Gravitation sensitiveness not confined to apex of root.

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With plate III and 6 figures in the text.

From the time that Charles and Francis Darwin[1]) in 1880 published their experiments on the behavior of decapitated roots toward gravitation down to the year 1895 when Czapek[2]) published his results obtained by the employment of glass caps, the contest waged over the question of the perceptive region of the root, a contest accompanied by numerous polemics and thousands of root-decapitations. With the publication of Czapek's work, however, the botanical world seems to have accepted the matter as ended, and has apparently given adherence to the view that only the apical one or two millimeters of the root-tip acts as the perceptive organ for gravitation. Rarely an author, as in the case of Richter[3]) and Jost[4]), states that the proof is still lacking.

Now it can be shown that neither Czapek's method nor any other method so far employed has or can prove the restriction of the perceptive region to the apical two millimeters of the root. And this demostration can be given without farther experiment, as a matter of logical reasoning.

Part I: Lack of evidence of localization of geotropic sensitiveness.

As is well known, most roots, when two millimeters of the apex are excised, show no farther response to gravitation. This result however has not been accepted as demonstrating restriction

[1]) Power of movement in plants. London.

[2]) Untersuchungen über Geotropismus. (Jahrb. wiss. Botanik. XXVII. 1895. 243.)

[3]) Zur Frage nach der Funktion der Wurzelspitze. Inauguraldiss. Freiburg i. Br. 1902.

[4]) Review of papers by Richter, Darwin and Massart. (Bot. Zeit. 61. 1903. Abt. II. 23.)

of the perceptive organ to the part excised; for it has been thought that the wounding might destroy the sensitiveness of the elongating zone posterior to the wound. By the ingenious employment of glass caps bent at a right angle into which the roots were forced to grow, Czapek was able to cause the apical one and half millimeters of the root to take an angle of 90° with the rest of the root; and thus one region of the root could be placed in its position of equilibrium with regard to gravitation, while the other region was 90° removed from this position.

If the seedling with the glass cap over the apex of the root was set up as shown in Fig. 1, in a short time it had changed to the relations shown in Fig. 2. If the seedling was laid hori-

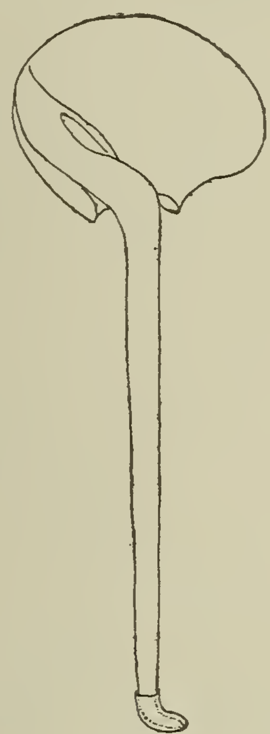

Fig. 1.
Seedling of *Lupinus albus* with glass cap over root-tip. After Czapek.

Fig. 2.
Seedling of *Lupinus albus* after the root has taken its position of equilibrium.

zontally as in Fig. 3, it continued to grow without changing the position of tip or elongating zone.

These results were interpreted to mean that only the apical one or two millimeters of the root was sensitive to gravitation. A moment of reflection will show that the results accord with an entirely different hypothesis. Suppose merely that in Fig. 1 the horizontal 2 mm of the root-tip is more sensitive to gravitation than the elongating zone above it; then the root will swing into or toward the position shown in Fig. 2. If the apical 2 mm are much more sensitive than the adjacent older part, the tip may attain the vertical position as shown in Fig. 2, wholly overcoming the effect of the sensitiveness of the elongating zone. Such a distribution of sensitiveness to light has been made out by Rothert[1])

[1]) Über die Fortpflanzung des heliotropischen Reizes. (Ber. d. d. bot. Gesellsch. X. 1892. 374.)

for the cotyledons of *Avena* and *Phalaris*, the whole cotyledon being sensitive, but the sensitiveness diminishing from the apex downward.

The hypothesis given will account for the growth of a seedling from the form shown in Fig. 1 to that in Fig. 2, and will account for the continuation of the root in the form shown in Fig. 3 (when the seedling is kept in the horizontal position). When, however, a root is forced into the form shown in Fig. 3, allowed to grow for some hours in that form and position, and then removed to the klinostat, and so revolved as to neutralize the effect of gravitation, we might expect, according to Czapek[1]) the stimulation previously induced in the horizontal part of the elongating zone, if that were sensitive to gravitation, to produce a geotropic curve. Since no such effect is seen, Czapek assumes that the part of the root

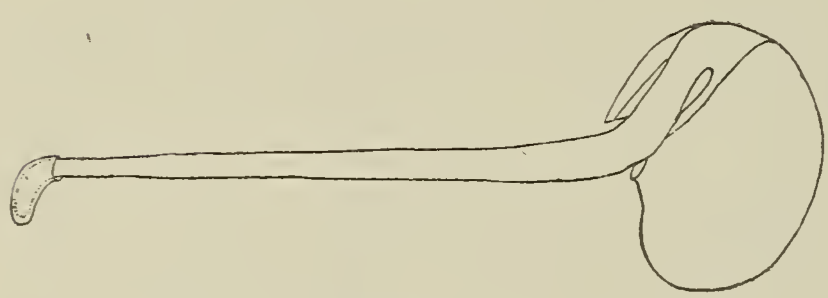

Fig. 3.
Seedling of *Lupinus albus* in position of equilibrium.

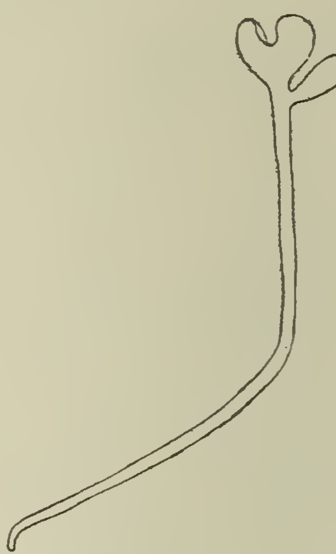

Fig. 4.
Seedling of *Brassica alba* after stimulation in stream of water.

posterior to the apical one to two millimeters must be insensitive to gravitation.

But this conclusion is not the only possible hypothesis. The tendency to bend, produced by gravitation, may be prevented by the autotropism of the root.

Referring to Czapek's experiments with the bent glass caps, it may be said that it is not necessary to use such a means to secure a great angular difference between the direction of the longitudinal axes of the root-apex and of the part just behind it. As Nemec[2]) has seen, so every one who has experimented with root curvatures has seen inverted orthotropic roots bend over into a horizontal or oblique position and subsequently for days continue on in the same direction, tho the tip all the time was bent downward as shown in Fig. 3. I have seen roots of *Brassica alba*, after curving upward into nearly a horizontal po-

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[1]) Über den Nachweis der geotropischen Sensibilität der Wurzelspitze. (Jahrb. wiss. Botanik. XXXV. 1900. 313.)

[2]) Über die Wahrnehmung des Schwerkraftreizes bei den Pflanzen (Jahrb. wiss. Botan. XXXVI. 1901. 78.)

sition when responding rheotropically to a stream of water, continue on in the same direction for days after the flow of water had ceased, producing a form like Fig. 4.

It is not unusual to find individual seedlings of *Vicia faba* and *Lupinus albus* when suspended horizontally in a damp chamber bending 2 or 3 mm of the tip obliquely downward, but straightening again in the elongating zone so that the course of the root continues horizontal or between the horizontal and the vertically downward position, thus producing a form quite similar to Czapek's preparation as shown in Fig. 3. Czapek obtained the straightening of bent roots by revolving the bent roots on the klinostat. But the cases just cited show that the straightening will often occur when the full stimulus of gravitation is applied to a horizontal root at rest. It is evident therefore that the tendency of a root to respond geotropically is opposed by its own autotropism. In the case of *Vicia faba* and *Lupinus albus* the autotropism of a horizontally lying root is sometimes able to prevent a complete response to gravitation.

Instead of ascribing, as Czapek does, the continued horizontal growth of a root, in the form shown in Fig. 3, to the absence of geotropic sensitiveness in the part posterior to the 2 mm of the apex, is it not just as reasonable to ascribe the straightening to autotropism combined with a greater sensitiveness to gravitation in the apex than in the straightening part?

If we assume that the apical 2 mm are much more sensitive to gravitation than the part behind, then the root shown in Fig. 1 must bend into the form of Fig. 2; and the seedling shown in Fig. 3 cannot bend its post-apical part downward, for in so doing it would throw its apex out of the vertical, out of the position of equilibrium.

Thus it is seen that Czapek's experiment with the glass-caps has not and cannot prove the absence of geotropic sensitiveness in the part of the root posterior to the apical one or two millimeters.

The argument against the methods and conclusions of Czapek applies with just as much force to those in his second paper[1]) and to those recently published by F. Darwin[2]), Massart[3]), Andrews[4]) and Cholodnyj[5]).

Thus there is presented here an hypothesis which will account for the results obtained by Czapek, and which implies the possession

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[1]) Über den Nachweis der geotropischen Sensibilität der Wurzelspitze. (Jahrb. wiss. Botanik. XXXV. 1900. 313.)

[2]) On a method of investigating the gravitational sensitiveness of the root-tip. (Journ. Linn. Soc. XXXV. 1902. 266.)

[3]) Sur l'irritabilité des plantes supérieures. (Mem. couron. par l'Acad. de Belgique. Bruxelles. 1902. — Review in Bot. Zeit. 61. 1903. Abt. II. 23.)

[4]) A natural proof that the root-tip alone is sensitive to the gravitation stimulus. (Proc. Indiana Acad. Sci. 1905. 189.)

[5]) Zur Frage über die Verteilung der geotropischen Sensibilität in der Wurzel. (Schriften des Naturforschervereins in Kiew. 1906. — Review in Bot Zeit. 65. 1907. Abt. II. 189.)

of geotropic sensitiveness by more than 2 mm of the root-tip. That the part of the root posterior to the 2 apical millimeters is sensitive to gravitation will be shown in the second part of this paper.

Part II. Demonstration of gravitation sensitiveness thru more than four millimeters of the root-tip.

In the first part of this paper it has been shown that the peculiar behavior of roots when subjected to the conditions imposed by Czapek, Fr. Darwin, Nemec, Andrews, Cholodnyj and others may be accounted for not only by the hypothesis of the restriction of the sensory region to the apical one or two millimeters, but just as well by the hypothesis of the possession of geotropic sensitiveness by the whole elongating region of the root, with the sensitiveness decreasing from the punctum vegetationis posteriorly. The ensuing pages will be devoted to a record of experiments which will show that the latter of the two hypotheses is the correct one, or, at least, will disprove the assumption of Darwin, that sensitiveness is localized in the tip of the root.

Since, as has already been pointed out, any method which depends for results on the bending of the apical 2 millimeters of the intact root into a different angle than that of the more posterior portion must fail to lead to a single hypothesis, some other method of experimentation must be used. That employed by Piccard[1]) would seem a little too precarious to be satisfactory. The old method of beheading roots and then laying them horizontal, to determine whether by the possible geotropic sensitiveness of the part left the root would curve downward, is generally condemned; for there is reason for supposing that the wounding disturbs or inhibits the normal behavior. This method led Darwin to believe that the sensitive region was confined to the apical one or two millimeters, and led Wiesner to reject that view. Roots so treated either do not bend at all or bend too irregularly to allow safe conclusions to be drawn.

Reflection on these matters brought the thought that, if more than the apical 2 millimeters of the root were sensitive to gravitation, a gravitation stimulus above the normal might overcome the autotropism and the effect of wounding sufficiently to bring the geotropism of decapitated roots to expression. This notion seemed all the more probable from the demonstration of Sachs[2]), Czapek[3]) and others that a more than normal gravitation stimulus brings a greater than normal geotropic response. The centri-

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[1]) Neue Versuche über die geotropische Sensibilität der Wurzelspitze. (Jahrb. wiss. Botanik. XL. 1904. 94.)

[2]) Wachstum der Haupt- und Nebenwurzeln. (Arbeiten d. bot. Inst. Würzburg. I. 1874. 607.)

[3]) Untersuchungen über Geotropismus. (Jahrb. wiss. Botanik. XXVII. 1895. 301.)

fuge method as introduced by Knight[1]) and employed by the two Authors just cited presented itself as the obvious way to make the test.

It was soon discovered by a search of the literature that Wiesner[2]) hat made precisely this test. He had cut off one or two millimeters of the root-tips of *Zea mais, Pisum sativum, Phaseolus multiflorus*, and *Vicia faba*, had revolved them at a velocity ranging from 20 g to 41 g, the roots being placed at right angles to the radii of revolution, and had obtained outward curves in all his beheaded roots. In some cases curves came in roots from which 3 mm had been removed. Wiesner, as we believe now, held an erroneous conception of the nature of the response; but he should have the credit of carrying out the experiment.

About the time that Wiesner's work appeared Brunchorst[3]) published an account of a few experiments made with decapitated roots of *Phaseolus* on the centrifuge revolving at 25 g. This Author filled the chamber holding his roots with moist sawdust to prevent the plastic bending of the roots, and therewith obtained no curves tho his roots made some growth.

Brunchorst used only one species of seedling in the foregoing experiment, excised apparently one to two millimeters of the root tip, and speaks of the tendency of the sawdust to dry out; yet on this small showing, Krabbe and others at the time discredited Wiesner's results, claiming that the latter's curves on the centrifuge were merely plastic. Czapek, in his extensive study of the geotropic sensitiveness of the root, pays no attention to the centrifuge experiments of Wiesner, tho the latter had offered good evidence that his curves were not plastic. This evidence was furnished by setting uninjured seedlings, like those decapitated, in a damp-chamber filled with carbon dioxide, and then revolving the preparation so as to give to the roots the same gravitation acceleration that had produced curves in the decapitated roots. In such a preparation there was not only no growth, but also no curving. Unless one will claim that we may get a plastic bend in a growing root, tho none in a non-growing living root, the result of Wiesner's is decisive, and it is remarkable that none of Wiesner's opponents has repeated the experiment. Czapek[4]), in his experiments employing the centrifuge to increase the gravitation stimulus, assumes that a speed equal to 40 g will not cause plastic curving in root-tips; but it was with a speed no greater than this and sometimes only half as great, that Wiesner obtained his curves in decapitated roots. Evidently Wiesner's results should have been taken more into account in determining the extent of the geotropically sensitive region in roots.

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[1]) Philos. Trans. I. 1806. 99.

[2]) Untersuchungen über die Wachstumsbewegungen der Wurzeln. (Sitzb. K. Akad. Wissensch. Abt. I. LXXXIX. 1884. 223.)

[3]) Die Funktion der Spitze bei den Richtungsbewegungen der Wurzeln. (Ber. d. d. bot. Gesellsch. II. 1884. 78.)

[4]) Jahrb. wiss. Botanik. XXVII. 1895. 305.

Experimental.

To test the geotropic sensitiveness of beheaded roots, resort was had to the centrifuge. An electric motor was used to drive several horizontal shafts, each shaft having at one end a heavy brass disk, to which by simple means a glass basin 22 cm in diameter could be secured. These glass-basins were used as damp-chambers, being lined with filter paper, and so covered with a heavy glass plate clamped over a thick rubber disk that after even 24 hours of revolution there was always free water remaining in the chamber. In the damp-chamber there was fitted a wooden cross of 2 bars, the bars occupying the position of diameters at right angles to each other. The wooden cross was easily removable and to it, perpendicularly to the diameters, were fastened the seedlings by means of strips of cloth and rubber bands. Such a preparation is shown in Plate III. The motor was so geared to the shafts turning the damp-chambers that the revolution was 300 times a minute. Such a revolution gives approximately as many times the acceleration of gravitation as the root-tips are distant in centimeters from the center of revolution. Nearly all the experiments were conducted with an acceleration equal to 7 g or 8 g. By the method indicated one could easily secure accelerations all the way from 1 g to 10 g in one preparation.

To insure accuracy in the length of root-tips excised and in cutting perpendicularly to the long axis of the root, a little guillotine was devised with guide posts for the razor and with a micrometer screw moving a little block back and forth, the root to be cut having its tip placed against the block, the position of the block determining the length of tip to be removed. This device did excellent service, cutting the tips with an error of less than one-tenth millimeter, end uniformly perpendicularly to the axis of the root.

The temperature during the experiments varied between 20° and 24° C. The seedlings were kept in the normally vertical position both before and after beheading, and never more than 10 minutes elapsed between the beheading and the beginning of revolution.

The seedlings employed were those of *Zea mais, Lupinus albus, Pisum sativum. Phaseolus muliflorus, Vicia faba, Ricinus communis,* and *Cucurbita pepo.* Several of these species showed the behavior recorded by Wiesner, but 3 of them showed behavior not before recorded, and some of them have been tested more thoroly than any before for the limitations of sensitiveness, and for other relations.

Zea mais. Twenty-nine seedlings had each 2 millimeters of the tip removed, and were revolved on the centrifuge at 8 g for 8 hours. Twenty roots curved outwards at angles varying from 10° to 25°, one root curved inward, and one curved in a direction at right angles to the plane of revolution. The other seven made no bend.

Thirteen seedlings had 2.5 mm excised, were revolved at 8 g for 8 hours, and then showed 4 roots with outward curves of 10° to 15°. The other 9 roots remained straight. In both this and the preceding experiment all roots elongated after beheading.

These 2 experiments indicate very clearly that with 2.5 mm of the root-tip removed, the root has in most cases lost the ability to respond to the centrifugal force, while that ability is retained generally when only 2 mm are excised. This lessening of the response, must depend, if the curves are geotropic, on the relation between the autotropism of the root and its geotropism, the latter being reduced either by an increasing inhibition from more proximal wounding, or by a greater loss of sensory tissue, or by the operation of both factors.

Pisum sativum. Fifteen seedlings had each 2 mm of the tip removed, and were revolved on the centrifuge at 7 g to 8 g for 14 hours. Ten roots curved outwards forming angles of 10° to 30°, one root bent inward, two bent obliquely and two grew straight.

Forty-two seedlings with 2.5 mm of the root excised, revolved at 8 g for 8 hours, showed 13 roots bent outward at angles from 10° to 30°, and 3 roots bent irregularly, the remaining 26 roots being straight.

Five seedlings had 3 mm cut from the tip of the root, were revolved at 8 g for 19 hours, and then showed 4 weak outward curves of 10° to 15°, and one weak inward curve.

The teaching here is the same as for *Zea mais.* When only 2 mm were excised the responses in the same period were proportionately more than twice as numerous as when 2.5 mm were excised.

The result when 3 mm were excised cannot be compared directly with the others, for the period of revolution was more than twice as great. The angles attained here were, however, considerably weaker than in the other experiments. However, the result shows that with even 3 mm of the tip removed, the roots still have the power to respond to centrifugal force.

Lupinus albus. In a total of 37 seedlings, from whose roots 2 mm had been cut, revolving at 8 g for 6 hours, 13 bent outward (unfortunately my notes fail to give the angles), 4 bent irregularly, and 20 grew straight.

In a total of 34 seedlings from whose roots 2.5 mm had been cut, revolving at 8 g for 7 hours, 10 bent outward at angles from 10° to 60°, 2 bent irregularly, and 22 grew straight.

The results here given do not certainly show that a greater inability to respond to centrifugal force is manifest the greater the amount of the root excised. Farther experiments are needed.

Phaseolus multiflorus. Only 8 seedlings were used to test the effect of removing 2 mm of the root-tip, and these gave only

2 outward curves of 15° during a period of 6 hours. Two and a half millimeters were cut from the tips of 45 roots and these seedlings as the others were revolved for seven and one-half hours at 7 g to 8 g. Among them, 13 roots curved outward at angles varying from 15° to 45°, 3 roots bent inward, and the remaining 29 roots grew straight.

These results may be accepted as demonstrating the ability of the beheaded roots of this species to respond to the centrifugal force, but the number of seedlings employed when 2 mm of the root were excised was too few to allow comparisons to be made with those from which 2.5 mm were removed. The large number of seedlings used when 2.5 mm were removed and the resulting large number of neutral roots makes certain the conclusion that, tho some individuals so treated are capable of responding, the large majority have lost that ability.

Ricinus communis. Fifty-two seedlings with tips amputated were revolved on the centrifuge at 8 g, temperature 20° to 22° C, and period 6 to 8 hours. None of them showed curves that could be called geotropic. All of the roots grew straight except 10 which curved but slightly in various directions. Twenty of these roots had 3 mm excised, 13 had 2.5 mm excised, 13 had 2 mm excised, and 6 had 1.5 mm excised. None of those in the last two groups showed any curvature.

This species is distinguished as the only one of the seven used in this work which does not respond to centrifugal action when 1.5 to 2 mm of the root are removed.

Vicia faba. The response of the roots of this seedling on the centrifuge was determined by Wiesner as possible but infrequent when 3 mm were amputated. In my experiments a beginning was made by amputating 2.5 mm, and subjecting the seedlings to a speed of 8 g in temperature varying from 20° to 23° C. Fourteen seedlings were revolved during 7 hours, and 8 curved outward at angles ranging from 15° to 66°, one curved toward the center and five grew straight.

When under the same conditions 41 seedlings were used from which 3 mm of the root had been removed, 34 made outward curves at angles ranging from 15° to 50°, averaging over 30°; only one root curved inward, while the other 6 grew straight.

Forty roots had 3.5 mm of the tip removed, were revolved at 8 g, in a temperature generally of 21° (for one set of 4 roots it was only 14° C, but the period here was lengthened to 10 hours), for a period of 6 to 8 hours. Twenty-six roots bent outward, one inward, 3 obliquely to the plane of revolution, and 10 grew straight. The angles formed by these roots averaged slightly less than those formed by the roots which had but 3 mm amputated. See Plate III for one set of these seedlings.

Thirty-five roots had each 4 mm removed from the tip, were revolved at 8 g, temperature was 20° to 23°, and the period 6 so 7 hours. Sixteen roots bent outward, and 19 grew straight, The most of the responding roots bent at an angle of about 20°, tho a few were as low as 10°, and one was 40_0 and one 80°.

Cucurbita pepo. Seedlings of this species show even more remarkable behavior on the centrifuge than those of *Vicia faba*. When 24 seedlings had 2.5 mm removed fromthe root-tip, and were revolved at 8 g, temperature 24°, period 7 hours, every root was found bent outward; the angles ranged from 10° to 75°, 13 of the roots showing angles of 45° or over, and only 3 having angles less than 30°.

An experiment made with 12 seedlings from whose roots 3 mm were removed, and the seedlings then revolved at 4 g, temperature 24°, period 5.5 hours, showed 10 roots curved outward at angles varying from 15° to 40°, and the other 2 roots straight.

Under the same conditions as the foregoing, except that the speed was equal to 8 g and the period was 6 hours, 26 roots from which 3.5 mm had been amputated, showed 23 outward curves at angles ranging from 10° to 45° — only 3 angles were less than 30° — while the other 3 roots were straight. Plate III shows one set of these seedlings.

Twelve seedlings with 4 mm of the root-tip removed, revolved at 8 g, temperature 24°, period 6 hours, gave 9 roots curved outward at angles from 15° to 40° — 5 being over 20° — and the other three roots straight.

The foregoing experiments show that the roots of all 7 species of plants used, except those of *Ricinus communis*, make bends on the centrifuge when not more than 2 mm of the root-tip are removed. Three of the seven — *Zea mais, Pisum sativum and Lupinus albus* — show a good proportion of curves when 2.5 mm of the root-tip are removed; and *Vicia faba* and *Cucurbita pepo* will curve on the centrifuge when 4 mm have been amputated.

The first question to determine is whether these curves are plastic. All writers who have followed Darwin's lead have concluded that the sensory tissue is confined to the apical one to two millimeters. Since now all of the 7 species used in this work, except one, show curves when 2 mm of the tip are excised, one must believe that the curves produced in these experiments are plastic, or he must admit the extension of the sensory tissue thru the most of the elongating zone.

Since all the devices hitherto used to demostrate the restriction of geotropic sensitiveness to the apical one or two millimeters of the root have, in the first part of this paper, been shown to fail of their purpose, the question of plasticity of the root on the centrifuge may be examined without bias.

There are four results which have been obtained with roots on the centrifuge which tell against the notion of plasticity.

1) As seen in my own experiments, the secondary roots of *Zea mais* on the centrifuge, at a speed of 8 g, assume their specific angle, not growing in the direction of the radii, where plasticity would carry them.
2) In nearly every one of the experiments recorded in this paper, some roots have continued to grow straight, while others have curved outward. Why should not all curve, if the curves are merely plastic?
3) The roots of *Ricinus communis*, as recorded above, fail to bend on the centrifuge even when as little as 1.5 mm are amputated. Yet the roots of *Ricinus* are most likely as plastic as those of *Cucurbita* or *Vicia faba*, which curve after 4 mm have been removed.
4) Unless Wiesner's results can be proved erroneous, he has shown the untenableness of the notion of plastic curves even at a speed of 41 g, by finding uninjured roots remaining unbent when revolved in a chamber of carbon dioxide.

The only evidence in favor of plastic curving is that offered by Brunchorst, when he states that by filling his revolving chamber with damp sawdust, no curves came on the centrifuge. He himself states that the sawdust was wont to become too dry, and my own experience proves that not only does the sawdust become dry in rapid revolution, but it packs hard against the peripheral walls of the revolving dish, and the water passes mostly to the periphery,

But after all this has been said, the reader will still feel uncertain of the indirect evidence offered and will look for direct evidence. This is given by the following experiments.

The floor of one of the damp chambers hitherto used was covered with thick sheet cork. Nine seedlings of *Vicia faba* had 3 mm excised from their tips and were then fastened in the damp chamber in the usual way. On the radially outward side of each root, in contact with the terminal 5 to 8 mm of the root, there was secured by pinning to the cork floor a strip of cork 15 mm long. This strip of cork would support the root, and prevent plastic bending when the centrifuge was revolved.

The revolution employed was at a speed nqual to 8 g for each root, the temperature was 24.5°, and the period 7.5 hours. At the end of the experiment, 7 of the 9 roots were found bent outward at angles ranging from 15° to 70°. The other 2 roots were straight, The 7 roots had curved by lifting their posterior part from the cork bar as the tip pressed against the cork, as illustrated in Fig. 5.

At the time of the examination just recorded, the cork bars were removed from the sides of the roots, and the preparation was continued in revolution at the rate of one revolution in 3 minutes.

Observation was next made at the end of 2.5 hours. The two roots which previously were found straight had now bent outward 15° and 20° respectively, while one root formerly curved had wholly straightened.

During all these tests, the damp chamber always contained several centimeters of free water in addition to that held in the filter-paper lining the chamber; as stated before, my damp-chambers were closed against the loss of water.

Fig. 5.
Seedling of *Vicia faba*. Method of bending when opposed by bar of cork.

The foregoing result would seem to demonstrate the geotropic sensitiveness of the part of the root behind the apical 3 mm. There can be no doubt that the curves are not plastic. Some, however, may hesitate to pronounce against the possible participation of hydrotropism and thigmotropism in producing the curves when the cork bars were employed. Such doubters are referred to my papers on The Rheotropism of Roots [1]) and Thigmotropism of Terrestrial Roots [2]), in which it is shown that, even in un-

Fig. 6.
Seedling of *Vicia faba*. Tip kept from bending by 2 bars of cork.

injured roots of *Vicia faba* and *Cucurbita pepo*, such curves as are recorded in this paper are never produced by cork in contact with one side either of the tip or the part behind the tip of the root.

To make the matter doubly sure, two other experiments were set up quite similar to the last, except that strips of cork were brought into contact with both sides of the tip of the root, as shown in Fig. 6: Six seedlings of *Vicia faba* had each 3 mm of the tip removed, and the seedlings were then prepared in the damp-chamber with their tips between cork bars as indicated, revolved for 7 hours at 8 g in temperature 24.5° and then observed. Only

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[1]) Bot. Gazette. XXXIII. 1902. 177.
[2]) Beih. z. Bot. Centralbl. XVII. 1904. 61.

5 of the roots had grown, and all were straight except one which had been able to make an outward curve while still between the cork bars.

The confining cork bars were now removed, and the preparation revolved for 2.5 hours longer at the rate of one revolution in 1.5 minutes. Observation then showed that all 5 of the roots which had grown had curved outward at angles of 10°, 15°, 30°, 45°, and 90° respectively.

Thirteen seedlings of *Cucurbita pepo* were treated precisely as the seedlings in the preceding experiment, having 3 mm of the apex removed, and cork bars fastened on both sides in contact with the terminal 5 to 7 mm of the roots. The speed was equal to 8 g, temperature 24.5°, and the period 7 hours. At the end of this period all 13 roots showed growth, and were still confined between the cork bars, and were straight. On removal of the cork bars, 11 of the 13 roots immediately curved outward at angles ranging from 15° to 70°, while the other 2 remained straight. The revolution was immediately resumed at the rate of once in 2 minutes, and after the lapse of 3.25 hours, the 2 roots formerly straight were curved at angles of 10° and 20° outward, while one of the roots formerly curved outward had entirely straightened. Thus all 13 roots had shown geotropic curves.

The method of experimentation here presented is so simple that any one may follow it out. The only difficult step is the proper amputation of the root-tips. If the experimenter will use seedlings of either *Vicia faba* or *Cucurbita pepo*, he cannot fail to obtain curves which will convince him that these plants possess gravitation sensitiveness in the part 4 millimeters distant from the apex, and even farther.

The geotropic sensitiveness of the root, having been, in my opinion, demonstrated to extend through 5 millimeters of some roots, we may now inquire as to several geotropic curvature-phenomena which present themseves in various kinds of experimentation.

Bearing in mind the results obtained with the centrifuge, how shall we offer an hypothesis in accord both with them and with the form of root-growth illustrated in Fig. 4. The latter form is often seen with *Cucurbita pepo, Phaseolus multiflorus, Lupinus albus* and *Vicia faba* when one places seedlings of these species horizontally in a damp-chamber. The apex of the root, as far as the zone of maximum growth, declines 45° more or less, but the main direction of growth is, in a considerable percentage of cases, horizontal or in a straight line dipping below the horizontal. This form must be attained by the tissue of the declining tip changing its direction as it passes behind the zone of maximum growth.

There are two hypotheses which are in accord with the phenomena mentioned in the last paragreph: (1) The gravitation sensitiveness is strongest at the apex of the root and diminishes rapidly posteriorly, where its effect is overcome by autotropism; or (2) the gravitation-sensitiveness is more equal thruout the elongating zone, but autotropism is stronger in the posterior part of the elongating zone than in the anterior part.

The behavior of *Ricinus communis*, both when the seedlings are laid horizontally at rest, and when those with beheaded roots are revolved on the centrifuge, is different from that of other species. The roots of *Ricinus* laid horizontally have never, in my experiments, shown a straightening behind the declining tip, but all have made a sharp geotropic curve downward, and continued in that direction; and on the centrifuge, with as little as 1.5 mm of the tip amputated, they have shown no curves when revolved at 8 g.

This behaviour may be accounted for by any of three hypotheses: 1) The geotropic sensitiveness of the root may be confined to the apical one and one-half millimeters, and autotropism may be weak; 2) geotropic sensitiveness may extend thru the elongating zone, but be much stronger in the apical one and one-half millimeters, and autotropism be weak; 3) geotropic sensitiveness may be more evenly distributed thru the elongating zone, and the roots may be highly sensitive to wounding, by which beheaded roots on the centrifuge are made non-responsive.

Nothing comes out more clearly in these experiments than the fact that roots, growing under the normal stimulus of gravitation, as well as beheaded roots on the centrifuge, behave very differently; and this difference manifests itself, not only between the different species, but also between the individuals of the same species. To substantiate this statement, I need recall merely the frequent failure of roots of *Lupinus albus*, *Phaseolus multiflorus*, and *Cucurbita pepo* to bend more than 45° downward after lying horizontally in a damp-chamber for 24 hours, and the difference in the curving on the centrifuge between such species as *Phaseolus multiflorus* and *Cucurbita pepo*.

What these differences in behavior depend upon is difficult to say. Wiesner related the reponse on the centrifuge to the length of the elongating zone, saying the longer the elongating zone, the greater the length of tip possible of removal without destroying the geotropic sensitiveness. My experiments do not confirm this view. *Phaseolus multiflorus* and *Cucurbita pepo*, for instance, have the same length of elongating zone, usually 7 mm, but occasionally 9 mm. Yet when 2.5 mm were amputated from the root-tips and both species were revolved on the centrifuge at 8 g, *Phaseolus* formed curves in only one-fourth of its roots, while *Cucurbita* formed curves in every one of its roots. A similar comparison of *Ricinus communis* and *Pisum sativum* shows elongating zones of about the same length, that of *Ricinus* sometimes appearing one millimeter longer. But the roots of *Pisum* on the centrifuge after removal of 2 mm from the apex, gave curves in two thirds of their number, while under the same circumstances, the roots of *Ricinus* gave no curves.

Summary.

1) All the attempts thus far made to demonstrate the limitation of gravitation-sensitiveness to the apical two millimeters of the root have failed, for the phenomena accord equally well with the hypothesis of the extension of sensitiveness thru the elongating zone, but diminishing from the apex backward; or the phenomena accord with the hypothesis of a more equable sensitiveness thru the elongating zone, and a stronger autotropism in the posterior than in the anterior part.

2) Experiments on the centrifuge with beheaded roots show that gravitation sensitiveness is present, in most of the species employed, more than 2.5 mm posterior to the tip, and in some species more than 4 mm distant from the tip.

3) The kind of geotropic curve which an orthotropic root will make when displaced from its position of equilibrium depends upon the relation of its geotropism to its autotropism. In frequent cases, the autotropism of the root prevents the horizontally placed seedling from sending its roots vertically downward.

4) The length of the elongating zone cannot be seen to have any relation to the extent of the geotropically sensitive zone.

University of Michigan, Ann Arbor, (U. S. A.).
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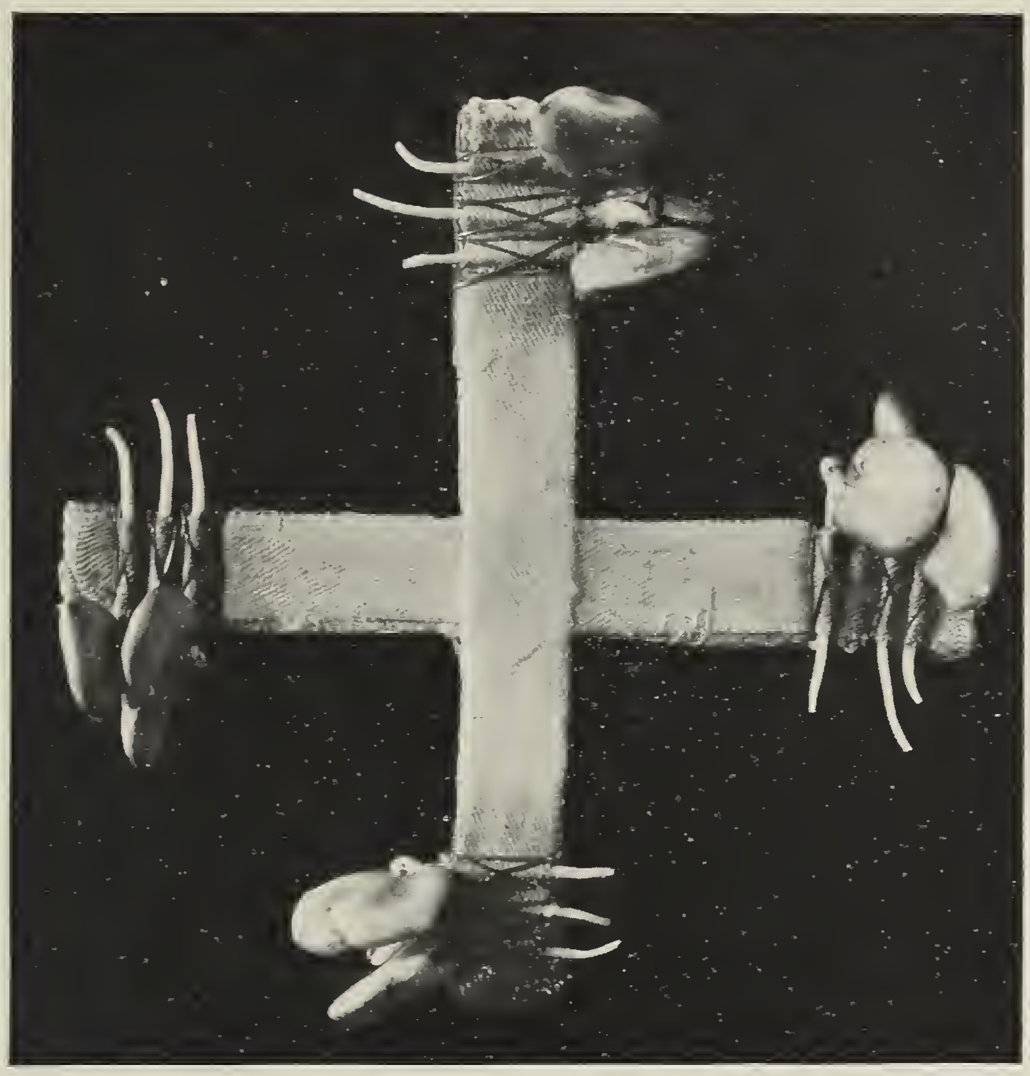
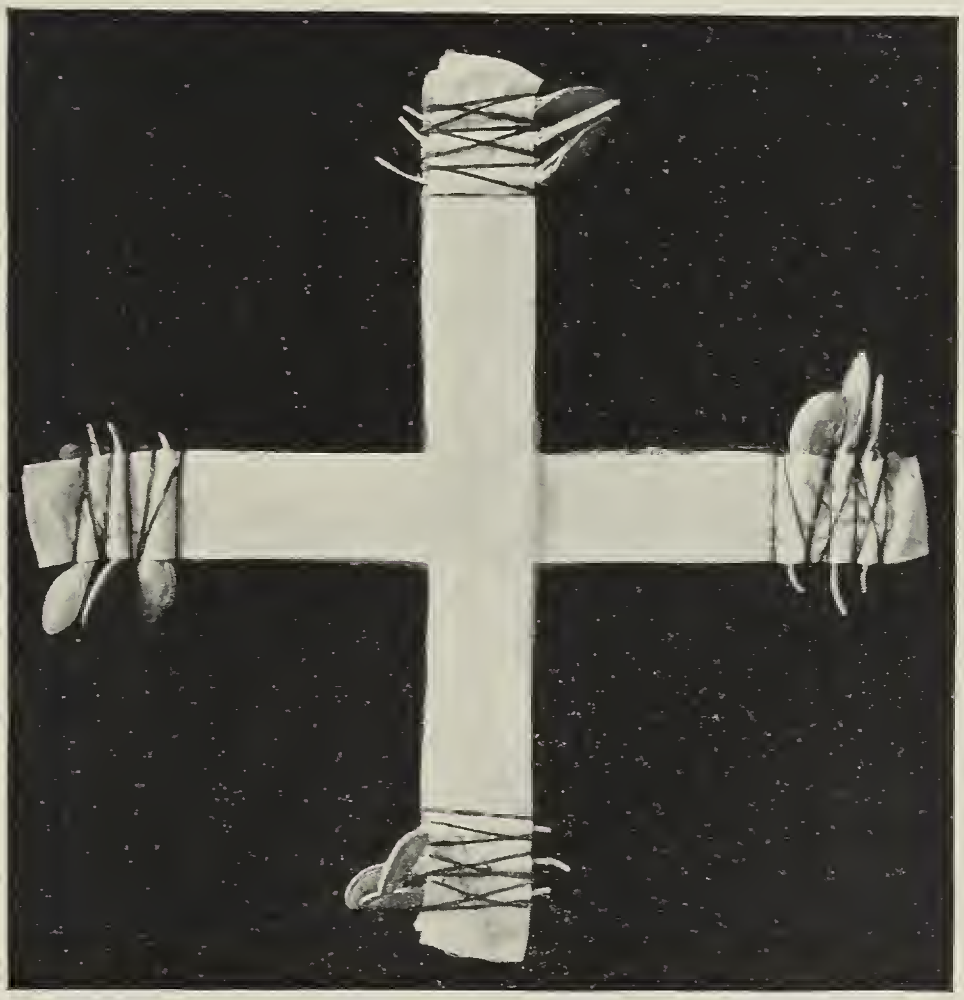
Explanation of plate.

The lower figure is made from a photograph of a preparation of *Cucurbita pepo*, 3.5 mm of the root-tips having been removed, and the preparation subsequently revolved on the centrifuge at 8 g for 6 hours. All the roots that have grown show outward curves.

The upper figure is a similar preparation of *Vicia faba*. The roots had 3.5 mm removed, and the preparation was subsequently revolved on the centrifuge at 8 g for 6 hours. Here there are 6 pronounced outward curves, one inward, one obliquely outward, and 4 roots nearly straight.





Frederick C. Newcombe.

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