UNIVERSITY OF CALIFORNIA, SAN DIEGO

Indirect effects of Argentine ant and honeydew-producing insect mutualisms on California red scale in a citrus agroecosystem

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in

Biology

by

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ABSTRACT OF THE THESIS

Indirect effects of Argentine ant and honeydew-producing insect mutualisms on California red scale in a citrus agroecosystem

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Michelle Cara Kizner

Master of Science in Biology

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Professor David A. Holway, Chair

In San Diego County, a major economic impact of the Argentine ant occurs in citrus agroecosystems, where ants interfere with biological control of key insect pests, especially California red scale. Ant control is considered a critical component of integrated pest management (IPM) of several citrus pests, but IPM recommendations fail to consider quantitative relationships between levels of Argentine ant abundance and those of the economic pests. This serious gap in understanding impedes development of economically and environmentally sustainable strategies for the management of these agricultural pests. In this study, we manipulated key members of a citrus food web to discover direct and indirect effects of a commonly-occurring mutualism. We found that there was a positive correlation between ants and red scale and an increase in parasitism on red scale when ants were removed. We also found that when ants were not present, key honeydew-producing insect abundance was reduced, as well as the converse: when honeydew-producing insects were removed, ant abundance was depressed. This study provides mechanistic and quantitative information required to engineer improved IPM strategies. For example, farmers could save money and labor by only applying pest control measures when ants reach the threshold level at which they positively affect hemipteran pests. Such ecologically informed strategies would reduce management costs while minimizing negative environmental effects resulting from existing, chemically intensive management practices.

INTRODUCTION

Mutualisms, reciprocally beneficial interactions between two species, are recognized as important ecological relationships that not only influence the players involved but also affect species outside the partnerships formed by mutualists. Indirect effects resulting from mutualisms may affect community structure in ways that exceed direct interactions (Wimp and Whitham 2006). Our research aims to identify the indirect effects of food-for-protection mutualisms between the Argentine ant and honeydew-producing insects in a citrus agroecosystem. Specifically, we explore the positive relationship between the Argentine ant and the California red scale (*Aonidiella aurantii*), a common citrus pest.

Linepithema humile, more commonly known as the Argentine ant, is a widespread invasive species, having invaded every continent except Antarctica. In California, Argentine ants displace most native ant species in the areas which they invade, due to their aggressive nature (Vega 2001, Holway 1999). Argentine ants increase in number and invade more easily in wet areas, which in southern California, include riparian ecosystems, irrigated lands, and urban areas (Holway et al 2002, Menke et al 2003).

Argentine ants commonly form mutualistic relationships with honeydew-producing insects, including many agricultural pests. Ants can be found tending aphids on tomato (Coppler et al. 2007) and soybean plants (Herbert and Horn 2008), green coffee scale on coffee plants (Liere and Perfect 2008), and assorted honeydew-producing insects in citrus, especially citrus mealybug (*Planococcus citri*), brown soft scale (*Coccus hesperidum*), and woolly whitefly (*Aleurothrixus floccosus*). These hemipteran pests produce honeydew, a carbohydrate-rich resource composed of partially digested plant sap that is highly attractive to ants. In return for food, ants protect Hemiptera from their parasites and predators (Itioka and Inoue 1996, Way 1963, Flanders 1945, Daane et al. 2003). Ant activity also benefits honeydew-producing insects by preventing the growth of sooty mold, which can result from honeydew being left on the tree (Markin 1970). These reciprocally beneficial interactions, known as food-for-protection mutualisms may attract ants into canopies of trees where their presence could give rise to a variety of effects. For example, in citrus, the Argentine ant may inadvertently protect California red scale, a hemipteran pest of citrus that does not produce honeydew, from *Aphytis,* a generalist parasitoid (Samways 1981, Martinez-Ferrer et al. 2003, Bartlett 1961, James et al 1997, Debach 1951).

California red scale represents the leading problem in citrus since it was accidentally introduced from Asia in the 1860s. Red scale are sucking herbivores that feed on all above ground portions of citrus trees and cosmetically damage fruit and also cause leaf drop, twig die back and sometimes even tree death. Pesticide campaigns in the 1950s were initially effective at reducing scale densities but eventually led to scale evolving resistance to insecticides (Grafton-Cardwell and Vehrs 1995). Beginning in the late 1940s, parasitic wasps (especially *Aphytis*) were introduced from Eurasia for biological control of red scale. These wasps remain a key tool for control of red scale because they are not harmful to the environment or human health, do not promote the development of resistance in red scale, and are approved for use in conventional and organic orchards (Reeve and Murdoch 1986). Other enemies of red scale, which are less important than Aphytis to biological control, are the generalist parasitoid wasps *Encarsia and Comperiella,* which also prey upon other hemipera (Murdoch 2006). Ants receive no known benefit from red scale but appear to deter *Aphytis* and other scale parasites simply by being present on trees (Murdoch et al. 1995). In many citrus-growing regions, however, *Aphytis* efficacy appears to be compromised by the ubiquitous presence of the Argentine ant (Fig. 1 summarizes the citrus food web considered in this study and illustrates the direct and indirect effects of Argentine ant presence).

The citrus industry has a history of cyclical dependence on different pesticides, followed by the development of resistance in pest populations and increased spraying. For example, pyriproxyfen was registered in the late 1990s in response to the declining efficacy of commonly used pesticides in citrus. Pyriproxyfen is an insect growth regulator that also has detrimental effects on some populations of beneficial insects. Some red scale populations are now showing signs of resistance to pyriproxyfen (Rill et al. 2007, Grafton-Cardwell et al. 2006). In conventional orchards, the use of broad-spectrum pesticides continues, but in organic orchards, boric acid is the primary registered chemical for ant control (USDA NOP 2008). Although widely used, boric acid baiting and other management practices remain largely based on the general recommendation to "control ants" and the effect of reducing ant levels on infestation levels of red scale, honeydew-producing insects, and other citrus pests has not been quantitatively studied.

In this study, we focus on the ecological effects of ant-hemipteran mutualisms in citrus. In San Diego County, citrus orchards now cover 14,650 acres and in 2008 generated $64.5 million (SD DAWM 2008), with organic citrus sales topping $14 million in 2007 (CDFA 2007). The county has the largest organic farming community of any US county (SD DAWM 2008) and contains over one-third of California's organic citrus acreage (CDFA 2007). Despite the commercial importance of the citrus industry in California and particularly in San Diego, there is much to still be discovered about the ecology of the system, such as how strong a role honeydew-producers play in attracting ants into trees and to what extent ants affect the numbers of red scale and honeydew-producing Hemiptera. In this study, the above questions were explored by selective removal of putatively key players of the system (ants, red scale, and honeydew-producing insects) from selected trees within an organic lemon grove. Populations were then monitored for nine months post removal. Based on the interactions described above, we hypothesize that ant abundance will positively correlate with the populations of both red scale and honeydew-producers. In turn, honeydew-producers are expected to have a positive effect on ant populations and, as a result, red scale should increase with increasing numbers of honeydew-producing insects (Fig. 1).

MATERIALS AND METHODS

Study System

We selected an organic lemon grove in Valley Center, San Diego County, CA (*33.2958°N, 116.9491°W*) (Fig. 2a). This site lies at a 430 m elevation and is approximately 50 km from the coast. Like many citrus agroecosystems in southern California (Markin 1970), our study site supports established populations of the Argentine ant, California red scale, and a variety of honeydew-producing Hemiptera. Within our study site, which contains over 400 lemon trees, we selected a total of 40 fruit-bearing trees, each of which supported densities of red scale. The trees had an average height of 3.4 m (range. 2.7 m - 4 m) and an average crown diameter of 2.4 m (range. 1.6 m - 3.4 m). Because the 40 trees were unevenly distributed within the orchard, we grouped trees into blocks based on size and location (n=10 blocks of 4 trees each). Within each block, trees were randomly assigned to one of four experimental groups: control, ant removal, red scale removal, and honeydew-producing insect removal. The primary honeydew-producing insects in this orchard at the time of the study included citrus mealybug, brown soft scale, black scale (*Saissetia oleae*), cottony-cushion scale (*Icerya purchasi*), citricola scale (*Coccus pseduomagnolarium*), and woolly whitefly. As reported by Markin (1970), we found that citrus mealybug was common throughout the orchard and was by far the most ant-tended hemipteran species (Fig. 2a).

Removal Experiments

In late July 2009, we initiated experimental treatments, which proceeded as follows. For trees in the ant removal treatment group, we prevented ants from accessing the tree canopy by placing Tanglefoot ® barriers at the base of each trunk. Prior to applying Tanglefoot ®, we wrapped trunks with a 15-cm wide band of high density foam (to prevent ants from travelling underneath the exclusion band) secured with zip ties. We then covered the foam with plastic wrap and duct tape and applied an approximately 3-cm wide band of Tanglefoot ® to the top 5 cm of plastic wrap (Fig. 2b). For the duration of the experiment, we monitored ant removal trees and added Tanglefoot ® as needed. To remove honeydew-producing insects, we scanned all parts of the tree for aggregations and manually removed those detected. In addition to carefully inspecting branches, stems, and leaves for honeydew-producing insects, we followed ant trails to the insects they were tending. We re-scanned trees approximately every two weeks and removed honeydew-producing insects as needed. Lastly, to remove red scale from the interior refuge of the tree, we scrubbed trunk and woody sections of primary branches with plastic scrubbers (Murdoch 1996). We performed red scale removals twice at the start of the study and then intermittently as needed.

Sampling

We sampled trees on five occasions between August and November 2009 to estimate the level of ant foraging and the abundance of honeydew-producing insects and red scale. We updated all removals in January 2010 and continued sampling through May of that year. We also measured these variables in one pre-removal survey in July prior to performing removals. To determine the level of ant activity, we counted the number of ants ascending trunks for one-minute time periods starting at approximately 11.

To estimate the abundance of honeydew-producing insects, we scanned approximately 12% of each tree's foliage. Areas selected for scanning consisted of two equal-sized sections: one in the upper half of the tree and the other in the lower half of the tree. We then randomly selected a compass coordinate and scanned all twigs between that coordinate and the next coordinate 45° clockwise. The upper and lower sections were 180° from one another (i.e. if the upper half of a tree was scanned between N and NE, the lower half was scanned between S and SW). Although we removed and counted all honeydew-producing insects, our statistical analyses focus primarily on citrus mealybug abundance. We found that this mealybug species was the most abundant and most commonly tended honeydew-producing insect by ants.

We measured red scale abundance both on the bark and in the canopy of each tree. To estimate the abundance of red scale on the tree's bark, we took four bark samples from each tree (Fig. 2d). We identified the number of primary branches per tree and took two, 1-cm bark samples from randomly selected branches; the branch and distance up the branch were chosen at random. Samples were taken using cork borers and a knife, and the tools were dipped in 75% ethanol between trees to prevent spreading of diseases. In 2009, to estimate the abundance of red scale in canopies, we counted red scale on randomly selected twigs. Four randomly chosen twigs were selected using height and direction coordinates produced with a random number generator. We then counted all red scale individuals within the first three flushes of each twig (Murdoch 1996). In 2010, we measured red scale in tree canopies by counting the proportion of infested fruit (i.e. an infested fruit is one with at least ten red scale) on each tree (Fig. 2e). This method is in alignment with UC-IPM guidelines and allowed for both a larger sample size, because we counted all fruit per tree, and less variance, because red scale are most commonly found on fruit, and are not as common on twigs and leaves.

During the 2010 season, we performed ant counts every two weeks, counting twice per day (once in the morning and once in the early afternoon) and recorded the number of ants both ascending and descending. We continued scanning trees for honeydew-producing insects. We continued taking bark samples but measured rates of parasitism along with total live red scale.

Statistical Analysis

Data were log transformed and then time averaged to improve normality and to increase homoschedasticity. Using JMP ® for data analysis, we averaged ant, honeydew-producer, red scale bark, red scale fruit infestation, and red scale parasitism counts across sampling periods and used the time-averaged mean values for each tree as data points. We performed simple linear regression on the pretreatment counts from 2009 of red scale twig counts and ants. We conducted t-tests to measure the effectiveness of our removal treatments. We also performed a t-test to compare mealybugs in control and ant removal trees in 2009 and an analysis of variance with a post-hoc least squares difference test on the ant trail data from 2009. We performed a regression of the red scale fruit infestation counts versus ants in 2010. Lastly, we performed a t-test comparing red scale parasitism rates taken in 2010 on bark in controls versus ant removal trees.

RESULTS

At the scale of individual trees within the lemon orchard surveyed, a positive relationship existed between the number of red scale on branches and number of ants on the trunks (Fig. 3). This relationship held for red scale counts on both bark and twigs. However, the relationship between red scale and ants was stronger on twigs ($F = 20.4$, $df = 1, 39$, $P<0.0001$, $R^2 = 0.34$) than on bark ($F = 10.8$, $df = 1, 39$, $P= 0.0022$, $R^2 = 0.22$).

For all three removal treatments, the target insect group declined sharply in abundance following treatment, confirming that treatments were effective (Fig. 4). Relative to controls, ant removals displayed a 93.1% reduction in ant activity for the duration of the experiment ($t = 4.22$, $P = 0.0011$, $df = 9$). Again compared to the relevant controls, honeydew-producing insect removal trees exhibited a 91.3% reduction in honeydew-producing insects ($t = 4.76$, $df = 9$, $P = 0.0005$), and red scale refuge removal trees exhibited a 81% reduction in red scale abundance on the bark refuge ($t = 5.62$, $df = 9$, $P = 0.0002$).

As hypothesized, ant foraging significantly decreased when honeydew-producing insects were removed from the canopies of lemon trees (Fig. 5). Compared to control trees, for example, ant activity, on average, was reduced by 63.6% ($t = 3.21$, $df = 9$, $P = 0.011$). In the honeydew-producing insect removal treatment, we observed ants visiting aggregations of honeydew-producing insects that we missed in our removal efforts. Ants also visited flowers for nectar.

In trees where we restricted ant foraging, numbers of citrus mealybug significantly decreased during the course of the study (Fig. 6). Compared to control trees, for example, mealybug density was reduced by 93.4% ($t = 4.07$, df = 9, $P = 0.0028$). This trend was not evident for other honeydew-producing insect groups; however, spatial heterogeneity and small sample sizes may have limited our ability to detect significant relationships for these other insects.

We also found a positive relationship between red scale and ants at the scale of fruit ($F = 15.16$, df = 1, 9, $P = 0.0004$, $R^2 = 0.27$), in our 2010 survey of infested fruit (Fig. 7), further supporting the relationship seen in the preliminary counts displayed in Figure 2.

For the red scale parasitism on bark counts taken in 2010, we found an increase in parasitism rates in trees where ants were removed when compared to control trees ($t = 2.22$, df = 9, $P = 0.027$) (Fig. 8).

We also came across some unexpected results. It was hypothesized that neither ant nor honeydew-producing insect abundance would be affected by removing the red scale refuge, but we found that ant abundance did decrease in red scale removal trees (Fig. 3) ($t = 1.83$, df = 9, $P = 0.05$). Ant abundance in red scale removal trees did not differ from that in honeydew-producing insect removal trees.

The full set of statistical results is provided in the appendix.

DISCUSSION

In San Diego County, a major economic impact of the Argentine ant occurs in citrus agroecosystems, where ants interfere with biological control of insect pests, especially California red scale. In this study, we found a positive correlation between ants and red scale both on the bark and in the tree canopy. We also confirmed positive relationships between honeydew-producing insects and ants at the tree level. Also at the tree level, we found both a reduction in ants when honeydew-producing insects were removed, as well as a reduction in mealybugs when ants were removed.

Honeydew-producing insects play an important role in attracting ants into the trees. When honeydew-producing insects were not present, we found that ants were much less likely to recruit into trees. However, as observed by Markin (1970), although citrus mealybug is the most preferred and constant source of honeydew, Argentine ants commonly recruit into trees for flower nectar, particularly during the spring bloom of April and May. We observed high level of ant recruitment into trees during these months, whether honeydew-producing insects were present or not, and found that ants were mostly recruiting to sources of floral nectar. Another possibility for ant presence in honeydew-producing insect removal treatments is that ants were recruiting to honeydew-producing insects that we did not remove. We removed honeydew-producing insects frequently and systematically, but considering the total area of the trees and the growth and reproduction rates of these insects, particularly in the warm summer months, it is reasonable to expect that, although a large portion of these insects were removed (91.3%), not all were found and removed (Fig. 4). This point is made clear by figure A.1, in which one can see that mealybugs were actually lower in ant removal trees than in honeydew-producing insect removal trees.

In this study, we also confirmed that red scale appear to benefit from ant presence. Before performing any removals, we observed a positive correlation between the two species, a relationship that continued throughout the study. However, neither ant removal nor honeydew-producing insect removal treatments showed any significant differences in red scale abundance either on bark or in the exterior. There was a trend for red scale to have higher abundance in controls than in ant removals, as expected, but this result was not statistically significant. We suspect that the lack of statistical significance in this case may be due to low sample size, for although many surveys were performed, red scale numbers per sample, remained low, as most individuals were found to be dead once inspected under a microscope. Moreover, we found that in ant removal trees, red scale on bark was more commonly parasitized (Fig. 8), confirming that the presence of ants negatively affects *Aphytis* and other parasitoids.

Beyond confirming our hypothesis that Argentine ants positively affect red scale, we also found the reciprocal to be true. In the red scale removal treatment group, we found that ant foraging was depressed. This was true throughout the study: during the summer and fall months when honeydew-producing insects were abundant, as well as during the spring months, when ants recruited to floral nectar. Ant abundance in red scale removal trees was not statistically significant from controls; however, it was in the same statistical group as honeydew-producing insect removals (Fig. 5). Although we expected ant removal trees to yield lower numbers of red scale, we did not expect for red scale removals to have lower ant counts. One potential explanation for this strange result could be that ants prey on red scale. It has been observed that ants feed on small scale (Murdoch 1970, Stadler and Dixon 2005), however, ants feeding specifically on red scale has yet to be directly observed. Another possibility is that ants use the presence of red scale as some sort of indicator of resources--perhaps red scale presence indicates general hemipteran abundance on the tree. Whatever the case, this unexpected result needs to be further explored.

Our research aims to further the knowledge of the ecological interactions that underlie citrus pest management by developing quantitative relationships between ant activity and economic thresholds for red scale and honeydew-producing citrus pests. We aim to use this ecologically-based information to develop practical, biologically-based management guidelines for citrus pests. Although growers commonly implement ant control in orchards, neither the mechanism by which ants disrupt biological control by parasitic wasps nor the numerical relationship between red scale and Argentine ant abundance are well understood. Without a better understanding of how ant abundance disrupts biological control and in turn drives red scale infestations, ant control efforts cannot be calibrated to anticipated pest infestations in an economically and environmentally sound manner.

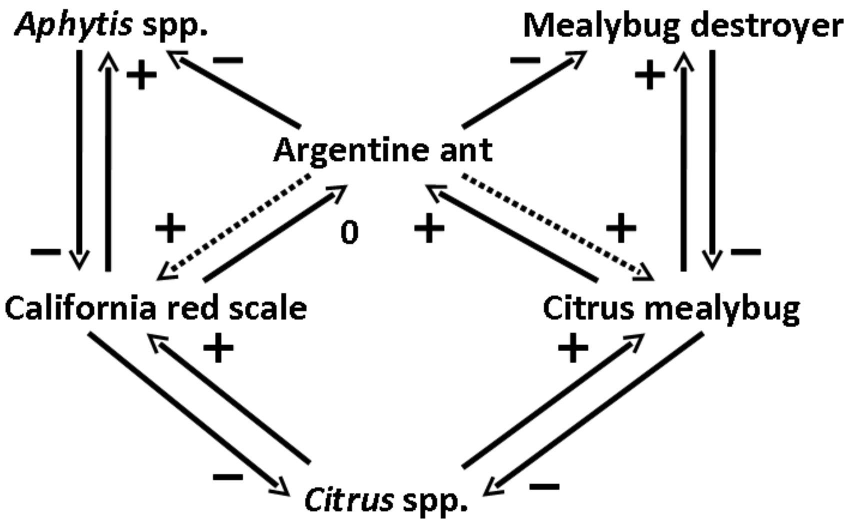

Figure 1. Food web diagram of the citrus agroecosystem. Solid lines represent direct relationships and dotted lines represent indirect relationships. Relationships indicated as positive (+), negative (-), or neutral (0).

Figure 2a. View of lemon orchard in Valley Center, CA where all experiments were performed.

Figure 2b. Argentine ants tending citrus mealybugs.

Figure 2c. Example of Tanglefoot ® barrier applied to ant removal treatment trees.

Figure 2d. Red scale on interior bark refuge.

Figure 2e. California red scale on a lemon.

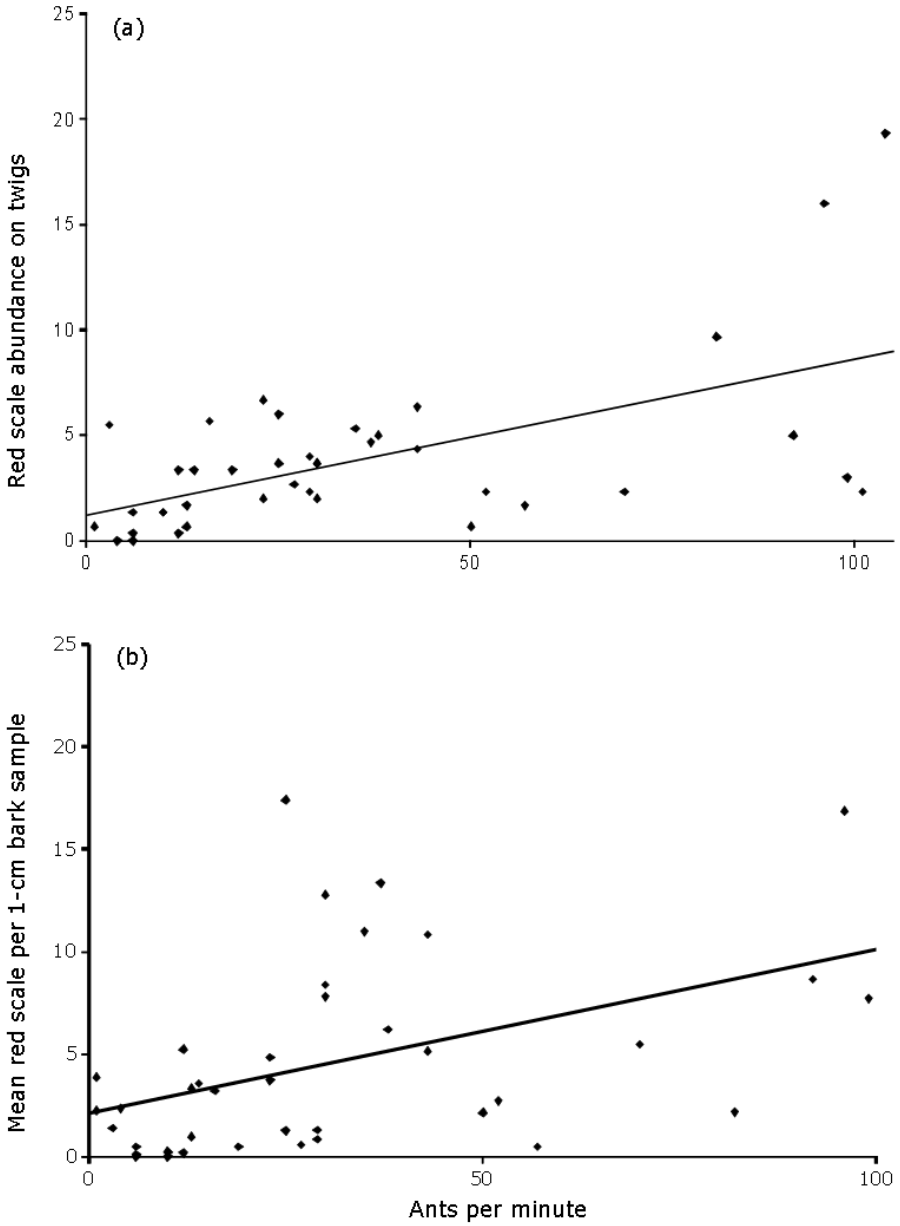

Figure 3. (a) Pre-treatment red scale on twigs versus ants per minute counts. (b) Pre-treatment red scale on bark versus ants per minute counts. Ants per minute measures number of ants ascending tree in one minute.

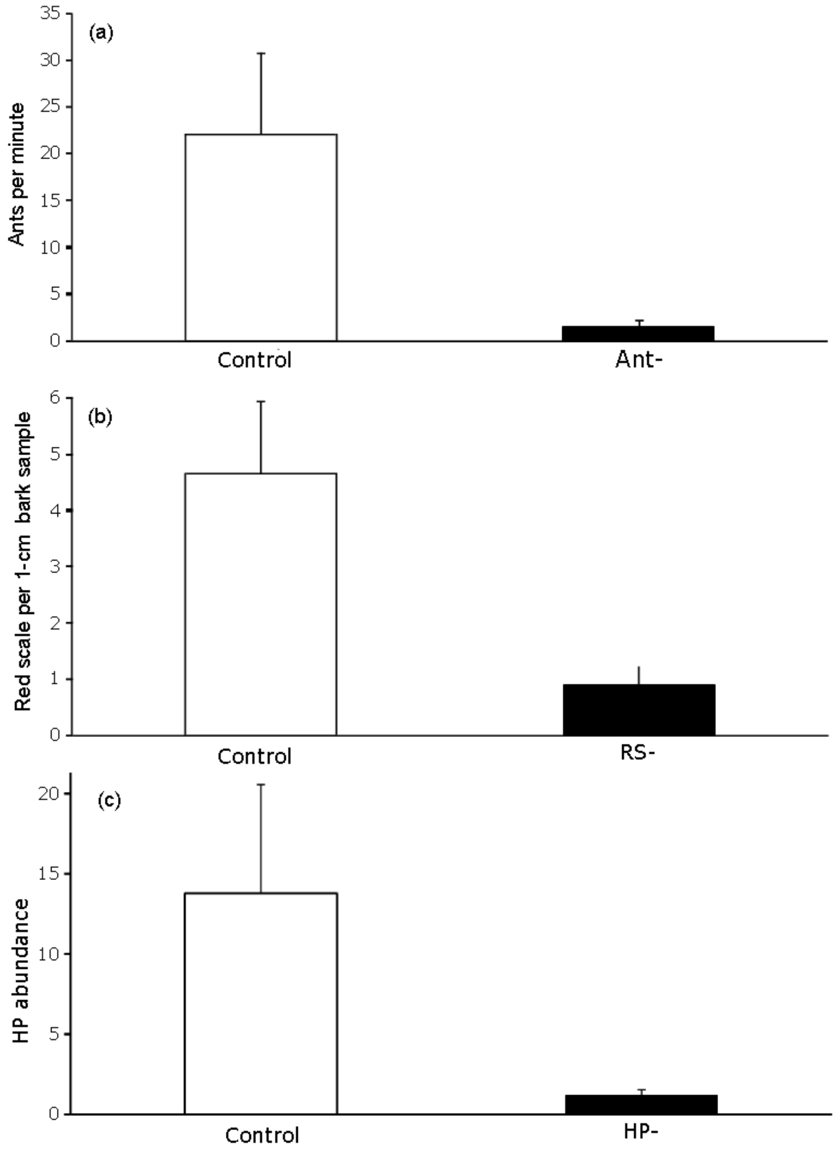

Figure 4. Comparisons of removal treatments and controls. (a) Ants per minute in control versus ant removal trees (Ant-). (b) Red scale bark counts in control versus red scale removal trees (RS-). (c) Honeydew-producing insect abundance (HP) in control versus honeydew producer removal trees (HP-).

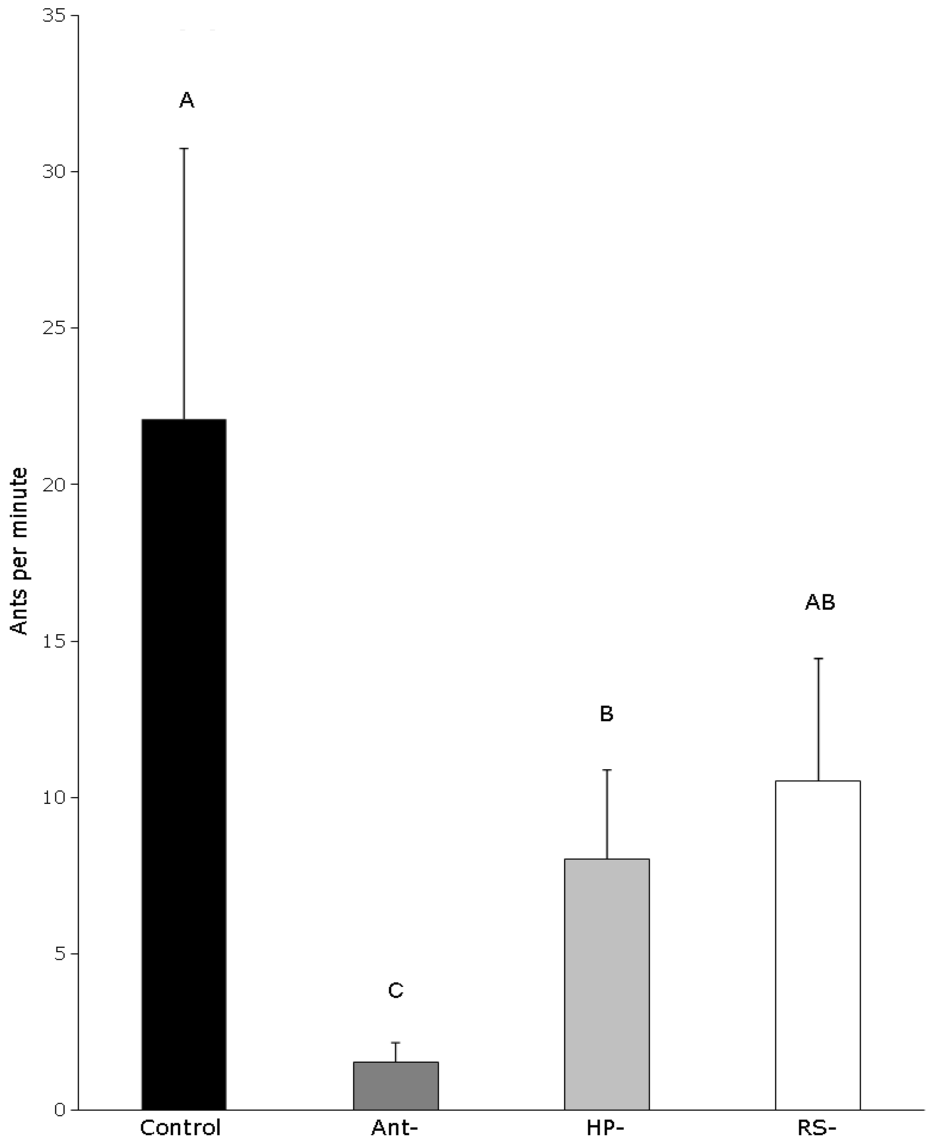

Figure 5. Mean ants per minute values (+1 standard error) for each experimental group compared using ANOVA. Letters indicate significance from post-hoc LSD test (see Fig. 4 for treatment group abbreviations).

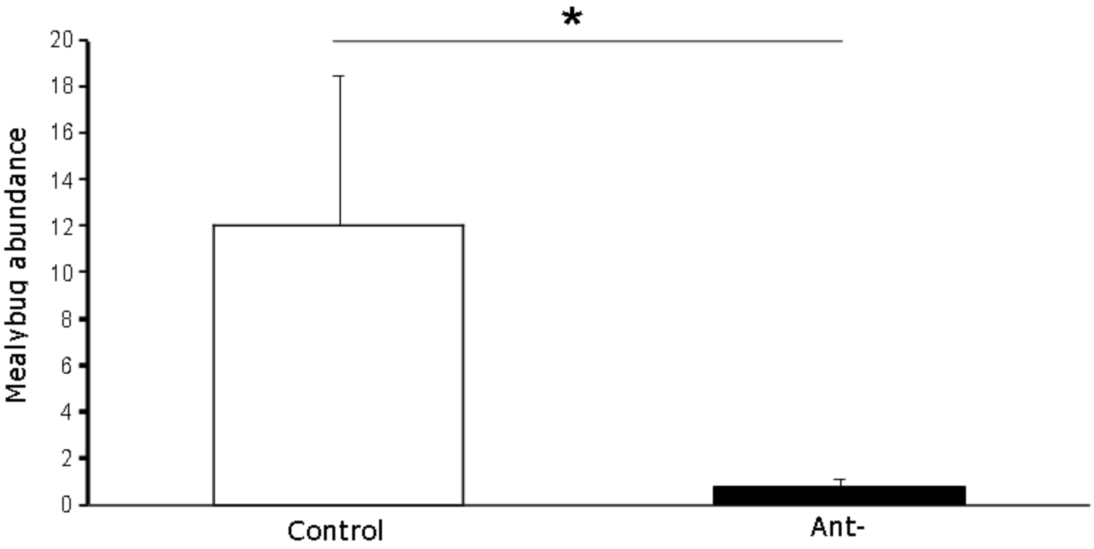

Figure 6. Mealybug counts in control versus ant removal trees (Ant-). Asterisk denotes statistical significance.

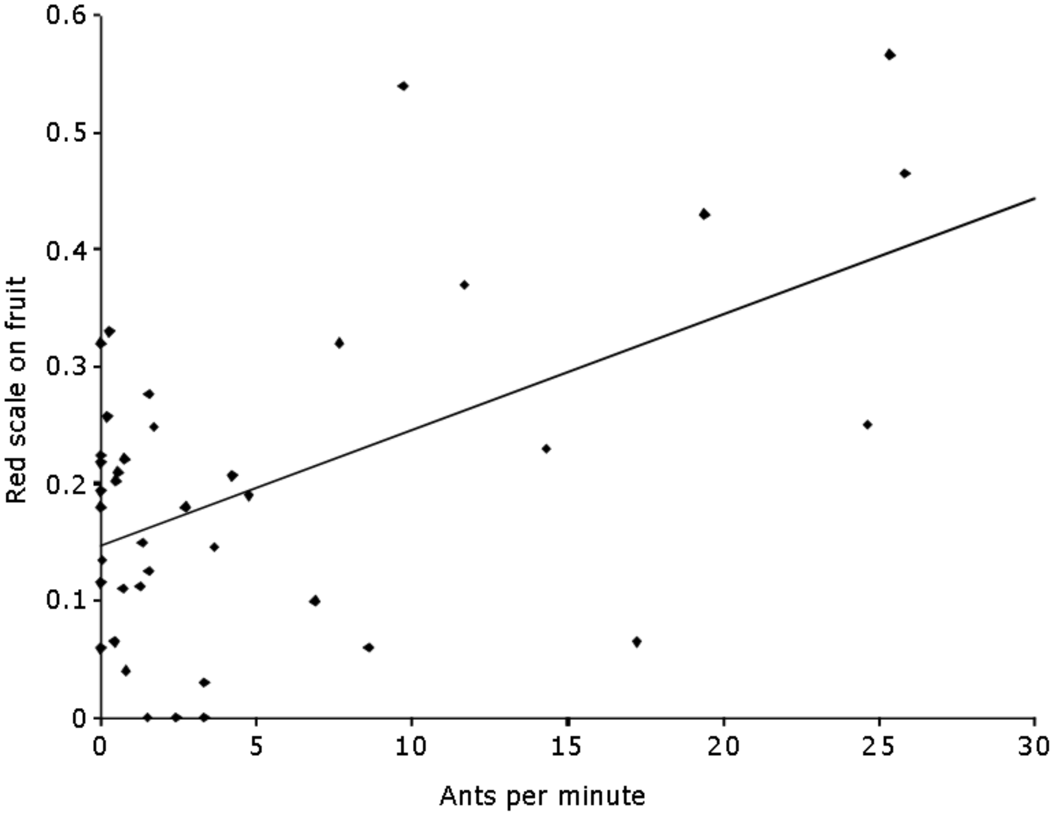

Figure 7. 2010 red scale fruit counts versus ants per minute.

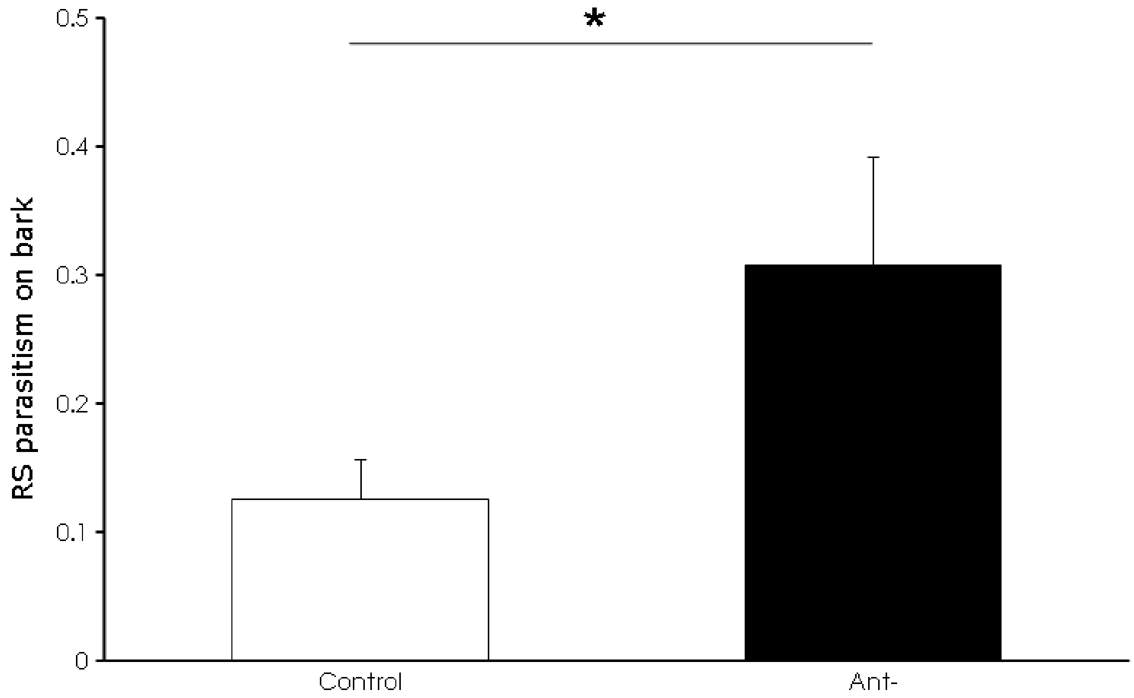

Figure 8. Red scale parasitism counts on bark in control versus ant removal trees (Ant-). Asterisk denotes significance.

APPENDIX

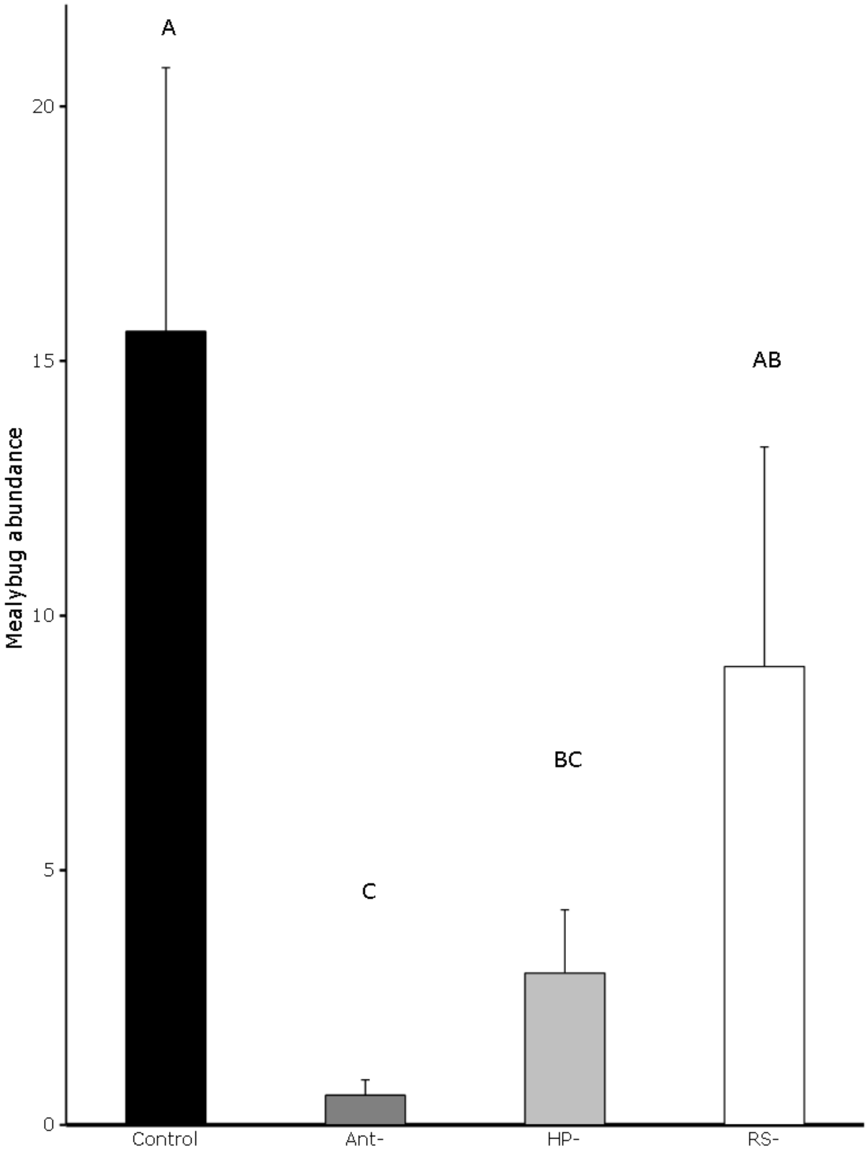

Figure A.1 Mean mealybug values from 2009 (+1 standard error) for each experimental group compared using ANOVA. Letters indicate significance from post-hoc LSD test (see Fig. 4 for treatment group abbreviations).

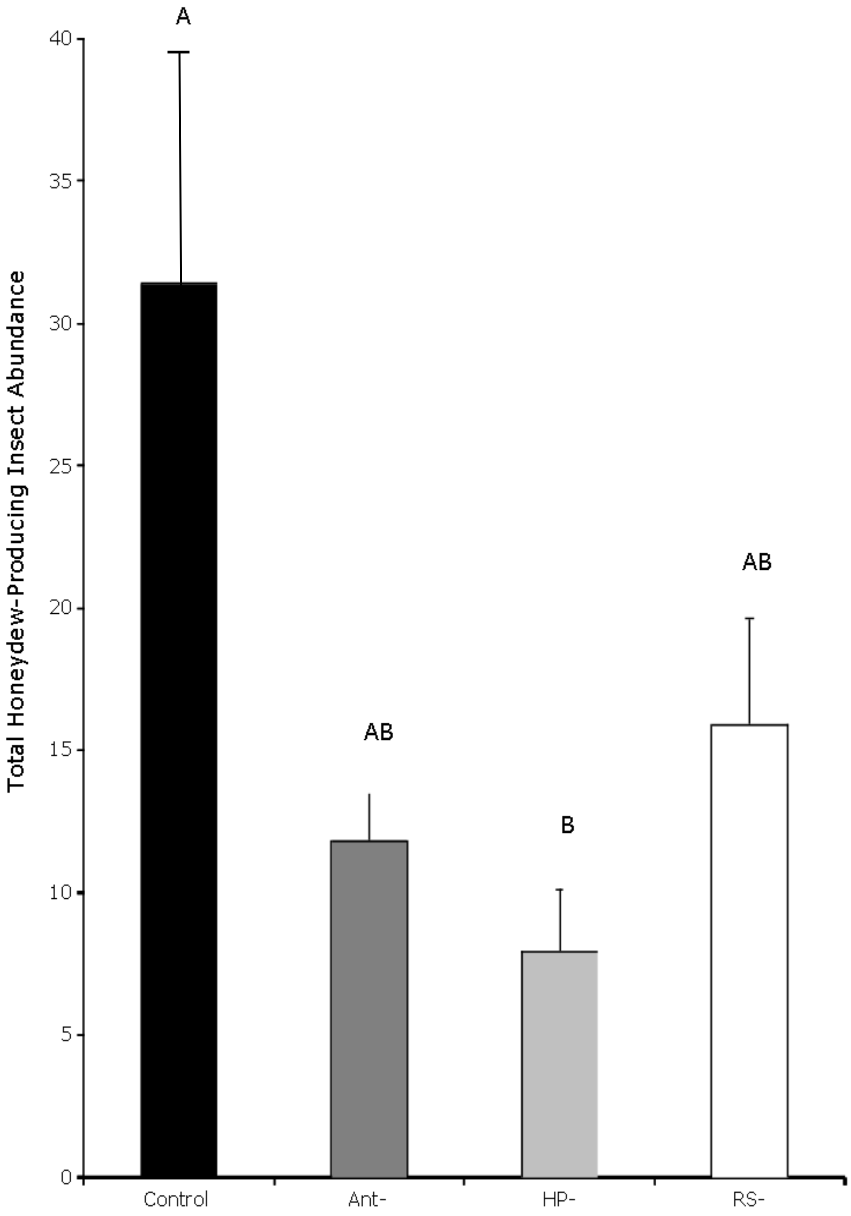

Figure A.2. Mean honeydew-producing insect values from 2009 (+1 standard error) for each experimental group compared using ANOVA. Letters indicate significance from post-hoc LSD test (see Fig. 4 for treatment group abbreviations).

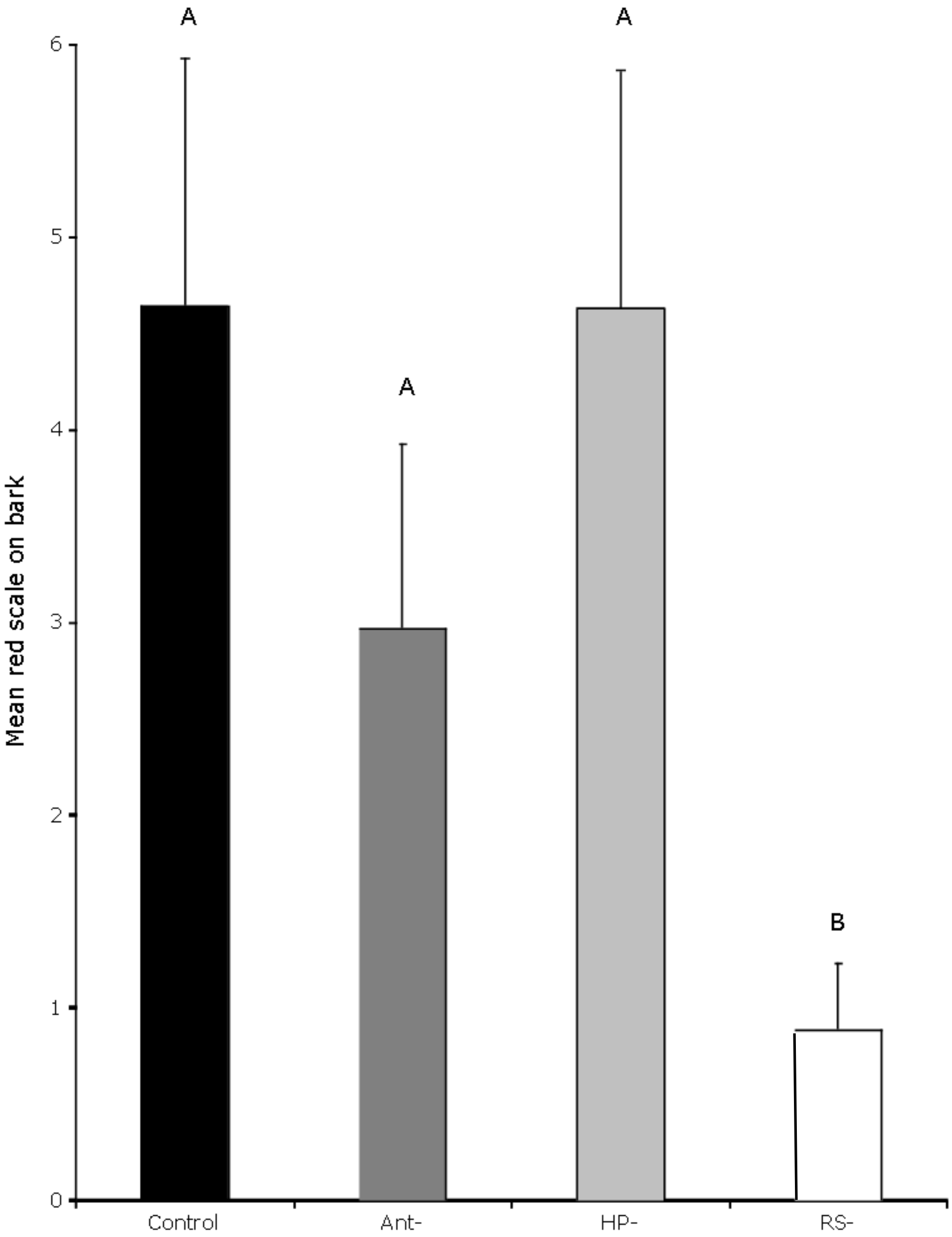

Figure A.3. Mean red scale bark values from 2009 (+1 standard error) for each experimental group compared using ANOVA. Letters indicate significance from post-hoc LSD test (see Fig. 4 for treatment group abbreviations).

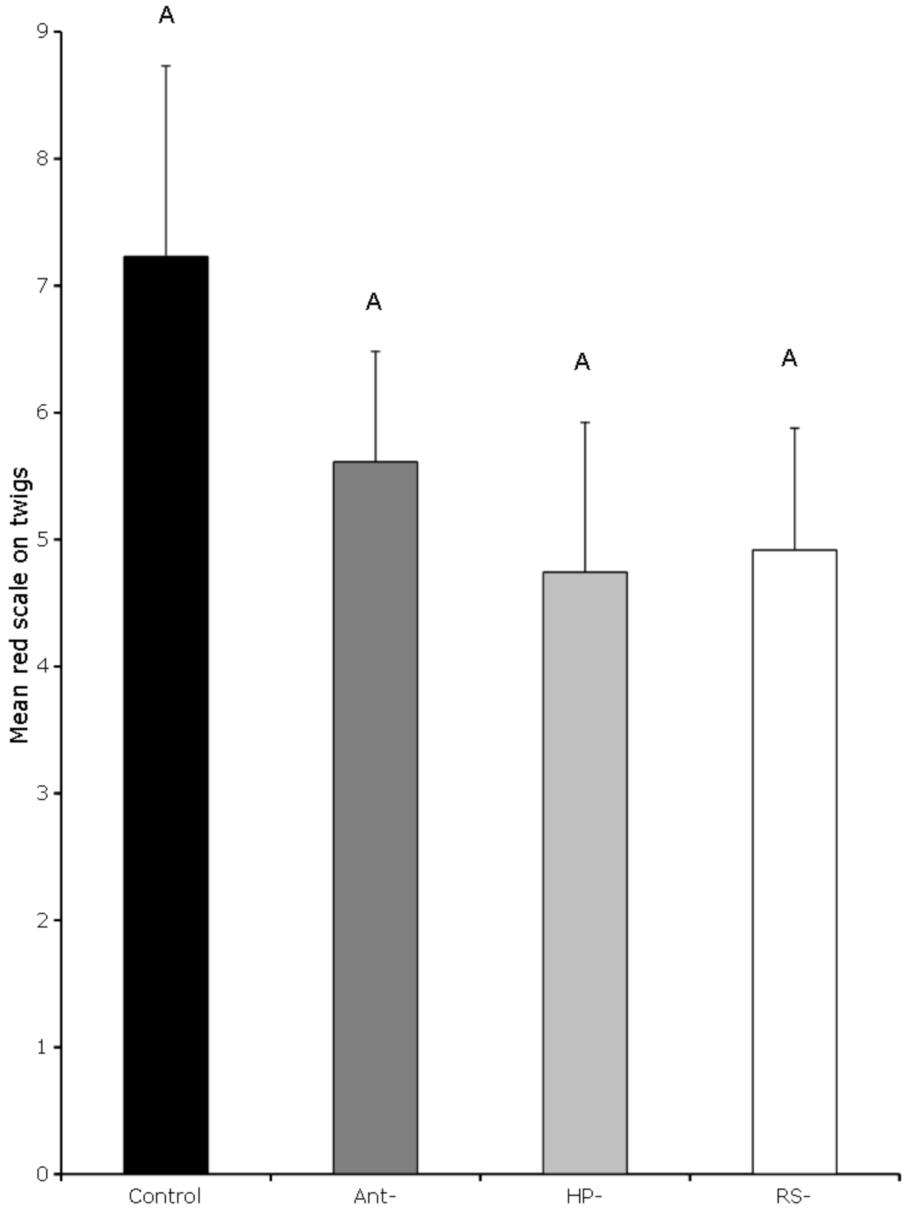

Figure A.4. Mean red scale twig values from 2009 (+1 standard error) for each experimental group compared using ANOVA. Letters indicate significance from post-hoc LSD test (see Fig. 4 for treatment group abbreviations).

Table A.1. Tree data and pretreatment ant and red scale data

Treatment	Block	Tree	Tree Height (m)	Ants	Red Scale on Twigs	Red Scale on Bark
RS-	1	09D	3.35	12	3.33	5.25
Ctrl	1	09E	3.05	3	0.00	2.37
HP-	1	10A	3.35	30	3.67	7.81
Ant-	1	13A	3.35	13	1.67	3.33
Ctrl	2	10C	3.35	1	0.67	2.25
RS-	2	10J	3.35	27	2.67	0.59
Ant-	2	12H	3.35	6	0.33	0.50
HP-	2	13B	3.66	10	1.33	0.25
RS-	3	09A	3.35	3	5.50	1.41
Ctrl	3	10K	3.66	19	3.33	0.50
Ant-	3	10L	3.66	30	2.00	8.40
HP-	3	11E	3.66	14	3.33	3.57
Ant-	4	12J	3.66	23	6.67	4.85
Ctrl	4	14G	3.05	29	2.33	1.31
RS-	4	19C	3.66	12	0.33	0.17
HP-	4	21I	3.66	13	0.67	0.97
Ant-	5	15G	3.05	6	0.00	0.00
Ctrl	5	15H	3.05	6	1.33	0.12
RS-	5	16F	3.05	10	1.33	0.00
HP-	5	22H	2.74	25	6.00	1.28
Ctrl	6	13J	3.66	52	2.33	2.73
HP-	6	18E	3.96	25	3.67	17.39
RS-	6	22C	3.66	92	5.00	8.67
Ant-	6	24F	3.66	96	16.00	16.85
RS-	7	16I	3.66	57	1.67	0.50
HP-	7	16K	3.35	29	4.00	0.87
Ant-	7	16L	3.66	35	5.33	10.98
Ctrl	7	16M	3.66	37	4.67	13.35
HP-	8	23E	3.35	43	6.33	5.16
RS-	8	24I	3.05	38	5.00	6.21
Ctrl	8	30H	3.35	23	2.00	3.72
Ant-	8	30I	3.66	101	2.33	1.26
RS-	9	25I	3.66	104	19.33	19.34
Ant-	9	26M	3.35	70	2.33	5.48
HP-	9	27M	3.66	82	9.67	2.18
Ctrl	9	30J	3.66	99	3.00	7.72
Ant-	10	29O	3.35	43	4.33	10.83
RS-	10	32N	3.35	16	5.67	3.21
Ctrl	10	34O	3.35	30	3.67	12.78
HP-	10	35M	3.66	50	0.67	2.16
Mean			3.44	35.35	3.84	4.91

Table A.2a. Time averaged ants per minute data from 2009

Block	Control	Ant-	HP-	RS-
1	0.20	1.60	1.00	0.80
2	0.40	0.40	1.00	3.20
3	4.60	0.00	0.20	1.60
4	11.40	2.20	3.40	2.80
5	21.20	0.00	4.40	5.80
6	13.80	0.40	6.40	18.00
7	11.20	0.00	6.40	6.80
8	31.00	6.50	9.80	10.20
9	92.40	2.20	27.00	41.80
10	34.80	2.00	20.80	14.40
Mean	22.10	1.53	8.04	10.54

Table A.2b. Time averaged ants per minute data from 2010

Block	Control	Ant-	HP-	RS-
1	0.00	1.27	0.23	0.00
2	0.00	0.00	0.64	0.00
3	0.00	0.05	1.09	0.50
4	0.50	0.00	2.50	2.55
5	1.05	0.36	2.73	0.65
6	0.18	1.41	7.14	4.35
7	8.95	0.64	3.27	1.30
8	16.55	3.30	7.73	6.25
9	26.73	2.14	21.82	11.15
10	25.23	3.45	19.82	12.50
Mean	7.92	1.26	6.70	3.93

Table A.3a. Time averaged honeydew-producing (HP) insect data from 2009

	Mealybugs				Total Honeydew-Producing Insects			
Block	Control	Ant-	HP-	RS-	Control	Ant-	HP-	RS-
1	0.17	0.00	0.60	8.33	5.92	7.50	3.15	13.67
2	0.00	0.17	0.00	1.50	2.58	11.63	1.70	19.58
3	1.50	0.00	0.00	0.00	6.50	10.67	3.40	2.71
4	35.67	0.00	1.80	2.00	51.00	13.63	20.05	8.50
5	28.33	0.00	1.00	46.67	39.33	0.33	1.75	46.67
6	13.50	0.17	6.00	6.83	38.25	9.75	8.80	12.38
7	1.67	1.00	0.40	5.33	7.96	12.63	1.45	7.92
8	23.33	1.83	10.60	2.17	26.42	7.75	14.60	8.21
9	44.50	2.67	8.60	9.67	72.58	20.25	17.05	12.88
10	7.17	0.00	0.80	7.50	18.21	12.17	5.05	19.38
Mean	15.58	0.58	2.98	9.00	26.88	10.63	7.70	15.19

Table A.3b. Time averaged honeydew-producing (HP) insect data from 2010

	Mealybugs				Total Honeydew-Producing Insects			
Block	Control	Ant-	HP-	RS-	Control	Ant-	HP-	RS-
1	0.75	0.00	0.00	0.25	3.33	5.00	0.00	1.00
2	0.25	0.00	0.25	0.00	2.33	1.00	1.00	0.67
3	0.25	0.50	0.00	0.00	3.00	2.67	0.33	0.33
4	0.25	0.00	0.25	0.75	2.67	1.33	0.33	16.67
5	0.00	0.00	0.00	0.25	2.33	1.00	2.00	0.33
6	0.00	0.50	0.25	17.50	5.33	4.33	1.67	24.33
7	2.50	0.25	0.50	0.00	9.67	2.33	2.67	1.33
8	18.75	2.25	1.00	1.75	45.00	5.33	3.00	16.00
9	20.75	0.25	1.25	3.75	65.67	1.33	6.33	5.33
10	41.50	1.00	1.25	0.00	59.67	6.00	5.33	4.33
Mean	8.50	0.48	0.48	2.43	19.90	3.03	2.27	7.03

Table A.4a. Time-averaged red scale bark data from 2009

Block	Control	Ant-	HP-	RS-
1	3.71	2.46	7.50	0.95
2	1.96	1.25	0.83	0.60
3	2.92	4.71	3.42	0.90
4	1.25	2.50	2.75	0.35
5	1.46	0.46	1.75	0.05
6	3.25	5.42	4.25	1.80
7	4.96	1.50	2.50	0.10
8	4.67	2.00	1.25	0.60
9	8.29	2.00	8.58	1.80
10	10.79	6.96	12.00	0.50
Mean	4.33	2.93	4.48	0.77

Table A.4b. Time-averaged red scale bark data from 2010

	Live Red Scale		Proportion of Red Scale Parasitized	
Block	Control	Ant-	Control	Ant-
1	2.63	1.81	0.17	0.36
2	0.69	1.94	0.00	0.33
3	2.00	2.75	0.21	0.19
4	1.44	0.19	0.06	0.25
5	0.75	0.13	0.25	1.00
6	1.25	2.88	0.33	0.25
7	3.88	3.00	0.25	0.12
8	0.44	2.38	0.00	0.22
9	3.44	1.31	0.06	0.04
10	5.56	3.56	0.15	0.08
Mean	2.21	1.99	0.15	0.28

Table A.5. Time-averaged red scale twig data from 2009

Block	Control	Ant-	HP-	RS-
1	4.00	4.74	9.56	5.38
2	4.14	2.35	3.05	1.20
3	4.00	8.70	2.63	2.00
4	3.43	5.52	2.47	0.50
5	4.57	2.52	3.29	1.75
6	8.65	10.92	3.79	11.25
7	10.73	8.13	4.32	2.50
8	3.39	3.83	3.16	18.00
9	17.09	5.13	3.95	5.00
10	16.26	8.67	9.84	15.25
Mean	7.63	6.05	4.61	6.28

Table A.6. Red scale fruit infestation data 2010

Block	Control	Ant-	HP-	RS-
1	0.12	0.28	0.33	0.18
2	0.19	0.06	0.11	0.32
3	0.23	0.14	0.15	0.21
4	0.20	0.22	0.18	0.00
5	0.11	0.07	0.00	0.04
6	0.26	0.15	0.32	0.19
7	0.54	0.22	0.03	0.00
8	0.06	0.15	0.06	0.37
9	0.57	0.13	0.25	0.10
10	0.46	0.21	0.43	0.23
Mean	0.27	0.16	0.18	0.16

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