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A Cybernetic Model of Growth Correlation in Young Apple Trees*

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Abstract. Growth correlations among lateral shoots of one-year-old apple trees *Malus* MILL., were described. The existence of a mechanism was postulated through which small original differences between buds or young shoots are quickly augmented, thus leading to differentiation of long shoots and short shoots. Existing hypotheses do not seem sufficient for explaining correlative phenomena of this type; a cybernetic approach was therefore applied. Studying growth correlations in terms of cybernetic revealed that previous hypotheses concerning correlations do not contradict each other as often thought, but depict different links in a more general chain of events. A cybernetic model points out the importance of root influences in interaction among shoots. It also shows that synergism between auxin, gibberellin and cytokinin in xylem and phloem differentiation and in starch metabolism is very important for understanding correlations in apple trees.

During the long history of investigation of plant growth correlations (see recent review by PHILLIPS 1969) several hypotheses attempting to explain their mechanism were put forward.

The best known hypothesis is that of THIMANN (1937). He maintained that auxin produced in the shoot apex directly inhibits the growth of axillary buds. Recently SACHS and THIMANN (1967) have modified this hypothesis as follows: Auxin external to the bud restricts its auxin production thus inhibiting its growth "just as external histidine can prevent E. coli from synthesizing histidine". Recently BURG and BURG (1968) showed that there is a possibility of "direct inhibition of buds" by the auxin, due to auxin-induced production of ethylene in the stem.

It was furthermore revealed, that cytokinin is able to protect buds from inhibition imposed by applied auxin (WICKSON and THIMANN 1958, HUGON 1967) or imposed by a growing apex, both in apple trees (CHVOJKA *et al.* 1961, PIENIĄŻEK and JANKIEWICZ 1966a, WILLIAMS and STAHLY 1968) and in herbaceous plants (SACHS and THIMANN 1964, ENGELBRECHT 1967, HUGON 1967). The experiments of BURG and BURG (1968) throw light on the possible mechanism of this cytokinin effect: They have shown that cytokinin drastically decreases the sensitivity of buds to the inhibitory action of ethylene. A few instances were also noted where cytokinin, applied together with auxin, enhanced inhibition of axillary bud growth (DAVIES *et al.* 1966, HILLMAN 1970), but these seem to be rather exceptional.

As early as 1908 DOSTÁL had postulated that specific factors responsible for correlative inhibition of buds are produced in leaves and cotyledons. The concept of specific correlative inhibitors was developed further by SNOW (1937) and other authors (LIBBERT 1961, LIBBERT and LIEBNOW 1964, GOODWIN and CANSFIELD 1967), however, they were unable to identify them chemically. The discovery of abscisic acid (ABA) in many plants (MILBORROW 1967), including apple trees (PIENIĄŻEK and RUDNICKI 1967), recently revived the search for specific inhibitors

*** This paper is dedicated to the 86th birthday of Prof. Dr. R. Dostál, member of the Czechoslovak Academy of Sciences.**

playing a role in growth correlations. DÖRFFLING (1966), WAREING *et al.* (1967), and ARNEY and MITCHELL (1969), suggest that ABA may indeed play an important role in growth correlations. However, HILLMAN (1970) has shown that ABA exhibits no direct inhibitory action on *Phaseolus* buds; he found that it was able only to enhance inhibition caused by other growth regulators.

The possible role of phenolic growth regulators in the correlations has been investigated by TOMASZEWSKI (1964). He assigned an important role to the balance between monophenols and polyphenols. This balance may regulate the activity of IAA oxidase which, in its turn, may significantly influence the level of auxin in the tissues.

The development of vascular connections between the bud and the main stem was considered by Van OVERBEEK (1938) as an essential factor in growth correlations. More recently SOROKIN and THIMANN (1964) have shown that applied cytokinin markedly stimulated the formation of vascular connections between the bud and the stele of the main stem, whereas auxin treatment impeded it.

The hypothesis of WENT (1939) assumes that correlative inhibition of lateral buds is a result of preferential transport of nutrients toward the growing apex or toward the source of applied auxin. "Auxin directed" nutrient transport was displayed in the experiments of several authors (BOOTH *et al.* 1962, NAKAMURA 1964, ŠEBÁNEK 1966a, b). The hormones may also be attracted toward the auxin source as shown by ŠEBÁNEK and HINK (1967). Recently SETH and WAREING (1967) revealed that attraction of nutrients toward the source of auxin is greatly enhanced when this compound is applied together with gibberellin and cytokinin. Some authors (ŠEBÁNEK 1966a, PHILLIPS 1968) suggest, however, that starvation of lateral buds does not take place as a result of preferential nutrient transport toward the auxin-treated part. They conclude that "auxin-directed transport" seems not to be the causal factor of correlative inhibition of axillary buds. Little is known about how hormones may regulate the transport of nutrients (ANTOSZEWSKI 1967).

Besides having a synergistic stimulatory effect on "auxin-directed nutrient transport", gibberellins (GA) also play several other roles in growth correlations. Gibberellin is known to enhance basipetal transport of IAA. In this way it can increase the inhibitory effect of IAA when applied together with it to decapitated stems (JACOBS and CASE 1965, RUDDAT and PHARIS 1966, SCOTT *et al.* 1967, TOMASZEWSKI 1970). On the other hand, GA stimulates growth of buds which have already started to develop (WICKSON and THIMANN 1958, HUGON 1967). This effect may explain the enormous stimulation of bud development by GA paste in HILLMAN's (1970) experiments with decapitated bean plants. For a more detailed discussion of the GA role in apical dominance, see also PHILLIPS' (1969) paper.

CHAMPAGNAT (1952, 1965a, b) and his coworkers (HUGON 1967, REMY 1961), as well as GREGORY and VEALE (1957) gave attention to the role of plant nutrition in growth correlations and to the inhibition of buds caused by a lack of nutrients and growth stimulators. Some investigators, for instance GREGORY and VEALE (1957), and MCINTYRE (1964, 1968), believe that the correlations among buds and shoots result primarily from competition for a limited nutrient supply.

This short review indicates that there are several groups of authors holding different and often contradictory views on the mechanism of growth correlations. This work is intended to present an explanation of growth correlations in the apple-tree in terms of cybernetics, since the cybernetic method of description is especially valuable for complex phenomena in which several processes are linked.

Plant Material Used

Intact one-year-old apple trees of several cultivars, McIntosh, Wealthy, Linda, and others, were chosen for this study. These were nonramified whips at the beginning of observations in early spring. Ramifications sometimes present in the lowest part of the trees were removed before bud swelling. Such trees in their middle and upper part have about 20—35 buds which all start development in the spring and have rather similar growth potential, this meaning that they have similar chances of forming long shoots or short shoots. Experiments with ringing and with bud thinning (JANKIEWICZ 1956, 1961, PLICH and JANKIEWICZ, in press) have shown that it is not difficult to turn a given bud toward the formation of a long shoot or a short shoot according to the wish of the experimenter. In untreated trees, the character of shoot growth is usually determined during an early phase of development (PLICH and JANKIEWICZ, in press). Soon after the shoots emerge, a part of them begin to develop vigorously, whereas others gradually

become inhibited (Fig. 1). The percentage of shoots on a tree which grow long seems to depend markedly on environmental conditions. It has therefore been concluded that there exists a correlative mechanism which drastically augments differences in the vigour between the shoots, thus causing their differentiation into long and short shoots.

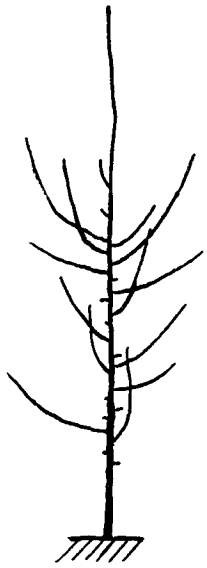

Fig. 1. Unpruned tree of the cultivar Linda. Part of the buds grew into long shoots whereas the others formed short shoots.

The Model of Growth Correlations Between Shoots

To simplify description, only two buds will be considered; only one of them is presented in Fig. 2. We must bear in mind, however, that on a tree each bud or shoot is influenced by many other buds or shoots.

It is assumed that there exists a minute initial difference between the two buds under con- sideration. For instance, they may differ in size or conditions for growth. As a result, one bud has an advantage resulting in somewhat better incipient growth and slightly higher auxin production (a), (letters in parenthesis in the following discussion refer to the schematic representation in Fig. 2). Part of this auxin is used for stimulating axis elongation (a'); the remainder augments the auxin pool which is transported basipetally toward the main axis (a''). An elongating shoot axis with its leaf primordia and developing leaves likewise produces auxin (b, b'), (Gunckel and Thimann 1949, Hatcher 1959). A part of the auxin pool transported toward the main axis is probably temporarily bound (d, d') or destroyed (e), the activity of the destructive system being influenced by the balance between polyphenols and monophenols (Tomaszewski 1964). The remaining auxin is transported basipetally in the main axis, causing several important phenomena along its path:

1. It stimulates cambial activity (f) and the production of new xylem and phloem elements (Söding 1952, Digby and Wareing 1966a, Pieniążek and Jankiewicz 1966b, Pieniążek and Saniewski 1968a). These newly produced vascular strands connect the bud with the main axis (f') and thereby also with the root system.

2. It evokes the attraction of nutrients toward the auxin source (g), thereby causing a part of the transporting system to begin working to the advantage of a particular bud.

3. It makes available for growth stored saccharide reserves by stimulating the conversion of starch into simple sugars (h), (Pieniążek and Saniewski 1968b).

These three effects result in a more efficient flow of stored sugars and nutrients from the roots toward the developing shoot having the small initial adventage (h', j, j'). Being better supplied with nutrients (k), the bud with the initial advantage becomes more vigorous, and produces an increasing amount of auxin. The difference between the two buds increases. Such cyclic dependence is referred to in cybernetics as positive feedback (Greniewski 1969).

The foregoing describes the first part of the model. The second part describes the role of the root system in growth correlations. In Fig. 2 the influence of the root system is represented by dashed lines.

The bud having a better connection with the vascular system of the main stem also has better access to hormones produced in the roots. There are numerous data indicating that cytokinins and gibberellins are produced in the roots (l) and are transported within the xylem sap, (Kulaeva 1962, Mothes 1964, Nitsch 1968, Reid and Burrows 1968). Cytokinin activity and gibberellin activity was found in apple xylem sap by Luckwill and Whyte (1968), and by Jones and Lacey (1968).

Moving with the transpiration stream to the apical region of a young lateral shoot (m'), cytokinins and gibberellins probably stimulate the meristem activity; however, this phenomenon is little known in apple trees. It has also been suggested that gibberellins are not only supplied from roots but are also produced in young leaves of apple shoots (Kato and Ito 1962, Luckwill 1968).

Cytokinins and gibberellins seem to be indispensable for the internode elongation of apple shoots (m''), Jones 1967, Pieniążek 1968, Plich and Jankiewicz 1970). Therefore, a shoot establishing better vascular connections with the main stem is better able to elongate.

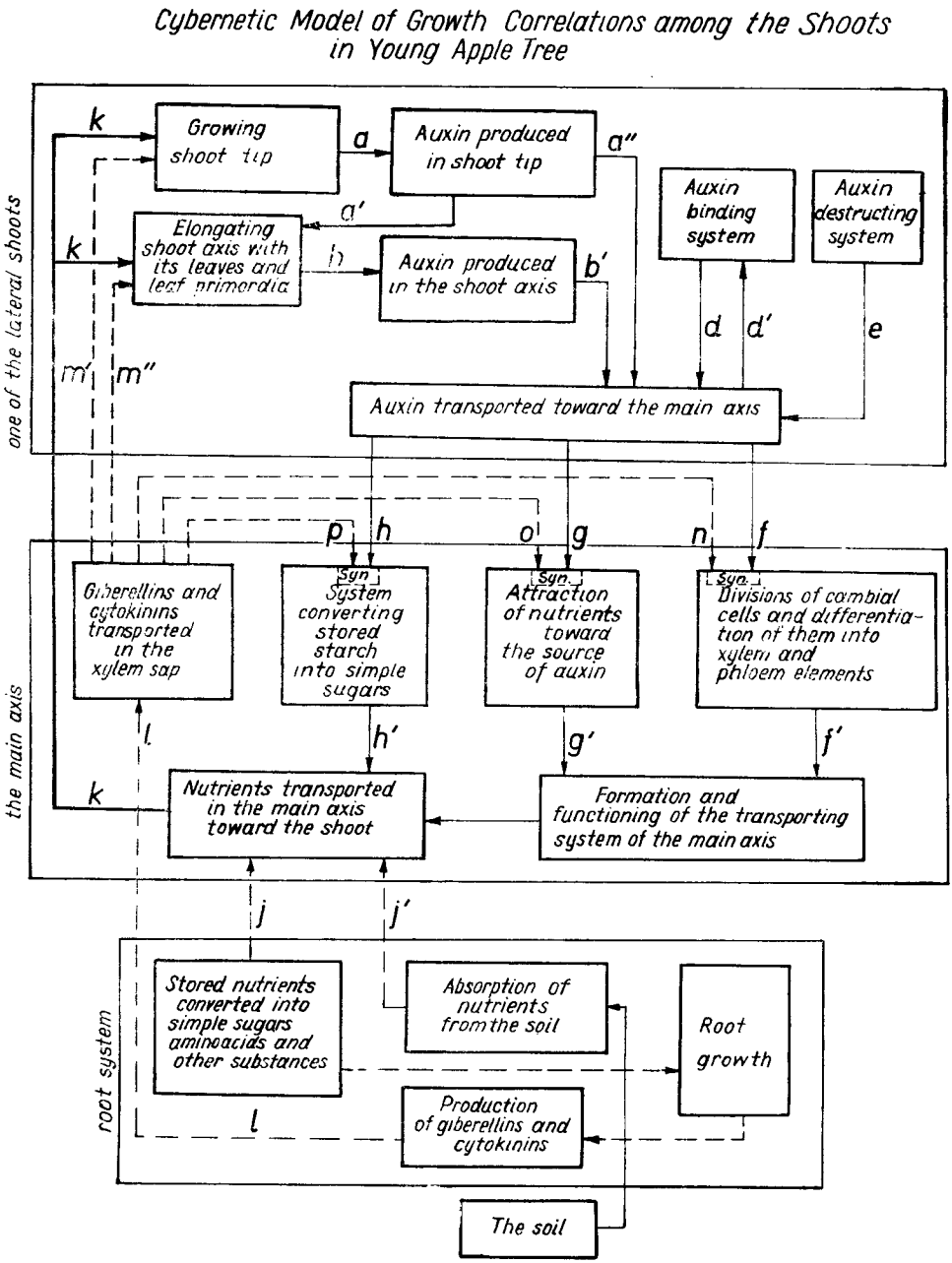

Fig. 2. Model of growth correlations among shoots. Only one lateral shoot is presented. The influence of the root system is indicated by broken lines. "Syn" refers to a subsystem responsible for synergism between auxin and other hormones.

The effects of gibberellins and cytokinins in the main axis appear to be of great importance in growth correlations. Together with auxins, these compounds act synergistically in stimulating cambial activity in apple tress (*n*), (PIENIĄŻEK and JANKIEWICZ, 1966b, PIENIĄŻEK and SANIEWSKI 1968a). Moreover, auxin alone is unable to cause normal xylem differentiation in apple trees. A differentiation pattern similar to that found in the spring wood may be obtained only when auxin is applied together with gibberellin or cytokinin, or both (PIENIĄŻEK and JANKIEWICZ, 1966b, PIENIĄŻEK and SANIEWSKI 1968a). The necessity of both auxin and gibberellin for normal xylem differentiation was also found in other broadleaved trees (DIGBY and WAREING 1966a, b). Recently FOSKET and TORREY (1969) have shown that both cytokinin and auxin are necessary for xylem formation in soybean tissue culture. As revealed by DIGBY and WAREING 1966a, b), the interaction of gibberellin with auxin is also necessary for normal phloem differentiation. Thus a shoot having better access to cytokinin and gibberellin produced in roots is better able to build the vascular system connecting it with the main stem and the roots.

The role of synergism between the auxin, cytokinin and gibberellin in the process of attraction of nutrients toward the source of auxin (*o*) has not been investigated in apple trees but it is very probable that the phenomena observed by SETH *et al.* (1967) occur in this plant.

Gibberellins also display synergism with auxin in stimulating the breakdown of starch stored in the main axis (*p*). In the presence of gibberellin the effects of auxin are more pronounced (PIENIĄŻEK and SANIEWSKI 1968b). The stronger shoot is thereby able to exploit a greater portion of the winter reserves of sugars.

To summarize, due to interactions between auxin, gibberellin and cytokinin, the shoot which initially starts with a little higher auxin production very quickly attains dominance over the weaker shoot. It monopolizes more and more of the limited supply of nutrients and hormones coming from the roots and the reserves of sugars stored in the main axis.

From a cybernetic point of view, the synergistic effects produced by auxin together with gibberellin and (or) cytokinin greatly enhance the positive character of the feedback presented in the first part of the model, and indicated by solid lines in Fig. 2.

The Possible Roles of Growth Inhibitors

The data concerning growth inhibitors in apple trees are not plentiful. Abscisic acid (ABA) has been found in apple leaves and fruits (PIENIĄŻEK and RUDNICKI 1967). Phenolic substances occur abundantly in apple trees (WILLIAMS 1960, SARAPUU 1964, GROCHOWSKA 1967). They may exhibit inhibitory action by stimulating the auxin oxidizing system (TOMASZEWSKI 1964). But it is also possible that they cause a direct inhibitory influence on extension growth or mitotic activity.

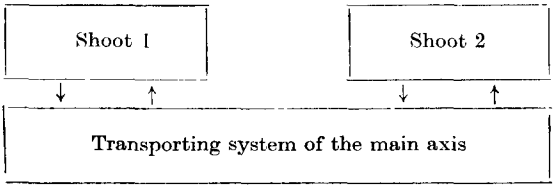

Fig. 3. Each shoot probably supplies inhibitors to the transporting system of the main axis but also reciprocally receives them.

It is very probable that every shoot produces ABA and other inhibitors and supplies them to the transporting system of the main axis, whence they are distributed throughout the tree (Fig. 3); thus every shoot not only produces but also receives inhibitors. The reaction of a vigorous and of a weak shoot to a given amount of inhibitory substance may be, however, quite different. A vigorous shoot has better access to nutrients, gibberellins and cytokinins transported from the roots. As shown by SONDHEIMER and GALSON (1966) and by RUDNICKI *et al.* 1971 gibberellins and cytokinins may play a protective role against the action of ABA. This results in the stronger shoot increasing its dominance over the weaker shoot.

From the cybernetic point of view, this "selective inhibition" of a weaker bud by inhibitors means additional strengthening of the positive character of the feedback.

Discussion

The model presents a mechanism by which differences among shoots may be augmented. It should be obvious that the growth of dominant shoots may be stimulated only to a certain level, at which limiting factors become prevalent, tending to keep further growth at a steady rate.

Competition between buds or shoots plays an important role in the presented feedback mechanism. Therefore, this mechanism acts only when at least one factor limits growth; in other words, competition cannot take place if there is nothing to compete for. Depending upon circumstances, hormones or nutrients may play a role as a limiting factor. Under poor nutritional conditions a smaller proportion of buds develop into long shoots. In well fertilized nurseries where nutrient competition is lessened, often most of the laterals form vigorous shoots.

The hormonal system of apple trees is not yet well understood. GUR and SAMISH (1968) have found two growth-promoting substances, supposedly indoleacetonitrile and IAA, in apple shoots. Indoleacetic acid and several indole derivatives were also found in apple by RAUSSENDORFF-BARGEN (1962). Gibberellin activity has been found in apple shoots (KATO and ITO 1962). Gibberellins A_4 and A_7 have been identified in apple fruitlets (DENNIS and NITSCH 1966) and in developing apple seeds (LUCKWILL *et al.* 1969). Gibberellin activity was detected in apple xylem sap by JONES and LACEY (1968). Cytokinin activity has been shown to occur in apple xylem sap (LUCKWILL and WHYTE 1968) and in apple fruitlets (ZWAR and BRUCE 1970). It is therefore clear that all 3 groups of hormones, auxins, cytokinins and gibberellins, occur in apple trees.

The results obtained with cytokinins by CHVOJKA *et al.* (1961), PIENIĄŻEK and JANKIEWICZ (1966a) and WILLIAMS and STAHLEY (1968), show that these compounds are able to release the bud from inhibition at different times of the year. It could be therefore suspected that cytokinins are very often limiting factors in growth correlations.

The release of buds from inhibition should include unblocking of mitotic activity in the shoot apex. Indeed, the observations of DWIVEDI and NAYLOR (1968) have shown that doubling of the DNA content in the nuclei of cells in the "zone of inhibition" in the apex is the earliest manifestation of incipient bud growth after release from inhibition. In apple trees, almost all buds start to develop after the winter, and hence for understanding growth correlations in this species it would be more valuable to study the progressive inhibition of meristematic activity n short shoot apices.

The presented model deals with apple trees. The question arises as to whether it may be generalized to include other plant species and other types of growth correlations. The author is of the opinion that this model may be useful for understanding correlations among the shoots in numerous species of woody plants. It may also help to explain cases where differences in vigour between buds or shoots increase rapidly, as for instance differences between two shoots developing from cotyledonary buds after decapitation. Such plants have been used by many authors (DOSTÁL 1959, ŠEBÁNEK 1966b, HUGON 1967, MC INTYRE 1968). It may also help to explain the classical example of growth correlation between the stem apex and lateral buds.

The presented model embraces in one system hypotheses which have often been considered contradictory or alternative. It includes elements of almost all the more important hypotheses concerning growth correlations: for instance that of THIMANN (1937) and SACHS and THIMANN (1964), that of CHAMPAGNAT (1952, 1965a) and GREGORY and VEALE (1957), as well as the "inhibitor hypothesis" of SNOW (1937) and GOODWIN and CANSFIELD (1967) and the hypothesis of OVERBEEK (1938) and SOROKIN and THIMANN (1964). In terms of the cybernetic model presented here, these

hypotheses depict only various links in a more general chain of events which the author has attempted to reconstruct in this paper for young apple-trees.

Some elements of cybernetic thinking may be found in earlier papers dealing with growth correlations, notably those by NAKAMURA (1964), MC INTYRE (1964), and LUCKWILL (1968). The concept of positive feedback was first applied to growth correlations by JANKIEWICZ (1967). The supposition that different hypotheses concerning growth correlations may not be contradictory was earlier expressed by CHAMPAGNAT (1965b).

Experiments are being continued in the hope of supplying more precise data concerning the importance of particular links in the model presented.

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L. S. JANKIEWICZ, Oddělení fysiologie rostlin, Výzkumný ústav ovocnářský, Skierniewice, Polsko: **Kybernetický model růstové korelace u mladých jabloní.** — Biol. Plant. **14** : 52—61, 1972.

Jsou popsány růstové korelace mezi postranními letorosty jednoletých jabloní *malus* MILL. a postulován mechanismus, který rychle zvyšuje původně malé rozdíly mezi pupeny a mladými letorosty, a tím vyvolává diferenciaci v dlouhé a krátké letorosty. Protože korelace tohoto typu nelze vysvětlit na základě dosavadních hypothes, bylo použito kybernetických metod. Kybernetickým studiem růstových korelací bylo zjištěno, že dřívější hypothesy o korelacích si navzájem neodporují, jak se často předpokládalo, ale že představují různé články v obecnějším řetězu případů. Kybernetický model zdůrazňuje význam vlivu kořenů na interakce mezi letorosty. Ukazuje dále, že synergický účinek auxinu, giberelinu a cytokininu na diferenciaci xylemu a floemu a na metabolismus škrobu je závažný pro pochopení korelací u jabloní.