SCIENCE

FRIDAY, APRIL 19, 1912

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MSS. intended for publication and books, etc., intended for review should be sent to the Editor of SCIENCE, Garrison-on-Hudson, N. Y.

THE EFFECT OF RESEARCH IN GENETICS ON THE ART OF BREEDING[1]

THE knowledge of breeding has advanced so rapidly in recent years that few of us realize the great change that has taken place in our understanding of the fundamental principles, and the effect that this change has had on the methods of practical breeding which we advocate. I had the good fortune to begin my studies and experiments in breeding in 1890, ten years before the rediscovery of Mendel's now famous principles of heredity, or the publication of de Vries's mutation theory. I have thus had the opportunity to follow this change through all its ramifications. From a condition of ignorance and largely of chaos, where all advance was taken as a lucky chance, we have developed to a position where practically each step may be taken intelligently. True, we touch the limits of knowledge on every hand and many of the most fundamental problems still remain unsolved, yet our understanding to-day, which enables us to analyze a plant into its component parts or characters, and then in turn by synthesis to build up a new structure by the combination of different characters into a new race or variety, is to our former understanding as light to darkness. The knowledge of breeding has developed into the science of genetics, and is fast assuming through the orderly presentation and classification of facts, the form of an exact science. Yet with all this advance in our understanding,

[1] Paper No. 27, Department of Plant Breeding, Cornell University, Ithaca, New York. Annual address of retiring chairman of the Plant Section, American Breeders' Association.

the methods of breeding that can be recommended for the use of practical breeders have changed but little in the last twenty years, the greatest change being primarily in the greater surety with which we now make recommendations. It is the speaker's purpose in this address to emphasize certain salient features of the advance that has been achieved, and point out what he conceives to be some of the most important problems awaiting solution.

Twenty years ago our understanding of the principles of breeding was derived largely from Knight's physiological papers and Darwin's "Origin of Species" and "Plants and Animals under Domestication." Verlot's admirable pamphlet "On the Production and Fixation of Varieties of Ornamental Plants" gave a general outline of the best methods then followed, and we derived our knowledge of the use of hybrids largely from Focke's excellent text, "Die Pflanzenmischlinge," published in 1880, and the work of the French experimenter Naudin.

At that time breeders clearly understood the fact that hybrids segregated in the second generation and gave new combinations of characters, and the suggestion was even then present in the minds of scientific breeders, that this segregation of characters took place during the reduction division. At that time breeders, just as definitely as now, planned experiments in hybridizing different varieties or species to secure certain recombinations of desired characters in the hybrids. The experiments in citrus hybridization conducted by Mr. W. T. Swingle and the speaker were planned in 1893 entirely on this basis, yet the principle was in no sense of the word original with us, but was at that time well understood by all practical breeders. This understanding, the speaker thinks, was largely derived from the investigations of Naudin, though various investigators contributed to it.

With a full understanding of the knowledge and practises of the breeders of two decades ago, it must be admitted that the conception of unit characters and Mendelian segregation was necessary to clarify this knowledge and bring out the latent possibilities of the material presented by nature for the use of the breeder, and it is doubtful whether we even yet adequately comprehend the almost infinite possibilities open to us.

To understand breeding to-day we must clearly understand the conception of unit characters. We no longer conceive the species, race or variety, as a fixed ensemble of characters. Following De Vries, we now commonly conceive the species or variety to be made up of a certain number of unit characters, that are in large measure associated together by the accident of evolution or breeding and which are separable entities in inheritance. We may liken these unit characters to bricks used in the construction of a building, each separate and yet dependent on the others for the maintenance of the structure; as each unit character is dependent on the other unit characters for the maintenance of the plant body. We may think of these unit characters as organic elements similar to chemical elements, that by their recombination through hybridization, form new compounds—new plants—of distinctly different appearance, but which in turn do not affect the unit characters, which may again be separated and led to form other compounds, again resulting in distinct organisms. Related species may possess many distinct unit characters, but ordinarily would be expected to possess many similar unit characters. Cultivated races or varieties ordinarily would differ only in a few unit characters, and difference in a single unit character would be sufficient to give a distinct and recognizable race or variety. Indeed, the difference between two varieties of a single unit character might mean that one variety would be exceedingly valuable and the other practically worthless. De Vries asserts that unit characters are discontinuous in inheritance and do not exhibit transitional forms. A plant can not be hairy and at the same time smooth, or a fruit yellow and at the same time red. While there is yet much difference of opinion on these questions the preponderance of evidence certainly favors the unit character conception.

If, then, we recognize that species are made up of unit characters and that different species differ in the possession of different unit characters, the great problem in the evolution of species becomes the question of how the new unit character is acquired. Have all unit characters existed from the beginning, or are new unit characters being continuously acquired? A few years ago we supposed that new characters, if acquired in any form, must be seized upon, as it were, by natural selection and preserved, or otherwise that they would be swamped by intercrossing and lost. We now know from Mendelian analysis that a unit character may be apparently lost in crossing, owing to the prevailing presence of its dominant allelomorph, but that in reality it is not lost or apparently changed and will reappear again when it happens that two gametes both bearing the character meet in fecundation. It may remain hidden for many years, but as we are now inclined to view the matter, the character or the determiner of the character would not be permanently lost to the species unless all individuals possessing it were killed before they produced seed. This unit character idea would lead us to the conception of the species as made up of all the unit characters that it has acquired by any means in its development and which still exist. The acquirement of any new unit character would add one more character to the species and double the number of possible varieties or races of the species.

In evolutionary studies we have long recognized that variation was the foundation of evolution and that no evolution was possible without variation, but we have assigned to selection an all-important part as guiding and even stimulating the variation in a certain direction. Darwin and particularly some of his more radical followers have assigned to selection a creative force, in that it has been assumed that when nature by a slight variation gave the hint of a possible change in a certain direction, natural or artificial selection, by choosing this variant and selecting from among its progeny the most markedly similar variants, could force the advance of the variation in the direction indicated. Since Darwin's time this cumulative action of selection has been emphasized so forcibly that we had come to recognize selection as an active force in creation rather than simply as a selective agency. To be the vital principle of evolution, as we now understand the species as made up of heritable unit characters, the selectionist must show that a new character can be created by selection, otherwise selection becomes a secondary principle.

When viewed from the standpoint of the production of a new and definitely heritable unit which mendelizes, the task of selection becomes more doubtful. Darwin's idea, that changes in species required many years and probably many centuries for accomplishment, took the subject largely out of the field of experimentation and in a measure developed a speculative science. One of the greatest contributions to science made by De Vries was to establish the study of evolution on an experimental basis. With the demonstration that evolution could be studied experimentally, the question of the effectiveness of selection was taken up, and we are now doubtless on the road to a solution of the problem. It is only possible for us here to call attention to a few of the researches in this direction.

The classical researches of De Vries, now familiar to us all, challenged the correctness of the selection theory and sought to show that species originated by sudden jumps or mutations. We may admit that De Vries proved that species or new characters were formed suddenly as mutations, but this would not prove that they might not also be formed or actually induced to mutate by a continuous process of selection. Indeed, in his experiments on the production of a double-flowered variety of *Chrysanthemum segetum* ("Mutationstheorie," Vol. I., p. 523), a few generations of selection led to markedly increasing the number of ray-florets before the ligulate corollas appeared among the disk-florets, the change which he interpreted as the mutation that gave him the double variety.

Johannsen has contributed much to our knowledge of selection and has given us a more exact method of experimentation by his conception of pure lines, biotypes, genotypes and phenotypes. His experiments in the selection of pure lines of beans in an attempt to produce large and small seeded types, have led him to conclude that selection within a pure line is ineffective in producing changes. He did, however, secure new types from pure lines through mutations.

Tower's experiments with the potato beetle in attempting to create by selection, large and small races, albinic and melanic races, and races with changed color-pattern, although conducted carefully for from ten to twelve generations, failed to give any evidence of producing permanently changed types. While strains of plus and minus variates gave populations with a range of variation apparently markedly restricted to their respective sides of the normal variation range, still these selected strains did not greatly exceed the normal range of variation in either direction, and when the selection was discontinued, in two or three generations, again produced populations exhibiting the normal range of variation. Clearly no new unit characters had been added by the selection. Tower, however, found that by subjecting the beetles, during the process of the formation of gametes, to certain abnormal conditions, he was likely to obtain mutations in the progeny that would immediately form the beginnings of new races.

Jennings in a series of selection experiments conducted with paramecium, which were continued for over twenty generations, obtained no evidence of a permanent modification of the type.

Pearl has conducted an extended experiment in the selection of chickens in the attempt to produce a breed of high egg-laying capacity. His results have led him to the conclusion that selection alone has no effect in producing a permanent improvement or a change of type.

Up to the present time these are the principal contributions to the subject, that discredit the effectiveness of selection as an active agency.

On the opposite side of the controversy we have the very careful and extensive researches of Castle and MacCurdy in the selection of Irish rats to increase the black-colored dorsal band on the one hand and to decrease or obliterate it on the other. Castle appears to have obtained very positive results favoring the gradual cumulative action of the selection, as he succeeded in markedly increasing the amount of black in one strain until the rats were almost wholly black, and in the other strain almost wholly obliterating the black. The speaker is not informed whether the inheritance in hybridization of these apparently new characters has been tested. If a new character has been added it should maintain itself and segregate after hybridization.

The experiments conducted by Dr. Smith and others at the Illinois Experiment Station on selecting high and low strains of corn with reference to oil and protein content, have resulted in markedly distinct strains possessing these qualities, which are inherited apparently as long as the selection is continued. It seems certain that the oil and protein content has been increased considerably beyond the maximum which existed in the original race. The writer is informed by Dr. Smith that experiments have been made in cultivating these varieties without selection and that the new characters have been maintained for several years without marked regression. We must apparently conclude then that new heritable characters have been acquired in the course of the selection, but it will probably be difficult to determine whether the advance is to be considered as a cumulative effect of the selection of fluctuations or the gradual purification by the selection, of mutants which occurred during the selection or possibly even before the first selections were made. The purification of a type even when the character concerned is easily observable is known to require a number of years unless both parents are carefully followed. Whether these qualities will segregate as unit characters after hybridization has not been determined so far as the writer is informed.

Very many cases of increases obtained in quantitative characters could be cited, but the majority of the experiments were undertaken primarily to obtain practical results, and whether such apparently new characters would stand the test of unit characters is doubtful.

The improvement of the sugar beet by selection forms a typical and instructive case of this kind. The careful selection of the sugar beet was started over sixty years ago by Louis Vilmorin, at which time a range of variation in sugar content of from 5 per cent. to 21 per cent. was known to exist. Since that time the industry has grown extensively until hundreds of thousands of beets are examined annually and the richest in sugar content selected for seed production. The process of selecting the beets richest in sugar content for mothers has now been continued for sixty years and is practised extensively every year, and yet there is no evidence that the maximum sugar content has been increased, and it is certain that the character of richness in sugar content has not been rendered permanently heritable, as sugar beet growers well know that their success depends upon the continuance of the selection. Here it is certain that no distinct unit character has been added by the continuous selection.

The strongest evidence as to the method of origin of new characters is derived naturally from our knowledge of known cases of the origin of such typical new characters. When we view the evidence critically, I think it must be admitted that in practically all, if not all, of the cases of new characters appearing, they have come into existence suddenly. The cut-leaved *Celedonium,* the cupid sweet pea, *Bursa heegeri,* the Otter sheep, the muley cow, are illustrations familiar to all and doubtless each of us could add several such illustrations from our own knowledge. Such new characters appearing suddenly are heritable and maintain themselves as unit characters in hybridization. We can not but admit that the evidence of these known cases counts against the origin of characters by gradual cumulative selection.

In summarizing this part of our discussion, we can only state that at present it appears that far the greatest weight of evidence is opposed to the origin of a new unit character through the cumulative action of selection.

Are we, then, to conclude that the practise of breeders in continually selecting from the best for propagation is useless, and must we advise practical breeders to discontinue their selection? How can we do this in the light of the success of the sugar beet breeders? Have not Sea Island cotton growers increased and maintained the length and fineness of their staple by continuous selection? Have not corn growers maintained high productiveness of different strains by selection? Are not the Jersey and the Holstein maintained at a high degree of efficiency by selection? Has not the speed of our trotting and pacing horses been increased and maintained at a high rate by the most careful selection? To one familiar with the history of agriculture and breeding these questions arise fast and are likely to be insistent. There can be no doubt that the practical breeders have made advances by selecting from the best individuals. No genetist or scientific breeder will deny this. It is simply the question of the interpretation of how the results were obtained that is in doubt and whether these results can be considered as permanent, new unit characters. Before we can thoroughly understand this subject it is probable that each individual case will require to be carefully analyzed, to determine the nature of the advance made and the interpretation of the process or processes concerned. At present we can only partially understand the phenomena presented.

It appears to me that we are dealing in breeding with two markedly distinct types of selection, based on different principles and arriving at different results, both right in principle and productive of equally valuable practical results, but of very different value, when considered from a strictly evolutionary standpoint.

It would seem that such cases of improvement as are illustrated by the sugar beet indicate that the continuous selection, generation after generation, of maximum fluctuations shown by a character, will result in maintaining a strain at nearly the maximum of efficiency; and that within a pure race the progeny of a maximum variate which would probably be classed as a fluctuation, does not regress entirely to the mean of the race in the first generation succeeding the selection, but that we only have a certain percentage of regression similar to the regression determined by Galton. It would further seem to be indicated by the evidence now available that in some cases we may even expect the continuously selected strain to exceed the ordinary maximum of the unselected population. In the Illinois corn experiments the maximum oil and protein content seems clearly to have exceeded the ordinary maximum, and is certainly maintained at a very high degree with a new mode and range of variation. If a new mutant of high protein content has been secured in the course of the experiments with a change of type it is probable that this high protein content will behave as a unit character in inheritance. Upon the other hand, if the results are interpreted as simply the maintenance by isolation of a strain produced by selecting fluctuations, there would probably be a rapid return to the normal range of variation of this character if the selection was discontinued.

De Vries has pointed out that natural selection can produce races and maintain them, but its power to develop races beyond the natural range of variability remains to be demonstrated.

With reference to his experiments with the potato beetle Tower states:

> It is demonstrated that among the fluctuating variations there are individuals which are able to transmit their particular variation and give rise by selection to a race, while the majority are not able to hand on their particular conditions to their progeny. Races developed by selection from such variations have not been carried beyond the normal limit of variability of the species.

These races or selected strains maintain themselves as long as the selection is continued, and when the selection is discontinued rapidly regress to the mean of the species.

The above examples from the sugar beet, corn and potato beetle will illustrate the type of improvement usually secured by practical breeders. By their selection they maintain a strain of high efficiency without having in general exceeded the limits of variation of the species or race and without having produced new unit characters which would be maintained without selection and segregate as pure units following hybridization.

Our different breeds of dairy animals are maintained in a state of high productivity by continuous selection. Cows are followed carefully with reference to their milk-producing capacity and their ability to transmit this quality to their offspring. The ability of bulls to beget high milk-producing daughters is taken as a test of their value. There can be no doubt, the speaker believes, that this selection within the breed maintains the breed in a state of high efficiency and is absolutely necessary to the success of dairying. Strictly speaking, in the course of this selection, however, no new type has been produced. It is well recognized that the continuous selection is necessary to the maintenance of high milk-producing capacity, and if the selection were discontinued the average milk production of any dairy herd would rapidly decline until it reached the normal mean for the breed concerned. The same can not be said, however, of the breed or race characters, that is, those characters which distinguish the breeds or races from other breeds. Selection is not necessary to maintain the general characters of the Holstein breed for, as long as it is not crossed with other breeds, it will in general maintain its characters so far as color, conformation, and dairy type are concerned. The same may be said of any of our breeds of cattle and horses. The high efficiency of our race horses is maintained by the most careful selection and yet probably in most cases no distinctly new character is added, which would maintain itself as a unit character in inheritance.

It is true that we are dealing here with complex phenomena and limited exact experimentation, and a distinct mutant in the direction of high efficiency might occur at any time and be chosen for breeding which would maintain itself without continuous selection.

It is interesting at this point to recall one of the most common differences between plant and animal breeding which is seldom clearly recognized by practical breeders. Plant breeders most commonly strive to produce new races or breeds with distinctive characters which will reproduce their desirable qualities without continuous selection; while animal breeders almost wholly limit their attention to selection within the breeds already established, to maintain them in the highest state of efficiency possible. The failure to understand this difference in purpose has frequently led to confusion in our discussions.

It is beyond the scope of this paper to discuss the kinds of variation used in these different types of selection, even if we possessed the requisite knowledge, which is doubtful. The speaker may be pardoned, however, for digressing far enough to state that it is his conviction that there is no very hard and fast line between that variation which is in considerable degree inherited, such as is found frequently in high milk-producing cows in selection within the breed, and the mutation which gives absolute inheritance and establishes a permanent new mode. The great difficulty in determining whether there is any true cumulative action of selection which will extend a character beyond the limits of the race or species is met in determining what are and what are not mutations. My experience has led me to conclude that the continuous selection of maximum fluctuations in a certain direction may in some cases lead to the gradual strengthening of the character until finally it may become, more or less suddenly, fully heritable and it would then be recognized as a mutation.

In many cases we find exceedingly small differences maintaining themselves generation after generation under different environments when the lines of descent are kept pure. A marked illustration of this is afforded by Mr. Evans's studies on pure lines of *Stellaria* reported at this meeting. The segregation of such characters in hybridization would be exceedingly difficult to recognize if it did occur. Again the occurrence of such small mutants, if we may so designate them, within a breed under selection, if not recognized and isolated, would be crossed with fluctuations and cause variations which would be recognized as regressions in the highly selected strain.

I think it will have become clear from the above discussion that in the present state of our knowledge of selection we can only advocate that practical breeders continue their selections as in the past. This is particularly true in the cases where it is the idea to maintain the race or breed at its highest efficiency. In the case of plant breeders working to produce new races, the mutation theory introduces a new element and leads the breeder to search for a mutant possessing desirable characters which he can isolate and which he may expect will reproduce its characters as soon as he has purified the type from mixtures derived through hybridization with other types. He will select the type to purify it rather than to augment its good qualities.

Returning again to the question of new characters, we may profitably question more definitely where such new characters come from, if they are not produced by selection. Clearly, no problem is of more importance to the breeder than to be able to definitely produce or cause such new characters to appear. If the breeder must await the pleasure of nature to secure the changes he desires, the waiting may be long and tedious. If he must watch thousands of plants of a certain race or species every year in order to find the apparently accidental variation or mutation in the direction of the improvement he has in mind which may rarely or never be found, the process will be so hazardous that we should have to await the accidental discovery of any new characters. Indeed, up to the present time we have had practically no other recourse than to await the accidental discovery of such new characters. We, however, have had many theorists and investigators who believed that changed environment would stimulate the production of variations in the direction of better fitting the organism to its environment. Lamarck and his followers have strongly maintained this hypothesis and many scientists even to-day believe in the effectiveness of environment in developing adaptive changes. Breeders have carried this principle so far as frequently to advocate the growing of plants in the environment most likely to produce the change desired, as, for instance, cultivating tall plants like twining beans in the north or at high altitudes if it is desired to produce a dwarf type or, *vice versa,* breeding the plants in the south and at a low altitude if a giant or tall type is desired. Weismann and his school of followers have apparently exploded this idea by demonstrating that characters acquired as a result of changed environment are merely physiological changes and are not inherited. The question, however, is by no means settled and we must await further evidence.

Knight believed that increased food supply caused an increase in the range of variation and that it was important for breeders to manure their plants heavily. De Vries, on the contrary, would have us believe that such variations are fluctuations and non-heritable. The studies of Weisse, Reinhold, MacLeod, Tammes and Love have given us many instances where the range of variation is increased as a result of food supply and other instances where the variation is apparently greater on poor or sterile soil.

It would seem that any treatment that would increase the range of variation, in plants that are grown for breeding purposes would be valuable, but it still remains to be definitely proved whether such increases in the range of variation are in any marked degree heritable and whether valuable maximum variates can be more frequently produced in this way than would be found in similar groups of plants under ordinary treatment.

It is only very recently that the idea has developed that we can go farther than possibly change the environment. With the publication of MacDougal's researches in 1906 describing mutations that were apparently caused by injecting the capsules of plants with certain solutions, such as zinc sulphate, magnesium chloride and the like, a possible new method of forcing variations was introduced. MacDougal apparently obtained marked variations as a result of his treatment, which were inherited in succeeding generations.

Tower, by subjecting potato beetles during the formation of the germ cells to extremely hot and dry or hot and humid conditions with changes of atmospheric pressure, was able to cause the development of marked changes or mutations which were found to transmit their characters true through several generations and which segregated as unit characters following hybridization. He concludes from his experiments "that heritable variations are produced as the direct response to external stimuli."

Gager has produced similar changes in plants by subjecting the developing ovaries of plants to the action of radium rays and a number of similar studies by Hertwig and others indicate that radium emanations have a very active effect on both plants and animals.

While the evidence favoring the value of such external stimuli as the above in producing new heritable characters is apparently definite and positive, the extent to which the method can be used in practical breeding has not been determined, and indeed we must await further evidence before we can finally accept the evidence, or the interpretation of the evidence, presented in these very valuable and suggestive researches. Dr. Humbert carried out experiments in the speaker's laboratory in which the capsules of a pure line of a wild plant *Silene noctiflora* were injected with the solutions used by Dr. MacDougal, and although the number of plants handled (about 15,000) was apparently as great or greater than was used in MacDougal's experiments, no mutations were found in the treated plants which were not also found in the untreated or check plants.

Some observations and experiments are recorded in literature which indicate that mutilations or severe injury may induce the development of mutations. Most noteworthy among such observations are those of Blaringham, who by mutilating corn plants in various ways, such as splitting or twisting the stalks, apparently produced variations which bred true without regression and which he described as mutations. My own observations on the great frequency of striking bud variations on recovering trunks of old citrus trees in Florida, following the severe freeze of 1894–5, also furnished evidence in support of this theory.

In general, it is assumed that in hybridization we are dealing merely with characters already present and that new characters which appear are due to the different reactions caused by new associations of unit characters in their mutual effect on one another. It is, however, possible that new unit characters may result from the commingling of the different hereditary units which are to be considered as mutations rather than new combinations. As is well known, Weismann long ago advanced the hypothesis that valuable variations in evolution were due to the commingling of protoplasms from different parents having different hereditary tendencies, a process which he called "amphimixis." He did not have in view, however, the formation of new unit characters as distinct from new combinations.

The most marked case known to the speaker, of the appearance of a new character which was apparently caused by the stimulation of hybridization, is the development of a marked spur or horn on the lip of a hybrid Calceolaria. This occurred among a series of hybrids between a herbaceous and a shrubby species made by Professor Atkinson and Mr. Shore, of the botanical department at Cornell University. One or two tapering horns about an inch in length and from 2 to 4 millimeters in diameter at the base, spring from the upper surface of the large corolla lip and grow erect to its surface. No such character, so far as can be learned, is known in the Calceolarias and it would seem to have been caused by the hybridization. It can not, apparently, be considered as a combination of any of the known characters of the species concerned.

Such apparently new characters appear rather commonly among large batches of hybrids, and while there is little evidence available on the subject, I am inclined to believe it will be found that hybridization may stimulate the production of new unit characters, which mendelize with the parental types.

While the evidence at our command regarding the artificial production of mutations is not yet sufficiently exact and trustworthy to enable us to draw definite conclusions and formulate recommendations for practical breeders, it may be stated that this is apparently one of the most profitable lines of experimentation for the immediate future.

Thus far I have only incidentally discussed hybridization and the advance of our knowledge in this direction. The scope of this address will not allow of an adequate treatment of this subject and it appeared wiser to discuss more in detail the problems of selection and variation. I can not, however, close this address without referring to this very important field of genetics.

No discovery in the field of breeding has had more effect or is more far reaching in its importance than the discovery of what have now come to be known as Mendel's principles of heredity. While, as stated in the beginning of this address, breeders had long before the rediscovery of Mendel's papers come to understand that there was a segregation of characters in the F_2 generation and that it was possible to recombine in certain hybrids the desired characters from different parents, there was no definite understanding of the underlying principles, and no conception of the almost infinite possibilities of improvement which the field of hybridization opened to us.

The law of dominance, while not universal, has explained many cases of prepotency in one generation and failure of certain individuals to transmit the character in the next generation. It has explained many cases of latency of characters and may account for all such cases.

The law of segregation has shown us that the splitting of characters follows a definite method and that we can in general estimate the frequency of occurrence of a certain desired combination, if we know the characters concerned to be simple unit characters.

The study of hybrids has been resolved into a study of unit characters and their relation to each other. By hybridizing related types having opposed characters and observing the segregations which occur in the later generations, we analyze the characters of each type and determine when we have a character pair. The researches on this subject by Mendel, Bateson, Davenport, Castle, Punnett, Shull, Hurst, Correns, Tschermak, East and dozens of other now well-known investigations, have developed a science of heredity of which we had no conception a few years ago.

We can now study the characters presented by the different varieties of a plant or of different species, which can be crossed with it and definitely plan the combination of characters desired in an ideal type, and can with considerable confidence estimate the number of plants it will be necessary to grow to get this combination. We now know in general how characters behave in segregation and inheritance so that we can go about the fixation of a desired type, when one is secured, in an orderly and intelligent way.

The farther the study of characters is carried the more we are coming to realize that the appearance of apparently new types following hybridization is due to recombinations of different units which in their reactions give apparently new characters. As an illustration, in a study of pepper hybrids which I have carried on during the past four years it has become evident that the form of plant and branching is due to three pairs of characters or allelomorphs; namely, first, erect or horizontal branches; second, large or small branches; and third, many or few branches. In crossing two medium-sized races, one with large, horizontal and few branches, and the other with small, erect and numerous branches, there result many new combinations of characters, among which appear some with small, horizontal and few branches, which gives a dwarf plant, and others will have a combination of large, erect and numerous branches, which gives a giant plant. These dwarfs on the one hand and giants on the other, appear as distinct, new creations, though they are very evidently merely the recombinations of already existing unit characters, and dwarfness and giantness are the results of the reaction of the different units combined.

When we remember the large number of distinct characters which are presented by the very numerous varieties of any of our cultivated plants, we arrive at an understanding of the possibilities of improvement which the field of hybridization affords, yet I doubt if many of us have even then an adequate conception of the possibilities. Possibly I may make this more clear by an illustration from my timothy breeding experiments. While the various characters presented by the different types under observation have not been carefully studied in inheritance, the following characters can be distinguished plainly, and from observations on accidental hybrids are known to segregate. The following is a list of 28 such character pairs which it is believed will prove to be allelomorphs.

TIMOTHY CHARACTER PAIRS

Heads

Long or short.
Thick or thin.
Dense or lax.
Greenish or purple when young.
Gray or tawny when ripe.
Simple or branched.
Erect or nodding.
Continuous or interrupted.
Apex blunt or pointed.
Base blunt or attenuated.
Seeds large or small.

Leaves

Long or short.
Broad or narrow.
Erect or reversed.
Rolled or flat.
Clustered at base or extending to top of culm.

Culms

Tall or short.
Thick or thin.
Straight or wavy.
Erect or bent outward.
Green or purplish.
Many or few.

Nodes

Many or few.
Green or brown.
Internodes long or short.

Habit Characters

Lodging or non-lodging.
Rusty or rust resistant.
Early or late season.

It is possible that some of these characters may be expressions of the same unit, but in a number of cases they certainly represent several different unit characters. For instance in length of head, height of culm, number of culms, and season of maturing, several different degrees are certainly present which are fully heritable. Doubtless there are many more than 28 pairs of unit characters which could be distinguished by careful study. If we have two pairs of characters, such as tall or short and early or late, we know that 4 homozygous combinations are possible. If three pairs are considered, 8 combinations are possible. Every time we add a different character pair we double the number of different combinations that are possible. Twenty-eight character pairs would thus give us as many possible combinations as 2 raised to the 28th power, or the astonishing number of 268,435,456. It would be possible then to produce this tremendous number of different varieties of timothy if there was any reason to do so, and each variety would be distinguished from any other variety by one distinct character and would reproduce true to seed.

The task of the breeder, then, is to find which among these character combinations gives the superior plant for commercial cultivation. He will soon eliminate certain characters as unimportant and concentrate his attention on those qualities that are essential.

It would be interesting to discuss the factor hypothesis, purity of germ cell, sexlimited inheritance and other important problems connected with inheritance studies, but I have already too severely tested your endurance.

As breeders and genetists we have every reason to congratulate ourselves on the rapid advance of our science and the growing recognition of the importance of the subject in practical agriculture. Colleges throughout the country are extending their courses of study to include genetics. In almost all of the experiment stations studies on genetics and practical breeding are now given fully as much attention as any other subject. With all of this advance, however, only in a few institutions have there been established special professorships or investigatorships in breeding or genetics. If the subject of genetics is to be properly taught or the investigations are to reach the highest standard, it is clear that men should have this as their special and recognized field. The subject should no longer be assigned indiscriminately to the horticulturist, agronomist, animal husbandmen or dairymen. We must establish more professorships of genetics or breeding.

Herbert J. Webber
Cornell University

GENERAL HYGIENE AS A REQUIRED COLLEGE COURSE[1]

During the last two or three decades, scientific method has been increasingly applied to the solution of problems bearing upon the health of the individual and of the community. Out of the region of controversy, in the study of problems of the maintenance and preservation of health, there has thus come to maturity during comparatively recent years a body of organized knowledge, of which the cardinal facts and broader methods may, perhaps, be grouped together under the title "general hygiene." The more technical and detailed side of the same subject is already taught as a professional course in some of our medical schools as "hygiene" or, with nominally a more specialized bearing, as "public health." On the other hand, a somewhat slight and semi-popular treatment of several hygienic topics is given in certain colleges by the instructors in physical training. Between these two types of instruction, a course in general hygiene, very substantial although non-technical, would strike a happy mean.

Before answering the question whether the teaching of general hygiene, thus defined, to every college undergraduate is necessary, it may first be enquired whether the average student is not already well-informed on this subject. On investigation, it will be found that he may have, in an informal way, attended one or two popular health lectures; that he has a hear-say, gossiping knowledge of the names of the commoner diseases, with a more personal but badly proportioned knowledge of one or two; has never seen a microbe, although he can use the word correctly; trusts implicitly to the initiative of the local civic authorities (who are less well educated than himself) for improvement in his supplies of water, milk and food; and is indebted to his newspaper or magazine for a variety of scraps of knowledge in the domain of preventive medicine, which scraps, if not partially forgotten, are admixed with much that is vague, or controversial or else fallacious. The fact is that his knowledge of general hygiene is altogether accidental and amateurish in character. Now, if the average undergraduate is in a twilight of ignorance in regard to aspects of this subject where knowledge would be vitally important to himself, he is in still greater darkness in

[1] The substance of an address given at Oberlin College, December 1, 1911.