

# Sensitive Life of *Asparagus plumosus*.

## A morpho-physiological Study

by

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### Introduction.

Few cultivated plants have become more widely distributed than the one from South Africa which forms the subject of the study here presented. *Asparagus plumosus* Baker var. *nanus* is now found thruout the civilized world as a house plant, and commercially shares with *Myrsiphyllum* the honors of extensive use for festive decoration. As stated by Miss Conover<sup>1)</sup>, this plant is seen in all sizes of growth, but commonly in homes in only the low form, 10 to 30 cm, but in hights up to several meters in greenhouses. The differences in appearance between the low form and the high are due merely to age and the methods of cultivation. From the seed rises a slender shoot which attains a hight of about 10 cm, and then bends 2 to 5 cm of its apex over into the inclined position, at the same time unfolding from its uppermost nodes lateral branches of 2 or 3 orders. The lateral branches at first take a position radial to the bearing axis, without much regard to the direction of gravitation. During the ensuing 2 weeks, the main tip and the branches pass gradually to the horizontal plane, tho  $\frac{1}{4}$  to  $\frac{1}{3}$  of the primary branches may remain permanently no farther than  $45^\circ$  from the vertical. The ultimate branches, the needles, show but slight regard to the direction of gravitation; for they grow out in all directions radial to their place of origin, and later show but small movement toward the horizontal plane.

The seedling develops a rhizome of a few millimeters length which grows but slowly beneath the ground, and which sends

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<sup>1)</sup> Conover, Behavior of *Asparagus plumosus* toward Gravitation and Light, (Plant World. XVI. 1913.)

above ground in slow succession shoot after shoot, the first rising a little higher than the seedling shoot, and each higher than its predecessor. These shoots turn their tips to the horizontal, and subsequently the branches begin unfolding. Unlike the behavior of similar members in seedlings, the branches on these shoots from the rhizomes unfold in the horizontal plane, and the needles, instead of radiating in all directions from their origin as in seedlings, radiate within the strict limits of the horizontal plane, giving to this horizontal part the appearance of having been in a plant-press. Of assimilating leaves, the plant produces none. The function of carbon-assimilation is assumed by all aerial parts of the plant except the rudimentary leaves, but chiefly by the last order of branches which are needles growing in clusters of 7 to 25, the needles being 3 to 7 mm in length and about 0.3 mm in diameter. The needles at the apex of the main axis are borne directly on this main axis, but, as one goes proximally, they are borne on branches of the 1st, 2d, 3d, and 4th order.

As this plant is seen in pots in houses, it presents only the appearance described above, and may attain a total length of not more than 30 to 60 cm even after the lapse of 3 years. The aerial shoots may live for 2 years at least, and thus there may persist from a single rhizome a half-dozen shoots, not differing greatly in height, clustered near together, and all turning the apical 8 to 20 cm over into the horizontal plane, and there dividing into hundreds of beautiful and delicate branches and needles, the branching being generally confined to the horizontal portion.

If, however, a 2- or a 3-year-old plant be set out in unconfined earth, it soon begins the formation of larger shoots. A shoot that rises to a height of 40 to 60 cm nearly always begins circumnutation at that height, and will twine, if a suitable support is offered. The tip bends from its formerly orthotropic course  $45^{\circ}$  to  $180^{\circ}$  or more, and describes in its movement a circuit 4 to 10 cm in diameter. Various tips, timed for periodicity when the temperature was  $28^{\circ}$ , were found to make their circuit, some in 2 hours, some in 8 hours, and others between these extremes.

These twining shoots show all gradations of length between a half-meter and several meters. A twiner produces no lateral branches till near the close of its elongation, and the first branches to develop are intermediate between the base and apex of the central axis. As the main axis is near the end of its growth, it ceases to circumnutate, 10 cm more or less of the tip straightens out horizontally from its supporting cord or stake, each node of this horizontal tip and of the stem below rapidly unfolds its branch, and we have a narrow spiral from which stand out in all directions the lateral branches as beautiful horizontal fronds, branching to the 4th or 5th order. An exception must be made to the last statement: The lowermost nodes of the central axis produce no branches. This leaves the lower portion of the shoot for a distance of 30 to 50 cm bare, except for the stout nodal scales.



These nodal scales on a stout shoot attain a considerable size — a centimeter or more in length — are closely appressed to the bearing axis, and are produced below into a stout divergent spine 3 to 7 mm in length. This rigid spine must certainly be of use in climbing in the plant's native habitat.

Twining is, in a certain sense, predestined. A shoot coming thru the ground with a diameter of more than 2 mm is almost certain to become a twiner. I have not seen shoots more than 4 mm in diameter. Should a twiner find no support to enable it to rise, it wanders about over the earth, or plant growth, as do other climbing plants, its cord-like stem of 2 or 3 meters length wholly destitute of any appendage except for the spinous nodal scales.

This *Asparagus* twines either clockwise or counterclockwise. I have seen a shoot start twining and make a complete turn about the supporting cord, then unwind itself and twine in the opposite direction for its final course.

## Experimental.

### A. Non-twining shoots from rhizomes.

#### I. Geotropic Relations.

In the paper by Miss Conover<sup>1)</sup>, already referred to, it has been shown that young shoots of this *Asparagus* are orthotropic and negatively geotropic. The same Author has shown also that the horizontal position assumed by the shoot when nearing its maturity is due to a reversal of response to gravitation, the shoot changing its negative geotropism to diageotropism.

This diageotropism pertains not only to the main axis but to all the branches also. As the branches of the first order start unfolding, they lie close to and parallel with the main axis. As they become a centimeter or more in length they swing thru an arc of approximately 90°, sometimes 180°, and always come to rest in the horizontal position. That the assumption of this position is not a heliotropic response can be shown by a klinostat experiment: Several pots, altogether with 8 developing shoots, have been revolved on the klinostat so as to neutralize gravitation, but not to neutralize light. The main axes and the lateral branches of the first order have shown positive heliotropic responses, but never negative nor transverse heliotropic, tho the revolution was continued till the plants had reached maturity. Were the horizontal position of main axis and branches due to the antagonistic working of geotropism and heliotropism, or to transverse heliotropism, we ought to have corresponding heliotropic movements in these klinostat

<sup>1)</sup> Conover, Behavior of *Asparagus plumosus* toward Gravitation and Light. (Plant World. XVI. 1913.)

experiments. Moreover, the main axis and the larger branches are positively heliotropic after both of these have taken the horizontal position, as has been seen many times in one-sided illumination.

The lateral branches of all orders seem to be from the beginning of their unfolding diageotropic. They do not begin to unfold till the main axis is near the end of its growth, and they have never been seen to assume the vertical position even temporarily. Since the lateral branches of all orders before they start unfolding lie appressed and parallel with the axis that bears them, and since, in the non-twining shoots, the main axis goes to the horizontal position before the lateral branches begin to unfold, it follows that these horizontal branches are already in the horizontal position when they begin unfolding. The shifting of position by these branches by which they come, all except the needles, to extend nearly at right angles to the respective axes which bear them, is therefore not due to diageotropic response, but must come from internal stimulation which causes each member, in the language of science, to assume its "proper angle". The needles, whether borne on main axis or a branch of any order, spread out in a horizontal layer like the spokes of a wheel, often filling a complete circle, but more often confining themselves to a semicircle. It is evident that the diageotropism of all of the horizontal members determines their horizontal position, but internal stimulation determines the position the branches shall occupy in this horizontal plane with respect to one another and to the main axis. So strong is this response to internal stimulation that a shoot which has taken the horizontal position and is placed parallel to a window with one-sided illumination will unfold its branches to the right and left of the main axis almost unaffected by the direction of light. That is to say, if we imagine a vertical plane to pass thru the axis of the horizontal shoot subjected to one-sided illumination, so that one side of the vertical plane is shaded and the other illuminated, we might expect that an unfolding branch which has its origin, say only  $10^{\circ}$  to the shaded side of the vertical plane, would bend across the vertical and place itself on the illuminated side. This result, however, does not follow in the experiment, but the branch swings out on the shaded side.

As pointed out by Miss Conover<sup>1)</sup>, the diageotropic shoots when still in a plastic condition make no effort to reverse when the plant is inverted; nor does main axis or branches twist thru an angle of  $90^{\circ}$  if the plane of the flanks of the horizontal members is revolved thru  $90^{\circ}$  about the horizontal axis. This result can mean nothing less than that the diageotropic members are radial and not dorsiventral as far as behavior is concerned. Structurally also, there is no evidence of dorsiventrality.

A young orthotropic shoot, revolved on the klinostat till grown to maturity, retains its orthotropic habit and retains also

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<sup>1)</sup> Conover, Behavior of *Asparagus plumosus* toward Gravitation and Light. (Plant World. XVI. 1913.)



its negative geotropism up to the cessation of growth. Plants, revolving as here indicated, have in 9 tests when the revolution was stopped before the plants were mature, shown negative geotropic curves in both the main axis and in the lateral branches.

## II. Relation toward Light.

The main axis of the seedling shoot and of the shoots arising from the rhizome are strongly positively heliotropic from their first appearance above ground to the cessation of growth with the tip in the horizontal position. The lateral branches of lower order than the needles are certainly less responsive to light than is the tip of the main axis, for they are but slowly and slightly deflected from their straight course by one-sided illumination. The lateral branches are under the domination of the 2 stimuli which cause them to take the horizontal position and their "proper angle" in this horizontal plane, and they are not easily diverted from their reaction to these two factors. The tip of the main axis, on the other hand, will readily bend aside from its straight course in response to light, even when the diageotropic shoot has unfolded the most of its branches and needles.

One of the effects of growing these *Asparagus* plants in the dark is to extend elongation enormously. A shoot that would grow to a total length of 15 or 20 cm in the light will attain an indefinite length in the dark. I have raised several such shoots to a height of over 200 cm, and discontinued the experiment with no indication of growth ceasing. This striking result in etiolation is accounted for to a limited extent by the greater length of internodes in the dark. The internode length of the main axis of a plant growing in light varies from 10 or 12 mm near the ground to 20 or 25 mm just below the first branch. In etiolated shoots, the length of internode varies from 12 mm to 60 mm, but the usual length is 25 to 38 mm. The increased length of internode would account for less than the doubling of the normal length of the plant. Since plants have been grown in the dark to 15 times the normal length, it follows that, in an etiolated plant, there are many more internodes formed. In other words, light, in the case of the normal plant, inhibits growth, speedily setting bounds to its duration. The shoots of my earlier preparations that grew to such great heights in the dark were grown in opaque black paper cones or cylinders, the neighboring green shoots from the same rhizomes being left in the light. It was then supposed that these etiolated shoots were supplied with assimilated material from the green shoots, and that we had here the unusual case of a shoot in the dark nursed by a neighboring assimilating shoot. To test the value of this hypothesis, the green shoots of several pots were wholly cut away and the pots were set in the dark. Within a week three rhizomes sent up each a new shoot. These were attended and watched for 6 months, when all plants were still living and had reached heights respectively of 177 cm, 74 cm, and 75.5 cm.



The tips of all 3 main axes and of some of the branches were dead. These shoots were now cut away, and the pots set again in the dark to watch developments. After 4 weeks, 2 of the rhizomes each sent up a slender shoot which continued to grow in the dark for over three and one-half months when engagements obliged me to end the experiment. From material stored in the rhizome and roots, therefore, two of these plants had continued growth for a year lacking 5 weeks. The 2 etiolated plants had borne altogether 7 branches. The total length of main axis and lateral branches was for one plant 266 cm, for the other 133.5 cm. This is a truly remarkable growth when one considers how small were the rhizomes and roots which furnished the material.

Besides the great elongation of the main axis, a characteristic of the etiolated shoot is the absence of branches. The appendages of the normal vegetative shoot are the nodal scales, the needle-bearing branches, and the needles. Of these 3, the etiolated shoot bears usually only the nodal scales. These scales seem, on the etiolated axis, to present about the same appearance as on an axis growing in the light. The needle-bearing branches of the first order would have numbered on the most of my experimental plants 10 to 20, had the plants been grown in the light. On only a few of the scores of etiolated axes have any needle-bearing branches appeared. Those axes that have shown branches were generally dead at the tip. However, 3 etiolated main axes did produce 1 to 4 lateral branches each, and with the main tip still living. Somewhat more numerous than the needle-bearing branches are the clusters of needles on the etiolated shoots. Since the main axis grown in the dark does not generally produce branches, one can look for the clusters of needles only at the nodes of the main axis. These needles are found on the etiolated shoot at not more than one node in twenty-five; most plants show none. When present on the etiolated shoot, their number in a cluster is greatly reduced, being from one to five, whereas on the shoot grown in the light, they would run from 7 to 25. The reduction in number probably is referable to the lack of elongation, as, with a lens, several very short needles can be seen in the clusters of the etiolated shoots.

No matter how long a shoot is kept in the dark, it remains remarkably sensitive to light, considering the fact that etiolated stems generally are more slowly responsive to a heliotropic stimulus than are those not etiolated.<sup>1)</sup> A reference to a single representative experiment will suffice for illustration. Five shoots that had been growing in the dark for 8 months were exposed in a window to light reflected from the sky. The temperature was 23°. In an hour all 5 shoots had made strong, positive, heliotropic curves of over 30°.

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<sup>1)</sup> Pringsheim, Einfluß der Beleuchtung auf die heliotropische Stimmung. (Beitr. Biol. Pflanzen. IX. 1907. p. 263.)

### III. Thermotropic Relations.

Inasmuch as subsequent study was to be made of the nutation of the shoots in the dark, and generally the method used to secure darkness was by covering the experimental shoots with black paper cylinders or inverted cones, thus allowing the uncovered shoots of the same rhizomes to carry on their carbon-assimilation, it was desirable to see how sensitive the covered shoots might be to differences of temperature on opposite sides of the opaque paper coverings. In this study it soon became evident that it would be unsafe to allow direct sunlight to fall on the covers even for brief periods. Sometimes in 40 minutes, and nearly always in an hour, strong negative thermotropic curves resulted from the shining of the sun on the covering, even tho the tips of the shoots were several centimeters away from the paper cover. When these thermotropic curves were made, the temperature within the covers varied from  $29^{\circ}$  to  $34^{\circ}$ .

### IV. Development of Diageotropism.

The following study enters into considerable detail of the development of diageotropism from negative geotropism in shoots from the seedling stage to the development of the twining condition, and hence deals with shoots up to an age of one and one-half to two years, except seedlings.

1. Heliotropism generally determines the plane of diageotropic curvature. If new shoots be allowed to come up from the rhizomes which already bear assimilating shoots, these growing shoots will be found, from the time they are 2 or 3 cm high, bending their tips from the vertical in response to the sunlight, making positive heliotropic curves from morning to night. During the night, the shoots erect their tips to the vertical position; and so this alternation of vertical with deflected direction goes on day and night till the development of diageotropism fixes the tip in a definite line of a horizontal plane. It is thus the influence of light which usually determines the direction of the plane of curvature of the diageotropic tip. But the heliotropic stimulus of light is not an absolute necessity to the taking of the horizontal position. If a potted plant with a vertical orthotropic shoot be placed in the dark some days before ready to assume the horizontal position, it takes this horizontal position in the absence of any heliotropic curve. But the plant in the dark offers gravitation, which causes the diageotropic curve, a footing for attack by the frequent nutations which carry the stem-tip  $10^{\circ}$  to  $20^{\circ}$  from the vertical.

2. Behavior of shoots never in light. The tests for this topic were carried out on shoots rising from rhizomes. In order to determine more exactly the effect of light, shoots were used that were never, from the origin of the bud on the rhizome, exposed to light. To obtain such shoots, pots of plants were examined



by digging the earth away from the base of the aerial shoots till unfolding buds were found on the rhizome. None of these buds were selected for experiment unless they had lain beneath at least a centimeter of earth; many of them were 2 cm below the surface. To shield these developing shoots from the light, cones were made of black cardboard, the smaller end 3 to 4 cm in diameter the larger about 15 cm in diameter. These cones were about 50 cm in height to start with, and were easily extended to any desired height by adding sections. To cover the young shoot, the earth was cleared away about it for a space large enough to receive the small end of the paper cone. The pot was then set on a heavy wooden base to whose sides had been fastened 2 upright wooden rods to serve as supports to the paper cone. The cone was then inverted over the bud on the rhizome and tied to the upright rods. About the base of the cone the earth was packed firmly to a depth of one to two cm so as to exclude light. The upper, larger, end of the cone was covered with several layers of black cloth, and over the cloth was pressed down a cap of black cardboard. These covering cones were very seldom removed during the progress of the experiment. Provision was made for observation by cutting windows in the sides of the cones, closing the windows with wrappings of black cloth or by partial cones of black paper sliding over the covering cones. A good many observations could be made by removing the cap over the upper end of the cone, and using a mirror to throw light into the cone. The assimilating shoots were left to continue their work outside the cones.

Altogether 20 shoots never exposed to light have been raised within these cones to heights varying from 30 cm to 200 cm, and observed for nutation. The general result, as far as the assumption of the diageotropic position is concerned, has been the absence of a fixed diageotropic position. Invariably the covered shoots have begun to lower their tips about the time they reached the height of the next youngest shoot outside the cone; and invariably, if the experiment was continued long enough, the tip has risen again before reaching the horizontal position, and continued growing erect for a period of days or weeks, to decline again later to  $15^{\circ}$  to  $45^{\circ}$  from the vertical, there to remain for a few hours to a few days, and again to assume the erect position. After one of these shoots had reached a height of a meter, more or less, its form was that of a straight cord except for an oblique portion, here and there, of one to a few centimeters in length, these oblique portions marking the positions at which the tip had remained for several hours to several days at an angle between the vertical and horizontal.

The following typical examples of detailed behavior will serve to put the case more precisely before the reader:

1) Covered shoot when 4 cm tall declined  $15^{\circ}$  for 2 to 3 hrs. — erected and grew vertical 30 days — then declined  $35^{\circ}$ , now 31 cm tall — after 1 day vertical again — after 12 hrs.



declined  $30^\circ$  — after 12 hrs. vertical — after 12 hrs. declined  $15^\circ$  — after 15 hrs. vertical, and so continued for 2 days when experiment ended. Total height 34 cm. Period of observation 36 days.

2) Shoot required 12 days to grow from 2 cm below surface of earth to 15 cm above earth, temperature averaging about  $22^\circ$ . All this time the shoot was erect, then 1.5 cm of apex bent  $15^\circ$  from vertical — thus for 27 hrs., then vertical — after 3 hrs. 45 min. declined  $15^\circ$  — after 55 min. vertical — after 10 hrs. 35 min. declined  $20^\circ$ ; from this time till the end of the experiment 35 days after the beginning, total height being 66 cm, the tip nutated up and down touching all points of the compass in irregular movements, never declining below  $40^\circ$  from the vertical, usually declining but  $15^\circ$  to  $20^\circ$ , never pausing more than 24 hrs. in one position, and erecting itself to the vertical position 11 times. For a period of 14 days, observations were made from 3 to 11 times daily.

3) Shoot 14 cm tall in cone when nutation began, 6 mm of tip declining  $10^\circ$  — after 1 day vertical — after 1 day declined  $10^\circ$  — after 1 day vertical — after 1 day declined  $20^\circ$  — next day declined to  $30^\circ$  — next day declined to  $45^\circ$  — after 1 hr. vertical — after 7 hrs. declined  $15^\circ$  — after 2 days declined to  $30^\circ$  — after 2 days declined to  $60^\circ$ , and so continued for 2 weeks when experiment ended. Total height of shoot 33 cm. Period of observation 35 days.

The foregoing three examples give the behavior of shoots thru a period within which these shoots in normal conditions would have developed the usual diageotropic frond. The following example is illustrative of the later behavior of 5 shoots which were followed to heights of from 109 cm as the lowest to 193 cm as the highest. All of these shoots were covered with the paper cones, or kept in a dark-room from the bud condition under the soil to the end of the experiment. Observations on number (4) were made every day, and for periods of several days at a time were made from 2 to 6 times a day. It is not to be supposed that all positions of these nutating stems were seen; but the observations were sufficiently frequent to detect any declination lasting 24 hours. Moreover a pause of 24 hours or more in one position, divergent by  $20^\circ$  or more from the vertical, must invariably be marked permanently in the stem by a considerable angle with the vertical. A summary of observations on one shoot follows:

4) For 22 days after coming above soil, plant, always in dark, showed no noticeable variation of tip from vertical, height then 39 cm — then declined  $30^\circ$  for less than 9 hrs. — then vertical for 45 hrs. — then declined  $25^\circ$  for 20 hrs. — then vertical for 24 hrs. — then declined  $30^\circ$  for 21 hrs. — then vertical for 5 hrs. — then declined  $40^\circ$  for 19 hrs. — then rose to  $20^\circ$  from vertical for 12 hrs. — then declined to  $40^\circ$  and for 6 days nutated up and down and laterally with declinations between  $20^\circ$  and  $70^\circ$  — then vertical for 24 hrs. — then declined to  $45^\circ$  for 9 days —



then rose to  $20^{\circ}$  below vertical for 2 days — then declined to  $45^{\circ}$  and experiment ended. Total height of shoot 109 cm. Total period of observation 46 days.

In the light this shoot would have made the diageotropic curve at a height of 15 cm to 20 cm.

The following is an example of 4 shoots which were never exposed to the light, which were not observed closely for details of nutation, but were followed in their later behavior to see whether they would adopt a constant direction of growth:

5) Shoot remained orthotropic for 18 days after appearing above ground, being then 23 cm tall. Mature assimilating shoots next older than one in the opaque cone averaged 21 cm vertical portion. From the beginning on thru a total period of 150 days, the shoot made a total growth of 177 cm, the tip then dying and a lateral branch being sent out later which continued the growth. During the whole period, after the first 18 days, the tip of the main axis alternately declined from  $45^{\circ}$  to  $70^{\circ}$  and rose to the vertical, remaining never more than a few days (1 to 8) in one position. The record shows the tip was vertical when the shoot was 48 cm tall, 61 cm, 79.5 cm, and 172 cm. The last height was attained only 8 days before the death of the tip.

3. Behavior of shoots exposed to light for one to several days. As clearly as the experiments illustrated by the foregoing examples demonstrate the inability of the plant in the absence of light to retain its plagiogeotropism, after relinquishing its negative geotropism, not less clearly does another set of experiments demonstrate the specific ability of light to make permanent this diageotropism even when light is cut off for days before the plant shows this reversal of response. This series of experiments has included the study of the behavior of 21 shoots of *Asparagus* from which light has been excluded after these shoots had been exposed to light from one to many days. The shoots were selected for exclusion from the light after they had attained various heights varying from 1 mm above ground to 8 cm above ground, the latter size belonging to shoots which were nearly ready to begin the diageotropic curve. The preparations were kept in the dark-room, or opaque covers as paper cones were used as in the former set of experiments, the assimilating shoots in the same pots being allowed to continue their functions. Representative experiments are given here.

6) Pot with a young shoot 8 cm above ground was removed from greenhouse to dark-room. Tip was already nutating preparatory to going to the transverse position. First day in dark, tip kept vertical position — second day, tip declined to  $25^{\circ}$  from vertical — after some nutation, tip reached the horizontal position on 4th day after placing in dark-room, held this position permanently and unfolded its branches, including needles.

7) Shoot 7 cm tall when covered — in the dark erect for 3 days — then declined  $30^{\circ}$  when 11 cm tall — 5th day declined to  $35^{\circ}$  — 7th day declined to  $80^{\circ}$  — 8th day declined to  $90^{\circ}$  —



9th and 10th day same position — 11th day lateral branches unfolding, and on to 14th day remained in same position with branches unfolded when observations ended.

8) Shoot 6.5 cm tall when covered, erect; older shoots outside cover, 9 cm tall when transverse bend was made. After 2 days, covered shoot bent  $45^\circ$  from vertical — after 3 days more declined to  $70^\circ$  — 1 day more same — during following 14 days declined to  $90^\circ$  and unfolded lateral branches. Numerous observations showed no considerable nutation of tip from time declination began. Total length of shoot 20 cm. Period of observation 26 days.

9) Shoot 7.7 cm tall when covered, erect; older shoots outside cover were 14 cm tall when transverse bend was made. After 2 days covered shoot declined to  $80^\circ$  — so continued for 10 days when lateral branches of first order were unfolded. Total height of shoot 18 cm. Period of observation 12 days.

The examples described under 6, 7, 8 and 9 above are clear cases of cessation of growth after the upper part of the shoots had reached the transverse position. The following 4 plants had perhaps not reached their definitive position, for they had not unfolded their lateral branches when the experiments were ended. These 4 shoots however declined steadily each in one plane, instead of nutating irregularly as did numbers 1, 2, 3, 4 and 5, indicating that light had some influence.

10) Shoot 1.7 cm above ground when covered, vertical; older shoots outside cover were 20 cm tall when transverse bend was made. After 8 days covered shoot declined to  $40^\circ$  — so continued for 12 days, when shoot 36 cm long — during next 8 days shoot declined to  $90^\circ$  where it remained for 6 days when experiment ended. Lateral branches were not unfolded. Period of observation 34 days.

11) Shoot 4.5 cm tall when covered — for 11 days mostly vertical, then declined  $30^\circ$  — 12th day same — 13th day same — 14th day declined to  $45^\circ$  when experiment ended.

12) Shoot 3.5 cm tall when covered — for 9 days vertical, then declined  $30^\circ$  — 11th day declined to  $35^\circ$  — 12th day same — 13th day declined to  $45^\circ$  — 14th day same when experiment ended.

13) Shoot 1.5 cm tall when covered — vertical till 11th day when tip declined  $15^\circ$  — 12th day same — 13th day vertical — 13th day evening declined to  $30^\circ$  — 14th day declined to  $40^\circ$ , and experiment ended.

The following 4 shoots were continued long enough under experiment to determine whether the plagiogeotropic position which they took was final. The effect of light is still evident:

14) Shoot 28 mm above ground when covered, grew erect for 10 days, when it reached height of 24 cm. Older shoots outside cover showed length of 21 cm, the diageotropic curve being 11 cm above ground. On 11th day, covered shoot declined  $15^\circ$  — so continued for 3 days, then declined to  $20^\circ$  — next day declined to  $30^\circ$  — 17th day vertical tip, leaving section below bent  $30^\circ$  —

18th day tip declined  $15^{\circ}$  — 19th day vertical — 20th day declined  $25^{\circ}$  — 21st day vertical in morning, declined  $30^{\circ}$  at evening — 22d day declined to  $40^{\circ}$  — 23d day declined to  $70^{\circ}$  — position maintained to 37th day, then rose to  $45^{\circ}$ , where it continued till 44th day — 45th day declined to  $70^{\circ}$  — 52d day vertical, and so continued for 4 days — 56th day declined to  $25^{\circ}$  — 59th day rose to  $10^{\circ}$ , and so continued for 3 days when experiment ended. Total height of shoot 117 cm. Period of observation 62 days. No lateral branches.

15) Shoot 22 mm above ground when covered. Older shoots outside cover about 20 cm long, bent to horizontal at middle. For 88 days this shoot was observed at intervals of 1 to 3 days, and seen to be behaving as number 14, now with tip vertical, now declined. On 88th day, tip was declined  $15^{\circ}$  from vertical, total height was 82.5 cm — 111th day, tip erect — 125th day, tip erect — 160th day, tip erect, experiment ended. Between these times when the tip was found erect, it was seen to be declined  $15^{\circ}$  to  $45^{\circ}$ , tho it probably erected and declined many times between observations. Total height of shoot 136.5 cm.

16) Shoot 18 mm above ground when covered. Next older shoot outside cone is 323 mm long, bent to horizontal about 17 cm above ground. 22 days after covering, shoot is 430 mm tall and is vertical — 37th day vertical — 48th day declined  $15^{\circ}$ , and so continued till 60th day when apex died at height of 95.5 cm. Experiment discontinued. Lateral branch continued the growth.

17) Shoot 3 mm above ground when covered. Next older shoot outside cone is 25 cm long, horizontal bend 17 cm above ground. 9th day covered shoot was 14 cm tall, declined  $15^{\circ}$  — 9th day, afternoon, tip vertical — next 5 days vertical — 15th day declined  $20^{\circ}$  — 16th day vertical and so remained 5 days — 21st day declined  $25^{\circ}$ , later in same day vertical — vertical 22d and 23d days, then bent  $20^{\circ}$  — 23d day vertical — 24th and 25th days vertical — 25th day declined  $30^{\circ}$  — next 3 days nutated up and down then vertical 2 days — 30th day declined  $15^{\circ}$  — 31st day declined to  $30^{\circ}$  — 32d day declined to  $45^{\circ}$  — 33d day declined to  $60^{\circ}$  — 35th day rose to  $30^{\circ}$ , same day declined to  $45^{\circ}$ , shoot 46 cm tall — 38th day vertical — during next 6 days tip nutated up and down from vertical to  $30^{\circ}$  declination, changing vertical plane of nutation daily or sometimes 2 or 3 times a day, observations made from twice to 7 times daily — 44th day tip declined to  $40^{\circ}$  where it remained without nutation for 2 days — 46th day declined in same plane to  $75^{\circ}$  where it remained 3 days — 49th day rose to  $45^{\circ}$  — 51st day rose to  $15^{\circ}$  below vertical — 53d day vertical and continued vertical for 10 days when experiment ended. Total height of shoot was 83 cm.

## V. Effect of Etiolation on Unfolding and Position of Branches.

On a former page of this paper it has been shown that a shoot grown in the dark adds greatly to the normal number of



internodes, shoots having been raised in the dark with 5 to 7 times as many internodes as they would have had in the light. To this phenomenon should now be added another, viz. the absence of branches, not including needles, on the etiolated main axis. Among several scores of shoots raised in the dark, 90% have shown not a single branch. And those giving rise to branches have produced in most cases but one on an axis, never more than 4. Except for the production of a few needles, the unfolding of branches has never gone farther than the primary, save in 3 instances in which the primary branches died at the tip and subsequently gave rise to secondary. These primary and secondary branches produced in the dark show no disposition to take the horizontal position as they do in the light; rather, they nutate, as do the main axes, between the vertical and the horizontal position, and in my experiments have often assumed the vertical position for periods of hours and days.

A little more numerous than the primary branches on shoots raised in the dark are the clusters of needles, as already mentioned when discussing the relations of growth toward light. These needles in the light spread out in a horizontal plane, but on etiolated plants they are stunted and grow out with a brush-like arrangement, as radii of a hemisphere, apparently uncontrolled by gravitation, but oriented by the position of the parent shoot and their relation to one another.

## VI. Development of Diageotropism on Removal of Etiolated Shoots to Light.

The etiolated shoots of *Asparagus* preserve their sensitiveness toward gravitation and light. In several instances, as already stated in this paper, these etiolated shoots have been tested with one-sided illumination, and found to make positive heliotropic curves within an hour.

These shoots retain their sensitiveness to gravitation also. A shoot that is vertical in the dark quickly bends back to the vertical when displaced. This was to be expected; but it is somewhat remarkable that the divergences which these etiolated, nutating shoots make with the vertical are also closely consequent on the change in response to gravitation. A shoot may be negatively geotropic today, plagiogeotropic tomorrow, and again negatively geotropic on the following day. Sixteen shoots confined in darkness from 1 to 6 months, and having various positions with relation to the direction of gravitation from  $0^{\circ}$  to  $90^{\circ}$ , were displaced from these positions. Some of them returned within 24 hours to their former directions, and the others left their new positions for directions more nearly coinciding with their former.

It is of interest to learn how these etiolated shoots which have never been exposed to light and have never developed a fixed diageotropic position will behave themselves toward gravitation when exposed to light. There have been in my experiments 13

shoots thus used. If these shoots were vertical when set out in the light, this direction was held for from 1 to 2 days, when the deflection to the horizontal position began. If the position of the shoots was  $45^\circ$  or more below the vertical when exposure to light began, the shoots invariably rose, reducing this angle by  $10^\circ$  to  $40^\circ$  during the first day and a half. The following is a representative instance of behavior:

18) Shoot grown in opaque cover to height of 66 cm with declination of  $30^\circ$  when set out under open sky at 7:30 A. M., and shaded from direct sunlight. Direction maintained for 36 hours, then tip rose  $15^\circ$  — next morning declined to  $30^\circ$ , but later in day rose again to  $15^\circ$  — 4th day morning declined to  $30^\circ$ , afternoon rose to  $15^\circ$  below vertical — 5th day declined to  $35^\circ$  and unfolded branches — 6th day declined to  $65^\circ$  — 7th day declined to the horizontal position and ceased nutation.

### VII. Behavior of Plants on the Klinostat.

Inasmuch as the development of diageotropism in normal growth is closely associated with the cessation of elongation of the shoot, it might be that that revolution on the klinostat might cause a greater than normal elongation. An additional reason for imagining that this might be so is the result of growing the plant in the dark — the production of a greater number of internodes and the absence of a final diageotropic position. When the test is made, however, it is found that revolution of the plant in the light with the axis of the klinostat horizontal causes no more than normal elongation. The shoot ceases growth at the usual size. Altogether 10 plants have been revolved on the klinostat to test this question, 6 with the axes of the shoots at right angles with the horizontal axis of the klinostat, and 4 with the axes of the shoots parallel with the horizontal axis of the klinostat. In the case of one of these plants, the revolution began before the tip of the shoot had come more than a millimeter above ground; the other shoots were from 1 to 6 cm high when revolution began. No unusual elongation was seen in any of them.

When revolution of these plants with the axis of the klinostat horizontal is conditioned so as to equalize light, the plant develops with all orders of branches related to the main axis as in *Asparagus officinale*. The aspect of the plant is very different from the usual. Instead of flattened frond, there is formed a central axis with branches growing out from it in several planes, these branches of the first order bearing their branches also in various planes, and finally the needles in brushes filling a hemisphere instead of flattened in a circle like the spokes of a wheel. Except for the needles, all of the branches of these plants grown on the klinostat make angles with the axis from which they arise of about  $80^\circ$  above and  $100^\circ$  below.

It is interesting to learn that as these plants grow to maturity on the klinostat, both main and lateral axes retain their



negative geotropism and positive heliotropism. At a time when branches of the first and second order are well unfolded, if the revolution of the klinostat is stopped at night, 3 or 4 hours suffice to produce upward curves at the tips of the main axis and branches. If the revolution is so carried out that the access of light is not equalized, the tips of the main shoot and branches will bend toward the stronger light. These results are wholly different from what one sees in plants in normal development; for in them main axis and branches are diageotropic as soon as the primary branches begin to unfold.

It has been shown in the work of Miss Conover, as well as my own, that the diageotropic axis of *Asparagus* is in a position of equilibrium however it may lie in the horizontal plane; and the same is true of the branches. Why then should this plant not develop diageotropism when revolved on the klinostat? Suppose that the plant is so revolved that its main axis is parallel with the horizontal axis of the klinostat. The main axis is always horizontal, but in spite of this it remains negatively geotropic. And in the same conditions of revolution the branches of the first order might place themselves in the horizontal position during revolution by bending forward or backward, parallel with the main axis.

Suppose, on the other hand, that the plant is fastened to the horizontal axis of the klinostat with the axis of the plant at right angles to the klinostat axis. In this position, some of the branches of the first order would be always in the horizontal direction if they merely grew out at right angles to the main axis. The main axis might place its tip in the horizontal (diageotropic?) position by merely turning  $90^{\circ}$  to the right or left of the direction of its older part. The evidence, however, is conclusive that diageotropism is not at all developed during revolution on the klinostat.

As the development of diageotropism has been detailed above for shoots placed in light after being raised in the dark, so the same process could be followed for shoots developed on the klinostat. But on the klinostat, main axis and branches hasten to their fixed position, while in the dark they make slow progress on their journey. Thus the development of diageotropism in plants raised to full maturity on the klinostat cannot be demonstrated by changes for which growth furnishes the evidence. The best that can be done is to remove such plants from the klinostat before they have wholly completed their growth. This has been done in the case of 2 pots with 5 shoots. The result was for the first one or two days a negatively geotropic elevation of the tips of the branches, followed after 3 days by a depression to the horizontal. The tip of the main axis also goes to the horizontal. The older parts of main axis and branches, which have unfolded in multiradial arrangement, retain this arrangement permanently, giving to the plant a very odd appearance.



## B. Behavior of Seedlings.

The fact that the normal mature aerial shoots of the seedlings differ in their appearance from those growing from rhizomes has already been pointed out. This difference consists in the position of needles and branches in the 2 kinds of shoots, the needles and all other branches on the shoots from rhizomes being flattened into a single horizontal plane, while the needles on seedling shoots spread out in many directions, and the branches bearing the needles are not all brot into a horizontal plane.

Not less striking than the difference noted above, is the difference between the behavior of seedlings and other shoots when grown in the dark. As already recorded, the shoots from rhizomes, if caused to form in the dark produce no branches and do not develop a definitive diageotropism, tho they do make transitory plagiogeotropic curves. The shoots of seedlings raised in the dark produce both branches and diageotropic apices.

Several small pots were planted with *Asparagus* seeds in the month of July. The shoots began appearing above ground after 26 days. As these shoots grew in hight they showed but little nutation till they were 8 to 10 cm high, about 10 days after appearing above ground. There were 14 of these seedlings growing in the dark. They all began declining but  $5^{\circ}$  to  $10^{\circ}$  the first day that declination began, the angle being 3 to 6 mm from the apex. For 2 or 3 days the tips nutated up and down, changing the plane of curvature, but not showing circumnutation. Soon the angle of curvature was seen to be 15 to 20 mm back from the tip while the declination went to  $15^{\circ}$  to  $30^{\circ}$ . After the first appearance of such a declination as this, the most of the shoots did not erect again and did not change the plane of curvature. The final planes of curvature were in about as many directions as there were shoots. Ten days to 2 weeks after the shoots began to decline at the tips, they had attained their final position. Six of the 14 had declined  $90^{\circ}$ , six were  $60^{\circ}$  to  $80^{\circ}$  below the vertical, one was  $45^{\circ}$ , and the other  $30^{\circ}$  from the vertical. The length of the declined portion varied from 7.5 cm to 2 cm.

These plagiotropic shoots bore branches also; only one of the 14 was without branches. The branches numbered from 2 to 6 on a shoot and varied in length from 3 mm to 45 mm. Each node of the plagiotropic part of the main axis, and each node of an unfolded branch bore needles; the apices of main and lateral axes also showed the needles diverging. The number of needles in a cluster was smaller than on a normal shoot, and the size of the needles was about one-half the normal. The smaller number in a cluster is probably due to the failure of many of the needles to elongate, as many short ones could be seen with a lens. The needles showed no control by gravitation in the positions they took, but the branches of lower order in general took the horizontal position; yet, a few branches on these seedlings, as already stated for seedlings grown in the light, took positions between the vertical and horizontal.



The tips of 3 of these 14 seedlings, for a length of about 3 mm, were declined at a smaller angle than the part lower down when the experiment ended; but in the rest of the plants, the tip continued at the same declination as the part below.

These preparations were continued for 7 weeks after the shoots began to appear above ground, for 34 days after the first seedling took its final diageotropic position, and 28 days after the last seedling took its final diageotropic position. These shoots have stopped growing; there is no indication of a resumption of the vertical position.

### C. Behavior of twining Shoots.

A description of the appearance and behavior of a normal twining shoot is given under the "Introduction" to this paper.

Several shoots growing in free earth in a bed in a greenhouse were chosen for experiment; all showed that they were, in ordinary conditions, destined to climb. They were tested for their behavior in darkness. These shoots were covered with sheetiron or cardboard cylinders 20 cm in diameter and of various heights.

1) The first shoot selected was 4 mm diameter at the ground, and 27.5 cm in height. It was orthotropic and bore no appendages except the nodal scales. Five days after exclusion of the light, the shoot had reached a height of 39 cm, and its tip diverged some  $45^\circ$  from the narrow bamboo stake stuck into the ground and rising in the axis of the cylinder. It showed no evidence of twining. The tip continued to rise in the same direction for 3 days more when it arched over, forming an arc of more than a semi-circle. Such a form of tip as this is taken in the normally growing plant as evidence of twining; but this tip did not twine. For two days more this shoot was watched, and then it died from over-heating in the cylinder unprotected from direct sunlight. The shoot had reached a height of 41.5 cm but had not twined about the stake. It is probable that, had it been growing in the light, it would have twined for the last 2 of the 10 days it was under experiment.

In subsequent experiments like the foregoing the covering cylinders were wrapped with several layers of white paper, air spaces being left between the layers. The removable caps, too, covering the upper ends of the cylinders were similarly protected from the sun, and there was no farther trouble from over-heating. The interior of the cylinders was thus kept cooler than the outside air in the hottest part of the day. This study was made thru the month of August.

2) A second shoot 35 cm in length, 4 mm diameter at the ground, was covered by a cylinder. Its tip at the time of covering had an S-shape curve 8 cm long. The shoot was tied to a bamboo stake about 7 mm in diameter. After 2 days under cover, the tip became vertical. On the 5th day in the dark, the shoot had grown to a length of 58.5 cm, and its tip was bent in an arc of



90°, radius about 5 cm. It had not twined. On 7th day, tip in arc of about 67°, but no twining. Observations were continued on this preparation for a total of 21 days, during which the shoot made a growth of 108.5 cm, reaching a total height therefore of 143.5 cm. Observations were made from once to 15 times a day. There was no twining. The most of the time, the tip nutated between the vertical and 90° below the vertical, often holding a declination of 45° below the vertical for a day. For the most of the time, however, the tip was in motion in both vertical and horizontal planes. These movements were followed by observations at intervals of 15 minutes for several hours on each of 3 days, and for shorter times on other days, in order to determine the character of the movements. The movements constituted irregular nutation, not circumnutation. Of course, if they had been circumnutation, the shoot would have twined, provided the tip was kept close enough to the stake, and the diameter of the circuit was great enough to carry the tip about the stake. Both of the last-named conditions were fulfilled: Tho the tendency of the tip was to grow off at an angle with the vertical — an angle of 15° to 45° — and the tip sometimes was found 6 cm in horizontal distance from the stake, the tip was frequently brot back to the vicinity of the stake by loosely looping a cord around stake and shoot 5 to 10 cm back from the tip of the shoot. Several times when the inclined tip was seen to be moving horizontally, the flank, a centimeter or two back of the apex, was brot against the stake so that a continuation of the movement would carry the tip around the stake; but the tip never continued long enough in the same direction to make a complete circuit. Several times the tip had risen to the vertical direction and remained for hours in the orthotropic position. When the cylinder was removed from the plant at the end of the experiment, the shoot showed a fairly straight stem with no coils, and no appendages except the nodal scales.

3) A shoot, 2 meters long and without any branches, that had wandered over the ground and among other plants in the same bed without finding any support to twine about was buried in earth 40 cm from its apex, and the distal portion brot upright and tied to a thin bamboo stake. After 24 hours, the shoot had made one and four-fifths turns about the stake. It was now covered with an opaque cylinder, and observed from day to day for 8 days. For 3 days the shoot continued to twine, making in all four and three-fourths turns about the stake. During these 3 days, the tip of the shoot approached nearer and nearer the vertical, straightening its arch, and thus narrowing the path of circumnutation and making a steeper coil than at the beginning of the period. For the last 5 days there was no more twining. The tip rose parallel with the stake, adding 9 cm to its length in these last 5 days. No branches were developed up to the conclusion of the observations.

4) A shoot that had already twined about a vertical cord, making a spiral 47.8 cm long, was covered by an opaque cylinder. This shoot was beginning to unfold lateral branches 30 cm below



the tip, the longest branch being 3 cm. No secondary branches had unfolded. The apex of the shoot at the time of covering was bent over into the horizontal plane and projected 3.5 cm laterally from the stake about which the stem was twining. The first day after covering, the shoot made 1 complete turn; the second day, 1 more complete turn, and shortened the free tip to 2 cm beyond the stake; the third day, 1 more complete turn, and shortened the free tip to 5 mm with a declension of  $45^{\circ}$ . The 4th day after covering, the shoot made half a turn and twined no more to the end of the experiment, 6 days later. As in former experiments, so in this, the tip was several times brot back to the stake so as to make it possible to twine if circumnutation was taking place. Observations at 15 minute intervals for several hours in each of several days disclosed that, as twining ceased, circumnutation ceased. Nutation continued thruout the experiment, but the oscillations became smaller and smaller toward the end. The greatest divergence from the vertical on the second day before the last was  $45^{\circ}$ , and the declination during the first eight and one-half of the last 27 hours extended from  $0^{\circ}$  to  $15^{\circ}$ . During these eight and one-half hours, the tip became vertical 4 times. As in the preceding case, the turns of the spiral became steeper as the shoot neared the end of the twining. The turns of the spiral made in the light were 53 mm apart, on the 2 last days of twining 60 mm apart, and the last half turn made at the conclusion of twining stretched a vertical hight of 80 mm. (All these turns were made about the same stake, the diameter being about the same thruout.) The total elongation after covering was 53 cm, of which 35 were made after twining ceased, and this section extended in a vertical line.

It should be said that in the middle of the experiment when the shoot had reached the top of the stake, a cord 2 mm diameter was tied to the stake and fastened taut to a cross bar in the top of the cylinder, thus affording a means for the shoot to twine even if the possible circumnutation was in a very narrow circuit. The absence of twining in these conditions, as well as my direct observations as before recorded, demonstrates that there was no circumnutation during the last 6 days.

The regaining of the ability to twine after etiolation had caused its loss was followed in the shoots of the last 2 experiments.

5) The covering cylinders were removed at midday, and behavior followed in a few observations. Twenty-four hours after exposure to light, both shoots had taken on a pale green color in their apical 10 cm, and both tips were declined about  $40^{\circ}$  from the vertical, the bent portion having increased from 1.5 and 2 cm when the coverings were removed to 3.5 and 4 cm respectively. Forty-eight hours after exposure to light, the tips had still longer portions declining from the vertical. This increase in length of curved apex was the most noticeable change since uncovering. Ninety-six hours after uncovering, one tip was declined  $40^{\circ}$ , and the other  $70^{\circ}$ , with the curved portions 5 cm and 8 cm long respectively. Both tips look as tho ready for twining, but both

have bent too far away from the cords to grasp them. The tips are now tied back to the cords. Thirty hours later both tips were found twining, one having made 2 turns, the other 3 and one-half turns about the cords. It is evident therefore that the shoots were circumnutating yesterday, and began twining as soon as tied in position to do so. Possibly they would have twined the day before if they had been in proper position.

## Discussion.

In the following discussion little time need be given to the consideration of the various activities of *Asparagus plumosus* which are similar to those of most orthotropic shoots. By reference to the experimental part of this paper, it will be seen that the aerial shoots of this plant, till they reach a height of 10 cm to 30 cm, are negatively geotropic and positively heliotropic, as are most plants. At least the extent of this study has not discovered important differences. The negative thermotropism of the shoots has been observed but not followed in detail. It is the peculiar behavior of this plant in turning the upper part of its aerial shoot to the horizontal, as does *Tropaeolum* and *Hedera helix*, that will here receive our chief attention.

### I. Cause of Plagiotropic Position.

In Miss Conover's<sup>1)</sup> paper, already referred to, very good evidence was given for regarding the plagiotropic position as due to diageotropism. This evidence, with my own added may be summarized here:

The plagiotropic declination is not due to negative heliotropism; for, in the first place, the shoot remains positively heliotropic while it is bending and after it has reached the horizontal position; and, in the second place, seedlings raised in the dark will go to the horizontal position, and shoots always in the dark, grown from rhizomes, will decline toward the horizontal.

The plagiotropic declination is not due to photonasty, for the same reasons as given in the last paragraph.

The plagiotropic position is not due to geonasty. The usual test for geonasty is made by inverting the plant so as to bring the formerly upper side of the shoot below; or the formerly upper side of the plagiotropic shoot is put in the flank position. The convex side of the curve should then become still more convex, on the supposition that the resistance of geotropism is removed by this change of position. This test, made for *Asparagus*, has given no indication that the plagiotropic curve in this plant is geonastic. Moreover, Miss Conover found by revolving a plant on the horizontal klinostat, the orthotropic part of the shoot being horizontal and the plant having recently made the plagiotropic

<sup>1)</sup> Conover, Behavior of *Asparagus plumosus* toward Gravitation and Light. (Plant World. XVI. 1913.)



bend, that the bend was promptly straightened out. If geonasty were the effective agent in bending the tip in normal conditions, then it ought not to be so readily overcome on the klinostat by autotropism.

I see no reason for calling this horizontal bend *geonyctonastic*, as Czapek<sup>1)</sup> applies this term to the bending of the flower stalk of *Papaver* and *Sedum*.

Diageotropism is the cause of the plagiotropic position. The horizontal position is assumed by the tips of seedling shoots kept in the dark from the seed. Revolution on the horizontal klinostat, started while the young shoot is orthotropic, causes the development of the shoot to maturity in the orthotropic condition, with all branches arranged radially and regularly spaced about the central axis. Miss Conover's result by the use of the centrifuge is also significant; since she found that if plants with young orthotropic shoots were kept on the centrifuge for several days, the tips of the shoots finally took a position parallel with the axis of revolution, this position corresponding to the plagiogeotropic position.

Altho the shoot becomes diageotropic on the centrifuge, it remains negatively geotropic on the klinostat, when revolved about its horizontal axis. As already noted, it might be that the main axis or its lateral branches would become diageotropic on the klinostat, since they are, or could place themselves by a small bend, in the horizontal position, that is, parallel with the axis of the klinostat. That they do not thus develop diageotropism is evidence that the plant must be at rest in order to give gravitation an opportunity to act for some time in the same direction on the cells which are active in the process of reversing the response to gravitation. A plant whose aerial shoot is in process of taking the diageotropic position may be reversed so as to place the formerly upper side downward. The bent portion of the shoot is uninfluenced by this change of 180°. But if the plant is revolved on the klinostat so that the horizontal axis of revolution passes thru the axis of the bent portion of the shoot, this bent portion being therefore in the horizontal position while revolving, the bent part goes back to the direction of the orthotropic portion of the shoot. This behavior shows again that, altho the cells acted upon by gravitation in bringing in plagiogeotropism may lie with any side directed toward the center of the earth, they must lie in the same position for a considerable time in order to give gravitation a footing for action.

## II. The Plagiotropic Shoot remains Radial.

Since the young shoot of *Asparagus*, while it is curving from the vertical to the horizontal, and still in a growing condition, may be inverted without changing the progress of the apical portion

<sup>1)</sup> Czapek, Geotropismus und Pflanzenform. (Wiesners Festschrift. 1908. p, 92.)

toward the horizontal, and since there is no torsion of the central axis after displacement from its former position, it follows that the plagiotropic shoot is radial and not dorsiventral. Unlike most plagiotropic shoots, that of *Asparagus* does not become plagiotropic till near cessation of growth. One may invert the plant at any time without causing the tips of main axis or branches to leave their horizontal position. This absence of dorsiventrality is evident in appearance as well as in behavior.

In the preservation of its radial condition, *Asparagus* resembles rhizomes,<sup>1)</sup> runners of *Fragaria vesca*<sup>2)</sup> and *Rubus caesius*.<sup>2)</sup>

### III. Effect of Light on Diageotropism.

The matter of the participation of light in the assumption by aerial shoots of the plagiotropic position is not at present in a satisfactory condition. Thus Czapek<sup>3)</sup> reports the shoot of *Glechoma hederacea* as horizontal in the dark, while both Oltmans<sup>4)</sup> and Maige<sup>5)</sup> report only the older shoots of this plant as horizontal in the dark, and state that the spring or young shoots grow vertically upward in the dark. Czapek<sup>3)</sup> reports the shoots of *Lysimachia numularia* as vertical in the dark, horizontal in the light; while Oltmans<sup>4)</sup> finds these shoots vertical in dark and in weak light, horizontal in strong light; and Maige<sup>5)</sup> finds them rising to the vertical position when transferred from diffused to direct sunlight. Illustrations of this sort could be multiplied. But, as Pfeffer<sup>6)</sup> points out, these differences would in large measure disappear, had all authors given attention as have Oltmanns and Maige, to the physiological state of the material they worked with — had they worked with plant — members of the same stage of development, and had they used the same intensities of illumination.

The earlier writings<sup>7)</sup> on the causes of change from the orthotropic to the plagiotropic position were wont to refer the behavior to a variety of responses, differing in different plants, such as negative heliotropism, positive geotropism, photonasty and

<sup>1)</sup> Elfving, Über einige horizontal wachsende Rhizome. (Arbeit. bot. Inst. Würz. II. 489.)

<sup>2)</sup> Czapek, Über die Richtungsursachen der Seitenwurzeln und einiger anderer plagiotroper Pflanzenteile. (Sitzber. Wien. Akad., Math.-naturw. Kl. CIV. Abt. I. 1895. p. 1197.)

<sup>3)</sup> Czapek, l. c.

<sup>4)</sup> Oltmans, Über positiven und negativen Heliotropismus. (Flora. 83. 1897. p. 1.)

<sup>5)</sup> Maige, Recherches sur les plantes rampantes. (Ann. Sci. Nat. Sér. 8. VII. 1900. p. 249.)

<sup>6)</sup> Pfeffer, Pflanzenphysiologie. Bd. II. 1904. p. 677.

<sup>7)</sup> Frank, Die natürliche wagerechte Richtung von Pflanzenteilen. Leipzig 1870. — Sachs, Über orthotrope und plagiotrope Pflanzenteile. (Arbeit. bot. Inst. Würz. II. 1879. p. 226.) — Czapek, l. c.



geonasty, as well as diageotropism; but the later writings<sup>1)</sup> show a tendency to refer the change in most plants to diageotropism alone, this diageotropism being, in many cases, induced by light. I fail to find anywhere in the literature a case in which the plagiotropic declination of a formerly orthotropic shoot may not be induced by the action of light. In the seedlings of *Asparagus plumosus*, however, we have such an instance. Raised in darkness from the seed, the aerial shoots make as great a declination as those raised in the light. The angles of declination run usually from  $45^{\circ}$  to  $90^{\circ}$ ; only one of my 14 seedlings showed its declination less than  $45^{\circ}$ . These angles are about the same as made by seedlings grown in the light; for while the declination of shoots growing from rhizomes is almost invariably  $90^{\circ}$ , that of normal seedlings is, in perhaps half of the number, less than  $90^{\circ}$ .

This prompt bending of the seedling shoot into the plagiotropic position in the dark was a surprise to me. One may assume that in phylogeny the appearance of this curve is secondary. Hence, on the principle that the seedling resembles, more or less, ancestral forms, one might expect the seedling in the dark to grow erect. The taking of the plagiotropic position in the dark under apparently the sole influence of gravitation might be interpreted as an inheritance, and the change of attunement to gravitation might be regarded as due to a phasogenic ekphory<sup>2)</sup> related to the approaching cessation of growth.

Altho it is evident by observation of seedlings kept always in the dark that light can have little if anything to do with the diageotropic position assumed by them, it is just as evident that light has considerable influence on the establishment of the diageotropism of shoots grown from rhizomes. It has been pointed out that the young orthotropic shoot of *Asparagus*, growing in light, usually has its vertical plane of curvature determined by the direction of light; that is, the positive heliotropism of the shoot keeps the tip more or less declined for a week or more before the diageotropism makes itself evident, and then the diageotropic decline is in the same vertical plane as the former heliotropic bend. This determination of the vertical plane of curving by light is exactly what takes place, according to Czapek<sup>3)</sup>, in the normal declination of the epicotyl of *Cucurbita pepo*. But this is not the only effect of light in this phenomenon. By reference to the part of this paper under the caption, „Behavior of Shoots never in Light“, it will be seen that without light, the shoots never attain a fixed plagiotropic position. They begin to make the plagiogeotropic decline in the dark, they may decline  $15^{\circ}$ ,  $30^{\circ}$ ,  $45^{\circ}$  or rarely go nearly to the horizontal, but after a pause of a few hours or a few days, they invariably erect themselves again to the vertical direction. And

<sup>1)</sup> Czapek, Weitere Beiträge zur Kenntnis der geotropischen Reizbewegungen. (Jahrb. wiss. Bot. XXXIII. 1898. p. 175.) — Maige, l. c.

<sup>2)</sup> Semon, Die Mneme. Engelmann, Leipzig 1908.

<sup>3)</sup> Czapek, Studien über die Wirkung äußerer Reizkräfte auf die Pflanzengestalt. (Flora. 85. 1898. p. 424.)



this alternate declension and erection of the tip continues as long as the shoot continues to grow in the dark, which may last for several months. This declension and erection of the tip is not mere ephemeral nutation. I could not see that *Asparagus* increased its ephemeral nutation in the dark, as Maige<sup>1)</sup> found to be true for *Stachys palustris* and *Mentha arvensis*. Each of the larger declinations that the tip took was immediately controlled by gravitation as was demonstrated several times by displacing the shoots from that position, and noting their quick return. There were also positions, divergent from the vertical, assumed often for but brief periods, an hour, more or less. Whether in such a case plagio-geotropism had taken the tip to its position, I had no means of determining, except to remember that on the horizontal klinostat in the dark such nutation did not take place.

By reference to that part of this paper entitled, „Behavior of Shoots exposed to Light for One to Several Days“, it will be seen that the effect of light on the assumption and retention of the diageotropic position makes itself felt at a distance of several days, 8 days at least. This is evidenced from the fact that those shoots which were covered from the light 8 days, or less, before they made the plagio-geotropic decline, retained the plagiotropic position permanently and unfolded their branches. Other shoots which were covered for a longer time before they made the decline, 11 days or more, probably would have erected later, but the experiments were not continued long enough to determine. But since the branches had not begun to unfold, it may be inferred that the shoot had not come to its definitive growth. Both in the normally growing plants and in those growing in the dark, the beginning of the unfolding of the branches was a sign that elongation of the main axis was about to end. The formation of the plagiotropic curve is thus a phase phenomenon, related to the physiological state, related to the approaching cessation of growth. Apparently, on the withdrawal of light, the inhibition of growth is removed and there arises a contest within the plant itself, on the one hand, for ending growth and making the plagiotropic curve, and, on the other, for continuing growth. Temporarily one tendency gains the ascendancy and temporarily the other, and thus the contest goes on indefinitely, but with the end-result favorable to growth; for the orthotropic elongation of the shoot in the dark is far in excess of the plagiotropic. In the case of seedlings, the exhaustion of stored food entails the cessation of growth in the dark. Whether the seedling shoots would make the plagiotropic bend in the dark, were there a continuing supply of food, we have no means of knowing.

That light bears some part in bringing the aerial shoot growing from the rhizome to the full diageotropic position, thru changing the response to gravitation is illustrated by the behavior of such

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<sup>1)</sup> Maige, Recherches sur les plantes rampantes. (Ann. Sci. Nat. Sér. 8. VII. 1900. p. 249.)



shoots when restored to the light after weeks or months in the dark. It has already been said that the position normally assumed by the shoots when growing in the light is the horizontal, and that etiolated shoots in the dark, as a rule, descend to an angle considerably above the horizontal, alternating up and down between the vertical position and a declination of  $15^{\circ}$  to  $45^{\circ}$ . On removing these etiolated plants to the light, diffused light because direct would be injurious in summer, they invariably lift their apex  $10^{\circ}$  to  $30^{\circ}$  after the lapse of 8 to 36 hours, then nutate narrowly up and down for 2 to 5 days, and then begin the rapid decline to the horizontal from which there is no return. Meantime, the branches begin to grow out, and growth of the main apex slows down. In watching the behavior of these plants, one cannot escape the conviction that the plagiogeotropism of the shoot in the dark is of a somewhat different quality from the plagiogeotropism of the shoot in the light. It might be more correct to say that the internal conditions surrounding the plagiogeotropism must be different in the two cases. Plagiogeotropism in the light is intimately associated with cessation of growth; in the dark, growth proceeds unchecked. The assumption of the transitory plagiotropic position in the dark is hesitating and variable; the movement to the plagiotropic position in the light is unhesitating and unvarying. One recognizes the phenomenon as a distinct change in behavior.

#### IV. Light as Related to Cessation of Growth.

Many times in the present paper the statement has been made that, if the shoots from the rhizomes are covered from the light early enough, these shoots have an indefinite elongation. These etiolated shoots not only have longer internodes than those growing in the light, but they have been raised with 7 times as many internodes as a normally growing shoot would have, and elongation was not then ended. It must be therefore that light acts as an inhibiting influence on growth, and in the absence of the inhibiting agent elongation finds no hindrance. Light alone, without the action of gravitation, is the inhibiting agent; for, on the klinostat in the light, a young shoot revolved about its axis laid horizontally ends its elongation as readily as when growing at rest. That the taking of the plagiotropic position is not the stimulus for cessation of growth is shown by the klinostat experiment in which growth ceased without a bend of the stem and without developing diageotropism. The inhibiting effect of light, however, is not direct. Changes are set in operation which continue to act for days after light is cut off. In the experiments cited in an earlier part of this paper the retardation of growth was not marked for at least 8 days, and the cessation did not occur for at least 12 days after light was excluded.

## V. Light as Related to Unfolding of Branches.

Goethe<sup>1)</sup> in his "Farbenlehre", stated that plants grown in darkness did not unfold their lateral buds. Sachs<sup>2)</sup> contradicted this statement, but Jost<sup>3)</sup> found that *Fagus sylvatica* did not unfold its lateral buds in the dark, and *Asparagus plumosus* follows the behavior of *Fagus*. In the case of seedlings, however, and in the case of shoots growing from the rhizomes, the shoots being removed from light not more than 6 to 8 days before ready to take the diageotropic position, the lateral buds unfold into branches not differing greatly from the normal. This unfolding of the buds of the seedlings and of the other shoots named is to be accounted a correlation when compared with the lack of unfolding in other shoots of *Asparagus*, since the shoots which unfold their lateral buds in the dark are all nearing the end of the growth of the main axis. This failure of etiolated shoots to unfold their lateral buds cannot be due to a lack of sufficient building material, since the main axis in many of my etiolated shoots grew for more than a meter after the normal time for unfolding the lateral buds. There was therefore enough material for forming the branches, but the plant did not dispose its supply of food for the unfolding of the lateral buds. Similar results are indicated by Sachs<sup>4)</sup> working with the growth of the leaves of *Cucurbita pepo*, and by Jost<sup>3)</sup> working with the leaves of some of the Leguminosae and the branches of *Fagus sylvatica*. Sachs' explanation of the smaller size of leaves in the dark is that the leaves become diseased; Jost has offered the hypothesis that it is due to the competition for food. There is a third possibility at least, that is that the plant disposes of its supply of food by correlation, correlation here not being equivalent to competition. None of these hypotheses attempts to show the mechanism of operation.

The lack of unfolding of the needle-bearing branches of the etiolated shoot extends also to the needles. Even in seedlings grown in the dark, which unfold the larger branches as well as tho in light, the needles are much reduced in size. The etiolated seedlings, therefore, agree in behavior with seedlings of most plants in failing to develop their assimilating organs in the dark.

## VI. Light as Related to Twining.

From the experiments already cited, it is evident that if a shoot destined for twining in the light is covered from the light

<sup>1)</sup> Goethe, Farbenlehre. Sämtliche Werke. Cotta'sche Ausgabe 1840. Bd. 37. p. 208.

<sup>2)</sup> Sachs, Bot. Zeitung. XXI. 1863. Beilagen. p. 11.

<sup>3)</sup> Jost, Über den Einfluß des Lichtes auf das Knospentreiben der Rotbuche. (Ber. d. D. Botan. Gesellsch. XII. 1894. p. 194.)

<sup>4)</sup> Sachs, Lectures on the Physiology of Plants. Translated by Ward. Oxford 1887. p. 532.



2 or 3 days before twining is to begin, the twining is wholly inhibited. Moreover, a shoot that has already been twining for some time may be made to cease twining in 3 days by depriving it of light. A shoot that has ceased to twine in the dark will, in the light, regain its ability to twine in 3 or 4 days in summer conditions. The relinquishment of twining is brought about by 2 changes in circumnutation: 1) The diameter of the circuit is greatly reduced, becoming zero when the tip rises to the vertical; 2) the regular movement of the tip of the stem changes to the irregular nutation of an ordinary orthotropic stem. The case has its points of resemblance to the behavior of the non-twining stem in the dark. In the latter, the plagiogeotropism alternates irregularly with negative geotropism; while with the twining shoots, the response to gravitation which leads to the regular circuit of the tip changes in the dark irregularly and transitorily to negative geotropism. But in the twining shoots in the dark, there is no temporary return to circumnutation long enough to permit one complete circuit; that is, there is not one complete turn about a support. The access of light restores to the plant its plagiogeotropism and its circumnutation, but only after the lapse of 3 or 4 days. The length of this restoration period indicates that here, as in the case of the non-twining shoots, there are internal processes concerned with the establishment of the plagiogeotropism which require considerable time for their consummation.

## VII. Biological Significance of the Behavior of *Asparagus*.

This *Asparagus* being in its greatest development a twining plant, and twining plants generally in their native habitat having to contend with the shade of the plants which give them mechanical support, one might wonder that the twining habit should be so readily relinquished in the dark. But it must be remembered that the degree of illumination necessary to insure twining has not been determined; it may be that weak light is sufficient. On the other hand, the plant, by growing straight instead of coiling, travels a considerably greater distance, and thus, other things being equal, stands a better chance of gaining the light. And, even without twining, the plant may be able to grow up thru a thicket by the aid of its hook-like nodal scales, which, it must be remembered, are the only appendages well developed on the etiolated shoot.

The advantage to the plant in changing, in the dark, its normally short shoots into vertical shoots of great elongation is too apparent to need comment. By this process the plant converts, as far as growth in the dark is concerned, its normally short, diageotropic shoots, and its normally long, twining shoots into shoots of a common habit of growth, a common appearance, both negatively geotropic and orthotropic; or, rather, it should be said that the resultant direction of growth is vertical or nearly so, so that the effect is as tho negative geotropism dominated the behavior.

However, tho the shoot at its earliest origin predestined to be a short non-twiner with horizontal tip, and the shoot predestined at its origin to be a twiner may be the same length, meters long, in the dark, may look alike and behave alike, the one is still in its inner capacity a non-twiner and the other a twiner, as subsequent exposure to the light demonstrates.

Lateral buds fail to unfold in the dark, and this may be regarded as an exemplification of the principle of conservation. The failure of the needles to attain their full size in the dark may be referred to the same class of phenomena as the stunted growth of leaves in the dark, since the needles are the assimilating organs.

The biological significance of the horizontal bend of the upper third to a half of the non-twinning normal shoots is not easy to perceive. If one were acquainted with the native environment of the plant the task might be easier. None of the benefits assigned to similar behavior on the part of *Hedera helix*, *Tropaeolum*, *Cucurbita*, *Glechoma*, *Vinca* and others will answer for *Asparagus*, for the reason that immediately on taking the horizontal position, *Asparagus* ceases to grow in length. If one observes a potted plant with 6 to 12 non-twinning shoots he sees that the horizontal portions of these shoots are in stories, one above another, the oldest below and the last formed the uppermost. The shoots interfere very little with one another, their arrangement in stories leaving horizontal spaces between the stories of fronds. This arrangement also can hardly cause sufficient shade to reduce the carbon-assimilation of the lowest story of shoots, for the fineness of the members of the branching system and their distance apart allow abundant light to penetrate to all shoots. But if the shoots grew erect, there would probably also be sufficient light tho the branches of the shoots would be crowded more closely together. If the plants grew closely together in beds, it would seem as tho the horizontal position would cause as much crowding as the vertical. Inasmuch as in nature we may suppose the direction of the plane of the diageotropic curve to be usually determined by the positive heliotropism of the shoot, it might follow that the shoot would receive more light in the horizontal position, because of shading from above, than tho it grew erect.

### Summary.

1. In form and behavior, *Asparagus plumosus* var. *nanus*, possesses 3 kinds of aerial shoots: 1) Seedling shoots which grow to a length of 10 cm to 15 cm, bend their terminal 3 cm to 5 cm into a plagiogeotropic position, while the branches not needles show a weak form of plagiogeotropism, and the needles are almost indifferent to gravitation; 2) non-twinning shoots from rhizomes which attain a length of 10 cm to 60 cm, bend the upper one-third or one-half of the shoot to the horizontal, while branches of all orders



including needles take the same horizontal, diageotropic position; 3) twining shoots from the rhizomes which grow erect for 40 to 60 cm, and then begin to twine, rising from one to several meters, finally bending the apical 10 to 15 cm over into the horizontal position, at the same time unfolding buds along the spiral stem and along the terminal horizontal portion, the branches of all orders taking the horizontal, diageotropic position.

2. The horizontal or oblique position taken by the various parts of the aerial shoot is due to a reversal of response to gravitation, the shoots being at first negatively geotropic.

3. Seedling shoots are able when grown in complete darkness to take the plagiogeotropic position as well as those grown in light; but aerial shoots from rhizomes require the presence of light to enable them to attain and retain the horizontal position.

4. Tho all kinds of shoots are positively heliotropic, the direction of light has nothing to do with the development of diageotropism, except that it may determine the plane of the diageotropic curve, by first causing a heliotropic curve, and thus giving gravitation a footing for the development of diageotropism. There is no evidence of geonasty or photonasty.

5. The influence of light on the development of diageotropism can be marked for at least 8 days after the plant has been placed in the dark.

6. Growing shoots, revolved about the horizontal axis of the klinostat, develop to maturity with no indication of diageotropism. The shoot develops its branching system with the same arrangement of parts as in an ordinary orthotropic plant, quite unlike the habit of this *Asparagus*.

7. When the aerial shoot becomes diageotropic and horizontal, it is still in morphology and physiology radial.

8. The elongation of the aerial shoot is brot to an end by the action of light. In the dark, growth seems capable of continuance as long as food lasts.

9. Only in seedling shoots do the lateral buds unfold in the dark.

10. The spinous nodal scales of the main axis of the aerial shoot are helpful in climbing, and develop about as well in darkness as in light.

11. The unfolding of lateral buds on the normal shoot seems to be phasogenic, as they do not unfold till the end of the growth of the main axis is near. This relation may indicate why the buds unfold on seedling shoots in the dark, growth being here brot to an end by lack of food, but do not unfold on shoots from rhizomes, these latter shoots while in the dark being supplied for a year or more with food from rhizome and roots.

12. The reversal of response to gravitation is also phasogenic, since it appears at the same time as the unfolding of lateral buds, being therefore related to the cessation of growth of the main axis.

13. The unfolding of lateral buds cannot be conditioned by the inception of diageotropism; for the branches develop on the

shoots revolved on the horizontal klinostat, while the shoot retains its negative geotropism.

14. The assumption of the diageotropic position by the apex of the shoot cannot be conditioned by the unfolding of the lateral buds; for, in one of my seedlings grown in the dark, the plagiogeotropic position was taken by a shoot whose buds never unfolded, and in the case of shoots from rhizomes, the shoots in the dark, temporary plagiogeotropic curves were made with no attendant unfolding of branches.

15. The assumption of the plagiogeotropic position by seedlings in the dark, and to a less degree by other shoots never exposed to light, has become hereditary.

16. The presence of light is necessary for the development of circumnutation, and hence for twining. A shoot that has been twining about a support will relinquish twining after the exclusion of light for 3 days.

17. The biological significance of various behaviors of *Asparagus*, like the removal of inhibition of elongation of the aerial shoot in the dark, the relinquishing of twining in the dark, the failure to unfold lateral buds in the dark, and the absence or stunted growth of needles in the dark, may be referred to the conservation of building material. The significance of the bending to the horizontal of the upper third or half of the aerial shoot from the rhizome and of the seedling may possibly bring the assimilating part of the plant into greater light.

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