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# THE CHANGE OF OPPOSITE TO ALTERNATE PHYLLOTAXY AND REPEATED REJUVENATIONS IN HEMP BY MEANS OF CHANGED PHOTOPERIODICITY [1]

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Hemp, *Cannabis sativa,* is typically an opposite-leaved plant but usually ends with an alternate phyllotaxy near or in the inflorescence. Occasionally, however, under normal conditions apparently, the change in leaf arrangement occurs some time before the flowering period and at some distance down the stem. Such instances are usually not common according to the observations of the writer who has studied the plant extensively in the field. If one considers the phyletic relationships of hemp it becomes plain that its immediate ancestors must have belonged to an alternate-leaved group, and the opposite-leaf heredity has been added to the original factors which now are expressed only in the last stages of the ontogeny.

Recapitulations of this nature appear very commonly in the higher plants, especially in the flower. The change from opposite to alternate expression must correspond to a certain physiological condition attained as the plant passes through a gradient of states on developing to maturity. In hemp then the new factor or factors for opposite phyllotaxy are laid down, so to speak, on top of or in addition to the old ones for alternate arrangement. So it becomes a matter of the activity or latency of the two sets of factors in accordance with physiological states in the cells. If this is approximately a correct analysis of the situation, it follows that all that is necessary to obtain a change of character expression at any point down the stem is to so manipulate the environmental stimuli as to induce a proper functional state in the cells and the proper character expression will follow.

After experimenting with hemp for a number of years and discovering a method of producing quite definite sex reversal (Schaffner, '21 and '23) the writer discovered that the expression of the phyllotaxy and other characters, as well as the expression of the sexual state, could be influenced decidedly. Accordingly a series of experiments has been carried on in which the phyllotaxy has been controlled in a number of ways, and other changes of character expression brought about in a very unusual and striking manner.

Garner and Allard ('20 and '23) have reported rejuvenation as a result of their work in photoperiodism, and the writer began to observe rejuvenescence with change of phyllotaxy in his winter hemp experiments in 1920

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and 1921, whenever plants came to maturity or old age about the time when the strength and length of daylight becomes pronounced in the springtime.

## Experiments with Photoperiodicity

If hemp is planted in the greenhouse on shallow-soil benches in January or February and receives only the short period of daylight, the plants will bloom in four or five weeks. The staminate plants will begin to go into senescence promptly and die. The carpellate plants will produce seed and go into a state of vegetative inactivity, and, in most cases, die or at least have dead tips by the last of April or the early part of May. A few, however, of the more vigorous plants will survive until they receive the stimulus of the increasing length of daylight and will then be rejuvenated. The new buds usually develop in the first or second node, and the rejuvenated branches which come from these buds have the alternate leaf arrangement.

In 1922 special experiments were begun. Hemp was planted on shallow benches in very rich soil on December 2. These plants began to bloom January 15, 1923, when 4 and 5 inches in height, and, after blooming for some time, were given a small amount of electric light which kept them from going into the senile state until with the advent of the longer daylight period of spring about half of the carpellate plants in the plot rejuvenated either in the terminal bud or in lateral buds and thus began a new period of growth. Most of the staminate plants died, but several survived and commenced a second period of growth like the carpellate plants. These plants mostly had from six to eight opposite leaf nodes. In the experiments the cotyledon node is not counted. The rejuvenated terminal buds continued their growth with alternate phyllotaxy the same as rejuvenated axillary buds. Some of the rejuvenated plants grew to be over three feet high, the part of the stem with opposite phyllotaxy being about six inches and the part with alternate phyllotaxy mostly about two and a half feet, when they began a second blooming period.

At the same time, on December 2, 1922, a large tank three feet in diameter and with soil three feet deep was planted with hemp seed and kept in continuous light from the beginning of sprouting. In the daytime they received the ordinary daylight through the greenhouse glass, and at night they were lighted with two 110 watt mazda electric light bulbs kept suspended about a foot above the tops of the plants. These plants made a remarkable growth as compared with the winter daylight plants. On February 10 the tallest were 56 inches high as compared with the control plants, the tallest of which at the time were, carpellate 6 inches, staminate 9 inches.

The plants in continuous light all changed from the opposite to the alternate phyllotaxy at the 7th, 8th, or 9th leaf node, without noticeable change in leaf character. At maturity the continuous-light plants were 7 to 10½ feet high. The last ones to bloom began anthesis on June 5, or six months after planting. The smaller plants, which were much shaded by the larger and

thus did not receive much benefit from the artificial light after a time, began blooming on March 5. The continuous light prolonged the vegetative growth of the most favorably situated plants more than three months as compared with normal summer plants in the field which usually bloom in about ten weeks. The change from opposite to alternate phyllotaxy took place while the plants were at the height of their vegetative vigor, both in respect to leaf development and elongation of the internodes. A few representative plants from the continuously illuminated plot are described below:

1. A plant 7 feet 7 inches high, staminate; 8 opposite leaf nodes below, 37 alternate leaf nodes above, but the seventh upward from the first alternate was also an opposite leaf node.
2. A staminate plant with 7 opposite leaf nodes below and 23 alternate leaf nodes above.
3. A carpellate plant with 10 opposite leaf nodes below and 24 alternate leaf nodes above.
4. A staminate plant 10 feet 7 inches high, dying on October 2, 1923, had 3 feet of stem at the lower end with 8 opposite nodes, and the 7½ feet had 53 alternate nodes. This plant began blooming on June 5, when it was 8 feet high, and continued producing flowers at a slow rate until October 2.

Another patch of hemp, planted in very rich shallow soil in the greenhouse benches on December 20, 1922, was allowed to develop flowers and to reach a rather advanced stage of maturity but was rejuvenated by means of continuous light before the terminal buds had died. Representative plants were:

1. A staminate plant with 5 opposite leaf nodes, one slightly irregular opposite node, and 50 alternate nodes, produced in the continuous light.
2. A carpellate plant with 7 opposite leaf nodes and 10 alternate leaf nodes. This plant was in bloom again and growth had stopped.
3. A carpellate plant with 8 opposite leaf nodes produced in the short light period, and 20 alternate leaf nodes produced from the terminal bud in the continuous illumination. When studied the plant was in the second blooming period.
4. A carpellate plant with several rejuvenated branches having alternate phyllotaxy. Two of these branches, after developing alternate leaves for some time, reversed to opposite phyllotaxy again and so continued to the end. This is a rare occurrence, but suggests that a means should be discovered to change the alternate phyllotaxy of rejuvenated shoots to opposite again by proper manipulation of the environment.

It thus became evident that the expression of the phyllotaxy of the hemp could be controlled experimentally in various ways, and consequently a number of special experiments were carried on in the winter of 1923–24 to gain further light on the influence of environment on the expression of the leaf arrangement and form in the hemp plant.

To test the influence of continuous light on extremely senile plants, hemp was planted on December 19, 1923, in a box of deep soil in rather poor light. All the staminate plants and most of the carpellate plants died soon after blooming. None produced seed. Several of the more vigorous carpellate plants, however, survived. After they had remained stationary for a long time, and when some of the weaker ones were beginning to show signs of approaching death, two 110 watt mazda electric light bulbs were turned on at

night beginning on March 14, 1924. Four of the surviving plants rejuvenated in the terminal bud. A study of these plants on April 9 showed the following conditions: The plants all rejuvenated promptly from the terminal bud with alternate phyllotaxy, which continued to the end. In one case, as listed below, the third node of the rejuvenated stem had opposite leaves and then continued alternate again. In another plant the fourth and fifth alternate nodes were very close together and were, therefore, nearly opposite. The other nodes of the rejuvenated stem were typically alternate, with normal internodes.

In every case the leaves either changed immediately to the simple type, and, after several nodes, developed 3-foliate or 5-foliate leaves, or, after producing one or two trifoliate leaves, passed over to the unifoliate condition and then back again to the compound, digitate type.

The individual record of the four rejuvenated plants, all carpellate, on April 9, when they were beginning a rapid development, is as follows:

1. Five nodes of opposite leaves; continuous illumination begun at about the time of the formation of the fifth node; plant at that time 2¾ inches high; rejuvenated at the tip and had at first two alternate leaf nodes which were followed by an opposite leaf node and then continued its growth with alternate phyllotaxy.
2. Four opposite leaf nodes when the night light was turned on; height of plant at that time 3 inches; rejuvenated at the tip and continued with the 5th and subsequent nodes with alternate phyllotaxy. The fourth and fifth of the alternate nodes were quite close together approximating to the opposite condition. The further development of nodes was typically alternate.
3. Five opposite nodes 3½ inches high when the light was turned on; rejuvenated at the tip and the sixth and subsequent nodes had alternate leaves.
4. Five opposite leaf nodes when the continuous illumination was begun and 2¼ inches high; rejuvenated at the tip and continued growth with alternate phyllotaxy.

Several months later all four plants had attained a height of over 3 feet and had continued the alternate arrangement, when the light was turned off and the experiment abandoned.

On January 11, 1924, hemp was planted in a tank 3 feet wide and with soil three feet deep. It was grown in the ordinary winter day and night conditions until February 20. Most of the numerous plants, both staminate and carpellate, had come to bloom by this time, and some of the carpellate plants had developed large seeds. A few, however, had only young flower incepts, and several showed no signs of developing flowers. Most of the plants in this lot were, therefore, stationary and ready or nearly ready to go into senile decline. Some of the staminate plants were already decidedly on the down grade. An attempt was made to have the plants in these various states when the light was turned on. On this date, therefore, February 20, two 110 watt mazda electric light bulbs were turned on at night and also on dark, cloudy days. All the plants, both staminate and carpellate, immediately began a process of rejuvenation, and all passed promptly from the opposite to the alternate phyllotaxy, those apparently most mature or senile immediately

and those which had not yet bloomed less promptly, but all after one to four leaf nodes had been produced. Several plants with young flower incepts responded to the continuous illumination very vigorously, with an unusually rapid vegetative growth, so that the reproductive function was entirely inhibited. The incipient flower buds developed no further and never came into bloom. One plant especially of this sort had shot up over a foot of new growth before the others which were in a more advanced reproductive or senile condition had overcome their inactivity. In general those plants

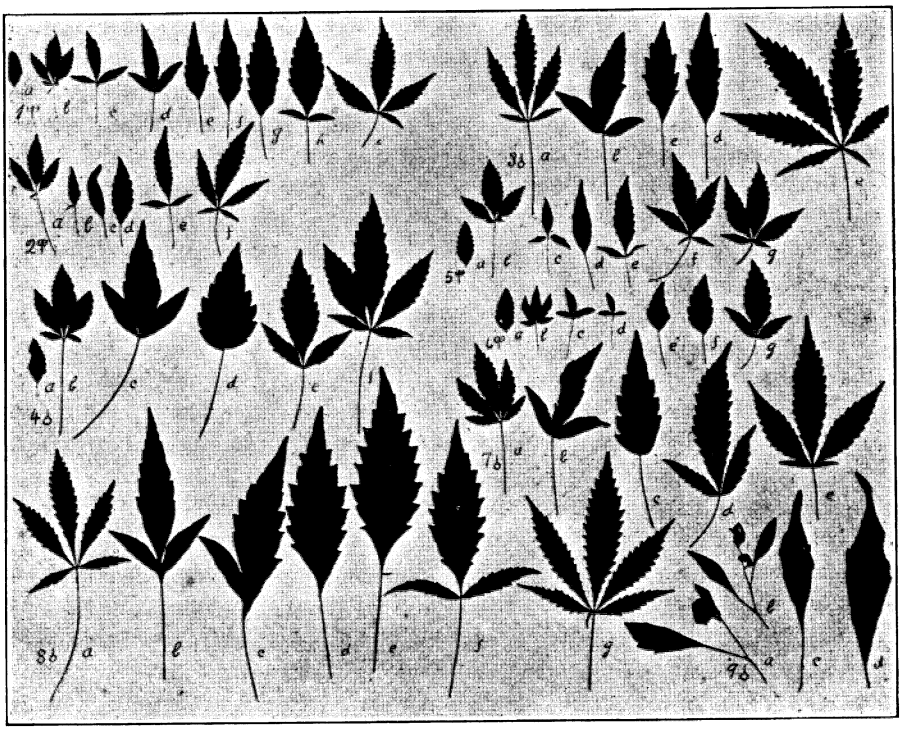

FIG. 1. Succession of leaf forms through the first rejuvenation period. 1. Staminate plant; *a*, first leaf; *b*, last leaf before rejuvenation. 2. Staminate plant; *b*, *c*, *d*, *e*, succession of leaves during rejuvenation period. 3. Carpellate plant; *a*, last leaf before beginning of rejuvenation; *b*, *c*, *d*, *e*, succession of leaves in rejuvenation period with a sudden jump from unifoliate to a leaf with six leaflets. 4. Carpellate plant; *a*, first leaf; *b*, last large leaf before rejuvenation; *c*, *d*, *e*, *f*, succession of leaf forms through the rejuvenation period. 5. Staminate plant; *a*, first leaf; *b*, last large leaf before rejuvenation began; *c–g*, succession of leaf forms through the rejuvenation stage. 6. Staminate plant; *a*, first leaf; *b*, last leaf before rejuvenation; *c–g*, succession of leaf forms through the rejuvenation period. 7. Carpellate plant; *a–e*, succession of leaf forms through the rejuvenation stage. 8. Carpellate plant; *a–g*, succession of leaf forms through the rejuvenation stage. 9. Carpellate plant; *a*, branch with one twisted crinkled leaf and one with inrolled margins; *b*, branch with two flat entire leaves and two crinkled leaves; *c*, *d*, leaves with inrolled margins.

which were the most advanced in the blooming condition were the slowest to continue growth but the most prompt to pass to the alternate phyllotaxy; while conversely, those which were in the best vegetative condition were the most prompt to continue growth and the slowest to change to the alternate phyllotaxy. Not only did the plants rejuvenate and change to the alternate leaf arrangement, but the first new leaves of the more extreme plants were mostly with entire margins, or with serrations only at the outer end. In some cases the first rejuvenated leaves were still compound, usually with three leaflets, but the following one to four nodes produced simple or unifoliate leaves, and then continued with two-lobed or three-lobed leaves, three-foliate leaves, five-foliate leaves, etc., in succession. In those plants which were not yet in the full blooming condition when the light was turned on, the rejuvenation was not so marked, for they merely passed from a five-foliate or seven-foliate leaf condition down to the three-foliate and then back again to the five- and seven-foliate. In such cases also no entire leaflets were produced, all being normally serrate. For change of leaves during rejuvenation see figure 1. In a few cases sporadic opposite leaf nodes appeared in the rejuvenated shoots.

A number of the plants in this experiment were pulled up and pressed for herbarium specimens on April 8, 1924, long before the second vegetative growth cycle was complete. Of these, 1 plant had 4 opposite leaf nodes before changing to alternate, 2 plants had 5, 2 had 6, and 2 had 7. All of the remaining plants in this experiment had a second reproductive period and were then allowed to die.

A plot was planted March 8, 1924 and raised with continuous light from the beginning, daylight and two 110 watt mazda bulbs at night. Of the 35 plants in this plot, 1 had 5 opposite leaf nodes before changing to alternate, 5 plants had 6, 14 had 7, 9 had 8, 5 had 9, and 1 had 10.

The change from opposite to alternate makes a fairly good probability curve. This change has apparently no relation to the size or vigor of growth of the individual plant.

A plot was planted in the greenhouse on June 5, 1924, and raised in continuous light from the first, daylight and (because the patch was rather large) three 110 watt mazda bulbs at night. The seventy-nine plants of the plot showed changes from opposite to alternate leaf arrangement as follows: 1 plant had 7 opposite leaf nodes before changing to alternate, 13 plants had 8, 30 had 9, 13 had 10, 13 had 11, 4 had 12, 4 had 13, and 1 had 14.

These plants developed a greater number of opposite nodes before changing to alternate than the plants of March 8. This must be ascribed to the influence of the longer daylight period and the shorter electric light period. The plants of March 18 changed after the 5th to 10th node while the June 5 plants changed after the 7th to 14th node. Although the number of March 8 plants is small, the evidence is satisfactory because those of June 5 are numerous enough to have included the lower fluctuation. These numbers are

interesting when compared with the rejuvenated short light plants which can be controlled to show alternate phyllotaxy after the 4th to 8th node.

Of the controls planted out of doors May 1, 1924, 3 plants had 16 opposite nodes before changing to alternate, 1 plant had 18, 2 had 20, 2 had 21, 1 had 22, 1 had 24, and 1 had 25. These plants changed after the 16th to 25th node. A comparison of these normally grown hemp plants with those grown in the greenhouse under continuous illumination shows a very striking difference in the hereditary expression.

The plumule of the embryo has at least two opposite leaf nodes already organized besides the cotyledon node, so the probable expectation of a possible change to alternate phyllotaxy through the stimulus of continuous light or rejuvenation by continuous light cannot be much below the fourth node. As shown above, the writer obtained two carpellate plants and one staminate plant that changed after the fourth node, the fifth being alternate. Perhaps with special care one might induce alternate phyllotaxy in the fourth node.

One of the most interesting results of rejuvenation is the repetition of the leaf form and other characters in the same succession as when the plant is developing from the seed. In both the normal out-of-doors plants, and in the winter greenhouse plants, whether in short light or continuous light, the cotyledons are simple and entire, the first leaves are simple and serrate, and are followed in succession by three-foliate, five-foliate, seven-foliate, etc., leaves up to a certain degree of compounding, depending on the size and vigor of the plant, and then down grade again to simple bracts in the inflorescence. In rejuvenated buds, whether terminal or lateral, the progression is the same if the bud starts from a senile plant. In the early rejuvenation stages, however, in the passage from simple leaves to three-foliate leaves there appear commonly intermediate, one-lobed or two-lobed forms which do not occur when the shoot develops from the seed in the original juvenile state. Nevertheless the physiological gradient must be essentially the same. The rejuvenation is a real rejuvenation, but whether the plant returns to the exact condition of the seedling is questionable. The changes produced by age and differentiation are probably not entirely overcome. We are probably safe in assuming that the degree of senility attained by the plant at the time of rejuvenation is in a general way indicated by the succeeding leaf forms. If maturity has not proceeded far the leaf forms will not go below the three-foliate, serrate condition. If the senility is well developed, the leaf form on the rejuvenated bud will at first be simple but still serrate. If senility is extreme the leaf will be partly or completely entire-margined and be simple or will be lobed or three-foliate at first but succeeded by the simple form to be followed by the regular series of more extreme compounding as the shoot develops.

An abnormality that frequently appears, especially in the carpellate plants, is a peculiar marginal curling or distortion of the leaf blade. Sometimes

there is a decided crinkling and sometimes a very one-sided development. These abnormalities are not developed after rejuvenescence is complete.

## Repeated Rejuvenations

Perhaps the most important and interesting results obtained were the repeated rejuvenations. As stated in the beginning of this paper, Garner and Allard ('20 and '23) reported rejuvenation for several species by means of lengthening the period of exposure to daylight. The writer had in the meantime observed cases of complete rejuvenation in staminate and carpellate hemp plants raised in winter, in 1919 and 1920. Reference was made to these rejuvenations in the article published in 1921. Later, very decided cases of rejuvenation appeared in *Acnida tamariscina* whenever the plants came into bloom late in the winter and had not died when the days were beginning to lengthen considerably. In *Acnida* the rejuvenescence was sometimes from the tips of the inflorescence branches. The development of leafy shoots from the slender naked flowering shoots gave a very striking and bizarre appearance to the plants.

After it became evident that apparently complete or nearly complete rejuvenescence was attained through the proper use of continuous light, it seemed desirable to find out how often the process could be repeated in the individual. Accordingly a plot of hemp, planted January 16, 1924, and developed in the winter short-light period, was allowed to bloom and continue until some of the plants began to die at the top naturally. The light was started on March 21, two 110 watt mazda bulbs being used. In the daytime the plants had nothing but the natural light as it came through the greenhouse glass. A considerable number of plants in this plot rejuvenated, although some were too decrepit to be revived. Two staminate plants were selected for the experiment, since the staminate plants are much shorter lived than the carpellate and usually die promptly after blooming. These two plants were 4 and 4½ inches high respectively. A carpellate plant was also preserved because of its peculiar sexual behavior after rejuvenation. The carpellate plant was 10 inches high when rejuvenated, had produced some seed, and was entirely dead at the top. It rejuvenated from several buds near the middle, and when the most vigorous branch was about 6 inches long it began to bloom and produced 12 typical, pure staminate flowers. The terminal bud of this branch, as well as the others, continued a vigorous vegetative growth and the flowers soon disappeared. On June 5 the electric light was turned off and the rejuvenated plant grew to be 6 feet tall by the 8th of September when the writer returned from a month's absence and found it in full bloom for the third time. At this period all the flowers were pure carpellate again as at the first blooming period. The plant was too tall to be properly cared for, as it was on a bench with a large root system and could not be transplanted. It was pruned back decidedly and the electric light was turned on again at night on September 9. By September 20 it was developing numerous

new buds which later grew into rather spindling shoots. Many of these branches were removed, and the growth continued more normally. Because of over maturity and the severe pruning after the third blooming period the plant was in a rather weak condition by December 1, and some of the branches had died. The artificial light was turned off on this date and by December 13 it began to die rapidly and was withered by the 15th. It was examined and incipient carpellate flowers with well-developed stigmas were found. This plant, therefore, had two successful rejuvenations, three vegetative periods, and four blooming periods, one of which was with pure staminate flowers. The death of this plant was not primarily due to senility but to the fact that it was too severely pruned, several large branches having been cut off too far down in the inactive leafless part.

The two staminate plants rejuvenated very slowly after the electric light was turned on at night, but finally each developed a spindling shoot from the side. The artificial light was turned off the last week in May, and they both began to bloom the first week in June. The flowers were pure staminate and were removed just at the time of opening. At the first blooming period some sex reversal to the female condition was present. On the 15th of June the plants were removed from the bench to large pots, and the electric lights turned on again during the night as at the first rejuvenation period. The plants were now each 8 inches high. Both rejuvenated from the second growth shoot, one from the tip and the other from the side. They were in continuous light until September 10, and made a remarkable growth when their original stunted nature is taken into account. Each plant was 4½ feet high and fairly robust. One would never have recognized the original, delicate, spindling shoots of the first and second periods. By September 20 both plants were in full bloom with numerous, normal staminate flowers. They were now cut back to 3 feet for convenience in handling, since they had grown too tall during the writer's absence in the latter part of the summer. Again, under the action of the two 110 watt mazda electric light bulbs turned on at night, they rejuvenated promptly and made a good growth with a considerable number of branches, and by November 25 one of them showed two sporadic flowers. The night light was again turned off on December 1, and the plants soon began to develop abundant flower buds. These flowers began to open December 14, 1924. Each plant had hundreds of staminate flowers entirely healthy and normal in appearance. They were all pure staminate which agreed with the expectation that hemp plants usually develop toward more extreme maleness in age. These two plants therefore had three successful rejuvenations, four periods of vegetative growth and four periods of blooming. On December 15 the light was turned on again and by January 5 the plants showed some slight signs of new bud and leaf development. On January 16, 1925, their first natural "birthday," they still showed considerable vigor, and had developed a few small new leaves in the inflorescence but were also showing signs of senility, one more so than the other. They were still

developing some flowers. One plant was dead by January 31, 1925, and the other was nearly withered by February 7. They, as well as the carpellate plant, continued the alternate phyllotaxy after the first rejuvenation. Control staminate plants, planted near the end of May out-of-doors, were, after their one " natural " blooming period, nearly all dead before the end of the fifteenth week.

If staminate hemp plants, with one natural blooming period and a maximum vegetative period of three to five months in the latitude of Columbus, can be rejuvenated three times with four vegetative and four reproductive periods, there is no reason why with carefully controlled environments they should not be rejuvenated several times more.

The writer cannot refrain from remarking that a certain degree of rejuvenescence must certainly be possible in senescent man; and these hemp experiments indicate that there may be various ways open to the human physiologist not only to induce vigorous life up to old age but actually to prolong the usual three score and ten or four score years of human life decidedly and to discover real rejuvenation agents.

## Summary

1. Although the change in hemp from opposite to alternate phyllotaxy is usually a regular occurrence toward the end of the sporophyte ontogeny, it can be induced at a much earlier stage by environmental control. The phylogenetically more primitive alternate heredity is normally latent during the greater part of the vegetative development while the more modern and specialized heredity for opposite phyllotaxy is active. This activity and latency depends on physiological gradients which in turn can be controlled to a considerable extent by ecological factors.

2. If hemp plants are developed in the short light period of winter, and thus brought to an early maturity and then rejuvenated by means of continuous light, either from the tip or from lateral buds, they will pass immediately from the opposite to the alternate phyllotaxy. This change can be induced after the fourth leaf node.

3. If hemp plants are brought to the blooming period with the short light period of late winter, and are then exposed to continuous illumination by using electric light at night, they will all rejuvenate from the terminal bud, both staminate and carpellate, and continue their growth with alternate phyllotaxy.

4. If hemp plants come to the blooming stage in early spring when the days are beginning to lengthen decidedly, some of them will rejuvenate naturally, usually from lateral buds below the inflorescence.

5. If hemp plants are grown in continuous light, daylight in the daytime and electric light at night, they will change their phyllotaxy at an early stage from opposite to alternate but without apparent change in leaf character; and the shorter the natural daylight is at the time the earlier usually will the change

occur. Plants from seed planted about the first of March will change at the 6th to the 11th node, and plants from seed planted about the first of June will change at the 8th to the 15th node.

6. Sporadically opposite leaf nodes occur along with the alternate nodes, and occasionally the alternate phyllotaxy will fall back completely to the opposite, but no method has been discovered to induce this change experimentally.

7. In rejuvenation through the application of continuous light, whenever regrowth originates in a rather extreme, senile condition, the new leaves have a strong tendency to have completely entire margins or to be toothed only on the outer end; and also they change to the simple or unifoliate type, either immediately or after the production of one or more tri-foliate leaves. If maturity or senility is not far advanced the new leaves do not develop entire margins, and may not go beyond the three-foliate stage in simplicity.

8. After any rejuvenation there is a succession of leaf forms corresponding to the succession of forms developed by the juvenile plant from the seed.

9. Repeated rejuvenations can be brought about both in staminate and carpellate plants. Three actual rejuvenations have been produced in individuals, with four periods of vegetative development and four periods of blooming.

10. Rejuvenated staminate hemp plants have been kept alive for over a year while naturally they usually die by the time they are 15 weeks old in the latitude of Columbus, Ohio.

## Literature Cited

1. **Garner, W. W., and Allard, H. A.** 1920. Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. Jour. Agr. Research, **18**: 553–606.
2. **Garner, W. W., and Allard, H. A.** 1923. Further studies in photoperiodism, the response of the plant to relative length of day and night. Jour. Agr. Research, **23**: 871–920.
3. **Schaffner, John H.** 1921. Influence of environment on sexual expression in hemp. Bot. Gaz., **71**: 197–291.
4. **Schaffner, John H.** 1923. The influence of relative length of daylight on the reversal of sex in hemp. Ecology, **4**: 323–334.