The Sensory Zone of Roots.

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With a Figure in the Text.

I. INTRODUCTION.

IN a recent paper¹, evidence was offered to show that the stimulus giving the response known as *rheotropism* is perceived by the apical millimetre of *Zea Mays*, L., and of *Raphanus sativus*, L. There was evidence to show also that, in the root of the latter plant, the stimulus was perceived throughout the elongating zone, and still more posteriorly, to a distance even 15 mm. back of the apex, this being at least 10 mm. beyond the limit of the elongating zone.

This discovery was of such interest that it seemed advisable to extend the research to other plants, to ascertain whether the phenomena, observed in *Raphanus*, might be found to be general. The results obtained in such an investigation are reported in the present paper.

By way of retrospect, it may be said that the various tropisms of roots so far determined have their sensory seat either in the apex or in the elongating zone. Confined to the apex in front of the elongating zone is the sensory tissue controlling the responses known as geotropism², and trauma-

¹ Newcombe, The Rheotropism of Roots. Bot. Gazette, xxxiii, 1902, p. 177.

² Czapek, Jahrb. f. wiss. Botanik, xxvii, p. 255; xxxv, p. 317.

tropism¹, and probably heliotropism² and hydrotropism³. Thermotropism⁴, aerotropism⁵, galvanotropism⁶ and rheotropism⁷, are responses known to be due to the sensitiveness of the elongating zone, but in these cases the root-apex is not known to be insensitive. Thigmotropism⁸, as such, has as yet no place among phenomena of irritability in any but aerial roots, for Wiesner⁹ and Spalding¹⁰ have shown the thigmotropism of Darwin to be traumatropism, and I shall shortly offer evidence to show the same thing regarding Sachs' thigmotropism.

The foregoing statement is enough to indicate that in roots no sensory area has been found posterior to the elongating zone. The following pages will show that several plants possess sensitive areas removed by a considerable distance from the elongating zone. Evidence will also be offered to show that the rheotropic sensitiveness of the root-apex of *Brassica alba* is to be assumed as well as that of *Raphanus sativus* and *Zea Mays*.

II. THE RHEOTROPIC SENSITIVENESS OF THE APEX OF THE ROOT.

In the paper¹¹ already referred to, experiments were detailed in which the rheotropic sensitiveness of the apical millimetre of the roots of *Helianthus annuus*, L., and *Brassica alba*, Boiss., was made probable by the application of fine

¹ Wiesner, Sitzb. d. k. Akad. d. Wissensch. Wien, Bd. lxxxix, I. Abth., 1884. Also Spalding, Ann. of Bot., viii, 1894, p. 423.

² Kohl, Die Mechanik der Reizkrümmungen, p. 26.

³ Molisch, Sitzb. d. k. Akad. d. Wissensch. (math.-nat. Cl.), Wien, Bd. lxxxviii, I. Abth., 1883, p. 897. Also Pfeffer, cited by Czapek in Jahrb. f. wiss. Bot., xxxv, p. 316.

⁴ Wortmann, Bot. Zeit., xliii, p. 232.

⁵ Molisch, Sitzb. d. k. Akad. d. Wissensch. (math.-nat. Cl.), Wien, Bd. xc, I. Abth., 1884, p. 175.

⁶ Brunchorst, Ber. d. D. Bot. Gesellsch., ii, 1884, p. 204.

⁷ Juel, Jahrb. f. wiss. Bot., xxxiv, 1900, p. 518.

⁸ Darwin, Power of Movement in Plants, p. 129. Also Sachs, Arbeit. d. Bot. Inst. Würzb., i, p. 437.

⁹ Wiesner, loc. cit.

¹⁰ Spalding, loc. cit.

¹¹ Newcombe, Bot. Gaz., xxxiii, 1902, p. 177.

jets of water to one side of the tip. Four seedlings of *Helianthus* were used, and all four roots responded with positive curves; while fourteen seedlings of *Brassica* were used, of which six roots gave positive curves, two gave negative curves, and six remained neutral. This evidence was not conclusive.

FIG. 24 (I). Illustration of a preparation to determine the sensitiveness of the apex of the root. The glass-tube with its seedling was fastened to a bar of wood. The packing of cotton is not represented. The arrows indicate the direction of the current of water.

(II). Illustration of a preparation to determine the extent of the sensory zone. In this preparation 15 mm. of the apex of the root is covered, the lowest circle of wire serving to mark the height at which the root-tip is to be kept during the experiment.

Better results were obtained by another method. This consisted in the employment of glass-tubes to shield all of the root, except the apex, from the action of a stream of water in which the lower part of the seedlings was immersed. Thin-walled glass-tubes with an inner diameter of 3 mm. were cut to suitable lengths, the roots and hypocotyls of the

seedlings passed into these, and wet cotton was used as packing to fix the seedling in the tube. The preparation is illustrated in Fig. 24 (I).

The seedlings with encasing tubes were secured to a bar of white pine 20 cm. in length, the bar was adjusted parallel with the diameter and just above the water of a glass basin 22 cm. in width. The roots and glass-tubes project into the water. The seedlings were now adjusted to the proper exposure of apex by moving them up or down the tubes, and the basin of water was set revolving. Such a preparation as this needs almost constant watching, for the growth of the roots necessitates the raising of the seedlings in the tubes at intervals of fifteen to thirty minutes.

Tested by this method, *Zea Mays* (popcorn), when only 1 mm. to 2 mm. was exposed to the action of the stream, gave nine positive curves out of a total of twenty-one roots, the twelve remaining neutral. The period of the experiment was only four hours in one case and eight hours in the other, thus accounting for the small number of curves. Since there were no negative curves, however, the positive ones may be counted as irritable responses. In a later experiment with the same species, ten roots were in the water-stream for seven hours with never more than 1.5 mm. exposed beyond the glass-tubes. Six positive curves resulted, and four roots remained straight.

Raphanus sativus tested by the foregoing method, with not more than 2 mm. of apex exposed, the duration of the experiment being six hours, gave positive responses in all of the thirteen roots used. In a second similar experiment lasting for eight hours, with never more than 1.5 mm. being exposed, nineteen roots became positive and one remained neutral. In a third experiment lasting nine hours, in which nineteen seedlings were used, with never more than 1 mm. of the root-apex exposed, eleven roots became positive, while the other eight remained neutral.

Since the publication of the foregoing results a third species has been tested as were the two others, this being *Brassica*

alba, Boiss. Only eight seedlings were used; the temperature of the water was 24°C.; the velocity of the water-steam ranged from 200 cm. per minute for the roots nearest the centre to 700 cm. for those most distant; the duration of the test was six hours, and there was never more than 1 mm. of apex exposed. Seven roots showed strong positive curves, and the eighth was neutral.

From the foregoing results there can be no doubt that the apex of these roots is rheotropically sensitive.

III. SENSITIVENESS OF THE POST-ELONGATING ZONE.

It has already been shown¹ that the root of the seedling of *Raphanus sativus* is sensitive to a rheotropic stimulus from its apical millimetre back to at least the fifteenth millimetre. Since the method in that study is the same as that used in the more recent testing of other species, it may be briefly summarized as follows:—Glass-tubing of 3 mm. internal calibre was cut into appropriate lengths, varying from 1 to 3 cm., and paired tubes were made by joining two pieces together by fine annealed iron wire, as shown in Fig. 24 (II). These tubes were washed in water for twenty-four or more hours before using. When the seedlings had attained a proper size, usually 3 to 5 cm. in length, the paired tube was filled with water, and the root of a seedling was passed in, the seedling being secured in the tube by packing wet cotton around the upper part of the root, or the lower end of the hypocotyl, as this was held in the upper section of the paired tube. A flattened needle with its point broken off did very good service in packing the cotton around the seedling. As each seedling was secured in a tube, the preparation was set vertically upright in a dish of water. When ten such seedlings were ready, a bar of wood about 1 cm. square and 20 cm. long was clamped in a vice at one end, and the glass-tubes with the contained seedlings were fastened to the bar. In fastening the preparations to the bar of wood, one side of the bar was first covered with wet blotting paper, the tubes were

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

laid against this, one by one, and secured in place by a strip of cloth and rubber bands. While these tubes and seedlings were being fastened to the bar, they were kept constantly in the vertical position, and hence throughout the whole preparation there was no chance for a geotropic stimulation. As these tubes were arranged on the bar, none of them came nearer than 2.5 to 3 cm. from the middle, and the extreme ones were about 9.5 cm. from the middle. The interval between two neighbouring tubes was about 1.5 cm. As the seedlings were secured in the paired tubes, they were adjusted so that any length of apex desired was enclosed by the lower piece of the paired tube. Thus when the bar of wood with its load was suspended over a revolving basin of water, with the glass-tubes projecting into the water, the only part of the root exposed to the water-stream was the portion, usually 5 to 10 mm. in length, between the two pieces of the paired-tube.

As stated elsewhere¹, it was with great surprise that I observed the roots of *Raphanus sativus*, L., making positive curves within glass-tubes when the part that was stimulated was 10 mm. distant from the apex, especially as observation with the horizontal microscope had shown that the elongating zone, when the roots are kept in water, is confined to the first 5 mm. of the apex. The roots of *Raphanus sativus*, when 10 mm. of the apex were enclosed in the tubes, showed thirty-four positive curves in a total of forty-eight seedlings; and when a length of 15 mm. of the apex was shielded, ten positive curves in a total of 23 seedlings. When, however, a length of 20 mm. of the apex was shielded from the water-stream, in a total of nineteen roots, only seven curved positively, while four became negative, and eight remained neutral.

Since this record was made for *Raphanus sativus* (early long scarlet), five other tests have been made with the same variety, and in the same manner as before. The total result obtained in all the experiments with this plant may be presented in the form of the following table:—

TABLE I. *Raphanus sativus* with root-tips shielded from

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

the water-stream by glass-tubes. Temperature of the water = 23° to 24° ; duration of experiments = from 9 to 12 hours; velocities = from 200 cm. to 700 cm. per minute.

<i>No. Seedlings.</i>	<i>Extent of Apex shielded.</i>	<i>Positive Curves.</i>	<i>Neutral Roots.</i>	<i>Negative Curves.</i>
48	10 mm.	34 = 71%	11	3
50	15 mm.	28 = 56%	18	4
33	20 mm.	14 = 42%	14	4

The results recorded in this table would seem to show that the root of *Raphanus sativus* is sensitive to the water-stream at least 20 mm. back from the apex. It is true that the number of positive responses is not large, but it is large enough to indicate clearly that some directive influence was at work, especially as there were but four negative curves. The roots of *Raphanus* do not distort in water, nor do they nutate through any considerable angle. The angles attained in all the curves counted as rheotropic were never below 10° , and were often 30° to 45° . A majority were above 15° .

The foregoing table also shows that the sensitiveness of the roots decreases with the distance from the elongating zone, though, when the stimulus is applied 10 mm. from the apex, nearly as many positive curves appear as when the whole root is exposed to the water-stream. My former paper¹ shows that this plant, when the whole root receives the stimulus, gives 87 per cent. of positive responses; when the apex to a distance of 10 mm. is shielded, positive curves equal to 71 per cent. appear.

A second plant whose irritability back of the elongating zone was tested is *Brassica alba*, Boiss. This plant was known to be highly sensitive to the action of a stream of water¹, and for this reason was selected for experiment. The preparation was made and the experiments carried out in the same way as for *Raphanus*, the plants being shielded

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

from the light also at all times, except for the few minutes when observations were being made.

TABLE II. *Brassica alba* with root-tips shielded from water-stream by glass-tubes. Temperature of the water = 22° to 24° ; duration of experiments = from 7.5 to 11.75 hours; velocities = from 200 cm. to 700 cm. per minute.

<i>No. Seedlings.</i>	<i>Extent of Apex shielded.</i>	<i>Positive Curves.</i>	<i>Neutral Roots.</i>	<i>Negative Curves.</i>
16	10 mm.	12 = 75%	4	0
33	15 mm.	28 = 85%	4	1
18	20 mm.	9 = 50%	9	0
22	25 mm.	11 = 50%	9	2

This summary, if it teaches what it seems to, is remarkable in showing that this plant is sensitive rheotropically at a place at least 25 mm. distant from the apex of the root. One must not, however, put too much faith in summaries. Let us examine the individual experiments to see whether they tend toward a constant result: there were three sets of seedlings prepared and carried through the experiment with 25 mm. of the apex shielded. One with ten seedlings gave seven positive curves, one with nine seedlings gave four positive curves, and one with three gave one positive curve. None of the curves counted were less than 10° , and the average was 22° . Inasmuch as the roots did not become contorted, and there were only two negative bends, I see no escape from the conclusion that the most of these positive curves were caused by the water-stream. Should we consider the experiments in which 20 mm. of the apex were covered by the tube, we should find the same relations. When, however, we consider the cases in which only 15 mm. of the apex were shielded by the tube, even the most sceptical must admit the evidence. The total of thirty-three seedlings used were distributed in six experiments, and in every experiment two-thirds or more of the roots responded with positive curves.

These curves varied between 10° and 90° , the most of them being between 15° and 30° .

To determine the extent of the elongating zone of *Brassica alba*, the roots of four plants were marked with India ink, and immediately measured with a horizontal microscope. Subsequent examination showed that three of these plants had elongated only in the first 5 mm., while the fourth had made a slight growth in the sixth millimetre also. These roots were kept in water both before and after the preparation for measurement.

Fagopyrum esculentum, Moench., when its naked roots are immersed in flowing water of suitable velocity¹, has shown a positive response in 92 per cent. of the total number of roots used. It is therefore highly sensitive rheotropically. But unlike *Raphanus sativus* and *Brassica alba*, it has the disadvantage of growing with a considerable number of contortions in water. It has been selected for experiment in the study of the extent of the sensitive area in roots, but it gives, as one would expect, a larger number of negative bends, these negative bends being considered not as rheotropic responses, but rather as the result of the objectional environment of water, whatever that may be. The tabular summary of the behaviour of *Fagopyrum*, when treated as the two preceding plants were, appears as follows:—

TABLE III. *Fagopyrum esculentum* with root-tips shielded from water-stream by glass-tubes. Temperature of the water = 23° to 24° ; duration of experiments = 10 to 11 hours; velocities = from 200 to 700 cm. per minute.

No. Seedlings.	Extent of Apex shielded.	Positive Curves.	Neutral Roots.	Negative Curves.
38	10 mm.	29 = 76%	3	6
41	15 mm.	24 = 59%	10	7
36	20 mm.	17 = 47%	5	14
5	25 mm.	0 = 0%	4	1

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

Compared with the tables for *Raphanus* and *Brassica*, this one for *Fagopyrum* shows a proportionally much larger number of negative curves and a smaller number of neutral roots, indicating that we cannot for *Fagopyrum* reckon all the positive curves as due to the water-stream. If we subtract from the positive curves in each group, the number of negative curves in the same group, we ought to obtain approximately the true number of rheotropic responses. This statement, of course, assumes that there is no such response as negative rheotropism, a belief in which I have been confirmed by all my work on rheotropism.

The individual experiments in the group with 10 mm. of the root covered, and also those with 15 mm. covered, are uniform in showing in all cases a majority of all roots with positive curves. The five experiments in the group with 20 mm. of the apex covered varied considerably in the results shown, three having a majority of positive curves, one a majority of negative curves, and two having an equal number of positive and negative curves. The apparent tendency toward positive curving is here so slight that no claim can be made for sensitiveness at a distance of 20 mm. from the apex.

The explanation of the relatively much larger number of negative roots when 20 mm. of the apex are covered than when 10 mm. or 15 mm. are covered, is found probably in the weaker effect of the stimulus of the water-stream when applied at 20 mm. from the apex. As a result of the lesser effect of this stimulus, the direction of growth of the root is left more under the control of the stimulus which leads to distorted growth. It has been shown elsewhere¹ that, in rheotropic experiments with the naked roots of this plant in water, the initial distortion curves are converted into positive rheotropic curves, or rather that the various directions taken initially, due to distortion, are later brought into a common direction which is parallel with the current of the water.

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

Helianthus annuus, L., like *Fagopyrum esculentum*, does not produce all its roots straight in water. It is a plant giving 70 per cent. of positive rheotropic curvatures when the naked roots are acted on by a stream of water, but the angles attained average less than 45° . This behaviour places this plant among those with a good degree of sensitiveness to a stream of water, but considerably below the grade of *Raphanus* and *Brassica*. The following table will show that, like *Fagopyrum*, this plant gives a considerable number of negative bends, which are to be interpreted as merely the result of the environment of water.

TABLE IV. *Helianthus annuus* with root-tips shielded from the water-stream by glass-tubes. Temperature of the water = 24° ; duration of the experiments = 11 hours; velocities = from 200 cm. to 700 cm. per minute.

No. Seedlings.	Extent of Apex shielded.	Positive Curves.	Neutral Roots.	Negative Curves.
30	10 mm.	22 = 73%	6	2
46	15 mm.	23 = 50%	14	9
29	20 mm.	11 = 38%	14	4
32	25 mm.	11 = 34%	15	6

The results of individual experiments carried through on various days agree very closely with the proportions shown in the totals of the table. For those roots with 10 mm. shielded, two experiments were made with fifteen seedlings in each. Each experiment gave eleven positive curves, while one experiment gave two negative curves and two neutral roots, and the other gave no negative curves, but four neutral roots. The experiments with 15 mm. of the root covered numbered four. The first one of these four sets of roots had eight individuals, and gave three positive curves, three negative, and two neutral roots; the second had fourteen individuals, and gave seven positive curves, two negative, and five neutral roots; the third set had twelve individuals, and gave seven

positive curves, one negative, and four neutral roots; the fourth set had twelve individuals, and gave six positive curves, three negative, and three neutral roots.

In a plant like *Helianthus annuus*, not growing well in water, it is not at all surprising that occasionally a set of seedlings will vary somewhat, as did the first set noted above, from the general behaviour. The result of the four experiments seems to me to teach unmistakably that the root of this plant is sensitive to a water-stream at the distance of 15 mm. from the apex. The negative curves appearing in these experiments would nearly all be turned into positive curves were the roots not covered by the tubes. This is shown in my paper on 'Rheotropism,' and is to be explained probably by supposing that the rheotropism of the roots overcomes in most cases the initial tendency to contorted growth. When the roots are partially shielded by tubes, the rheotropic stimulus affects the plant to a much less degree, and the tendency to contorted growth manifests itself much more strongly.

If we assume a sensitiveness of the root of *Helianthus* at a distance of 15 mm. from the apex, the recorded results will hardly warrant such an assumption for the part of the root 20 mm. distant from the apex. For if we take the four negative curves as due to contortion and assume an equal number of contortions among the positive roots, we shall have left but seven positive roots in a total of twenty-nine, a proportion almost too small to serve as a basis for any conclusion. We cannot assume that the root of *Helianthus* is insensitive 20 mm. distant from the apex, but rather that the method employed gives no sufficient evidence for a judgement either way.

Five roots of *Helianthus annuus* were marked and observed with the horizontal microscope for the extent of the elongating zone, the roots being kept in water, and light excluded. Of these, four roots showed growth in the first 7 mm. only, while the fifth root showed growth in the first 5 mm. only. It must be therefore that the root of this plant is sensitive to

the rheotropic stimulus at least 8 mm. back of the limit of the elongating zone.

Zea Mays, L. (the variety commonly called *white popcorn*), unlike its near relatives, the *sweet* and the *field corn*, produces mostly straight roots in water, and shows a good degree of rheotropic sensitiveness. In seventy-nine seedlings whose naked roots were subjected to a stream of water, 72 per cent. showed positive curves. This plant was selected therefore as promising results by the employment of glass-tubes. In the experiments with 15 mm. of the apex of the root shielded from the water-stream, so many roots responded, that it was thought unnecessary to experiment with but 10 mm. of the apex covered.

The roots of this plant are so large, that larger glass-tubes were used, viz. tubes of 4 mm. internal diameter.

TABLE V. *Zea Mays* (white popcorn) with root-tips shielded from the water-stream by glass-tubes. Temperature of the water = 24°; duration of the experiments = 10 hours to 12 hours; velocities = from 200 cm. to 700 cm. per minute.

No. Seedlings.	Extent of Apex shielded.	Positive Curves.	Neutral Roots.	Negative Curves.
30	15 mm.	23 = 76%	5	2
30	20 mm.	21 = 70%	8	1
30	25 mm.	11 = 37%	13	6

These ninety seedlings were used in nine sets, each set having ten seedlings. The results for the various sets were remarkably consistent, and each group of ten showed about the same proportionate number of curves and neutral roots as shown by the total of its class in the table.

Measured with the horizontal microscope as they were growing in water, one seedling of *Zea* (popcorn) showed the elongating zone of its root to be confined to the first 8 mm., three showed growth in the first 9 mm., and a fifth showed growth in the first 10 mm. 10 mm. may be assumed as the

limit of elongation for most individuals of this variety. At the distance of 20 mm. from the apex, the sensitiveness of the roots is so great as to bring approximately the same percentage of curves as is produced when the whole root is subjected to the water-stream. It is probable, though not certain, that the roots are sensitive 25 mm. from the apex.

In the effort to extend the study of the phenomena here treated over as wide a range as possible, an attempt was made to add a representative of the *Leguminosae* to the number of those included in the experiments. So far as tested, only two species of this family could be thought of with any hope of success, these two being *Pisum sativum*, L., and *Vicia sativa*, L. In my tests¹, I had found *Pisum* somewhat more sensitive than *Vicia*. Both plants give a rather high proportion of crooked roots in water, and both have been shown to respond rather slowly to a rheotropic stimulus. Individual roots in both species, when the whole root received the stimulus², have been seen to respond within two hours after the application of the stimulus, but the majority of roots in both species show no curves till after the lapse of six to eight hours.

Pisum sativum was selected for experiment, and over one hundred seedlings tested by shielding various lengths of root from the water-stream. The roots curved, but in all directions, and the curves were evidently due to the objectionable environment of water, and not to the water-stream. A control was set up in still water, without using the glass-tubes, and the curves came in the same way. Ten seedlings with naked roots were tested for rheotropism, but gave no rheotropic curves, only distortion curves, during twelve hours. The attempt to use this plant with the glass-tubes was thereupon abandoned.

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

² Juel, Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. f. wiss. Botanik, xxxiv, p. 507. Newcombe, loc. cit.

IV. SUMMARY AND CONCLUSION.

As far as we know, there is no reason in the nature of the case why the sensitiveness of roots to stimuli should be confined to the region capable of elongation. A grass-stem receives and responds to the gravitation stimulus when under ordinary conditions its growth has ceased¹; the cotyledon of *Panicum*² is sensitive to light after growth has ceased; and the leaves of *Mimosa* and of numerous other plants continue to receive and respond to stimuli long after growth has ended. The region of roots shown in the foregoing pages to be sensitive to stimuli, though no longer capable of elongation, may still grow in diameter. And it may be said here that the assumption of the limitation of sensitiveness of roots for certain stimuli to certain regions is not in all cases justified. Czapek³ appears to have tenable ground for limiting the perception of gravitation to the root-apex. But that moisture stimulates only the apex, cannot be maintained until the elongating zone and the part back of it are tested in the neutralization of gravitation. So also with thermotropism, aerotropism, and the like; for aught we know, the stimuli for these responses may be received beyond as well as in the elongating zone.

In carrying out the experiments detailed in the foregoing pages, there are various difficulties involved and various objections which may be raised. These will now be briefly considered. In the first place, I may admit that the employment of glass-tubes is but an imperfect method; the tubes necessarily obstruct the flow of water. If, however, fibres of cotton are attached to the glass-tubes, they are seen to trail constantly in the direction at right angles to the diameter of the revolving basin of water, showing that a current approximately constant in direction is maintained. The current, after being disturbed by the tubes and seedlings in one-half of the diameter, is re-composed by its undisturbed progress through the following

¹ De Vries, Ueber die Aufrichtung des gelagerten Getreides. Landw. Jahrbücher, ix, 1880, p. 473.

² Rothert, Ueber Heliotropismus. Cohn's Beitr. z. Biol., vii, p. 176.

³ Czapek, Jahrb. f. wiss. Botanik, xxvii, p. 255; *ibid.* xxxv, p. 317.

half-circle before it reaches the row of seedlings in the other half of the diameter. The speed of revolution (this being twelve times to the minute) is rapid enough to overcome in large measure the tendency to eddies and cross-currents. The constancy of response by the roots indicates a constancy in direction of water-stream.

A second criticism that might be advanced against the method here employed may be found in the assumed possibility of a current through the tubes, even if a very slow one, thus bringing the current against the elongating zone. This notion is worth considering, for it has been shown that a velocity of only one centimetre, or less, per minute is sufficient to call forth a rheotropic response in *Raphanus sativus*¹, and a velocity of 2 cm. per minute will call forth a response in the roots of *Zea Mays*², *Vicia sativa*², and *Brassica alba*¹. There are three reasons why this possible explanation of the cause of the curves will not suffice. (1) The glass-tubes with the seedlings were kept as nearly vertical as the eye could detect. If the glass-tubes were vertical in the water, no current could pass through the tubes, though there might be a little movement of the water a slight distance within the opening of each end of the tube. In all my experiments the lower end of the root was kept three or more millimetres (usually 10 to 12 mm.) above the lower end of the tube. It seems impossible to assume that any movement of water in a constant direction could have taken place within the tube at such a distance from its opening. (2) If the tubes were in some cases slightly inclined from the vertical direction, thereby causing possibly a very slow stream through the tubes, only those streams which flowed from above downward through the tubes could have caused the curves of the roots; for a stream flowing from below upward through the tube would keep the root from bending, the tendency of the rheotropic response being to turn the root-tip toward and parallel with the current of water. It

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

² Juel, Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. f. wiss. Botanik, xxxiv, 1900, p. 515.

is, however, out of any possibility that so many tubes should have been inclined in a direction favourable to a downward flow of a stream, and that, owing to this flow, so many roots should have been bent in a constant direction as to give the percentages of responses shown in the tables. (3) To guard against the possibility of a flow of water in the tubes, several experiments were carried through in which the lower ends of the tubes were closed by a firm plug of cotton. In these cases the curves came just as promptly and as numerous as when the tubes were left open.

There was no possibility of mistaking geotropic or heliotropic curves for rheotropic; for, as stated elsewhere, during the preparation the seedlings were kept in the vertical direction, and all the experiments were carried on in the dark-room. Moreover, the preparations often stood at rest for hours after setting up before the revolution of the basins of water was begun, thus affording time for overcoming the effect of any preceding geotropic or heliotropic stimulus. Besides all this, the initial bends in my experiments never came in less than two hours, and, in the majority of roots, not till five or more hours after the beginning of the revolution. Such a latent period as this is not at all unusual for rheotropism, as shown by the work of Berg¹, Juel², and myself³.

It might be thought that the contact of the root with the glass-tube would cause a curvature. To this it may be said that no response to contact has been demonstrated for roots. Moreover, experiments set up to test the effect of contact between roots and glass-tubes have shown no curves resulting.

From all the considerations presented in the foregoing pages, the rheotropic sensitiveness of the root at a considerable distance from the limit of the elongating zone may, I believe, be accepted as demonstrated. Juel⁴ had obtained curves in two roots of *Vicia sativa* covered with collodion caps for a distance of 7 to 8 mm. from the apex. This number was

¹ Berg, Studien über Rheotropismus. Lunds Univ. Årsskrift, xxxv, II, No. 6.

² Juel, Jahrb. f. wiss. Botanik, xxxiv, 507.

³ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

⁴ Juel, loc. cit., p. 519.

too small to serve as a demonstration, and it is probable that the caps did not cover the whole of the elongating zone. In the present paper not only was the whole of the elongating zone covered, but several millimetres beyond. It may with safety be said that the root of *Zea Mays* (popcorn) is sensitive at a place 10 mm. back of the limit of the elongating zone; that of *Fagopyrum esculentum*, 9 mm., or more, from the elongating zone; that of *Helianthus annuus*, 8 mm., or more, from the elongating zone; and those of *Brassica alba* and *Raphanus sativus*, certainly 10 mm. and probably 15 mm. to 20 mm. from the elongating zone.

As to the velocity of the water-stream causing these curves, it should be noted that it was not so great as given in the tables, since there no account was taken of the resistance offered by the glass-tubes and the roots. Elsewhere¹ it has been shown that velocities of current between 100 cm. and 500 cm. per minute bring good rheotropic responses in the uncovered roots of eighteen species of plants tested. It may well be believed that in spite of the obstruction offered by the glass-tubes and the roots, the velocities of flow fell within the limits for good responses.

The results here given should not be taken as showing the limit of the sensory tissue. With better means, not only might the limit of sensitiveness be extended, but a greater percentage of curvatures might be obtained. In my work on rheotropism² it was found that many individuals of many species did not show a response for twelve to twenty hours after the application of the stimulus of the water-stream. It is however, when glass-tubes are used, not advisable to continue an experiment more than about twelve hours. A longer period brings distortion to several of the roots. These distortions are apparently due to want of exchange of water in the tubes surrounding the roots, the excreta from the roots accumulating in the imprisoned water. It is probably not due to a lack of oxygen; for the roots still

¹ Newcombe, Bot. Gazette, xxxiii, 1902, p. 177.

² Ibid.

continue to grow, and a lack of oxygen does not cause distortion so far as my observation goes.

A final reference may be made to the significance and nature of rheotropism. Of biological significance, it is difficult to perceive any. The nature of the stimulus remains as obscure as ever. Of course there is pressure against the roots by the stream of water. But thigmotropism has not been and probably cannot be demonstrated in ordinary roots by ordinary means. If rheotropism is not thigmotropism, we do not know what the nature of the stimulus is; but until thigmotropism has been demonstrated in roots, no claim can be made for the identity of these two responses.

Newcombe, Frederick C . 1902. "The sensory zone of roots." *Annals of botany* 16, 429–447. <https://doi.org/10.1093/oxfordjournals.aob.a088882>.

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