Changes of Electrical Conductivity under Geotropic Stimulation.

By James Small, M.Sc. (Lond.), F.L.S.

(Communicated by Dr. A. D. Waller, F.R.S. Received May 11, 1917.)

The very short perception period* for the epicotyl and hypocotyl of various plants, which Fitting (3) has proved, and the presence of geotropic response in the absence of starch grains in many fungi and higher plants tend to indicate that the starch grain or statolith apparatus is not absolutely necessary for the perception of gravity by plants. The differential effect of gravity on the permeability of the upper and under sides of the pulvinus of *Phaseolus* indicates the possibility of a similar effect being produced in the roots of the plants.

Fitting's numerous experiments were examined in order to ascertain whether the strength of the geotropic reaction bore any constant relation to the geotropic stimulus. Putting the data given in Fitting's Table 10 [(3), Teil I, p. 282] in the form of a graph, we get a curve (fig. 1) which is

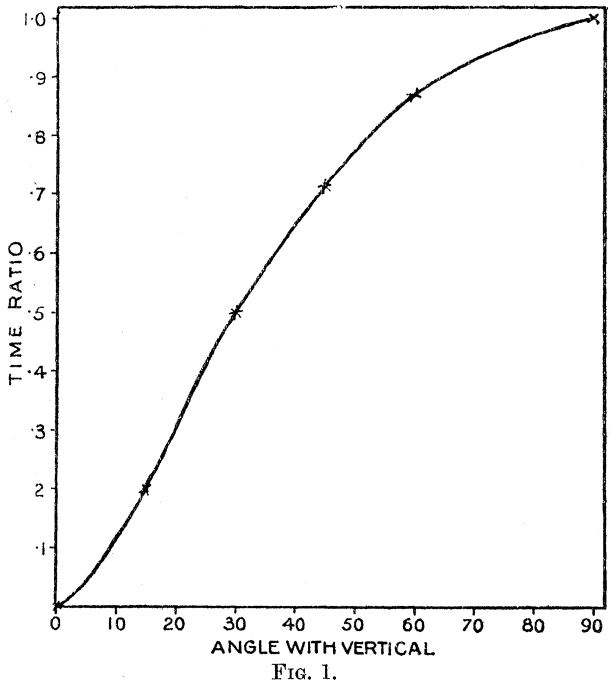

Fig. 1.

* *Perception period* is used here, not in the psychological sense, but in the sense generally accepted among botanists, and defined as the smallest fraction of the *presentation time* which gives a cumulative effect when the stimulus is repeated for a sufficient number of times with less than the *relaxation time* between the successive stimulations.

logarithmic in the centre and shows divergences at the extremities, the ordinates being the ratios of the times of exposure at 90° to the times at other angles to the vertical, and the abscissæ being the angles with the vertical. In this way we get the strength of the reaction, which varies directly as the time of exposure, plotted against the strength of the stimulus, which varies directly as the angle with the vertical. The resulting graph is the typical sigmoid curve obtained by Waller (9) for the response by animals to various stimuli. This more or less logarithmic relation is also proved by the fifty-eight experiments on the perception of minimal angle differences by the epicotyls of *Vicia Faba* and *Phaseolus multiflorus* and by the hypocotyls of *Helianthus annuus*, which Fitting (3, Teil I, pp. 306–310) has published (fig. 2).

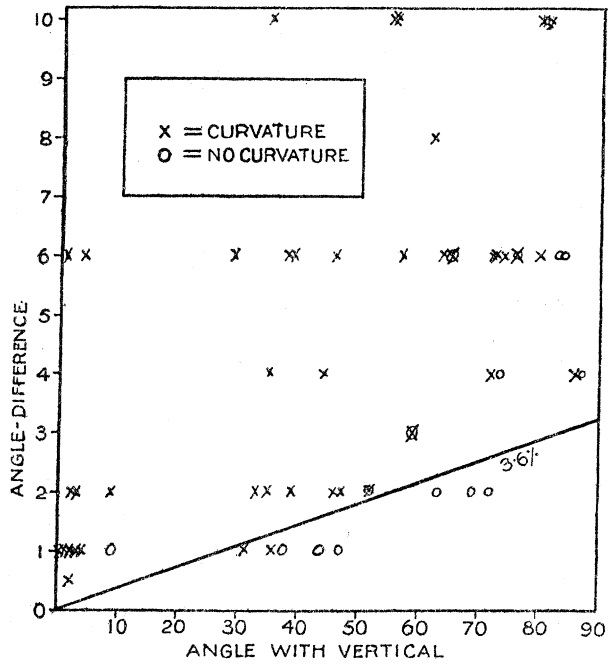

FIG. 2.

From these published results of other investigators the hypothesis was formed that the proximate mechanism of geotropic response in plants is a change in the permeability of the protoplasm in the cells of the perceptive region. Such changes involve changes in the electrical resistance of the tissue [*cp.* McClendon (5) and Osterhout (6*b*)].

Experimental Proofs.

Method.

The hypothesis was tested by some preliminary experiments with the Kohlrausch bridge, and it was found that the turning of the root horizontal always caused an immediate decrement of the resistance, which was interpreted, as in McClendon's experiments (5), as increase in permeability to ions. This decrement of resistance was distinctly less in the upper side of the root than in the lower. A more accurate apparatus, which will now be described, was then set up, and the results are given below.

The Kohlrausch modification of the Wheatstone bridge consists in (1) the use of an alternating current which prevents local electrolysis in the tissue; (2) the use of a telephone by which the position of the sliding contact is regulated so that the least amount of sound is heard in the telephone. This "silence" point or position of minimum sound is the point at which the resistances have the well known relationship to one another. Fig. 3 shows

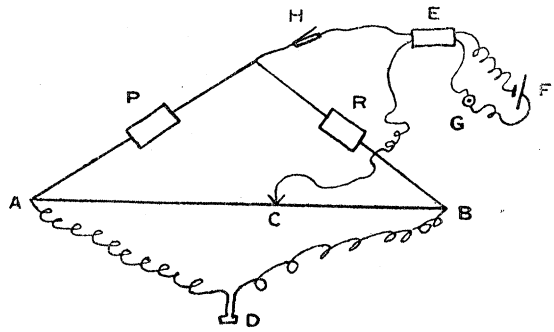

Fig. 3.

the arrangement of the apparatus diagrammatically, AB being the metre bridge, C the sliding contact, D the telephone, E the induction coil, F a single accumulator, G a plug key for putting the accumulator into or out of action, H a tapping key, R a resistance box, and P the plant or unknown resistance. By means of the tapping key the injurious effects of the passage of the current through the tissue are minimised. When the silence point is obtained the position of C is read off and the resistance calculated from the ratio AC : CB : : P : R.

The resistance to be determined was that of the tissue at one side of the root-tip of *Vicia Faba* from 1 mm. to 2 mm. from the apex. The ends of two fine platinum wires were bent at right angles, the bent ends being 0·75 mm. to 1·5 mm. in length. About 1·5 cm. of the root was covered with paraffin wax melted at a temperature of 45° C. As the root was dipped into the wax

and quickly withdrawn, no injurious effects were observed. This was tested by removing the wax tip and growing the beans for about 10 days afterwards. The wires were inserted on the same side of the root, the first 1 mm. from the apex and the second 2 mm. from the apex. This operation requires much practice and a considerable amount of patience if the root is not to be injured to such a degree that the succeeding stages are useless. The wax covering serves the double purpose of keeping the root from drying and of insulating the wires from the surface of the root. A root-tip covered with wax in this way will remain fresh for hours after the unwaxed portion is strongly withered, and the aërating system of the root of *Vicia Faba* is efficient enough to provide the necessary opportunities for respiration in the covered portion of the root (4). The wires were fixed in position by a plug of wax melted around them, so that a longitudinal section of the root-tip, fitted with wires, would show something like fig. 4. The

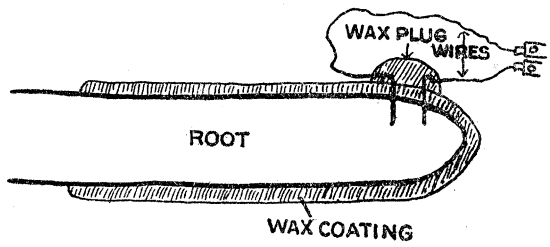

FIG. 4.

placing of the plant at any desired angle was accomplished by means of the apparatus figured (fig. 5).

The supports C and E were clamped to a shelf, AB. A wooden support, D, with a socket in it, was supported by C. The angle was indicated upon a scale, O, marked upon a smooth piece of mahogany with a socket at the centre of the semicircle. The scale was divided into 36 angles of 5° each, and holes were made in the proper places so that a plug, P, could be inserted to support the swinging portion of the apparatus at any required angle. The orientation of this scale was checked by means of a plumb line T. For convenience in fixing the plant a piece of sheet cork, H, was screwed to a wooden base, G. This base had a vertical line drawn along the centre of the length and another line at right angles to it, at about one-third of the length from the top. At the ends of the latter line steel rods, G′, G′, were inserted to give an axis upon which the part swung when the free ends were inserted in the sockets of D and O. The sheet cork was thoroughly waxed, and a thread, S, was fixed along it coinciding with the vertical line on the wooden base. The orientation was checked with a set square, a plumb line, R, and

the thread, which was waxed over for insulation. Two blocks of paraffin wax, K, K, were fixed to the cork near the base, and to each a brass binding

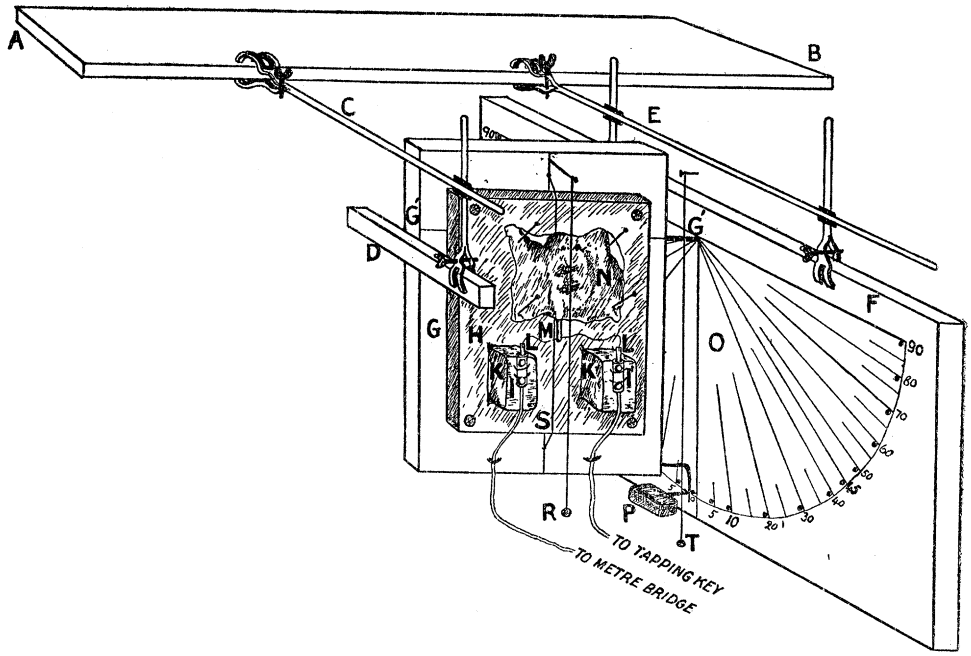

FIG. 5.

screw, I′, was fixed by means of wire staples, which were sunk in the wax, but did not penetrate to the cork. Two terminals, L, L, consisting of thin platinum wires fixed to small strips of zinc, were then attached to the binding screws. Connection with the induction coil and the metre bridge was made with insulated wires fixed in the binding screws. To the side of G was fixed a large pin bent so that it formed an indicator on the scale, O, and by resting on the plug, P, kept the whole in position. The bean, after the root-tip had been coated with wax, was fixed with two pins to the sheet cork, so that the root was parallel to the surface of the cork and to the vertical thread, S. The wires were then inserted on the "front" of the root, M, with all due precautions. After the plug of wax had been placed in position to keep the wires from moving, the unwaxed portion of the plant was covered with wet lint to keep it moist.

By tilting G and fixing it in position by means of the indicator pin and the plug P, the root could be placed so that the wires were in either the upper or the lower side. In the records of the experiments given below + angles were taken as those where the wires were in the physically upper side of the root and − angles as those in which they were in the physically lower side.

The scale O acted as a light screen, so that the root was not subject to any heliotropic stimulus.

The Wound Reaction.

It may be supposed that two wires cannot be inserted into the root-tip without inducing some sort of a wound reaction, and the passage of even an alternating current is almost sure to have some effect on such a delicate structure. The first experiment was, therefore, to determine the resistance at given intervals of time with the root in the vertical position. Preliminary experiments had shown that the effect of the current could be eliminated by taking the readings within a minute and allowing 15 mins. between each. Fifteen-minute readings, therefore, were taken with the root vertical, and the results show that during the first 30—40 mins. there is an injury response which is represented by a decrement of resistance followed by an increment of resistance in two distinct waves, the second being much weaker than the first. The first increment is, in fact, followed by a period of relative quiescence, during which the resistance remains almost constant for 1—2 hours, after which the vitality decreases rapidly, as is shown by the great decrement of the resistance. Fig. 6 is a typical series of readings in

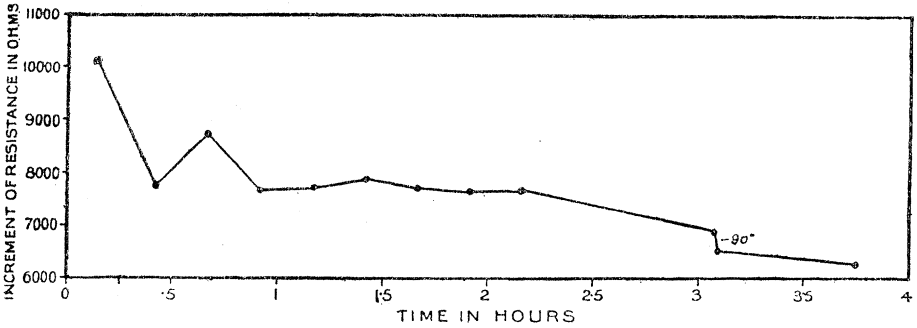

Fig. 6.

the form of a graph. During the final decrement of resistance the plant can still perceive a change to the horizontal, as is proved by the sudden drop in the graph at $-90°$. Sometimes if the root was about 2 cm. long it proved very vigorous and the resistance increased for a considerable time (fig. 7) before the loss of vitality began to show.

The extent of the injury was also tested by growing the beans after they had been used for an experiment. If the readings extended for an hour and a half to two hours, the root afterwards recovered more or less and continued growth with slight abnormalities. If, however, the experiment lasted over 2 hours the side of the root-tip in which the wires had been placed decayed

and the growth of the other side produced various twistings. In other cases the whole tip died and numerous lateral roots were produced about 1 cm.

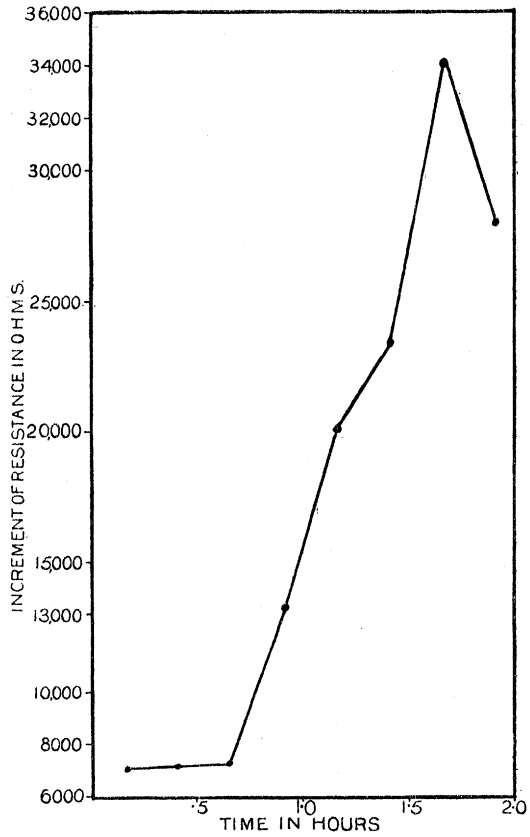

FIG. 7.

behind the apex of the main root, which grew very thick for a distance of 2–3 cm. from the point. In several cases where the wires were left in roots 2–3 cm. long for 48 hours after the experiment, the root grew out of the wax coat and left the wires, being itself apparently unaffected by the injury.

The changes in the resistance produced by tilting the root were then studied during the period of quiescence. The plant was mounted and readings taken every 15 min. with the root vertical until two consecutive readings were similar, then the root was placed at various angles with the vertical.

Changes in Resistance and Geotropic Stimulation.

In all the following experiments roots from 2 to 4 cm. in length were used and the beans were germinated upon a vertical board covered with blotting

paper and with a cloth arranged over several nails to form a chamber which was kept moist by running water. In this way most of the roots were obtained straight and vertical and the preparatory manipulation was carried out with the root as nearly as possible in the position of rest.

The decrement of resistance furnishes a standard for the measurement of the degree of excitation, instead of the time-ratio used in fig. 1. The resistance was measured with the root vertical at intervals of 15 min. until two similar readings were obtained as explained above, then after another interval of 15 min. the root was tilted at an angle of 20° and a reading taken as quickly as possible. The time taken to get the silence point varied from 15 to 20 sec. As the ratio of the relaxation time to the time of excitation in *Vicia Faba* is 5 : 1,* the root was returned to the vertical position immediately after the reading had been obtained and an interval of 10–15 min. allowed to elapse between each reading. Other angles were taken in succession. The advantage of the present method over previous methods lies in the fact that the behaviour of the same bean root towards different stimuli can be studied; this eliminates to a certain extent that individual variation (*cf.* Tröndle (8)) which complicates the interpretation of most results in geotropism.

The resistance is calculated thus:—P : R : : AC : CB, $\quad \therefore P = \frac{AC}{AB} \times R.$

Experiment 1 : Fixed resistance or R = 6400 ohms.

Angle of root to vertical	...	0°	−20°	−30°	−45°	−60°	−90°
Total resistance in ohms	...	9600	8660	8145	7667	9600	8839
Decrement of resistance	...	—	940	1455	1933	0	761

It will be seen that the first part of the curve, fig. 8, closely approximates

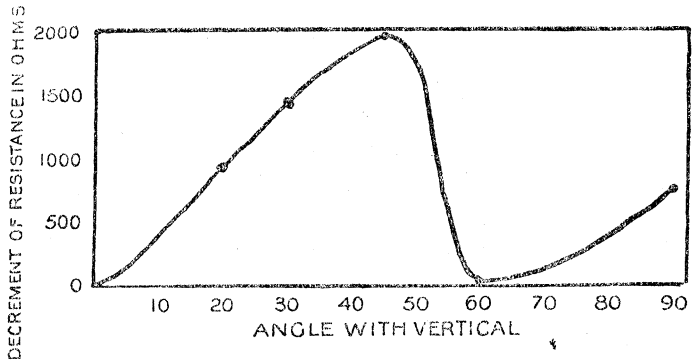

Fig. 8.

* Fitting (3), Teil II, p. 340.

that in fig. 1. The remainder of the curve shows the injury effects, which are, however, more than counterbalanced by the excitation effects at $-90°$.

Experiment 2: R = 6000 ohms.

Angle to vertical	0°	0°	−10°	−20°	−30°	−40°	−70°	−90°
Total resistance	7783	7636	7333	6958	6850	6738	6474	6875
Decrement of resistance ...	—	—	303	678	786	898	1162	761

Here the curve is flatter, fig. 9, but the sigmoid character is quite obvious.

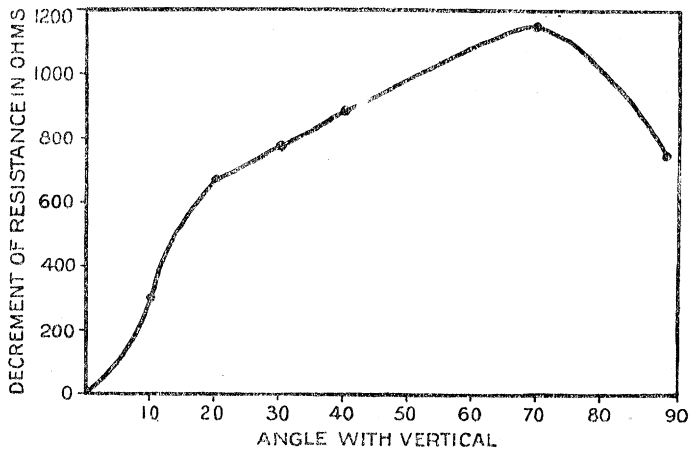

Fig. 9.

Experiment 3: R = 10,000 ohms.

Angle to vertical	0°	0°	−5°	−10°	−20°	−30°	−40°
Total resistance	10,325	10,325	10,040	9417	8869	8691	8552
Decrement of resistance ...	—	—	285	908	1456	1634	1773

Angle to vertical	−45°	−50°	−60°	−70°	−80°	−90°	+90°
Total resistance	8484	8348	7825	7211	7111	6751	7007
Decrement of resistance ...	1841	1977	2500	3114	3214	3574	3320

Although not regularly sigmoid the curve in this case (fig. 10), even after 5 hours, shows a perception of the difference between $-90°$ and $+90°$. The curve up to $-40°$ is quite regular and as $2\frac{1}{4}$ hours had then elapsed from the commencement of the experiment the irregularities are quite comprehensible.

The upper half of the curve was investigated in the next two experiments.

Experiment 4: R = 4000 ohms.

Angle with vertical ...	0°	0°	−45°	−50°	−60°	−70°	−80°	−90°
Total resistance	3767	3767	3561	3476	3462	3421	3407	3407
Decrement of resistance ...	—	—	206	291	305	346	367	367

This curve (fig. 11), although the actual reduction is less than in most experiments, confirms the sigmoid character of the curve. Variation is to be

expected with the physiological variation of the individuals (*cf.* Tröndle (8)), and the difference between the *percentage* reductions is much less variable, *i.e.* 5–15 per cent.

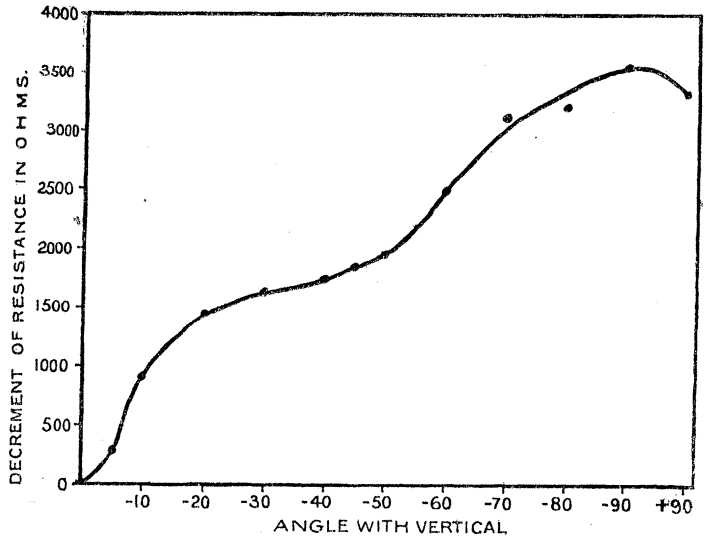

Fig. 10.

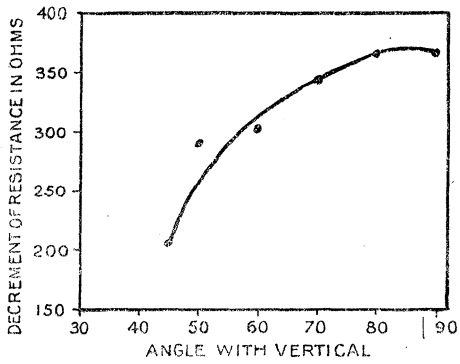

Fig. 11.

Experiment 5 : R = 10,000 ohms.

Angle with vertical ...	0°	0°	−45°	−50°	−60°	−70°	−80°	−90°
Total resistance	12,321	12,222	10,493	10,040	9802	9531	9267	9342
Decrement of resistance	—	—	1,729	2,182	2420	2691	2955	2880

The curve of these results (fig. 12) closely approximates the upper part of the curve in fig. 10 and displays the sigmoid character again.*

* Loeb and Osterhout (6) agree with Waller (9) in regarding the Weber-Fechner Law as governing many phenomena of stimulation, and Osterhout has suggested a dynamical explanation of the law.

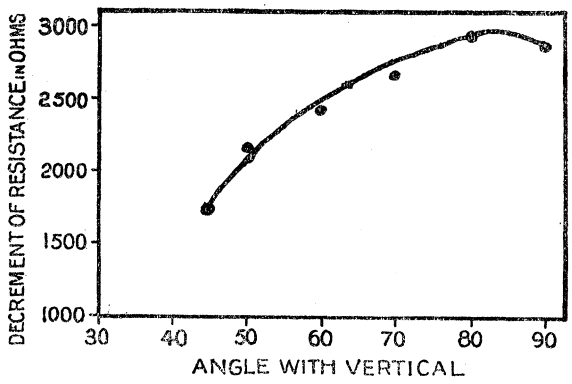

FIG. 12.

Differential Permeability of Upper and Under Sides.

Preliminary experiments indicated that the permeability of both upper and under sides of the root-tip increased, and this was further investigated in the following experiments.

Experiment 6: R = 7000 ohms.

Angle with vertical ...	0°	0°	−10°	+10°	−20°	+20°
Total resistance	8696	8730	8217	8418	7958	8250
Decrement of resistance ...	—	—	513	312	772	480

Experiment 7: R = 6000 ohms.

Angle with vertical ...	0°	0°	−45°	+45°	−70°	+70°	−90°	+90°
Total resistance	6073	6073	5194	5765	4851	5606	4753	5584
Decrement of resistance ...	—	—	879	308	1222	467	1320	489

The results of Experiments 6 and 7 are graphed in fig. 13. The relative flatness of the upper part of the curve is again demonstrated, especially in Experiment 7, where the difference between −90° and +90° is distinctly greater than that between −70° and +70°. Therefore, although the actual permeability is greater at 90°, and the turgor as a consequence less, than at smaller angles with the vertical, the difference between the turgor of the upper and under sides is greater and it is this differential permeability that produces the curvature. This explains the stronger curvatures obtained with the root horizontal.

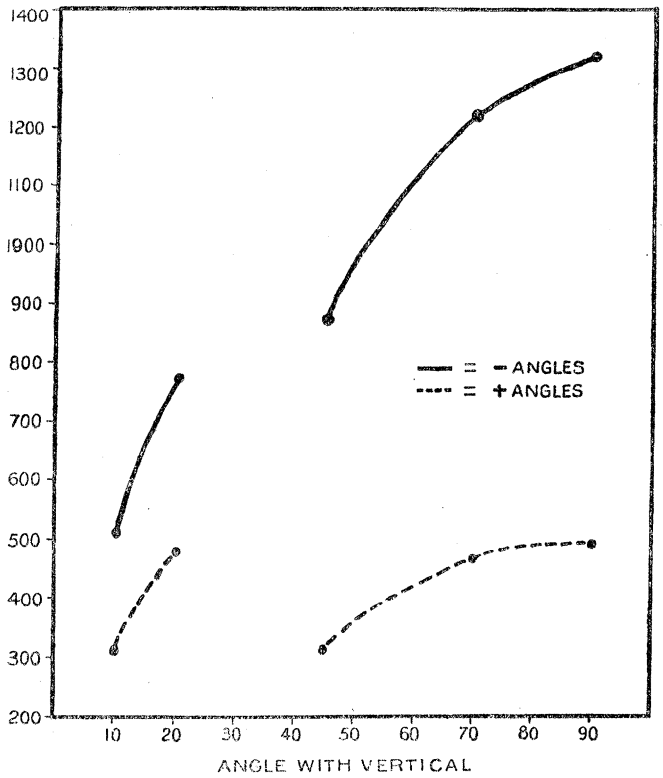

FIG. 13.

Diffusion Effects.

One of the results of increased permeability is more rapid diffusion of salts and a consequent dilution of the cell sap. Such dilution would increase the resistance and was investigated in the following experiments.

Experiment 8 : R = 7000 ohms.

Angle with vertical ...	0°	0°	−90°	−90°	−90°	−90°	−90°
Total resistance	8283	8318	6958	7345	7645	7798	7798
Decrement of resistance ...	—	—	1360	1073	673	520	520
Interval in mins.	—	15	2	8	5	5	15

Angle with vertical ...	−90°	−90°	−90°	−90°	−90°	−90°
Total resistance	7738	7171	7026	6673	6645	6539
Decrement of resistance ...	580	1147	1292	1645	1673	1779
Interval in mins.	10	15	15	15	45	15

Experiment 9 : R = 7000 ohms.

Angle with vertical ...	0°	0°	+90°	+90°	+90°	+90°	+90°	+90°
Total resistance	9365	9356	8660	8802	9018	9090	9128	8521
Decrement of resistance ...	—	—	696	554	338	266	228	735
Interval in mins.	—	15	2	8	6	5	15	10

Angle with vertical ...	+90°	+90°	+90°	+90°	+90°	+90°	+90°
Total resistance	7863	7767	7705	7584	7584	7614	7404
Decrement of resistance ...	1493	1589	1651	1772	1772	1742	1952
Interval in mins.	15	15	15	15	15	15	15

It will be seen from the graphs (fig. 14) that the turning of the root horizontal results in a considerable increase of permeability in both cases, the

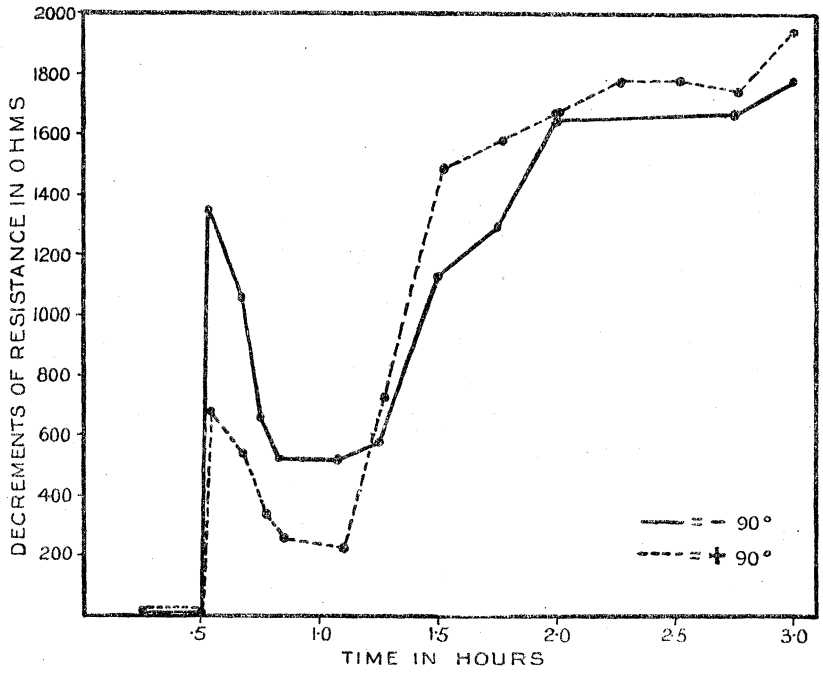

FIG. 14.

increase being much less when the root was turned so that the side which was being investigated was uppermost. Different beans were used, however, one for Experiment 8 and another for Experiment 9. The root was left in the horizontal position for the remainder of the experiment and the dilution due to diffusion is represented by the downward curves, these giving an increment of resistance from that of the root when it was first turned horizontal. The decrement of resistance due to loss of vitality starts 15–30 min. earlier than was usual in the other experiments, where no time was given for diffusion to take place as the plant was returned to the vertical immediately after each reading.

CONCLUSIONS.

From the time of M. C. Bose (2) to the time of J. C. Bose (1) and Fitting (3) very little advance had been made in the explanation of geotropism. J. C. Bose added to the experimental proof that geotropism is due to protoplasmic action, and interpreted his results as proving a differential change in the turgor on the concave and convex sides of the curve in stems and roots.

He also carried out experiments which proved that the responsive peculiarities of the root are shared by the shoot.

The present investigation proves that the mechanism of geotropic response by the root depends upon permeability changes. These changes in permeability explain the general curvature, the stronger curvature at 90° to the vertical, and the retardation of the elongation of the axis during curvature (Sachs, 7). The perception of gravity by plants is thus brought into line with the response in animals to the same stimulus. It is suggested that it is a general property of protoplasm to react to stimuli according to the sigmoid relation, and that the perception of gravity by protoplasm in general attains an accuracy of between 3 and 4 per cent. of the total stimulus [*vide* fig. 2 and Weber (10) on the perception of gravity by man with an accuracy of 3·3 per cent.].

SUMMARY.

1. That the perception of gravity by the root is a protoplasmic phenomenon is proved by the record of the changes in the electrical resistance of the second millimetre of one side of the root-tip of *Vicia Faba* at various angles to the vertical. These changes show the same sigmoid curve as is shown by animal tissue in response to stimuli.

2. The permeability of the cortical cells of both the upper and the under sides of the root-tip increases when the root is placed at an angle with the vertical, but that of the underside does so to a greater extent. The consequent relatively greater turgidity of the cells of the upper side explains the curvature. The increase in permeability, *i.e.*, decrease in turgor and electrical resistance, of the upper and under sides increases with the angle to the vertical, but the permeability of the upper side increases at a slower rate than that of the under side; this explains the stronger curvature when the plant is horizontal (*vide* fig. 13).

3. The increased permeability, giving decreased turgor, on both sides of the root explains the retardation of the elongation of the axis shown by Sachs (7) to take place during curvature.

In conclusion, I would record my indebtedness to my colleagues of the Chemical, Physiological, Physical and Psychological Departments at Bedford College, especially to Dr. J. S. Edkins and Dr. J. F. Spencer, for valuable assistance and advice.*

* It is obviously desirable to confirm the results obtained with the telephone method by the galvanometer, for two reasons: (1) the induction currents used in the telephone method produce alterations of resistance; (2) the subjective determination of the minimum-sound point is sometimes dubious and cannot be demonstrated to an audience. Experiments with the galvanometer are in progress but are not yet completed.

[*April* 19, 1918.—Experiments with the galvanometer have been carried out in Dr. Waller's laboratory, but the results with that apparatus were vitiated by a temperature effect due to the moist, non-polarisable electrodes used. It is important, however, that the subjective Kohlrausch method should be supplemented by an objective method, and the writer hopes to develop a suitable apparatus for the necessary confirmation of the results given above.]

BIBLIOGRAPHY.

(1) Bose, J. C., 'Plant Response,' London, 1916.
(2) Bose, M. C., 'De Motu Plantarum Sensus Aemulo,' Leipzig, 1729.
(3) Fitting, H., "Untersuchungen über geotropischen Reizvorgang," 'Teil I u. II. Jahrbuch. f. wiss. Botanik,' vol. 41 (1905).
(4) Hunter, C., "The Aerating System of *Vicia Faba*," 'Ann. Bot.,' vol. 29 (1915).
(5) McClendon, J. F., "The Increased Permeability of Striated Muscle to Ions during Contraction," 'Amer. Jour. Physiol.,' vol. 29, p. 302 (1912).
(6) Osterhout, W. J. V., (*a*) "Antagonism and Weber's Law," 'Science,' N.S., vol. 44, p. 318 (1916); (*b*) "The Permeability of Protoplasm to Ions," *ibid.* N.S., vol. 35, p. 112 (1912).
(7) Sachs, J. v., 'Physiology of Plants' (Eng. trans.), 1887.
(8) Tröndle, A., "Ueber Physiologische Variabilität," 'Bericht. Natur. Gesell. Freiburg,' vol. 21 (1914).
(9) Waller, A. D., (*a*) "Points relating to the Weber-Fechner Law," 'Brain,' p. 205 (1895); (*b*) "On the Excitability of Nervous Matter," 'Brain,' 1900; (*c*) 'The Signs of Life,' London, 1903.
(10) Weber, E. H., 'De Tactu: Annotationes anatomicæ et physiologicæ,' Leipzig, 1851.