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GA_{4+7} Rate and Timing Interact to Suppress Return Bloom of Young "Honeycrisp" Apple Trees and Improve Tree Growth

Todd Einhorn[1*], Denise Ruwersma[1], Mokhles Elsysy[1,2], Drew Hubbard[3]

[1]Department of Horticulture, Michigan State University, East Lansing, MI, USA
[2]Department of Pomology, Assiut University, Assiut, Egypt
[3]Fine Americas, Inc., Walnut Creek, CA, USA
Email: *einhornt@msu.edu

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Abstract

Newly planted apple orchards in the USA comprising the highly biennial cultivar, "Honeycrisp", are prone to flower within the first two years from planting and set fruit. These processes limit canopy development and subsequent yield potential. GA_{4+7} can inhibit floral formation processes of apples. The timing and dose for eliminating return bloom of young "Honeycrisp" trees, however, is unclear. A factorial experimental design to test GA_{4+7} application timing and rate produced significant reductions in return bloom for both factors and their interaction. Treatment responses demonstrated that florigenic processes in "Honeycrisp" occurred early. The most pronounced reduction in return bloom followed the 2-week after full bloom (WAFB) application timing, increasing with increasing rate. The effect on return bloom was progressively diminished over the next two weeks of applications but remained significantly lower than the control. Three successive applications timed one week apart eliminated return bloom of spurs at the highest rate. Both factors and their interaction also significantly reduced return bloom of terminal buds of leaders; in contrast to floral buds on spurs, the response of terminal buds on leaders improved with delayed application timings. Timing exerted a stronger effect than rate on return flowering of the terminal buds of leaders. Leader growth was positively affected by GA_{4+7}, the year of application, when three successive applications were made. Tree height, overall growth, expressed as the increase in trunk cross-sectional area, and limb number were also significantly improved by GA_{4+7} but varied in their responses to application timing and rate, and were inconsistent. Overall, successive applications of GA_{4+7} had good efficacy for inhibiting floral initiation of meristems on spurs and terminals while improving the vegetative growth of young "Honeycrisp" trees.

Keywords

Floral Inhibition, Floral Initiation, Floral Induction Gibberellins, Flowering, Fruit Set, Crop Load Management

1. Introduction

"Honeycrisp" is a low-vigor cultivar capable of flowering and fruiting within the first years from planting, especially when combined with dwarfing and precocious rootstocks. These processes negatively affect flower formation for the subsequent year [1] [2]. "Honeycrisp", like other biennial cultivars that are allowed to carry a crop in the first years from establishment enters an "on" and "off" cycle of production that compromises yield potential and crop consistency. This precocity may seem advantageous for early production and profitability, but given "Honeycrisp's" inherently low vigor, the cropping of young trees will comprise canopy growth. Because the maximum yield potential of an apple orchard depends upon the total light intercepted by canopies [3] and, thus, canopy growth and development, trees that fail to fill their allotted space cannot attain maximum productivity. This scenario cannot be easily reversed by vigor-promoting techniques, e.g. fertilization, plant growth regulators (PGRs), irrigation, etc. The type of nursery planting material can also affect tree development in the orchard. US nurseries produce a diverse portfolio of fruit trees to include bare-root (one-year-old lightly feathered trees, one-year-old whips, two-year-old knip boom trees) and air-pruning containerized trees (one-year or younger including green trees delivered in spring with only 60 cm of new growth from bench grafts). Many producers of "Honeycrisp" remove the feathers (*i.e.*, the initial limbs) of nursery trees leaving short stubs to promote leader growth and produce weak, flat renewal limbs; thus, priority is placed on achieving maximum height in the orchard since feathers and fruiting both limit leader extension of "Honeycrisp" trees. Alternatively, preemptive strategies that promote vigor and delay and/or inhibit flowering are needed.

The developmental timing of floral initiation of apple cultivars is considerably wide, with the onset of initiation occurring between 40 and 150 days after full bloom (DAFB) and durations, typically, lasting between 1 and 2 months [4]-[6] Based on anatomical observation of meristem doming [7], as a proxy for floral initiation and meristem commitment to flowering, "Honeycrisp" had an earlier date of initiation onset and a shorter bud initiation period relative to several other cultivars [8], though year also affected the onset and duration of floral initiation. Understanding the timing of floral commitment would be requisite for applying crop load management strategies to mitigate biennialism of "Honeycrisp".

Gibberellins (GAs) are negative regulators of flower formation of apples [9], and their application in apple orchards has been widely studied for managing return bloom and fruit russeting (see reviews, [10] [11]). Bioactive GAs appear to play a role in the control of key flowering genes [12] through interaction with sugars and other hormones to mediate floral induction [13]. GA concentrations in apple fruit were maximum between 4 and 6 WAFB [14] and tended to be higher in fruit-bearing spurs than vegetative spurs [1], though the peak of endogenous GA in seeds and diffusates did not always relate with GA activity of spurs [1]. The link between GA and biennialism is supported by higher concentrations of GA in spurs of biennial cultivars than those of annual cultivars [15]. Of the active GA isomers, GA_7 is widely accepted as the most efficacious for inhibiting floral initiation of apple [16]-[18], though GA_3 [17] and GA_4 [19] have also been efficacious. Commercial formulations of GA_{4+7} contain approximately equivalent portions of each isomer. Exogenous GAs also induced the growth of apple shoots [2] and increased the transcript level of MdTFL1, a key gene associated with vegetative growth of apple trees [20]. Conversely, silencing MdTFL1 was concomitant with floral induction of apple meristems [21] [22]. Application of GA_{4+7} to "Honeycrisp" inhibited flowering and increased the expression levels of MdTFL1-1 in apical buds [23]. The potential use of GAs, then, to maintain meristems of young trees in a vegetative state might improve canopy infill, which would be of significant benefit to an orchard's future productivity.

Extrapolating from previously published GA protocols to inhibit floral initiation of young "Honeycrisp" trees is difficult given the disparate application timings and doses and the different cultivar responses observed; all generally on mature trees. [24] applied four sequential GA_{4+7} sprays (250 and 500 $mg \cdot L^{-1}$), one month apart after petal fall and effectively suppressed "Delicious" return bloom. [16] applied various rates and GA formulations (GA_4, GA_7 and GA_{4+7}) to "Delicious" and "Golden Delicious" in successive applications-one to four WAFB and observed mixed results depending on cultivar, GA source, and year; though, GA_7 was more efficacious than GA_4. Given the use of successive applications, the exact efficacy of an individual timing could not be ascertained; though, other reports indicated single applications within two weeks from bloom were as effective as multiple applications for inhibiting floral initiation of spurs [18] [25]. On the contrary, delayed applications (+6 WAFB) were necessary to suppress floral initiation of lateral-borne buds of one-year-old shoots [17]. Collectively, these reports support the use of GA to suppress flowering of apple but a clear protocol for their use across cultivars does not emerge. Thus, our objective was to evaluate the rate and timing of GA_{4+7} applications to young Honeycrisp trees to inhibit floral initiation and eliminate return bloom. A secondary objective was to assess the effects of GA on promoting canopy development. The hypothesis was that a one-year application of GA to young Honeycrisp trees (*i.e.*, 2nd to 3rd leaf) will promote growth to facilitate canopy infill and better support fruiting in future years. The research was carried out using a new GA_{4+7} formulation comprising highly concentrated GA_7.

2. Materials and Methods

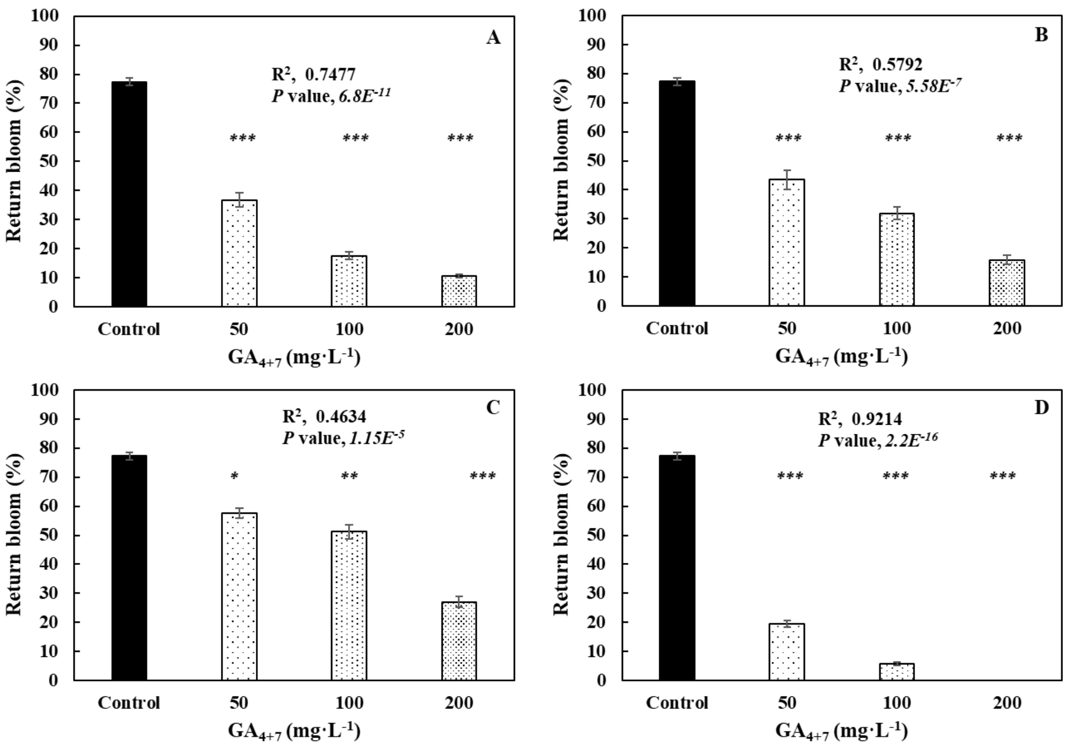
Plant material. The study was performed on a commercial orchard in Sparta, Michigan (43.1 lat. −85.7 long.) using a two-year-old "Honeycrisp" orchard (*i.e.*, entering the 3rd leaf). Trees were grafted on Budagovsky 9 rootstock and planted 1 m × 3.4 m and trained to a tall spindle. Trees were received as one-year-old nursery trees. Soil is a sandy loam. The climate of Michigan is insulated by the Great Lakes and is a relatively cool and humid temperate-zone fruit growing region; climatic data can be observed using the Michigan Automated Weather Network (MAWN) and Enviro-weather program https://mawn.geo.msu.edu/dod.asp. All cultural practices were performed according to commercial standards except treatments as described below.

Experimental design. The experiment was an augmented two-way factorial design [26] with three levels of factor 1 (rate) and four levels of factor 2 (application timing) compared to a non-treated control, arranged in a CRD with 10 single-tree replicates. In 2022, 130 trees with an average of 39 clusters at full bloom were selected for uniformity at green tip based on trunk circumference (±0.25 cm) and randomized across 13 treatments: a non-treated control and 50, 100 or 200 $mg \cdot L^{-1}$ of GA_{4+7} (*i.e.*, 0.95% GA, Arrange TM, Fine Americas, Walnut Creek, CA), applied at 2, 3 and/or 4 WAFB. The ratio of GA_4 to GA_7 in Arrange TM is proprietary and differs from other formulations by purportedly comprising a higher concentration of GA_7 to GA_4. Therefore, the absolute concentration of each isomer in solution cannot be directly compared to results from previously published work related to GA_{4+7}. All solutions included a non-ionic surfactant (Regulaid, KALO Inc., Overland Park, KS) at 0.1% v: v to promote leaf penetration. Solutions were applied to canopies to ensure uniform coverage (*i.e.*, to drip) with a pressurized handgun applicator. All treatment trees were separated in each direction by a minimum of one guard tree to avoid spray contamination of other treatments and solutions were applied early in the morning under high humidity, moderate temperatures and low wind to facilitate penetration and minimize drift. Guard trees adjacent to sprayed trees had no leaf wetness when observed visually while sprays were applied. Full bloom occurred on 12-May and was based on 80% of flowers having visible anthers. Application dates for the 2-WAFB, 3-WAFB and 4-WAFB sprays were 26-May, 3-June and 11-June, 2022 respectively.

Measurements. At "pink" to first bloom timing in the spring of 2023, the total number of flower clusters was counted and divided by the total number of potential fruiting sites per tree (fruiting spurs; n - 100) to produce return bloom percentages. The leader of each tree (n = 1) was also observed in spring of 2023 for presence or absence of a terminal flower cluster (binomial data) to generate return bloom data for leaders. The circumference of all trees was recorded in the spring of 2022 at 30 cm distance from the graft union and, again at the same location, at leaf abscission in 2023. Trunk circumference was converted to trunk cross-sectional area (tca) and reported as the increase in tca between measurement dates. Annual leader growth (in length) was measured at leaf abscission in 2022 and 2023. The total number of limbs per tree was determined following leaf senescence in 2023. Any limb ≤ 2 years old with an origin at the central axis (*i.e.*, trunk) was counted.

Statistical analysis. All statistical analyses were performed with the R statistical package R (v. 4.3.3 R Foundation, Vienna, Austria). A separate linear model for the effect of GA_{4+7} application rates (0 [*i.e.*, Control], 50, 100 and 200 ppm) within each application timing was assigned to explain the effect of application rates at different timings on each explanatory variable (leader growth termination, tree growth, tree height, leader length, limb number and return bloom), and significance at $P < 0.05$ was reported along with R squared values (Table 1 and Figure 1). An overall statistical model was designed to illustrate the effect of application timing, rate and their interactions on the same explanatory variables (Table 1).

3. Results



Rate and application timing each significantly affected flower promotion at the terminals of leaders as well as their interaction (Table 1). All applications, except 50 and 100 mg·L^{-1} applied 2 WAFB, significantly reduced the return bloom of terminals, 100% of which flowered when left untreated. Low sample populations of leader terminals per tree (n = 1) may have contributed to numerical inconsistencies in the rate and/or timing effects when compared to results for spurs (n - 100). A highly significant timing effect, that improved with later applications, contrasted the observed response of spurs.

Figure 1. The effect of 2022 GA_{4+7} applications of 0 [*i.e.*, Control] 50, 100 or 200 mg·L^{-1} applied 2 WAFB (A), 3 WAFB (B), 4 WAFB (C) and 2, 3, and 4 WAFB (D) to 3rd leaf Honeycrisp apple trees in 2022 on 4th leaf return bloom in 2023. Return bloom is expressed as the total potential fruiting sites on spurs divided into the number of flower clusters per tree in spring 2023. Means were calculated from 10 single-tree replicates (±SE). Asterisks above data bars within each panel (*i.e.*, application timing) indicate significant differences for individual treatments compared to the control via a t-test. The R^2 and P values describe the rate effect within each panel (*i.e.*, application timing). P values for the augmented 2-factor model for timing, rate and their interaction were 0.0025, <0.0001, and 0.05, respectively.

Table 1. The effect of 2022 GA_{4+7} applications to 3rd leaf Honeycrisp apple trees at varying dose and application timings on the return bloom of terminal buds of leaders, cumulative growth of trees expressed as an increase in trunk cross-sectional area between spring 2022 and autumn 2023, final tree height (measured from the graft union), the annual incremental length of the leader in 2022 and 2023 and the average number of branches per tree in autumn 2023 after leaf abscission. Means are the average of 10 single tree replicates. R^2 and model P values below individual timings describe the rate response within an application timing for the response factors.

GA	Application timing	Return bloom	Tree growth	Tree height	Leader length (cm)		Limbs
(mg·L^{-1})	(wafb)	(% leader terminals)	(% TCAi)	(m)	2022	2023	(no.)
	Control	100	35.6	2.52	22.6	18.3	30.3
50	2	70	48.5	2.57	20.8	20.6	36.4**
100	2	66	45.5	2.55	24.2	17.7	32.9
200	2	44*z	57.5*	2.67	26.9	19.9	35.5*
	R^2	0.09	0.04	0.01	0.13	−0.029	0.16
	Model P value	0.1	0.2	0.3	0.05*	0.6	0.03*
50	3	0***	47.5	2.54	21.2	19.2	32.8
100	3	14***	55.4*	2.56*	24.7	22	34.1
200	3	50**	47.4	2.57	24.9	18.5	34.1
	R^2	0.6	0.06	0.1	−0.06	−0.05	0.03
	Model P value	<0.0001***	0.2	0.06	0.8	0.7	0.3
50	4	30***	49.8	2.65*	26.1	21.6	34.1
100	4	11***	53.7	2.61*	25.1	23.1	34.3
200	4	30***	52.8	2.67*	24.4	21.8	33.6
	R^2	0.4	−0.002	0.12	−0.014	0.004	0.03
	Model P value	0.0003***	0.4	0.05*	0.49	0.39	0.27
50	2, 3, 4	0***	59.8*	2.58	24.6	21.7	34.1
100	2, 3, 4	60*	65.2**	2.68**	27.4*	20.3	34.7
200	2, 3, 4	25***	50.5	2.65*	28.7*	21.6	33.5
	R^2	0.51	0.18	0.2	0.1	−0.01	0.03
	Model P value	<0.0001***	0.02*	0.01*	0.05*	0.5	0.3
	Timing	<0.0001***	0.03*	0.06	0.5	0.4	0.09
	Rate	0.04*	0.1	0.9	0.4	0.9	0.045*
	Interaction	0.01*	0.2	0.8	0.7	0.9	0.09

*, **, *** assigned to treatments within columns represent significance at P < 0.05, P < 0.01, P < 0.0001, respectively, between an individual treatment and the control via a t-test.

GA_{4+7} rate and application timing had a marked, significant effect on reducing the return bloom of "Honeycrisp" spurs (P < 0.0001 and 0.0025, respectively; Figure 1(A-D)). The interaction of these two factors was also significant (P, 0.05). Inhibition of spur floral initiation was positively, linearly related to GA_{4+7} rate within each application timing. On average, there were 93 potential fruiting sites per tree in 2022 and these were unaffected by GA treatments; thus, the absolute number of flower clusters was similar to the percent of potential fruiting sites returning bloom as provided in **Figure 1**. The return bloom response was explained to a progressively lesser degree with delayed application timings (**Figure 1(A-D)**); however, three successive applications of GA_{4+7} were clearly additive and could explain ~92% of the return bloom response. Our results demonstrate the earliness, *i.e.*, 2 WAFB, of floral formation processes of "Honeycrisp", underscored by the diminishing response at 3 and 4 WAFB.

Leader length the year of application (2022) responded positively to GA_{4+7} with higher rates applied over successive applications producing significantly longer leaders than the control (**Table 1**). GA_{4+7} rate also statistically increased the number of limbs per tree (**Table 1**). Our interest in quantifying additional direct effects of GA_{4+7} on tree growth over the 2-year duration of the experiment was confounded by the persistence of fruit in 2023 due to a miscommunication with the grower (*i.e.*, to eliminate all fruit borne from return bloom the year following GA application); thus, profound differences according to GA efficacy in return bloom resulted in a spectrum of fruit set and crop that likely affected tree vigor. Trees ranged from having no fruit when treated with three successive applications of the highest GA_{4+7} dose to ~15 fruit on untreated control trees (data not shown). Tree growth, expressed either as the increase in trunk cross-sectional area or tree height over the 2-year period, was numerically higher in all treatments compared to control, albeit only significantly when successive applications were applied (**Table 1**). While these data do not distinguish the effects of GA_{4+7} on tree growth as either indirect (crop load) or direct (hormonal regulation), they do underscore the negative impact of flowering and fruiting processes on young trees and the practical consequences of unwanted bloom that, in turn, requires additional cost and time for their elimination.

4. Discussion

Previous reports have demonstrated GA efficacy on flower formation of spurs at similarly early timings but with extended efficacy over a wider timeframe than assessed in the present study [16] [18]. Within a population of meristems, floral formation occurred asynchronously over a period of 39 to 149 DAFB [5]-[7]. Similar durations were reported for vegetative to floral transitions of pear (*Pyrus communis* L.) cultivars [27]. The onset and duration of "Honeycrisp" flower initiation occurred markedly earlier than "Gala", "Fuji" or "Empire" over two years and was complete at a markedly earlier date than other apple cultivars [8]. Our application timings plausibly interacted with floral induction that precedes the actual doming of meristems, *i.e.*, the morphological "marker" of floral initiation typically used to timestamp a meristem's commitment to flowering [7]. GAs have been shown to alter gene expression within regulatory florigenic networks [20] [23]. These upstream processes ultimately "induce" floral initiation. The implication of these data for crop load management of "Honeycrisp" cannot be overstated and help to explain why efficacious fruitlet thinning at 10 - 12 mm fruitlet diameters (generally occurring between 2 and 3 WAFB) is insufficient to mitigate poor return bloom. These data further support early crop load intervention of "Honeycrisp", by bloom-thinning [28] or reducing floral bud load via dormant pruning to a threshold bud number [29].

The disparate effects of GA on flower formation of spurs and terminals are corroborated by these organs having different floral initiation timings attributed to their plastochron [30]. GA-inhibition of lateral meristems on one-year-old wood of apple required delayed application timing compared to spurs [17] [18] since spur growth is completed earlier in the season than the terminal cessation of extension shoots. Thus, the different floral inhibition responses to application timing of GA_{4+7} observed within buds on spurs and leaders would require different application timings.

A considerable challenge faced by growers of "Honeycrisp" trees is overcoming the deleterious effect of early flowering and fruiting on vigor, primarily in the growth of the leader which is prerequisite to filling the orchard space and maximizing future productivity. Apical vegetative buds that transition to floral meristems (though still possessing vegetative meristems in the compound bud of apple) are limited in growth by the highly determinant bourse shoot, that, in turn, assumes the role of surrogate leader [31] [32]. This process is independent of fruit set, which will further impact tree growth due to the strong carbohydrate demand of the competing fruit sink [3]. The significant effect of GA_{4+7} rate on increasing the number of limbs per tree may also not have been a direct effect of GA_{4+7} and was not consistently observed among application timings. Branch induction in young sweet cherry (*Prunus avium* L.) trees was promoted by exogenous GA (without the addition of cytokinin) but at concentrations profoundly higher than those applied in the present study [33]. Lateral branching of apple is generally induced by early, green tip' applications of combination PGR treatments (cytokinin plus GA) and/or notching [34] before sufficient concentrations of auxin are synthesized in terminal buds to re-establish apical dominance. The significant branching response observed in the present study at the early timing, and well in advance of "green tip", is physiologically supported by the literature but given the relatively weak response further experimentation is required.

5. Conclusion

Our results demonstrate that early GA treatment can inhibit floral formation processes in the highly biennial cultivar, "Honeycrisp" (*i.e.*, by 2 WAFB). The significant effects of GA_{4+7} rate, application timing, and their interaction on reducing floral initiation and return bloom were most pronounced when three successive applications were applied. GA_{4+7} significantly reduced floral initiation within terminal buds of leaders also, but at later timings than spurs. Leader growth during the year of application was improved by higher GA_{4+7} rates when applied in successive applications. Tree growth was significantly affected by GA_{4+7} timing and limb number was significantly related to rate; both tended to be greatest for successive GA_{4+7} treatments, though effects among treatments were inconsistent and likely compounded by the existence of fruit the year following treatment applications. The practical importance and implications of the results are in the elimination of return bloom, which maintains meristems as vegetative, avoids additional labor and time required to remove unwanted flowers and fruitlets from inhibiting return bloom when cropping is desired, and leads to improved canopy infill. Future work in this area could address even earlier timings (*i.e.*, pink to full bloom timing) and further identify the efficacy of mid to late-season application timings to eliminate floral formation in terminal buds of leaders and extension shoots. Additional research of interest could determine if GA_{4+7} could be effectively used to control return bloom in fully bearing Honeycrisp trees to reduce thinning pressure and mitigate biennialism.

Author Contributions

Individual contributions are as follows: Conceptualization, T. E.; methodology, T. E., D. R., D. H.; formal analysis, M. E., T. E.; investigation, T. E., D. R.; data curation, D. R, T. E., M. E.; writing, T. E.; writing—review and editing, T. E., M. E.; supervision, T. E.; project administration, T. E. All authors have read and agreed to the published version of the manuscript.

Data Availability Statement

The raw data supporting the conclusions of this article will be made available by the authors on request.

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Conflicts of Interest

The authors declare no conflicts of interest.

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