overcome. Sir George Savage referred to the great amount of interest he found in the old herbals in his possession, although some of them were difficult to follow. He had spent four years in a very wide country practise in Cumberland, and he recalled his indebtedness to a man who made a great many of the simpler remedies from dandelions and other plants, and saved a great deal of trouble. British bed-straw was a useful herb; in the *British Medical Journal* of forty years ago he found a note on its efficacy in certain cases. He concluded by quoting a remark of Rousseau to the effect that the field of botany had not been studied by scientists, but had been exploited by medical men who wished the public to have faith in their simples.

SPECIAL ARTICLES

THE CHEMICAL BASIS OF REGENERATION AND GEOTROPISM

1. IT is a well-known fact that in many plants after the removal of the apex some restoration of the old form is accomplished by the growth of a hitherto dormant bud near the wound. This process has been called regeneration. It is also well known that in certain fir trees the old form is restored in such a case in an apparently different way, namely by one or more of the horizontal branches next to the apex beginning to grow vertically upwards (negative geotropism). One may wonder how it can happen that the same result, namely the restoration of the old form, is accomplished in the organic world in such different ways; and it is quite natural that occurrences of this kind should suggest to one not a mechanist the conception of mystic forces acting inside or outside the living organism towards a definite purpose, in this case the restoration of the lost apex. The writer pointed out not long ago that both phenomena, the restoration of form of a mutilated organism by geotropic bending as well as by the growing out of hitherto dormant buds may be caused by one and the same agency; namely the collection of certain chemical substances near the wound.[1] New experiments which the writer has since made seem to prove this idea to be correct.

2. In a previous paper the writer had shown that when an isolated piece of stem of *Bryophyllum calycinum,* from 10 to 15 cm. long, with one leaf attached to its apical end, is put in a horizontal position the stem will gradually bend and assume the shape of a U, with the concave side upwards and that this bending is due to the active growth of a certain layer of cells in the cortex on the lower side of the stem. When the same experiment is made with stems without a leaf attached some geotropic bending of the stem still occurs, but at a much slower rate. From this observation the writer drew the conclusion that the leaf furnishes material to the stem which causes the growth of the cortex of the lower side of the stem, resulting in the subsquent geotropic bending of the stem.[2] The leaf forces this material into that part of the stem which is situated more basally than the leaf; since the part of the stem situated in front of a leaf does as a rule not show any geotropic bending. The fact that the growth leading to the geotropic curvature takes place in the cells of the lower side of a horizontally placed stem indicates that the material causing the growth collects on the lower side of the stem, which appears quite natural, since this material is a liquid, possibly containing some solid particles in suspension. A slight leakage of sap from the conducting vessels might be sufficient to account for such an accumulation of material on the under side of a horizontally placed stem.

3. Since the publication of these observations on geotropism in *Bryophyllum* the writer has been able to show that the mass of shoots which an isolated leaf can produce from its notches is a function of the mass of the leaf and that sister leaves of equal size when isolated from the stem produce equal masses of shoots under equal conditions and in equal time, even if the number of shoots produced differs considerably in the two leaves. When

1 Loeb, J., SCIENCE, 1916, XLIV., 210; *Bot. Gazette,* 1917, LXIII., 25; "The Organism as a Whole," New York, 1916, p. 153.

2 *Loc. cit.*

the mass of one set of isolated leaves is reduced by cutting out pieces from their center while their isolated sister leaves remain intact the mass of shoots produced by the two sets of sister leaves varies approximately in proportion with the mass of the leaves.[3]

If it is true that the geotropic bending of a horizontally placed stem depends upon the mass of material furnished to the stem by the leaf we should expect that a reduction of the mass of the leaf would correspondingly retard the rate of geotropic bending in the stem. The writer has recently carried out such experiments and they corroborate this expectation. If two sets of stems of equal length are suspended in an aquarium, each with one leaf attached to its apical end, and if the size of the leaf is reduced in one set by cutting away pieces of the leaf, the geotropic bending takes place the more slowly the smaller the mass of the leaf. It is difficult to conceive of a more striking experiment. When the mass of the leaf is reduced to zero, the bending is extremely slow.

4. These experiments suggest that the growth of the cells of a horizontally placed stem which gives rise to the geotropic bending is accelerated by substances furnished to the stem by an apical leaf; and that these substances might be the same as those which serve for the formation of roots and shoots in the isolated leaf. If this were true, a leaf attached to a piece of stem should form a smaller mass of shoots and roots than its sister leaf entirely detached from the stem, since in the former part of the material available for shoot formation should go into the stem.

It has been known for some time that a piece of stem inhibits the shoot formation in a leaf of *Bryophyllum calycinum,* but this inhibition was attributed by former writers to an influence of roots formed on such a piece of stem. By suitable experiments it can be shown, however, that the inhibition takes place also when no roots are formed on the stem.

It seemed to the writer that the inhibiting influence of the stem on the shoot production in the leaf was due, as stated, to the absorption of material from the leaf by the stem which would have served for the growth of roots and shoots in the leaf if the latter had been detached from the stem; and that the material flowing from the leaf into the stem was causing the growth of the cells in the lower side of a horizontally placed stem, thereby giving rise to the geotropic bending of the stem (and incidentally also to the callus formation at the base of the stem). If this were true there should exist a simple quantitative relation between the inhibiting power of the stem upon shoot formation in a leaf and the increase in the mass of the stem; namely, the two quantities should be approximately equal. The writer has carried out such experiments in large numbers and found that this relation holds true, namely that a piece of stem attached to a leaf increases its weight by approximately the same amount by which the shoot production in the leaf is diminished. For these experiments the following method was adopted.

5. A piece from the stem of *Bryophyllum,* containing one node with its two leaves, is cut out from a plant and the stem split longitudinally in the middle between the two leaves, leaving one half of the stem attached to each leaf. The half stem is removed from one leaf and weighed directly. The leaf whose half stem is cut off and the leaf with a half stem still attached to it serve for the experiment. After several weeks the amount of shoots in both leaves is determined by weight and it is found that the leaf without stem had produced a larger mass of shoots than the leaf with a piece of stem attached. The latter is then removed from the leaf and weighed. It is invariably found that it has increased in weight and that this increase approximately equals the diminution in the mass of shoots in the leaf under the influence of the stem. The following may serve as an example.

Three sets of experiments were made simultaneously on 6, 7 and 7 pairs of sister leaves prepared in the way described above; one leaf was without stem and the other with one half of the split stem. The three experiments dif-

[3] Loeb, J., Science, 1917, XLV., 436; *Bot. Gazette,* 1917 (in print).

fered in regard to the length of the stem, which was in the three experiments 2 (*A*), 1 (*B*) and 0.5 cm. (C), respectively. The leaves dipped with their apices in water. The results are given in Table I. In this table we call the difference in the mass of shoots produced in the leaves *without* and *with* stems the inhibiting action of the stem. This quantity should equal approximately the sum of the mass of shoots produced in the axil of the leaf attached to the stem plus the increase in weight of the stem attached to the leaf during the duration of the experiment. The ratio of the two values should therefore approximately equal 1 (Table I.).

TABLE I

DURATION OF EXPERIMENT 23 DAYS

	Shoots Produced by Leaves		Shoots Produced by Stem		Increase in Weight of Stems, Gm.	Inhibiting Action of Stem / Increase in Weight of Stems (Including Weight of Shoots Produced by Stem)
	Number	Weight, Gm.	Number	Weight, Gm.		
Experiment A. Length of stem 2 cm. 6 pairs of sister leaves from the same plant.						
Leaves without stems......	17	1.396				
Leaves with stems..........	5	0.266	5	0.454	0.888	$\frac{1.130}{1.342}$
Experiment B. Length of stem 1 cm. 7 pairs of sister leaves from the same plant.						
Leaves without stems.......	19	1.606				
Leaves with stems..........	13	0.823	4	0.335	0.400	$\frac{0.783}{0.735}$
Experiment C. Length of stem 0.5 cm. 7 pairs of sister leaves from the same plant.						
Leaves without stems......	15	1.006				
Leaves with stems..........	12	0.464	4	0.105	0.289	$\frac{0.542}{0.394}$

The experiments show that within the limit of error the mass of the stem increased in such a way as to approximately equal the inhibiting effect of the stem on shoot production in the notches of the leaf. The mass of roots produced in the leaves is neglected since it is small compared with the mass of stems.

It is almost impossible to split the living stem so perfectly that the two pieces are absolutely equal and in this way an error creeps in which can only be eliminated by a large number of experiments. In 19 different sets of experiments the leaves *without* stems produced 27.898 grams of shoots and the leaves *with* stems 9.797 grams. The inhibiting action of the stems, *i. e.*, the difference in shoot production between the leaves *without* stems and their sister leaves *with* stems was therefore 18.101 grams. According to our theory the weight of the stems which were left attached to the leaves should have increased by the same amount. The actual increase in the weight of the half stems attached to the one set of leaves was in the same time 16.695 grams. This includes the increase due to shoot production in the axil of the leaf, which was slight, amounting in all to less than 1.5 grams. The two values, 18.101 and 16.695 differ by 8.5 per cent.

It seems, therefore, probable that the inhibiting effect of the stem upon the mass of shoots produced in the leaves is due to the absorption of a corresponding quantity of material from the leaves by the stem.

6. *Summary and Conclusions.*—(1) The writer had shown in a former note that the mass of shoots produced in isolated sister leaves of *Bryophyllum calycinum* is in direct proportion to the masses of the leaves and that this remains true if the mass of one leaf is reduced by cutting out pieces from the center of the leaf, while the sister leaf remains intact. In this paper it is shown that the rate of geotropic bending of horizontally placed stems of *Bryophyllum calycium,* if one apical leaf is attached to the stem, occurs at a rate increasing with the mass of the leaf. When the mass of the leaf is diminished by cutting away pieces the rate of geotropic bending is diminished also.

(2) It had been known for a long time that when a piece of stem is attached to a leaf of *Bryophyllum calycinum* the shoot production in the latter is diminished or completely inhibited. It is shown in this paper that the mass of a piece of stem attached to a leaf increases by approximately the same amount by which the shoot production in the leaf is diminished through the influence of the stem. The inference is drawn that the inhibiting effect of the stem upon shoot production in the leaf is due to the fact that the same material which would have been available for shoot production in the leaf, had the latter been detached from the stem, is now absorbed by the stem.

(3) This material gives rise in the stem to callus formation and to that growth of certain cells of the cortex which causes the geotropic bending; and if the buds of the stem are not removed it causes also shoot production on the stem. The comparatively large masses involved indicate that this material must consist chiefly of the common material required for growth, *i. e.,* water, sugars, amino acids, salts; but the accessory substances and the hypothetical specific organ-forming substances of Sachs may be included in this mass; and this is suggested by the fact that on the lower side of a horizontally placed stem, roots grow out, while shoots grow out from the upper side. There must, therefore, be associated with the material which causes geotropic bending also something which favors the growth of roots and this may be one of the hypothetical substances of Sachs.

(4) These facts give a simple explanation of the "resourcefulness" of the organism referred to in the beginning of this paper, namely that plants may restore their lost apex either by the growth of the hitherto dormant buds near the wound or by a geotropic bending of former horizontal branches next to the wound (fir trees). Our experiments suggest that the cause is the same in both cases, namely, a mass action of the nutritive, and possibly also of some specific substances, upon the cells of dormant buds or upon the cells of the lower side of horizontal branches which leads to a rapid synthesis and growth in these cells. Without the removal of the old apex this growth would not have taken place, for the simple reason that the nutritive material would have had no chance to collect near the wound in masses sufficient for the growth.

(5) The phenomena of geotropism thus turn out to be phenomena of mass action, probably of the common nutritive material circulating in the sap and they are apparently of the same nature as the growth of dormant buds, which is also due to a mass action of the same substances. Gravity need play only a passive rôle, allowing masses of liquids to "seek their level." In the literature of geotropism this phenomenon is treated as a case of "stimulation," but this treatment misses the essential point, namely, the chemical mass action involved, and it substitutes a fictitious factor, the "stimulus" of gravitation, which in all probability does not exist. The case is similar to that of heliotropism when the orientation of animals to light is treated as a "reaction to a stimulus" instead of as an instance of the photochemical law of Bunsen and Roscoe.

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