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ENHANCING FEATHERING OF ONE-YEAR-OLD GALA AND JONAGOLD APPLE TREES THROUGH APPLICATION OF 6-BENZYLAMINOPURINE AND GIBBERELLINS

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Abstract

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In apple, synthetic cytokinin 6-benzylaminopurine (BA), either alone or combined with gibberellins 4+7 (GA_{4+7}), plays an important role in overcoming apical dominance and in the production of well-feathered apple nursery trees. The solutions of BA and BA+GA_{4+7} corresponding to the concentrations of 250, 350 and 450 μl l^{-1} of active ingredient (BA) were applied three times at 7-day intervals during vegetative period. Feather formation is strongly influenced by type and concentration of plant growth regulators. Increasing concentrations of BA and BA+GA_{4+7} led to a greater number of feathers, increased feather length, and expanded branching zone. Applied in combination with GA_{4+7}, BA has stronger positive effect on total feather number, feather length, branching zone and tree height, than when applied alone. Compared to BA+GA_{4+7}, BA has a stronger effect on the growth rate of the shoot, resulting in a greater feather angle and a lower tree height, which can be eliminated by addition of GA_{4+7}. The treatments also had different effects on trunk diameter. In Gala, a minor adverse effect of BA on trunk diameter was noted, whereas it was positive in Jonagold.

Key words: apical dominance, auxins, feathers, *Malus domestica*, nursery trees

Introduction

For a high-quality tree, the presence of a sufficient number of feathers is desirable because they form flower buds in the second year of nursery production and enable the tree to bear fruit in the first year following planting (Robinson et al., 2006; Sadowski et al., 2007; Elfving, 2010). Moreover, as feathered trees facilitate earlier canopy structure formation, pruning is consequently simplified and management costs reduced (Robinson, 2007). Nursery-grown apple cultivars vary greatly in their tendency to form feathers (Wertheim and Webster, 2003). Some one-year-old apple cultivars exhibit poor feathering (Volz et al., 1994; Hrotko et al., 2000; Sazo and Robinson, 2011). Important factors in feathering are nutrient availability (Tromp, 1996), ecological conditions (Tromp, 1996; Tromp and Boertjes, 1996) and apical dominance (Cline, 1991; Volz et al., 1994; Sazo and Robinson, 2011), i.e., the control that the terminal bud exerts over the development of lateral buds (Cline, 1997). This dominance establishes certain branching patterns characteristic of each woody plant species (Wilson, 2000). In an attempt to explain the mechanism of apical dominance, several hypotheses emerged, including hormonal hypothesis, photosynthetic hypothesis, and the hypothesis of water and mineral nutrient transport (Wilson, 2000). Hormonal hypothesis suggests that auxins play a role in apical growth dominance, which can be overcome by cytokinins (Cline, 1991; Cook et al., 2001; Wang et al., 1994). Auxin is mainly synthesized in the shoot apex in young leaves (Aloni, 2007) and is subsequently transported basipetally (downward, from the tip to the base) (Aloni, 2007; Müller and Leyser, 2011). The application of 6-benzylaminopurine (BA) affects the flow of auxins (Müller and Leyser, 2011) and temporarily impedes the main shoot growth (Sazo and Robinson, 2011), which helps overcome apical dominance and creates favourable conditions for feather formation. In apple varieties, BA – either alone

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or in combination with gibberellins 4+7 (GA_{4+7}) – plays an important role in overcoming apical dominance and in the production of well-feathered nursery trees (Volz et al., 1994; Wertheim and Estabrooks, 1994; Hrotko et al., 2000; Rossi et al., 2004; Sazo and Robinson, 2011).

Gala and Jonagold, as well as their mutants, are still among the most important apple cultivars in Europe (WAPA, 2012). The objective of this paper is to determine the effects of a range of concentrations (250-450 µl l^{-1} BA) of BA and BA+GA_{4+7} on feather formation on one-year-old Gala and Jonagold apple trees.

Materials and Methods

The experiment was carried out in 2011 and 2012, in a commercial nursery situated in Kanjiža, Serbia (46º03'N, 20º01'E, 77 m a.s.l.), using one-year-old Gala and Jonagold apple trees on M9 T337 rootstocks.

The experimental procedure followed a randomized block design with four replications, each represented by five plants (corresponding to 20 plants per treatment). The rootstocks were planted in March, at a 1.1×0.1 m distance. In August, during the first vegetative period, the plants were grafted by chip budding at 20 cm above ground. At the time of the second vegetative phase, during the growth of the main shoot, all feathers that emerged below 62-64 cm height were removed with a sharp knife. During the second vegetative period, the apical section of the main shoot was sprayed (15 cm in length in the first spraying and 10-15 cm in the second and third sprayings) using a hand sprayer until run-off. Three spray treatments were performed at 7-day intervals. The first treatment was applied in mid-June, when the growth of the main shoot reached 78-80 cm. Irrigation utilizing a sprinkler system was carried out as required.

The treatments used consisted of Gerba 4 LG, containing 4% BA, and Progerbalin LG, containing 1.8% BA and 1.8% GA_{4+7} ("L-Gobbi", Italy), each with varying concentrations of active ingredient BA (250, 350 and 450 µl l^{-1}). A surfactant, Trend® 90 ("Du-Pont", USA), was added to each treatment at the rate of 500 µl l^{-1}.

At the end of the vegetative period, the following parameters were measured: number of feathers, feather length, feather angle (for feathers longer than 10 cm), tree height and trunk diameter (10 cm above the graft union), height of the lowest and highest feather, and branching zone (based on the distance between the highest and lowest feather).

Using Statistica 12 (StatSoft Inc., Tulsa, USA), the data were statistically processed by analysis of variance (ANOVA) and mean values were compared by applying Duncan's multiple range test ($P < 0.05$).

Results and Discussions

Total number of feathers

In both experimental years, the controls of both cultivars had very few feathers—with Gala having 3.7-4.3 and Jonagold 0.6-2.8 (Figures 1 and 2). Nursery trees with such

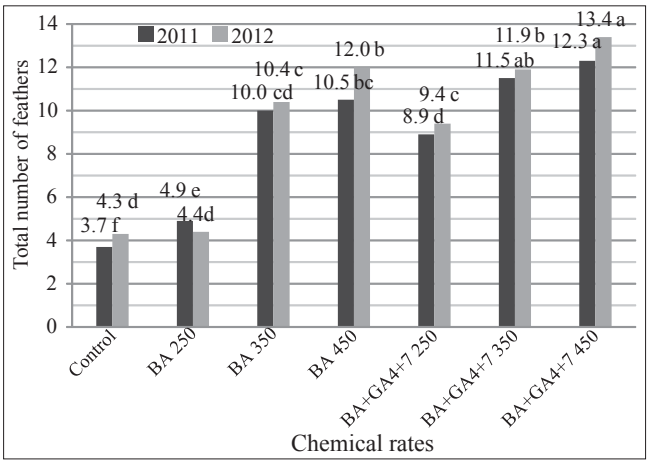

Fig. 1. Effects of BA and BA+GA_{4+7} on the total number of feathers in one-year-old Gala trees

[1] Number indicates the amount of active ingredient (BA) in the spraying solution (expressed in µl l^{-1})

[2] Means followed by different letters are significantly different at $P \leq 0.05$, as established by the Duncan's Multiple Range Test

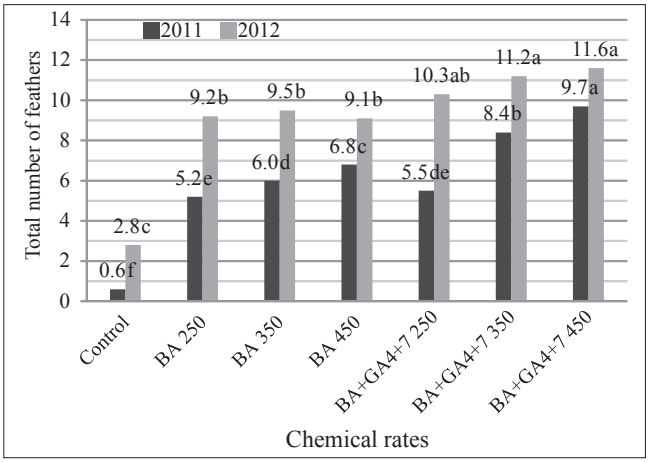

Fig. 2. Effects of BA and BA+GA4+7 on the total number of feathers in one-year-old Jonagold trees

[1] Number indicates the amount of active ingredient (BA) in the spraying solution (expressed in µl l^{-1})

[2] Means followed by different letters are significantly different at $P \leq 0.05$, as established by the Duncan's Multiple Range Test

a small number of feathers are not suitable for intensive orchard planting, as cropping is significantly delayed (Robinson et al., 2006; Elfving, 2010). The treatments with BA and BA+GA_{4+7} significantly affected the formation of feathers. Increasing the BA concentrations (250-450 µl l^{-1}) resulted in significant increase in the total number of feathers in all samples except Jonagold in 2012. Findings of previous studies of one-year-old apple trees indicate that increasing BA concentrations from 200 to 400 µl l^{-1} (Hrotko et al., 2000) and BA+GA_{4+7} from 250 to 750 µl l^{-1} BA (Rossi et al., 2004; Jacyna and Barnard, 2008) led to the emergence of a greater number of feathers.

All treatments in which BA+GA_{4+7} was applied resulted in a significantly higher number of feathers compared to application of only BA. Other authors claim that BA is responsible for overcoming apical dominance (Cook et al., 2001; Müller and Leyser, 2011) and enhancing feathering in apple nursery trees (Wertheim and Estabrooks, 1994; Hrotko et al., 2000; Sazo and Robinson, 2011), while the main role of GA is to elongate feathers (Volz et al., 1994; Hrotko et al., 2000). However, in pears, when applied on its own, GA_{4+7} are capable of enhancing feathering (Palmer et al., 2011). Our results show that, when GA_{4+7} are applied in combination with BA, it has a positive effect on total feather number in Gala and Jonagold apple nursery trees.

In all treatments of both cultivars, except Gala in treatment BA 250, a higher number of feathers were obtained in 2012 than in 2011, possibly due to more favourable environmental conditions in 2012. Soil temperature, air humidity and air temperature are important factors affecting feather formation and growth on an apple tree (Tromp, 1996; Tromp and Boertjes, 1996). Soil is another important factor affecting the variable plant quality. As Palmer et al. (2011) noted, in order to avoid apple tree diseases, nurserymen often rent new land; hence, soil quality may have an effect on tree growth characteristics as well. The differences noted in the two years of the research were particularly pronounced in Jonagold.

Feather length

Feather length is also important in determining the tree quality. According to Sadowski et al. (2007), feather length and orchard tree productivity are linked. Apple cultivars differ in their ability to form feathers in the nursery (Wertheim and Webster, 2003; Cvetković, 2010), whereby Gala and Jonagold tend to form longer feathers (Kviklys, 2006; Cvetković, 2010; Atay and Koyuncu, 2013). In Gala cultivar, length of most feathers on the control trees exceeded 30 cm (Table 1). In 2011, most feathers developed on the Jonagold control trees were 10-30 cm long, exceeding 30 cm in 2012 (Table 2). Apart from a different feathering potential, in the absence

Table 1
Effects of BA and BA+GA_{4+7} application on feather number (< 10 cm, 10–30 cm, > 30 cm) and feather length in one-year-old Gala trees

Treatment	Total number of feathers <10 cm	Total number of feathers 10–30 cm	Total number of feathers >30 cm	Total feather length, cm	Mean feather length, cm
2011					
BA+GA_{4+7} 450[1]	0.5	6.4ab[2]	5.4a	369.9a	29.1b
BA+GA_{4+7} 350	0.0	7.4a	4.1ab	328.2b	28.7b
BA+GA_{4+7} 250	0.5	4.7bc	3.7ab	230.2c	27.6b
BA 450	0.0	6.2ab	4.3ab	296.6b	28.4b
BA 350	0.6	6.8ab	2.6bc	210.2c	21.1c
BA 250	0.3	3.2c	1.4c	126.1d	26.2bc
Control	0.0	0.6d	3.1bc	127.4d	34.7a
2012					
BA+GA_{4+7} 450	0.0	7.1a	6.3a	413.5a	29.8c
BA+GA_{4+7} 350	0.2	7.1a	4.6bc	351.8b	29.6c
BA+GA_{4+7} 250	0.4	4.7b	4.3bc	263.2c	29.6c
BA 450	0.0	6.7a	5.3ab	359.8b	30.1c
BA 350	0.5	6.9a	3.0c	237.5c	22.9d
BA 250	0.2	1.3c	2.9c	154.2d	35.5b
Control	0.0	1.0c	3.3c	174.6d	41.2a

[1] Number indicates the amount of active ingredient (BA) in the spraying solution (expressed in µl l^{-1})

[2] Means followed by different letters are significantly different at $P \leq 0.05$, as established by the Duncan's Multiple Range Test

Table 2
Effects of BA and BA+GA_{4+7} application on feather number (< 10 cm, 10–30 cm, > 30 cm) and feather length in one-year-old Jonagold trees

Treatment	Total number of feathers <10 cm	Total number of feathers 10–30 cm	Total number of feathers >30 cm	Total feather length, cm	Mean feather length, cm
2011					
BA+GA_{4+7} 450[1]	2.6a[2]	4.2a	2.9a	245.7a	25.3c
BA+GA_{4+7} 350	2.3a	4.0a	2.1b	173.2c	20.7d
BA+GA_{4+7} 250	1.4b	3.0b	1.1c	105.9d	19.4d
BA 450	1.5b	2.3bc	2.9a	201.6b	29.4bc
BA 350	1.4b	2.2bc	2.4ab	151.3c	25.8c
BA 250	0.6c	1.7c	2.9a	168.9c	32.8b
Control	0.0c	0.3d	1.7bc	84.7d	44.8a
2012					
BA+GA_{4+7} 450	1.0a	6.8b	3.8a	313.7a	27.0a
BA+GA_{4+7} 350	1.2a	7.4ab	2.6b	280.6a	24.9ab
BA+GA_{4+7} 250	0.6ab	9.0a	0.7c	201.7b	19.6d
BA 450	0.1b	7.4ab	1.6bc	214.0b	23.7abc
BA 350	1.1a	6.8b	1.6bc	210.0b	22.2bcd
BA 250	1.3a	6.8b	1.1c	180.9b	20.3cd
Control	0.1b	1.6c	1.3c	95.2c	27.1a

[1] *Number indicates the amount of active ingredient (BA) in the spraying solution (expressed in µl l^{-1})*
[2] *Means followed by different letters are significantly different at $P \leq 0.05$, as established by the Duncan's Multiple Range Test*

of exogenous hormones, apple cultivars may respond differently to the application of branching agents (Jacyna and Barnard, 2008). In Gala cultivar, BA and BA+GA_{4+7} treatments did not affect the formation of feathers shorter than 10 cm, while in Jonagold, the number of such feathers increased. In both cultivars, the application of BA and BA+GA_{4+7} significantly increased the number of feathers longer than 10 cm. In addition, in both cultivars, across all treatments, the branches of 10-30 cm length were predominant.

The results indicate positive correlation between the total number and total length of branches. In both cultivars, total feather length increased with increasing BA and BA+GA_{4+7} concentrations. Moreover, irrespective of concentration, application of BA+GA_{4+7} was more effective than BA alone. The effect of GA_{4+7} on feather length was thus positive. In Jonagold cultivar, mean feather length increased with increasing BA and BA+GA_{4+7} concentrations. The only exception is BA 250 treatment in 2011, which resulted in greater mean feather length than BA 350 in both years, and BA 450 in 2012. In Gala, while increasing concentrations of BA+GA_{4+7} resulted in the increased mean feather length, the differences were not statistically significant. BA treatments did not always show this tendency. Due to low BA concentrations in BA 250 treatments, both cultivars had significantly fewer feathers compared to those treated with BA and BA+GA_{4+7}. In 2011, when subjected to BA 250 treatment, the trees formed longer feathers because the nutrients were used for the growth of a smaller number of shoots. As the main shoot and feathers are in competition for water and nutrients (Cline, 1991), an increase in the number of feathers enables variation in mean feather length (Dorić et al., 2013). These results are in accordance with earlier research findings, which confirmed that GA affects shoot elongation on apple trees (Volz et al., 1994; Bulley et al., 2005).

Branching zone

Under all BA and BA+GA_{4+7} treatments, except BA 250 and BA+GA_{4+7} 250 applied on Jonagold in 2011, feathering occurred at a satisfactory height of 65-67 cm (Tables 3 and 4). In Jonagold, the height of the first feather indicates that the lower BA concentration (250 µl l^{-1}) was not sufficient for feathers to form at a desired height. It is very important that the first spraying is performed at the right time and with appropriate concentrations of BA or BA+GA_{4+7}, so that the first feather forms at the right height, as this is indicative of the success of the first spraying treatment (Dorić et al., 2013). In apple, BA+GA_{4+7} should be applied when the tip of the shoot is 4-20 cm from the desired height of the first feather (Elfving and Visser, 2006). If trees are not sprayed with appropriate concentrations of BA or BA+GA_{4+7}, it is possible, as was the case with Jonagold that the first feather will not emerge at the right height.

Table 3
Effects of BA and BA+GA_{4+7} application on the height of the lowest and highest feather, branching zone, feather angle, tree height and trunk diameter in one-year-old Gala trees

Treatment	Lowest feather height, cm	Highest feather height, cm	Branching zone, cm	Feather angle, °	Tree height, cm	Trunk diameter, mm
2011						
BA+GA_{4+7} 450[1]	65.1b[2]	112.1a	46.9a	52.5cd	166.5bc	13.6a
BA+GA_{4+7} 350	65.0b	105.9b	40.9b	52.2d	166.3bc	13.7a
BA+GA_{4+7} 250	65.0b	102.4bc	37.4bc	55.6bc	166.5bc	13.7a
BA 450	65.1b	100.7bc	35.6bcd	57.6ab	164.6cd	13.5a
BA 350	66.9a	101.0bc	34.1cd	58.2ab	161.1d	12.0b
BA 250	66.5ab	79.7d	13.2e	57.4ab	170.6b	12.1b
Control	66.2ab	96.5c	30.3d	60.6a	175.5a	13.6a
2012						
BA+GA_{4+7} 450	65.3b	113.5a	48.2a	51.9c	169.6b	13.0ab
BA+GA_{4+7} 350	65.0b	105.5b	40.5b	51.7c	168.0bc	13.2ab
BA+GA_{4+7} 250	65.2b	103.0bc	37.8b	54.6bc	164.8bc	13.0ab
BA 450	65.1b	104.9b	39.8b	60.6a	168.7bc	13.3ab
BA 350	66.2ab	102.8bc	36.6bc	57.7ab	162.3c	12.4b
BA 250	66.5ab	86.9d	20.4d	57.2ab	171.1ab	12.6b
Control	66.9a	96.5c	29.6c	59.4a	176.2a	13.8a

[1] *Number indicates the amount of active ingredient (BA) in the spraying solution (expressed in µl l^{-1})*
[2] *Means followed by different letters are significantly different at $P \leq 0.05$, as established by the Duncan's Multiple Range Test*

Table 4
Effects of BA and BA+GA_{4+7} application on the height of the lowest and highest feather, branching zone, feather angle, tree height and trunk diameter in one-year-old Jonagold trees

Treatment	Lowest feather height, cm	Highest feather height, cm	Branching zone, cm	Feather angle, °	Tree height, cm	Trunk diameter, mm
2011						
BA+GA_{4+7} 450[1]	65.4b[2]	100.6a	35.2a	59.2bc	154.9ab	12.2ab
BA+GA_{4+7} 350	65.5b	94.8b	29.3b	58.8c	155.9a	11.7bc
BA+GA_{4+7} 250	72.0a	91.9b	19.8c	54.1d	156.3a	11.3c
BA 450	65.9b	92.9b	27.0b	64.3a	152.5bc	12.8a
BA 350	66.0b	83.5c	17.5c	62.4abc	151.6c	11.9b
BA 250	70.8a	90.4b	19.6c	63.2ab	151.8bc	12.0b
Control	68.3ab	74.4d	5.1d	63.5a	154.3abc	11.3c
2012						
BA+GA_{4+7} 450	65.4b	104.7a	39.3a	52.3b	153.1a	12.7a
BA+GA_{4+7} 350	66.9b	105.1a	38.2a	49.2bc	154.8a	12.3ab
BA+GA_{4+7} 250	68.3ab	105.9a	37.6a	45.8c	155.2a	11.0cd
BA 450	65.7b	93.9b	28.1b	57.2a	129.8c	11.0cd
BA 350	66.6b	94.0b	27.4b	52.0b	130.8c	11.6bc
BA 250	66.7b	93.7b	27.0b	52.1b	134.6bc	10.2d
Control	71.0a	84.7c	13.7c	48.2bc	138.3b	10.6d

[1] *Number indicates the amount of active ingredient (BA) in the spraying solution (expressed in µl l^{-1})*
[2] *Means followed by different letters are significantly different at $P \leq 0.05$, as established by the Duncan's Multiple Range Test*

In both experimental years, increasing BA and BA+GA_{4+7} concentrations resulted in the expansion of the branching zone. Irrespective of BA concentration, branching zone values were significantly higher when BA+GA_{4+7} - rather than BA alone - was applied. It has been shown that GAs has significant effect on the elongation of the shoots in various woody species. Studies of apple trees have also established a significant effect of GA on the number and length of shoot internodes (Bulley et al., 2005). In line with these findings, our results indicate that application of GA_{4+7} significantly affects the elongation of the main shoot.

Feather angle and tree height

Feathers initially emerge at a very sharp angle, which increases with further growth. This is preferable to wide angle branching, as the resulting feathers bloom early and are more easily trained after planting (Warner, 1991). By affecting apical dominance, BA and BA+GA_{4+7} also impact feather angle and tree height (Wertheim, 1978; Elfving and Visser, 2005). In this research, significant differences between control and treatment samples of both cultivars were found (Table 3 and 4). Thus, we can conclude that, in both cultivars, BA treatments achieved a wider feather angle than BA+GA_{4+7}.

In the case of Gala cultivar, BA and BA+GA_{4+7} exhibited a minor negative effect on the main shoot growth (Table 3). The negative effect of BA on Jonagold cultivar was not significant in 2011, whereas it was much more pronounced in 2012 (Table 4). Extant studies have shown that Idared (Hrotko et al., 2000) and Fuji one-year-old apple nursery tree height (Sazo and Robinson, 2011) could be negatively affected by BA application. When applied alone, cytokinins reduce tree height, while gibberellin sprays consistently increase tree height in pears (Palmer et al., 2011). In the present study, similar results were obtained for Jonagold. In 2011, BA+GA_{4+7} application produced results that did not differ significantly from the control. In the following year, the trees treated with BA+GA_{4+7} were significantly taller than both controls and BA-treated trees. Thus, it can be concluded that GA_{4+7} can eliminate the negative effect of BA on the growth of the main shoot.

Trunk diameter

In Gala cultivar, trunk diameter values measured following application of BA and BA+GA_{4+7} were lower compared to control. In Jonagold, trunk diameter increased with increasing BA and BA+GA_{4+7} concentrations. Wertheim and Estabrooks (1994) reported a small positive linear correlation between BA concentration and trunk diameter in Red Boskoop apple trees. In contrast, following their study of one-year-old Catarina apples, Rossi et al. (2004) found that increasing concentrations of BA+GA_{4+7} from 250 to 750 µl l^{-1} BA resulted in the decrease in trunk diameter; however, the differences were not statistically significant. Studies of some other fruit species, such as plum (Magyar and Hrotko, 2002), and cherry (Magyar and Hrotko, 2005) also confirmed that BA can result in the decrease in trunk diameter to a certain degree, if higher concentrations of BA are applied. In pear, application of BA as a means of enhancing the formation of feathers did not affect the trunk diameter (Palmer et al., 2011). However, based on present and previous results, the mechanism by which BA and BA+GA_{4+7} affect tree diameter cannot be precisely determined. The four major hormonal signals that induce and control wood formation in trees are auxin, cytokinin, gibberellin and ethylene. The movement of IAA via the cambium regulates cambial activity (Aloni, 2007). Since BA affects the synthesis of auxins in shoot tip, it is possible that it also affects cambial activity, i.e., the thickening of the tree, both of which need further research.

Conclusions

BA and BA+GA_{4+7} treatments significantly affected feather formation in Gala and Jonagold one-year-old nursery trees. Increasing BA and BA+GA_{4+7} concentrations from 250 to 450 µl l^{-1} leads to an increase in the total number of feathers. In both cultivars, the application of BA and BA+GA_{4+7} results in an increase in the number of feathers exceeding 10 cm in lenght, while in Jonagold, increase was also noted in feathers shorter than 10 cm.

Total feather length increased with increased BA and BA+GA_{4+7} concentrations. As GA_{4+7} has a significant positive effect on feather length, BA+GA_{4+7} treatments are more effective than BA treatments.

The branching zone increased with increased BA and BA+GA_{4+7} concentrations. Low concentrations of BA and BA+ GA_{4+7} failed to induce the formation of feathers at the right height.

In addition to apical dominance, application of BA and BA+GA_{4+7} also affects tree height and feather angle. Compared to BA+GA_{4+7}, when applied alone, BA facilitates the formation of a wider feather angle. BA has a stronger effect on the growth rate of the main shoot, which can negatively affect tree height. As these negative effects of BA can be eliminted by GA_{4+7}, application of BA+GA_{4+7} can positively affect tree height, which was the case with Jonagold in 2012.

BA can reduce the trunk diameter, as evidenced by our results pertaining to Gala. In this cultivar, a minor adverse effect of BA on trunk diameter was detected, whereas it was mildly positive in Jonagold. Effects of BA and BA+GA_{4+7} on trunk diameter need to be further researched.

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