Gibberellic Acid Accelerates 'Honeycrisp', but not 'Cameo', Apple Fruit Maturation

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SUMMARY. **Gibberellins inhibit flowering in apple (*Malus domestica*) and show promise as tools to promote annual bearing. The authors validated the efficacy of gibberellic acid (GA) to reduce return bloom dramatically in two biennial cultivars. 'Honeycrisp' fruit treated in 2004 with GA_{4+7} at 0, 200, 400, or 600 mg·L^{-1} demonstrated advanced maturity in terms of starch levels, flesh firmness, and titratable acidity, whereas 'Cameo' fruit showed variable treatment effects. In 2005, 0, 300, 600, 900, or 1200 mg·L^{-1} GA_{4+7} was applied to 'Cameo', and fruit maturity was once again unaffected. Two commercial GA products (GA_4, GA_{4+7}) were applied in 2005 to 'Honeycrisp' at 400 mg·L^{-1}. Both formulations caused fruit to have less flesh firmness and acidity, and increased levels of starch conversion compared with the untreated control at harvest and after 140 d of common storage. All GA treatments in all four trials profoundly diminished flowering in the season after treatment. Results demonstrate differences in sensitivity to GA between the two cultivars.**

Biennial bearing is a major problem for apple producers, who need new options to manage cropping and to ensure consistent yields of high-quality fruit. Flowering promoters such as Ethephon or naphthaleneacetic acid (NAA) are widely used in the United States to improve return bloom after moderate to heavy crops. Floral initiation inhibitors, specifically gibberellins, show potential as crop load management tools by reducing return bloom after light crops. Literature widely reports the effects of various gibberellic acid (GA) isomers on flowering in apple in the season after application (Bertelsen and Tustin, 2002; Marino and Greene, 1981; McArtney, 1994; Meador and Taylor, 1987; Tromp, 1982). However, little has been reported on the effects of GA on apple fruit present during treatment (i.e., current season fruit).

In sweet cherry (*Prunus avium*), GA_3 can delay fruit maturation (Proebsting, 1972). The Pacific northwestern U.S. industry widely uses 10 to 20 mg·L^{-1} to increase fruit size and quality and to extend commercial harvest. The use of GA_3 has also been shown to delay maturity and improve fruit quality of prunes and plums (*Prunus domestica*) (Looney, 1996). Impacts of GA on apple maturity are not widely reported, but Greene (1989) found softer fruit at harvest and increased storage breakdown of GA-treated 'Empire' apples, suggesting that 50 to 150 mg·L^{-1} GA_{4+7} might accelerate ripening. Looney et al. (1992) saw no effect from 7.5 or 15 mg·L^{-1} GA_4 or GA_{4+7} on firmness of 'Golden Delicious', but did report higher sugar levels and decreased russeting in treated fruit. If growers are to use GA to help manage cropping in apple, the secondary effects of those programs on the current season's crop must be better understood.

The capacity of GAs to improve fruit finish is well documented (Looney, 1996). Taylor (1978) found GA_{4+7} to be more effective than similar rates of GA_3 to reduce russet in 'Golden Delicious'. The ability of GA_{4+7} to reduce russet in 'Golden Delicious' was later confirmed by Meador and Taylor (1987) and Elfving and Allen (1987). Reuveni et al. (2001) reported similar reductions in fruit russet from three different commercial bioregulator formulations containing GA_{4+7}. In addition to improving fruit finish, GA can affect other quality parameters. Unrath (1974) and Looney et al. (1992) observed increased fruit length and length-to-diameter ratio in apples treated with GA_{4+7}. Spray concentrations used in these studies were 10 to 20 times less than those typically used to manipulate flowering, making extrapolation of their results to significantly higher rates tenuous.

The trials reported here explore the collateral effects on in-season apple fruit maturity in two highly biennial cultivars from GA programs designed to inhibit return bloom as part of a comprehensive crop load management program.

Materials and methods

EXPERIMENTAL DESIGN. In both 2004 and 2005, two field trials were

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Units

To convert U.S. to SI, multiply by	U.S. unit	SI unit	To convert SI to U.S., multiply by
0.3048	ft	m	3.2808
3.7854	gal	L	0.2642
2.54	inch(es)	cm	0.3937
25.4	inch(es)	mm	0.0394
6.4516	inch^2	cm^2	0.1550
4.4482	lbf	N	0.2248
1	ppm	mg·L^{-1}	1
6.8948	psi	kPa	0.1450
(°F – 32) ÷ 1.8	°F	°C	(1.8 × °C) + 32

conducted in commercial apple orchards in three distinct growing districts of Washington state. Aside from elimination of bioregulator programs that affect flower initiation, standard orchard management strategies were followed by grower-cooperators. Each trial used a randomized complete block design with six replicates. In two 'Cameo' trials, whole individual trees served both as experimental and sampling units. Whole trees were also treated in two 'Honeycrisp' trials, but sampling units for bloom counts were restricted to an eastern- and western-oriented scaffold limb as a result of large tree size. Fruit for harvest analysis were randomly selected from entire trees. The 2005 'Honeycrisp' trial was located near the 2004 trial in the same orchard block. To isolate treatments, at least one buffer row was maintained between rows receiving treatment. In addition, a minimum of 3 m (one to three trees) of separation between treated trees was maintained within the row for all trials.

Data were analyzed with SAS (9.0) (SAS Institute, Cary, NC). Means were separated with the General Linear Models procedure (GLM) using Tukey's Studentized range test at 0.05 following a significant analysis of variance. When fixed-effects variables allowed regression analysis, the GLM procedure of SAS was used to evaluate the homogeneity of slopes, curvatures, and intercepts of the regressions on bioregulator concentration. Only significant findings are included in this report.

2004 TRIALS. We established a trial in a 7-year-old 'Cameo'/Budagovsky 9 (Bud.9) orchard near Tonasket, WA (lat. 48°46′N, long. 119°27′W). Trees were planted 1 × 3.5 m and trained to a three-wire vertical trellis in a spindle system. Treated trees were sprayed with 200, 400, or 600 $mg \cdot L^{-1}$ GA_{4+7} at 10-mm fruitlet size; control trees were left unsprayed.

A second trial was conducted near Brewster, WA (lat. 48°7′N, long. 119°46′W) on 6-year-old 'Honeycrisp' grafts on 14-year-old 'Regent' interstems on Poland 18 (P.18) rootstocks. These free-standing central leader trees were spaced 3 × 5 m. Spray applications were identical to those in of the 'Cameo' trial.

2005 TRIALS. A trial was established in 9-year-old 'Cameo'/M.9 'Nicolai 29' (M.9 'Nic.29') near Quincy, WA (lat. 47°16′N, long. 119°49′W). Trees were spaced 1.5 × 4 m and were trained to a five-wire V trellis. Because of modest response from treatments in the 2004 'Cameo' trial, more aggressive concentrations of 300, 600, 900, or 1200 $mg \cdot L^{-1}$ GA_{4+7} were applied.

Twelve-year-old 'Honeycrisp'/P.18 trees near Brewster, WA (lat. 48.2°N, long. 119.7°W) were selected for a study of fruit maturity effects of fruit untreated or sprayed with 400 $mg \cdot L^{-1}$ GA_4 or GA_{4+7}.

SPRAYS. The commercial GA_{4+7} formulation ProVide (Valent Biosciences, Libertyville, IL) was used in all four trials; Valent Biosciences declined to disclose the relative ratio of GA_4 to GA_7 in ProVide. The 2005 'Honeycrisp' trial also included a commercial GA_4 product, Novagib 10L (Fine Agrochemicals, Worcester, UK), which is comprised of 92% to 97% GA_4 and 1% to 2% GA_7. Gibberellic acid 7 is widely reported to be a stronger inhibitor of apple floral initiation than GA_4 (Bertelsen and Tustin, 2002; Marino and Greene, 1981; Tromp, 1982), but recent studies in Washington found similar responses from both isomers (Schmidt, 2006). All applications were sprayed at 10-mm fruitlet size as determined by the mean diameter of king apples of 30 randomly selected fruit clusters measured with digital calipers (Mitutoyo Corp., Kawasaki, Japan) in the respective trial blocks (13–15 d after full bloom). This timing had been determined to maximize treatment effects by other recent regional GA studies (Schmidt, 2006). Applications were made by handgun with a 25-gal 'Nifty' power sprayer (Rears Manufacturing, Eugene, OR) adjusted to a fine mist at 200 psi pressure. Whole trees were sprayed until all visible foliage was wet, but not to the point of dripping from more than 10% of all leaves. No adjuvants were used for any spray.

DATA COLLECTION. Initial flower cluster counts in similarly cropped trees were recorded for each sampling unit during the late pink stage of bloom development in the season of treatment. After terminal bud set, final shoot length was measured on 10 upright, 1-year-old shoots in each tree. Return bloom was assessed the subsequent spring by counting flower clusters in the same sampling units used for initial counts; pruning effects were assumed to be equivalent among treatments. Trunk or branch circumferences were measured at the time of both bloom counts.

In all trials, 30 fruit were randomly collected for harvest quality analyses from each tree 1 to 3 d before commercial harvest. A second random sample of 30 fruit was simultaneously taken for medium-term storage (90–140 d) and subsequent quality analyses in all cases except the 2004 'Honeycrisp' trial. Fruit were held in 1 °C air storage until they could be processed, typically within 48 h unless they were intended for storage.

All fruit were weighed and measured for length and diameter before running across a single-lane color grader (Falcon grading system; Aweta Corp., Nootdorp, The Netherlands) programmed to replicate a commercial packing line with standard color grades. A 20-fruit subsample from the 30-fruit sample from each tree was rated for visual defects, including sunburn, bitter pit, and splitting. Fruit russet incidence and severity was recorded in categories of stem bowl, fruit shoulder, smooth solid, and net type on fruit flanks. Fruit firmness was measured by punching two opposite sides of each peeled apple with a standard 7/16-inch penetrometer (EPT-1 Pressure Tester; Lake City Electric, Osoyoos, BC, Canada) used for Magness-Taylor tests. All 20 fruit were bisected laterally at the equator; calyx halves were treated with 10% iodine solution for standard starch readings (0–6-point scale) and tissue pieces from the stem halves of each fruit were mechanically juiced to produce a bulk sample for evaluation of soluble solids concentration (0% to 35% digital refractometer; Sper Scientific, Scottsdale, AZ) and titratable acidity (DL50 Graphix titrator; Mettler Toledo, Columbus, OH). For all parameters, statistical analyses were conducted using mean values for each tree, rather than values for individual subsamples.

After 90 to 140 d in 1 °C storage, the samples were analyzed similarly to initial harvest samples except for starch readings, which were omitted as a result of the nearly complete loss of starch reserves during storage.

Results and discussion

2004 'Cameo' gibberellic acid 4+7 concentration trial. The effects of GA_{4+7} on 'Cameo' fruit maturity were inconsistent. Control fruit were softer than treated fruit (Table 1), suggesting advanced maturity. In contrast, control fruit had higher acidity, which would indicate less advanced maturity (Mattheis, 1996). Fruit size, shape, and finish were unaffected by any treatment (data not shown). In addition, no significant treatment effects for any maturity parameter were observed in fruit analyzed after 90 d of cold-air storage.

Return bloom was profoundly diminished by GA_{4+7} in a curvilinear fashion (Table 1). The use of GA_{4+7} at 400 mg·L^{-1} and higher concentrations completely eliminated flowering the subsequent season. This trial was conducted during the "on" year of a severe biennial bearing cycle in conjunction with other trials not reported here. According to grower records, yields from this block during "on" years were ≈400% of yields in "off" seasons. This extreme alternation accounts for the relatively poor 2005 return bloom in control trees. Vegetative shoot extension was unaffected.

2004 'Honeycrisp' gibberellic acid 4+7 concentration trial. Treated fruit in this trial showed advanced maturity across several indices (Table 2). Strong linear effects of elevated starch conversion, decreased flesh firmness, and reduced titratable acidity suggest that maturity of treated fruit was 2 to 5 d more advanced than control fruit. Soluble solids concentration was unaffected by any treatment.

The experimental design initially included collection of fruit samples for maturity evaluation at three timings: commercial harvest minus 7 d, commercial harvest, and commercial harvest plus 7 d. Unfortunately, only the first sample was secured before the grower strip-picked the entire trial block 5 d ahead of schedule, including trial trees. Flowering in 2005 was significantly diminished in direct linear relation to spray concentration. No effect on shoot growth was observed.

2005 'Cameo' gibberellic acid 4+7 concentration trial. As in 2004, maturity effects of GA_{4+7} on maturity of 'Cameo' were inconclusive. Although not statistically significant, increased levels of starch conversion (Table 3) at high spray concentrations would likely be sufficient to drive commercial decisions regarding harvest timing and storage regimes. Clear trends could not be discerned from firmness, sugar, acidity, or fruit finish data in either fruit analyzed at harvest or after 120 d of storage. Overall, the data suggested little effect of the postbloom GA treatments on fruit physiological behavior during and after harvest.

Diminished fruit diameter and weight were consistently associated with higher concentrations of GA_{4+7} in both 'Cameo' trials (data not shown), but the effects were not significant (P = 0.05). This trend is corroborated by a series of trials by the Washington Tree Fruit Research Commission, which found that benzyladenine (BA) + GA_{4+7} formulations had a tendency to reduce fruit diameter in numerous strains of 'Delicious' (J. McFerson, unpublished). Because 'Cameo' is believed to be a chance seedling of 'Delicious', it is reasonable to expect GA_{4+7} to act similarly on both cultivars. 'Honeycrisp', conversely, showed neutral or positive effects on fruit size resulting from the application of GA_{4+7}.

Trees in this orchard demonstrated a good balance between

Table 1. Effects of concentration of GA_{4+7} (applied in 2004) on fruit quality/maturity parameters and return bloom of 'Cameo'/Budagovsky 9 apple.

Concn (mg·L^{-1})[z]	Starch index (1–6 scale)	Flesh firmness (N)[y]	Soluble solids (%)	Titratable acidity (%)	Russeted fruit (%)	2005 return bloom [flower clusters (no./cm^2 TCSA)][x]
Harvest						
0	4.4	62.0	11.8	0.39	11	0.6
200	4.3	64.3	12.2	0.35	8	0.1
400	4.1	63.5	12.1	0.34	10	0.0
600	4.1	63.3	12.2	0.36	14	0.0
Significance						
Concentration						
Linear	NS	*	NS	**	NS	****
Quadratic	NS	NS	NS	*	NS	**
Model r^2	0.20	0.32	0.15	0.64	0.42	0.77
Harvest + 90 d						
0	—	54.4	11.7	0.42	13	—
200	—	53.5	11.9	0.43	23	—
400	—	55.2	11.9	0.43	9	—
600	—	55.6	12.0	0.43	16	—
Significance						
Concentration						
Linear	—	NS	NS	NS	**	—
Quadratic	—	NS	NS	NS	**	—
Model r^2	—	0.55	0.68	0.28	0.52	—

[z]1 mg·L^{-1} = 1 ppm.
[y]1 N = 0.2248 lbf.
[x]TCSA, trunk cross-sectional area; 1 cm^2 = 0.1550 inch^2.
NS,*,**,****Nonsignificant or significant at P = 0.05, 0.01, or 0.0001 respectively.
Fruit were analyzed at harvest or after 90 d of regular-atmosphere cold storage.

Table 2. Effects of concentration of GA_{4+7} (applied in 2004) on fruit quality/maturity parameters and return bloom of 'Honeycrisp'/Poland 18 apple.

Concn ($mg \cdot L^{-1}$)[z]	Starch index (1–6 scale)	Flesh firmness (N)[y]	Soluble solids (%)	Titratable acidity (%)	2005 return bloom [flower clusters (no./cm^2 LCSA)][x]
0	4.4	65.5	12.6	0.45	4.9
200	4.7	62.8	12.7	0.42	3.2
400	4.9	60.4	12.3	0.36	1.3
600	5.2	59.2	12.7	0.38	0.7
Significance					
Concentration					
Linear	****	****	NS	*	****
Model r^2	0.74	0.79	0.27	0.52	0.73

[z]1 $mg \cdot L^{-1}$= 1 ppm.
[y]1 N = 0.2248 lbf.
[x]LCSA, limb cross-sectional area; 1 cm^2 = 0.1550 $inch^2$.
[NS,*,****]Nonsignificant or significant at P = 0.05 or 0.0001 respectively.

Table 3. Effects of concentration of GA_{4+7} (applied in 2005) on fruit quality/maturity parameters and return bloom of 'Cameo'/ M.9 'Nicolai 29' apple.

Concn ($mg \cdot L^{-1}$)[z]	Starch index (1–6 scale)	Flesh firmness (N)[y]	Soluble solids (%)	Titratable acidity (%)	Russeted fruit (%)	2006 return bloom [flower clusters (no./cm^2 TCSA)][x]
Harvest						
0	4.8	69.5	12.3	0.24	13	9.2
300	4.9	69.4	13.5	0.25	13	2.3
600	5.1	71.1	12.9	0.22	12	0.4
900	5.3	69.3	12.7	0.22	13	0.3
1200	5.5	68.2	12.3	0.22	12	0.3
Significance						
Concentration						
Linear	NS	NS	*	NS	NS	****
Quadratic	NS	NS	**	NS	NS	****
Model r^2	0.50	0.32	0.42	0.59	0.28	0.82
Harvest + 120 d						
0	—	55.6	12.3	0.27	20	—
300	—	51.2	13.3	0.26	15	—
600	—	54.5	12.4	0.28	33	—
900	—	53.0	12.7	0.25	14	—
1200	—	55.3	12.0	0.24	23	—
Significance						
Concentration						
Linear	—	NS	NS	NS	NS	—
Quadratic	—	NS	NS	NS	NS	—
Model r^2	—	0.35	0.24	0.55	0.09	—

[z]1 $mg \cdot L^{-1}$= 1 ppm.
[y]1 N = 0.2248 lbf.
[x]TCSA, trunk cross-sectional area; 1 cm^2 = 0.1550 $inch^2$.
[NS,*,**,****]Nonsignificant or significant at P = 0.05, 0.01, or 0.0001 respectively.
Fruit were analyzed at harvest or after 120 d of regular-atmosphere cold storage.

vegetative and reproductive growth, and consistent harvest yields indicated no biennial bearing habit. Upright shoot growth was rather modest in control plots (≈10 cm). Final shoot length was unaffected by any treatment. Return bloom was significantly inhibited in both linear and curvilinear fashion with respect to concentration, with little difference among results for 600, 900, or 1200 $mg \cdot L^{-1}$ (Table 3).

2005 'HONEYCRISP' GIBBERELLIC ACID ISOMER TRIAL. Fruit maturity was not as clearly accelerated by GA in 2005 as in the 2004 'Honeycrisp' trial. Both GA_4 and GA_{4+7} produced fruit at harvest with decreased titratable acidity (Table 4), but effects on fruit firmness, starch conversion, and soluble solids content were not significant.

Fruit finish was improved by GA_4, which reduced overall incidence of fruit russet by ≈50%. Most russet was observed in the stem bowl or on fruit shoulders, with few blemishes appearing on the flanks of fruit. Assessment of russet on fruit stored for 140 d was confounded by decay and other postharvest disorders, and results are excluded from this report. Gibberellic acid treatments caused a 12% to 15% increase (P = 0.05) in shoot extension. Gibberellic acid 4 and GA_{4+7} significantly increased fruit length and the length-to-diameter ratio, but fruit diameter was unaffected. Incidence of bitter pit trended slightly higher in all GA treatments, perhaps associated with increased vigor in treated trees, but sample size was inadequate to draw robust conclusions (data not shown).

Both GA treatments reduced return bloom by more than 80%—an excessive correction for most commercial circumstances. We chose an aggressive concentration of 400 $mg \cdot L^{-1}$ GA to increase our odds of producing clear results. Future studies examining more modest concentrations (50–200 $mg \cdot L^{-1}$) of these materials would likely provide more practical information to growers trying to decide how to manage alternate bearing blocks.

Gibberellins are often the hormonal antithesis of ethylene, producing opposite effects with respect to shoot growth and floral initiation. However, the ethylene-inducing growth regulator Ethephon accelerates ripening of apple (Greene, 1996) and many other fruits. The advanced maturity of GA-treated 'Honeycrisp' suggests upregulation of the ethylene synthesis pathways, perhaps as part of a wounding response from damaging levels of GA early during the growing season. In future studies of this type, regular analysis for the presence of ethylene or its metabolic precursors such as s-adenosyl methionine or aminocyclopropane carboxylic acid might provide insight regarding how the application of high levels of exogenous GA accelerates maturity. The maturity response of GA-treated fruit could also be explored with field

Table 4. Effects of 400 mg·L^{-1} a.i. GA_4 and GA_{4+7} (applied in 2005) on fruit quality/maturity parameters and return bloom of 'Honeycrisp'/Poland 18 apple.

Isomer	Starch index (1–6 scale)	Flesh firmness (N)[z]	Soluble solids (%)	Titratable acidity (%)	Russeted fruit (%)[y]	2006 return bloom [flower clusters (no./cm^2 LCSA)][x]
Harvest						
Control	5.2	67.7	12.9	0.25 a	40 a	2.8 a
GA_4	5.4	64.2	13.1	0.21 b	20 b	0.5 b
GA_{4+7}	5.3	62.7	13.2	0.21 b	35 ab	0.3 b
P value	0.71	0.06	0.79	0.01	0.02	0.0002
Harvest + 140 d						
Control	—	63.4 a	12.6	0.32 a	—	—
GA_4	—	57.2 b	12.1	0.26 b	—	—
GA_{4+7}	—	56.3 b	12.4	0.27 b	—	—
P value	—	0.002	0.45	0.001	—	—

[z]1 N = 0.2248 lbf.
[y]n = 120 fruit/treatment.
[x]LCSA, limb cross-sectional area; 1 cm^2 = 0.1550 inch^2.
Fruit were analyzed at harvest or after 140 d of regular-atmosphere cold storage. Means followed by the same letter are not significantly different within a column (n = 6, $P \leq 0.05$).

applications of 1-methylcyclopropene, theoretically inhibiting ethylene perception.

Apple cultivars responding differently to various bioregulators is a common phenomenon. Published reports document cultivar-specific responses to daminozide (Crowe, 1968; McLaughlin and Greene, 1991; Walsh and Kender, 1982), prohexadione–calcium (Buban et al., 2004), Atonik (Koupil, 1997), BA (McLaughlin and Greene, 1991), Ethephon (Walsh and Kender, 1982), NAA (Elezaby and Hasseeb, 1995; Krzewinska et al., 2002), and two triazoles (paclobutrazol and uniconazole) (Zimmerman and Steffens, 1995). Based on unique responses to an unspecified GA applied to root collars of 'Shampion', 'Paulared', and 'Lobo', Grochowska et al. (1995) proposed that individual cultivars have cultivar-specific patterns of endogenous hormones or gibberellin metabolic pathways.

'Honeycrisp' crop load is relatively easy to moderate with blossom and postbloom chemical thinners. In contrast, 'Cameo' requires more aggressive thinning programs. Phenotypic differences between these two cultivars are numerous, and the relative sensitivity of 'Honeycrisp' to GA and insensitivity of 'Cameo' to GA and Ethephon observed in related studies (Schmidt, 2006) support the hypothesis of cultivar-specific hormone profiles and unique metabolic pathways.

Gibberellins show promise as floral inhibitors to mitigate biennial bearing in mature apple trees, as well as in young plantings to minimize early cropping and to encourage trees to fill their space more rapidly. Concentrations of GA designed to influence flowering advanced fruit maturity in 'Honeycrisp', but not 'Cameo'. Results suggest both formulations of GA tested induced early ripening of 'Honeycrisp'. Cultivar-specific responses in our trials highlight the need for GA programs to be customized for individual cultivars. Other factors to consider may include rootstock, cropping history, and bloom and postbloom chemical thinning programs. Future research in apple genomics likely holds the ultimate answers regarding cultivar-specific responses to bioregulators. Until those metabolic pathways are elucidated, further exploration of primary and collateral effects of using GA to promote annual flowering would be useful to assist growers in making more informed management decisions.

Literature cited

Bertelsen, M.G. and D.S. Tustin. 2002. Suppression of flower bud formation in light cropping trees of 'Pacific Rose' apple using gibberellin sprays. J. Hort. Sci. Biotechnol. 77:753–757.

Buban, T., L. Csiszar, P. Sallai, and A. Varga. 2004. Experiences with the bioregulator prohexadione-Ca used in apple and pear orchards. Acta Hort. 633:67–74.

Crowe, A.D. 1968. Results from sprays of the growth regulator "Alar" on certain apple varieties. Annu. Rpt. Nova Scotia Fruit Growers Assn. 103:63–70.

Elezaby, E. and G. Hasseeb. 1995. Fungicidal inhibition and growth regulator promotion of pollen germination and germ-tube elongation in apple. Acta Hort. 409:179–183.

Elfving, D.C. and O.B. Allen. 1987. Effect of gibberellin A_{4+7} applications on 'Golden Delicious' fruit russet. Crop Res. (Hort. Res.) 27:11–18.

Greene, D.W. 1989. Gibberellins A_{4+7} influence fruit set, fruit quality, and return bloom of apples. J. Amer. Soc. Hort. Sci. 114:619–625.

Greene, D.W. 1996. Ethylene-based preharvest growth regulators, p. 149–159. In: K. Maib, P. Andrews, G. Lang, and K. Mullinix (eds.). Tree fruit physiology: Growth and development. Good Fruit Grower, Yakima, WA.

Grochowska, M.J., M. Hodun, A. Mika, H. Morgas, and D. Chlebowska. 1995. High responsiveness of apple trees to single application of growth regulators to the root collar. J. Fruit Ornamental Plant Res. 3:91–101.

Koupil, S. 1997. Effect of growth regulator Atonik on some apple cultivars: Effect on growth and quality of fruits. Zahradnictvi (Hort. Sci., Prague) 24:85–87.

Krzewinska, D., A. Basak, and A. Mika. 2002. Effect of fruit set regulation on return bloom in some apple cultivars. Annales Universitatis Maraie Curie – Sklodowska Section EEE 10:221–227.

Looney, N.E. 1996. Effects of gibberellin-based plant bioregulators on fruit quality, p. 137–147. In: K. Maib, P. Andrews, G. Lang, and K. Mullinix (eds.). Tree fruit physiology: Growth and development. Good Fruit Grower, Yakima, WA.

Looney, N.E., R.L. Granger, C.L. Chu, L.N. Mander, and R.P. Pharis. 1992. Influences of gibberellins A_4, A_{4+7} and A_4+iso-A_7 on apple fruit quality and tree productivity. II. Other effects on fruit quality and importance of fruit position within the tree canopy. J. Hort. Sci. 67:841–847.

Marino, F. and D.W. Greene. 1981. Involvement of gibberellins in the biennial bearing of 'Early McIntosh' apples. J. Amer. Soc. Hort. Sci. 106:593–596.

Mattheis, J. 1996. Fruit maturity and ripening, p. 117–123. In: K. Maib, P. Andrews, G. Lang, and K. Mullinix (eds.). Tree fruit physiology: Growth and development. Good Fruit Grower, Yakima, WA.

McArtney, S.J. 1994. Exogenous gibberellin affects biennial bearing and the fruit shape of 'Braeburn' apple. N. Z. J. Crop Hort. Sci. 22:343–346.

McLaughlin, J.M. and D.W. Greene. 1991. Fruit and hormones influence flowering of apple I: Effect of cultivar. J. Amer. Soc. Hort. Sci. 116:446–449.

Meador, D.B. and B.H. Taylor. 1987. Effect of early season foliar sprays of GA_{4+7} on russeting and return bloom of 'Golden Delicious' apple. HortScience 22:412–415.

Proebsting, E. 1972. Chemical sprays to extend sweet cherry harvest. Wash. State Univ. Ext. Multilith 3520. Cooperative Extension Service, Wash. State Univ., Pullman, WA.

Reuveni, M., D. Sheglov, and R. Rulf. 2001. The influence of fungicides and gibberellin (A_{4+7}) applications of russet control on 'Golden Delicious' apple fruit. J. Hort. Sci. Biotechnol. 76:636–640.

Schmidt, T.R. 2006. Manipulation of crop load with bioregulators to mitigate biennial bearing in apple. MS thesis, Washington State University, Pullman, WA.

Taylor, B.K. 1978. Effects of gibberellin sprays on fruit russet and tree performance of Golden Delicious apple. J. Hort. Sci. 53:167–169.

Tromp, J. 1982. Flower-bud formation in apple as affected by various gibberellins. J. Hort. Sci. 57:277–282.

Unrath, C.R. 1974. The commercial implications of gibberellin A_4A_7 plus benzyladenine for improving shape and yield of 'Delicious' apples. J. Amer. Soc. Hort. Sci. 99:381–384.

Walsh, C.S. and W.J. Kender. 1982. Effect of cultivar, strain, and growth regulator treatments on shoot development and ethylene evolution in apple trees. J. Amer. Soc. Hort. Sci. 107:198–202.

Zimmerman, R.H. and G.L. Steffens. 1995. Cultivar, planting density, and plant growth regulator effects on growth and fruiting of tissue-culture apple trees. J. Amer. Soc. Hort. Sci. 120:183–193.