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LIFE MOVEMENTS IN PLANTS

BY

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PREFACE

THE publication of the third and fourth volumes of Transactions for 1920 and 1921 had been greatly delayed on account of my prolonged absence in Europe, and of post-war difficulties in publication. The fifth volume of the series for 1922, "On the Ascent of Sap" is expected to be published at about the same time as these.

The present two volumes will be found to contain accounts of investigations on geotropism, on dia-heliotropic attitude of leaves as regulated by transmitted nervous impulse, on assimilatory and dissimilatory changes under light, on new methods of recording the effects of protoplasmic changes under stimulus; and also of various methods and appliances for detection of the two fundamental reactions to which all plant movements are due. In regard to geotropism of higher plants, electric investigations have been described which lend strong support to the theory of statoliths, indeed practically confirm it. Investigation by means of the Electric Probe has made it possible to explore the interior of the plant, and map out the excitatory changes from layer to layer under the stimulus of gravity. The results of these investigations show that while the layers of tissue contiguous to the upper perceptive layer undergo a contraction, those contiguous to the lower perceptive layer exhibit an expansion. The cause of this difference has also been discovered in the fact that the geotropic stimulus due to the pressure of heavy particles acts directly on the upper, and indirectly on the lower layer of the responding cells. Another discovery, namely, the critical angle for immediate geotropic excitation, also lends fresh and independent support to the theory of statoliths. An explanation of the dia-geotropism of dorsi-ventral organs has been found in the differential excitability of the two sides of the organ. In regard to the dia-heliotropic attitude of many leaves, it is shown to be due to transmitted impulse of a nervous character initiated in the lamina and conducted to the motile organ. The nervous tissue which conducts excitation has been localised in the phloem of the fibro-vascular bundle. As regards the pulvinus of *Mimosa* it is found to be a highly complex organ, each of its four quadrants responding in a definite way by a down- or up-movement, or by a right- or left-handed torsion.

The method of resistivity-variation has been further perfected and the responses of the vegetable tissue to various modes of stimulation—mechanical, electric, and photic—have been recorded. The characteristic responses have been shown to correspond to the mechanical and electromotive responses. The new Quadrant method has been rendered extremely sensitive, enabling us to record the response to light emitted by a single spark.

The response of the plant is modified by the changing intensity of light during the course of the day; but no sensitive appliances had hitherto been available for the continuous record of the variation of light. This difficulty has been overcome by the invention of the Automatic Radiograph.

The movement of plants is affected by the ascent of sap which causes an increase of turgor in the tissue. Prolonged investigations on the "Physiology of the Ascent of Sap" have shown that the propulsion of sap is brought about by the pulsating and pumping action of the cells of the inner layer of the cortex; it is also shown that the state of turgor of the plant at any hour of the day is determined by the gain or loss of liquid by the plant, the relative variations of which are definitely traceable to external agencies.

In the general review it has been shown that the innumerable variations in response are produced by the different combinations of numerous factors, some concordant and others antagonistic. This is the secret of the great complexity of the plant movements, which are by no means capricious. By the isolation of individual factors and separate investigations on them, it is possible to unravel the complexity and discover a generalisation for the life-movements in plants.

BOSE INSTITUTE, CALCUTTA, J. C. BOSE.
October, 1921.

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LII.—ON ELECTRIC LOCALISATION OF THE GEO-PERCEPTIVE LAYER.

By Sir J. C. Bose,
Assisted by
Satyendra Chandra Guha, m.sc.

In the second volume of the Transactions of the Institute (1919), a very sensitive electric method is described for the determination of the exact position of the sensitive layer in the interior by which the plant is enabled to perceive the vertical direction, so that the shoot or the petiole places its length parallel to the direction of the lines of force of gravity, with the apex upwards. This directive movement is accomplished by a responsive curvature, the upper side becoming concave and the lower convex. The concavity of the upper side is brought about by an excitatory contraction, which I have shown takes place under all forms of stimulation, mechanical, electrical, chemical and photic. It has also been shown that the characteristic signs of excitation—diminution of turgor, contraction, and diminution of the rate of growth—may be detected electrically by an induced change of galvanometric negativity. If suitable electric connections are made so that one contact is on one side of the stem, and the other on a distant indifferent point, then on laying the plant horizontal, the upper side of the stem is found to exhibit an electric change of galvanometric negativity indicative of excitation. The geotropic irritation and the electric sign of excitation disappears as soon as the plant is restored to the normal vertical position.

The seat of geotropic irritation is at the perceptive layer itself; hence the electric response of the perceptive layer is the maximum possible. I have thus been able to localise the geo-perceptive layer by means of the Electric Probe, fully described in the previous volume: the principle of the method will be understood from the following description:—

As every side of a radial organ is geotropically excitable, the geo-perceptive cells must be disposed in a cylindrical layer at some unknown depth from the surface, which in a longitudinal section of the shoot would appear as two straight lines G and G, (Fig. 221). In a vertical position, the geo-perceptive layer will remain unaffected, but rotation through 90° would initiate the excitatory reaction. Let us first centre our attention to the geo-perceptive layer G, which occupies the upper position. This sensitive layer perceives the stimulus, and is, therefore, the focus of irritation; the state of excitation is, as we have seen, detected by induced galvanometric negativity, and the electric change would be most intense at the perceptive layer itself. The excitation of the perceptive layer will irradiate into the neighbouring cells in radial directions with diminishing

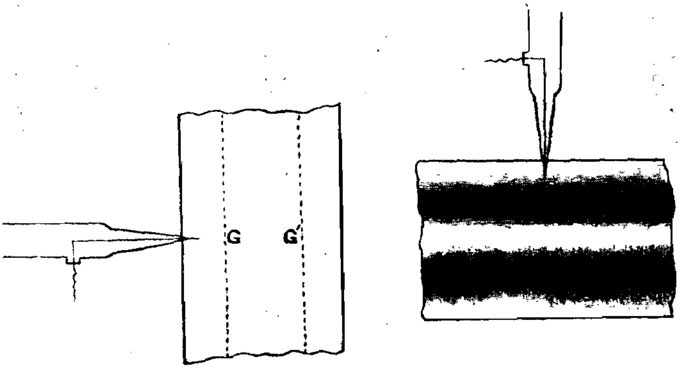

FIG. 221 Diagrammatic representation of the geo-perceptive layer in the unexcited vertical, and in excited horizontal position.

intensity. Hence the intensity of the responsive electric change will decline in both directions, outwards and inwards.

The distribution of the excitatory change, initiated at the perceptive layer and irradiated in radial directions, is represented by the depth of the shading, the darkest shadow being on the perceptive layer. Had excitation been attended with the change of light into shade, we would have witnessed the spectacle of a deep shadow (vanishing towards the edge)

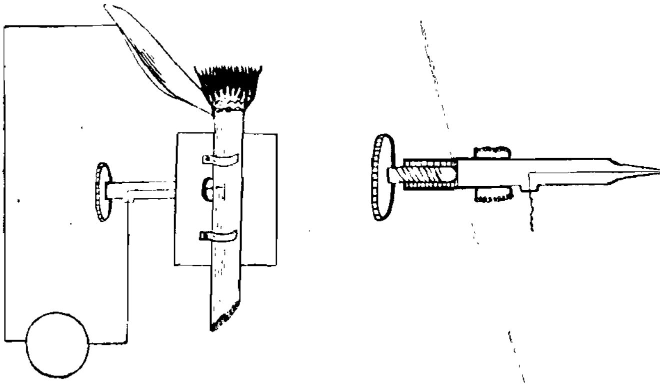

FIG. 222 The Electric Probe. Figure to the left represents one electric contact made with sepal of *Nymphaea*, and the other, with the flower stalk by means of the probe; the included galvanometer is represented by a circle. Figure to the right is an enlarged view of the probe.

spreading over different layers of cells during displacement of the organ from the vertical to the horizontal; the shadow would have disappeared on the restoration of the organ to the vertical position.

Different shades of excitation in different layers are, however, capable of discrimination by means of the Electric Probe, insulated except at the tip, which is gradually pushed into the stem from outside (Fig. 222). It will at first encounter increasing excitatory change during its approach to the perceptive layer, where the irritation would be at its maximum. The indicating galvanometer in connection with the Probe will thus indicate increasing galvanometric negativity, which will reach a maximum value when the probe reaches the perceptive layer. After this, as the Probe passes beyond the perceptive layer, the electric indication of excitation would undergo decline and final abolition. The characteristic effects described above are to be found only under the action of gravitational stimulus; they will be absent when the organ is held in a vertical position and thus freed from geotropic excitation.

The electric investigations with the Probe on the lines indicated above enabled me to map out the induced electric variation inside an organ under the stimulus of gravity. The induced galvanometric negativity of the *upper side* of the stem (indicative of excitation) is found to undergo variation at different depths, and attains a maximum value at a definite layer, beyond which there is a decline. The geo-perceptive layer is thus experimentally localised by measuring the depth of the intrusion of the Probe for the maximum galvanometric negativity.

The electric response of the lower side of the organ to gravitational stimulus is, however, of an opposite sign to that of the upper side, a *galvanometric positivity* indicative of expansion and increase of turgor. The electric indication on the lower side also exhibits variations in different layers, the maximum positivity occurring at the *perceptive* layer. These responsive electric variations indicate that the layers of tissue contiguous to the upper perceptive layer undergo a contraction, while those contiguous to the lower perceptive layer show an expansion.

In certain lower animals it has been found that the weight of the heavy particles acting on a sensitive layer causes the perception of the direction of gravity. From histological considerations Haberlandt and Nemec came to the conclusion that the heavy particles, such as starch grains, performed a similar function in many plants. The electro-physiological investigation which I undertook was for the exact localisation of the sensory cells *in situ*, and in a condition of *normal living activity*. I also wished to record the entire cycle of reaction, from the onset of geotropic stimulus to its cessation in the living plant. My physiological investigations fully confirm the conclusion that it is the "starch sheath" containing a number of large-sized starch grains which is the geo-perceptive organ.

The experiments were first carried out with two

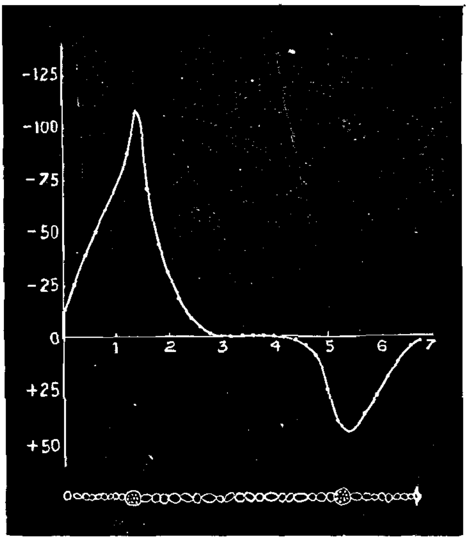

FIG 223

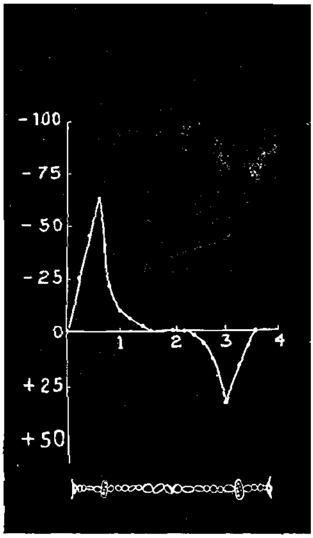

FIG. 224

FIG. 223 Curve of geo-electric excitation in different layers of *Nymphaea*. Ordinate represents geo-electric excitation; abscissa, distance from upper surface of flower stalk. Diagrammatic section underneath shows the position of the geo-perceptive layer (starch-sheath) corresponding to maximum induced galvanometric negativity and positivity on the two sides.

FIG. 224 The curve of geo-electric excitation in different layers of *Bryophyllum*.

different species of plant, the flower stalk of *Nymphaea* and the stem of *Bryophyllum*. The curves obtained from results of numerous experiments show that the maximum electric reaction takes place in the particular layer which contains the starch grains (Figs. 223, 224). As regards the geo-electric reactions it was found that the response is strong at the particular season, when the physiological vigour of the plant is at its height; later in the season, the response undergoes a rapid decline and final abolition. Microscopic examination revealed the cause of this difference. In the favourable season, the starch grains in the sheath are present in great abundance; but they disappear later. The presence of starch grains thus appears to be associated with the sensitive reaction of the perceptive layer.

In addition to the effect of seasonal *variation, there is* an additional factor, namely the influence of normal variation of temperature on geotropic response: it was found that while the response was vigorous on cold days of Calcutta winter (average temperature 20°C.), it declined rapidly on the return of warmer days. It thus appeared that within a moderate range of variation, a rise of temperature depresses geotropic action, while a fall of temperature accentuates it. This found independent support from my investigations on the diurnal up and down movements of organs subjected to the action of gravity. The "Praying Palm" of Faridpore is a striking example of this. The tree which grew at an inclination to the vertical was subjected to the action of gravity. The maximum geotropic reaction causing the highest erection of the apex of the tree, was found to take place at about 6 A.M. when the temperature was at its minimum. The maximum fall of the tree, caused by diminished geotropic action, occurred at about 3 P.M. when the temperature was at its maximum. I have shown further that this thermo-geotropic reaction explains the diurnal movements of leaves of many plants.*

As regards the effect of temperature on geotropic response, I found once more that while the geo-electric response was very marked in the colder months of February

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* Life Movements of Plants—Vols. I and II.

(temperature 20°C.), it disappeared by the middle of April when the average temperature was about 30°C. With *Tropaeolum majus* I could get no response even in March. I afterwards renewed my experiments with this plant three months later at the Mayapuri Research Station at Darjeeling. I was considerably surprised to find that the geo-electric response of the plant which had disappeared in Calcutta in March was fully vigorous in May and June at the hill station; the temperature at Darjeeling was lower than 20°C. This shows that geo-electric response is accentuated, within limits, by a fall of temperature and and depressed by a rise of temperature.

I have recently (1921) been able to renew the investigations on the localisation of the geo-perceptive layer in a large number of plants, the results of which are given below.

GEO-ELECTRIC RESPONSE OF THE PETIOLE OF TROPAEOLUM.

Detailed results of experiments on the localisation of the geo-perceptive layer in the petiole of the Tropaeolum, are given below as typical of the reaction in other plants. *Tropaeolum* has the following special advantages. Geotropically it is very sensitive; its latent period of response is very short, the horizontally laid petiole beginning to bend upwards in the course of a few minutes. The leaf may be isolated from the plant, and the cut end of the petiole placed in moist cotton. The normal geotropic irritability of the cut specimen is found to be fully restored in the course of half an hour. The manipulation of a cut specimen, alternately in a vertical or in a horizontal position, presents no difficulty. A very large number of specimens is, moreover, obtained from the same plant. As regards geo-electric reaction of the petiole of *Tropaeolum*, the induced electromotive variation is considerable and attains the maximum value within a short time; the recovery is practically complete after restoration to the vertical.

The mode of experimental procedure is as follows; the Probe is thrust into the petiole by successive steps of 0.05 mm. and the electric response observed on displacement of the petiole from the vertical to the horizontal position, in which latter case the organ is subjected to geotropic irritation. The induced electric variation, as already stated, is of considerable intensity. The irritation caused by the prick of the Probe is slight, since the fine Probe insinuates itself into the tissue, rather than makes any marked rupture. The immediate effect of the insertion of the Probe is a negative deflection of the galvanometer, which declines and practically disappears in the course of about 5 minutes. The geotropic irritability moreover is fully restored in the course of less than 15 minutes, after which records of geotropic response are obtained by photographic method.

LOCALISATION OF GEO-PERCEPTIVE LAYER IN THE PETIOLE OF TROPAEOLUM.

Geo-electric excitation at different layers.—I give below the photographic records of responses to the stimulus of of gravity at various layers as the Probe was thrust in from outside by successive steps of 0.05 mm. (Fig. 225). It will be seen that the geo-electric response underwent a continuous increase till the maximum excitation occurred at a depth of 0.20 mm. A rapid decline occurred beyond this point and the response disappeared at a depth of 0.50 mm. The following table gives the quantitative results of the experiment.

Experiment 230

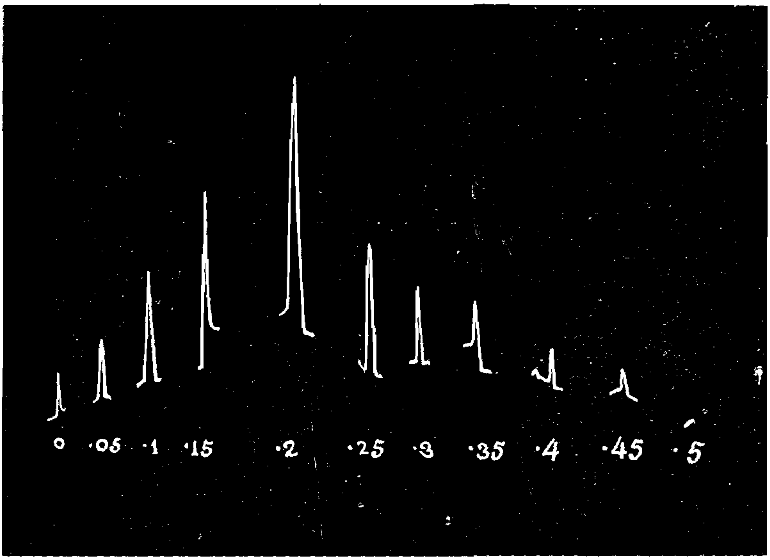

FIG. 225. Intensity of Geo-electric response at different depths in the petiole of Tropaeolum.
Note the maximum excitation at a depth of 0.20 mm.

TABLE XLVII.—SHOWING GEO-TROPIC REACTION AT DIFFERENT LAYERS IN THE PETIOLE OF *Tropaeolum*.

Distance from surface in mm.	Geo-electric response of galvanometric negativity
0.00	5 divisions
0.05	9 ,,
0.1	18 ,,
0.15	29 ,,
0.20	42 ,,
0.25	20 ,,
0.30	11 ,,
0.35	7 ,,
0.40	5 ,,
0.45	2 ,,
0.50	0 ,,
Position of the starch sheath at a depth of 0.20 mm.	

Subsequent microscopic section showed the maximally excited layer at a depth of 0.20 mm. was the sheath which contained the starch grains. The geo-perceptive layer is thus found to coincide with the starch sheath.

Maximum excitability of the geo-perceptive layer.—The maximum excitation induced at the perceptive layer appears to be due to two factors; we have first the direct stimulation caused by the fall of the starch grains; secondly the *general excitability* of the geo-perceptive layer is greater than that of the neighbouring ones. As regards the relatively greater excitability of the perceptive layer, this became evident from the effects observed during the passage of the Probe with the specimen held vertical. The insertion of the Probe then acts as a mechanical stimulus, and the response by galvanometric negativity is found to be maximum at the starch sheath, proving that this is relatively the most excitable. This particular response takes place *during* the thrust of the Probe; the resulting irritation disappears, however, when the Probe is left in a stationary condition. The normal excitability of the cells is restored, after a period of rest of about 10 minutes. The geo-electric response is observed after restoration of the normal excitability.

A few words may be said about the relative position of the maximally excited layer, as found from the readings of the Probe and subsequent determination of the position of the starch sheath by microscopic examination of the transverse section. In the example given above, the two are found to be identical. There is, however, the possibility of a slight variation; the Probe, as already stated, is inserted by steps of 0.05 mm., and may, therefore, in the successive steps of its passage lie slightly on one or the other side of the sensitive layer. The error introduced from this is, however, slight. As regards the micrometric determinations, the section at the line of the passage of the Probe should be slightly moistened for microscopic examination; for too long an immersion in water is liable to cause a swelling of the cells, and thus vitiate the measurements.

The following table gives the results obtained with twelve different specimens of the petiole of *Tropaeolum*. The specimens were unequally thick: hence the sensitive layer was found at a depth of 0.15 mm. in thin, and at 0.20 mm. in thick specimens; the maximum electric excitation was in all cases found to occur at the starch sheath.

TABLE XLVIII.—GEO-ELECTRIC RESPONSE AT VARIOUS DEPTHS IN DIFFERENT SPECIMENS (PETIOLE OF *Tropaeolum*).

No. of Specimen.	Responsive galvanometric negativity at depths of:							Position of starch sheath from surface
	0 mm.	0.1 mm.	0.15 mm.	0.20 mm.	0.25 mm.	0.30 mm.	0.40 mm.	
1.	7dns.	16dns.	**50**dns.	35 dns.	25 dns.	0. dns.	0. dns.	0·16mm.
2.	10 ,,	24 ,,	47 ,,	**84** ,,	65 ,,	57 ,,	7 ,,	0·20 ,,
3.	0 ,,	6 ,,	10 ,,	**25** ,,	8 ,,	2 ,,	0 ,,	0·20 ,,
4.	5 ,,	35 ,,	**57** ,,	30 ,,	19 ,,	13 ,,	0 ,,	0·15 ,,
5.	6 ,,	15 ,,	22 ,,	**30** ,,	24 ,,	15 ,,	0 ,,	0·18 ,,
6.	5 ,,	8 ,,	**15** ,,	6 ,,	4 ,,	1 ,,	0 ,,	0·15 ,,
7.	3 ,,	5 ,,	**14** ,,	5 ,,	3 ,,	0 ,,	0 ,,	0·15 ,,
8.	0 ,,	16 ,,	31 ,,	**48** ,,	14 ,,	12 ,,	8 ,,	0·22 ,,
9.	3 ,,	12 ,,	**15** ,,	11 ,,	8 ,,	6 ,,	0 ,,	0·15 ,,
10.	2 ,,	10 ,,	**22** ,,	7 ,,	3 ,,	1 ,,	0 ,,	0·15 ,,
11.	3 ,,	18 ,,	32 ,,	**43** ,,	35 ,,	23 ,,	7 ,,	0·21 ,,
12.	0 ,,	2 ,,	5 ,,	**26** ,,	7 ,,	3 ,,	0 ,,	0·20 ,,

DECLINE OF GEO-ELECTRIC EXCITATION ON TWO SIDES OF THE PERCEPTIVE LAYER

The experimental localisation of the perceptive layer is greatly facilitated by the abrupt enhancement of excitation at the layer. This will be fully realised from the resultant curve obtained from data derived from twelve different specimens. We take the perceptive layer itself as the point of reference, and measure successive distances say of 0.05 mm. to the left and to the right of the point of reference.

The abscissa to the left is towards the centre, that to the right, towards the surface. The mean values of the excitatory action at the different points are the ordinates for the construction of the curve. It will be seen how abruptly it rises to the maximum at the perceptive layer and falls beyond it inwards and outwards (Fig. 226).

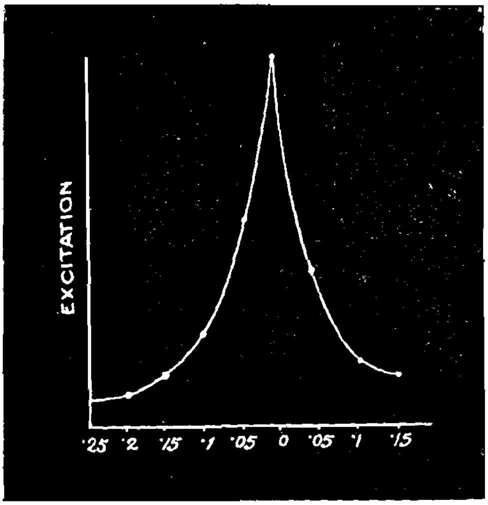

FIG 226 Curve showing geo-electric distribution. Maximum excitation occurs at geo-perceptive layer O. Excitatory reaction rapidly declines inwards and outwards (See Text).

GEO-ELECTRIC EXCITATION AT THE UNDER SIDE.

The experiments with *Nymphaea* and *Bryophyllum** brought out the striking fact that under the stimulus of gravity the excitatory electric reaction at the lower side is of opposite sign to that at the upper side, a positive, instead of a negative electric variation, the maximum positivity occuring at the starch sheath. Since the galvanometric negativity is associated with contraction and galvanometric positivity with expansion, the geotropic curvature of the

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* Life Movements of Plants.—Vol. II.

stem or the petiole is thus due to the joint effect of contraction of the upper and expansion of the lower side.

GEO-ELECTRIC RESPONSE AT THE LOWER SIDE OF PETIOLE OF TROPAEOLUM.

Experiment 232

The account of an experiment on the electric response induced at the lower side under the action of gravity is given below. The galvanometric response of the epidermal layer was +6 divisions. At a depth of 0.05 mm. it increased to +15, at 0.1 to +26 divisions. At a depth of 0.15 mm. the response attained its maximum value of +40 divisions. It declined beyond that layer to +11 divisions at a depth of 0.20 mm., and to +2 at 0.25 mm. The geo-electric response disappeared at a depth of 0.30 mm. The geo-electric distribution is thus similar to that at the upper side, the characteristic difference being in the change of the sign of the response from negative to positive (Fig. 227).

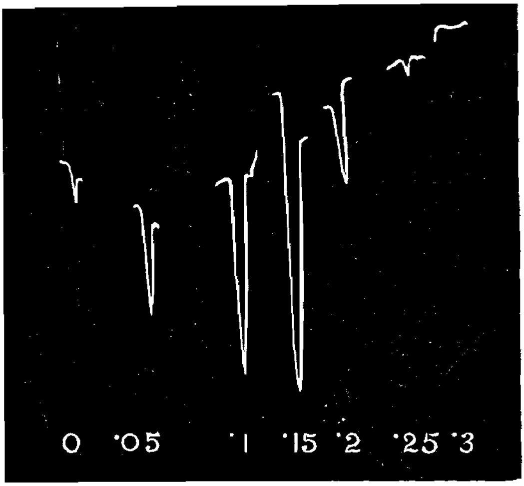

FIG. 227 Intensity of geo-electric excitation at different depths at the underside of petiole of Tropaeolum. Maximum excitation attained at a depth of 0.15 mm. which is the starch-containing layer.

Note electro-positivity of response indicated by down-curve.

GEO-PERCEPTIVE LAYER IN THE STEM OF TROPAEOLUM.

The next investigation was undertaken with the stem of *Tropaeolum*, which is also sensitive to geotropic action. Three specimens were chosen of approximately the same thickness, and the geo-perceptive layer localised by means of the Probe.

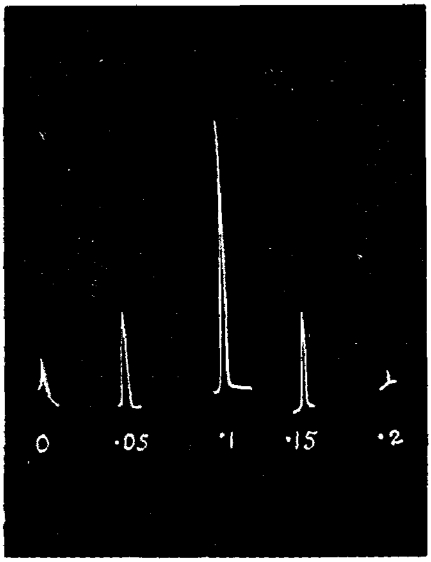

FIG 228 Geo-electric response at different depths in the stem of Tropaeolum. Maximum response at a depth of 0.10 mm. which contained the starch-sheath.

In the first of these the response by galvanometric negativity was 5 divisions at the epidermis, which increased to 15 divisions at a depth of 0.05 mm. and to 37 at 0.10 mm. This was the climax, for the response underwent a rapid diminution and abolition as the Probe passed further into the stem (Fig. 228). Microscopic section showed that the layer at a depth of 0.10 mm., which gave the maximum geo-electric response, was the one which contained the starch grains.

Experiment 232

Similar results were obtained with two other specimens. The results are given in detail in the following table.

TABLE XLIX.—LOCALISATION OF GEO-PERCEPTIVE LAYER IN STEM OF *Tropaeolum*.

Specimen	Response of galvanometric negativity at depths of ;						Distance of starch sheath from surface
	0	0·05 mm.	0·1 mm.	0·15 mm.	0·2 mm.	0·25 mm.	
I ...	5 dns.	10 dns.	**37** dns.	19 dns.	7 dns.	0 dns.	0·10 mm.
II ...	7 ,,	16 ,,	**35** ,,	15 ,,	2 ,,	0 ,,	0·11 ,,
III ...	10 ,,	22 ,,	**58** ,,	33 ,,	9 ,,	6 ,,	0·10 ,,

Localisation of Geo-perceptive layer in other plants.—The geo-perceptive layer of a large number of other plants was similarly localised, by the Probe, a short account of which is given below.

Commelyna.—The geotropic sensibility of the stem of this plant is shown by its erectile movement from a horizontal to a vertical position. The geo-electric response at the surface was 0. At 0.1 mm. it was 6, which increased to a maximum of 18 at a depth of 0.2. After this the response underwent a rapid decline. The maximally excited layer was subsequently found to contain the starch grains.

Myosotis.—The stem of Forget-me-not also gave strong geo-electric response, the maximum excitation occuring at a depth of 0.20 mm. In the microscopic section the starch containing layer was also found at the depth of 0.20 mm.

Centaurea.—The flower stalk of corn-flower was found to exhibit electric response of moderate intensity under the stimulus of gravity. It is sensitive before the opening the flower buds, but this disappears later after the opening of the flower. The maximally excited layer was at a depth of 0.3 mm. which also contained the starch grains.

Tiger Lily.—The flower bud of this plant is strongly geotropic. It gave the maximum geo-electric response at a depth of 0.3 mm. The starch grains occurred very near this layer.

Convolvulus.—This gave the maximum geo-electric response at a distance of 0.3 mm. from the surface, and the starch layer was found at a depth of 0.28 mm.

The table given below embodies the above results, and also those previously obtained with *Bryophyllum* and in *Nymphaea.* Though the maximal excitation occurs at unequal depths in different species of plants, the maximally excited layer is always found to coincide with the starch-sheath.

TABLE L.—GEO-ELECTRIC RESPONSE AT VARIOUS DEPTHS IN DIFFERENT PLANTS.

Specimen	Galvanometric negativity at depths in mm.											Position of starch sheath at depth of :
	0.	·1	·2	·3	·4	·5	·6	·7	·8	1·4	1·6	
Commelyna	0	6	**18**	2	0							0·21 mm.
Myosotis	15	27	80	**31**	7	5	0					0·3 ,,
Centaurea	0	10	22	**40**	8	7	0					0·3 ,,
Tiger Lily	7	11	25	**54**	7	5	3					0·3 ,,
Convolvulus	0	3	13	**33**	20	5	0					0·28 ,,
Bryophyllum	0		24		45		**63**		21	3	0	0·6 ,,
Nymphaea	10		26		40		50		62	**108**	72	1·4 ,,
Tropaeolum (stem)		**37**	7	0								0·10 ,,
,, (petiole)	0	6	**25**	2	0							0·20 ,,

The numerous experiments carried out with different plants thus show, that the maximum excitation occurs at a definite layer, and that this particular layer contains the falling starch grains.

DUPLICATION OF GEO-PERCEPTIVE LAYER.

The experiments described above brought out the definite fact that during the passage of the Probe from the surface to the central pith it encounters a particular starch layer, at which the geo-electric response is at its maximum.

From this it might at first appear that the geo-perceptive ayer must always be single. There is however, an interestng variation which is described below.

Experiment 233

While experimenting with a specimen of plant which was supplied from a nursery as the Cape Marigold (Calendula stellata?), I was at first greatly puzzled by the fact that this plant exhibited two definite electric maxima during the passage of the Probe from the surface to the pith. Thus in a given specimen, while geo-electric response of galvanometric negativity at a depth of 0.1 mm. was 60 divisions, it increased abruptly to 115 divisions at 0.2 mm., and declined to 15, at the greater depth of 0.30 mm. The response continued to decline till a depth of 0.60 was reached, when the response exhibited a second maximum, this time of 105 divisions. Below this the excitatory reaction underwent a decline and abolition. Detailed results are given in the following table.

TABLE LI.—SHOWING DUPLICATION OF GEO-PERCEPTIVE LAYER.

Distance from surface.	Geo-electric response
Surface 0 mm.	10 divisions
0·10 mm.	60 ..
0·20 ..	**115** ..
0·30 ..	15 ..
0·40 ..	14 ..
0·50 ..	14 ..
0·60 ..	**105** ..
0·70 ..	12 ..

The two starch-sheaths occurred at depths of 0·17 and 0·58 mm.

Similar duplication of geo-electric maximum was also obtained in a second specimen of the same plant. After cutting section of the plant it was a matter of agreeable surprise to find that there were two definite starch layers separated from each other by a distance of about 0.4 mm ;

it was at these starch-sheaths that the maximum excitations were observed. In the first specimen, the maximum excitation occurred, as we have seen, at a depth of 0.2 mm. The microscopic section showed the first starch-sheath to be at a depth of 0.17 mm. Corresponding to the second electric maximum at 0.60 mm. there was the second starch-sheath at a depth of 0.58 mm. In the second specimen, the positions of the electric maxima and the starch-sheaths exactly coincided, the first at a depth of 0.30 mm. and the second at 0.70 mm. The curve given above (Fig. 229) illustrates the geo-electric distribution at different layers and the occurrence of the two electric maxima.

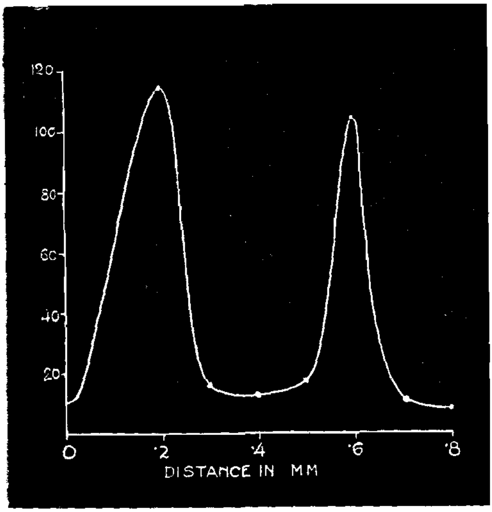

FIG. 229 Curve showing duplication of geo-electric maximum (see Text).

The above results afford another striking demonstration of the fact that the layer which contains the starch grains becomes the focus of irritation when the organ is displaced from the vertical to the horizontal position, and that in cases of two distinct starch layers, there are two foci of irritation which coincide with the two layers.

Another significant fact was noticed in regard to the geo-electric response of Calendula (?) that the geo-electric excitability was very marked at the beginning of its proper season, the sensitiveness disappearing later. Microscopic section showed that this insensitive condition was associated with the disappearance of the starch grains in the two layers. Of these the starch grains in the layer near the centre were the first to become reabsorbed.

THE EFFECT OF AGE ON GEO-ELECTRIC RESPONSE.

In connection with this, several interesting results were obtained. While working with the peduncles of several flowers it was noticed that a very strong geo-electric response occurred before the opening of the flower, but the response declined after the opening. Again, in the petiole of *Tropaeolum*, while moderately young specimens exhibited a marked response, very young and very old specimens exhibited little or none. The following investigation was undertaken to obtain more definite results in regard to the effect of age on geo-electric excitability. The uncertainty arising from the employment of different plants was eliminated by determining the excitatory action in different members of an identical plant; variation of age was secured by choosing different leaves of the same *Tropaeolum*, the leaf near the apex being the youngest, while those lower down were of increasing age. I chose for my experiments the second, the fourth, and the seventh leaves, counting from the apex. The Probe was thrust in till the petiole gave the maximum geo-electric response at an inclination of 90° to the vertical.

Experiment 234

In a particular series of experiments the second leaf gave the maximum response of 4 mm; the response of the fourth leaf showed a great enhancement, of 26 mm.; the response of the 7th was found to have declined to 7 mm. In the table given below I give the results obtained in three other series of experiments.

TABLE LII.—EFFECT OF AGE ON GEO-ELECTRIC RESPONSE.

Sequence of leaves	Maximum Negative electric response			
	Series I	Series II	Series III	Mean
Second petiole ...	4 mm.	12 mm.	17 mm.	11 mm.
Fourth „ ...	26 „	33 „	37 „	32 „
Seventh „ ...	6 „	8 „	5 „	6 „

It is thus seen that the geo-electric sensibility is but feeble in very young and old specimens.

SUMMARY.

The geo-perceptive layer, in the numerous specimens examined, was found to coincide with the starch-sheath.

The geo-electric response is diminished at high temperatures. The response which was found abolished in summer in the plains was found to persist in the colder climate of the hill station.

In certain plants, the geo-electric distribution exhibits two maxima. The focus of irritation is not single but double. Microscopic section showed that the starch-sheath in these is not single but double, and that the positions of the two electric maxima coincide with those of the two starch-sheaths.

Geotropic irritability is modified by age; it is strong in the middle-aged, and feeble in very young and old specimens.

LIII. THE RELATION BETWEEN THE ANGLE OF INCLINATION AND THE GEO-ELECTRIC EXCITATION.

By Sir J. C. Bose,
Assisted by
Satyendra Chandra Guha, m.sc.

If the pressure of heavy particles on the sensitive ectoplasmic layer of the cell be the efficient cause of stimulation under gravity, it would follow that the irritation caused by them will increase with the angle of inclination. In the vertical position there would be no effective stimulus; it would be most intense at an inclination of 90°. The effective pressure and the resulting stimulation will evidently vary as the sine of the angle of inclination to the vertical. The theory of the pressure of the particles being the efficient cause of geotropic action will thus find strong support if it could be shown that the induced irritation varies as the sine of the angle of inclination.

As regards the measurement of the induced irritation, it is theoretically possible to determine it from the mechanical or the electric response at various inclinations. But the practical difficulties in the measurement of the mechanical response are so numerous that it is impossible to obtain with it any accurate result. No such difficulty is encountered in the electric determination, the relative advantages of which are as follows: in the mechanical response the induced curvature is brought about by the modification of the normal rate of growth, which takes place a considerable time after the perception of the stimulus; the latent period of the mechanical response may thus be as long as an hour; the rate of responsive curvature is moreover indefinite, being sluggish at the beginning, rapid in the middle, and slow towards the end, when the organ becomes nearly vertical. Again the method of reversal, by which many sources of error are eliminated, cannot conveniently be applied with mechanical response. With the electric response, on the other hand, the above difficulties are practically absent. The latent period is very short and the maximum excitatory reaction is attained in the course of a minute or so. The excitatory reaction of galvanometric negativity disappears on the return of the specimen to a vertical position. Again, the errors caused by the inaccurate reading of the angular scale and the physiological asymmetry of the organ may be eliminated by the Method of Reversal. When the plant is inclined to the right through +90°, the current of response flows in one direction; when it is inclined to the left through -90°, the responsive current becomes reversed; the experimental error of a single determination is eliminated by taking the mean of the two galvanometric deflections. The details of the procedure will be understood from the *diagram given in* Fig. 230. The specimen is first vertical, with the two symmetrical contacts at the two sides, the electrodes being connected in the usual manner with the indicating galvanometer; after inclination through +90° the upper side A, becomes galvanometrically negative (right hand figure). The *excitatory reaction at the upper side finds* mechanical expression by the contraction and concavity, with positive up-curvature. The differential excitations of

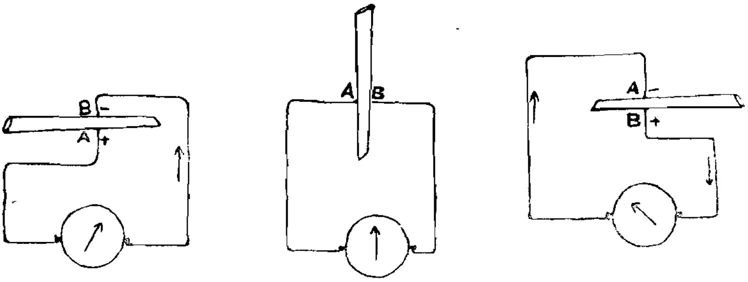

FIG. 230 Diagrammatic representation of the geo-electric response of the Shoot.

A and B and the resulting electric response disappear on the return of the specimen to the vertical or zero position. The specimen is next inclined to -90°; A now becomes the under, and B the upper and the excited side (left hand figure). The electro-motive change now undergoes a reversal, B becoming galvanometrically negative. The induced electromotive variation thus obtained is of considerable intensity, often exceeding 15 millivolts.

We shall now describe the experimental results on the relation between the angle of inclination and the resulting geo-electric excitation.

Excitatory Reaction at 45° and 90°.—In this investigation the first difficulty encountered is the accurate determination of the angle of inclination. An index is attached to the plant, and a stationary circular scale enables us to find the angle through which the plant is inclined to the vertical. But the vertical or zero reading itself is subject to an error of a few degrees; this is accentuated by the fact that we have no means of knowing whether the perceptive layer inside the plant is exactly parrallel to the surface of the stem or the petiole. The only means of eliminating the error is by obtaining two responses, say at $+45^\circ$ and -45°, by the Method of Reversal; in the first the *index reading* is $+45^\circ$ subject to the correction E, which is the error of the setting of the index. Now this error will make the actual angle $45^\circ + E$ and $45^\circ - E$ in the two readings for inclinations to the right and the left, *i.e.*, the angle will be greater in one case and correspondingly smaller in the other. Hence the mean of the two responses obtained through *successive positive* and negative inclinations of the specimen will reduce or eliminate not only this error, but also that due to the physiological asymmetry.

Experiment 235

I give below a series of galvanometric responses of the petiole of *Tropaeolum*, when carried through the entire cycle of inclination from the vertical to $+45^\circ$ (as read by the movement of the index), back to zero, and then to -45°, and back once more to zero. The same procedure was followed in the case of inclination to 90°; the records are given in Fig. 231. The response to +45° is seen in an up-curve, with subsequent recovery on return to the vertical. Inclination to -45° gave a reverse response of down-curve with *subsequent recovery*. The amplitude of two responses are 19 and 17 divisions respectively, the mean being 18 divisions. Inclinations to +90° and -90° gave rise respectively to the two responses of 24 divisions and 30 divisions, the mean being 27 divisions. The ratio of the excitations at 90 and 45 is therefore 27 : 18 or 1 : 1.5. The relation of sin 90° : sin 45° is 1 : 1.41. The ratio of excitatory actions at the two angles may thus be regarded as approximately the same as between the sines of the angles of inclination.

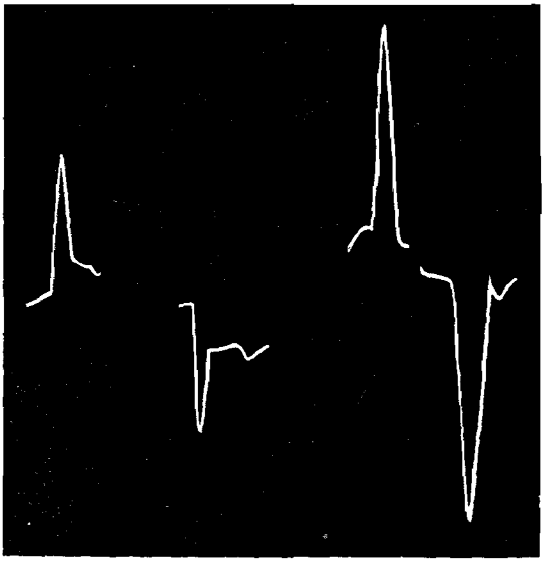

FIG. 231 Alternate geo-electric response at +45° and 45°, also at +90° and - 90°.

The following embodies the results of the observed actions at 45° and 90° in six different specimens of the petiole of *Tropaeolum*.

TABLE LIII.—EXCITATORY ACTIONS FOR INCLINATIONS OF 45° AND 90°. (PETIOLE OF *Tropaeolum*).

No.	Electric response		Ratio $\frac{b}{a}$
	(a) for 45°	(b) for 90°	
1.	37 divisions	55 divisions	1·488
2.	28 ,,	40 ,,	1·428
3.	192 ,,	274 ,,	1·426
4.	22 ,,	32 ,,	1·454
5.	31 ,,	44 ,,	1·420
6.	37 ,,	53 ,,	1·432
Mean ratio of excitation			1·44
Ratio of sines			1·41

The mean ratio of excitatory actions at the two angles is 1.44 while the ratio of the sines is 1.41. It will be noted that there is a persistent small difference between the two ratios, the excitation at the larger angle being greater than the value deduced from the ratio of the sines. The relatively greater excitation at the larger angle may have a physiological significance of which reference will be made later.

Excitatory Reactions at 45°, 60°, **and** 90°.—The relative excitatory actions with a different batch of petioles of *Tropaeolum*, was next obtained for the three angles of inclination of 45°, 60°, and 90°.

Experiment 236

TABLE LIV.—*EXCITATORY ACTION AT ANGLES OF INCLINATION OF* 45°. AND 90° (*Petiole of Tropaeolum*).

No.	Electric response at		
	(a) 45°	(b) 60°	(c) 90°
1.	39 dns.	49 dns.	54 dns.
2.	32 ,,	40 ,,	47 ,,
3.	31 ,,	40 ,,	46 ,,
4.	22 ,,	29 ,,	34 ,,
5.	14 ,,	19 ,,	25 ,,
6.	19 ,,	22 ,,	25 ,,
Mean	26 ,,	33 ,,	38 ,,
Ratio of excitations	1 :	1·26 :	1·47
,, sines	1 :	1·22 :	1·41

The determinations given above show once more that the excitation is but approximately proportional to the sines of the angles of inclination, the ratio of excitations at larger angles being relatively greater. The next series of observations were with angles of inclination which increased by steps of 10° degrees.

Experiment 237

I took photographic records of the responses at the successive angles of inclination of 45°, 55°, 65°, 75° and 90°, which are reproduced in Figure 232. The table gives the detailed results.

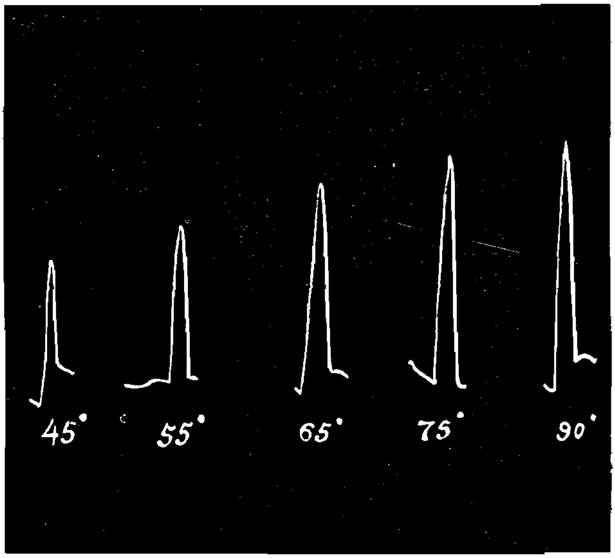

FIG. 232 Records of geo-electric responses at various angles.

TABLE LV.—GEO-ELECTRIC RESPONSES AT INCLINATIONS OF 45,° 55,° 65,° 75° AND 90.°

Angles	45°	55°	65°	75°	90°
Responses	44 dns.	52 dns.	57 dns.	61 dns.	63 dns.
Ratio of excitations	..	...	1·30 :	1·38 :	1·43
,, sines	..	...	1·28 :	1·36 :	1·41

Experiment 238

Further experiments were carried out with twelve different specimens of petiole of *Tropaeolum* and the mean *excitatory action* at the different angles are given in the following table :

TABLE LVI.—GEO-ELECTRIC EXCITATIONS AT VARIOUS ANGLES.

Angles	45°	55°	65°	75°	90°
Responses	40·8 dns.	47 dns.	55 dns.	60·5 dns.	63·3 dns.

Ratio of excitations ... ... 1 : 1·18 : 1·34 : 1·48 : 1·55
,, sines ... ... 1 : 1·15 : 1·28 : 1·36 : 1·41

The ratio of excitations, compared with the ratio of sines is thus seen to undergo a gradual increase with increasing angles of inclination. Thus to take the two extreme cases, the divergence between the two at 55° is 2.6 per cent. whereas at 90°, it is 9 per cent. This definite divergence which is persistent in all the determinations points to certain physiological difference.

In *attempting to find an explanation of the* relatively greater excitation at larger angles of inclination we have to take account of two different factors, first of the pressure exerted by the particles, and second the irritability of the ectoplasmic layer pressed by the particles. As regards the first, the effective pressure exerted by the particles is proportional to the sine of the angle of inclination. As regards the irritability of the ectoplasmic layer, this may not be the same throughout the length of the cell but greater towards the apical end. At the smaller angle of inclination, say to the right, the statoliths, originally at the base of the cell, accumulate to the right hand corner of the cell; a portion of the basal side of the cell is thus subjected to pressure. When the angle of inclination is increased, the statoliths pass along the whole length of the cell, including the apical end. The relatively greater excitation with increasing angle of inclination may therefore be explained on the assumption that the excitability of the ectoplasm is greater towards the apex. We shall next consider facts which appear to lend support to this view.

EXCITATORY ACTIONS AT 45° AND 135°.

A controversy has arisen in regard to the question as to whether the intensity of geotropic excitation is the same or different at the angles of inclination of 45° and 135°. The effective pressure exerted by the particles are the same at the two angles; the only difference in the two cases is in the collection of the particles at the basal end at 45° and at the apical end at 135°. Czapek has found that the effective stimulus of gravitation is greater when the organ is held at 135° than when held at 45°, though his results have not been accepted by others. In my work on *Plant Response* (1906) experiments have been described on geotropic response at 45° and 135°. The specimen employed was the unopened flower of *Crinum* lily, the response being mechanical. The results showed that the response to geotropic stimulus at 135° is greater than at 45°.

Experiment 239

I have recently carried out further experiments on this subject employing the independent method of electric response which is more reliable and accurate than the method of mechanical response. Allowance was made for any possible change in the excitability brought on by fatigue. This was secured by carrying out the experiments in the following sequence of observation (1) of response for 45°, (2) of response for 135° and (3) of response once more at 45°. The comparison of the first and the third responses would show hether any change in the excitability had occurred on count of fatigue; allowance for this is made by taking the mean of the two responses for 45° at the beginning and at the end of the series.

Experiment 240

Geo-electric response at 45° and 135°.—Observations with the petiole of *Tropaeolum* were made as follows; the first and the third responses for 45° were found to be 47 and 45 mm. respectively, the mean of the two being 46 mm. The second or intermediate response, taken for 135° gave 55 mm. The excitatory actions at 45° and 135° are thus seen to be in the proportion of 46 : 55, or as 1 : 1.2. In a second series with a different specimen the first and the third responses at 45° were both 25 mm. (Fig. 233). There was in this case no fatigue. The intermediate response at 135° was 31 mm. The ratio of the excitatory effects at the two angles are thus in the proportion of 25 : 31 or as 1 : 1.2. The excitation at 135° is thus about 20 per cent. greater than at 45°.

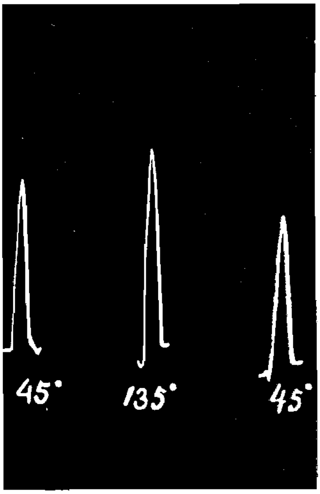

FIG. 233. Geo-electric response in sequence of 45°, 135° and 45°.

Experiments were next carried out with the stem of *Convolvulus*; at 45° the excitatory deflection was 26 divisions; when the angle was increased to 135°, the deflection was enhanced to 31 divisions. That the excitation at 135° was greater than at 45° was evidenced in a convincing manner by the return of the angle to 45° when the galvanometric spot of light was immediately restored almost to the first deflection; there was a slight fatigue and the deflection was 25 divisions instead of the former value of 26 divisions. The ratio of the two excitations at 45° and 135° is thus 25.5 : 31 or 1 : 1.23. In a second experiment the two excitatory deflections were as 18 : 21 or 1 : 1.31; the mean ratio from the two experiments is 1 : 1.27. The various results that have been given all tend to show that the excitation is greater at 135° than at 45°.

TABLE LVII.—GEO-ELECTRIC ACTIONS AT 45° AND 135°.

Specimen	Electric response at		
	45°	135°	45°
Tropaeolum	47 dns.	55 dns.	45 dns.
,,	25 ,,	31 ,,	25 ,,
Convolvulus	26 ,,	31 ,,	25 ,,
,,	16 ,,	20 ,,	16 ,,

Ratio of excitations at 135° and 45° Tropaeolum 1 : 1·2
,, ,, ,, ,, Convolvulus 1 : 1·27

We found from the indications of the experiments already described in regard to the effects of the angle increasing from 45° to 90°, that excitation is relatively enhanced with the increase of the angle. The relative effects at 45° and 135° may therefore be taken as extension of that generalisation. It would thus appear that the ectoplasmic layer is not uniformly irritable at all points, but that it undergoes a variation, the apical being more excitable than the basal end.

GEOTROPIC ACTIONS AT THE UPPER AND LOWER SIDES OF THE HORIZONTALLY LAID ORGAN.

We shall next consider the very difficult problem relating to the geotropic curvature of a shoot or a petiole. The upward curvature could only be due to the differential actions at the upper and the lower sides of the organ, otherwise the antagonistic effects at the opposite sides would neutralise each other. The responsive up-curvature is only possible (1) if the contractile effect at the upper side is greater than at the lower side, or (2) if the effects on the two sides are of opposite signs, namely, a contraction at the upper and an expansion at the lower side; in this latter case the two effects would be concordant. The investigations with the Electric Probe already described, indicate that the physiological effects induced at the upper and lower sides are of opposite signs, a galvanometric negativity indicative of contraction at the upper, and a galvanometric positivity indicative of expansion, at the lower side. The physiological actions are thus concordant in bringing about the upward geotropic curvature of the stem or the petiole.

These opposite actions at the upper and lower sides being thus established, we are confronted with the further difficulty of finding an explanation for this characteristic difference. The solution of this problem will be given in a subsequent chapter.

SUMMARY.

The geotropic excitation is found to vary approximately with the sine of the angle of inclination.

The results of numerous experiments tend to show that the excitatory reaction at increased angle of inclination is relatively greater than the value deduced from the law of sines.

This enhancement may be explained on the supposition that the excitability of the ectoplasmic layer at the apical end of the geo-perceptive cells is greater than at the basal end.

This consideration finds support from the fact that the geo-electric excitation at 135° is about 1.2 times greater than at 45°. In the first case, the starch grains accumulate at the basal, and in the latter case, at the apical end.

The geotropic up-curvature is only possible by a differential reaction at the upper and the lower sides of a horizontally laid stem or petiole. Electric investigations show that the tissue contiguous to the upper perceptive layer undergoes contraction, while that contiguous to the lower perceptive layer undergoes expansion.

LIV. THE CRITICAL ANGLE FOR GEO-ELECTRIC EXCITATION.

By

SIR J. C. BOSE,

Assisted by

SATYENDRA CHANDRA GUHA, M.SC.

A new line of investigation will be described in the present chapter which will afford an independent and crucial test as regards the falling starch grains being the effective factor in geotropic excitation. The results, to be presently described, will be better understood if we visualise the process of the fall of the starch grains in consequence of the inclination of the organ to the vertical. Let us take a mechanical model in which a layer of sand particles are resting on a flat surface. On gradually increasing the inclination of the surface to the horizon, there will at first be no displacement of the particles; for on account of friction and cohesion they will remain sticking against the surface. During the continuous increase of the angle, a point will be reached when there will be an abrupt sliding down of the particles.

This angle of sliding we shall designate as the critical angle; it will be relatively high if the surface be rough, and low when the surface is smooth. Again a rough surface may be smoothed down by the repeated sliding down of the particles. The critical point may thus be lowered by repetition of the sliding process.

Let us further imagine the flat surface to be bounded by vertical walls. The lateral pressure of the particles will be slight and constant at the two sides. But after inclination above the critical angle, the fall of the particles and the resulting increase of pressure on one side will be very abrupt.

The mechanical model described above may be taken as representing the statolithic cell. If the geotropic stimulus be brought about by the falling starch grains we should expect that :

(1) The particles will not be displaced at small angles of inclination and there would thus be no excitation.

(2) On gradually increasing the angle of inclination, the particles will slide down and press against the side of the cell, as soon as the critical angle is exceeded. This abrupt fall of particles and the resulting increase of pressure will constitute a stimulus and give rise to an excitatory response.

(3) Repetition of the process is likely to lower the critical angle to a certain extent.

(4) Had the weight of the fluid contents of the cell in higher plants been the only means of stimulation by gravity, the excitatory reactions would have been proportional to the sines of the angles of inclination above zero. But there would be a hiatus in this relation, if the fall of the solid particles be the efficient cause. There will be no excitatory response at angles lower than the critical. Even at a slightly greater angle than the critical, some of the particles may remain sticking at the base, and the excitation would be disproportionately lower than what is demanded by the law of sines. It is only after the critical angle has been considerably exceeded that the relation of sines will be found to hold good, at least approximately.

We shall now subject the above theoretical considerations to the test of experiment. We shall first attempt to discover if there be any discontinuity in the responsive reactions at angles below 45°, above which they have been found approximately proportional to the sines of the angles of inclination. After discovering this break of continuity we shall attempt to discover the critical angle and its exact value in different species of plants.

EXCITATORY ACTIONS AT 35°, 45°, AND 60°.

From the results of experiments detailed in the previous chapter it is found that the geo-electric excitation is approximately proportional to the sines of the angle of inclination. In order to observe whether the relation holds good at lower angles, a series of observation were made with six different specimens of the petiole of *Tropaeolum* at 35°, 45°, and 60°. The results are given in the following table.

TABLE LVIII.—GEO-ELECTRIC EXCITATIONS AT 35°, 45° AND 60°.

Specimen	Electric Response		
	35°	45°	60°
1	19 dns.	39 dns.	49 dns.
2	19 ,,	32 ,,	40 ,,
3	7 ,,	31 ,,	40 ,,
4	7 ,,	22 ,,	29 ,,
5	5 ,,	14 ,,	19 ,,
6	5 ,,	19 ,,	22 ,,
Mean	10·3	26·1	33·1

From the above we find that by *increasing* the angle above 45° the ratio of excitations at 60° to 45° is as 1.34 : 1, while the ratio of sines of 60° to 45° is as 1.22 : 1.

By *decreasing* the angle on the other hand we obtain the following :—

Ratio of excitation at 45° and 35° is as 1 : 0.39.
,, ,, sines of 45° ,, 35° ,, ,, 1 : 0.81.

In order to avoid decimals we multiply the above ratios by 100 and obtain the following results.

	35°	45°	60°
Excitations	39	100	134
Sines	81	100	122

The dotted thin curve given in Figure 234 represents the sines of the various angles of inclination ; the continuous line represents the excitations at the corresponding angles. It will be noticed that while the divergence between the sines and the excitations is slight above 45°, it is very pronounced at the lower angle of 35° ;

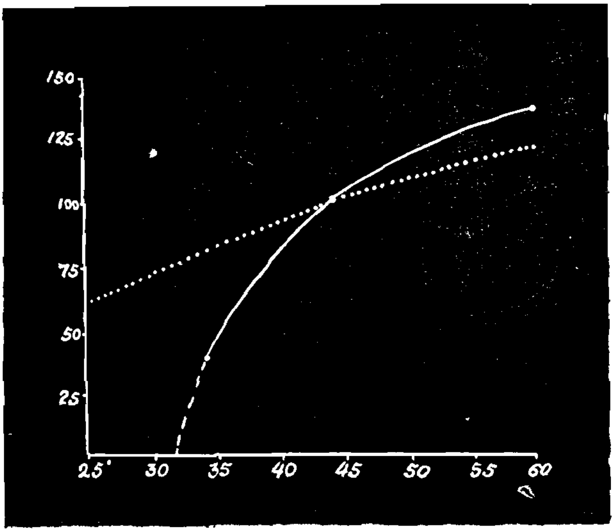

FIG. 234 Curves showing values of sines (dotted) and of excitations (thick line). The latter produced cuts abscissa at 31·5°, indicating absence of excitation at a critical angle. Ordinate represents excitation, abscissa the angle of inclination.

it indicates the approach of some hiatus or discontinuity. By producing the curve backwards we find it to cut the abscissa at 31.5° at which angle the excitation would be reduced to zero. This is the critical point; above this angle the excitatory reaction will be abrupt.

We shall next investigate whether such a critical point actually exists as foreshadowed by the curve and by the theoretical considerations detailed at the beginning of the chapter.

DETERMINATION OF THE CRITICAL ANGLE.

The discovery of the critical angle was the outcome of my investigations on the geo-electric response of *Nymphaea* (1919). The electric response was being recorded by inclining the specimen from the vertical to the horizontal. This was done very gradually in order to avoid any mechanical disturbance likely to disarrange the electric contacts. There was at first no indication of geo-electric excitation as the angle was gradually increased from zero upwards, and it was a matter of great surprise to note the sudden excitation which occurred as the inclination reached the approximate value of 33°. The excitatory action was detected by the sudden deflection of the hitherto quiescent galvanometer spot of light. On return to the vertical position the excitatory deflection disappeared. A repetition of the experiment gave the same result. As the excitatory action was due to the fall of the starch grains, it was clear that these particles had remained sticking at the base of the cell till they were precipitated above the critical angle.

Further experiments with *Nymphaea* had to be abandoned for the year, as the proper season of the plant was over. I have since been engaged in finding out whether a critical point for geo-electric excitation could be detected in other plants as was surmised from the trend of the curve given in Figure 234, from which critical point for the petiole of *Tropaeolum* appeared to be about 31.5°. It is very remarkable that the critical point of *Nymphaea* should be so near the above value. The critical point of 33° found for *Nymphaea* was very approximate. The following experiments were carried out for the determination of the critical angle of different plants, every precaution being taken for securing the highest accuracy.

Determination of the Critical point for the petiole of Tropaeolum.—I shall first give a continuous photographic record of the electric response of the petiole of *Tropaeolum* as it was gradually inclined from

Experiment 241

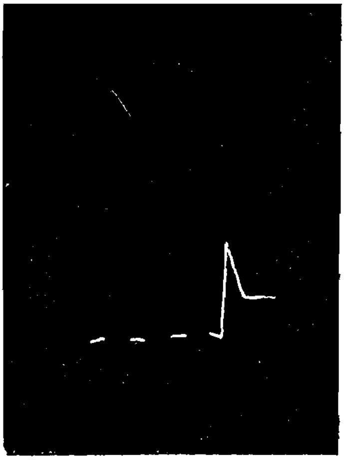

FIG. 235. Abrupt geo-electric response at an inclination of 31° (Tropaeolum).

25° to 31°, by successive steps of 2°. There was no response at 25°, 27° and 29°. When the angle was increased to 31° the response occurred abruptly, (Fig. 235). The restoration to the vertical was attended by a recovery.

I may dwell once more on the special advantages offered by the electric method in investigations on the excitatory action under the stimulus of gravity. The electric response is almost instantaneous; as the angle is gradually increased we obtain an immediate effect at the critical point, indicating the moment when the particles begin to slide down. In contrast with this are the difficulties inseparable from the mechanical method which render any accurate determination a matter of impossibility. For mechanical response, which is at all appreciable, takes place after a considerable length of time. The autonomous movement of the plant which must take place during this interval, will obviously produce a slow displacement of the particles downwards, even at an angle lower than the critical. These drawbacks are absent in the electric determination, where the critical angle at which the particles are abruptly precipitated becomes immediately detected.

The possible error in the exact setting of the index at zero of the scale is eliminated by the alternate inclination to the right and to the left. The mean of the two effective inclinations thus gives the true value of the critical angle.

Detailed accounts will now be given of determination of the critical angle of the petiole of *Tropaeolum*. Experiment 242 The angle of inclination to the right was gradually increased and the hitherto quiescent spot of light exhibited a sudden deflection to the right at 30°. On return to the vertical the excitatory action disappeared. Inclination to the left gave a sudden deflection at −35°, the deflection being now to the left. And nothing could be more striking than the unerring certainty with which an invisible force was evolved at definite points of alternate inclinations, which gave a sudden push to the galvanometric indicator, now to the right, then to the left. The mean of the two angles in this experiment gives the true value of 32.5° for the critical angle. The results of five observations are given in Table LIX. The mean of these determinations with six different petioles of *Tropaeolum* is found to be 31.7°, which is in remarkable agreement with the value of the critical point of 31.5° as deduced from the point where the excitation curve crosses the abscissa (see Fig. 234).

Determination of the Critical point for the stem of Tropaeolum.—The critical point for the stem was next determined, the procedure adopted being the same as in the last case. The minimum angle at which the response occurred by the right-handed rotation was +33° : rotation in the left direction gave the response at −30°. Hence the true critical angle for the specimen was 31.5°. Five other determinations were made with other specimens, and the mean critical angle obtained was 32.7°, which is very nearly the same as the critical angle for the petiole.

Experiment 243

Critical angle for the stem of Commelyna bengalensis. With this plant an inclination of +30° gave the excitatory response; inclination in the opposite direction gave the response at −33°. The true critical angle is thus 31.5°. In a second specimen the mean value of the critical angle was found to be 31°.

Experiment 244

TABLE LIX.—THE CRITICAL ANGLE FOR VARIOUS PLANTS.

Specimen	No.	Inclination to right or left	Critical angle	Mean
Petiole of Tropaeolum	I	+30 . . . —35	32·5	31·7
	II	+30 . . . —34·5	32·25	
	III	+35 . . . —30	32·5	
	IV	+29 . . . —32	30·5	
	V	+25 . . . —37	31·0	
	VI	+31 . . . —32	31·5	
Stem of Tropaeolum	I	+33 . . . —30	31·5	32·6
	II	+35 . . . —30	32·5	
	III	+36 . . . —30	33	
	IV	+35 . . . —32	33·5	
	V	+34 . . . —33	33·5	
	VI	+33 . . . —30	31·5	
Stem of Commelyna	I	+30 . . . —33	31·5	31·25
	II	+32 . . . —30	31	

The mean critical value for various plants examined is thus 31.8, the maximum variation from this is less than 1° It is very remarkable that the critical angle for different plants observed should exhibit so close an agreement.

THE EFFECT OF REPETITION.

Experiment 245

I stated at the beginning that repetition of the experiment is likely to *reduce the friction* and lower the sliding angle, and with it the critical point. It is very interesting to find that this was found to be the case as regards critical angle for geo-electric response. I took three different specimens of the petiole of *Tropaeolum*, the experiments being carried out three times in succession. In every case it was found that the effect of repetition was to produce a considerable lowering of the critical point. In the first specimen the critical point was lowered from 32.5° to 28.5°, in the second from 31° to 22.5°, and in the third from 30° to 22.5°. In *Commelyna*, however, the diminution was slight, namely from 31.5° to 30°, at the second repetition.

TABLE LX.—THE EFFECT OF REPETITION ON THE CRITICAL ANGLE.

Specimen		Direction of inclination		Mean Critical Angle
		Right	Left	
Petiole of Tropaeolum I	1.	30	35	32·5
	2.	30	32	31
	3.	27	30	28·5
II	1.	30	32	31
	2.	25	28	26·5
	3.	20	25	22·5
III	1.	29	31	30
	2.	24	30	27
	3.	20	25	22·5

The experiments that have been described offer the strongest confirmation of the statolithic theory. It has been shown that the geo-electric excitation is produced when the organ is held in a horizontal position. But when the organ is gradually inclined from the vertical there is no excitation till the critical angle is reached. The abrupt excitatory reaction must therefore be due to the sudden fall of heavy particles from the base to the side of the cells.

SUMMARY.

The excitatory reaction under stimulus of gravity, is reduced disproportionately with diminution of angle of inclination. This indicates the approach of some hiatus or discontinuity. By producing the curve of excitation backwards, it cuts the abscissa at about 31.5° at which angle the immediate excitatory reaction would be reduced to zero.

The critical angle for geo-electric excitation has been found in a large number of plants to be about 32°.

The effect of repetition of inclination is found to lower the critical angle.

The abrupt excitation above the critical angle can only be due to the sudden fall of the particles from the base to the side of the sensitive cells. The experiments therefore offer the strongest support to the theory of statoliths.

LV.—RESEARCHES ON THE EFFECT OF ANAESTHETICS ON GROWTH.

BY

SIR J.C. BOSE,

Assisted by

GURUPRASANNA DAS, L.M.S.

The effect of various anaesthetics on geotropic curvature will be given in detail in the next chapter. Since the fundamental mechanism of geotropic curvature is the differential growth at the upper and lower sides of the organ, we shall in this chapter investigate the effect of various anaesthetics on growth itself.

The difficulty in investigations on longitudinal growth arises from its excessive slow rate, on account of which a long period elapses before any perceptible elongation can be detected. But the prolongation of the period of observation introduces other complicating factors such as the variation of temperature and of light, which modify the growth. These difficulties are overcome by the device of the High Magnification Crescograph* in which a system of compound levers produces a magnification which may be raised to ten thousand times. Any change in the rate of growth is thus immediately detected, the experiment being completed in the course of a few minutes during which external conditions could be maintained constant.

METHOD OF RECORD.

The specimen of plant, suitably mounted, is attached to the first lever at a short distance from the fulcrum; the

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* Life Movements in Plants, Vol. I., p. 152.

second or recording lever produces a further magnification. The total magnification employed in the following experi-

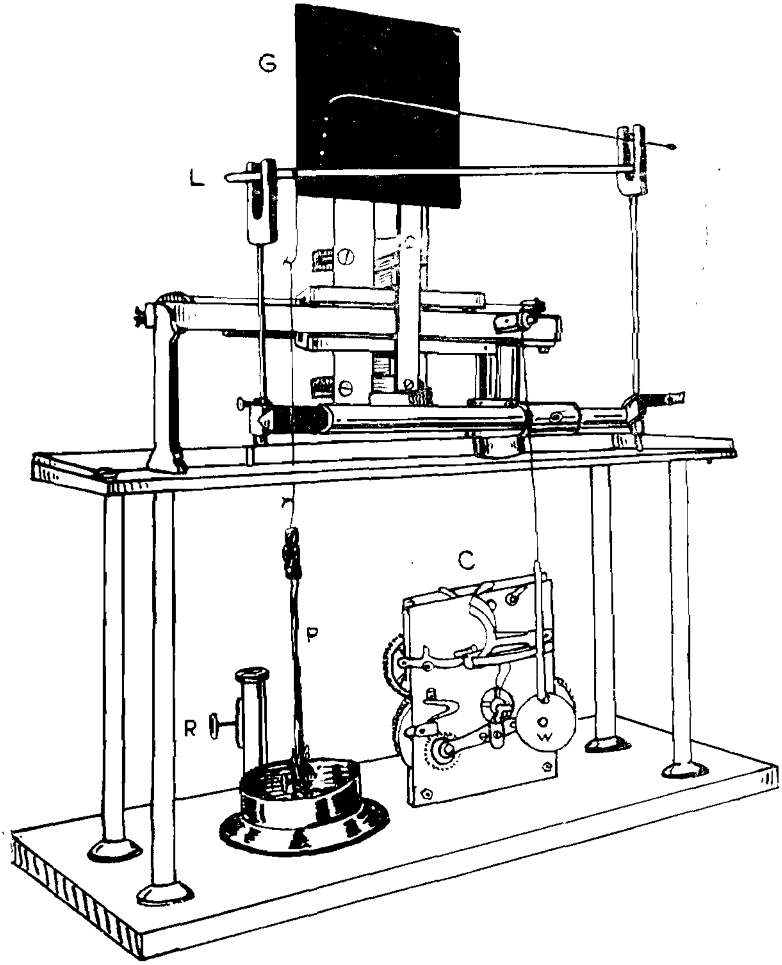

FIG 236. The High Magnification Crescograph. Plant P. attached to first lever; second lever records successive dots of growth-elongation on smoked glass G, kept oscillating by clockwork C. Adjustment of recording point is made by making plant move up or down by rack and pinion R. (One-fourth normal size.)

ments is 1000 times. (Fig. 236). The recording plate is kept oscillating at intervals of 15 seconds, so that successive dots give the time-record. The plate is also moved in a horizontal direction and the normal rate of growth and its induced variation is found from the recorded curve. Enhancement of growth causes an erection of the curve and also wider spacings between the successive dots. Diminution of the rate is shown by the flattening of the curve and the closeness of the dots; *arrest of growth* is indicated by a horizontal record, and an actual contraction by the reversal of the curve downwards.

APPLICATION OF ANAESTHETICS.

Much difficulty was at first experienced in devising an effective method for subjecting the specimen of plant to the action of anaesthetic acting uniformly on all sides of the organ. This was overcome by the following device in which

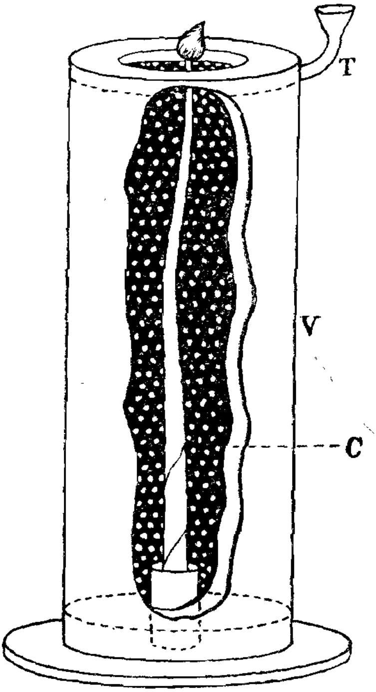

FIG. 237. Chamber for application of anaesthetics (see Text).

a detachable cylinder acts as a cover; it has a layer of thick absorbant cloth lining the inside. The pill box cover which closes the cylinder (with a hole for the protrusion of the specimen for attachment with the Crescograph) has a circular tube soldered underneath, with a series of small holes; one end of the tube is provided with a funnel into which is poured a given dose of ether or chloroform. The anaesthetic drips down into the absorbing cloth and the specimen soon becomes uniformly surrounded by vapour of the anaesthetic (Fig. 237). As the plant slowly absorbs the vapour, the immediate effect is due to a small dose; at the second stage, the effect of a 'moderate' dose makes its appearance. And finally, the effect of an excessive dose is found from the record at the third stage. The effects of different doses of application are thus found in the course of a few minutes by the record given by an identical specimen.

EFFECT OF ETHER ON GROWING ORGANS.

The following may serve as typical examples of results obtained from an extensive series of investigations carried out with various organs of different plants; among these may be mentioned the seedlings of Wheat; the stems ot *Helianthus* and of *Dahlia*; the petiole of *Tropaeolum*; the tendril of *Cucurbita*; the penduncles of *Hibiscus*, of *Centaurea*, of *Daffodil* and of *Allium*; the flower bud of *Crinum* lily; and the pistil of *Datura*. The results obtained are similar in all these cases; out of these, three representative experiments will be described in detail.

Experiment 246

Seedlings of Wheat.—The specimen was an intact seedling with roots; it exhibited a fairly rapid rate of growth as seen in the first part of the record (Fig. 238a). On application of ether the growth-rate became very greatly enhanced in less than 15 seconds and persisted for a considerable length of time.

This is seen in the erection of the curve and wider spacings between the successive dots. Continued application of ether caused a subsequent depression of the rate.

Crinum lily.—The result seen in this record is similar to that obtained with the seedling of Wheat. The acceleration occurred within 30 seconds of the application of ether vapour; the enhanced rate persisted for a period of 3 minutes, after which

Experiment 247

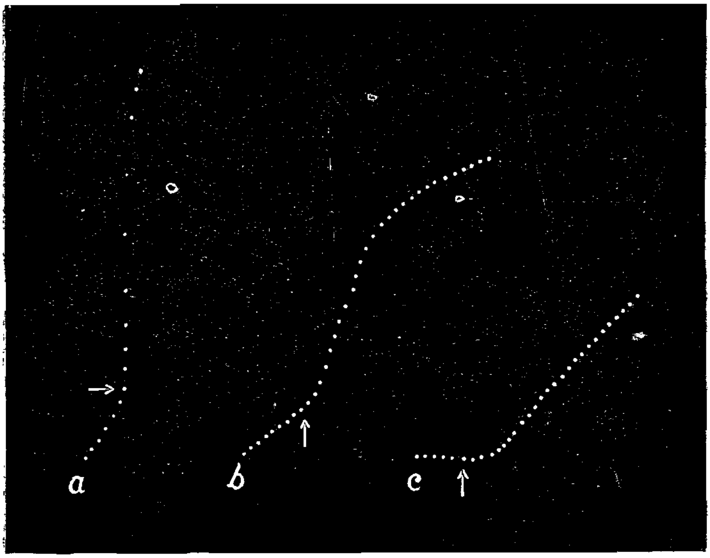

Fig. 238 Effect of ether vapour applied at arrow in enhancing the rate of growth in :

(a) Seeding of wheat ; (b) *Crinum* lily and (c) Stem of *Helianthus*. In this last, there is a renewal of arrested growth.

the depressing effect of a large dose is seen to occur as illustrated by the response curve (b) tending to become horizontal.

Stem of Helianthus.—The cut specimen was found to be in a state of arrested growth and the result obtained under ether is of much interest. It shows that ether not only enhances the rate of existing growth but *brings about a renewal of arrested growth.* In

Experiment 248

this case, the growth-renewal occurred within 90 seconds of the application of ether vapour (curve c), the growth persisting for a long time.

EFFECT OF CHLOROFORM.

Experiment 249

Petiole of Tropaeolum.—The preliminary effect of chloroform vapour is an acceleration of the rate of growth. In the petiole of *Tropaeolum* this acceleration occurred 4 minutes after the application of the anaesthetic and persisted for a period of 4 minutes and 15 seconds; this was followed by an arrest of growth for 45 seconds after which there was the abrupt contraction due to the death-spasm (Fig. 239a).

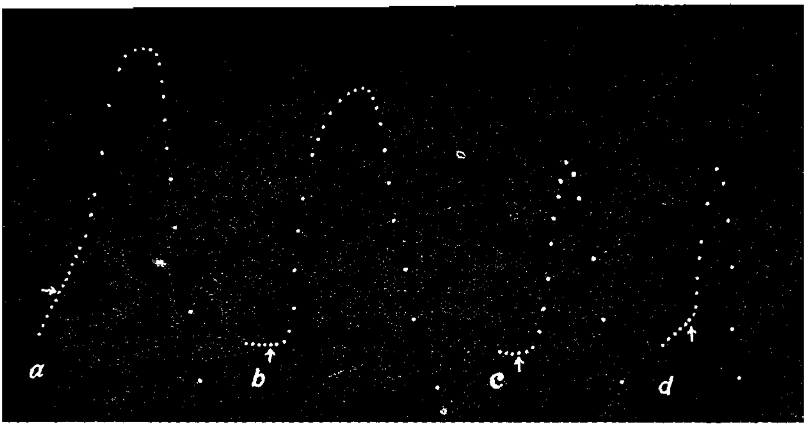

FIG. 239 Effect of chloroform vapour on growth; records exhibit effects characteristic of three stages, an enhancement, an arrest, and a spasmodic death-contraction.

(a) Petiole of *Tropaeolum*; (b) Peduncle of *Centaurea*; (c) *Crinum lily* and (d) Pistil of *Datura*.

Experiment 250

Peduncle of Centaurea.—The specimen was in a state of arrested growth, as seen from record (b); application of chloroform vapour induced a vigorous growth after an interval of 30 seconds. Here also we obtain the renewal of growth under a small dose of the anaesthetic. The revived growth persisted for 3 minutes, after which there was an arrest followed by the spasmodic death-contraction.

Crinum lily.—The specimen in this case was also in a state of arrested growth. Application of chloroform renewed the growth in less than 30 seconds (curve *c*). Under the continued action of chloroform the revived growth which had persisted for 2 minutes and 15 seconds was arrested; this was followed by a violent spasmodic contraction.

Experiment 251

Pistil of Datura.—Having described the effect of the anaesthetic on peduncles and on flower-buds I shall next describe the response of the pistil. The effect of chloroform on normal growth was a great enhancement which occurred in the course of 30 seconds (curve *d*). This persisted for nearly 2 minutes after which there was an arrest and subsequent spasmodic contraction.

Experiment 252

The growing organ under chloroform, thus exhibits a preliminary expansion followed by contraction. The contraction by itself should not be regarded as the sign of death, for we shall find later, that there are agents which induce a temporary contraction from which a revival is possible. The test of death-spasm is an irreversible change, from which the plant cannot be revived by substituting fresh air for the anaesthetic. This contraction under the prolonged action of chloroform, (by which even the interior of the tissue becomes affected) may be taken as the death-spasm, since a renewal of fresh air in the plant chamber does not bring about the revival of the plant. Another interesting phenomenon observed after chloroforming the plant is the profuse deposit of minute drops of liquids on the surface. This is due to the forcing out of the sap during death-contraction, the escape being facilitated by the increased permeability of the cells at death. Dark spots of discoloration soon begin to appear, and spread rapidly over the surface of the organ, which soon becomes wilted from the loss of turgor.

As regards death-spasm under an anaesthetic, it is instructive to compare with it the parallel effects of strong stimulus of an electric shock. When this is very strong, the response is by marked contraction of both pulvinated and growing organs. The plant is killed by the strong stimulus and there is no subsequent recovery. But if a moderate stimulus be applied to a fresh specimen, the plant will be found to recover from its excitatory contraction, and respond once more to stimulus. The excitatory contraction may thus pass from a reversible to an irreversible condition of death. We shall find later that this is equally true of the action of anaesthetics, a strong dose of which causes a contraction and death; but a mild dose of anaesthetic induces, after a time, a contraction from which there is a recovery brought about by substitution of fresh air.

SUMMARY.

The various growing organs, the stem, the petiole, the peduncle, the flower-bud, and the pistil exhibit similar reaction under a given anaesthetic.

A small dose of ether induces a great enhancement of the rate of growth; arrested growth is revived by it. The effect of a large dose, or of prolonged action, is to paralyse growth; timely substitution of fresh air is attended by a revival.

The effect of continued action of chloroform vapour is as follows:—

At the first stage there is produced a great acceleration of growth, or a renewal of arrested growth; at the second stage the growth becomes arrested; at the third, or final stage there is a violent contraction.

As chloroform in large doses is toxic, its prolonged application gives rise to the spasm of death. After this the surface of the plant is found to be covered with minute drops of liquid forced out from the plant during its death-contraction, the escape being facilitated by the increased permeability of the cells at death. After this, death discoloration spreads out rapidly and the specimen becomes wilted from loss of turgor.

LVI.—THE EFFECTS OF ANAESTHETICS ON GEOTROPIC RESPONSE.

BY

SIR J. C. BOSE,

Assisted by

LALIT MOHAN MUKERJI, B.SC.

An upward geotropic curvature takes place when the growing stem, the peduncle, the petiole or the flower-bud is placed in a horizontal position. This is due to the concordant effects of induced retardation of growth or contraction of the upper, and enhancement of the rate of growth and expansion of the lower side of the organ. The co-ordinated effects on the upper and the lower sides were independently demonstrated by the results of electric investigations. The upper side exhibits increasing galvanometric negativity, characteristic of excitatory contraction; the lower side exhibits, on the other hand, an increasing galvanometric positivity indicative of expansion and enhancement of the rate of growth. In pulvinated organs, the upward geotropic curvature is due to diminution of turgor and contraction of the upper, and enhanced turgor and expansion of the lower side.

Results of investigations by the electric method also show that the geo-electric response occurs a short time after the onset of the geotropic stimulus. But on account of the sluggishness of growth and its induced variation, the initiation of geotropic curvature becomes greatly delayed. This is accentuated by another complicating factor, namely, that of the weight, which causes a bending down of organ. The upper side of the organ is thus subjected t tension and the lower side to a compression. T differential action causes, at the beginning, a downw curvature, which has to be reversed by the true geotro action. The geotropic curvature is thus delayed, often more than an hour. The complications described above serious obstacles for accurate determination of the geotro response and its induced variation. These difficulties h been overcome (1) by the choice of a specimen which quick in its response, and (2) by reducing the weight of specimen by cutting off portions which are non-essent These conditions are fulfilled by the petiole of *Tropaeolu* The lamina is cut off, the weight of the short length of petiole being thus greatly reduced. The cut ends wrapped in moist cotton, and after a rest of half an hour irritability of the specimen is found to be fully restor Finally, (3) the beginning of geotropic response can be eas detected by the employment of a magnifying lever. T sensitiveness of the petiole of *Tropaeolum* is, however, great that a magnification of five times is quite sufficient the purpose of record, which is taken on a plate oscillat once in three minutes, the successive dots representing t interval of time.

This plant *Tropaeolum* grows in Calcutta during winter months from November to January and during months of February and March which are the spring seas the plant begins to die off by the beginning of April. T experiments described below were commenced in Febru 1920, and continued till March, 1921. The experime were thus carried on during two springs and one winter; records given by the spring and the winter specimens exhi certain differences which are characteristic. In the spr specimen, the latent period, or the period which elap between the application of the stimulus of gravity and the commencement of the geotropic up-movement is six minutes or less, after which the rate of movement becomes uniform for about half an hour. The slope of the curve, and the distance between the successive dots indicate the geotropic activity; any induced enhancement of the normal rate is, as already explained, exhibited by the erection of the curve and greater separation of the successive dots; depression, on the other hand, is indicated by the opposite change. In the winter specimens, owing to the general depressed rate of growth, the geotropic response is very sluggish, as seen in the prolonged latent period, which in the particular experiment is seen to be 48 minutes; the sluggish character of the response is also indicated by the gentle slope of the geotropic curve (Fig. 240).

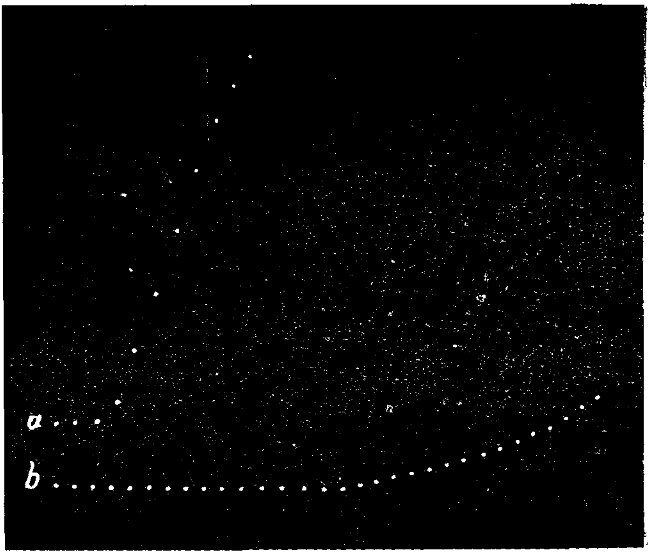

Fig. 240. Geotropic curve: (*a*) of a spring, and (*b*) of a winter specimen. The latent period of the former is six minutes, of the latter forty-eight minutes.

Note the relatively erect curve of the spring specimen indicating a more intense geotropic action.

The uniformity of the erectile response cannot be maintained for an indefinitely long period, since any further response is impossible after the full erection of the specimen. It should therefore be held a few degrees below the horizon, and record continued till it rises through the same angle above the horizontal position. The slope of the curve is then found to remain practically uniform for about half an hour, which is more than sufficient for the completion of the experiment on the action of the anaesthetic. Having described the experimental method, we shall next study the effect of ether on geotropic curvature of (A) pulvinated and (B) of growing organs. The effect of chloroform will also be studied in these two different types.

EFFECT OF ETHER ON GEOTROPIC CURVATURE OF PULVINATED ORGANS.

Mimosa.—The leaf of *Mimosa*, normally speaking,

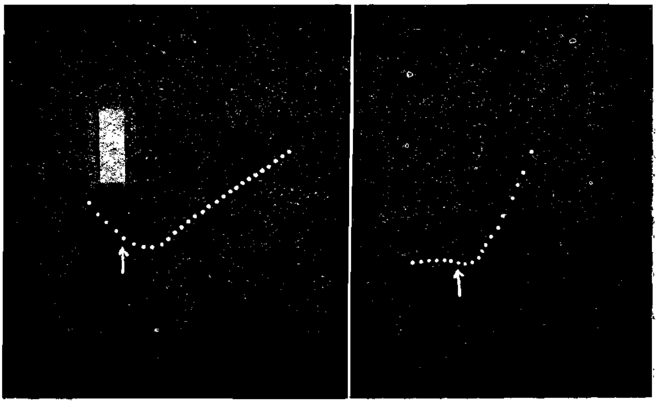

FIG. 241 FIG. 242

FIG. 241. Effect of ether on geotropic response of the leaf of *Mimosa*.

FIG. 242. The geotropic response of the terminal leaflet of *Desmodium gyrans* under the action of ether.

assumes the so-called dia-geotropic position, which is approximately horizontal. Enhancement of geotropic action would cause an erection of the leaf. In the experiment described below, the leaf on

Experiment 253

account of its diurnal movement, was exhibiting a fall; application of ether vapour at the point marked with the arrow arrested this fall; afterwards an erectile movement was initiated which indicated an enhancement of geotropic action. This occurred in the course of 40 seconds, and the erectile movement persisted for a further period of 7 minutes (Fig. 241). Continued action of the anaesthetic was afterwards found to arrest all further movement.

Experiment 254

Terminal leaflet of Desmodium.—The leaflet was in a stationary dia-geotropic position. Application of ether vapour induced in a short time, a great enhancement in the geotropic curvature as seen in figure 242.

EFFECT OF ETHER ON GEOTROPIC CURVATURE OF GROWING ORGANS.

Experiment 255

Petiole of Tropaeolum.—After the attainment of uniform geotropic up-movement, a specimen of *Tropaeolum* was subjected to the action of ether vapour; this induced a very great enhancement of geotropic movement in the course of 3 minutes, as seen in the erection of the curve and in wider spacings of the successive dots (Fig. 243).

Experiment 256

Having thus obtained a definite proof of the enhancement of the geotropic action under ether, two batches of six similar petioles of *Tropaeolum* were taken and placed horizontally; of these the first batch was placed in a chamber containing air, the second batch being placed in a chamber which contained a small quantity of ether vapour. On examining the two batches after an hour, it was found that while a slight curvature was produced in specimens under normal condition, those subjected to the vapour of ether had become highly erected the tips being bent even backwards. The striking difference between the two will be seen in the reproductions from a photograph of the normal and the etherised specimen (Fig. 244). The experiments on pulvinated and on growing organs thus exhibit similar results, namely, an enhancement of geotropic action under moderate application of ether vapour.

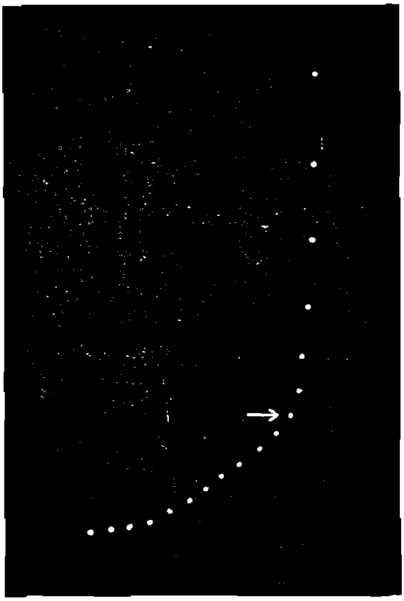

FIG. 243. Effect of ether in enhancement of geotropic response (Petiole of *Tropaeolum.*)

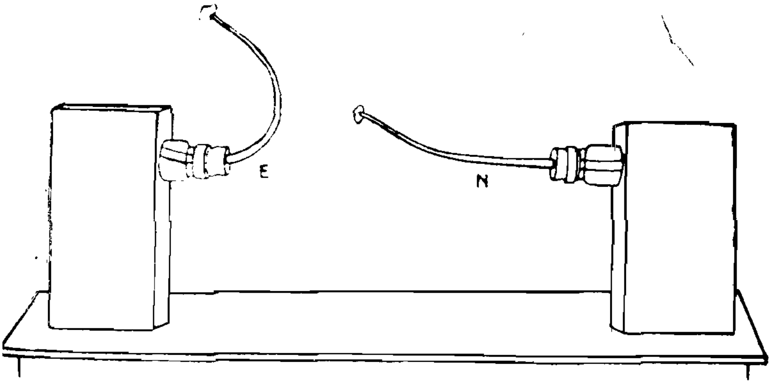

FIG 244. The effect of ether vapour on geotropism. N, the normal action in air; E, the effect in an atmosphere of ether vapour.

EFFECT OF CHLOROFORM ON GEOTROPIC RESPONSE OF PULVINATED ORGANS.

Experiment 257

Mimosa.—The preliminary effect of chloroform vapour is seen to induce, in the course of 80 seconds, a great enhancement of the geotropic action, as seen in the rapid erectile movement; this was arrested in the course of three minutes after which there occurred a very rapid contractile movement (Fig. 245).

Experiment 258

Desmodium leaflet.—The leaflet was executing a slow up-movement. Application of chloroform induced preliminary enhancement of geotropic action in the course of 40 seconds. This persisted for two minutes and a half, after which the movement underwent a reversal (Fig. 246).

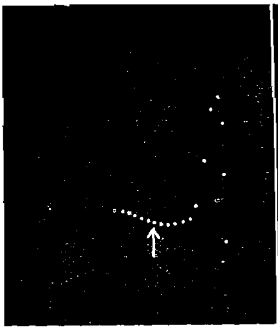

FIG. 245

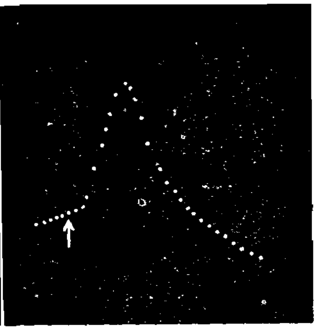

FIG. 246

FIG. 245 Effect of chloroform vapour on geotropic response of *Mimosa.*

Note enhancement at the first stage, arrest at the second, and reversal at the third stage.

FIG. 246 Similar effect of chloroform on geotropic response of the terminal leaflet of *Desmodium.*

EFFECT OF CHLOROFORM ON GEOTROPIC RESPONSE OF GROWING ORGANS.

The following experiments on the action of chloroform were carried out with two different species of plants, the seedlings of *Eclipta erecta*, and the petiole of *Tropaeolum*, with the object of bringing out certain characteristic differences.

Seedling of Eclipta.—The skin of *Eclipta* is somewhat impervious to vapour; hence a relatively small quantity of chloroform vapour is absorbed by the plant. The characteristic effect is seen to be a great enhancement of geotropic action which persisted for a considerable length of time (Fig. 247*a*).

Experiment 259

Petiole of Tropaeolum.—In the last experiment,

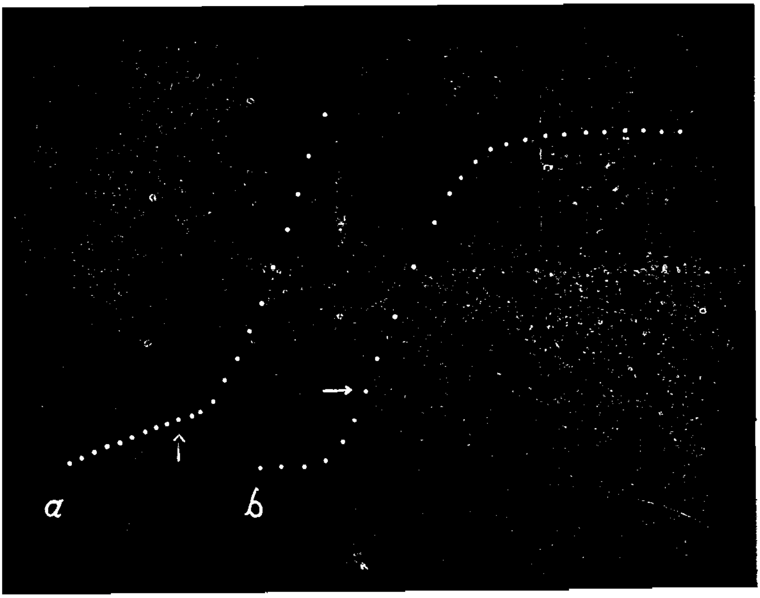

FIG. 247 Effect of chloroform on geotropic response: (*a*) enhancement f geotropic action in *Eclipta*, (*b*) preliminary enhancement followed by rrest in *Tropaeolum* [See text].

absorption of small quantity of chloroform gave rise to acceleration which is characteristic of the first stage. In *Tropaeolum*, the petiole absorbs the vapour more readily, and we observe an enhancement of geotropic action at the first stage, and an arrest at he second stage (Fig. 247*b*).

Experiment 260

In reviewing the effect of anaesthetics on geotropism in growing organs, we are able to trace it to the *induced* modification of growth itself. For ether has been shown to enhance the rate of growth; it also enhances the rate of geotropic movement. Chloroform induces a preliminary enhancement of growth followed by an arrest. In geotropic response under chloroform we also obtain a preliminary increase followed by arrest of geotropic movement. Effects parallel to these are also obtained with pulvinated organs.

SUMMARY.

The geotropic action in growing organs is dependent on its growth-activity. In spring, the latent period is relatively short and the rate of erectile movement rapid. In winter, the latent period is prolonged and the geotropic movement is sluggish.

Ether induces an enhancement of geotropic action both in pulvinated and in growing organs.

The effect of chloroform in a moderate dose, is an enhancement of geotropic action followed by an arrest. Excessive application may, however, give rise to the reversed contractile movement.

VII.—THE EFFECT OF CARBON DIOXIDE ON GEOTROPIC ACTION.

BY

SIR J. C. BOSE,

Assisted by

SURENDRA CHANDRA DAS, M.A.

In considering the action of different anaesthetic agents we found that the effect of chloroform is very intense and ultimately fatal; ether is less toxic and does not, under normal conditions, produce the death of the plant. The effect at the first stage in both is the same, namely, an enhancement of growth and of geotropic curvature. At the second stage, we obtain a paralysis of sensibility, the geotropic response being thereby arrested. Substitution of fresh air often brings about a restoration and the renewal of geotropic action. The effect of ether, generally speaking, stops at the second stage; but with chloroform in excessive dose, the effect of the third stage makes its appearance—a spasmodic contraction followed by the death of the organ.

Carbonic acid gas may be regarded as a mild narcotic, its effect being comparable to that of ether. One would therefore expect, that its effect on geotropic response would be similar to that of ether, that is to say, an enhancement of response at the commencement followed by an arrest under its continued action. The normal geotropic action might also be expected to be restored on substitution of fresh air.

EFFECT OF CARBONIC ACID GAS ON GEOTROPIC RESPONSE OF GROWING ORGANS.

Experiment 261

Effect on winter specimens of Tropaeolum.—The results anticipated were fully verified in all the experiments carried out during the winter season of 1920, of which a record is given in Figure 248*a*; owing to the sluggishness of response in the cold season, the latent period (the first part of the record not shown) was found to be 40 minutes. The geotropic curvature was then initiated at a slow rate, as seen in the

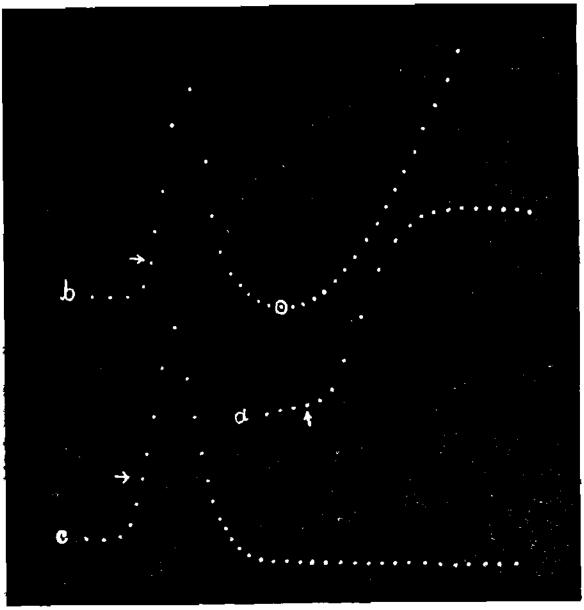

FIG. 248 Effect of CO_2 on geotropic response of *Tropaeolum*:
(*a*) Effect on winter specimen; CO_2 applied at arrow induced preliminary enhancement followed by arrest.
(*b*) Effect on spring specimen; CO_2 applied at arrow and fresh air substituted at circle. The effect induced is a preliminary enhancement followed by a *reversal*. Substitution of fresh air renewed normal geotropic action.
(*c*) Enhancement of geotropic response followed by persistent reversal under continued action of the gas.

slightly inclined curve of ascent. Carbonic acid gas was next passed into the plant-chamber; this caused a great enhancement of the geotropic action in the course of about 3 minutes. The induced enhancement is clearly seen in the very erect curve, and in the separation of the successive dots; the acceleration persisted for 20 minutes, after which the geotropic movement became arrested. This arrest was not permanent, for introduction of fresh air was found to bring about the subsequent renewal of geotropic up-movement.

Response of Spring Specimens.—The experiment with the winter specimen is described at the beginning since its responsive characteristics are easily explained. But the response of specimens in the earlier months of the year, in the spring of 1920, presented peculiarities which appeared at first to be quite inexplicable. This will be understood from the records (Fig. 248*b*), in which the latent period is as short as six minutes and the erect curve shows the considerable geotropic sensibility of the spring specimen. After the attainment of uniform erectile movement, carbonic acid gas was made to fill up the plant-chamber; this induced a great enhancement of geotropic movement in the course of 3 minutes, a result characteristic of the first stage. The erectile movement was temporarily arrested in the course of 21 minutes. There next followed the astonishing, and at first inexplicable, result of the reversal of normal geotropic movement which carried the tip of the specimen *below* the horizontal position. It thus appeared as if carbonic acid gas caused a reversal of the normal geotropic response. Fresh air was next introduced into the chamber, with the result that the normal geotropic up-movement was renewed after an interval of five minutes.

Experiment 262

In another experiment, a stream of carbonic acid gas was maintained throughout the experiment lasting for more than an hour. It gave the same sequence of effects as before, namely, an enhancement at the first stage, a temporary arrest at the second, and a reversal at the third stage. The tip of the specimen under the continued action of gas persisted in its reversed position below the horizon. The results given above were so unexpected that I was at first inclined to attribute it to some unknown and abnormal condition. But repetition of the experiment a year later, in the spring of 1921, fully corroborated the previous observations.

The results described above relate to the action of carbonic acid gas on the geotropic response of *Tropaeolum*. For determination of the universality of the phenomenon, further investigations were undertaken with a large number of growing and pulvinated organs of different plants.

Response of the peduncle of Tube-rose.—This specimen gave the normal geotropic response, though the effects were relatively sluggish. The latent period was 45 minutes. Continued action of carbonic gas induced a reversal of normal geotropic response in the course of six minutes. On the substitution of fresh air in the plant-chamber, the normal up-movement was once more initiated. Continued action of carbon dioxide is thus seen to produce in the Tube-rose a reversal of geotropic action similar to that in *Tropaeolum*.

Experiment 263

EFFECT OF CARBONIC ACID GAS ON GEOTROPIC RESPONSE OF PULVINATED ORGANS.

The geotropic excitability of the upper half of the pulvinus of *Mimosa* is very much less than that of the lower half. It thus happens that the leaf of *Mimosa* is in a state of equilibrium in a horizontal or the so-called dia-geotropic position. But if the plant be inverted so that the relatively more excitable lower half is above, the geotropic excitation and the resulting curvature are greatly enhanced, the leaf becoming continuously erected in this inverted position. The experiment may be carried out with a small piece of cut stem of *Mimosa* bearing the lateral leaf; the sub-petioles may also be cut off, thus reducing the weight of the petiole. In order to prevent drying, the cut ends of the stem and of the petiole are covered with small pieces of moist cloth. The sensibility of the pulvinus is fully restored in the course of an hour, when mechanical stimulation is found to cause the normal fall of the petiole.* The cut specimen may now be easily manipulated and held in the inverted position (Fig. 249) for obtaining the normal record of geotropic up-movement, which is brought about by the joint effects of contraction of the more excitable half B, and the expansion of the less excitable half A.

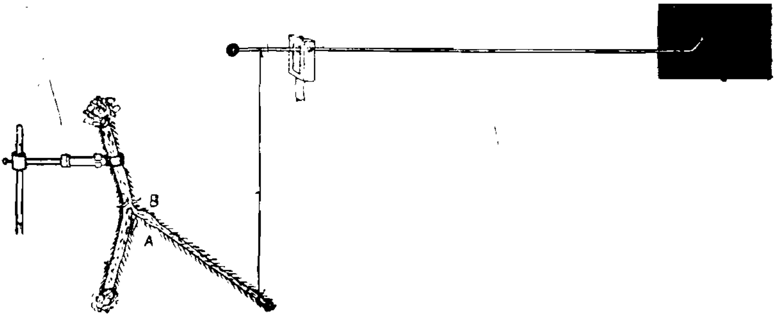

FIG. 249 Method of record of geotropic response of *Mimosa*, held in an inverted position with the more excitable half of pulvinus B facing upwards.

Effect of CO_2 on Geotropic Response of Mimosa.—The first part of the record in Figure 250 shows the uniform geotropic response in the inverted position. The plant-chamber was next filled with carbon dioxide. This caused an arrest, and a subsequent reversal of geotropic response, which occurred 2 minutes after the application of the gas. By this reversal, the leaf was

Experiment 264

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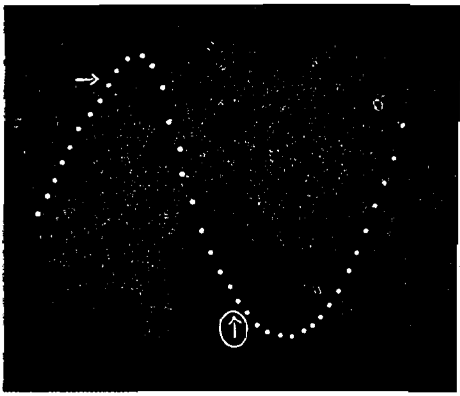
* Life Movements in Plants.—Vol. I., p. 81.

brought below its original position and maintained there. Substitution of fresh air brought about a restoration, and the normal geotropic response was renewed in the course of four minutes.

Experiment 265

Erythrina indica.—The pulvinus of *Erythrina* is less sensitive than that of *Mimosa*; the characteristic effects are, in other respects, the same in the two cases. The cut specimen was held in an inverted position, and after the attainment of uniform up-movement, carbonic acid gas was applied; this caused a reversal of the normal geotropic movement in the course of four minutes and twenty seconds; the petiole was thus lowered below its original position. Introduction of fresh air gave rise, in the course of two minutes, to the renewal of the normal erectile movement (Fig. 251.)



FIG· 250

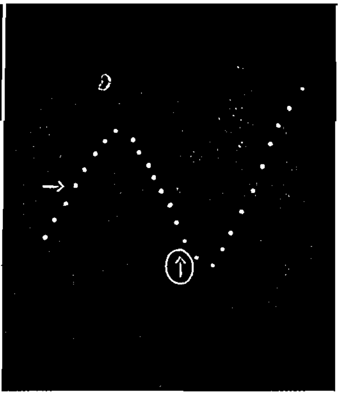


FIG. 251

FIG. 250 Effect of CO_2 on geotropic response of *Mimosa* applied at arrow; second arrow within a circle represents substitution of fresh air.

FIG. 251 Effect of CO_2 on geotropic response of *Erythrina indica*. Successive dots are at intervals of a minute.

The results obtained with various growing and pulvinated organs thus show that the normal geotropic response is reversed under the continued action of carbonic acid gas.

Lynn* has also shown that a reversal of geotropic curvature occurs when the hypocotyls of *Helianthus annuus* are fixed horizontally in an atmosphere containing from 9 to 30 per cent. of carbon dioxide. On the removal of the carbonic acid, the seedlings showed a normal upward curvature by next morning. Lynn did not notice any preliminary enhancement of geotropic curvature, the method of eye observation employed being not adequate for the purpose. For an explanation of the phenomenon he suggests the theory of hydrion concentration; an assumption is made that the stem is a relatively alkaline structure, because the carbon dioxide of respiration does not accumulate (most of it being used up by the plant during photosynthesis); it is further supposed that as a result of the relative alkalinity of the continuous phase of the protoplasm in the perceptive cells, a horizontally placed stem under normal conditions turns upwards in response to stimulus of gravity. In an atmosphere of carbon dioxide, on the other hand, the stem is rendered less alkaline with the result of reversal of normal response.

This explanation is not satisfactory since there is no evidence in support of the Hydrion Differentiation Theory of Geotropism propounded by Prof. Small; on the contrary, accumulation of carbonic acid in the plant in the absence of photosynthesis has practically little effect towards reversal of normal geotropic response. Most of the records given in this chapter were obtained with petioles of leaves, the photosynthetic lamina being cut off; moreover the specimens were kept in a dark box. In spite of these conditions the geotropic response produced was a normal up-curvature. Finally, the immediate effect of carbon dioxide is an enhancement of normal geotropic action—a result which contradicts the hydrion theory.

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* M. J. Lynn, M.SC., "The Reversal of Geotropic Response in the stem." The New Phytologist—August, 19, 1921.

EXPLANATION OF THE REVERSAL.

In regard to the reversal of the normal response it might be thought that the geotropic perception might in some way undergo change in an atmosphere of carbon dioxide. In reference to this, investigations with the Electric Probe, previously described, have fully confirmed the theory that in higher plants, it is the falling starch grains that cause geo-perception; since the weight of these particles remains constant, there could be no possibility in the variation of this factor. It might be argued that the starch grains become absorbed in an atmosphere of carbonic acid gas, the particular factor of stimulation being thus eliminated. This argument is, however, untenable, since the reversal under carbonic acid and restoration of normal response on removal of the gas take place in the course of a few minutes: the disappearance and reappearance of the starch grains could not possibly have taken place within such a short time

Returning to the question of normal geotropic curvature in growing organs I have shown* that this is brought about by differential growth, that the upper side of the horizontally laid organ undergoes a retardation of growth, while an acceleration of growth and expansion takes place on the lower side. A satisfactory explanation of the effects of various narcotics—an acceleration, an arrest, or a reversal—may therefore be found from the determination of the effects of various narcotics on growth itself. Let us first consider the enhancement of geotropic up-curvature under moderate application of ether vapour. This increased up-curvature may be brought about:

(1) by the increased *contraction* of the upper side due to diminished rate of growth under the anaesthetic, or

(2) by the induced *expansion* and enhanced growth of the lower side of the organ.

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* Life Movements in Plants.—Vol. II, p. 502.

We are in a position to decide between the two alternatives, by finding whether ether induces a retardation or an enhancement of growth. If it induces a retardation, the enhanced geotropic curvature would be due to the contraction of the upper side : an acceleration of growth under ether would, on the other hand, show that the enhancement of geotropic curvature was brought about by the increased rate of growth at the lower side of the organ. The results of investigation on the effect of ether already described show definitely that it induces an enhancement of the rate of growth. *Hence the modification of geotropic curvature under the anaesthetic is due to the induced change of growth of the lower side.* This deduction also follows from the general consideration that the upper side of the organ is contracted under the geotropic stimulus, whereas the lower side is in a state of active growth. Modification in the rate of growth is likely to occur in the growing portion of the tissue rather than in the portion where it has become arrested under the action of stimulus. A crucial experiment will be described which will show that carbonic acid gas exerts little or no effect on the contracted side of the organ.

Our attempt to discover the cause of reversal of the geotropic response under carbon dioxide must, therefore, be concentrated on the determination of the effect of the gas on growth. In regard to this, the only information that has been available is that the presence of oxygen is necessary for normal growth, and that growth comes to a stop in an atmosphere of carbonic acid gas. This does not however explain the increased geotropic curvature at the beginning, nor the reversal under its continued action. Certain results which were obtained with the High Magnification Crescograph showed that the preliminary effect of carbonic acid is an enhancement, while continuous action causes a retardation of growth.* This would fully explain the

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* *Life Movements in Plants.*—Vol. II, p. 265.

initial increase of the geotropic curvature under carbonic acid and the subsequent arrest. Further investigations are however necessary to determine the effect of continued action of carbonic acid in inducing a reversal, and the after-effect on the removal of the gas. The following investigations were therefore carried out on the effect of carbonic acid on growth as regards: (1) the immediate effect, (2) the persistent effect, (3) the after-effect on the removal of the gas, and (4) the effect of carbonic acid gas on an organ contracted under continuous stimulation.

INVESTIGATION ON MODIFICATION OF GROWTH UNDER CARBONIC ACID GAS.

The High Magnification Crescograph was employed for record of the normal growth and its induced variation. The flower-bud of *Crinum* lily was found suitable for this research, as its normal rate of growth is very uniform. The magnification employed was a thousand times, and the successive dots in the record indicate intervals of 20 seconds. The specimen was enclosed in a chamber which could be filled with pure carbon dioxide for a definite length of time, air being afterwards substituted for the gas.

Experiment 266

The rate of normal growth of the *Crinum* lily was taken on a moving plate, and the slope of the curve and the closeness of the successive dots indicated the normal rate. Carbonic acid gas was introduced into the chamber; this is seen to have induced an almost immediate enhancement of the rate of growth as seen in the erection of the curve and the wider spacings between the dots (Fig. 252). This induced enhancement of growth lasted for 4 minutes, *after which a contraction took place on account of which the specimen became shorter than at the beginning; this contraction persisted throughout the application of* *the gas. On substitution of fresh air the normal growth elongation was resumed.* This resumption occurred in the course of about 4 minutes.

This remarkable result of contraction which persists during the application of gas, and the restoration of growth on removal of the gas, offer full explanation of the reversal of geotropic response and the subsequent restoration of the normal response on introduction of fresh air. The preliminary enhancement of growth under CO_2 also explains the immediate enhancement of the geotropic curvature. The up-curvature has been explained to be due to the differential growth of the upper and lower sides of the organ. Considerations have also been adduced to show that the modification of geotropic curvature under anaesthetics is brought about by the induced change of growth at the lower side of the organ, the effect on the contracted upper side being

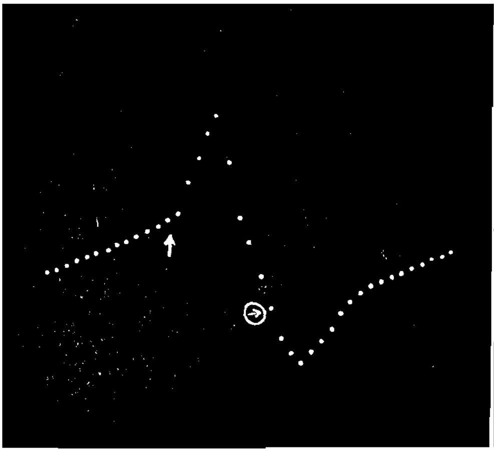

FIG. 252

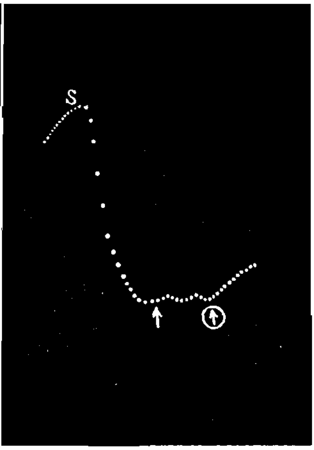

FIG. 253

FIG. 252 Effect of CO_2 on growth.

Note preliminary enhancement followed by active contraction, under which the organ became shorter than at the beginning. Substitution of fresh air at arrow (within a circle) caused a renewal of growth.

FIG. 253 Organ contracted under stimulus S; application of CO_2 at arrow produces no effect. Renewal of growth on cessation of stimulus and removal of gas.

negligible. It would, however, be interesting to obtain a direct proof of this by observing the effect of carbon dioxide on the growth of an organ contracted under constant stimulus.

Effect of CO_2 on an Organ Contracted under Stimulus.—The record was taken of the normal rate of growth of *Crinum* lily, which was next subjected to constant stimulation under tetanising electric shocks of moderate intensity. This is seen to induce a maximum contraction. Carbonic acid was next introduced into the chamber; the organ remained contracted in spite of the introduction of the gas. A transient disturbance sometimes occurred on the introduction of the gas, which quickly disappeared, and the organ remained practically in the same contracted condition as before. The stimulus was next discontinued, and fresh air introduced into the chamber; the normal growth was now found renewed (Fig. 253). It is thus seen that in a geotropically curved organ the upper and contracted half remains practically unaffected by the introduction of the carbonic acid gas. A preliminary enhancement of growth of the lower half of the organ followed by contraction explains the increase of geotropic curvature followed by a reversal.

Experiment 267

VARIATION OF GEO-ELECTRIC RESPONSE UNDER CARBONIC ACID.

The experiments that have been described offer the fullest explanation of the preliminary increased geotropic response and its reversal under carbonic acid gas. The subject is, however, of sufficient importance to justify investigation by the altogether independent method of electric response.

It has already been shown that under the action of stimulus of gravity the upper side of a horizontally laid organ undergoes an electric change of galvanometric negativity, indicative of excitatory contraction; the lower side of the organ undergoes, on the other hand, a change of galvanometric positivity which is the electric concomitant of enhancement of rate of growth and expansion. The resultant geo-electric response is thus due to the joint effects of negativity of the upper and positivity of the lower, just as the erectile response under the stimulus of gravity is due to joint effects of contraction of the upper and expansion of the lower side of the organ. The electric and mechanical responses are but different expressions of the fundamental reactions which occur at the opposite sides of the organ. This being so, we would expect that any agent which increases the existing geotropic curvature will also increase the existing geo-electric current. Conversely, other agents which cause a reversal of the geotropic curvature will also cause a reversal of the electric current.

Geo-electric Response.—The peduncle of the Tuberose, which exhibits strong geotropic curvature, was found suitable for the following investigations on the geo-electric response. Two electric contacts were made at opposite sides of the organ by thrusting in two thin platinum electrodes in circuit with a sensitive galvanometer (Fig. 254). After the subsidence of the irritation caused by the slight wound, photographic records of the deflection are taken when the organ is held vertical; in the absence of geotropic excitation, the galvanometric deflection is found to be practically zero. But as soon as the specimen is inclined to a horizontal position a deflection occurs, the lower contact becoming galvanometrically positive, and the upper negative; this deflection soon attains a maximum value, and remains constant as long as the specimen is held in the horizontal position. The deflection disappears on the removal of geotropic stimulus by restoring the plant to the vertical position. After making the two diametrically opposite

Experiment 268

contacts with the peduncle, the specimen was placed in a horizontal position; this gave rise to the geo-electric response which attained in a short time the maximum value. Carbonic acid gas was next passed into the plant-chamber. *This gave rise to preliminary enhancement of the electric response followed by reversal. On substitution of fresh air, there was restoration of the normal response.* The experiment was repeated a number of times with the same specimen and it was invariably found that the geo-electric response was reversed and restored by alternate application of the gas and its removal. The result of the electric response is thus parallel to that of the mechanical response.

ISOLATION OF RESPONSE OF ONE SIDE OF THE ORGAN.

In the above experiments the electric response was due to the joint effects on upper and lower sides of the organ.

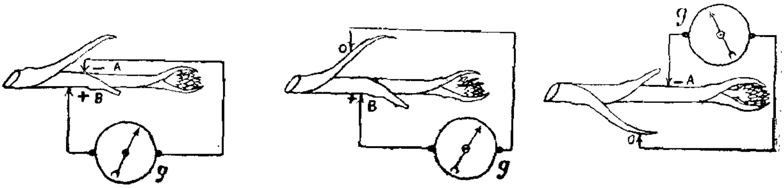

FIG. 254. Electric connections for geo-electric response. The first illustration shows electric contacts with upper and lower sides of organ, the contracted upper, exhibiting galvanometric negativity, and the expanded lower a galvanometric positivity. *Second illustration shows isolated contact with the lower* B, the second contact being made with indifferent point O, in the leaf. In the third illustration, the isolated contact is made with the upper side A. The isolated lower contact B exhibits an electric positivity and the upper A, an electric negativity.

The electric method of enquiry, however, offers the unique advantage of isolation of the effects of the lower and the upper sides. For this we make one electric contact B, which is to be the lower side; the second contact O is made with an indifferent point, *i.e.*, the lamina of a lateral leaf. The responsive variation would in this case be due to the change induced on the lower side of the organ. For observation of the induced change on the upper side, the electric contacts are made with A, and the indifferent point, O (Figure 254).

Effect of CO_2 on the Lower Side.—The two contacts thus made with O and B, gave no deflection when the organ was held vertical. The specimen was next inclined so as to make it horizontal; a large galvanometric deflection was now induced by the geotropic stimulus, the lower side B becoming galvanometrically positive (up-curve), indicating an expansion, enhancement of turgor, and increased rate of growth. On introduction of carbonic acid into the plant-chamber, *there occurred a short-lived increase of response; after this the positive deflection was suddenly reversed into negative, indicating that the lower side had undergone a contraction.* On the introduction of fresh air, the normal expansion of the lower side was once more restored, as indicated by the restoration of positive electric response (Fig. 255).

Experiment 269

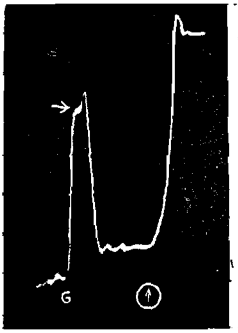

FIG. 255

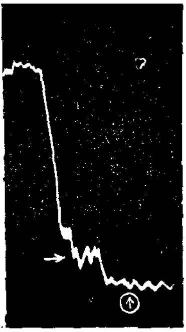

FIG. 256

FIG. 255 Effect of CO_2 on geo-electric response of lower side. Inclination to horizontal position induced galvanometric positivity of lowe side (up-curve). Application of CO_2 at arrow induced a reversal. Removal of gas at arrow (within circle) renewed the normal response.

FIG. 256 Effect of CO_2 on upper side. Normal electric response is negative (down-curve). Application of CO_2 or its removal induced little change.

Effect of CO_2 on the Upper Side.—The isolated electric contact was next made with the upper side A. On placing the specimen in a horizontal position the geotropic response of the upper side was

Experiment 270

negative (down-curve). Introduction or removal of carbonic acid gas produced little or no change (Fig. 256).

The results described above prove once more that the effect induced on the upper side is negligible compared with that induced on the lower side of the organ. The strict concomitance of the mechanical and electric responses, and their induced variations will be seen in the following *tabular statement of the results.*

TABLE LXI.—EFFECT OF CO_2 ON GEOTROPIC ACTION OF THE MORE EFFECTIVE LOWER SIDE OF THE ORGAN.

Effect of *Carbonic acid*:	Mechanical response.	Electric response.	Resultant geotropic response.
On introduction.	Increased expansion.	Increased galvanometric positivity.	Enhanced geotropic response.
Persistent effect.	Contraction.	Galvanometric negativity.	Reversal of response.
Effect of removal of gas.	Normal expansion.	Normal positive response.	Normal geotropic response.

SUMMARY

The immediate effect of carbonic acid gas on geotropic response of growing and pulvinated organs is an *enhancement above the normal.*

Continued action of carbonic acid gives rise to a reversal of the normal geotropic response.

This reversal persists during continued action of the carbonic acid. The *normal response is restored after removal of the gas.*

Investigation with the mechanical method of response shows that it is the lower side of the organ which is relatively more affected by the anaesthetic than the upper side. The lower side thus exhibits an initial expansion and increased rate of growth under carbonic acid gas, with the resulting enhancement of geotropic response. Continuous application of the gas induces a contraction of the lower side causing a down movement or reversal of the normal response. Growth of the lower side is renewed on the removal of the gas with consequent restoration of the normal response.

Electric response under the stimulus of gravity exhibits effects parallel to those of mechanical response. The effect of carbonic acid gas is a preliminary enhancement of geo-electric response followed by reversal. The reversal persists during the continued application of the gas; the normal geo-electric response becomes renewed on the removal of the gas.

Investigation on the isolated response of the lower side of the organ offers an independent corroboration of the above. Introduction of the carbonic acid induces a preliminary enhancement of galvanometric positivity of the lower side; this is subsequently reversed to galvanometric negativity. Removal of the gas is followed by the restoration of the normal positive response. The electric response of the upper side exhibits little or no change by the introduction or removal of the gas.

The reversal of the geotropic response under carbon dioxide is thus due to the contractile action of the gas, which is more effective on the lower side of the organ.

LVIII.—ON PHYSIOLOGICAL ANISOTROPY INDUCED BY GRAVITATIONAL STIMULUS.

By Sir J. C. Bose,
Assisted by
Surendra Chandra Das, M.A.

Plants have been usually classified as 'sensitive' and ordinary; the former is examplified by *Mimosa pudica* which responds to stimulus by a conspicuous movement of the fall of the leaf. Ordinary plants, on the other hand, appear to be insensitive under shocks of every kind. I have, however, shown that every plant, and every organ of every plant, responds to stimulus, the induced excitation being detected by the electric response of galvanometric negativity.*

It is, moreover, not true that the organs of ordinary plants do not exhibit any mechanical response under stimulus. In *Mimosa* the lower half of the pulvinus is relatively the more excitable; hence under stimulus, the greater contraction of the lower half pulls the leaf down; the actual contraction in the lower half is, however, not very great, but the slight movement is magnified by the petiolar index. Had the upper half of the pulvinus been as excitable as the lower half, it is obvious that the two antagonistic contractions would have neutralised each other. In such a case excitatory contractions would have occurred, without any external manifestation of responsive movement.

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* Response in the Living and Non-Living.

In radial organs of ordinary plants the excitability is the same all round; hence the organ is unable to exhibit any lateral movement on account of the antagonistic contractions of opposite sides.

For exhibition of any conspicuous lateral movement the organ should be anisotropic, its opposite sides being unequally excitable. This anisotropy is normally found in dorsi-ventral organs like the pulvinus of *Mimosa.* It may, however, be induced by the one-sided action of stimulus, on account of which the stimulated side of certain organs becomes permanently contracted. An example of this is found in various tendrils, where the stimulus of contact causes them to coil round the support. It is evident that the tissue already contracted under stimulus, can undergo little or no further contraction; whereas, the expanded nd unstimulated length would exhibit a responsive conraction. It thus follows that the contracted and concave ide of the tendril would prove to be less excitable and ontractile, than the expanded convex side. A physiological nisotropy may thus be induced by the unequal action of he stimulus on two opposite sides of an organ, and in the ase of the coiled tendril, the anisotropy is permanent he fact of the coiled tendril being physiologically anisoropic may be tested by subjecting it to the diffuse stimulus f tetanising electric shocks. The response of the tendril s then found to be a movement of uncoiling due to the reater contraction of the hitherto unstimulated convex side.

These considerations lead us to expect that under uitable conditions, a temporary anisotropy could be conerred on radial organs by the unilateral action of stimulus When a radial stem is laid in a horizontal position, a georopic curvature is induced, a particular side A, which appens to be above, becomes contracted while the opposite ide B becomes expanded. One would, therefore, expect that under these conditions an induction of anisotropy by which the upper side A is rendered less excitable than the opposite side B. The *anisotropy* would, however, be not permanent; for by turning round the stem through 180°, the above relations would be reversed. B would now become contracted and A expanded; A would now be rendered more excitable than B. From theoretical considerations detailed above, we see the possibility of an ordinary radial organ being rendered 'sensitive' after being subjected to the stimulus of gravity. For a geotropically curved organ is no longer radial but anisotropic, and the more excitable convex side would thus function like the more excitable lower half of the pulvinus of *Mimosa*. The response to diffuse stimulation would be similar in the two cases, namely, a down-response due to the greater contraction of the lower side. The only difference between the two would lie in the fact that in the geotropically curved stem, the induced differentiation is temporary, whereas, in the dorsi-ventral pulvinus it is permanent. We shall next inquire whether the above inference is found verified by experimental results.

METHOD OF INVESTIGATION.

We take various radial organs of plants, and subject them to electric shocks. No lateral response is produced, since their different sides are equally excitable; the antagonistic reactions thus neutralise each other.

This absence of effect under diffuse stimulation is obtained *immediately* after laying the radial organ in a horizontal position. For, a certain length of time is required for induction of physiological anisotropy under the action of the stimulus of gravity. After the attainment of geotropic up-curvature the lower or convex side is rendered the more excitable, and diffuse stimulation by electric shock induces a *down-movement* by the greater contraction of the lower side. If next a geotropically curved specimen be held inverted with the convex side above, diffuse shock would cause a contraction of the upper convex side with a resulting *up-movement*. The intermediate case is the one in which sufficient time had not been allowed for physiological differentiation when there is no response. Diagrammatic representation of the three cases are given in Fig. 257; the following experiments are in verification of the above. The results described below may be obtained with different curved organs. As a typical case we may take the seedling of *Eclipta erecta* which is very sensitive to geotropic action.

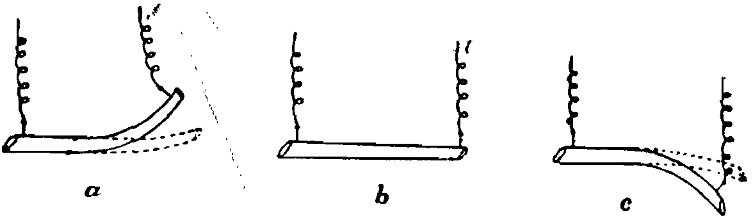

FIG. 257 *Diagrammatic representation of responsive movements under* diffuse stimulus in geotropically curved organs:
a) Organ curved upwards. Responsive movement downwards seen in dotted outline,
(b) No response in specimen before induction of anisotropy,
(c) Geotropically curved specimen held inverted. Response by up-movement.

RESPONSE OF GEOTROPICALLY CURVED ORGAN.

Response before induction of physiological anisotropy.—The responsive movement of the specimen is obtained by means of an Oscillating Recorder, the successive dots being produced at intervals of 40 seconds, the recording lever producing a magnification of 20 times. The radial stem of *Eclipta* is laid horizontal, and tetanising electric shocks passed through it before the induction of geotropic curvature. The applied stimulus induced no responsive movement, either up or down (Fig. 258*b*).

Experiment 271

Experiment 272

Response of up-curved organ.—The stem was next allowed to curve upwards under geotropic action, and record of response obtained under electric stimulus. It was thus found that responsive down-movement occurred under a minimal stimulus which was just effective in inducing the responsive movement of *Mimosa.* Thus as regards minimally effective stimulus the sensitiveness of ordinary plants is found to be of the same order as that of the much lauded *Mimosa.* As regards the *apex time* and the period of recovery the responsive characteristics of the ordinary stem are intermediate between those of sensitive plants, *Mimosa pudica* and *Neptunia oleracea.* In the former the apex time, *i.e.*, the period for the attainment of maximum contraction, is three seconds, the period of recovery being 15 minutes. In *Neptunia* the maximum contraction is attained in the course of 180 seconds, and the recovery is only complete after 60 minutes. In regard to the above, it is to be remembered that the recovery is relatively quick after feeble, and very much protracted after strong stimulation.

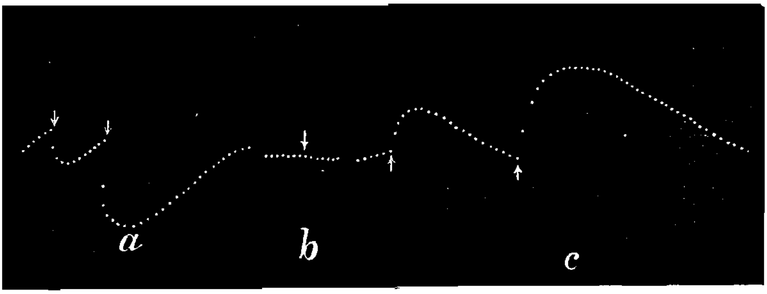

FIG. 258 Response of geotropically curved organ under external stimulus:
(*a*) Response of up-curved organ by down-movement. The two records are for feeble and moderate stimulus,
(*b*) No response before induction of anisotropy,
(*c*) Response by an up-movement in an up-curved organ, held inverted.

In the response of geotropically curved organ the apex time is about 120 seconds, which is slower than in *Mimosa* but quicker than in *Neptunia.* The period of recovery after feeble stimulation is 5 minutes and after strong stimulus 15 minutes (Fig. 258*a*). The period of recovery is about same as in *Mimosa* but quicker than in *Neptunia.*

Response of an inverted organ.—The geotropically curved organ is next placed in an inverted position, the convex side being up. Response to electric stimulation is now *upwards* due to the greater contraction of the expanded upper side. Two successive responses were obtained with (1) feeble and (2) strong electric stimulus (Fig. 258*c*).

Experiment 273

REVERSAL OF ANISOTROPY WITH CORRESPONDING REVERSAL OF RESPONSE.

After obtaining the response in the inverted position the specimen was allowed to remain in that position. The geotropic stimulus now tended to reverse the curvature of the organ placed in the inverted position. The convexity of the upper side gradually disappeared and with it, the induced anisotropy; the stem became straight and radial: electrical stimulus now induced no responsive movement. After a further interval of time the original curvature became reversed, the lower concave side now became convex and relatively the more excitable. Electric stimulation was now found to induce a responsive movement downwards. Thus experimenting with an identical specimen, held with the convex side up, the response was at first upwards; under geotropic action the organ became straight, when there was no responsive movement. The organ then became concave, and gave the downward response. The changing internal differentiation in an identical specimen is thus detected by a definite transformation from an up-response to zero, and finally to a down-response.

Experiment 274

The response of a geotropically curved organ has thus been shown to be similar to that of the pulvinus of the *Mimosa*; in both we obtain a responsive down-movement under external stimulus such as that of tetanising electric shocks. We shall presently find that this resemblance extends even in all essential details. Thus the response of *Mimosa* is modified in a definite way by the condition of sub-tonicity. It is also affected by the action of anaesthetics, the effect being modified by the dose and duration of application.

ABNORMAL POSITIVE RESPONSE UNDER CONDITION OF SUB-TONICITY.

Experiment 275

Positive response in Mimosa.—An experiment has already been described (Expt. 50, Vol. I, p. 147) which showed that when the *Mimosa* plant is kept in unfavourable condition such as darkness, its tonic condition falls below *par*. In this sub-tonic condition the response to stimulus is not by the normal *fall* of the leaf (negative response) but by the abnormal positive or *erectile* movement. Under the action of successive stimulations, the tonic condition of the tissue is improved and the response becomes gradually converted from the abnormal positive to the normal negative.

The experiment is varied in the following way; a cut specimen of *Mimosa* is taken in a vigorous condition; the response of the leaf to moderate electric stimulus is found to be normal negative. The specimen is next kept in a dark cupboard for about 12 hours, when the response is found to be converted into the abnormal positive. After exposure to day light outside, response of the specimen is found to be restored to the normal negative.

Experiment 276

Abnormal positive response of geotropically curved stem.—We shall next observe the most striking parallelism in the response of *Mimosa* and of geotropically curved organ under condition of subtonicity. We found that the normal response of a geotropically curved organ is always by a *down-movement* in a specimen held with the concave side upwards. Half a dozen curved specimens were next placed in a dark room for 5 or 6 hours, and all of them exhibited a reversal of response, which was now by an *up-movement.* The specimens were next exposed to diffuse light of the sky or of sunlight for an hour. After this the response of all the specimens was found to be normal, *i.e.*, by a down-movement.

MODIFYING ACTION OF ANAESTHETICS ON RESPONSE TO EXTERNAL STIMULUS.

Account of detailed investigation on the effect of anaesthetics has already been given in the previous chapters. It was shown that the effect of an anaesthetic like ether is to cause an enhancement of response; continued application however causes a depression or abolition of irritability.

Experiment 277

Effect of ether on geotropically curved organ.—The normal response of the geotropically curved organ is first obtained, after which dilute vapour of ether is introduced into the plant-chamber. Successive responses to equal stimulus are next obtained after etherisation lasting for 1 minute, for 15 minutes, and for 30 minutes. From the record of responses thus obtained we find that the amplitude of the normal response is 4 mm.; after one minute's application of ether the amplitude is enhanced to 14 mm., or more than three times the normal; after 15 minutes there is a further enhancement, the amplitude being 24 mm. or six times the normal. But after thirty minutes all responsive movement is found paralysed (Fig. 259).

Effect of Carbonic acid and of Chloroform.—The effects of these mild and strong anaesthetics are found essentially similar to that of ether, the only difference being in the relative rapidity of the characteristic changes, which is very quick under chloroform and slow under carbonic acid.

Experiment 278

The immediate effect of all kinds of anaesthetics is an enhancement of response of the geotropically curved organ to external stimulus; continued action of anaesthetics causes an abolition of response.

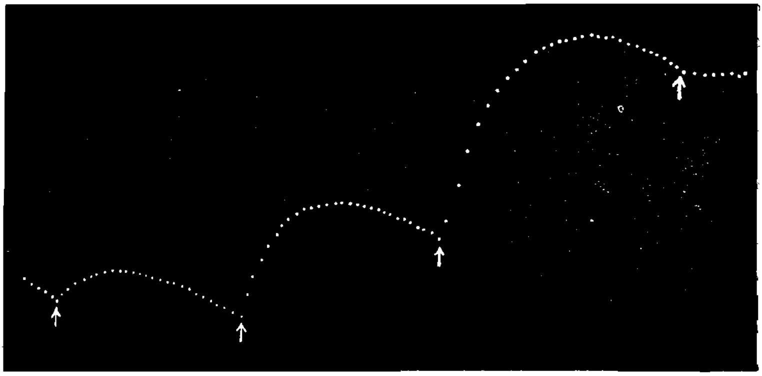

Fig. 259. Effect of ether vapour on response of geotropically curved organ. The first is the normal, the second, third and the fourth are responses under continued action of ether.

Note the increase of response followed by an arrest.

The effect of anaesthetics on response to external stimulus is precisely the same as that to internal stimulus of gravity. For the rate of geotropic movement is enhanced under the immediate action of anaesthetics and arrested after continued application.

A wide generalisation is thus reached as regards the effects of anaesthetics in regard to response under external and internal stimulation.

SUMMARY.

A radial organ is equally contractile on its different sides; hence diffuse stimulation induces no resultant lateral movement, which is prevented by equal and antagonistic contractions at diametrically opposite sides of the organ.

In dorsi-ventral organs like the pulvinus of *Mimosa*, there is a physiological anisotropy which is permanent. The pulvinus under diffuse stimulus responds by a fall, due to the induced greater contraction of the lower side.

In ordinary plants a physiological anisotropy is induced by unilateral action of stimulus. In a tendril coiled round a support, the contracted and concave side is rendered less excitable than the expanded convex side. Diffuse stimulus induces greater contraction of the convex side with the resulting movement of uncoiling.

In the two cases described above, the anisotropy induced is permanent. But the anisotropy induced by the stimulus of gravity is temporary. In a geotropically curved organ, the contracted and concave side is less excitable than its diametrically opposite convex side. Diffuse stimulus is found to give rise to a responsive down-movement, *i.e.*, in a direction opposite to the existing curvature.

The sensitiveness of ordinary plants thus rendered anisotropic under geotropic action, is of the same order as that of the 'sensitive' *Mimosa*. The apex time is 2 minutes and the period of recovery 15 minutes.

The anisotropy of the geotropically curved organ, held in an inverted position, undergoes continuous change culminating in a reversal. The internal transformation is detected by the responsive reaction evoked under external stimulus. Thus response of a curved organ (held in an inverted position) is found to change from an up-movement through zero to a down-movement. The first is the case when the upper side of the organ is convex, the second, when the organ is straight, and the third when the upper side is concave.

The sign of response of geotropically curved organ, like that of the pulvinus of *Mimosa,* becomes reversed under condition of sub-tonicity. Application of stimulus, raises the tonic condition to the normal with corresponding restoration of the normal sign of response.

Anaesthetics induce a preliminary enhancement of responsive movement followed, under continued action, by an abolition.

The effects of anaesthetics on response to external stimulus are in every way similar to those of internal stimulation under gravity. The response of a curved organ and the rate of geotropic curvature is enhanced under the immediate action of anaesthetics and abolished under continued action.

A generalisation is thus reached of the identical effects of anaesthetics, in regard to both external and internal stimulation.

IX.—THE DEATH-SPASM IN GEOTROPICALLY CURVED ORGANS.

By Sir J. C. Bose,

Assisted by

Apurba Chandra Nag, m.sc.

We have seen in a previous chapter that a spasmodic leath-contraction occurs under toxic doses of chloroform. n radial organs this spasm is exhibited by the shortening of he length (Experiment 249). In pulvinated organs it is hown by the greater contraction of the more excitable half f the pulvinus (Experiment 257). This irreversible change, ssociated with death, is shown by the fact that substitution f fresh air for chloroform vapour does not revive the plant; death discoloration soon spreads over, and the plant ecomes *flaccid from loss of* turgor. Since the particular pasm indicates the onset of death in plants, it might be ossible to detect the critical point of death brought about y other means. Thus a plant subjected to the gradual ise of temperature would succumb as soon as the fatal temerature is reached. I have shown elsewhere* that this leath-temperature may be accurately determined by aking a continuous record of the responsive movement of he plant caused by the rise of temperature. Thus on ubjecting the sensitive plant *Mimosa pudica* to a gradual ise of temperature at the standard rate of one degree per

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*Bose—Plant Response, p. 168.
,, Comparative Electro-Physiology, p. 546

minute in a thermal bath, the leaf was found to be continuously erected till the temperature reached the critical degree: the erectile movement was then suddenly reversed into a spasmodic down-movement, this latter, being in fact the excitatory fall of the leaf. The critical temperature was found to be at or near 60°C. After this the plant was found to be permanently irresponsive. Repetition of the experiment showed neither the preliminary expansion nor the final spasmodic contraction. In plants with thick stems, the attainment in the interior of the plant of outside fatal temperature, must be a slow process; hence such plants have to be subjected for a long time to the critical temperature to ensure death. But seedlings quickly succumb to the action of death-temperature. Thus similar seedlings of *Mimosa* were divided into two batches and placed in the same bath, the rate of rise of temperature being 1°C. per minute. The first batch

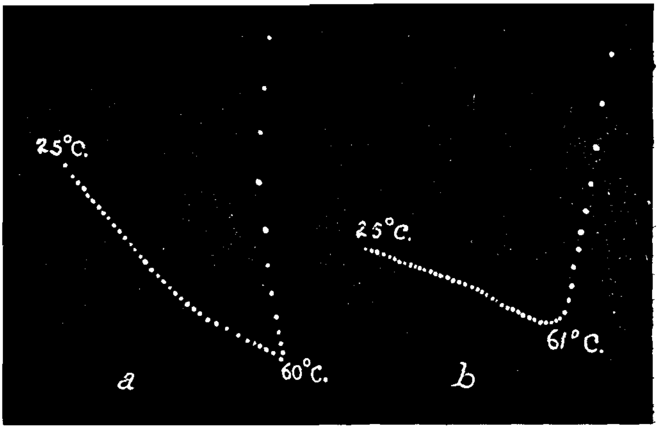

FIG. 260 Death-spasm at the critical temperature:

(*a*) First part of the curve shows continuous erection of the leaf of *Mimosa* during rise of temperature from 25° to 60°. The death-spasm of sudden fall of the leaf occurred at 60°C.

(*b*) Death-spasm of seedling of *Helianthus annuus* at 61°C.

'ere taken off from the bath at the temperature of 58°C., 'hich was two degrees short of the fatal temperature, and eplaced in water. The second batch, placed in the thermal ath, exhibited the spasmodic fall of the leaves at 60°C.; hese were also taken out and placed in water at ordinary emperature. The first batch exhibited after two hours, enewed signs of life and excitability, whereas, the second alf never revived. Hence the spasmodic movement of the ll of the leaf may be regarded as the death-spasm, corresonding to the death-throe in animals. The occurrence of eath-spasm I have shown to be very general, not merely in ensitive, but also in ordinary plants, and in all their gans. Thus ordinary growing shoots and also

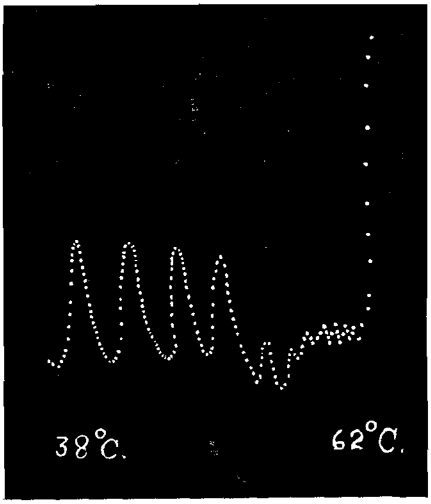

FIG. 261 Death-spasm in the pulsating leaflet of Desmodium gyrans

Note spasmodic contraction at 62°C.

the roots are found to exhibit a similar spasmodic death-contraction at temperatures between 60° and 62°C. (Fig. 260). This death-spasm also takes place in the actively rhythmic leaflets of *Desmodium gyrans*. In Fig. 261 is seen a continuous record of pulsations of this leaflet as the temperature of the plant-chamber was continuously increased from 30° to 63°C. The frequency of pulsation was found at first to be enhanced; this was followed by an arrest and subsequently a contractile spasm occurred at 62°C. The characteristic spasmodic death-contraction is thus exhibited by all vegetable tissues, ordinary, sensitive, and rhythmic.

The fact that a temperature of about 60°C. is generally fatal to plants, is supported by independent results of electric investigations. The electric response of galvanometric negativity which characterises the living condition of the plant, is found abolished when the specimen is raised above 60°C. This may therefore be regarded as the fatal temperature for most plants.

One plausible explanation of the sudden contraction at the critical temperature is, that it is not an excitatory reaction, but due to the coagulation of the protoplasm. The following evidence, however, strongly supports the view that the phenomenon is one of excitation.

1. Were the phenomenon one of mere coagulation, we should expect a steady and continuous contraction with the rise of temperature, the contraction remaining persistent with the completion of coagulation. But instead of this, we find at first a growing expansion at a moderate rate, on account of which the leaf of *Mimosa* becomes erected. On the attainment of the critical temperature, however, there is an abrupt inversion of the erectile movement shown by the sudden fall of the leaf. Moreover, after this spasmodic contraction, there is often a gradual disappearance of the rigor, parallel to the post-mortem relaxation of the animal tissue. These three phasic reactions, the preliminary expansion, the death-contraction, and the post-mortem relaxation, are exhibited by a specimen which had been

alive. But once it had passed through the temperature at which the spasm takes place, there is an abolition of all response; repetition of the experiment shows neither the preliminary expansion, nor the spasm which had been previously exhibited at the fatal temperature.

2. In the case of coagulation, the shrinkage would be non-discriminative and general, in contrast to the excitatory responsive movement, the direction of which is determined by the differential excitability of the two halves of the motile organ. The spasmodic movement exhibited by different plants at the critical temperature is directive, there being induced a greater contraction of the more excitable half. In *Mimosa*, it is the lower half which is the more excitable, hence the spasmodic fall is downwards. In a spirally cut peduncle of *Allium*, the inner half of the spiral is the more excitable, hence the response at the critical temperature is a sudden curling movement. But the spiral tendril of *Passiflora*, in which the outer half is the more excitable, exhibits the death-spasm by an uncurling movement.

3. If the phenomenon were one of physiological excitation, it would be appropriately modified by physiological change in the tissue: this is actually found to be the case. Thus fatigue lowers the temperature at which death-spasm takes place, proportionately to the extent of fatigue; in a particular experiment the death-point was thus lowered from the normal 60°C. to 37°C. Poisonous solutions are also found to lower the death-point.

4. The question whether the spasmodic movement is due to coagulation or to excitation may be decided by a definite test. Excitation may not only be detected by a visible movement, but also by an electrical manifestation, totally independent of the mechanical movement; a tissue thus becomes galvanometrically negative under excitation. Employing this test I found that, at the fatal temperature, an abrupt negative electric variation takes place in the tissue.

5. Excitation also gives rise to a concomitant diminution of the resistance of the tissue. A sudden diminution of resistance is found to take place at the critical death-temperature. The two records given in Figure 262 exhibit the sudden inversion of the curves at the critical temperature by the electromotive change of galvanometric negativity and by the sudden diminution of the electric resistance.

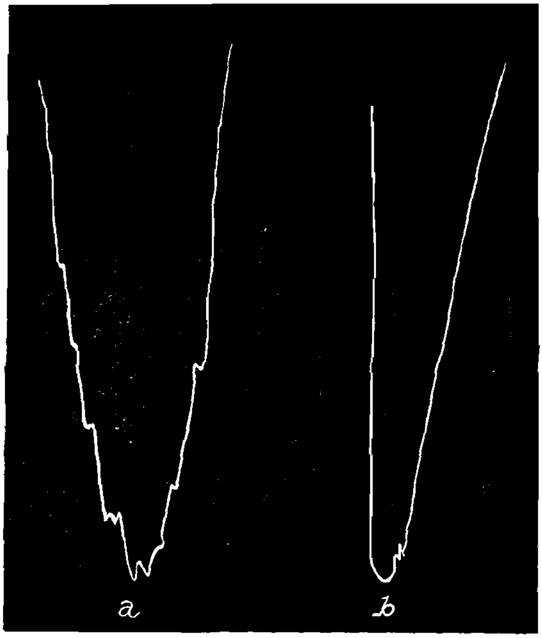

Fig. 262 Determination of the death-point by
(*a*) electromotive, and
(*b*) resistivity variation. In the former the electromotive variation at the critical point is a *change from electro-positivity to* electro-negativity; in the latter, from an increasing to a suddenly decreasing electric resistance. The death-point is about 6 .°C.

The considerations adduced above would appear to be decisive in support of the conclusion that there is an excitatory reaction in the tissue at the moment of death. A conclusive proof of this will be found in a later chapter, where an independent method will be found described in demonstration of the excitatory impulse generated at the moment of death.

DEATH-SPASM IN GEOTROPICALLY CURVED ORGANS.

We have seen that in a permanently anisotropic organ like the pulvinus of *Mimosa*, a death-spasm occurs at or about 60°C., the excitatory reaction causing a violent contractile movement; this gives rise to the fall of the leaf. We shall next observe whether a radial organ, rendered anisotropic by the action of gravity, also exhibits a spasmodic movement at a critical point, and if so, determine, the death-temperature.

Death point of a geotropically curved organ.—For this, a specimen of *Basella alba* was taken which had undergone a geotropic curvature. The specimen was placed in a water bath whose temperature was gradually raised from 40°C. upwards. By a simple

Experiment 279

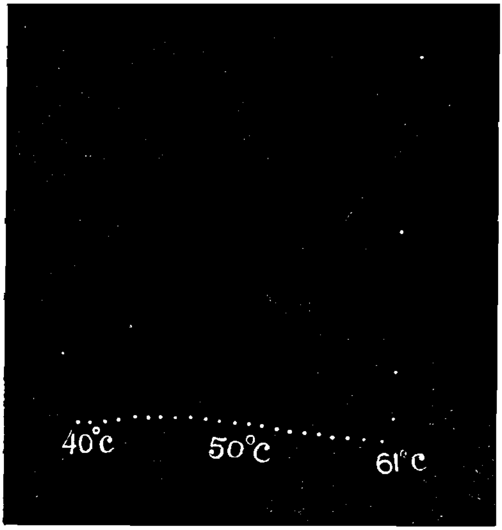

Fig. 263 Death-spasm in the geotropically curved *Basella alba*. A sudden down-movement occurred at 61°C

device the plate was made to oscillate for each degree rise of temperature, hence successive dots represent rise of temperature of 1°C. As the temperature rose gradually there was a slight movement of erection; but as soon as the temperature reached 61°C., there was produced a sudden and violent down-movement which represented a contraction of the more excitable lower and convex side of the organ. This intense reaction is independently exhibited by the very erect curve of down-movement (Fig. 263).

SUMMARY.

Different plants under a toxic dose of chloroform exhibit a death-contraction. In the case of radial organs this is shown by sudden shortening of the length; in pulvinated organs, the death-contraction causes a sudden fall of the leaf.

The critical temperature for death of the plant may be determined from continuous record of movement of the plant under rising temperature. It is thus found, that a spasmodic contraction takes place at the critical point which is at or near 60°C. The plant is killed after being subjected to a temperature above this critical point.

In radial organs this death-contraction is exhibited by a sudden shortening of the length. In *Mimosa* the death spasm is exhibited by a sudden fall of the leaf due to greater contraction of the more excitable lower half of the organ.

The death-point may also be determined by the sudden electromotive variation of galvanometric negativity and by an abrupt diminution of electrical resistance which takes place at or about 60°C.

In a geotropically curved organ the death spasm also takes place near 60°C. This is exhibited, as in the case of the pulvinus of *Mimosa*, by a sudden down-movement caused by the contraction of the more excitable lower side of the organ.

LX.—THE COMPLEX RESPONSE OF PULVINUS OF *MIMOSA* TO TRANSMITTED EXCITATION.

By Sir J. C. Bose.

Assisted by

Satyendra Chandra Guha, M.Sc.

The pulvinus of *Mimosa* translates the invisible excitation transmitted from a distance into movement. It may, therefore, be termed as the *Effector*. We are accustomed to regard this organ to consist only of two functional halves, the upper and the lower, the responsive action being supposed to be a simple rectilinear down- and up-movement. In reality, the responding organ is highly complex; for it is found to give certain other responses which had hitherto not been suspected. Thus, in addition to the down- and up-movements, it exhibits right-handed and left-handed twists, that is to say, torsional responses clockwise or anti-clockwise. The motor organ thus consists of four *effectors* by which the four distinct types of responses are brought about.

Record of torsional response.—The torsional response is obtained as follows: in order to eliminate the effect of the weight of the leaf, and also for obtaining pure torsion, the petiole is enclosed in a hooked glass support with a smooth internal surface. Friction and the effect of weight are thus practically eliminated; the circular support prevents any up- or down-movement, yet allows freedom for torsional response. The torsion is magnified by an L-shaped piece of aluminium wire appropriately tied to the petiole, so that the long arm is at right angles to the petiole. The end of the arm is attached by a silk thread to the short arm of a recording lever; there is thus a compound magnification of the torsional movement, a left-handed torsion producing an up-curve, and a right-handed torsion a down-curve. The record is obtained by the Oscillating Recorder, the successive dots being at definite intervals of time, which may be varied, according to requirements, from 20 to 60 seconds. The same apparatus may be used for obtaining the up and down records. For this, the hooked support is removed and the short arm of the lever directly attached by a thread to the petiole (Fig. 264).

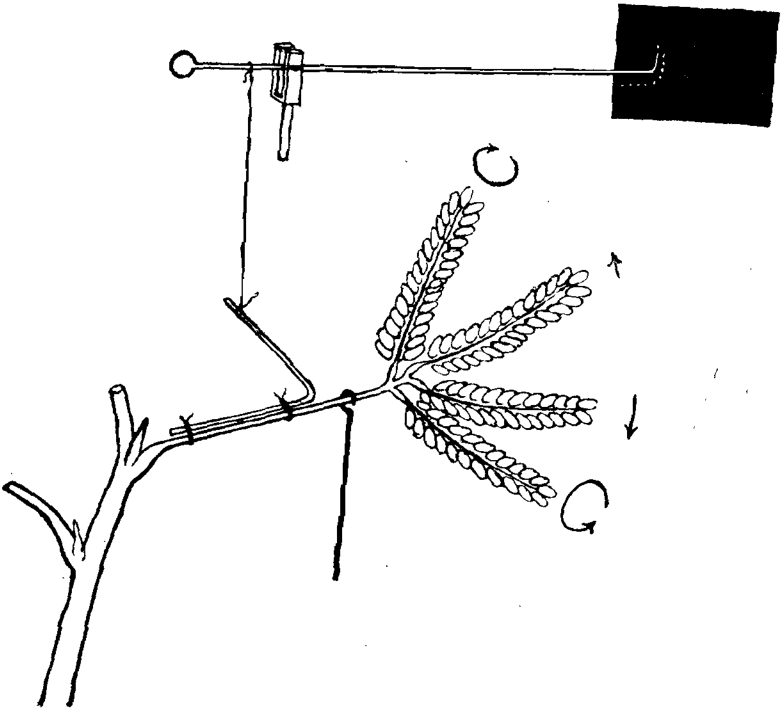

Fig. 264 Method of obtaining torsional response. Stimulation of the first sub-petiole to the left induces left-handed, and of the fourth sub-petiole, a right-handed torsion. Stimulation of the second sub-petiole induce a rapid down-movement, that of the third sub-petiole, a slow up-movement. For record of rectilinear movement, the hooked support is removed.

We shall now study the effect of transmitted excitation caused by successive stimulation of the 4 sub-petioles. The characteristic responses are found to be the same whatever be the mode of stimulation, mechanical, electric, or photic. Care, however, has to be taken so that the stimulus is not too strong, for excessive stimulation becomes diffused and thus causes a fall of the leaf by the *predominant contraction* of the lower half of the pulvinus. Electric stimulation by tetanising electric shocks has the advantage that the intensity may be reduced to any extent desirable; again, strong light from an arc lamp may be thrown down on a particular sub-petiole, and the intensity of stimulation suitably increased by prolonging the duration of application. The stimulation produced by light, generally speaking, is less intense than that caused by electric shocks, and the reaction under light is, therefore, relatively sluggish. The different sub-petioles will be distinguished by definite numbers, counting from the left, the observer being supposed to face the central stem. The sub-petioles 1 and 4 are the two extremes, the two intermediate ones being 2 and 3.

Response to electric stimulation of sub-petioles 1 and 4.—The sub-petiole number 1 is first stimulated by moderately feeble electric stimulus of short duration; the response is seen to be a *left-handed* torsion, represented by an up-curve: The response is initiated in a short time, and there is a recovery on the cessation of the stimulus. The sub-petiole number 4 is next subjected to stimulation and we obtain a similar torsional response, but now in a *right-handed* direction, seen as a down-curve. The first pair of records are seen one below the other (Fig. 265E).

Experiment 280

Response to photic stimulation of 1 and 4.—In order to demonstrate that different modes of stimulation induce an identical effect, the sub-petiole 1 is now stimulated for a certain length of time, by throwing down on it a strong beam of light from an electric

Experiment 281

lantern. The response is, as in the last case, a left-handed torsion. Stimulation of number 4 induces, on the other hand, a right-handed torsion. (Fig. 265L).

Stimulation of sub-petioles 2 and 3.—We next observe the responsive movements caused by stimulation of the two intermediate sub-petioles, numbers 2 and 3. We shall presently find that the responses in the two cases are *down* and *up*; the record is obtained

Experiment 282

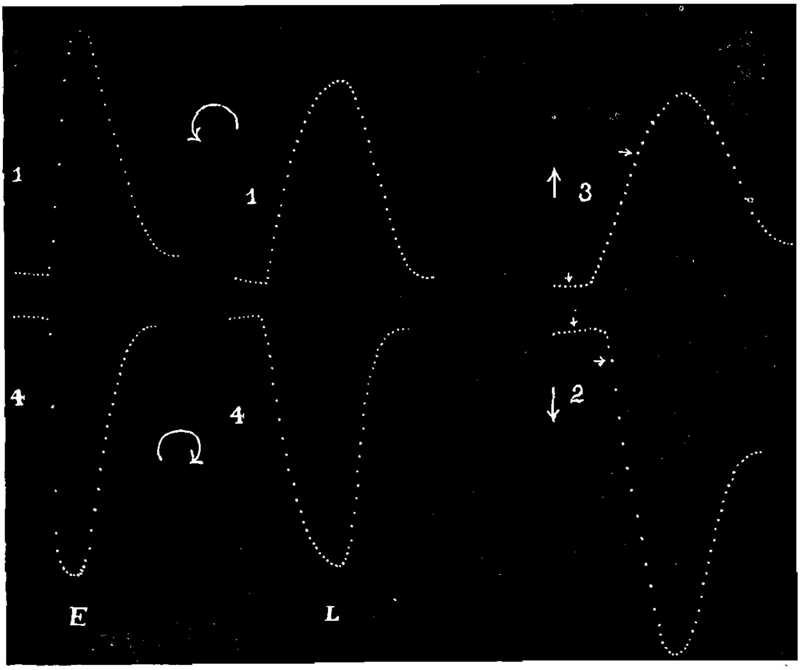

Fig. 265 Record of responses due to stimulation of the different sub-petioles. E, torsional responses under electric stimulus; stimulation of 1, causes left-handed torsion (up-curve) that of 4, a right-handed torsion (down-curve). L, similar torsional responses under stimulus of light. The records to the extreme right show the rectilinear responses induced by stimulation of 2 (rapid down-movement) and of 3 (slow up-movement). Duration of application of light represented by two succeeding arrows. (*Mimosa.*)

by attaching the short arm of the lever to the petiole and removing the hooked glass support. In the following experiments we employ the moderate stimulus of light.

The sub-petiole number 2 is first stimulated; this causes a rapid *responsive fall*, followed by subsequent recovery on the cessation of light. Stimulation of the sub-petiole 3 gives rise to a relatively slow up-response; the duration of application of light had, in this case, to be prolonged for obtaining a moderate amplitude of response; the recovery is also relatively sluggish. These responses are seen in the third pair of records given in Figure 265.

The results of experiments described above are definite and are as follows: stimulation of sub-petiole 1, causes a left-handed, that of number 4, a right-handed torsion; the amplitudes of response in the two cases are approximately equal. Stimulation of sub-petiole 2 causes a rapid and intense down-response, that of 3, a relatively sluggish and less intense up-response. The effectors for these characteristically different responses must, therefore, be distinct; they must, moreover, be in conducting communication with the four sub-petioles in which excitatory impulses are generated. We shall presently find that definite links of communication exist, between the points of reception of stimulus and the distant effectors.

LOCALISATION OF NERVOUS TISSUE IN MIMOSA.

In my previous work, it has been shown that in *Mimosa* stimulus gives rise to an excitatory impulse, which is transmitted with a definite velocity, that this impulse has all the characteristics of the nervous impulse in animals.* The most important problem in connection with this subject is the localisation of the conducting or nervous tissues. I succeeded in isolating a length of such a tissue in ferns and was able to obtain with it many results which are regarded as characteristics of the nervous tissue in animals. In *Mimosa*, however, it is impossible to isolate the nervous tissues

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* Irritability of Plants, p. 154.

without injury, and I have, for many years, been confronted with the problem of localising *in situ* the particular tissue which serves as the conductor of excitation. I have recently been successful in my efforts, the method employed being that of the Electric Probe, already described, by which it has been possible to localise the geo-perceptive layer in plants.

The principle of the method will be understood if we take the somewhat analogous case of a cable along which electric messages are being transmitted. The conducting strand is here embedded in a non-conducting sheath. We can localise the embedded conductor, and pick up the transmitted message by gradually thrusting in the Electric Probe, which is insulated except at the extreme tip. A galvanometer included in the circuit of the Probe will begin to pick up messages that are being transmitted from the moment of *contact of the tip of the probe with the conducting strand*. The depth of insertion for contact can be read on a suitable scale, and the position of the conductor may thus be determined.

We may similarly localise the exact position of the conducting nerve embedded in the petiole of *Mimosa* (Fig. 266). Excitation of the sub-petiole will give rise to an excitatory impulse which travels in a centrifugal direction along the nerve. This excitatory impulse in the nerve is detected by an induced change of galvanometric negativity. The conducting nerve will be most intensely excited by the transmitted impulse, and the induced electrical change of this particular tissue will be maximum. Excitation will no doubt be irradiated to the adjoining tissue, but this will undergo a rapid diminution in radial directions outwards. If the stimulus be moderate or feeble the irradiation will be slight.

The experimental procedure is as follows :—The Probe is thrust perpendicularly to the diameter of the petiole (Fig.

266). The intrusion of the probe is by steps, say of 0.05 mm. at a time. The slight wound produced by the insertion of the tip of the probe causes an excitation, which subsides completely in the course of about fifteen minutes. A sub-petiole is now stimulated by suitable stimuli, which may be chemical, thermal, mechanical, or electric. The excitatory impulse is propagated preferentially along certain conducting channel in the petiole. The results to be described were obtained with all the different modes of stimulation. The electric method of stimulation has the advantage that it can be maintained constant or varied in a graduated manner. Special precautions are taken that there should be no disturbance caused by leakage of the stimulating current; this is verified by the fact that reversal of the primary current which actuates the secondary coil causes no change in the electric response: the excitatory

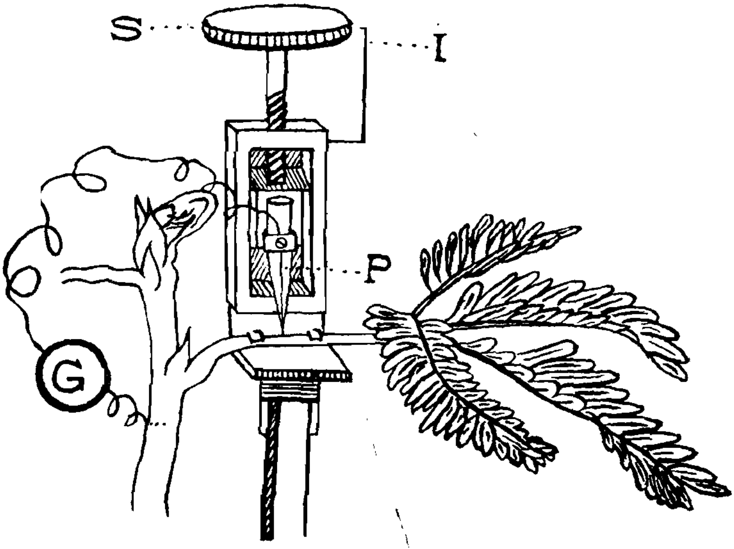

Fig. 266 The Electric Probe for localisation of nervous tissue in plants P, the probe in circuit with the galvanometer, G; S, the screw head, by the rotation of which the probe enters the petiole in successive steps; I, index by which the depth of intrusion may be determined.

electric change in the different layers is, moreover, definitely related to the character of the tissue.

I shall anticipate results by describing the characteristic effects. The excitatory electric change, detectable in different layers as the probe passes from the epidermis to the central pith, is found to rise suddenly to a maximum in the phloem portion of the fibro-vascular bundle; the xylem shows little or no transmitted excitation. Hence we arrive at the conclusion, that it is the phloem which functions as the nerve of the plant. The characteristic electric maximum was not found in experiments where the probe missed the phloem; greater experience now enables me to direct the passage of the probe so as not to miss the nerve tract.

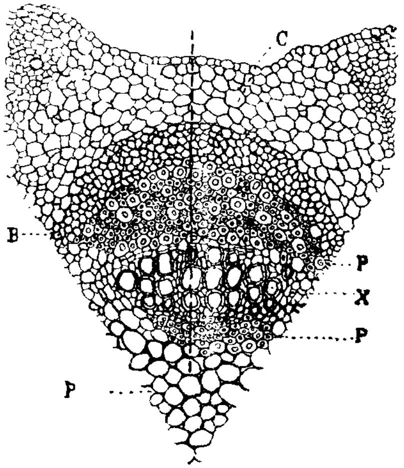

Fig. 267 Micro-photograph showing a quadrant of the petiole and the fibro-vascular bundle. The tissues seen in the section are: the epidermis; C, the cortex; B, the bundle sheath; P, the first phloem; X, the xylem; P, the second phloem; and p, the central pith. The dotted vertical line shows direction of passage of the Probe. (*Mimosa*)

In the diagram of the transverse section of the petiole of *Mimosa*, usually given in text-book, there is in each bundle a single phloem strand outside the xylem. I was, therefore, considerably puzzled by the fact, that in traversing the bundle two electric maxima are obtained, one before reaching the xylem, and the second, after passing it. In order to determine the cause of this anomaly, a transverse section of the petiole of *Mimosa* was made, and differential staining clearly brought out the fact that the phloem strand is not single but double, one above, and the other, below the xylem (Fig. 267) The second electric maximum coincided with the inner phloem.

It may be stated here that in petioles provided with four sub-petioles, there are four distinct bundles with four nerve trunks. The micro-photograph (Fig. 267) shows one of the bundles.

Electrical excitation in different layers.—I shall now give detailed results of localisation of the conducting tissue.

Experiment 283

The probe enters the epidermis and is pushed in by steps of, 0.05 mm.; it passes in succession the cortex, C, the outer phloem, P, the xylem, X, the inner phloem, P′, and the central pith, p. The thickness of the different layers is modified by age of the specimen. In the records given below (Fig 268) the electric response of the epidermis was +12 divisions of the galvanometer. I have shown elsewhere, that the epidermis, which protoplasmically is more or less dead, gives either a zero or a positive, in contradistinction to the normal negative response of living tissues. The probe at a depth of 0.1 mm. encountered the cortex and the response there was −17 divisions. We next arrive at the region of the phloem which extends through 0.15 mm., the average depth being 0.2 mm. The response in this region underwent a sudden enhancement, as seen in the three responses −61, −65 and −40 divisions. The xylem, which was at a depth of 0.3 mm., showed no response, proving that it was a non-conductor. When the probe reached a depth of 0.35 mm. it encountered the second phloem, where the response underwent a second enhancement of −56 divisions. The probe reached the border of the pith at a depth of 0.4 mm. and the response underwent a diminution to −26 divisions. In cases where the incident stimulus on the sub-petiole is feeble, the irradiation effects are greatly diminished: the excitatory transmission is then found only in the phloem.

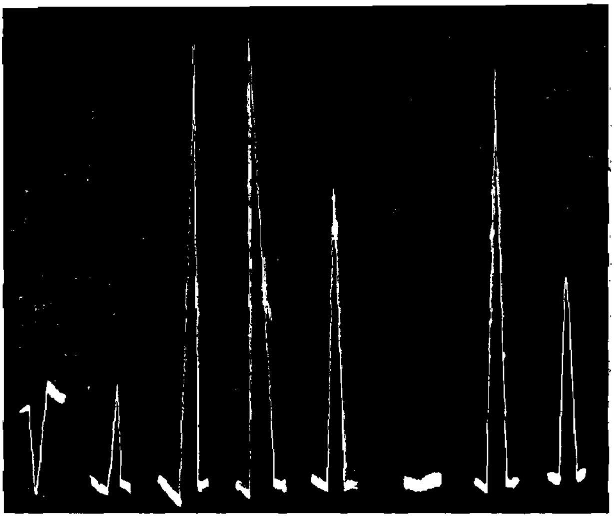

Fig. 268 Galvanometric record of transmitted excitation in different layers of the petiole: the first is the positive response of the epidermis, the second is the feeble negative response of the cortex, the third, fourth, and the fifth are the enhanced responses in the first phloem, the sixth shows absence of excitation in the xylem, the seventh is the enhanced response in the second phloem, the eighth is the diminished response in the pith.

I give below a summary of results obtained with ten different specimens:—

TABLE LXII.—SHOWING INTENSITY OF TRANSMITTED EXCITATION IN DIFFERENT LAYERS IN TEN DIFFERENT SPECIMENS.

Different layers.	Transmitted excitation.										
	I.	II.	III.	IV.	V.	VI.	VII.	VIII.	IX	X.	Mean.
Epidermis...	+1	0	0	0	0	0	0	+4	0	0	+0·5
Cortex ...	-2	-3	50	0	0	0	0	0	0	0	-5·5
Phloem ...	-30	-30	—100	30	-36	-44	-33	-18	-20	—24	36·5
Xylem ...	—8	-9	0	0	0	10	0	—4	-8	—8	-4·7
Phloem ...	-30	-30	-84	10	36	20	-12	-18	—2	-16	—26·8
Pith ...	0	-6	-29	0	0	-7	0	0	0	0	—4·2

It will be seen that in all cases the phloem is invariably found to be the best channel for conduction of excitation. The following curve (Fig. 269), plotted from the mean values given in the Table LXII illustrates this in a striking manner.

The transmitted nervous impulse.—The fibro-vascular bundles, as stated before, are four in number, of which two are vertical, one above the other, and the other two lateral.

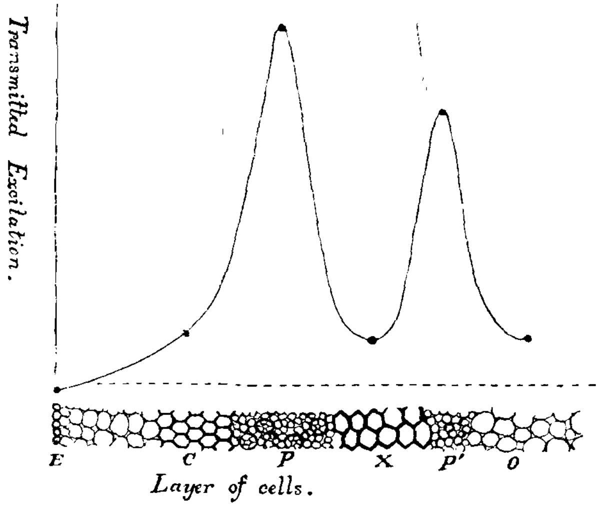

Fig. 269 Curve showing the different intensities of transmitted excitation in different layers: E, epidermis; C, cortex: P, first phloem: X, xylem; P', second phloem: O, pith.

In certain experiments the probe was passed vertically through the petiole, when it encountered the upper and lower bundles. I thus obtained maximum transmitted excitations in the phloems of the upper fibro-vascular bundle, and a similar maximum in the phloems of the lower bundle, the intervening layers of tissue being practically non-conducting. *From this it follows, that excitatory impulse is propagated along definite channels through the length of the petiole.*

DEFINITE INNERVATION.

We shall now follow the nervous strands from the sub-petioles to the motor organ. The excitation is conducted along the phloem strand of the sub-petiole, and thence through the connected phloem in the petiole. There are four main bundles which ultimately reach the motile organ, the pulvinus. There the fibro-vascular bundles apparently fuse, but very fine section of the pulvinus shows lines of separation. (cf. Fig. 274). The nerves thus terminate in the four effectors, of which two are lateral, the right and the left; the other two, are upper and lower effectors. (Fig. 270).

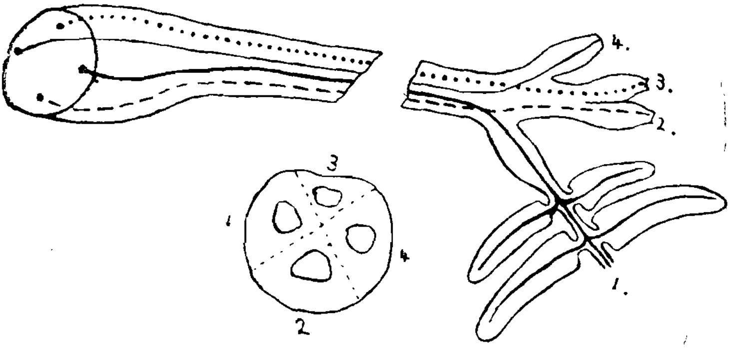

Fig. 270 The course of four nervous strands from the four sub-petioles to the pulvinus. The lower figure is a diagrammatic section of the pulvinus with its four effectors. Effectors 1 and 4, which give rise to left- and right-handed torsions are respectively in nervous connection with sub-petioles 1 and 4. The lower effector 2 is connected with sub-petiole 2, the response being a rapid down-movement. The upper quadrant 3 is in connection with sub-petiole 3, the response being a slow up-movement. (*Mimosa*.)

The four quadrants of the pulvinus are thus the four effectors; each of which consists of a nerve with the contractile cortex. The nerve in effector 1, is in conducting communication with the sub-petiole 1; stimulation of that sub-petiole causes excitation of the nerve in the effector 1, giving rise to the response characteristic of that effector, namely a left-handed torsion; nervous stimulation of the quadrant 2, causes a rapid down-movement; that of 4, a right-handed torsion; finally, stimulation of the nerve in 3 causes a slow up-movement. The reason of the more energetic down-movement of 2, relatively to the up-movement of 3, is due to the fact that the cortex of the lower quadrant is more excitable than that of 3.

The four quadrants have been numbered in the particular way to bring out their nervous connections with the sub-petioles numbered from left to right. It might sometimes be more convenient to describe the quadrant 1, as the left quadrant, the quadrant 4 as the right, quadrant 3 as the upper, and quadrant 2 as the lower. The fundamental reactions underlying the four types of response are now fully understood; these excitations may be regarded as internal as far as the pulvinus is concerned; for in the cases described above, the pulvinus was not directly stimulated; the excitation came from a distance and it is the four stimulated nerves within the pulvinus, that caused the four definite responses.

SUMMARY.

The pulvinus is a highly complex organ consisting of four distinct effectors, each giving rise to a definite and characteristic response.

The four quadrants of the pulvinus serve as different effectors, each consisting of a nerve and a contractile tissue.

The four nerves in the four quadrants lead separately to the four sub-petioles. These nerves have been localised by the Electric Probe in the phloem of the four fibro-vascular bundles in the petiole.

The four nerves in the four quadrants may, thus, be separately stimulated by nervous excitation transmitted from the four sub-petioles, the resulting response being determined by the characteristic reaction of the particular effector.

Stimulation of the nerve in the upper quadrant, however produced, is thus followed by a relatively slow up-movement; that in the lower quadrant, by a rapid down-movement. Stimulation of the nerve in the left quadrant gives rise to a left-handed torsion, that in the right quadrant, to a right-handed torsion.

LXI.—INVESTIGATIONS ON DIA-GEOTROPISM OF DORSI-VENTRAL ORGANS.

BY SIR J. C. BOSE,
Assisted by
SURENDRA CHANDRA DAS, M.A.

The geotropic response in higher plants has been shown to be brought about by the differential excitation caused by the falling starch grains, this differential action being in some way due to the pressure of particles on the inner and outer tangential walls of the statolithic apparatus. It has been shown further, that there is no specific difference in irritability of the shoot and of the root, as is assumed by the terms ' negative ' and ' positive ' geotropism. These terms are mere descriptive phrases which offer no real explanation of the phenomenon. The difference in the sign of response in the two cases have been shown to be due to the fact that in the one case, stimulation is direct, and in the other, indirect.*

We have a different type of geotropic reaction, described as ' dia-geotropic.' A concrete example of this is found in the motile pulvinus of *Mimosa*; the leaf, under normal condition, places itself in an approximately horizontal position, the vertical lines of force of gravity being perpendicular to it.

In the case of the so-called negative geotropism, a radial stem is found ultimately to erect itself so that its length is parallel to the lines of force of gravity. If the stem is rotated through 180°, that is to say, held in an inverted position, it still erects itself as before. The organ has a

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* Life Movements in Plants. Vol. II, p. 476.

definite reaction which is constant, whether it is held 'direct' or 'inverted.' Though the term 'negative' geotropism does not explain the phenomenon, yet it is a correct descriptive phrase; the organ places itself vertical, whichever side of the organ faces upwards.

But the term 'dia-geotropism' neither offers any explanation of the phenomenon nor is it even a correct descriptive phrase. It may be supposed that the reaction is due to some unknown specific irritability which is characteristic of the organ. If the *Mimosa* be held in a normal position, the motile pulvinus (with the attached leaf) places itself horizontally. But if the plant be held in an inverted position, the leaf becomes erect, *i.e.*, it assumes a 'negative' geotropic position. It is evident that an identical organ cannot be endowed with both 'negative' and 'dia-geotropic' sensibilities.

Detailed investigation on the characteristic responses of *Mimosa* leaf, not only under geotropic but under stimuli in general, appeared to hold out hopes of throwing light on the obscure subject, and of offering a rational explanation of the phenomenon of dia-geotropism. The results of the previous investigations have shown, that the pulvinus is a highly complex organ consisting of a group of distinct effectors; that these distinct effectors are actuated by distinct nerves which had been localised. We shall presently find that a definite mechanism exists by which the nerve in each effector becomes stimulated under the stimulus of gravity, and that such nervous stimulation in different quadrants give rise to geotropic responses which are very characteristic.

GENERAL DESCRIPTION OF THE PHENOMENON.

Experiment 284

Returning to the dia-geotropic pulvinus, one important fact to be noticed is that the upper and the lower halves of the organ are differentially excitable. Further, the dia-geotropic position is assumed by the leaves when its upper side is struck by vertical lines of force of gravity, the direction of the lines of force being supposed to be the same as the direction of the fall of a heavy particle. If now the plant be held inverted, the more excitable lower half being struck by the lines of force, the geotropic action is greatly increased and the leaves place themselves parallel to the lines of force. Figure 271 is the sketch of a *Mimosa* plant in a normal and in an inverted position. In the former, the attitude of the leaves is dia-geotropic, and in the latter, negatively geotropic. Another characteristic effect will be noticed in the inverted position. The very young leaves near the top exhibit little or no geotropic action. This may be due to the geo-perceptive layer not being functionally developed in too young a specimen: evidence in support of this will be given later. The third leaf exhibits the geotropic action in a very pronounced manner, this leaf being erected almost vertical. Still older leaves exhibit a decline in geotropic action. Here, we have a result parallel to what

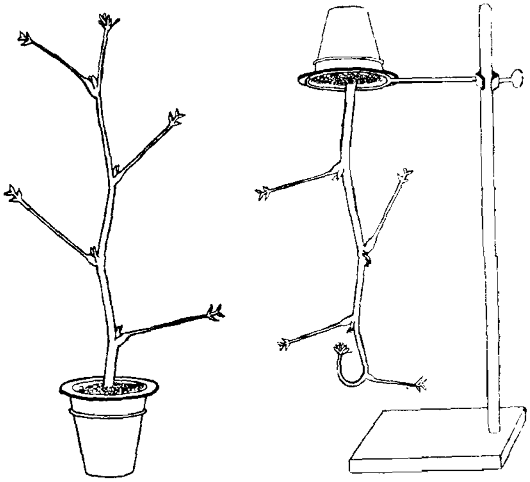

Fig. 271 Diagrammatic representation of the posture of leaves of *Mimosa* in normal, and inverted positions.

was obtained with the petiole of *Tropaeolum*, in which the middle-aged leaves are found to be the most sensitive, while the too young and too old, the least sensitive to geotropic stimulus.

Another interesting result is the curving upwards of the young shoot at the upper end of the stem. We thus have in the same *Mimosa* plant: (1) a dia-geotropic response of the leaf in the normal position, (2) a negative geotropic response of the leaf in an inverted position, and (3) a negative geotropic response of the radial shoot. In the shoot itself we obtain, however, a transition from negative to dia-geotropic response. Thus in a procumbent stem, a differential excitability is induced by continued action of sunlight on the exposed upper side in consequence of which its excitability becomes reduced. The stem is no longer radial but anisotropic, the shaded side of the stem being comparable with the lower half of the pulvinus; such an anisotropic stem exhibits a dia-geotropic reaction.

The important characteristics of a dia-geotropic organ are: (1) *that it exhibits differential excitability, the lower half being relatively the more excitable, and (2) that the dia-geotropic response takes place when the less excitable half of the organ is struck by the vertical lines of the force of gravity.* The dia-geotropic response is thus due to the differential action of the stimulus of gravity on an anisotropic organ.

CHARACTERISTIC RESPONSES OF PULVINUS TO STIMULUS OF GRAVITY.

We have seen in the last chapter how the different responses of the pulvinus, right-handed or left-handed torsions, and up- and down-movements, are brought about by the stimulation of each nerve in the four effectors. Hence if any source of internal irritation causes a left-handed torsion, this can only be due to the stimulation of the nerve in the left quadrant: similarly, right-handed torsion must be due to stimulation of the nerve in the right quadrant, the slow up-movement, to the irritation of nerve in the upper, and the quick down-movement, to the stimulation of the nerve in the lower quadrant.

We shall now study in detail the characteristic responses of the pulvinus under the stimulus of gravity. Here also we find the four definite types of responses, namely, the up or down, and the left- and right-handed torsions; these are induced, as we shall presently find, by the effective stimulation of one or other of the four quadrants by the gravitational stimulus (Fig. 272).

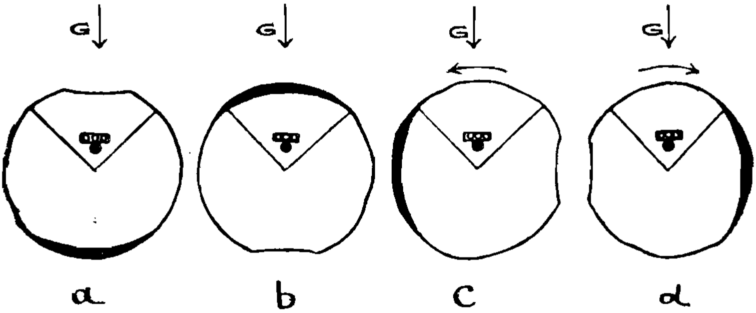

Fig. 272 Diagrammatic representation showing the four quadrants, in (a) the upper, in (b) the lower, in (c) the left, and in (d) the right, subjected to stimulus of gravity, G. The thick outline represents the more excitable lower quadrant. The starch grains press against the nerve respresented by thick dot in each quadrant.

Response to geotropic stimulation of the upper and the lower quadrants.—We hold the leaf in the normal position slightly inclined below the horizon, so that the upper quadrant faces the lines of force; and the response is a slow up-movement. The leaf is next held inverted so that the more excitable lower quadrant faces the lines of force; the rectilinear response is now found to be more energetic than in the last case.

Experiment 285

Response to geotropic stimulation of the left and the right quadrants.—When the plant is so held that the left quadrant is subject to the vertical lines of force, the response is by a left-handed torsion, followed by recovery on restoration of the plant to the normal position. Similar torsional response, this time in a right-handed direction, takes place when the right quadrant is subjected to the vertical lines of force. Records of torsional responses, right-handed and left-handed, induced by gravitational stimulus, are seen in Figure 273.

Experiment 286

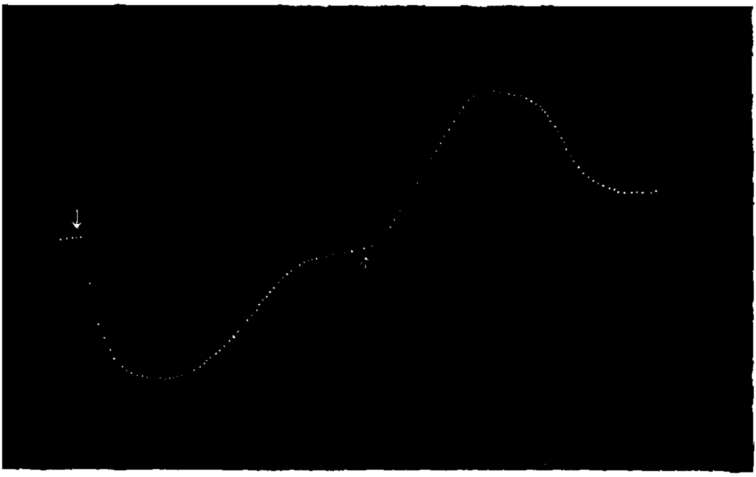

Fig. 273 Records of responses of the right and left quadrants to the stimulus of gravity. The responses are by right-handed (down-curve) and left-handed (up-curve) torsions. (*Mimosa.*)

By subjecting the four quadrants to the action of the vertical lines of force we thus obtain the responses which are characteristic of excitation of the nerve present in each quadrant. What, then, is the mechanism by which gravitational force causes the irritation of the nerve in each effector?

In higher plants, it is the pressure of the heavy particles which causes geo-perception and the subsequent response.

The mechanics of this is not yet fully understood, but the characteristic response of the pulvinus of *Mimosa* will be found to elucidate the obscurity which surrounds the subject. In regard to a satisfactory explanation of the characteristic geotropic responses of the four effectors, it is thus necessary :

(1) to discover the statolithic apparatus in the pulvinus;
(2) to determine the precise manner in which the weight of the heavy particles excite the nerve in each of the four quadrants and thus cause the response characteristic of the particular effector,
(3) to discover the cause of the difference in the geotropic reaction in the upper and the lower halves of the organ, the upper undergoing a contraction and lower an expansion. And finally, we have,
(4) to discover an explanation of the response peculiar to the dia-geotropic organ. A radial organ is in equilibrium when its length is vertical, but a vertically placed dia-geotropic organ moves downwards towards the horizon; whereas, when placed inclined below the horizon, it moves upwards, *i.e.*, towards the horizontal position of equilibrium.

THE STATOLITHIC APPARATUS.

In examining a section of the pulvinus, it was a matter of great surprise and disappointment not to find any starch grains, the pressure of which is the effective means of geotropic stimulation. Yet the geotropic response of the pulvinus is more pronounced than in radial stems, in which the presence of statoliths is such a striking feature The failure of detection of starch grains by iodine was afterwards found to be due to the presence of chlorophyll bodies; previous treatment with chloral hydrate is, however, effective in bringing out the starch grains in the clearest manner. *The starch-sheath is found to abut directly on the phloem of the* *four bundles present in the pulvinus.* Figures 274, 275, and 276 are reproduced from photo-micrographs of transverse sections of different pulvini and stem. The first gives a clear idea of the arrangement of four quadrants in the pulvinus of water Mimosa (*Neptunia oleracea*), in which the disposition of the four separate bundles and the starch-sheath is similar to that in *Mimosa pudica.* The section of the pulvinus was taken near the petiole and the four bundles are distinctly separated from each other (Fig. 274). As we approach inwards, the four bundles approach each other and appear to form an almost continuous ring; each bundle is, however, physiologically distinct from its neighbours. Each quadrant, *from out to inwards,* is seen to consist: (1) of the sensitive cortex, (2) of the starch-

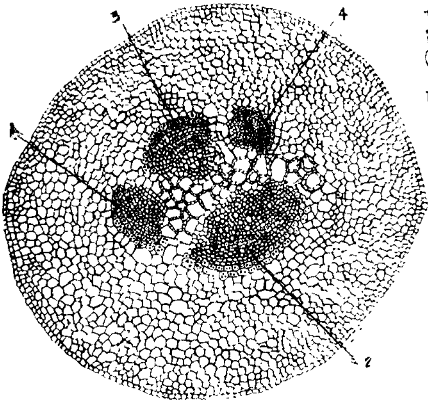

FIG. 274

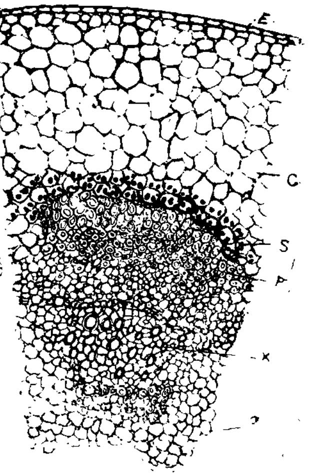

FIG. 275

Fig. 274 Photo-micrograph of transverse section of the pulvinus of *Neptunia* showing four distinct quadrants; 1 and 4 are lateral, 3 and 2 are upper and lower respectively. Starch-sheath containing starch grains abut against the phloem.

Fig. 275 Enlarged photo-micrograph of the lower quadrant of *Mimosa pudica.* E, epidimis; C, sensitive cortex; S, starch-layer two cells thick with numerous starch-grains, which press against the phloem, P; X, the xylem; O, pith. (The top represents the lower side).

sheath of two layers of cells studded with numerous starch grains, which under ordinary conditions are dispersed diffusely, but fall on the lower side when subjected to long continued action of the force of gravity. The statocysts, as already stated, abut directly against the phloem of the bundle which functions as the nerve. We have next the phloem, the xylem, and the central pith. In a very young pulvinus the starch grains are not formed, which probably explains its insensitiveness to the stimulus of gravity.

A transverse section of the lower quadrant of the pulvinus of *Mimosa pudica* is reproduced, much enlarged, in Figure 275. The characteristic distribution of the different elements will be found to be similar to that in *Neptunia.*

Figure 276 shows the transverse section of the upper side of the stem of *Impatiens*, as representative of ordinary dicotyledonous plants. The section was made after the commencement of the upward geotropic curvature. We observe the cortex, and a starch layer which abuts against the phloem. *The starch grains have fallen on the lower side and are practically pressing against the nerve.* The physiological machinary in an ordinary stem is, thus, essentially the same as in the pulvinus; the minor difference is in the greater contractility of the sensitive cortex in the pulvinus. But this is merely a question of degree and not of kind; for we have seen that the cortical tissue in an ordinary plant undergoes contraction under stimulation. The real difference between a radial stem and the pulvinus is this, that in the former, the excitability is the same all round, whereas, in the dorsi-ventral organ, the lower side is relatively more excitable than the upper side. We shall presently find, that it is this differentiation which causes the characteristic difference in the responses of dia-geotropic and negatively geotropic organs.

The geotropic curvature has been explained to be due to the joint effects of contraction of the upper, and expansion of the lower side. We take a seedling of *Eclipta*, which is found to be very sensitive to geotropic action. It is laid horizontally, and a vertical section is made after the production of the upward curvature. The illustration (Fig. 277) shows the physiological changes induced at the upper and lower sides. The cortex in the *upper side shows a relative contraction, while that in the lower side, a relative expansion.* A single starch layer is seen to abut against the upper and the lower nerves. *The starch grains in the upper statocyst*

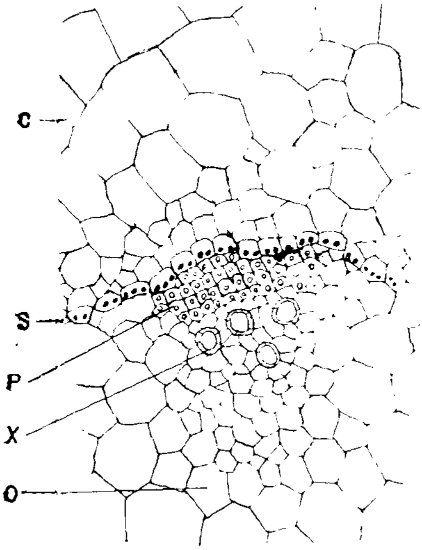

FIG. 276

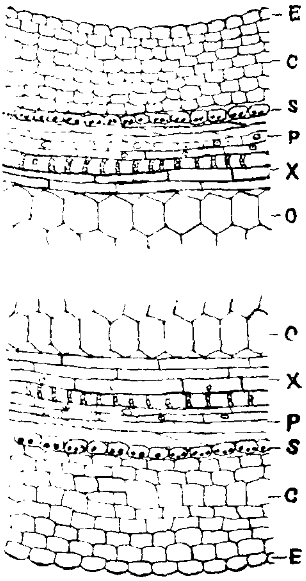

FIG. 277

Fig. 276 Photo-micrograph of transverse section of upper side of geotropically curved *Impatiens*.

Note the starch grains fallen on the inner tangential wall of statocysts, S, pressing against the phloem P C, cortex; X, xylem; O, pith.

Fig. 277 Vertical longitudinal sections of upper and lower sides of geotropically curved stem of *Eclipta*.

Note contraction of the upper, and expansion of lower cortex. The starch grains are pressing against the phloem of the upper side and inducing contraction. The starch grains in the lower statocysts are pressing against the outer tangential wall away from the phloem.

are found pressing against the inner tangential wall of the cells nearest the phloem; in the lower side of the stem, the starch grains in the cells are, on the other hand, pressing on the outer tangential wall furthest from the phloem. It is important to bear in mind this characteristic difference in modes of stimulation on opposite sides of the organ.

Returning to the pulvinus of Mimosa, the motile apparatus has been shown to consist of four effectors, each containing a nerve. The excitation of each nerve causes the response characteristic of the particular effector. We shall now inquire, how the nerve in each quadrant becomes stimulated under the action of gravity, when that quadrant is above and facing the lines of force.

In regard to the action of gravity, it is important to bear in mind that the stimulus is *internal.* It is the weight of the particles, the conjoint action of gravity and mass, that exerts the pressure necessary for excitation. Fixing our attention to one of the quadrants, say, the upper, held at an angle inclined to the horizon and with its upper side facing the lines of force, we find that the cells containing the starch grains are practically in contact with the phloem which functions as the nerve; there is thus only a cell wall which intervenes, and which is probably perforated and traversed by protoplasmic threads. In any case, the nerve of the upper quadrant becomes directly stimulated by the pressure of the starch grains above, and the cortex of that quadrant undergoing contraction gives rise to an up-movement. If the pulvinus be held in an inverted position, the lower quadrant faces the lines of force, and the responsive movement is relatively more intense. This may be due to the greater stimulation of the nerve by the pressure of a more abundant or heavier starch grains, also on account of the greater excitability of the lower quadrant. A large number of sections of the pulvinus showed a greater abundance of starch-grains in the starch-sheath of the lower quadrant. This, along with the greater excitability of the cortex explain the more intense geotropic response of the lower quadrant. When the left quadrant is exposed to the vertical lines of force, the nerve in that quadrant becomes stimulated by the pressure of the particles, and the response is by a left-handed torsion, characteristic of the left effector. Similarly, exposure of the right quadrant to gravitational stimulus gives rise to a right-handed torsion.

NEGATIVE AND POSITIVE REACTIONS ON OPPOSITE SIDES OF A RADIAL ORGAN.

The most perplexing problem in the geotropic action is the difference in the signs of reaction on the opposite sides

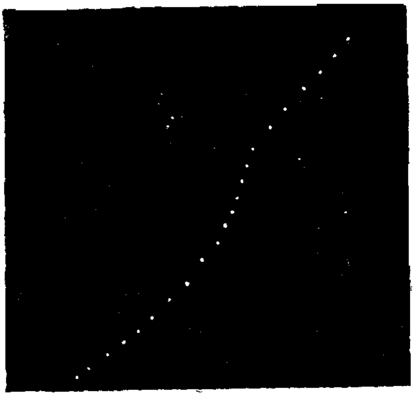

Fig. 278 Effect of feeble stimulus in enhancing the rate of growth. The curve at the beginning exhibits the normal rate; feeble stimulus applied for a short time enhanced the normal rate (as seen in the erect curve) followed by recovery.

of the organ. We have seen that the upper side exhibits an excitatory contraction with diminution of turgor, and retardation of the rate of growth. This we shall designate as the negative response. The reaction on the lower side is, however, diametrically opposite, namely a positive response, an increase of turgor, expansion, and enhancement of the rate of growth. At first sight these opposite effects under the identical stimulus of gravity seem to be inexplicable. I shall, however, be able to adduce facts and considerations which will fully explain the phenomena which appear to be so anomalous.

Before entering into the detailed study of this subject, I would draw attention to the very important results obtained on the effect of intensity, and of point of application of stimulus on growth (Expts. 86 and 89, pp. 215-224, Vol. I). It is there shown, that while normal intensity of stimulus causes a retardation, sub-minimal stimulus induces the *opposite effect of acceleration of growth* (*Fig.* 278). *Again* while indirect stimulus accelerates growth, direct stimulus is found to inhibit it (Fig. 279). *These fundamental effects* are demonstrated by application of different modes of stimulation, and also by the employment of methods of record as diverse as mechanical and electrical (cf. Expts. 85, 103).

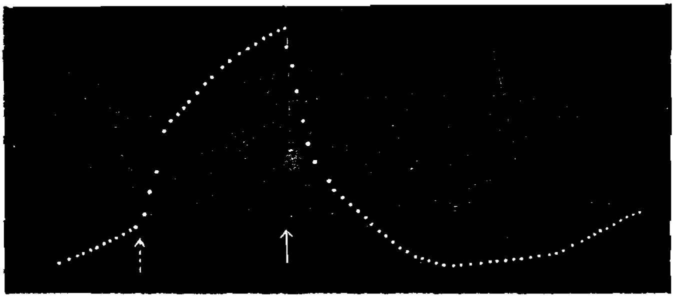

Fig. 279 Effect of indirect and direct stimulus on growth. Indirect stimulus at dotted arrow is seen to accelerate, while direct stimulus at the second arrow, to stop growth. Direct stimulus in the present case has induced an actual contraction.

Let us next consider the excitation caused by geotropic stimulus on the upper and the lower sides of the organ. We saw that the responsive movement is caused by stimulation of the nerve by the pressure of the heavy particles. Now, there is a characteristic difference as regards stimulation of the nerves in the upper and the lower sides. As already stated, the particles exert on the upper nerve a pressure, which is intense and direct, hence the upper effector undergoes contraction. But the case is different as regards stimulation of the lower nerve. The starch grains in the statocyst are seen to press against the outer tangential wall furthest from the nerve (cf. Fig. 277). The stimulation is thus indirect and minimal. Hence the response is positive, *i.e.*, an acceleration of growth. The lower effector thus undergoes an expansion; a change of growth thus occurs which is of opposite sign to that in the upper effector. The conjoint effect of contraction at the upper, and expansion at the lower side brings about the upward geotropic movement.

DIA-GEOTROPIC RESPONSE OF THE PULVINUS.

The only question, which still remains to be explained, is the dia-geotropic attitude of the leaf of *Mimosa; in radial* organs the position of geotropical equilibrium is vertical, whereas, in the pulvinus it is approximately horizontal.

A radial organ held vertical remains in that position, the length of the organ being parallel to the lines of force of gravity. But if the *Mimosa* plant be so placed that the leaf is vertical, it does not remain in that position, but moves downwards till the upper half of the pulvinus is approximately perpendicular to the lines of force. What, then, is the underlying physiological cause which would account for the characteristic differences of response in radial and dorsi-ventral organs? The physiological difference which we found in the two cases is, that in radial organs the excitability of two opposite sides is the same; so that similar stimulation of the two sides produces similar contractions which counteract each other. But in the dorsi-ventral pulvinus, owing to the difference of excitability, the more excitable lower half exhibits under the same stimulation a more pronounced contraction than the less excitable upper half.

ELECTRIC INVESTIGATION.

I have already explained how the physiological change associated with expansion or excitatory contraction of any portion of the tissue may be detected by the concomitant electrical change. We introduce the Electric Probe into the tissue in connection with a galvanometer. A positive electric variation indicates an expansion, while a negative variation, the opposite reaction of contraction.

Geo-electric response of radial organs.—We take the radial stem of *Tropaeolum*, and introduce two probes on opposite sides of the organ, a galvanometer being interposed in the circuit. We incline the specimen at increasing angles, and observe the geo-electric deflection; centering our attention to the electric change induced at the lower side we find, that the electric variation thus induced is one of galvanometric positivity, indicative of expansion of that side. (It is understood that the electric variation of the upper side is negative, indicating contraction of that side.) The inclination may be continuously increased, and the electric change of the lower side is found to remain persistently positive, though the intensity of reaction may undergo some variation. Inclination of a radial organ, thus, gives rise to an expansive response of the lower, and a contractile response of the upper side, and this throughout various angles of inclination.

Experiment 287

Geo-electric response of the dorsi-ventral pulvinus.—Electric connections similar to the above are made with the pulvinus of *Mimosa*. A necessary condition for success of the experiment is to place the specimen outside, exposed to diffuse light; the two connecting

Experiment 288

wires are led to the galvanometer inside the laboratory. It is necessary to take this precaution since long maintenance of the plant in a dark room is apt to bring about a condition of *sub-tonicity with consequent disappearance*, or even a reversal, of the normal response. After the electric connections are made in the manner described, the specimen is adjusted so as to place the pulvinus and the attached leaf vertical. With a radial organ there is no electric response in this vertical position; but the pulvinus of *Mimosa* exhibits in this position a strong geo-electric response, the more excitable (lower) half becoming *galvanometrically negative*. In a typical experiment the deflection was 45 divisions. This negative deflection of the more excitable side of the organ shows that a contraction of that side is induced in the vertical position; the corresponding geotropic response thus tends to bring down the leaf towards the horizontal. This, in reality, is what actually takes place.

Experiment 289

The leaf is next inclined at an angle of about 35° below the horizon. The geo-electric response is now found to undergo a reversal, the more excitable half being now *galvanometrically positive* with a deflection of +50. The specimen was next brought back once more to the vertical position, with the restoration of the original galvanometric negativity of the more excitable side. The positivity of the lower side when inclined to 35° below the horizon indicates that there is a responsive reaction of expansion of the lower half by which the leaf is raised towards the horizontal. There is thus a transition through zero, between the negative response in the vertical, and the positive response at 35° below the horizon; at this point of transition, when the response disappears, the leaf is in a state of geotropic equilibrium. This is the dia-geotropic position of the leaf which may be regarded as approximately horizontal.

We shall next attempt to discover the reason for the characteristic differences of response in radial and dorsiventral organs. A diagrammatic representation of a geotropic organ is given in Figure 280, first in a vertical position, then inclined at about 35° below the horizon; N and N' are the two nerves at the opposite sides, the stimulations of which, by the pressure of starch grains, cause the excitatory contraction of the cortex of directly stimulated side, and the expansion of the indirectly stimulated opposite side. The side which is to be the under-side after inclination is represented as shaded.

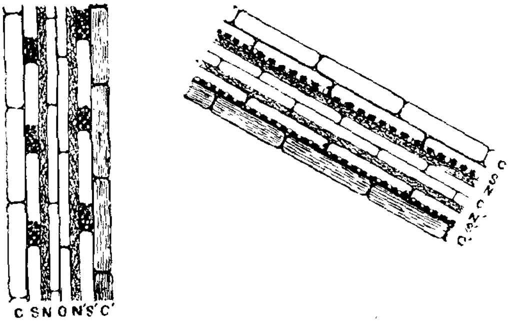

Fig. 280 Diagrammatic representation of a geotropic organ in a vertical and in an inclined position. The shaded is to be the underside. It also represents the more excitable half of a dia-geotropic organ. C, C', cortex; S, S', statocysts. N, N' nerves; O, pith. In vertical position of a radial organ excitation induced by lateral pressure of starch grains is same on the two sides in dia-geotropic organs the excitation on the right side is greater (see text).

Response of radial organs.—As the starch grains become piled up at the base of the cell, they exert not only a vertical but also a lateral pressure. Now in a radial organ held vertical, the stimulations of the two nerves are the same; moreover, the excitability of the cortex at the two sides are also the same; hence the two antagonistic reactions balance each other. But when the organ is inclined, say, 35° below the horizon, it is the upper nerve, as already explained, that becomes directly and intensely stimulated; whereas, the lower nerve undergoes an indirect and feeble stimulation.

The result is a contraction of the upper and an expansion of the lower side, this explains the upward or negative geotropic curvature of radial organs.

Response of dorsi-ventral organs.—In the above diagram, let us regard the right and shaded side to be also the more excitable. In a vertical position of the leaf the lateral pressure, exerted by the particles on the two sides, may be the same but the excitatory contraction of the more excitable cortex of the lower half of the pulvinus will be relatively greater. The greater excitation of the more excitable half of the pulvinus in a vertical position is also demonstrated by the induced galvanometric negativity of that side. There can, therefore, be no balance, and the organ moves downwards. But at 35° below the horizon, the upper nerve N, becomes directly stimulated by the pressure of the particles, whereas, the lower nerve N′ becomes feebly and indirectly stimulated. The response is thus upwards, *i.e.*, towards the horizontal position. The position of geotropic balance thus lies between the above two extreme cases.

This position of balance will evidently depend on the differential excitability between the two halves of the anisotropic organ. If the difference in the excitability is very great, the dia-geotropic position will approximate to the horizontal. If the difference is slight, the balancing position will be nearer the vertical, which is the normal position of geotropic equilibrium in radial organs. The above consideration will explain the different dia-geotropic attitudes of various dorsi-ventral organs, in which the inclination to the vertical is found to vary widely from an almost erect to a horizontal position.

SUMMARY.

It has been shown that the stimulus of gravity causes definite responsive movements depending on the particular quadrant which faces the lines of force.

Geotropic stimulation is effected by the pressure of starch grains in the statocysts which directly abut on the nerve. When the upper quadrant of the pulvinus of *Mimosa* faces the vertical lines of force, the result is a moderate up-movement; exposure of the lower quadrant gives rise to a more intense rectilinear-movement. Again, stimulations of nerves of left and right quadrants by the pressure of particles, give rise respectively to left- and right-handed geotropic torsions.

The opposite reactions at the upper and lower sides of a radial organ are due to the fact that the stimulation of nerve at the upper side is intense and direct, whereas at the lower side, it is feeble and indirect. The response induced by moderately strong stimulus being a retardation of growth and contraction, the upper side becomes concave. The effect of sub-minimul stimulus at the lower side is an acceleration of growth and expansion, which induce the convexity of the lower side. The geotropic curvature of the organ is thus due to the concordant effects induced at the upper and lower sides.

A dorsi-ventral organ placed in a vertical position has its opposite sides stimulated by the lateral pressure exerted by the starch grains: the responsive contraction is greater at the more excitable lower side of the organ. Hence the organ moves downwards. At an angle of 35° below the horizon, the upper half is subjected to direct and the lower to indirect stimulation. The response is thus upwards, towards a horizontal position.

The balancing position between these extreme cases is determined by the differential excitability of the two halves of the anisotropic organ. This balancing position approximates to the horizontal when the difference of excitability is great; it becomes nearly vertical when the difference is slight. These considerations explain the different dia-geotropic attitudes of various dorsi-ventral organs.

VOLUME IV

MECHANICAL AND ELECTRIC RESPONSE OF PLANTS

LXII.—THE DIA-HELIOTROPIC ATTITUDE OF LEAVES.

By Sir J. C. Bose,

Assisted by

Satyendra Chandra Guha, M.Sc.

In the previous chapter we obtained an explanation of the dia-geotropism of various dorsi-ventral organs, and found that the effect was due to internal stimulation of the nerve by the pressure of starch grains. The diverse responses of the pulvinus,—by up or down movement, by left-handed or right-handed torsion—were shown to be brought about by definite reactions of the four distinct effectors in the main pulvinus.

We shall in the present chapter describe investigations on the phenomenon of dia-heliotropism.* In geotropic response, the stimulus, as already stated, is internal; but in heliotropic action, the stimulus is external. The heliotropic movement takes place, not only when light acts directly on the motor organ, but also when it acts indirectly at some distance from the motor organ.

As a result of the effects of the direct and indirect light, the leaves adjust themselves in various ways in relation to the incident light. The heliotropic fixed position is assumed by means of curvatures and torsions of the motor organ, which may be the pulvinus, or the petiole acting as a diffuse pulvinoid. In some cases the motor organ alone is both

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* cf. Bose and Guha—Proc. Roy. Soc. B-vol. 93, p. 153.

perceptive and responsive; in others, the leaf blade exerts a directive action, the perceptive lamina and the motor organ being separated by an intervening distance. This directive action of the lamina has been found by Vochting in *Malva verticillata*, and by Haberlandt in *Begonia discolor*, and in several other plants. In connection with this, it should be borne in mind that this characteristic does not preclude the possibility of the motor organ being directly affected by the stimulus. In a nerve-and-muscle preparation, the muscle is excited, not merely by indirect but also by direct stimulus. As regards the heliotropic adjustment of leaves, the stimulus of light acts, in the cases just mentioned, both directly and indirectly, the indirect stimulation being due to some transmitted effect from the perceptive lamina. We may regard the coarse adjustment to be brought about by direct, and the finer adjustment by indirect stimulation.

Certain leaves thus assume a heliotropic fixed position so that the blades are placed at right angles to the direction of light, the directive action being due to certain transmitted reaction, hitherto unknown. No explanation has, however, been forthcoming as regards the physiological reaction to which this movement must be due. Suggestions have been made that the dia-heliotropic position of leaves is of obvious advantage, since this position assures for the plant the maximum illumination. But such teleological considerations offer no explanation of the definite physiological reaction. It is, moreover, not true, as I shall show in the course of this paper, that there is something inherent in the plant-irritability by which the surface of the leaf is constrained to place itself perpendicular to the incident light.

I have for many years been engaged in pursuing investigation on the subject, and have recently succeeded in discovering the fundamental reaction to which the directive movement is due. I shall be able to show that the particular attitude assumed by the leaves is brought about by transmitted "nervous impulse," which reaches the motor organ, which is not simple but highly complex; that there are several distinct impulses which react on the corresponding effectors grouped in the motor organ.

The dia-heliotropic phenomena, will be studied not only in 'sensitive' but also in ordinary plants. It will be shown that the responsive reactions in both these cases are essentially similar. As a type of the former I shall take *Mimosa pudica*, and for the latter, *Helianthus annuus*.

GENERAL DESCRIPTION OF THE DIA-HELIOTROPIC PHENOMENA.

Before entering into the experimental investigation of the subject, it is desirable to describe the dia-heliotropic phenomena, as typically exemplified by *Mimosa* and *Helianthus*. A photograph of the former is reproduced in Figure 281*a*, in which the plant placed in a box had been exposed to the northern sky and not to direct sunlight. It will be seen that the leaves which directly front the light have been raised, and so placed that the sub-petioles, with their leaflets, are at right angles to the strongest illumination. The side or lateral leaves have, on the other hand, undergone appropriate torsions—the plane of the leaflets being adjusted perpendicular to the light. It will be noticed that in executing this, the petioles to the right and the left have undergone opposite torsions. After the assumption of this position, the pot containing the plant was turned round through 180°. This brought about a new adjustment in the course of twenty minutes, the plane of all the leaflets being once more at right angles to the light. The new adjustment necessitated a complete reversal of the former movements and torsions. Such perfect adjustment is brought about by bright light from the sky, and not so well by direct sunlight, for reasons which will be given later.

In Figure 281*b*, is seen the heliotropic adjustment of the

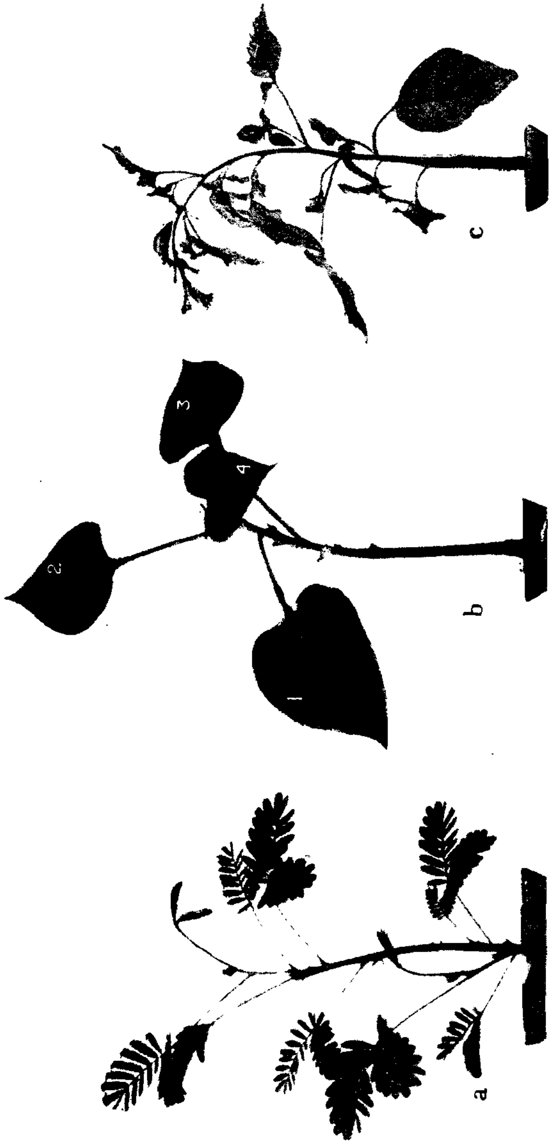

Fig. 281 Dia-heliotropic adjustment of leaves: (*a*), in *Mimosa*; (*b*), in *Helianthus annuus*; and (*c*), in a different species of *Helianthus*. [From photographs.]

leaves of sunflower, grown near a wall, the plant being exposed to light from the western sky. The adjustment is essentially similar to that seen in *Mimosa*. The lateral leaves, 1 and 3, have undergone appropriate torsions—right-handed or left-handed—so that the leaf-blades placed themselves at right angles to the light. The leaf numbered 2 has been raised, placing its lamina perpendicular to the light. A contributing factor in this is the bending over of the stem, due to positive heliotropic curvature, which accentuated the rise of the leaf number 2. The same bending often causes an apparent fall of the leaf marked 4. When the stem is tied to a stake, the bending over of the stem is prevented; the leaf numbered 2 is then found raised by heliotropic action; but there is little or no fall of the opposite leaf.

Another photograph is reproduced (Fig. 281*c*) of the heliotropic curvature and adjustment of a different species of sunflower, which was grown in the open. In the morning the plant bent over to the east and all the leaves exhibited appropriate movements and torsions. In the afternoon the plant bent over to the west, all the previous adjustments and torsions being completely reversed. The plant continued to exhibit these alternate swings day after day till the movement ceased with age.

CHARACTERISTICS OF THE MOTOR ORGAN.

I have shown elsewhere that there is *no essential* difference between the response of "sensitive" and "ordinary" plants. I shall now show that all the characteristics of the response of the leaf of *Mimosa* are also found in the leaf of *Helianthus*. These will be specially demonstrated as regards normal response and recovery, the response of adaxial and abaxial halves of the organ to stimulus, the effect of direct and indirect stimulus in inducing heliotropic curvature, the daily periodic movements of the leaves, and the torsional response to lateral stimulation.

MECHANICAL RESPONSE DUE TO DIFFERENTIAL EXCITABILITY.

It has already been explained that on account of the differential excitability of the upper and lower halves of the pulvinus, a diffuse stimulus causes a responsive fall of the leaf of *Mimosa*. I shall now show that a similar reaction takes place in *Helianthus*.

Experiment 290

In *Helianthus*, the entire petiole acts as a motor organ, of which the upper half is relatively less excitable. Diffuse stimulation by electric shock induces a responsive fall, followed by a recovery on the cessation of stimulus. The response-records thus obtained are very similar to those obtained with the leaf of *Mimosa*. In *Helianthus* the reaction is relatively sluggish and the contraction is not so great as in *Mimosa*. The difference between the two responsive reactions is one of degree and not of kind.

RESPONSE TO STIMULATION OF ADAXIAL AND ABAXIAL HALVES OF THE ORGAN.

The upper half of the pulvinus of *Mimosa* responds to application of light by local contraction; the leaf is thus erected and the movement towards light may be described as positive heliotropism. The leaflets attached to the sub-petioles are thus made to face the light. Under strong and long continued sunlight the excitation is transmitted across the pulvinus, and causes at first a neutralisation, and finally a reversed or negative movement by the contraction of the more excitable lower half of the organ. This is the reason why the dia-heliotropic adjustment is less perfect under strong sunlight.

We obtain parallel reaction with *Helianthus*: here the petiole acts as an extended pulvinoid. Light applied from above, causes an erectile movement: when applied below it causes a more energetic down movement. As the transverse conductivity of the petiole is feeble, the positive heliotropic response, induced by light acting from above, is rarely reversed into negative.

Experiment 291

THE MECHANISM OF HELIOTROPIC CURVATURE.

A few words may now be said of the mechanics of curvature by which the stem of *Helianthus* bends towards light. All forms of stimuli, including that of light, induce a diminution of turgor and consequent *contraction, and retardation* of the rate of growth of the *directly excited side*. But this is not the only factor in bringing about the positive curvature. I have shown that while the effect of direct stimulus at the proximal side of the stem induces diminution of turgor and contraction, its effect on the distal side, where it acts indirectly, is the very opposite, namely, an *increase* of *turgor and expansion*. The positive curvature is thus due to joint effects of direct and indirect stimulus at the two opposite sides. I have been able to demonstrate the induced increase of turgor at the distal side by experimenting with the stem of *Mimosa*. The stimulus of light is applied at a point directly opposite to the motile leaf, which by its movement indicates the change of turgor, the induced increase of turgor being indicated by an erection, and diminution of turgor by a fall of the leaf. Application of light at a point on one side of the stem was thus found to induce an *increase* of turgor at its diametrically opposite point, as evidenced by the erectile movement of the leaf.

Parallel experiments which I have recently carried out with *Helianthus* gave *identical* results. Arc light was continuously applied at a point opposite the indicating leaf;

this induced an increase of turgor, as exhibited by a continuous erection of the leaf. We thus find that while direct stimulation induces a diminution of turgor at the proximal side, indirect stimulation causes an increase of turgor at the distal side. The positive heliotropic curvature is thus due to the joint effects of contraction of the proximal and expansion of the distal side.

THE DIURNAL MOVEMENT.

The daily periodic movements of the leaf *Mimosa* and of *Helianthus* exhibit a further similarity which is remarkable. I have shown elsewhere* that in plants sensitive to light the operative factors in the diurnal movement are :—

a. The variation of geotropic action with changing temperature. A rise of temperature is found to inhibit the geotropic action; a fall of temperature accentuates it. In consequence of this the leaf, subject to geotropic action, undergoes a periodic up-and-down movement; the maximum fall of the leaf takes place at thermal noon, which is about 2 P.M., the maximum rise is at thermal dawn, about 6 A.M.

b. The action of light is, generally speaking, antagonistic to that of temperature. In the forenoon, rise of temperature causes a fall of the leaf, but continuous light acting from above tends to raise it. The rapid diminution of light towards evening acts virtually like a stimulus, causing an abrupt fall of the leaf.

The diurnal movements of *Mimosa* and *Helianthus* exhibit four phases which are very similar :—

(1) The leaf, owing to fall of temperature erects itself from 2 to 5-30 P.M., or thereabouts.

(2) After 6 P.M. there is a rapid diminution of light, and the leaf undergoes a sudden fall, which continues till about 9 P.M.

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* Life Movements in Plants, Vol. II., p. 597.

(3) After 9 P.M. the leaf begins to erect itself with the fall of temperature, the maximum erection being attained at thermal dawn, which is at 6 A.M., approximately.

(4) In the forenoon the leaf is acted on by two antagonistic reactions, the effects of rising temperature and of increasing light, the effect of rise of temperature being predominant. The leaf thus continues to fall till thermal noon, which is about 2 P.M.

TORSIONAL RESPONSE TO LATERAL STIMULUS.

When the nerves of the left and right flanks or quadrants of the pulvinus of *Mimosa* are stimulated by excitations transmitted from the left and right sub-petioles, there are produced left-handed and right-handed torsions (see Fig. 265). We also obtain similar results through direct stimulation of the left and right flanks of the pulvinus by light. Direct stimulation of the left flank induces a left-handed torsion; that of the right flank, a right-handed torsion.

The response just described above takes place when the pulvinus is exposed to lateral light, the leaflets carried by the sub-petioles being completely shielded from it. The differentially excitable organ thus undergoes a twist, in consequence of which the less excitable upper half of the pulvinus is made to face the stimulus. The leaflets attached to the sub-petiole are thus carried passively, like so many flags, to face the hypothetical source of light. It is obvious that the response is brought about by a definite physiological reaction and not for the utilitarian purpose of securing maximum illumination of the leaflets or the lamina. Teleological considerations, often adduced, offer no real explanation of the phenomena; such arguments are, moreover, highly misleading, for similar responsive torsion is induced, not merely by light, but by modes of stimulation so diverse as electrical, thermal, geotropic, and chemical.

Torsional response of petiole of Helianthus.—The above results are also exhibited by the petiole of *Helianthus* under various stimuli applied laterally.

Experiment 292

Two fine pins are thrust about 1 cm. apart on the right flank of the petiole of *Helianthus*, to serve as electrodes for application of induction shocks from a secondary coil; a similar pair of electrodes are attached to the left flank. On application of a feeble tetanising shock to the right flank, the petiole exhibited a right-handed torsion; stimulation of the left flank induced a left-handed torsion. Electric stimulation quickly stirs up the internal tissue, hence the latent period is short, and the responsive reaction is rapid (Fig. 282*a*). I next took a different specimen, and applied the stimulus of light to the right and the left flanks alternately. This gave rise to right- and left-handed torsions as under electric stimulus, the only

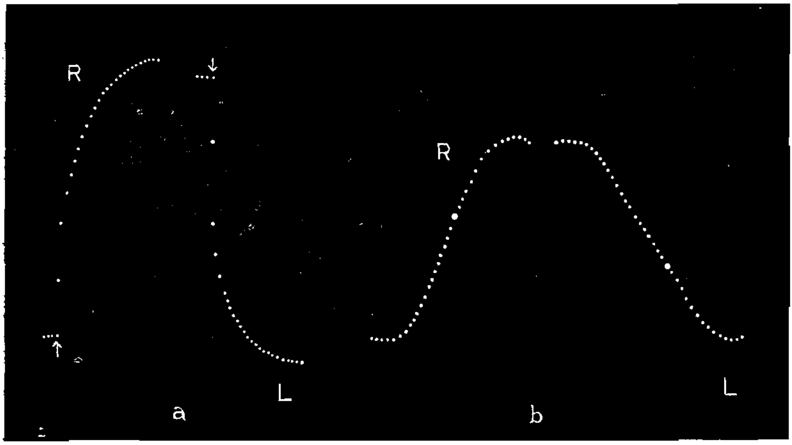

Fig. 282 Torsional response of petiole of Helianthus in response to (*a*), electric stimulus, and (*b*), to stimulus of light. R and L are the opposite responses, due to stimulation of the right and left flanks. Successive dots are at intervals of 20 seconds. The prolonged latent period under light is not shown in the record. The portion of record exhibiting recovery is also omitted. The two thick dots in (*b*), represent the moments of cessation of light.

difference being in the slower reaction and prolonged latent period of 15 minutes (Fig. 282*b*). It must be remembered that in the case of light the excitation is gradually transmitted from the outer surface to the inner tissue. As regards the direct action of light, the results given above show that the responsive reactions of sensitive and ordinary plants are not different, but essentially similar. With reference to the heliotropic adjustment of leaves, we found that, when light strikes symmetrically in front, the leaf bends towards it. The growing stem itself is excitable, and its *induced curvature* is a *contributory factor* in placing the surface of the lamina at right angles to the light. Leaves struck laterally by light undergo torsion which is definite, being determined by the direction of the incident light. The torsion thus induced places the leaflets or the lamina at right angles to the light. These effects are produced, as stated before, when the responding pulvinus or petiole are directly exposed to light, the leaflets or the lamina being protected from it.

The heliotropic adjustment of leaves often takes place, as we have seen, when the motor organ is in the shade, or is artificially kept so. There must, therefore, be transmitted impulses by which the distant motor apparatus is so actuated that the leaflets or the lamina are placed at right angles to the light. The transmitted impulse, if single or diffuse, cannot evidently exert the necessary directive action. I have already explained (p. 706) that the transmitted impulse is of a nervous character, that the impulses are more than one, and distinct from each other, and that they travel by different channels from the lamina which perceives light to the distant effectors where movement is produced in response to transmitted excitation.

THE DIRECTIVE ACTION OF PROPAGATED IMPULSE IN HELIOTROPIC LEAF-ADJUSTMENT.

As in *Mimosa*, so also in *Helianthus*, the nervous channels were traced from the receptor to the effector. The most difficult problem that confronts us now is to explain the responsive movement and torsion of the *motor organ*, by which the expanded leaf-surface faces the light. I shall now describe the motor reaction when *different* parts of the leaf are locally stimulated, not only by light, but by diverse modes of stimulation.

HELIOTROPIC ADJUSTMENT OF THE LEAF OF MIMOSA.

I have already shown (Experiments 280, 281) that stimulation of the right sub-petiole by induction shock or by light induces a right-handed, that of the left sub-petiole, a left-handed torsion. We shall consider in detail the effects induced by vertical light on leaflets of *Mimosa*.

Experiment 293

When the leaflets of the right petiole were acted on by vertical light, the distant pulvinus underwent a torsion, and the amount of light absorbed by the leaflets thus became reduced. Hence it is obvious that it is not the advantage of the plant, but the inevitable physiological reaction, that determines the movement. Stimulation of the leaflets of the left sub-petiole induced a left-handed torsion. If the leaflets of the two intermediate sub-petioles are kept shaded, and the leaflets of the right and left sub-petioles are illuminated by vertical light, the two resulting torsions are found to balance each other. While in this state of dynamic balance, if the intensity of light on one of the sub-petioles, say the left, be diminished by interposition of a piece of paper, the balance is at once upset, and we find a right-handed torsion. The movements caused by transmitted excitations from the intermediate sub-petioles number 2 and number 3, similarly balance each other. It is thus seen that equilibrium is only possible when the entire leaf-surface is equally illuminated; and that would be the case when the surface is perpendicular to the incident light. The dia-heliotropic attitudes of leaves is thus brought about by distinct nervous impulses, initiated at the perceptive region actuating the different effectors.

TRANSMITTED EXCITATION IN HELIANTHUS.

In *Helianthus* we can distinguish three main veins or nerves, which gather excitation from different regions of the lamina. The nervous function of these are demonstrated by two different methods of investigation, electrical and mechanical. In *Helianthus* we notice three main nerve-endings in the lamina in continuation of the nerves in the petiole (Fig. 283) the petiole itself serves, as we have seen, as an extended motor organ.

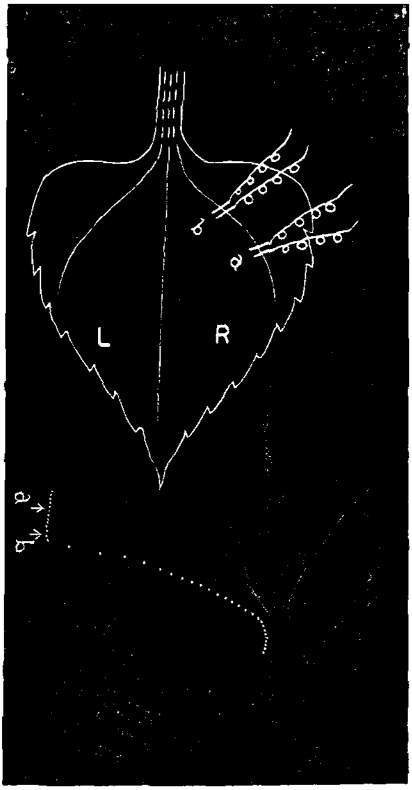

Fig. 283 The upper figure is a diagram of stimulation of nerve-ending of Helianthus. The record below shows that stimulation beyond the cut gives (*a*), no response; while stimulation at (*b*), induces right-handed torsion.

Method of electric response.—One electrode was pricked in so as to make contact with the phloem of the right bundle embedded in the petiole; the second contact was made with a distant indifferent point. Electric stimulation of the right nerve-termination in the lamina gave rise to an electric response of galvanometric negativity, the response being monophasic Application of thermal and chemical stimulations produced similar results. In the two last cases, the intense stimulus gave rise to multiple responses. In the next experiment

Experiment 294

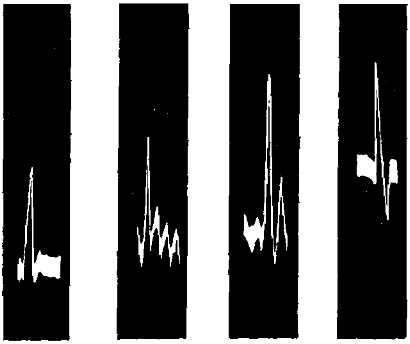

Fig. 384 Galvanometric record of transmitted excitation in the nerve of *Helianthus*. The first is in response to electric stimulus, the second and the third to thermal and chemical stimulus. The fourth is a diphasic response. Note the multiple response due to strong stimulation. [See text].

both the electrodes leading to the galvanometer were connected with the nerve in the petiole, 1 cm. behind the other. The response was now diphasic, since excitation reached the two points in succession. (Fig. 284).

Method of Mechanical Response.—The effect of transmitted excitation was now observed by characteristic responsive movement of the petiole, which is the motile organ. The stimulation employed is electrical and photic. The electrodes for induction shock are inserted in the manner seen in Fig. 283.

Electric stimulation; effect of discontinuity.—A cut is made between *a* and *b*, thus interrupting the continuity of the nerve to the right. Electric stimulation at *a* induced no responsive movement; stimulation at *b*, however, induced the normal response by right-handed torsion (see lower record, Fig. 283).

Experiment 295

Alternate Electric Stimulation.—The right and left nerve endings in the lamina were stimulated alternately. This gave rise to right-handed and left-handed torsions respectively. In figure 285*a*. is given the record of right-handed torsion.

Experiment 296

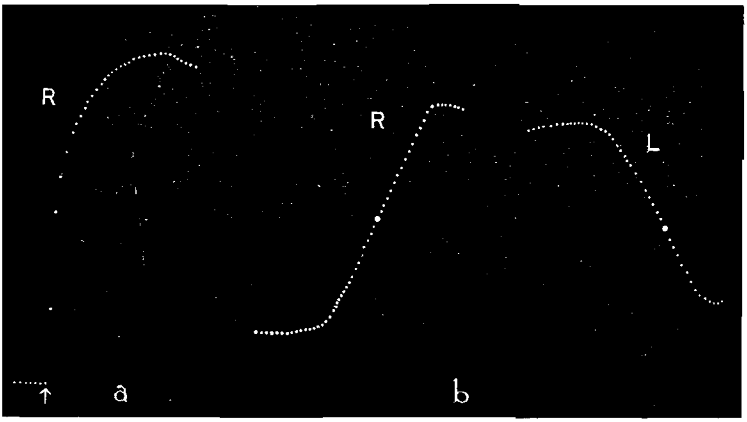

Fig. 285 Torsional response due to transmitted excitation in *Helianthus*; (*a*), right-handed torsion due to electric stimulation of the nerve-ending in the right half of the lamina; (*b*), right-handed and left-handed torsions due to transmitted excitations caused by alternate illumination of the right and left half of the lamina. Light was stopped after the thick dot.

The following experiments will show that photic stimulus induces a reaction which is similar to that of electric stimulus:—

Stimulus of Light.—Sunlight was thrown first on the right half and then on the left half of the lamina. The transmitted excitations induced corresponding torsional responses (Fig. 285*b*). A balance was produced when the two halves of the lamina

Experiment 297

excitatory impulse on the left flank (the electric indication of which is galvanometric negativity) would oppose and thus neutralise the particular directive movement. Hence for ensuring a steady directive motion, in response to stimulation of the right half of the lamina, all excitatory impulse to the left flank of the petiole should be inhibited. Further, the directive movement induced by the stimulation of the right half of the lamina would be actively helped if the motor reaction of the left flank of the petiole be of an opposite character to that in the right flank. We found that the right-handed torsion is induced by a differential contraction of the right flank and for concordant effect the reaction of the left flank should be opposite, *i.e.*, a differential expansion. The nervous impulse which actuates the right effector when the right half of the lamina is alone stimulated, is indicated by *galvanometric negativity*; for concordant movement under the above condition, the impulse which actuates the left effector should be of oppesite sign, *i.e.*, of *galvanometric positivity*.

I carried out two sets of experiments on the above lines with an identical leaf *Helianthus*. For electric detection of transmitted excitatory impulse, along the right nerve, one of the contacts was made with that nerve, the second being with a distant indifferent point. The nerve endings on the right half of the lamina were electrically stimulated and the transmitted impulse along the nerve gave the usual excitatory reaction of galvanometric negativity. A second pair of contacts were made for detection of transmitted impulse in the nerve of the left flank of the petiole. Stimulation of the nerve termination of the right half of the lamina gave in the left nerve a reaction of *galvanometric positivity*. In practice stimulus was always applied to the right half of the lamina, and galvanometric connections were made alternately with the

Experiment 29

right and left nerve. The results were always the same and showed that excitation of a nerve gave rise to an opposite reaction in the contiguous nerve. There is no doubt that these two nervous impulses of opposite signs reaching the antagonistic tissues of the two flanks of the motor organ must be of importance in the co-ordination of the resulting movements.

SUMMARY.

In certain leaves the heliotropic adjustment is brought about by transmission of nervous impulse to the motor organ. A continuity is shown to exist in the response of "sensitive" and ordinary plants. *Mimosa pudica* is taken as a type of the former, and *Helianthus annuus* of the latter. Mechanical response is brought about in both by the differential excitability of the upper and lower halves of the motile organ. The lower half in both is the more excitable. Local stimulation of the abaxial half of the organ induces an erectile movement, that of adaxial half a more rapid downward movement.

Heliotropic curvature of a stem is due to the joint effects of contractile reaction of the proximal and expansion of the distal side.

The daily periodic movements of the leaves of *Mimosa* and of *Helianthus* are essentially similar. The diurnal movement is brought about by the variation of the geotropic action with changing temperature, and by the varying intensity of light. The leaves erect themselves during the fall of temperature from thermal noon at 2 P.M. to about 5-30 P.M. Owing to the rapid diminution of light in the evening the leaves undergo an abrupt fall which continues till 9 P.M. After this the leaves erect themselves, till the maximum erection is attained at 6 A.M., which is the thermal dawn. The movement of the leaves is then reversed and there is a continuous fall till the thermal noon at 2 P.M.

A very important motile reaction in the adjustment of leaves is the torsional response to lateral stimulus. The following is the law which determines the directive movement: An anisotropic organ when laterally stimulated by any stimulus undergoes torsion by which the less excitable side is made to face the stimulus. In a dorsi-ventral organ the upper side is, generally speaking, the less excitable side, and the response of such an organ to lateral stimulus may be expressed in the following simple terms. Lateral stimulation of a dorsi-ventral organ induces a torsion which is right-handed, when the right flank is stimulated. Left-handed torsion is induced by the stimulation of the left flank.

The effects described above take place by direct stimulation of light. They also take place under transmitted excitation.

The pulvinus of Mimosa may be regarded as consisting of four effectors; the response of the right effector is by a right-handed torsion, and of the left effector by a left-handed torsion. The upper and lower effectors respond by rectilinear up-and-down movements.

Excitation at the receptive region is propagated along a definite conducting channel, which is traced from the receptive area in the lamina to the corresponding effector in the motor region.

In a petiole of *Mimosa,* provided with sub-petioles carrying rows of leaflets, stimulation of the right row of leaflets by light gives rise to an excitatory impulse which reaches the right effector and induces a right-handed torsion. Stimulation of the left row of leaflets induces the opposite, or left-handed torsion. The illumination of the second sub-petiole induces an up-movement; that of the third sub-petiole a down-movement. The leaf is thus adjusted in space by the co-ordinated action of four reflexes, equilibrium being attained when the leaf-surfaces is perpendicular to the incident light.

The dia-heliotropic attitude of leaves is thus brought about by distinct nervous impulses initiated at the perceptive region actuating the different effectors.

Results similar to the above were also obtained with *Helianthus*.

For the movement of the eye the contraction of the muscle opposing the movement has to be inhibited. In the torsional movement of the leaf, it is found that the stimulation of one nerve causes in a contiguous nerve an opposite reaction. The nervous impulses of opposite signs reaching different flanks of the motile organ is thus of importance in the co-ordination of the resulting movement.

LXIII.—THE ELECTRIC RESPONSE OF *MIMOSA PUDICA*.

BY SIR J. C. BOSE,
Assisted by
SURENDRA CHANDRA DAS, M.A.

All plants and their various organs have been shown to exhibit an electric response under stimulation, the stimulated tissue being rendered galvanometrically negative. In *Mimosa* we have a conspicuous response by mechanical movement. The effect of changes of environment on the plant may thus be detected by induced variations in the mechanical response, which may be automatically recorded by the Resonant and Oscillating Recorders. A study of the electric response of *Mimosa* is of interest, because it enables us to find out whether the two independent methods of record correctly indicate the fundamental physiological change which is induced in the organism by external variations.

The pulvinus of *Mimosa* is a dorsi-ventral organ, the excitability of the lower half being very much greater than that of the upper. Hence an identical stimulus induces a relatively greater excitatory reaction at the lower side. It has been shown, that the induced change of galvanometric negativity depends on the intensity of excitation; hence, on making electric connections with the upper and lower sides of the pulvinus, a diffuse stimulation would be expected to exhibit a resulting galvanometric negativity of the lower half of the organ. Having explained the general principle, we have next to devise practical methods for obtaining the electric response.

THE EXPERIMENTAL METHOD.

The electric connections with the upper and lower halves are made with gold or platinum wires. In order to secure good contact, two separate pieces of cork are held together by four short lengths of elastic. The connecting gold wires, above and below, have their terminal ends flattened, so as not to cause any wound to the pulvinus; a drop of kaolin paste in normal saline makes a perfect electric contact; a small quantity of glycerin is added to the saline solution to prevent rapid drying of the kaolin paste. The slightly stretched elastic keeps the pressure of contact constant. The small pieces of cork are light and, therefore, do not exert any appreciable weight on

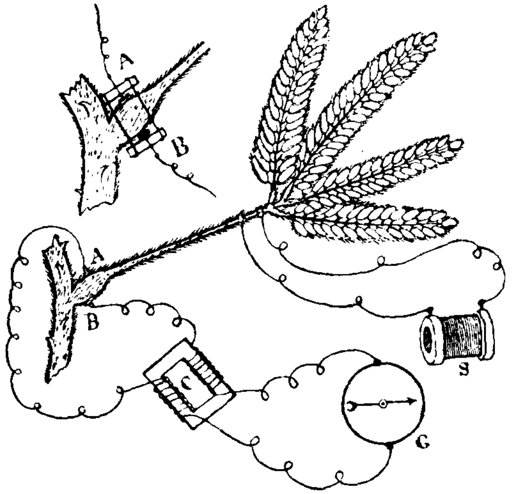

Fig. 286 Method for obtaining electric response of the pulvinus of *Mimosa*. Stimulus of electric shock obtained from the secondary S, of an induction coils. The choking coil C, prevents leakage of shock-current into the galvanometer *circuit*. The upper illustration shows the electric connections with the two halves of the pulvinus.

the leaf (Fig. 286). The complicated method of electrolytic contact by means of non-polarisable electrodes is not only unnecessary, but often harmful; for unless great precautions are taken the zinc sulphate solution may leak and come in contact with the plant abolishing its excitability. The amalgamated zinc rods, moreover, are not absolutely iso-electric. These drawbacks are not present in the platinum or gold contacts, for pure specimens of these metals could be made iso-electric after annealing. The direct method of contact reduces the resistance to a minimum. The object of non-polarisable contacts is to diminish the counter-electromotive force due to the passage of the current. This counter E. M. F. depends on the strength of the current; since the responsive current of the plant is very feeble, it does not in practice give rise to any appreciable polarisation.

The problem which offered the greatest difficulty in this investigation is in securing uniform stimulations in succession, or in increasing the stimulus in a perfectly graduated manner. The only means by which this can be secured is by tetanising electric shocks of definite intensity and duration. The intensity may be continuously increased by pushing the secondary coil nearer the primary. The duration of application may be kept the same in successive experiments by completing the primary circuit of the coil (provided with the usual vibrating hammer) for a definite length of time by means of a metronome. The two terminals of the secondary coil are applied to the petiole at certain distance from the pulvinus, and the electric responses to successive transmitted excitations are recorded on a moving photographic plate by the excursion of the spot of light reflected from the galvanometer.

The oscillatory induction shock introduces, however, a complication by the leakage of the shock-current into the galvanometer. This difficulty has, however, been completely removed by the interposition of a magnetic choking coil, which prevents the rapidly alternating current to enter the galvanometer circuit.

An important condition for obtaining the normal electric response is the maintenance of the plant in a favourable tonic condition. It is thus necessary to expose the plant to diffuse light of the sky. As the photographic records require a dark room, the leading wires from the plant are carried to the galvanometer in the photographic room.

Electric response to Transmitted Excitation.—Electric stimulus of uniform intensity is applied at intervals of 10 minutes or so, and the resulting response recorded. The photographic plate was moving at a slow rate, hence the record of response and recovery are almost superposed; it will be noted that the amplitude of successive responses under uniform stimulus is the same (Fig. 287). The response is by galvanometric negativity of the more excitable lower half of the pulvinus. This corresponds with the responsive *fall* of the leaf by the relatively greater contraction of the lower half.

Experiment 299

EFFECT OF EXCESSIVE ABSORPTION OF WATER BY THE PULVINUS.

A muscle immersed in distilled water loses its power of contraction. Application of water to the pulvinus also renders it irresponsive. This is seen on rainy days, when the sensibility of the pulvinus is found to be practically abolished. A more definite result was obtained in the following experiments. After obtaining the normal mechanical response, a drop of water was applied to the pulvinus, and the resulting absorption of water in excess caused a complete abolition of motile excitability. In connection with this it should be remembered that excitatory contraction is brought about by the expulsion of the sap from the pulvinus; its over-inflated condition may, therefore, oppose the excitatory contraction with resulting abolition of the mechanical response.

A question now arises, whether this absence of mechanical response is due to the abolition of irritability, or merely to physical restraint imposed by the over-turgid tissue. This subject may be experimentally tested by means of electric response, which is independent of mechanical movement.

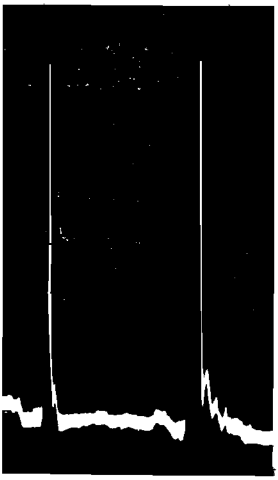

FIG. 287

FIG. 288

Fig. 287 Uniform response of galvanometric negativity under uniform stimulations of moderate intensity (*Mimosa*).

Fig. 288 Positive electric response in *Mimosa*, under feeble stimulus.

For, the leaf of *Mimosa* may be held fixed without interfering with its electric response. This fact explains the occurrence of electric response in ordinary plants, in which there is no conspicuous movement in response to stimulus.

The pulvinus of *Mimosa* was made mechanically irresponsive by application of water. In this condition, mechanical or electrical stimulation did not cause the normal fall of the leaf. An electric record was next obtained, and it was found that the

Experiment 300

mechanically insensitive leaf gave the normal electric response of galvanometeric negativity, proving that the tissue was still irritable though unable to manifest it outwardly by mechanical movement.

EFFECT OF FEEBLE STIMULUS.

The transmitted excitation due to stimulus of moderate intensity causes, as we have seen, a response of galvanometric negativity of the more excitable lower half of the pulvinus. *Experiment 301* The intensity of stimulus in the following experiments is reduced by removing the secondary coil away from the primary. *Feeble stimulus is now found to induce a response which is of opposite sign to that of the normal, namely by galvanometric positivity, indicative of expansion instead of normal contraction* (Fig. 288). The opposite responses observed under feeble and strong stimulus appears to be of general occurrence. We have already found that while strong stimulus induces a contraction and retardation of growth, a feeble stimulus induces the opposite effect of expansion and acceleration. (see Fig. 278). Similar effects are also found in geotropic response where the upper side, subjected to moderate stimulus, exhibits contraction, and the lower side, under enfeebled stimulation, shows expansion (p. 629).

If the stimulus be gradually increased, the response changes from positive to normal negative, sometimes through a diphasic response, positive followed by negative. The particular intensity above which the response is transformed from positive to negative, may be termed the *critical intensity*. This critical value is found to depend on the tonic condition of the tissue. In a highly excitable specimen, the critical point is low, and the normal negative response takes place even under moderately feeble stimulus. The critical point is, however, raised when the tissue falls nto a sub-tonic condition; the positive response under eeble stimulus may then be obtained without difficulty.

Experiment 302

Positive response of Sub-tonic tissues.—The plant is kept in diffuse light, and the particular intensity of stimulus which invariably gives negative response is determined. A cover is next placed over he plant so as to maintain it in darkness for about an hour, hus inducing a condition of sub-tonicity. Application of he stimulus which previously induced a negative response s now found to bring about a positive response. The plant s next exposed to light, for improving its tonic condition. The response is now found once more to be a normal negative.

We found the occurrence of a similar positive mechanical response in *Mimosa* in a sub-tonic condition (Vol. I, Experiment 50); the characteristic effects of stimulus on growth are also similar, that is to say, while in the normal condition of the plant stimulus causes a retardation of growth, in a sub-tonic condition, it gives rise to an enhancement of growth (Experiment 88).

CONDUCTING PATH FASHIONED BY STIMULUS.

Experiment 303

It has been shown that the phloem of the fibro-vascular bundle functions as the nerve by which the excitation is transmitted. In young leaves the phloem is anatomically present, but its power of physiological conduction has not yet been developed. It is of extreme interest to follow the manner in which the conducting power in young tissues is functionally developed by the action of stimulus. We take a young leaf of *Mimosa*, and apply stimulus of moderate intensity to the petiole at some distance from the responding pulvinus, the distance of the secondary coil from the primary being noted at the same time. The tissue is found to be non-conducting to the stimulus, as indicated by the absence of normal response of galvanometric negativity. The stimulus is next increased by bringing the secondary nearer the primary coil; the block to conduction is now found to be suddenly removed, and the conducted excitation gives rise to the normal negative response. We next remove the secondary away from the primary to the first ineffective position. But the formerly ineffective stimulus is now found to be effectively transmitted, the response being the normal negative. Stimulus is thus found to fashion its own conducting path.

SUMMARY.

The normal electric response of the pulvinus of *Mimosa* to transmitted excitation is by an induced galvanometric negativity of the more excitable lower half of the pulvinus.

Excessive absorption of water abolishes the mechanical response of the pulvinus. The electric response is, however, found to persist, proving that the tissue is still irritable though unable to manifest it outwardly by mechanical movement.

Feeble stimulus gives rise to a response which is of opposite sign to that of strong stimulus.

The critical intensity of stimulus for normal negative response depends on the tonic condition; it is low when the tissue is highly excitable, and high when the tonic condition falls below par.

In young plants, the nervous elements are present though not functionally developed for conduction of excitation. In such a condition, stimulus is found to fashion its own conducting path.

LXIV.—SIMULTANEOUS DETERMINATION OF VELOCITY OF EXCITATION BY MECHANICAL AND ELECTRIC METHODS.

By Sir J. C. Bose,

Assisted by

Basiswar Sen, B.Sc.

It has been shown in the last chapter that the more excitable lower half of the pulvinus exhibits, under transmitted excitation, a galvanometric negativity in reference to the upper side. This differential effect is parallel to the greater contraction of the lower side by which the leaf undergoes the normal fall.

The excitatory impulse generated at a distance has been shown to be of nervous character. A certain time elapses between the application of stimulus and the response given by the pulvinus. The period of transmission, and our knowledge of the intervening distance between the point of application of stimulus and the responding pulvinus, enable us to determine the velocity of transmission of excitation. Allowance must be made for the physiological inertia of the pulvinus, the latent period of which has been found to be about a tenth of a second.

DETERMINATION OF VELOCITY BY THE MECHANICAL METHOD.

The determination of the velocity of transmission by mechanical response is made by the Resonant Recorder, fully described elsewhere.* The writer W, made of fine

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* Irritability of Plants, p. 140.

steel wire with a bent tip, is at right angles to the lever and is maintained by electromagnetic means in a state of to-and-fro vibration, say ten times in a second. The writing index is previously tuned so as to vibrate at this rate. The steel wire is supported at the centre of the pole of an electromagnet which is periodically excited by a current interrupted by a reed; when the reed is exactly tuned to vibrate ten times in a second, the writer is thrown into sympathetic vibration. The successive dots of records thus indicate intervals of a tenth of a second (Fig. 289). Employing

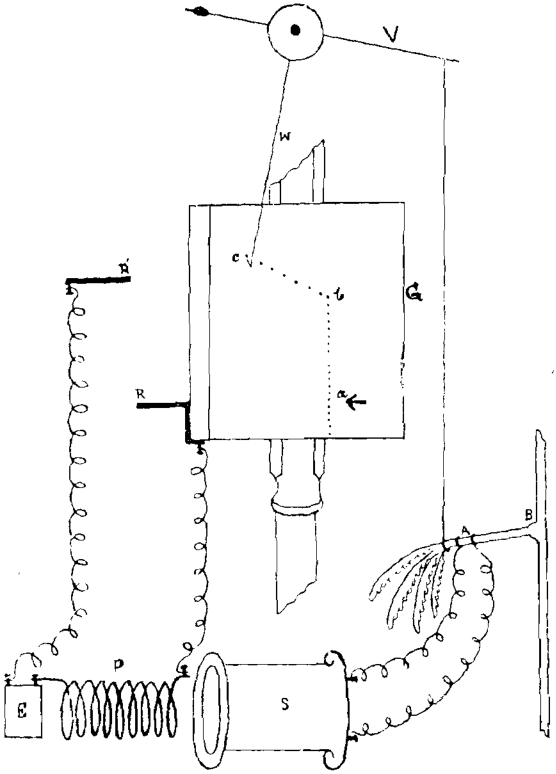

FIG. 289 Resonant Recorder for determination of velocity of transmission of excitation. The falling plate during descent made electric contact of R with R' for induction shock by the secondary coil S.

this method, the velocity of transmission in the petiole of *Mimosa* was found to be about 30 mm. per second in an excitable specimen of the plant. The velocity depends on the physiological condition; under depressed condition in winter, the velocity is found lowered to about 4 mm. per second.

We have hitherto employed the Resonant Recorder for the mechanical, and the galvanometer, for the electric response of *Mimosa*. The problem that now confronts us is the determination of the mutual relation of these two different modes of response, whether they indicate the same fundamental physiological reaction which underlies excitation. For this, it is necessary to devise some means of obtaining simultaneous records of the two responses given by an identical specimen. We may carry out this idea further and determine the velocity by the two independent methods of mechanical, and electrical responses. The identity of the two results thus obtained will afford conclusive proof that the mechanical and electric responses are but different expressions of the excitatory change induced by stimulus. In connection with this it should be borne in mind that the inertia of the mechanical and the electric recorders are not the same; but the difference may be so slight as to be negligible in practice. The electric response is, in general, obtained by a galvanometer, with its high sensitivity, a moderately delicate apparatus giving a deflection of 1 mm. for a current of 10^{-10} ampere. This great sensitiveness is, to a certain extent, nullified by the high electrical resistance of the plant, on account of which the current in the circuit is greatly diminished. There is another drawback in the use of the galvanometer in certain experiments on the absolute determination of the electromotive variation induced by stimulus, for it also gives rise to a diminution of electrical resistance of the tissue. The increased deflection may therefore, be not solely due to an increase in the induced electromotive force. For certain special investigation it is, therefore, of advantage to employ an electrometer, instead of a galvanometer. In the electrometer, the circuit is open, and its indications are, therefore, independent of resistance.

THE ELECTROMETRIC METHOD.

It does not appear that the Quadrant Electrometer has been used for physiological work. The prevailing impression is (1) that it is not sufficiently sensitive, (2) that it is difficult to keep the needle charged for days to the same potential so that its sensitiveness and zero position remain constant, and finally, (3) there is a misgiving that its deflections are affected by external disturbances.

As regards the sensitiveness, it has been possible to raise it sufficiently high by employing a long suspension of fine quartz thread rendered conducting by the usual method. The sensitiveness may, with care, be thus raised so as to give a deflection of 1 mm. for a thousandth of a volt.

The dry cells are unsatisfactory for charging the needle; Cu-Zn elements in water are, on the other hand, fully satisfactory. The cells are made by scooping out a series of large sized holes in a thick block of solid paraffin. A sufficient number of Zn-Cu elements are placed in series so as to give a terminal difference of potential of 110 volts. The zero position of the reflected spot of light is then found to remain constant for many days in succession.

The insulated pair of quadrants is suitably connected with the lower half of the pulvinus. The pot containing the plant is connected with the second pair of quadrants, which is earthed.

SIMULTANEOUS MECHANICAL AND ELECTRIC RECORDS.

For obtaining simultaneous records, the recording glass plate for mechanical, and the photographic plate for the electric record, are allowed to fall at the same rate by means of a clockwork. The spot of light reflected from the mirror of the electrometer falls on the photographic plate and records the electric response. We have next to employ some device for obtaining the time-relations of the two curves.

As regards the mechanical record given by the Resonant Recorder, the successive dots represent intervals of tenths of a second. Hence the curve of response is its own chronogram. For obtaining the time-relations of the electric curve, the reed which actuates the Resonant Recorder, is interposed in the path of light reflected from the mirror of the electrometer. The reed has a piece of aluminium,

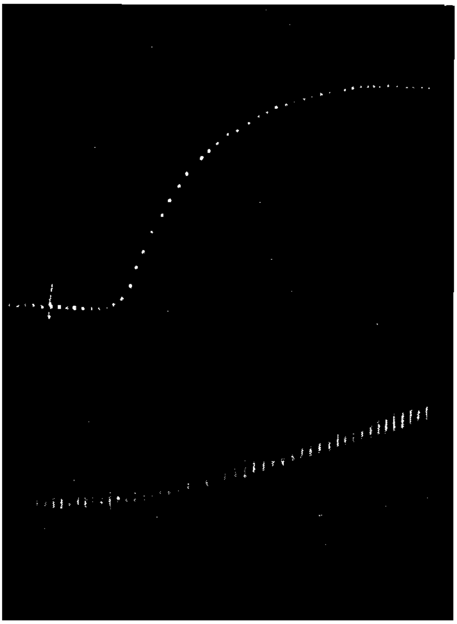

Fig. 290 Simultaneous records for velocity of transmission. The upper is the mechanical, and the lower, the electric record. The time-interval for initiation of response is found in both cases to be 0.7 second.

which interrupts the light ten times in a second. The photographic record thus consists of lines of light alternating with darkness; the successive dots in the mechanical record thus correspond with these lines of light.

After making the arrangements described above the two plates are allowed to fall at the same rate. Stimulus of electric shock was now applied to the petiole at a distance of 20 mm. from the pulvinus. There was no immediate response either mechanical or electrical; but after an interval of 7 dots, the leaf began to fall, causing a mechanical record upwards. The interval between the application of stimulus and the initiation of response is thus 0.7 seconds. Making an allowance of 0.1 second for the latent period of the pulvinus, the time required for transmission of excitation through 20 mm. is thus 0.6 seconds. The velocity is thus 33 mm. per second.

Experiment 304

The electric record gave an identical result; the response was initiated at the 7th strip of light, that is to say at the same time as the mechanical response (Fig. 290).

It is thus seen that the transmitted excitation, which induces a fall of the leaf by relatively greater contraction of the more excitable half of the pulvinus, also induces a simultaneous electromotive change of galvanometric negativity of the lower half of the organ. The velocity of transmission obtained by the two methods are thus practically the same.

SUMMARY.

A Quadrant Electrometer may be employed for obtaining electric response of plants. The advantage of this method lies in the fact that the observed response is due to ıduced electromotive variation, unaffected by the resistance of the circuit.

A simultaneous determination of the mechanical and electric responses is made by the employment of the Resonant and Electric Recorders connected with the same leaf. The records thus obtained show, that the mechanical response of the leaf has an electric concomitant in a negative electromotive variation.

LXV.—THE MULTIPLE RESPONSE IN *MIMOSA*.

By Sir J. C. Bose,

Assisted by

Surendra Chandra Das, M.A.

The character of different modes of response—by electric variation, by the movement of the leaf, and by variation of the rate of growth—has been shown to be determined in a definite way by the intensity of stimulus. Under sub-minimal stimulus the response is positive,—a positive electric variation, an expansion and erectile movement of the leaf, and an acceleration of the rate of growth. Stimulus of moderate intensity induces, on the other hand, a negative electric variation, a contraction and fall of the leaf, and a retardation of the rate of growth. The critical intensity of stimulus for transformation of the positive into negative response is modified by the tonic condition of the tissue; under sub-tonic condition the critical point is high, so that even a moderate intensity of stimulus induces a positive response. The tonicity of the tissue is, however, improved by the action of the stimulus, and in consequence of previous stimulation the positive response is transformed into the normal negative.

Having observed the effects of sub-minimal and of moderate stimulus, we shall next study the effect of intense stimulation. For this purpose we may take a leaf of *Biophytum* or of *Averrhoa* in which there are numerous pairs of sensitive leaflets. We attach one of these leaflets to an Oscillating Recorder, and observe the response induced by stimulus applied at the petiole at some distance from the leaflet. The effects of feeble and moderate stimulus are similar to what we have already observed, namely, a positive and negative response respectively. We next apply a stronger stimulus and find that the response is not single but multiple (see Fig. 295). For obtaining records of these multiple responses it is necessary to prevent the complete closure of the leaflets by which further response is rendered impossible. This is secured by applying a light counterpoise in the second arm of the lever, which, exerting a tension, opposes the complete closure of the leaflet.

These multiple responses are found to occur under any form of strong stimulation, the stimulus being as diverse as induction shocks, strong light, thermal shock, and chemical excitation.

MULTIPLE ELECTRIC RESPONSE IN MIMOSA.

Having seen that a recurrent series of responses occur under a single strong stimulus in multiply responding plants like *Biophytum* and *Averrhoa*, we shall next try to find out whether similar responses may be obtained from *Mimosa* which, generally speaking, gives but a single response to a single stimulus. For this we shall first employ the electric method of investigation.

Electric connections are made in the usual manner with the upper and lower halves of the pulvinus, and the galvanometric response recorded on the photographic plate. The petiole, at a distance of 3 cm. from the pulvinus, was strongly stimulated by application of a hot wire. This gave rise to a very large response of galvanometric negativity, so large as to take the spot of light away from the plate; after the spot of light came back to the plate during recovery, there occurred

Experiment 305

a second response followed by a recurrent series of other responses. In order to keep the spot of light within the plate, a less excitable specimen was next employed, and strong stimulus applied as before. This is seen to have given rise to a series of six recurrent responses. (Fig. 291).

MULTIPLE MECHANICAL RESPONSE.

Though the multiple electric response may be obtained with *Mimosa* without much difficulty, yet I failed for a long time to obtain corresponding mechanical responses which were multiple. This failure I have since been able to trace to the following; (1) the heavy leaf is unable to follow the relatively quick recurrent responses, (2) strong stimulus gives rise to a fall which is maximum and in this state of complete fall, further responses cannot be detected, (3) the subsequent responses are relatively small compared to the

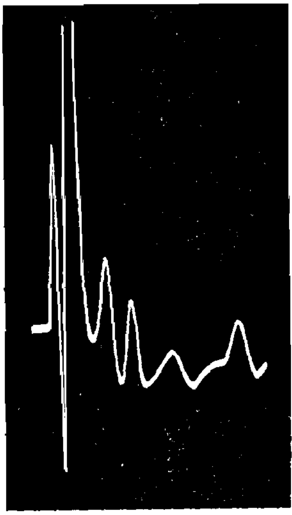

FIG. 291

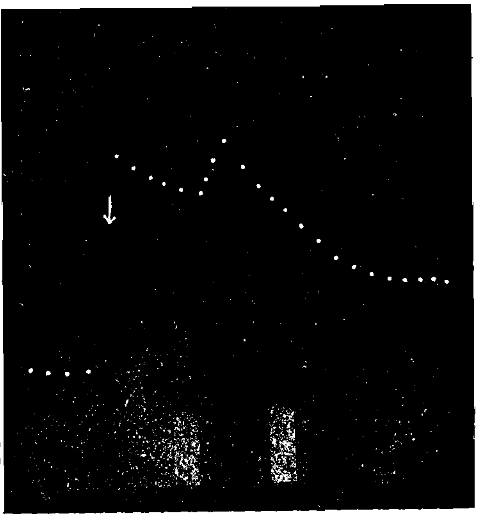

FIG. 292

Fig. 291 Multiple electric responses under a single strong stimulus (*Mimosa*).

Fig. 292 Multiple mechanical response in *Mimosa* under strong stimulus.

amplitude of the first response; hence a higher magnification is necessary. A high magnification, however, makes the first record go completely out of the plate. The practical difficulties in obtaining multiple mechanical responses are thus seen to be very numerous. They have been to a certain extent removed by the following devices.

The weight of the leaf is reduced to a minimum by cutting off the sub-petioles, leaving a short length of the petiole for attachment to the recording lever. The shock of operation makes the plant temporarily insensitive; but after a period of rest of one or two hours the excitability is found to be restored.

For preventing the complete fall of the leaf a suitable counterpoise is placed on the opposite arm of the lever to exert a tension. Finally a moderate magnification is employed so as to keep the record within the smoked glass plate.

Experiment 306

After taking these precautions record was taken of the effect of strong stimulus caused by application of a heated wire to the stem below the leaf. This gave rise first, to a large response of the fall of the leaf, followed by a partial recovery; there then occurred a second response (Fig. 292); in other cases there were three recurrent responses of the *Mimosa* leaf under a single strong stimulus.

A continuity is thus established between the multiple responding plants like *Biophytum* and ordinarily responding plant like, *Mimosa*. Feeble stimulus induces in these plants a positive response and a moderate stimulus causes a single negative response. Strong stimulus, however, gives rise in all these cases, to a multiple series of responses. We shall, in the next chapter, find that this continuity is extended to the autonomous response which is caused by some internal stimulation.

SUMMARY.

The response of plants exhibits three different characteristics, depending on the intensity of stimulus applied. Under sub-minimal stimulus, both the mechanical and the electric responses are single and positive; under moderate stimulus, it is negative. But under strong intensity, a single stimulus gives rise to a recurrent series of responses. This is true of all plants, ordinary and sensitive.

Multiple response under strong stimulus is typically exemplified by the leaflets of *Biophytum* and *Averrhoa*. In these, strong stimulus of all kinds,—electric, thermal, photic, and chemical—gives rise to multiple responses.

In the ordinarily responding plant like *Mimosa*, which gives a single response under a single moderate stimulus, multiple electric and mechanical responses occur under the action of a single strong stimulus. A continuity of response is thus established in all types of plants.

LXVI.—THE EFFECT OF CARBON DIOXIDE ON THE MECHANICAL AND ELECTRIC PULSATIONS OF *DESMODIUM GYRANS*.

BY SIR J. C. BOSE,

Assisted by
BASISWAR SEN, B.SC.

We found in a previous chapter that the autonomous activity of growth is arrested by the action of carbonic acid, and that a renewal of the activity takes place on substitution of fresh air. The pulsating movements of the lateral leaflets of *Desmodium gyrans* is a striking example of autonomous or internal activity, and we shall in the present chapter study the effect of carbon dioxide on the 'spontaneous' movements of the leaflet.

It may be stated here that strictly speaking, there is no such thing as spontaneous movement. The energy which expresses itself in pulsatory movements is derived by the plant either directly from the immediate external sources, or from excess of such energy already accumulated and held latent in the tissue. When the storage is exhausted, as when the plant is kept in a dark room, the rhythmic pulsations are found to come to a stop. The pulsation of the leaflet can, however, be renewed by the application of fresh stimulus, the persistence of the pulsatory movements being dependent on the quantity of incident stimulus. The responsive characteristic of the *Desmodium* leaflet in a state of standstill is similar to that of the leaflet of

Biophytum. It gives rise to a single response to a single moderate stimulus, and to multiple responses to a strong stimulus. A continuity is thus seen to exist between the multiple responding leaflet of *Biophytum*, and the automatically pulsating leaflet of *Desmodium*.

EFFECT OF CARBONIC ACID GAS ON MECHANICAL PULSATION.

Experiment 307

A cut stem with the petiole bearing the lateral leaflets is suitably mounted in a test-tube filled with water; the shock of operation passes away in the course of about an hour when the pulsations become renewed. One of the leaflets is now attached to an Oscillating Recorder for obtaining tracings of its normal pulsations. A stream of carbonic acid gas is next passed into the plant chamber; this is seen to induce a complete arrest of the pulsations (Fig. 293). Fresh air is next substituted in the plant-chamber; this renews the arrested pulsation. In fact, the pulsations are now found to be more vigorous than at the beginning. It seems as if the

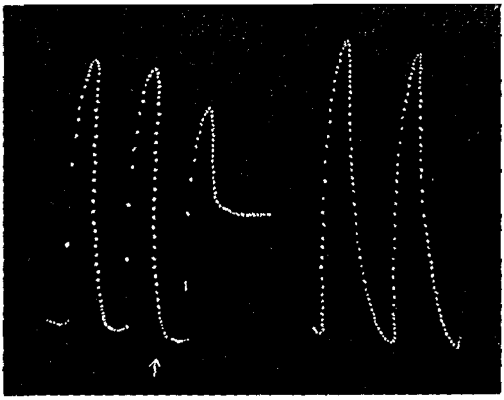

Fig. 293 Effect of CO_2 on autonomous mechanical pulsation of *Desmodium gyrans*.

Note arrest under CO_2 applied at arrow and subsequent revival on introduction of fresh air.

energy of pulsation, hitherto held in restraint, now found an enhanced expression.

EFFECT OF CARBONIC ACID GAS ON ELECTRIC PULSATIONS.

Each pulsation of the *Desmodium* leaflet consists of a rapid down-movement followed by a slow up-movement. The maximum rate of down-movement is about 1.5 mm. per second, while the corresponding rate of up-movement is only 0.5 mm. per second. It would appear that the down- and up-movements are brought about principally by the alternate contractions of the lower and upper sides of the pulvinule. Thus the lower half contracts rapidly, followed by a recovery; during this recovery the upper half contracts. The pulsations are thus due to alternate variations of turgor on the opposite sides of the organ. A parallel instance is found in circumnutation of certain growing organs, in which alternations of growth at the two opposite sides of the organ give rise to lateral oscillations.

Experiment 368

I have succeeded in obtaining records of the electric pulsations of the *Desmodium* leaflets in the following manner. We make two electric contacts, one with the more effective lower half of the pulvinule, and the other, with a distant indifferent point. The electric pulsations, to be presently described, take place independently of the mechanical movement, hence the leaflet may be held fixed without interfering with the electric pulsations. During the phase of contraction of the lower half, that half becomes galvanometrically negative, and we obtain a large electric pulsation. This pulsation is often attended by a small subsidiary pulsation, probably due to comparatively feeble excitation of the upper half of the pulvinule.

The records given in Figure 294, exhibit uniform electric pulsations. On introduction of carbonic acid gas into the plant-chamber, the pulsations declined rapidly and ultimately came to a stop, as in the case of the mechanical pulsation. Carbonic acid gas was next removed by blowing in fresh air, when the electric pulsations were renewed even with additional vigour.

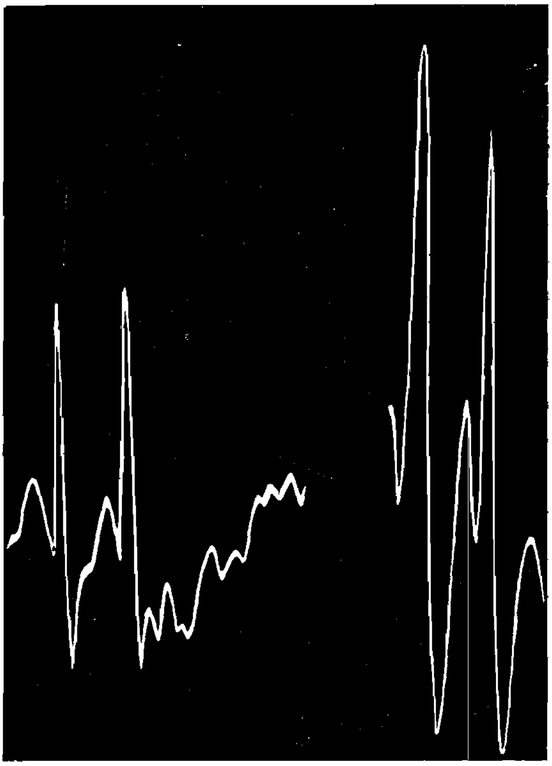

Fig. 294 Effect of CO_2 on electric pulsations of *Desmodium gyrans.* Note the two normal electric pulsation and subsequent arrest under CO_2. Last record shows enhanced pulsation on renewal of fresh air.

SUMMARY.

There is a continuity of response in multiple responding plant like *Biophytum* and the automatically responding plant like *Desmodium*. On depletion of absorbed energy, *Desmodium* leaflet comes to a state of standstill. It gives then, like *Biophytum* leaflet, a single response to a single moderate stimulus, and multiple responses to a strong stimulus.

The mechanical pulsation of *Desmodium* leaflet is arrested by carbonic acid gas. Introduction of fresh air renews the pulsations.

The leaflet of *Desmodium* exhibits electric pulsations in response to internal activity which maintains the mechanical pulsation. The electric pulsation is, however, independent of mechanical movement; it persists even after the leaflet is fixed so as to prevent its mechanical pulsation.

The effect of carbonic acid gas on electric pulsation is similar to that on mechanical pulsation. It arrests the pulsations during the continued action of the gas. Substitution of fresh air is followed by the renewal of electric pulsation.

LXVII.—THE TRANSMISSION OF DEATH EXCITATION.

By Sir J. C. Bose,

Assisted by

Basiswar Sen, B.Sc.

Experiments have been described in a previous chapter which showed that plants exhibit a death-spasm at a critical temperature, which is at or about 60°C. Considerations were adduced to prove that this was not a phenomenon of coagulation, but an excitatory reaction which occurs at the moment of death.

This will find an independent support, if we succeed in demonstrating the occurrence of an excitatory impulse at a point distant from the indicator. Thus, on the exposure of a portion of the stem of *Mimosa* to rising temperature, it may be expected that an intense excitatory impulse would be initiated at the critical temperature and transmitted to the distant leaves causing their fall. The fact of this transmitted excitation would undoubtedly afford crucial proof of the excitatory reaction at death. The experiments described below were carried out not with *Mimosa* alone, but with other sensitive plants such as *Biophytum* and *Averrhoa*.

EXPERIMENTAL ARRANGEMENT.

It may be stated that the leaves and leaflets of cut specimens of *Mimosa*, of *Averrhoa* and of *Biophytum* can be made to exhibit all the irritable reactions of the intact plant. After section of the stem or the petiole the shock of operation causes a temporary abolition of excitability; but after a period of rest, the sensibility is found restored. The stem or the petiole is then so supported that its cut end is immersed in a water-bath to a depth of 2 cm. The bath consists of a thin-walled water vessel with arrangements for electric heating by means of a coil of wire. It is easy to regulate the rise of temperature, to a standard rate of 1°C. per minute, by means of the rheostat included in the circuit.

CRITICAL TEMPERATURE FOR TRANSMISSION OF DEATH-EXCITATION IN MIMOSA.

Transmitted excitation at death-point in cut specimens.—In carrying out the experiment in the manner described above, it was found that the steady rise of temperature in the bath did not at first produce any effect on the distant leaves; but on the attainment of a certain critical temperature, an intense excitatory impulse was generated in the immersed portion of the stem, which, travelling upwards, caused an abrupt fall of the leaves in a serial succession. This could only be due to the *transmitted* effect of excitation occurring at the *local* death of the immersed portion of the stem; for the leaves re-erected themselves, and recovered their normal excitability after a period of about 20 minutes. That the excitation was due to the death of the immersed portion was proved by repeating the experiment. This time there was total absence of any responsive fall of the leaves, showing that the immersed portion had permanently lost its power of initiating any further excitatory impulse on account of its death. But the result was quite different, when the experiment was repeated for the third time after

Experiment 309

lowering the same stem through further 2 cm. in the heating bath. A new excitatory impulse was found to be initiated at the critical temperature by the death of the freshly immersed portion of the stem, the impulse causing the usual fall of the leaves.

The experiment, just described, demonstrates conclusively the occurrence of an intense excitatory reaction in the tissue at the moment of its death.

It was shown in a previous experiment that the death-point of the pulvinus is at or near 60°C. An interesting question now arises: Is the death-point of an ordinary non-motile tissue of the stem the same as that of the contractile tissue of the pulvinus, or is it different? In carrying out experiments with fresh preparations of cut specimens, the temperatures at which transmitted death-excitations occurred were found in four typical cases to be at 64°C., 64°C., 65°C., and 65°C. respectively. The distance of the nearest leaf was, in all cases, 20 mm. from the immersed portion of the stem. A slight error is introduced in the determination of the death-point from the fall of the leaf, since there is a short time-interval between the initiation of excitation in the immersed stem and its detection by the leaf at a distance of 20 mm. Taking the average value of the velocity of transmission in the stem under normal conditions to be about 5 mm. per second, the fall should occur 4 seconds after the initiation of the excitation. The rate of rise of temperature in the bath is 1°C. per 60 seconds; hence the error introduced in the determination of the death-point by the adoption of the indirect method of excitation would amount to a fraction of a degree, which may be regarded as quite negligible.

The velocity of transmission in intact specimens has been taken as of the order of 5 mm. per second. This may not, however, be the actual value in a cut specimen; for I find that the injury caused by the operation causes a depression in the conducting power. Hence in a cut specimen there may be induced a great delay in the passage of the excitatory impulse, on account of which an error of several degrees may be introduced in the determination of the death-point.

The conducting power in an isolated preparation is, in general, more or less completely restored after a prolonged period of rest. In the next batch of preparations, the experimental determination of the death point was undertaken six hours after isolation from the parent plant; the different values of the death-point were now found to be: 62°C., 62°C., 63°C., and 63°C. respectively.

Experiment with intact specimens.—From the fact that the disappearance of the effect of injury tended to bring the death-point nearer the normal 60°C., I was next led to experiment with intact plants. For this, I took a batch of young seedlings of *Mimosa* and carefully removed them from the ground without injuring the roots. The lower part of the plant was placed in the bath in the usual manner and the death-points observed in four typical cases were: 60°C., 60°C., 59.6°C., and 60°C. respectively. It will thus be seen that an excitatory impulse is generated at the critical death-temperature, and that the death-point in an ordinary tissue is the same as that in sensitive pulvinated organs.

CRITICAL POINT FOR TRANSMITTED DEATH-EXCITATION IN AVERRHOA.

Similar experiments were next carried out with cut petioles of *Averrhoa*, and one of the sensitive leaflets was chosen for detection of transmitted excitation. This was attached to a delicate Oscillating Recorder for obtaining record of transmitted

Experiment 310

excitation. As regards the character of this excitation in *Averrhoa* and *Biophytum*, I have shown elsewhere that under intense stimulation, the response instead of being single becomes multiple. The death-excitation, if intense, is thus expected to give rise to a multiple series of responses.

The cut end of the long petiole was gradually raised in temperature at the standard rate of one degree per minute. The indicating leaflet was at a distance of 50 mm. from the cut end. The velocity of transmission of excitation is relatively slow, less than 1 mm. per second; hence by the time the excitation reaches the distant leaflet the observed temperature in the bath would have risen one or two degrees higher. Figure 295 shows that a death-excitation was generated at the critical temperature, which had given rise to a multiple series of responses. The temperature at which this occurred was 62°C., which for reasons explained above was one or two degrees above the true death-point. The bath was allowed to cool down and the temperature was raised once more; but there was no transmitted excitation since the immersed portion had been previously killed. The

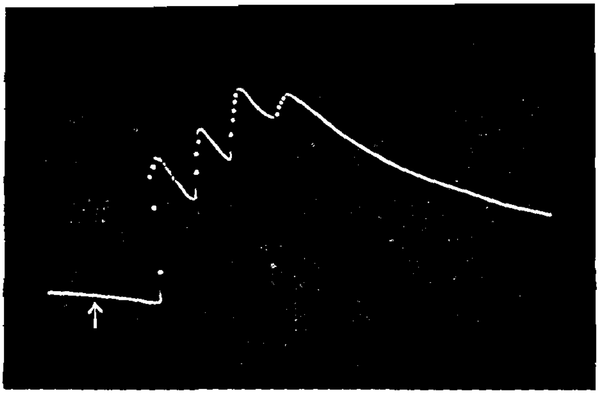

Fig. 295 Transmitted death-excitation giving rise to multiple response in *Averrhoa*; this occurred at 62°C.

petiole was next lowered by 2 cm. thus bringing a fresh unkilled portion in operation, and the transmitted death-excitation was found to occur once more as at the beginning. This proves conclusively that the transmitted excitation is generated at the critical temperature at the moment of death of the living tissue. The fact that heat caused only local death was independently proved by the effect of direct stimulation of the leaflet after the multiple response of the transmitted excitation had come to a stop. Stimulation of the indicating leaflet gave rise to the normal response. The effects described above were also found in *Biophytum*.

EXCITATORY IMPULSE AT DEATH BY POISON.

The determining cause of the excitatory impulse lies not in the manner of death but in death itself. The same excitation may be initiated in the complete absence of scalding or of coagulation. A quick method of bringing about death is in the administration of poison. We might thus be successful in discovering the transmitted excitation at the death of the tissue under poison.

Experiment 311

Transmitted excitation in Mimosa.—For this investigation I first took intact seedlings of *Mimosa*; the roots and the stem were immersed in a beaker of water, the distance of the nearest motile leaf being 2 cm. above the point of immersion. Another beaker was kept ready containing poison of a definite strength, either 1 per cent. or 5 per cent. solution. This was applied by substituting the beaker containing the poison for the beaker of water. It is obvious that the quickness with which a tissue is killed will depend on the strength of the poison: the transmitted death-excitation, if any, will be exhibited earlier under a strong than under a feeble poison The effective intensity of a poison will depend not only on the strength, but also on its relative virulence.

The application of a poisonous solution to the root might conceivably, through plasmolysis, cause certain hydrostatic disturbance in the plant. I carried out an investigation to show that such a disturbance, supposing it to occur, does not cause any excitation. Thus a solution of KNO_3 applied to the root of the seedlings of *Mimosa* did not produce any excitation.

In investigations on the effect of poisons, I first selected potassium cyanide, as previous experiments proved it to be one of the most effective toxic agents. One per cent. solution of this substance was applied to the root of the *Mimosa* seedling in a manner that has already been described. The nearest motile leaf-indicator was always at a distance of 20 mm. above the point of application. After a certain interval, the poison was found to take effect and the death-excitation was exhibited by the sudden fall of all the leaves. I give below the periods found to elapse in four typical cases, between the application of poison and the exhibition of excitatory reaction. The initiation of death-excitation at the point of application itself must have taken place about four seconds earlier, this being the time lost in transmission through the intervening distance of 20 mm.

TABLE LXIII.—PERIOD ELAPSING BETWEEN APPLICATION OF 1 PER CENT KCN SOLUTION AND EXHIBITION OF DEATH-EXCITATION.

No.	Time.
1	236 seconds.
2	256 ,,
3	193 ,,
4	180 ,,
Average time, 216 seconds.	

The time necessary for the appearance of death-excitation will depend, as stated before, on the strength of application and on the effective virulence of the poison. Experiment 312 With regard to the first, we saw that the average time taken by 1 per cent. KCN solution to cause death-excitation was 216 seconds. For observing the effect of stronger solution, I next applied 5 per cent. solution to a second batch of seedlings with the following results.

TABLE LXIV.—PERIOD ELAPSING BETWEEN APPLICATION OF 5 PER CENT. SOLUTION OF KCN AND EXHIBITION OF DEATH-EXCITATION.

No.	Time.
1	42 seconds.
2	60 ,,
3	61 ,,
4	58 ,,
Average time, 55 seconds.	

As regards the relative virulence of different poisons, I knew from my previous investigations that mercuric chloride is less toxic in its action than Experiment 313 potassium cyanide. The average period required for exhibition of death-excitation with 1 per cent. solution of this agent was found to be 650 seconds, as against 216 seconds required for 1 per cent. solution of potassium cyanide.

Transmitted death-excitation in Biophytum.—The thin and long flower stalks of *Biophytum* are very effective in the conduction of excitation. When Experiment 314 these are stimulated in any way, excitation travels downwards, and the sensitive leaflets exhibit successive closures from the centre outwards. For local application of poison, a small piece of cloth was wrapped round the upper portion of the flower stalk which was moistened with a small quantity of 5 per cent. solution of KCN; special care was taken that the poison did not leak downwards. After an interval of three minutes the death-excitation was initiated which caused the successive closure of the leaflets. A record of the response of a single leaflet showed that it was multiple (Fig. 296). After the cessation of the multiple pulsation, the leaflet was locally stimulated by a moderate stimulus at the point marked with the cross. This gave rise to a single response, proving that the poison did not reach the leaflet; the multiple response was thus due to the intense excitation from the distant poisoned area.

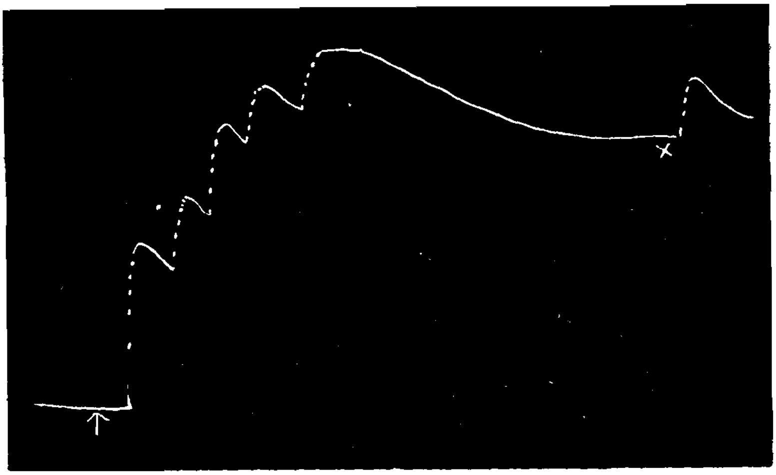

Fig. 296 Multiple responses of leaflet of Biophytum under transmitted death-excitation due to poisoning.

Local stimulation of the leaflet at cross gave rise to a single response (see text).

SUMMARY.

On subjecting *Mimosa* to steady rise of temperature in a bath, a sudden fall of the leaf is observed at the critical temperature of 60°C. This in reality is the death-spasm of the plant.

In order to show that the movement of the fall of leaf is not due merely to shrinkage of cells in the pulvinus by coagulation of their protoplasm, but to excitatory reaction, the motile organ was kept free from the action of heat, a distant point lower down the stem being subjected to the action of rising temperature. At the critical temperature of 60°C., an excitatory impulse was generated at the dying portion of tissue, which, travelling upwards, caused the fall of the leaves. On repetition of the experiment the killed portion did not initiate any fresh excitatory impulse; but exposure of fresh portion of stem to the critical temperature gave rise to a new impulse. Similar effects were also found to occur in *Averrhoa* and in *Biophytum*.

The death-points of motile and ordinary tissues are found to be practically identical.

Death-excitation is also locally initiated under the action of poison, and the excitatory impulse is then transmitted to a distance. The period necessary for the initiation of the excitatory spasm is shortened by the increased strength and virulence of the poison.

The occurrence of an intense excitatory reaction in the tissue at the moment of its death, is thus conclusively proved by the results of experiments on scalding and poisoning.

LXVIII.—THE SPREAD OF THE WATER-HYACINTH.

BY SIR J. C. BOSE.

Perhaps few pests have caused such a wide devastation and threatened the economic existence of a country as the Water-Hyacinth. (*Eichornia Crassipses*). It is spreading over large areas in certain States of America, in Australia, Java, Burma, Ceylon and India. The danger is specially ominous in Bengal; a few years ago it was growing sporadically in the eastern district which is one of the most fertile provinces in India. Its spread is now beyond control; many of the smaller rivers and canals are so densely packed with it that navigation has become impossible. The floods carry the Hyacinth to the arable lands; once it gets a foothold there the plants under cultivation succumb in the struggle for survival. A single root of the Hyacinth has been known to spread through an area of 600 square metres in the course of a few months. The economic danger from the spread of this pest has become very acute and the Government of Bengal recently appointed a commission under the presidentship of the author, to enquire into the subject. Certain preliminary investigations have been carried out at the Bose Institute in regard to the efficacy of different methods which had been employed in various countries to check the spread of the pest. A short account of the investigation is given below

In Figure 297 is reproduced a photograph of a stretch plant-growth in the large water course adjoining the Experimental Research Station at Sijbaria on the Ganges. The weeds grow to a height of more than three feet. The leaf-stalk of the plant is expanded like a bladder to give it sufficient buoyancy for floating in water. The wind caught by the leaves presses the plants against each other; a compact mass is thus formed, the plants in the interior being completely sheltered by those outside. The growth is so dense that in many places it is possible to walk over the floating mass; navigation under these circumstances is an impossibility. The plants have thus spread over rivers, canals, and shallow stretches of water through many square miles which are not easily accessible; this has introduced additional difficulties to the destruction of the pest.

Fig. 297 A stretch of Water-Hyacinth, near Sijbaria on the Ganges.

POSSIBLE METHODS OF DESTRUCTION.

The theoretical methods for the destruction of the plant and the question of their effectiveness are described below.

Introduction of fungi.—Fungal parasites might be found which would cause the destruction of the Hyacinth; but there is a considerable danger of the fungus attacking valuable crops.

THE METHOD OF STEAM.

In the United States attempts have been made to destroy the plant by turning on the steam-hose and thus scald the plant to death. A similar method has been employed in Burma; in certain experiments the nozzle of the hose was made to touch the plant and the issuing jet actually split the leaves which were killed as evidenced by the death-discoloration. But many new leaves came out in the course of a few days from the plant supposed to have been scalded to death. It has since been thought that high pressure steam might prove to be more effective; this is however a gratuitous assumption. For I have shown elsewhere that the death-temperature of a plant is very definite; as determined by the Death-Recorder this point has invariably been found to be at or about 60°C. Ordinary steam of 100°C. is thus 40°C. higher than the fatal temperature; there can, therefore, be no necessity for the use of a still higher temperature by the employment of high pressure steam.

For the removal of any possible misgiving in regard to the fatal temperature for Hyacinth, the leaf of the plant was placed in a bath suitably attached to the Death-Recorder previously described. Experiment 315 The record seen in Figure 298 was taken, as the temperature of the bath rose from 50°C. upwards, each dot representing a rise of 1°C. The death-spasm of Hyacinth is thus seen to occur, as in other plants, at 60°C.

Setting fire to the plant.—The effect of the still more drastic method of setting fire to the plant was next observed. The upper part of the plant floating in water was wrapped round with a piece of Experiment 316 cloth soaked in petrol. On setting the cloth on fire, the plant was burnt to ashes down to the edge of the water. The submerged portion of the plant, however, sent out fresh leaves in the course of a fortnight and growth was found renewed as if nothing untoward had happened to it.

DISCOVERY OF THE CAUSE OF FAILURE.

Large number of tanks in every district of Bengal are used for irrigation and for supply of drinking water; they are often overgrown with the Hyacinth. After clearing the tanks a new crop of Hyacinth is found to appear in the course of a few months, though the growth is now less dense than before the clearing. *From this, it is clear that detached fragments from submerged portion are effective in the propagation of the plant.*

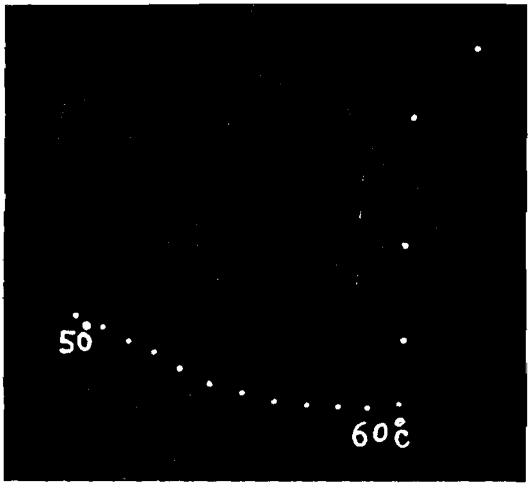

Fig. 298 Determination of the death-point of the Water-Hyacinth. Death-spasm at 60°C is seen in the up-curve.

The above inference was next subjected to experimental test. The upper part of the plant was cut off and a small portion of the submerged plant with roots was buried under mud; in the course of

Experiment 317

three weeks new leaves sprang up from the detached portion of the plant.

The failure of the various methods hitherto employed has arisen from ignoring the important part played by the submerged portion of the plant in its propagation. The seeds no doubt germinate under favourable conditions; but this is practically negligible compared with the vegetative mode of propagation. The photograph reproduced in Figure 299 shows the submerged portion of the plant which is as large as the part above water. The number of roots in each plant is as many as 150 or more. In a vertical section of the plant numerous buds are seen to occur at the

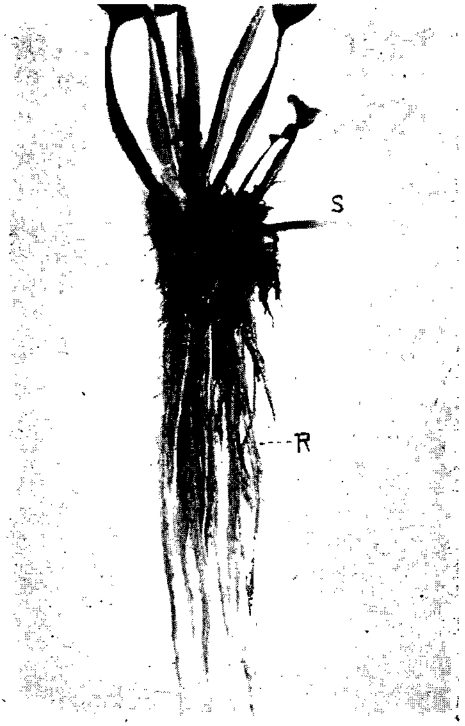

Fig. 299 Photograph of R, root and S, stolon of Water-Hyacinth.

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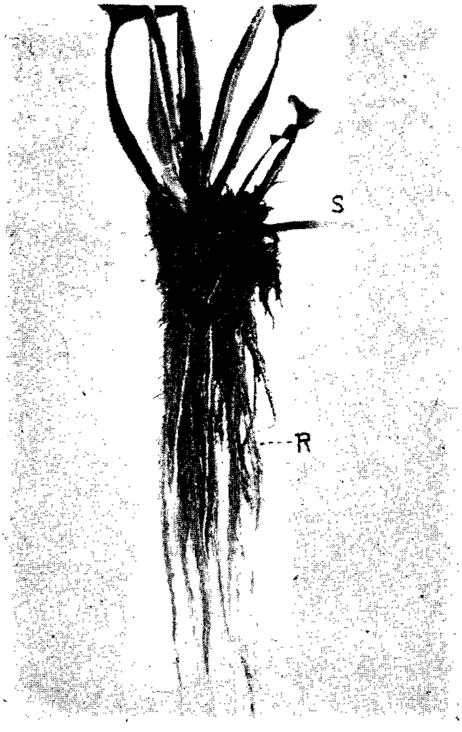

Fig. 299 Photograph of R, root and S, stolon of Water-Hyacinth.

this is practically negligible compared with the vegetative mode of propagation. The photograph reproduced in Figure 299 shows the submerged portion of the plant which is as large as the part above water. The number of roots in each plant is as many as 150 or more. In a vertical section of the plant numerous buds are seen to occur at the axils of the leaves; these grow out into horizontal runners, each of which gives rise to a new plant. Numerous runners spring out from a single plant and the vegetative multiplication is thus extraordinarily rapid.

It is thus seen that *no method for eradication of the pest can be satisfactory which does not ensure the destruction of the submerged portion of the plant.*

METHOD OF POISONOUS SPRAY.

A very large number of poisons are known which, if properly applied, cause the death of the plant. Even strong solution of common salt is found effective. Attempts have been made to destroy the Hyacinth plant by spraying it with poisonous solutions. But for reasons to be presently described, this particular method would prove to be quite ineffective. The enormous areas covered by the Hyacinth are, as already stated, difficult of access; hence powerful machinery would be required to send the sprayed solution to a distance. But there is little chance of the poisonous solution effectively reaching an individual plant in the interior, sheltered by the dense mass outside. A single plant which escapes the poisoning would become a new focus for the spread of the pest.

Assuming, however, that the poison did reach the plant, its application would be found ineffective in causing the destruction of the plant as a whole. Local death of the upper part of the plant by steam did not, as we saw, kill the submerged portion. In the case of poison, the sprayed solution cannot directly reach the plant under water; the only possibility for this lies in the conduction of the poison by the plant downwards, from the leaves to the roots.

But my recent investigations on the physiological machinery for the ascent of sap* have shown that while a

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* Bose—Physiology of the Ascent of Sap (In the press). Longmans & Green.

poisonous or any other solution is easily conducted by the ascent of sap upwards, it cannot be carried downwards to the submerged roots. Hence application of poison to the root kills the plant throughout its length; application of the poison to the shoot, on the other hand, causes a local death which does not, normally speaking, spread downwards. The following experiments give a striking demonstration of the different effects of application of poison to the root and the shoot.

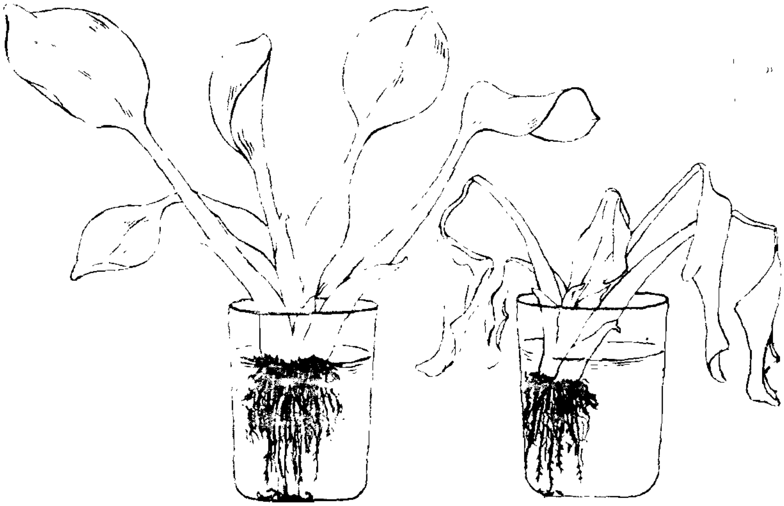

Fig. 300 Effect of poison applied to the root of the Hyacinth. The illustration to the left is the appearance of the plant before, to the right, after application of poison.

Experiment 318

Effect of poison applied to the root of Hyacinth.—The effect of formaldeyde solution may be taken as typical of the action of other poisons. A vigorous plant of Hyacinth seen to the left of the Figure 300, was afterwards placed with its roots in a 5 per cent. solution of formaldehyde. The roots absorbed the poison which rose with the ascent sap and killed the plant from below upwards; this upward march of death was easily followed by the advancing death-discoloration which crept upwards. The plant was killed throughout its length in the course of from six to eight hours, when it collapsed and became a mass of dying and dead tissue.

Experiment 319

Effect of poison applied to the cut end of the stem of Chrysanthemum.—The effect described above takes place in all plants. In Figure 301 are seen the photographs of cut stems of *Chrysanthemum coronarium*; one was placed in water, and the other in a poisonous solution. The poison ascended with the sap, and reached the first pair of leaves, which underwent an immediate collapse. The fall of the other leaves followed in succession with the ascent of the poison; the appearance of the plant thus poisoned to death is seen on the right side of the illustration.

Fig. 301. Photographs of cut stems of *Chrysanthemum* placed in water and in a poisonous solution.

Experiment 320

Effect of poisoning the leaf.—In sharp contrast with results given above, we next observe the effect of the application of poison to the upper end of the Hyacinth as is done by spraying of the poisonous solution. The poisoning is made even more upwards. The plant was killed throughout its length in the course of from six to eight hours, when it collapsed and became a mass of dying and dead tissue.

Experiment 319

Effect of poison applied to the cut end of the stem of Chrysanthemum.—The effect described above takes place in all plants. In Figure 301 are seen the photographs of cut stems of *Chrysanthemum coronarium*; one was placed in water, and the other in a poisonous solution. The poison ascended with the sap, and reached the first pair of leaves, which underwent an immediate collapse. The fall of the other leaves followed in succession with the ascent of the poison; the appearance of the plant thus poisoned to death is seen on the right side of the illustration.

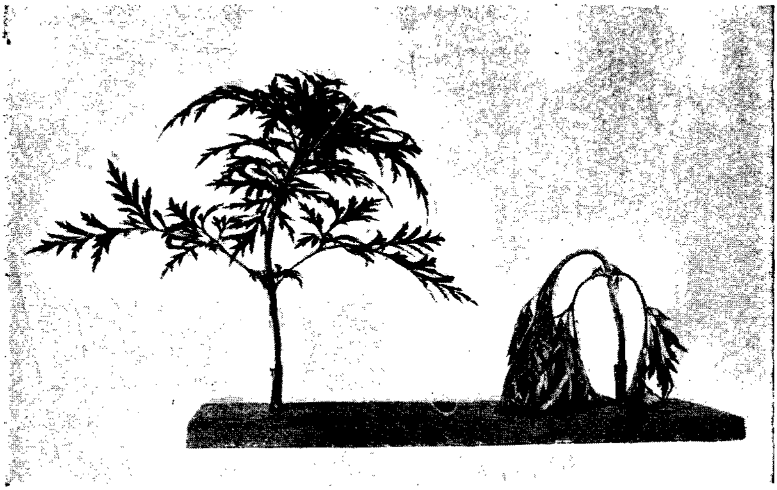

Fig. 301 Photographs of cut steams of *Chrysanthemum* placed in water and in a poisonous solution.

Experiment 320

Effect of poisoning the leaf.—In sharp contrast with results given above, we next observe the effect of the application of poison to the upper end of the Hyacinth as is done by spraying of the poisonous solution. The poisoning is made even more effective by enclosing the leaf in a close-fitting funnel filled with formaldehyde solution; the lamina became discoloured and crumpled up by the direct action of the poison. There was, however, no transmitted effect and no downward march of death. The leaf stalk immediately below remained green and fully alive. (Fig. 302.)

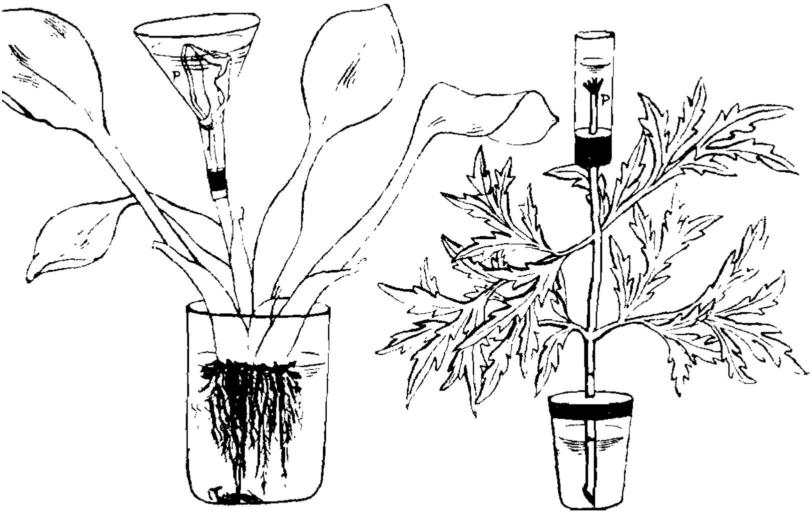

Fig. 302 Effect of poison P applied to the upper part of shoot in Hyacinth and in *Chrysanthemum*. The lower part remains fully alive.

Experiment 321

Effect of application of poison to the upper end of the shoot.—A parallel experiment was carried out with the shoot of the *Chrysanthemum*, the upper end of which was placed in a glass tube filled with the poison. The poison did not work downwards as was shown by the leaves below remaining green and expanded in a living condition.

The definite results of investigations described above thus clear up the obscurity that had surrounded the subject, and thereby narrow down the problem to the essential element, namely, the destruction of the submerged portion effective by enclosing the leaf in a close-fitting funnel filled with formaldehyde solution; the lamina became discoloured and crumpled up by the direct action of the poison. There was, however, no transmitted effect and no downward march of death. The leaf stalk immediately below remained green and fully alive. (Fig. 302.)

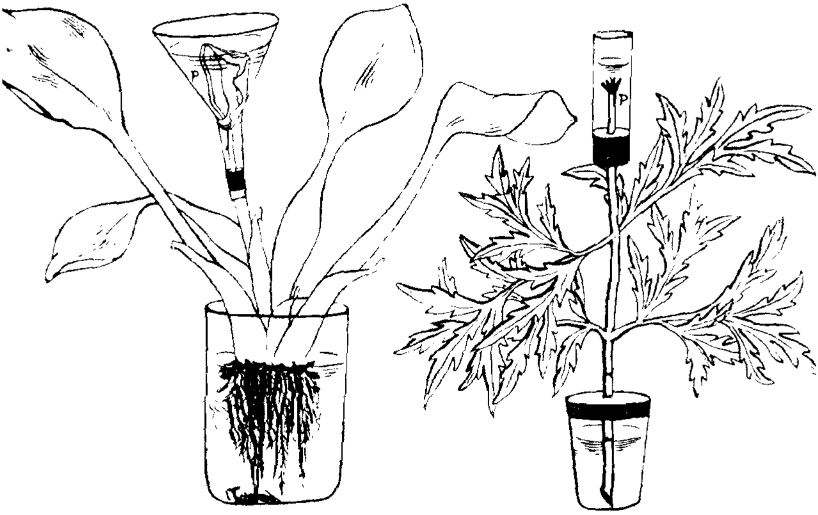

Fig. 302 Effect of poison P applied to the upper part of shoot in Hyacinth and in *Chrysanthemum*. The lower part remains fully alive.

Effect of application of poison to the upper end of the shoot.—A parallel experiment was carried out with the shoot of the *Chrysanthemum*, the upper end of which was placed in a glass tube filled with the poison. The poison did not work downwards as was shown by the leaves below remaining green and expanded in a living condition.

Experiment 321

The definite results of investigations described above thus clear up the obscurity that had surrounded the subject, and thereby narrow down the problem to the essential element, namely, the destruction of the submerged portion of the plant which is the most effective means of propagation. This cannot be done with steam or by spraying with poisonous solutions. The only effective means is in the mechanical collection and destruction. There are various possibilities in the economic utilisation of the plant, from which a large portion of the cost of collection could be recovered.

SUMMARY.

The rapid spread of the Water-Hyacinth is brought about by vegetative propagation. The submerged portion of the plant sends out a large number of horizontal runners, each of which gives rise to a new plant.

Steam kills the portion of the plant above water; the submerged portion remains alive and thus brings about a rapid propagation.

Poisonous solutions applied to the root are carried upwards with the ascent of sap and thus kill the plant throughout the length.

Application of poisonous solutions by means of the spray causes only the local death of the upper portion of the plant. The poison is not conducted downwards. The spraying method is therefore ineffective in the destruction of the plant.

LXIX.—RESPONSE TO MECHANICAL STIMULUS BY VARIATION OF ELECTRIC RESISTANCE.

By Sir J. C. Bose.

Assisted by
Narendra Nath Neogi, M.Sc.

Two independent means have been described for the determination of physiological changes induced in the plant, namely, the methods of mechanical and of electromotive response. In addition to these a third method had already been employed in my previous work on Comparative Electro-physiology (1907). This method of response by variation of resistance is considerably extended in the following series of papers.

I have already shown that all modes of stimulation, mechanical, electric, or photic, induce an identical excitatory effect, as recorded by the mechanical and the electromotive response. The above will be found fully supported by the Method of Resistivity variation which will be separately employed for investigations on response (1) to mechanical stimulus, (2) to electric stimulus and (3) to the stimulus of light. Of these the mechanical stimulus has certain advantages, since in the first stage of the inquiry it is preferable to employ a non-electrical mode of stimulation for obtaining response by variation of electric resistance. The drawback in the employment of mechanical stimulus is the difficulty in obtaining stimuli of equal intensity in succession or in increasing it in a graduated manner. The above difficulties have, however, been completely removed by the invention of certain devices for uniform stimulation. The necessity for the maintenance of successive uniform stimuli is sufficiently obvious. For it is only by such means that it is possible to secure uniform responses under normal conditions; the effect of an external agent may then be found from the induced variation in the amplitude of the normal response.

The advantage of electric stimulation is that the intensity may be maintained constant, or varied from sub-minimal value. This is a matter of importance, since it enables us to determine whether the responsive reaction is of the same sign throughout the whole range of stimulation from the subminimal to the maximal. The drawback in the application of induction shocks as stimulus is the liability of the leakage of high tension current into the galvanometer circuit, which would vitiate the result. It is to be borne in mind, that in obtaining record of electric response we have to employ a very sensitive galvanometer. It is therefore of utmost importance to remove all elements likely to disturb the normal deflection. We shall, however, find that it is possible, by taking sufficient precautions, to eliminate all sources of error.

Finally, as regards the photic stimulus, it offers no difficulty in application. Particular care has, however, to be taken to keep the metallic contacts made with the plant shaded from light, as this might give rise to photo-electric effect. The stimulus caused by light is obviously less intense than that induced by tetanising electric shocks.

EXPERIMENTAL ARRANGEMENTS.

We take stems of various plants and mount them as in the diagram (Fig. 303). The plant is clamped in the middle, and its two lengths P and Q form the two arms of the Wheatstone Bridge; the electric contacts with the plant are made by means of two platinum pins which are thrust into the plant. The two other arms of the bridge are made by a rheostat with a sliding contact. There is a balance when PS=QR; successive completions of the battery and galvanometer circuits by means of a double contact key (not shown in the figure) now cause no galvanometer deflection. But if the portion of the plant P undergoes a diminution of resistance, the fact is demonstrated by the resulting deflection, say to the right; a deflection to the left indicates, on the other hand, an increase of resistance of P.

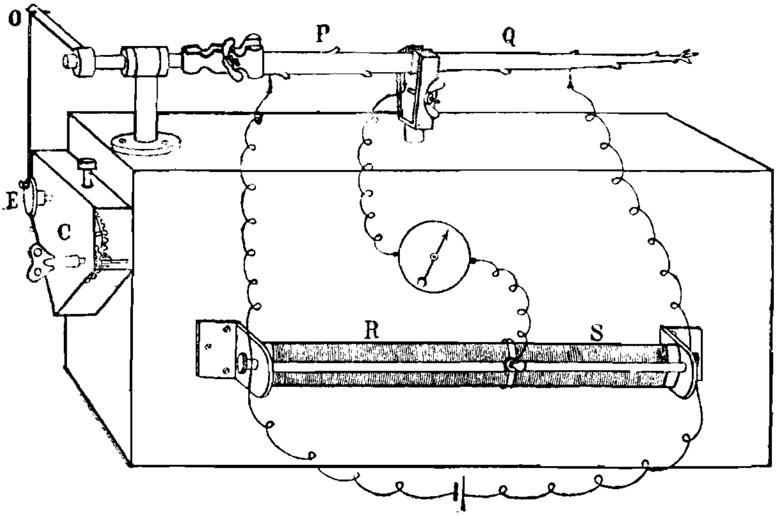

Fig. 303 Experimental method for obtaining response to mechanical stimulus by resistivity variation. P and Q are lengths of plant which form two arms of the Bridge, of which P alone is subjected to torsional vibration by means of the revolving eccentric E, worked by clockwork, C. The two other arms of the Bridge, R and S, are formed by the rheostat with sliding contact, seen below

The balance is easily secured in the following manner; the sliding contact of the rheostat is at first placed in the middle, and the resistance of Q gradually diminished by moving the platinum contact inwards from the extreme right. After obtaining an approximate balance the plant is allowed a period of rest for about 15 minutes, after which the irritation caused by the pin-prick would be found to disappear. A very perfect balance is next obtained by the careful adjustment of the sliding contact of the rheostat. The electric contacts with the plants are made, as previously stated, by means of platinum pins; this method of contact is in practice far preferable to that of the non-polarisable electrode.

The next question which demands our attention is the polarisation caused by the brief passage of the battery current required for the measurement of the electric resistance. This difficulty was at first overcome by the use of a rotating cummutator by which equi-alternating current was sent through the circuit, the polarisation being thus neutralised. This necessitated the reversal of the galvanometer connections at the same time, which was secured by the employment of a second commutator mounted on the

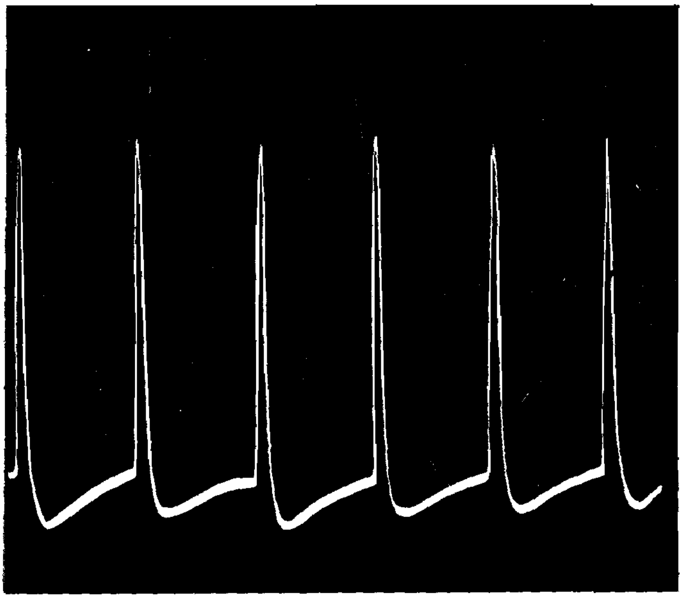

Fig. 304 Records showing uniformly diminished resistance (up-curve) on uniform mechanical stimulation. *(Calotropis gigantia).*

axis of the first. I found later, that the use of an alternating current was an unnecessary refinement, since the polarisation under the actual condition of the experiment is practically zero. The storage cell used for the experiment has an E. M. F. of two volts; the electrical resistance of the plant is however more than a million ohms. Hence the intensity of the current is about 2×10^{-6} ampere. The galvanometer attains its maximum deflection in the course of about three seconds and the circuit is completed, by the double tapping key, for less than 5 seconds. The polarisation produced by the brief passage of such a feeble current is quite negligible It does not in any way affect the uniformity of responses under successive equal stimulations as will be found demonstrated in the record of responses given in Figure 304.

METHOD OF MECHANICAL STIMULATION.

The greatest difficulty which confronts us is in securing successive stimulations of equal intensity and in increasing this intensity in a definite manner. The tissue could be stimulated by a spring tapper but the excitation in such a case would have remained localised at the point struck, the adjoining tissue exhibiting the effect of indirect stimulation: it has been shown that the effect of the indirect is of opposite sign to that of direct stimulation. Hence the result would have been complicated by the algebraical summation of the two opposite reactions. For avoiding this, it is necessary to stimulate the whole length of the tissue. This has been secured by the method of torsional vibration.

If after securing the balance the arm of the plant P be slowly twisted, say to the right through 5°, the physical distortion is found to cause no measurable variation in the resistance. But a rapid torsion is found to give rise to a responsive deflection of the galvanometer, say to the right, indicating *a diminution of resistance*. It is the *suddenness* of the disturbance which

Experiment 322

constitutes a stimulus. If now we produce a sudden twist of 5° to the left, we obtain the same excitatory deflection to the right as before. It is not the twist as such, but the sudden mechanical disturbance which causes stimulation. The plant is next subjected to a rapid alternating torsion to the right and left through 5°; the response is now found to be nearly doubled. Torsional vibration is thus found to be a very effective method of stimulation; the intensity of stimulus, within limits, is found to increase with the amplitude of torsional vibration.

Experiment 323

Additive effect of stimulus.—Keeping the angle of torsional vibration constant, the stimulus is found to be increased with the number of repetitions. *An important result is that a singly ineffective stimulus becomes effective after repetition.* Thus while a single torsional vibration of 2° is ineffective, it becomes effective after a number of repetitions. The advantage of this is that with small angles there is little physical distortion produced in the tissue. We have here an instance parallel to the cumulative effect of repeated electric shocks, a single one of which is ineffective. The mechanical stimulation is effected by automatic means; the end of the plant is fixed in a torsional clamp, and rapid alternating torsions are given to P by means of the clockwork C. Suitable adjustments are provided for regulating the angle of torsion. After the clock is fully wound, a press button releases it, with the result that twenty successive torsional vibrations are produced in rapid succession. The responsive deflection induced by stimulus is recorded on a photographic plate.*

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* A feeble E. M. F. is generated at the mid-point of P by the torsional vibration; there is, however, no electric variation at the fixed points of contact, and no electromotive force round the circuit. This is seen in the fact that the deflection produced by the induced variation of resistance remains the same after the reversal of the connections of the voltaic cell in the Wheatstone Bridge.

UNIFORM RESPONSE UNDER UNIFORM STIMULUS.

A series of uniform responses to constant stimulus applied at intervals of 10 minutes is seen in Figure 304. The experimental specimen was a stem of *Calotropis gigantea*. Other plants also give similar results, though some are more sensitive than others. This sensitiveness is further modified by age, by season, and by the physiological condition of the tissue. The responsive variation under stimulus may amount to ten per cent. of the *normal resistance*.

Experiment 324

EFFECT OF ANAESTHETICS.

The physiological character of the response is demonstrated by the application of chloroform vapour. We found that the excitability of a vegetable tissue is depressed under the continued action of this anaesthetic The first record (Fig. 305) shows the normal

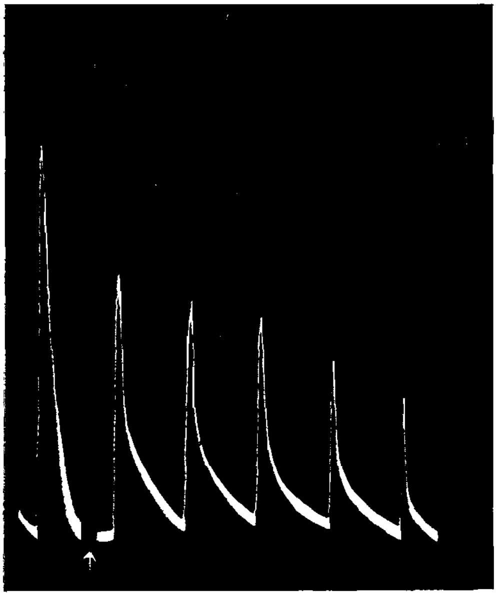

Fig. 305 Effect of chloroform in inducing depression of response.

Experiment 325

response; chloroform was applied at the point marked with an arrow, the subsequent responses being obtained at intervals of 10 minutes. The response by variation of resistance is thus seen to undergo a decline under the continued action of the anaesthetic.

PRELIMINARY EFFECT OF DILUTE VAPOUR OF CHLOROFORM.

The spark record.—The galvanometric records given above were obtained by photographic means with the inconvenience inseparable from working in a dark room. A different method has, however, been devised for obtaining direct record of the deflection of the galvanometer index on a moving piece of paper which is perforated by electric sparks. A full description of the apparatus will be found in a subsequent chapter. A record obtained by the spark-method is seen in Figure 306.

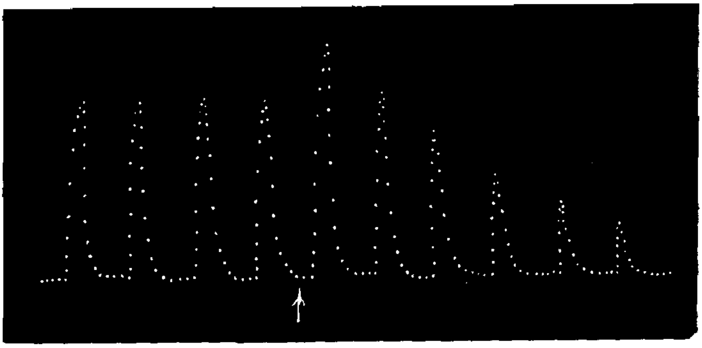

Fig. 306 The spark record of galvanometric response. Dilute vapour *of chloroform* applied at arrow induced a preliminary enhancement of response followed by depression.

Experiment 326

We found certain characteristic effects of chloroform which depended on the duration of application. The immediate effect at the first stage was found to be an enhancement of excitability, followed at the second stage by a depression. In the present experiment, the first four are the normal and uniform responses; the next record was obtained after a minute of the introduction of the chloroform vapour. The response is seen to have *undergone a marked enhancement*. Continued action of chloroform, however, caused the subsequent *depression* (Fig. 306).

SUMMARY.

The response to mechanical stimulus is obtained by the employment of the Wheatstone Bridge, the plant forming the two arms of the bridge; the other two arms are made of a rheostat with sliding contact for the adjustment of balance.

Torsional vibration is shown to be an *effective means* of stimulating the tissue. The intensity of excitation is increased by increasing the angle of torsion.

The effect of stimulus is found to be additive; a singly ineffective stimulus thus becomes effective by repetition.

The effect of mechanical stimulus is to induce a diminution of the electrical resistance of the tissue.

The physiological character of the response is demonstrated by the action of an anaesthetic like chloroform vapour. During the first stage of its action, the amplitude of response is enhanced; continued action of the anaesthetic is, however, followed by a depression.

LXX.—RESISTIVITY VARIATION IN PLANTS UNDER ELECTRIC STIMULUS.

BY SIR J. C. BOSE,

Assisted by

GURUPRASANNA DAS, L.M.S

A *generalisation has previously been established that* all modes of stimulation, mechanical, electrical or photic, give rise to similar excitatory reaction. Mechanical stimulus has already been shown to induce this, by a diminution of electric resistance. We shall in the present chapter study the effect of electrical stimulus in inducing a responsive variation of the resistance of the tissue.

The great advantage of electric mode of stimulation is in its constancy and in the wide range of its possible variation. The stimulus may thus be increased from zero to a maximum. In the former, the secondary coil is at a very great distance from the primary, and in the latter it is pushed in so as to enclose the primary coil. The duration of application of stimulus can be accurately regulated by means of a metronome; in the following experiments the duration of stimulus is half a second.

THE METHOD OF EXPERIMENT.

The experimental arrangements are shown in Figure 307. Two platinum pins are thrust about 5 cm. apart in the middle portion of the plant growing in a pot. Records are taken of the variation of resistance induced by stimulus in this particular portion of the plant which forms the fourth arm of the Wheatstone's Bridge. The electric shock from the induction coil is passed through the length of the plant, between the tip and the root, thus causing uniform stimulation of the intermediate portion of the plant.

In obtaining electromotive response of *Mimosa*, the electric stimulus was applied at some distance from the

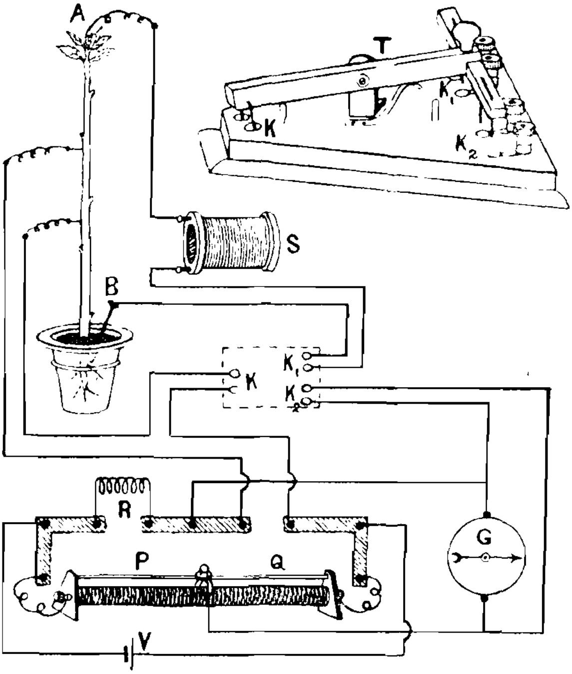

Fig. 307 Method of resistivity variation for response to electric stimulus. Pressure of the tilting key T causes stimulation of the plant by induction shock from coil S at the time when galvanometer circuit is cut off (see text).

pulvinus the upper and lower halves of which were connected with the galvanometer. The interposition of a chocking coil was then found effective in preventing the leakage of the shock-current into the galvanometer circuit. In the present case, the electric stimulation is direct and the prevention of the leakage of the shock-current presents certain difficulties. These are, however, completely removed by cutting off the galvanometer connections with the plant during the passage of the induction shock. The shock-circuit S had, moreover, to be cut off from the plant during the determination of the resistance and its induced variation; otherwise the coil S would have acted as a shunt.

The method of procedure is therefore as follows: The ey K is closed and K_1 and K_2 opened. The exact balance is obtained by the sliding contact by which the ratio of P nd Q is varied. The balancing condition is found from the galvanometer deflection being reduced to zero. The plant is now cut off from the galvanometer and put on in the shock circuit; this is done by opening the key K, and closing K_1; K_2 is simultaneously closed so as to short-circuit the galvanometer. The electric shock is thus allowed to pass through the plant for half a second after which K_1 and K_2 are opened and K closed. The variation of resistance induced by stimulus, causes an upset of the previous balance of resistance with the resulting deflection of the galvanometer spot of light.

In practice, the successive manipulations of making, breaking and remaking of the connections are performed almost automatically by a momentary pressure on the tilting key T, and the release of that pressure. The relative position of the three keys and the sequence of their action will be understood from the illustration at the upper corner of Figure 307.

In the following investigations, intact or cut specimens of various plants have been successfully employed; among these may be mentioned the seedling of *Helianthus annuus* and of *Impatiens*, also the climbing stem of *Ipomea pulchella*, and *Porana paniculata*. The sensibility depends on age, season, and the previous history of the plant. Under favourable circumstances very pronounced response is obtained under an electric shock so feeble as to be beyond human perception.

After making suitable electric connections by means of platinum electrodes, the specimen is allowed a period of rest for complete subsidence of irritation caused by manipulation. The characteristic responses by variation of electric resistance are then obtained under sub-minimal, moderate and strong stimulations.*

EFFECT OF STIMULUS OF MODERATE INTENSITY.

Experiment 327

The intensity of stimulus is continuously increased by the approach of the secondary coil to the primary till a particular distance is found at which the amplitude of response is about three centimetres. The duration of electric stimulation is only half a second, and successive stimuli of equal intensity are applied at intervals of eight to ten minutes. Figure 308 shows: (1) that the response is by a *diminution* of resistance as indicated by the up-curve, (2) that the recovery is complete on the cessation of stimulus, and (3) that the amplitudes of successive responses are equal under uniform stimulation. If successive stimulations are at shorter intervals than 5 minutes, the protoplasmic recovery is incomplete, and we observe signs of fatigue. This is shown by a diminution in the amplitude of successive responses. Another interesting phenomenon, sometimes observed, is the occurrence of alternating fatigue, that is to say, a large response is followed by a small one, and this, in a recurrent series.

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* An autonomous pulsation is sometimes observed, due to the pulsatory activity of certain cells which maintain the ascent of sap. The electric pulsation may, however, be made to disappear by separating the points of contact on the stem, till the pulsatory activities at the two points are in the same phase. A detailed account of the phenomenon will be found described in the *Physiology of the Ascent of Sap* to be shortly published by Messrs. Longmans. In all experiments, the iso-electric condition of the two contacts is assured by observing the quiescent condition of the galvanometer spot of light.

For the study of the effect of external agents, it is important that the normal responses should be uniform, and the conditions for securing such uniform responses have been fully described. The stimulating or depressing character of an agent may now be discovered from the induced modification in the normal response; an enhancement of excitability thus will be detected by a concomitant increase in the amplitude of response; a lowering of excitability will, on the other hand, be indicated by the amplitude of response undergoing a depression.

FIG. 308

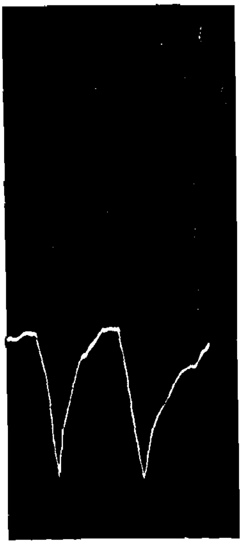

FIG. 309

Fig. 308 Effect of stimulus of moderate intensity. Response by diminution of resistance seen in the up-curve.

Fig. 309 Effect of sub-minimal stimulus. Response by increase of resistance exhibited by the down-curve *(Helianthus)*.

EFFECT OF SUB-MINIMAL STIMULUS.

Experiment 328

We have seen that the sign of response under sub-minimal stimulus is opposite to that of the normal. Thus, while moderate stimulus induces a retardation of growth, sub-minimal stimulus induces an enhancement of the rate, (p. 224). In the electromotive method, the response under feeble stimulus is galvanometric positivity, instead of the normal negative. In *Mimosa* feeble stimulus induces an expansive erectile response instead of the contractile fall of the leaf, (p. 147). This positive response is more easily observed when the critical point of transition from positive to negative becomes raised by the subtonic condition of the tissue.

It is very remarkable that in the method of resistivity variation we also obtain, under feeble stimulation, a response of opposite sign to that of the normal; that is to say, the resistance of the tissue exhibits an increase, instead of the normal diminution. Figure 309 shows such positive responses under feeble stimulus, by an increase of resistance (down-curve) followed by recovery.

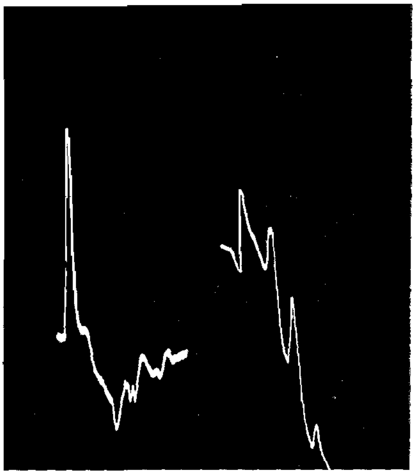

Fig. 310 Multiple response to strong electric and thermal shocks.

EFFECT OF STRONG STIMULUS.

If the intensity of stimulus be gradually increased, the amplitude of normal negative response by diminution of resistance becomes enhanced till a limiting value is reached. Further increase of intensity is then found to give rise to the very interesting

Experiment 329

phenomenon of *multiple response*, the resistance of the tissue undergoing a recurrent variations, analogous to the multiple mechanical and electromotive responses under strong stimulus.

As the strong stimulus gives rise first to a very large response which is followed by a multiple series, it is difficult to obtain a complete record since the first response goes off the photographic plate. It is, however, easy to observe them by watching the alternate movements of the galvanometer spot of light which persist for a considerable length of time. It has sometimes been possible to obtain the multiple response within the plate, by employing a stimulus which is not excessively strong. The record seen to the left of Figure 310 shows five multiple responses, under moderately strong electric stimulus; the record to the right of the figure shows multiple response under thermal stimulus. I have also obtained similar multiple responses under the stimulus of strong light.

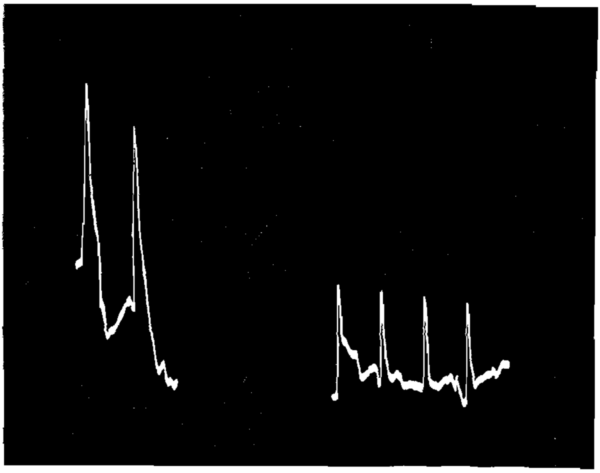

Fig. 311 Effect of CO_2 in depressing response by resistivity variation.

Having studied the responses under feeble, moderate and strong stimuli we shall next observe the characteristic effects of physiological change induced by the action of anaesthetics.

EFFECT OF CARBON DIOXIDE.

We found that prolonged application of carbon dioxide induces a depression of all modes of response. The method of resistivity variation also exhibits similar depression of response. In Figure 311 the first two responses are normal; the introduction of carbon dioxide into the plant-chamber is seen to have induced a marked depression.

Experiment 330

EFFECT OF ETHER AND CHLOROFORM VAPOUR.

Dilute vapour of ether has already been found to induce a marked enhancement in the mechanical and the electromotive response. The response by resistivity variation also exhibits a great increase under the action of this anaesthetic (Fig. 312). The enhanced excitability under dilute chloroform vapour is so great that,

Experiment 331

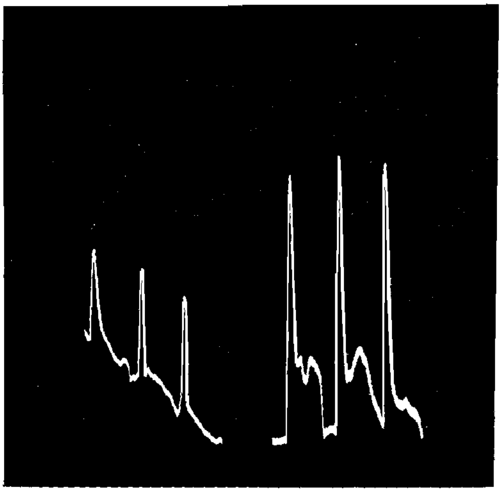

Fig. 312 Effect of dilute ether vapour in enhancing the response by resistivity variation.

a single stimulus often gives rise to a multiple series of responses.

SUMMARY.

The response of normal tissues to electric stimulus is by a diminution of electrical resistance, followed by a recovery.

The response to sub-minimal stimulus is of an opposite sign to that of the normal, *i.e.*, an increase of resistance instead of a diminution.

Strong stimulus gives rise to a multiple series of responses by resistivity variation.

Prolonged action of carbon dioxide induces a diminution in the amplitude of response.

The various characteristics of response by resistivity variation are parallel to those of mechanical response of sensitive plants, the responsive variation of growth in growing organs, and the response of electromotive variation in all vegetable tissues.

Dilute ether vapour causes a great enhancement in the response. The excitability of the tissue is also increased by dilute vapour of chloroform, on account of which a single stimulus is often found to give rise to repeated responses.

LXXI.—THE QUADRANT METHOD OF RESPONSE TO STIMULUS OF LIGHT.

By Sir J. C. Bose,

Assisted by

Apurba Chandra Nag, M.Sc.

We have found in the two previous chapters that modes of stimulation, as diverse as mechanical and electrical, induce an excitatory reaction exhibited by an induced diminution of resistance. We shall now study the effect of the stimulus of light on the resistance of the tissue; a new method of very great sensitiveness has been devised for this investigation, so sensitive indeed as to detect the effect of light of so brief a duration as a hundred thousandth part of a second. This is due to the fact that the galvanometer deflection by this method is not simply proportional to the induced variation of resistance of one arm, but to the product of variations in two arms.

The principle of the method will be understood from the diagram given at the lower end of Figure 313, which represents a leaf blade of *Tropaeolum* in which its four quadrants P, Q, R, S, serve as the four arms of a Wheatstone Bridge. The diagonal connections are made with the battery and the galvanometer respectively. The three contacts with the leaf may be fixed, and the fourth moved slightly to the right or to the left till an exact balance is obtained in darkness, when PQ=RS. One of the pairs of opposite quadrants P and Q is shaded by a double of the balance and the galvanometer deflection is now in an opposite direction.

The reliability and the sensitiveness of the Quadrant Method may thus be tested by obtaining equal and opposite responses under alternate illumination of the two pairs of quadrants; the test in confirmation of the above will be found in records given in Figure 314.

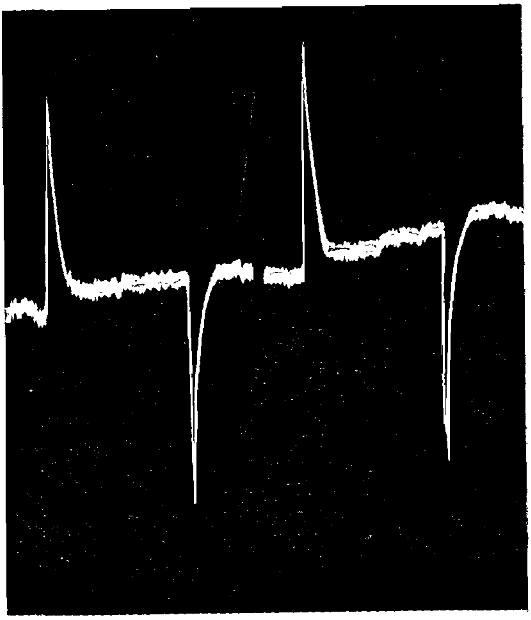

Fig. 314 Equal responses in opposite directions by alternate illumination of the two pairs of quadrant.

After securing such perfect adjustments, the double V-shaped screen is kept fixed, and the leaf mounted in a rectangular dark chamber closed except at the front, which carries a photographic shutter by which one pair of quadrants is exposed to light for a definite duration. The electric connections with the leaf are led to four binding screws; the petiole protruding from the box is dipped in an U-tube filled with water. (cf. right-hand illustration of Fig. 313).

and the response is seen to consist of a priliminary positive twitch followed by a large negative response. indicative of normal diminution of resistance. The leaf exhibited a complete recovery.

EFFECT OF INCREASING INTENSITY OF LIGHT.

Experiment 333

The arc lamp is taken out of the lantern, and the diverging beam employed for the following experiment. As the intensity of light varies as the square of the distance, suitable marks were made on the scale fixed on the table, so that the intensity of light incident on the leaf was increased in the proportion of 1 : 3 : 5 : 7 by bringing the arc nearer the leaf at the particular distances marked on the scale. The duration of exposure was kept the same.

Fig. 317 Effect of carbonic acid gas on response to light. Note preliminary enhancement followed by decline.

The responses under increasing intensities of light in the ratio given above are seen in Figure 316. The resistance is seen to undergo a diminution with the increasing intensity of stimulus.

We shall next study the effects of anaesthetics on response to the stimulus of light.

EFFECT OF CARBON DIOXIDE

After taking a series of normal responses, carbon dioxide was passed into the plant-chamber. This is seen to give rise to a preliminary enhancement of responses followed by increasing depression. (Figure 317). The effect of carbon dioxide is thus the same on all responses under diverse modes of stimulation.

Experiment 334

EFFECT OF DILUTE VAPOUR OF CHLOROFORM.

Dilute chloroform has been shown to induce a preliminary enhancement of response followed by a decline. This anaesthetic is seen to induce a similar effect on response to light; after the introduction of the chloroform vapour, the three successive responses are found to be increased by about 50 per cent; the subsequent responses exhibit a great depression (Fig. 318).

Experiment 335

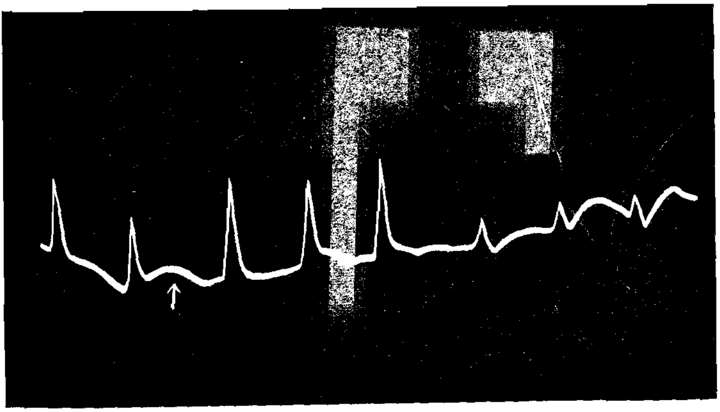

Fig. 318 Effect of chloroform. The preliminary enhancement was followed by a depression.

VARIATION OF PERMEABILITY UNDER STIMULUS.

The excitatory fall of the leaf of *Mimosa* is due to the expulsion of the sap from the excited cells in the pulvinus. This may be due to an active contraction or to an increase of permeability of the protoplasmic lining of the cell. Our present state of knowledge in regard to the mechanism of contraction of vegetable tissue is as incomplete as that of the phenomenon of muscular contraction. According to Schafer, the contraction of a muscle is brought about by a transfer and redistribution of fluid material; the contraction of the pulvinus of *Mimosa* is also due to the transfer of fluids. All movements of living organism whether animal or plant may be said to be effected by essentially the same means, *i.e.*, by the contractile protoplasm, of which the highly specialised form is seen in the muscular tissue of the animal.

It has been supposed that the mechanical response of the pulvinus is not due to active contraction, but to the escape of water from the distended cells by an induced increase of permeability. The observed diminution of the electric resistance of vegetable tissues under stimulus may be regarded as offering some support to the theory of increase of permeability under stimulus.

The high resistance of a tissue has been imagined to be due to the impermeability of the cell membranes to salts, the salt solution being conductors of electric current. The diminution of resistance after stimulation is regarded as due to increase of permeability and resulting escape of fluid containing salts, which confers increased electric conductivity or diminished resistance of the tissue. But this theory does not explain all the facts; (1) for the escape of sap in one direction would produce an increase of conductivity, more or less persistent. But the normal resistance is found restored in the course of as short a time as 2 minutes; (2) it does not explain a temporary increase of resistance, which is often found to be the after-effect of a stimulus (see Fig. 308); (3) it offers no explanation of the multiple response under strong stimulus, where we observe a recurrent diminution and increase of resistance; (4) and finally, the *increase* of resistance induced by feeble stimulus is a further and insuperable difficulty in the way of the above theory.

The permeability variation, according to the above theory, is regarded as selective or one-directioned, by which the fluid is expelled *outwards* from the cell. But this is not a correct interpretation of fact, for there is an alternating phasic change on account of which the sap is not merely expelled *outwards*, but also absorbed inwards; instead of selective permeability in one direction, there are, as it were, alternate directioned changes by which the fluid is periodically expelled and taken in across the boundary of the cell. This is clearly seen in rhythmic cells of the lateral leaflets of *Desmodium gyrans*, where the recurrent down and up movements of the leaflets are associated with periodic expulsion and absorption. This is also the case in the propulsion of sap in plants, which I have shown to be caused by periodic expulsion and absorption of fluid by the active layer of cells in the cortex.

This periodic expulsion and absorption is the common characteristic of all modes of response; I have shown that a continuity exists between the autonomous, the multiple, and ordinary response. In multiple responses under strong stimulus, (*e.g.*, in *Biopytum* leaflet) there is produced a recurrent contraction and expansion concomitant with the periodic expulsion and absorption. The single response under stimulus in ordinary cases also exhibits this periodic change of expulsion with subsequent absorption during recovery.

The facts described above indicate that a simple theory of permeability-variation is not sufficient for a full explanation of the observed phenomena. These and other results point rather to the existance of two definite protoplasmic reactions, which may be described as the A- and the D-effects. The A-effect, usually induced by sub-minimal stimulus, finds outward expression, by induced expansion, increase of turgor, enhancement of the rate of growth, galvanometric positivity and increase of electrical resistance. The D-effect (predominantly induced under stimulus of moderate intensity) is outwardly manifested, on the other hand, by contraction, diminution of turgor, diminished rate of growth, galvanometric negativity and diminution of electric resistance. The following table shows the parallel effects exhibited by diverse modes of response.

TABLE LXV.—SHOWING PARALLELISM IN DIFFERENT MODES OF RESPONSE.

External change	Mechanical response	Variation of growth	Electromotive response	Resistivity variation
Sub-minimal stimulus	Expansion: erectile response	Acceleration of growth	Galvanometric positivity	Increase of resistance
Moderate stimulus	Contraction; fall of leaf	Retardation of growth	Galvanometric negativity	Diminution of resistance
Strong stimulus	Multiple response	Multiple response	Multiple response	Multiple response
Carbonic acid gas	Diminished response	Diminished response	Diminished response	Diminished response
Vapour of ether	Enhanced response	Acceleration of growth	Enhanced response	Enhanced response

SUMMARY.

In the Quadrant Method for determination of variation of resistance under the stimulus of light, the quadrants of the lamina serve as the four arms of the Wheatstone Bridge. One of the two pairs of opposite quadrants is shaded by a screen. Exposure of the other pair to light gives rise to a responsive variation of resistance.

The method is found to be extremely sensitive, response being obtained of the effect of light from a single spark.

The response to the stimulus of light is by a diminution of resistance, followed by recovery on the cessation of light.

Increasing intensity of light induces a corresponding diminution of the resistance of the tissue.

Anaesthetics like carbon dioxide or dilute chloroform induce a preliminary enhancement of response followed by depression.

All modes of stimulation, mechanical electrical or photic, give rise to similar response by diminution of electric resistance.

Feeble stimulus gives rise to the opposite change of an increase of electric resistance.

A phasic change is observed by which the sap becomes alternately expelled from, and absorbed by, the cell. The expansion under feeble stimulus is associated with absorption and contraction under stronger stimulus, with expulsion.

The indications of effects induced by external change given by the method of resistivity variation are similar to those obtained from responsive variations of electromotive force, of the rate of growth, and of mechanical response. They are thus different expressions of the fundamental protoplasmic change in response to external variation.

These changes may be generally described as the A- and the D-effects. The former is exhibited by expansion, enhancement of the rate of growth, positive electromotive change and the increase of resistance; the latter is expressed by contraction, retardation of growth, galvanometric negativity and diminution of electric resistance.

LXXII.—THE SELF-RECORDING RADIOGRAPH.

By Sir J. C. Bose,

Assisted by

Narendra Nath Neogi, M.Sc.

A diurnal periodicty is generally exhibited in the various activities of the plant; a daily periodicity is also shown in the movements of different plant organs. These diurnal periodicities must be related to the daily variation of temperature and the recurrent changes of light and darkness; they must be thus brought about by the algebraical summation of effects induced by variation temperature and of light. It would thus be impossible to analyse the phenomenon unless a continuous record of changes in the intensity of light is secured with the same exactitude as the variation of temperature. As regards these two factors, the effect induced by the rise of temperature is often antagonistic to that of increasing intensity of light. Thus a rise of temperature enhances the rate of growth up to an optimum; light, on the other hand, acts as a stimulus retarding the normal rate of growth. Variation of temperature affects the organ as a whole, whereas light may act unilaterally, depressing the rate of growth of the particular side subjected to the action of light.

For a full analysis of diurnal periodicity in plants, it thus becomes necessary to devise means for continuous record of variation of temperature and the changing intensity of light. As regards variation of temperature, a simple and reliable type of thermograph was described in one of the volumes of this series, by which it is easy to obtain a continuous record of the variation of temperature throughout the day and night. No apparatus is, however, available at present for the continuous registration of variation of the intensity of light.

THE SELENIUM CELL.

The method for obtaining record of intensity of light and its variation depends on utilising the property of a substance sensitive to light. Selenium is well known for the characteristic diminution of its electric resistance under illumination. Thus a definite deflection is produced in a galvanometer when the selenium cell is placed in the dark in series with a battery of voltaic cells. Exposure to light, causing a diminution of resistance, gives rise to an increase of deflection. The variation in the deflection of the galvanometer thus indicates the variation in the intensity of light. Several difficulties are, however, encountered in practice in obtaining a continuous record for the whole day. The resistance of selenium undergoes a change under the continued action of an electric current; this is due to polarisation caused by the current, which increases with the strength and the duration of the current. But the effect of polarisation is negligible, if the current be feeble and of short duration. Another difficulty, which might possibly interfere with the accuracy of the readings is the effect of daily variation of temperature on the normal resistance of the selenium cell. This effect may be eliminated by observing, at different hours of the day, the difference of the resistance of the cell (1) in the dark, and (2) after exposure to light. Finally, we have to devise some means for automatic record of the galvanometric deflection under changing intensities of light.

THE RADIOGRAPH.

The difficulties enumerated above have been completely removed by the following devices :

a. The Wheatstone Bridge for balancing electric resistance of the selenium cell in dark and its upset on exposure to light.

b. The arrangement of three electric keys which are automatically put on and off in regular sequence and at predetermined intervals.

c. The Self-recording Galvanograph.

THE WHEATSTONE BRIDGE

This is diagrammatically represented in B, (Fig. 319). The resistance of the particular selenium cell S is 76,000 ohms in the dark. An approximately equal resistance is placed in the second arm of the bridge. A rheostat having a large number of turns of fine wire with a sliding contact is used for the two variable arms of the bridge, diagrammatically represented by a straight line. An approximate balance is obtained when the sliding contact is in the middle ; a slight movement to the right or to the left secures the exact balance when the galvanometer deflection is reduced to zero. The balance is upset when the selenium cell is exposed to light and the resulting deflection gives a measure of the intensity of light.

THE AUTOMATIC KEYS.

After previous adjustment of the balance in the dark the electric circuit is completed by the closure of key K_1 after which the selenium cell is exposed to light by an automatic door is seen in the diagram immediately above the dark box. In reality it is at the upper end of a vertical tube the inside of which is coated with lamp-black to prevent side reflection. The light that falls on the selenium cell is thus from a definite area of the sky. The intensity of light from the sky at different periods of the day causes deflection of the galvanometer which is proportional to that intensity. The maximum deflection of the galvanometer employed is attained in the course of 3 seconds after the exposure.

The third key K_3 is for completion of spark circuit R for record of the maximum galvanometric deflection, three seconds after the exposure of the selenium cell. This key actuates a sparking coil R, the vibrating interrupter of which is not shown in the figure. The spark, thus produced, punctures the maximum deflection of the galvanometer index on a moving piece of paper attached to the plate M.

The successive closure and opening of the keys are made automatically and in proper sequence by means of a clockwork, the whole process being repeated at intervals of 15 minutes.

THE GALVANOGRAPH.

We now come to the most difficult problem concerning the automatic record of the galvanometer deflections. This may be secured without great difficulty by means of photography. A spot of light reflected from the galvanometer mirror may be allowed to fall on a photographic plate which descends at an uniform rate by clockwork. This, however, entails the use of a dark room and subsequent development of the plate. The trouble was avoided by the device of direct record of the galvanometer deflection by means of electric sparks.

The sparking method has been previously employed in which the deflected index of the galvanometer in connection with one electrode of an induction coil leaves a spark record on a moving piece of paper. Several difficulties are, however, encountered in the employment of this method with a highly sensitive galvanometer. There is a liability of leakage of the high tension current into the galvanometer circuit. Secondly, the discharge of the spark gives a backward kick to the index by which the normal deflection undergoes an unknown variation.

The above difficulties are removed in the following manner. The moving coil of the sensitive D'Arsonval galvanometer, has a long glass index I, at right angles to the plane of the coil. The glass index is coated with shellac varnish to render it highly insulating. The index is projected to a short distance on the opposite side, for attachment of a counterpoise; this takes the form of a vertical vane of mica which acts as a damper. The galvanometer itself is of an aperiodic type, and the addition of the damper makes it perfectly dead-beat. The sensitveness of the galvanometer is such that a micro-ampere of current produces a a deflection of 10 mm. of the index. The recording index has attached to it a short vertical piece of thin platinum wire pointed at its two ends; this end of the index moves between a sheet of metal M, and a semi-circular piece of narrow metal sheet C. The metal sheet M is mounted on wheels and moves at an uniform rate by clockwork. Record is made by sparks. One electrode of the sparking coil is in connection with C, and the other with M. The sparking thus takes place simultaneously, above and below the vertical and double-pointed platinum wire carried at the end of the index. There is thus no resultant kick, and the index remains undisturbed. The sparking, as previously stated, takes place three seconds after exposure of the selenium cell to light, by which time the deflection reaches its maximum. The record thus consists of successive dots at intervals of 15 minutes, the dots representing the maximum deflections of the galvanometer corresponding to the intensity of light.

The record given in Figure 320 was taken about the end of January; the sun rose at about 6-45 A.M. and set at

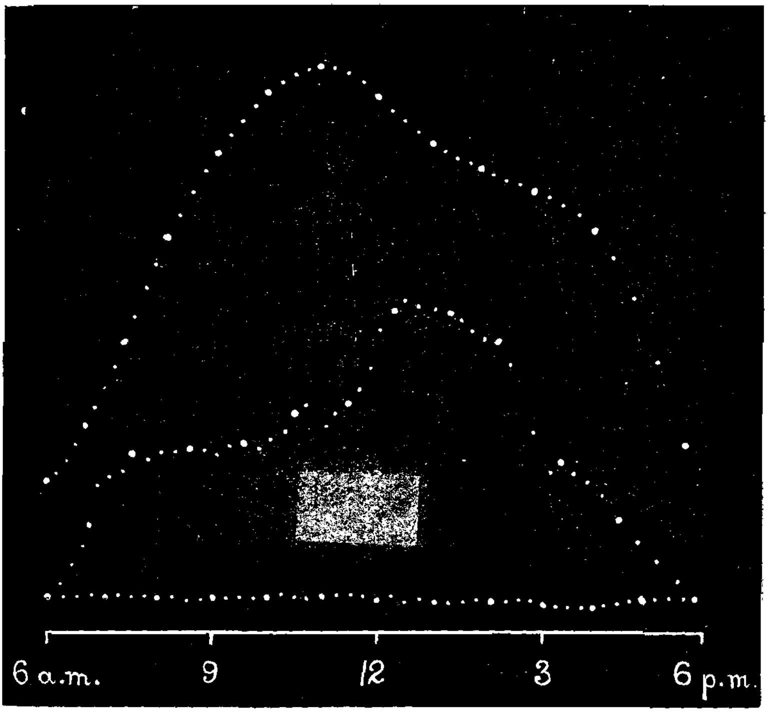

Fig. 320. Radiograph of variation of intensity of light from the sky during 12 hours in winter. The upper record shows the variation on a bright day, the maximum intensity being attained at 12 noon. The lower record exhibits irregular variation on a cloudy day. The horizontal record above the base line shows that the electric resistance of selenium cell is practically unaffected by variation of temperature. Successive thin dots at 15 minutes' interval, thick dots at intervals of an hour.

5-30 P.M. The twilight is very short in the tropics; the sky is feebly lighted about 6 A.M.: it becomes dark about 6 P.M. The record shows the intensity of light to be exceedingly feeble at 6 A.M. The rise in the intensity was rapid, attaining the maximum at 12 noon. This will be designated as the light-noon. The intensity of light then declined at a rate slower than the rise. But after 5 P.M. the fall of intensity was extremely rapid.

It was stated that there is a possibility of change of resistance induced by diurnal variation of temperature. In order to determine the extent of this variation, a spark record was also obtained before exposure to light. The dotted record near the base shows that the resistance remained practically constant, inspite of the variation of the temperature.

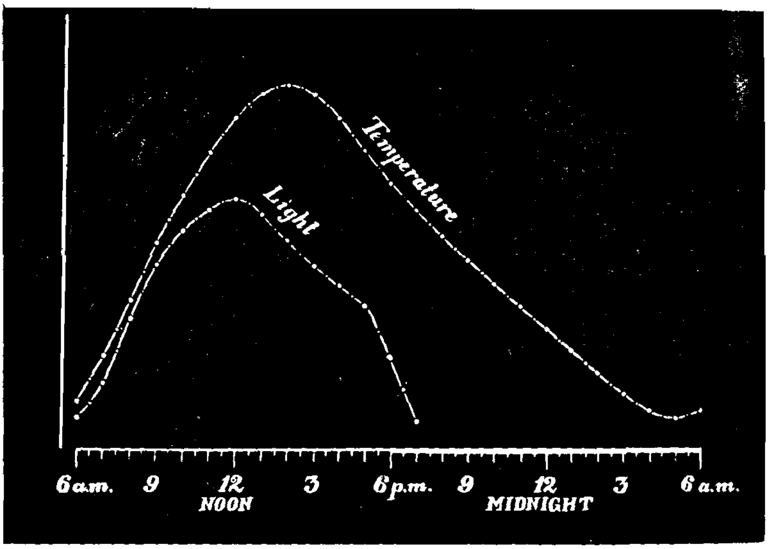

Fig. 321. Record of diurnal variations of light and of temperature in summer.

An important point arises as regards the diurnal variation of light and of temperature, and determination of their periods of maximum and minimum. For this purpose records of diurnal variations of temperature and of light were taken on the same day in summer with the thermograph and the radiograph. The two curves are given in Figure 321.

It will be seen that while the maximum intensity of light is at 12 noon, the thermal maximum is at about 2 P.M. The thermal noon is thus two hours later than the light-noon. Light disappears at night from 6 P.M. to 6 A.M., that is to say, the period of minimum is prolonged for 12 hours. But the fall of temperature is gradual, and the minimum is attained at about 5 A.M. which is the thermal dawn. The characteristic variations of these two important factors should be borne in mind, since the diurnal movements of plants are modified by the algebraical summation of the effects of light and of temperature.

It is sometimes desirable to carry out researches during a period when the intensity of light remains approximately constant. This period is found to be between 11 A.M. and 1 P.M. for the variation is only ± 5 per cent. of the mean.

The record given of the diurnal variation of light is true of days when the sky is clear. But the passage of cloud causes change in the intensity which is accurately recorded by the Radiograph. A record of such irregular variation in a stormy day is given in the lower record of Figure 320.

SUMMARY.

The Radiograph gives a record of the diurnal variation of light. On a clear day in January, the intensity was found to increase rapidly from 6 A.M. to 12 noon, when it reached its maximum. Light began to decline slowly up to 5 P.M., the decline being less rapid than the rise at the forenoon. The fall of intensity was extremely rapid after 5 P.M.

Any fluctuation of light due to passage of a cloud is accurately recorded by the Radiograph.

The fall of intensity of light is abrupt after 5 P.M., and the minimum persists from 6 P.M. to 6 A.M. In contrast to this, is the periodic variation of temperature which attains its maximum at 2 P.M. and its minimum at 5 A.M. The former may be regarded as the thermal noon, and the latter as the thermal dawn.

LXXIII.—ON A VEGETABLE PHOTO-ELECTRIC CELL.

By Sir J. C. Bose,

Assisted by

Guruprasanna Das, L. M. S.

Vegetable tissues have been shown to exhibit an excitatory reaction under the stimulus of light, the response being by contraction (p. 208) and by diminution of resistance (p. 816). The corresponding electromotive response under excitatory action of light would be by an induced change of *galvanometric negativity*. This normal electric response under the stimulus of light has been demonstrated in my work on Comparative Electro-physiology.

Some observers have, however, obtained in green leaves a response of galvanometric positivity. This anomalous result would seem to indicate that the response to light is of an opposite sign to that induced by other modes of stimulation. It would, however, be shown that the normal response to light is by induced galvanometric negativity, the positive response being brought about under certain specific conditions.

NORMAL RESPONSE TO LIGHT.

For obtaining the normal response, we take a vigorous leaf and pin it on a paraffined block of wood. Two pieces of thin muslin in connection with non-polarising electrodes are spread over two areas of the leaf A and B; when these pieces of muslin are

Experiment 336

moistened with normal saline, they become practically transparent. When light from an arc lamp is thrown on A, that area becomes galvanometrically negative and the direction of the responsive current is in the direction of GAB. Light thrown on B (A being shaded) causes a response in the opposite direction, (left illustration Fig. 322).

The fact, that the electromotive response under light is the same as that under any other form of stimulus such as mechanical, is demonstrated as follows. The moist piece of cloth on A is rubbed against the surface of the leaf by means of a glass rod; or the leaf may be struck with a glass hammer. In both these cases, A becomes galvanometrically negative, the direction of the current of response being the same as when A is stimulated by light.

Having given a simple demonstration of the fundamental reaction, we shall now describe the photo-electric cell made of two pieces of leaf. In the experiment described above, the resistance of the circuit is very great, first on account of the high resistance of the two non-polarisable electrodes, and secondly because of the resistance offered by the leaf. The non-polarisable electrode, moreover, is a source of much trouble; an attempt was therefore made to discard it, and employ means for diminishing the resistance of the circuit. For the following experiments we employ the leaf of *Musa sapientum* which are divided into two longitudinal halves by a slit along the thick midrib. Two pieces of leaves are thus obtained about 10 × 10 cm. which are hung parallel and separated from each other in a rectangular glass vessel filled with normal saline; the distance between the two leaves is 3 cm. Two gold wires are thrust through the length of the two divided midribs; they serve as the external electrodes of the photo-voltaic cell, leading to the galvanometer G. The glass trough is placed inside a rectangular wooden chamber with two hinged doors on opposite sides, by which the leaf A or B could be alternately exposed to light (Fig. 322). When the doors are closed, A and B are in darkness; they are practically iso-electric, there being no current in the galvanometer. But exposure of A to light gives rise to a difference of potential between A and B, A becoming galvanometrically negative, the resulting deflection being in one direction. Exposure of B gives rise to a responsive deflection in the opposite direction. The two leaves serve as the two plates in a voltaic cell; but unlike ordinary voltaic cell with elements of different metals, the two plates of the vegetable cell are made of two halves of the same leaf, the electromotive force being generated by the excitatory action of light on one of the two half leaves. The advantages of this method of obtaining electromotive response are: (1) that the troublesome employment of the non-polarisable electrodes with their high resistance is dispensed with; (2) that the area of the surface of the leaf exposed to light is considerably increased; (3) that the electric resistance of the circuit is greatly decreased, since the interposed resistance is that of normal saline about 3 cm. thick with a broad section of 100 square cm.; and

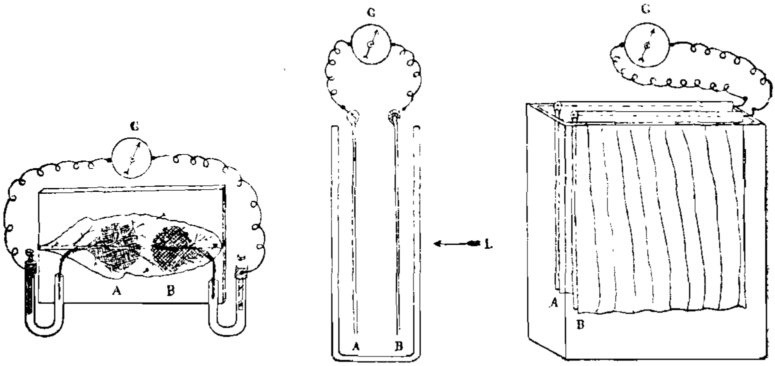

Fig. 322. Diagrammatic representation of a vegetable photo-electric cell. The first illustration shows electric connections with two portions of the leaf A, B, by non-polarisable electrodes The second and third illustrate (side and front views) of the photo-voltaic cell made of two half-leaves.

(4) that alternate and opposite responses may be obtained by successive exposures of the two leaf-plates to the parallel beam of an arc lamp, this being easily secured by turning the rectangular plant chamber round a revolving base.

RESPONSE OF THE LEAF TO LIGHT.

Experiment 337

The photo-voltaic cell thus constructed is stimulated by light from an arc lamp which passes through a trough of alum solution for absorption of the heat rays. Successive exposures are made for 10 seconds and records obtained on a moving photographic plate. The normal responses are uniform, exhibiting induced galvanometric negativity as seen in the up-curves. On the cessation of light there is a complete recovery; in fact, the recovery shows an overshooting towards galvanometric positivity from which it returns almost to the original zero position before stimulation. There is a curious resemblance of this after-effect of electromotive variation to that of resistivity variation (see Fig. 308); both the records indicate that stimulus often gives rise to dual effects, a negative variation or D-effect followed by a positive variation or the the A-effect.

POSITIVE RESPONSE TO LIGHT.

We shall next consider the anomalous result which sometimes occurs, namely, the positive response to light. It has been shown (p. 810) that a positive response occurs under a stimulus below the critical intensity, and that this critical point is low in highly excitable tissues, whereas it is relatively high in others in condition of depressed excitability. It has been further shown (p. 757) that while the excitability is relatively high at a certain age of the specimen, it is lowered when the tissue is either very young or very old. We may, therefore, expect that the same stimulus which evokes a negative response in a vigorous middle-aged leaf of *Musa*, would give rise to a positive response in a very young leaf or in a leaf which is becoming yellow with age.

Experiment 338

The above anticipations have been found verified in the following experiments. In Figure 324 is seen the positive response of a very young leaf. *Figure* 325 shows similar positive response given by a very old leaf. There is an additional element which tends to produce a positive response of which reference will be presently made.

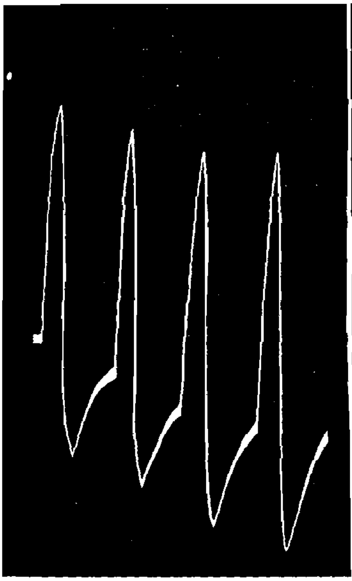

FIG. 323

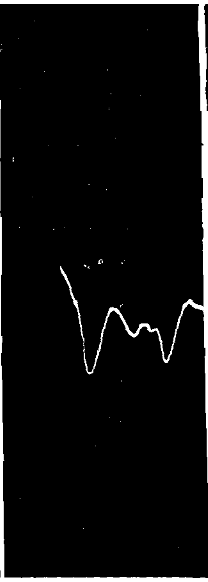

FIG 324

FIG. 325

Fig 323. Normal electromotive response in a vigorous specimen. Note the transient positive after-effect.

Figs. 324 and 325. *Abnormal positive response in a very young* and in a very old specimen.

Experiment 339

It has been shown that the reaction under light, is within limits, proportional to the quantity of light, that is to say, on the intensity multiplied by duration of light (p. 345). Keeping the intensity constant, we obtain responses to increasing durations of light, of 5 seconds, 10 seconds, and 15 seconds. The responses are seen to undergo an increase with the increased duration of exposure (Figure 326). But this increase does not go on indefinitely, for the continuous action of light causes a maximum negative response beyond which a decline sets in. There must, therefore, be an opposing element which tends to neutralise the normal excitatory D-effect.

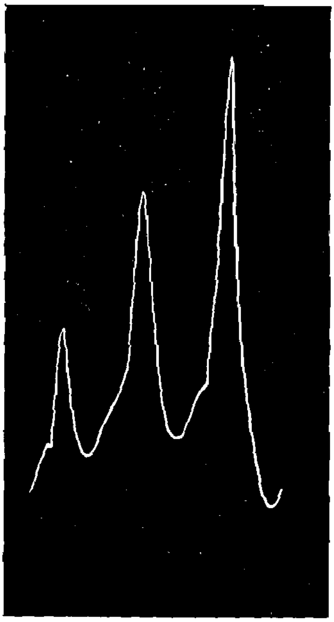

Fig. 326. Effects of increasing durations of exposure of 5, 10, and 15 seconds.

The existance of this opposing A-reaction has already been seen in the transient after effect in Figure 323. We have already seen that stimulus in general, induces both the D- and A-effects; in excitable specimens the D-effect is predominant and therefore, masks the A-effect; this positive A-effect is, however, exhibited under feeble stimulus or even as an after-effect of strong stimulation.

There are again certain conditions which are specially favourable for the exhibition of the A-effect. When the green leaf has an abundant supply of chlorophyll, the photosynthetic process of building up becomes specially marked. I have thus obtained under the action of light, a positive response with the green leaf of *Lactuca sativa* in which chlorophyll is present in such a great abundance.

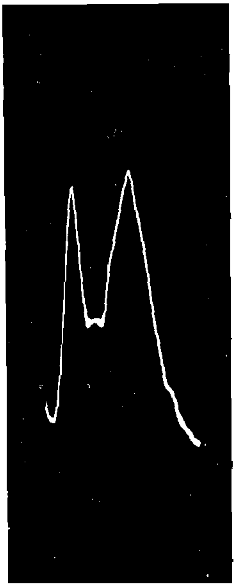

Fig. 327. After-effect of light. *The maximum negative is reversed* and attains a balance in the horizontal portion of the curve Stoppage of light causes the unmasking of the negative followed by recovery.

The fact that positive response is associated with assimilation is proved by my recent experiments on photo-electric response of water plants. The photosynthesis under light is here independently demonstrated by profuse evolution of oxygen. These water plants exhibit marked positive electric response during strong illumination, the response disappearing on the cessation of light.

EFFECT OF CONTINUED ACTION OF LIGHT.

Experiment 340

The positive element in the response may be indirectly demonstrated even in the normal *Musa* leaf. In Figure 327 is seen the effect of continuous action of light which at first exhibits the predominant negative response attaining a maximum; the positive element now begins to increase with the duration of light; at a certain stage, the two elements, D and A, balance each other the resulting response being horizontal. On stoppage of light, the antagonistic A element ceases to be active, while D appears to be persistent. The result is a sudden unmasking of the negative, held in balance during exposure to light. A negative response with subsequent recovery thus occurs on the cessation of light (Fig. 237).

SUMMARY.

A photo-electric cell is constructed of two half-leaves of *Musa*, supported parallel, in a trough filled with normal saline. The two halves act as two metallic plates of a voltaic cell. The resistance of the circuit is thus greatly reduced.

An electromotive force is generated by exposure to light, the stimulated leaf becoming galvanometrically negative; there is a recovery on the cessation of light.

In vigorous leaves, increasing duration of light gives rise to increasing negative response which tends to reach a limit.

The excitability of a very young or a very old leaf is below par; the response in such cases is by galvanometric positivity.

On account of photosynthesis there is a positive element n the response which is often masked by the predominant egative. The positive is often found as an after-effect in he normal negative response. Under continued action of ght the negative is opposed by the increasing positive, bringing about a condition of balance. On the stoppage of light the masked D-effect exhibits itself as a short-lived negative response.

LXXIV.—GENERAL REVIEW

OF

VOLUMES I TO IV.

The movements of plant organs under the manifold and changing forces of the environment are extremely varied and complicated. The most important of these are the effects of variation of temperature, of the stimuli of contact, of gravity and of light. The effects of these diverse agencies are not always concordant, but often contradictory. The same stimulus is found, moreover, to produce sometimes one effect, and at other times precisely the opposite. It has thus appeared almost hopeless to discover an underlying unity in phenomena so extremely diverse. A tendency has thus arisen towards the belief that it was not any definite physiological reaction, but the individuality of the plant that determined the choice of movement for its ultimate advantage. Teleological argument of this character confuses the real issue, and diverts attention from the discovery of the fundamental physiological mechanism. Terms and phrases have been employed for different movements, such as positive heliotropism when the organ turns towards, negative heliotropism when it moves away, and dia-heliotropism when it places itself at right angles to the direction of light. Similarly the terms positive and negative geotropism have been used to denote the movement towards or away from the earth. These terms offer no real explanation of the phenomena, and their use, as pointed by Bayliss, have proved to be " mischievous, leading to the belief that new knowledge has been obtained when a phenomenon is described by a name derived from the classical tongue instead of in English."

The advance of physiology of plant-movements has been delayed, mainly from the lack of definite knowledge in regard to (1) the fundamental reaction induced by different forms of stimuli, (2) the modification of the effect brought about by changes in the tonic condition of the tissue, (3) the different effects of feeble, moderate, and strong stimuli, and (4) the variation of effect which arises from the direct and indirect applications of stimulus.

As regards the first, it has been thought that the effects of different stimuli are specifically different. In reality there is no such difference, for the investigations described in these volumes show that all stimuli induce similar excitatory reaction by contraction. Perception of stimulus and the consequent reaction arises from the disturbance of the sensitive protoplasm. Though certain anatomical structures, such as tactile hairs and others facilitate the perception of a particular form of stimulus by causing deformation of the sensitive protoplasm in an affective manner, yet all forms of stimuli are found to induce similar reactions, as exhibited by contraction or by the concomitant response of galvanometric negativity.

The second point relates to the modifying influence of tonic condition; it has been shown that while in the normal condition of the tissue, the response is by *contraction*, in a sub-tonic condition it undergoes a reversal of sign, the response being by expansion.

In regard to the effects induced by varying intensities of stimulus, it has been found that a feeble stimulus induces an expansive reaction, in contrast with the contractile effect of a moderate stimulus. Strong stimulus, again has been shown to give rise to a multiple series of responses.

And finally, the existence of a very important factor had not previously been suspected, namely, the differing effects induced by change in the point of application of stimulus. It has been shown that while direct stimulus induces a diminution of turgor and contraction, indirect stimulus causes the opposite effect of increase of turgor and expansion (p. 139). The explanation of this is found in the fact that owing to the semi-conducting nature of the vegetable tissue, the excitatory impulse from a distance undergoes rapid diminution, and becomes minimal when it reaches the responding organ; but minimal stimulus is shown to induce an effect which is of opposite sign to that of normal intensity (p. 809). In the second place, the local contraction caused by stimulus causes an expulsion of fluid giving rise to a hydraulic wave which forces water into the responding organ at a distance and causes an expansion.

The following generalisations have been experimentally established :—

I. *Under normal conditions, all forms of stimuli of moderate intensity give rise to* negative *responses, seen exhibited by contraction, diminution of turgor, fall of leaf, electromotive change of galvanometric negativity and a diminution of electric resistance.*

II. *Feeble stimuli give rise to responses which are* positive, *i.e., of opposite sign to the normal negative.*

III. *In the sub-tonic condition of a tissue the response under moderate stimulus is* positive.

IV. *Strong stimuli give rise to* multiple responses.

V. *All forms of Direct Stimuli induce* contraction; *Indirect Stimuli, on the other hand, cause* expansion.

The diverse movements of plants are explained on the principle broadly stated above. Some of the more important investigations described in the four volumes may now be classified as follows.

1. Similarity of response in pulvinated, growing, and non-growing organs.

(*a*) Response of *Mimosa*.
(*b*) Diurnal variation of moto-excitability.
(*c*) Response of ordinary plants.
(*d*) Response of growing organs.

2. Different methods of detection of negative and positive responses.

(*a*) Mechanical response.
(*b*) Electromotive response.
(*c*) Response by variation of electric resistance.
(*d*) Permeability variation under stimulus.

3. Identical excitatory reaction under different modes of stimulation.

4. Positive response under feeble stimulus.

5. Modification of response in sub-tonic tissues.

6. Opposite effects of direct and indirect stimulation.

7. Multiple response under strong stimulus, and the continuity of multiple and autonomous responses.

8. Autonomous response, and the movement of growth.

9. Effect of anaesthetics on various responses.

(*a*) Carbon dioxide on electric response, on growth, and on geotropic response.
(*b*) Ether vapour on electric response, on growth, and on geotropic response.
(*c*) Chloroform vapour on *Desmodium* pulsation, on growth, on geotropic response, and on electric response.

10. Death-spasm in plants and the transmission of death-excitation.

11. Nervous impulse in plants.

12. The Nervous and the Hydraulic reflex.

13. Tropic movements under unilateral stimulus.

14. Mechanotropism.

15. Phototropism.

(*a*) Quantitative relation.
(*b*) Negative phototropism.
(*c*) Effects of different rays of the spectrum.
(*d*) The complete phototropic curve.
(*e*) Phototropic torsion.

16. Dia-heliotropic adjustment of leaves under transmitted excitation.

17. Photonastic curvatures.

18. Night and day movements of plants.

(*a*) Thermonastic movements.
(*b*) Thermo-geotropism.
(*c*) The Self-recording Radiograph.
(*d*) Movement due to alteration of light and darkness.
(*e*) Diurnal movement of *Mimosa*.

19. Geotropism.

(*a*) Mechanical response.
(*b*) Electric response.
(*c*) Explanation of opposite reactions at upper and lower sides.
(*d*) Geotropic excitations at various angles.
(*e*) Effect of narcotics.
(*f*) Effect of variation of temperature.
(*g*) Localisation of geo-perceptive layer.
(*h*) Dia-geotropism of dorsi-ventral organs.
(*i*) Geotropism of roots.

The main results of these enquiries may now be briefly outlined under the above headings.

RESPONSE IN PULVINATED, GROWING, AND NON-GROWING ORGANS.

Mechanical response of Mimosa.—Both the upper and the lower halves of the pulvinus are sensitive, but the lower half is about 80 times more excitable than the upper. Diffuse stimulation induces responsive fall by the greater contraction of the lower half. For a long time it has been assumed that the expansive force of upper half of the pulvinus and the weight of the leaf are important factors in the responsive fall of the leaf. Experiments carried out after cutting off the sub-petioles, and the amputation of the upper or the lower half of the pulvinus show that the responsive movement is mainly due to the active force of contraction exerted by the lower half of the pulvinus (p. 85).

Diurnal variation of moto-excitability of Mimosa.—The moto-excitability of *Mimosa* undergoes a diurnal variation. The plant is almost insensitive in the morning; the excitability is gradually increased to a maximum at 1 P.M., which remains constant for several hours. A continuous fall of excitability begins in the evening, the minimum being reached in the morning. This variation of excitability is primarily due to the diurnal change of temperature, and in a minor degree to variation of light (p. 71).

Response of ordinary plants.—The distinction between sensitive and ordinary plants is arbitrary, since sensitiveness can be demonstrated throughout plant life. Thus radial organs exhibit a shortening of length under stimulus. The characteristics of the response of ordinary plants are the same as those of the sensitive *Mimosa* (p. 37). As the different flanks of the radial organs are equally excitable, there is no lateral movement under diffuse stimulus. In a radial tendril a physiological anisotropy is, however, induced by the action of stimulus on one side of the organ. In such a curved tendril, the concave side is less excitable than the convex. Diffuse stimulus tends to straighten the curved tendril by greater contraction of the convex side (p. 41). Under geotropic action, a radial organ is rendered temporarily anisotropic; diffuse stimulus then causes a responsive movement by which the curved organ becomes straightened. The temporary anisotropy may be neutralised and reversed by inverting the organ, the response undergoing corresponding reversal (p. 681).

Response of growing organs.—By means of the High Magnification Crescograph the normal rate of growth and its induced variation are determined in the course of a few seconds. The magnification thus obtained may be as much ten thousand times, while the Magnetic Crescograph can give an amplification up to ten million times, thus enabling us to observe and measure the rate of growth, and its slightest variation. The effect of stimulus is found to induce an incipient contraction, exhibited by a diminution of the rate of growth: this retardation increases with the increasing intensity of stimulus, culminating even in an actual shortening of the organ (p. 166).

The sensitiveness of these methods for detection of induced variation of growth can be yet further increased by the use of the Balanced Crescograph. In this the movement of growth upwards is exactly compensated by an equal movement of the plant downwards, with the result that the record remains horizontal. The effect of an external agent is immediately detected by the upsetting of the balance; up-record representing acceleration above normal, and down record, the opposite effect of depression. The sensitiveness of the method of Balance is so great as to enable us to detect the retardation of growth induced by a single flash of light lasting for about a hundred thousandth of a second (pp. 263, 325).

DIFFERENT METHODS OF DETECTION OF NEGATIVE AND POSITIVE RESPONSES.

It is convenient, and often necessary, to have at our disposal independent methods of detection of excitatory reaction in plant tissues. I have shown elsewhere* that every plant, and every organ of every plant exhibits excitatory response by an induced change of galvanometric

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* Responses in the Living and Non-Living, (1902).

negativity. That the electromotive response is but a different expression of protoplasmic excitation has been shown by obtaining a simultaneous record of mechanical and electrical response of *Mimosa* (p. 763). Another method has also been described by which the excitatory reaction is detected and recorded by the induced diminution of the electric resistance of the tissue (pp. 796, 805). The Quadrant Method devised for obtaining response by change of electric resistance is found to be extremely sensitive.

NEGATIVE AND POSITIVE RESPONSES.

There are two fundamental reactions distinguished as *negative* and *positive* which underlie all physiological variation. The outward manifestations of the excitatory negative are, (a) diminution of turgor, (b) contraction, (c) fall of motile leaf, (d) diminution of the rate of growth, (e) electromotive change of galvanometric negativity, and (f) diminution of the electric resistance. While the positive reaction is associated with, (a) increase of turgor, (b) expansion, (c) erectile movement of the motile leaf, (d) increase of the rate of growth, (e) electromotive change of galvanometric positivity, and (f) increase of electrical resistance. The excitatory effect is seen in response to moderate stimulus of all tissues in normal vigorous condition. The positive effect is demonstrated by irrigation of the plant, with the resulting ascent of sap by which the turgor of tissue is increased. The same effect may also be produced by application of hydrostatic pressure. In another aspect, the negative and the positive responses are associated respectively with the breakdown, D-change, and the building up, A-change. Stimulus induces both D- and A-changes, the separate existence of which has been demonstrated.

The closest parallelism has been established between the results obtained with mechanical and electrical responses of non-growing organs under stimulus, and the responsive variation of growth. Circumstances which give rise to negative mechanical and electrical responses also give rise to negative variation or retardation of the rate of growth. Other circumstances which cause positive mechanical and electric responses bring about positive variation or enhancement of the rate of growth. The physiological machinery is alike in pulvinated, non-pulvinated, in growing, and in non-growing organs.

Rise of temperature, within limits, induces an expansion, and an acceleration of the rate of growth. The reaction induced by a rise of temperature is often antagonistic to that induced by stimulus.

Mechanical response.—The negative response is seen in the fall of the *Mimosa* leaf and in the retardation of the rate of growth (p. 197). That the positive response due to the enhancement of turgor is shown by the erectile movement of the leaf of *Mimosa* (p. 39), and by the enhancement of the rate of growth (p. 190).

Electromotive response.—The normal excitatory response of galvanometric negativity has been shown to occur under mechanical stimulus (p. 836), under electric stimulus (p. 744) and under stimulus of light (p. 838).

I have in my later experiments found that an enhancement of turgor gives rise to an electromotive change of galvanometric positivity.

Both the D- and A-changes occur under the action of stimulus; since the excitatory D-reaction is, under normal conditions, relatively predominant the negative electric variations masks the positive. The positive A-change may, however, be unmasked on the cessation of stimulus, when it is exhibited as a short-lived positive after-effect (p. 838). Under continuous stimulation by light the increasing A-effect neutralises the negative; on the stoppage of light the balanced D-effect is unmasked (p. 842) with resulting negative response. I have recently succeeded in obtaining he pure assimilatory response of galvanometric positivity under the action of light in actively photosynthetic water plants like *Hydrilla verticillata.* Here active assimilation is imultaneously exhibited in two different ways: (1) by volution of oxygen, and (2) by the positive electric variation.

Response by variation of electric resistance.—The excitatory negative reaction has been demonstrated by the nduced diminution of electric resistance under mechanical stimulus (p. 801), under electric stimulus (p. 808), and under he stimulus of light (p. 816). In the Quadrant Method he two opposite quadrants are shaded, and illumination of he unshaded quadrants upsets the previously balanced resistance. The sensitiveness of the method is so great that t detects and records the diminution of resistance induced by the almost instantaneous flash of light given by a single electric spark (p. 817).

Contraction and permeability variation.—The excitatory fall of the leaf of *Mimosa* is due to the expulsion of the sap from the excited cells in the pulvinus. This may be due to an active contraction or to an increase of permeability of the protoplasmic lining of the cell. According to Schafer, the contraction of a muscle is brought about by a transfer and redistribution of fluid material; the contraction of the pulvinus of *Mimosa* is also due to the transfer of fluids. All movements of living organism, whether animal or plant, may be said to be effected by essentially the same means, *i.e.*, by the contractile protoplasm, of which the highly specialised form is seen in the muscular tissue of the animal. It has been shown that a simple theory of permeability variation is not sufficient for a full explanation of the observed phenomena (p. 820). These rather point to the existence of two definite protoplasmic reactions, which may be described as the A- and the D-effects.

IDENTICAL EXCITATORY REACTION UNDER DIFFERENT MODES OF STIMULATION.

Among the different forms of stimuli are: contact and friction, prick and wound, induction electric shock or shock of condenser discharge, the 'make' of an electric current at the kathode, the action of certain chemical agents, the action of the rays of light from the more refrangible portions of the spectrum, the infra-red thermal radiation, the electric radiation, and the action of gravity.

Mechanical and electrical stimuli alike cause a fall of the leaf of *Mimosa*, a diminution of the rate of growth (p. 239), an electromotive change of galvanometric negativity (p. 744), and a diminution of electrical resistance of the tissue (p. 808). Stimulus of light causes the fall of *Mimosa* leaf (p. 245), retardation of the rate of growth p. 206); positive tropic curvature in growing organs (p. 318), electric variation of galvanometric negativity (p. 838), and diminution of electric resistance (p. 816).

Thermal radiation by diminishing the rate of growth induces a positive tropic curvature in growing organs.

Electric radiation of wireless stimulation of moderate intensity induces a retardation of growth (p. 422) and an electric variation of galvanometric negativity.

POSITIVE RESPONSE UNDER FEEBLE STIMULUS.

This is seen in the erectile response of *Mimosa*, in the enhancement of the rate of growth (p. 224), in the response of galvanometric positivity, and in the response of the increase of electric resistance of the tissue (p. 809)

MODIFICATION OF RESPONSE IN SUB-TONIC TISSUES.

The normal negative response undergoes a reversal in sub-tonic specimens seen in positive mechanical response, in an acceleration of the rate of growth (p. 221). Continuous stimulation converts the abnormal positive into normal negative response. The *abnormal* response finds explanation in the fact that stimulus give rise simultaneously to two reactions, the positive associated with an 'up' or A-change and the excitatory *negative, associated* with the 'down' or D-change. In excitable condition of the tissue, the negative D-change is predominant; conversely, the positive A-change is very pronounced in a tissue whose tonic condition is below par. The A-change enhances the potential energy of the system. Hence successive stimulations, by enhancing the functional activity of a sub-tonic tissue, convert the abnormal positive into normal negative response.

OPPOSITE EFFECTS OF DIRECT AND INDIRECT STIMULATION.

Every stimulus is shown to give rise to two separate and distinct impulses:—the positive, which is independent of the conductivity of the tissue for its transmission, and the excitatory negative which is dependent on the conducting power. The former is transmitted quickly; the latter, being a phenomenon of conduction of protoplasmic change, is conducted slowly. The positive impulse gives rise to *expansion, positive electric response*, and an acceleration of the rate of growth. The excitatory negative gives rise to contraction, negative electric response, and to retardation of the rate of growth. The negative reaction, is more intense than the positive. When the intervening distance between the point of application of stimulus and the responding organ is sufficiently great, the negative impulse lags behind the positive; the response is then diphasic, positive followed by negative. Reduction of the intervening distance causes a masking of the positive by the predominant negative.

A negative response has been shown to take place under a direct stimulation of the responding organ. When the stimulation is applied at a sufficient distance, the excitatory impulse becomes weakened to the point of extinction: the response is then positive as seen in the erectile response of various motile leaves and leaflets (p. 138), and in the enhanced rate of growth in growing organs (p. 214).

MULTIPLE RESPONSE UNDER STRONG STIMULUS, AND THE CONTINUITY BETWEEN MULTIPLE AND AUTONOMOUS RESPONSE.

When a plant organ is subjected to a strong stimulus, it exhibits a series of multiple responses. This is seen in the multiple mechanical response (p. 784), in multiple electromotive response (p. 744) and in multiple response of resistivity variation (p. 811). These multiple responses are induced by various modes of strong stimulation, such as induction shock, constant electric current, strong light, thermal shock, and mechanical excitation. In such cases the excess of stimulus is, as it were, held latent as may be observed in the subsequent multiple responses.

These recurrent responses under strong stimulus are strikingly demonstrated by the leaflets of *Biophytum*, the characteristics of which are like those of the cardiac tissue of the animal. Both are characterised by a long refractory period and response on " all or none " principle. In both, a single moderate stimulus gives rise to a single response: and a strong stimulus causes a multiple series of responses.

There is no strict line of demarcation between the phenomenon of multiple response as examplified by the leaflets of *Biophytum* and that of autonomous response as exhibited by the leaflets of *Desmodium*. Under very favourable conditions of absorption of energy from without, an ordinarily responding plant like *Biophytum* becomes converted into an " automatically " pulsating plant like

Desmodium. Conversely, under unfavourable conditions,—.*e.*, when the sum total of its energy is below par—the automatically responding *Desmodium* becomes reduced to an ordinarily responding plant like *Biophytum*. Its leaflets hen come to a standstill. Their pulsations may then be enewed by external stimulus, the persistence of which is ound to depend on the intensity and duration of the stimulus bsorbed.*

AUTONOMOUS RESPONSE AND THE MOVEMENT OF GROWTH.

The pulsating movement of the lateral leaflet of *Desmodium* is a striking example of the spontaneous activity of plant tissues. The general characteristics of a pulsating tissue are: (1) the periodic increase and diminution of turgor, (2) the dependence of activity on internal hydrostatic pressure,—a diminution causing an arrest, and an increase bringing about a renewal of pulsation, (3) the storage of external stimulus in the maintenance of rhythmic activity,—a run-down of absorbed energy being followed by an arrest and a renewal of arrested activity after the application of fresh stimulus; and finally, (4) the modifying influence of temperature, seen in the arrest of pulsations at a critical temperature, and in the maximum activity at an optimum temperature.†

All the above characteristics are found in the autonomous activity of growth, which is also found to exhibit pulsations (p. 169). Growth is arrested under diminished internal hydrostatic pressure produced artificially or under drought; it is enhanced by increased internal pressure after irrigation (p. 189). Growth arrested under condition of sub-tonicity becomes revived by the action of stimulus. The

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* Bose—Irritability of Plants, p. 289.

†*Ibid*, p. 291.

critical temperature for the arrest of growth in many tropical plants is about 22°C. (p. 177), the optimum temperature for maximum rate being about 34°C.

In my forthcoming work on the " Ascent of Sap " it is shown that the ascent is brought about by the pulsatory activity of the cells of the internal cortex which extends throughout the length of the plant, the movement of the sap being essentially due to the pumping action. Furthermore, that the rate of ascent is diminished by the diminution of the internal hydrostatic *pressure*; that the arrested ascent in a plant in a condition of sub-tonicity is revived by the action of external stimulus; that the ascent in many tropical plants is arrested at a similar critical temperature; and that the transpiration from leaves exhibits a maximum at the similar optimum temperature, of 33° or thereabouts.

THE EFFECT OF ANAESTHETICS.

Carbon dioxide may be taken as a mild anaesthetic, ether vapour being stronger in its action. The effect of chloroform vapour is more intense and liable to produce fatal results. The action of anaesthetics is modified by the strength of the dose and the duration of application. Under the continued action of an anaesthetic different reactions are generally found to occur at three different stages.

Carbon dioxide.—The preliminary effect of this gas is an increase of activity followed by a decline.

This is seen in the preliminary enhanced response by resistivity variation under the stimulus of light; continued action of the gas causes a depression in the response (p. 819). Similar results are seen in response under electric stimulation (p. 812).

In growing organs the preliminary effect of this gas is an enhancement of the rate followed by a retardation (p. 365). Continued action of this gas may even cause an active contraction which persists during the application of the gas, the normal growth being restored after renewal of fresh air (p. 668).

Geotropic response is brought about by differential growth induced at the upper and lower sides of the organ. The acceleration of growth caused by CO_2 at the first stage gives rise to an enhancement of geotropic response. But continued action of this gas causing contraction brings about a reversal of the normal geotropic response from an up- to a down-curvature. This explains the apparent reversal of normal geotropic response under carbonic acid gas (p. 644).

Effect of ether vapour.—Dilute vapour causes an increase of activity seen in *the enhancement of electric* response (p. 812), in the initiation or enhancement of growth, and in inducing a great increase in the rate of *geotropic response (p. 663).*

Effect of vapour of chloroform.—The application of this anaesthetic gives rise to different effects at three different stages. The immediate effect at the first stage is an enhancement of activity; at the second stage, there is an arrest; and at the third stage, there occurs a spasmodic death-contraction. The effects of these three stages are well exhibited by changes induced in the rate of growth. An arrested growth becomes revived or the normal rate becomes enhanced at the first stage. At the second stage, growth becomes arrested; and finally, at the third stage there is produced a contractile death-spasm.

In the geotropic response the immediate effect of chloroform vapour is a great enhancement followed by an arrest under continued action of the narcotic (p. 656).

In the response of leaves to light obtained by the method of resistivity variation, the preliminary effect of chloroform is an enhancement which is followed by a depression (p. 812).

DEATH-SPASM IN PLANTS AND TRANSMISSION OF DEATH-EXCITATION.

When a plant organ is gradually raised in temperature, a death-spasm occurs, at a certain critical temperature, at or near 60°C. A pulvinated leaf, or an anisotropic organ exhibits a spasmodic down-movement; a radial organ shows sudden contraction. The plant is killed after the attainment of the fatal temperature. The intense death-excitation is also exhibited by an abrupt electric response of galvanometric negativity, and by a sudden diminution of electric resistance (p. 692).

The occurrence of the death-excitation is also demonstrated by the transmitted effect; when the lower end of the plant is subjected to the death-temperature, an excitatory impulse is generated at or about 60°C. which causes the successive fall of the motile leaf or leaflets higher up the plant.

The onset of local death caused by application of poison gives rise to a similar excitatory impulse, which is transmitted to a distance (p. 781).

NERVOUS IMPULSE IN PLANTS.

Ordinary tissues are semi-conducting and the contractile effect of stimulus remains localised. There are, however, certain tissues characterised by a more or less *protoplasmic continuity*; excitation initiated at any point of such a tissue is transmitted to a distance with a definite velocity. By means of the Electric Probe this conducting tissue has been localised in the phloem of the fibro-vascular bundle. The xylem is a non-conductor: and this is more or less true of the mass of the cortex and of the pith (p. 703). The conduction of excitation is arrested by the application of various physiological blocks: thus an electrotonic block arrests the conduction *during* the application of the current, the conduction being restored on its cessation of the current. Rise of temperature enhances, and fall of temperature lowers the rate of conduction. Excitation is transmitted in both directions; the centrifugal velocity is greater than the centripetal. Local application of cold depresses or arrests conduction, while application of poison permanently abolishes the conduction.

The power of conduction is modified by season, being higher in summer than in winter; it is also modified by age. The conducting power is low in *young specimens, and* maximum in fully grown organs; a decline of conductivity sets in with age. The tonic condition of the tissue has an influence on the conductivity. In an optimum condition the velocity of transmission of excitation is the same for feeble or strong stimulus. Excessive stimulation induces a temporary depression of the conducting power. The effects are different in a sub-tonic specimen; in such a case, velocity of transmission increases with the intensity of stimulus, and the after-effect is an enhancement of the conducting power. In non-conducting young organs a conducting path is canalised by the action of stimulus (pp. 106, 757).

There is a particular aspect of the action of stimulus which is of fundamental importance in the life of the plant. The continuance of its normal functions depends on external stimulus to maintain the tissue in an optimum tonic condition; for deprivation of stimulus reduces the plant to an atonic condition, in which all life-activities are brought to a standstill. The internal activity of the plant is also dependent on external stimulation. Turning our attention to particular instances, we find that growth and movement in plants depend on the turgid condition of the tissue, which is determined by the *cellular activity* which maintains the ascent of sap. When the plant is cut off from the stimulus of its environment, the ascent of sap undergoes a decline which culminates in an arrest.

It is thus clear that for the maintenance of the ascent of sap in a tree the internal cortex should be excited throughout its length either by direct or by transmitted stimulation. As for the great length of the cortex in the trunk of the tree, covered as it is by the thick bark, direct stimulation of the active internal cells by external stimulus is impossible; it can only be effected by transmitted stimulation. There thus arise two questions: the first relates to the external stimulus which by its transmitted excitation maintains the cellular activity of the internal cortex; the second relates to the nervous path by which the excitation reaches that active layer.

Among the external stimuli, none is so wdely available as that of light. Its stimulating effect can be transmitted to a distance by the nervous channel, which is the phloem in the vascular tissue. The vascular bundles again are spread out in fine remifications as veins in the leaves. The expanded lamina is thus not merely a specialised structure for photosynthesis, but also a catchment-basin for the stimulus of light, the excitatory effect of which is gathered into larger and larger nerve trunks for transmission to the interior of the plant. It is very significant that the internal cortex in which pulsatory activity is to be maintained abuts against the phloem through which excitation from outside is being conducted.*

It is thus seen how all parts of the plant are, by means of nerve-conduction, become not merely energised but also put in the most intimate communication with each other. It is then in virtue of the existence of such nerves, that the plant constitutes a single organised whole, each of whose parts is affected by every influence that falls upon any other.

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* cf. Physiology of the Ascent of Sap.

THE HYDRAULIC AND THE NERVOUS REFLEX.

In a plant subjected to drought, irrigation at the root causes a movement of water upwards with a definite velocity: this hydraulic impulse causes an increase of turgor from below upwards, and the drooping leaves become erected. An example of this was given where irrigation of *Mimosa* gave rise to the erectile response of the distant leaf p. 39). If instead of irrigation we apply a strong stimulus to the root, say a prick with a pin or an electric shock from an induction coil, the transmitted nervous impulse induces a *fall* of the leaf. *The hydraulic impulse is thus antagonisti to the nervous impulse.* Even in ordinary response and recovery we observe these opposite actions. The erectile movement of the leaf is due to the ascent of sap to the pulvinus along a definite channel. Stimulation of the leaf induces a contraction and expulsion of water from the pulvinus which escapes by the same channel through which the ascent took place, but this time in a reverse direction. The two phases of the normal response, *viz.*, the excitatory down movement followed by erectile recovery are thus brought about by the excitatory and hydraulic actions respectively. The fact that the hydraulic expansion opposes and may even neutralise the excitatory action is seen in the response of *Mimosa*. The apparent insensitiveness of the plant early in the morning is partly due to the excessive turgor of the pulvinus at that time of the day. Again, application of water to the pulvinus induces an expansion and inhibition of response which may be restored by the withdrawal of the excess of water by glycerin.*

The term 'reflex' has been defined as the reaction in which there follows on an initiating reaction, an end-effect reached through the mediation of a conductor itself incapable of the end-effect.

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* Irritability of Plants, p. 88.

Now the invisible hydraulic impulse initiated by the irrigation of the root causes an end-effect, namely the erectile response of the leaf at a distance; we may therefore regard the particular effect produced at a distance as the *hydraulic reflex*. There is a different end-effect, due to transmission of excitation through the plant-nerve which causes the fall of leaf; this is the *nervous reflex*; the hydraulic reflex induces, as already stated, an expansive and the nerve-reflex a contractile end-effect A complexity thus arises in the motile response of growing and of pulvinated organs due to the two reflexes antagonising each other. The recognition of the existence of these two distinct reflexes makes it possible to offer a full explanation of various effects which have hitherto appeared to be anomalous.

TROPIC MOVEMENT UNDER UNILATERAL STIMULUS.

All tropic curvatures under diverse modes of stimulation in pulvinated and growing organs are due to: (*a*) the action of stimulus causing a diminution of turgor and contraction at the directly stimulated proximal side of the organ, and (*b*) increase of turgor and expansion at the indirectly stimulated distal side. In growing organs an induced diminution of turgor is attended by a retardation, and an increase of turgor by an enhancement of growth. Positive curvatures towards the stimulus are thus caused by the joint effects of the contraction of the proximal and expansion of the distal side. The fact that the stimulus applied at one side causes an increase of turgor at the diametrically opposite side has been demonstrated, by stimulation of one side of the stem, which caused the erectile movement of the motile leaf at the opposite side (p. 281).

The following laws of effects of Direct and Indirect stimulus determine the varied movements of plants.

1. All forms of Direct stimuli induce contraction or etardation of growth, and Indirect stimuli expansion or cceleration of growth.

2. Unilateral stimulus induces a positive curvature by he contraction of the proximal, and expansion of the distal ide.

3. Transverse conduction of excitation neutralises, or reverses the positive curvature. This effect is accentuated by the differential excitabilities of the upper and the under halves of the anisotropic organ. Excitation internally diffused induces effect similar to diffuse external stimulus.

4. The effect of rise of temperature is opposite to that of the stimulus of light.

MECHANOTROPISM: TWINING OF TENDRILLS.

It has been repeatedly shown that direct stimulations of all kinds induce contraction, and retardation of growth, while indirect stimulations cause an acceleration of the rate of growth (p. 291). Under unilateral mechanical stimulus of short duration, the directly stimulated proximal side of a tendril undergoes contraction, and the indirectly stimulated distal side shows the opposite effect of expansion; a positive curvature is thus produced, with a movement towards the stimulus. The after-effect of direct stimulus is an acceleration of growth above the normal, hence after brief unilateral stimulation, the stimulated side undergoes an acceleration of growth and expansion, by which the recovery is hastened (p. 300). This positive after-effect of stimulus on growth is seen in the balanced record of growth (p. 325). Stimulation of one side of the tendril induces an expansion of the opposite side (effect of indirect stimulus), even in cases where the contractility of the stimulated side is feeble. Hence response to direct stimulation of the more excitable side of the tendril may be inhibited by the stimulation of the opposite side (p. 300).

PHOTOTROPISM.

Quantitative relation.—The positive heliotropic curvature of pulvinated and growing organs is explained by considerations given above, namely, the contraction of the proximal and expansion of the indirectly stimulated distal side. It is shown that the amount of heliotropic curvature depends, (1) on the intensity of light, (2) on the sine of the directive angle, and (3) on the duration of exposure. The intensity of phototropic action is thus dependent on the quantity of incident light (p. 345).

Negative heliotropism.—When the light is very strong and long continued, the excitation is transmitted across the organ and induces contraction of the further side, which neutralises the positive curvature. The organ now places itself at right angles to the light, this being the dia-heliotropic position. In certain cases, the transverse conductivity is considerable, the result of which is an enhanced excitation of the further side, while the contraction of the near side is reduced on account of fatigue caused by over-excitation. The organ thus bends away from light, exhibiting the so-called negative heliotropism (p. 337).

Effects of different rays of the spectrum.—The retardation of growth is one of the factors in the induction of the phototropic curvature. The ultra-violet rays induce the most intense reaction in retardation of growth; the blue rays are also effective, but the yellow and the red rays are relatively ineffective (p. 211). In the infra-red region the thermal rays also are very effective in inducing tropic curvature; we thus obtain positive, dia-, and negative radio-thermotropic phenomena, parallel to those under visible radiation (p. 415). The effects of rise of temperature and of direct radiation are, however, antagonistic to each other (p. 415).

Beyond the infra-red we enter the vast range of electric radiation and to this also the plant is shown to be sensitive. Like light, feeble electric radiation gives rise to an acceleration, and strong radiation to a retardation of growth. Parallel effects are obtained in the electric response of plants to wireless stimulation (p. 424).

The complete phototropic curve.—This consists of four parts: (1) the stage of sub-minimal stimulation, (2) the stage of increasing positive curvature reaching a maximum, (3) the stage of neutralisation, and (4) the stage of reversal into negative. Confining our attention to the second stage, the susceptibility for excitation is found to be feeble at the beginning; it increases very rapidly with increasing intensity or duration of stumulus; the reaction then reaches a limit. As regards the complete phototropic curve, the first part is negative due to the physiological expansion induced by sub-minimal stimulus. The curve then crosses the abscissa upwards, and the positive curvature reaches a maximum. Owing to transverse conduction of excitation, there is a subsequent neutralisation and reversal into negative. Weber's law is not applicable for the entire range of stimulation. His quantitative relation fails in the region of sub-minimal stimulus, where the physiological reaction becomes *qualitatively* different, (p. 361).

Phototropic torsion.—Lateral stimuli of all kinds induce a torsional response in a dorsi-ventral organ, the direction of torsion being such that the less excitable half of the organ is made to face the stimulus. The torsional movements of leaves and leaflets of many plants are explained by the above definite reaction. The excitatory efficiencies of two different stimuli may be compared by the

Torsional Balance by allowing them to act on the two flanks of the organ (p. 409).

DIA-HELIOTROPIC ADJUSTMENT OF LEAVES UNDER TRANSMITTED EXCITATION.

Dia-heliotropism is characteristically exhibited by dorsiventral organs such as leaves. Heliotropic adjustment is shown to take place under transmitted excitation in *Mimosa* and in *Helianthus*, chosen as representatives of sensitive and ordinary plants. The four quadrants of the pulvinus of *Mimosa* function as four distinct effectors. There are separate nerve strands which connect the four sub-petioles with the four quadrants of the pulvinus. Hence the stimulation of the right sub-petiole by light gives rise to a transmitted nervous impulse which reaches the right quadrant and causes a right-handed torsion. Stimulation of the left sub-petiole causes, on the other hand, a left-handed torsion. Finally, stimulus applied to the second and the third sub-petioles causes respectively the down- and up-movements

A single reflex caused by the stimulation of one of the sub-petioles gives rise to a purposeless movement in one direction which carries the plane of the leaflet away from the position perpendicular to the incident light. But when the two sub-petioles : (1) and (4) are simultaneously exposed to light of the same intensity, the two resulting torsions balance each other. Hence the lateral adjustments of the leaf as a whole are made by the two sub-petioles (1) and (4) which are situated outside: the balancing adjustments up or down, are made in response to the excitations transmitted, by the two middle sub-petioles (2) and (3). It is thus seen that equilibrium is only possible when the entire leaf-surface (consisting of the rows of leaflets carried by the four sub-petioles) is equally illuminated; and this can only ccur when the leaf surface as a whole is perpendicular to e incident light. The leaf is adjusted in space by the -ordinated action of the four reflexes. The dia-heliotropic ttitude of the leaves is thus brought about by distinct ervous impulses, initiated at the perceptive region actuating e different effectors at a distance (p. 746).

PHOTONASTIC CURVATURES.

There is no line of demarcation between tropic nd nastic movements. In an organ exhibiting ifference of excitability at the opposite sides, strong nilateral stimulus becomes internally diffused, and auses greater contraction of the more excitable side of the rgan. Two different effects are produced which are deternined by the transverse conductivity of the organ. In the bsence of transverse conduction, the positive curvature eaches a maximum without neutralisation or reversal. The eaflets of *Erythrina indica* and of *Clitoria ternata* thus fold pwards, the apices of their leaflets pointing towards the un. But in organs in which the power of transverse conluction is considerable, the excitation under strong light ecomes internally diffused, and gives rise to the greater ontraction of the more excitable half of the organ. This xplains the so-called "midday sleep" by the upward olding of the *Mimosa* leaflet and downward folding of the eaflet of *Biophytum* and of *Averrhoa*, under the action of he rays of the sun (p. 543).

NIGHT AND DAY MOVEMENTS IN PLANTS.

The diurnal movements of plants are complicated by several phenomena, the most important of which are, (1) thermonastic movement caused by the differential growth of the two sides of the organ under diurnal variation of temperature, (2) thermo-geotropism, due to variation of temperature intensity of light gradually declines till about 5 P.M., after which the diminution of light is very abrupt.

Diurnal movement due to alternation of light and darkness.—In the leaflets of *Cassia alata* the effect of light is predominant, compared with that of temperature. The leaflets begin to close when the light is undergoing a rapid diminution after 5 P.M., the closure being completed by 9 P.M. The leaflets remain closed till 5 A.M. next morning, after which they begin to open with the light, and become fully expanded by 9 A.M. (p. 544). The large terminal leaflet of *Desmodium* exhibits diurnal movement similar to that of *Cassia* (p. 542).

Diurnal movement of the leaf of Mimosa.—The leaf is responsive both to the action of gravity and of light. The operative factors in the diurnal movement are: (*a*) the variation of geotropic action with changing temperature, and (*b*) the response to the action of light which, generally speaking, is antagonistic to that of rise of temperature. Under thermo-geotropic action the maximum fall of the leaf takes place at thermal noon, which is about 2 P.M. the maximum rise being at thermal dawn, about 6 A.M.

In the forenoon, rise of temperature causes a fall of leaf, but continuous light acting from above tends to raise it. The rapid diminution of light towards evening acts virtually as a stimulus, causing an abrupt fall of the leaf. The diurnal movement of *Mimosa* thus exhibits four phases, (1) The leaf owing to fall of temperature erects itself from 2 to 5-30 P.M. or thereabouts, (2) About 6 P.M. there is a rapid diminution of light and the leaf undergoes a sudden fall, which continues till about 9 P.M. (3) After 9 P.M. the leaf begins to erect itself during the fall of temperature, the maximum erection being attained at thermal dawn which is at or about 6 A.M. (4) In the forenoon the leaf is acted on by two antagonistic reactions, the effect of rising temperature and of increasing light, the effect of temperature being predominant. The leaf thus continues to *fall till thermal noon, which is about 2 P.M.* The diurnal curves of the petioles of *Cassia alata* and of *Helianthus annulus* are similar to that of *Mimosa* (p. 597).

GEOTROPISM.

Mechanical response.—The stimulus of gravity is shown to induce an excitatory reaction similar to that under other forms of stimulation. The upper side of the horizontally laid shoot is directly stimulated and undergoes contraction (p. 440).

Electric response.—The excitatory reaction of the upper side is exhibited by an induced change of galvanometric negativity. The lower side shows a change of galvanometric positivity indicative of increase of turgor and enhancement of the rate of growth (p. 447). The method of geo-electric response is more sensitive in the detection and quantitative determination of the effect of stimulus of gravity than the method of mechanical response.

Explanations of opposite reactions at different sides of the organ.—The geotropic up-curvature is only possible by differential reaction at opposite sides of the organ; this is demonstrated by the results of electric investigations which show that the upper side exhibits contraction, while the lower undergoes expansion. It is further shown that this difference in the reaction is due to the fact that the stimulus is direct at the upper and indirect at the lower side (p. 610).

Geotropic excitations at various angles.—The excitation is found to increase as the sine of the angle of inclination. This relation is only approximate, for the excitation is relatively greater at larger angles than the value deduced from the law of sines (p. 625)

The critical angle for immediate geotropic excitation.—The excitation at lower angles is disproportionately less; the divergence between the sines and excitations is very slight above 45°, while it is very pronounced at the lower angle of 35°. The curve of excitation at diminishing angles when produced backwards cuts the abscissa at about 31.5° at which angle, the geo-electric excitation would be reduced to zero. The results of experiments show the existence of such a critical angle at about 32°. The theory of statoliths obtains strong support from this particular phenomenon, for an increase above the critical angle is found to give rise to an abrupt excitatory geo-electric response (p. 636) This must evidently be due to the sudden fall of the heavy particles from the base to the side of the geo-perceptive cells.

Geotropic torsion.—In dorsi-ventral organs lateral application of any form of stimulus gives rise to a torsional response by which the less excitable half of the organ is made to face the stimulus. A geotropic torsion is produced when the plant is placed on one side, so that the vertical lines of force of gravity strike at one of the two flanks of the organ. Geotropic stimulation of the right flank gives rise to a right-handed, that of the left flank, to a left-handed torsion (p. 504). Torsions induced by two different modes of stimulation, say of gravity and of light, may thus be compared by making them act simultaneously at the two opposite flanks of the organ (p. 505).

Effect of narcotics.—The general effects of narcotics have already been explained in connection with their action on all modes of stimulation. Carbon dioxide induces a preliminary enhancement of geotropic response followed by a decline and even a reversal. The effect of dilute vapour of ether is to cause a great increase in geotropic curvature. Chloroform vapour causes an enhancement followed by an arrest of geotropic action.

Effect of variation of temperature.—The thermo-geotropic action has been shown to cause a diminution in geotropic curvature during rise, and an increase during fall of temperature. The geotropic torsion is similarly decreased during the rise and increased during the fall of temperature. Variation of temperature also modifies the position of dia-geotropic equilibrium (p. 519).

Localisation of geo-perceptive layer.—Electric investigations support the theory that it is the weight of the heavy particles which causes geotropic stimulation in the higher plants. The geo-perceptive layer has been localised by the Electric Probe and found to coincide with the endodermal starch-sheath. In certain plants the geo-electric distribution exhibits two maxima. Microscopic section showed that the starch-sheath in these is not single but double, and that the positions of the two electric maxima coincide with those of the two starch-sheaths (p. 618).

Dia-geotropism of dorsi-ventral organs.—This particular adjustment under geotropic stimulation is shown to be due to the irritation caused by pressure of heavy particles on cells which are unequally excitable at the upper and lower sides of the organ (p. 726).

Geotropism of roots.—On subjection of the tip of the root to the stimulus of gravity, its upper side exhibits excitatory reaction of the galvanometric negativity. This shows that the root-tip undergoes direct stimulation.

The electric response in the growing region above the stimulated point of the root-tip is positive, indicative of increase of turgor and expansion. This is due to the effect of indirect stimulus.

The stimulus of gravity is perceived at the root-tip and the responsive movement takes place at the distant growing region. Geotropic stimulation of the root is thus indirect (p. 473).

In contrast with the above is the fact that the growing region of the shoot is both sensitive and responsive to geotropic stimulus.

As the effects of direct and indirect stimulation on growth are antithetic, the responses of shoot and root to the direct and indirect stimulus must be of opposite signs. There is thus no necessity for postulating two different irritabilities for the shoot and the root, since tissues in general exhibit positive and negative curvatures according as the stimulus is direct or indirect (p. 476).

A plant is acted on by gravity, by light and its diurnal variation, by changing temperature, by drought and rain, not to mention many other stimuli of its environment. For obtaining some idea of the great complexity which arises from the varied reactions we may watch a *Mimosa* plant watered at intervals and observe specially the effects of two out of many stimuli of its environment, namely those of light and of gravity. In the movement of *Mimosa* leaf there are then the following variable factors: (1) the hydraulic reflex due to the ascent of sap which causes an erectile movement antagonistic to the excitatory fall of the leaf; (2) the different effects of direct and indirect stimulation, examplified by the fall of the leaf under stimulus directly applied to the pulvinus in contrast with the erectile movement caused by a similar stimulus indirectly applied, *i.e.*, at the point of the stem opposite to the pulvinus (p. 281); (3) the reflex caused by the stimulus of light acting on the four sub-petioles bearing the leaflets, in this there are four modifying sub-factors which depend on the relative intensities of excitation transmitted from the four distinct receptors of light-stimulus; (4) the geotropic stimulus which acts on the four quadrants of the pulvinus, the responsive peculiarity of each of these quadrants is different from that of the others; and (5) the effect of thermal variation in modification of geotropic action.

The above example illustrates the extremely numerous variations in the response which must arise from the combination of effects of a large number of factors, some of which are concordant and others antagonistic. The problem of plant-movement which confronts us though bewildering at first sight, is, however, not insoluble. By the isolation of individual factors and separate investigations on them, it is possible to unravel the complexity and discover a generalisation for the life-movement in plants.

LITERATURE

Bayliss, W. M.—" Principles of General Physiology "—(1915).

Blackman, V. H. and Paine.—" Annals of Botany "—vol. xxxiii, No. cxxxv—(1918).

Bose J. C.—" Response in the Living and Non-Living "—(1902).

,, " Plant Response "—1906.

,, " Comparative Electro Physiology "—1907.

,, " An Automatic Method for Investigation of Velocity of Transmission of Excitation in *Mimosa* "—Phil., Trans., B, vol. 204, 1913.

,, " Researches on Irritability of Plants "—1913.

,, " On Diurnal Variation of Moto-Excitability of Plants "—Annals of Botany, vol. xxvii. No. cviii,—1913.

,, " The Influence of Homodromous and Heterodromous Electric Current on Transmission of Excitation in Plant and Animal "—Roy. Soc. Proc. B, vol. 88—1915.

,, and S. C. Das—" Physiological Investigation with Petiole-Pulvinus Preparation of *Mimosa pudica.*" Roy. Soc. Proc. B, vol. 89, 1916.

,, and G. Das—" Researches on Growth and Movement in Plants by Means of the High Magnification Crescograph "—Roy. Soc. Proc. B, vol. 90,—1919.

,, and S. C. Guha—" The Dia-Heliotropic Attitude of Leaves as determined by Transmitted Nervous Excitation,"—Roy. Soc. Proc. B, vol. 93, 1922.

Haberlandt, G.—" Physiological Plant Anatomy," (English translation)—(1914).

Jost, L.—" Lectures on Plant Physiology," (English translation)—(1907).

Lynn, M. J.—" The Reversal of Geotropic Response in the Stem," The New Phytologist—(1921).

Pfeffer, W.—" Plant Physiology," (English Translation)—(1903).

Vines, S. H.—" Lectures on Physiology of Plant,"—(1886)

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