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PHYSIOLOGICAL FACTORS ASSOCIATED WITH THE SHOOT GROWTH OF APPLE TREES

By

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Introduction

Profitable fruit production is due to blooming and fruit set over wide bearing surface. Wide bearing surface is formed by the shoot growth over the good frame work of the fruit tree.

The main physiological foundation of shoot growth and flower formation is nitrogen and carbohydrates metabolism. Since Kraus and Kraybill (1), many investigators (1~9, 11,) have pursued these metabolism in the shoots of various kinds of fruit trees. The senior author (13) previously reported on these metabolism in the shoots of the Japanese pear.

In addition to nitrogen and carbohydrates, phytohormones play a great role in the development of the shoots (10, 14, 15, 17, 19, 20).

The present paper reports on the relationships between the length growth of apple shoots and the above related phygiological factors.

Materials and methods

Seven years old McIntosh Red apple trees, planted in the field of the Tohoku University, were used.

Shoots, selected for uniformity, were sampled from the branches facing south between 10 A.M. and 12 A.M. to determine the chemical constituents, auxin and gibberellin-like substances in the terminal bud of apple shoots.

1) Carbohydrates and nitrogen compounds:

Hot 80 per cent ethyl alcohol was used to separate the soluble and insoluble fractions of the samples taken from the terminal parts, about 10 cm long. The soluble fraction was used for soluble nitrogen, total sugars and reducing sugar determination. The residue, after alcohol extraction, was used for insoluble nitrogen, starch and polysaccharides determination. The nitrogen was determined by the Semi-micro Kjeldahl method. The reducing sugar was determined by the Somogyi method. The other carbohydrates were determined by the Somogyi method after hydrolysis respectively.

Namely, Total sugars: Hydrolysis with 1 cc of 25% HCI (sp. gr. 1.125) for 15 hr at 25°C.

Starch: Hydrolysis with 3% diastase at the initial pH 5.6 for 3 hr at 48°C, after 1 hour boiling of 0.2 gr samples in 20 cc of distilled water.

Polysaccharides: Hydrolysis with 20 cc of 25 % HCI (sp. gr. 1.125) : H_2O (v/v1:20) for 2.5 hr.

2) Auxin:

Ten buds (0.5 gr fresh weight) were collected and extracted for 20 hr with three changes of peroxide free ether approximately at eight hours intervals. The ether extracts were combined and condensed. The method employed in the bioassay of ether extracts was similar to that described by Went (12) and Hemberg (16).

3) Gibberellin-like substances:

The extraction of leaves and terminal buds was carried out for 48 hr with four changes of 80 per cent alcohol. The bioassay of gibberellin-like substances was determined by the modified rice seedling test described by Kato and Ito (25).

Result

I Length growth of apple shoots

1) Growth of various types of shoots.

March of the growth of vertical, horizontal and weeping vegetative shoots is shown in Fig. 1.

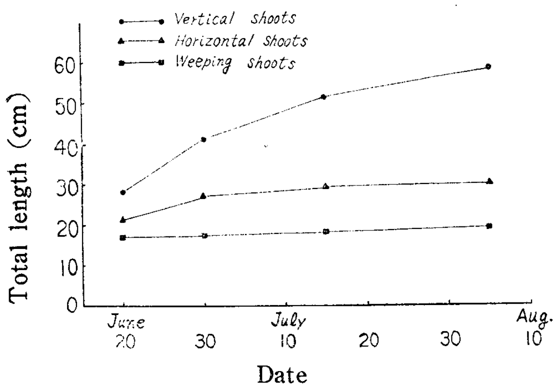


Fig. 1. Growth of various types of apple shoots. (1958)

The weeping vegetative shoots reach the maximum length on June 20. By the end of June the horizontal shoots reach the maximum.

The vertical vegetative shoots grow out to the end of July, secondary growth arising very often.

It is suggested that there is a close relationship between the growth direction of shoot and the vigor of the shoot growth.

2) The relationships between the number of nodes, internode and the shoot length.

The length of shoot is determined by the number of nodes and individual internode length.

Table 1. The characteristics of various types of apple shoots.

Sample No.	Total length (cm)	No. of inter-node	Av. length of inter -node	No. of internodes 0~0.5	0.6~1.0	1.1~1.5	1.6~2.0	2.1~2.5	2.6~3.0	3.1~3·5	3.6~4.0	4.1~4.5	Type of shoot
1	21.0	16	1.31	6	2	1	1	3	2	0	1	0	Weeping shoot
2	29.2	21	1.39	8	4	1	3	0	3	2	0	0	〃
3	33.0	22	1.50	7	4	1	2	2	2	3	1	0	Horizontal shoot
4	41.5	26	1.60	9	3	1	3	4	3	2	1	0	〃
5	52.8	32	1.65	10	2	1	8	3	2	3	1	2	〃
6	59.4	33	1.80	10	2	0	3	5	9	4	0	0	〃
7	74.0	40	1.85	10	2	2	3	8	8	4	3	0	Vertical shoot
8	78.5	42	1.87	9	2	1	3	11	9	3	4	0	〃
9	91.2	45	2.04	9	2	0	1	21	7	5	0	0	〃
10	94.8	46	2.06	9	2	4	5	7	9	7	3	0	〃

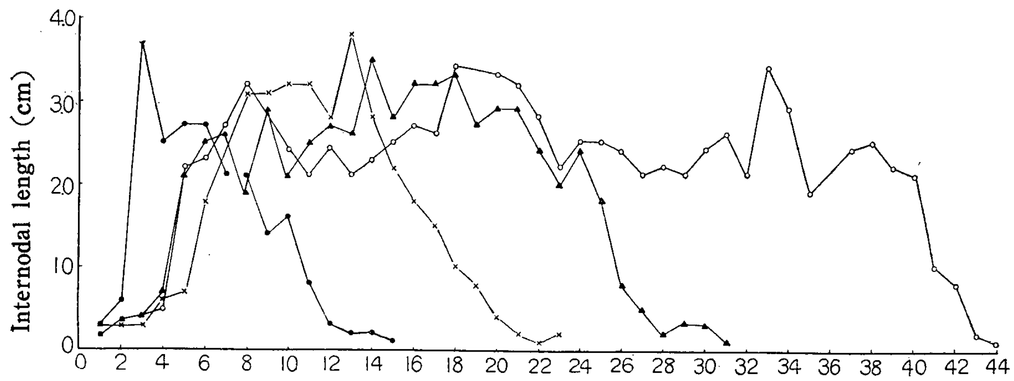


Fig. 2. The trends of internodal length of apple shoot of the various length. (1960)

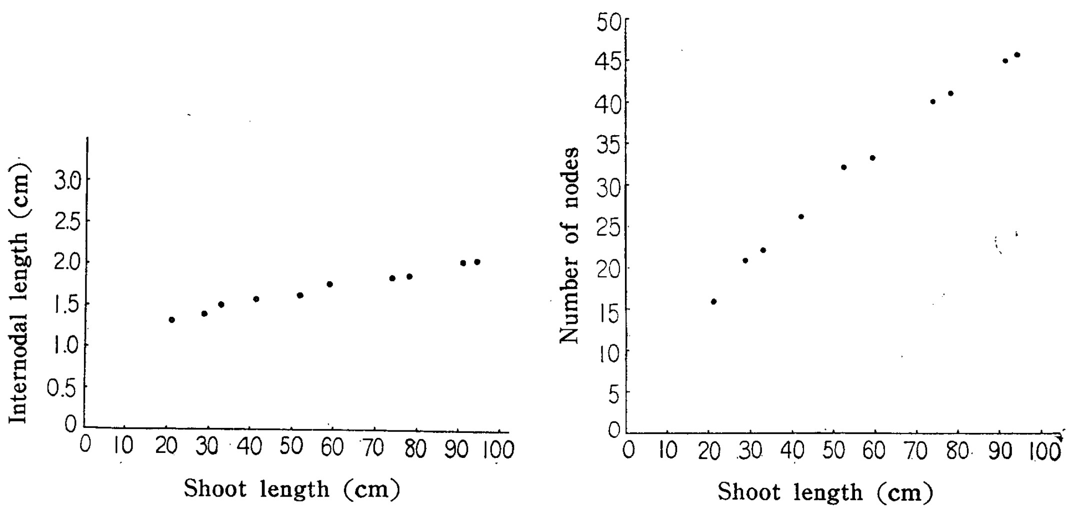


Fig. 3. The relationships between the average length of mature-leaf-bearing internodes, the number of nodes and the whole length of apple shoots. (1960)

On Nov. 20, various types of shoots were collected and the number of nodes and the lengths between the nodes were measured. The longer shoots have much more number of nodes than the shorter ones (Table 1). There is a close correlation between the number of nodes and the shoot length as shown in Fig. 3.

The length of successive individual internodes from the base to the tip of the shoot shows a remarkable pattern of fluctuation completely independent of climatic variations, as previously reported by Hancock and Barlow (24) (Fig. 2), but the average length of the mature-leaf-bearing internode shows a curvilinear relationship with the whole length of the shoot (Fig. 3).

II Physiological factors associated with the length growth of the shoots.

1) Auxin content in the terminal bud of apple shoots.

To investigate the seasonal changes of auxin content in the terminal bud of apple shoots during the course of experiment, 0.5 gr samples of the terminal buds (fresh weight) were collected from ten shoots.

After cut into pieces, the samples were extracted with peroxide free ether for 20hr at 0°C. The ether extracts were bioassayed by the Avena curvature test described by Went (12).

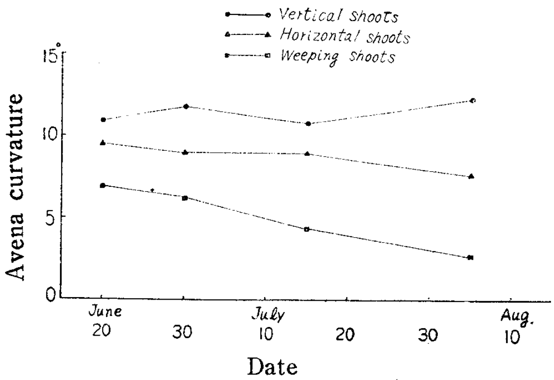


Fig. 4. The trends of seasonal changes of auxin content in the terminal bud of apple shoot. (1958)

Fig. 4. shows the result of Avena curvature test on the ether extracts of apple shoots.

It is evident that the auxin content in the terminal bud of vertical vegetative shoots is highest.

There occurs a gradual decline in the auxin content in the terminal bud of apple shoots until early August, and this tendency is more acute in the weeping shoots than the others.

It is very noticeable that the auxin content in the terminal bud increases in advance of the commencement of the rejuvenile shoot growth.

2) Carbohydrates and nitrogen constituents in the apical part of the apple shoots.

The apical parts of horizontal shoots (10 cm long from the terminal bud) were gathered and analysed. The trends of the chemical constituents in the terminal part of the shoots are shown in Figs. 5, 6.

It is evident that the rapid increase in the total carbohydrates to the maximum occurs about the beginning of August.

This seasonal tendency is manifested mostly by a rise and fall of polysaccharides. Up to the end of June, the starch content increases very slowly, and is thereafter followed by the rapid increase which corresponds to the decrease of the other polysaccharides.

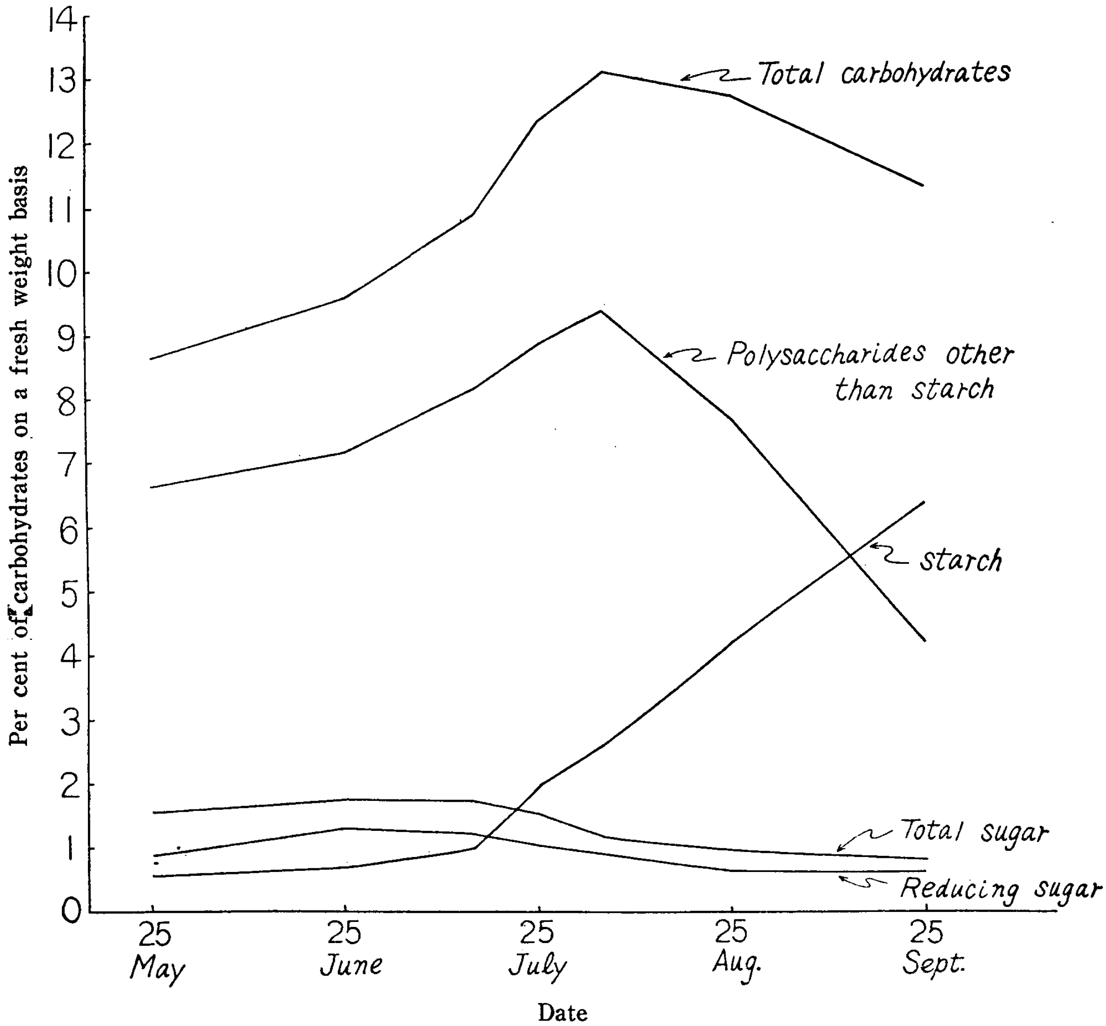


Fig. 5. The trends of seasonal changes of carbohydrates in the apical part of horizontal shoots.

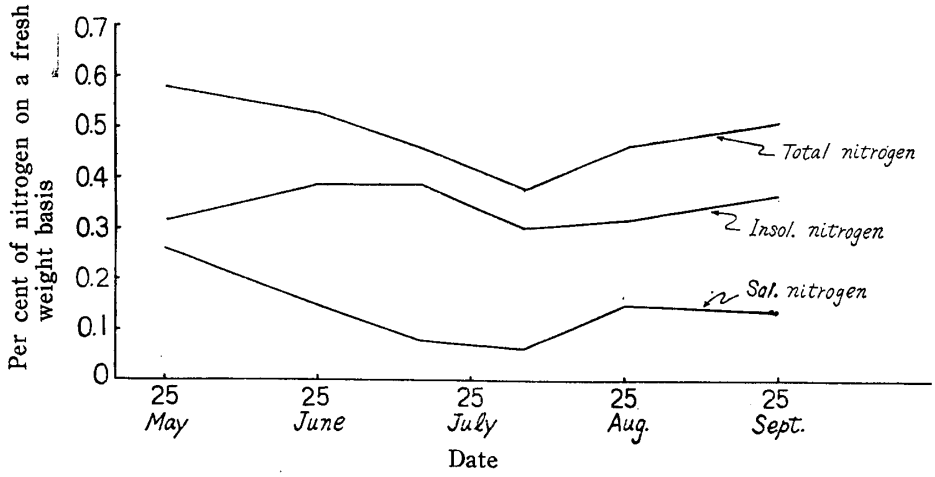


Fig. 6. The trends of seasonal changes of nitrogen compounds in the apical part of horizontal shoots. (1958)

During the course of shoot growth, the content of soluble sugars is constantly low up to the end of July, and thereafter further decreases gradually (Fig. 5).

Fig. 6 shows the trends of seasonal changes of nitrogen compounds in the apical parts of apple shoots.

Up to the end of June, the insoluble nitrogen content increases, being accompanied by a decrease of soluble nitrogen and, thereafter the content of both nitrogen fraction shows the slow increase.

It is suggested that the increase of insoluble nitrogen is the result of protein synthesis.

III Studies on the length growth, as affected by fruiting, girdling and defoliation.

(1) Effect of whole mature-leaf defoliation, girdling and fruiting.

Horizontal shoots (20~25 cm long) were selected for uniformity to examine the effect of defoliation, girdling and fruiting on the length growth.

The experiments were carried out in three replicates, each replicate comprising 50 shoots.

i) The length growth as affected by defoliation, girdling and fruiting.

It is shwn in Fig. 7 that the defoliation promotes the shoot growth, but, on the contrary, fruiting and girdling prohibit the length growth, inducing the earlier cessation.

ii) Auxin content in the terminal bud of the shoots.

The result of the Avena curvature test on the ether extracts from the terminal bud is represented in Fig. 8.

It is clear that the rapid increase of auxin content goes on up to July 15 by the defoliation, and fruiting or girdling treatment, on the contrary, induces a considerable derease of auxin.

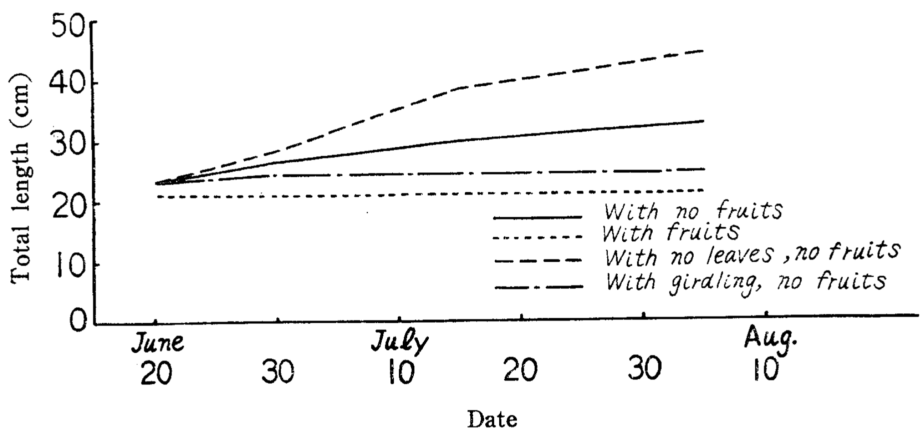


Fig. 7. Effect of defoliation, girdling and fruiting on the length growth of horizontal shoots. (1958)

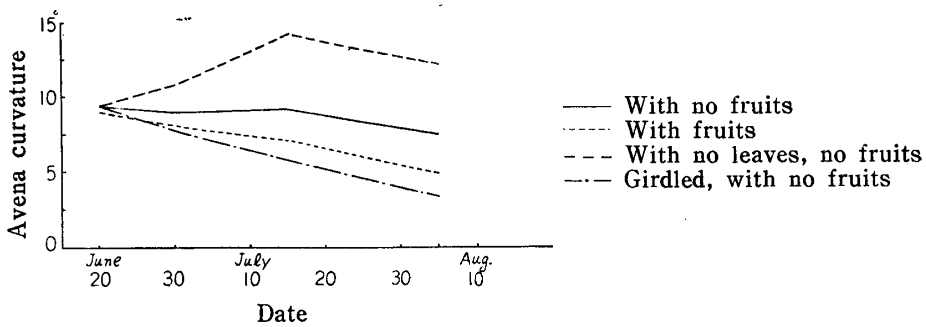


Fig. 8. Effect of defoliation, girdling and fruiting on the auxin content in the terminal bud of apple shoots. (1958)

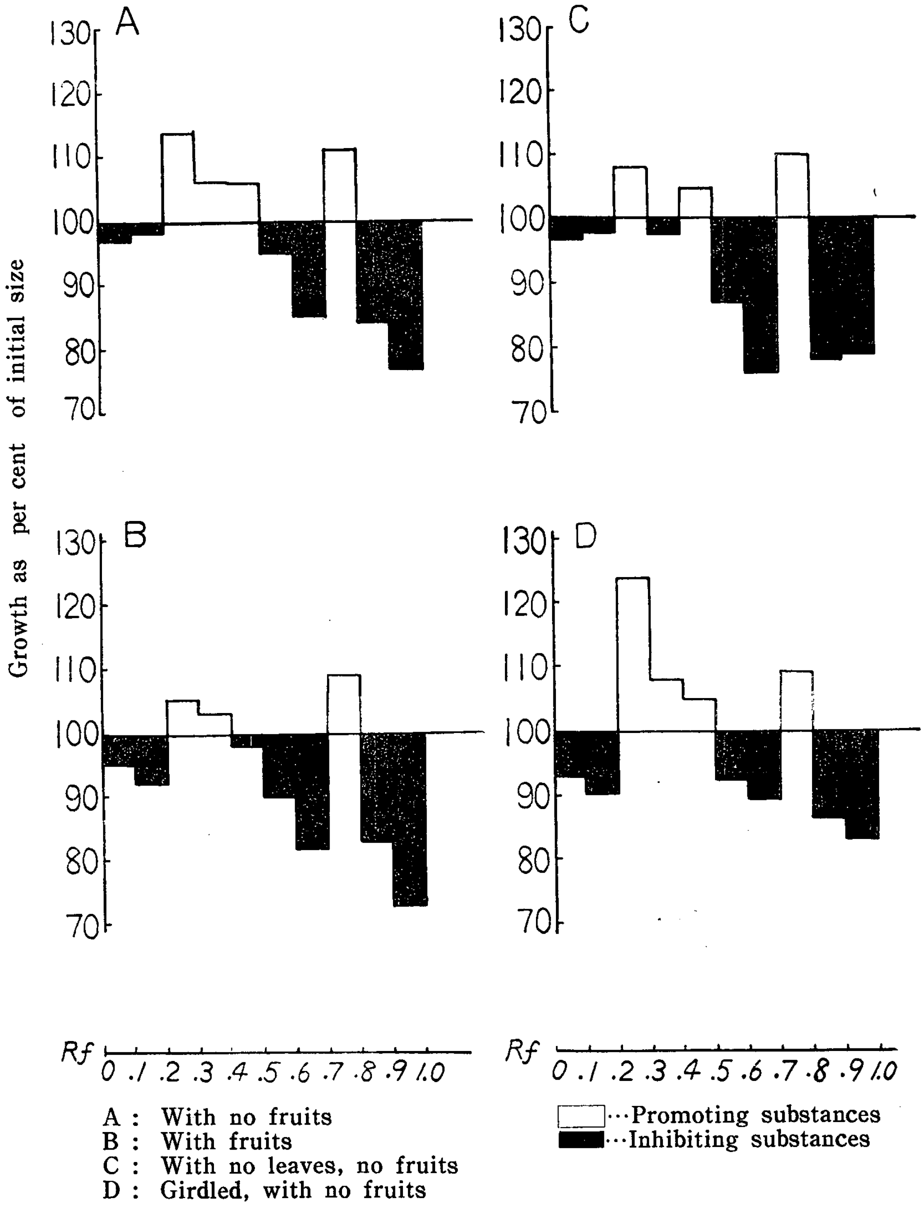


Fig. 9. Chromatograms of crude ether extracts in the terminal bud of apple shoots. (1958)

The auxin content in the terminal bud is affected by defoliation, girdling and fruiting. The increase of auxin content is due to the increase of promoting substances and the decrease of auxin content depends upon both the decrease of promoting substances and the increase of inhibiting substances as shown in the chromatograms of crude ether extracts of the apple shoots collected on July 15, bioassayed by the Avena straight growth test (Fig. 9).

iii) Carbohydrates and nitrogen constituents.

Table 2 shows the result of the chemical analysis of the materials sampled on Aug. 5.

Table 2 includes the carbohydrates and nitrogen constituents of the vertical shoots as a check.

Table 2. Effect of defoliation, girdling and fruiting on the chemical constituents in the apical part of apple shoots. (1958)

(Per cent on fresh weigth basis)

Chemical constituents / Plots	Reducing sugar	Non-reducing sugar	Total sugar	Starch	Polysaccharides	Total carbohydrates	Soluble nitrogen	Insoluble nitrogen	Total nitrogen	C/N
Vertical shoot with no fruits	0.81	0.17	0.98	0.55	4.59	5.57	0.11	0.37	0.48	11.6
Horizontal shoot with no fruits	0.93	0.15	1.08	2.44	12.20	13.28	0.07	0.30	0.37	35.9
Horizontal shoot with fruits	0.83	0.31	1.14	2.20	10.72	11.86	0.15	0.23	0.38	31.2
Horizontal shoot with no fruits, no leaves	1.34	0.16	1.50	0.83	6.86	8.38	0.03	0.23	0.26	32.2
Horizontal shoot with no fruits, girdled	0.93	0.37	1.30	3.45	14.55	15.85	0.07	0.28	0.35	45.3

The vertical vegetative shoots show the higher amount of nitrogen compounds, and less carbohydrates than the others.

Fruiting is followed with the decrease of carbohydrates, but not of nitrogen compounds, and the girdling induces the accumulation of carbohydrates, but not of nitrogen compounds.

In the defoliated shoots, both carbohydrates and nitrogen compounds decrease remarkably as compared with the shoots with no fruits.

iv) The relationships between the carbohydrates, nitrogen and the auxin content in the terminal bud.

Comparing the shift of auxin content in the terminal bud with that of carbohydrates and nitrogen constituents of apple shoots sampled on August 5, a very interesting relationship is found as shown in Fig. 10.

The increase of auxin content in the terminal bud is correlated with the decrease of carbohydrates content, especially starch content, but not with the nitrogen content in the apical part of the shoots.

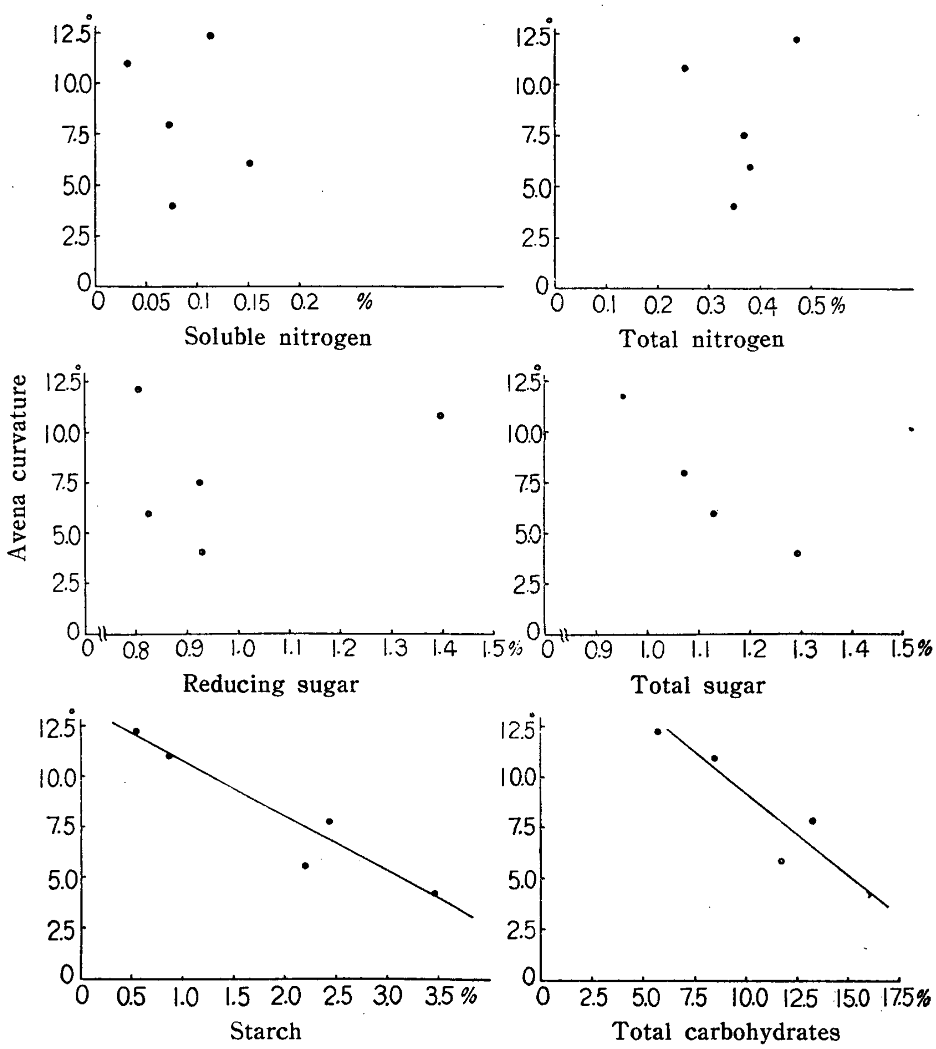


Fig. 10. The correlation between auxin content in the terminal bud and chemical constituents in the apical part of apple shoots. (1958)

(2) Effect of partial mature-leaf defoliation during the course of shoot growth.

As mentioned above, mature-leaf defoliation promotes the shoot growth. In 1959, tests on the effect of partial defoliation on the shoot growth was carried out during the course of shoot growth and after the growth cessation.

In these experiments, shoots on the wide-angled framework were selected and divided into four plots, A) control (non-treatment), B) 1/3 upper leaves defoliation, C) 1/3 middle leaves defoliation, D) 1/3 lower leaves defoliation.

i) During the course of shoot growth.

On May 20, the defoliation was carried out with about 20 cm long shoots. The subsequent growth of the treated shoots is shown in Fig. 11.

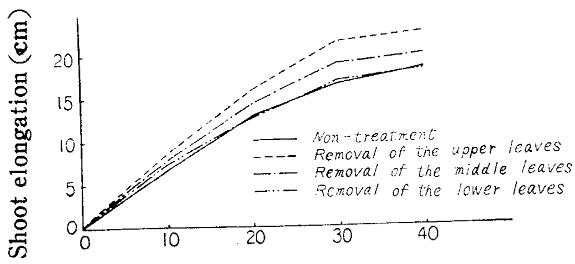


Fig. 11. Effect of mature-leaf defoliation at various parts of shoots on the length growth. (1959)

The effect of removal of the leaves resulted in the promotion of shoot growth, and is in the following descending order, B>C>D=A.

The changes of carbohydrates and nitrogen constituents in the apical part of apple shoots 10 and 20 days after defoliation are shown in Table 3.

The partial defoliation induces the same changes of chemical contituents as the previous whole mature-leaf defoliation experiment.

It is shown that starch accumulation is depressed and on the other hand, the soluble sugars, especially the reducing sugar, and nitrogen constituents, especially the insoluble nitrogen, increase.

Table 3. Effect of partial defoliation on the chemical constituents in the apical part of apple shoots during the course of shoot growth. (1959)
(Per cent on fresh weight basis)

Plots	Chemical constituents	Reducing sugar	Non-reducing sugar	Total sugar	Starch	Polysaccharides	Total carbohydrates	Soluble nitrogen	Insoluble nitrogen	Total nitrogen
after 10 days	Control	0.82	0.12	0.94	1.62	4.28	5.22	0.04	0.45	0.49
	Removal of upper leaves	1.10	0.02	1.12	1.20	3.18	4.30	0.06	0.50	0.56
	Removal of middle leaves	0.89	0.05	0.94	1.26	3.51	4.45	0.06	0.46	0.52
	Removal of lower leaves	0.86	0.09	0.95	1.40	3.94	4.69	0.03	0.44	0.47
after 20 days	Control	0.97	0.14	1.11	2.85	4.74	5.85	0.10	0.49	0.59
	Removal of upper leaves	1.32	0.04	1.36	1.85	2.53	3.89	0.15	0.58	0.73
	Removal of middle leaves	1.24	0.08	1.32	2.14	3.19	4.51	0.12	0.54	0.66
	Removal of lower leaves	0.98	0.19	1.17	2.78	4.35	5.51	0.10	0.48	0.58

This tendency is reduced as the part of defoliation becomes lower.

The results shown in Fig. 12 indicate that the auxin and the total carbohydrates content shifts with a close correlation.

This coincides with the result shown in Fig. 9.

ii) After the growth cessation.

Shoots of various lengths were sampled 10 days after defoliation.

It seems that the carbohydrates and nitrogen contents are less in the longer shoots than the shorter ones. The rise and fall of nitrogen and carbohydrates in the shoots show the same tendency as the previous experiment, but the effect is less severe. Among the treated shoots, the shorter ones are much more affected by the defoliation than the longer ones (Table 4).

3) Effect of the unexpanded-leaf defoliation.

To examine the effect of unexpanded-leaf defoliation, 30 cm long shoots, elongating horizontally, were treated on May 20, 1960, as follows, A) control (non-treatment), B) whole expanded-leaf defoliation, C) whole unexpanded-leaf defoliation. Thirty days after the treatment, the number of nodes, length of internodes and the leaf size were measured.

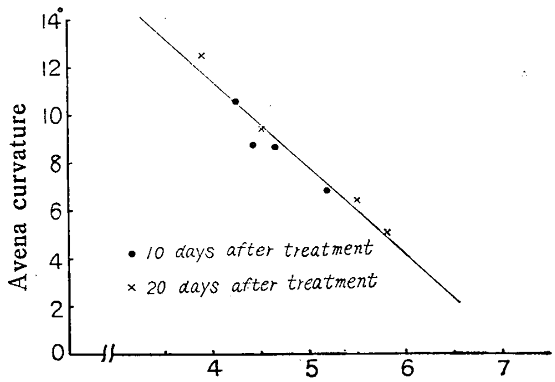


Fig. 12. The correlation between auxin content in the terminal bud and carbohydrates content in the apical part of apple shoots. (1959)

Table 4. Effect of partial defoliation on the chemical constituents in the apical part of apple shoots after the growth cessation. (1959)
(Per cent on fresh weight basis)

Plots \ Chemical constituents		Reducing sugar	Non-reducing sugar	Total sugar	Starch	Polysaccharides	Total carbohydrats	Soluble nitrogen	Insoluble nitrogen	Total nitrogen
Control	LS	0.66	0.43	1·09	2.72	7.45	8.54	0.15	0.60	0.75
	SS	0.69	0.54	1.23	2.89	7.68	8.91	0.13	0.61	0.74
Removal of upper leaves	LS	0.76	0.02	0.78	2.32	7.26	8.04	0.16	0.62	0.78
	SS	0.85	0.01	0.86	2.44	7.43	8.29	0.17	0.63	0.80
Removal of middle leaves	LS	0.68	0.08	0.76	2.63	7.42	8.18	0.16	0.62	0.78
	SS	0.72	0.15	0.87	2.75	7.63	8.50	0.14	0.61	0.75
Removal of lower leaves	LS	0.70	0.24	0.94	2.69	7.43	8.37	0.15	0.61	0.76
	SS	0.72	0.24	0.96	2.89	7.64	8.60	0.12	0.61	0.73

* LS … shoots, 50~60 cm long
SS … shoots, 30~40 cm long

It is shown in Fig. 13 that shoot growth is remarkably promoted by the expanded-leaf defoliation and is inhibited by the unexpanded-leaf defoliation. Shoot growth is due to the individual internodal length growth as shown in Fig. 14. It appears that the unexpanded-leaf defoliation reduces the length growth of individual internode and increases the number of nodes.

The effect of defoliation on the other leaf size is repersented in Fig. 15. The leaf size is diminished by the defoliation, especially by mature-leaf defoliation.

4) Content of gibberellin-like substances in the leaves.

From the experiment mentioned above, the removal of mature or immature leaves affects the promotion of the internodal growth. And further, it is well

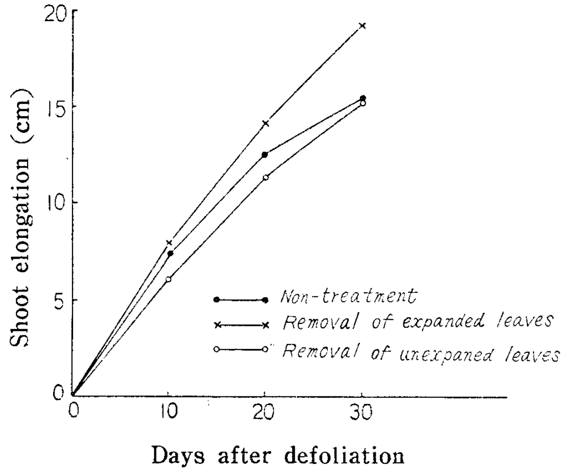


Fig 13. Effect of unexpanded immature-leaf defoliation on the length growth of apple shoots. (1960)

known that gibberellins are very effective in increasing internodal length and leaf size. The content of gibberellin-like substances in the leaves is shown in Fig. 16.

The half-sized leaves have the most abundant gibberellin-like substances on the leaf unit basis and, on the fresh weight basis, unexpanded-leaves have the most abundant. Consequently it appears that the younger tissues contain much more gibberellins and their precursors.

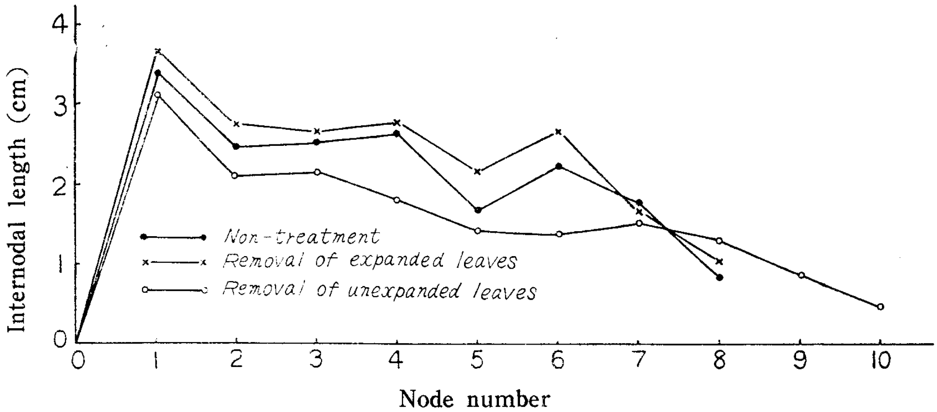


Fig. 14. Effect of unexpanded immature- leaf defoliation on the individual internodal length of apple shoots. (1960)

* The node bearing the first unexpanded immature-leaf next to the expanded leaf was designated as the 1st node and in the acropetal order, as 2nd, 3rd, 4th, ... to the apical bud.

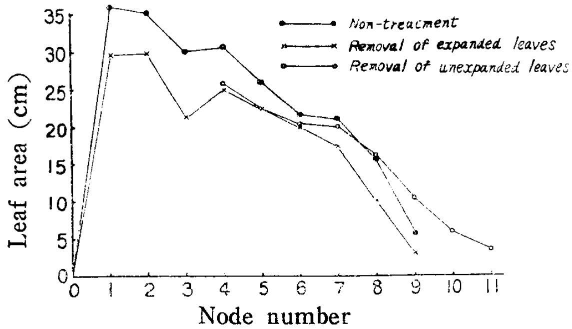
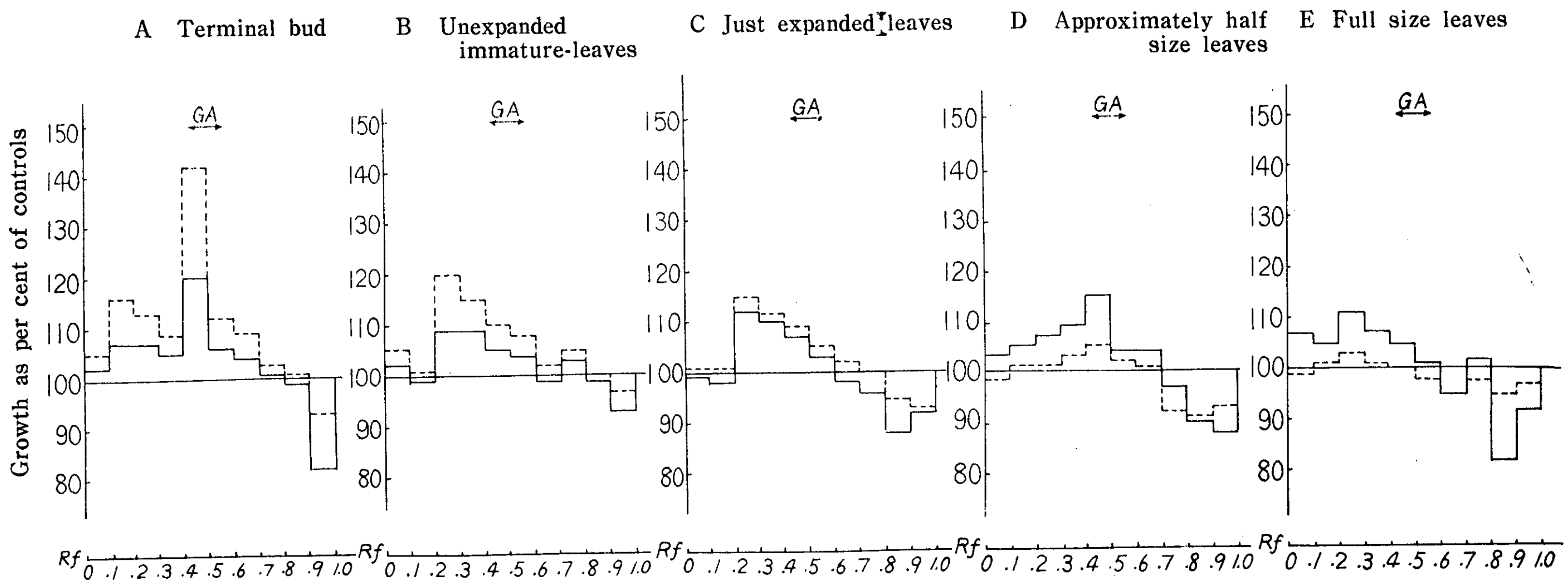


Fig. 15. Effect of unexpanded immature-leaf defoliation on the leaf size of apple shoots. (1960)

IV Studies on the length growth with special reference to the influence of gibberellin.

1) Effect of foliage application of gibberellin on the shoot growth of apple trees.

Gibberellin solution of 100 ppm was sprayed with the hand atomizer over ten shoots, 20~25 cm long, five times every other day, beginning on June 16, 1959.



[solid box] ......Gibberellin-like substances per 20 sections (terminal buds or leaves).

[dashed box] ......Gibberellin-like substances per fresh weight of 2.0gr.

The solid line indicates the growth of controls.

Fig. 16. Chromatograms of ether fraction of alcohol extracts in the terminal bud and leaves of apple shoots. Assayed by rice seedling test. (1960)

Although Powell *et al* (22) have reported that except at the highest concentration applied twice weekly or once weekly, limited or no response in several physical measurements was obtained, gibberellin sprays in this experiment resulted in the marked promotion of shoot growth as shown in Fig 17.

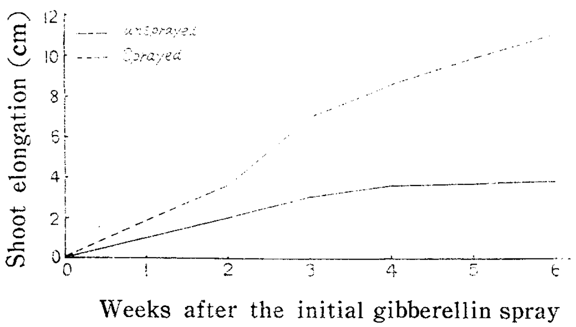


Fig. 17. Growth of apple shoots treated with gibberellin. (1959)

* Foliar spray application was made five times with the solution of gibberellin at 100 ppm every other day, commencing on June 16.

The total new growth of gibberellin-treated shoots shows about three times as long as that of control. It is suggested that the elongating effect varied with the time of gibberellin application, the concentration of gibberellin, the replication number and the intervals of spray applications is ultimately reflects the shift of the internal condition of shoot.

2) Effect of gibberellin application on the growth of various types of shoots.

On June 23, 1960 three types of shoots, just ceased the length growth, namely, the vertical shoots 40～50 cm long, the horizontal shoots, 20～30 cm long, and the weeping shoots, 20～30 cm long, were sprayed with gibberellin.

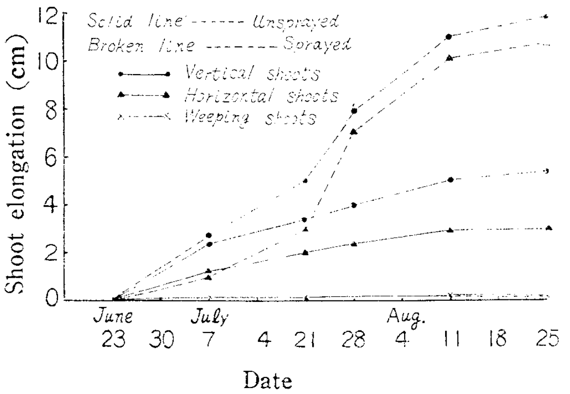


Fig. 18. Effect of gibberellin on the length growth of various types of apple shoots. (1960)

The result of gibberellin application five times every other day is shown in Fig. 18.

Gibberellin promotes considerably the length growth of both vertical and horizontal shoots, but scarcely affects the growth of the weeping shoots.

It appears that gibberellin is effective for the growth acceleration of shoot only during the course of growth.

3) Gibberellin-like substances in the terminal buds of various types of shoots.

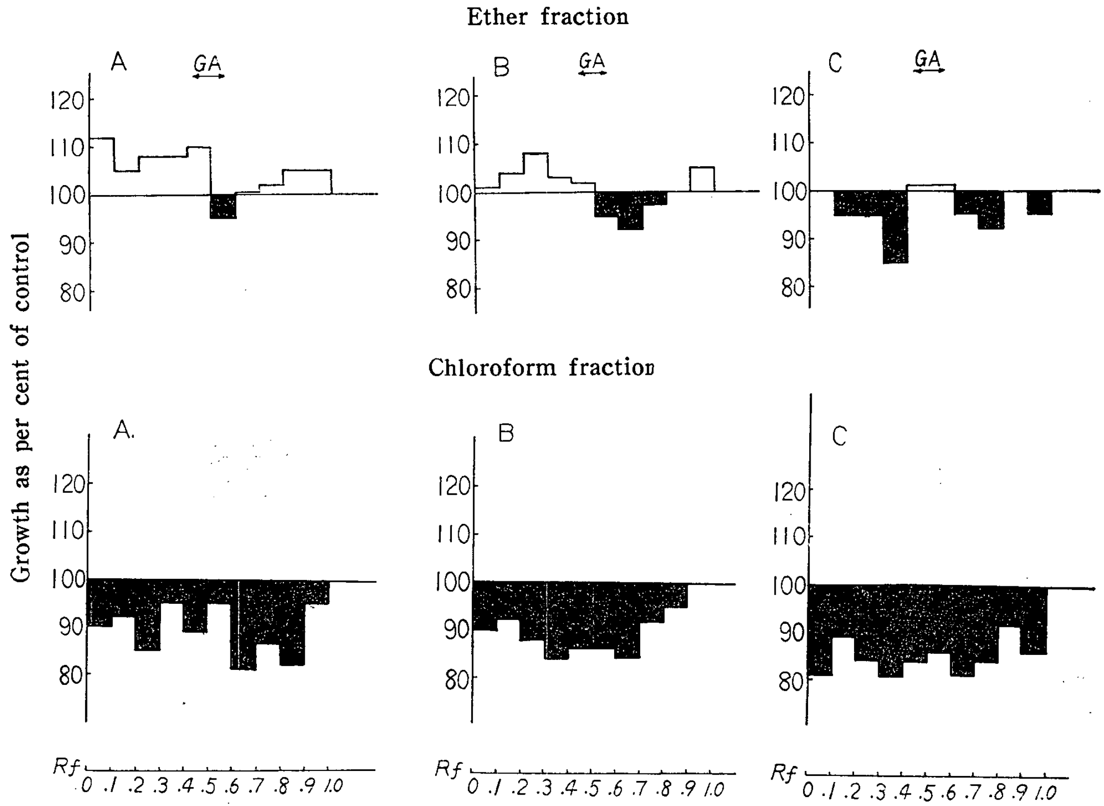
Ten shoots were collected from the three types of shoots respectively as mentioned above, to investigate the gibberellin-like substances in the terminal bud. Three grams (fresh weight) of ten terminal parts of each type of shoots, about 3 cm long from the tip, were taken and cut into pieces to extract with 80 per cent alcohol.

The fractionation of alcohol extracts was carried out after 48 hours extraction. The bioassay of gibberellin-like substances in each fraction was made by Kato and Ito's method (25).

Fig. 19 shows the result of the bioassay of gibberellin-like substances in the terminal buds.

It is apparent that much more gibberellin-like substances and less anti-gibberellin are found in the vigorous shoots than the weak ones.

The weeping shoots, entering into the growth decline have very small amount of gibberellin-like substances. Consequently, it seems that the native gibberellin-like substances disappears with the growth cessation of shoots.



A : Vertical shoots B : Horizontal shoot C : Weeping shoots

The solid line gives the growth of controls

Fig. 19. The content of gibberellin-like substances in the terminal bud of various types of apple shoots. (1960)

Discussion

1) Shoot growth

The present investigation shows that shoot growth varies closely relating to its growth angle. The vertical vegetative shoots with greater number of nodes and longer internodes continue to grow out vigorously to the end of July. In other words, the weeping or horizontal shoots result in shorter growth with less number of nodes and rather shorter internodes (Fig. 3). The results above obtained is similar to Barlow's findings (23).

Shoot growth is affected by the defoliaiton and girdling (Fig. 7). Namely, the mature-leaf defoliation promotes the length growth and the girdling treatment prohibits the elongation of shoots, but the effect of mature-leaf defoliation is different by the time of removal, number of removed leaves and defoliated portion of shoots. The earlier the time of removal, the more severe the defoliation and the more upper the part of defoliation is, the larger the shoot growth is.

As shown in Fig. 14, the mature-leaf defoliation is effective in promoting the length growth through the elongation of internodal length and not through the increase of nodes and leaves. On the contrary, the immature-leaf defoliation increases the number of nodes and leaves. Length growth, therefore, is attributed to the synergistic action of products synthesized by the mature- and immature-leaves.

2) Chemical constituents in the apical part of apple shoots.

(1) Auxin

Gunckel and Thiman (15) show that auxin in the terminal bud is transformed from its precursor translocated from the leaves.

Hatcher (20) reports that the free auxin content declines throughout growth with a steady positioning of the auxin peak in the upper shoots.

As reported here, it is clearly shown that the auxin level is closely associated with the behavior of shoot growth which is strengthened in the vertical direction or by defoliation and depressed in the horizontal direction or by girdling

It is very noticeable that after the defoliation treatment, before rejuvenile growth, the auxin content increases in the terminal bud.

These results are considered to agree with Shalucha's finding (14) that the vigorous growth is correlated with high auxin yields.

(2) Carbohydrates and nitrogen compounds.

Studies on the chemical composition of apple shoot concerning flower bud formation and shoot growth have been reported by Hooker (2), Harvey (3), Kraybill (4), and Potter (6).

The results in this paper are almost the same as those reports, but it is very noticeable that the chemical constituents in the apical part of shoot are influenced by the growth direction.

Horizontal growth results in the earlier accumulation of carbohydrates, particularly starch, and in the earlier decrease of the nitrogen content.

It is considered that the accumulation of starch in the apical part of shoot is the physiological basis of flower bud formation, being accompanied by the growth cessation or induced by girdling. The higher content of insoluble nitrogen in the non-bearing horizontal shoots or girdled shoots than in the fruiting or defoliated ones suggests that insoluble nitrogen may also play a role in the flower bud fomation (Table 2).

Kessler's finding (21) may be taken as an illustration of this suggestion.

(3) Translocation of carbohydrates.

The results of girdling and defoliation experiments (2, 3) suggest that the modes of translocation of carbohydrates is influenced by the leaf location, the number of leaves being associated with the stage of shoot growth.

Namely, in the early course of shoot growth, most of the carbohydrates photosynthesized translocates to the tip, but later as the shoot growth advances the photoproducts from the lower leaves tend to translocate to the roots and not to the tip of apple shoots. Finally only the carbohydrates photosynthesized in the upper leaves translocate to the tip.

This tendency is more markedly shown in the longer shoots in the shorter ones the lower leaves contributing to some extent to the tip even after growth cessation.

(4) The relationships between the carbohydrates, nitrogen and the auxin content in the terminal bud of apple shoots.

Shalucha (14) reported that there was no direct correlation between the auxin and nitrogen content in peach shoots.

In this experiment, however, a close correlation is found between auxin and carbohydrates, especially starch, and scarcely with nitrogen as shown in Figs. 10, 12.

Auxin content in the terminal bud decreases with the progress of growth and increases by mature-leaf defoliation.

(5) Gibberellin-like substances.

The results of foliar application of gibberellin and quantitative extraction of gibberellin-like substances from the various types of shoots suggest that gibberellin is involved in the shoot growth process. Nitsch (19) has reported that the growth cessation of shoot might be due to the decrease of gibberellin-like substances.

The vigorous shoots have large amount of gibberellin-like substances, whereas weak shoots or shoots which had ceased the terminal growth contain a less amount.

Comparing the internodal growth induced by the expanded-leaf defoliation with that induced by gibberellin spray, it may be considered that gibberellin-like substances or their precursor in unexpanded immature-leaves is translocated to the terminal bud and contribute to the internodal growth.

The shift of amount of active gibberellin-like substances in immature-leaves proves the relation mentioned above (Fig. 16).

3) The mechahism of shoot growth

On the basis of the foregoing results, the internal conditions controlling the growth of apple shoot are proposed in Fig. 20. Photosynthesized products

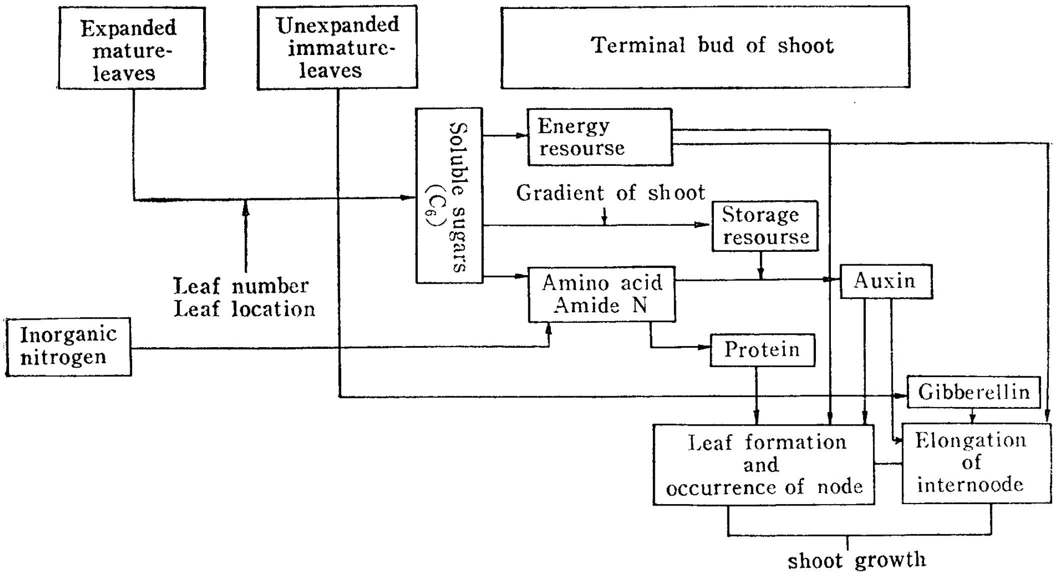


Fig. 20. Diagram showing the internal factors concerning the shoot growth of apple tiees.

are classified as (1) materials for energy resource, (2) storage materials and (3) soluble nitrogen such as amino acid, or amide, some of them being transformed into auxin and protein.

The leaves and nodes differentiate with abundant supply of protein, auxin and carbohybrates (energy resource).

Gibberellin, on the other hand, supplied from the immature-leaves promote the internodal growth with auxin.

Barlow and Hancock (18) have framed the hypothesis concerning the mechanism of shoot growth from the observed effects of defoliation treatment. It is suggested that the immature-leaves produce the internode factor and the leaf growth factor, and the mature-leaves produce the basic food material for the growth of leaves, internodes and axillary bud alike.

It may be concluded that the basic food material is carbohydrates and controls the auxin metabolism and the internode factor is gibberellin-like substances.

The girdling treatment inhibits the downward translocation of carbohydrates, and those accumulate in the apical part of shoot.

The increase of carbohydrates followed by the decrease of the auxin content as shown in Figs. 10, 12.

The mature-leaf defoliation, especially in the upper part of the shoot, decreases the carbohydrates content in the terminal bud and increases the auxin content.

This internal conditions in the terminal bud promote the internodal length associated with gibberellin-like substances translocated from the immature-leaves.

On the contrary, the immature-leaf defoliation inhibits the internodal growth owing to the shortage of gibberellin-like substances in the terminal bud, but promotes the leaf expansion and increases number of nodes with the synergistic action of auxin and protein.

Summary

1. In order to establish the reasonable management of apple trees, clarifying the internal factors concerning the growth process of shoot, the experiments were conducted with seven years old McIntosh Red apple trees growing in the field of the Tohoku University since 1958.

2. Shoot growth is controlled by the growth direction of the shoots. The vertical vegetative shoots grow out most vigorously and longer than the horizontal and weeping ones. The longer shoots consist of a great number of nodes with longer individual internode, while the shorter ones with less number of nodes.

3. The mature-leaf defoliation promotes the shoot growth with the increase of internode length, while the unexpanded immature-leaf defoliation decreases the shoot growth with individual short internodal length in spite of the increase of the number of nodes. The girdling and fruiting prohibit the shoot growth, resulting in the earlier growth cessation.

4. Chemical constituents in the apical part of apple shoots.

(1) Auxin; It is shown that auxin content in the terminal bud decreases with the progress of shoot growth, and considerably increases before the rejuvenile growth of the shoots. Shift of auxin content responds to the vigor of vegetative shoot growth. The auxin in the vigorously growing shoots as vertical shoots is higher than that in the poorly growing ones as horizontal and weeping.

The girdling and fruiting induce the decrease of auxin content, while the mature-leaf defoliation increases the auxin content.

(2) Carbohydrates and nitrogen compounds; As the shoots grow out, the insoluble nitrogen increases, accompanied by the decrease of soluble nitrogen, but total nitrogen content decreases and reaches the minimum by the beginning of August, followed by the subsequent increase.

Carbohydrates, especially starch content increase with the progress of growth and reach the maximum by the beginning of August, while soluble sugar content is fairly constant.

Carbohydrates content of vertical shoots is less than that of horizontal and weeping ones, whereas the nitrogen content of vertical shoots is higher than

that of horizontal and weeping ones.

The defoliation and fruiting reduce the content of carbohydrates and nitrogen compounds in the apical part of apple shoots, and the girdling increases the carbohydrates, especially starch content.

During the course of initial growth, total amounts of carbohydrates from the mature-leaves may be translocated to the tip and in the later course of growth the photosynthesized products of the lower mature-leaves tend to translocate to the roots.

It appears that the amount of carbohydrates in the tip is also influenced by fruiting and the growth direction of shoots.

(3) It is very noticeable that the decrease of auxin content in the terminal bud is closely related to the increase of carbohydrates content, especially starch content in the apical part of apple shoots.

(4) Gibberellin foliar application promotes the growth in elongating shoots, but fails to stimulate growth in shoots which have ceased growth. The content of native gibberellin-like substances in the terminal bud is in the following descending order,

vertical shoots>horizontal shoots>weeping shoots.

In the case of the individual leaf, the content per leaf unit is in the following descending order,

half-size expanded leaf>just expanded leaf>full-size leaf>folded immature-leaf, and the content per fresh weight unit is as follows,

folded immature-leaf>just expanded leaf>half-size leaf>full-size leaf.

(5) On the basis of the foregoing results, the physiological factors influencing the apple shoot growth are proposed and discussed.

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