OBSERVATIONS ON THE NUTATION OF HELIANTHUS ANNUUS.[1]

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IN the year 1890 Kellerman[2] reported some observations on the nutation of the sunflower, in which he concluded that, contrary to an almost universal popular belief, the heads of *Helianthus annuus* do not turn with the sun, facing toward the east in the morning and gradually moving westward until evening. He considered the belief mainly traditional, although he found some movement through a very small space, but rarely if ever through a space approaching a half circle. He suggested, however, that nutation might be more marked in the head previous to anthesis.

Having been a firm believer in the supposed nutation, and recalling numerous instances which seemed to support the belief, the writer desired to ascertain for himself the true facts in the case and also the conditions which may have given rise to the traditional belief. Accordingly a long series of observations were made in Clay county, Kansas, during the summers of 1896 and 1897, extending in both years from June to September. The summer of 1896 was especially favorable for the study, there being a more abundant and luxuriant crop of this characteristic western weed than usual. The western variety of *Helianthus annuus* differs considerably in many anatomical characters from the common cultivated variety which was not included in the study. The observations of the second season were entirely a confirmation of those recorded during the first.

[1] Contributions from the Botanical Laboratory, Ohio State University. II.

[2] Observations on the nutation of sunflowers. Trans. Kan. Acad. Sci. 12: 140–158. 1889–90.

1898]

NUTATION OF THE GROWING PLANT.

The observations were commenced on plants from three to five feet high, with stems varying from a half inch to an inch and a half in diameter. Observations were taken on a large number of individual plants, as well as on large patches of plants in general. In the morning, at sunrise, when the weather is clear, the plants all nutate toward the east or northeast at an angle of 45° to 75° from the vertical. The leaves stand out with rigid petioles so that their upper surfaces face the morning sun. When one stands looking toward the west, all the terminal buds and upper leaf surfaces face him. As the sun rises from the horizon, the plants gradually become erect and the leaves move at the same time so as to present their upper surfaces directly at right angles toward the rays of light. At noon the stems and terminal buds are vertical. During the afternoon the tops gradually nutate towards the west at an angle of 60° to 90° from the vertical. Usually the nutation is 90°. The upper surfaces of all the upper leaves have changed their positions so that they face due west and all those near the terminal bud have thus a more or less vertical position. The bending of the stem usually takes place about four or five inches from the tip and the curve represents merely the quadrant of the circumference of a circle, although sometimes it is more abrupt and angular (*fig. 1*).

By about 10 o'clock P.M. most of the stems have regained the vertical position, but at this time some may still be curved toward the west from 20° to 40°. The leaves now are turned downwards, drooping in such a manner that the apices all point vertically toward the earth. The curving is mainly in the petiole. This "sleeping" position contrasts quite strikingly with the day position, and it is taken both on cloudy and on starry nights. About 2 o'clock A.M., and usually much earlier, the leaves begin to be raised, and the tops of the stems turn toward the east gradually until sunrise, when they are again nutating from 45° to 75° toward the east.

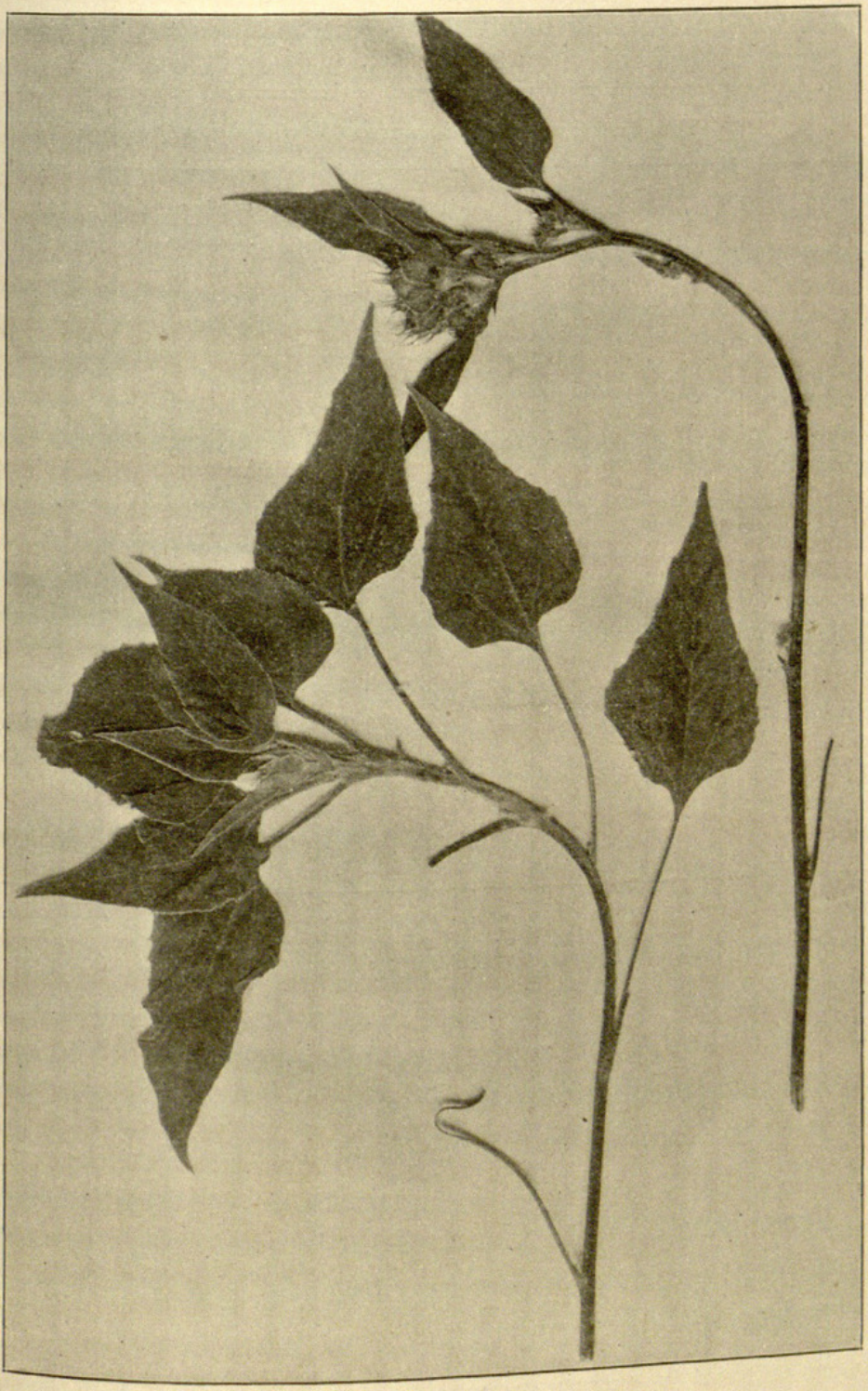

FIG. 1.—Two small plants of Helianthus showing westward nutation at sunset; photographed from pressed specimens with the natural curvature.

The following is a typical table of the nutation during twenty-four hours. July 11–12, 1897; two days after rain; sunshine and full moonlight throughout the period of observation; moderate wind from the northeast.

Time	Temperature	Angle of nutation	Direction	Remarks
5 p. m.	28° C	35°	West	Sunshine
6 p. m.	27	60	West	Sunshine
7 p. m.	24	75	West	Sunshine
Sunset				
8 p. m.	21	90	West	Full moon
9 p. m.	19	70	West	Full moon
10 p. m.	19	40	West	Full moon
12 m.	19	0	Vertical	Full moon
1 a. m.	19	30	East	Full moon
Sunrise				
5 a. m.	16	55	East	Sunshine
6 a. m.	17	70	East	Sunshine
7 a. m.	18	70	East	Sunshine
8 a. m.	19	40	East	Sunshine
10 a. m.	21	20	East	Sunshine
12 m.	22	0	Vertical	Fleeting clouds
2 p. m.	23	15	West	Fleeting clouds
3 p. m.	23	20	West	Fleeting clouds
5 p. m.	22	40	West	Fleeting clouds

There are thus four distinct periods in the daily nutation of the plant.

1. From shortly after sunrise, when the plant is nutating about 60° east, until sunset there is a gradual movement westward until the terminal bud faces west and the upper part of the stem nutates 90°.

2. From sunset until about 10 o'clock P.M., during which time the plant regains its vertical position and the leaves drop downward so that their apices point vertically toward the earth.

3. From 10 o'clock P.M. to 1 o'clock A.M., the period of repose.

4. From 1 o'clock A.M. until sunrise, a gradual turning eastward, accompanied by a rising of the leaves by which they are

again brought with their upper surfaces at right angles to the light.

Of course there is considerable difference to be observed in different individuals. Some regain the vertical position after sunset much sooner than others, and some begin to turn eastward long before 1 o'clock A.M. The nutations described here are not exceptional, but under ordinary conditions they occur in nearly all individuals, some nutating more prominently, however, than others. As soon as side branches are developed they partake of the movements to nearly as great an extent as the main axis.

If the bending of the stem and the diaheliotropism of the leaves is due to the direct stimulus produced by sunlight, then it is easy to see why the nutation should be considerably less in the morning than in the evening, since the light has much less time to produce the stimulus. But it may be that other causes have an influence on nutation. Thus at 11 o'clock P.M., while the leaves are all drooping, the crowns can frequently be seen turning toward the east which just two hours before were nutating 90° west. At 1 o'clock A.M., when it is evident no direct light can come from the sun, the tops of the stems are frequently seen nutating toward the east 30° or more, and the leaves are beginning to rise and stand up rigidly. Nor does it seem that the period of repose is brought on entirely by the falling of the temperature. From sunset until midnight there is a rapid fall in temperature, and during this period the "sleep" position is assumed. But there is also a rapid fall from 1 o'clock A.M. until sunrise, when the plant responds exactly in the opposite way. The drooping of the leaves then is not to be explained entirely as a means of protection against excessive radiation, for when the temperature is the lowest the leaves are already standing up rigidly and turning toward the east. Whether fluctuations in the humidity of the atmosphere had anything to do with this action, I did not attempt to investigate. I believe that this action is largely due to the fatigue of the protoplasm which must have expended an enormous amount of energy to keep up

the turgidity of the cells in the petiole during the day, and it resumes its work, after a period of rest, long before there seems to be any direct stimulus from the light.

EFFECT OF WIND, CLOUDS, DRYNESS, AND MOISTURE.

A moderate wind has little or no effect on nutation, no difference from what direction it comes. In Kansas the wind is very variable, but no important effect could be detected. However, when the wind blows very strongly it interferes somewhat with nutation. On some days when there was a very strong southwest wind the plants still turned west from 70° to 90°.

Cloudy weather has little effect on nutation. However, on some days it seems to check it a little. On some days, as for instance on July 27, 1897, it was cloudy nearly all the afternoon, but there was a strong nutation of 90° to the west.

Continued drought has a marked effect on nutation. When the ground is dry and the weather clear and hot the plants wilt, the leaves droop, and there is little or no nutation of the stem.

During rainy weather on cloudy days the nutation in the evening was scarcely noticeable. Also on a rainy day with sunshine in the latter part of the afternoon little or no nutation was discovered. When the ground was saturated with moisture and the atmosphere was very humid, although clear, very little nutation was observed. Thus in rainy weather, nutation is checked when it cannot be ascribed to a lack of sunshine. This was especially noticeable in the evening, but it was also very marked on mornings when the ground and atmosphere were saturated. When the ground is moderately moist and the air clear and dry with a light breeze, the conditions for nutation are at the optimum. At such times it is simply astonishing to notice a sunflower patch just at the setting of the sun. It thus appears that excessive moisture interferes greatly with the normal nutation of *Helianthus annuus*. This agrees with the observations of Cunningham,[3] who finds that plants react least readily to stimuli in a saturated atmosphere.

[3] The causes of fluctuations in turgescence in the motor organs of leaves. Ann. Roy. Bot. Gar. Calcutta 6 [Part 1, 4to. pp. 161]. 1895.

EFFECTS OF DECAPITATION, DEFOLIATION AND WOUNDING.

In order to determine through what organs the stimulus was received which caused the stems to bend, the terminal buds of a large number of plants were removed, and it was found that this treatment had no effect whatever, at least no noticeable effect, on the daily nutation. The decapitated plants acted in the same way as others not thus treated, nutating from 40° to 60° in the morning and from 60° to 90° in the evening. When conditions were favorable the decapitated plants nutated 90° west in the evening both on the day on which the operation was performed and for any number of days afterward.

Plants were also wounded by cutting slices from the side of the stem midway between the terminal bud and the central point of curvature, both on the east side and on the west. But this seemed to have no more effect on the nutation than would follow from the mechanical interference caused by the wound.

Plants were next treated by cutting off the leaves. In some the leaves were cut close to the stem, while in others the laminæ were cut off, the petiole being left. Plants thus treated immediately lost their power of nutation. They would stand perfectly upright, while their neighbors not so treated would nutate 90°. Some delaminated in the evening were found to be still inclining toward the west in the morning, while others had regained the upright position. When the leaves were cut in the morning the plants were found to be perfectly upright in the evening, while the natural ones and some decapitated the same morning nutated 90° west.

Thus it appears that decapitation has no effect on nutation. Wounding the side of the stem affects nutation only to the extent that it produces mechanical interference. Delamination, whether of the blade or of the entire leaf, stops nutation entirely. It was observed in some plants which had been delaminated that after the leaves and stems of the terminal bud had grown out again nutation was continued in the new parts, but the bending was confined to those parts and did not extend below.

From the above it is demonstrated that the irritability which is responsible for the bending of the stem is not inherent in the stem itself, but the stimulus is received by the lamina of the leaf, and the impulse transmitted through the petiole to the stem produces a response from both these parts.

NUTATION OF THE HEADS BEFORE ANTHESIS.

About July 15 the behavior of the young heads began to be observed. It was found that both the terminal heads and those on side branches nutated to the same extent as the leaf buds. Young heads on long, naked stems coming from the axils of leaves nutated also, the bracts of the involucre acting no doubt the same as the ordinary leaves. When the leaves were removed from the stems bearing heads, the nutation did not cease. Thus, on August 2 the leaves were removed from plants having young heads, and the next day these nutated 50° east in the morning, and 90° west in the evening. This experiment was repeated many times with both terminal and lateral heads, always with the same results. After the leaves have been removed from a plant having forty or fifty heads the effect of the nutation becomes quite striking.

THE DISK DURING ANTHESIS.

The nutation of the heads continues until anthesis begins. At this time the stem below the head hardens, which makes further nutation impossible. During anthesis the head is tipped sidewise until it stands with its face almost vertical, and this nodding is nearly always toward the northeast, although it may be east or north also. During favorable weather, at least 90 per cent. of the open disks will be found facing the northeast, both in the morning and in the evening. The heads are not disturbed by light wind, but a strong wind twists the stems and thus greatly disturbs the normal position of the heads. Whole acres of plants were observed in regard to these points. The eastward position of the disks readily deceives one into thinking that the face moves with the sun, especially when observations

are taken only in the morning. The nodding of the heads takes place about the time when the ligulate florets have all expanded; sometimes, however, it begins earlier. When the disk nods toward the northeast, the bracts of the head are brought with their outer surfaces into the most advantageous position for the process of photosyntax, and can thus continue to manufacture food which can no longer be transferred so readily through the elongated and hardening stem. This is of great advantage to the developing seeds of the large disk. There is also another advantage. The disk is turned away from direct sunlight, bringing the conditions to an optimum for the processes of pollination and fertilization.

Meehan[4] has observed an eastward turning of the heads of *Helianthus mollis*. He states that it has a southeasterly face on opening, and that it turns not with the sun but eastwardly as the head progresses toward maturity.

HELIANTHUS RIGIDUS.

During the summer of 1897, observations were also made on the nutation of *Helianthus rigidus*. Nutation in this plant is even more marked than in *H. annuus*. Young leafy stems and some with young heads were observed to nutate from 70° to 80° east in the morning and 90° west in the evening. The point of bending is quite low, usually about eight inches from the tip. Because of the naked and slender stems which bear the heads and the vigor with which they nutate, this plant should be an exceedingly favorable object for the study of curvature in stems, since it could be manipulated almost as readily as can the roots of seedlings.

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[4] BOT. GAZ. 9 : 49–50. 1884.