

Effects of Heading-back Pruning on Shoot Growth and IAA and Cytokinin Concentrations at Bud Burst of Columnar-type Apple Trees

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To elucidate the possible relationship between growth characteristics and apical dominance of columnar-type apple trees, the growth response to heading-back pruning and the concentration of indoleacetic acid (IAA) and cytokinins in apical and lateral buds on one-year-old shoots after sprouting were investigated. Terminal shoot growth in columnar-type ‘Trajan’ was not inhibited, whereas distal lateral shoots displayed significant length growth by heading-back pruning. The IAA concentration of columnar types was higher in apical shoots than in lateral shoots. The cytokinin concentration of both apical and lateral shoots was higher in columnar type than in the normal one. The kind of cytokinins that directly influences the growth regulation of columnar types was not determined. The ratio of total cytokinins to IAA concentration for cultivars and nodal positions was not significantly different suggesting that apical dominance is more involved in growth characteristics of columnar type than it is in normal apple trees.

Key Words: apple, columnar type, cytokinins, GC-MS-SIM, IAA.

Introduction

‘McIntosh Wijcik’, discovered as a bud mutation of ‘McIntosh’ in Canada (Fisher, 1969), is unique among tree mutant forms. This mutant is called a columnar-type apple tree because it has numerous spurs on its trunk with short internodes. Both a single dominant gene, *Co*, and several polygenes control ‘Wijcik’ growth characteristics (Lapins, 1969, 1976).

The intensity of apical dominance, which is mediated by the auxin, IAA, affects lateral bud growth of older shoots in apple trees. IAA plays a central role in the correlative phenomenon, which determines acrotony and tree architecture in apple trees (Bangerth, 1989; Faust, 1997; Greene and Autio, 1994). Apical dominance of columnar-type apple trees is likely to be stronger than that of normal apple trees because the apical buds of the columnar-type trees grow into shoots, whereas lateral buds develop into spurs. Lee and Looney (1977) reported that the apical dominance of compact seedlings is stronger than that of normal seedlings. However, treatment of an auxin transport inhibitor on decapitated compact seedlings increased the intensity of apical dominance. Thus, the relationship between shoot growth and apical dominance of columnar types still remains unclear.

Analyses for endogenous auxin and cytokinins between columnar-type and normal-type trees showed that the free indoleacetic acid (IAA) ratio to total IAA of bourse buds in mid-June was higher in ‘Wijcik’ than in ‘McIntosh’ (Looney and Lane, 1984). However, no significant differences in IAA concentrations between columnar and normal shoots were found during the entire growing season (Watanabe et al., 2004). Cytokinin-like substance concentrations were higher in shoots of ‘Wijcik’ than in those of the other strains of ‘McIntosh’ mutants (Looney et al., 1988). Cytokinin concentrations in shoots of columnar-type ‘Maypole’ and ‘Tuscan’ were higher than that of ‘McIntosh’ (Watanabe et al., 2004) indicating that both cytokinin and auxin levels might be involved in determining growth habits of apple trees. Apical dominance results in correlative inhibition whereby apical buds, mediated via an auxin, inhibit lateral shoot growth in many plant species. Therefore, in this study, endogenous IAA and cytokinin levels in young apical and lateral shoots related to correlative inhibition were determined to clarify the relationship between growth characteristics and apical dominance in columnar type apple trees. The correlative growth relationship was investigated in response to heading-back pruning of one-year-old shoots and the concentrations of the growth regulators in young apical and lateral shoots after bud burst in columnar-type apple trees.

Materials and Methods

1. Effects of heading-back pruning on 'Trajan' shoot growth

Three-year-old columnar-type 'Trajan' apple trees grafted on Marubakaidou (*Malus prunifolia* Borkh. var. *ringo* Asami) rootstocks and 24-year-old normal-type 'Fuji' apple trees grafted on M.26 rootstocks were used for this experiment in 2002. In both cultivars, the terminal 10 cm of shoots from 15 one-year-old vertical shoots of 50–60 cm were headed back in mid-April; the control shoots were left intact. The terminal lateral bud, after removal of the distal part of the shoot, is called the apical bud in the pruned shoot. The length and number of shoots, emerging from the apical and lateral buds, were counted in late October. The lateral shoots were quantified by counting and measuring lateral shoots longer than 1 cm that emerged from the previous season's growth. The number of lateral shoots per centimeter of one-year-old shoots was recorded. The average lateral shoots length was determined by measuring the mean length of lateral shoots emerging from the previous year's shoots. The frequency of the emerging lateral shoots was determined by counting the shoots, emerging from each lateral bud located by the ninth node below the apex for 15 pruned and intact shoots. The lateral shoot lengths were determined by calculating the mean length of shoots emerging from each lateral bud located by the ninth node below the apex for 15 shoot.

2. IAA and cytokinins in burst buds of columnar-type apple trees

1) Plant materials

In 2002, five-year-old columnar-type 'Maypole', 'Tuscan', and 'Wijcik' apple trees, which were grafted on seedling rootstocks, and 40-year-old normal 'McIntosh' apple trees, which were grafted on seedling rootstock growing at the Department of Apple Research, National Institute of Fruit Tree Science were selected. Budburst in the apple cultivars occurred with 1 to 3 April, new apical and lateral shoots located on the tenth nodes below the apex on the previous year's shoot were collected at random from several trees on 25 April. Those young shoots that had no developed xylem tissue consisted of expanding and unfolded leaves, and the growing apices. The expanding leaves were removed and the remaining parts were pooled and stored at -30 until analyzed.

2) Extract and purification procedure for IAA

Extracts and purification procedures for IAA were performed according to Watanabe et al. (2004), i.e., a 500-mg (FW) sample was macerated in cold 80% (v/v) methanol containing 50 mg soluble polyvinylpyrrolidone (K-30; Tokyo Kasei Kogyo Co. Ltd., Tokyo, Japan) with 5 nmol of [¹³C₆]-IAA as an internal standard. Extracts were partitioned with diethyl ether. The diethyl ether phase was evaporated to dryness in vacuo. Then the

residue was dissolved in 20% (v/v) methanol, an aliquot of which was injected into a high performance liquid chromatograph (HPLC), equipped with an internal OSD-2 column (10 mm i.d. × 150 mm; GL Science Inc., Tokyo, Japan). The column was eluted with a linear gradient from 30% (v/v) to 80% (v/v) methanol in 0.5% (v/v) acetic acid. The eluates were collected as the IAA fraction based on retention time. Each sample was prepared in duplicate.

3) Extract and purification procedure for cytokinins

Extracts and purification procedures for cytokinins were performed according to Watanabe et al. (2004), i.e., a 500-mg (FW) sample was macerated in cold 80% (v/v) methanol with 100 ng each of [²H₅]-zeatin (Z), [²H₆]-zeatin riboside (ZR), [²H₅]-isopenyladenine (iAde), [²H₆]-isopenyladenosine (iAdo) as internal standards. The extracts were passed through a column of polyvinylpyrrolidone and the eluate was partitioned with water-saturated n-butanol. The n-butanol phase was evaporated to dryness in vacuo and the residue was dissolved in 20% (v/v) methanol. An aliquot of the methanolic sample was injected into the HPLC as above for IAA analysis. The column was eluted with a linear gradient from 5% (v/v) to 80% (v/v) methanol in 0.5% (v/v) acetic acid. The eluates were collected based on their individual retention times as fractions of Z, ZR, iAde and iAdo. Analyses of respective samples were replicated.

4) Gas chromatograph mass spectrometry-selected ion monitoring (GC-MS-SIM) analysis

The IAA and cytokinin derivatives were quantified with a GC-MS-SIM (QP5000; Shimadzu Corp., Kyoto, Japan), equipped with a fused-silica capillary column (0.22 mm i. d. × 25 m, CBP1, Shimadzu Corp., Kyoto, Japan). Selected ion monitoring was conducted at *m/z* 130/136 for IAA/[¹³C₆]IAA, and respectively at 230/235, 216/221, 231/237, and 391/397 for Z/[²H₅]Z, ZR/[²H₅]ZR, iAde/[²H₆]iAde, and iAdo/[²H₆]iAdo.

3. Statistics

Data for shoot growth between treatment on the same cultivars were compared by using the least significant difference (LSD) test at the 5% level. All data for IAA and cytokinins concentration were analyzed by using two-way (cultivars × position) analysis of variance (ANOVA). Furthermore, IAA and cytokinins concentrations between position on the same cultivars were compared by using the LSD test at the 5% level.

Results

1. Effects of heading-back pruning on 'Trajan' shoot growth

Heading-back did not increase the total shoot length significantly in either cultivar compared to that of the controls (Table 1), but the treatment reduced terminal shoot length of 'Fuji' significantly compared to that of the control. Total shoot growth and the number of lateral

Table 1. Effects of heading-back pruning on shoot growth in columnar-type ‘Trajan’ and normal-type ‘Fuji’.

Cultivar	Treatment	Total shoot length (cm)	Terminal shoot length (cm)	Lateral shoot length (cm)	Number of lateral shoots on previous year's branch (number/cm)
Fuji	control	67.4 ± 26.2 a	36.4 ± 8.4 b	7.8 ± 7.7 a	0.05 ± 0.04 a
	heading	76.9 ± 36.8 a	28.6 ± 8.3 a	12.2 ± 7.9 a	0.07 ± 0.05 a
Trajan	control	59.5 ± 22.7 a	51.3 ± 19.4 a	2.2 ± 2.2 a	0.05 ± 0.04 a
	heading	77.7 ± 31.8 a	53.8 ± 19.3 a	8.2 ± 6.2 b	0.05 ± 0.01 a

Data are means ± SD (n = 15). Different letters indicate significant difference ($P < 0.05$) by LSD test.

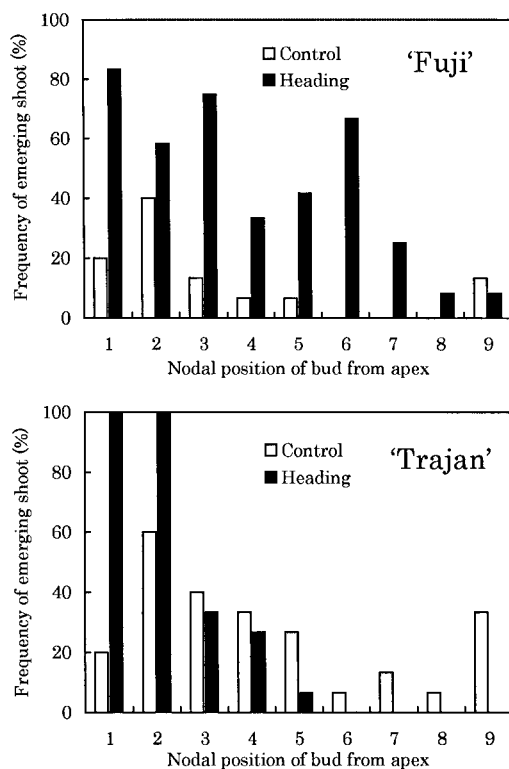


Fig. 1. Effects of heading-back pruning on frequency of the emerging shoots from all lateral buds of one-year-old shoots in ‘Fuji’ (upper) and ‘Trajan’ (lower) apple trees. The first and ninth buds below apical buds are respectively indicated as “1” and “9”.

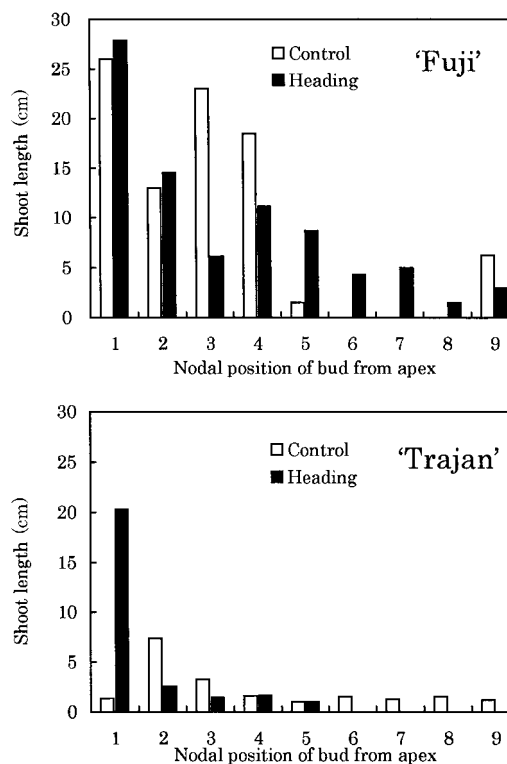


Fig. 2. Effects of heading-back pruning on the mean length of shoots emerging from all lateral buds of one-year-old shoots in ‘Fuji’ (upper) and ‘Trajan’ (lower) apple trees. The first and ninth buds below apical buds are respectively indicated as “1” and “9”.

shoots of ‘Trajan’ was unaffected by heading, but the treatment increased lateral shoot length.

The range of bud position of emerging shoots in ‘Fuji’ was expanded by the heading, but narrowed in ‘Trajan’ (Fig. 1). Heading increased the frequency of emerging shoot in ‘Fuji’ and increased the frequency of emerging shoots from lateral buds; it occurred only at first and second nodes below the apex in ‘Trajan’.

Lengths of lateral shoots located by second node below the apex in ‘Fuji’ were unaffected by the heading, whereas the treatment decreased the lengths of lateral shoots located at the third and fourth nodes below the apex (Fig. 2). In ‘Trajan’, the lateral shoots length was shorter than about 7 cm in the control, but that of lateral shoots, located at the first node, was increased from 1.3 to 20.3 cm by heading.

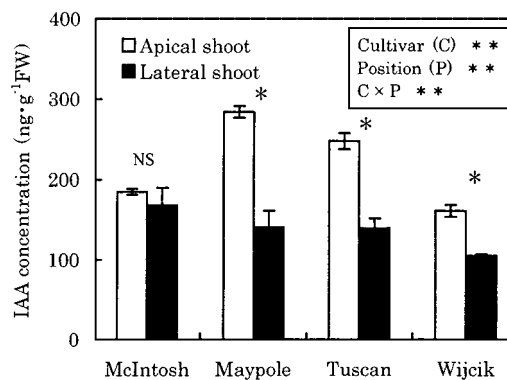


Fig. 3. IAA concentration in young apical and lateral shoots of one-year-old shoots after bud bursting in ‘McIntosh’, ‘Maypole’, ‘Tuscan’ and ‘Wijcik’. Vertical bars indicate SD (n = 2). NS and * above column: Not significant (NS) or significant ($P < 0.05$) by LSD test, ** in frame: Significant at $P < 0.01$ by two-way ANOVA.

2. IAA and cytokinins in burst buds of columnar-type apple tree

The IAA concentration differed significantly among cultivars and nodal positions (Fig. 3). In ‘Maypole’, ‘Tuscan’, and ‘Wijcik’, the IAA concentrations were significantly higher in young apical shoots than in young lateral shoots, but they were not significantly different between the two organs in ‘McIntosh’. The total cytokinin concentration differed significantly among cultivars; it was higher in ‘Maypole’, ‘Tuscan’, and ‘Wijcik’ than in ‘McIntosh’ in both apical and lateral shoots (Fig. 4). No differences were apparent in Z and iAdo concentrations among cultivars and positions (Fig. 5), but ZR and iAde concentrations differed significantly

among positions. In ‘McIntosh’ and ‘Tuscan’, apical shoots contained significantly higher ZR than did lateral shoots. The iAde concentration in ‘Wijcik’ showed significant differences between apical and lateral shoots. The ratio of total cytokinin to IAA concentration (IAA/CK) was not significantly different among cultivars and nodal positions (Fig. 6).

Discussion

Heading-back by removing two-thirds of the previous seasons’ terminal growth in ‘Delicious’ engendered significantly more lateral buds to develop into shoots (Elfving and Forshey, 1977). Likewise, the traditional pinching treatment in ‘Idared’ created significantly more lateral shoots per tree and longer lateral shoots. That treatment was also associated to significantly shorter terminal shoots (Hrotko et al., 1997). Consequently, decapitation distal apple shoots generally inhibits terminal shoot growth and promotes lateral shoot growth. In this experiment, however, ‘Trajan’ terminal shoot growth was not inhibited by heading-back in that both terminal and distal lateral shoots were forced into growth. Heading might substitute distal lateral buds for apical buds immediately and apical dominance might be reestablished. This induced dominant growth of distal shoots in ‘Trajan’ which suggests that the columnar type has stronger apical dominance than dose ‘Fuji’.

Pruning removes plant parts that are sites of plant growth regulator production (Faust, 1989). Dormant pruning upsets shoot/root ratio; thus, it promotes the growth of lateral buds without treatment from plant growth regulators. This growth response is caused by the change of endogenous plant growth regulators in

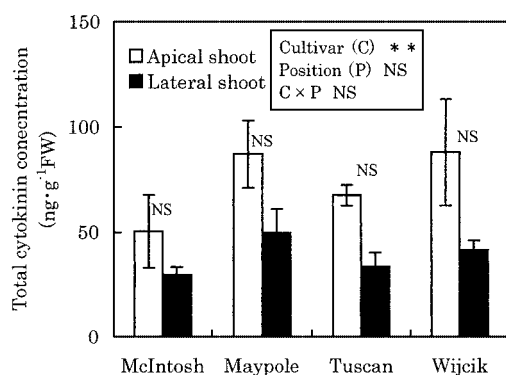


Fig. 4. Total cytokinin concentration in young apical and lateral shoots of one-year-old shoots after bud bursting in ‘McIntosh’, ‘Maypole’, ‘Tuscan’ and ‘Wijcik’. Vertical bars indicate SD ($n=2$). NS above column: Not significant ($P<0.05$) by LSD test, NS and ** in frame: Not significant or significant at $P<0.01$ by two-way ANOVA.

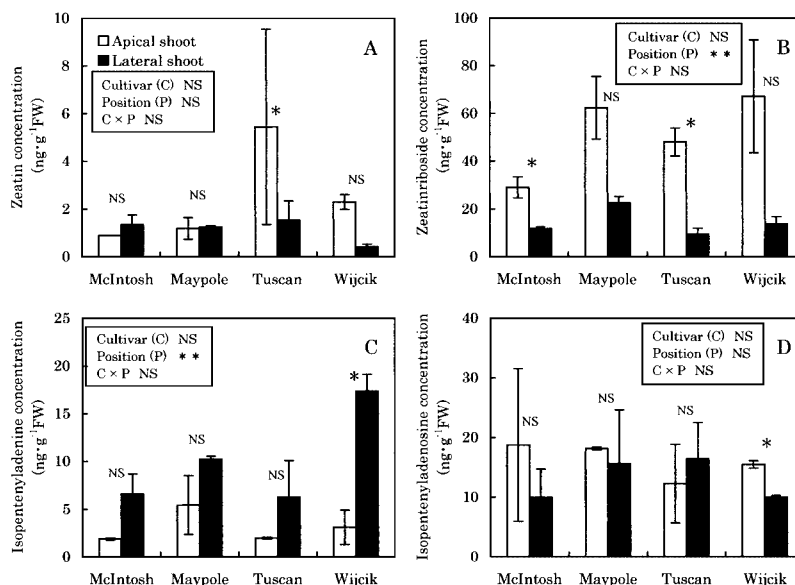


Fig. 5. Concentration of zeatin (A), zeatin riboside (B), isopentenyladenine (C) and isopentenyladenosine (D) in young apical and lateral shoots of one-year-old shoots after bud bursting in ‘McIntosh’, ‘Maypole’, ‘Tuscan’ and ‘Wijcik’. Vertical bars indicate SD ($n=2$). NS and * above column: Not significant or significant ($P<0.05$) by LSD test, NS and ** in frame: Not significant or significant at $P<0.01$ by two-way ANOVA.

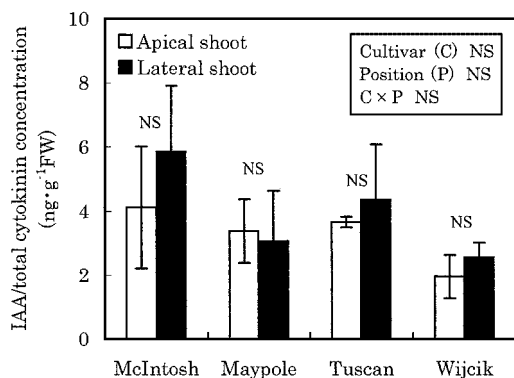


Fig. 6. Ratio of total cytokinin concentrations to IAA concentration (IAA/CK) in young apical and lateral shoots of one-year-old shoots after bud bursting in 'McIntosh', 'Maypole', 'Tuscan' and 'Wijcik'. Vertical bars indicate SD ($n=2$). NS above column: Not significant ($P < 0.05$) by LSD test, NS in frame: Not significant $P < 0.01$ by two-way ANOVA.

apple trees (Grochowska and Karaszewska, 1978). Our experiment showed that heading-back might have different effects on the respective endogenous plant growth regulators of 'Trajan' and 'Fuji'.

The role of endogenous IAA in columnar-type trees' shoot growth remains controversial (Lane and Looney, 1984; Watanabe et al., 2004). In this experiment, IAA concentration in columnar types was higher in apical shoots than in lateral ones. In *Brassica oleracea*, *Xanthium strumarium* and *Phaseolus vulgaris*, IAA concentrations of lateral buds are lower than the apical ones. Hence, decapitation releases the shoot from apical dominance, thereby, it increases IAA concentration in lateral buds (Gocal et al., 1991; Thomas, 1972; Tucker and Mansfield, 1973). The difference in IAA concentrations between apical and lateral shoots suggests that apical shoots inhibited lateral shoot growth more in columnar types than that in 'McIntosh'. The initial growth of lateral buds on one-year-old shoots somehow involve IAA concentration in columnar-type trees. It is well known that auxin, produced in apical buds, inhibits the growth of lateral buds through polar transport (Bangerth, 1989). The diffusive auxin from apical buds in the columnar type should be determined.

Looney et al. (1988) and Watanabe et al. (2004) showed that higher cytokinin concentrations in the shoots are related to shoot growth regulation of the columnar type. In this study, cytokinin concentrations of both apical and lateral shoots on one-year-old shoots after bud burst were higher in the columnar type than in the normal type which indicates that cytokinins are related to the initial growth of apical and lateral shoots in the columnar type.

ZR might be the predominant growth regulator involved in spring bud burst in apples (Cutting et al., 1991; Tromp and Ova, 1990). Watanabe et al. (2004) suggested that the high ZR concentration of shoots is related to growth characteristics in columnar-type trees.

In this experiment, apical buds contained more ZR than did lateral buds, but no distinct differences were found between columnar and normal types. Hence, the kind of cytokinin that is directly concerned with the growth regulation of columnar types was not ascertained.

Lateral bud elongation is inhibited by IAA (Bangerth, 1989), whereas benzyladenine (BA) increased endogenous cytokinin concentrations in apple trees (Carboni et al., 2002) and promoted the number of shoots that emerge from lateral buds in all apple trees (Hrotko et al., 1997; Wertheim and Estabrooks, 1994). These results indicate that low IAA/CK ratio promotes bud burst of lateral buds. The IAA/CK in lateral buds in our study tended to be lower in 'Maypole', 'Tuscan', and 'Wijcik' than in 'McIntosh'. Although lateral buds in 'Maypole', 'Tuscan', and 'Wijcik' were inhibited by the apical bud, they had high cytokinin concentrations. The numerous spurs on its young lateral shoots in the columnar type might be attributed to the low IAA/CK ratio.

Both 'Maypole' and 'Tuscan' are 'Wijcik' progenies, but their growth habits differ. In our experiment, the IAA and cytokinin concentrations in 'Wijcik' differ not only from those of 'McIntosh', but also from those of 'Maypole' and 'Tuscan'. The relationship between growth characteristics such as node length, number of spurs, spur length, and endogenous plant growth regulators among the columnar cultivars should be investigated to elucidate the growth components of columnar-type apple trees. In experiments 1 and 2, different columnar- and normal-type cultivars were used for comparison; we should have included identical cultivars in our trials.

In conclusion, heading-back of 'Trajan' induced more terminal and distal lateral shoot growth than it did on 'McIntosh'. The IAA concentration of the columnar phenotypes, 'Maypole', 'Tuscan', and 'Wijcik' were higher in apical shoots than in lateral shoots, indicating that shoot growth in columnar type is directed more toward apical dominance than in the normal phenotype. Auxin and cytokinins play a small role in growth of columnar type, such as less growth of lateral bud and vertical shoot elongation. Therefore, future studies should examine other plant growth regulators such as gibberellin and abscisic acid.

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カラムナータイプリンゴ樹における切り返しせん定が新しょう成長に及ぼす影響ならびに発芽後の
芽中の IAA およびサイトカイニン含量

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リンゴカラムナータイプ樹の生育特性と頂芽優勢性との関係を明らかにするため、切り返しせん定に対する成長反応および発芽後の若い頂生新しょうおよび腋生新しょうのインドール酢酸 (IAA) およびサイトカイニン含量を調査した。切り返しせん定により‘トラジャン’では頂生新しょう長は抑制されず、腋芽の先端部が優勢な成長を示した。‘メイポール’‘タスカン’および‘ウィジック’の IAA 含量は腋生新しょうよりも頂生新しょう

中で高かった。頂生および腋生新しょう中のサイトカイニン含量は‘旭’よりも‘メイポール’‘タスカン’および‘ウィジック’で高かった。カラムナータイプ樹の新しょう成長に関与するサイトカイニンの種類は特定できなかった。IAA/ サイトカイニンは品種間および部位間に有意な差は認められなかった。以上の結果から、カラムナータイプ樹の生育特性には頂芽優勢性が普通タイプ樹よりも強く関与することが推察された。