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THE INFLUENCE OF RELATIVE LENGTH OF DAYLIGHT ON THE REVERSAL OF SEX IN HEMP[1]

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Since investigating, by observation and experiment, the fundamental nature of sex in organisms, especially plants, the writer has been impressed by the great influence of the environment in determining the characteristics of the individual. The inevitable conclusion has been reached that ecological factors are of prime importance, in many species, in determining directly the actual sexual nature of the individual or in inducing actual reversals of the sexual state in case the sex had already been determined. The results on which these conclusions have hitherto rested have been published in various papers, the most important of which from the ecological point of view are those on *Arisaema triphyllum* (L.) Torr. (Schaffner, '22), where it was shown that the sexual expression of the perennial individual could be changed absolutely from year to year through control of the nutrition and water supply, and on *Cannabis sativa* L. ('21), in which it was shown that ordinary hemp produces pure diecious (two sexes separate) individuals when planted in the field in spring, but that about 90 per cent of both male and female plants reversed their sexual expression, the carpellate individual giving rise to male structures and the staminate to female, when planted in the greenhouse during the winter period.

Davey and Gibson ('17) have presented evidence that changes in the sexual state of sweet gale, *Myrica gale,* are in some way associated with the environment. In wet areas they found the relative proportion of carpellate plants to be greater than in dry areas. They found variations of the sexual state of individuals from year to year. Plants entirely carpellate one year would produce some staminate catkins the following year. They also observed several cases of the reverse change.

It will thus be seen that the problems of sex, sexual expression, and sex reversal apparently continue to be ecological in spite of the more recent trend

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of genetic hypotheses which would remove them entirely to the domain of cytology and Mendelian heredity, so far at least as the individual is concerned.

In reporting on the abnormal sexual expression in plants of the common hemp in 1918, the writer ('18) made the statement that: "The great abundance of intermediates in the winter, greenhouse plants was probably due to the abnormal environment, mainly a lack of light." In the meantime, ever since 1917, a large number of experiments have been carried on to determine to what extent the intensity of light, and more especially the relative length of the daylight period, were the cause of sex reversal.

It was not evident from the first experiments what was the efficient agent in the light factor. The reversal might be due to the intensity of illumination, the comparative length of the illumination period or daylight, or it might to some extent be due to the quality of the light at the time of the year, together with its possible modification as it filtered through the glass of the greenhouse.

In 1920, Garner and Allard ('20) published the results of extensive experiments on the influence of length of daylight on the growth, period of maturity, and the reproduction of various plants. This paper influenced the writer to carry on similar experiments in his studies of sex reversal and sex determination. From previous experience it was decided that the common hemp would be the most suitable plant for experimentation on the possible influence of relative length of day on reversal of the sexual state in individuals where the male or female state is already established at the time of the sprouting of the seed.

Plantings have been made in the spring and summer out of doors since 1918, and the seed obtained from the summer garden plants has been used each year for the following winter experiments in the greenhouse and for the next year's plantings out of doors. In the variety used there was no moneciousness (both sexes on one plant) or sex reversal in any of the out-of-doors, summer plants, either carpellate or staminate. The individuals were either pure carpellate or pure staminate. A record of the field plantings is given in the table below.

TABLE I. *Record of field plantings, showing all plants pure female and pure male during the period of long daylight*

Date of planting	Carpellate		Staminate	
	Pure	Intermediates	Pure	Intermediates
Early May, 1918	all	0	all	0
Early May, 1919	124	0	122	0
June 24, 1919	86	0	83	0
May 18, 1920	134	0	121	0
May 18, 1921	all	0	all	0
Aug. 1, 1922	*	*	75	0
Aug. 15, 1922	98	0	94	0

* Carpellate plants not studied.

It will be seen that the carpellate and staminate plants were approximately equal in number for each planting where counts were made, and that among the hundreds of plants grown in the five years not a single individual with intermediate sexual expression was discovered. Sex reversal is evidently very rare in summer in the region of Columbus, Ohio, in the variety of hemp used for the experiments.

The hemp planted out of doors in the spring began to bloom in eight to nine weeks after the date of planting. A patch planted on May 18, 1920, began to expand flowers on July 18, or in 61 days. Another patch planted on June 24, 1919, began to bloom on August 18, or in 55 days.

To test the influence of relative intensity of illumination on sex reversal, three plots were planted side by side on May 18, 1920. One patch was fully exposed to sunlight, the second was covered with a single layer of thin gunny sack cloth, and the third was covered with a double layer of the same cloth. The plants under the single layer of cloth obtained enough light to continue growth, but those under the double layer of cloth were so densely shaded that one layer was occasionally removed to allow more light to penetrate in order to keep the plants alive. Finally the second layer was permanently removed, since it became evident that otherwise the plants would all die before the blooming period. On July 7 the fully exposed plants averaged 32 inches in height, the tallest being 7 feet; those under the single layer of cloth averaged 16 inches, the tallest being 2 feet; and those which were part of the time under the double layer of cloth averaged 8 inches, the tallest being 15 inches. At maturity the tallest plant in the fully exposed patch measured 8¾ feet, the tallest under the single layer of cloth measured 5½ feet, and the tallest under the double layer measured 3½ feet.

The exposed plants began to bloom on July 6, those under the single layer of cloth on July 18, and those under the double layer on July 26; thus the exposed plants began blooming 20 days before those under the double cloth. It is possible that some of the individuals which perished under the double cloth might have been in bloom somewhat earlier than the earliest that survived, since there seems to be some individual difference in the vegetative period of growth; nevertheless, the greater part of the difference of 20 days in the blooming period must have been due to the relative intensity of the light.

In the patch fully exposed to daylight there were 134 carpellate plants and 121 staminate. In that covered with a single layer of cloth there were 50 carpellate plants and 38 staminate. In the patch with double shading only 21 plants survived to the blooming period, 14 carpellate and 7 staminate. The plants of all three plots were carefully studied for sex reversal, but all, both staminate and carpellate, were apparently pure in sexual expression except one carpellate plant which grew beside one of the corner posts in the plot with the single cloth screen. This plant, besides hundreds of carpellate flowers, developed 23 staminate flowers, all at or near the ends of branches of the inflorescence. Seed from this individual planted out of doors the following season gave nothing but pure staminate and pure carpellate plants.

It is evident, therefore, that a long daylight period of low illumination decreases the size of the hemp plants decidedly and increases the period of vegetative growth before anthesis. But a long daylight period of low illumination has apparently no effect on the sexual state.

Plantings were also made in a shallow box out of doors on May 4, 1921, and covered during the entire 24 hours except from 9 A.M. to 2 P.M., when they were exposed each day to direct daylight. The number of plants was small and most of them died before blooming, but of the five staminate plants which developed to maturity three were pure in sexual expression and two were intermediate. The carpellate plants were not yet in bloom when the experiment had to be abandoned because of the writer's leaving for a distant state. But in the light of the results obtained from the winter plants as presented below, even the small number obtained shows that with a series of properly controlled plants it is probable that the percentage of reversal would correspond very closely to the length of the daily period of exposure. A series of plots with exposures varying by hour or half-hour differences, from 2 to 14 hours should give a curve of reversal approximating those obtained by successive plantings during the shorter daylight seasons. Such experiments should be made by some one with suitable time and equipment for the work.

The writer thus came to the conclusion that one of the main factors, if not the only one, responsible for the confusion of the sexual state in his winter plants must be the relative length of the daylight period rather than the intensity of illumination. Consequently a series of plantings at more or less regular intervals was begun in the greenhouse and has been continued, as time permitted, for the past two years. The temperature was not especially under control, but was such as is ordinarily maintained in a greenhouse. The soil was a rich sandy loam well supplied with manure and has not been changed since the experiments began. The conditions of environment for the winter plants were, therefore, such as obtain in shallow soil benches in ordinary greenhouse practice.

The results of the two years' plantings are given in the tables following. Since it was found that there is no essential difference in the mode or rate of sex reversal of the staminate and carpellate individuals, only the staminate plants were studied during most of the second year. This permitted the same space to be planted more frequently than would have been possible had the carpellate plants also been studied, since these develop much more slowly.

The difference in length of day between the winter and summer solstices differs slightly from year to year. An approximate daylight and darkness chart for Columbus, Ohio, is given in figure 1. The difference from sunrise to sunset is about 15:01 hours at the summer solstice, and about 9:19 at the winter solstice, or a difference of about 6:20 hours in the length of day between the winter and summer solstices.

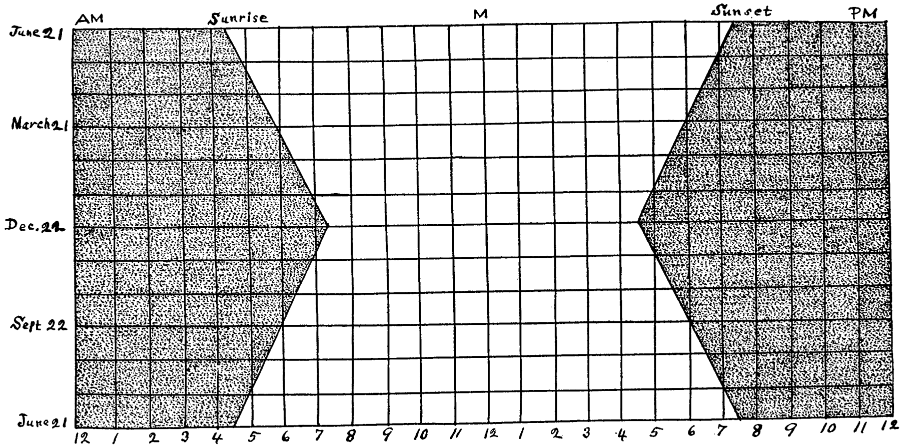

FIG. 1. Chart showing approximate length of daylight and night at Columbus, Ohio.

In depending on difference in length of day for the illumination period there is some fluctuation inevitable, since on a cloudy day the effective light is cut short both in the morning and in the evening. Nevertheless, the progression of the reversal ratio is quite remarkable for its uniformity and its conformity to the decreasing and increasing daylight periods.

TABLE II. *Record of plantings in the greenhouse, showing the relative percentages of sex reversal in relation to length of daylight*

	Carpellate				Staminate			
	Number pure	%	Number intermediate	%	Number pure	%	Number intermediate	%
1920–21								
Nov. 1	28	23+	92	76+	12	10	104	90
Dec. 1	13	20	53	80	4	6+	62	93+
Dec. 15	4	13+	25	86+	3	7	39	93
Feb. 1	24	34+	46	65+	25	34+	47	65+
Mar. 15	39	66	20	34	20	40	30	60
May 2	30	100	0	0	17	94+	1	5+
1921–22								
Sept. 20	11	61+	7	38+	9	42+	12	57+
Oct. 19	15	46+	17	53+	13	32+	27	67+
Nov. 21	—*	—	—	—	19	26+	54	73+
Dec. 20	—	—	—	—	3	10	27	90
Jan. 20	—	—	—	—	8	32	17	68
Feb. 20	—	—	—	—	16	43+	21	56+
Mar. 20	—	—	—	—	20	66+	10	33+
Apr. 20	—	—	—	—	28	100	0	0
May 1	—	—	—	—	91	97+	2	2+
May 20	24	100	0	0	32	100	0	0
Aug. 19	—	—	—	—	102	85	18	15
Sept. 1	—	—	—	—	13	65	7	35

* Carpellate plants not studied.

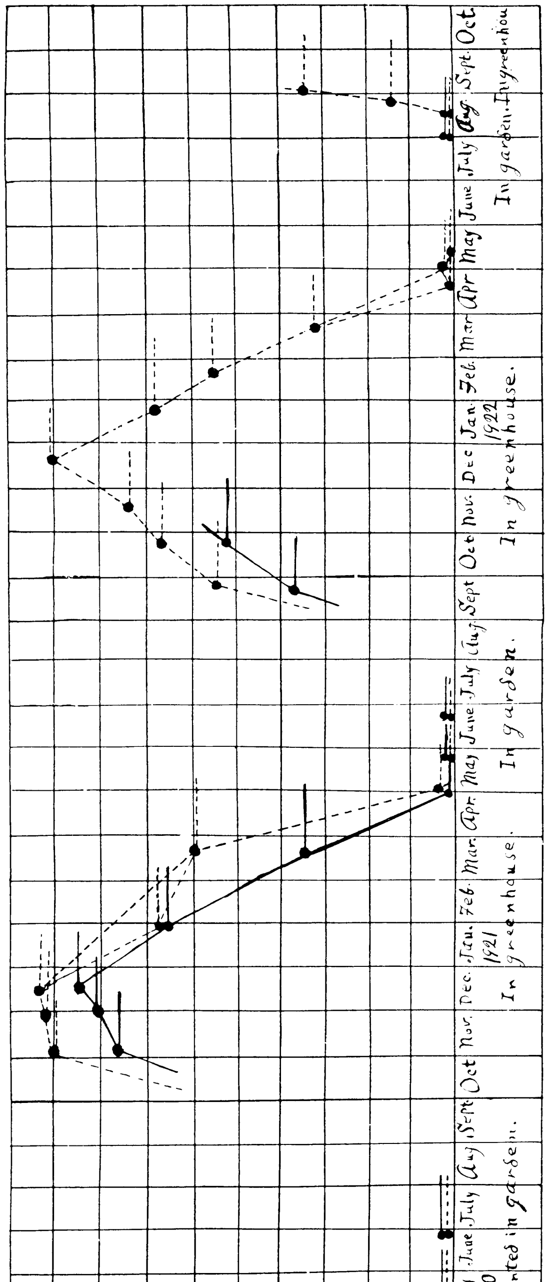

FIG. 2. Graph showing the relative percentages of sex reversal in relation to length of daylight. Continuous lines, female plants; broken lines, male plants.

The percentages of sex reversals of all the plantings, both in the garden and in the greenhouse, are shown graphically in figure 2, which may be compared with the daylight graph, figure 1.

Combining the data obtained for the staminate plants for two years gives a rather close progression of sex reversal from 0 to 93 per cent and then a regression to 0 again. Comparatively few records are greater or less than the expectation from the time of planting.

TABLE III. *Combined percentages of pure and intermediate sexes for staminate plants, showing the progression of sex reversal with relative length of daylight*

	Percent Pure	Percent Intermediate
Aug. 15 *	100	0
Aug. 19	85	15
Sept. 1	65	35
Sept. 20	42	57
Oct. 19	32	67
Nov. 1	10	90
Nov. 21	26	73
Dec. 1	6	93
Dec. 15	7	93
Dec. 20	10	90
Jan. 20	32	68
Feb. 1	34	65
Feb. 20	43	56
Mar. 15	40	60
Mar. 20	66	33
Apr. 20	100	0
May 1	97	2
May 2	94	5
May 20	100	0

The combined records of the percentages of reversal of the carpellate plants, although less complete, are equally significant.

TABLE IV. *Same as Table III, only for carpellate plants, and with less data.*

	Percent Pure	Percent Intermediate
Aug. 15 *	100	0
Sept. 20	61	38
Oct. 19	46	53
Nov. 1	23	76
Dec. 1	20	80
Dec. 15	13	86
Feb. 1	34	65
March 15	66	34
May 2	100	0
May 20	100	0

* These planted in the garden.

That there is a direct relation between length of day and percentage of sex reversal in the hemp is beyond question; however, a few experiments so far conducted seem to indicate that the percentage of reversal for any given length of daylight will be greater in a rich soil with abundant nitrogen than in a poor substratum low in nitrogen. Because of the fragmentary nature of the experiments hitherto carried on, this aspect of the problem will not be considered further at present.

The general results obtained may be stated as follows: In the latitude of Columbus, Ohio, with proper illumination in the greenhouse or in the field or garden, the ordinary varieties of hemp are pure in sexual expression, developing the typical diecious state when planted at any time between the 10th of May and the 10th of August, and usually also for a week or two outside of these dates. But if the planting is done in the greenhouse between the 20th of August and the 1st of May, sex reversal is almost certain to take place in inverse proportion to the length of daylight at the time of planting and the subsequent period of growth. At the beginning or near the end of this nine months' period only a small percentage of individuals, either carpellate or staminate, reverse some of their tissues to the opposite sexual condition, while during December about 90 per cent or more of both the carpellate and staminate individuals will show sex reversal. The percentage of reversal on either side of the maximum period decreases quite regularly in harmony with the increasing daylight period until zero is reached at the time of the suitable light period for pure sexual expression.

The plants in the greenhouse usually come up out of the ground on the fifth or sixth day, and between October 1 and April 1 are usually in bloom in 30 days or less from the date of planting. The shortest period obtained in any of the experiments was just 20 days from the day of planting to the extrusion of stigmas from reversed staminate plants. Seeds planted May 1, 1922, in the greenhouse did not come into bloom until June 18, or in 49 days.

The winter staminate plants, whether pure or with sex reversal, commonly have but two nodes of leaves besides the cotyledons, with a small inflorescence which may or may not have rudimentary leaves. The carpellate winter plants usually develop more leaves, although they may also be blooming when the second pair of leaves is expanded. The December plants are usually but 4–6 inches high. The vigorous summer plants usually develop twenty or more leaf nodes before growth ceases. An interesting phenomenon in relation to the December plants is the rapid elongation of the slender staminate plants at the beginning of anthesis, by which they are rapidly lifted above the general level of the carpellate plants. In a few days the staminate plants become on the average about twice as tall as the carpellate plants, making the sexual dimorphism of the vegetative shoot very pronounced. The elongation of the second internode above the cotyledons is especially prominent, being commonly more than twice as long as the corresponding carpellate internode.

Another remarkable phenomenon of the short-lived winter plants is the frequent rejuvenescence which takes place in plants that are becoming senile just about the time that the lengthening daylight period is beginning to have a decided effect on the functional activity. Plants which appear to have gone into the last stages preceding death may develop one or more side buds that begin a vigorous and normal period of growth, the same as a seedling beginning its vegetative cycle at the time, while the upper part of the plant with the old inflorescence and seed dies away in the same manner as the entire individual of an earlier date does after passing through the short inflorescence and fruiting period.

One of the most remarkable effects of the short light period on the hemp plants, both staminate and carpellate, is the production of endless numbers and patterns of confused flowers. One can find almost any abnormality possible from the characters involved. It would be a bewildering and hopeless task for a systematist to attempt to describe the diversity in which parts of stamens and carpels are mingled together in irregular sex mosaics. In the past a few abnormal flowers have been described and figured by various authors. A résumé of such reported abnormalities has been published by Prain ('04). As stated, such forms can be obtained in great profusion from the ordinary diecious hemp by putting it in the proper light environment. It is not necessary to have a monecious or abnormal parentage. A few examples are presented here (fig. 3) to show the general character of the sex mosaics produced.

Through the kindness of Mr. Lyster H. Dewey, in charge of Fiber Plant Investigations, U. S. Department of Agriculture, the writer obtained seed of a simple-leaf, or pinnatifid-leaf variety of hemp, which was reported to have originated in 1917 in the Department's trial grounds as a second generation hybrid of a cross between "Kymington" staminate and "Italian Ferarra" carpellate. Seed labeled "1944(24)—monecious plant, crop of 1919" was used as a test to detect differences in "moneciousness" under different daylight periods. A plot out of doors planted June 20, 1921, developed 6 staminate plants, all apparently pure in sexual expression, and 15 carpellate plants, 2 of which had some staminate flowers and the remaining 13 were apparently pure in sexual expression. Plants raised from the same package of seed and planted in the greenhouse on December 9, 1921, showed 12 staminate intermediate individuals and no staminate pure or 100 per cent staminate intermediate; and 7 carpellate intermediate individuals and 2 carpellate pure, or 77 per cent carpellate intermediate and 22 per cent carpellate pure. From the same package of seed, plantings were made on January 9, 1922, and from this planting 13 staminate intermediate plants were obtained and 9 staminate pure, or 59 per cent staminate intermediate and 40 per cent staminate pure; and 15 carpellate intermediate individuals and 7 carpellate pure, or 68 per cent carpellate intermediate and 31 per cent carpellate pure. A normal palmateleaf "monecious" variety was also tested by several plantings with results essentially similar, namely, a higher percentage of "moneciousness" was obtained in the winter than in the summer. It will be seen, therefore, that the limited number of experiments with so-called "monecious varieties"

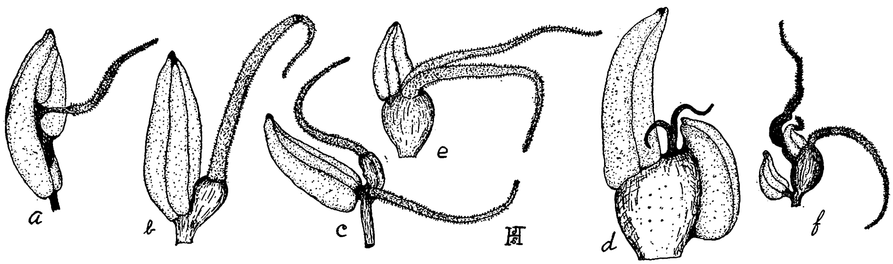

FIG. 3. Drawings of sporophyll, sex mosaics from winter plants of *Cannabis sativa*. All somewhat magnified.

a. Abnormal stamen with four microsporangia, two normal and two short, and a well-developed stigma—from a staminate plant.

b. Complex with a normal anther and a rudimentary ovulary with a normal stigma—from center of staminate flower on staminate plant.

c. Stamen-carpel complex with a normal anther and a structure intermediate between anther and ovulary with a typical stigma at the top and another coming from the base—from carpellate plant.

d. Stamen-carpel complex showing a well-developed ovulary, but with two imperfect stigmas and two bi-locular anthers, the one coming out from near the top and the other from the side of the ovulary wall—carpellate plant.

e. Carpel-stamen mosaic with a well-developed ovulary and two normal stigmas and a tri-locular anther coming from the top besides the stigmas—carpellate plant.

f. Flower complex showing a normal stamen and an ovulary with one normal stigma and another abnormal stigma which is connected at the base with an imperfect, bi-locular anther which also ends in a minute stigma—young flower from carpellate plant.

indicate the same kind of reaction as those which were pure in sexual expression in the normal growing season. The "monecious" varieties showed a much higher percentage of moneciousness during the short days of winter than in the summer. It is, however, conceivable that a "monecious" variety of hemp might be found or developed that would produce all monecious individuals under normal seasonal conditions, and the problem would then be to find an environment in which the response would result in dieciousness.

CONCLUSIONS

The experiments carried on with hemp during the past few years show that the ecological factor of relative length of daylight has a profound effect on the plant, not only in changing its size and complexity, its period of vegetative growth and maturity, and its conditions of senility and rejuvenescence, but also in determining the nature of its sexual expression. The most remarkable phenomenon observed is the fact that the single factor of relative length of daylight to darkness causes a reversal of the sexual state in both directions. In the staminate plants the reversal is from maleness to femaleness, and at the same time it is from femaleness to maleness in the carpellate plants. The action of the light, therefore, probably goes deeper than merely the reduction of the food supply by reducing photosynthesis. It is conceivable that there may be a direct effect on the ultimate chemical and electrical activities of the cell. As was shown in the paper on *Arisaema triphyllum,* the control of the sexual state in this plant by means of the supply of nutrients and food was entirely in one direction for the given environment. Under one set of ecological factors maleness changed to femaleness and femaleness remained female, while under the opposite set of ecological factors femaleness changed to maleness and maleness remained male.

It becomes evident that the dimorphisms so prominently expressed between the staminate and carpellate hemp individuals are not caused by hereditary differences in the individuals, since both staminate and carpellate plants have the potentiality and power to produce all of the opposite sexual characters, both primary and secondary, and actually do produce them under the proper environment.

The sexual dimorphism expressed between the individuals or between different parts of the same individual is due to reversible states induced by environmental factors, the ecological factor apparently of the greatest efficiency in producing reversal of the sexual state in the hemp plant being the relative length of the intermittent light period. Long periods of daylight with short periods of night induce pure sexual expression in the individual, while comparatively short daylight periods with long night periods cause sex reversal in the vegetative tissues of the body, the shortest daylight periods in the vicinity of Columbus, Ohio, usually giving 90 per cent or more of individuals, both staminate and carpellate, with some degree of sex reversal. The percentage of reversal between the maximum and minimum periods of efficiency is roughly inversely proportional to the length of the daylight period.

The experiments show that the attempt to explain sexual expressions by hypothetical, homozygous and heterozygous, Mendelian, hereditary factors is of little value in the analysis of the sexual nature of diecious, dimorphic organisms like the hemp, even though a single sexual state seems to be established in the egg either before fertilization or in the zygote at or soon after the fertilization period. The problem is primarily physiological and ecological, the expression of the one sex or the other in the cells of the vegetative body, or its reversal to the opposite sex at any stage in the cell lineage of the vegetative cycle, being dependent on the character, intensity, and duration of the ecological factors involved, whether internal or external. In other words, the fundamental nature of sexuality is physiological rather than morphological.

The notion that the sexual state is fixed and that the state is due to irreversible hereditary units in control will have to be given up and a theory developed in harmony with known experimental phenomena and comparative morphology. Whatever theory one may hold must agree with the fact that the sexual state is changeable and reversible through the action of environmental factors even in organisms strongly dimorphic. The study of sexuality then has an ecological aspect and the main line of attack must be toward finding the factors efficient in each specific case to establish maleness, femaleness, or neutrality in a cell, tissue, organ, or individual, or to reverse any one of these conditions to the other. Annual, diecious plants appear to be favorable objects for experiments, but there is no inherent reason why experimental control should not be exercised on sporophytes with bisporangiate and monecious flowers and also on hermaphroditic gametophytes. In fact, it is well known that hermaphroditic gametophytes have been developed as unisexual individuals through the influence of a special environment, and on the other hand unisexual gametophytes have been changed to hermaphrodites.

So far the writer has found two efficient ecological methods for inducing sex control or sex reversal. In *Arisaema* the sexual state can be controlled through the nutrition and water supply, and in *Cannabis* the relative length of daylight induces sex reversal in a high degree. It must be recognized that a mere beginning has been made, but long avenues of research and investigation seem to open up for the future. For it is now known that sex can be changed by ecological factors in various monosporangiate sporophytes, and that it is not primarily Mendelian in reaction, nor caused by specific sex factors or chromosomes. Sex must, therefore, be due, as stated above, to some fundamental physical or chemical state in the living cell, either in the protoplasm itself or in its inclusions. This state may be positive, negative, or neutral, and thus the sex of a cell or its vegetative descendants may be successively female, male, or neutral, in any order, the reversal being brought about both quantitatively and qualitatively by varying the factors of environment.

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