Correlations among lateral shoots in young apple trees

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(Received: March 30, 1974)

Abstract

Growth correlations among axillary buds and young shoots in one-year-old apple trees were investigated. Darkening of every second bud for 3-5 days during bursting time resulted in the formation of mainly short shoots. Thinning of part of the buds caused a higher percentage of the remaining ones to form long shoots. High nutrition level favored the formation of long shoots. When no special treatment was given to the trees, the initial size of the buds played an important role in the determination of future shoot vigor. The medium-size and large buds, in most cases, showed an ability to accumulate more $^{32}\text{PO}_4^{3-}$ per unit of dry weight than did the smaller ones. This indicates that the initial differences among the buds are amplified by a positive feedback mechanism. In horizontally placed trees, the buds on the lower side showed inhibited phosphate uptake. Different growth regulators applied in very small amounts, in a droplet of water to every second bud or shoot tip, markedly changed the correlative interrelations among the developing shoots. The development of vascular connections between the main axis and the lateral buds and shoots of different sizes was investigated.

INTRODUCTION

Apple trees usually form few or no branches during their first season of growth after budding but during the second they produce laterals from almost all buds, except a few near the soil surface. The laterals develop variably, however, some of them form long shoots, whereas others develop as short shoots. The mechanism causing this differentiation in vigor is correlative, i.e. the development of one bud is dependent on the development of the others (G unckel and Th imann 1949; Ch am-p agnat 1965). Little is known, however, about the nature of this differentiating mechanism. It may be supposed that the vigor of a branch, during the first season of growth, is predetermined in the bud. On the other hand, it has been suggested that differentiation of branch vigor occurs only during active growth, through the amplification of minute

initial differences among the buds and young shoots by a positive feedback mechanism (Jankiewicz 1972): the bud which is a little stronger than the others at the beginning, produces slightly more auxin, stimulating the formation of a somewhat better vascular connection of this bud with the main axis, thus providing it with better nutrition and a better supply of hormones transported from the root system. This, in consequence, causes still better growth of this bud and gradually gives it more and more opportunities to dominate over the neighbouring buds.

The authors, in this study, have attempted to approach the problem of differentiation of branch vigor with experimental methods.

METHODS

Some of the experiments were conducted in a nursery near Skierniewice on a moderately fertile pseudopodsolic soil, well fertilized (60 kg N, 120 kg K₂O) in the spring. Other experiments were performed in a greenhouse maintained at a temperature range of 15-28°C on trees growing in pails containing a mixture of sterilized compost soil, sand and peat (2 : 1 : 1 by volume). The potted trees were kept in a cold storage over winter and then were transferred to the greenhouse.

The experiments with radioactive phosphorus were conducted with one-year-old stems of 'Cortland' or of 'Antonowka' apple seedlings grown in pails and kept in a field during the winter with their roots protected against excessive freezing. They were brought into the greenhouse in early spring. When the buds had swollen and had begun to open, the trees were severed at the soil level and the cut ends were immersed for 20 hours in a nutrient solution containing $^{32}\text{PO}_4^{3-}$. Subsequently, the buds were excised, dried and divided into classes according to dry weight. Radioactivity of the buds was then determined with a Geiger-Müller (G-M) counter.

In one experiment the buds were taken from non-radioactive trees treated differently. The buds were excised, placed on agar blocks containing radioactive phosphate and kept in Petri dishes in a humid atmosphere (about 100% RH). After 20 hours of absorption the buds and the agar blocks were dried separately. The buds were then weighed and the radioactivity of the agar blocks and of the buds was determined using the G-M counter. This experiment was performed with 7 trees which had a total of about 100 buds.

In order to examine the capacity of particular parts of the bud to absorb radioactive phosphate, the buds taken from the trees previously immersed with their lower ends in the solution of $^{32}\text{P}_4^{3-}$ were divided into 3 parts: the "meristematic part" (including a small piece of the

primordial axis), the leaf primordia and the scales. Each part was checked separately for radioactivity.

In the experiment concerning the effect of gravity on bud development and $^{32}\text{PO}_4^{3-}$ absorption, the trees were brought into the heated greenhouse in early spring and after a few days, when their buds started to swell, they were placed in a horizontal position. Further details of this experiment are given later.

To investigate the vascular connection between the main axis and buds of different sizes, cross sections taken from the base of each bud or shoot were fixed in 75% ethanol, embedded in paraffin and later examined for thick-walled xylem elements with polarized light.

In another experiment, growth regulators were applied to nursery trees on every second bud or shoot starting with the moment of bud bursting. One droplet (0.04 ml) of the water solution of growth regulators (with Tween 20 at 4 droplets per 100 ml as a surfactant) was applied every second day with total of 5 applications. Control trees were treated in the same manner but with water plus Tween 20 only.

If not otherwise indicated, the experiments were set up in 7-8 randomized blocks using one tree as a plot. The results of both nursery and greenhouse experiments were examined statistically with the method of analysis of variance using Duncan's multiple range test for significance. The numbers of shoots per tree were transformed for statistical analysis according to Freeman and Tukey's transformations for binominal and Poisson distribution (Mosteller and Youtz 1961; Caliński 1964).

RESULTS

The differences in weights among buds and their changes during swelling. Although the dormant buds in the middle section of the maiden apple trees usually did not show any macroscopically visible variation in size, their dry weights varied (Fig. 1), and these differences tended to increase during swelling. The group of the uppermost buds showed the most weight increase, so that in spite of their very low initial weight, most of them became equal in weight to the middle buds during swelling.

Attempts to experimentally change the relative number of short shoots and long shoots in a tree. In order to check experimentally if the future spring growth of a branch is predetermined in the bud, attempts were made to "direct" the development of a given bud into a long or a short shoot.

Darkening of every second bud with aluminum foil or with black paper for 3-5 days was done during the time of bud bursting or during the early development of the shoots. Precautions were taken to ensure that the paper or aluminum foil did not touch the buds. This treatment

Fig. 1. Dry weights (ordinate) of consecutive buds (abscissa) on 3 different trees during dormancy (Oct.) and on 3 other trees during bud swelling time (April)
The buds were counted from the apex downward

caused the subsequent growth of darkened buds to be markedly inhibited (Tables 1 and 2). They formed mainly short shoots.

On the other hand, the removal of every second bud at different dates markedly stimulated the growth of the remaining shoots and caused them to form much fewer short laterals than on the untreated control trees (Table 3). With 'Hibernal' and 'McIntosh' trees, the later the thinning was done the less effective it was. In 'Wealthy' trees, thinning done

Table 1

The ratio of the sum of growth increments of darkened to non-darkened buds of Hibernal trees

Date of starting the experiment	Stage of growth	Date of measurement	Control trees	The trees with buds darkened for:	
				3 days	5 days
28 IV 1969	bud-bursting	10 VI	0.91 b	0.26 a	0.10 a
04 V 1970	bud-bursting	05 VII	0.94 b	—	0.56 a
11 V 1970	shoots 2.5 cm long	05 VII	0.94 b	—	0.47 a

The numbers marked with the same letter do not differ significantly at $P = 0.05$.

Table 2

The influence of darkening every second pair of buds for 5 days on the number of short shoots per ten buds in Hibernial trees

Treatment of the buds or shoots	Control trees	Experiment started	
		at bud-bursting	when the shoots were 2.5 cm long
Darkened	—	5.4 b	6.8 c
Non-darkened	4.1 ab	2.8 a	2.9 a

The darkened and 10 non-darkened buds were taken on each tree. Other details as in Table 1.

Table 3

Effect of bud or shoot thinning on the number of short shoots (shorter than 10 cm)

Cultivar	Control trees *	Number of short shoots on trees in which every second bud or shoot was removed on the following dates:					Number of all shoots on a tree**
		April 29 bud-swelling	May 6 bud-opening	May 14 shoots 3 cm	May 21 shoots 6 cm	May 28 shoots 9-13 cm	
nursery							
Hibernal	7.0 b	—	1.0 a	4.3 b	3.2 ab	5.3 b	14
Wealthy	9.5 b	4.2 a	5.2 a	4.2 a	5.1 a	6.1 a	15
greenhouse ***							
McIntosh	13.4 d	May 26 bud-swelling	May 31 bud-opening	June 5 shoots 3 cm	June 10 shoots 5 cm	—	14
		7.3 a	8.3 ab	9.0 bc	9.5 c	—	

For a given cultivar, numbers marked with the same letter do not differ significantly at $P=0.05$.

* In control trees every second shoot was omitted in calculations.

** The zone 0 to 20 cm above soil level was not taken into account.

*** Trees kept in a cold room to May 20.

after May 15 caused a resumption of growth of some of the shoots which had already started the formation of the terminal bud. Such shoots later showed a peculiar transition zone with scales instead of leaves and with nearly normally elongated internodes (Fig. 2).

The experiment designed to investigate the effect of nutrition upon the number of short and long shoots in trees was performed with 'McIntosh' trees grown in pails in a greenhouse. They were provided with two

Fig. 2. A shoot which renewed growth after a period of inhibition showing a zone with scales (indicated by arrows) attached to elongated internodes

Fig. 3. The numbers of shoots of different classes of length on unfertilized (A) and fertilized (B) 'McIntosh' trees, on different dates. White columns = rosettes less than 1 cm in length; hatched columns = short shoots 1-10 cm in length; and crossed columns = long shoots > 10 cm

drastically different nutrition levels: one group was watered only with tap water, whereas the other group was fertilized weekly, during the first month of growth, with Azofoska at 5 g per pail. Azofoska contains a mixture of macro- and micro-nutrients. The difference in the number of short shoots on the trees belonging to these 2 groups was already vi-

Table 4

Activity of the buds on one-year-old stems of cv. Antonówka seedlings.

The $^{32}\text{PO}_4^{3-}$ was uptaken for 20 hours through cut lower end

Classes of weight in mg	Average weight in mg	imp · min ⁻¹ · bud ⁻¹	imp · min ⁻¹ · mg of dry weight
Below 10	5.5	938	159
10-20	14.4	3889	260
Above 20	26.9	6329	239

Fig. 4. An illustration of the specific activities — broken line — and dry weights of consecutive buds on a single tree

sible after 2 weeks of growth and was stabilized after an additional 3 weeks (Fig. 3). The majority of buds on unfertilized trees formed rosette shoots, whereas most of the buds on well-nourished trees formed long shoots.

Investigations on the early stages of shoot vigor differentiation by the isotope method. Buds of different sizes were taken from the trees 20 hours after administration of $^{32}\text{PO}_4^{3-}$ to the cut lower end. It was found that the activity of buds depended largely on their size: the larger was the bud the higher was its total activity (Table 4). Specific activity (Fig. 4), was lowest in small buds and highest in medium buds. The large buds, those heavier than 20 mg, showed somewhat lower specific activity than the medium ones (Table 4). This phenomenon has also been observed in other experiments by Borkowska (unpublished data). To obtain further information on these differences, a separate experiment was performed in which the activity of particular parts of buds was measured. After the trees had absorbed radioactive phosphate their buds were removed, dried and divided into sizes according to their weight. They were then dissected into scales, leaf primordia and "meristematic part" as previously described. As shown in Figure 5, it was found that the meristematic part accounted for nearly the same percentage of the total

Fig. 5. Dry weights of scales (Sc), leaf primordia (Lf) and meristematic part (Mr) as percentages of the total dry weight of small buds, < 10 mg (white columns); medium buds, 10-20 mg (hatched columns) and large buds > 20 mg (crossed columns)

Fig. 6. Specific activity of scales, leaf primordia and meristematic part in small, medium and large buds. For other details see Fig. 5

dry weight of buds of all sizes (35-38%). Leaf primordia percentages were higher: 44% in small buds, 52% in medium ones and 60% in large ones. Specific activity was much lower in small buds than in medium or large ones (Fig. 6). Specific activity in leaf primordia was the highest in medium-size buds. These results cast more light on the data presented in Table 4. The characteristic feature of small buds was low specific activity in their meristematic part and in their leaf primordia. They also contained a rather large proportion of almost inert scales. Due to this, the specific activity in whole small buds was always relatively very low. The medium buds showed the highest specific activity in the meristematic part and in the leaf primordia — therefore, the specific activity in entire medium buds was the highest. The somewhat lower specific activity in the largest buds, in comparison with medium ones, seems natural. As the buds grew larger, they contained larger leaf primordia (60% of their total dry weight) which were evidently less meristematic and showed a lower capacity to uptake $^{32}\text{PO}_4^{3-}$. Also, their "meristematic part" contained a larger proportion of more inert axial tissues.

The uptake of $^{32}\text{PO}_4^{3-}$ by the upper and lower buds on horizontally treated trees. Five-day long horizontal treatment of apple trees during bud-bursting time was sufficient to evoke marked differences in the further development of buds situated on their lower and upper sides. It thus seemed desirable to investigate the influence of this treatment on the uptake of $^{32}\text{PO}_4^{3-}$ by the buds.

One-year-old stems of 'Antonovka' seedlings, growing in pails, were placed in a horizontal position for 4 days. Subsequently they were severed at the soil level and immersed with the cut end in the $^{32}\text{PO}_4^{3-}$ solution for 20 hours. During this time they also were kept in a horizontal position, so that the horizontal treatment altogether lasted approximately 5 days. Then the upper and lower buds were removed separately, dried and weighed. There were 15 trees in this experiment, each having 5 upper and 5 lower buds on the average. The buds were divided into 4 size classes as indicated in Table 5.

At the end of the 5-day horizontal treatment the upper and lower buds did not show any marked difference in size, however, their ability to uptake $^{32}\text{PO}_4^{3-}$ differed markedly. In each size class the upper buds showed much higher activity per bud and much higher specific activity than the lower buds (Table 5). This experiment was repeated with seedlings of the same cultivar during the other year and very similar results were obtained.

In a modification of this experiment the non-radioactive trees were placed in a horizontal position for 5 days and then the upper and lower buds were excised and placed separately on 4 mm³ agar blocks containing radioactive phosphate (1 μ Ci per 1 ml of agar). Blocks with buds placed on them were kept in Petri dishes in a humid atmosphere (about 100% RH) for 20 hours. It seems interesting that in this experiment the interdependence between bud size and the uptake of $^{32}\text{PO}_4^{3-}$ was completely reversed as compared with the experiments in which the buds remained on the trees during $^{32}\text{PO}_4^{3-}$ treatment (compare Tables 5 and 6): the smaller the bud the greater was its specific activity. There also was no difference in activity per bud and in specific activity between the buds taken from the upper and from the lower sides of the trees. Thus the buds must be attached to the tree during $^{32}\text{PO}_4^{3-}$ feeding in order to be able to exhibit gravimorphically induced differences in its uptake.

The development of vascular connections between the main axis and the buds of different size. Increasing differences in vascular tissue development among buds play an important role in a cybernetic model of shoot vigor differentiation (Jankiewicz 1972). It seemed necessary, therefore, to investigate them in detail. The observation of the cross sections taken at the bases of buds and shoots showed that on April 18,

Table 5

Activity of the upper and lower buds on Antonovka seedlings kept in a horizontal position for 5 days. $^{32}\text{PO}_4^{3-}$ was uptaken for 20 hours
All data are for dry weight

Classes of weight in mg	Upper buds			Lower buds		
	average weight in mg	imp/min/bud	imp · min ⁻¹ · mg ⁻¹	average weight in mg	imp/min/bud	imp · min ⁻¹ · mg ⁻¹
Below 5	2.7	410	171	3.2	291	89
5-10	7.6	1721	254	6.9	795	120
10-20	13.8	5318	373	13.6	2618	195
Above 20	22.8	5994	260	—	—	—

Table 6

Activity of the buds severed from the trees kept in horizontal position for 5 days.
The $^{32}\text{PO}_4^{3-}$ was uptaken by the excised buds from agar blocks for 20 hours

Classes of weight in mg	Upper buds			Lower buds		
	average weight in mg	imp/min/bud	imp · min ⁻¹ · mg ⁻¹	average weight in mg	imp/min/bud	imp · min ⁻¹ · mg ⁻¹
Below 10	6.0	1880	360	6.5	1930	327
10-20	14.8	2300	160	14.1	2360	170
Above 20	23.4	2290	107	23.8	2240	96

when the buds were bursting they contained protoxylem elements almost exclusively (Fig. 7). "Large" and "small" buds differed very little in the number of these elements. Six days later, on April 24, when the leaves had already emerged from the buds the difference among the larger and smaller buds was visible: the larger ones contained more metaxylem elements. This difference remained constant later. The number of protoxylem elements diminished in all categories of buds, which is a normal phenomenon. Secondary xylem vessels were observed first in the shoots collected on May 2. The number of secondary wood vessels was larger in the large shoots than in small ones. This difference has augmented later. The meaning of the differences in the content of protoxylem, metaxylem and secondary wood between small and large buds is clearer when one takes into account that the average cross section area of a protoxylem vessel is $27 \mu^2$ and that of a metaxylem vessel is $134 \mu^2$. The secondary wood vessels of small buds had cross section area $370 \mu^2$ and those of large buds $477 \mu^2$. These results show that the number of vessels is increasing much more rapidly in large buds and that these buds differentiate secondary wood much earlier than do the small ones.

Fig. 7. Numbers of vessels of protoxylem (solid lines), metaxylem (dashed lines) and secondary wood (dotted lines) in large (L) and small (S) buds or shoots on different dates. Cross sections taken at the base of a bud or shoot

Fig. 8. In poorly nourished trees only the strongest buds (those above the solid line) developed vigorous shoots. In a well nourished tree much more buds developed vigorous shoots (those above the dashed line).

Other details as in Fig. 1

Influence of growth regulators on the correlations among shoots. To observe this influence, every second bud or shoot on a one-year-old stem was treated, as described in "Methods". In such a system, the treated buds or shoots were in a correlative balance with those that were untreated, thus a substance which stimulated the growth of treated buds could cause concomittant inhibition of untreated ones.

The influence of growth regulators on the number of short shoots (shorter than 10
Every second buds were treated on a tree.

Treatment	Control trees	BA 100	BA 200	GA ₃ 400	BA 100 GA ₃ 400	IAA 100
Treated buds	5.2 bcd	2.8 ab	2.0 a	5.1 bcd	3.0ab	9.1 f
Untreated buds		5.4 cde	7.7 def	6.1 cde	7.1 def	6.1 cde

The number of short shoots that developed from treated buds depended markedly on the growth regulator used (Table 7). In control trees, 5.2 of 11 treated buds developed short shoots. Treatment with benzyladenine (BA), at a concentration of 200 mg/l, decreased markedly the number of short shoots. Gibberellin (GA₃) did not influence shoot elongation. Indoleacetic acid (IAA) showed a strong inhibitory effect. A similar effect was produced by abscisic acid (ABA). A mixture of BA at a concentration of 100 mg/l with GA₃ showed an effect similar to that of BA alone at a concentration of 100 mg/l. Benzyladenine applied in a mixture with IAA or ABA neutralized their inhibitory effect on shoot growth and the shoots grew as if treated with water only. GA₃ although non-active when used alone, nullified the inhibitory effect of IAA.

The number of short shoots among those which were produced by untreated buds did not differ consistently in this experiment. This does not mean, however, that the treatments used had no effect on the growth of untreated shoots. The indication that such an effect might exist was supplied by a comparison of the length ratio of treated to untreated shoots on differently treated trees. This ratio expressed the differences between the effects of particular treatment much better than did the number of short shoots among the treated ones (Table 8).

Table 8

The ratio between the sums of the lengths of treated and untreated shoots
of Wealthy trees. Measurements taken on July 5 1970

P=0.01

BA 100	BA 200	GA ₃ 400	BAI00 GA400	IAA 100	IAA I00 BA 100	IAA I00 GA 400	ABA 100	ABA 200	ABA I00 BA 100
1.74 d	2.47 e	1.17 c	1.94 d	0.36 a	1.21 r	0.83 abc	0.59 ab	0.38 a	0.99 bc

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cm) on Wealthy trees. Measurements taken on July 5. Concentrations in mg/l. Buds on the control trees were treated with water $P=0.05$

IAA 100 BA 100	IAA 100 GA ₃ 400	ABA 100	ABA 200	ABA 100 BA 100	Average number of shoots per tree
4.9 bcd	5.9 cde	8.1 ef	7.4 def	4.9 bcd	11
6.1 cde	5.0 bcd	6.0 cde	5.0 bcd	6.4 cde	11

DISCUSSION

This paper presents the results of experiments designed to investigate the process of differentiation of apple buds into short and long shoots. Part of the additional data related to this problem was published earlier (Jankiewicz et al. 1973). The buds in the middle part of apple tree are usually of similar size. Examination of their dry weight shows, however, some differences.

Since these initial differences among buds were not very pronounced, it was easy to experimentally direct the development of any particular bud toward the formation of a long or a short shoot. Thus, such a mild influence as darkening of certain buds for 3-5 days at bursting time caused them to develop into short shoots. In this case, the correlative positive feedback mechanism postulated by Jankiewicz (1972), which tends to inhibit all weaker buds, "struck" those that were weakened by short duration darkening. The authors have found no data in the literature concerning the effect of short duration darkening on bud development. However, the detrimental effect of prolonged darkening on peach bud growth has been reported by Erez et al. (1966).

On the other hand, reducing the competition among buds by thinning them favored the formation of long shoots (compare also the data of Jankiewicz et al. (1973). The decreasing effectiveness of thinning on later dates may be explained by the fact that the shoots which are correlative inhibited for a longer time gradually become dormant (Witkowska-Żuk and Kapuściński 1974). The weakest shoots, those forming only 1-3 small leaves, began to form the terminal bud at May 2, approximately.

A natural factor which markedly influences the correlations among buds is gravity (Wareing and Nasr 1961; Borkowska 1966; Jankiewicz 1971; Lakhoua 1972). Placing the trees in a horizontal position for only 5 days during bud bursting time stimulated markedly

the further development of the buds which were on the upper side of the tree during horizontal treatment and inhibited the buds on the lower side (Borkowska 1968). As previously reported (Jankiewicz et al. 1967, the poplars are even more sensitive to gravity and 1 day of horizontal treatment during bud bursting time was sufficient to change markedly the subsequent development of buds situated on the upper and lower sides of the trees.

When no special treatment was applied to a tree, the vigor of any particular bud depended to a large extent on the relation of its size to the size of other buds. The process of amplification of the small initial differences among buds during the course of their subsequent growth was observed in this work in several ways.

The difference in the ability to accumulate phosphate ions between the small buds on the one hand and medium and large buds on the other hand was very marked. Phosphate may be considered as representative of nutrients in general, and one may suppose that the other nutrients behave similarly. The small buds weighing less than 10 mg showed not only less uptake per bud than the larger buds, but also less uptake per mg of dry weight. Also their meristematic part was able to uptake less phosphate per mg of dry weight. This, consequently, probably brought about their weaker rate of development in comparison with larger buds.

Changes in the development of vascular strands in buds and shoots of various sizes paralleled increasing with time differences in their vigor. At bursting time (April 18), the buds of different sizes showed almost indiscernable differences in the number of protoxylem vessels. Later, profound differences appeared among the buds in the number of metaxylem and secondary xylem vessels.

The effect of nutrition on growth correlations may be presented as an interaction of 2 factors: initial bud size and nutrition level. In conditions of lowered competition for nutrients in abundantly fertilized trees, many buds formed long shoots (those above the dashed line in the model presented in Fig. 8) and only the weakest ones developed short shoots. In the case of acute competition for nutrients only a few of the strongest buds formed long shoots (those above the solid line in Fig. 8). Such a mechanism which causes the available nutrients to nourish abundantly only a few branches seems to be very important for tree survival in nature. Due to this mechanism, even in very poor nutritional conditions, the plant forms at least a few vigorous shoots that are necessary to gain the space and light for leaves; to build up the scaffold of the future crown and to suppress the competing neighbours. The effect of nutrition on growth correlations may be easier understood in the light of the results of Wagner and Michael (1971) and Woolley and

Wareing (1972) suggesting higher cytokinin production in the roots of plants on a high nitrogen level.

The experiment with different nutrition levels presents one more problem: why 2 particular buds differing only slightly in their initial size will produce a pair of similarly long shoots in conditions of good nutrition and a pair of shoots differing very markedly in their vigor in conditions of poor nutrition. This question was also set forth by McIntyre (1968) from his work with "two-bud" flax seedlings.

When it is assumed that these 2 buds initially possess an unequal number of vascular strands, it seems natural that they should grow equally well in conditions of very good nutrition, i.e., when even the bud with a thinner vascular connection receives enough nutrients and root-produced hormones from the main axis for maximal growth. However, in conditions of poor nutrition the bud which possesses a larger vascular connection receives a sufficient amount of nutrients and hormones for vigorous growth whereas the other bud will be undernourished and gradually inhibited by the correlative feedback mechanism.

For example: let us assume that the smaller bud of the pair has only 2 vessels, whereas the larger one has 3. Let us assume also that each bud needs 30 units per hour of nutrients and root-produced hormones for vigorous (maximal) growth. If, in good nutrition conditions one vessel brings 15 units per hour, both buds grow equally vigorously, because they both receive 30 units or more per hour. In poor nutrition conditions, when one vessel brings only, say, 10 units per hour, only the larger bud will receive enough nutrients for vigorous growth, whereas the other will be undernourished and gradually more and more inhibited.

As it was shown, 5-day horizontal treatment induced marked differences in the ability of the upper and lower buds to uptake $^{32}\text{PO}_4^{3-}$. This result corroborates the earlier findings of Smith and Wareing (1966) with *Betula* seedlings. The reduced ability of the buds situated on the under side of a tree to uptake phosphate and probably other nutrients also may be considered as a symptom of their "primary" inhibition due to the action of gravity on a system composed only of a stem and the buds. Such partially inhibited buds are further inhibited "secondarily" (even after reverting a tree to the normal vertical position) by a normal correlative feedback mechanism which tends to suppress all weaker buds (Borkowska and Jankiewicz 1972).

Another phenomenon which may influence the correlations among buds is their differential demand for chilling in various zones of the tree (Crabbé 1968; Champagnat 1969; Barnola 1970). This problem, however, was not investigated in this work and seems to be of minor importance in the plant material used.

The experiment in which the growth regulators were applied shows that a tree whose every second bud is treated is a good model for the investigation of correlative interdependence among buds of a young tree.

Marked growth promotion due to BA application which was observed in this experiment may indicate that cytokinins are in short supply in young apple trees and that buds or shoots compete for them. This is in accord with the important role ascribed to cytokinin in a positive feedback mechanism of growth correlations (Jankiewicz 1972). Several earlier papers have reported that cytokinins were able to induce growth of correlatively inhibited buds of apple trees (Chvojka et al. 1961; Pieniążek and Jankiewicz 1966; Williams and Stahly 1968; Kender and Carpenter 1972) and in other plants (Hugon 1961; Engelbrecht 1967; Sachs and Thimann 1967; Thimann et al. 1971; Weinberg 1969). The supposition that competition for cytokinins is an important factor in growth correlations was advanced by Thimann et al. 1971 and it is gaining more and more support recently (Wooley and Wareing 1972).

As it was shown earlier (Jankiewicz et al. 1973), the internodes of decapitated apple shoots elongate markedly in response to GA_3 and GA_{4+7} . The lack of such response when GA_3 was applied on the tips of uninjured shoots might indicate that they contained sufficient amounts of their own gibberellins, produced in young parts of shoots (Gauslund 1972) or supplied from the roots (Jones and Lacey 1968).

Indoleacetic acid is known to stimulate internode elongation of decapitated apple shoots (Jankiewicz et al. 1973) and *Pisum* shoots (Ockersee and Galston 1967) but its effect on apical meristem function is inhibitory, probably due to IAA-induced ethylene production (Apelbaum and Burg 1972). Possibly, only exceedingly low concentrations of IAA support meristem development (Šebánek 1971). The inhibition of apical meristem activity by applied IAA may be considered as a simulation of the action of natural auxin which reaches the apex of a given branch, being transported from other parts of a plant basipetally in the main axis and then acropetally in a given branch. It is known (Münch 1938) that each branch tends to inhibit the branches situated below it and to induce epinasty in them. Fulford et al. (1968) have shown an important acropetal movement of an auxin in intact shoots of fruit trees.

The inhibitory action of ABA on shoot growth found in this work is a well known phenomenon (Addicott and Lyon 1969). It is also known that ABA occurs in apple plants (Pieniążek and Rudnicki 1967; Powell 1973). It may be supposed, therefore, that ABA plays a role in correlative phenomena in apple trees. However, the concentrations needed to partly inhibit the growth of the buds were very high

in this experiment. Tucker and Mansfield (1973) attributed an important role to ABA in the mechanism of apical dominance.

The fact that treatment with cytokinin or GA_3 protected the buds or shoots against IAA or ABA-induced inhibition corroborates the findings of Sondheimer and Galson (1967), Burg and Burg (1968) and of Rudnicki et al. (1971). This makes very probable the supposition of Jankiewicz (1972) that the buds or shoots which have gained better vascular connection with the main axis and receive more root produced cytokinins and gibberellins are protected against the action of inhibitors and supraoptimal, inhibitory concentrations of natural auxin.

The results presented in this paper for apple trees support fully the conclusion of Wooley and Wareing (1972) for *Solanum andigena* that lateral shoot development is controlled by an interaction between auxin, gibberellin and cytokinin. The results presented also fit well with the cybernetic model of growth correlation (Jankiewicz 1972) which suggests how such an interaction may operate in an apple tree in coordination with nutritional factors and inhibitors.

This paper was partly supported by the U.S. Department of Agriculture, Agricultural Research Service, Grant No FG-Po-265. The authors are indebted to Dr. K. Szczepański for advice concerning statistical analyses and to Prof. dr R. Antoszewski for facilities in the Isotope Laboratory. The skillfull technical help of Mrs. F. Domostowicz, Mrs. W. Matysiak and Miss K. Galer is gratefully acknowledged. We are also greatly indebted to Dr. C. C. Zych for reviewing the manuscript.

REFERENCES

- Apelbaum A., Burg S. P., 1972. Effect of ethylene on cell division and deoxyribonucleic acid synthesis in *Pisum sativum*. Plant Physiol. 50: 117-124.
- Addicott F. T., Lyons J. L., 1969. Physiology of abscisic acid and related substances. Ann. Rev. Plant Physiol. 20: 139-164.
- Barnola P., 1970. Recherches sur le déterminisme de la basitonie chez le framboisier (*Rubus idaeus* L.) Ann. Sci. Nat. Botanique (Paris) ser. 12(11): 129-152.
- Borkowska B., 1966. Gravimorphism in young apple trees: sensitivity to gravity stimulus during dormancy and growth. Bull. Acad. Pol. Sci. Cl. V, 15: 563-567.
- Borkowska B., 1968. Studia nad grawimorfizmem u jabłoni. Praca doktorska. Instytut Sadownictwa. Skierniewice.
- Burg S. P., Burg E., 1968. Ethylene formation in pea seedlings, its relation to the inhibition of bud growth caused by indole-3-acetic acid. Plant Physiol. 43: 1069-1074.
- Caliński T., 1964. Podstawy metodyczne polowych doświadczeń z ochrony roślin. Instytut Ochrony Roślin, Poznań.
- Champagnat P., 1965. Carances et inhibition corrélative. [In:] Travaux de biologie végétale dédiés au professeur Plantefol. Masson et Cie. Paris.
- Champagnat P., 1969. La notion de facteurs de précéances entre bourgeons. Bull. Soc. bot. Fr. 116: 323-348.
- Chvojka L., Vereš K. and Kozel J. 1961. The effect of kinins on the growth

- of apple-tree buds and on incorporation of radioactive phosphate. *Biol. Plant.* 3: 140-147.
- Crabbé J., 1968. Evolution annuelle de la capacité intrinsèque de débourrement des bourgeons successifs de la pousse de l'année chez le pommier et le poirier. *Bull. Soc. Roy. Bot. Belg.* 101: 195-204.
- Engelbrecht L. von, 1967. Die Bedeutung verschiedener Cytokinine für die Überwindung der apikalen Dominanz bei *Nicotiana glauca*. *Wiss. Z. Univ. Rostock Matem. Naturwiss. Reihe 16*: 647-649.
- Erez A., Samish R. M., and Lavee S., 1966. The role of light in leaf and flowerbud break of the peach (*Prunus persica*). *Physiol. Plant.* 19: 650-659.
- Fulford R. M., Quinlan J. D., Lacey H. J., and Barlow H. W. B., 1968. The acropetal movement of growth substances from young leaves on woody shoots. [In:] Wrightman F., Setterfield G. (eds.): *Biochemistry and physiology of plant growth substances*. Ruge Press, Ottawa.
- Gunckel J. E., Thimann K. V., 1949. Studies of development in long shoots and short shoots in *Ginkgo biloba* L. III. Auxin production in shoot growth. *Amer. J. Bot.* 36: 145-151.
- Hugon E., 1961. Influence comparée de quelques vitamines et de la cinétine sur la dominance apicale. *Comptes Rendues Acad. Sci. (Paris)* 252: 776-778.
- Jankiewicz L. S., 1971. Gravimorphism in higher plants. [In:] Gordon S. A., Cohen M. J., (eds.): *Gravity and the organism*. Univ. Chicago Press pp. 317-331.
- Jankiewicz L. S., 1972. A cybernetic model of growth correlation in young apple trees. *Biol. Plant. (Praha)* 14: 52-61.
- Jankiewicz L. S., Plich H., Borkowska B. and Moraszczyk A., 1973. Growth correlations and the shape of young trees and shrubs. *Acta Hort.* 34: 107-116.
- Jankiewicz L. S., Szrednicka W. and Borkowska B., 1967. Gravimorphism in the poplar (*Populus* sp.). *Bull. Acad. Pol. Sci. Cl. V*, 15: 111-113.
- Kender W. J., Carpenter S., 1972. Stimulation of lateral bud growth of apple trees by 6-benzylaminopurine. *J. Amer. Soc. hort. Sci.* 97: 337-380.
- Lakhoua H., 1972. Étude de l'arcure et du gravimorphism chez jeunes pommier (*Malus sylvestris* (L.) Mill.) en tant que facteurs de la ramification. *These Doct. Univ. Paris. VI*.
- McIntyre G. I., 1968. Nutritional control of the correlative inhibition between lateral shoots in the flax seedlings (*Linum usitatissimum*). *Can. J. Bot.* 46: 147-155.
- Mosteller F., Youtz C., 1961. Tables of the Freeman-Tukey transformation for the binominal and Poisson distributions. *Biometrika* 48: 443-440.
- Ockerse R., Galston W., 1967. Gibberellin-auxin interaction in pea stem elongation. *Plant Physiol.* 42: 47-54.
- Pieniążek J., Jankiewicz L. S., 1966. Development of collateral buds due to benzylaminopurine in dormant apple shoots. *Bull. Acad. Pol. Sci.* 14: 185-187.
- Pieniążek J., Jankiewicz L. S., 1967. Initiation of cambial activity during dormancy due to naphthaleneacetic acid, 6-benzylamino-purine and gibberellin in the apple shoot. *Wiss. Z. Univ. Rostock Matem. Naturwiss. Reihe 16*: 651-652.
- Pieniążek J., Rudnicki R., 1967. The presence of abscisin II in apple leaves and apple fruit juice. *Bull. Acad. Pol. Sci. Cl. V*, 15: 251-254.
- Rudnicki R., Kamiński W., Pieniążek J., 1971. The interaction of abscisic acid with growth stimulators in germination of partially after-ripened apple embryos. *Biol. Plant.* 13: 122-127.
- Sachs T., Thimann K. V., 1967. The role of auxin and cytokinins in the release of buds from dominance. *Amer. J. Bot.* 54: 136-144.

- Sebánek J., 1971. Výklad vrcholové dominance v rostlině na podkladě studia korelace mezi dělohami a kotylárními pupeny u hrachu (*Pisum sativum* L.). Acta Univ. Agric. Brno. 7: 393-418.
- Smith H., Wareing P. F., 1966. Apical dominance and the effect of gravity on nutrient distribution. Planta 70: 87-94.
- Sondheimer E., Galson E. C., 1966. Effects of abscisin II and other plant growth substances on germination of seeds with stratification requirements. Plant Physiol. 41: 1397-1398.
- Thimann K. V., Sachs T. and Mathur K. N., 1971. The mechanism of apical dominance in *Coleus*. Physiol. Plant. 24: 68-72.
- Tucker D. J., Mansfield T. A., 1973. Apical dominance in *Xanthium strumarium*. Jour. exp. Bot. 24: 731-740.
- Wagner H., Michael G., 1971. Der Einfluss unterschiedlicher Stickstoffversorgung auf die Cytokininbildung in Wurzeln Sonnenblumenpflanzen. Biochem. Physiol. Pflanzen 162: 147-158.
- Wareing P. F., Nasr T. A. A., 1961. Gravimorphism in trees. 1. Effect of gravity on growth and apical dominance in fruit trees. Ann. Bot. 25: 321-340.
- Weinberger J. H., 1969. The stimulation of dormant peach buds by a cytokinin. Hort Science 4: 125-126.
- Williams M. W., Stahly E. A., 1968. Effect of cytokinins on apple shoot development from axillary buds. Hort Science 3: 68-69.
- Witkowska-Zuk L., Kozłowska W., 1973. Investigations on the dormancy of *Fraxinus excelsior* L. buds. Sequence of growth period, correlated inhibition and rest of shoot apex in the annual cycle. Acta Soc. Bot. Pol. 42: 627-636.
- Woolley D. J., Wareing P. F., 1972. The interaction between growth promoters in apical dominance. I. Hormonal interaction, movement and metabolism of a cytokinin in rootless cuttings. II. Environmental effects on endogenous cytokinin and gibberellin levels in *Solanum andigena*. New Phytol. 71: 781-793, 1015-1025.

Korelacje między pędami bocznymi u młodych drzewek jabłoni

Streszczenie

Badano korelacje wzrostowe między pąkami pachwinowymi i wyrastającymi z nich pędami u jednorocznych jabłoni. Zaciemnienie co drugiego pąka na 3-5 dni w czasie pęknięcia pąków sprzyjało tworzeniu się krótkopędów. Usunięcie co drugiego pąka lub pędu powodowało, że z pozostałych powstały przeważnie długopędy.

Obfite odżywianie mineralne drzewek sprzyjało tworzeniu się na nich długopędów. Gdy drzewek nie poddawano żadnemu specjalnemu traktowaniu i gdy były one nie przycięte na wiosnę, początkowe, niewielkie różnice w wielkości pąków grały ważną rolę zapoczątkowując różnicowanie się długopędów i krótkopędów. Pąki średniej wielkości i duże wykazywały zdolność do akumulacji większej ilości radioaktywnego fosforanu na jednostkę suchej masy niż pąki małe. To wskazuje, że początkowe niewielkie różnice między pąkami są wzmacniane przez korelacyjny mechanizm. U drzewek umieszczonych w pozycji poziomej na okres 5 dni pąki wszystkich klas wielkości położone na dolnej stronie wykazywały osłabione pobieranie radioaktywnego fosforanu. Regulatory wzrostu, zastosowane w bardzo małej ilości, w kropli wody, na wierzchołek wzrostu co drugiego pąka lub pędu, zmieniały w znacznym stopniu korelacje między nimi. Rozwój połączeń waskularnych między pąkami różnej wielkości a osią główną był częścią procesu szybkiego różnicowania się pąków co do siły wzrostu.