is not more theory or discussion, but more observation and experiment. I believe that the chromosome theory as applied to the sex problem presents a sufficiently plausible face to be taken for a time as a guide to further examination of the facts. Perchance the true explanation may be found on the way, even should our working hypothesis prove a false leader.

EDMUND B. WILSON
COLUMBIA UNIVERSITY

## SEX-DETERMINING FACTORS IN PLANTS

IT is generally agreed that no true sex-determining factors for plants have as yet been recognized, and naturally a botanist would hardly choose the topic which has been assigned to me in this discussion. Claims are, however, constantly made that this or that environmental influence has been observed to modify slightly at least the percentage of the sexes in dicœcious plants. The extensive literature of such experiments and observations was summarized very fully and critically by Strasburger in 1900, and I need only allude to it here.

A great variety of factors have been tested both singly and in combination, but without positive results. Conditions of nutrition, as to both kind and amount, have been exhaustively studied and reports of success in influencing the sex ratio by this or that fertilizer are constantly made, and quite as constantly fail of confirmation. Laurent has recently (1903) claimed that an excess of nitrogen or lime favors the development of males in spinach, hemp, etc., while potash and phosphoric acid favor the development of females, but his results are not convincing.

Temperature, light and moisture conditions, relative age of parents, relative maturity of pollen, early and late planting, pruning, etc., have all been more or less elaborately tested without achieving results.

Gallardo (1901) reported that wild female plants of *Dioscorea* and *Clematis,* when transplanted into the botanic garden at La Plata, became hermaphrodite the next year, and the year following returned again to the female condition. The experiment was repeated the following year, with the same results, but it is hardly clear just what factor or factors were here concerned, and it is certain that transplanting generally has no such effects.

That the sex of seed plants can be changed by environmental conditions is, however, further shown beyond the possibility of question by the case of the anther smut (*Ustilago violacea*) which infects the campion (*Lychnis dioica* L.). Here the fungus, when present in the female plants, regularly leads to the development of stamens and the suppression of the pistil. The capacity to develop stamens must, in this case, be assumed to be present in the female plant, and the fungus is able to induce the conditions necessary to their formation and the suppression of the pistils, and thus provide for the development of its own spores. Elaborate experimental attempts by Strasburger to duplicate on uninfected plants the effects produced by the parasite led, however, to no results.

In the absence of positive data as to sex-determining factors in plants it may be well to note briefly some of the more conspicuous facts as to sex differentiation with which the student of reproduction and heredity in plants is confronted.

In plants at least sex-determining factors are to be sharply distinguished from factors which lead to sexual as contrasted with asexual reproduction. We must be careful, in discussing the factors which may determine sex, to distinguish two questions: first, as to the causes which lead to the occurrence of sexual cell fusion as con-

trasted with asexual spore formation, and second, as to the cause or causes of the differences which exist between the egg and antherozoid cells which fuse and of the secondary sexual characters of the individuals which produce these cells. This distinction has not always been clear in the work of those who have studied the so-called cyclic alternation of parthenogenesis and sexual reproduction in animals.

The interesting results obtained by Klebs and others on a wide variety of fungi and algæ show conclusively that a very high degree of plasticity characterizes these plants as to the time of occurrence and relative predominance of asexual spore formation and sexual reproduction by cell copulations. Environmental stimuli and conditions of all sorts may determine whether the plant reproduces itself sexually or asexually or merely continues vegetative growth. We have in these simpler plants numerous cases like Penicillium in which sexual reproduction occurs only at very long intervals or not at all, while in many of the mildews, for example, a period of asexual spore formation is quite regularly followed by sexual reproduction. The same differences are abundantly illustrated in the algæ. It is quite possible, however, as I have elsewhere pointed out, that the very apparent influence of environmental conditions in determining whether sexual or asexual reproduction shall occur is, after all, only an accessory manifestation and that there is really a more fundamental series of cyclic changes in the organism which are primarily responsible for the result.

Functionally there can be little question that this cyclic succession of asexual spore formation followed later and under special conditions by sexual reproduction is equivalent to the alternation of parthenogenetic and sexual stages in the Aphides, etc. Asexual spores have the same advantages for the rapid spread and multiplication of the plant as parthenogenetic eggs have for the animal. In both cases environmental conditions seem to play a large part in determining which stage shall occur at all or predominate, and in these environmental conditions there are probably two sets of factors to be distinguished. First, the factors which lead to sexual as contrasted with asexual reproduction, and second, the factors which lead to the differentiation of the male and female organisms and sex cells.

It is quite clear in the case of the plants that reproduction by conjugation is by no means necessarily the fusion of visibly differentiated cells. It consists in its essential nature and in its most primitive occurrence merely in the union of two cells, whether like or unlike, in size, etc. The facts of heredity give, in general, no evidence that the gametes differ in any respect in their capacity to influence the offspring, and cytological data are in harmony with the assumption of the essential equivalence of the gametes even when their visible differentiation is most conspicuous.

In the simpler plants this functional equivalence is paralleled by an entire resemblance between the gametes in size, form, relative activity, etc. We may assume that there are inner and sexual differences between the gametes of *Sporodinia, Mesocarpus,* etc., but the assumption is based on no observable facts of structure and behavior and tends rather to mysticism than to an explanation of the phenomena of cell fusion. The changed relations of surface area and volume, and the known effects of an increase of the chromosome number on cells and nuclei may just as well be regarded as the first direct effects of conjugation, as the satisfaction of any mysterious sexual affinity due to some invisible sexual differentiation in the gametes.

The phenomenon of prepotency is also to be sharply distinguished from sexual

differentiation. I do not refer to such prepotency as is characterized by plant and animal breeders as the power of certain individuals in a given cross to transmit their qualities to the offspring with the suppression of those of the other parent, but to the prepotency established by Darwin's classic experiments in cross pollination and whose correlative is the partial or complete self sterility observed in so many hermaphroditic flowers. This prepotency is a very widely spread phenomenon among plants and appears almost with the first development of gametic fusions. It is a common fact among algæ that even before there is any sexual differentiation between the gametes, the tendency to conjugation is very much stronger between swarm spores from mother cells of separated origin.

Sex differentiation itself seems to arise in entire independence of this prepotency as an expression of the universal tendency to specialization of function with differentiation of structure, on the one hand, toward increased motility with relatively reduced size, on the other, toward increased size and storage of metaplasmic materials as is so perfectly shown in the *Volvox* series and many other groups of algæ.

As to the stage in the life cycle at which sex differentiation occurs, plants show the widest possible variety. Marchal has recently shown that the spores from a single capsule in some of the dicœcious mosses are of both sexes, but that the sex of each spore and of the protonema and moss plants which come from it is fixed. It is quite possible that here sex differentiation is accomplished in connection with the reduction divisions and spore formation—the same stage as that at which the differential distribution of chromosomes is described for certain insects, but far removed from egg formation and fertilization. The stage of sex differentiation in Equisetum may be the same as that in these mosses with dicœcious gametophytes.

In the ferns and lycopods, however, sex differentiation is accomplished in the gametophyte. In the ferns the older and first formed regions of the prothallus produce antheridia and later on the newer growth produces archegonia. In the heterosporous fern allies Marsilia, Isoetes, etc., and in hermaphroditic seed plants, sex differentiation appears in the spore sacs and the asexual spores themselves. The gametophytes are thus unisexual and their sex is determined by the sex of the spores from which they come.

In dicœcious seed plants sex differentiation apparently may occur in the egg so that the entire sporophyte is male or female for its lifetime, but the determination here is of a rather indefinite sort, since a large proportion of such dicœcious plants have been reported as occasionally producing a few hermaphroditic flowers. The gametophytes in all seed plants are strictly and unchangeably unisexual.

The flowers of hermaphrodite or perfect shrubs and trees offer a most interesting case of successively repeated sex determinations in the life of the same individual. With each succeeding blooming period the stamens and pistils are differentiated anew in the flower buds out of what must be regarded as the strictly non-sexual new cell growth of the year. Such hermaphroditism, requiring the operation of sex-determining factors with each successive season, is sharply in contrast with that in animals in which the sex glands are fixed for life.

Polygamous and polygamodicœcious seed plants complicate the conditions still further, but it is sufficiently plain that no simple differential distribution of chromosomes on Mendelian principles at the period of chromosome reduction could in any

way account for the conditions presented by the higher plants.

The existence of dicœcious races with a widely varying percentage of the sexes is also against the assumption that sex is transmitted as a Mendelian character. Heyer found the hemp plants about Halle showed a ratio of 100 males to 114 females. Fisch at Erlangen found the ratio was 100 males to 154 females.

The conditions noted as to the stage at which sex differentiation occurs, etc., suggest at least the universal presence in plant cells of the potentiality for development in the direction of either sex when the necessary environmental conditions are given.

Robert A. Harper
University of Wisconsin

## Sex-determining factors in animals

There are few biological questions that appeal more directly to the human race than whether the sex of the child can be determined by the external conditions under which the parents live, or whether the conditions are internal and, therefore, beyond the power of control. This problem has been examined by the statistician, argued by philosophers, discussed by the naturalists and exploited by the quack. Theories of sex determination have flourished like weeds, and, while perennial, are apt to be like their prototypes, short lived. The history of these theories is, nevertheless, full of interest and not without significance. Even a brief survey will bring out the salient points.

Aristotle refuted the opinion of Anaxagoras that the male comes from the right side and the female from the left side of the father; that of Empedocles, who held that the temperature of the uterus influences the sex of the offspring; and that of Democritus, who suggested that the excess of the male or of the female element is the essential factor. Aristotle, in turn, held that the temperature of the germ-material determines the sex, for, he said, more males are born to young and to old parents than to those of middle life, because in youth the temperature of the body has not reached its maximum and in old age it has begun to abate. In recent years we find that one external factor above all others has been supposed to have an intimate relation to sex determination, namely, nutrition. An experiment of Landois in 1867 furnished the first erroneous evidence in favor of this view. He claimed that he could produce at will males or females of the butterfly *Vanessa* by regulating the amount of food. A similar conclusion was reached by Mrs. Treat and by Gentry in 1873. Riley, Bessels, Briggs, Andrews, Fletcher, and Kellogg and Bell have shown that no effects of this kind are produced by starving or by feeding. At most there occurs a greater mortality of the female caterpillars through starvation, leaving more males alive. The futility of the experiment is now manifest, since it has been shown that the reproductive organs of the male and female are already laid down when the caterpillar leaves the egg.

Equally inconclusive have been the experiments with the tadpole of the frog. The work of Born and of Yung has been upset by the experiments of Pflüger, Cuénot and of Richard Hertwig. The earlier observers failed to take into account the great mortality of the tadpoles kept under artificial conditions, hence a possible source of error is present in their results, and the conclusions are unsatisfactory so long as we do not know whether in the frog one sex is more susceptible than the other to unfavorable conditions. Aside from this possibility there seems to be something very peculiar about the proportions of the sexes in these amphibians.

Düsing has applied the statistical method of study to the proportion of males and