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# INHERITANCE AND RESPONSE[1].

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I am to deal with some fundamental phases of biology which are to the front just now, and which teachers of biology should realize. They have not invaded our textbooks seriously as yet, but they are somewhat revolutionary. Such illustrations as I shall need to use are naturally taken from my own field, but they are duplicated in our experience with animals; so that although the illustrations may be botanical, the principles involved are biological.

The modern history of botany is a series of segregations of subjects. Each new segregate has attracted a certain number of recruits from the older subjects. There have always been two categories of botanists: those who move on promptly to the newer phases of their subject, and the old guard that never moves on. The latest segregate of the series is plant genetics, which is making so large an appeal to botanists that if the epidemic continues all botanists are in danger of becoming geneticists. What I wish to present has a bearing upon the work of this important modern field of botanical activity. In this presentation, however, I shall not introduce the details of material. These details are too numerous for the time at command, and too technical for any audience excepting one of professional geneticists.

Plant geneticists have begun, just as did plant morphologists, by using the most complex material. So long as plant morphologists focused their attention upon seed plants, they were accumulating data that could be interpreted only empirically. When they included a study of the lower forms, the simpler groups became keys to the more complex ones, and interpreta-

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tion became scientific. In plant genetics we are still mainly in the stage of complex material. Sexual reproduction is selected as the method of reproduction to be investigated, and the particular sexual structures selected are so peculiarly involved with other structures that it is impossible to analyze the factors involved in the results. Not only are the sexual structures beyond the reach of observation and of experimental control, but there is an alternation of two forms of reproduction, inheritance being carried through one generation to express itself in the next.

Furthermore, the origin of embryos produced in seeds is not assured. While we may assume that for the most part they are the result of fertilization, which in its gross aspects can be controlled, the increasing number of cases of parthenogenesis, vegetative apogamy, and sporophytic budding introduces a serious element of uncertainty. The program between pollination and fertilization, and between fertilization and the escape of the embryo from the seed, is a very long one, and not a single stage of it is under observation, much less under control. In other words, we are working empirically upon our problem as yet.

Everyone is interested more or less in the problem of inheritance, and a vast amount of literature is developing, ranging from the records of scientific experiments to the unscientific phases of eugenics.

When men began to think of inheritance as possibly having a scientific basis, they hit upon the obvious effects of environment upon structures. Plants and animals were then conceived of as plastic organisms molded by their environment. In other words, we are what we are because of our surroundings. This was a natural first view, based upon the observation of superficial phenomena.

Later, the internal structures of plants and animals came under observation, and a wonderful mechanism was discovered which seemed adequate to account for the facts of inheritance. We could see the actual material that guides inheritance from generation to generation. As a result, inheritance came to be looked upon as an inevitable fate, bound up with a machine that grinds out the same product, no matter what the environment may be. In other words, it was the theological doctrine of foreordination applied to inheritance.

Then experimental work in the breeding of plants began, and data began to multiply which indicated that the hereditary machine does not always turn out an identical product, but that variation is constant and in every direction. Especially was this assumed to be true in the case of sexual reproduction, in which two individuals of different ancestry combine in the product. This was purely an assumption, as it turns out. No similar experimental work had been done with spores, which produce more new individuals among plants than do eggs; but it was assumed that the product of spores must be invariable. In fact, it is a common statement that the significance of sex in the plant kingdom is to introduce variation and therefore a chance for evolution. Recent experimental work has shown that inheritance by spores is just as variable as inheritance by the sex method. However, this is just beginning to be realized and has not penetrated the camp of geneticists very far.

Then came the explanation of the variable product observed in sex inheritance. The machine had been constructed in such a rigid way that an expanation of variations presented difficulties. These difficulties were met by terminology; and if genetics had done nothing else, it would be remembered for having greatly enriched our vocabulary. All sorts of mimic combats were imagined as occurring within a fertilized egg; names were given to the victors and the defeated, but the result was never in doubt, for it could be stated with precision in a mathematical formula. If an unexpected result appeared, it was easy to explain it by reconstructing the formula.

All the time there was lurking in the background spore reproduction, with fully as variable results, but with no mimic combats or formulas to explain them.

Finally, it began to be discovered that the machine was subject to change; that it could be changed experimentally; and that it responded to varying conditions. A machine that is a variable has lost the rigidity of a machine, and cannot determine an invariable result. And so we have begun to swing back to environment as a factor in the result. It is environment, however, with a new definition. It may be the old-fashioned environment, entirely external to the plant or animal; or it may be the internal conditions in which a living cell is working. In either case, the living substance *responds*, and the result is recorded in the product. As a consequence, we have come to recognize that two factors determine the product of reproduction, namely, inheritance and response. They are easily defined.

Response includes those results whose cause has been discovered; while inheritance includes those results whose cause has not been discovered, as yet. It is needless to say that the territory covered by response is increasing as experimental work progresses; and that the territory covered by inheritance is correspondingly diminishing.

When variations occur, it has always been a question whether they are inheritable or not. This has become the fundamental distinction between what are called fluctuating variations and mutations. Recent experiments with certain lower plants, which reproduce by spores, have shown that if the conditions which induce the variation remain constant, the variation is inheritable. Any response, therefore, becomes inheritable if the conditions are static. In other words, what we call inheritance is simply a record of static conditions; and since in nature the succession of conditions is fairly uniform, it is no wonder that the results are fairly uniform, and seem to be ground out by a rigid machine.

It is generally assumed that there are certain unchangeable features in every plant and animal which may always come under the category of inheritance. This is probably true; at least we have no other way of explaining why the egg of a sunflower, for example, even with the wildest change of conditions, can produce nothing but a sunflower. It may be made to produce a new kind of sunflower, but the fundamental sunflower structure is there. So we are content at present to recognize inheritance and response as two factors in reproduction, the one dealing with fundamental structure and the other with its variations. The real question today is: What are the limits of response and at what point does it encounter the dead wall of inheritance?

Of course there is a terminology applied to inheritance as here defined. Terminology is always ready to explain what baffles knowledge. The explanation is that inheritance involves the essential organization of the germ plasm. But what is the organization of the germ plasm, essential or unessential? This definition simply introduces us to an unknown factor. We shall have to know the factor before we can discover whether it can be controlled or not.

I wish now to give a few illustrations of responses; and you may determine for yourselves whether they are superficial responses, such as all will allow, or somewhat fundamental.

In the days of rigid morphology, a plant was supposed to go through a definite routine during its life. For example, certain of the algae live vigorously for a time, then produce spores, finally produce sexual cells, and then die. It was natural to infer that the production of spores and the production of sexual cells belong to definite periods in the life of the plant, periods fixed in the definite program of the life history. Now it is known that these three stages of the plant (vegetative activity, spore production, sexual cell production) do not represent definite periods, fixed like the orbit of a planet, but are responses to three different conditions. Any one of these responses can be secured at any period in the history of the plant, and in any order. If the conditions favor maximum vegetative activity, neither spores nor sexual cells are produced; if the conditions for vegetative activity become less favorable, spores are produced; if the conditions become still less favorable, in fact quite unfavorable for vegatative activity, sexual cells are produced. In this case, also, any cell may be made to do any of these things. Here are a lot of fundamental responses that loosen up our former rigid morphology and suggest that perhaps all structures may arise as responses rather than as inevitable, foreordained results, no matter what the conditions may be.

To carry this same situation further, I wish to report a result obtained in connection with experiments upon certain algae. One of the much-stressed distinctions among certain groups of algae has to do with the behavior of the fertilized egg in germination. In some cases an egg produces a new plant directly; in other cases it produces spores, which in turn produce new plants. To the morphologist this has seemed quite a fundamental condition. The experiments referred to undertook to apply to these eggs what had been discovered in reference to vegetative activity and spore production. Eggs which were known to produce only spores were placed in conditions favorable to maximum vegetative activity, and instead of producing spores they produced new individuals directly. Also, eggs which were known to produce only new individuals directly were placed in conditions less favorable to vegetative activity, and instead of producing new individuals they produced spores. In neither case had these eggs been known to behave this way in nature; but it was needed only to change the conditions of germination to change the result. This does not suggest the work of a machine, but a response to conditions that result in different reactions.

I wish to use as my second illustration some observed conditions of cotyledon formation. You recall the two great groups of angiosperms, dicotyledons and monocotyledons, the former having two cotyledons and the latter one. This distinction is regarded as so fundamental that, when other features fail to distinguish the two groups, this cotyledon feature is appealed to as the court of last resort. In tracing the development of embryos, we found that at least two cotyledons always start, but that in monocotyledons one of them does little more than start and the other one finally appears as the only cotyledon. This naturally suggests the question: What checks one of the cotyledons in monocotyledons? The only difference in the conditions for development that we could observe in the two cases was that in monocotyledons the first leaves emerging between the two cotyledons begin a vigorous development about as soon as the cotyledons start. This suggested the possibility that one of the cotyledons might be crowded out by the cluster of precocious leaves.

This suggestion was emphasized by the fact that in dicotyledons the first leaves are relatively late in appearing, and do not grow at all until both cotyledons are fully formed.

We now find in traversing a considerable range of monocotyledons that in some of them the first leaves are not quite so precocious as usual, and in consequence both cotyledons develop. Sometimes they are unequal, but in an increasing number of cases the embryo is quite normally dicotyledonous. In other words, one can transform a monocotyledon into a dicotyledon, so far as the embryo is concerned, by checking the development of the first leaves.

There is no need to multiply illustrations. The two I have used are selected from many, all of which indicate that the field of response is widening, and that it is beginning to include some of the characters which we have regarded as fundamental and therefore inevitable.

In conclusion, I wish to indicate a field of experimental work which bids fair to uncover some of the fundamental facts in reference to inheritance and response.

If sexual reproduction must be studied, it would seem desirable to use material selected from the more primitive sexual forms, material in which the sexual structures are not so involved with other structures, in which the whole performance of fertilization and embryo development is in sight and capable of control.

The difference between a sex act and an embryo development under cover, and in the open, when experimental control is the end in view, is too obvious to need further explanation.

Furthermore, in these simpler sexual forms the origin of sex is observable, so far as it is represented by the sexual cells, and the general conditions of origin are known, conditions which are sadly in need of analysis in experimental work. It must be evident that a knowledge of the factors involved in the origin of sex may throw some light on the function of sex in general. But the origin of sex involves a still more fundamental problem.

Sexual cells are related to spores; that is, spores are historically intermediates between vegetative cells and sexual cells. This suggests that the origin of spores and inheritance through them deserve attention as a preliminary to the origin of sexual cells and inheritance through them. In other words, there are certain things that all forms of reproduction have in common, and these should be kept distinct from the things which are peculiar to sexual inheritance.

The plant geneticist may not be interested in the conditions that result in sexual cell formation, and even less interested in the conditions that result in spore formation, but these are fundamental to the problem of reproduction, and therefore fundamental to the problem of inheritance. A practical plant breeder may be interested only in the fact that he can obtain a new individual from a seed, the pedigree of whose embryo in the nature of things cannot be demonstrated, but only inferred; but a scientific plant breeder, whom we now call a geneticist, must be interested in the conditions that determine inheritance, and these include the conditions that determine reproduction in general.

No more favorable material for determining the fundamental facts of inheritance can be found among plants than spores of the simpler forms. They are accessible, and therefore capable of control; a succession of spore-produced individuals represents a line whose purity cannot be questioned; the so called "modification of the germ plasm" can be accomplished with a precision that is impossible in an ovary and ovule-enclosed egg, to say nothing of the sperm. In short, freed from all entanglements of sex, the possibilities of variation in pure lines can be determined, and the possibilities of the inheritance of such variations. Such work will establish the facts common to all inheritance, and will enable us to recognize the contribution of sex to inheritance.

This work demands not merely the technique of plant breeding, but it involves also the technique of cytology to discover the structural changes; and the technique of physics and of physiological chemistry to determine the conditions and substances that are factors in the various processes. Perhaps of largest significance is the fact that, just as the doctrine of evolution broke up a static taxonomy, so this experimental work with inheritance is breaking up a static morphology, and a static genetics, encrusted with rigid definitions, and is making these great fields dynamic.

Those who wish to project the facts of inheritance and response into the field of eugenics may find some fertile suggestions to consider. If these two factors are involved in every result of reproduction what is the contribution of each? Is the control of inheritance the only problem of eugenics? Our present picture of reproduction is something as follows. A fertilized egg includes a wide range of possibilities. Inheritance determines the number and nature of these possibilities; for our possibilities are limited by those we have received. No one of us ever develops a tithe of his possibilities; in other words, our stock in trade is always much larger than we use. The parental selection of possibilities may be no clue to our own; that is, we are not necessarily doomed by the selection our parents have made, for they pass on to us possibilities they have never called upon.

If inheritance limits us only in the number and nature of our possibilities, what determines the selection? Here is where the role of response appears and the response follows what may be called *opportunity*. The conclusion is, that while we must see to it that inheritance is as favorable as possible, it is even more important to see to it that every child shall have a *stimulating opportunity*.

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## THE JUNEAU GOLD BELT.

The large mining developments near Juneau, Alaska, have attracted attention to the northern extension of the Juneau gold belt. Though relatively little productive mining has yet been done in that area, some developments are under way. The region is heavily timbered and therefore difficult to prospect. In spite of the difficulties detailed topographic and geologic maps of this region have been made. The maps are published, together with a description of the geology and mineral resources, in a report entitled *The Eagle River Region, Southeastern Alaska,* by Adolph Knopf (*Bulletin* 502), which may be procured on application to the Director of the United States Geological Survey, Department of the Interior, Washington.