Band LXI. No. 5. XVI. Jahrgang.

Botanisches Centralblatt.

REFERIRENDES ORGAN

für das Gesammtgebiet der Botanik des In- und Auslandes.

Herausgegeben

unter Mitwirkung zahlreicher Gelehrten

von

Dr. Oscar Uhlworm und **Dr. F. G. Kohl**

in Cassel. in Marburg.

Zugleich Organ

des

Botanischen Vereins in München, der Botaniska Sällskapet i Stockholm, der Gesellschaft für Botanik zu Hamburg, der botanischen Section der Schlesischen Gesellschaft für vaterländische Cultur zu Breslau, der Botaniska Sektionen af Naturvetenskapliga Studentsällskapet i Upsala, der k. k. zoologisch-botanischen Gesellschaft in Wien, des Botanischen Vereins in Lund und der Societas pro Fauna et Flora Fennica in Helsingfors.

Nr. 5.	Abonnement für das halbe Jahr (2 Bände) mit 14 M. durch alle Buchhandlungen und Postanstalten.	1895.

Die Herren Mitarbeiter werden dringend ersucht, die Manuscripte immer nur auf *einer* Seite zu beschreiben und für *jedes* Referat besondere Blätter benutzen zu wollen. Die Redaction.

Wissenschaftliche Original-Mittheilungen.*)

The Sensitive Movements of some Flowering Plants under Colored Screens.

By

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(Schluss.)

Summary.

We can now summarice the results of the above observations. In all cases it has been found that Sachs' statement is so far correct, viz: that when sensitive plants are placed under colored screens the leaflets fold as in the nyctitropic state, most powerfully under red, less so under yellow, only feebly or not at all

*) Für den Inhalt der Originalartikel sind die Herren Verfasser allein verantwortlich. Red.

under green, and that under blue screens the leaflets remain open as in ordinary day-light. But expansion under the red and yellow screens soon takes place, the rapidity of expansion varying according to the brightness of the light and the species experimented on. An imperfect knowledge of this subsequent change has caused Vines*) to give Sachs' statement a fallacious interpretation, for he says „with regard to the particular rays of the spectrum which determine these movements it appears from the observations of Sachs and Bert that the highly refrangible rays are those which are specially concerned. When a plant with its leaves fully expanded is exposed to yellow light, the leaves soon close, whereas if under the same circumstances the plant be exposed to blue light, the leaves will remain expanded. Yellow light acts like darkness, blue light like day-light.“ This condition is a short-lived one, lasting at longest in the species experimented with for about eight hours.

In time then all of the screened plants had their leaves fully expanded and presented this position during the morning (from 5.30 till 8 or 8.30 on the average), and before sunset (from 4 to 5.30 on the average) of each day. It will readily be noted, from a comparison of the species studied, that the sunset variations are considerable. Thus the Cassias show nyctitropism sooner than does *Oxalis stricta.*

If the light be diffuse and thus of moderate intensity the flat morning position of the leaves is retained throughout the entire day, or part of it if the sun ultimately shines out, as happened on September 13th in the above records. If the light become more intense no alteration, or it may be slight deflection in *Cassia* or inflection in *Oxalis* occurs to leaflets of plants under the red and yellow screens. When plants are under a green screen and exposed to intense illumination the leaflets either remain flat or assume a more or less paraheliotropic position, the angular change at times amounting to 25^{0}. In all cases under blue screens the leaflets become paraheliotropic more or less powerfully, the amount of angular movement being proportioned to the intensity of light. It is impossible at present to say whether the blue or violet rays are the more powerful.

In all cases normal nyctitropic movement is accelerated a half to one and a half hours under a red screen. But the movements of the leaves and leaflets then are very peculiar. In *Cassia nictitans* and *C. chamaecrista* some of the leaves fall, others slightly rise, and in closing of the leaflets a pair, or even one here and there, may shou inflexion when others onf the same leafhave not moved.

Under a yellow screen nyctitropism is not quite so accelerated as under red, but the closing movements are nearly or quite regular in sequence, and in Cassias are first visible at the leaf

*) Physiology of Plants, p. 539.

extremity. Under a green screen the time movement practically coincides with that of exposed plants, and is beautifully regular in sequence. According to the climatic environment for each day, variations in the time movement of the species are shown. This is seen from the record of Oct. 3rd for *Oxalis stricta*. These variations are probably due to moisture, illumination and temperature effects either separately or combined.

Under the blue light there is always a distinct retardation of the normal nyctitropic period to the extent of from $^1/_2$ to $2^1/_2$ hours, the variations seeming to depend on temperature, on length of exposure to the blue light, and on relative intensity of the light for the day.

The relative period of unfolding in the morning has not been determined with sufficient accuracy as yet, but likewise varies under the different screens. If the peculiar results that were got on September 17th when the plants were uncovered, prove to be trustworthy and general, they indicate a remarkable reversal of the behavior exhibited when the plants were first covered, and an equally remarkable reversal of the nyctitropic relations that obtained while the plants were covered.

These observations seem further to warrant us in concluding that up to 38° C, or even 43° C in some species, heat rays either fail to stimulate the tissues, or if they do that their actions is interrupted or antagonized by some other form of energy, though this is scarcely likely. The same is true of the less refrangible light rays, and of these the orange-yellow, yellow and yellow-green seem to give the most uniform results, for so long as plants were exposed to intense light the leaflets remained either quite flat or became slightly reflexed. Under the green screen the leaflets of *C. nictitans* and *C. chamaecrista*, when strongly illuminated remained flat or became inflexed in some cases to 25°, but those of *C. Tora* under equal illumination inflexed through an angle of 15°; those of *Oxalis stricta* remained flat. The paraheliotropic movement thus started under the green screen in some species became greatly more pronounced under the blue in all, and during intense illumination in Oxalis almost amounted to the nyctitropic position.

Grouping the above facts, the conclusion is reached that the heat rays, the less refrangible rays, and the more refrangible rays are all trophic up to a certain point. When that point is crossed the heat rays and less refrangible rays continue to be trophic up to a much higher point, but the more refrangible rays (from green-blue to violet) act as a stimulant or irritant.

Oltmanns*) concludes from his experiments with white light that Darwin's division of leaf positions into diaheliotropic and paraheliotropic is superfluous, since he considers that the transition from the one to the other is gradual and is determined by relative

*) Flora, 1892, p. 251.

light intensity. My observations show that for any one species of plant there is a definite optimum that varies somewhat according to temperature, moisture, etc. -- and that up to the optimum point all of the rays contribute to maintain the diaheliotropic position. Beyond this the more refrangible rays cease to be trophic, and acting as a stimulant cause movements that correspond in amount with the intensity of the light-stimulant. That at a definite temperature the less refrangible and more refrangible rays are alike trophic is highly probable, from the fact that plants grown for days under all of the colored screens are not permanently injured, even though in the active growing state. Thus the four plants of *Cassia Tora* were under screen for seven days, and were then placed in my plant house, where they have since grown well. It should be said however that the growth of the plant from under the blue screen, has been less active than in the case of those fromthe first two. That the blue-violet as well as the red-yellow rays are trophic, seems to be a probable explanation of the behavior of plants when first placed under a red or orange-yellow screen, for the closing of the leaflets then seems only to be accounted for by the cutting off of the more refrangible rays of optimum intensity, and accompanying disturbance of the normal functions. The re-expansion of the leaflets within a few hours at longest, proves that the disturbance is temporary and not deep-seated.

Oltmann's further says: „Alle dorsiventralen Organe eine besondere Lage zum Licht einnehmen, indem sie demselben eine ganz bestimmte Seite zukehren, welche ausserdem einen für jede Intensität des Lichtes bestimmten Winkel mit den einfallenden Strahlen bildet."

The writer so far agrees with the above statement, but believes that when the intensity of the more refrangible rays reaches such a point that these rays cease to be trophic, the highest limit of diaheliotropism is reached, and paraheliotropism ensues.

It may be worth emphasizing here that sensitive movements are most pronounced in tropical plants, are less so in sub-tropical and warm-temperate species, and are rare or feebly expressed in temperate and sub-artic plants. But, as is well known, leaves that are exposed to an intense light show more rapid metabolic changes than those that are shaded. Any change, therefore, in the tissues of a plant which would insure protection of the lamina from the intense blue-violet rays, and its exposure again advantageously when these rays become subdued, would have every liklihood of perpetuation in sub-tropical and tropical regions, and such is the state of matters as we find them. We do not know accurately as yet the mechanism involved in a sensitive pulvinus, or the changes effected on stimulation of it, but anyone can readily prove that every gradation from non sensitive to highly sensitive leaves is met with in such groups as the *Oxalideae* and

Leguminosae, and that broadly speaking the sensitiveness increases as we pass froms regions where the sun's rays are of minor intensity, to others where the rays are of increased intensity.

The writer therefore regards the action of the more refrangible rays when of a definite intensity as one of stimulus, because 1) the angular inflexion of leaflets is proportionate to the intensity of the stimulating rays; 2) the movement is not due to indirect action from the green laminar substance to the pulvinus cells, but is wholly centred in the latter; 3) if the inflexion movement is considerable, the white cushion of the pulvinus shows a visible change from white to a dull leaden green color; 4) when the more refrangible rays are cut off by a color screen the stimulus is removed, and then neither the heat rays nor the less refrangible light rays cause closure.

Under the first head it is worthy of note here that the parallelism between mechanical, thermal and chemical stimuli and stimulus by the more refrangible rays is complete, a weak stimulus causing slight inflexion and a strong stimulus powerful inflexion.

Under the third head it should be stated that the same molecular change takes place in the pulvinus region of *Cassia nictitans* and *C. chamaecrista* as I have already demonstrated to occur in species of *Mimosa* and *Schrankia**). After mechanical stimulus a latent period of fully five seconds in *C. nictitans* ensues before this change occurs, but then the difference between a stimulated and non- stimulated leaflet is striking. By careful observation it can be shown that the same change occurs from light stimulus by the more refrangible rays.

The above experiments then indicate that by the paraheliotropic movement leaflets are protected from the intense action of the blue-violet rays, and for this end all of the leaflets on any one leaf need not move through the same angle. Oltmanns (p. 238) says: „Die Blätter der *Robinia* sind in hervorragendem Maasse photometrisch; jede Veränderung der Lichtintensität beantworten sie mit einer veränderten Stellung der Spreite" . . . . „das Blatt lässt Licht von bestimmter Intensität unter einem genau definirten Winkel auf sich wirken. Der Lichteinfallswinkel hängt wieder von der Stimmung der Blätter ab."

Those cases are not rare where even adjoining leaflets show very diverse movements that it would be difficult to explain on the above grounds. Thus on a bright, warm day a plant of *Oxalis stricta* was observed at 2 : 15 p. m. having several leaves whose leaflets were in pronounced paraheliotropic position, but one leaf had its petiole so placed that a leaflet next to the incident rays had bent down through an angle of 78°, another away from the source of light by falling only 25° then had its

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*) Biological Lectures at Wood's Holl. 1893. p. 205.

surfaces parallel to, and therefore well protected from, the rays, while the third had fallen through 55°, and then presented one edge and parallel surfaces, to the rays. If we consider the movement of each leaflet to be caused by changes in the pulvinus cells, the pulvinus of the first leaflet having been fully exposed to the intense rays, the leaflet would become strongly reflexed. The pulvinus of the second leaflet would be protected after movement of the leaflet through a small angle, while the rays would pass parallel to the surface of the third leaflet after it had fallen to the extent indicated above. But here and in every movement of sensitive plants the writer considers that there is an intimate relation between the pulvinus cells and the entire living tissue of each leaflet, so that any change occurring in the pulvinus tissue is probably not confined to it alone, since vice versa his experiments on *Dionaea*, *Mimosa*, *Cassia*, *Oxalis* etc. prove that stimulation of any part of a leaf or leaflet is propagated to the motile centre.

If we attempt now to answer the questions: Are the more refrangible rays injurious to plant life when above an optimum intensity for each species; and if so, why are they injurious? several publications of recent years seem to help us.

The consensus of opinion now is, that metabolic changes go on most actively under the more refrangible rays of the spectrum. As proof, mention need only be made of the results obtained by Wiesner, George Henslow, Purjewicz and Engelmann among others. These normal processes which are often carried on at rather low temperatures and in weak sunlight, are characterized by the setting free of secondary products, not a few of which are useless or even deleterious for plant growth. An increase above the optimum light intensity will be associated with increased chemical activity, and the setting free of greater quantities of decomposition products. The para heliotropic movements will so act as to prevent this. The fact that exposure of non-sensitive leaves on a tree to direct and intense light causes more rapid decomposition of the food stuffs than on other leaves or even parts of the same leaf, is well known and is apparently to be explained on the same principle.

But a light intensity greatly less than that needed to insolate any sensitive plant may affect the growth of tissue by its more refrangible rays. Thus Ludwig Klein*) proved that the cessation of growth during day in the conidial stalks of *Botrytis cinerea* is solely due to the blue-violet rays and that growth as well as spore-formation is promoted by red-yellow rays. Ward's experiments with plate cultures of *Bacillus anthracis***) prove that a certain intensity of the more refrangible rays is prejudicial and in most instances fatal to this fungus. Sorokin's older experi-

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*) Bot. Zeitung. 1885. p. 14.
**) Proc. Roy. Soc. Vol. LIII. p. 25.

ments likewise prove this. In the case of sensitive plants each species is not affected alike by the same intensity of the more refrangible rays. Thus if we attempt a rough approximation by noting temperature, *Oxalis stricta* and other species are visibly affected at 20° C; *Cassia Tora* at 24° C, *C. nictitans* at 26° C, *Oxalis dendroides* at 28° C and *Mimosa pudica* at 30° C. The various relations thus indicated by temperature hold also for light intensity. This being so for flowering plants, a much greater range of action may be expected amongst Fungi and allied groups. The above facts then indicate that the more refrangible rays promote active chemical change, and that above a certain optimum of intensity they are decidedly destructive.

If we attempt now to answer the second question as to why the blue-violet rays are injurious, we are met by difficulties that are due chiefly to want of information. The information however may soon be forthcoming. Ward's suggestion for *Bacillus anthracis* is that „it appears at least possible that the bactericidal action of the light is due to its destructive influence, in presence of oxygen, on the fatty matters or other oxidisable substances forming the reserve materials of the spores.“ And later he says: „Of course it may turn out that the action of the light is more profound than the simple explanation offered assumes, and that the physiological properties of the protoplasm are deeply concerned.“

If we apply these theoretical considerations to sensitive plants we are met by the fact that the visible results of the intense blue-violet rays are the same as for other kinds of stimuli, whether mechanical, thermal, chemical, or electrical. I have already expressed the view*) that such movements may be more readily explained by chemico-physical activity of the protoplasm itself. But it should be stated that in every leguminous sensitive plant yet examined by the writer each contractile cell of the primary pulvinus tissue, or as in *Cassia Tora*, each epidermal cell of the leaflet pulvinus, contains a clear refractive sphere that has a definite position in relation to light. This body gives all the reactions of an oil, and usually has traces of tannin. During and after its solution the cell nucleus is revealed within, surrounded by small granules that had been imbedded in the oily matrix. We get some idea from this of the extreme complexity of the chemico-physical mechanism, but at present our knowledge is not sufficient to permit of any explanation of the presence of the oil.

These observations emphasize the view already expressed by several investigators that orange, yellow, and green screens to the protoplasm, whether in the form of pigmented walls, of pigmented cell sap, or of chlorophyll are of a protective character, and permit the normal functions to be carried on unimpeded by the action of the more intense blue-violet rays. But while such pigments are

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*) Biological Lectures.

specially effective, the writer would suggest a similar function for the thick, highly cuticularized epidermis that covers so many desertic plants, or plants that grow in places exposed to intense sunlight. One can easily prove by experiment that on a hot day a thin sheet of white paper considerably reduces the light intensity. A piece of *Opuntia* epidermis similarly obstructs the light rays, and even though the heat rays pass, we have seen that up to 40—43 C no injurious effect follows to many plants. It might further be pointed out, as Wiesner has already done, that the hair covering on the leaves of certain plants will contribute to the same end.

A very remarkable movement, however, has been studied by the writer during the past two summers, which need only be shortly referred to here. During the warmer days of July and August, when the shade temperature rises to 35—38° C, leaves of some sensitive plants that are fully exposed, and which under a greatly less intense illumination have already exhibited paraheliotropic movement, begin to incurve their leaflets so as at once to expose their under surface and shade the actively assimilating upper surface. At first this was supposed to be a sign of drooping, but more careful study proved it to be a normal movement, and one also that is shown by many plants that are not sensitive. Among sensitive plants *Desmodium canadense*, and among non-sensitive ones *Arisaema Dracunculus*, *Zinnia hybrida* and *Ambrosia trifida* may be mentioned. The conditions that bring about this remarkable movement need not be discussed now, but we regard it as another means of protection from the intense blue violet-rays.

Philadelphia, 2nd November 1894.

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