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Gibberellin Treatment Toward Off-crop Season as a Practical Tool to Increase Yield in 'Orri' Mandarin

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Abstract. **Multiannual fruit bearing in fruit trees varies from regular bearing, with an almost steady yield from season to season, to alternate bearing, during which a year with a high fruit load (on-crop) is followed by a year of a low fruit load (off-crop). 'Orri' mandarin [Temple (Citrus temple hort. ex Y. Tanaka) × Dancy (*Citrus tangerine* hort. ex Tanaka)] exhibits a nonregular bearing pattern: steady for a few years and alternate for others. In nonregular or alternate-bearing cultivars, fruit load is thought to regulate flowering induction and development negatively the following year. In citrus, the bud meristem develops into a leafless inflorescence (generative), leafy inflorescence (mixed type, containing leaves and flowers in various ratios), or vegetative shoot, or remains dormant. Mixed-type inflorescences contribute to most of the final yield. Gibberellins inhibit flowering when applied at relatively high concentrations during the flowering induction period in the winter, but they are suggested to induce yield when applied at relatively low concentrations. We determined the effect of mild gibberellin application in an off-crop year on the productivity of 'Orri' mandarin, and whether it occurs through the induction of mixed-type inflorescences. Low-concentration, low-frequency gibberellin treatments were applied to trees during the winter when fruit load was high, resulting in a greater number of mixed vs. generative inflorescences at anthesis. An average increase of 40% in fruit number and yield weight was recorded in off-crop seasons at harvest, whereas no change was recorded in on-crop seasons. We discuss treatment efficiency in on-crop and off-crop years as a practical tool for increasing yield in low-crop seasons of 'Orri' mandarin.**

Multiannual fruit bearing can vary among fruit trees species or cultivars. Cultivars with regular bearing produce a more or less steady amount of yield from one season to the next, whereas other cultivars exhibit either nonregular or alternate bearing, with fluctuations in yield from season to season. Cultivars with nonregular bearing can produce similar yields over a period of time—for instance, a few years of high fruit load (on-crop), followed by a year of low fruit load (off-crop), or vice versa. In contrast, cultivars exhibiting alternate bearing tend to display a predictable pattern of an on-crop year followed by an off-crop year in multiannual cycles (Goldschmidt and Sadka 2021). In these cultivars, heavy fruit load in one year is thought to inhibit flowering induction the following year, resulting in a pronounced reduction in yield (Agustí et al. 2022; Goldschmidt and Sadka 2021; Krasniqi et al. 2017; Sharma et al. 2019).

Citrus species are very popular worldwide (Liu et al. 2012), but fruit production is restricted by nonregular or alternate bearing in some of the most important commercial cultivars, mainly of mandarins and oranges (Monselise and Goldschmidt 1982). 'Orri' mandarin, an important commercial cultivar in Israel, displays a nonregular bearing pattern, which may vary from a regular-bearing pattern to various degrees of alternate bearing. In citrus, the floral transition takes place in the winter in subtropical regions, and depends on the accumulation of cold hours, which initiates the process of flowering induction (Goldschmidt and Sadka 2021). The signal is thought to be transferred to the axillary buds or apical meristem, where it drives differentiation to inflorescence (Nishikawa et al. 2007). This process coincides with fruit presence on the tree or begins shortly after harvest, and thus fruit load is thought to affect yield the following season, such that the greater the number of fruit, the stronger the inhibition (Agustí et al. 2022; Goldschmidt and Sadka 2021). After flower induction and differentiation, the bud can develop into an inflorescence or a vegetative shoot, or remain dormant. There are two types of inflorescences in citrus: generative (also called "pure" inflorescence), containing only flower buds, and mixed ("leafy" inflorescence), containing flower buds and leaves in various ratios (Agustí et al. 2022). The number of mixed inflorescences is usually less than that of the generative ones during anthesis, although the former contribute most of the final yield (Jahn 1973).

In fruit trees, flowering induction and differentiation are affected negatively by gibberellic acid (GA) treatments applied during the flowering induction period (Garmendia et al. 2019). This seems to contrast with the case in Arabidopsis, where GA treatment induces flowering (Wilson et al. 1992). However, even in Arabidopsis, although GA treatment promotes the phase transition (i.e., bolting of the inflorescence column), it then needs to be removed or it will decrease the number of flowers (Yamaguchi et al. 2014). When applied to citrus trees at a relatively high concentration and frequency, the effect is most pronounced for the development of generative inflorescences, which are dramatically reduced, whereas the number of mixed inflorescences is reduced, induced, or remains unchanged in response to these treatments (Goldberg-Moeller et al. 2013; Goldschmidt et al. 1985; Muñoz-Fambuena et al. 2012; Tang and Lovatt 2019). Based on the effect of the hormone on flowering, it was suggested that, along with auxin, GA plays a role in fruit-load inhibition on flowering induction (Bangerth 2009; Goldschmidt et al. 1985; Haim et al. 2021; Sadka et al. 2023).

Mild GA treatments during the flowering induction period of 'Valencia' orange resulted in an induced and reduced proportion of leafy and leafless inflorescences, respectively, but overall fruit number was remarkably reduced (Moss 1970). Similar treatments were examined for yield improvement toward off-crop year, and for mitigating alternate bearing in 'Nour' clementine (Benhamou et al. 2004). Although control trees showed two consecutive off-crop years following an on-crop year, treated trees exhibited only one off-crop year, demonstrating the potential of the treatment. Mild GA treatments were also tested in Huanglongbing-affected 'Valencia' sweet orange, resulting in improved productivity, mostly as a result of induced vegetation and reduced canopy dieback (Shahzad et al. 2024; Singh et al. 2022; Tang et al. 2021). These reports indicate that such treatments during the flowering induction period may be effective for yield improvement when flowering rates in the next season are expected to be low.

The yield-inducing potential of mild GA treatments through enhanced formation of mixed inflorescences was tested in 'Orri' mandarin toward an expected off-crop season. GA was

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applied at a low frequency (one or two treatments) and low concentrations (from 25 to 50 ppm) during the winter. The number of inflorescences (generative and mixed type), vegetative shoots, and dormant buds was quantified during anthesis, and total yield, fruit number, and fruit weight were recorded at harvest.

Materials and Methods

Multiannual yield of 'Orri' mandarin. Data of annual yield (from 2009 to 2020) of 'Orri' mandarin ['Temple' mandarin (Citrus temple hort. ex Y. Tanaka) × 'Dancy' mandarin (Citrus tangerine hort. ex Tanaka] plots from the central region of Israel were kindly provided by Mehadrin-Tnuport Export L.P. (Beerot Yitzhak, Israel).

Plant material and experimental design. The experiments were carried out in Winter 2019 (first season), 2020 (second season), and 2021 (third season) on trees of 'Orri' mandarin. The harvest time of 'Orri' mandarin took place from the end of January until the end of February; thus, the treatments were applied when the previous year's yield was present on the trees. On-crop plots with trees bearing at least 40 $ton \cdot ha^{-1}$ (according to the grower's estimation, which took place in November of each year) and expected to carry a low yield the following season were chosen as follows: In 2019, a plot of 2.2 ha planted in 2007 in Safaria (lat. 31°58′36.9″N, long. 34°51′33.9″E) with a tree spacing of 20 ft between rows and 11 ft between trees, grafted on 'Troyer' orange (Citrus sinensis 'Washington' × *Poncirus trifoliata* L. Raf.). In 2020, a plot of 1.5 ha planted in 2007 in Kfar Habad (lat. 31°58′32.9″N, long. 34°50′43.0″E) with a tree spacing of 18 ft between rows and 11 ft between trees, grafted on 'Sour Orange' (*Citrus ×aurantium*) (plot A); and a plot of 2.2 ha planted in 2007 in Safaria (lat. 31°58′36.9″N, long. 34°51′33.9″E) with a tree spacing of 20 ft between rows and 11 ft between trees, grafted on Troyer orange (plot B). Last, in 2021, a plot of 0.8 ha planted in 2007 in Kfar Habad (lat. 31°59′22.6″N, long. 34°50′11.6″E) with a tree spacing of 20 ft between rows and 10 ft between trees, grafted on 'Sour Orange'. All plots were irrigated by drip irrigation according to the standards determined by the Extension Service, Ministry of Agriculture and Food Security, using Penman-Monteith reference evapotranspiration. In 2019 and 2020, four blocks were labeled randomly in the plots. Each block contained two proximate trees per treatment and one border tree on each side, with eight trees per treatment overall. In 2021, 10 blocks were labeled randomly in the plot. Each block contained three proximate trees per treatment and one border tree on each side, with 30 trees per treatment overall.

In the first season (2019–20), GA (Giberllon® GA_3; GADOT Agro, Givat Brenner, Israel) mixed with 0.025% w/v Triton X-100 (Sigma-Aldrich, St. Louis, MO, USA) was applied to the trees by foliar spray (5 L per tree) during flowering induction at three time points (beginning of December, mid-December, and end of December) using two concentrations (25 and 50 ppm). Treatment groups included a control, receiving 0.025% w/v Triton X-100; a single treatment of 25 ppm GA (treatments 1–3) or 50 ppm GA (treatments 6–8) at one of the three time points (Table 1); two GA treatments of 25 ppm at the first and second time points (treatment 4, Table 1); and two GA treatments of 25 ppm at the second and third time points (treatment 5, Table 1). Considering the practical aspect of this work, in the following season (2020–21), two 'Orri' plots were used to reexamine the effects of three treatment groups that seemed promising in the previous trial: a single treatment of 25 ppm GA in mid-December (treatment 2), two applications of 25 ppm GA at the beginning of December and mid-December (treatment 4), and two applications of 25 ppm GA at mid-December and the end of December (treatment 5) (year 2, Table 1). In the third season (2021–22), two treatments were applied: a control, receiving 0.025% w/v Triton X-100, and two GA treatments of 25 ppm in mid-December and at the end of December (treatment 5) (year 3, Table 1).

Because each plot was trialed once, long-term effects of the treatment were not evaluated.

Inflorescence determination and fruit harvest. Branches of similar size were labeled on each tree before budbreak in January. In the first and second years, three branches per tree were counted in each treatment ($n = 24$). In the third year, 10 branches per tree were counted in five random blocks ($n = 150$). Counting of generative inflorescences, mixed-type inflorescences, and newly developed vegetative shoots was performed close to or at full bloom, and the numbers were standardized to the number of nodes present on the branch. As mentioned earlier, GA was applied when fruit was present on the trees. Because variance in harvest time may affect inflorescence development and therefore the efficiency of the GA treatments, dates of harvest are provided for the yield present on the tree during the applications as follows: 7 Feb 2020 in the first year, 28 Jan 2021 (plot A) and 30 Jan 2021 (plot B) in the second year, and 2 Feb 2022 in the third year. Dates of harvest of the yield resulting from the treatments were as follows: 6 Feb 2021 in the first year, 28 Jan 2022 (first plot) and 3 Feb 2022 (second plot) in the second year, and 8 Feb 2023 in the third year. Fruit yield (measured as kilogram per tree), number, and weight were recorded.

Statistical analysis. Statistical analyses of the treated and control trees consisted of data distribution assessments, robust fit, and goodness-of-fit tests, followed by one-way analysis of variance (ANOVA) when data distribution was normal (yield parameters) or Welch's ANOVA when data distribution was not normal (inflorescence numbers). Following ANOVA, Student's t test or pooled t test parametric comparisons were conducted. Following Welch's ANOVA, Steel's test or the Wilcoxon rank-sum test, nonparametric comparisons were conducted. Analyses were performed using JMP software (v. 18; SAS Institute, Cary, NC, USA). Log transformation was applied to fruit count data of year 1 and year 2 (plot B) to enhance normality before statistical analyses.

Results and Discussion

'Orri' mandarin is a nonregular-bearing cultivar. Annual yield of 'Orri' mandarin, studied here because of its high commercial value, varies from regular to alternate bearing, as shown for 72 plots located in the central region of Israel from 2009 to 2020 (Supplemental Table 1, total weight data are obtained from packing houses). Years 2011–12 and 2012–13 were generally characterized by two consecutive on-crop seasons, as were 2018–19 and 2019–20, whereas years 2013–14 to 2018–19 showed a year-to-year alternate-bearing pattern in many of the plots. These data demonstrate the complex fruit-bearing behavior of this cultivar compared with alternate-bearing cultivars such as 'Murcott' mandarin or regular bearers (Agusti et al. 2014).

Effect of GA applications on inflorescence number, fruit number, and yield weight. The GA treatments were applied throughout the flowering induction period during on-crop

Table 1. Gibberellic acid (GA) treatments (control and treatments 1–8) according to GA concentration (25 or 50 ppm) and time points (beginning of December, mid-December, end of December) in different research years. During year 2, the experiments were conducted on two plots, as indicated.

Treatment	Time point	Year 1		Year 2, plot A	Year 2, plot B	Year 3
		25 ppm GA	50 ppm GA	25 ppm GA	25 ppm GA	25 ppm GA
Control						
1	Beginning of December	+				
2	Mid-December	+		+	+	
3	End of December	+				
4	Beginning + mid-December	+		+	+	
5	Mid- + end of December	+		+	+	+
6	Beginning of December		+			
7	Mid-December		+			
8	End of December		+			

seasons (toward projected off-crop seasons). These off-crop seasons were characterized by a low number of flowers and, by using mild GA treatments, we aimed to increase fruit number and to test whether the effect occurs through induced development of mixed-type inflorescences over generative ones, as the latter is shown to be less productive for the final yield in other citrus cultivars (Goldschmidt 1999). The experiments were repeated in four plots during 3 years of research, and the chosen plots exhibited an on-crop year with an expected off-crop year the following season, based on data from previous seasons. The practical aspect of this work consisted of reducing the number of treatments from year to year, where only promising ones were selected for the second and third years of testing. Using this approach, year-to-year variations that may affect treatment efficiency could be ignored. In the first season (2019–20), 25 or 50 ppm GA was applied to ‘Orri’ mandarin on-crop trees by foliar spray at the beginning of December, mid-December, and the end of December (treatments 1–3 and 6–8, Table 1). In addition, two treatments of 25 ppm were applied at two time points (treatments 4 and 5, Table 1). Including the control treatment (no GA application), nine treatments were considered. All of the GA treatments reduced the number of generative inflorescences, compared with the control, by 50% to 100%, with the strongest effect detected in trees treated twice with 25 ppm (treatments 4 and 5) (Fig. 1A). In contrast, mixed inflorescences were induced 3- to 5-fold compared with the control in most GA treatments (Fig. 1B). Vegetative shoots barely developed in the control group, with no significant differences detected among the treatment groups (Fig. 1C). Total inflorescences were reduced by ≈30% in all GA treatment groups compared with the control, with the exception of treatment 1 (Fig. 1D). As expected, in control trees, two-thirds of the fruit originated from mixed inflorescences and one-third from generative ones (Fig. 1E). However, treatment 5 significantly altered the proportion, with 87% of the fruit resulting from the mixed-type inflorescences and only 13% from generative ones (Fig. 1E). Fruit counting on the trees in November showed no effect of the treatments (not shown). However, as treatments 2, 4, and 5 seemed to have the greatest effect in respect to inflorescence development, they were harvested and retested in the 2020–21 season. Remarkably, regardless of the effect on inflorescence number and proportion, none of the harvested treatments affected yield, fruit number, or average fruit weight (Fig. 1F–H). Overall, average yield in the plot was ≈45 ton·ha^{-1}, clearly indicating that the year was not an off-crop one, as initially projected. It was apparent that two consecutive on-crop seasons had occurred and, therefore, the treatment might have failed to induce the yield, although the mixed-type inflorescences were induced significantly. We assume that the trees were already at their full fruit-load potential, preventing an increase in yield. This is similar to other studies in which other flowering induction treatments in citrus failed to increase yield when fruit load was already high (Benhamou et al. 2004; Martínez-Fuentes et al. 2013).

To increase the probability of obtaining an off-crop year following the treatment, two ‘Orri’ mandarin on-crop plots were selected during the second season (2020–21). Based on the first year’s inflorescence results, 25 ppm GA was applied as follows: in mid-December (treatment 2, single treatment), at the beginning of December and in mid-December (treatment 4), and in mid-December and at the end of December (treatment 5) (Table 1). In the first plot (Fig. 2), only treatment 2 reduced the number of generative inflorescences by about 2-fold compared with the control, whereas the other treatments had no significant effect (Fig. 2A). Mixed inflorescences were not altered by any of the treatments, but the number of vegetative shoots was induced significantly by about 7-fold in treatment 2 compared with the control and by about 3-fold in treatment 5 (Fig. 2B and C). Total inflorescences were reduced almost 2-fold in treatment 2 compared with the control, whereas their numbers in treatments 4 and 5 were not significantly different from the control (Fig. 2D). Surprisingly, only treatment 5

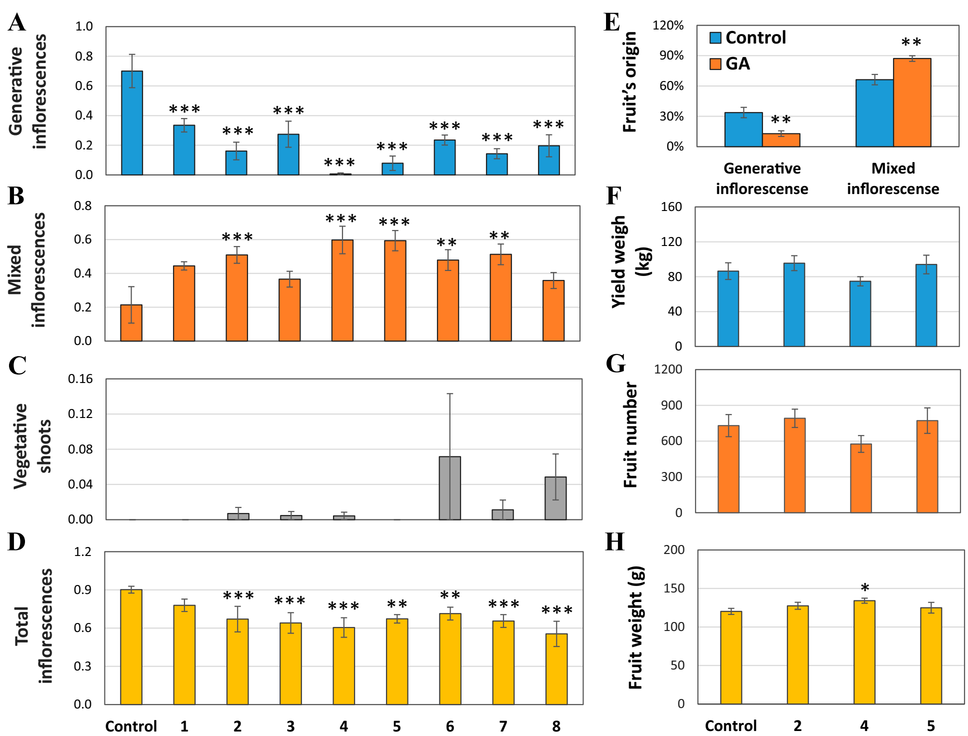

Fig. 1. Effect of gibberellic acid (GA) treatments on citrus ‘Orri’ mandarin flower development, fruit number, and overall yield in the first experiment (2019–20 season). Single treatments of GA were given at each of three time points in 2019 (treatments 1–3, 25 ppm; treatments 6–8, 50 ppm; beginning of December, mid-December, and end of December); treatments of 25 ppm GA were also given at two time points: beginning of December and mid-December (treatment 4), and mid-December and end of December (treatment 5). Generative inflorescences (**A**), mixed inflorescences (**B**), vegetative shoots (**C**), and total inflorescences (**D**) were counted and quantified by standardization to the number of nodes on the branch (n = 24). Fruit origin was determined as either generative or mixed inflorescence in the control group (Control) and treatment 5 (GA). Mean yield weight (**F**), fruit number (**G**), and fruit weight (**H**) were calculated per tree after harvesting the control and treatment 5 groups (n = 8). Asterisks denote a significant difference between treatments and control (*$P \leq 0.1$, **$P \leq 0.05$, ***$P \leq 0.01$) by Steel’s test (**A–D**), by pooled *t* test (**E**), or by Student’s *t* test for each pair (**F–H**).

resulted in improved yield, with 40% greater fruit weight per tree ($P \leq 0.08$), and an increase of ≈50% in fruit number ($P \leq 0.1$) compared with the control. Individual fruit weight was not altered by the GA treatment. The total yield in the plot was about 35 ton·ha^{-1} (Fig. 2E–G). In the second plot (Fig. 3), generative inflorescences were reduced in treatment 2 by about 2.5-fold compared with the control, and in treatment 5 by about 2-fold, whereas treatment 4 did not differ significantly from the control (Fig. 3A). In addition, mixed inflorescences were only induced in treatment 5, about 2-fold compared with the control (Fig. 3B). The numbers of vegetative shoots and total inflorescences were similar in all treatment groups (Fig. 3C and D). Although all other tested treatments did not affect yield compared with control, treatment 5 increased yield weight ($P \leq 0.05$) and fruit number ($P \leq 0.05$) by ≈40% compared with the control, whereas individual fruit weight was unaffected (Fig. 3E–G). The overall yield in this plot was ≈27 ton·ha^{-1}. Despite the lack of increase in mixed inflorescences in the first plot, in both plots treatment 5 increased yield weight and fruit number by ≈40% ($P \leq 0.1$ in the first plot, $P \leq 0.05$ in the second plot). In these two plots, an off-crop season occurred, as initially projected.

In the third season (2021–22), an on-crop 'Orri' mandarin plot was treated with 25 ppm GA at two time points: mid-December and end of December (treatment 5, Table 1). The treatment resulted in a more than 10-fold reduction in generative inflorescences compared with the control, whereas the number of mixed inflorescences did not differ (Fig. 4A). In addition, the number of vegetative shoots was induced about 10-fold in treated trees compared with the control, and the number of total inflorescences was reduced by ≈30% (Fig. 4A). The treatment resulted in approximately twice as many dormant buds as control trees (Fig. 4A). As demonstrated in the first year, 67% and 86% of the fruit originated from mixed inflorescences in the control and treated trees, respectively (Fig. 4B). No significant differences were found between treated and untreated trees with respect to yield, fruit number, or individual fruit weight (Fig. 4C–E). The overall yield in the plot was estimated to be 62 ton·ha^{-1}. This plot exhibited two consecutive on-crop seasons, further demonstrating the nonregular fruit-bearing pattern of this cultivar (Goldberg-Moeller et al. 2013; Schneider et al. 2009). As mentioned earlier, previous reports have shown that mild GA treatments during the flowering induction period can improve yield in Huanglongbing-affected 'Valencia' sweet orange (Singh et al. 2022; Tang et al. 2021), and in 'Nour' clementine (Benhamou et al. 2004). Adding our data, mild GA treatments appear to enhance yield in various commercial citrus cultivars. However, as the treatments were not effective during year 1 and year 3, which

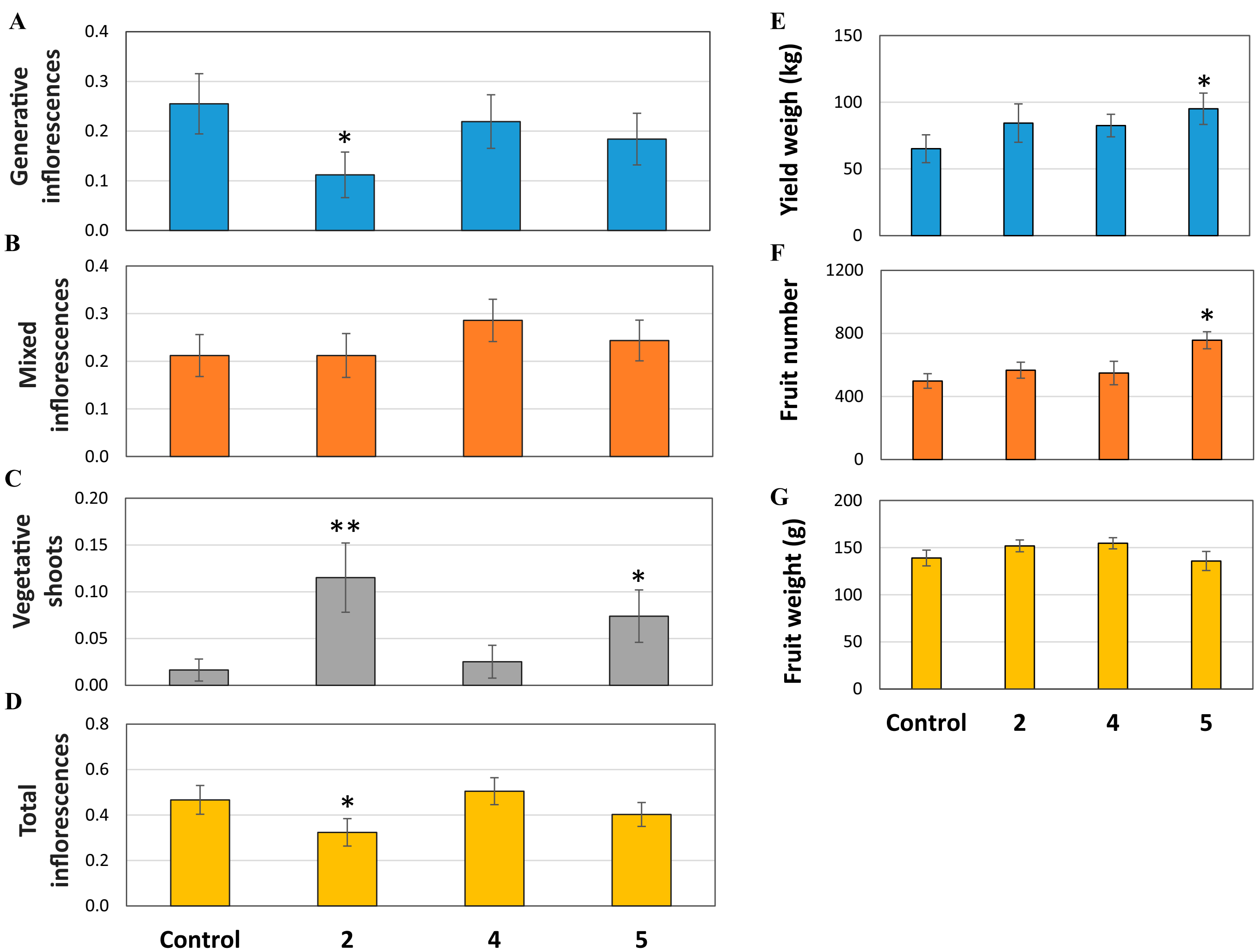

Fig. 2. Effect of gibberellic acid (GA) treatments on citrus 'Orri' mandarin flower development, fruit number, and overall yield in the second experiment (plot A, 2020–21 season). Treatments of 25 ppm GA were given once in mid-December (treatment 2), twice at the beginning of December and mid-December (treatment 4), or in mid-December and the end of December (treatment 5). Generative inflorescences (**A**), mixed inflorescences (**B**), vegetative shoots (**C**), and total inflorescences (**D**) were counted and quantified by standardization to the number of nodes on the branch (n = 24). Mean yield weight (**E**), fruit number (**F**), and fruit weight (**G**) were calculated per tree after harvesting the control and treatment 5 groups (n = 8). Asterisks denote a significant difference between treatment and control (*$P \leq 0.1$, **$P \leq 0.05$, ***$P \leq 0.01$) by the Wilcoxon rank-sum test for each pair (**A–D**) or by Student's *t* test for each pair (**E–G**).

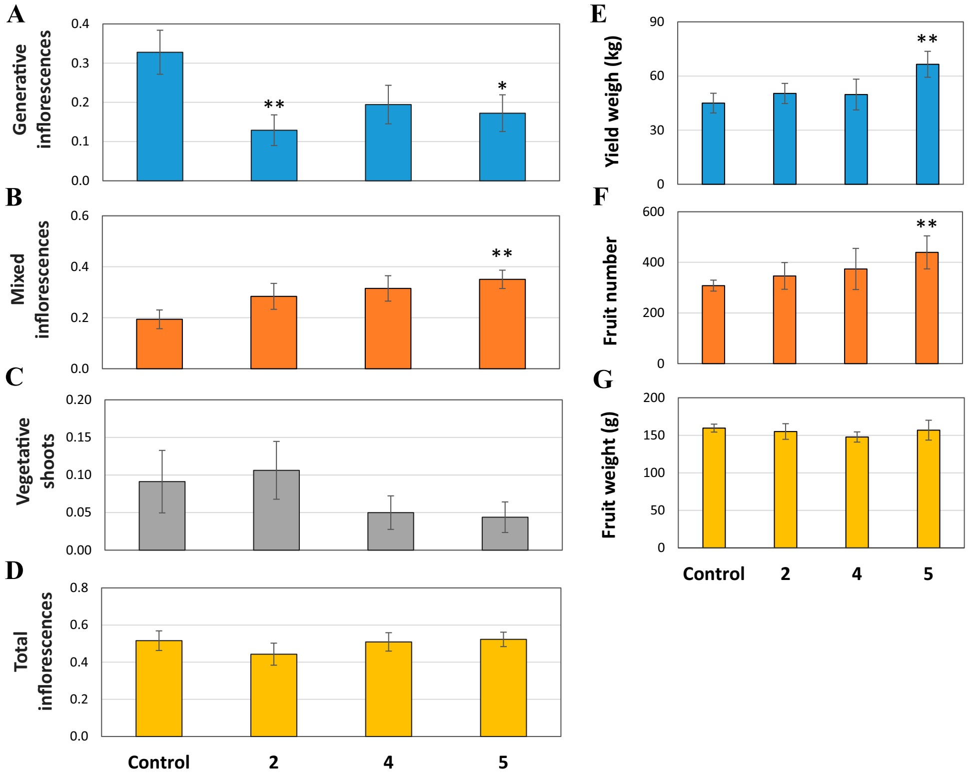

Fig. 3. Effect of gibberellic acid (GA) treatments on citrus 'Orri' mandarin flower development, fruit number, and overall yield in the third experiment (plot B, 2020–21 season). Treatments of 25 ppm GA were given once in mid-December (treatment 2), twice at the beginning of December and mid-December (treatment 4), or mid-December and at the end of December (treatment 5). Generative inflorescences (**A**), mixed inflorescences (**B**), vegetative shoots (**C**), and total inflorescences (**D**) were counted and quantified by standardization to the number of nodes on the branch (n = 24). Mean yield weight (**E**), fruit number (**F**), and fruit weight (**G**) were calculated per tree after harvesting the control and treatment 5 groups (n = 8). Asterisks denote a significant difference between treatment and control (*$P \leq 0.1$, **$P \leq 0.05$, ***$P \leq 0.01$) by the Wilcoxon rank-sum test for each pair (**A–D**) or by Student's *t* test for each pair (**E–G**).

were on-crop years, but rather only in year 2, in the two plots showing off-crop, it was concluded that the treatments were effective only when an off-crop season followed. Furthermore, data for year 2, plot B suggest that the induced yield in treatment 5 resulted from the induced number of mixed-type inflorescences. However, in plot A, no induction in these inflorescences was detected, but rather was seen in the vegetative ones. This may suggest that induced yield is caused either by induced mixed-type inflorescences or by induced vegetative shoots. Similarly to treatment 5,

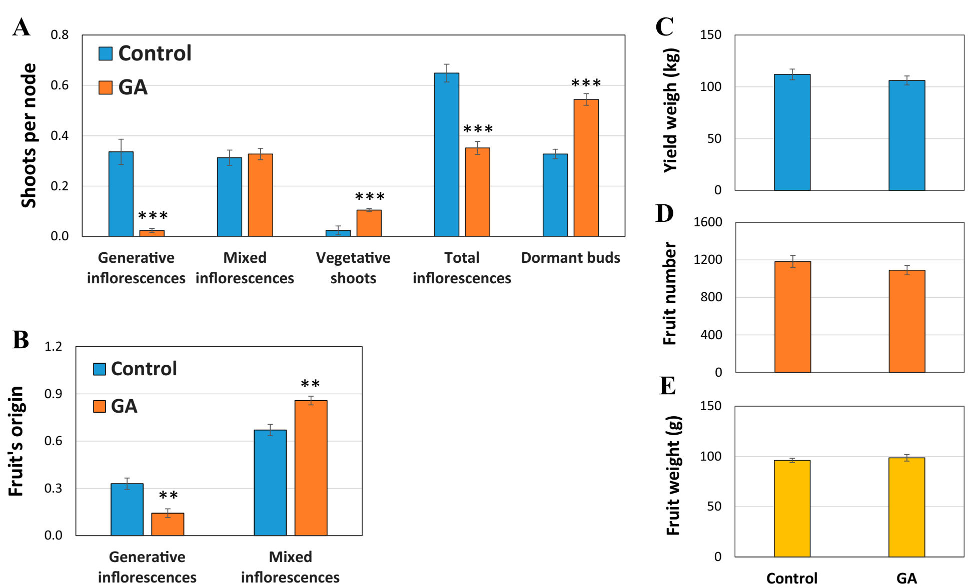

Fig. 4. Effect of gibberellic acid (GA) treatments on citrus 'Orri' mandarin flower development, fruit number, and overall yield in the fourth experiment (2021–22 season). Treatment of 25 ppm GA was given twice, in mid-December and the end of Dec 2021 (designated GA, previously treatment 5). (**A**) Generative inflorescences, mixed inflorescences, vegetative shoots, total inflorescences, and dormant buds were counted and quantified by standardization to the number of nodes on the branch in the control group (Control) and the treatment group (GA) (n = 150). (**B**) Fruit origin was determined as either generative or mixed inflorescences in the Control and GA groups. Mean yield weight (**C**), fruit number (**D**), and fruit weight (**E**) were calculated per tree after harvesting the control and GA groups (n = 20). Asterisks denote a significant difference between the treatment and control (*$P \leq 0.1$, **$P \leq 0.05$, ***$P \leq 0.01$) by the Wilcoxon rank-sum test for each pair (**A**) or by pooled *t* test (**B–E**).

treatment 2 in plot A also resulted in an induced number of vegetative shoots, but still with no induced yield. However, although treatment 5 resulted in 3-fold induction in vegetative shoots, in treatment 2 the vegetative shoots induced by 7-fold. It was well established that although vegetation was required for flowering, over-vegetation competed with reproductive growth, which might well be the case in treatment 2 (Goldschmidt 1999). Furthermore, treatment 2 also resulted in a reduced number of total inflorescences, supporting this notion. Regardless, the varied response of these two plots to the same treatment depended most likely on additional parameters, which are not identified here.

Here, the treatments were applied only once in each plot, raising a question in regard to the effect of multiannual GA treatment on the same trees. Although multiannual GA treatments in 'Valencia' orange during three consecutive years did not change the alternate bearing index (Benhamou et al. 2004), other cultivars might respond differently. Therefore, this question deserves further investigation.

Fruit set, and therefore yield increase, is suggested to be enhanced as a result of the abundance of carbohydrates produced in "source" organs, usually referring to mature leaves (Paul and Foyer 2001; Salazar-García and Lovatt 2000). In 'Hass' avocado, GA treatments of 25 or 100 ppm toward the off-crop season, depending on the timing, turned the determinate inflorescences into indeterminate ones, characterized by a vegetative apex, thus possibly supplying the newly set fruit with valuable photoassimilates (Salazar-García and Lovatt 2000). Although the number of mixed-type inflorescences was not always affected by the treatment, it is tempting to assume that the leaves present in the mixed-type inflorescence act as a carbohydrate source for the developing flower buds and fruitlets, ultimately increasing fruit number (Agusti et al. 2014). This notion is supported by a study in which citrus tree defoliation reduced carbohydrate content in fruitlets and increased their rate of abscission (Agusti et al. 2014). Furthermore, the treatment barely stimulated the development of vegetative shoots and, therefore, competition for resources could be limited (Goldschmidt 1999), which may contribute to the sink strength of the flower buds on the mixed-type inflorescence. However, this assumption is challenged by previous findings of no difference in carbohydrate levels, or vascular development, in mixed-type vs. generative inflorescences (Erner and Shomer 1996). Therefore, further research is needed to understand the treatment's mechanism of action and the different outcomes when applied at high vs. low concentrations.

Although the number of mixed-type inflorescences was not always affected by the treatment, the reduction in the number of generative inflorescences was quite consistent. The inconsistent relationship between mixed-type inflorescences and yield could be derived from the variability in 'Orri' mandarin shoot emergence at anthesis, resulting from yearly girdling of two-thirds of its branches at that stage (Agusti et al. 2014). This usually leads to the emergence of branches with a high number of generative inflorescences next to branches with high vegetative growth. Therefore, mixed-type inflorescences, which are present in a considerably lesser proportion than the generative ones, could be misquantified. Another point worth mentioning is the nonregular bearing of 'Orri' mandarin when two consecutive on-crop years occur (Supplemental Table 1). Although in classical alternate-bearing cultivars it is assumed that heavy fruit load inhibits flowering induction, a question could arise with regard to why 'Orri' mandarin can "escape" occasionally from this inhibition. We suggest that during the off-crop year, this cultivar is capable of storing reserves that are sufficient for 2 years. However, further research is needed to validate this assumption.

Conclusion

Nonregular and alternate bearing is a major concern in horticulture because it limits the multiannual yield of many cultivars, such as 'Orri' mandarin. GA treatments during the flowering induction period greatly reduce flower number when applied at high concentration and frequency. However, mild GA treatments may promote the development of mixed-type inflorescences, which contribute to most of the final yield, with a relatively marginal effect on the total number of flowers. Despite the inconsistent fruit-bearing behavior of 'Orri' mandarin, the potential of these treatments to increase yield in off-crop seasons, thereby increasing profitability, is suggested.

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