Growth Responses from One-year-old Apple Branches to Heading as a Factor Governing Terminal Shoot Length in Cultivars with Different Branching Habits

Takuro Kikuchi*, Yunosuke Shiozaki**, Toshiyuki Adachi***, Fernando Setsuo Yassunaka****, Yasutomo Otake***** and Tsutomu Nishide*****

Faculty of Agriculture, Hirosaki University, Hirosaki 036–8561

Summary

A series of one-season experiments were carried out with ‘Fuji’ and ‘Jonathan’ trees of different ages and with young ‘Hokuto’ trees. Twigs (1-year-old branches) on trees that were trained to the central leader or open center systems were headed to elucidate the twig-to-twig relationships on terminal shoot growth. Terminal shoots were almost the same length between pruned and unpruned twigs in ‘Fuji’ and ‘Hokuto’ trees, whereas those of ‘Jonathan’ grew longer when headed. Unpruned twigs of ‘Fuji’ sent out a few shoots but the number of shoots and total shoot length that developed from headed twigs were almost the same as those from unpruned counterparts. Unpruned twigs of ‘Jonathan’ tended to develop a large number of shoots, whereas heading cuts caused a significant reduction in the number of shoots and total shoot length. The foregoing cultivar-specific responses to pruning also occurred in experiments with water sprouts. The above observations were integrated into the following assumptions: (1) The strength of shoot growth on twigs is determined to a considerable extent by inherent twig conditions and the circumstances under which they developed. Twig location on the crown and distance from the tree base as well as length and thickness of the twigs seem to be important factors related to the shoot growth. (2) Terminal shoot length is a product of conditions determined by the individual twig and the mutual interaction between terminal and lateral shoots. (3) In cultivars with infrequent branching habits, such as ‘Fuji’, in which the terminal shoots have a strong dominance over lateral shoots, heading cuts do not encourage terminal shoot growth because growth relations between terminal and lateral shoots are little changed by pruning. (4) In cultivars having frequent branching habits, i.e., ‘Jonathan’, in which the terminal shoot is weakly dominant, heading induces the remaining terminal shoots to grow longer by reducing the number of active buds on the twig; it favors the early stage of terminal shoot growth and reduces subsequent inhibition of terminal shoots by lateral ones.

Key Words: apple cultivars, branching habit, branch systems, heading pruning, terminal shoot growth.

Introduction

A large number of studies have been made on the effect of pruning and the following seems to be the widely accepted consensus: a) pruning increases the growth of new shoots, but decreases the growth of other parts of the tree, especially the trunk (diameter) and roots (Mika, 1986). b) pruning reduces the number of buds so that the remaining shoots receive more food

reserves stored in the tree and mineral nutrients and water from the soil, at least until reduction in root growth reestablishes the balance between root and top (Chandler, 1957a). Saure (1971, 1992) tried to interpret the invigorating effect of pruning on the hormonal growth control of trees based on the feedback interaction between roots and shoots. These explanations are apparently concerned with mechanisms involving whole tree relations.

In pruning apple trees, thinning is usually performed; heading is often applied only to certain 1-year-old branches (previous year’s shoots, which will be called “twigs” occasionally for simplicity) under the assumption that this encourages terminal shoot growth. However, this assumption is questionable because pruning in this case seems to deal with relations in a relatively small range of branch system in which tested twig is located. In this connection, Kikuchi, one of the present authors, found in preliminary studies (unpublished) that

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*Corresponding author (E-mail: kikuchi-takuro@saturn.sannet.ne.jp)

Present address: 7-jo Goshonouchi-kita, Kyoto 600–8861.

**Present address: Faculty of Agriculture and Life Science, Hirosaki University, Hirosaki, 036–8561.

***Present address: Takahata Town Hall, Yamagata Pref.

****Mr. Yassunaka died in a car accident June 2002. We will all miss his friendship and invaluable inputs as a scientist.

*****Present address: Snow Brand Seed Co., LTD., Sapporo.

*****Present address: Aiful Corporation, Kyoto.

heading 1-year-old branches did not always have invigorating effects on terminal shoot growth depending on cultivars.

This study was conducted to clarify the relations observed in the preliminary studies on a more generalized basis. A series of separate one-season experiments were carried out over several years mainly with 'Fuji' and 'Jonathan' trees. 'Hokuto' trees were given preparatory treatments to produce trees which have various tree conditions. The test trees differed in tree age and form. Treatments were applied to twigs placed in various positions. An attempt was made to integrate the findings from these trials into a hypothesis which would support the methodology proposed by Kikuchi (2001).

Materials and Methods

A series of one-season experiments were carried out in 1990, 1992, 1993, 1994 and 1995 separately with established 'Fuji' and 'Jonathan' trees of different ages and with young 'Hokuto' trees. In this paper these experiments will be grouped for convenience by the year when they were conducted, e.g. Expt. '90, Expt. '92, etc.

Experiments were carried out at the experimental farm of Hirotsuki University on deep alluvial soil classified as clay loam. The orchard was under permanent grass sod that was mowed 5 times during the season. Fertilizers had not been applied since late 1970s to prevent overly vigorous tree growth and to maintain a stable production of well-colored apples.

Trees used for the experiments were grafted on Marubakaido (*Malus prunifolia* Borkh. var. *ringo* Asami) rootstock. The 1-year-old branches (previous year's growth) on experimental trees in guard rows were pruned in early April. Treatments were made to all twigs on a tree (except Expt. '90 where only bottom scaffold branches were tested) in the following ways: all twigs, which met requirements for each experiment, were counted in a fixed direction on the scaffold branches, and treatments were assigned in an order previously determined at random. The current season's growths were divided into two groups according to their lengths; shoots, 6 cm or more and spurs, less than 6 cm. Current year's shoot lengths were measured in late fall. The terminal shoot is designated in this paper as the longest shoot arising from the terminal portion of the parent twig whether pruned or unpruned. The trees were given conventional fruit thinning by hand except where otherwise stated: a single fruit was left on each flower cluster, and the ratio between the numbers of fruit and terminal buds of the previous year's growth was reduced to; one in every three for 'Jonathan', and one in every four for 'Fuji'. Test twigs were deblossomed if flower clusters developed:

Expt. '90

Three 16-year-old 'Fuji' trees (spaced 6.0 m × 4.0 m and trained to a central leader) were given the

following treatments: twigs 30 cm or longer, whether arising terminally or laterally from 2-year-old branches were headed: (1) one-third of the length cut off (1/3 P), (2) two-thirds of the length cut off (2/3 P), and (3) unpruned (UP). All blossoms on the trees were removed immediately after full bloom. The angles of the twigs from the vertical were recorded at the time of shoot measurement.

Expt. '92

A group of 47 central leader 5-year-old 'Hokuto' trees (spaced 7.0 m × 3.5 m) were divided into three groups and given the following preliminary treatments to produce different tree conditions: (1) In late March 1992, 15 trees were pruned heavier than for conventional Japanese fruit production and all fruit were removed in early June (unringed, pruned, defruited trees). The remaining 32 trees were ringed by removing a ring of bark, 5 mm in width, from the trunk in June 1991. They were not dormant-pruned thereafter. (2) Sixteen of these ringed trees were defruited in early June 1992 (ringed, unpruned, defruited trees). (3) On the remaining 16 trees, the crop was hand-thinned lightly in early June, leaving single fruit on each clusters (ringed, unpruned, heavily cropped trees). The average crop weight per tree was 59.1 kg (s=4.4 kg) and the average number of fruit per tree was 199.4 (s=55.1). Three pruning treatments were applied to twigs 25 cm or longer, whether terminal or lateral, which were positioned above the horizontal; (1) one-third of the length of the twigs cut off (1/3 P), (2) two-thirds of the length of twigs cut off (2/3 P), and (3) unpruned (UP). The angle of twigs from the vertical was measured at the time of the shoot length measurement.

Expt. '93

Eleven 20-year-old, central leader 'Fuji' trees (spaced 6.0 m × 4.0 m) and 33, 7-year-old central leader 'Jonathan' trees (spaced 5.0 m × 3.5 m) were pruned as follows: twigs 30 cm or longer arising terminally or laterally from 2-year-old branches at an angle of 40–90 degrees from the vertical were headed: (1) two-thirds of the length of the twigs cut off (2/3 P) and (2) unpruned (UP).

Expt. '94

Eleven 17-year-old, central leader 'Fuji' trees and 39 central leader, 8-year-old 'Jonathan' trees (spaced 5.0 m × 3.5 m) were pruned as follows: (1) two-thirds of the length of the twigs cut off (2/3 P) and (2) unpruned (UP). Treatments were applied to twigs that were 30 cm or longer, oriented between 40 and 90 degrees from the vertical, and developed terminally ('Fuji') or terminally and laterally ('Jonathan') on unpruned 2-year-old branches. In 'Jonathan' trees, the same treatment was applied to 1-year-old water sprouts 60 cm or longer arising from latent buds on branches

thicker than 3 cm.

Expt. '95

Thirty-two, 20-year-old, central leader 'Fuji' trees (spaced 4.0 m × 2.5 m), 16, 31-year-old, open center 'Fuji' trees, (spaced 9.0 m × 9.0 m), 44, 9-year-old, central leader 'Jonathan' trees (spaced 5.0 m × 3.5 m), and 10, 35-year-old, open center 'Jonathan' trees (spaced 10.8 m × 10.8 m) were pruned as those trees in

Expt. '94. Water sprouts were tested in both cultivars in the same way as with Expt. '94.

Results

Heading of 1-year-old branches (twigs) on 'Fuji' trees (Fig. 1, 2, 3) did not significantly increase terminal shoot lengths compared with those on unpruned twigs. This was irrespective of tree age, with or without crop load, and whether twigs were of terminal or lateral

Fig. 1. Effect of heading 1-year-old branches with different inclinations (<45°, >45° from the vertical) on terminal and total shoot length in 16-year-old 'Fuji' trees (Expt. '90). One-year-old branches were not divided into terminal and lateral origin. UP: unpruned, 1/3 P: one-third of the branch length cut off, 2/3 P: two-thirds of the branch length cut off. Different alphabetical letters denote significance by Duncan's multiple range test at $P < 0.05$, $n = 40, 100$ for each pruning treatment on <45° branches and >45° branches, respectively.

Fig. 2. Effect of heading 1-year-old branches on terminal and total shoot length in 20-year-old 'Fuji' trees (Expt. '93). Terminal, Lateral: origin of 1-year-old branches. UP, 2/3 P: See Fig. 1. NS, *: non-significant and significant at $P < 0.05$ by t -test, respectively, $n = 70, 57$ for each pruning treatment on terminal and lateral branches, respectively.

Fig. 3. Effect of heading 1-year-old branches on terminal and total shoot length in 17 (Expt. '94)-, 20 (Expt. '95)- and 31 (Expt. '95)-year-old 'Fuji' trees. One-year-old branches are of terminal origin. UP, 2/3 P: See Fig. 1. NS, *, **: non-significant and significant at $P < 0.05$ and $P < 0.01$ by t -test, respectively, $n = 49, 126, 156$ for each pruning treatment on 17, 20, 31-year-old trees, respectively.

Fig. 4. Effect of heading 1-year-old branches on terminal and total shoot length in 7-year-old 'Jonathan' trees (Expt. '93). Terminal, Lateral: See Fig. 2. **: significant at $P < 0.01$ by t -test, $n = 75, 69$ for each pruning treatment on Terminal and Lateral branches, respectively.

Fig. 5. Effect of heading 1-year-old branches on terminal and total shoot length in 8-year-old 'Jonathan' trees (Expt. '94). Terminal, Lateral: See Fig. 2. UP, 2/3 P: See Fig. 1. **: significant at $P < 0.01$ by t -test, $n = 55, 56$ for each pruning treatment on Terminal and Lateral branches, respectively.

Fig. 6. Effect of heading 1-year-old branches on terminal and total shoot length in 9- and 35-year-old 'Jonathan' trees (Expt. '95). One-year-old branches are of terminal origin. UP, 2/3 P: See Fig. 1. NS, **: non-significant and significant at $P < 0.01$ by t -test, respectively, $n = 86, 64$ for each pruning treatment on 9- and 35-year-old trees, respectively.

origin, or the inclination of the twigs. Total shoot length was, likewise, not significantly affected by pruning. In 'Jonathan' trees (Fig. 4, 5, 6), in contrast with 'Fuji', terminal shoots were longer on pruned twigs than on unpruned counterparts, irrespective of terminal or lateral origin of the twigs and of tree age. Total shoot length of unpruned twigs on 7- and 8-year-old 'Jonathan' were much longer compared with that of 'Fuji' trees; total shoot length was greatly reduced by pruning. The unringed, pruned, defruited 'Hokuto' trees grew vigorously in terms of their terminal shoot length compared with trees given other preliminary treatments. Pruning did not accelerate terminal shoot elongation irrespective of tree vigor, terminal or lateral origin of the twigs and with or without crop load (Fig. 7). In the ringed trees, the 1/3 P treatment tended to produce shorter terminal shoots as compared with the other

treatments, irrespective of cropping or non-cropping, or terminal or lateral origin of twigs.

The number of shoots developed on individual twigs is given in Fig. 8 for 'Fuji' and 'Jonathan'. Unpruned twigs of 'Jonathan' produced many more shoots than did 'Fuji'; the reduction in shoot number due to pruning was also greater. Heading reduced the number of spurs in both cultivars (Fig. 9).

Heading 1-year-old water sprouts in 'Jonathan' trees increased terminal shoot lengths (Fig. 10), but it had no effect in 'Fuji' trees. Total shoot lengths (Fig. 10) and the number of shoots developed on 1-year-old section of unpruned water sprouts (Fig. 11) were much greater in 'Jonathan' than of 'Fuji', and their reduction due to pruning was also much greater in the former. In 'Jonathan' trees, secondary shoots (feathers) developed particularly on terminal shoots of pruned twigs (data not

Fig. 7. Effect of heading 1-year-old branches on terminal shoot length in 5-year-old 'Hokuto' trees preliminarily treated with different orchard practices (Expt. '92). Terminal, Lateral: See Fig. 1. UP, 1/3 P, 2/3 P: See Fig. 1. Different alphabetical letters denote significance by Duncan's multiple range test at $P < 0.05$, $n = 111, 48, 110, 54, 153, 78$ for each pruning treatment on terminal and lateral branches of unringed, pruned, defruited trees, terminal and lateral branches of ringed, unpruned, defruited trees, and terminal and lateral branches of ringed, unpruned, heavily cropped trees, respectively.

shown).

Discussion

In these pruning studies, heading of twigs in 'Fuji' and 'Hokuto' did not invigorate growth of terminal shoots as compared with those on unpruned twigs irrespective of tree age, vigor of trees, with or without crop load, inclination of twigs, or whether twigs were of terminal or lateral origin. Contrarily, heading twigs of 'Jonathan' increased terminal shoot length significantly over that of unpruned twigs.

Fig. 8. Effect of heading 1-year-old branches on the number of shoots in 'Fuji' and 'Jonathan' trees. Tested 1-year-old branches are of terminal origin and the same with those in Fig. 2–6. UP, 2/3 P: See Fig. 1. *, **: significant at $P < 0.05$ and $P < 0.01$ by t -test, respectively, $n = 49, 91, 126, 156$ for each pruning treatment on 17 (Expt. '94)–, 20 (Expt. '93)–, 20 (Expt. '95)–, 31 (Expt. '95)– year-old 'Fuji' trees, respectively. $n = 75, 55, 86, 64$ for each pruning treatment on 7 (Expt. '93)–, 8 (Expt. '94)–, 9 (Expt. '95)–, 35 (Expt. '95)– year-old 'Jonathan' trees, respectively.

It is widely accepted that heading the vertical stem of maiden apple trees causes new terminal shoots to grow longer with increasingly severe pruning (e.g. Jonkers, 1982). This may have influenced people engaged in pruning practices to assume that terminal shoots are always invigorated when headed even in branching systems of older trees.

In pruning 1-year-old trees, the amount of dry matter partitioned to the stem decreased, and a nearly comparable amount of dry matter was added to shoot production excluding leaves (Kikuchi et al., 1996; Maggs, 1959). This relation constitutes the material basis of the invigorating effect of heading on shoot growth in 1-

year-old trees. This mechanism works particularly well in 1-year-old trees which have a simple closed structure consisting of the roots and 1-year-old stems. In the same context, the same mechanism is not expected to work when twigs in older trees are headed.

The differences between 'Fuji' and 'Jonathan' were also found in the experiments with water sprouts arising from branches thicker than 3 cm in diameter, indicating that the differences are not related to the way nor the degree of ramification of the branches from which tested twigs arose, but is attributed to characteristics inherent in the parent twigs.

Asami (1928) and Fujimura (1932), studying Japanese persimmon (*Diospyros kaki* Thunb.) trees, demonstrated that the total length of shoots produced on 1-year-old branches was in proportion to the bark area (surface area) of the branches. Maggs (1964) observed that on mature apple trees trained to a vase form the length of the current season's shoots growing at various heights on the stem could be related to the distance from the base of the tree to the shoot insertion. It is also recognized in forest trees that branches and twigs that grow vigorously one year tend to produce more and bigger

twigs the following year, whereas, branches on less vigorous tree parts frequently die back or remain dormant. This responses are thought to be adaptive tactics of trees to take advantage of favorable environmental conditions; while minimizing investment in areas that are shaded or otherwise inappropriate for growth (Waller, 1986).

These findings and considerations suggest that the strength of shoot growth on the twigs is determined to a considerable extent by the inherent vigor of the twigs and the circumstances under which they developed. Twig location on the crown and distance from the tree base as well as length and thickness of the twigs are important factors related to subsequent shoot growth, although the specific growth mechanisms are unknown. Terminal shoot length represents the strength of a twig to extend, that can be influenced by interrelations between new growths on the twig and the environment.

As to the mechanism by which buds or shoots on a twig compete with one another in the spring, Abbot (1984) explained that growth is initially sustained by locally stored metabolites. Subsequently, as more active growing points with higher hormone output, become active, they attract metabolites through the enlarging vascular systems from storage cells in the distant large limbs, trunk and roots to ensure self-perpetuation at the expense of weaker buds. On the other hand, Brunner (1990) stated that it is not only the apical bud and apical shoot which affect lateral buds but reversely, the latter may react to the apex and may correlatively inhibit its development and growth. Suzuki (1990) studied 1-year-old stems of 12-year-old low pruned mulberry (*Morus alba* L.) and found that besides inhibition of lower laterals by the upper, leading shoots, there was evidence for mutual inhibition (competition for nutrients and water) of neighboring laterals along the stem.

Abbot's view offers possible causes of the different responses between 'Fuji' and 'Jonathan' to our pruning method. In unpruned twigs of 'Fuji' there were fewer active buds so that the terminal shoot quickly established a dominant position over lateral shoots. The number of active buds was decreased little even though heavy cuts reduced the number of spurs. This would explain why the same pattern of terminal and total shoot length was obtained whether the twigs were headed or not. However, on unpruned 'Jonathan' twigs that have many active buds, the terminal shoot failed to establish dominance over lateral ones, and subsequent terminal shoot growth was inhibited by lateral shoots.

These differences in the pattern of shoot growth between cultivars are attributed to the inherent growth characteristics of individual cultivars. 'Jonathan' trees often produce lateral flower buds (Shima, 1934, Chandler, 1957b), indicating that their lateral buds develop well in the year when they are laid down, leading to many lateral shoots in the following spring. Forshey et al. (1992) classified 'Jonathan' into the group of apple

Fig. 9. Effect of heading 1-year-old branches on the number of spurs in 'Fuji' and 'Jonathan' trees. Tested branches are the same with those in Fig. 8. UP, 2/3 P: See Fig. 1. *, **: significant at $P < 0.05$ and $P < 0.01$ by t -test, respectively, $n = 49, 126, 156$ for each pruning treatment on 17 (Expt. '94) -, 20 (Expt. '93) -, 31 (Expt. '95) - year-old 'Fuji' trees, respectively. $n = 55, 86, 64$ for each pruning treatment on 8 (Expt. '94) -, 9 (Expt. '95) -, 35 (Expt. '95) - year-old 'Jonathan' trees, respectively.

Fig. 10. Effect of heading 1-year-old water sprouts on terminal and total shoot length in 'Fuji' and 'Jonathan' trees. UP, 2/3 P: See Fig. 1. NS, **: non-significant and significant at $P<0.01$ by t -test, $n=126, 158$ for each pruning treatment on 20 (Expt. '95)-, 31 (Expt. '95)-year-old 'Fuji' trees, respectively, $n=64, 106, 66$ for each pruning treatment on 8 (Expt. '94)-, 9 (Expt. '95)-, 35 (Expt. '95)-year-old 'Jonathan' trees, respectively.

Fig. 11. Effect of heading 1-year-old water sprouts on the number of shoots in 'Fuji' and 'Jonathan' trees. Tested branches are the same with those in Fig. 10. UP, 2/3 P: See Fig. 1. **: significant at $P<0.01$ by t -test.

cultivars with frequent branching habit, while 'Fuji' was classified into the group of less-frequent branching cultivars. The relatively small number of shoots on

unpruned twigs of 35-yr-old trees of 'Jonathan' is probably the result of reduced vigor.

'Hokuto' can be classified into the group of less-frequent branching cultivars, an inherent characteristic that would explain why terminal shoot length was influenced little by heading like in 'Fuji' (a parent of 'Hokuto'). The length of terminal shoots of 1/3-pruned twigs in 'Hokuto' trees was a little shorter than in 2/3-pruned and unpruned twigs; no information on lateral shoot growth was obtained to give a satisfactory discussion.

In 35-year-old 'Jonathan' trees, the shoot number and total shoot length in unpruned twigs and the degree of their reduction due to heading are comparable with those of 'Fuji' trees. Heading encouraged the growth of terminal shoots probably because buds near the cut end were well-developed and sprouted relatively early.

Asami (1928) demonstrated that total shoot length from headed twigs was in proportion to the bark area (surface area) after pruning. In our studies, the surface area of twigs was not measured. However, because total shoot length of 'Fuji' trees was changed little even by the 2/3 P treatment, it can be said that Asami's principle does not always hold true in all apple cultivars. We contend that it depends on the branching habit of the cultivar.

From the above observations, we conclude that: (1) Terminal shoot length is a product of conditions determined by the individual twig and the mutual interaction between terminal and lateral shoots. (2) In cultivars

having infrequent branching habits, such as 'Fuji' and 'Hokuto' in which the terminal shoots have a strong tendency to be dominant over lateral shoots, heading shoots does not encourage terminal shoot growth. (3) In cultivars having frequent branching habits, e.g. 'Jonathan', in which terminal shoots are not dominant over lateral shoots, heading of 1-year-old shoots causes terminal shoots to grow longer by reducing the number of active buds on the twig; it favors the early stage of terminal shoot growth and reduces subsequent inhibition of terminal shoots by lateral ones. Because longer twigs tend to send out more lateral shoots than short ones, there is more possibility that terminal shoots are invigorated by being headed.

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リンゴの同一樹上における切り返しせん定の有無が頂端新梢生長に及ぼす影響、
特に品種の分枝特性との関係

菊池卓郎・塩崎雄之輔・安達敏幸・安中フェルナンド節夫・大竹康友・西出 勉

弘前大学農学部 036-8561 弘前市文京町

摘 要

リンゴの同一樹上における一部の1年生枝(前年の新梢)の切り返しせん定が、頂端新梢長に及ぼす影響を明らかにするため、主として‘ふじ’と‘紅玉’、一部‘北斗’のさまざまな樹齢の樹のさまざまな状態の1年生枝を用いて、1年単位の一連の実験を5年間にわたって行った。‘ふじ’と‘北斗’においては頂端新梢長は、せん定区と無せん定区の間で差が見られなかった。一方、‘紅玉’においては頂端新梢はせん定によって長くなった。‘ふじ’では無せん定1年生母枝上の新梢数は少なく、せん定によって新梢数と総新梢長は減少しなかった。‘紅玉’の無せん定枝は比較的多くの新梢を発生し、せん定は新梢数と総新梢長の減少をもたらした。‘ふじ’と‘紅玉’の間に見られた上記の違いは、徒長枝を用いた実験でも同様に認められた。一連の実験の結果を総合して下記の推論に達した。(1)1年生母枝からの新梢の生長の強さは、かなりの程度まで母枝の長さや太さ、樹上における位置、樹の基部からの距離等、母枝自体の状態と樹上において母枝のおかれた条件

によって決定される。(2)頂端新梢の生長は、このような母枝に固有の生長の可能性と、母枝上の芽の間の相互の影響の結果としてもたらされる。(3)‘ふじ’のような側生新梢を発生しにくい品種では、頂端新梢の側生新梢に対する優位性が確立される傾向が強い。このような品種ではせん定は頂端新梢長にほとんど影響しない。それは頂端新梢の優位性に加え、せん定によって母枝上の新梢数の変化が少なく、頂端新梢と側生新梢の相互間の関係に変化がないためである。(4)‘紅玉’のような側生新梢を発生しやすい品種では、頂端新梢の側生新梢に対する優位性は強くない。このような品種ではせん定は頂端新梢の長さを増大させる。それはせん定によって側芽の数を減少させることにより、生長初期の段階において頂端新梢の生長に有利な状態をもたらすとともに、その後の側生新梢の頂端新梢に対する抑制を減少させるためである。