Biological Control 65 (2013) 184–189

Contents lists available at SciVerse ScienceDirect

Biological Control

journal homepage: www.elsevier.com/locate/ybcon

Compact plants reduce biological control of *Myzus persicae* by *Aphidius colemani*

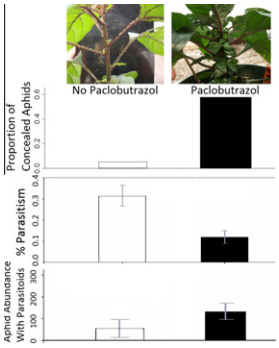
Sara Guiti Prado *, Steven D. Frank

Department of Entomology, North Carolina State University, Campus Box 7613, Raleigh, NC 27695-7613, USA

HIGHLIGHTS

- Paclobutrazol-treated plants had a higher proportion of concealed feeding locations.
- Proportionally more aphids fed in concealed locations when parasitoids were present.
- We observed lower aphid suppression by *Aphidius colemani* on paclobutrazol treated plants.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 13 June 2012
Accepted 3 March 2013
Available online 14 March 2013

Keywords:
Foraging efficiency
Paclobutrazol
Plant growth regulator
Prey behavior

ABSTRACT

Common horticultural practices, such as the use of plant growth regulators, may negatively influence the outcome of biological control programs. Plant growth regulators are applied to many ornamental and agricultural crops and can result in compact plants that have more branches and are bushier than untreated plants. Since plant architectural complexity can have strong effects on natural enemy foraging efficiency and pest suppression, our hypothesis was that the use of plant growth regulators would reduce aphid suppression by the parasitoid *Aphidius colemani*. In this study we investigated how the plant growth regulator paclobutrazol and the parasitic wasp *A. colemani* interact to affect the abundance and behavior of *Myzus persicae*. We found that paclobutrazol alone reduced aphid abundance compared to untreated plants. However, when parasitoids were present, paclobutrazol and associated changes in plant architecture reduced parasitism and increased aphid abundance compared to untreated plants. A likely mechanism for this result is that significantly more *M. persicae* fed in concealed locations on paclobutrazol-treated plants than on untreated plants. This study demonstrates that paclobutrazol reduced the efficacy of biological control by *A. colemani* and suggests that plant growth regulators could also affect biological control of other organisms.

1. Introduction

Horticultural practices that alter plant architecture and quality may have unexpected consequences on the efficacy of biological control programs. Plant growth regulators are non-nutrient, organic compounds used in ornamental plant production to modify plant growth and/or development (Basra, 2000). Plant growth regulators 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, plant growth regulators may alter arthropod behavior and development (Singer and Smith, 1976; Andow and Prokrym, 1990; Kaur and Rup, 2002). Although plant growth regulators are widely used in horticulture and agriculture, very little is known about their effects on herbivores, natural enemies, and their interactions.

Plant growth regulators could affect herbivore abundance directly via herbivore biology or indirectly via their parasitoids. For example, high doses of chlormequat chloride adversely affect

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

1049-9644/$ - see front matter © 2013 Elsevier Inc. All rights reserved.
http://dx.doi.org/10.1016/j.biocontrol.2013.03.004

aphid reproduction (Singer and Smith, 1976). Similarly, gibberellic acid significantly reduces melon fruit fly (*Bactrocera cucurbitae* Coquillett) fecundity and fertility (Kaur and Rup, 2002). Thus, plant growth regulators could reduce pest herbivore population growth making biological control more effective. Alternatively, plant growth regulators may affect parasitoid fitness or abundance via the resources the chemically-altered plants provide for the parasitoid hosts. Uçkan et al. (2008) found that when herbivore hosts were fed high doses of gibberellic acid, endoparasitoid emergence time increased and longevity decreased. Hence, the quality of the plant consumed by the herbivore host can negatively affect parasitoid fitness by compromising the resources available during its development (Ode et al., 2005). Unfortunately, few studies have documented the effects of plant growth regulators on herbivores (Robinson, 1960; Singer and Smith, 1976; Kaur and Rup, 2002) and even less have determined their effects on parasitoid fitness. Therefore, predicting the impact of plant growth regulator induced changes in plant quality on biological control programs is difficult.

Plant architectural changes caused by plant growth regulators could also affect aphid abundance through changes in parasitoid foraging behaviors. Increasing plant architectural complexity can reduce parasitoid foraging efficiency and suppression of herbivores (Andow and Prokrym, 1990). Traits that increase plant complexity and are relevant to parasitoid foraging efficiency include the size, heterogeneity, and connectivity of plant structures (Cloyd and Sadof, 2000; Gingras, 2003) and leaf texture (Andow and Prokrym, 1990; Lukianchuk and Smith, 1997). These traits can reduce parasitoid foraging efficiency by increasing searching time or by otherwise decreasing the odds of encountering prey (Price et al., 1980). For instance, the attack rate of the citrus mealy bug parasitoid was negatively correlated with plant size, height, leaf number, leaf surface area, and branch number (Cloyd and Sadof, 2000). In addition, complex plants can provide herbivores with concealed feeding locations, thus decreasing biological control efficacy (Gardner and Dixon, 1985; Stadler and Volkl, 1991; Clark and Messina, 1998). Understanding the ways in which plant architecture can affect pest suppression by parasitoids will improve our ability to implement successful 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 (Basra, 2000). Biological control of *M. persicae* in greenhouse crops often entails releasing *Aphidius colemani* Viereck (Hymenoptera: Braconidae) (van Steenis, 1995; Rabasse and van Steenis, 1999), a solitary, koinobiont, endoparasitoid (Starý, 1975). *A. colemani* development is closely tied to its hosts' development, making it vulnerable when its host feeds on toxic or low quality plant material (Kalule and Wright, 2005). In addition, foraging efficiency and pest suppression by *A. colemani* and other parasitoids can be influenced by plant structure and aphid distribution (Stadler and Volkl, 1991). Therefore we feel this herbivore-parasitoid system is an ecologically and economically relevant system in which to determine how plant growth regulators and parasitoids interact to affect aphid abundance. Specifically our objectives were to (1) Determine the effect of plant architecture on aphid feeding location; (2) Determine how paclobutrazol and *A. colemani* affect aphid abundance; and (3) Determine how plant architecture and *A. colemani* affect aphid distribution and parasitism on exposed and concealed plant parts. To achieve our objectives, we compared *M. persicae* abundance and distribution on pepper plants (*Capsicum annuum* 'Black Pearl') treated with paclobutrazol to untreated plants in the presence and absence of *A. colemani*. Our research is the first to examine the direct and indirect effects of plant growth regulators on pest abundance and should provide important management information to improve greenhouse plant production.

2. Methods

2.1. Study system

For all experiments, *A. colemani* were purchased from Koppert Biological Systems (Howell, MI). Upon receipt, the mummies were placed in a 61 × 61 cm cage where the parasitoids could emerge and mate. The cage was placed on a counter in a laboratory with an average temperature of 24 °C. During that time, they were provided with a 25% sucrose-water solution. Only mated, female parasitoids were selected for the experiments in order to ensure that both male and female offspring could be produced. All parasitoids were used less than 72 h after emergence. We used *M. persicae* from a laboratory colony that was started from parasitoid-free, field-collected aphids. The aphids were reared on pepper plants for over two months (*Capsicum annuum* 'Black Pearl') in an incubator at 25 °C and 70–80% RH.

Black Pearl pepper plants were obtained from Raker and Sons (Litchfield, MI) as plugs (128 plugs <7 cm in height). Plants were inspected upon receipt to confirm that they were aphid- and parasitoid- free. Sixty plants were repotted into 15.2 cm-diameter pots filled with Fafard 2P soil mix (Agawam, MA) with 8.86 g of Scotts Osmocote (N-P-K: 14–14-14) fertilizer (Marysville, OH) per pot. When plants were 2.5 weeks old, paclobutrazol (Bonzi®, Syngenta Crop Protection, Greensboro, NC) was applied as a drench to 30 plants with 1.5 mg a.i. given to each pot through a 118.3 ml solution. Plants were 4 weeks old at the start of each experiment.

2.2. Effect of plant architecture on aphid feeding locations

To determine how plant growth regulator-induced changes in plant architecture affect aphid concealment, we compared the proportion of aphids feeding in concealed locations on paclobutrazol-treated and untreated pepper plants. We performed 18 replicates per treatment, in which 10 *M. persicae* of random instar were placed on the soil 1–2 cm from the pepper plant's stem. Aphids were allowed to climb up and establish feeding sites for one hour after which we searched the plants to determine if the aphids were feeding in 'concealed' or 'exposed' locations. Aphids were categorized as 'exposed' if they were surrounded on fewer than three sides by plant structures, such as leaves or stems, less than 1 cm away. Aphids were categorized as 'concealed' if they were surrounded on three or more sides by plant structures less than 1 cm away. Other studies have found that herbivores hidden between plant structures are parasitized less successfully than herbivores that are more exposed (Gardner and Dixon, 1985). A chi-squared test was performed to determine if the proportion of aphids feeding in concealed locations was different between treated and untreated plants, using R version 2.13.1 (R Development Core Team, 2010).

2.3. Effect of paclobutrazol and A. colemani on aphid abundance

To determine how paclobutrazol affects aphid population growth and parasitism by *A. colemani*, we conducted a 2 × 2 factorial experiment that crossed two paclobutrazol treatments ('untreated' or 'treated') with two parasitoid treatments ('absent' or 'present'). Every treatment combination was replicated 12 times for a total of 48 pepper plants. The plants were placed on a greenhouse bench and randomly assigned to one of the four treatment combination. Greenhouse temperatures were maintained at an average of 75.5 ± 0.2 °C for duration of the experiment. Every pot

Fig. 1. Untreated plant (left) and treated plant (right). The stem (dashed line) is exposed for the untreated plant but protected for the treated plants. The buds (solid line) on both plants were considered exposed.

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 by randomly placing 10 *M. persicae* of random instars on the plants' leaves. All *M. persicae* were randomly selected from highly infested leaves from the laboratory colony. After 24 h, one mated female *A. colemani* was released into cages assigned to the parasitoid 'present' treatments. In accordance with the recommended release rates for light infestations, only one parasitoid was released.

One week after parasitoids were released, we inspected plants to record aphid and mummy abundance and distribution. Mummy abundance was used as a measurement of aphid parasitism. Along with a complete count of all aphids and mummies on the plant, aphids and mummies were counted separately on the buds and the stem. This process was repeated five times, every 72 h, following the first data-collection day. Based on findings from the first experiment, we categorized the buds of both treated and untreated plants, and the stems of untreated plants as 'exposed'. The stems of treated plants were categorized as 'concealed' due to the high number and the proximity of plant parts or leaves concealing the stem (Fig. 1). In 10 of the plants (four from treated, six from untreated) the parasitoid died before parasitizing any aphids so these were removed from the analysis.

A two-way repeated measures ANOVA was used to determine how paclobutrazol, parasitoids, and their interaction affected total aphid abundance, mummy abundance, and percent parasitism. Percent parasitism was calculated by dividing the total number of parasitized aphids (mummies) by the total number of aphids and mummies. The total number of aphids were $\log(x+1)$ transformed. As mummy abundance and percent parasitism could not be normalized, a nonparametric factorial repeated measures analysis was performed using the package nparLD (Noguchi et al., 2012) to determine how time, paclobutrazol, and their interaction affected total mummy abundance, and percent parasitism. To determine how paclobutrazol and *A. colemani* affect aphid distribution and parasitism, a repeated measures ANOVA was performed for both aphid abundance on stems and buds over time. All proportions including the percent parasitism were arcsine square root transformed, to correct non-normal distribution.

The nonparametric factorial repeated measures analysis was performed using R version 2.13.1 (R Development Core Team, 2010). All other statistical analyses were performed in SAS version 9.2 (SAS Institute Inc., 2010).

2.4. Effect of paclobutrazol on plant height and biomass

Plant height and dry biomass were measured to determine how treated and untreated plants varied in architecture. Plant height was measured in centimeters, from the base of the stem to the top of the plant, at the beginning and end of the experiment. To determine plant biomass, all plants were cut at soil level, washed in soapy water to remove aphids and mummies, rinsed, placed in paper bags, and dried in an oven for 30 h at 69 °C. Once dried, all plants were weighed to obtain their dry mass.

A two-way ANOVA was used to determine how paclobutrazol, parasitoids, and their interaction affected final plant dry biomass. *T*-tests were used to compare plant height before and after the experiment for paclobutrazol-treated and untreated plants. In addition to providing information on plant architecture, plant biomass was used to determine the effect of plant size on aphid abundance with and without parasitoids. This step was taken to see if

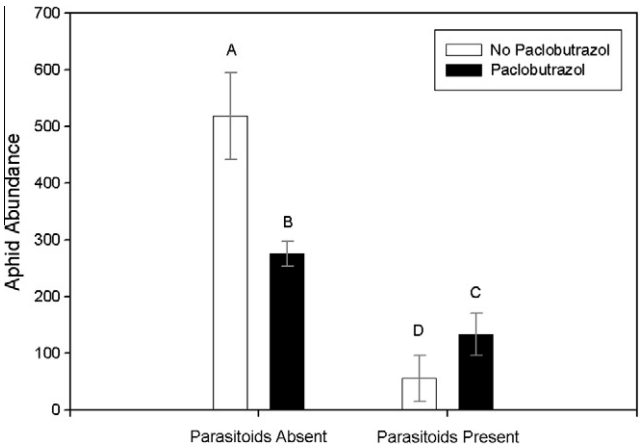


Fig. 2. Mean (± SE) number of aphids on caged pepper plants during a three week experiment in which plants were untreated or treated with paclobutrazol and had parasitoids absent or present within the cages. Means with different letters are significantly different at the $P < 0.05$ level.

the smaller, paclobutrazol-treated plants limited aphid population growthf. The final aphid abundances were divided by the dry plant biomass and analyzed using an ANOVA. All statistical analyses were performed in SAS version 9.2 (SAS Institute Inc., 2010).

3. Results

3.1. Effect of plant architecture on aphid feeding locations

A chi-squared test showed that significantly more aphids were feeding in 'concealed' locations on the treated plants than on the untreated plants $\chi^2_1 = 43.85$; $P < 0.0001$). Only 5.07% of the 180 aphids placed on the untreated plants were concealed, while 57.69% of aphids were concealed on the more compact, paclobutrazol-treated plants.

3.2. Effect of paclobutrazol and A. colemani on aphid abundance

There was a significant interaction between parasitoid presence and paclobutrazol on aphid abundance, such that aphids were less abundant on paclobutrazol-treated plants than untreated plants when no parasitoids were present, but more abundant on treated plants when parasitoids were present ($F_{1,170} = 29.58$; $P < 0.0001$) (Fig. 2). Parasitoids reduced aphid abundance by 93% on untreated plants but only reduced aphid abundance by 52% on treated plants.

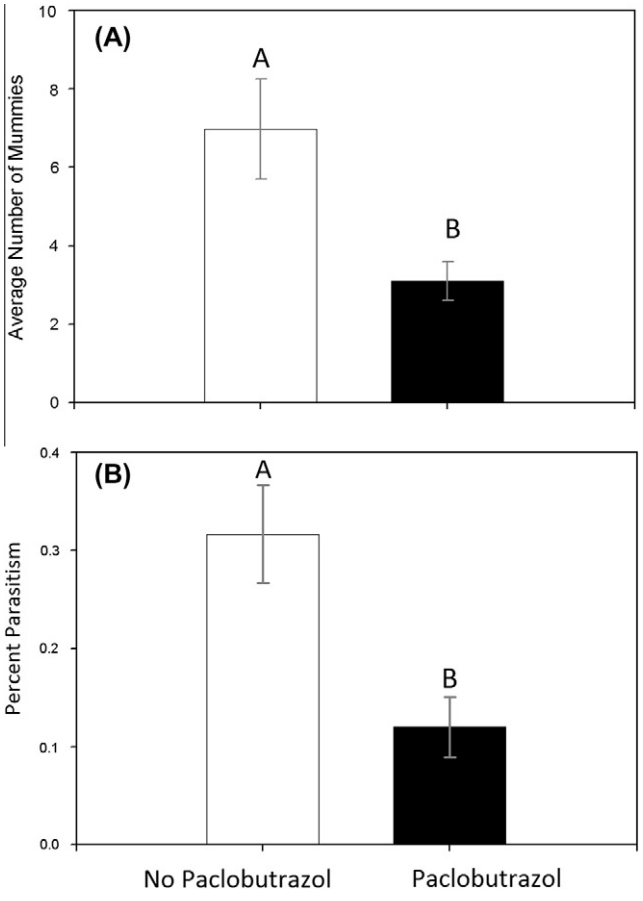


Fig. 3. (A) Mean (± SE) number of aphid mummies on caged pepper plants with parasitoids during a three week experiment in which plants were untreated or treated with paclobutrazol. Means with different letters are significantly different at the $P < 0.05$ level. (B) Percent parasitism (mummies/aphids) (± SE) observed on caged pepper plants during a three week experiment in which plants were untreated or treated with paclobutrazol and had parasitoids within the cages. Means with different letters are significantly different at the $P < 0.05$ level.

There was also a significant interaction between parasitoid presence and time ($F_{4,170} = 2.60$; $P = 0.0378$) wherein aphid abundance declined over time when parasitoids were present, but increased when they were absent. The main effects of time and parasitoids were also significant ($F_{4,170} = 37.90$; $P < 0.0001$; $F_{1,170} = 199.04$; $P < 0.0001$, respectively), however there was no significant main effect of paclobutrazol ($F_{1,170} = 1.44$; $P = 0.2311$). The interaction between time, parasitoid presence, and paclobutrazol was not significant ($F_{4,170} = 0.43$; $P = 0.7874$).

There were significant main effects of paclobutrazol and time on mummy abundance ($F_{1.00,\infty} = 4.53$; $P = 0.0334$; $F_{2.13,\infty} = 7.11$; $P < 0.0001$; respectively) wherein mummy abundance was 66% lower on treated plants than on untreated plants (Fig. 3A). There was no significant interaction between paclobutrazol and time on mummy abundance ($F_{2.13,\infty} = 0.73$; $P = 0.4917$). There was a significant main effect of paclobutrazol on percent parasitism ($F_{1,\infty} = 4.98$; $P = 0.025$) such that the percent parasitism on untreated plants was 2.5 times greater than on treated plants (Fig. 3B). There was no significant main effect of time on percent parasitism nor was there a significant interaction between time and paclobutrazol ($F_{1.83,\infty} = 1.84$; $P = 0.1625$; $F_{1.83,\infty} = 0.97$; $P = 0.3740$, respectively).

There was a significant interaction between parasitoid presence and paclobutrazol on the proportion of aphids feeding on buds, an exposed location, such that parasitoids reduced the proportion of aphids feeding on the buds of untreated plants by 77% but it was only reduced by 34% on treated plants ($F_{1,169} = 19.94$; $P < 0.0001$) (Fig. 4). The main effects of parasitoid presence, paclobutrazol, and time were also significant ($F_{1,169} = 48.02$; $P < 0.0001$; $F_{1,169} = 10.78$; $P = 0.0012$; $F_{4,169} = 2.63$; $P = 0.0360$, respectively). The interaction between time and parasitoid presence, and between time and paclobutrazol did not have a significant effect on the proportion of aphids feeding on the buds ($F_{4,169} = 1.06$; $P = 0.3777$, $F_{4,169} = 0.94$; $P = 0.4443$, respectively). The three-way interaction between parasitoid presence, paclobutrazol and time was also not significant ($F_{4,169} = 0.72$; $P = 0.5804$).

There was a significant interaction between time, parasitoid presence, and paclobutrazol on the proportion of aphids feeding on the stem ($F_{4,169} = 2.42$; $P = 0.0504$) which is considered concealed in treated plants but exposed in untreated plants (Fig. 5). Parasitoid presence significantly decreased the proportion of aphids feeding on the stems of untreated plants but not of treated plants and this effect became stronger over time. There was a significant interaction between parasitoid presence and paclobutrazol

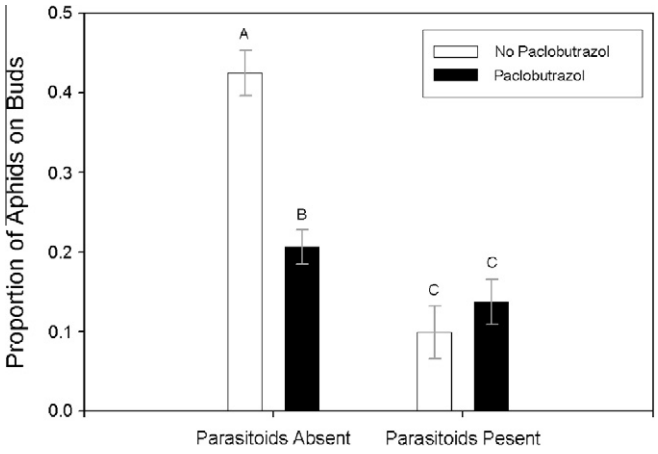


Fig. 4. Proportion of aphids observed feeding on the exposed buds (± SE) of caged pepper plants during a three week experiment in which plants were untreated or treated with paclobutrazol and had parasitoids absent or present within the cages. Means with different letters are significantly different at the $P < 0.05$ level.

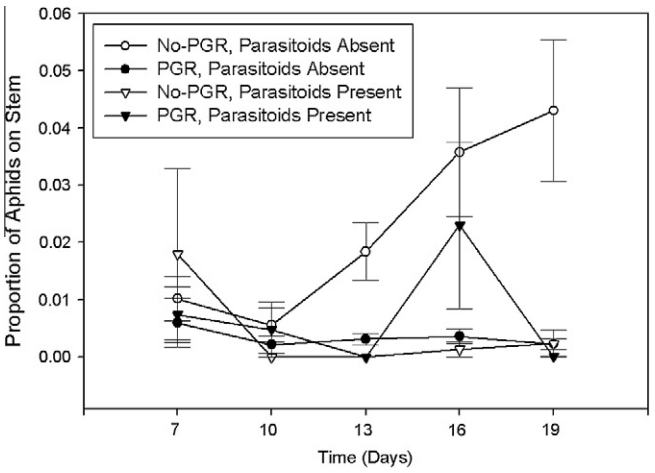


Fig. 5. Proportion of aphids observed feeding on the stems (± SE) of caged pepper plants during a three week experiment in which plants were untreated or treated with paclobutrazol and had parasitoids absent or present within the cages. Aphids feeding on paclobutrazol-treated plant stems were considered concealed, and those feeding on paclobutrazol-untreated plant stems were considered exposed.

on the proportion of aphids feeding on the stem ($F_{1,169} = 17.92$; $P < 0.0001$) and a significant interaction between parasitoid presence and time ($F_{4,169} = 3.25$; $P = 0.0135$). There was no significant interaction between time and treatment on the proportion of aphids feeding on the stems ($F_{4,169} = 1.66$; $P = 0.1615$). The main effects of effect of parasitoid presence, paclobutrazol and time were also significant ($F_{1,169} = 18.29$; $P < 0.0001$; $F_{1,169} = 10.91$; $P = 0.0012$; $F_{4,169} = 3.05$; $P = 0.0186$, respectively).

3.3. Effect of paclobutrazol on plant height and biomass

The average height of the untreated plants (21.74 ± 1.067) was significantly greater than that of the treated (11.07 ± 0.38) plants at the beginning ($t_{20} = 9.01$; $P < 0.0001$) and at the end (33.92 ± 2.17; 12.71 ± 0.58, respectively) of the experiment ($t_{20} = 9.21$; $P < 0.0001$). Plant biomass was also significantly greater for the untreated plants (4.45 ± 0.56) than it was for the treated plants (1.69 ± 0.21) ($F_{1,34} = 19.91$; $P < 0.001$). Parasitoid presence did not significantly affect plant biomass ($F_{1,34} = 0.12$; $P = 0.7363$) nor was there a significant interaction ($F_{1,34} = 0.00$; $P = 0.9698$).

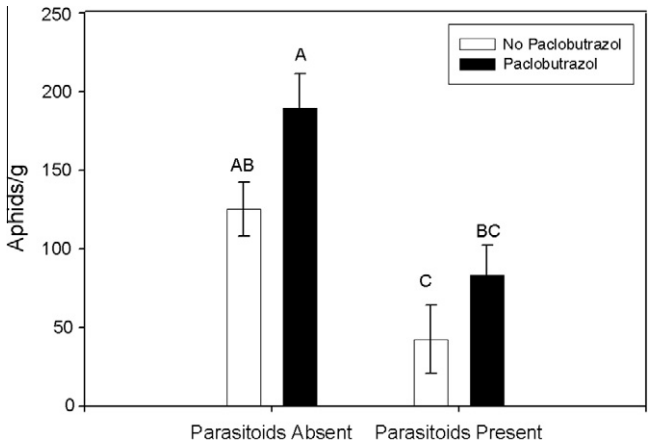


Fig. 6. Proportion of aphids/gram of biomass (± SE) on caged pepper plants during a three week experiment in which plants were untreated or treated with paclobutrazol and had parasitoids absent or present within the cages. Means with different letters are significantly different at the $P < 0.05$ level.

Aphid abundance was significantly affected by plant dry biomass and parasitoid presence, as the number of aphids per gram of dry biomass was significantly lower when parasitoids were present than when they were absent ($F_{1,34} = 14.36$; $P = 0.0006$) (Fig. 6). Paclobutrazol had a marginally significant effect on the number of aphids per gram ($F_{1,34} = 3.81$; $P = 0.0591$), wherein a greater number of aphids per gram was observed on treated plants than on untreated ones. There was no significant interaction between parasitoids and paclobutrazol on the number of aphids per gram ($F_{1,34} = 0.00$; $P = 0.9823$).

4. Discussion

This study assessed how paclobutrazol-induced changes in plant architecture affect *M. persicae* suppression by *A. colemani*. Previous studies have investigated the effect of plant architecture on pest suppression by natural enemies (Gardner and Dixon, 1985; Andow and Prokrym, 1990; Randlkofer et al., 2010), however, none have done so using the same plant species. For example, some have compared the effects of plant architecture using artificial plants made from paper or plastic (Andow and Prokrym, 1990; Lukianchuk and Smith, 1997; Gingras et al., 2002). Others have used two or more cultivars with different architectural features (Cloyd and Sadof, 2000; Gingras, 2003) or manipulated plant structures (Gontijo et al., 2010; Randlkofer et al., 2010). Our novel approach was to use plant growth regulators to manipulate the architecture of a single pepper plant species. We found that plant growth regulators, which are frequently used in agriculture and horticulture, can significantly reduce aphid suppression by parasitoids. Our findings suggest that aphids may have been more concealed from parasitism due to the more compact plant structure.

We explicitly tested the combined effects of paclobutrazol and parasitoids on aphid abundance and found that paclobutrazol-treated plants had about half as many aphids as untreated plants when parasitoids were absent. Despite this, parasitoids reduced aphid abundance to the lowest level on the untreated plants indicating reduced parasitoid efficacy on paclobutrazol-treated plants. We believe a primary mechanism for this is that aphids were more likely to be concealed from parasitoids on the smaller paclobutrazol-treated plants, than on untreated plants. Although we did not test whether aphids categorized as 'concealed' were in fact parasitized less often, other studies have found that herbivore susceptibility to parasitism is reduced when feeding within tight plant structures (Gardner and Dixon, 1985; Clark and Messina, 1998). For example, Gardner and Dixon (1985) found that aphids feeding on wheat ears were parasitized at a lower rate than those feeding on the blades, and hypothesized that aphids feeding in the tight spaces between the grains were less accessible to parasitoids. Likewise, boll weevil larvae concealed beneath wide cotton bracts are parasitized eight times less than those beneath narrow 'frego' type bracts that leave the larvae more exposed (McGovern and Cross, 1976). As in these examples, in our caged experiment we observed fewer parasitized aphids on the treated plants than on the untreated ones, suggesting *A. colemani* had reduced access to *M. persicae*.

In addition to feeding in concealed locations, aphids have a wide range of escape responses with which they can defend themselves from natural enemy attacks (Dixon, 1958). Among these responses is predator avoidance wherein an aphid can walk away from a threat (Dixon, 1958). In our study, we observed a lower proportion of aphids feeding on the exposed plant parts when parasitoids were present compared to when they were absent. We suspect that the threat of parasitism when foraging on exposed locations, such as the buds or stems, caused aphids to move to more concealed locations. This is consistent with findings by Costa-

magna and Landis (2011), who also observed a shift in aphid within-plant distribution from high predation risk to low predation risk locations. We believe that more aphids were able to move from exposed to concealed locations on the treated plants than on the untreated plants. Thus, aphid suppression on treated plants was likely reduced by the combination of aphid escape behavior and the greater probability of feeding in refuges.

When no parasitoids were present, aphid abundance was close to 2.5 times lower on treated than untreated plants. This is consistent with previous findings that plant growth regulators reduced herbivore reproduction or population growth (Honeyborne, 1969; Coffelt and Schultz, 1988) and may suggest that plant growth regulators reduced plant quality for aphids. However, based on our assessment of plant dry biomass and height, we suggest that paclobutrazol reduced aphid abundance by reducing the carrying capacity of the pepper plants, rather than by decreasing plant quality per se. The smaller paclobutrazol-treated plants likely limited aphid population growth (Gadgil and Solbrig, 1972; Yano, 2006). Our finding that the number of aphids per gram did not differ between the treated and untreated plants when parasitoids were absent corroborates our hypothesis. Interestingly, there was no significant difference between the number of aphids per gram on the treated plants when parasitoids were present and the number of aphids per gram on the untreated plants when parasitoids were absent. The smaller plant size played an important role in reducing aphid abundance when parasitoids were absent, but the compact architecture of these smaller plants reduced *A. colemani* efficacy at suppressing *M. persicae*.

In this study parasitoid and aphid movement was restricted to one caged plant, so future studies should investigate the effects of plant growth regulators on pest suppression at larger scales. Nevertheless, we demonstrated that one of the most commonly used types of agricultural chemical, plant growth regulators, can reduce the efficacy of biological control by *A. colemani*. To compensate for this reduced efficacy, growers may need to increase the number or frequency of natural enemies released or integrate chemical and biological control (e.g. Tremblay et al. 2008) to achieve satisfactory pest suppression. Our study sheds light on the unexpected effects agricultural practices may have on the outcome of biological control programs.

Acknowledgements

We thank George Kennedy, Fred Gould, Emily Meineke, and Adam Terando for useful discussions and comments on previous versions of this manuscript. We also thank Raker and Sons for donating Black Pearl pepper plants for this experiment. We thank Brian Whipker and Ingrid McCall for providing us with information about paclobutrazol. This work was supported by the NCSU Department of Entomology, a USDA SARE Graduate Student grant (GS11-099) to SGP and SDF, and grants to SDF from the American Floral Endowment and Fred C. Gloeckner Foundation.

References

Andow, D.A., Prokrym, D.R., 1990. Plant structural complexity and host-finding by a parasitoid. Oecologia 82, 162–165.

Baker, 1994. Insect and related pests of flowers and foliage plants: some important, common, and potential pests in the southeastern United States, revised. ed. North Carolina Cooperative Extension Service.

Basra, A.S., 2000. Plant Growth Regulators in Agriculture and Horticulture: Their Role and Commercial Uses. Psychology Press.

Clark, T.L., Messina, F.J., 1998. Plant architecture and the foraging success of ladybird beetles attacking the Russian wheat aphid. Entomol. Exp. Appl. 86, 153–161.

Cloyd, R.A., Sadof, C.S., 2000. Effects of plant architecture on the attack rate of *Leptomastix dactylopii* (Hymenoptera: Encyrtidae), a parasitoid of the citrus mealybug (Homoptera Pseudococcidae). Popul. Ecol. 29, 535–541.

Coffelt, M.A., Schultz, P.B., 1988. Influence of plant growth regulators on the development of the azalea lace bug (Hemiptera: Tingidae). J. Econ. Entomol. 81, 290–292.

Costamagna, A.C., Landis, D.A., 2011. Lack of strong refuges allows top-down control of soybean aphid by generalist natural enemies. Biol. Control 57, 184–192.

Dixon, A.F.G., 1958. The escape responses shown by certain aphids to the presence of the coccinellid *Adalia Decempunctata*. Trans. Royal Entomol. Soc. Lond. 110, 319–334.

Gadgil, M., Solbrig, O.T., 1972. The concept of r- and K-selection: evidence from wildflowers and theoretical considerations. Am. Nat. 106, 14–31.

Gardner, S.M., Dixon, A.F.G., 1985. Plant structure and the foraging success of *Aphidius rhopalosiphi* (Hymenoptera: Aphidiidae). Ecol. Entomol. 10, 171–179.

Gingras, D., 2003. Effect of plant structure on host finding capacity of lepidopterous pests of crucifers by two *Trichogramma* parasitoids. Biol. Control 27, 25–31.

Gingras, D., Dutilleul, P., Boivin, G., 2002. Modeling the impact of plant structure on host-finding behavior of parasitoids. Oecologia 130, 396–402.

Gontijo, L.M., Margolies, D.C., Nechols, J.R., Cloyd, R.A., 2010. Plant architecture, prey distribution and predator release strategy interact to affect foraging efficiency of the predatory mite *Phytoseiulus persimilis* (Acari: Phytoseiidae) on cucumber. Biol. Control 53, 136–141.

Heathcote, G.D., 1962. Suitability of some plant hosts for the development of the peach-potato aphid, *Myzus persicae*. Entomol. Exp. Appl. 5, 114–118.

Honeyborne, C.H.B., 1969. Performance of *Aphis fabae* and *Brevicoryne brassicae* on plants treated with growth regulators. J. Sci. Food Agric. 20, 388–390.

Kalule, T., Wright, D.J., 2005. Effect of cultivars with varying levels of resistance to aphids on development time, sex ratio, size and longevity of the parasitoid *Aphidius colemani*. BioControl 50, 235–246.

Kaur, R., Rup, P.J., 2002. Evaluation of regulatory influence of four plant growth regulators on the reproductive potential and longevity of melon fruit fly (*Bactrocera cucurbitae*). Phytoparasitica 30, 224–230.

Lukianchuk, J.L., Smith, S.M., 1997. Influence of plant structural complexity on the foraging success of Trichogramma minutum: a comparison of search on artificial and foliage models. Ecology 84, 221–228.

McGovern, W.L., Cross, W.H., 1976. Affects of two cotton varieties on levels of boll weevil parasitism [Col.: Curculionidae]. Entomophaga 21, 123–125.

Noguchi, K., Latif, M., Thangavelu, K., Konietschke, F., Gel, Y.R., Brunner, E., 2012. Nonparametric analysis of longitudinal data in factorial experiments.

Ode, P.J., Hopper, K.R., Coll, M., 2005. Oviposition vs. offspring fitness in *Aphidius colemani* parasitizing different aphid species. Entomol. Exp. Appl. 115, 303–310.

Price, P.W., Bouton, C.E., Gross, P., Mcpheron, B.A., Thompson, J.N., Weis, A.E., 1980. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annu. Rev. Ecol. Syst. 11, 41–65.

Rabasse, J., van Steenis, M., 1999. Biological control of aphids. In: Albajes, R., Gullino, M.L., Van Lenteren, J.C., Elad, Y. (Eds.), Integrated Pest and Disease Management in Greenhouse Crops. Kluwer Academic Publishers, Netherlands, pp. 235–243.

Randlkofer, B., Obermaier, E., Casas, J., Meiners, T., 2010. Connectivity counts: disentangling effects of vegetation structure elements on the searching movement of a parasitoid. Ecol. Entomol. 35, 1–10.

Robinson, A.G., 1960. Effect of maleic hydrazide and other plant growth regulators on the pea aphid, *Acyrthosiphon pisum* (Harris), caged on broad bean, *Vicia faba* L. Can. Entomol. 92, 494–499.

Singer, M.C., Smith, B.D., 1976. Use of the plant growth regulator chlormequat chloride to control the aphid *Hyperomyzus lactucae* on black currants. Ann. Appl. Biol. 82, 407–414.

Stadler, B., Volkl, W., 1991. Interspecific larval competition between *Lysiphlebus testaceipes* and *Aphidius colemani* (Hym., Aphidiidae). J. Appl. Entomol. 111, 63–71.

Starý, P., 1975. Aphidius colemani Viereck: its taxonomy, distribution and host range (Hymenoptera, Aphidiidae). Acta Entomol. Bohemoslov. 72, 156–163.

Tremblay, E., Belanger, A., Brosseau, M., Boivin, G., 2008. Toxicity and sublethal effects of an insecticidal soap on *Aphidius colemani* (Hymenoptera: Braconidae). Pest Manag. Sci. 64, 249–254.

van Steenis, M.J., 1995. Evaluation of four aphidiine parasitoids for biological control of *Aphis gossypii*. Entomol. Exp. Appl. 75, 151–157.

Yano, E., 2006. Ecological considerations for biological control of aphids in protected culture. Popul. Ecol. 48, 333–339.