On the Galvanotropism of Roots.¹

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With Four Figures in the Text and two Curves.

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I. HISTORICAL.

ELFVING² observed that roots responded to electrical stimuli. He grew seedlings with the tips only of their radicles dipping vertically into water, between two electrodes, and found that the roots curved towards the positive electrode. He obtained the same result when the current traversed the root longitudinally and also with decapitated roots. With some seedlings (*Lepidium*, *Sinapis*, *Raphanus*) he could not get constant results, and with one (*Brassica*) the curve was always towards the negative

¹ An abstract of much of the work included in this paper was communicated to the Royal Society by Dr. Francis Darwin, Nov. 23, 1905.

² Elfving, Bot. Zeitung, 1882.

electrode. The currents used by him were so strong that the roots usually died.

In 1883, Müller-Hettlingen¹ published the results of his researches in the same subject. He used a horizontal glass plate, covered with a piece of flannel which dipped at opposite ends into water: on this flannel the seedlings were laid, and then covered with another glass plate which was prevented from touching the lower by glass supports: the current passed through the flannel, and so presumably through the roots. Here the curvature was towards the negative electrode, and these radicles seldom died.

Little reliance can, however, be placed on these experiments, for it is very uncertain how much, if any, current passed through the roots: also rheotropic, hydrotropic, and geotropic reactions were not rendered impossible.

Müller-Hettlingen's work was closely followed by that of Brunchhorst,² whose investigations seemed to reconcile these conflicting results. He drew the conclusion that the positive curvature observed by Elfving was due to the action of a strong current, while Müller-Hettlingen's negative curvature was due to the latter using a much weaker current. The positive curvature he considered to be of a traumatropic nature, due to injury of the anodal side of the root, whereas the curvature to the negative electrode he supposed to be the result of a directive influence, and to be analogous to geotropic and heliotropic curves.

In experiments with strong currents, Brunchhorst used a similar apparatus to Elfving, but when working with weak ones he used a glass cylinder rotating horizontally on a clinostat, thereby eliminating geotropic action.

The strength of the currents used by these investigators is not very definitely stated; Elfving used 2, 4, or 6 Leclanché cells, and Müller-Hettlingen 4 Grove's cells; but as these cells are liable to rapid and pronounced polarization when in constant use, the currents obtained could not have been of a very reliable or uniform nature.

Brunchhorst estimates the strength of the currents he used by the amount of deposit of copper per hour; but even this does not convey a very satisfactory idea of the current used. The current passed through water in which the roots were immersed, and since these and water have dissimilar resistances, the amount of current passing through them could not be determined from external measures of current strength. The current density in each root would depend as much upon the area of cross section of the surrounding water as upon the current strength in the external circuit.

¹ Müller-Hettlingen, *Pflüger's Archiv*, xxxi, 1883.

² Brunchhorst, *Ber. d. Deutsch. Bot. Gesellsch.*, 1884.

Further research of a less restricted character was obviously needed ¹, and this investigation was initiated and carried on in the Botanical Laboratory of the University of Birmingham, under the direction of Dr. (now Professor) A. J. Ewart, to whom the author is greatly indebted for much kind and valuable assistance. She also wishes to express her thanks to Professor Hillhouse for the use of the resources of the Botanical Laboratory and for his kindness in criticizing the work, and also to Professor Poynting for the use of apparatus belonging to the Physical Department and for his help when referred to on points of technical detail.

2. PREPARATION OF MATERIAL.

To prepare material for the following experiments seeds of *Vicia Faba* (both broad bean and horse bean), *Phaseolus multiflorus*, *Zea Mais*, *Pisum Sativum*, *Helianthus annuus*, *Helianthus giganteus*, *Cucurbita Pepo*, and *Ricinus zanzibarensis* were soaked in water for usually twenty-four hours.

The seeds after soaking were germinated for a further twenty-four hours in moist sawdust, then carefully withdrawn, and the germination continued for a time in a vertical position in a damp chamber so as to avoid the possibility of accidental or injury curvatures. As an alternative their germination was continued horizontally in a moist chamber which was rotated on a clinostat.² To ascertain whether the radicles grew, or not, after stimulation, the apical centimeter was marked with Indian ink into spaces 1 mm. wide.

3. EXPERIMENTS WITH SEEDLINGS GROWING IN GELATINE.

Instead of using water, as in Elfving's and Brunchhorst's experiments, seedlings were arranged in a glass vessel containing 3 per cent. gelatine between two platinum electrodes, 10 to 12 cm. apart, and a current of 4.2 voltage passed through. In order to trace the limits of acid and

¹ See Pfeffer, Physiology of Plants, vol. iii, Eng. trans., section 42.

² The clock clinostats used in these experiments are a hitherto undescribed adaptation, by Professor Hillhouse, of American eight-day clocks, in which the full eight-day working power is retained—a point of some importance in prolonged experiments, since disturbance for winding purposes is reduced to a minimum. The face, hour-hand, and spindle are removed, and a new toothed wheel on the minute spindle engages another wheel borne upon a new spindle, of the same thickness as the minute spindle, which is fixed upon the clock framework a short distance away. The rate of rotation of this second spindle depends upon the relative number of teeth in the two wheels. A perforated brass disc, or table, fits upon either of these spindles by means of a split sleeve, and thus each clock gives rotation at one-hour periods, and at longer or shorter periods according to construction. For safety, the face is replaced by a metal plate, pierced for spindles and key. To exclude water when in horizontal use, another plate, with slit for the spindle, can be slipped on. With vertical axis, this clinostat carries freely upon its rotating disc a weight of several kilos. Its use with horizontal axis is illustrated, in an extreme case, in the accompanying Fig. 2, a flat cork of suitable size being then attached to the disc by means of the perforations. In a more recent form of the instrument, each clock bears two supplementary spindles with different rates of rotation.

alkaline diffusion from the respective poles the faintly alkaline gelatine was tinged slightly with phenolphthalein. After about twenty hours the roots in the strongly alkaline and acid zones near the negative and positive electrodes respectively, showed curvatures towards those electrodes, and after a further twenty hours the roots in the intermediate regions curved also but to a lesser degree, and then chiefly to the negative electrode.

Thus, in one experiment, with 15 seedlings after 48 hours, 9 curved to the alkaline pole, 2 to the acid, and 4 remained straight, while with another set of 11 seedlings, 5 curved to the alkaline pole, 4 to the acid, and 2 did not curve. These radicles were situated at distances varying from

FIG. 1. Seedlings growing in gelatine.

.5 to 12 cms. from the electrodes (see Fig. 1). For some experiments the gelatine was rendered slightly acid by a few drops of H_2SO_4 . The greater number of curvatures were still to the alkaline pole, even in the intermediate region, which was now slightly acid instead of alkaline.

To ascertain how far geotropic irritability was affected by growth in gelatine, a few seedlings were laid horizontally in that medium, and compared with a control set grown in a damp, well-aerated vessel. After seventeen hours the control seedlings had curved nearly 90° , while those in gelatine were still straight; and only after two days did the latter begin to curve slightly, no doubt because their geotropic sensitiveness was in large measure suppressed by lack of proper aeration.

Some of these experiments were now repeated, using 4 per cent. gelatine with holes cut in and kept open by means of small chips of wood. Here the better aeration brought about a quicker response, for the roots in the zone intermediate between the strongly acid and alkaline zones showed decided curves within the first twenty-four hours after the current had been put on.

Through one set of radicles growing in gelatine a very strong electric current (220 volts) was passed for a few minutes, and then the radicles were wiped and divided longitudinally at right angles to the direction of the current and pressed on to litmus-paper, but no trace of any internal differential polarization could be detected. Both halves of those radicles taken out of the strongly alkaline region contained local acid areas surrounded by alkaline ones: in the strongly acid region both halves were strongly acid, and an acid reaction similar to that of unstimulated roots was all that could be detected in the intermediately placed roots.

4. EXPERIMENTS WITH POLARIZABLE ELECTRODES DIRECTLY APPLIED TO THE ROOT.

But more definite results were found by placing the electrodes directly on the roots.

Strong currents were applied by means of tapering platinum electrodes touching appropriate points on the root, which was kept moist during the process. The voltage used in such cases was 4.2, but the current naturally depended mainly upon the variable resistance of the interposed tissues.

After marking with Indian ink the side (not the place) which the

FIG. 2. Diagram showing apparatus used when passing a weak constant current through a root.

positive electrode had touched, the seedlings were pinned to a cork (perforated for aeration) which fitted into a small moist chamber lined with moist blotting-paper. This chamber was now attached to a clinostat and

so placed that the roots were horizontal and parallel to the axis of rotation, and at right angles with the incident light.

When working with very *weak currents* a more complicated apparatus was used. A glass cylinder 30 cm. $\times$ 8 cm. was fitted at either end with a cork, through which a glass rod was passed. This cylinder was so attached to the clinostat that the glass rod constituted a horizontal axis of rotation, and its end remote from the clinostat rested upon friction wheels (Fig. 2).

Surrounding the cylinder at each end was a ring of wire with radiating projections. Beneath each ring was a small vessel of mercury, and as the cylinder revolved the projections dipped into the mercury. Inside the cylinder the glass rod passed through a large cake of paraffin wax, which served as support for two small platinum electrodes, and wires from these passed out of the cylinder at opposite ends, and were joined up with those forming the rings. A cork disc arranged parallel with the other corks served to support the seedling, so that, when the electrodes touched the radicle, and the ends of the conducting wires from the battery were dipping in the vessels of mercury, a complete circuit was formed.

The same precautions as before were taken to ensure moist and oxygenated air.

For some time there was a great difficulty in getting a current which after passing for some hours did not kill the roots. For the supply of electricity an accumulator of voltage 4.2 was used, and in the circuit at first was placed a resistance box of 14,000 ohms. This current proved too strong, so water resistances, in the form of 1, then 2, then 3 metre-length tubes filled with very slightly acidulated water, were added. The current now seemed about the right strength, but was so feeble that it could not be measured even by a milli-ampere metre.

After ten days or so the water resistances did not act well, owing to polarization, and had to be discarded. Ultimately instead of the accumulator a dry cell, voltage 1.35, was used, and this with two resistance coils of 100,000 ohms. and 50,000 ohms. respectively, gave a workable current, and one easily measured from the formula $C = \frac{E}{R}$. The 150,000 ohms. resistance was so great as to render the other resistances negligible.

With these two kinds of apparatus electric currents were passed through several hundreds of seedlings—a tedious process, since from the nature of the apparatus only one could be treated at a time.

4 *a*. RESULTS WITH WEAK CURRENTS.

Weak constant currents varying in duration from five hours to two days, when stronger than $\frac{4.2}{150,000}$ ampere, gradually killed roots, but from

$\frac{4.2}{150,000}$ to $\frac{1.35}{150,000}$ ampere they produced a curvature to one or other electrode according to its position.

Of 13 seedlings, in which the positive and negative electrodes were placed exactly opposite one another, at about 1.5 mm. to 2 mm. from the root apex, 8 curved to the positive electrode, 4 curved to the negative electrode, and 1 between the two: there was frequently blackening and signs of injury, more especially at the place where the positive electrode touched.

To add more resistance and thus still further weaken the current, the electrodes were placed 1.5 cm. or more apart; and now the curvature was towards the apical electrode, whether positive or negative, and usually there was no sign of injury. The results from 15 seedlings tested in this way, during 15 nearly consecutive days, gave 13 curvatures to the apical electrode, whether positive or negative. Two only died; the others showed no sign of injury.

4b. RESULTS WITH STRONG CURRENTS.

With strong currents of 3 to 8 minutes duration voltage 4.2 and resistance that of the root tissue only, the results were as follows:—

α. With electrodes on opposite sides, at a distance from the apex varying from 1.5 to 5 mm., out of 29 radicles, 27 curved to the positive electrode, 1 remained straight, and the other curved to the negative electrode.

β. With electrodes on opposite sides, one placed 1.5 mm. from the apex and the other 5 to 10 mm. away, out of 21 radicles, 12 curved to the apical electrode, whether positive or negative, 4 remained straight, 3 curved in the opposite direction, and 2 were doubtful.

γ. With electrodes on the same side of the root, one 1.5 or 2 mm. from the apex, and the other varying from 5 mm. to 4 cm. away, out of 69 seedlings, 37 curved to the apical electrode, 14 curved away, 20 did not curve, and the other three died.

δ. With one electrode flat against the apex, and the other 1.5 to 3 mm. away, out of 33 seedlings, 16 curved to the current side (7 only slightly), 16 did not curve, 1 curved away.

ε. With one electrode flat against the apex, and the other more than 5 mm. away, out of 9 radicles none curved.

It was quite possible to get these positive and negative curvatures without visible injury to the root, even when examined microscopically, although in some cases the epidermis and perhaps one or two cortical layers of cells were injured, and in a few the injury extended even to the stele.

4c. SUMMARY OF RESULTS WITH POLARIZABLE ELECTRODES.

From these results it will be seen that a strong electric current applied to the root for a short time will produce just the same kind of curvature as a weak constant current for a long period, and that the direction of the curvature evidently depends on the position of the electrodes, not on whether the current is strong or weak.

If both the electrodes are on the sensitive zone of the root, and the same distance from the apex on opposite sides, the curve is always to the positive electrode.

If one electrode is on the sensitive zone, and the other some distance away, either on the same side or opposite side, the curvature is always towards the apical electrode, whether positive or negative. A few experiments performed without the use of a clinostat showed that electrical stimulation could produce curvatures even in opposition to the stimulus of gravity.

Some lateral roots were tested and gave similar results to primary ones.

4d. THE ANGLE OF CURVATURE.

The angles of curvature were usually sharp, and varied in extent from a few degrees to 180° or more, according to the duration and amount of stimulation (cp. Fig. 1). After about twenty-four hours or less the effect of the stimulus passed off; the autotropic tendency of the root would then assert itself, and the last centimetre or so would take an 'S' form. Sometimes when the stimulation had been feeble and the curve only slight the root straightened itself completely.

4e. THE SENSITIVE ZONE.

To find the length of the sensitive zone of the root the position of one or both electrodes was varied from time to time, and beyond the fourth or fifth millimetre from the apex no response to stimulation took place. The most sensitive part was at from 1 mm. to 2 mm., but a slight curve could be obtained even when one or both electrodes were placed 4 or 5 mm. from the root-tip.

4f. DECAPITATED ROOTS.

With decapitated radicles there was usually no response, either when decapitation took place before stimulation or when stimulation preceded decapitation, as the following results show:—

11 radicles with 1.5 or 2 mm. of their tips cut off were stimulated, and of these 8 remained straight, 2 curved slightly, and 1 curved 30° .

6 radicles were stimulated, and their tips (1.5 mm.) then cut off, and of these 5 did not curve.

In these experiments electrodes were applied from 1.5 to 2 mm. from the apex, and then just the tip or 1.5 mm. of the root was removed.

4g. DURATION OF STIMULUS.

To find the duration of stimulus, roots were stimulated with strong currents, as in 4 *b* (α), fixed in plaster of paris, and rotated on a clinostat. On opening the casts after one or two days and again rotating, there was a curvature in an hour or so, but after three or four days in the plaster frequently no curvature took place. For example, 7 radicles were stimulated and put in plaster of paris, and released at the end of one or two days and all curved: whereas of 12 radicles similarly treated but released after three or four days, 7 remained straight and only 5 curved.

5. EXPERIMENTS WITH NON-POLARIZABLE ELECTRODES DIRECTLY APPLIED TO THE ROOT.

Some experiments were made, using non-polarizable electrodes with the platinum electrodes in the circuit, and at the same time control experiments, using platinum electrodes with the non-polarizable ones in the circuit, so that the total resistance was the same in both cases.

The non-polarizable electrodes were made by fitting a small brush of camel's hair into a tiny tube 1.5 cm. long, down the centre of which extended a copper wire from the accumulator: the brush was kept moist by diluted slightly acid cell-sap extracted from pressed roots, slowly flowing down from the glass tube. The current from the lighting main (220 volts) was used, and a large resistance of 2,200 ohms. in the form of three resistance lamps arranged in series was added.

The current was passed for fifty seconds; 54 roots were separately tested, and out of these 43 remained straight and 11 curved, but only slightly in most cases.

In the control experiment 40 roots were tested, and of these 9 remained straight and 31 curved, and these very frequently showed scars and other signs of injury.

The non-polarizable electrodes seldom caused any injury. When the 220 volt current was passed for longer than fifty seconds, even with the non-polarizable electrodes, a curvature took place.

6. ACTION OF LOCAL ACID AND ALKALI.

To ascertain whether there was any appreciable production of acid or alkali the cell-sap near the electrodes was tested with litmus-paper: there was a well-marked acid reaction at the positive electrode contact,

but at the negative electrode only a weak alkaline reaction was evident, this being probably due to partial neutralization by the CO_2 of respiration. These reactions suggested that possibly touching the sensitive zone of the root with acid or alkali might produce similar curvatures to those produced by an electric current, so pieces of blotting-paper, 1 sq. mm. in extent, soaked in either a solution of sodium carbonate or sulphuric acid, were placed on roots about 1.5 mm. from the apex, with the following results:—

Of 11 roots on which decinormal solution of the alkali was placed 8 curved towards it.

Of 42 roots treated with decinormal or weaker H_2SO_4 , 31 curved to the acid, 6 away, and 5 did not curve.

Of 11 roots on each of which a tiny slice of electrolysed acid tissue had been placed 8 curved to the acid.

Of 11 roots on each of which a slice of electrolysed alkaline tissue (or the sap only) had been placed 8 curved to the alkali.

A few experiments were tried in which decinormal acid and decinormal alkali were placed opposite one another, when the curve was to the acid side (thus producing a curve analogous to the one obtained when the positive and negative electrodes were placed opposite one another).

These acid and alkaline curvatures could be obtained without injury to the root, although when the acid or alkali was strong injury did take place.

7. LATENT PERIOD OF RESPONSE.

The response to the electrical stimulus is slow, and is not apparent to the naked eye until after at least three or four hours at a temperature of 19° to 22°C. , while at a lower temperature (15° to 18°) often twelve hours or more elapse before there is any sign of a curve. With a horizontal microscope, however, a curvature can be detected within an hour of stimulation.

8. THE ABNORMAL THICKENING OF MANY ROOTS.

Accompanying the curvature of the roots there was very frequently a thickening just above the electrode which was placed between the apex and the fourth and fifth millimetre space (Fig. 3). Microscopic sections of this showed merely a slight increase in the size of the cortical cells. This thickening appeared even when growth had been stopped for a few days by imbedding in plaster of paris.

This could hardly be a correlative action due to arrest of growth at the apex causing an increased tendency to lateral swelling behind, for when unstimulated root-tips were fixed in glass caps or glass collars no such result was produced. Hence this phenomenon must be due to the stimulatory action of the electric current, or more probably of the products

of electrolysis in the cell-sap, since a similar thickening frequently appeared in the neighbourhood of the stimulated spot when radicles curved as the

FIG. 3. Roots showing an abnormal thickening.

result of the external application of acid or alkali. The same kind of thickening took place when the tips of broad beans were allowed to grow against a pellet of blotting-paper saturated with a very dilute solution of sodium carbonate (Fig. 4).

Nemec¹ in a recent paper drew attention to a thickening of roots in the strongest growing part produced by allowing them to grow for an hour in a solution of either chloral hydrate or benzine, and then transferring to pure water: after forty-eight hours or so the normal growth was resumed again.

FIG. 4. A root of Broad Bean, showing an abnormal thickening due to growing against a pellet of blotting-paper saturated with dilute sodium carbonate. The curve is geotropic.

9. ABNORMALLY ELONGATED CELLS.

There should be mentioned another feature which was to be seen when any injury extending two or more cells below the epidermis occurred.

To the naked eye nothing was apparent except a brown scar, but microscopic examination revealed cells, two or three rows deep, with greatly extended radial walls; and between these cells and those forming the endodermis the cells were of the normal size, though the protoplasm in them appeared to have contracted and was probably dead. A few of these cells when measured had radial walls of lengths .51 mm., .68 mm., .85 mm., and 1.53 mm., compared with the normal diameter of .34 mm. or .51 mm.: the tangential walls were nearly normal, and did not differ much from one another.

Injured places on roots which had been made to curve by the external

¹ Nemec, Pringsheim's Jahrbücher, vol. 39, p. 689.

application of acid or alkali, when examined microscopically, also showed a tendency in the cell walls to elongate radially.¹

10. RATE OF GROWTH OF STIMULATED ROOTS.

From time to time measurements were taken to see whether the normal rate of growth was disturbed by stimulation. The average rate of growth per hour during the twenty-four hours preceding stimulation was taken, and also during the twenty-four hours following it and during the next day: the results showed stimulation was followed by retardation.

The following measurements illustrate this:—

	<i>Rate per hour during 24 hours before stimulation.</i>	<i>Rate per hour 24 hours after stimulation.</i>	<i>Rate per hour 24 hours later still.</i>
<i>Phaseolus multiflorus</i>	·44 mm.	·24 mm.	·42 mm.
<i>Vicia Faba</i>	·14 „	·06 „	·23 „
<i>Vicia Faba</i>	·3 „	·25 „	·04 „
<i>Phaseolus multiflorus</i>	·66 „	·49 „	·17 „

In many cases where no curvature took place after stimulation there was a complete stoppage of growth. That growth took place on both sides of the root was readily seen by covering the root after stimulation with a thick layer of Indian ink, and observing the cracks which formed on the concave as well as on the convex side of the curved root.

By using a horizontal measuring microscope, and taking periodical observations, the rates of growth on both sides of the curving root were more accurately measured. The readings were taken during the two or three hours preceding stimulation, and then continued for three or four hours.

During the first and second hour or longer after stimulation, when prolonged weak currents were used, there was usually an acceleration of growth on both sides of the curve; but it was greater, and lasted longer, on the convex side. Ultimately growth was retarded, if not quite checked, on both sides of the root.

10a. DIAGRAMMATIC REPRESENTATION OF THE GROWTH IN LENGTH OF CURVING ROOTS.

The following diagrams are selected from many to give an illustration of the curves of growth usually obtained. The three black lines to each figure except Figs. 6 and 7 represent the curves of the three apical zones marked out on each root, each zone of about 1·5 mm. length: the red line represents a general curve made by regarding the three zones as one. Each cm. length on the base line represents a period of one hour, and a cm. length on the ordinate line a unit of increment in length. The asterisks

¹ The question of these abnormal thickenings is being made a subject for further study.

Concave side of root

Convex side of root

NOTE.—The 'red' line mentioned on p. 398 is represented in this diagram by a dotted line.

mark the time at which a strong current (4.5 volts) was passed for three minutes; or, in curves where two appear, the period during which a weak current (1.5 volts R 100,000 ohms.) was passing.

The signs + and — indicate the sides of the root touched by the + or — electrode.

In each case the lines on the left-hand side indicate the concave side of the curve, and on the right the convex.

In Figs. 6 and 7 the curves represent the growth in length of the root as indicated merely by change in the position of the root-tip.

11. EXPERIMENTS WITH ACID AND ALKALI DIFFUSING THROUGH GELATINE.

Lilienfeld¹ has recently published some experiments of tropic responses induced by different salt solutions in radicles growing in gelatine. No very definite results were obtained, and in some cases they were even contradictory; yet a few might well be classed as of an ordinary chemotropic nature.

With a view to seeing whether there was any analogy between these curvatures, especially those produced by acid and alkaline solutions, and the curvature due to an electric current, similar experiments in a slightly modified form were made.

Seedlings were grown in a round glass vessel about 12 cms. wide containing a neutral solution of agar (5 or 6 per cent.) from the centre of which a small rod (.5 cm. diameter) of the jelly had been cut out, and the hole thus made was plugged with a roll of blotting-paper which was moistened with the solution to be tested, either H_2SO_4 , NaHO, or sodium carbonate of $\frac{N}{10}$ or other strength, or phosphoric acid neutralized by KHO. In some instances the solid jelly was stirred up to ensure better aeration. Each experiment lasted about two days, during which time the blotting-paper was moistened several times. The atmosphere above the seedlings was kept damp and well aerated. A few of these experiments were carried out on a clinostat.

No definite results were obtained, probably because the method was incapable of proper control, diffusion taking place too rapidly to allow of one side of the root perceiving and responding to the stimulus before its whole surface was equally affected. An attempt to secure slower diffusion was made by plugging the stem of a very small thistle funnel with blotting-paper, and inserting it in the gelatine instead of the usual roll, but with no satisfactory results.

¹ Lilienfeld, Ber. d. Deutsch. Bot. Gesellsch., March, 1905.

Similar experiments were carried out using troughs of sand, silver or coarse red, the salt solution being placed at one end of the trough in a little cubical chamber, of which the side facing the seedlings was made of plaster of paris.

In these experiments also the results were very conflicting. Some rather better results were obtained when using two plugged thistle funnels containing, respectively, decinormal solutions of NaHO and H_2SO_4 , and placed 10 to 12 cms. apart, with the seedlings in rows between them; the gelatine being coloured with phenolphthalein so that the extent of diffusion might be traced.

On the whole this series of experiments gave no conclusive results. Possibly the lack of aeration in gelatine delayed the curvatures until diffusion had gone too far; while in the troughs of sand the drainage and other currents may have been too rapid to allow of any difference of concentration being maintained on opposite sides.

The direct application of acid and alkali, however, on opposite sides gave very decided and consistent results.¹

12. SUMMARY OF RESULTS.

From the details which have been given there is enough evidence to connect these galvanotropic curvatures with those of a chemotropic character—the chemical stimuli being here the acid and alkaline ions formed during electrolysis.

In support of this view the following facts may be summarized:—

1. Acids and alkalies are formed in appreciable quantities at the places where the + and – electrodes touch the roots. (Section 6.)
2. Similar curvatures to galvanotropic ones are produced by acids and alkalies placed on the sensitive zone of the root. (Section 6.)
3. If a piece of root tissue under a + or – electrode be cut out and applied to another root, the latter curves to the acid or alkaline tissue. (Section 6.)
4. Acids and alkalies applied to the sensitive zone of roots can produce signs of injury similar to those produced by an electric current. (Sections 8 and 9.)
5. When one electrode is placed flat against the apex, and the other at some distance beyond the elongating zone of the root, there is no curvature: in this case the acid or alkali is produced in the root cap, and by diffusion affects the sensitive zone equally in all directions, and hence there is no differential response. But if the hinder electrode is on the sensitive zone, usually the root curves to this electrode, but sometimes remains straight,

¹ In the research as carried out, the experiments with seedlings grown in gelatine (section 3) were consequent upon this series of observations.

possibly because of the nearness of the electrodes to one another. (Section 4 *b*, *d* and *e*.)

6. When a current is passed through gelatine in which a number of roots are growing, both kinds of curvatures take place. (Section 3.)

7. When non-polarizable electrodes are used, with a strength of current sufficient to produce a curvature if applied by polarizable electrodes, no curvature takes place. (Section 5.) With these electrodes any acid or alkali would be chiefly formed in the glass tubes, and diffusion would hardly take place with sufficient rapidity for the acid or alkali to be long enough in contact with the root to cause a curvature.

13. THEORY AND CRITICAL.

During the passage of an electric current through a root there are two influences to be taken into account :—

(1) The accumulations of ions near the electrodes, (2) the ions en route between the electrodes, either or both of which may be concerned in the tropic response.

Taking into consideration the action of either the acid or alkaline ions, it will readily be seen that a stimulus given by the accumulation, say, of acid ions will act in a direction quite contrary to that of travelling acid ions ; and thus in the case of a current across a single root between directly applied electrodes there would be four possible stimulatory actions coming into play, namely those due to the accumulated acid ions and the travelling alkaline ones acting in one direction, and the accumulated alkaline ions and the travelling acid ions acting in the opposite direction ; and the response would depend on whether one set of stimuli predominated over the other.

Since with transverse currents directly applied a curvature to the positive electrode is always carried out in preference to one to the — electrode, it is evident that the acid ions have a greater stimulatory effect than alkaline ones ; and this is what might be expected, since it is a well-known fact that acid ions travel, and hence accumulate, more quickly than alkaline ones, and also are more chemically active.

Where the current traverses the root longitudinally, the curvature no doubt is due to the stimulating action of whichever ions have accumulated in the sensitive zone, since this region, being the actively growing one, is the only part of the root capable of curving.

Now, comparing the effects of a transverse current acting directly on a root, and one passing through gelatine, in which a number of roots are growing, a striking difference is apparent. It was remarked in this latter instance, that the curvatures in that portion of the gelatine which was intermediate between the zones extending about 2.5 cms. from either electrode were chiefly to the — electrode whether the medium was acid or alkaline.

An explanation of this may be found by supposing these curvatures to be due chiefly to the travelling ions, and since evidence points to the acid ions being the more effective, the impingement of these on the sides of the roots facing the — electrode would bring about a curvature in that direction.

Another argument which might be put forward to account for this apparent peculiarity is that since roots are normally acid, they might, according to Weber's Law, be more responsive to alkali at first, whereas when the acidity reached a certain intensity its primary greater stimulating action would come into play, and overcome the predominant influence excited by the first traces of alkali. Also roots growing in gelatine would, owing to poor aeration, have more CO_2 in their tissues, and hence might even be more acid than normal.

The curvatures to the + and — electrodes in the immediate vicinity of these electrodes are without doubt due mainly to the direct action of the accumulated acid and alkali in these regions, the ions diffusing to the root in the opposite direction to that in which they are carried by the electric current.

To test how far a curvature was due to the action of an accumulation of ions or to the impingement of travelling ions when the electrodes were directly applied, a few experiments were made, using chloroform to render the protoplasm non-irritable during the time the ions would be travelling through it. At first a saturated solution of chloroform in distilled water was used: the effect of the chloroform lasted so long that no curve was visible within twenty-four hours of stimulation; but a half-saturated solution answered well.

The roots were placed in the liquid for four minutes, stimulated for four minutes, then washed, and after seventeen hours they were compared with a control set, stimulated but not chloroformed. The chloroformed ones curved to a greater extent, and showed more vigorous growth, hence a conclusion might be drawn that this was due to the antagonistic action of the travelling ions being eliminated owing to the non-irritable condition of the roots during the passage of the current, and only the action of the accumulated ions allowed to be effective, since this action comes into play as the effect of the chloroform passes away. An electric current was passed through a dilute salt solution saturated with chloroform, and it was found that the chloroform did not appreciably effect the conductivity of the liquid, so that the presence of chloroform in the root does not alter its conductivity, and hence allow more or less current to pass than through unchloroformed roots. Also some seedlings were chloroformed as above, and laid horizontally, and their feeble curvatures after seventeen hours showed that the chloroform had lowered their geotropic irritability considerably.

The above results show that, although Brunchhorst's facts are correct

as far as they go, the conclusions he draws from them need extension and amplification.

Thus in regard to the — curvatures obtained by him with weak currents acting on roots arranged in water, the stimulatory effect of the travelling ions would preponderate, and of these the acid ones especially, which, impinging first on the sides of the roots facing the — electrode, would produce a curvature in that direction: convection currents, aided by those due to the rotation of the cylinder of water, would prevent any great accumulation of ions at the two electrodes, so there would be no strongly marked acid or alkaline zones as in gelatine, and hence there would be no + curvatures.

This arrangement of growing roots completely immersed in water is not a good one, since they must necessarily lack proper aeration. The curve to the + electrode obtained by using strong currents Brunchhorst considered to be of a traumatropic nature, because his roots, and Elfving's, usually died: but this term is certainly inapplicable to all + curvatures, since it is quite easy to obtain them without injury: though it is quite possible that Brunchhorst's and Elfving's curves were really curves of injury.

Also Spalding¹ has shown that traumatropic curvatures will take place even when growth is arrested for seven or eight days by means of plaster of paris imbedding; whereas an electrically stimulated root, if allowed to remain as long as five days in a cast, will not curve after release.

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POSTSCRIPT.

After the completion of the foregoing work on the Galvanotropism of Roots it seemed desirable to ascertain whether a powerful magnetic field would also produce stimulatory effects. It is well known that a plant cell is made up of constituents possessing different magnetic permeabilities, and hence, theoretically, a field of sufficiently great power could hardly fail to influence growth in some way or other.

A horseshoe electro-magnet with adjustable pointed pole-pieces was used: each iron core was 7.95 cms. diameter, and its length 32 cms. A current of about 15 amperes, produced from twenty cells (the E.M.F. of each being 2 volts), passed through the coils, against a resistance of 4.15 ohms. The pole-pieces were adjusted so that their distance apart varied from 7.5 cms. to 3.7 cms. in different experiments; and the roots of very young seedlings of *Pisum sativum* and *Vicia Faba* were placed between

¹ Spalding, Annals of Botany, December, 1894.

them in vertical and horizontal positions. The seedlings were either fixed in narrow glass troughs or pinned with brass or silver pins to very thin sections of cork, covered with cotton wool, and were kept moist by frequent supplies of water of suitable temperature. The room was kept at a temperature of about 23°C ., but a thermometer inserted among the seedlings during the exposure to magnetic action registered 25°C . The seedlings were arranged as close as possible to the poles without touching, and kept in that position 40 min., 60 min., 2 hrs., 4 hrs., or 6 hrs.; in every experiment light was excluded, and a control was arranged.

When the roots were removed from the magnetic field and examined, some were transferred to a clinostat for twenty-four hours, and others were fixed in chrom-acetic acid, and, after the usual treatment, microtome sections obtained.

These experiments gave only negative results; hence it seems quite conclusive that to produce any influence on the growth of roots a very much more powerful magnetic field would be necessary.

Microscopic examination of the microtome sections fails to give evidence of any change or alteration in the position of the cell contents: also, since in a few experiments, though not in the majority, the geotropic curvatures of the roots placed horizontally just above one pole slightly exceeded those of the roots placed horizontally just below, special attention was directed to the position of the statoliths in the root-cap; but no difference between either set and those of the control roots was to be noted.

Some further experiments were carried out at an electric light station, using the magnetic field produced by a small dynamo through which passed a current of 25 amperes produced from an E.M.F. of 250 volts. The roots were exposed to magnetic action for twenty-five or twenty-nine hours at a temperature of 24°C . Here again no positive results were obtained.

I should like also to make brief reference to the recently published work of Dr. Gustav Gassner (Bot. Zeit., Sept. 1906) on 'Der Galvanotropismus der Wurzeln.'

His method of experimenting was as follows:—A seedling was fixed in a vessel of definite size ($20 \times 9 \times 8.5$ cms.) with its root immersed in water or sometimes gelatine: using carbon electrodes, a current of known strength was passed through the water or gelatine and so through the root for periods of time varying from a few seconds to fifteen hours or more: the current density seems to have varied between .005 and 4.5 M.A. per qcm.

He arrived at the conclusion that Galvanotropism was nothing more than a special case of Traumatropism, and that the + or - direction

of curvature was brought about by differences of current density or by passing the current for varying periods of time, keeping the density constant.

Dr. Gassner does not appear in any of his experiments to have tried the method of applying the electrodes directly to the root and then by varying the points of application changing the direction of the current. His current always traversed the root horizontally; and thus, by using only this one direction he has missed most of the evidence which in my experiments leads to a different interpretation of Galvanotropism.

Moreover, although his work shows that the utmost care has been taken to avoid any source of error, the experiments were conducted without the use of a klinostat—a sufficiently obvious precaution wherever possible, in dealing with root curvatures: also with the exception of the experiments on root-tips, the roots were entirely immersed in water or gelatine—a condition under which they lack aeration in greater or less degree, and in consequence have a diminished power of response.

It seems highly probable, then, that the curvatures obtained by Dr. Gassner were essentially traumatropic, and that, so far as they are concerned, the interpretation of them given in section 7 is a correct one. But it is a far cry from this to the assertion of the identity of Galvanotropism with a special form of Traumatropism ('Auf Grund eingehender Untersuchungen und Vergleiche kam ich zu dem Ergebnis, dass der Galvanotropismus auf Traumatropismus zurückzuführen ist'). Galvanic currents *can* cause injury, in which case the resulting curvature is traumatropic.

My own experiments, however, make it clear that galvanotropic curvatures can be obtained without injury to the root. Similar curvatures can be produced by dissimilar causes; in the one case of injury; in the other as response to a stimulus which no more involves injury than does the shifting of 'statoliths' in response to a changed direction of geotropic action; and that the term traumatropic could in no way be applied to these.

Further, by constantly varying the direction of the current it was proved quite conclusively that the + or — direction of the curve depended on the position of the positive or negative electrodes: moreover, further experiments all pointed to the analogy of these curves with those produced by a chemotropic stimulus.

Jan., 1907.

J. S. B.

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