The Correlation of Growth under the Influence of Injuries.

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IT has been the purpose of the experiments which form the basis of this paper to determine in what time, through what distance, and to what extent an injury inflicted upon one part of a plant will influence the growth of the injured and of the uninjured parts. The experiments have been carried on in the Botanical Institute at Leipzig during the years 1896-7, under the direction of Professor Dr. Pfeffer, to whom I wish to express my sincere thanks for his invaluable suggestions, and also for the use of his splendidly equipped laboratory.

The correlation of growth has received considerable attention from investigators either directly or indirectly, but the observations have been made for the most part under the influence either of long-continued irritation or of a series of irritations produced at more or less irregular intervals, and extending over a considerable period of time¹. In the following experiments special attention has been given to first effects of injury upon the curve of growth,

¹ Pfeffer, Druck und Arbeitsleistung, 1893. Hering, Ueber Wachsthumscorrelation in Folge mechanischer Hemmung des Wachsens; Pringsheim's Jahrbuch, Vol. 29, p. 132, 1896. Kny, On Correlation in the Growth of Roots and Shoots; Annals of Botany, Vol. viii, p. 265, 1894.

while previous investigators have concerned themselves for the most part with final results.

It is well known that the removal of some of the branches of a tree will often cause the other branches to become more vigorous and the fruit to be more perfectly developed; also that the disturbance of the roots of garden-plants, through the process of cultivation, often causes a more vigorous and rapid development of all their parts. However, no systematic study of injured plants has heretofore been made, in regard either to the effect of a single irritation of short duration or to the time required for such effect to manifest itself.

MATERIAL AND METHODS.

As far as possible in the experiments herein described, the external causes of the variation of the rate of growth were eliminated in order to study more accurately the internal influence of the irritation. With this object in view the plants were grown in damp chambers, in diffused light, and in all possible cases at a constant temperature.

The larger number of the experiments were performed with seedlings. Satisfactory results were obtained with seedlings of *Phaseolus multiflorus*, *Vicia Faba*, *Lupinus albus*, *Helianthus annuus*, *Cucurbita Pepo*, *Zea Mais*, *Avena sativa*, *Hordeum vulgare*, and *Secale cereale*. Experiments with older plants were carried on with the same material, also with *Calla*, and with a few cuttings of *Salix*. A number of experiments have also been performed with *Phycomyces nitens*.

Seedlings.—The seeds were soaked for about twenty-four hours, and then placed in damp sawdust at the temperature under which the experiments were to be carried on¹. When the roots and shoots had attained the desired length, the seedlings were placed in glass boxes containing damp sawdust, or the seeds were wrapped in damp cotton, and the roots were suspended in water or in damp chambers. In

¹ True, On the Influence of Sudden Changes of Turgor and of Temperature on Growth; *Annals of Botany*, Vol. ix, p. 363, 1895.

order to study the growth of the roots after the shoots were injured, the roots were marked with indian ink about 15 mm. from the tip (distance accurately measured) before the seedlings were placed in the glass boxes. They were then left for several hours in order to determine the normal rate of growth. The plumule or shoot was afterwards removed from the odd numbers, by means of a sharp knife or a pair of scissors, leaving the even numbers in a normal state for control-plants. In other experiments seedlings were prepared as above, but the shoots were split for several millimeters instead of being removed. If it became necessary to remove one of the cotyledons in order to treat the plumule as desired, one cotyledon was also removed from each of the control-plants.

In studying the growth of the shoot when the root was injured, the seedlings were prepared as before, and the shoot was marked near the base. In some cases only the root-tips were removed; in other experiments nearly the whole root was cut away; while in still other experiments the roots were split, either near the base or near the tip, for a distance of ten millimeters. Cultures in which the roots were grown in water or in damp chambers were especially convenient in all experiments in which the roots were to be treated, and in the study of the growth of secondary roots.

To determine the effect upon the growth of the leaves when the tips of the leaves themselves were injured, seedlings of *Avena*, *Hordeum*, and *Mais* were grown in damp sawdust, and, after determining the rate of growth for a given number of hours, the tips of the leaves were cut off from two to fifteen millimeters. In like manner the effect was observed upon the growth of stems when an entire leaf was removed from the stems of *Phaseolus*, *Vicia*, and *Cucurbita*.

A series of experiments were carried on to determine the effect of an atmosphere of ether upon growth. For this purpose *Hordeum*, *Avena*, and *Secale* were found convenient. The seedlings were grown in small pots of damp sawdust under large bell-jars. After the normal rate of growth had

been determined, a shallow dish containing 200 cc. of water, in which a definite amount of ether had been dissolved, was introduced under one of the bell-jars, the other preparation being left in a normal state for control. In some of the experiments the seedlings were kept in a dilute atmosphere of ether as long as they continued to grow, while in other cases they were placed in a strong atmosphere of ether for a short time. In order to measure the leaves, it was necessary to remove the plants from the bell-jars from time to time; and, as this allowed more or less of the ether to escape, a fresh mixture of ether and water was introduced under those bell-jars in which it was desired to maintain a constant atmosphere of ether.

Older Plants.—In preparing the older plants, seedlings were first started in damp sawdust, and then transferred to pots of damp earth and kept for several weeks under bell-jars. In order to have the root-tip in view, the main root was directed through the hole in the bottom of the flower-pot and allowed to extend into a damp chamber.

To study the growth of the root after the stem was injured, the root was marked 15 mm. from the tip, and the normal rate of growth observed. Only a part of the stem and a few of the leaves were then removed, and the growth of the root noted from time to time.

In considering the influence upon the stem when the roots were injured, a knife-blade $5\frac{1}{2}$ cm. in length was passed around the main root at a distance of only a few centimeters, thus severing a larger or a smaller number of the secondary roots. In order to determine accurately the degree of injury which was inflicted by removing the roots, and also to eliminate the influence of transpiration, seedlings were placed in cylinders of plaster of Paris from three to four centimeters in diameter, the bottoms of which were composed of cotton-netting. The netting prevented the earth from falling through, but allowed the roots, which were directed into damp chambers, to pass freely. By this means a definite number and desired length of roots could be removed. *Calla* plants

which had been grown for several months in pots of earth, were studied with reference to the growth of young leaves and roots when a full-grown vigorous leaf was removed. A few cuttings of *Salix* were prepared according to the method used by Kny¹.

Phycomyces.—A drop of gelatine containing the proper nourishing material was placed on a glass slide, and on the gelatine was deposited a single spore of *Phycomyces*. The preparations were kept in damp chambers in the dark until one or more sporangium-stalks formed. The damp chambers for these experiments consisted of air-tight boxes open at one end and two or three centimeters square by five or six centimeters long. These were lined on two opposite sides with moist filter-paper, and placed over the drop of gelatine on which the spore rested. By this means the growth of the sporangium-stalk could be observed in the damp chamber with the aid of a horizontal microscope. Having determined the rate of growth of the sporangium-stalk for a given interval, the damp chamber was removed for a moment, and the plant subjected to the following treatment:—

1. One or more of the mycelia were cut at a distance of from one to two millimeters from the base of the sporangium-stalk under investigation;
2. One of two or more sporangium-stalks produced by the same plant was cut off;
3. The mycelia were treated with a solution of potassium nitrate of definite strength.

In the experiments in which potassium nitrate was used, the volume of the gelatine-drop was liable to increase, causing an apparent elongation of the sporangium-stalk; hence in these experiments the sporangium-stalks were marked with indian ink below the growing zone².

In all higher plants the growth was measured at intervals of three, six, twelve, or twenty-four hours by means of a scale divided into half millimeters. For shorter intervals

¹ L. c., p. 276.

² Études sur la Turgescence chez le *Phycomyces*, p. 22, 1885.

the growth of the higher plants, as well as of *Phycomyces*, was measured by means of a horizontal microscope. Control-plants were used in all cases except with *Phycomyces*, and were selected according to their equality in size and rate of growth with those to be treated.

EXPERIMENTS.

Seedlings.—Owing to the high degree of independence existing between roots and shoots, it was necessary to perform a large number of experiments in order to reach definite and satisfactory conclusions. No attempt will be made to give a detailed description of the individual experiments, but rather the general results obtained. In the following tables a series was made up from the averages of growth of a large number of seedlings for a definite period. In the second column *P.* indicates the period during which the injured and the uninjured plants were compared. The periods were often determined from a large number of observations made at short intervals and combined; e.g. if four observations were made at intervals of six hours, and each observation showed an acceleration of growth, the four observations were combined and given as one observation of twenty-four hours. All the numbers opposite *a* were made up from the averages of nine or more experiment-plants; while the numbers opposite *b* were made up in the same manner from the same number of control-plants. The original length of roots and shoots indicates the length of these parts when measured for the determination of the normal rate of growth. The normal rate of growth was determined for all experiment as well as control-plants. The column headed 'Average growth during first period after injury' usually covered the time within which a change in rate of growth became apparent. The last column in each table is given for the purpose of showing how long the plants were under observation after treatment, and also for the purpose of comparing the growth of the injured and of the

control-plants for the total period after injury. The difference between the increase of the injured and of the control-plants, however, does not indicate the actual acceleration or retardation of growth if the several short periods show both acceleration and retardation.

TABLE I.

Growth of root after shoot was injured.

Series I. { *a.*—Entire shoot removed.
Zea Mais. { *b.*—Control.
 Series II. { *a.*—Entire shoot removed.
Vicia Faba. { *b.*—Control.
 Series III. { *a.*—Plumule removed.
Vicia Faba. { *b.*—Control.

Temperature, 22° (constant).

Series.		Average original length of root of twelve seedlings.	Average original length of shoot of twelve seedlings.	Average normal rate of growth of root.	Average growth of root, 1st period after injury.	Average growth of root, 2nd period after injury.	Average growth of root, 3rd period after injury.	Average total growth of root after injury.
I.	P.			24 hrs.	24 hrs.	48 hrs.	48 hrs.	120 hrs.
	<i>a.</i>	21 mm.	9.5 mm.	38 mm.	43 mm.	83 mm.	66 mm.	192 mm.
	<i>b.</i>	21 "	9 "	39 "	36 "	68 "	47 "	151 "
II.	P.			24 hrs.	24 hrs.	48 hrs.	144 hrs.	216 hrs.
	<i>a.</i>	50 mm.	14 mm.	14 mm.	21 mm.	36 mm.	124 mm.	181 mm.
	<i>b.</i>	50 "	16 "	14 "	27 "	36 "	72 "	135 "
III.	P.			24 hrs.	24 hrs.	24 hrs.	48 hrs.	96 hrs.
	<i>a.</i>	34 mm.		33 mm.	43 mm.	42 mm.	68 mm.	153 mm.
	<i>b.</i>	36 "		32 "	42 "	38 "	69 "	149 "

If we examine Table I, Series I and II, we shall find that the injury produced an acceleration in the growth of the root as a final result in both series. In Series I the acceleration began within twenty-four hours, and continued for five days. In Series II a retardation was observed during the first twenty-four hours, followed by a period of normal growth,

which in turn was followed by a period of acceleration. Series III, Table I, shows neither acceleration nor retardation.

If we now turn to Table II, it will be seen that the shoot was influenced by an injury produced upon the root. The final result of Series I, Table II, would indicate that no change

TABLE II.

Growth of leaf after root was injured.

Series I. { *a.*—5 mm. removed from root-tip.
Hordeum. { *b.*—Control.
 Series II. { *a.*—Three-fourths of each root removed.
Zea Mais. { *b.*—Control.
 Series III. { *a.*—Entire root removed.
Zea Mais. { *b.*—Control.

Temperature, 22° (constant).

Series.		Average original length of root of twelve seedlings.	Average original length of shoot of twelve seedlings.	Average normal rate of growth of leaf.	Average growth of leaf, 1st period after injury.	Average growth of leaf, 2nd period after injury.	Average growth of leaf, 3rd period after injury.	Average total growth of leaf after injury.
I.	P.			24 hrs.	24 hrs.	24 hrs.	24 hrs.	72 hrs.
	<i>a.</i>	28 mm.	8 mm.	20 mm.	30 mm.	37 mm.	31 mm.	98 mm.
	<i>b.</i>	29 "	8 "	19 "	38 "	40 "	19 "	97 "
II.	P.			24 hrs.	24 hrs.	48 hrs.	96 hrs.	168 hrs.
	<i>a.</i>	48 mm.	29 mm.	26 mm.	24 mm.	57 mm.	123 mm.	204 mm.
	<i>b.</i>	48 "	26 "	25 "	29 "	70 "	88 "	187 "
III.	P.			24 hrs.	24 hrs.	48 hrs.	48 hrs.	120 hrs.
	<i>a.</i>	57 mm.	23 mm.	16 mm.	17 mm.	31 mm.	19 mm.	67 mm.
	<i>b.</i>	56 "	21 "	15 "	20 "	39 "	61 "	120 "

had taken place in the rate of growth, but an examination of the figures under the first period after injury shows a distinct retardation, while the figures under the third period indicate a slightly stronger acceleration. In Series II, Table I, the retardation became apparent within twenty-four hours, and continued for three days, followed by a period of acceleration which also lasted for three days. Series III of the

TABLE III.

Growth of shoot after root was injured.

Series I. $\left\{ \begin{array}{l} a.—10 \text{ mm. removed from root-tip.} \\ \textit{Helianthus.} \left\{ \begin{array}{l} b.—\text{Entire root removed.} \\ c.—\text{Control.} \end{array} \right. \end{array} \right.$

Temperature, 22° (constant).

Series.		Average original length of root of nine seedlings.	Average original length of shoot of nine seedlings.	Average normal rate of growth of shoot.	Average growth of shoot, 1st period after injury.	Average growth of shoot, 2nd period after injury.	Average growth of shoot, 3rd period after injury.	Average total growth of shoot after injury.
I.	P.			24 hrs.	24 hrs.	48 hrs.	144 hrs.	216 hrs.
	a.	66 mm.	22 mm.	10 mm.	17 mm.	65 mm.	92 mm.	174 mm.
	b.	64 „	21 „	10 „	13 „	35 „	41 „	89 „
	c.	62 „	22 „	9 „	20 „	50 „	60 „	130 „

TABLE IV.

Growth of root and shoot after root-tip was slightly injured.

Series I. $\left\{ \begin{array}{l} a.—1 \text{ mm. (as nearly as possible) removed from root-tip.} \\ \textit{Vicia Faba.} \left\{ \begin{array}{l} b.—\text{Control.} \end{array} \right. \end{array} \right.$

Temperature, 22° (constant).

Series.		Average original length of root of ten seedlings.	Average original length of shoot of ten seedlings.	Average normal rate of growth of root.	Average growth of root, 1st period after injury.	Average growth of root, 2nd period after injury.	Average growth of root, 3rd period after injury.	Average total growth of root after injury.	Average total growth of shoot after injury.
I.	P.			24 hrs.	24 hrs.	48 hrs.	144 hrs.	216 hrs.	216 hrs.
	a.	20 mm.	3 mm.	15 mm.	18 mm.	22 mm.	41 mm.	81 mm.	53 mm.
	b.	19 „	3 „	14 „	18 „	32 „	78 „	128 „	32 „

same table shows a constant retardation, although the retardation during the first period of twenty-four hours was no more marked than in Series I and II, in which the degree of injury was much less.

Table III shows the same general results with *Helianthus* as those shown in Table II with *Hordeum* and *Mais*. The

TABLE V.

Growth of leaf after leaf-tip was injured.

Series I.	{	a.—10 mm. removed from leaf-tip.		
<i>Avena</i> .	{	b.—5 " " "		
	{	c.—Control.		
Series II.	{	a.—5 mm. removed from leaf-tip.		
<i>Zea Mais</i> .	{	b.—2 " " "		
	{	c.—Control.		

Temperature, 22° (constant).

Series.		Average original length of leaf of ten seedlings.	Average normal rate of growth of leaf.	Average growth of leaf, 1st period after injury.	Average growth of leaf, 2nd period after injury.	Average growth of leaf, 3rd period after injury.	Average total growth of leaf after injury.
I.	P.		24 hrs.	24 hrs.	48 hrs.	72 hrs.	144 hrs.
	a.	36 mm.	12 mm.	12 mm.	61 mm.	54 mm.	127 mm.
	b.	35 "	13 "	13 "	61 "	63 "	137 "
	c.	36 "	13 "	13 "	58 "	33 "	104 "
II.	P.		24 hrs.	24 hrs.	48 hrs.	168 hrs.	240 hrs.
	a.	18 mm.	10 mm.	11 mm.	25 mm.	93 mm.	129 mm.
	b.	20 "	9 "	11 "	33 "	135 "	179 "
	c.	19 "	10 "	11 "	29 "	71 "	111 "

periods of variation in the rate of growth, however, were longer in the experiments with *Helianthus*.

According to Table IV even one millimeter cut from root-tips produced an acceleration in the growth of the shoots, although the growth of the root was of course retarded. During the first twenty-four hours after cutting no change

could be detected in the rate of growth of either root or shoot, but during the following nine days the rate of growth of the roots was distinctly retarded, while the rate of growth of the shoots was just as distinctly accelerated, though not to the same extent.

When leaf-tips were cut off as in Table V, the growth of the leaves cut was accelerated if the growing zone was not injured. In Series I, Table V, the acceleration began after the first twenty-four hours after injury, and continued for five days, i. e. during the whole growth of these leaves of the seedlings.

TABLE VI.

Growth of shoot after one leaf was removed.

Series I. { *a.*—One leaf removed.
Phaseolus. { *b.*—Control.

Temperature, 23° (constant).

Series.		Average original length of shoot of twelve seedlings.	Average normal rate of growth of shoot.	Average growth of shoot, 1st period after injury.	Average growth of shoot, 2nd period after injury.	Average growth of shoot, 3rd period after injury.	Average total growth of shoot after injury.
	P.		24 hrs.	24 hrs.	96 hrs.	192 hrs.	312 hrs.
I.	<i>a.</i>	164 mm.	9 mm.	22 mm.	104 mm.	66 mm.	192 mm.
	<i>b.</i>	162 "	9 "	17 "	63 "	31 "	111 "

In Series II *a* shows a slight retardation after the first twenty-four hours followed by acceleration, while *b* shows continuous acceleration after the first twenty-four hours, returning to a normal growth after about nine days.

The effect of removing one of the leaves from young shoots was next investigated. For this purpose *Phaseolus multiflorus* was found to give very satisfactory results. Table VI shows that the acceleration in growth began within twenty-four hours after injury, and continued for about thirteen days, showing a total acceleration of more than 70 % of the normal growth.

In Table VII, in which the shoots were split along one side, a retardation in the growth of the shoots was appreciable during the first twenty-four hours. This was followed by a period of acceleration which continued for five days, at the end of which time the growth-rate had again become normal.

When the roots were split, no variation was noticeable in either root or leaf during the first period of twenty-four

TABLE VII.

Growth of shoot after the shoot was split on one side.

Series I. { *a.*—Shoot split 10 mm. on one side near the base.
Helianthus. { *b.*—Control.

Temperature, 22° (constant).

Series.		Average original length of shoot of nine seedlings.	Average normal rate of growth of shoot.	Average growth of shoot, 1st period after injury.	Average growth of shoot, 2nd period after injury.	Average growth of shoot, 3rd period after injury.	Average growth of shoot, 4th period after injury.	Average total growth of shoot after injury.
	P.		24 hrs.	24 hrs.	48 hrs.	96 hrs.	96 hrs.	264 hrs.
I.	<i>a.</i>	29 mm.	13 mm.	15 mm.	35 mm.	27 mm.	19 mm.	96 mm.
	<i>b.</i>	30 "	12 "	22 "	26 "	18 "	18 "	84 "

hours; but after the first twenty-four hours acceleration began, and continued for five days in both root and leaf, as shown in the last two columns in Table VIII. The secondary roots were longer and more numerous in the injured than in the uninjured plants¹.

A closer study of secondary roots showed that their growth was first retarded and afterwards strongly accelerated under the influence of injury as seen in Table IX. Experiment *b* shows that the splitting of the roots caused acceleration in the growth of shoots as well as of main and secondary roots. The number of secondary roots was also increased if too much of the main root had not been removed, or if the main root was split (*b*, Table IX).

¹ Pfeffer, *Druck und Arbeitsleistung*, p. 343, 1893.

TABLE VIII.

Growth of leaf and root after the root was split near the tip.

Series I. { *a.*—Roots split 10 mm., beginning 5 mm. from the tip.
Zea Mais. { *b.*—Control.

Temperature, 22° (constant).

Series.		Average original length of root of twelve seedlings.	Average original length of shoot of twelve seedlings.	Average normal rate of growth of leaf.	Average growth of leaf, 1st period after injury.	Average growth of leaf, 2nd period after injury.	Average growth of leaf, 3rd period after injury.	Average total growth of leaf after injury.	Average total growth of root after injury.
I.	P.			24 hrs.	24 hrs.	48 hrs.	72 hrs.	168 hrs.	168 hrs.
	<i>a.</i>	26 mm.	10 mm.	15 mm.	15 mm.	55 mm.	78 mm.	148 mm.	166 mm.
	<i>b.</i>	25 "	11 "	15 "	16 "	43 "	62 "	121 "	134 "

TABLE IX.

Growth of roots and shoots after the roots were injured.

Series I. { *a.*—10 mm. removed from root-tips.
Phaseolus { *b.*—Roots split 10 mm., beginning 5 mm. from the tip.
multiflorus. { *c.*—Control.

Temperature, 22° (constant).

Series.		Average original length of root of eleven seedlings.	Average original length of shoot of eleven seedlings.	Average length of secondary roots at end of 1st period.	Average length of secondary roots at end of 2nd period.	Average length of secondary roots at end of 3rd period.	Number of secondary roots at end of experiment.	Average total length of main root.	Average total length of shoot after injury.
I.	P.			24 hrs.	24 hrs.	240 hrs.	288 hrs.	288 hrs.	288 hrs.
	<i>a.</i>	38 mm.	17 mm.	68 mm.	260 mm.	3100 mm.	26	28 mm.	225 mm.
	<i>b.</i>	37 "	18 "	53 "	210 "	3300 "	42	215 "	213 "
	<i>c.</i>	35 "	17 "	82 "	210 "	2100 "	34	180 "	176 "

When the plants were kept in a constant atmosphere of ether derived from 1 cc. of ether in 200 cc. of water (Series I, Table X), a constant retardation was observed, although the plants remained alive and grew for the same length of time as the control-plants, viz. about six days. If a stronger atmosphere than the above was used, a still more marked

TABLE X.

Growth of leaves in a constant atmosphere of ether.

Series I. { *a.*—1 cc. of ether in 200 cc. of water (under bell-jars).
Avena. { *b.*—Control.

Series II. { *a.*— $\frac{1}{10}$ cc. of ether in 200 cc. of water (under bell-jars).
Avena. { *b.*—Control.

Temperature, 20° (constant).

Series.		Average original length of leaves of twelve seedlings.	Average normal rate of growth of leaves.	Average growth of leaves, 1st period in ether.	Average growth of leaves, 2nd period in ether.	Average growth of leaves, 3rd period in ether.	Average growth of leaves, 4th period in ether.	Average total growth of leaves in ether.
I.	P.		24 hrs.	24 hrs.	24 hrs.	48 hrs.	48 hrs.	144 hrs.
	<i>a.</i>	39 mm.	16 mm.	21 mm.	25 mm.	38 mm.	12 mm.	96 mm.
	<i>b.</i>	39 "	16 "	27 "	34 "	56 "	17 "	134 "
II.	P.		24 hrs.	24 hrs.	48 hrs.	48 hrs.	72 hrs.	192 hrs.
	<i>a.</i>	26 mm.	11 mm.	21 mm.	66 mm.	40 mm.	34 mm.	161 mm.
	<i>b.</i>	26 "	11 "	28 "	58 "	31 "	17 "	134 "

retardation was apparent. On the other hand, if a weaker atmosphere of ether was used, e. g. $\frac{1}{10}$ cc. of ether in 200 cc. of water (Series II, Table X), the growth was first retarded and then distinctly accelerated, the younger plants being more easily retarded in their growth than were the older ones. If less than $\frac{1}{10}$ cc. of ether was used, no change which could not have been due to individual differences could be detected.

Series I, Table XI, shows that seedlings may be shocked for one hour with strong ether without producing any marked effect upon the rate of growth of the leaves. If the shock lasted one and a half hours, as in Series II, an acceleration was noticeable, beginning after the first twenty-four hours

TABLE XI.

Growth of leaves after shocking with ether.

- Series I. { *a.*—1 hour in atmosphere of ether (5 cc. ether in 200 cc. water).
Avena. { *b.*—Control.
- Series II. { *a.*—1½ hours in atmosphere of ether (5 cc. ether in 200 cc. water).
Avena. { *b.*—Control.
- Series III. { *a.*—2 hours in atmosphere of ether (5 cc. ether in 200 cc. water).
Avena. { *b.*—Control.

Temperature, 23° (constant).

Series.		Average original length of leaf of twelve seedlings.	Average normal rate of growth of leaves.	Average growth of leaves, 1st period after shocking.	Average growth of leaves, 2nd period after shocking.	Average growth of leaves, 3rd period after shocking.	Average growth of leaves, 4th period after shocking.	Average total growth of leaves after shocking.
I.	P.		24 hrs.	12 hrs.	12 hrs.	24 hrs.	72 hrs.	120 hrs.
	<i>a.</i>	25 mm.	21 mm.	14 mm.	14 mm.	22 mm.	29 mm.	79 mm.
	<i>b.</i>	26 "	22 "	17 "	15 "	25 "	25 "	82 "
II.	P.		24 hrs.	24 hrs.	24 hrs.	24 hrs.	48 hrs.	120 hrs.
	<i>a.</i>	33 mm.	27 mm.	30 mm.	30 mm.	25 mm.	11 mm.	96 mm.
	<i>b.</i>	35 "	25 "	30 "	25 "	16 "	2 "	73 "
III.	P.		24 hrs.	12 hrs.	36 hrs.	24 hrs.	48 hrs.	120 hrs.
	<i>a.</i>	26 mm.	29 mm.	15 mm.	32 mm.	20 mm.	7 mm.	74 mm.
	<i>b.</i>	28 "	28 "	21 "	46 "	22 "	7 "	96 "

and continuing four days, i. e. as long as the leaves of the seedlings grew. If the shock was allowed to continue for two hours, a marked retardation during the first forty-eight hours was observed, followed by a return to the normal rate of growth, but without acceleration (Series III). A shock

of longer duration than two hours usually caused either a continuous retardation or death.

Older Plants. Stems.—Satisfactory results were obtained in studying the growth of the stems when the roots were injured in plants of *Phaseolus multiflorus* about two weeks old. In the experiments with these older plants a single root was allowed to pass through the bottom of the flower-pot in the manner already described. This root was then allowed to attain a length of from thirty to forty centimeters below the bottom of the flower-pot before cutting away, but no

TABLE XII.

Growth of stem after a number of secondary roots were removed.

Series I. { *a.*—About two-thirds of the secondary roots removed 2 cm. from base.
Phaseolus. { *b.*—Control.

Temperature 22° (constant).

Series.		Average original length of stem of ten plants.	Average normal rate of growth of stems.	Average growth of stems, 1st period after injury.	Average growth of stems, 2nd period after injury.	Average growth of stems, 3rd period after injury.	Average growth of stems, 4th period after injury.	Average growth of stems, 5th period after injury.	Average total growth of stems after injury.
	P.		24 hrs.	12 hrs.	12 hrs.	24 hrs.	24 hrs.	120 hrs.	192 hrs.
I.	<i>a.</i>	149 mm.	27 mm.	17 mm.	19 mm.	41 mm.	33 mm.	149 mm.	259 mm.
	<i>b.</i>	147 "	26 "	12 "	13 "	29 "	31 "	172 "	257 "

appreciable variation in the rate of growth of the stem could be detected. Subsequent experiments showed that the injury in this case was not strong enough to produce any decided change in the rate of growth. However, when a large number of the secondary roots were cut off at a distance of about two centimeters from the main root, as in Table XII, a decided acceleration in the growth of the stem took place within twelve hours after injury, and continued for about forty-eight hours. This was followed by a period of normal growth lasting about twenty-four hours, after which came a period of retardation lasting about five days, at the end of which time the stems were again practically equal in

length, and the normal rate of growth was resumed. It was possible to determine approximately the degree of injury which had been inflicted upon these plants when they were removed from the earth at the end of the experiments. When a number of the roots were forced to grow into the damp chambers and were then cut away, the results were similar to those given in Table XII, though in most cases not so marked, since the injury in the latter experiments was not so great, and since it was necessary for the influence to act through a greater distance. The number of roots cut off

TABLE XIII.

Growth of a leaf after another leaf was removed.

Series I. $\left\{ \begin{array}{l} a, b, \text{ and } c. \text{—One leaf removed.} \\ \text{Calla. } d. \text{—Control.} \end{array} \right.$

Temperature, 17–21°.

Series.		Average original length of leaf of five plants.	Average normal rate of growth of leaves.	Average growth of leaves, 1st period after injury.	Average growth of leaves, 2nd period after injury.	Average growth of leaves, 3rd period after injury.	Average growth of leaves, 4th period after injury.	Average growth of leaves, 5th period after injury.	Average total growth of leaves, after injury.
I.	P.		24 hrs.	6 hrs.	24 hrs.	24 hrs.	24 hrs.	96 hrs.	174 hrs.
	a.	245 mm.	22 mm.	10 mm.	32 mm.	30 mm.	27 mm.	68 mm.	167 mm.
	b.	150 "	17 "	8 "	25 "	18 "	10 "	40 "	101 "
	c.	211 "	20 "	13 "	37 "	45 "	25 "	78 "	198 "
	d.	185 "	18 "	4.5 "	19 "	18 "	17 "	64 "	122.5 "

was only about one-third as many as in the previous experiments, and the irritation had to act through nearly twice the distance.

Leaves.—The growth of young leaves of *Calla* was found to be nearly uniform from day to day when the conditions were normal and constant. If however the plant was disturbed by the removal of one of the full-grown vigorous leaves, the rate of growth of the young leaves was decidedly

accelerated within six hours. The acceleration continued from one to five days, after which came a period of normal growth, followed in some cases by a period of retardation (Table XIII).

Roots.—No appreciable change in the rate of growth of roots could be detected in the older plants, even when the entire stem, of *Phaseolus* for example, was cut away, leaving only the first pair of leaves. Also in *Calla* no change was produced in the rate of growth of the roots by the removal of a leaf, although this same injury produced such a comparatively sudden and marked change in the rate of growth of the young leaves.

Cuttings.—A few experiments were performed with cuttings of *Salix*, the results of which were similar to those already shown. Owing however to the small number of experiments and to the slight changes in the rate of growth, further investigations are necessary before the results can be tabulated with satisfaction.

Phycomyces.—When the mycelia were cut near the base of the sporangium-stalk, the rate of growth of the stalk was immediately reduced in a very marked degree, but in no case examined did the growth entirely cease. The sporangium-stalk began in a few minutes to recover its rate of growth, and in from thirty to sixty minutes was growing again at the usual rate. No change was observed in the rate of growth of the sporangium-stalk if the mycelia cut were comparatively thin, or if the larger mycelia were cut only near the tips. In those experiments in which one of two or more sporangium-stalks was cut off, the uninjured stalk showed a still stronger retardation in the rate of growth than when the mycelia were cut, and the retardation in some cases continued for a longer time. But, as in the preceding experiments, the growth did not absolutely cease.

While the above table would indicate that observations were made only at intervals of ten minutes, it was really the case that the plants were not removed from before the microscope. The treating and refocussing required but a few

seconds, and the stalks were watched closely for the first few seconds after treating. After the rate of growth of a stalk had recovered from the effect of cutting one mycelium,

TABLE XIV.

Growth of sporangium-stalks of *Phycomyces* after other sporangium-stalks or mycelia were cut off or treated with KNO_3 .

Temperature, 17–20°.

Observation periods.	Growth of sp.-stalk after mycelia cut once.	Growth of sp.-stalk after mycelia cut twice.	Growth of sp.-stalk after another sp.-stalk was cut once.	Growth of sp.-stalk after another sp.-stalk was cut three times.	Heliotropism of sp.-stalk after mycelia were cut once.	Growth of sp.-stalk after KNO_3 applied to mycelia.
	Spaces.	Spaces.	Spaces.	Spaces.	Spaces.	Spaces.
N { 10 min.	11	7	20	20	3	8
„	12	7	20	22	3	8
„	12*	8*	21*	23*	3*	9*
„	3	3	1	1	$\frac{1}{2}$	5
„	4	4	8	10	$\frac{1}{2}$	2
„	5	6	15	14	1	0
„	7	8*	20	18*	$1\frac{1}{2}$	0
„	10	3	20	18	2	0†
„	11	5	22	20*	3	0
„	13	8	25	22	3	0
„	14	9	26	22	3	1
„	15	9	26	25	4	3

One space = $\frac{1}{80}$ of a millimeter.

N shows normal growth for three periods.

* Indicates the time of injury.

† In the last column indicates that the 5% KNO_3 solution was gradually displaced by water.

the rate of growth was again reduced to the same extent if another mycelium of the same size was cut, the period of recovery being shorter usually in the second case

(Table XIV, column 3). If a stalk was cut, the reduction in growth was greater than when a mycelium was cut (Table XIV, column 4). In column 5, Table XIV, the same stalk was cut three times. The first time about one-third of the stalk was removed, causing a decided retardation in growth of another stalk on the same plant. The second and third cuttings removed the remaining two-thirds of the same stalk, but produced no change in the rate of growth of the stalk under observation.

When a solution of from 3 to 5% of KNO_3 was applied to the mycelia of *Phycomyces*, the growth of the stalk was gradually retarded until it finally ceased. If the turgor was restored by displacing the KNO_3 solution with water, the growth began again in from twenty to sixty minutes. The length of time required for the resumption of growth depended upon the strength of the KNO_3 solution used, and upon the time during which the growth had ceased. Cross-walls formed in the mycelia in from one to two hours after cutting, while the return to the normal rate of growth usually took place in from thirty to sixty minutes; hence it is clear that the formation of cross-walls could not have influenced the return to the normal rate of growth.

CONCLUSIONS.

*Distance through which the irritation acted*¹. When nearly the entire root of seedlings was removed, the point of injury was only from one to ten millimeters from the lowest point of the growing-zone of the shoot. Likewise when the leaf-tips were removed (as in Table V), or a leaf was cut from the growing shoot (as in Table VI), the shortest distance to the zone of growth did not exceed a few millimeters. On the other hand, if the root-tip alone was removed or split, the irritation had to act through nearly the

¹ Rothert, Ueber Heliotropismus; Cohn's Beiträge zur Biologie der Pflanzen, Vol. vii, p. 66, 1896.

entire length of the root in order to affect the growth of the shoot. This distance, as shown by the tables, varied from twenty to fifty millimeters. In like manner, when the shoot was injured, it was necessary for the influence of the irritation to travel nearly the entire length of the root in order to affect the growing-zone. Furthermore it was not sufficient for the irritation simply to reach the growing-zone, but it was necessary for it to extend through a part or all of the cells of the zone in order to affect the growth.

In the older plants the distance through which the irritation acted was much greater than in the seedlings. In *Phaseolus*, for example, the entire growth of the stem, after the roots were injured, took place above the first pair of leaves, which were from 95 to 150 mm. above the root. The secondary roots were injured at least 20 mm. from the main root, so that the distance from the point of injury to the growing-zone of the stem was from 115 to 170 mm. In the *Phaseolus* plants in which the roots extended into damp chambers before injury, the distance was still greater. The flower-pots used were 110 mm. deep. This added to the 95 or 150 mm. made a distance of from 205 to 260 mm. through which the influence must have acted. In *Calla* the distance between the point of injury and the zone of growth varied from 50 to 80 mm. In *Phycomyces* the distance was from 10 to 50 mm.

These distances are by no means to be regarded as the limits through which such irritation will influence growth. The distance through which an influence will act depends upon the degree of injury and upon the external and internal conditions of the individual plants.

Time.—In experiments relative to the time required for the influence of the irritation to exhibit itself, observation with the horizontal microscope showed that there was no sudden change, due to injury, in the rate of growth of higher plants. It was only by extending the period of observation over several hours that a distinct difference in the rate of growth could be detected. It is therefore impossible to say definitely at what time an acceleration or a retardation of growth began.

In some of the experiments a distinct difference in the rate of growth was observed in six hours, while in other cases no change could be seen within twenty-four hours after injury. Even among plants of the same species and under the same conditions there were individual differences in the time required for the variation in the rate of growth. It was rare that a change in the rate of growth which could not be accounted for by individual differences was noticeable in less than six hours. The duration of the retardation or acceleration depended largely upon the degree of injury. If the injury was sufficiently severe, the retardation continued throughout the life of the seedling; while with a less severe injury the retardation lasted only from one to three days, and was often followed by a period of acceleration (Table II, Series II and III). If the injury was slight, it was usually followed by acceleration without an intervening period of retardation (Table VI). The influence of the irritation upon the seedlings was usually much more gradual than upon the older plants. The total period covered by a variation in the rate of growth due to a single irritation varied from one to twelve days, and depended upon the condition of the individual plant and upon the degree of injury. It was possible for the retarding and accelerating influences to neutralize each other so that the final result was the same as if no injury had been inflicted. Indeed it was possible for the final result to indicate a slower growth than the normal even though the injury was followed by a period of acceleration, provided that a strong retardation followed or preceded the acceleration.

With *Phycomyces* a reduction in the rate of growth took place immediately after cutting, as shown in Table XIV. The retardation was evidently due to a change of turgor rather than to an irritation produced by cutting. At any rate, it is impossible to know what part the irritation plays in these experiments so long as the influence of turgor is not eliminated.

Extent of variation in growth.—It is apparent from a study of the preceding tables that a change in the rate of growth

due to injury may vary from 0 to 70% of the normal rate. It is evident that some plants respond much more readily to the influence of an irritation than others. This accounts in part for the great variation in different species. It appears however that an injury has two opposite effects upon growth, one of acceleration, the other of retardation. It is clear that these opposing tendencies may be so nearly equal that, although the plant is a sensitive one, no appreciable change in the rate of growth can be observed. If the tendency of the irritation to retard the growth is weaker or of shorter duration than is the tendency to acceleration, the plant will soon show signs of acceleration and *vice versa*. It is seen from the tables that the retarding influence is stronger than the accelerating influence under a severe injury, but that the retarding influence diminishes more rapidly than does the accelerating influence. It is impossible to determine if the retarding influence ever ceases entirely, or if the highest degree of acceleration is ever reached. We can only say that the amount of variation in growth is the difference between the accelerating and the retarding tendencies. If these opposing tendencies are in a state of equilibrium, the growth will be constant from period to period. The activities of growth¹ may serve as an irritant to disturb this state of equilibrium, as shown by the almost constant variation in the rate of growth of normal plants.

SUMMARY.

A single irritation produced by cutting or splitting the shoots or roots or removing the leaf-tips of seedlings tends to produce a change in the rate of growth of the injured and of the uninjured parts.

If the injury is slight, signs of an acceleration in the rate of growth will be apparent in from six to twenty-four hours, and will continue for from one to several days. If the injury

¹ Pfeffer, Studien zur Energetik der Pflanze, 1892.

is severe, the acceleration will be preceded by a period of retardation of longer or shorter duration, depending upon the severity of the injury and upon the condition of the plant injured.

The growth of the stems of older plants is accelerated by removal of a number of the roots or leaves, but is not affected by a slight injury to the roots.

The roots of older plants as well as of seedlings are more independent than are the stems or shoots¹.

The change in the rate of growth of higher plants under the influence of a single irritation begins gradually, reaches its maximum in from twelve to ninety-six hours, and gradually diminishes until the normal rate is resumed.

A dilute but continuous atmosphere of ether, or a strong shock of ether of short duration, will produce an acceleration in growth.

The total variation in the growth of higher plants due to the influence of a single irritation is from 0 to 70% of the normal growth for the same period.

The growth of sporangium-stalks of *Phycomyces* is suddenly and strongly retarded by cutting either the mycelia or another sporangium-stalk on the same plant. The growth does not entirely cease, and gradually recovers its normal rate in from thirty to sixty minutes.

The influence of an irritation due to cutting or other injury is capable of acting through a distance of several hundred millimeters.

¹ Kny, l.c., p. 280.

Townsend, Charles Orvin. 1897. "The correlation of growth under the influence of injuries." *Annals of botany* 11, 509–532.

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