Tritrophic effects of plant growth regulators in an aphid-parasitoid system
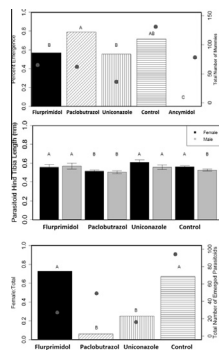
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HIGHLIGHTS

- We did not observe any significant effect of PGR on aphid abundance.
- We observed significantly less mummies on paclobutrazol treated plants.
- PGRs can significantly reduce parasitoid emergence, size and female ratio.

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Plant growth regulators (PGRs) have the potential to negatively affect the outcome of biological control via plant architectural changes and plant chemical changes. Despite studies demonstrating the negative effects of PGRs on herbivore survival and development, to date, no studies have investigated the tritrophic effects of PGRs on parasitoid life history traits. In this study we investigated the effect of four commonly used PGRs on *Myzus persicae* abundance and suppression, and *Aphidius colemani* fitness in a greenhouse experiment. None of the PGRs reduced aphid abundance alone or affected aphid suppression by *A. colemani*. However, paclobutrazol reduced the number of mummies that developed on plants. PGRs had a range of negative effects on parasitoid fitness. No adult parasitoids eclosed from mummies on ancymidol treated plants. Paclobutrazol reduced parasitoid size, and paclobutrazol and uniconazole reduced female:total ratio. This study shows that PGRs can negatively affect parasitoid fitness, and reduce parasitism, suggesting the potential for negative long-term effects on the efficacy of biological control.

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1. Introduction

The efficacy of augmentation biological control is often unpredictable as it is influenced by many biotic and abiotic factor (Collier and Van Steenwyk, 2004; Frank, 2010). Although the effect of many ecological interactions on biological control efficacy has been well studied (Holt and Lawton, 1994; Martinou et al., 2010; Fill et al., 2012), we know little about the impact of common horticulture practices such as the use of plant growth regulators (but see Oetting and Latimer, 1995 and Uçkan et al., 2008). Plant growth regulators (PGRs) are non-nutrient, organic compounds used in ornamental plant production to modify plant growth and development (Basra, 2000). PGRs can be used to reduce plant growth rate, improve coloring, increase branching and bushiness, or synchronize flowering times (Basra, 2000). By changing plant chemistry, physiology, and architecture PGRs may alter arthropod behavior and development (e.g. Prado and Frank, 2013). Although PGRs are widely used in horticulture and agriculture, still much remains to be known about their effects on herbivores, natural enemies, and their interactions.

PGRs have the potential to reduce pest population growth by reducing fecundity, egg viability, and increasing development time (Visscher, 1980; Coffelt et al., 1993; Kaur and Rup, 2002). For

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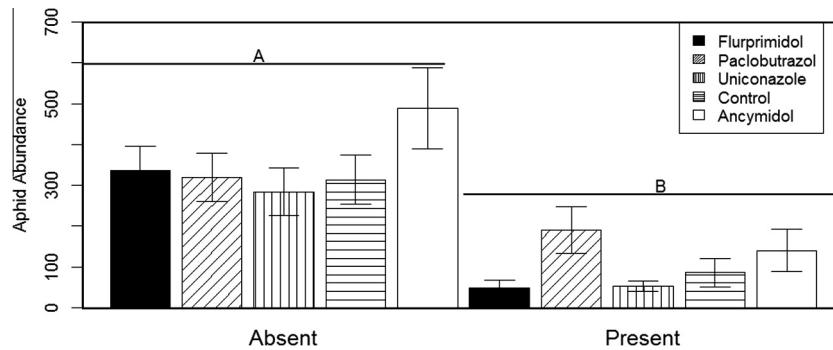 E-mail address: sprado@ncsu.edu (S.G. Prado).

Fig. 1. Overall mean (±SE) number of aphids on caged pepper plants during a three week experiment in which plants were untreated or treated with one of four PGRs and had parasitoids absent or present within the cages. Though a non-parametric mixed-effects ANOVA was performed to determine the effects of parasitoids and PGRs on aphid abundance, the untransformed aphid abundances are presented in this graph. Different letters above horizontal bars indicate significant ($P < 0.05$) main effect of parasitoids on aphid abundance.

example, Coffelt et al. (1993) showed that high doses of paclobutrazol significantly slowed the development and decreased the survival of *Anisota senatoria* Smith (Lepidoptera: Saturnidae). Several phloem feeding insects including aphids and lace bugs are also negatively affected by PGRs (Honeyborne, 1969; Coffelt and Schultz, 1988). Chlormequat chloride was found to reduce *Aphis fabae* Scopoli (Hemiptera: Aphididae) fecundity and survival, and ethylene-bisnitrourethane to reduce its size (Honeyborne, 1969). Although we have some evidence that PGRs can compromise herbivore development (e.g. Visscher, 1980; Coffelt et al., 1993; Kaur and Rup, 2002), few studies have investigated the effects of these chemicals on natural enemies.

By affecting the quality of aphid hosts, PGRs could alter parasitoid abundance, fitness, or efficacy. For example, Honeyborne (1969) found that chlormequat chloride and N-dimethylaminosuccinamic acid (B995) reduce aphid size. Parasitoids developing in these smaller hosts may also be reduced in size (Sequeira and Mackauer, 1992) resulting in reduced fecundity (Ellers et al., 1998; Eijs and van Alphen, 1999; Sampaio et al., 2008). Parasitoids developing in small hosts also tend to have higher male sex ratio and mortality rates than those developing in large hosts (Jarosik et al., 2003). Additionally, small parasitoids tend to have fewer fat reserves (Ellers et al., 1998; Eijs and van Alphen, 1999), thus reducing their dispersal potential (Ellers et al., 1998) and their ability to survive when food is unavailable (Ellers et al., 1998; Eijs and van Alphen, 1999). Along with altering parasitoid life history traits, PGRs can reduce parasitism by increasing plant architectural complexity (Prado and Frank, 2013). Thus, the potential benefit of PGRs to reduce pest population growth could be nullified if negative effects on parasitoids disrupt biological control programs.

Myzus persicae Sulzer (Hemiptera: Aphididae) is one of the most important pests of greenhouse ornamental and vegetable crops (Heathcote, 1962). *M. persicae* feeds on over 100 vegetable and ornamental plant species (Baker, 1994), many of which are treated with plant growth regulators during greenhouse production. *Aphidius colemani* Viereck (Hymenoptera: Braconidae) is a solitary, koinobiont, endoparasitoid (Starý, 1975) used for biological control of economically important pest aphids including *M. persicae* (van Steenis, 1995). As such, *A. colemani* development is closely tied to its hosts' development, making it vulnerable to changes in host quality, when its host feeds on toxic or low quality plant material (Kalule and Wright, 2005). In a previous experiment, we showed that the PGR paclobutrazol reduced aphid suppression by *A. colemani* by increasing plant architectural complexity (Prado and Frank, 2013). In this study, we expand on our previous research to include four of the most commonly used PGRs (Whipker and Evans, 2012) to determine (1) how different PGRs interact with *A. colemani* to affect *M. persicae* abundance and suppression, and (2) how different PGRs affect *A. colemani* fitness and abundance. To achieve our objectives, we compared aphid populations on ornamental Black Pearl Pepper plants (*Capsicum annuum* 'Black Pearl') treated with one of four plant growth regulators to each other and to untreated plants in the presence and absence of *A. colemani*. Furthermore, we compared life history traits of parasitoids reared on treated and untreated plants. This research will be the first to document the effects of multiple PGRs on an aphid parasitoid's fitness and efficacy, and should assist in improving biological control programs.

2. Methods

2.1. Study system

A. colemani were purchased from Koppert Biological Systems (Howell, MI) (product: Aphipar). Upon receipt, the mummies were placed in a 61×61 cm cage where the parasitoids could emerge and mate. During that time, they were provided with a 25%
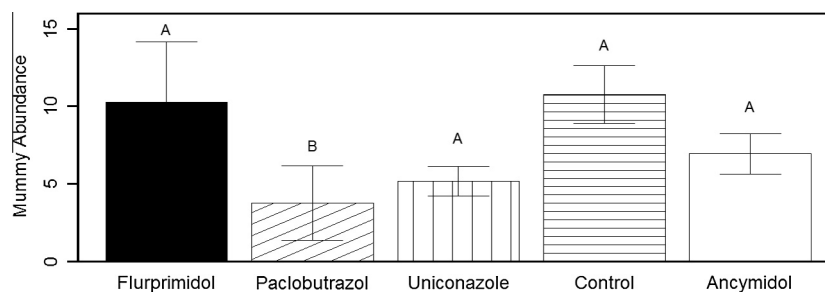

Fig. 2. Overall mean (±SE) number of aphid mummies on caged pepper plants with parasitoids during a three week experiment in which plants were untreated or treated with PGRs. Though a non-parametric mixed-effects ANOVA was performed to determine the effect of each treatment on mummy abundance, the untransformed mummy abundances are presented in this graph. Means with different letters are significantly different at the $P = 0.05$ level.
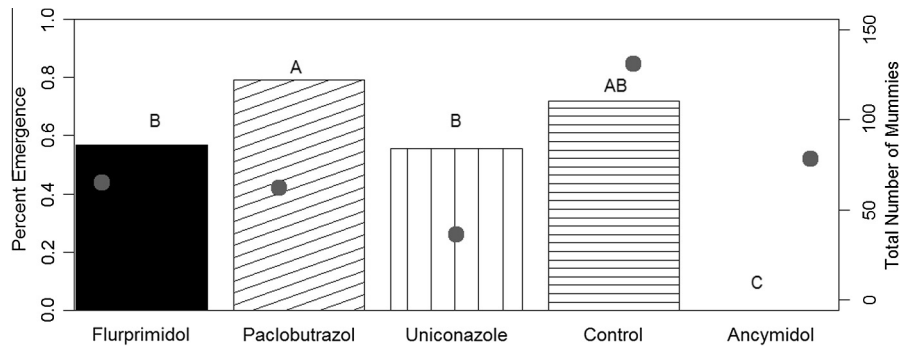
Fig. 3. Total number of parasitoids that emerged from mummies removed from pepper plants that were untreated or treated with PGRs. Bars with different letters are significantly different at the $P = 0.05$ level. The gray dots indicate the total number of mummies that were removed from the pepper plants (right y-axis) from which the parasitoids emerged.

sucrose-water solution. All female parasitoids were used less than 72 after emergence. We used *M. persicae* from a laboratory colony that was started from field collected aphids. The aphids were reared on Black Pearl Pepper plants (*Capsicum annuum* 'Black Pearl') in an incubator at 25 °C and 70–80% RH.

All Black Pearl pepper plants were obtained from cuttings. Source plants were cut 5–10 cm below the bud. The cut tips were then dipped into "Rhizopon AA Dry Powder Rooting Hormone #1" (Active ingredient (a.i.): 0.1% 3-Indolebuteric acid) (Earth City, MO) and planted in 48 pot trays (56 cm by 25.5 cm tray) with sifted Faf-ard 2P mix (Agawam, MA) for germination. The cuttings were left to root in a misting area for 6 weeks before they were transplanted into 15.2 cm-diameter pots with Farfard 2P soil mix with 396.44 g of Scotts Osmocote (N-P-K: 14-14-14) fertilizer (Marysville, OH) for every 0.08 m^3 of soil. Each PGR was applied as a drench to 12 plants 2.5 weeks after transplanting the cuttings. 118.29 ml of solution were applied to each pot. Rates were as follows: 8 ppm of Bonzi® (a.i. paclobutrazol 0.4%), 2 ppm of Topflor® (a.i. flurprim-idol 0.38%), 14 ppm of Abide® (a.i. ancymidol 0.0264%) and 2 ppm of Sumagic® (a.i. uniconazole 0.055%). Twelve plants were left un-treated as controls. Plants were left to grow for another 10 days be-fore the experiment began.

2.2. Effect of four PGRs on aphid abundance

To determine the effects of four plant growth regulators on aphid abundance and suppression, we conducted a 2×5 factorial experiment that crossed 5 plant growth regulator treatments ('Ancymidol', 'Paclobutrazol', 'Control', 'Uniconazole' and 'Flur-primidol') with two parasitoid treatments ('absent' and 'present'). Every treatment combination was replicated 6 times for a total of 60 'Black Pearl' pepper plants. Every pot was covered in a bag made of organdi fabric that was supported from within by 45 cm bamboo

stakes and fastened around the base of the pot using a binder clip. On the first day, we infested each plant with 15 *M. persicae* of ran-dom instars from the laboratory colony. After 4 h two mated fe-male *A. colemani* were released into cages assigned to the parasitoid 'present' treatments. One week after parasitoids were released, we recorded total aphid and mummy abundance on each pepper plant. This process was repeated five times, every 72 h, fol-lowing the first data-collection day.

2.3. Effect of four PGRs on A. colemani life history traits

On the last day of the experiment (day 19), mummies were picked off the plants from all the parasitoid 'present' treatments and placed in glass vials plugged with cotton. All mummies were grouped by PGR treatment for a total of five vials. Parasitoids were reared out of mummies in the laboratory and preserved in 90% alcohol upon emergence. We examined each parasitoid under a dissecting microscope with an ocular micrometer to determine their gender and measure the length of their left hind tibia. Parasit-oid percent emergence was determined by dividing the total num-ber of emerged parasitoids by the total number of mummies from each treatment. In 5 of the plants (1 from Paclobutrazol, 1 from the untreated, and 3 from the Flurprimidol) no mummies formed over the course of the experiment, so they were included as replicates in the parasitoid 'absent' treatment.

2.4. Statistical analysis

As total aphid abundance and mummy abundance could not be normalized, a nonparametric factorial repeated measures analysis was performed using the package nparLD (Noguchi et al., 2012) to determine how time, PGRs, parasitoids, and their interaction af-fected their numbers. Differences in parasitoid percent emergence
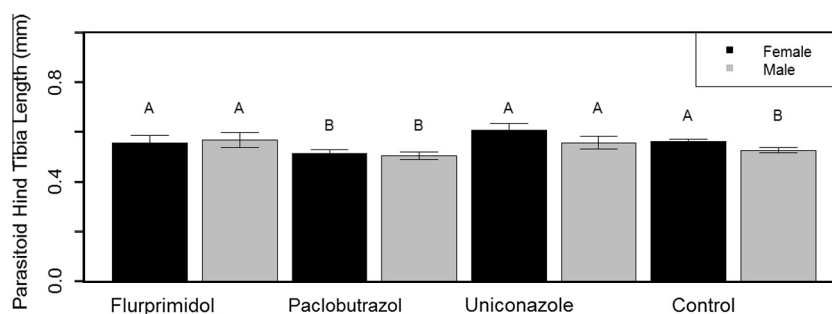

Fig. 4. Overall mean (±SE) hind tibia length of parasitoids emerging from mummies removed from pepper plants that were untreated or treated with PGRs. No parasitoids emerged from ancymidol, and therefore no hind tibia length measurements could be taken. Means with different letters are significantly different at the $P = 0.05$ level.
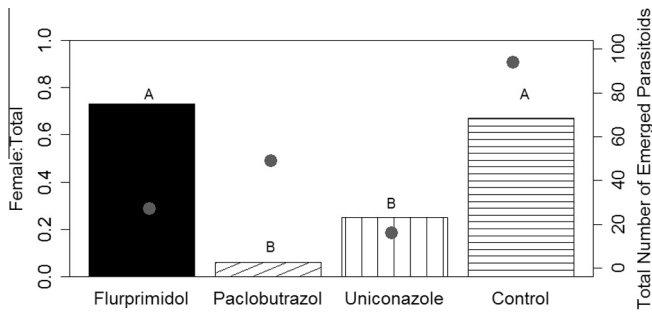
Fig. 5. Overall ratio of female:total number of emerged parasitoids. Means with different letters are significantly different at the $P = 0.05$ level. The gray dots indicate the total number of emerged parasitoids (right y-axis) from which the female ratio was calculated.

across PGRs was determines using a Pearson's Chi square test. A Chi square test was also used to calculate the differences in parasitoid sex ratio between PGR treatments. Lastly, a two-way analysis of variance (ANOVA) was used to determine how PGRs and parasitoid sex interact to affected parasitoid size. All analyses were performed using R version 2.14.2.

3. Results

3.1. Effect of four PGRs on aphid abundance

There was a significant interaction between parasitoid presence and time on aphid abundance, such that aphid abundance increased more slowly when parasitoids were present than when they were absent ($F_{1.94,\infty} = 9.74$; $P < 0.0001$). The main effects of time ($F_{1.94,\infty} = 188.34$; $P < 0.0001$) and parasitoids were also significant ($F_{1,\infty} = 52.95$; $P < 0.0001$, Fig. 1), however there was no significant main effect of PGR ($F_{3.50,\infty} = 1.38$; $P = 0.24$). The interaction between time, parasitoids and PGR was not significant ($F_{6.00,\infty} = 0.97$; $P = 0.44$) nor were the interactions between PGR and time or PGR and parasitoids ($F_{6.00,\infty} = 1.122$; $P = 0.35$; $F_{3.50,\infty} = 0.54$; $P = 0.68$, respectively).

There was a significant main effect of PGR on mummy abundance ($F_{3.47,\infty} = 3.71$; $P = 0.0077$) (Fig. 2) wherein mummy abundance was significantly lower on paclobutrazol-treated plants than for the other treatments. There was also a significant effect of time ($F_{2.19,\infty} = 13.66$; $P < 0.0001$) on mummy abundance. However, there was no significant interaction between PGR and time on mummy abundance ($F_{6.16,\infty} = 0.78$; $P = 0.59$).

3.2. Effect of four PGRs on A. colemani life history traits

A chi-square test showed a significant effect of PGR on the frequency of emerged parasitoids ($\chi_4^2 = 123.99$; $P < 0.0001$) (Fig. 3). There was also a significant interaction between parasitoid sex and PGR on parasitoid size ($F_{3192} = 2.83$; $P = 0.0392$), wherein female parasitoids emerging from paclobutrazol treated plants were significantly smaller, and male parasitoids emerging flurprimidol and uniconazole treated plants were significantly larger than females and males emerging from the control (Fig. 4). The main effects of sex and PGR were also significant ($F_{1192} = 32.73$; $P < 0.0001$; $F_{3192} = 10.05$; $P < 0.0001$, respectively). Parasitoid female ratio (female:total) was also significantly affected by PGR ($\chi_3^2 = 63.52$; $P < 0.0001$), resulting in highly male-biased populations on paclobutrazol and uniconazole treated plants and female-biased populations on flurprimidol and the untreated control plants (Fig. 5).

4. Discussion

In this study we assessed how four of the most commonly used PGRs affect *M. persicae* abundance and suppression, and *A. colemani* fitness. Previous studies showed that PGRs can decrease herbivore reproduction rate (Visscher, 1980; Kaur and Rup, 2002), increase their development time (Coffelt and Schultz, 1988), and decrease their survival (Coffelt et al., 1993). Despite the generally negative effects of PGRs on herbivores, only one study has documented the effect of a PGR on parasitoid development and reproduction (Uçkan et al., 2008). Prado and Frank (2013) found that paclobutrazol reduces biological control of *M. persicae* by increasing plant architectural complexity. However, they did not consider physiological effects on parasitoid life history traits as a mechanism for this reduced aphid suppression. Based on these previous studies, our hypothesis was that PGRs would reduce aphid abundance and suppression by *A. colemani*. We also predicted that PGR treated plants would have indirect negative effects on parasitoids via their aphid hosts. We did not find any significant effect of PGRs on aphid abundance or suppression but three of the four PGRs tested had negative effects on at least one aspect of *A. colemani* life history.

To understand the ways PGRs may affect natural enemy efficacy, we began by looking at the percentage of adult parasitoids successfully emerging from their hosts. We found a significantly lower percentage of adult parasitoids emerging from ancymidol, flurprimidol, and uniconazole treated plants than from paclobutrazol treated plants. While about 56% of adult parasitoids emerged from mummies on flurprimidol and uniconazole treated plants, 0% of the parasitoids successfully emerged in the ancymidol treatment. Several factors are known to affect *A. colemani* emergence, among which are temperature, desiccation, and declining parasitoid energy reserves (Colinet et al., 2006). As all mummies were placed in the same sized vials and in the same environmental chamber during emergence, we do not believe that temperature or humidity could have affected parasitoid emergence between treatments. Uçkan et al. (2008) suggested that changes in host hormones caused by the ingestion of the PGR, gibberellic acid, reduced host survival and increased its developmental abnormalities, potentially affecting parasitoids. We do not know whether the PGRs in our study had a toxic effect on parasitoids, or reduced the nutritional quality of their hosts but both of these have been shown to reduce parasitoid survivorship to adulthood (Slansky, 1986; Thorpe and Barbosa, 1986; Holton et al., 2003). What is clear is that if the 0% emergence observed in the ancymidol treatment were to continue, the *A. colemani* population on these plants would eventually be reduced to zero, and along with it, aphid suppression. Though we did not observe reduced aphid suppression in this study, we suspect that prolonging the experiment for a few more parasitoid generations would have intensified the population-level effects of the PGRs on both aphids and parasitoids, resulting in more distinct differences in aphid abundances.

As only female parasitoids can parasitize aphids, the sex ratio of the emerged parasitoids can greatly affect aphid suppression (Hagen and van den Bosch, 1968). For instance, although the greatest number of parasitoids emerged from the paclobutrazol treated plants, only 6% of these parasitoids were female and able to contribute to biological control of *M. persicae*. The reduced female ratio observed for paclobutrazol and uniconazole reared parasitoids could be due to reduced host quality. Resource limitation during parasitoid larval development has been shown to cause female larval mortality, resulting in a higher male survivorship, and consequently a male-biased sex ratio (Jarosik et al., 2003). Aphid hosts may have been resource limited either because of direct toxicity effects (Uçkan et al., 2008) or because of the reduced nutritional

value of the uniconazole and paclobutrazol treated plants (Fox et al., 1990, 1996; Rademacher, 2000).

While a high female ratio is important for effective biological control (Heimpel and Lundgren, 2000), not all females perform equally. In general, large parasitoids have higher fitness and have higher host searching efficiency than small parasitoids (Visser, 1994). Large parasitoids have more fat reserves than small parasitoids, allowing them to disperse farther and to survive longer when food is unavailable (Eijs and van Alphen, 1999). Parasitoid size is also positively correlated with egg number (Heimpel and Rosenheim, 1998; Eijs and van Alphen, 1999; Sampaio et al., 2008), meaning that smaller parasitoids may become egg-limited and consequently less effective biological control agents earlier in their life (Rosenheim and Rosen, 1991; Heimpel and Rosenheim, 1998). In our study, we found that female parasitoids reared on paclobutrazol treated plants were significantly smaller than parasitoids from the other treatments. As with female ratio, and parasitoid percent emergence, we can only hypothesize how parasitoid size was affected by the PGR. For instance, it is possible that parasitoid size was reduced via a reduced host size caused by toxic effects of paclobutrazol (Honeyborne, 1969). It is also possible that direct PGR toxicity affected parasitoid development, reducing its body size (Couty et al., 2001).

Whatever the mechanism may be, of the four PGRs tested, ancymidol resulted in parasitoids with the lowest fitness since none completed development. Of the PGRs that resulted in adult parasitoids, paclobutrazol had the most negative effects on parasitoid fitness. It is evident from this study that PGRs can have strong, but variable effects on parasitoid life history traits. However, further research is needed to uncover the mechanism through which these effects occur, and their long-term effects on biological control. This work highlights how a common horticultural practice can contribute to the unpredictable outcome of biological control.

Acknowledgments

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