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Correlative Growth of Lateral Bud in *Ipomoea Batatas* Shoot[1)]

By

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The phenomenon of apical dominance has long been studied by many investigators, but the mechanisms involved are still in dispute. The author has been studying for years the correlative inhibition of lateral bud growth using young shoots of *Ipomoea Batatas* LAM. This material is very useful because sufficient number of uniform cuttings can be easily obtained, cuttings are healthy without fail during the experimental period and bud growth is uniform among cuttings in an experimental set. However, determination of auxin content of tissues is difficult because of the latex.

In his recent review on correlations AUDUS (1) distinguished three phases in the bud growth, namely, phases of bud initiation, determination of bud structure and bud expansion. The investigation reported in the present paper, as well as in the preceding ones (5, 6 and 7), is concerned with the last phase. As actively growing part of shoot excised from the rest was used and adult leaves which might send out food factors were removed when such nodes were included in the experimental cutting, correlative growth relationships could be observed apparently in many experiments. It will be stressed in this paper that auxin inhibits lateral buds indirectly through activating the growth of other tissues, while it may also inhibit them directly. It will be shown that one or the other way of bud inhibition may be prominent according to cases. The paper, however, will not deal with mechanisms of the direct bud inhibiting action of auxin.

The author wishes to thank Professor Joji ASHIDA for his guidance and criticism.

Material and Methods

Cuttings of young growing stems of sweet potato plant (*Ipomoea Batatas*, var. Norin No. 1) were used throughout the experiments. The age of node

1) This work was aided by the Grant in Aid for Fundamental Scientific Research of the Ministry of Education.

will be represented as follows: the lowermost (oldest) node bearing a leaf the blade of which is yet folded is named A1, younger nodes being called A2, A3, ..., successively towards the apex. The node that bears the youngest expanded leaf is named B1, and older nodes are numbered B2, B3, ..., successively towards the base. Leaves and lateral buds are named according to the nodes which bear them.

Materials were selected so as to be as uniform as possible and cuttings were prepared immediately before every experiment.

The basal end of stem piece was put in a salts solution, as in the experiments reported previously (5). Unless stated otherwise, the cut surfaces of stem and petiole to be exposed to air were smeared with unhydrous pure lanolin to prevent loss of water from them. For the experiments using rooted cuttings, slips 25 cm in length were planted in pots with the two basal nodes burried in the soil. They were used for experiments after eleven to twenty days when they had taken roots. Unless stated otherwise, cuttings were placed about 1.5 m apart from a large south window of a room, the direct sunlight being avoided. In the experiments in the dark, cuttings were kept in a cabinet.

The length of lateral buds was measured at the beginning and at the end of experiment, and the number of leaves which had expanded on them during the experimental period was counted. The dry weight of lateral buds was determined by excising and drying them at 98°C.

The growth regulators used were β-indoleacetic acid (hereafter referred to as IAA), α-naphthaleneacetic acid (NAA), 2, 4-dichlorophenoxyacetic acid (2, 4-D), 2, 3, 5-triiodobenzoic acid (TIBA), gibberellin (GB) (a mixture of 55.6% A_1 and 28.6% A_3) and kinetin. They were applied as lanolin pastes smeared, according to cases, over the apical cut surface of stem or petiole, around the stem or petiole forming a collar about 2 mm broad, or over the lateral bud itself. The concentration of pastes will be given by weight percentage of unhydrous lanolin. Other procedures are to be referred to the previous reports (5, 7).

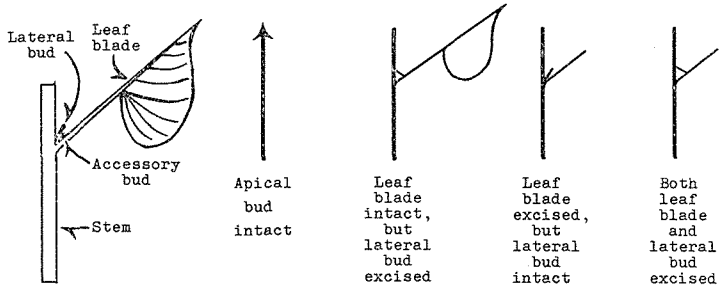


Fig. 1. Diagrams to represent the presence and absence of the apical bud, the lateral bud and the leaf blade in the following tables. In cuttings having more than one node, petioles and lateral buds will be drawn as if they are arranged in a 1/2 phylotaxy, instead of 2/5.

Conditions of cuttings at the beginning of experiment will be shown diagrammatically in tables in the manner as illustrated in Fig. 1.

Results

A. *General pattern of lateral bud inhibition.*

At the outset of the investigation, an experiment was made in order to compare the inhibiting effects of the apical bud and young developing leaves on the growth of the lateral bud standing on the lowest node.

Fourteen cm long shoot cuttings which had B1-node as their oldest node were prepared. The leaf blade of B1 and the lateral buds standing on the nodes of A1 and younger were cut off. The cuttings were divided into four groups according to the presence or absence of the apical bud and the young leaves (A1–A3), as shown in Table 1. The apical bud as meant here held the apical meristem and the leaf blade shorter than 5 mm at the beginning of experiment.

Table 1. Inhibiting effect of the apical bud and upper young leaves (A1–A3) exhibited on the growth of lateral bud of B1. Beginning on Aug. 2, measured after 8 days. Mean of 5 samples.

	(I)	(II)	(III)	(IV)
Apical bud → A3 → A2 → A1 → B1 →				
Elongation of B1 lateral bud (mm)	17.4	2.6	0.4	0.2
Ratio	*100*	*15*	*2*	*1*
Dry weight of B1 lateral bud (mg)	17.7	1.2	0.6	0.6
Ratio	*100*	*7*	*3*	*3*
No. leaves unfolding on B1 lateral bud	1.0	0	0	0
No. leaves unfolding on stem	——	——	2.4	1.4

A representative set of results is depicted in Table 1. In the control cuttings (I in Table 1) which had none of the apical bud and young developing leaves, the lateral bud of B1-node elongated 17.4 mm and let one new leaf

expand on it in eight days. The apical bud (II) and the three young leaves (III) strongly inhibited the lower lateral bud, the inhibiting effect of the former being weaker than that of the latter. The inhibition was strengthened by the presence of the two together (IV).

Since the number of the leaves which expanded on the stem during the course of the experiment was 2.4 in group III and 1.4 in group IV, the apical bud seems to inhibit also the development of young leaves.

B. *Experiments with single-node cuttings.*

It was demonstrated in the foregoing experiment that young leaves as well as the apical bud inhibit the growth of a lateral bud. In the following experiments, single-node cuttings were used in order to simplify the relationship between leaf and lateral bud.

a) *A young growing leaf inhibits the growth of its axillary bud, while a fully expanded leaf promotes it.*

An experiment was undertaken in order to see if a leaf inhibits its axillary bud, and if the inhibiting effect differs according to the age of the node used.

Single-node cuttings were prepared with the nodes from A2 to B3. Stems were excised for a length of 4 cm in the cuttings of from B1 to B3, but 3 cm in A1 and 2 cm in A2 as internodes were not long enough in these very young parts. Cuttings of each age were grouped into two, one bearing the leaf blade and the other debladed at the distal end of petiole. All were kept standing in diffuse light for eleven days.

Table 2. Differential effect of a leaf exhibited on the growth of its axillary bud according to the age of the node in single-node cuttings. Beginning on Aug. 4, measured after 11 days. Mean of 5 samples.

Age of node	A2		A1		B1		B2		B3	
Leaf blade*	−	+	−	+	−	+	−	+	−	+
Elongation of bud (mm)	3.8	0.6	8.2	2.2	14.2	10.0	14.5	23.2	14.8	28.0
Ratio	*100*	*16*	*100*	*27*	*100*	*70*	*100*	*160*	*100*	*189*
No. leaves unfolding on lateral bud	0.2	0	1.2	0	1.4	0	1.4	1.0	1.4	1.4

*) + : Leaf blade present, − : debladed.

The results summarized in Table 2 indicate that the leaf-blade inhibits the growth of the axillary bud in B1 and the nodes younger than this, while it promotes in B2 and B3. The leaf-blade seems to have two kinds of effect on the growth of its axillary bud, inhibiting and promoting. And the result may be expressed in either way: the younger the node, the stronger the inhibition by the leaf; or, the younger the node, the less the promotion by the leaf.

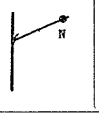
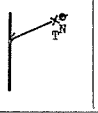
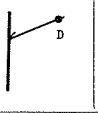
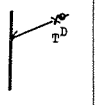
b) *Bud inhibiting effect of leaf can be replaced by IAA, NAA and 2, 4-D.*

The author (5) has reported that IAA applied in place of a leaf-blade inhibits the growth of the lateral bud to the same extent as the blade and the inhibition by IAA is reversed to some extent by TIBA applied at the middle part of the petiole. And he has reached a conclusion (6) that the reversion of bud inhibition by TIBA is due to an inhibition of IAA translocation. Recently, according to the experiments using IAA-C^{14}, VARDAR (18) suspected the blocking effect of TIBA on auxin or IAA translocation, but unpublished results accumulated by the present author are confirming that auxin, at least in its active form, cannot pass the site of TIBA treatment and increases the growth of the apical portion of the petiole.

An experiment was performed in order to see if synthetic growth regulators other than IAA also exert a similar inhibition on bud growth and if the inhibition, if any, is reversed by TIBA as in the case of IAA.

Single-node cuttings of B1, 8 cm long, were debladed at the distal end of petiole. Around the petiole, close to the distal end, 0.1% lanolin paste of NAA or 2, 4-D was smeared in a ring form. Two per cent paste of TIBA was further applied to an adjacent proximal part of the petiole in a half number each of NAA and 2, 4-D cuttings. Thus five groups were prepared including control (I to V in Table 3).

Table 3. Effect on the growth of lateral bud of NAA, 2, 4-D and TIBA applied as lanolin pastes smeared around the petiole near the cut end. Node B1. ●N, ●D and ×T indicate the application sites of pastes of NAA, 2, 4-D and TIBA, respectively. Beginning on Sept. 22, measured after 6 days. Mean of 5 samples.

	(I)	(II)	(III)	(IV)	(V)
					
Elongation of bud (mm)	15.2	5.0	13.2	7.2	13.0
Ratio	*100*	*33*	*87*	*47*	*86*
Dry weight of bud (mg)	12.1	1.5	10.2	2.6	9.9
Ratio	*100*	*12*	*84*	*21*	*82*
No. leaves unfolding on lateral bud	1.4	0	0.4	0	1.2
Elongation of petiole (%)	9	119	13	96	29

The results summarized in Table 3 are the same in the general trend as in the case of IAA (I, V and VI in Table 1 in the previous report (6)). NAA and 2, 4-D inhibited the bud growth (II and IV in Table 3), as reported by WICKSON and THIMANN (20), and TIBA applied on the proximal side of auxin reversed the inhibition (III and V).

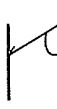
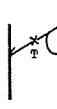
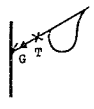
NAA and 2, 4-D promoted the elongation of petiole remarkably, and their effect was reversed by TIBA. Percentage elongation of petiole was a little larger in the TIBA-treated ones (III and V) than in the control (I), largely owing to the elongation of the part of petiole between the auxin-paste and TIBA-paste. In petiole, therefore, it seems that TIBA does not move significantly to the acropetal direction and that it blocks the basipetal translocation of auxin as reported before (5, 6).

c) *Gibberellin applied to petiole inhibits the growth of its axillary bud.*

In the course of studies attention was paid to the growth of petiole, and it was found that GB cannot produce its growth-promoting effect unless the tissue contains auxin, natural or exogenously supplied (7). Presented here are the results concerning the bud growth observed in some of the experiments described in that paper.

The treatments may be apprehended by the schema in Tables 4 and 5. For detailed description of the experiments, refer to the previous report (7).

Table 4. Effect of GB and TIBA on the growth of lateral bud and of petiole. ▲G and ×T indicate the application sites of pastes of GB and TIBA, respectively. Node A1. The cuttings were kept in the dark during the experimental period, Sept. 18–25. Mean of 5 samples.

	(I)	(II)	(III)	(IV)	(V)
					
Elongation of bud (mm)	7.4	1.6	7.8	1.0	6.2
Ratio	*100*	*22*	*105*	*14*	*84*
Dry weight of bud (mg)	2.5	0.9	2.8	0.8	2.1
Ratio	*100*	*36*	*112*	*32*	*84*
Elongation of petiole (%)	7	91	50	134	56

It is seen in Table 4 that the leaf blade inhibited the axillary bud strongly (II), and the inhibition was reversed completely by TIBA (III), just as reported previously (6). When GB was applied to the petiole (IV), bud growth was

inhibited more strongly than without it (II). And TIBA reversed the inhibition (V).

The growth of bud appears to be correlated negatively with the elongation of petiole. It thus may be concluded that the factor of compensatory growth exercises a remarkable effect on the growth of bud, as concluded previously (6).

Table 5. Effect of GB and TIBA on the growth of lateral bud and of petiole. ●I, ▲G and ×T indicate the application sites of pastes of IAA, GB and TIBA, respectively. Node A1. Beginning on Sept. 19, measured after 8 days. Mean of 5 samples.

	(I)	(II)	(III)	(IV)	(V)
					
Elongation of bud (mm)	9.0	4.0	6.6	2.4	5.4
Ratio	*100*	*44*	*73*	*27*	*60*
Dry weight of bud (mg)	4.8	1.8	2.6	1.0	1.8
Ratio	*100*	*38*	*54*	*21*	*38*
No. leaves unfolding on lateral bud	0.6	0	0	0	0
Elongation of petiole (%)	7	52	28	114	40

Table 5 shows the result of a similar experiment in which 0.1% IAA-paste substituted the leaf blade. The general trend was the same as in Table 4, although the bud inhibition and petiole elongation are less in the present case. The photograph showing a representative set of cuttings is presented in Fig. 5 in the previous report (7).

GB thus can reduce the bud growth while it promotes the growth of other tissues.

d) *The more distal the site of IAA application, the stronger the bud inhibition.*

Stem cuttings bearing A1-node, 5 cm long, were debladed at the distal end of petiole. The petiole was smeared with 0.1% IAA-paste in a ring form near the distal end, at the middle or near the base, as illustrated in Table 6. The growth of bud and petiole was observed after nine days.

The results are summarized in Table 6. Both the bud growth inhibition and the petiole elongation were the largest when IAA was applied near the distal end of petiole (II), and the smallest when it was applied near the base (IV). The elongation of petiole was mainly located in the part between the

Table 6. Effect of site of IAA application on the growth of lateral bud. Node A1. ◉I indicates the site of IAA application. Beginning on Sept. 4, measured after 9 days. Mean of 5 samples.

	(I)	(II)	(III)	(IV)
				
Elongation of bud (mm)	12.6	3.2	5.2	5.6
Ratio	*100*	*25*	*41*	*45*
Dry weight of bud (mg)	9.0	1.2	2.1	2.8
Ratio	*100*	*13*	*23*	*31*
No. leaves unfolding on lateral bud	1.2	0	0	0.2
Elongation of petiole: (%)				
Apical half	10	77	29	15
Basal half	6	62	65	36
Entire petiole	8	70	47	26

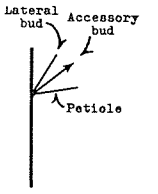
site of IAA application and the base (see Table). So that the more distal the IAA treatment, the larger the elongation of whole petiole. And the bud growth inhibition may best be explained by growth compensation.

It was reported in etiolated pea seedlings that the inhibition of lateral bud increased with the distance from the bud to the apical bud or a young growing leaf (13) and to IAA applied in place of the apical bud (19). If attention had been paid to the stem growth in these experiments, the bud growth might have been found to be negatively correlated with it.

e) *Accessory bud can be inhibited in several ways.*

In normal sweet potato plants, an accessory bud becomes apparent at A1-node, but it grows hardly any more. An experiment was tried to see the relationship between an accessory bud and the other organs, stem, leaf and lateral bud. Stem cuttings, 6 cm long, of B3-node were debladed and kept standing in a nutrient solution as usual for two days. In the meantime, the lateral bud elongated to about 15 mm long while accessory bud was only about 0.5 mm. The lateral bud was decapitated leaving 10 mm of its axis. The cut surfaces of the stem and petiole were renewed, and 0.1% IAA-paste was smeared on the cut surface of the stem, the petiole or the lateral bud (see Table 7).

Table 7. Inhibition of growth of accessory bud by IAA applied on the cut ends of stem, petiole and lateral bud. Node B3. The lateral buds were decapitated after 2 days of their growth, and all the IAA treatments were made simultaneously on Aug. 31. Measured and harvested after 6 days. ●I indicates the site of IAA application. Mean of 5 samples.

	(I)	(II)	(III)	(IV)
				
Length of accessory bud (mm)	24.2	5.6	14.8	3.2
Ratio	*100*	*23*	*61*	*13*
Dry weight of accessory bud (mg)	14.4	0.8	4.2	0.4
Ratio	*100*	*6*	*29*	*3*
No. leaves unfolding on accessory bud	1.2	0	0.4	0
Fresh weight of 6mm segment of lateral bud stump (mg)	16.6	18.0	17.1	40.6
Ratio	*100*	*108*	*103*	*242*
Dry weight of 6mm segment of lateral bud stump (mg)	1.2	1.2	1.1	2.2
Ratio	*100*	*100*	*92*	*183*

On the seventh day of the treatment, the length of the accessory bud was measured, and 6 mm segments excised from the stumps of lateral buds were weighed in order to estimate the growth in thickness. The results are summarized in Table 7.

The elongation of the accessory bud was inhibited by IAA applied on the cut surfaces of lateral bud (IV), main stem (II) and petiole (III), the grade of inhibition being in the order as mentioned. On the other hand, the decapitated lateral bud grew remarkably in thickness when its cut end was smeared with IAA-paste (IV), while IAA applied on the stem and petiole had practically no effect in this respect (II and III).

Summarizing the results of the experiments so far described, it may be stated that the organ which grows actively following application of auxin can exert an inhibiting effect on the bud growth, and the bud growth is inhibited

conspicuously when much growth occurs between the bud and the site of auxin application.

f) *Glucose reverses bud-inhibiting effect of a leaf-blade.*

Cuttings with B1-nodes, 4 cm long, were divided into two groups. For one group the leaf blade was cut off at its base, while for the other the blade was left intact. The usual nutrient solution was used for a half number of each group and the nutrient solution enriched with 1% glucose was used for the rest. All the cuttings were kept standing for twelve days in the dark.

Table 8. Effect of glucose on the correlation between a leaf and a lateral bud. Node B1. Beginning on Oct. 16, measured after 12 days of darkness. Mean of 5 samples.

Culture solution	No glucose added		1% Glucose added	
Leaf blade	(I) Cut off	(II) Intact	(III) Cut off	(IV) Intact
Elongation of bud (mm)	3.8	3.0	4.0	6.8
Ratio	*100*	*79*	*105*	*179*

The results represented in Table 8 show that the lateral bud was inhibited by the leaf when glucose was not given (compare II with I), as already shown in a preceding experiment (Table 2). When the culture solution was enriched with glucose, however, the lateral bud was conspicuously promoted, instead of being inhibited, by the leaf-blade (IV), while the lateral bud of debladed cuttings grew only a little better with glucose (III) than without it (I). Hence, it is confirmed that a food factor may play a role in the correlative growth between a bud and a leaf, as proposed by the author in the previous report (6).

g) *Discussion.*

In the experiments described above, it was found that the organs which inhibited the lateral bud were actively developing ones, such as the apical bud (Table 1) and very young leaves (either leaf blade or petiole) (Tables 1, 2, 4, 5 and 6). These inhibiting organs were characterized by high auxin content, either natural or experimentally supplied.

The inhibition of bud growth came about when an organ was growing actively. In the experiment shown in Table 6, for instance, the more distal the site of IAA application on a petiole, the larger the petiole growth and the stronger the bud growth inhibition. When IAA was applied near the distal end of debladed petiole the growth was induced along its entire length, the distal half of petiole being more active in growth than the basal half. The bud inhibition, however, cannot be accounted for solely by the correlation with the petiole growth because the bud growth was only 45 per cent of control even when IAA was applied to the base of petiole. Since the growth at the basal part of petiole, in length and in thickness, could not be measured in this case, there

remains a possibility of correlative inhibition. But here a direct effect of auxin on the bud may also be taken into consideration. This point will be discussed later.

In the experiments summarized in Tables 4 and 5, GB applied to the petiole promoted its growth and heightened the bud inhibiting effect of the leaf blade or IAA given in place of it. And, in the experiment shown in Table 8, glucose reversed the bud inhibition caused by a young leaf. These results may indicate that the food factor is a factor controlling the bud inhibition in such a restricted system as single-node cuttings, especially in the young cuttings which are composed of actively growing tissues.

In the experiment summarized in Table 1, it was found that the shoot apex inhibited not only lower lateral buds but also the development of young leaves near the apex. And, when the shoot apex was cut off, young leaves grew and exerted an inhibiting effect on the bud. The results shown in Table 7 indicate that an accessory bud is inhibited when IAA is applied to the cut surface either of stem, lateral bud or petiole. Hence, it may be said that young leaves are inhibited by the apical bud, the lateral bud by the apical bud and young leaves, and the accessory bud by the apical bud, young leaves and the lateral bud.

When a principal inhibiting organ is lost, the organ which will grow most actively will become the principal inhibiting organ. This will be apparent in the experiment shown in Table 13 below.

C. *Experiments with two-node cuttings.*

In the preceding experiments, the relationship between a leaf and a bud at its axil was observed. In the next place, experiments using two-node cuttings will be reported. They were planned in order to see the effect of a bud or a leaf of a node to be exerted on the bud standing on the neighbouring node, and to see how the bud-inhibiting effect was conducted along the stem.

a) *Growth relationship between the upper and lower buds.*

Shoots including in them B4 as the oldest node were harvested and selected for uniformity. All the leaf blades not younger than A3 were cut off, and the debladed shoots were kept standing in the nutrient solution as usual. On the next day the internode between B2 and B3 nodes was cut and the cuttings which were 10 cm in length and included the two nodes, B3 and B4, were obtained. Keeping them in a dark cabinet, the lengths of the two buds were measured every day or every two days. Figure 2 shows the growth process of the two buds in seven days.

Soon after the isolation from the younger part of stem, the two buds began to elongate. But the lower bud grew more slowly than the upper one. The bud at the axil of B4 node had grown roughly as the bud of B3 if it had been on a single-node cutting. Hence, the growth of the lower bud is considered to be inhibited by the upper bud.

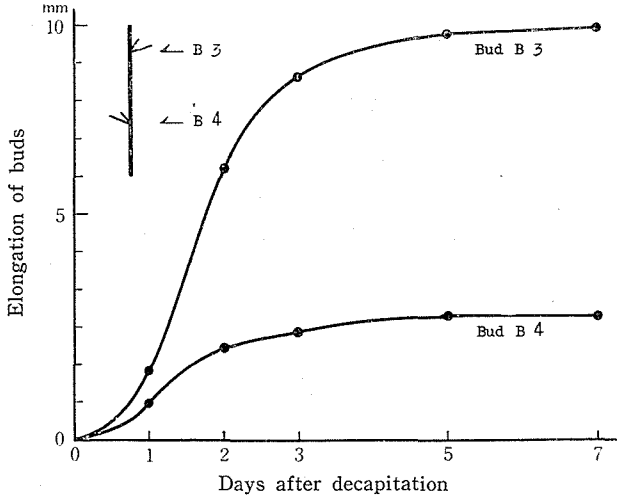


Fig. 2. Growth of the two buds of the two-node cutting in the dark. Decapitation was performed on Oct. 16. Mean of 9 samples.

b) *Inhibiting effect of a bud travels through a girdled part of the stem, but not through a scalded part.*

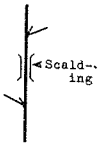
An experiment was carried out to see if the inhibiting effect of an upper lateral bud reached a lower one through a girdled or scalded portion of the stem.

Two-node cuttings, consisting of B3 and B4 nodes and 9 cm in length, were debladed and divided into the three groups, girdled, scalded and intact. A one cm stretch of stem was girdled or scalded at the middle of the internode between the two nodes. A thirty seconds' exposure to steam, jetting out from a fine glass tube, was sufficient to kill the innermost tissue of the stem. Girdled and scalded portions of stem were covered doubly with sulphate paper to prevent loss of water.

The results represented in Table 9 show that the total elongation and the total dry weight of the two buds were reduced by either girdling or scalding. However, the proportion of elongation, the upper bud to the lower one, differed conspicuously between the girdled group (86 : 14) and the scalded group (41 : 59), while it was the same between the former and the control (85 : 15). The same was true with the final dry weight of buds.

Hence the inhibiting effect of the upper bud traveled through the girdled part, but not through the scalded part. The scalding appears to separate the cutting into two portions which are independent of each other with respect to growth regulators and nutrients, except water and probably minerals.

Table 9. Effect of girdling and scalding on the interaction between the upper and the lower buds. A 1 cm stretch at the middle of internode was girdled or scalded. Treated on Sept. 6, measured after 8 days. Mean of 5 samples.

	(I)		(II)		(III)	
B3 → B4 →						
	B3	B4	B3	B4	B3	B4
Elongation of bud (mm)	23.4	4.0	16.0	2.6	9.4	13.8
» B3+B4 (mm)	27.2		18.6		23.2	
Ratio	*85* :	*15*	*86* :	*14*	*41* :	*59*
Dry weight of bud (mg)	27.6	1.2	20.9	0.8	7.4	14.1
» B3+B4 (mg)	28.8		21.7		21.5	
Ratio	*96* :	*4*	*96* :	*4*	*34* :	*66*
No. leaves unfolding on lateral bud	1.6	0	2.2	0	0.7	1.4

Snow has obtained similar results using *Phaseolus multiflorus* as to girdling and *Vicia Faba* as to scalding (12).

c) *Inhibiting effect of a leaf or IAA travels in acropetal as well as basipetal direction in the stem.*

In the experiment shown in Table 2, the leaf of A1 node strongly inhibited the growth of the bud at its axil. The experiments to be described here were carried out to see the effect of A1 leaf on the growth of lateral buds standing on the neighbouring nodes.

The two types of two-node cuttings, A2–A1 and A1–B1, were prepared. Buds and leaf blades were excised as illustrated in Fig. 3, in which the results obtained were also represented. Since all the cuttings of an experimental set were kept under the same conditions and since the bud growth is represented in percentage of the control specific to each, the effects of leaf blade and IAA may be compared with one another.

The young leaf, A1, inhibited the growth of the bud (A2) above it, although the inhibition was not so large as on the lower bud (B1). The inhibiting effect on the bud at its own axil situated midway between the upward and the downward effects. The same pattern of bud inhibition was observed also when 0.1% IAA-paste was given in place of A1 leaf blade, though the inhibition was weaker than in the above case.

Upward translocation of the inhibiting effect was reported also by Snow (14) and Libbert (8).

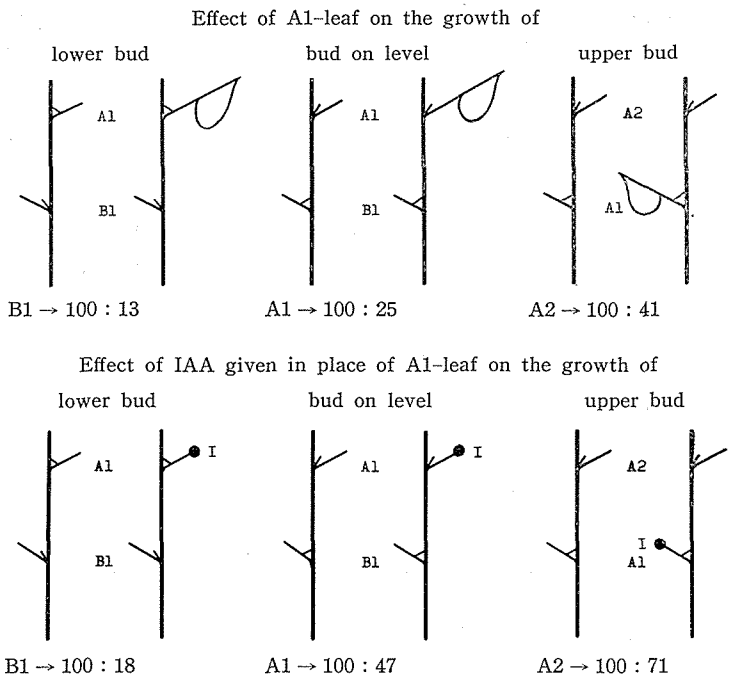


Fig. 3. Effect of A1-leaf, as well as of IAA given in place of it, on growth of the bud standing on the lower, the same and the upper nodes in two-node cuttings. Elongation of bud is expressed in percentage of respective control for each case. Mean of 2 to 7 experiments performed under the same conditions. ●I indicates the site of IAA application.

d) *Discussion.*

The experiment illustrated in Fig. 2 indicated that both the upper and the lower buds began growing soon after the shoot apex was removed, and the dominance of the upper bud increased then. It may be difficult to explain how the upper bud becomes dominating when the two buds begin growing at the same time. Since, however, the upward inhibiting effect of a leaf or IAA was weaker than the downward one in the preceding experiment (Fig. 3), the same relationship may have been present between the two buds. This relationship may elucidate the dominance of the upper bud.

The polarity, which is not absolute, in the transmission of inhibitory effect shown in Fig. 3 may be ascribed to a corresponding polarity in auxin translocation, though the upward movement of auxin has not been examined directly. The effect of correlative growth should also be taken in consideration, since the growth capacity of tissues is larger in the upper part of the cutting.

The results shown in Table 9 indicate that the bud-inhibiting effect is

transmitted downward through the living tissues remaining in the girdled part of stem, but not through dead ones. Using *Phaseolus* SNOW (12) found that the inhibiting effect of the apical bud crossed the cut surface of tissue, and concluded for the first time that a diffusible substance is responsible for the effect. HARVEY (4), on the other hand, observed that the inhibiting effect did not pass through a steam-killed stretch of the stem of *Phaseolus*. So that the effect of scalding observed does not seem to be restricted to the sweet potato stem. When LIBBERT (8), using *Pisum* seedling, replaced an excised shoot apex on the stump, laterals were inhibited again when the tissue connection was reestablished.

D. *Experiments with rooted cuttings.*

The experiments described so far were conducted using rootless cuttings. At the close of experimental period, callus had been formed at their basal end and, when they carried leaf blade or were treated with IAA, several roots had appeared on them. When, on the other hand, cuttings which had already rooted in the soil were used for experiments, they looked more healthy than the rootless ones throughout the experimental period. Buds grew larger than the latter during an experiment, perhaps partly because of richer food factor.

Experiments using rooted cuttings will be described below. It may be considered that physiological conditions of plants under experiment were better than in unrooted material.

a) *Effect of the site of gibberellin application on the bud growth.*

Cuttings, 25 cm long, were planted in pots, five in each, so that the two basal nodes might be in the soil. After eleven days in a glass house the leaf blade of the third oldest node above the soil surface was in the state of A1. The cuttings were well rooted. In four of five pots the apical part of plants was removed by cutting at the middle of the internode between A1 and A2 (I to IV in Table 10). All the leaf blades and the lateral buds on the nodes, B1 and B2, were excised. Then as illustrated in Table 10, 0.5% GB-pastes were smeared on the apical cut end of the stem (II), on the node A1 forming a half ring on the opposite side of the lateral bud (III) and on the lateral bud itself (IV and V).

The results represented in Table 10 show that GB promoted the growth of lateral bud when applied close to the bud (III) and strikingly so when applied on the bud directly (IV), while a slight inhibition was observed when applied on the cut end of the stem (II). It should be noted, on the other hand, that the lateral bud did not grow at all when the apical part of stem was left intact, even if GB was applied directly on it (V).

In the experiments with single-node cuttings (Tables 4 and 5), it was found that inhibition of bud growth by leaf blade, or by IAA given in place of it, was intensified when the growth of petiole was promoted by GB. A slight

Table 10. Effect of site of GB application on the growth of lateral bud. Rooted shoots. ●G indicates the site of GB application. Beginning on July 3, measured after 12 days. Mean of 5 samples.

	(I)	(II)	(III)	(IV)	(V)
A1 → B1 → B2 →					
Elongation of bud (mm)	25.1	23.3	34.7	136.9	0
Ratio	*100*	*93*	*138*	*545*	*0*
Dry weight of bud (mg)	39.4	28.4	38.8	41.2	——
Ratio	*100*	*72*	*98*	*105*	——
No. leaves unfolding on lateral bud	2.4	1.8	2.0	1.8	0

inhibition caused by GB applied on the apical cut end (II) may be ascribed to a slight increase in the growth occurring in the stem.

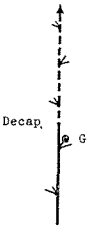
GB exerts an inhibitory effect on the bud growth when it is applied so that it may promote the growth of other tissues. GB promotes the bud growth, on the other hand, when it is applied directly on (IV), or very near to (III) the bud. It may be considered that a tissue which is affected by GB strongly is made to grow more actively and "attract" food factors.

Even if the bud is treated with GB directly, it does not grow at all when the shoot apex is present (V). The bud-inhibiting effect of the apex is strong. And the growth-promoting effect of GB cannot be manifested, when a tissue has no growth capacity, whether this condition may be owing to its age or be induced by auxin or lack of auxin (7).

b) *Gibberellin is ineffective on the growth of the completely inhibited bud.*

Next experiment was performed in order to reconfirm that the apical part of shoot was responsible for the ineffectiveness of GB applied on the lateral bud. Cuttings similar to those used in the preceding experiment were planted in pots. After thirteen days all the leaf blades with the midrib longer than 5 mm were removed from all the rooted cuttings. The lowest aerial node was named *b* and the upper next node *a*. The lateral bud on *a*-node was covered with 0.5% GB-paste in half of the plants (II and IV in Table 11), and not in the rest (I and III). No bud growth was observed in all of the plants after three days.

Table 11. Effect of apical part of shoot on the growth of GB-treated lateral bud. The shoot apex was intact throughout the experimental period in I and II, and it was cut off 3 days after the beginning of experiment in III and IV. ⊛G indicates the site of GB application. Beginning on Aug. 18, measured after 3 days and 8 days. Mean of 5 samples.

		(I)	(II)	(III)	(IV)
Bud *a* → Bud *b* →					
Elongation of bud *a* (mm)	in the first 3 days	0	0	0	0
	in the following 5 days	0	0	15.8	60.2
Elongation of bud *b* (mm)	in the first 3 days	0	0	0	0
	in the following 5 days	0	0	2.2	3.2
No. leaves unfolding on bud *a*		0	0	2.0	1.8

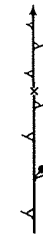
Then, half of the GB-treated plants and half of the untreated ones were decapitated at the middle of the internode above *a*-node (III and IV). Five days after this, it was found that the bud grew only on the decapitated stems, and that the effect of GB promoting the bud growth appeared only on them. The bud (*b*) not treated by GB also grew in the decapitated stumps. Thus the growth-promoting effect of GB on the lateral bud cannot be apparent unless the inhibition by the apical part of stem is released.

c) *Bud inhibition is caused by auxin in dual ways.*

Next experiment was undertaken to see, under similar conditions as above, the effect of blocking of auxin translocation by TIBA. Cuttings were planted in pots and grown for twenty days. All the leaf blades of all the cuttings were excised. And all the buds except the apical one and the one standing on the second oldest aerial node were removed. In one third of the planted cuttings the apical part of shoot was cut off leaving four aerial nodes (I and II in Table 12). In another third, 2% TIBA-paste was smeared around the stem at the middle of the internode corresponding to the cut just mentioned (V and VI). The lateral bud was smeared directly with 0.5% GB-paste in half

the plants each of the above-mentioned two groups and the rest (II, IV and VI). The growth of lateral bud and shoot apex was observed after eight days. The results are represented in Table 12.

Table 12. Effects of TIBA and GB on the growth of lateral bud and young leaves. ●G and ×T indicate the application sites of GB and TIBA, respectively. Beginning on July 18, measured after 8 days. Mean of 5 samples.

	(I)	(II)	(III)	(IV)	(V)	(VI)
B1 →						
Elongation of lateral bud (mm)	27.0	177.4	0	0	2.4	9.4
Ratio	*100*	*659*	*0*	*0*	*9*	*35*
Dry weight of lateral bud (mg)	46.3	51.3	0.3	0.3	0.5	1.3
Ratio	*100*	*111*	*0.7*	*0.7*	*1.1*	*2.8*
No. leaves unfolding on lateral bud	2.0	4.2*	0	0	0	0
No. leaves unfolding on the main axis	——	——	1.8	2.0	3.2	2.6

*: The unfolded leaves were very small as compared with those in group I.

The lateral bud did not grow at all when the apical part of shoot was present (III), and GB applied on the bud was ineffective in this case (IV). The bud grew, and GB promoted its growth remarkably, when the apical part was not present (I and II). And TIBA applied on the stem made the bud grow (V) and also made the effect of GB apparent (VI); in other words, TIBA simulated the removal of the apical part of stem in the effect on the bud growth, though the effect was not so large.

Since TIBA on the stem is considered to block the translocation of auxin coming down from the apical part, the theory of direct effect of auxin in the bud inhibition, as maintained by THIMANN (15), is preferable.

On the other hand, the number of the leaves that had unfolded on the main axis during the experimental period was larger in the TIBA-treated plants than those not treated, whether the lateral bud was treated with GB or not (compare V with III, and VI with IV, respectively). It seems that the auxin

from the apical bud promoted the growth of the shoot above the site of TIBA application, because the downward translocation of auxin was blocked there.

The reason for the smaller growth of the lateral bud in V compared to I, and that in VI compared to II, may be found in that the blocking of the apical dominance effect by TIBA is incomplete, and also in that the growth of the apical part diverts the food factors which can be used by the lateral buds in decapitated cuttings. The inhibiting effect of auxin through the growth stimulation of tissues other than the one in question may be called the indirect growth-inhibiting effect of auxin.

d) *Gibberellin alters dominance relationship between buds.*

It was shown in the foregoing experiment that GB does not promote the growth of the lateral bud so far as the inhibiting effect of the apical bud reaches it. Then it may be interesting to see the mutual effect between two adjoining lateral buds.

Cuttings were planted for rooting as usual. Eleven days after planting, all the shoots were pruned leaving the three aerial nodes, and the lowest lateral bud was cut off. Of the two remaining buds, the upper one was referred to as *a* and the other *b*. 0.5% GB-paste was smeared directly on *a*-bud for one group (II in Table 13) and on *b*-bud for another (III), the buds not being treated for control (I). The results obtained after thirteen days are summarized in Table 13.

Table 13. Effect of GB on the dominance relationship between two lateral buds. ●G indicates the site of GB application. Beginning on July 8, measured after 13 days. Mean of 5 samples.

	(I)		(II)		(III)	
Bud *a* → Bud *b* →						
Buds	*a*	*b*	*a*	*b*	*a*	*b*
Elongation of bud (mm)	28.8	17.6	153.0	12.2	12.2	179.6
a : *b*	*62* : *38*		*93* : *7*		*6* : *94*	

In the control group (I), the buds elongated together but the domination of the upper bud became apparent ($a:b=62:38$). And, when the upper bud was treated with GB (II), its dominance was intensified ($a:b=93:7$). When, on the other hand, the lower bud was treated with GB (III), this bud elongated

no less than the upper bud in the case of group II and inhibited the upper bud as effectively as the GB-treated upper bud did to the lower one ($a:b=6:94$). The dominance relation was thus changed by GB.

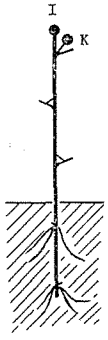
It may be concluded that the center of growth metabolism functions as the center of dominance.

e) *Kinetin does not reverse the bud inhibition caused by IAA.*

WICKSON and THIMANN (20), using etiolated single-node stem sections and etiolated and green entire shoots of Alaska pea, have found that kinetin reverses the lateral bud inhibition to be exhibited by shoot apex and IAA, and suggested that the normal phenomenon of apical dominance depends on an interaction between auxin and a kinetin-like substance in the plant. An experiment was conducted to see the effect of kinetin in the present material.

Rooted cuttings were prepared as usual. Shoots were cut at the internode above the third oldest aerial node, and all the leaf blades and the lower two of the lateral buds were removed, thus the stumps as illustrated in Table 14 being obtained. The cut surface of stem was smeared with pure lanolin and 0.1 and 0.5% lanolin pastes of IAA, and the lateral bud with the same concentration series of kinetin pastes. Elongation of the bud was measured after three and thirteen days of the treatment. The results are summarized in Table 14.

Table 14. Combined effect on the growth of lateral bud of kinetin applied on the bud and IAA applied on the stem. Elongation of the bud observed 3 days and 13 days after the treatment made on July 1. ●I and ●K indicate the application sites of IAA and kinetin, respectively. Mean of 5 samples.



Kinetin concn., %	Bud elongation, mm					
	In 3 days			In 13 days		
	IAA concn., %			IAA concn., %		
	0	0.1	0.5	0	0.1	0.5
0	4.8 *100*	0 *0*	0 *0*	9.6 *100*	8.8 *92*	2.2 *23*
0.1	5.6 *117*	0 *0*	0 *0*	14.2 *148*	7.4 *77*	0.6 *6*
0.5	5.8 *121*	0 *0*	0 *0*	13.0 *135*	5.5 *57*	0.6 *6*

In the first three days, the elongation of the lateral bud was inhibited completely by IAA irrespective of kinetin. Kinetin, on the other hand, favoured the elongation slightly provided that no IAA was given. Thus, kinetin applied directly to the lateral bud did not reverse the inhibiting effect exerted by 0.1 and 0.5% pastes of IAA applied to the cut surface of stem not far from the bud.

As days passed, the IAA-inhibited buds began to elongate as the so-called "breakaway", but they did not overtake the control in thirteen days. Without IAA application, the growth-promoting effect of kinetin became conspicuous in these days. In the stumps receiving IAA, on the other hand, the bud growth was reduced by kinetin. Hence kinetin did not show an effect of reversing the inhibition by IAA, unlike the results of WICKSON and THIMANN (20).

f) *Discussion.*

It is well known that GB promotes the elongation of stem and petiole. The results shown in Tables 4, 5 and 10 indicate that GB is most effective for growth when it is applied to the organ that is growing or is going to grow. And when it is applied to a growing organ, the growth of another organ may be inhibited. The dominance relationships among organs seem to be conditioned by their growth. This was clearly demonstrated by the experimental result summarized in Table 13, namely, either of the two buds could inhibit the growth of the other by being induced to grow more actively by GB-application.

Experimental results represented in Tables 10, 11 and 12 have shown that the growth-promoting effect of GB is not operative when the bud treated with GB is inhibited completely by the apical bud. The author found previously that the growth of petiole was not promoted by GB unless the tissue contained natural auxin or exogenously supplied IAA (7). Thus, a "no auxin, no GB-effect" principle was suggested. However, since GB is not effective also when the bud growth is inhibited by auxin, it may be better to say "no growth, no GB-effect".

It is seen in Table 12 that, when the bud growth is small due to a partial inhibition, the growth increment brought about by GB is also small. In this respect, it may be stated that GB amplifies the growth. The GB-induced growth is zero when the growth activity of an organ is zero, and it is small when the latter is small.

As to the effect of kinetin on the apical dominance, the discrepancy between the present result and those of WICKSON and THIMANN (20) awaits further studies for elucidation.

General Discussion

In the experiments using decapitated cuttings, the cutting was conducted just prior to other treatments. The young leaf left remaining on these cuttings continued its growth even after the treatment. The leaf may be a source of auxin and, at the same time, a growing organ which consumes food, especially in the dark. Through decapitation the lateral bud left on the cutting was released from the inhibition exerted by the apical part of shoot. In such cases, the organs then growing have a capacity of being dominant. Competition for food is a significant factor for the dominance relationships, as demonstrated by the experiment shown in Table 8, and also by GREGORY and VEALE (3).

On the other hand, the inhibition of lateral bud by the apical part of shoot is so powerful that GB can exert no direct effect on the inhibited bud.

It may be relevant to draw a distinction between complete inhibition and partial inhibition. By the former is meant the case where a bud does not grow at all during the experimental period, while in the case of partial inhibition, the problem concerns how much the growth of an axillary shoot is influenced by other parts of the body (a cutting, etc.). The two ways may be mentioned in the bud-inhibiting action of auxin, namely, the *direct* one, the mechanism of which is under much discussions (2, 9, 10, 11, 15, 16, 17, 20 and 21), and the *indirect* one through diversion of food supply by enhancement of growth in tissues to which auxin is applied or translocated. The indirect effect is an important factor in the partial inhibition, while it is not apparent when the bud is completely inhibited by the direct effect of auxin.

Summary

Using single-node and two-node cuttings and rooted cuttings of young sweet potato shoots, observed were the effects exerted on the growth of a lateral bud by a leaf, another lateral bud, the apical bud, and lanolin pastes of growth regulating substances applied on various parts of the cutting.

1) A young growing leaf inhibited the growth of its axillary bud, while a fully expanded leaf promoted it.

2) Bud-inhibiting effect of a leaf could be substituted by β-indoleacetic acid, α-naphthaleneacetic acid or 2, 4-dichlorophenoxyacetic acid.

3) Gibberellin applied onto a petiole inhibited the growth of its axillary bud, instead of promoting it.

4) The more distal the site of indoleacetic acid application on a petiole, the more strongly the bud on its axil was inhibited.

5) An accessory bud was inhibited by either the lateral bud on the same axil, a young leaf or the apical bud.

6) Supply of glucose reversed the bud-inhibiting effect of a leaf.

7) When the apical part of shoot was removed, remaining two buds began to elongate, but the upper one dominated over the lower one.

8) The inhibiting effect of a bud reached the neighbouring lower bud through a girdled part of the stem, but not through a scalded part.

9) The inhibiting effect of a leaf, or of indoleacetic acid given in place of it, traveled upward, as well as downward, along the stem.

10) Growth of a lateral bud was promoted by gibberellin applied directly on it when the apical part of the shoot was removed, but no growth, and accordingly no growth promotion by gibberellin, was observed when the shoot apex was present.

11) Of the two neighbouring lateral buds, the one the growth of which was promoted by gibberellin inhibited the other.

12) Growth inhibition of lateral bud by indoleacetic acid applied near to it was not reversed by kinetin given directly on it.

The results mentioned in 1 to 6 show that the growth of a lateral bud correlates negatively with the growth of other parts of the cutting. Thus, auxin can inhibit lateral buds *indirectly*, namely by increasing the growth of other tissues. The counterpart, the *direct* inhibition, is mentioned when auxin inhibits a bud by reaching its base, as in the effect of the apical bud on lateral buds.

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