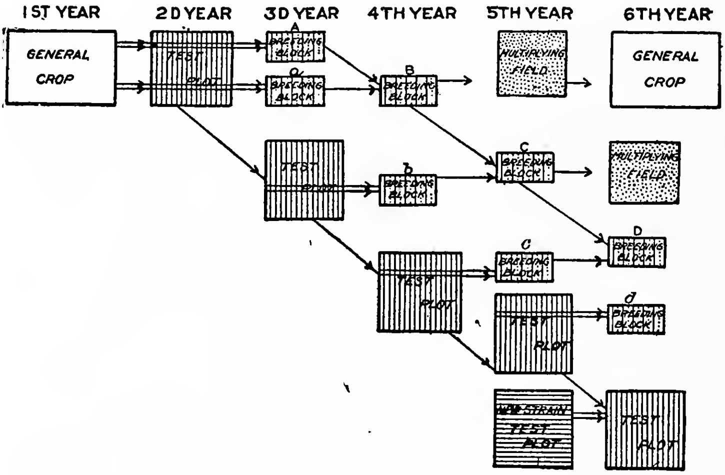

FIG. 6. Williams' method of maize breeding. (After Shamel.)

This method has two advantages: it does away with any possibility of the selected ears having been crossed during their ear-to-the-row test with pollen of inferior types and yet does not allow the strain to deteriorate through inbreeding. Its disadvantages are:

1. There is only a small number of ears in the first breeding plot which makes the chance of isolation of the best types relatively small. This is supposedly obviated by taking the ears for the test rows each year from the general field; but the objection to this proceeding is that new mixtures of elementary types are thereby introduced into the improved strain. High fluctuations are thus continually brought into the strain, but the isolation of the best type is further than ever from attainment.
2. It is necessary to grow three isolated plots each year, which on many seedsmen's farms is almost an impossibility.
3. There is not sufficient range for the selection of fluctuating variations in such small plots, after the individual ear crosses are made.

It appears, therefore, that there are advantages and disadvantages belonging to each method, without there having been suggested a particularly desirable combination of the two. Where there is sufficient uniform soil available, and where the breeder is going to devote his whole time to the development of maize, the following method is proposed as worthy of consideration, although it also leaves much to be desired. In the first year let the breeder obtain select ears of the variety from different growers, of as many different desirable types as possible. Let these ears be selected from standing plants where possible, paying strict attention to the character of the plants that bear the selected ears. The stalks should be firm and erect, with a good secondary root system and plenty of foliage. The ears should be borne between three feet six inches and five feet high, on medium length ear shanks, and should be covered with only a moderate amount of husk. They should be mature, and should contain the largest possible weight of kernels of uniform size and shape, where the time of maturity is not an object. In places where the growing season is short, smaller ears should be selected, but from plants that produce more than one ear, for we have found that a pound of corn can be produced by a plant bearing two ears, in a shorter time than a pound of corn can be produced upon a single ear. Other fancy score card points need be given little attention, as what we wish to obtain is a variety that produces the greatest profit per acre. This we shall find out by actual test without carrying into it a preconceived notion of just which type is the most productive.

At least three hundred of these ears should be planted in the first year's ear-to-the-row test, and five hundred or more should be grown if possible. These ears should each be numbered and only one-half of the kernels of each planted in single rows in the test plot. Our object is to have the greatest possible probability of obtaining the best natural types from the first year's test. Notes should be taken of the desirable or undesirable qualities shown by the plants of each row, at various stages of growth, and at the end of the season each row should be cut, husked and weighed separately.

All of the corn from the best fifteen or twenty rows should be saved separately and the ears and plant records of these rows carefully studied. All rows whose products show a number of undesirable characteristics should be entirely discarded. Some rows will have shown a marked superiority over all others. The ears from those rows should be examined minutely to see whether they bear any peculiarities that may be correlated with productive efficiency. If any such peculiarities are found, note them in the record book, for the value of the knowledge of such a correlation to the breeder can hardly be estimated.

The next season plant the remnants of the four ears that had this season produced the four rows with the most marked superiority over the rest. These ears will possess the superiority shown in the test, uncrossed by inferior pollen in the test plot to the previous season. They will probably not be distinct and uniform types, for it is likely that they contain blood of other types from previous natural crosses in the field; but they are the pick of a large number of ears, and partially or wholly true to type as the case may be; they are good foundation stock for a uniform variety.

There are now two methods of procedure open:

1. To begin at once to select high fluctuations, without trying to isolate further a single type.

2. To risk evil effect from inbreeding and work to isolate further a more uniform foundation stock.

In the first method the plan of planting can be arranged by planting in alternate rows with as many combinations as possible. Then by detasseling the upper half of each odd numbered row and the lower half of each even numbered row, force as many different crosses as possible on these rows. Save the best ears of these crosses and begin a regular ear-to-the-row fluctuation breeding* plot and continue it annually, using from fifty to one hundred rows.

The second method can be followed most practically by planting the remnants of the best four ears in pedigree plots. Each plot is then surrounded by two rows of some very high growing ensilage corn planted one kernel every eight inches. These rows are to obstruct foreign pollen and should be *carefully detasseled* each season. Personally I prefer to use immediately the fluctuation plot on account of danger of continued inbreeding, but I am free to confess that the question is not permanently settled. There may be individuals that will stand continued inbreeding like Darwin's morning glory, Hero.

The point of extreme importance is the advantage of isolating immediately from the general field as fine a foundation stock as possible. The relative probability of doing this increases directly with the number of ears used in the first test plot; hence as large a number as possible should be used. If we obtain a fine foundation stock we are on the road to success; if we have left the best stock out of our first test plot, no amount of continued breeding from the inferior stock can obtain it.

CONCLUSION.

These pages are designed only to give the practical plant breeder an introduction to the theoretical side of his subject. There are hundreds of agriculturists who are interested in the work of improving their important field crops, and yet who know nothing of the work of their colleagues in the science either pure or applied. In many cases the methods in use are primitive as those of several centuries past. In other instances much impractical advice is followed blindly. We now have plant breeder's associations in a large number of our states, as well as a national organization† with over a thousand members, where information can be obtained upon special subjects. It is hoped that readers of this paper that expect to do plant breeding work, will become members of some of these associations and take up a course of

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* A breeding plot in which high fluctuations in yield are selected.

† The American Breeders' Association. For information address, Hon. W. M. Hays, Secretary, Washington, D. C. The Connecticut Plant Breeders' Association, Prof. C. D. Jarvis, Secretary, Storrs, Conn.

reading along the lines suggested in the appended list. The reading will be found fascinating as well as instructive and the association with men interested in similar lines of work will prove to be of great value.

The writer is well aware that he can be accused of a pronounced De Vriesian view of this paper. He can only plead that the view is from the standpoint of the principles and theories that give at present the most practical and efficient help in actual plant breeding. As was stated in the beginning, the studies of the evolution student and of the plant breeder should be and are parallel, but only in so far as theories are proposed that can be experimentally demonstrated. Experimental proof on all points is the ideal of the modern biologist, but it is absolutely essential to the modern breeder. The philosophical side of biology can have but little weight with the latter. It may be admitted that certain forces may have been of great value in effecting an evolution through eons of time, and still be ineffective agents in the time allotted to the man who wishes to make changes under domestication from the standpoint of commercial gain. It is here that the two lines part company; and it is the plant breeder who remembers this distinction between natural and artificial evolution when studying disputed theories of variation and heredity, that will obtain the greatest aid from the results of the experimental biologist. We may admit, for instance, that the believer in Lamarckian factors as agents in evolution can say that experiments concerning the inheritance of acquired characters have been carried on only for a period of time that would be negligible in a geological epoch; we may admit the justness of the same criticism of our conclusions regarding the ineffectiveness of the selection of fluctuations in permanently changing characters: but we are justified in retorting that only such theories can be of use to us that produce results within the span of a human life. With this point in mind the writer believes that a fair view has been taken of the questions touched upon in this paper.

Our three main theses we will again summarize:

1. Organisms are composed of numbers of characters which are inherited as units. These units are inherited by definite laws of which Mendel's law is the first to have been discovered. Since these characters are inherited as units it is most reasonable to

suppose that each one has been originated fully formed, i. e., as a mutation. The addition of a new unit character is the only real difference between this mutating organism and its progenitors, and is the true and only foundation for domestic improvement.

2. The object of hybridization is to shuffle and recombine these unit characters. Hybridization, therefore, actually produces nothing new in spite of its wonderful manifestations. Just as chemical units,—the elements,—can be combined and recombined into different compounds, so can the unit characters of organisms be combined and recombined by hybridization.

3. The value of the selection of fluctuations is slightly to increase or to decrease the manifestations of a unit character after it has been formed by nature. Selection can never produce a unit character, for there is obviously no basis upon which it could work.

READING LIST.

This list of publications is suggested as a course of supplementary reading in English, concerning the questions that have been under discussion, and is available to most readers through the public libraries. The reading should be done cautiously, for it must be remembered that most of these publications were issued previous to the rediscovery of Mendel's work, in 1900. If the works of De Vries, Mendel and later workers of the Mendelian school are studied first, the reader will appreciate how great has been the change of opinion during the last seven years concerning these questions, and will not be confused by the different points of view of the early writers. The recent work is scattered through the files of many journals, and is for the most part in foreign languages. For these reasons it is not available to many readers and has therefore been omitted from the list. To remedy this omission, it is recommended that the reader obtain from his bookseller, as soon as they are published, the two forthcoming volumes on the problems of variation and heredity by Wm. Bateson, M.A., F.R.S., Fellow of St. John's College, Cambridge.

Bailey, L. H. Plant Breeding. Ed. 4. N. Y. Macmillan. 1906.

Contains a fairly complete bibliography to the end of 1905.

Bailey, L. H. Evolution of our Native Fruits. N. Y. Macmillan. 1898.

Gives a popular historical account of the development of American varieties of fruits.

Darwin, Chas. Cross and Self-fertilization in the Vegetable Kingdom. N. Y. D. Appleton.

Read chapters one and twelve, giving the plans of the experiments and results.

Darwin, Chas. Animals and Plants under Domestication. 2 v. Ed. 2. N. Y. D. Appleton.

The historical parts of the first volume are still of great interest. The theoretical discussions in volume two will only be confusing to the reader and had best be omitted. Our views concerning the explanation of the phenomena brought together in volume one have entirely changed since Darwin's time.

De Vries, Hugo. Species and Varieties: Their Origin by Mutation. 2d Ed. Chicago. Open Court. 1906.

A large book which goes rather deeply into the subject. It has in it more of interest to plant breeders than any other book concerned with evolution.

De Vries, Hugo. Plant Breeding. Chicago. Open Court. 1907.
A work that is of special interest to plant breeders. It should be read before the larger work. Gives an account of Nilsson's work in Sweden and Burbank's work in the United States.

Kellogg, V. L. Darwinism To-day. N. Y. Henry Holt. 1907.
Gives the best summary of modern criticism of Darwin. The author does not accept the mutation theory.

Lock, R. H. Variation, Heredity and Evolution. London. John Murray. 1906.
The best popular presentation of the subject from the modern viewpoint. Contains the summation of important researches up to 1906.

Morgan, T. H. Evolution and Adaptation. N. Y. Macmillan. 1903.
A good criticism of Darwin by one who accepts the mutation theory.

Punnett, R. C. Mendelism. Ed. 2. Cambridge. Macmillan. 1907.
A short and readable account of Mendelism to date of publication.

Romanes, G. J. Darwinism. Ed. 3. Chicago. Open Court. 1901.
An excellent account of Darwin's theory of natural selection; the early criticisms and Romanes' replies.

The following articles, although written without a knowledge of Mendelism, which would change their statements to some extent, are recommended as a set of interesting papers that may be obtained free from any Congressman or from the Secretary of Agriculture, Washington, D. C. Either the complete year books will be sent or the separate articles may be obtained as reprints.

Bailey, L. H. The Improvement of our Native Fruits. Year book U. S. D. A. 1896: pp. 297-304.

Hays, W. M. Progress in Plant and Animal Breeding. Year book U. S. D. A. 1901: pp. 217-232.

Swingle, W. T. and Webber, H. J. Hybrids and their Utilization in Plant Breeding. Year book U. S. D. A. 1897: pp. 383-420.

Webber, H. J. Influences of Environment in the origination of Plant Varieties. Year book U. S. D. A. 1896: pp. 89-106.

Webber, H. J. Improvement of Plants by Selection. Year book U. S. D. A. 1898: pp. 355-376.

Webber, H. J. and Bessey, E. A. Progress of Plant Breeding in the United States. Year book U. S. D. A. 1899: pp. 465-490.