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**A GENETIC VIEW OF SEX EXPRES-
SION IN THE FLOWERING
PLANTS¹**

It seems a conservative statement to say that stud-

¹ Address of the president of the American Society of Naturalists, forty-first annual meeting, Cincinnati, December 29, 1923.

Paper No. 117, Department of Plant Breeding, Cornell University, Ithaca, New York.

ies of the past twenty years among animal forms have tended increasingly to link the phenomena of sex inheritance with the behavior of chromosomes. To this result, cytology and genetics have contributed perhaps almost equally. The number of forms in which one sex is known to have a morphologically different chromosome complex from the other sex are many. That, with respect to the chromosomes, the female of certain forms produces gametes of a single kind, whereas the male produces two kinds, and that in turn an egg fertilized by one kind of sperm gives rise to a female and with the other kind to a male, cytological studies leave no doubt. In other forms it is the female that produces two kinds of gametes and the male one kind. The fact that in some animals sex dimorphism is associated with unequal numbers of chromosomes while in others, though the numbers are the same, the sex chromosomes differ morphologically in the two sexes, makes it seem not unlikely that functional dimorphism may exist even where no morphological differences in the chromosomes are seen.

No less important than these cytological discoveries and quite in accord with them are the results of genetic studies of sex-linked characters. The exact parallelism between genetic phenomena and chromosome behavior as normally exhibited, for example, in criss-cross inheritance of sex-linked characters is no more striking than that shown in aberrant cases involving primary and secondary non-disjunction, the occurrence of gynandromorphs, and the like. In fact, the unity of the results obtained by cytological and genetic methods of attack may well be regarded as among the most brilliant achievements of recent biological research.

Letting these statements represent the present trend of research on the animal side and, for the moment, omitting any reference to results that are interpreted on quite a different basis, we may now inquire into the present status of the sex problem among the higher plants. Here, it must be confessed, there is found a very different situation. If among zoologists there are still some whose results lead them to dissent more or less mildly from the current chromosome theory of sex inheritance, among botanists there are crusaders on whose banners are inscribed a quite different device. In making this statement, I do not overlook the fact that some botanists have made bold to suggest a Mendelian interpretation of sex inheritance in dioecious plants, regarding one sex as a homozygous recessive and the other as a heterozygous dominant. But it will scarcely be denied, I think, that the present trend of botanical thought is strongly counter to any current chromosome theory of sex inheritance.

Indeed there are botanists who apparently are not convinced that there is any relation between chromo-

somes and the genetic factors concerned in the development of even such characters as color of seeds and flowers or the numerous other qualities which are the stock in trade of geneticists. In fact, there are botanists—there may be zoologists too for all I know—who, I am told, are not at all favorably disposed toward the notions of geneticists that there really exist as entities such things as genetic factors, botanists whose rallying cry, it is said, is “Down with the gene.” I have used the expressions “I am told” and “it is said” because I confess that I can not quite follow the published statements of these authors. To them I am not now addressing my remarks. Evidently, we neither read nor speak the same language.

But there are other botanists who accept in whole, or in large part, the orthodox genetic faith for ordinary Mendelian characters, even to the linear arrangement of genes on the chromosomes, and who, none the less, will have nothing to do with hypotheses that in any way connect chromosomes with sex even in dioecious plants. They seem to regard sex and sex characters as wholly different from other plant characters both in their inheritance and in their expression. To them sex development is in no way conditioned by genetic factors.

Never before have I admitted having in my own genotype much of the missionary spirit, but now I must confess to an inclination to convert the class of botanists I have just alluded to. Surely their souls are worth saving.

You doubtless will have gathered from all this that my thesis is that sex characters differ in no essential way from other organic characters, as regards either mode of inheritance or manner of development. In defending this thesis, it will be necessary to inquire why one might possibly suppose that sex characters are essentially different from other characters of plants or animals.

Perhaps a prime consideration in forcing one to question seriously whether sex in the higher plants is influenced by genetic factors in any way related to the chromosomes is the prevalence of the hermaphroditic condition among these organisms. Another difficulty, one more apparent than real, is the obvious complexity of sex differentiations in contrast to the supposedly simple conception of sex chromosomes. Again, how can one account for the environmental modification of sex characters or the outright reversal of sex? Whether or not such effects of environment have actually been proved for animals, it is waste of time even to raise the question for plants. We must begin by admitting that, in at least some plants, sex expression is reversible.

COMPLEXITY OF SEX EXPRESSION

Let us consider first the manifest complexity of sex

expression in the flowering plants.² I need give no extended account of this. The diverse forms and arrangements of stamens and pistils are familiar to all. Starting with types in which both stamens and pistils are found in the same flower, we pass, by no very abrupt stages, through monoecious types with staminate separated widely in distinct inflorescences, to dioecious forms, not overlooking along the way various combination types exhibiting andro- and gynodioecism and andro- and gynodioecism. How can such complexity be harmonized with the conception of simple unit factors as expounded by geneticists? If we grant that genetic factors do exist and that they do play their part, even though in an unknown way, in the development of ordinary characters such as form, size or color of seeds or other plant parts—and please recall that I am addressing my remarks only to those who do accept some part of all this—it may be profitable to inquire whether these ordinary characters are in reality so very simple in their manner of inheritance.

The notion that some or all of these characters are inherited in a very simple way is, I fear, largely the fault of geneticists, an error that was excusable perhaps in the early stages of our studies. When, to use an example with which I am personally familiar, it was found that a single genetic factor pair in maize differentiates normal green seedlings from ones wholly devoid of green color, it doubtless was correct to conclude that a single recessive factor is sufficient to prevent the development of chlorophyll. Even at that time, however, it was going much too far to infer as a corollary to this that the dominant allelomorph of this factor for white seedlings is alone concerned in the normal development and distribution of chlorophyll. No wonder physiologists were unable to accept so simple an explanation of the inheritance of so complex a substance as chlorophyll. We now know at least four distinct recessive factors, any one of which assures the production of white seedlings, and others which accomplish this end only when acting together. And there are other factors for virescent, pale green, yellow and striped seedlings, and still others for various kinds of abnormal development of chlorophyll in

² Although many may not sanction my use of the term sex as applicable to what we commonly regard as the plant body, the sporophyte, of flowering plants instead of limiting its application to what phylogenetically is the sexual generation, the gametophyte, they will certainly admit that there is precedent for this usage and perhaps also that there is some real justification for it both on the basis of convenience in comparing the higher plants with the higher animals and on the more fundamental ground that in the flowering plants sex differentiation of the all but vestigial gametophyte is anticipated in the sporophyte.

older plants. In all, there are known more than thirty recessive genetic factors, any one of which is able to retard or to prevent the normal development of chlorophyll. From this it must follow that all the thirty or more dominant allelomorphs of these recessive factors are essential to the normal development of chlorophyll in the maize plant. This should be complex enough even for a physiologist. And we have only begun the genetic investigation of chlorophyll inheritance in maize.

Although this may be an extreme example, it is more or less typical of other common characters. If we grant that the complexity of the situation here is no bar to a factorial interpretation, why worry about the complexity of sex characters? But, is not the chromosome theory of sex inheritance a relatively very simple thing? What is more simple, for instance, than the conception that two X chromosomes in *Drosophila* make a female and one X a male?

Let us see just how simple the sex situation in *Drosophila* is not. It was realized long ago that the case could not be explained by the assumption that there was merely a factor for femaleness in one or both of the X chromosomes of the female and a factor for maleness in the X chromosome of the male, for normally the X chromosome of every male is derived directly from its mother. Although explanations of this situation were not wanting, they were none too plausible. There might perhaps be a maleness factor in the Y chromosome, but then how account for sex dimorphism in forms lacking the Y chromosome?

It was not until individuals with triploid autosomes were found that the situation began to clear. It seems highly probable now that the X chromosomes of *Drosophila* carry female tendencies—perhaps male ones also, but with the balance on the female side—and that the autosomes, or some of them, carry a balance toward the male side. With diploid autosomes, two X chromosomes throw the balance strongly to the female side, whereas one X chromosome is insufficient to accomplish this result and the maleness of the autosomes completely overbalances it. It is easy to believe, then, that the several possible combinations of haploid, diploid and triploid chromosomes might well result in supermales, males, sex intergrades, females and superfemales, all of which have been observed in *Drosophila* and some of which have been noted in other forms. The usual sharp distinction between males and females in *Drosophila* is apparently due to the fact that normally the displacement of a single X chromosome is enough to throw the balance from one sex tendency completely to the opposite tendency.

Granting the probability of all this, is not sex inheritance still very different from the inheritance of other characters? Other characters of *Drosophila* are

referred to specific genes assigned definite *loci* on the chromosomes. This has never been done with sex genes. Must we conclude, therefore, that sex is not dependent on specific genes but that there are merely somewhat different sex tendencies among the several chromosomes, a kind of "organism-as-a-whole" conception narrowed down to the chromosomes? This conclusion does not necessarily follow, even though at present we may have no direct evidence against it. There might be a hundred distinct sex factors in *Drosophila* without the possibility of assigning a single one of them to a definite *locus* so long as they were all in the homozygous condition. The same thing was true of the allelomorphs of some hundreds of mutant genes for other characters of *Drosophila* before the mutations occurred or the mutants were discovered, and there are perhaps hundreds of other genes that remain unplaced and unknown merely because they have not mutated or the mutants have not been studied.

The genetic situation in maize, though on the whole much less well known than that in *Drosophila*, may perhaps afford some help toward a solution of sex problems. Normal maize plants are monoecious, with maleness expressed in the terminal and femaleness in the lateral inflorescences. There are, however, mutant types of maize which, under ordinary conditions, are wholly female, the terminal as well as the lateral inflorescence bearing pistillate flowers only. Four distinct recessive genes are known, the influence of any one of which results in femaleness. Moreover, two of these have been definitely placed with respect to genes for such characters as color of seeds, color and form of leaves, and the like, and their *loci* are in non-homologous chromosomes. Although no entirely male strains of maize are known, there are three types which ordinarily produce only a few pistillate flowers and some individuals of which have no such flowers. And each of these again is due to one or more recessive factors, each one being transmitted independently of the others. Moreover, there are two types in which the normal monoecious condition has been modified to an andromonoecious one; and each of these two types also is due to the influence of one or other of two recessive genes. In all, then, there are at least nine pairs of genetic factors which influence the expression of sex in maize.

It is not yet known whether all these nine pairs of genetic factors are to be assigned to nine of the ten pairs of chromosomes, but certainly several of them are inherited independently. Although no dioecious strain of maize is known to exist and the sex situation in this plant may not be closely similar in some other respects to that in *Drosophila*, it none the less adds to the plausibility of the present interpretation of sex, namely, that sex is probably an ex-

pression of the interaction of several, perhaps many, factors located in different chromosomes. In any event sex inheritance is not the simple affair that it has been supposed to be. In this respect, sex inheritance corresponds closely to the hereditary behavior of other characters.

SEX REVERSAL

We may now consider the problem of sex reversal particularly in dioecious plants. Numerous instances are known of the appearance of a few or many staminate flowers late in the life of plants that earlier had produced none but pistillate flowers, or of plants in which this behavior is reversed. Some monoecious plants usually first have staminate flowers alone, then both staminate and pistillate flowers, and finally, under certain environmental conditions, only pistillate ones. Plants of one sex, which under ordinary conditions do not usually produce flowers of the opposite sex, can often be made to do so by appropriate cultural conditions. I have referred to a wholly pistillate flowered condition of maize as being dependent on the presence of one or other of certain recessive genetic factors. Normal strains of monoecious maize can be so grown that they produce no staminate flowers and are then indistinguishable in appearance from the "genetically" pistillate flowered kinds.

Does this behavior set off sex inheritance and sex development in any way from the inheritance of other characters? The behavior of numerous vegetative characters answers this question in the negative. A single extreme example may be noted. In some strains of maize a red pigment develops in the pericarp if the ear is exposed to light at the proper time and no such color is produced if the ear is not so exposed. Long exposure to strong light results in strong color whereas shorter exposure or weaker light gives correspondingly weaker color. Is this then a matter of environmental influence alone with which genetic factors have nothing to do? Obviously not, for there are other strains of maize whose ears have never been observed to develop such color under any condition of light. Again there are strains that have red color in the pericarp whether the ears are exposed to light or kept in darkness. The genetic factors concerned in the expression of color in these several strains are well known and their *loci* in the chromosome complex of maize have been determined. In short, the development of this so-called sun-red color in the pericarp of maize is just as much a genetic phenomenon as that of any other character of this plant. Merely because its expression is influenced more by environment than is true of some other characters, it does not follow that the genetic contribution is any less real or any less important.

I should not dare affirm that there is any character

whose expression is not at all influenced by environment and I confess to an abiding faith that characters of all sorts are influenced by genetic factors. I assume—and admit that my position is an assumption—that characters in general, whether of sex or of other nature, develop through the cooperative influences of genetic factors and of factors of the environment, the internal as well as the external environment. I say cooperative influence because I see no need to assume antagonistic effects of heredity and environment. While it is conceivable that a favorable environment may force the development of a character beyond the normal expression of its inheritance and that an unfavorable one may stop its development short of its inherent possibilities, is not such a conception a bit absurd? Just what is inherited? Is not after all what is inherited merely the possibility—indeed the necessity—of reacting in a particular way to a particular internal and external environment? I never think of sun-red maize as inheriting red pericarp and of a certain environment, darkness, inhibiting the full expression of this inheritance. Nor do I think of it as inheriting a colorless pericarp which a particular environment, sunlight, changes to red. To me it inherits merely the ability to react to sunlight so as to produce red color and to darkness in such a way that the end result is colorless pericarp. And other strains of maize inherit the ability to react to these same environments in quite different ways as respects pericarp color.

You now have my creed of inheritance and development. True, we know very little of how these reactions begin or of what they are. Do we know much less about these processes when they concern sex development than when vegetative characters are in question? All I care to risk saying is that in many animals, and perhaps in some dioecious plants, the balance of genetic factors is so strongly toward maleness or toward femaleness that the reactions give a definite result in any environment as yet tried, whereas in many dioecious plants, and perhaps in some animals, the genetic balance is so delicate that the reaction may go one way in one environment and the other way under other surrounding conditions, with the occurrence of various sex intergrades when the environment is less extreme or less constant. By substituting pericarp color in maize for sex in animals and plants, the foregoing statement need not be otherwise changed to make it fit the observed results. In short, we have as yet come upon no fundamental difference between the inheritance of sex and the inheritance of other characters.

HERMAPHRODITISM³

There remains the difficulty of accounting for the

³ Following zoological precedent, I here use the term hermaphroditism with its common-language meaning to

hermaphroditic condition so prevalent among the higher plants. How can hermaphroditism be reconciled with the idea of definite genetic factors for sex? The staminate and pistillate flowers of a monoecious plant differ from each other as sharply in form and function as do these two kinds of flowers on related dioecious plants, and there is the same sharp difference between stamens and pistils when they occur together in the same flower as when separated in different flowers or on different plants. Is there the slightest cytological evidence of the existence of any chromosome mechanism which could conceivably distribute allelomorphous sex factors to the different parts of a single plant in somewhat the same way that the reduction division may do in case of dioecious plants?

If you have followed me thus far, you doubtless have anticipated my treatment of this problem. It is idle in the face of the negative evidence of cytological studies to postulate any chromosome behavior, analogous to the reduction division, for the distribution of sex difference to different parts of the same plant. Moreover, I am aware of no critical genetic evidence in support of the idea that unit factors are ever, or at all commonly, separated in the sporophyte body in any way analogous to Mendelian segregation. On the contrary, there is strong genetic evidence that bud sports and related phenomena, often ascribed to segregation of factors, are due at least in some instances to chromosome elimination or non-disjunction or to somatic gene mutations.

If then there is neither cytological nor genetic evidence of the segregation of unit factors within the plant body, how are we to account for sex differentiation in hermaphroditic plants? Again I answer that the explanation is to be sought in the same way that an understanding of the differentiation of other characters will, let us hope, some day be gained. I grant that it is not an explanation of sex differences to say that the fundamental processes concerned in the differentiation of other characters are little known. But I do believe that it will clarify our ideas of sex differentiation to get away from the notion that it is necessarily different in any essential way from the differentiation of other characters.

It seems unreasonable to suppose that sex in hermaphroditic plants can in no way be related to sex genes merely because there presumably is the same gene complex in the cells of a stamen that there is in the cells of a pistil of the same plant, the same gene complex in a microsporocyte as in a megasporocyte

denote the expression of both maleness and femaleness in the same individual, rather than with the restricted significance given it by botanists to designate individuals or species in which each flower is bisexual. Botanists may, if they choose, with little or no violence to my meaning, substitute for it here the term bisporangeateness.

of the same individual. This is also true doubtless of other plant parts. Aleurone color of maize is seen in only one or two layers of cells, the outer layers of the endosperm. Just what there is in the internal or external environment of these cell layers that induces the color to develop in them, while no such color is ever seen in the underlying cells of the endosperm, is not known. It does not follow from this, however, that genetic factors are not concerned in aleurone-color development. Indeed, the genetic complex concerned with aleurone color is as well understood as any in maize. Several distinct aleurone-color genes have long been recognized and the relative positions of their *loci* in the chromosomes are in large part known. I see no reason to doubt that the same complex, the same relative position of genes, holds for all cells of the endosperm, but the deeper lying cells do not exhibit the colors seen in the aleurone layer. Is the association of pistils and stamens in a single flower either more or less mysterious than the differentiation of the aleurone layer from the rest of the endosperm?

The aleurone-color comparison can be carried still further. Certain genes are known to influence aleurone-color patterns. In the speckled and in the blotched patterns, smaller or larger groups of aleurone cells develop color while neighboring groups do not. In the Navajo pattern the distal end of the seed is solidly colored and the remainder colorless. No one, I presume, would suggest that in these cases certain aleurone cells have a different complex of aleurone-color genes from other nearby aleurone cells.

If the aleurone-color situation is open thus to factorial analysis, need we despair of accomplishing as much for sex differences even in hermaphroditic plants? True, little along this line has been accomplished as yet, but it is worth recalling that a beginning has been made with maize. It was noted earlier that any one of nine recessive factors is sufficient even under ordinary conditions of growth to upset the typical monoecious habit. It follows from this that the presence of all nine of the dominant allelomorphs of these factors is necessary for the expression of the typical monoecious condition. True, it is not known how this complex of nine dominant genes, with perhaps many others not as yet recognized, results in the production of male flowers in the terminal inflorescences and female flowers in the lateral ones; but do we know less about this than about how a particular complex of endosperm and aleurone genes results in definite color patterns?

SUMMARY AND CONCLUSIONS

In concluding this discussion let us recall that, according to the view here presented, sex characters of

the flowering plants are to be interpreted on the basis of genetic factors associated with chromosomes just as vegetative characters are interpreted. In typically hermaphroditic forms where both male and female tendencies are exhibited in the same individual, factors for maleness and for femaleness are thought of as being in so delicate a balance that influences analogous to those responsible for the differentiation of vegetative characters effect a more or less regular differentiation of sex organs. The question of heterozygosity of factors for one sex or the other does not enter here any more than it does in cases of inherited color patterns where pigmented and unpigmented parts may appear in some forms as irregular mosaics and in others as regular patterns. Genetic factors influencing the development of male and female organs in the monoecious species, *Zea mays*, have been shown to behave quite as do other genes.

In prevaillingly dioecious forms of the flowering plants also, factors for maleness and for femaleness presumably are present both in male and in female individuals, but here the balance is more strongly to the one or to the other condition. The approximate numerical equality of individuals of the two sexes in these forms at once suggests a chromosome mechanism similar to that known to exist in numerous animal groups. The occurrence of sex linkage in a dioecious species of *Lychnis* favors this assumption, although certain irregularities of behavior in this instance are still to be explained. There has appeared recently a preliminary cytological account of chromosome dimorphism of the X-Y type in another species of *Lychnis*. That morphologically unlike sex chromosomes have not been found, and may not exist, in many plants need not disturb us greatly, for why should sex factors be presumed necessarily to influence the size or form of chromosomes more than do other genes? The suggestion that the difference frequently observed between the X and the Y chromosomes of many dioecious animals may be due to the opportunity for the indefinite accumulation of recessive zygotic lethals, which is afforded by the enforced heterozygosity of one sex, appeals to me strongly. If these lethals were at all frequently of the nature of chromosome deficiencies, it is conceivable that they might modify profoundly the form and size of the Y chromosome. I see no reason, however, to assume that lethals of this kind occur in all dioecious organisms. Moreover, it seems likely that the occasional self-fertilization of prevaillingly dioecious individuals among flowering plants may tend to prevent the accumulation of recessive lethals in the heterozygous sex. But there is little use in discussing such possibilities until we have much more information about the genetic behavior of dioecious plants than is now available.

The existence of sex intergrades is no bar to the conception of sex relations in dioecious plants here outlined. The distinctness of predominantly male and predominantly female individuals ordinarily is marked and may well be ascribed to a pair of differential genes distributed with homologous chromosomes at the reduction division. The difference between this and instances of absolute dioecism, if such exist, is to be sought in the nature of the respective genes rather than in chromosome behavior. Even the occasional appearance of sex intergrades approaching the condition of typical hermaphrodites may well be due to the influence of several heterozygous sex factors of relatively minor influence—the geneticist's old friends, modifying factors, in a somewhat unfamiliar rôle.

I have reserved for this, the position of emphasis at the close of my discussion, the strongest evidence against my view of sex relations in dioecious plants. When, as not uncommonly happens, an otherwise female plant produces a few male flowers or a male plant a few female flowers, it is possible to obtain self-fertilized seeds. If, then, one sex is heterozygous for a strongly differential pair of sex factors and the other sex is homozygous for the recessive allelomorph, the latter should, of course, breed true and the former presumably throw the two types in the numerical relation typical of a Mendelian monohybrid. Results reported for at least one form, *Mercurialis*, indicate that individuals exhibiting a predominantly female condition breed true when self-fertilized. But there is no evidence, so far as I am aware, that predominantly male plants of this form throw the two types. Indeed, the available evidence is quite the opposite of this.

Unfortunately, *Mercurialis* is not well adapted to an investigation of this kind. When relatively few female flowers are produced by a male plant and such flowers produce only a few seeds, the number of plants resulting is correspondingly small. Perhaps, however, the numbers actually reported for *Mercurialis* are sufficient to carry conviction to one who does not have preconceived notions contrary to the observed results. The results with *Mercurialis*, as well as the striking departure from normal sex ratios in the progenies of certain individuals of *Lychnis*, emphasize the importance of thoroughgoing analyses of similar material to the end that such possibilities as the presence of differential gametic lethals, and the like, may be checked.

It is just here that one finds *Mercurialis*, and in fact most dioecious plants, unsatisfactory material at the present time. The genetic complex of none of these forms is at all well known. If for some dioecious species of plant we could know the chromosome *loci* of numerous genes, we should hold a much more favorable position than at present from which

to attempt an analysis of its sex behavior. I am not suggesting that we wait until such material is available, but I am not optimistic about the possibility of obtaining crucial evidence from any species until its genetic analysis has proceeded to a point that makes available the tools essential to any critical genetic investigation of its sex expression.

Finally, let me observe that, even though this missionary epistle to the brethren who dwell in darkness fail to convert them, it should at least afford them a somewhat unfamiliar point of attack. And, if their subsequent efforts result in my own conversion, I, at least, shall feel that I have not labored in vain.

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