CHEMICAL BASIS OF CORRELATION[1]

I. PRODUCTION OF EQUAL MASSES OF SHOOTS BY EQUAL MASSES OF SISTER LEAVES IN BRYOPHYLLUM CALYCINUM

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(WITH EIGHTEEN FIGURES)

In this paper the term correlation will signify the inhibiting influence which the growing buds of a leaf of *Bryophyllum calycinum* have upon the growth of other buds of the same leaf. It is generally known that in a complex organism the growth in one organ of the complex may inhibit the growth in other organs of the same complex.

In former papers[2] the writer has shown that when in *Bryophyllum calycinum* one organ inhibits the growth of buds in another organ the inhibited organ contributes in some cases material to the growth in the inhibiting organ. It was known through the experiments of WAKKER and DEVRIES[3] that if a piece of stem is left attached to a leaf of *Bryophyllum* the stem will inhibit the growth of shoots in the notches of the leaf, while such shoots will grow if the leaf is entirely isolated from the stem. The writer was able to show that in such a case the leaf accelerates the growth of a shoot in the stem attached to the leaf. Thus figs. 1 and 2 are sister leaves, that is, leaves from the same node of a stem of *Bryophyllum*. Both are dipping with their tips in water.[4] Leaf 1, without a stem, has formed a shoot in 22 days, while the sister leaf in fig. 2 has formed no shoot, due to the inhibiting effect of the piece of stem attached to the leaf. The latter has accelerated the growth of the shoot in the piece of stem attached to the leaf, however, for a piece of stem of

[1] From the Laboratories of The Rockefeller Institute for Medical Research.

[2] LOEB, J., BOT. GAZ. 60:249. 1915; 62:293. 1916; Science 41:704. 1915; The organism as a whole, p. 153. Putnam's Sons, New York. 1916.

[3] DEVRIES, H., Jahrb. Wiss. Bot. 22:35. 1890–91.

[4] The result is the same when the leaves are suspended in moist air instead of dipping into water.

equal size without a leaf attached to it will in the same time form
no shoot or only a very tiny shoot (fig. 3).   The inference was drawn
that the inhibiting effect of the stem upon the leaf in fig. 2 was due
to the fact that the leaf furnished the material required for the
growth of shoots to the stem instead of to its own notches.   This
takes place even when no shoot is formed in the stem; in that case
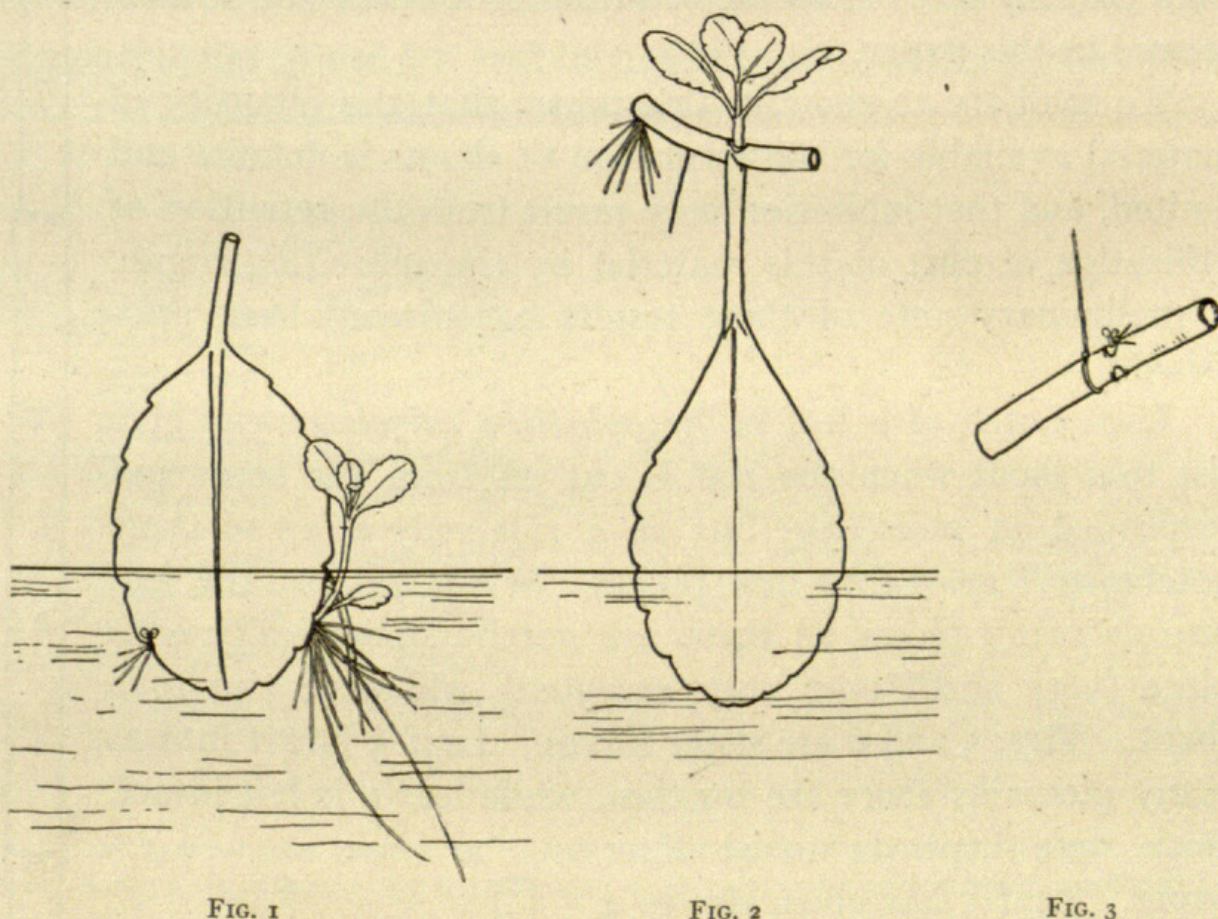the material furnished by the leaf is stored in or consumed by

FIG. 1   FIG. 2   FIG. 3

FIGS. 1–3.—Figs. 1, 2, sister leaves; leaf of fig. 2 still attached to stem, showing
stem inhibits shoot formation in leaf; fig. 2 shows inhibition is accompanied by
accelerating effect of leaf upon growth of shoot from stem, since in a piece of stem,
suspended in moist air, as in fig. 3, production of shoots is suppressed or retarded.

certain cells of the stem, as indicated, for example, by callus for-
mation and by geotropic curvature.[5]

The same principle was shown to hold if stems without leaves
are suspended in moist air.   In such cases the two buds of the
most apical node of a long piece of stem grow out (fig. 4), and
it can be shown that the basal part of the stem whose buds are
inhibited from growing furnishes to the growing buds at the apex

[5] LOEB, J., Science 46:547. 1917.

the material required for their growth, for if we cut out short pieces with one node only (fig. 4, *a, b, c, d*), the growth of the shoots from the buds is retarded. This is not the only factor of inhibition in this case, since the writer has recently shown[6] that a growing bud, as well as a leaf, seems to send out inhibitory substances toward the base of the stem which prevent the buds in the stem, situated more basally, from growing out. This factor of inhibition will not be considered in this paper.

We shall try to show in this paper that the quantity of material available for the formation of shoots is definite and limited, and that inhibition may result from the retention or utilization of part of this material by the inhibiting organ. A preliminary note of these results has already been published.[7]

Each notch of a leaf of *Bryophyllum calycinum* can give rise to a shoot when the leaf is cut off from the stem and suspended in moist air, but as a rule only a few of these notches will grow into new plants. When we cut the leaf into as many pieces as there are notches, practically each piece (very small ones only excepted) will give rise to a shoot. Figs. 5 and 6 are sister leaves. Leaf 5 is cut into as many pieces as there are notches, while leaf 6 is left intact. Both were kept on moist filter paper. Leaf 5 has given rise to a new shoot in practically each notch, while leaf 6 has formed only 4 shoots. We assume that in the latter leaf the shoots which

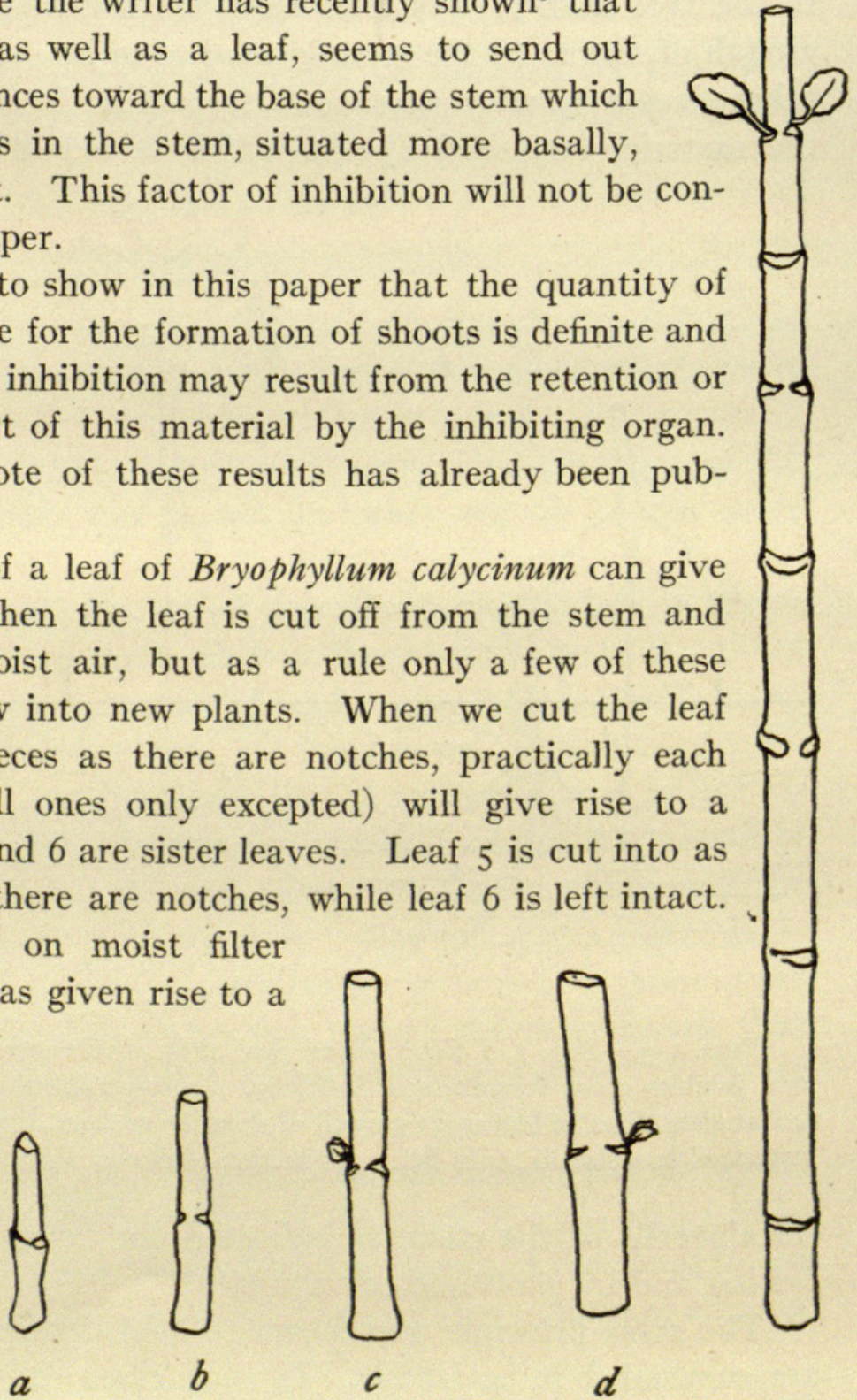a   b   c   d

Fig. 4.—Shows that inhibited basal part of the long stem accelerates growth of the two apical buds, since in pieces with one node only (*a, b, c, d*) the buds do not grow at all, or much more slowly.

[6] Loeb, J., Science **46**:547. 1917.   [7] *Ibid.*, **45**:436. 1917.

grow out first inhibit the growth in the other notches. (No part of the leaf of *Bryophyllum calycinum* except the notches is able to give rise to shoots or roots. The formation of roots will be omitted from consideration in this paper in order to simplify the discussion.) Our contention is that this inhibition in leaf 6 is due to the absorption of all the material available for shoot formation by the 4 notches that happened to grow out first, thus depriving the other notches of the material needed for the growth of shoots. By comparing figs. 5 and 6 it will be noticed that 3 of the shoots which leaf 6 produced are considerably larger than the individual shoots
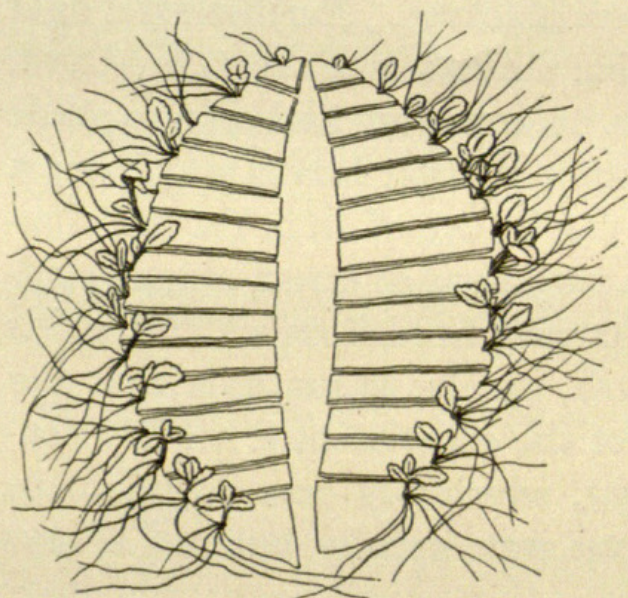

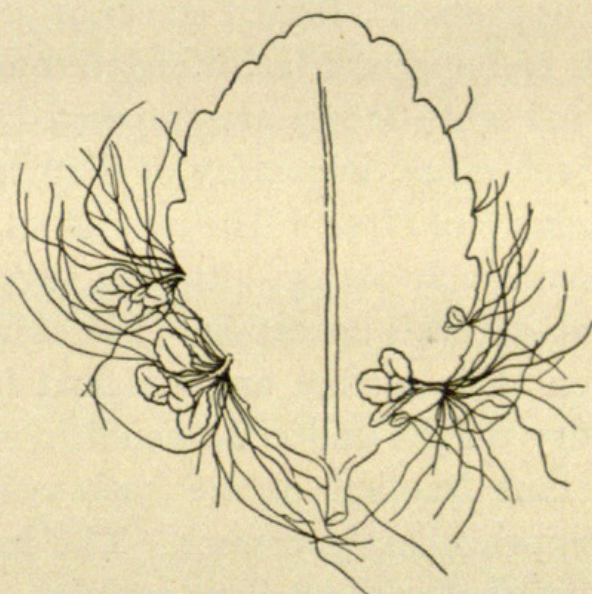FIG. 5   FIG. 6

FIGS. 5, 6.—Sister leaves: fig. 5, leaf cut into as many pieces as notches; almost every notch forms a shoot; fig. 6, leaf intact, only 4 shoots formed, 3 being considerably larger than those shown in fig. 5, thus indicating tendency of both leaves to produce equal masses of shoots, although number of shoots may vary considerably.

of leaf 5, and this suggests the possibility that the isolation of a piece with one notch simply prevents the material needed for the growth of the notch being taken away by some of the other notches which by chance start growing a little earlier.

In order to prove this we must be able to show that if we isolate two sister leaves (which are of equal size, age, and history) and keep them under equal conditions, they will produce in equal times approximately equal masses of shoots. It is necessary, of course, that both leaves are healthy and not yet beginning to etiolize, and that they should not do so during the course of the experiment.

It is necessary also that the experiment be continued long enough (that is, a month or longer at about 23°C.) to allow the shoots to reach a sufficiently large size, since if the shoots are too small the error in measuring their masses prevents exact results. On the other hand, the experiment must not last too long, for if the shoots become too large they produce themselves too considerable a share of the material needed for their own growth. The leaves were generally kept on wet filter paper in flat dishes with a loose glass cover. One of the greatest sources of error or variation in the results was probably the differences in the absorption of water by the roots of different leaves or pieces of leaves. Furthermore, light is an important factor in determining the masses of shoots produced, and when leaves are suspended in an aquarium and able to shade each other, inequality of illumination of sister leaves also forms a source of error. The new shoots can be cut off from the leaf comparatively neatly, although slight variations or errors are unavoidable in this operation. The shoots were freed from water droplets on their surface and weighed fresh, on the assumption that the dry weight under the conditions of the experiment is a fairly constant fraction of the fresh weight, which has been found to be approximately correct. The leaves were usually but not always weighed without their petioles.

TABLE I

Sister leaves		Number of shoots produced from leaf	Mgm. of shoots produced in 33 days
I.	Leaf 1.........	3	350
	Leaf 2.........	3	345
II.	Leaf 1.........	1	290
	Leaf 2.........	2	306
III.	Leaf 1.........	2	375
	Leaf 2.........	4	385
IV.	Leaf 1.........	5	594
	Leaf 2.........	4	607
V.	Leaf 1.........	4	457
	Leaf 2.........	5	455

Table I gives the weight of the shoots produced by 5 pairs of sister leaves in 33 days (February 15—March 20). The two sister

leaves are always designated as 1 and 2. It is found that each of two sister leaves which were of equal size produced almost identical masses of shoots in the same period of time and under equal conditions, although the number of shoots by two sister leaves differed.

Table II gives another experiment of the same kind. The two sister leaves produce in each case almost identical masses of shoots

TABLE II

MARCH 29—APRIL 20, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaf 1............	7	0.2560	2.3030	111
	Leaf 2............	9	0.2455	2.2555	109
II.	Leaf 1...........	5	0.1920	1.783	108
	Leaf 2...........	4	0.2075	1.8735	111
III.	Leaf 1..........	5	0.2005	2.262	89
	Leaf 2..........	3	0.1605	1.982	81
IV.	Leaf 1...........	5	0.1910	1.668	114
	Leaf 2...........	4	0.1570	1.402	112
V.	Leaf 1...........	4	0.3205	2.5125	128
	Leaf 2...........	7	0.3760	3.0770	122
VI.*	Leaf 1..........	3	0.1790	2.191	82 etiolized
	Leaf 2..........	?	0.0595	1.597	37 leaves
VII.	Leaf 1..........	6	0.2355	2.6495	89
	Leaf 2..........	4	0.216	2.288	94
VIII.	Leaf 1.........	2	0.109	1.326	82
	Leaf 2.........	4	0.132	1.505	88
IX.	Leaf 1...........	3	0.172	1.927	89
	Leaf 2...........	5	0.187	2.093	89
Average	Leaves 1...	....	1.675	16.430	102
	Leaves 2...	....	1.682	16.476	102

* Pair VI is not included in the average.

in the same time, although the number of shoots varies quite often. The shoots produced by the two leaves of the sixth pair differ considerably, but those two leaves were etiolized. They were excluded from the calculation of the average shoot production, which is exactly the same for each set of leaves, namely 102 mgm. of shoots for 1 gm. of leaf.

Tables III and IV show a slightly greater variation than tables I and II, owing to the inevitable errors in such experiments (errors in cutting off and ascertaining the weight of the small shoots, errors in evaporation, differences in the condition of the two sister leaves,

TABLE III

APRIL 11—MAY 10, 1917

Sister leaves	Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I. { Leaf 1............	2	0.180	1.655	109
{ Leaf 2............	1	0.201	1.590	126
II. { Leaf 1............	2	0.115	1.050	109
{ Leaf 2............	2	0.166	1.505	110
III. { Leaf 1...........	3	0.155	1.081	143
{ Leaf 2...........	2	0.140	1.098	127
IV. { Leaf 1...........	3	0.123	1.158	106
{ Leaf 2...........	3	0.126	1.245	101
V. { Leaf 1...........	2	0.110	1.038	106
{ Leaf 2...........	2	0.089	0.995	90
VI. { Leaf 1...........	2	0.183	1.646	111
{ Leaf 2...........	2	0.153	1.383	111
VII. { Leaf 1...........	3	0.231	1.617	143
{ Leaf 2...........	3	0.178	1.463	122
VIII. { Leaf 1...........	4	0.220	1.547	142
{ Leaf 2...........	2	0.146	1.172	125
IX. { Leaf 1...........	3	0.119	1.230	97
{ Leaf 2...........	3	0.149	1.410	106
Average { Leaves 1...	....	1.436	12.022	119
{ Leaves 2...	....	1.348	11.861	114

and in the external conditions of moisture and light, and others). The fact that these errors are accidental is proved by the proximity of the average shoot production in each set of leaves, which is 119 and 114 mgm. of shoots per gm. of leaf in table III, and 106 and 100 mgm. in table IV.

We may make the following statement, therefore: *Two healthy, isolated sister leaves of equal mass will produce in equal times and under equal conditions approximately equal masses of shoots, although*

the number of shoots in the two leaves may differ. The variations in the results lie within the limits of the unavoidable errors of the experiments.

TABLE IV

INTACT SISTER LEAVES; MARCH 20—APRIL 18, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf in 29 days
I.	Leaf 1............	3	0.127	1.310	97
	Leaf 2............	2	0.128	1.170	109
II.	Leaf 1............	2	0.150	1.595	94
	Leaf 2............	3	0.1325	1.323	100
III.	Leaf 1............	4	0.2085	1.9175	109
	Leaf 2............	2	0.1575	1.722	91
IV.	Leaf 1............	3	0.270	2.286	118
	Leaf 2............	4	0.145	1.586	91
V.	Leaf 1............	2	0.147	1.3385	110
	Leaf 2............	5	0.2075	2.061	101
VI.	Leaf 1............	4	0.211	1.9735	107
	Leaf 2............	3	0.220	2.0275	107.5
VII.	Leaf 1............	2	0.1065	0.9435	113
	Leaf 2............	3	0.105	1.062	99
VIII.	Leaf 1............	5	0.233	2.332	100
	Leaf 2............	4	0.228	2.2595	101
Average	Leaves 1...	....	1.452	13.69	106
	Leaves 2...	....	1.322	13.21	100

It would follow that if we cut a leaf into two symmetrical halves each half should produce equal masses of shoots in the same time and under the same conditions. This is approximately correct, as table VI shows.

The experiment was repeated (table V), and we may confine ourselves to a statement of the average result. The two halves are designated as right and left, when facing the observer with their basal end and when lying on their lower side.

It is obvious, therefore, that if leaves are cut symmetrically, the two halves will produce in equal times and under equal conditions on the average exactly the same mass of shoots, even when the number of shoots in the two halves varies.

While in the preceding experiments the number of shoots produced in sister leaves was not identical, yet it seemed of interest to find out whether the law of the production of equal masses of shoots by equal masses of sister leaves was true also if the number

TABLE V

APRIL 12—MAY 15

	Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
20 left halves of leaves.....	33	2.916	19.307	151
20 right halves of leaves....	31	2.790	18.466	151

TABLE VI

SISTER LEAVES, EACH CUT INTO TWO SYMMETRICAL HALVES; APRIL 3—MAY 4

Sister leaves			Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaf 1	Left half....	2	0.188	0.936	203
		Right half...	2	0.183	0.959	191
	Leaf 2	Left half....	1	0.202	1.009	200
		Right half...	2	0.254	1.241	205
II.	Leaf 1	Left half....	1	0.057	0.427	133
		Right half...	2	0.053	0.398	133
	Leaf 2	Left half....	1	0.063	0.441	143
		Right half...	1	0.056	0.398	141
III.	Leaf 1	Left half....	1	0.120	0.820	146
		Right half...	3	0.111	0.758	146
	Leaf 2	Left half....	1	0.116	0.713	163
		Right half...	1	0.115	0.721	160
IV.	Leaf 1	Left half....	1	0.070	0.497	141
		Right half...	1	0.072	0.580	124
	Leaf 2	Left half....	2	0.073	0.595	122
		Right half...	1	0.068	0.522	130

of shoots produced in the two leaves differed considerably. For this purpose one leaf was cut into 4 pieces while its sister leaf remained intact. The whole leaves produced fewer shoots than the leaves cut into 4 pieces; nevertheless, the masses of shoots produced in the two sets of leaves remained the same. Thus 12

intact leaves produced 25 shoots, while their sister leaves cut into
4 pieces each produced 50 shoots.   Yet the average weight of shoots
produced per gm. of leaf was 156 mgm. for the intact leaves and

TABLE VII

SISTER LEAVES, ONE INTACT, THE OTHER CUT INTO FOUR PIECES;
APRIL 18—MAY 18, 1917

Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaf 1, intact......	2	0.198	1.170	169
	Leaf 2, 4 pieces....	4	0.2025	1.205	168
II.	Leaf 1, intact......	2	0.216	1.596	135
	Leaf 2, 4 pieces....	4	0.214	1.560	137
III.	Leaf 1, intact......	1	0.305	1.925	158
	Leaf 2, 4 pieces....	4	0.368	2.110	174
IV.	Leaf 1, intact......	2	0.340	1.9015	177
	Leaf 2, 4 pieces....	4	0.2635	1.475	179
V.	Leaf 1, intact......	2	0.197	1.072	184
	Leaf 2, 4 pieces....	4	0.200	1.227	163
VI.	Leaf 1, intact......	3	0.265	1.743	152
	Leaf 2, 4 pieces....	6	0.292	1.675	174
VII.	Leaf 1, intact......	2	0.2415	1.741	138
	Leaf 2, 4 pieces....	4	0.255	1.745	146
VIII.	Leaf 1, intact......	1	0.195	1.260	155
	Leaf 2, 4 pieces....	4	0.109	0.660	165
IX.	Leaf 1, intact......	2	0.218	1.198	182
	Leaf 2, 4 pieces....	4	0.209	1.110	188
X.	Leaf 1, intact......	2	0.223	1.514	147
	Leaf 2, 4 pieces....	4	0.180	1.280	140
XI.	Leaf 1, intact......	4	0.258	1.820	142
	Leaf 2, 4 pieces....	5	0.2615	1.818	144
XII.	Leaf 1, intact......	2	0.227	1.498	151
	Leaf 2, 4 pieces....	3	0.191	1.205	158
Average	Intact leaves	25	2.884	18.435	156
	Leaves cut into 4 pieces	50	2.747	17.070	161

161 mgm. for the leaves cut into 4 pieces, in spite of the difference
in the number of shoots produced.   Table VII gives the results in
detail.   These experiments again confirm the conclusion that equal

masses of sister leaves produce equal masses of shoots in equal time, even if the number of shoots in the two cases is in the ratio of 1:2.

In order to test further this law it seemed necessary to modify the experiment. For this purpose the mass of one of two sister leaves was reduced by cutting out a large piece from the center, leaving the edge intact (fig. 8), while the other leaf remained intact (fig. 7). If the law just expressed is correct, it should follow
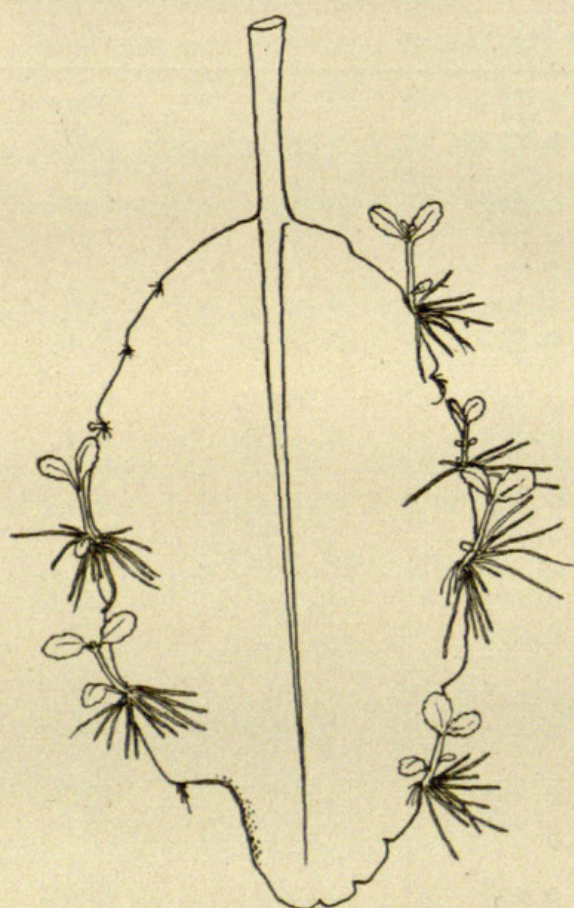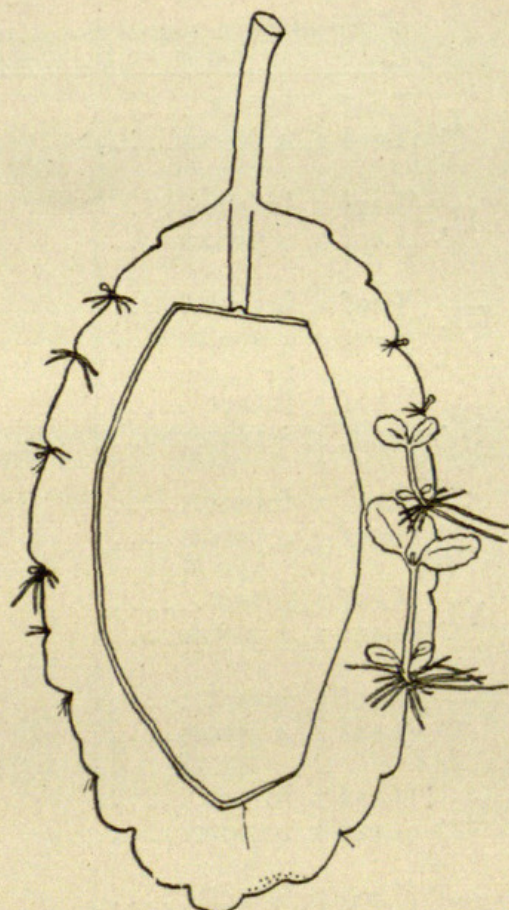

FIG. 7   FIG. 8

FIGS. 7, 8.—Sister leaves suspended in moist air: fig. 7, leaf intact; fig. 8, leaf with mass reduced by cutting out large piece from center of leaf; mass of shoots produced smaller than that produced by intact leaf; drawn 23 days after beginning of experiment.

that the mass of shoots produced by such sister leaves (one set of which remained intact while the mass of the other set was reduced by cutting out pieces from the middle) would no longer be equal, but would differ in proportion to the mass of the two sets of leaves. This was found to be approximately true, as table VIII indicates.

Thus in experiment I (table VIII) the 5 intact leaves weighing 13.8 gm. produced in 37 days 1405 mgm. of shoots, while their 5

sister leaves, whose weight was reduced from approximately 13.8 gm. to 7.6 gm. (by cutting out pieces from the center of the leaf as indicated in fig. 8), produced in the same time and under the same condition 755 mgm. of shoots. While the proportion of the mass of the two sets of leaves was $\frac{7.6}{13.8}$, the proportion of the mass

TABLE VIII

Number of experiment	Sister leaves		Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots produced per gm. of leaf
I.	Leaves dipping in water; duration of experiment 37 days	(a) 5 leaves, with center cut out ..	11	0.755	7.61	99
		(b) 5 sister leaves, intact..........	9	1.405	13.80	101
II.	Leaves dipping in water; duration of experiment 25 days	(a) 7 leaves, with center cut out...	21	1.213	9.899	122
		(b) 7 sister leaves, intact..........	25	1.995	16.935	118
III.	Leaves dipping in water; duration of experiment 32 days	(a) 9 leaves, with center cut out ..	22	2.292	10.522	218
		(b) 9 sister leaves, intact..........	30	3.430	17.852	192
IV.	Leaves dipping in water; duration of experiment 27 days	(a) 12 leaves, with center cut out ..	33	2.175	11.245	194
		(b) 12 sister leaves, intact..........	33	2.761	19.395	142
V.	Leaves kept in moist air; duration of experiment 38 days	(a) 5 leaves, with center cut out ..	13	0.690	5.42	109
		(b) 5 sister leaves, intact..........	20	1.207	11.81	102

of the shoots produced was $\frac{755}{1405}$. These two quotients are almost identical. The same is true for experiments II, III, and V, while in IV there is a greater discrepancy. Experiments III and IV indicate that if there is such a discrepancy it seems to be in favor of the leaf reduced in size. Since light plays such an important rôle in the production of shoots the discrepancy may possibly be due to the accidental fact that the intact leaves shaded

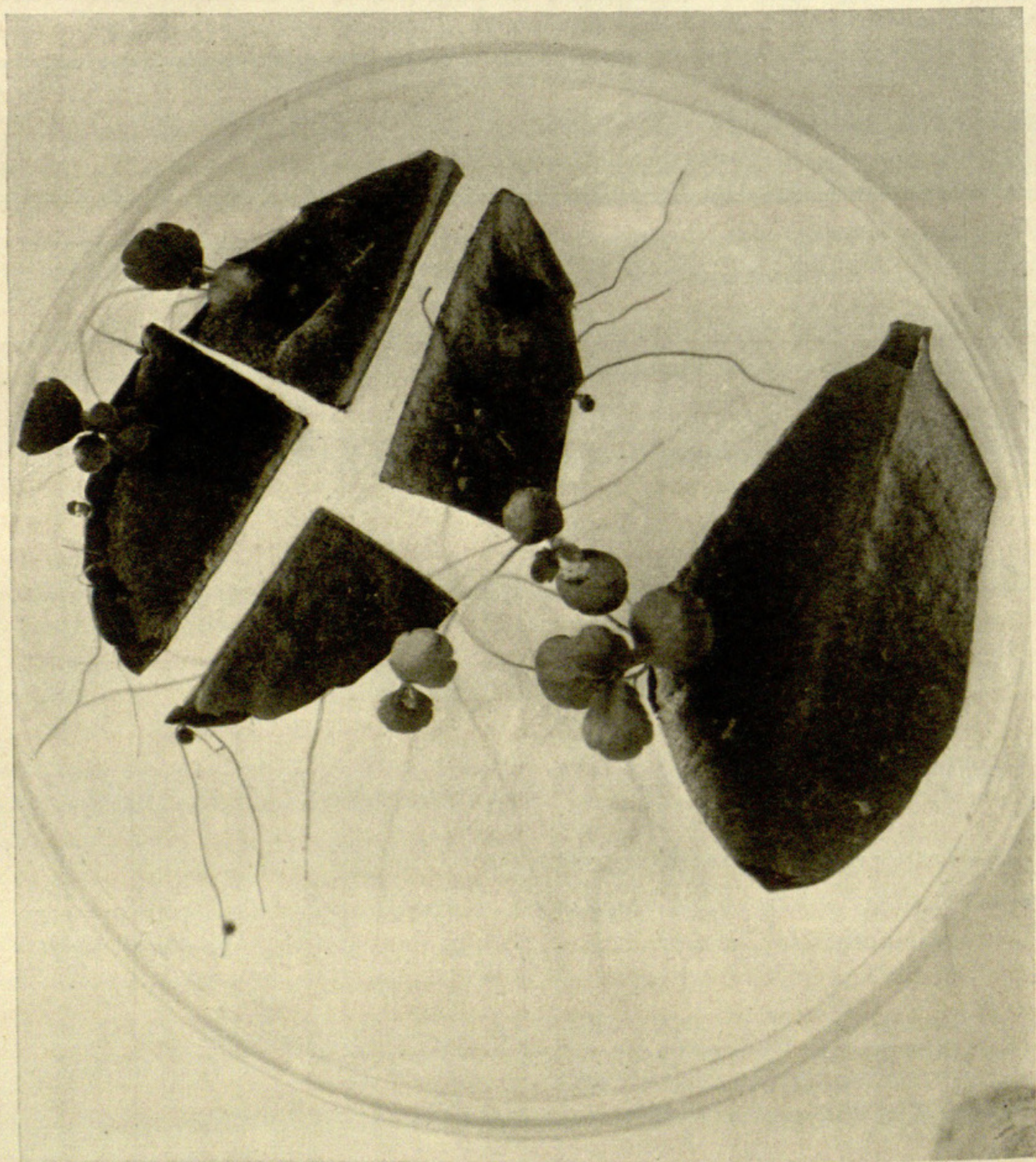each other more in these experiments than the leaves with their centers cut out.

FIG. 9.—Sister leaves: one cut into 4 pieces, other not subdivided, but all notches except one removed; from this notch a shoot is produced considerably larger than each of shoots produced from the 4 smaller pieces of other leaf; photographed 19 days after beginning of experiment.

The shoots produced by the whole leaves and by the leaves reduced in mass, therefore, were approximately in proportion with the masses of the two sets of leaves; or in other words, each set of sister leaves produced

*approximately the same weight of shoots per gram of leaf in the same
length of time.*

When a leaf is isolated and put on moist filter paper or if it is
suspended in moist air, as a rule more than one notch grows out
into a shoot (fig. 6). This seems to indicate that the material
available for shoot formation in one leaf does not all flow easily into
one notch, so that we should expect that the material available in a
leaf might be utilized more completely if the leaf were cut into
several smaller pieces than if all the material had to go into one
shoot only. This fact is evident from the following experiment.

In one leaf the whole edge (containing the notches) with the
exception of one notch was removed (fig. 9). Such a leaf could
form only one shoot. The sister leaf was cut into 4 pieces but the
edges were left intact. These 4 pieces could form at least 4 shoots.
Fig. 9 shows such a pair of sister leaves. It was to be expected that
the total weight of the shoots formed by the 4 pieces would be
approximately equal to that of the one shoot in the sister leaf, or
exceed it slightly for the reason indicated. Table IX shows that
6 shoots produced in 6 whole leaves differed very little in weight
from the 32 shoots produced by their 6 sister leaves, each of which
was cut into 4 pieces, but that the difference was in favor of the
leaves cut into 4 pieces. The latter produced per gram leaf 93 mgm.
of shoots, the former 84 mgm. In a second set of experiments the
difference was in the same direction, but a little larger, namely
98 mgm. and 74.5 mgm. (table IX). While these experiments con-
firm the law of equal production of shoots by equal masses of leaf,
they also indicate that several shoots can consume the material
available in one leaf more quickly than if only one shoot is present.

A second complication is encountered when small pieces con-
taining one notch are cut out from a leaf (fig. 6). In this case it
may happen that when the piece is too small the notch of the small
piece may not form any shoot at all, or the growth may be materially
delayed. This is intelligible on the assumption that if the quantity
of material available falls below a certain minimum no shoot can
grow out. Fig. 10 illustrates this statement. A large and a small
piece were cut out from the same leaf, each piece containing one
notch only, the notches in each set of two pieces originally being

symmetrical. The photograph was taken 36 days after the beginning of the experiment. It will be seen that the size of the shoot varies with the size of the piece, but that some of the smallest pieces have failed to form shoots. This fact is to be considered in experiments in which one leaf is left intact and the sister leaf cut into as many pieces as there are notches. In that case it may happen that the law of equal production of shoots by equal masses of leaves

TABLE IX

SISTER LEAVES: (*a*) WHOLE LEAF, BUT ALL NOTCHES WITH EXCEPTION OF ONE REMOVED; (*b*) CUT INTO 4 PIECES, BUT NO NOTCH REMOVED; APRIL 5—APRIL 25, 1917

Sister leaves	Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots per 1 gm. of leaf
I. (*a*) Whole leaf......	1	0.1935	2.403	81
I. (*b*) 4 pieces.........	6	0.206	2.267	91
II. (*a*) Whole leaf......	1	0.110	2.234	49
II. (*b*) 4 pieces.........	6	0.105	2.431	43
III. (*a*) Whole leaf......	1	0.136	1.647	83
III. (*b*) 4 pieces.........	5	0.185	2.083	89
IV. (*a*) Whole leaf......	1	0.196	1.8325	107
IV. (*b*) 4 pieces.........	7	0.2975	2.387	125
V. (*a*) Whole leaf......	1	0.201	2.035	99
V. (*b*) 4 pieces.........	4	0.246	2.225	110
VI. (*a*) Whole leaf......	1	0.110	1.086	101
VI. (*b*) 4 pieces.........	4	0.154	1.4015	109
	Total number of shoots	Total weight of shoots	Total weight of leaves	Shoots per gm. of leaf; mgm.
Average (*a*) Whole leaves.	6	0.9465	11.237	84
Average (*b*) Cut leaves...	32	1.193	12.794	93

may not hold strictly, for two reasons: (1) some of the small pieces may not form any shoot at all or form it only too late; (2) a complication may vitiate the result in the opposite direction, namely, that the shoots formed by small pieces can use the material available for shoot formation more readily than the shoots in the whole leaves. Table XI gives the results of such an experiment on 3 pairs of sister leaves, one leaf remaining intact or cut into two symmetrical halves, while the other was cut into as many pieces as there were notches.

In spite of the enormous difference in the number of shoots in both cases, the weight of shoots produced by one gram leaf in a given time was not very different, the average being 143 mgm. of shoots in one set and 150 mgm. in the other set per gram of leaf.

The law of equal production of shoots by equal masses of leaves explains why the shoots growing out from the notches of a leaf grow the more rapidly the smaller their number. It does not explain

TABLE X

SISTER LEAVES: (*a*) WHOLE LEAF, BUT ALL NOTCHES WITH EXCEPTION OF ONE REMOVED; (*b*) CUT INTO 4 PIECES, BUT NO NOTCH REMOVED; APRIL 4—APRIL 25, 1917

Sister leaves	Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots per 1 gm. of leaf
I. {(*a*) Whole leaf......	1	0.201	2.202	90.5
{(*b*) 4 pieces.........	6	0.316	2.542	124
II. {(*a*) Whole leaf......	1	0.144	2.0325	71
{(*b*) 4 pieces.........	4	0.2335	2.3235	100.5
III. {(*a*) Whole leaf......	1	0.162	1.832	88
{(*b*) 4 pieces.........	4	0.179	1.950	92
IV. {(*a*) Whole leaf......	1	0.147	2.152	68
{(*b*) 4 pieces.........	4	0.256	2.5145	102
V. {(*a*) Whole leaf......	1	0.150	2.710	55
{(*b*) 4 pieces.........	4	0.191	2.667	72
VI. {(*a*) Whole leaf......	1	0.084	0.986	85
{(*b*) 4 pieces.........	4	0.111	1.107	100
	Total number of shoots	Total weight of shoots	Total weight of leaves	Shoots per gm. of leaf; mgm.
Average {(*a*) Whole leaves.	6	0.8889	11.915	74.5
{(*b*) Cut leaves ...	26	1.2875	13.104	98

how it happens that in an isolated leaf not all the notches grow out into shoots.

When we cut off a leaf and suspend it in moist air (the air not being completely saturated with water vapor), after some time most of the notches form roots, as the leaf in fig. 11 indicates, which was drawn 18 days after the beginning of the experiment. If there are any notches which do not form roots, they are usually found at the apex and at the base of the leaf (fig. 11). After the roots are

formed, shoots begin to grow out of the notches, and now a remark-
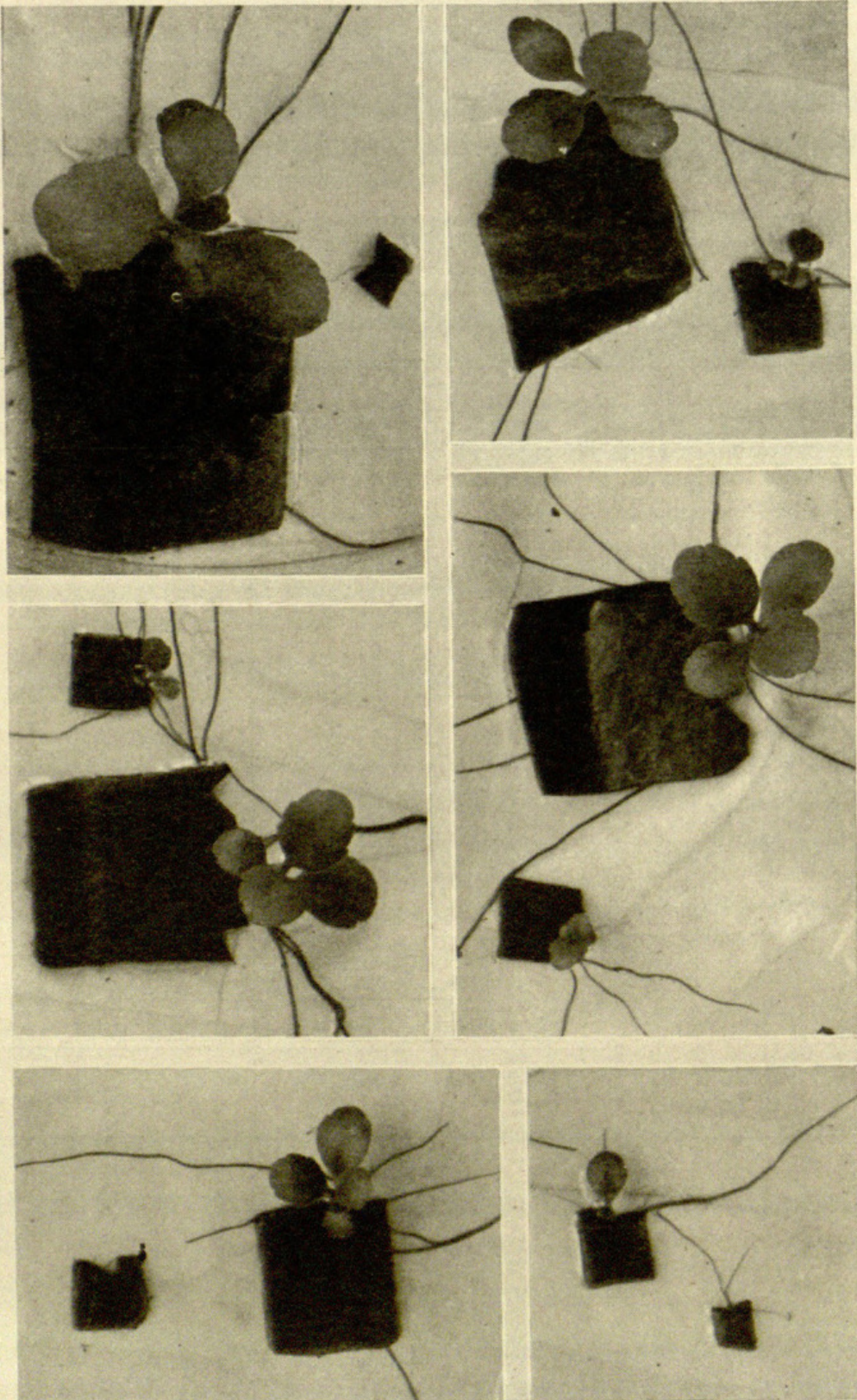able change occurs.   Fig. 12 shows the same leaf as fig. 11, 10 days

FIG. 10.—Large and very small pieces, each with one notch cut from one leaf;
smallest pieces have not yet formed shoots (in 4 weeks); parallelism between size of
leaf and size of shoot obvious.

later. Two of the shoots in the notches in the middle of the leaf have grown into shoots, and in these notches the roots have continued to grow; while the roots formed in the other notches have shriveled up and no new shoots have grown out.
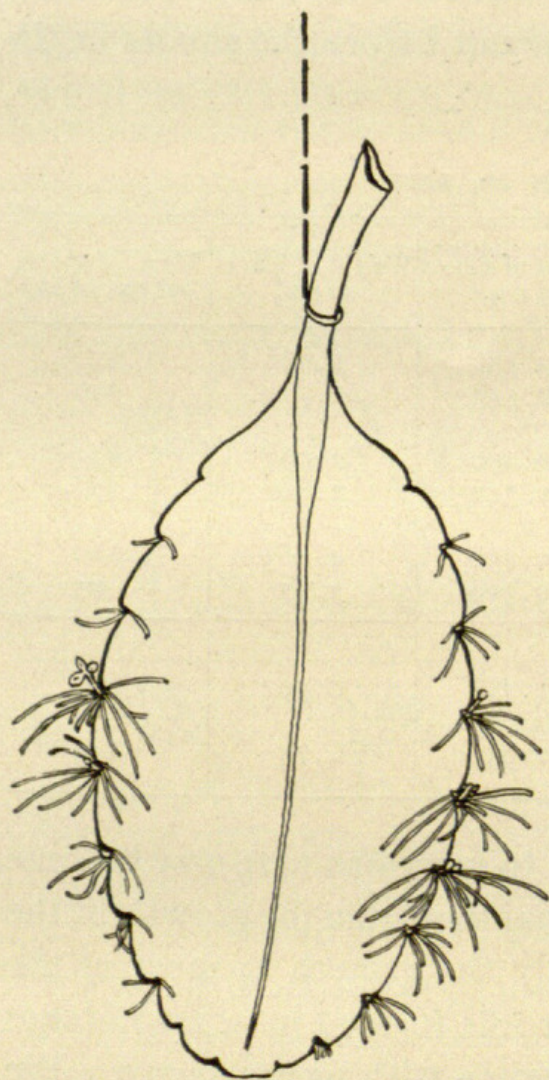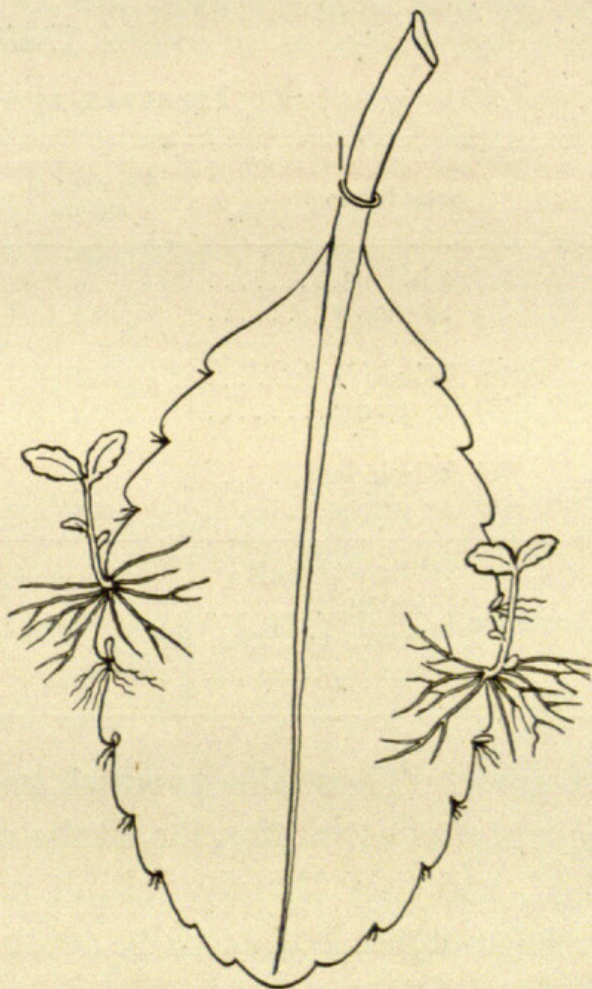
FIG. 11   FIG. 12

FIGS. 11, 12.—Same leaf suspended in moist air, in fig. 11 after 18 days, in fig. 12 after 28 days; at first all notches in middle of leaf form roots and in some of them shoots begin to develop (fig. 11); later (fig. 12) only two of these shoots in middle of leaf grow, while roots in other notches not only ceased to grow but are shriveled up; proves inhibiting effect of most rapidly growing notches on others.

From this observation, which is typical and which has been verified many times, we are inclined to draw the following conclusion. As long as the leaf is part of the normal plant, its sap flows into the stem of the plant and the notches cannot grow out. When the leaf is separated from the plant and suspended in moist air, this flow ceases and the material carried in the form of sap

remains in the leaf and becomes available for the notches. As a consequence the notches in the leaf begin to grow out. The chances for growth are apparently not equal for all the notches of a leaf suspended in moist air, but are as a rule better for those in the middle of the leaf, where the leaf is thicker and where probably more sap is available. The roots grow out before the shoots begin

TABLE XI

FEBRUARY 15—MARCH 20, 1917

Sister leaves	Number of shoots	Weight of shoots in gm.	Weight of leaves in gm.	Mgm. of shoots per gm. of leaf
I. (a) 2 halves.........	3	0.316	1.866	170
(b) 16 pieces........	14	0.345	1.727	200
II. (a) Whole leaf......	4	0.490	2.061	233
(b) 14 pieces........	14	0.312	1.810	172
III. (a) Whole leaf......	2	0.450	4.465	100
(b) 17 pieces........	15	0.300	3.17	95
Averages { Whole or half leaves.........	9	1.256	8.392	150
Leaves cut into small pieces ...	43	0.957	6.71	143

to grow. Those shoots which happen to grow out first now become a center of attraction for all the material available for growth in the leaf, and they thereby inhibit not only the growth in most of the other notches but actually cause the roots formed in other notches to dry out again, as a comparison of fig. 12 with fig. 11 shows. We cannot yet tell how it happens that the more rapidly growing leaf attracts the sap to itself.

We have mentioned that as a rule the notches which will grow out first are not the ones at the apical or basal ends, but in the middle of the leaf, where the leaf is thickest and where apparently more sap is available. That it is possibly only the quantity of water which decides the initiation of growth[8] is suggested by the fact that a leaf, like the one in fig. 12, which, when suspended in moist air forms no shoots in the apical notches, can be caused at

[8] This refers only to the initial step of starting the growth in a dormant bud; its actual growth, of course, depends upon the supply of sugar, amino acids, salts, and other solutes from the leaf.

any time to form new shoots in these notches if we let the apex dip into water. As soon as this happens these notches will form shoots and these shoots will soon equal or exceed in size the old stems, and in turn may now inhibit the growth of the latter.

The leaf in fig. 12 was drawn on January 30. On February 7 its apex was suspended in water and soon new shoots formed in the apical notches (figs. 13, 14). Fig. 13 was drawn 9 days, and fig. 14,
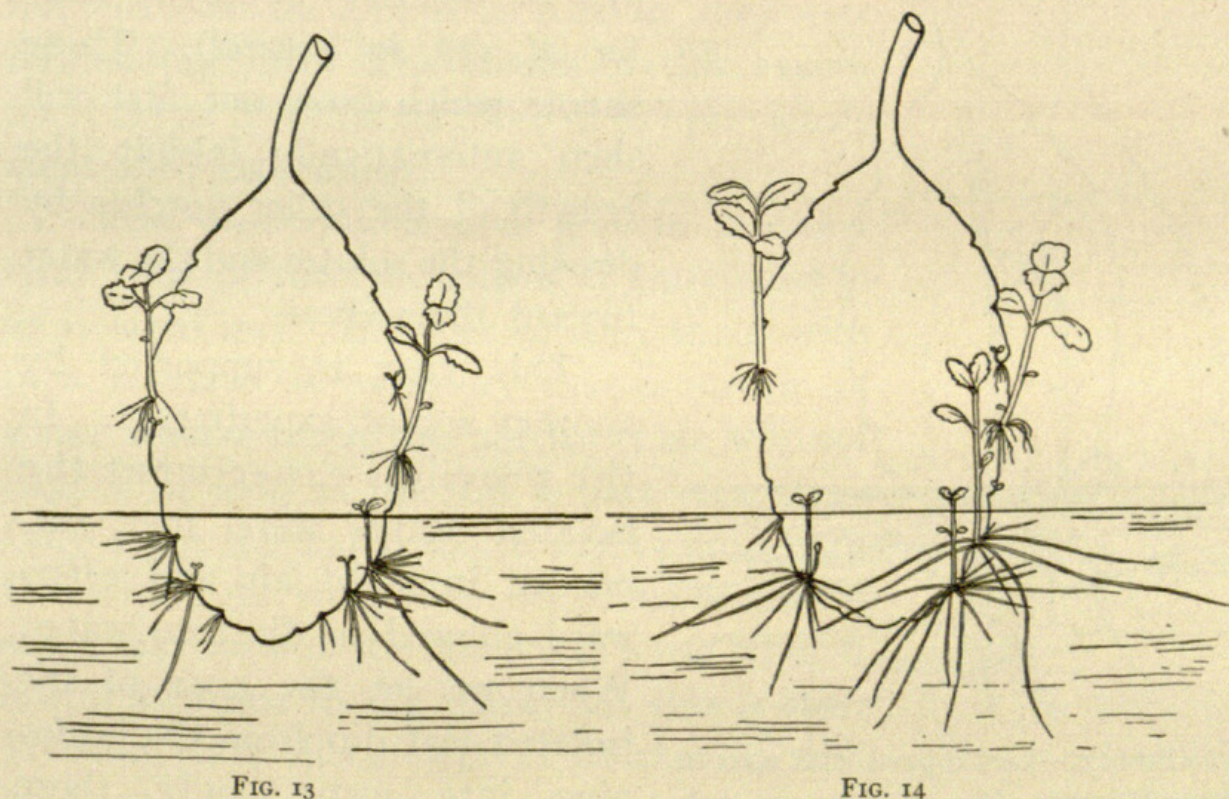

FIG. 13   FIG. 14

FIGS. 13, 14.—Same leaf as in figs. 11 and 12, after 45 and 52 days; on 33d day leaf was dipped with apex in water and now new shoots are formed in watered notches, which grow rapidly and soon reach size of two original shoots; proves that amount of water determines which notches shall grow into shoots.

16 days after the apex was put into water. It will be noticed that new shoots have grown out from three of the apical notches dipping in water. This never happened when the leaves remained in moist air. It can be shown that such a leaf when dipping in water absorbs water, and we are justified therefore in assuming that the increase in the contents of water in a notch or the starting of a current of water through the notch starts its growth.

We may compare the conditions for the initiation of the growth of a notch in a leaf to those of the growth of a seed, inasmuch as in both cases an absorption of water is necessary to initiate growth.

In both cases the water may play the rôle of accelerating the velocity of certain chemical processes which are needed for the formation of roots and shoots.

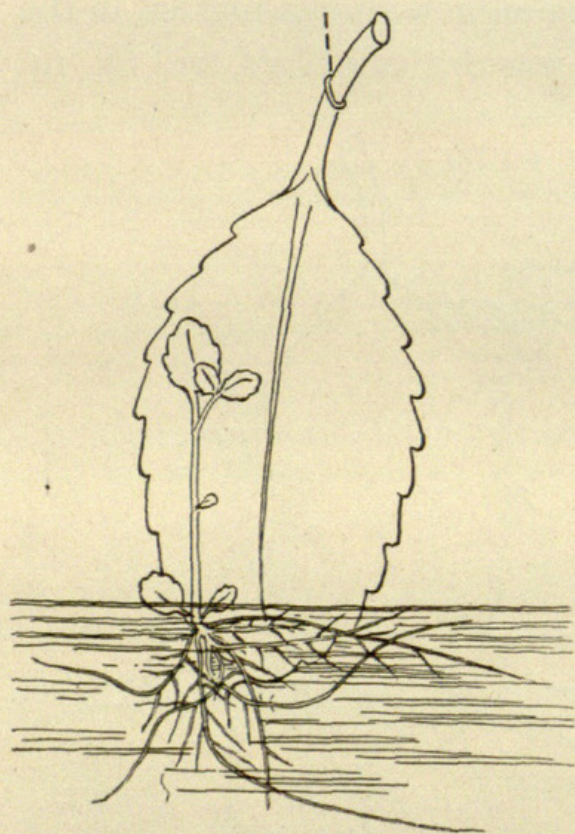The experiment just described never fails, and we may therefore say with some justification that *in an isolated leaf suspended in moist air those notches will grow out first which by chance have at first the necessary supply of water (or of sap in general).* Those shoots which grow out first will then automatically inhibit the growth of the other notches by drawing the solutes and the water toward themselves.

This view is supported by another set of experiments. In the previous experiment the isolated leaves were first suspended in moist air and afterward allowed to dip into water. When we let the apex of the isolated leaf dip from the beginning into water, only those notches will give rise to shoots which are just under the level of the water or just above it (fig. 15). Such shoots grow more rapidly than the shoots of leaves suspended entirely in moist air,

Fig. 15.—Leaf dipped with apex in water; drawn after 28 days: in such cases the shoot from one of watered notches will grow out so rapidly that as a rule it suppresses root and shoot formation in notches in middle of leaf, where growth is most rapid, when leaf is suspended in moist air, as comparison of figs. 15 and 11 will show.

and this fact also suggests that it is the quantity of water which decides which notches grow out first. It is also noticeable that when an isolated leaf dips into water from the beginning the notches in the middle of the leaf, which would have given rise to roots (fig. 11) if the leaf had been suspended entirely in air, now generally fail to do so (fig. 15), if the leaf is not too large, presumably because the greater rate of growth of the notch dipping into water inhibits the growth of roots in the rest of the notches. With the greater

rate of growth of a notch is linked a greater inhibiting power upon the growth of the other notches, inasmuch as the flow of sap is directed toward a rapidly growing notch. The leaf in fig. 15 was then taken out of water and suspended in air on February 4. No new notches grew out, as was to be expected. The rapidly growing original shoot attracted all the sap available. A few roots started in some of the notches, but shriveled up almost as soon as they were formed (fig. 16). The results of this experiment are as constant as those of the previously mentioned experiment.

These observations thus give us a rather clear view of the mechanism of correlation in an isolated leaf. In order to start the growth of a notch it is necessary that a stream of water should reach the notch. This will not happen as long as the leaf is part of a stem. Only when the leaf is old, ready to drop from the plant, do we notice occasionally that a shoot may form in the notches of a leaf while it is still attached to the plant, but this is rare. We can start the growth of notches at will, however, when the leaf is cut off. In that case that notch or those notches will grow first which happen to receive the greatest water supply (from within or without). Those which begin to grow more rapidly than the rest will automatically cause a current of sap toward themselves, in a way not yet understood.

FIG. 16.—Same leaf as fig. 15: on 33d day leaf was removed from water and suspended in moist air; rapidly growing old shoot prevents any further growth in other notches.

They thereby inhibit or retard the growth in the other notches. This inhibition can be overcome at any time by supplying more water to an inhibited notch from without, whereby we accelerate the rate of chemical reactions in this notch, which in turn will now cause a flow of sap toward itself, but we can also increase the flow of sap to certain notches from within. The writer's former observations have shown that the sap in the leaf can flow around a corner, a fact which suggests the existence of

many interlocking channels for the sap flow. It occurred to us that if we suspend such leaves in moist air with their longitudinal axes put horizontally (figs. 17, 18), the notches on the lower side of the leaf should form more shoots than the notches on the upper side, since the sap should collect in larger masses on the lower edge of the leaf. This is apparently the case, since very often shoots form only on the lower side of such a leaf, as in fig. 17 (where the notches in *a*, *b*, *c* had been removed before the experiment began). In fig. 18 three notches formed on the lower and one on the upper side. The
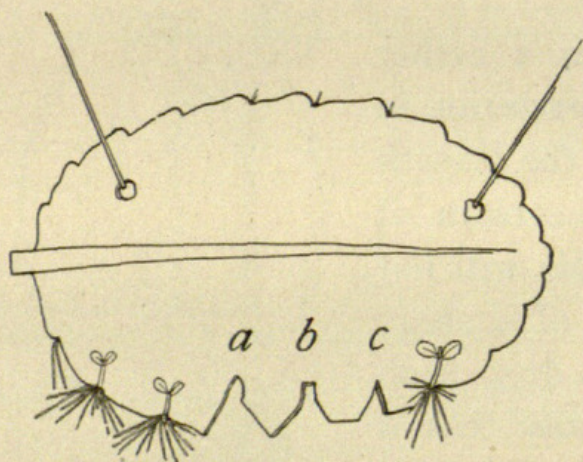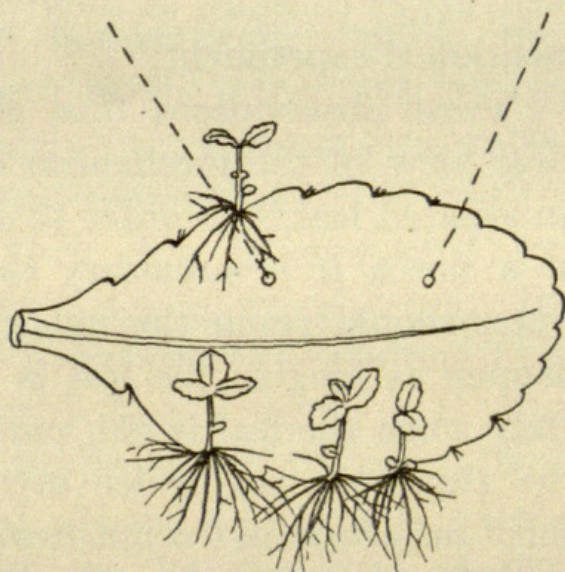
FIG. 17   FIG. 18

FIGS. 17, 18.—Leaves suspended in moist air with main axis in horizontal position: shows formation of shoots is favored on lower side, where water is bound to collect in larger masses; in fig. 17 notches at *a*, *b*, *c* had been removed.

experiment just mentioned and which has often been repeated supports the idea that the first shoots grow out where the water or sap collects, the water naturally having the tendency to flow downward.

Light is an important factor in the shoot production of the leaf of *Bryophyllum calycinum*. Isolated leaves kept in the dark produce a considerably smaller mass of shoots than their sister leaves kept in light, as the following experiment shows. Six leaves taken from different plants or nodes were suspended in the dark, either in moist air or were dipped with their apices in water; while their sister leaves were suspended in the same way but in light. Table XII shows the difference in the amount of shoot production.

It is obvious that in both cases the shoot formation is considerably greater in the light than in the dark. The experiment seems to indicate that either the process of assimilation contributes directly or indirectly to the formation of material for shoots in the leaf, or that the light in some other way contributes to the shoot formation. It is obvious that among the conditions which are to be considered in the production of equal masses of shoots by equal masses of leaves equality of illumination is of special importance. The writer observed deviations from the rule of equal production of shoots by equal masses of sister leaves when the leaves were able to partially cover or shade each other.

TABLE XII

	SHOOTS PRODUCED		WEIGHT OF LEAVES IN GM.	MGM. OF SHOOTS PRO GM. OF LEAF
	Number	Weight in gm.		
I. 6 pairs of leaves suspended in moist air				in 30 days
In dark............	3	0.016	11.65	1
In light............	24	0.543	8.03	68
II. 7 pairs of leaves dipping in water				in 26 days
In dark............	14	0.406	13.377	30
In light............	17	1.725	17.270	100

In this paper we have considered only the production of equal masses of shoots by equal masses of sister leaves of *Bryophyllum calycinum*. The law is probably correct for leaves of *Bryophyllum* in general, provided a sufficiently large number of leaves are compared, so that the influence of individual differences in the leaves (age, amount of chlorophyll, etc.) is eliminated.

It is also very probable that this form of correlative inhibition of growth is not confined to the leaf of *Bryophyllum*, but is a more general phenomenon. Thus it seems to exist in the potato, where the growth of one bud seems to inhibit the growth of other buds of the same tuber, and perhaps for reasons similar to those set forth here.

Summary

1. Equal masses of sister leaves produce approximately equal masses of shoots in equal time and under equal conditions, even if the number of shoots varies considerably.

2. Those shoots which grow out first attract automatically the material available for shoot formation, thus withholding it from the other buds; the mechanism of this automatic attraction is not yet known.

3. These two factors, the limited amount of material available for growth and the automatic attraction of the material by the buds which grow out first, explain the inhibiting effect of these buds on the growth of the other buds.

4. The relative amount of water in a notch determines which notches give rise to shoots first; by supplying a liberal water supply from without or from within we can determine at will which notches shall grow out first.

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