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Preliminary Notes on the Epinasty and Hyponasty of Raphainus Cotyledons

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auxanometer methods to root-stocks by uncovering the root-stock attaching a silver thread, running it horizontally to the open side of the box passing over a horizontal roller and upward and finally adding the linen (or silken) thread which runs on the small circumference of the first wheel. Or in this case one wheel alone could doubtless be used. This study of underground stems, as in the grass root-stock, the potato rhizome or any other underground stem, would throw some light upon the tuber and its method of growth. A comparison of underground organs should be made along this line.

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PRELIMINARY NOTES ON THE EPINASTY AND HYPONASTY OF RAPHAINUS COTYLEDONS.—*E. P. Sheldon.*

In presenting this evening some of the phases of our present knowledge regarding the various positions assumed by dorsiventral organs during their period of growth and development, I think I can do little better than to give a short outline of the views held by prominent botanists on this point, and follow somewhat the course of development of such views as outlined by Sydney H. Vines, in his article on Epinasty and Hyponasty.*

First in importance are the views of De Vries.†

Here we have the first recognition of the fact that the growth of the two sides of a dorsiventral organ is not equal. There may be some growth on both sides of such an organ, but when the growth of the upper side preponderates over the growth of the lower organ it is said to be in a state of epinasty. When the reverse is true it is said to be in a state of hyponasty.

De Vries does not agree with Frank‡ in regard to the cause of the position of such members.

Instead of explaining their position by peculiar forms of geotropic and heliotropic irritability, he considers them as a resultant of the various forms of epinasty, hyponasty, and negative or positive heliotropism or geotropism. The observation of Sachs§ on

*Annals of Botany. Aug., 1889.

†De Vries: Arb. d. bot. Inst. in Würzburg, I, 1874.

‡Frank: Die natürliche wagerichte Richtung von Pflanzentheilen Leipzig, 1870.

§Sachs: Arb. d. bot. Inst. in Würzburg, II, 1879.

the thallus of *Marchantia* are directly in this line, and tend to uphold the position of De Vries. The observations of Darwin¶ have shown us that dorsiventral organs tend to place themselves at right angles to the direction of the light rays, and further that the phenomena of epinasty and hyponasty are to be considered as a modified form of circumnutation. One of the most important contributions to our knowledge of the subject is that of Detmer.**

By means of a series of observations in which dorsiventral organs were subject to varying intensities of illumination, Detmer comes to the conclusion that the position assumed by such are due not to the *photonic*, but to the *paratonic* action of light; and therefore instead of a condition of epinasty, it is in reality one of "photo-epinasty."

Coming now to the observations of Vines†† we find that he states the primary object of his experiments to be:

(1) "To ascertain whether epinasty and hyponasty are spontaneous movements, or are induced by light or other causes as stated by Detmer; and (2) whether the curvatures of dorsiventral members which have hitherto been ascribed to negative geotropism, are or are not due to this cause." He repeats the experiments of Detmer with the cotyledons of *Cucurbita* seedlings and with the primordial leaves of *Phaseolus*, and comes to the conclusion that "the effect of light is not '*paratonic*,' as Detmer would have it to be, but it is '*phototonic*;'" or in other words, that epinastic growth can take place in darkness.

It will be noted that these conclusions render the term "photo-epinasty" of Detmer useless.

To further establish his position, Vines notices that in seedlings of *Helianthus, Dahlia, Fuchsia,* and *Urtica*, epinasty is stimulated by the absence of light rather than bv its presence.

Continuing his experiments with *Plantago media* and *Taraxacum officinale*, he finds that specimens of these plants kept in darkness for 72 hours become decidedly hyponastic, and this happens whether the plant was placed in its normal position, or rotated on the clinostat. From this he comes to his second conclusion viz: that "Dorsiventral members are not negatively geo-

¶F. Darwin: Journal Linnean Society, XVIII, London, 1881. See also "Movements of Plants," 1880.

**Detmer: Bot. Zeitg, 1882.

††Vines, l. c.

tropic." Early last spring Professor MacMillan of the University brought a plant of *Solanum tuberosum* from the greenhouse and placed it upon a desk in his lecture room. The plant while in the greenhouse was under the influence of strong illumination. In the lecture room it had only diffuse light. In the course of 24 hours a remarkable change took place in the position of the leaves. Instead of being horizontal or slightly epinastic as they were under normal conditions, they were curled downwards so that the tips touched the stem. At the same time transverse epinastic curvatures had taken place.††

This seemed to show that the absence of light of a certain degree of intensity tends to promote epinastic curvatures. It was a realization of this peculiar state of our knowledge regarding epinasty and hyponasty that led Professor MacMillan to suggest to me the advisability of selecting some normally epinastic dorsiventral organ and subjecting it to varying degrees of intensity of light, as well as to varying intensities of light from different directions. Not only was a study of the action of light upon such an organ suggested, but also of all other natural conditions which might influence epinastic or hyponastic growth.

For this purpose the cotyledons of *Raphanus sativa* have been chosen. So far as I have been able to determine, no continuous observations have been made upon the epinastic and hyponastic curvatures of these normally epinastic organs.

The experiments were conducted in the University greenhouse, and the temperature in all cases was approximately the same, varying from a minimum of 60°-65° Fahr. by night, to a maximum of 75°-80° by day.

The seeds were planted Dec. 20th, in four-inch flower-pot saucers, and were constantly kept at the same degree of moisture. Before proceeding to a consideration of the phenomena observed it might be well to note in regard to the germinating seed of *Raphanus*, that in all cases when the cotyledons break from the seed-coats they are folded together, the lower and larger cotyledon always being strongly hyponastic, while the smaller and inner cotyledon is always strongly epinastic.

Two groups of cultures were made:

A. Those grown under normal conditions from the first.

B. Those grown under special conditions from the first.

††MacMillan: Botanical Gazette, Vol. xv, p. 121.

A.

NORMAL CONDITIONS.

For purposes of comparison let us first note the growth of the organs selected when exposed to ordinary conditions of strong illumination on a shelf in plant-house.

After 24 hours. Seeds swollen, but cotyledons not leaving seed coats so that no observations could be taken.

After 48 hours. Cotyledons have left the seed coat. The lower and larger are strongly hyponastic, fiwhile the inner and upper ares trongly epinastic. Slightly turned downward.

After 72 hours. Upper cotyledons slightly hyponastic, both now being curved outwards: *i. e.* both hyponastic. Not separated.

After 96 hours. Cotyledons separated, owing to the epinastic curvature of the hypocotyls. Strongly epinastic, upright.

After 120 hours. Cotyledons epinastic, separated. Plants 1 inch high.

It is interesting to note with regard to these that if one observes them early in the morning they are nearly always slightly hyponastic, especially if the weather is dark or cloudy. Later in the day, (*i. e.* 9 to 10 o'clock) they are found to be epinastic. The organs with which we have to do are evidently very irritable.

B.

SPECIAL CONDITIONS.

The special conditions may now be followed in the order of experimentation.

1. *Diffuse daylight.*—This was secured by selecting a convenient place under the shelves of the plant-house, sheltered from the rays of the sun and the reflection from the glass roof.

After 48 hours. The same phenomena are to be noted as in A, but less vigorous; cotyledons less opened, turned downward.

After 72 hours. Curvature less than in A. Cotyledons parallel, turned downward.

After 92 hours. Cotyledons most of them upright and parallel. The upper has overcome its epinasty and become slightly hyponastic, while the lower is still slightly hyponastic. Sometimes slightly epinastic, often straight.

After 96 hours. Cotyledons hyponastic. Not separated.

After 120 hours. Cotyledons hyponastic. Not separated.

After 144 hours. Cotyledons hyponastic. Separated

After 168 hours. Cotyledons hyponastic. Unchanged.

2. *Total Darkness.*—Using boxes placed one within the other

and lined with tin and tar felt, so as to preclude all possibility of the entrance of light.

After 48 hours. Same curvatures as in A, but cotyledons not opened as much. Strongly etiolated.

After 72 hours. Cotyledons hyponastic. Not separated, turned downwards.

After 92 hours. Cotyledons hyponastic, upright. Not separated.

After 96 hours. Cotyledons hyponastic. Slightly separating.

After 116 hours. Cotyledons strongly hyponastic. Slightly separating.

After 140 hours. Cotyledons strongly hyponastic. Unchanged.

3. *Faint illumination.*—Made by placing the saucers under square frames, covered with shades of cloth.

After 48 hours. Cotyledons separating (opening) upper epinastic, lower hyponastic, turned downwards.

After 72 hours. Upper cotyledons epinastic, lower hyponastic. The tendency is toward parallelism of the cotyledons.

After 96 hours. Cotyledons hyponastic. As compared with No. 1, (Diffuse light) they are more sŏ at this age.

After 120 hours. Cotyledons hyponastic. Not separating.

After 144 hours. Cotyledons hyponastic. Not separating.

After 168 hours. Cotyledons hyponastic. Separating. Upper cotyledon with shorter pedicel, lower with longer.

After 192 hours. Cotyledons hyponastic. Separating.

4. *Illumination from the side.*—Produced by placing saucers at the back of low boxes with one side wanting, and exposing open side toward strongest light direction, *i. e.,* the path of the sun. In this manner we get light coming mainly from the one direction, and by placing the seedlings so that illumination may be directed toward the side of the cotyledons we may study this condition. Light here is necessarily somewhat diffuse. By arranging a mirror strong illumination may be secured.

After 48 hours. Upper cotyledons epinastic, lower hyponastic.

After 72 hours. Cotyledons turned downward. Upper epinastic, lower hyponastic. It is to be noted that the upper cotyledons are presented toward the direction of the incident light rays.

Three saucersful placed in opposite direction, *i. e.,* with lower cotyledons toward light direction.

After 96 hours. The result has been that those so placed have turned around, and persist in presenting their upper cotyledons toward the light. Cotyledons hyponastic.

After 120 hours. Those turned yesterday so as to have side illumination, have turned around and persist in presenting their faces to the incident light rays. Hyponastic.

5. *Strong illumination from end (toward notch between cotyledons).* Planted under same conditions as No. 4.

After 48 hours. Upper cotyledons epinastic, lower hyponastic.

After 72 hours. Same as No. 4. A number of plants so placed as to throw direction of light rays toward notch between cotyledons.

After 96 hours. Cotyledons hyponastic. Those placed so as to throw illumination toward notch between cotyledons have closed. More may now be so placed.

After 120 hours. Cotyledons all strongly hyponastic. Separating, owing to the epinastic curvature of the hypocotyls. They have all turned so that the light is directed toward the notch.

6. Exposed for 12 hours to total darkness, 6 to strong illumination, 18 to total darkness, and 12 to diffuse daylight, (repeat.)

These were planted Dec. 20th, 6 p. m.

After 12 hours. Put in strong illumination.

After 18 hours. Put in dark. Germinating.

After 36 hours. Put in diffuse light.

After 48 hours. Put in dark. Same phenomena of curvature as in A.

After 60 hours. Put in strong illumination. Upper cotyledons epinastic, lower hyponastic.

After 66 hours. Put in dark. Cotyledons strongly epinastic. In many cases they are parallel. The epinasty of the upper cotyledon being lessened, with tendency toward hyponastic curvature. The upper cotyledon does not become hyponastic, but does become less epinastic until the lower cotyledon overcomes its hyponastic curvature.

After 84 hours. Put in diffuse light. Cotyledons hyponastic, upright, separating, owing doubtless to the epinastic curvature of the hypocotyls.

After 96 hours. Put in dark. Cotyledons hyponastic, but less so than 12 hours ago.

After 108 hours. Put in strong illumination. Cotyledons hyponastic.

After 114 hours. Put in dark. Cotyledons hyponastic, but less so than 6 hours ago.

After 132 hours. Put in diffuse light. Cotyledons epinastic.

After 144 hours. Put in dark. Cotyledons present a very peculiar appearance. They are still slightly epinastic, but the edges are curled upwards, showing tendency toward hyponasty.

After 156 hours. Put in strong illumination. Cotyledons epinastic with edges curled upward.

After 162 hours. Cotyledons epinastic, with edges not curled upwards.

The plants were now put in total darkness, and kept in this condition for ten days. Observations were made at 12 M. on each day, but in all cases they were strongly epinastic. Some of these were repeatedly exposed first to light then to darkness, but this produced no further curvatures.

7. Exposed for 12 hours to dark, 12 hours to diffuse light, 18 to dark, 6 to strong light, 12 to dark, 6 to strong light, 6 to diffuse light, 12 to dark, 6 to diffuse light, 18 to dark, and 12 to strong light. (*Repeat*). These also were planted Dec. 20th, 6 p. m.

After 12 hours. Put in diffuse light. Seeds swollen and sending out roots, but not opened enough to see different curvatures. This seems to be the most favorable condition for germination.

After 24 hours. Put in dark.

After 42 hours. Put in strong illumination. Upper cotyledons epinastic, lower hyponastic.

After 48 hours. Put in dark.

After 60 hours. Put in strong illumination. Cotyledons barely opened, showing no tendency to curvature which might separate the cotyledons.

After 66 hours. Put in diffuse light. Cotyledons separated. The epinasty of the upper has become less apparent, as has the hyponasty of the lower, turned downwards.

After 72 hours. Put in dark.

After 84 hours. Put in diffuse light. Cotyledons slightly epinastic, upright.

After 90 hours. Put in dark. Cotyledons hyponastic. Not separated.

After 108 hours. Put in strong illumination. Cotyledons hyponastic. Not separated.

After 114 hours. Cotyledons hyponastic, but less so than 6 hours ago. Not separating.

After 120 hours. Put in dark. Cotyledons slightly epinastic. Separating.

After 132 hours. Put in diffuse light. Cotyledons epinastic. Separated.

After 144 hours. Put in dark. Epinastic.

After 162 hours. Put in strong illumination. Cotyledons slightly hyponastic.

After 168 hours. Put in dark. Cotyledons hyponastic but less so than 6 hours ago.

After 180 hours. Put in strong illumination. Cotyledons slightly hyponastic.

After 186 hours. Cotyledons epinastic.

To summarize these results we find that the cotyledons of *Raphanus sativa* are always epinastic when grown under normal conditions of light, temperature and moisture. Considering the temperature and moisture the same in all cases, we find in respect to these organs, that when grown under a condition of total darkness, diffuse or faint light, they are always hyponastic. When grown in total darkness the cotyledons are very sensitive to the influence of light.

In the case of one trayful, 72 hours old, which was exposed to diffuse light while taking notes, the cotyledons curved perceptibly, so that they were but slightly hyponastic. It is to be noted also that after 96 HOURS in the dark, epinastic curvature of the hypocotyls took place, thereby separating the cotyledons.

The illumination in the case of the light coming from only one direction must be toward the notch between the cotyledons.

Before the cotyledons are 96 hours old, however, they will close if illumination is directed toward the notch. This may be assigned to hyponastic curvature of the hypocotyls.

It might seem as if this is a wise protection for the tender epicotyl. With this is to be correlated the fact that in total darkness a certain period of time elapses before epinastic curvature of the hypocotyl takes place.

When we consider the cultures in which the organs under consideration were exposed to varying conditions, as in Nos. 6 and 7, we find that a broad field of investigation opens out before us. Let us first look carefully at No. 6.

After 66 hours we find that by 18 hours exposure to total darkness the cotyledons become changed from a strongly epinastic to a hyponastic condition. This seems to show that the absence of light in this case is favorable to a hyponastic position.

After 108 hours, the cotyledons being at that time hyponastic, they were placed in strong illumination for 6 hours. At the end of this period they were placed in dark for 12 hours, then in diffuse light. Not until this latter change took place did the cotyledons show any marked epinastic curvature. This, and the peculiar appearance of the cotyledons in the two succeeding states have led me to think that we have here a manifestation of a latent period of growth with respect to epinastic curvature. It is peculiar that when this epinastic condition was obtained the absence or presence of light should have no further effect on the cotyledons.

With respect to No. 7, it is only necessary to point to the difference in the results. In the latter we have without doubt a set of changes which instead of tending towards fixation of position, tend in exactly the opposite way, *i. e.* toward extreme irritability. It has now become apparent that what is needed is accurate permutations of these conditions, varying the time to secure results which explain the phenomena noted in this paper.

That the influence of light upon dorsiventral organs which produces epinastic or hyponastic growth is dependent on the intensity of light-vibrations is beyond a doubt. To determine the intensity of vibrations required to produce a given curvature, and to solve some of the problems indicated by these notes is the object of further experiments being conducted at the University. A series of permutations are now under way and an effort will be made to cover as much of the debated ground as possible.

February 3, 1891.