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Factors influencing lateral-branch formation in woody plants

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One of the most appealing characteristics of a plant, even to inexperienced observers, is its branching habit, i.e. the way the plant builds up its system of ramifications.

With young, especially maiden woody (perennial) plants this natural branching is called *syllepsis*. *Syllepsis* originates from axillary primordia showing no rest symptoms (Jankiewicz 1984). It occurs mainly during the early developmental years in tree life indicating tree vigor (Crabbe 1987). The type of *syllepsis* ultimately determines future natural plant shape. Sylleptic branching could be used as an early characteristic to evaluate the later branching behavior of woody plant cultivars (Costes and Guedon 1997).

Plant branching pattern is an important quality indicator for ornamental trees and shrubs (De Silva et al. 1976, Karhu 1997), landscape trees (Haserodt and Snydor 1983) and fruit trees (Plich and Basak 1978, Quinlan and Pakenham 1981). An effective process of shaping ornamental plants aims to provide uniform appearance (ex. *Azalea, Bougainvillea, Fuchsia, Geranium, Kolanchoe spp.*, et.) or prevent tree breakage due to canopy malformation (ex. Callery pears) (Gerhold and McElroy 1994, Bailey 1997). The use of quality branched fruit trees in the orchards greatly contributes to improved future performance since the laterals provide sites for flower bud setting.

Various procedures are used to promote lateral-branch formation in young fruit and ornamental trees (Keever and Foster 1990, Volz et al. 1994). A direct effect of applying different techniques to promote branching is an improvement in tree structure, which is usually accompanied by both an increase in the amount of feathers and a thickening of the stem (Van Oosten 1978). In fruit trees, far more important, however, is a secondary effect of branching: the induction of earlier and heavier cropping of feathered trees at the initial stage of orchard establishment in comparison with their unfeathered counterparts (Johann 1985, Quinlan 1985). Although the difference in cropping between initially branched and unbranched trees diminishes with tree age (Poniedziałek et al. 1994), it provides for some income in the first years after orchard establishment (Ferree and Rhodus 1987) thus a quick return on the money invested.

APICAL DOMINANCE

Plants demonstrate a great number of mutual correlations. The most common example of correlative inhibition is apical dominance, that is when apical portions of the shoot exert control over the outgrowth of the lateral buds or shoots. The way this inhibitory influence is transmitted within a plant is not fully understood. Progress in studies on apical dominance during the past several decades has been slow (Cline 1991). Part of the difficulty in understanding the phenomenon of apical dominance is that it involves variable, uncontrolled features of the environment which can override genetic features and thus alter chemical events regulating its mechanism (Martin 1987). There are two main conceptions explaining the mechanism of apical dominance: the first a 'hormonal' and the second, 'nutritive' (Phillips 1975). The 'hormonal' theory assumes that the growing apical bud of a parent shoot is the source of some correlative signal, probably of auxin origin, which restricts the development of axillary buds. This signal carries integrated information about the development, size and environment of individual shoots (Sachs 1993). Li and Bangerth (cited by Jankiewicz in Jankiewicz 1997) believe that the mechanism of apical dominance consists in preventing auxin export from axillary buds and shoots to the parent shoot by a basipetal stream of auxin from terminal bud(s), thus inhibiting the outgrowth of axillary buds. The other role is imputed to cytokinins (Phillips 1975). It is thought then, that the rate of development of axillary buds, thus branching is controlled by interaction of endogenous hormones, with auxins and cytokinins playing major role (Sachs and Thimann 1967). Cytokinin effect, however appears to be secondary in most cases, to the inhibitory effect of some signals originating from the upper bud (Cline 1991). Li and Bangerth (cited by Bangerth 1993) showed that cytokinin stimulated auxin transport thus reducing its concentration in the sap of parent shoot; in this way, cytokinins may contribute to releasing axillary buds from apical dominance. However, the degree of bud release from apical dominance appears to be specifically related to the place of application of exogenous cytokinin (Bangerth 1993). It is also believed that other endogenous bioregulators, such as ethylene or ABA, may also effect to some extent apical dominance (Jankiewicz 1984 after Burg and Burg). At present time, there is no sufficient evidence to support the role of ethylene and/or ABA in controlling lateral outgrowth (Cline 1991, Chen et al. 1997). Recent studies on many plants indicated that exogenous gibberellins (GA) alone do not initiate bud outgrowth in intact plants (Cline 1991). GA strengthens apical dominance, probably by promoting elongation of the main shoot (Quinlan and Tobutt 1990).

However, it was found that the endogenous level of GA_3 increased after combining BA treatment and decapitation, suggesting that gibberellins may play some role in axillary bud outgrowth (Chen et al. 1997). The 'nutritive' theory states that apical dominance is controlled by the internal competition between lateral buds and the parent shoot for water, mineral nutrients and carbohydrates. Kasperbauer (1971) reported that exposure of tobacco plants to red light promoted branching, whereas no such effect has been found with maiden apple trees (Tromp 1993). Studies showed that the basic inorganic nutrients, with nitrogen as one of the major elements, affected apical dominance (Martin 1987). Research by McIntyre (cited by Martin 1987) showed that plant water status overruled nitrogen and light regimes in influencing apical dominance. Wang et al. (1994) believe that auxins presumably produced by the terminal bud restrict the movement of water to lateral buds inhibiting tree growth, thus accentuating apical dominance. It is known that cytokinins, gibberellins and ABA level are markedly affected by water content in plants (Phillips 1975). Results of recent studies on the role of soil temperature and air humidity in promoting lateral branch formation support a 'nutritive' theory (Tromp 1996). However, a review of the literature on apical dominance shows that in most instances both 'hormonal' and 'nutritional' theories complement each other (Phillips 1975, Martin 1987, Cline 1991). Jankiewicz (1972) has presented a cybernetic model of growth correlations in young apple trees. This model links together all existing growth correlation hypothesis and explains why some buds become dominant over others. The principle of this model is based on the assumption that small differences between buds at the moment of growth initiation are quickly augmented, thus leading to differentiation of long and short shoots. This model also shows that synergism between auxin, gibberellin and cytokinin in vascular tissues and in starch metabolism is very important for understanding correlations in apple trees.

Releasing axillary buds from apical dominance forms the basis for feather induction. The ability to form laterals differs markedly among various species and cultivars of fruit trees. The phenomenon of apical dominance plainly has practical implications for the horticulturist because it influences natural branching of many plants, especially woody species. However, it can be modified by various endogenous and exogenous factors, which allows for the shaping of trees in a way that meets the cultural requirements of fruit, landscape and/or ornamental plant industry.

NATURAL SYLLEPSIS IN PLANTS

The rate of plant vegetative growth and the pattern of its development depend upon plant genotype, environmental factors and/or applied growing technologies (Howard et al. 1974 and 1975, Keever and Foster 1990, Palmer et al. 1994, Czarnecki 1996, Sadowski and Dąbrowski 1998). However, the branching ability is mainly under genetic control (Quinlan and Tobutt 1990). There have been attempts to use molecular biology to transfer gene(s) regulating branching behavior into newly bred apple cultivars (Brown and Weeden – pers.com.). Ruiz-Sifre et al. (1995) reported that when a free-branching poinsettia hybrid (donor) was grafted onto a poinsettia restricted-branching cultivar (receiver), the length and number of axillary shoots increased on receiver plant. *Syllepsis* in the plant world varies immensely. Temperate fruit species are characterized by rather limited ability to branch; yet there are great differences among the species, and also among the cultivars within the same species. Broadly speaking, apples, pears and sweet cherries do not branch readily in contrast with peach, apricot, sour cherry and plum cultivars. Many plants including some woody ornamentals and subtropical fruit species also face problems with inadequate branching that are similar to those found in temperate fruit species (Nauer and Boswell 1981, Joyroe-Cournoyer and Newman 1995, Al-Jouboory et al. 1997). Regardless of growing conditions, any plant has its own ability to naturally induce sylleptic shoots. This is commonly known under the term „*branching ability*" (Larsen 1979, Costes and Guedon 1997). It is also known that different cultivars of the same species that are grown in comparable environmental and cultural circumstances may behave differently if forced to induce branching. Thus the ability of a cultivar to induce a given type of branching under the influence of aforementioned circumstances ought to be named „*branching potential*" (Jacyna – unpublished data). The notion of „*branching potential*" would have a very practical implications since it is essentially an index of responses to exogenously induced feathering. For example: both apple cultivars 'Liberty' and 'Paulared' have very low natural ability to branch, yet 'Liberty' does have high branching potential while 'Paulared' does not; 'Liberty' branches readily if treated with low doses of chemicals, whereas 'Paulared' usually fails to feather when treated chemically. Both 'Rubinstar' and 'Ginger Gold' apple trees are known to branch freely. But if treated chemically or manually, they do not respond with a significant increase in feather number; thus they have low branching potential despite having high branching ability (Jacyna 1996, Reźnićek and Salas 1998).

VEGETATIVE GROWTH COMPONENTS OF MAIDEN FRUIT TREE

Cook et al. (1999) describe the formation of sylleptic shoots as the partial expression of apical dominance. Complete expression of apical dominance results in no *syllepsis*. A developed maiden tree framework usually consists of a dominant parent shoot (leader) and laterals which are subordinated to it. In this context the „framework" refers to the location, distribution and length of the axillary sylleptic shoots and their relative crotch angles. A maiden tree framework does not form a static model with a uniform development of side shoots along the tree leader. Quantitatively, the degree of parent shoot dominance is negatively correlated with total extension growth of tree shoots. Depending upon the location of sylleptic shoot formation, a tree may exhibit *acrotonic* or *basitonic* growth habit. If the most distal or apical buds appear to be dominant and tend to form extension shoots, this tendency is referred to as acrotony. Cook et al. (1998) reported that due to insufficient chilling and delayed foliation under south African climate, maiden fruit trees with acrotonic tendencies developed some basitonic tree type. Trunk formation is the result of acrotony (Crabbe 1987, Cook et al. 1998 after Rauh and Champagnat). If *syllepsis* originates from basal and/or proximal buds, it is referred to as *basitony* (Cook et al. 1998 after

Rauh). Either *acrotony* or *basitony* can play an important role in tree shaping while in the nursery. Basitonic sylleptic shoots usually are of little value in tree training for commercial orchard use because of their low position on tree leader relative to the soil line. Jankiewicz and Kemula (1962), and Quinlan and Pakenham (1984) have shown that removal of sylleptic shoots from the basal part of the parent shoot stimulated syllepsis in the distal zone. Therefore proper management of orchard trees should be based on understanding tree behavior and its physiological responses to the applied training technique (Mika 1986). Lespinasse (1981) has put apple varieties into four groups depending upon their growth/fruiting behavior, recommending for cultivars from each of these groups different tree training and management approach.

Costes and Guedon (1997) used a mathematical approach called a hidden semi-Markov chain to capture embedded structure of apple nursery trees: a tree of any apple cultivar is characterized by its own pattern of development which may be either sylleptic, spur, or may mix different types of shoots in specific zones. The magnitude of the sylleptic zone indicates the degree of branching probability; the balance between short and long sylleptic shoots determines the degree of spuriness. The results of this research suggest that *syllepsis* can be used as an early indicator of future branching behavior of apple cultivars.

The quality of a maiden tree is usually determined by its height, diameter (caliper), branching and abundance of root system. Numerous studies on different species of temperate fruit trees revealed that tree caliper or tree cross-sectional area of tree trunk (TCSA) are related in some way to sylletpic shoot number and/or their total extension growth (Poniedziałek et al. 1996, Chełpiński et al. 1998, Lipecki and Janisz 1999). Extensive studies by Ostrowska and Chełpiński (1997 a and b), and Chełpiński et al. (1998) using maiden trees of 14 cultivars of pear on Quince (*Cydonia oblonga*) and *Pyrus caucasica* rootstocks, 18 apple cultivars on several Malling rootstocks, and 5 cultivars of sour cherry on *Prunus mahaleb* rootstocks demonstrated that both the shoot number or their total extension growth were highly correlated with the TCSA. It is assumed that in maiden apple trees the relation between TCSA or tree diameter and total extension growth or the number of lateral shoots is positively correlated to tree vigor (Słowiński and Sadowski 1996, Lipecki and Janisz 1999). Yet some cultivars, especially those with low branching ability, do not fit this definition (Słowiński and Sadowski 1996). The most recent study by Lipecki and Janisz (1999) on 'Jonagold' and 'Elstar' apple maidens showed closer positive correlation between tree diameter and either total extension growth or the number of shoots rather than between tree height and the characteristics mentioned before. Therefore these authors suggest to use a tree diameter instead of tree height to estimate the quality of apple nursery trees.

EFFECT OF ROOTSTOCK

It is commonly accepted that rootstock may affect as well the vegetative growth of scion, as its generative development. However, it is also known that a reverse action is possible whereby the scion influences rootstock behavior (Rejman and Makosz 1994). The mechanism by which the rootstock controls the growth of fruit scion is not fully understood, but there is evidence to suggest some hormonal involvement (Abbas 1978, Soumelidou et al. 1994, Jones cited by Kamboj and Quinlan 1997, Kamboj et al. 1997). Abbas (1978) reported that shoot tips from 'Cox's' apple maiden trees on M.27 contained a greater amount of auxin-like substances during the stage of lateral shoot formation than did those on MM.106. In another comparison using rootstock M.9, Abbas (1978) found that shoot tips of naturally poor-branching 'Tydeman's Early' apple maiden trees contained more endogenous auxin-like compounds than did those of free-branching 'Cox's' apple trees. Kamboj and Quinlan (1997) and Kamboj et al. (1997) found that apple trees on vigorous rootstocks exhibited greater polar movement of auxins than did dwarfing rootstocks. Kamboj and Quinlan (1997) and Kamboj et al. (1999 a) found a higher concentration of cytokinin in root pressure exudate in invigorating rootstocks versus dwarf rootstocks. Consequently, the amount of cytokinin in the shoot sap increased with increasing of rootstock vigor. ABA content in the bark of dwarfed rootstocks was higher compared with that in vigorous rootstocks (Kamboj and Quinlan 1997). It was reported that dwarfing rootstocks exhibited greater ratios of ABA:IAA than the invigorating rootstocks. This ratio gradually increased from May to July (Kamboj et al. 1999 b). These findings suggest that ABA may be involved in auxin movement since it is known that greater concentration of ABA reduces auxin transport (Basler and McBride 1977).

A greater velocity of auxins moving to the roots in invigorating rootstocks than in dwarfing ones (Soumelidou et al. 1994, Kamboj and Quinlan 1997, Kamboj *et al.*1997) may apparently contribute to faster release of parent shoot from apical dominance, thus enhancing branching. This is likely to be brought about by lower concentrations of auxins above the bud union in vigorous rootstocks than in dwarf rootstocks. More efficient basipetal transport of auxin in invigorating rootstocks contributes to the increase of internodal elongation (Kamboj et al. 1997 after Young), and stimulation the production of longer sylleptic shoots in scions on vigorous rootstocks compared with dwarf ones (Kamboj et al. 1997). It is not clear why rootstocks differ in their auxin transport characteristics, but it has been suggested that they may differ in the intristic ability to transport IAA (Soumelidou et al. 1994). According to Lockard and Schneider (1981) auxins transported from the parent shoot to the roots stimulate metabolism there, which includes the synthesis of cytokinins. An efficient system of polar basipetal transport of auxins to the roots associated with stimulation of cytokinin synthesis followed by cytokinin acropetal movement to the parent shoot, and reduced presence of ABA in the bark of invigorating rootstocks may partially explain the role of vigorous rootstocks in inducing *syllepsis* in the scion.

It is commonly agreed that maiden trees tend to produce more laterals if propagated on vigorous rootstocks (Abbas 1978, Jaumień et al. 1993, Słowiński and Sadowski 1996, Ostrowska and Chełpiński 1997 a and b, Basak 1998). It is known that quality rootstocks contribute to the production of quality maiden trees. Howard et al. (1975) and Poniedziałek et al. (1996) advise the use of apple rootstocks with diameter 6–10 mm of collar root. Blaźkova (1997) recommends PHL and Colt rootstocks with a diameter of 14-18 mm for raising sweet cherries. Like fruit trees, ornamental trees and shrubs require adequate length and diameter of cuttings to produce quality plant materials (Montarone et al. 1997, Henry and Preece 1997). Montarone et al. (1997) reported that the branching effect in *Protea sp.* was especially affected by cutting's diameter and weight.

EFFECT OF CULTURAL PRACTICES

A prerequisite for obtaining well branched trees is their continuous and strong growth throughout the season. Site selection, its preparation and further management should aim at creating the best possible environment for growing nursery trees (Howard et al. 1975, Czynczyk 1991, Poniedziałek et al. 1996).

Advantages resulting from adequate weed control and fertilization are well established (Lipecki 1994, Poniedziałek et al. 1996). Szwedo and Murawska (1999) found in maiden apple trees a high positive correlation between the uptake of N, P, K, Ca and the number of feathers and tree diameter. Maiden trees of less vigorous cultivars were characterized by lesser nutrient uptake than those growing vigorously (Szwedo and Murawska 1999). Planting density may also influence maiden tree performance (Lipecki and Lipecki 1994, Theron et al. 2000). Olwell and Andrews (1992) found that apple trees spaced 40 cm within-row induced more feathers than did those at 20 cm. Kool and Lenssen (1997) found no influence of plant density on basal-shoot induction of rose. Many authors believe that within-row spacing in the nursery ranging from 25 to 40 cm generally meets „space" requirements of many temperate fruit species, provided that the other cultural practice requirements are met (Yong-Koo et al. 1984 a, Rejman and Makosz 1994, Poniedziałek et al. 1996).

Method of propagation plays an important role in maiden tree development and its final quality. Studies by Howard and coworkers (1974) proved that chip-budded trees were of higher quality than those propagated by T or inverted T-budding in terms of number of feathers and their length. Anatomical studies showed that chip-budded trees formed a complete union between scion and stock during autumn following budding, whereas T-budded did not. Chip buds developed very little callus at the bud union but there was a noticeable increase of new xylem in the scion. The amount of xylem in the scions was in the order chip > T inverted > T shield (Howard et al. 1974). These authors also reported that leaves of chip-budded trees contained more of NPK than T-budded. A recent review of world experiments by Ananda and Negi (1998) on propagation of deciduous fruit and nut trees showed that chip-budding significantly outperformed other propagation methods in terms of its ease of application, rapid bud union formation, high bud take, tree uniformity, tree quality and low labor input. Bench-grafting is used to shorten production cycle of fruit trees in the nursery. Yet apple bench-grafting seldom produces trees of acceptable quality in one season (Rejman and Makosz 1994).

Other procedures considered useful in increasing branching in maiden trees are *pinching* (removal of a short piece of shoot terminal), pruning a parent shoot (**heading back** or **tipping**), partial or total removal of several uppermost leaves on parent shoot (**cutting off**), **twisting** the tip of parent shoot, removal of basal sylleptic shoots or removal of several uppermost buds below the terminal bud on parent shoot (Marek 2001). Such techniques as leader decapitation used in the training of „**knipbaum**" type apple may offer some help in shaping either nursery or orchard trees (Jacyna and Brown 1989 a and b, Czarnecki 1998). The whole concept of lateral shoot induction by means of aforementioned practices is based upon counteracting of apical dominance. Plant responses on above-mentioned practices are different and due to species, cultivars, climate, soil and the specifics of method applied. Wertheim (1978), Volz et al. (1994) and Quellette et al. (1996) consider top-leaf cutting as being of little value for lateral branch formation. Olwell and Andrews (1992) found that apple 'Fuji' on M.9 increased branching when trees were pinched and several lower immature leaves cut off. Removal of five immature leaves from the tip of apple rootstocks MM 106 or M.26 brought about satisfactory branching when executed during the initial flush of spring growth (Quellette and Young 1994) compared with no such effects when mature leaves were removed (Mika 1971). These studies indicate that the developmental stage of leaf removed may influence axillary bud growth. Pinching usually brings better results in branching than leaf cutting (Wertheim 1978, Quellette and Young 1994). Gibbs and Volz (unpublished data) assume that immature leaf removal repeated over several weeks may have been more successful than a single operation. Combination of leaf removal and tipping with chemical application may increase branching in low-branching ability apple cultivars (Basak 1998). Repeated twisting of parent shoot may be of some help in increasing branching (Poniedziałek et al. 1996). Removal of incipient low-positioned shoots that emerge from the scion and/or rootstock, favors the growth of more and longer feathers, especially in the tree region, where primary branching is required (Quinlan 1978, Yong-Koo et al. 1984 a and b, Blażkova 1997). According to Sadowski and Dąbrowski (1998) multiple shoot removal is more effective in stimulating feather growth than less frequent operation, especially with vigorous cultivars. Yong-Koo et al. (1984 b) reported that the level of abscisic acid was higher in the scion stems of multi-shoot sweet cherry maidens than in single-shoot ones, suggesting that the extra basal shoots may become the source of additional amounts of ABA. These authors provided strong evidence that ABA might inhibit lateral-shoot induction. Further support for the inhibiting role of ABA in outgrowth of axillary buds was obtained through inhibition of lateral growth by application of exogenous ABA to single stem cherry trees; the content of auxins in both single and multi-shoot type of trees was similar (Yong-Koo et al.1984 b).

EFFECT OF ENVIRONMENTAL FACTORS

The role of the environmental factors such as air and soil temperature, humidity or solar radiation in causing year-to-year variation in the branching has been widely recognized (Abbas et al. 1980, Tromp 1992 a and b, Lindhagen 1998).

However, the way they modify plant growth habit is not fully known yet (Barr and Pellett 1972, Tromp 1992 a) because of interactions of different environmental factors. Therefore in this research an emphasis has been put to studying the complexity of soil and climatic factors affecting plant syllepsis (Abbas et al. 1980, Tromp and Boertjes 1996).

Abbas et al. (1980) showed that apple scions exposed to a 5-day cooling period (10° C) induced branching without reducing the growth of parent shoot. Plants exposed to a 10-day cold reduced parent shoot growth and did not stimulate any branching. These authors suggest that the early stage of maiden tree development may affect branching pattern. Tromp and Boertjes (1996) found that the temperature affected less growth of parent shoot than branching. When apple trees were subjected to either 15° C, 25° C and/or alternating outside temperature, and/or to different temperature combinations during three consecutive periods, the syllepsis occurred chiefly in periods when ambient temperature was 25° C throughout, which coincided with the highest growth rate of parent shoot. Tromp (1993) and Tromp and Romer (1996) found that when apple trees in the first year after budding were exposed to continuous all-season temperature from 16° C to 26° C, tree growth was reflected mainly in lateral shoot growth, with most pronounced effects at 21° C. Extensive research on the combined effects of soil temperature and air humidity using maiden apple trees showed that, irrespective of soil temperature, shoot growth was greater at higher relative air humidity.

Research by Barr and Pellet (1972) demonstrated that relatively small changes in soil temperature can bring about large differences in growth of many woody plants. Optimum temperature for shoot growth expressed as shoot elongation was species-dependent (Barr and Pellet 1972). Tromp (1992 a and 1996) reported that by alternating soil temperature and air humidity during three consecutive periods, treatment effects were mainly reflected in sylleptic shoot growth and its distribution, but not otherwise. The effect of soil temperature on *syllepsis* was confined to a relatively short period. The effects of combined air humidity and soil temperature were mainly expressed in the increase of the number of feathers. Lateral shoot distribution was mainly influenced by soil-temperature and depended greatly on the period in which *syllepsis* occurred. Tromp (1992 b) believes that the effect of soil temperature on *syllepsis* must be due to some factors originating in roots, thus the *syllepsis* is partly controlled by the balance between the stage of bud rest and the quantity of cytokinins moving up from the roots. Under low supply of cytokinins due to low soil temperature, basal older buds (that are more inhibited by their dormancy status) are unable to grow and thus the growth occurs in the later-formed and less dormant, higher inserted buds; higher soil temperatures then stimulate growth of basal shoots. The results of these studies support findings by Abbas et al. (1980), and Tromp and Boertjes (1996), suggesting that buds are only able to respond to syllepsis-induction factors at a certain stage of their development.

Light quality and its intensity may influence apical dominance thus plant branching pattern (McIntyre 1977, Mor and Halevy 1980, Lindhagen 1998). Mor and Halevy (1980) reported that rose plants grown in red light branched profusely whereas those grown in far-red light did not. Tromp (1993) found no effect of low-intensity red light on vegetative growth of maiden apple trees. McIntyre (1977) believes that such factors as high intensity of light, high relative air humidity and abundant supply of nitrogen are prerequisites for lateral branch formation. Having assumed that the number of growing lateral shoots depends on the number of unfolding leaves already formed on the parent shoot, and also that increasing light intensity promotes the outgrowth of side shoots, a dynamic model predicting branching in young apple trees has been developed (Lindhagen 1998). This model links climatic factors with branching thus allowing a simulation of optimal climatic conditions for different pattern of branching.

CHEMICAL INDUCTION OF FEATHERING

The idea of use chemical compounds to suppress apical dominance, thus stimulate branching in maiden apple trees was invented in Poland by Jankiewicz in 1960 (Jankiewicz 1960). Application of chemical branching agents (CBA) has been shown to be one of the most efficient and predictable ways of stimulating lateral-branch formation (Johann 1985, Quinlan and Tobutt 1990, Bailey 1997). The use of CBA causes partial or total removal of apical dominance. Most of the CBA fall into three basic groups, namely: **1) *Auxin Transport Inhibitors*** such as TIBA (2,3,5-triodobenzoic acid), or MB-25105 (n-propyl-3-t-butylphenoxyacetate). These compounds reduce apical dominance by temporary blocking basipetal movement of auxin (Quinlan and Pakenham 1980, Wilkinson 1981). **2) *Terminal Bud Inhibitors*** such as MH (maleic hydrazide), methyl esters of fatty alcohols C_6+C_{12} or P528 [ethyl-5-(4-chlorophenyl)-2-H-tetrazole-2-acetate] (Jankiewicz 1960, Ryan 1974, Plich and Hegazi 1977, Larsen 1979). Some chemicals from this group are classified as morphactines (morphologically active substances): dikegulac-sodium [sodium 2,3:4,6-Bis-*O*-(thylethylidene)α(-L-xylo-2-hexulofuranosonic acid] or chloroflurecolmethyl esters (Baldini et al. 1973, Bocion and De Silva 1975, Ramirez et al. 1983, Bailey 1997), which promote feathering through partial or total destruction of terminal buds. **3) *Cytokinins alone or supplemented with gibberellins***, which are synthetic derivatives of adenine (Kender and Carpenter 1972, Elfving 1985, Karhu 1997), or urea (Baldini et al. 1973), or recently released synthetic urea-type cytokinin [N-(2-chloro-4-piridynyl)-N-phenylurea] called forchlorfenuron (CPPU). In contrast with the CBA from the 1st and 2nd group, cytokinin-like compounds do not bring any detrimental effects to treated plant. It has been suggested that BA + gibberellin(s) may play sequential roles in overcoming apical dominance, with the initiation of axillary buds stimulated by BA, and then their subsequent elongation by gibberellins (Cody et al. 1985, Cline 1991). There have been other chemicals examined for potential use in feathering such as: CEPA – ethylene generator, AVG – inhibitor of ethylene biosynthesis, GA_3 – gibberellic acid, and CCC – chloromequat (Ugolik 1978, Edgerton 1983, Lewis and Warrington 1988). There were some earlier reports that ethylene or GA_3 may be involved in releasing buds from apical dominance (Philips 1975), however, most of the reports appearing since then have failed to confirm their role in correlative inhibition (Cline

1991). Recently, Haver and Schuch (1998) reported that a single application of ethylene generator (ethephon) reduced apical dominance in *Petunia x hybrid* and increased length of already induced laterals.

Most CBA are applied as foliar sprays, which proved to be effective and inexpensive ways of branching plant materials. Other methods of application such as smearing, watering, soaking or painting have been studied. Basak (1997) observed no great differences in some growth characteristics between smeared and foliar treated young apple trees. Kiang (1984) reported that both root growth and stem diameter of lemon seedlings increase when plants were irrigated with water containing ($BA+GA_{4+7}$). Henny and Fooshee (1985) observed an increase in the number of basal shoots in *Spathiphyllum sp.* when treated with BA as soil drench. Jayroe-Cournoyer and Newman (1995) showed that tea roses induced axillary shoots if grown in floral foams saturated with either BA or dikegulac-sodium. Zhang et al. (1990) achieved improved bud development and root initiation by soaking bulbs of *Lilium elegans* in aqueous solution of ($BA+GA_{4+7}$). Grochowska and Karaszewska (1989) found that single application of GA_3 and anti-oxidant BHT in lanolin paste applied to the collar root of young apple trees of several cultivars stimulated growth and branching. Jackson (1997) reported that hydrogen cyanamide along with ($BA+GA_{4+7}$) applied in water solution by painting have broken dormacy that resulted in satisfactory feathering of young apple trees grown in the subtropical climate of Zimbabwe. Plich and Basak (1978), Larsen (1979), Veinbrants and Miller (1981), Miller (1983 a) and most recently Wustenberghs and Keulemans (1999) did not obtain adequate feathering from foliar treated sweet cherry trees. Veinbrants and Miller (1981), and Miller (1983a) observed a significant improvement in feathering sweet cherry trees when buds on one-year-old wood were treated with ($BA+GA_{4+7}$) dissolved in brown latex paint.

Single application of CBA is usually less effective than multiple applications in lateral-branch induction (Wertheim and Estabrooks 1994, Hrotko et al. 1997 a and b). If the same cumulative rate of CBA is given to the plant as single or split application, it is the last one which is far more effective in promoting the outgrowth of axillary buds (Cody et al. 1985, Jacyna 1996). It is suggested that a smaller and gradual supply of exogenous bioregulator is more efficiently used by treated plant, resulting in satisfactory lateral branch formation. Wertheim and Estabrooks (1994) reported that branching increased with the increase of treatment frequency. Hrotko et al. (1996 b, 1997 a) found that six consecutive BA applications were more effective in branching apple trees than three or four sprays.

The time of the first treatment coincident with a certain stage of plant development, the number and frequency of applications, and concentration of CBA determine the final effects of CBA on maiden tree growth characteristics. It is likely that the effectiveness of CBA multiple sprays depends upon the time elapsed between the applications (Plich and Hegazi 1977, Hrotko et al. 1996 b). Basak et al. (1993), and Wertheim and Estabrooks (1994) recommended weekly intervals between the applications be used to secure high effectiveness of CBA applications. The height of maiden tree at the time of CBA application greatly effects the distribution of side shoots (Wertheim 1978). Treated maiden trees, however, may induce feathering at any stage of their development provided the parent shoot is still actively growing and treated axillary buds are not dormant (Jankiewicz and Grzymała 1964). Edgerton (1983) found that when the timing of benzyladenine application was delayed or its concentration was too low to induce branching, the buds in the treated area enlarged in size, and eventually the trees produced high quality laterals next year while planted in the orchard. Bangerth (1993) showed that when BA is uniformly applied to uppermost axillary buds, it can decrease apical dominance but if BA is applied to terminal bud or very few buds below, it can increase apical dominance. Practically, the optimum timing for application of CBA, or first of a series of multiple applications, depends upon the height of the desired branching (Hibbitt and Hardisty 1979). Most of the laterals induced by BA alone or in combination with GA_{4+7} usually occur at and/or above the application zone (Miller 1983 a) since BA is readily transported above the treated area (Sterett and Hopkins 1980). Occasionally, branching responses may appear below the application zone (Jacyna et al. 1994) because the compound is also translocated down (Pieniążek and Jankiewicz 1966).

The main effect of CBA applications is the increase of the number of feathers. However, the variation in tree performance and its branching habit result from changing such tree features as elongation of shoots, total extension growth of newly induced shoots, magnitude of crotch angle, size and shape of leaf, height and diameter of parent shoot, and development of root system. There is a *consensus* that the net branching effect is above all associated with the type of a compound used, concentration applied and the frequency of application.

Commonly used BA or its derivatives compounded with gibberellins, mostly stimulate outgrowth and elongation of axillary shoots (Greene and Miller 1984). Elongation of lateral shoots is also found where BA was used on its own (Cody 1985). Yet shoot length is not always affected by either BA or BA+gibberellins (Basak et al. 1993). However, in some instances it may even be reduced (Miller 1983 b, Olwell and Andrews 1992). Usually, an increase of CBA concentrations leads to an increase in the number of laterals (Wertheim and Estabrooks 1994, Hrotko et al. 1997 a) and both these factors are positively well correlated (Elfving 1985). Yet data on application of BA, or ($BA+GA_{4+7}$) by Greene and Miller (1984), and Koen et al. (1989), respectively, indicated high negative correlation between the number of shoots induced and/or their length, and the compound concentration if this last exceed a certain level. Sometimes cytokinins have inhibitory effect on growth (Jankiewicz – pers.com.). In general, CBA treated trees are characterized by greater total extension growth than those untreated; this results from the increase in shoot number (Veinbrants and Miller 1981, Volz et al. 1994).

The increase in shoot number by CBA is usually coupled with the enlargement of total tree foliage area due to an increase of a plant's total extension growth. An increase in the number of leaves with simultaneous reduction in leaf size in ($BA+GA_{4+7}$) treated apple maidens was reported to be concentration-dependent (Johann 1984 and 1985, Basak in Jankiewicz 1997).

Higher CBA rates and/or more sequential applications tend to noticeably reduce tree height, that sometimes is compensated for by an increase in feather number. These events are found mostly in difficult-to-feather apple cultivars (Basak and Soczek 1986, Hrotko et al. 1996 b). One of the possible reasons for tree height to be reduced may be a decrease in internodal length. Hrotko et al. (1997 a and b) found that BA treated apple maiden trees developed shorter internodes, but their number was similar to that of untreated trees. In contrast with these data, both Keever and Foster (1990), and Carswell et al. (1996) have noticed no reduction in internode length with hollies (*Ilex sp.*) and azaleas, and *Sophora sp.* plants, respectively.

Jankiewicz (1964) found that the crotch angle width greatly depends on the supply of auxins to the tissues of the crotch, and its magnitude is likely correlated with growth substances, presumably auxins, flowing down the leader.

Few reports indicated that application of exogenous BA or its combinations with GA, may influence to some extent root development. Hrotko et al. (1996 a) found that BA treated 'Idared' apple maidens developed more fibrous roots, whereas those untreated did not. Johann (1984 and 1985) reported an increase in dry matter and starch content in roots, leaves and shoots of maiden apples treated with either ($BA+GA_{4+7}$) or MB 25-105 (auxin transport inhibitor). Kiang (1984) pointed out that drench application of ($BA+GA_{4+7}$) increased root growth of citrus seedlings. In contrast with the few chemical branching agents that are frequently used in fruit tree nurseries, the choice of CBA available for ornamental plants is greater including dikegulac-sodiun or methyl esters of fatty alcohols, and ethylene generators. These compounds are used worldwide for indoor or outdoor ornamental plants including temperate zone and (sub)tropical plants (Wilkinson 1981, Keever and Foster 1990, Al-Jouboory et al. 1997, Karhu 1997, Haver and Schuh 1998).

It is well known that the quality of maiden tree influences future tree performance (Howard et al. 1975). However, if the tree quality is to be considered as an important factor, a young orchard tree should produce its first crops in the second or third year after transplanting from the nursery, otherwise the effect of the initial tree quality is lost (Poniedziałek et al. 1996). Van Oosten (1978) reported that during the first two years in the orchard, branched apple trees of cv. 'Booskop' almost doubled yields compared with trees with no laterals present at planting time. Similar data regarding 'Jonagold', 'Gloster' and 'Melrose' was published by Poniedziałek et al. (1994).

Besides known direct changes in tree morphology induced by CBAs, those agents also bring about different carry-over effects. Residual effects of CBA applications in the nursery (with no further sprays in the orchard) usually increase cropping and return bloom as compared with untreated trees (Jackson 1981, Johann 1984 and 1985, Ferree and Rhodus 1987). However, excessive BA foliar applications were reported to have adverse effects on flower-bud formation Wertheim and Estabrooks (1994). These authors suggested that stimulation of numerous shoots, which may be a potential source for gibberellin production, could inhibit flower-bud induction. Formation of flower buds, fruit set, cropping level and the amount of return bloom are priority issues because they directly affect tree performance, thus the profitability, at the very beginning of orchard life.

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Czynniki wpływające na tworzenie się bocznych rozgałęzień (*syllepsis*) u roślin gatunków drzewiastych

Streszczenie

Charakterystyczna cechą wielu gatunków roślin drzewiastych jest zdolność do tworzenia w pierwszym roku po okulizacji w szkółce bocznych pędów zwanych syleptycznymi. Obecność tych pędów w dużej mierze decyduje o szybkości wejścia roślin gatunków sadowniczych w okres owocowania, natomiast u drzew ozdobnych wpływa na ich walory estetyczne stanowiące isitny element architektury krajobrazu.

Indukcja pędów syleptycznych uwarunkowana jest stopniem występowania dominacji dominacji wierzchołkowej, co ma swoje bezpośrednie źródło w genotypie

danej rośliny. Ograniczenie dominacji wierzchołkowej jest odwrotnie proporcjonalne do *syllepsis* rośliny. Takie gatunki sadownicze jak brzoskwinie lub wiśnie charakteryzują się dużymi zdolnościami do wydawania pędów syleptycznych w przeciwieństwie do jabłoni lub czereśni, które pod tym względem wykazują duże zróżnicowanie między odmianami.

Stymulowanie *syllepsis* polega na ograniczeniu lub eliminacji dominacji wierzchołkowej. *Syllepsis* roślin drzewiastych może być modyfikowane czynnikami biotycznymi jak podkładka oraz czynnikami abiotycznymi takimi jak klimat, gleba i technologia produkcji szkółkarskiej. Jednakże dominującą rolę w indukcji pędów syleptycznych odgrywają genetyczne predspozycje rośliny.

Praca ta ma charakter przeglądowy i omawia wyniki wielu badań prowadzonych w ostatnich trzydziestu latach w wielu krajach nad anatomicznymi i morfologicznymi aspektami *syllepsis* (gatunek, odmiana, podkładka oraz korelacje między cechami jakościowymi okulantów), klimatycznymi warunkami indukcji i stymulacji wzrost pędów syleptycznych (temperatura i wilgotność powietrza oraz podłoża) oraz czynnikami technologicznymi, takimi jak sposoby rozmnażania, metody agrotechniczne i stosowanie syntetycznych bioregulatorów.