

FY 97 FINAL PROJECT PROGRESS REPORT

1. PROJECT TITLE Biological and chemical control of the Nantucket pine tip moth to increase fiber yields in Georgia forests

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3. EXECUTIVE SUMMARY OF WORK COMPLETED

The project is on schedule. All of the objectives for FY97 have been met. High variability in tip moth populations has reduced the amount of data which potentially could have been collected.

4. <u>DELIVERABLES</u>		
<u>Major Milestones & Dates</u>	<u>Original Proposal</u>	<u>Actual</u>
July 1996 – June 1997	Evaluate 2 nd year of systemic insecticide tests	2 nd year results show some efficacy but reduced from year 1.
July 1996 – March 1997	Continued rearing and identification of natural enemies in the Coastal Plain	The complex of parasites appears to consist of 12 species. <i>Campoplex</i> is almost absent from the Coastal Plain.
September 1996 – July 1997	Evaluate the effect of vegetation control on tip moth parasitism	Data show that vegetation management increased tip moth parasitism at low infestation rates and lowered it at high rates.

5. <u>BUDGET</u>		
State Funds	<u>Total FY 97</u> \$ 87,000	<u>9-Month Expended</u> \$ 87,000
Matching Funds	<u>Original Proposal</u> \$ 89,000	<u>Actual</u> \$ 89,000

6. Additional Information/Results/Graphics/Manuscript are attached.

**BIOLOGICAL AND CHEMICAL CONTROL OF THE NANTUCKET PINE TIP MOTH
TO INCREASE FIBER YIELDS IN GEORGIA FORESTS**

FINAL PROGRESS REPORT - FY 1997

TO

GEORGIA CONSORTIUM FOR COMPETITIVENESS IN PULP AND PAPER

FROM

C. W. BERISFORD

DEPARTMENT OF ENTOMOLOGY

UNIVERSITY OF GEORGIA

ATHENS, GA 30602

Evaluation of Progress

The research is generally on schedule and all of the objectives have been met or exceeded through the second year of the three year project. We anticipate that all of the original objectives will be met by the end of FY 1998.

Insecticide Tests

Insecticide evaluation experiments were installed at various locations around the South. Some of the tests produced less data than expected due to a collapse in tip moth populations or to a failure for high populations to develop. However, we were able to collect adequate data at most of the locations. Most of the information reported here was collected during the 1996 field season; data from 1997 are still being collected and/or analyzed.

Granular Insecticide Tests

In March of 1996, a trial of 2 systemic insecticides in granular formulation was installed on a wet, heavy organic soil site in the Coastal Plain of North Carolina north of New Bern (Weyerhaeuser Co. Land). Furadan 15g at 0.5 g a.i./tree was included as an internal standard for comparison. The test compounds were applied at the following rates:

<u>Treatment</u>	<u>Product</u>	<u>Rate (gm a.i./tree)</u>
1	Counter 20CR	0.5
2	Counter 20CR	1.0
3	Counter 20CR	2.0
4	Merit	0.5
5	Merit	1.0
6	Furadan 15g	0.5

The trial was a complete randomized block design with 6 replicates and 6 trees per rep. The appropriate amount of product was applied to 1 (low rate of Counter) or 2 dibble marks 10 cm deep and 10cm from the seedlings.

Continuing Systemic Insecticide Test from 1995: Piedmont Site

A similar study which had been installed on the Piedmont near Athens last year was monitored for tip moth infestation, and year end heights were taken (end of year 2). This site experienced very low incidence of tip moth throughout both years. Additionally, growth of seedlings was minimal due to unknown site factors other than tip moth (probably drought in 1995). The highest infestation level in year one was 13% of the top whorl in the check plots. This was not significantly different from the best treatment (3.7% infestation for Counter 20CR at 2.0 gm a.i./tree). No trends were apparent for the remaining treatments which varied between 4 and 10 percent infestation. At years' end, there was zero new growth on the seedlings in 3 of the 4 reps. No apparent mortality or phytotoxic effects were observed.

In 1996, tip moth population levels remained low. Measurable damage did not occur until the second generation of moths. All treatments had significantly fewer damaged shoots than the check, but were not different from each other. Trends in the data did appear for Counter 20CR where infestation declined with increasing treatment rate. Results were anomalous for the remaining treatments (Figure 1). Percent infested terminal shoots was greatest in the check plots with all treatments except the two low rates of imidacloprid and the high rate of Biodac 15g being significantly less than the check (Figure 2). Treatments were not different from one another. Again in the third

generation, infestation levels were extremely low, ranging from 1 to 9 % over all plots. No differences or trends were detected. Year end heights were taken , but there were no significant differences among the treatments (Figure 3). Results here should be interpreted very cautiously given the low tip moth population and obvious negative site effect on seedling growth.

North Carolina Coastal Plain Site:1996 Results

Tip moth levels were low during the first generation as expected. Terminal infestation ranged from 6 to 24 percent with no detectable differences among treatments. Survival and phytotoxicity were similar among all treatments and replicates. Tip moth populations increased considerably during generation 2. Terminal infestation was not significantly different among any treatments except for the Furadan plots, and was highest in the Counter 20CR 1.0gm plots (78%). Most treatments averaged close to 50% terminal shoot infestation (Figure 4). Total percentage of infested shoots reflected a different trend with check plots being highest (36%), and the high rate of imidacloprid being lowest (1.6%). The trend for a treatment effect was strong (see Figure 5), with imidacloprid and furadan treatments performing significantly better than the check. We had some anomalous results with the high rate of Counter (terbufos), but the 2 lower rates showed a strong trend regarding efficacy. Unfortunately, due to high variance within and among replicates, significant differences were not detected. Tip moth populations were low during the 3rd generation, averaging only 16% in check plots (Figure 6). The furadan standard treatment seemed to lose effect during this time, although efficacy results were non-significant. Basal diameters were similar among all treatments (Figure 7), but heights showed a positive trend regarding treatment effect (Figure 8). Only the furadan treatment was significantly different from the check plots.

Historically, tip moth has been difficult to control on these pocosin, high organic

content soils. We are hoping for larger moth populations next year to provide sufficient pressure on these trees, and allow a more critical look at efficacy.

Foliar Application Trials

Products tested for 1996 were similar to those in 1995 with the addition of Orthene and an Orthene/Tame tank-mix. These were applied on the same date as the other treatments which was timed for efficacy of a pyrethroid. Additionally, Orthene and Orthene/Tame were applied to additional untreated plots 7-8 days after the initial spray date. The products and application rates were as follows:

Product	Percent Active Ingredient Of Finished Spray
Capture 2EC	0.025
Pounce 3.2EC	0.024
Tempo 2S	0.0078
Mimic plus	0.014
Latron CS (surfactant)	
Foray 48B	NA
Foray 48B plus extender	NA
Orthene 75WSP	0.11
Orthene plus Tame 2.4EC	0.04 plus 0.025

Two tests were conducted during the first generation of tip moths in Spring of 1996. One site was in the Coastal Plain of Alabama on Jefferson Smurfit Corp. Land near Brewton, and the other in the Upper Coastal Plain of Georgia on Union Camp Corp. land near Waynesboro. Tip moth population was low on the Alabama test with the check plots

averaging only 24%. All treated plots contained significantly fewer infested shoots in the top whorl than the control (Figure 9) with a strong trend towards treatment efficacy in terminal shoot infestation. Infestation levels were held below 10% in all treatment plots, with several treatments averaging less than 5%. Tip moth pressure was not high enough to provide a rigorous test in this instance. The Upper Coastal Plain site in Georgia had similarly low tip moth populations with the infestations in the top whorl averaging 26% (Figure 10). Once again, all treated plots had significantly fewer infested shoots in the top whorl than untreated control plots. Most treatments were at or below 6% infestation in top whorl shoots. Terminal shoot infestation showed a strong trend for treatment efficacy but were non-significant due to large variances between and among replicates. As in the Alabama test, tip moth pressure was considered to be minimal.

A third foliar application test was conducted on Union Camp Corp. land in the Upper Coastal Plain of Virginia during the third generation of tip moths. Tip moth pressure was extreme, approaching 100% of available shoots for untreated trees during the previous generation. Susceptible life stages become increasingly difficult to target with each successive tip moth generation, and the developmental stages present in this plantation were predictably strung out from early larvae through pupae. Infestations of top whorl shoots in the check plots were above 60%. This was a purposefully conservative count on our part because damage from the previous generation was so extreme and persistent that it was difficult to sort out from the currently infested shoots. All treatments had fewer infested shoots than the untreated checks (Figure 11). Considering the very high tip moth population and the strung out nature of this third generation, all treatments performed well. It appeared that the pyrethroid compounds were more effective than others as a group. This could be an artifact of spray timing, however.

Figure 1.

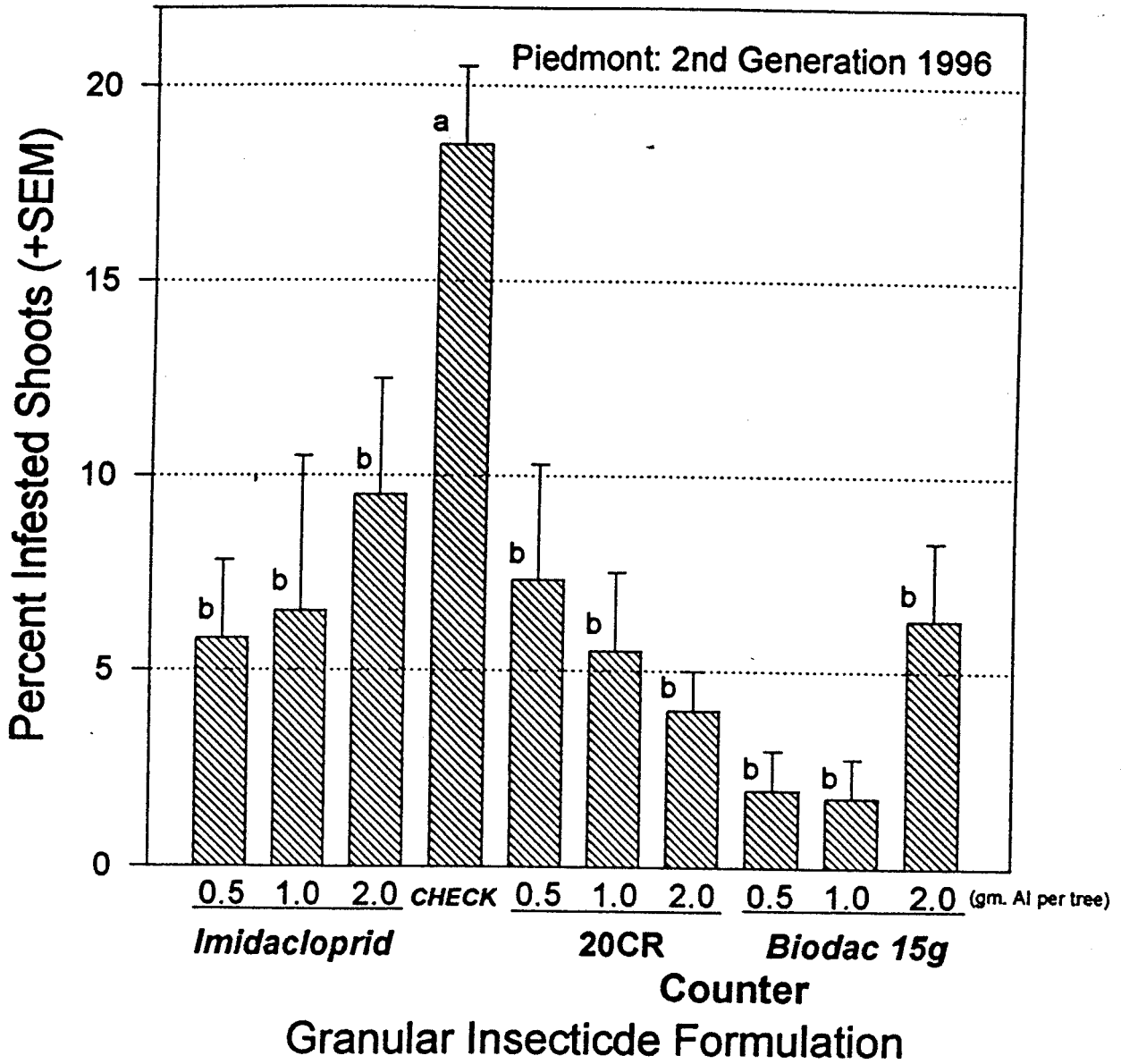


Figure 2.

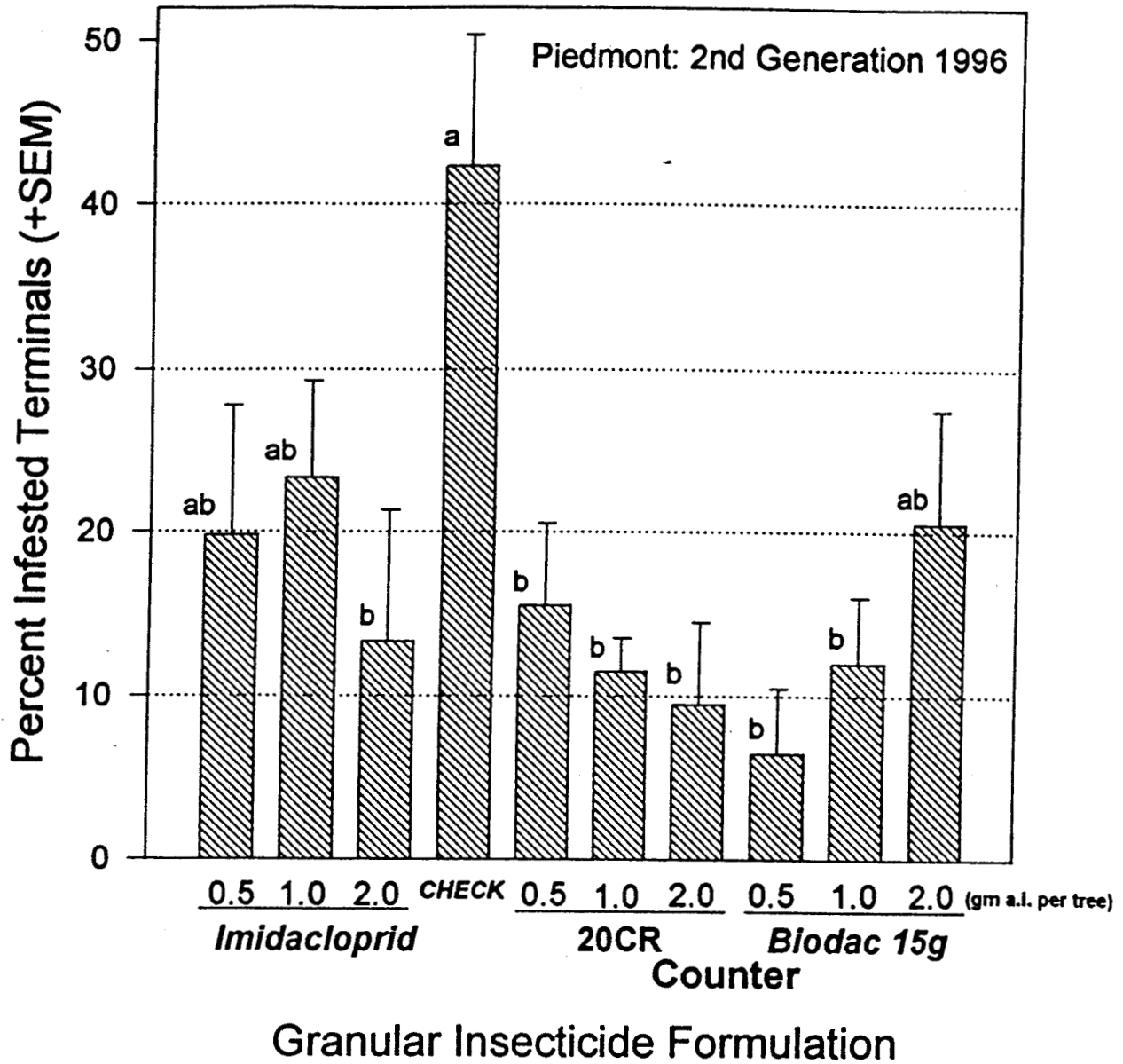


Figure 3.

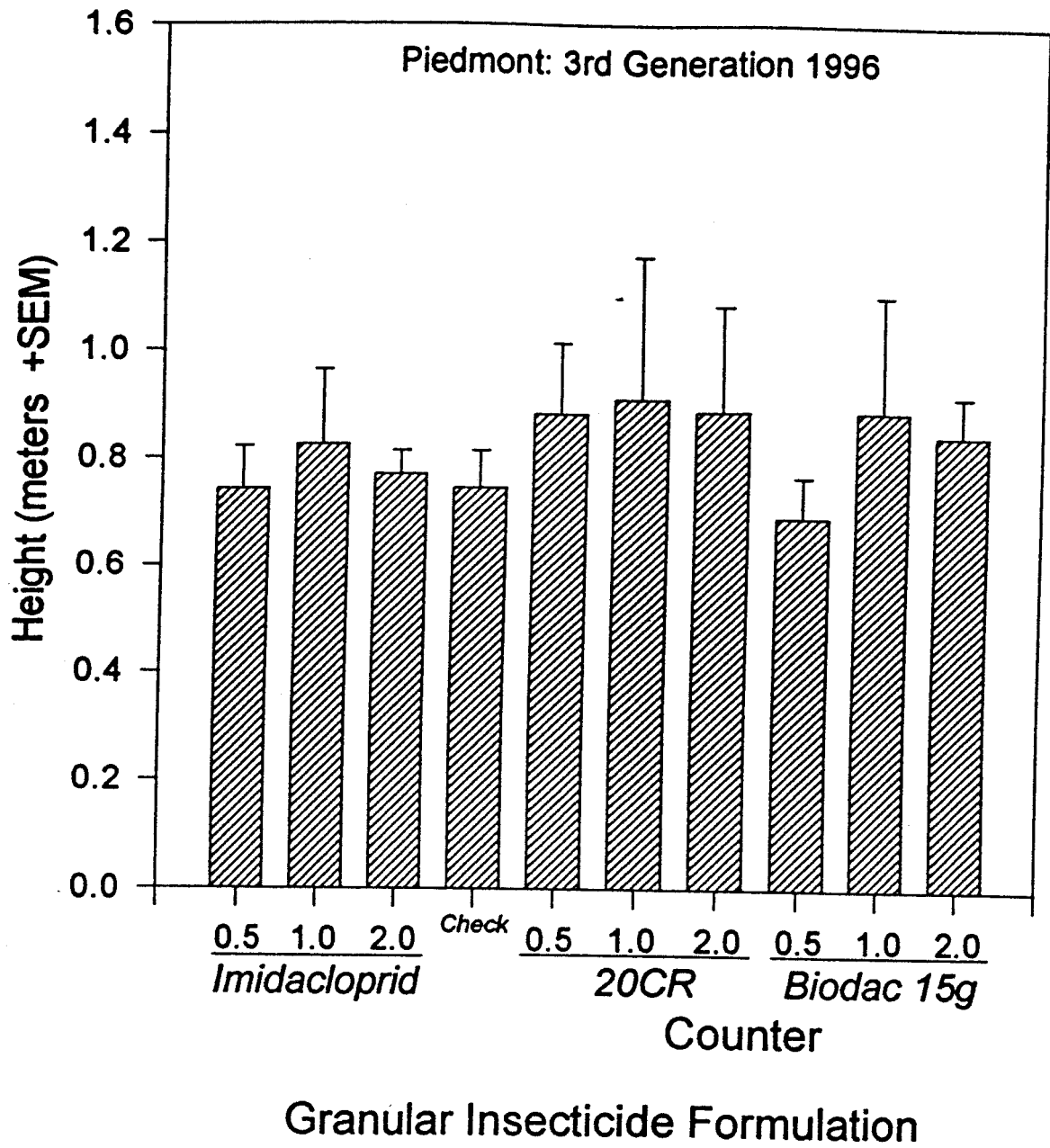


Figure 4.

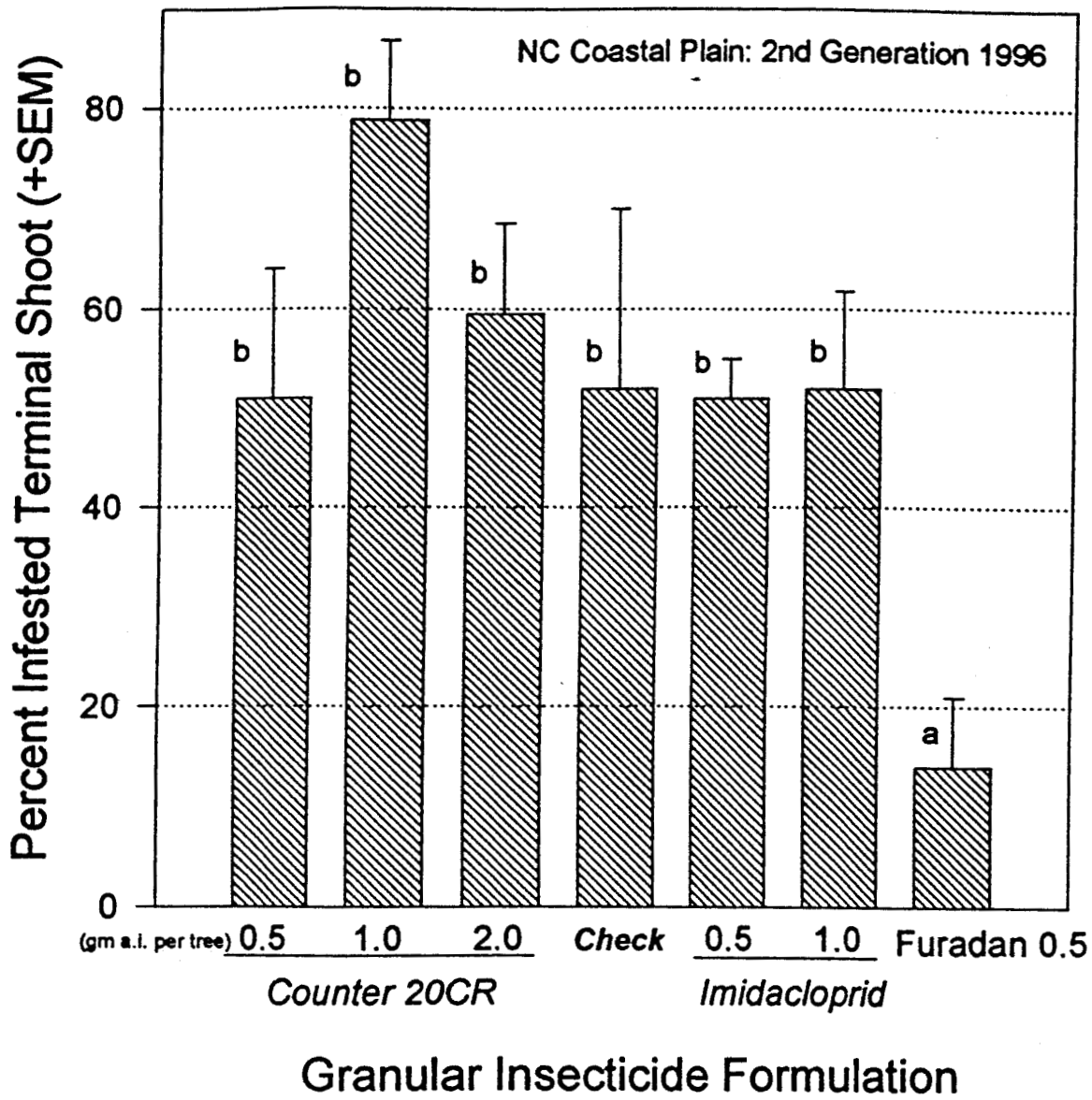


Figure 5.

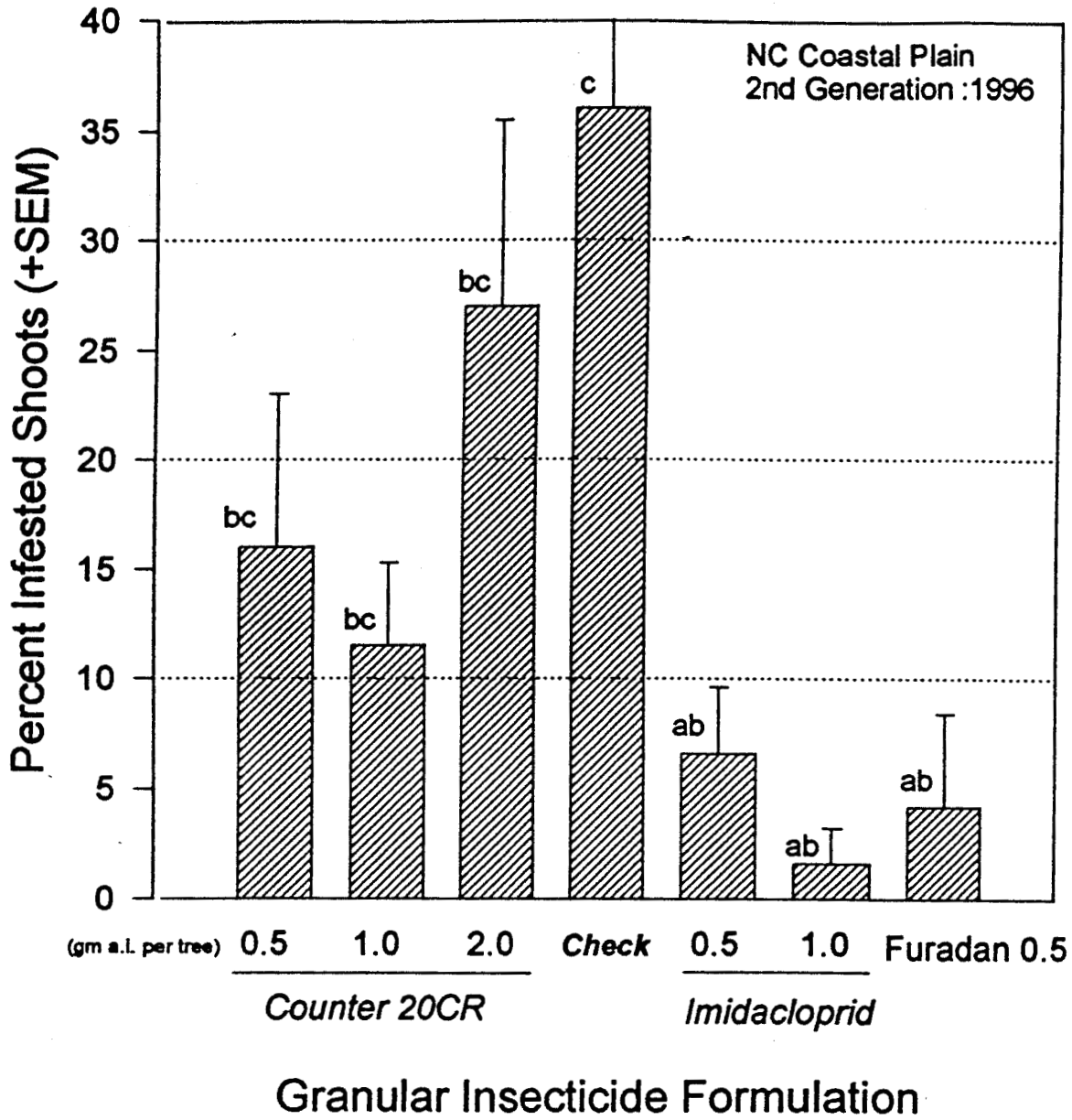


Figure 6.

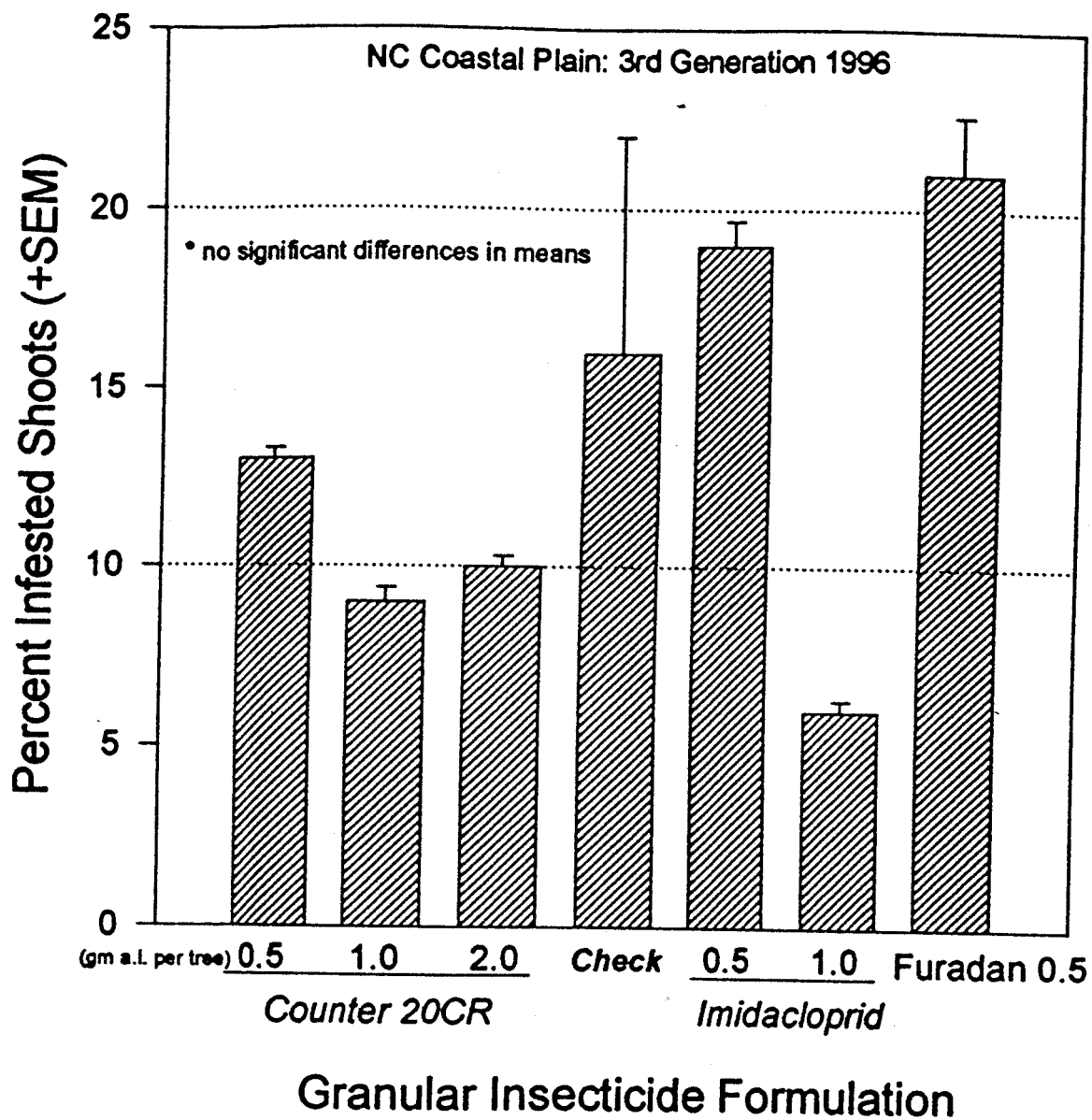


Figure 7.

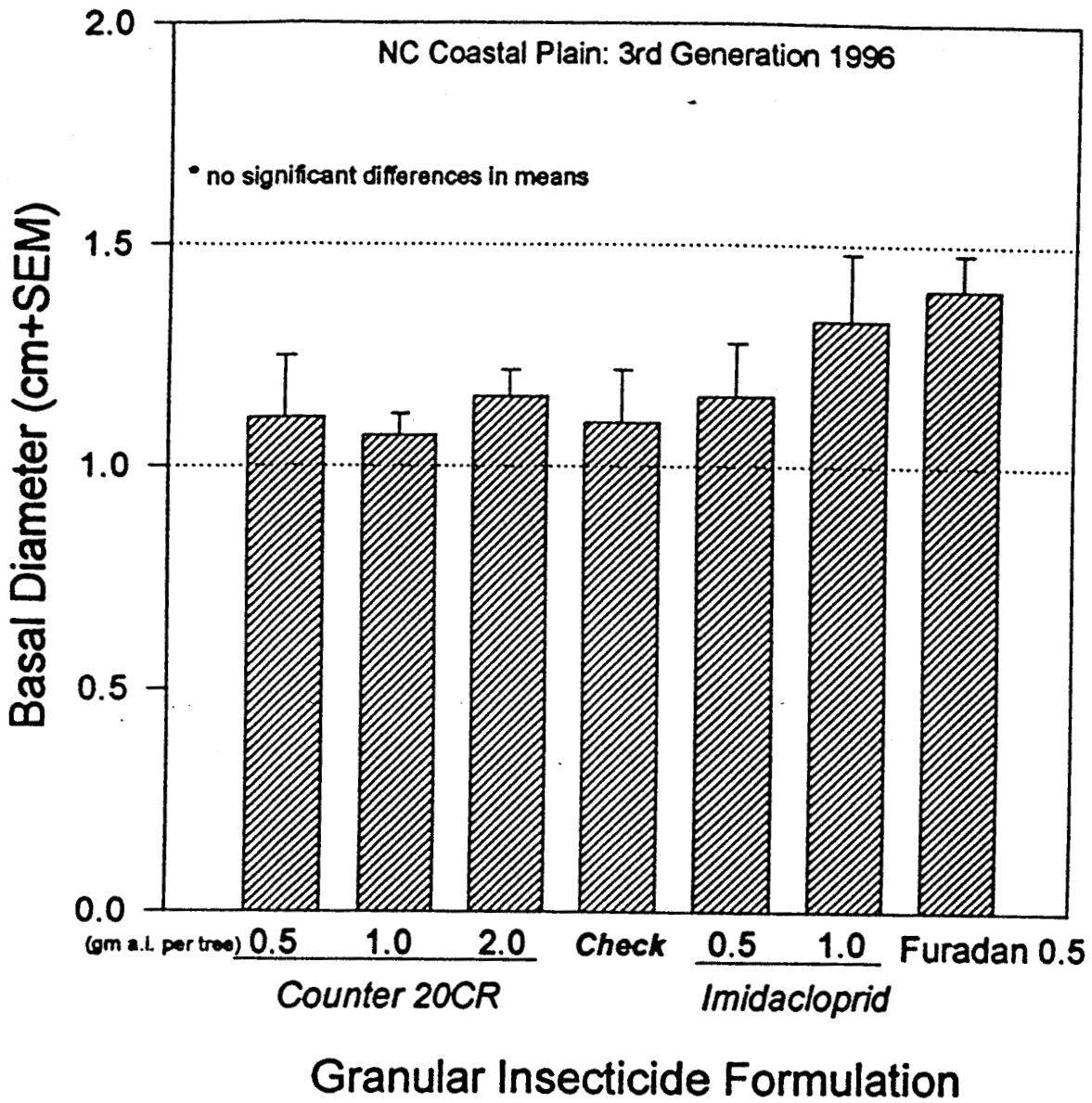


Figure 8.

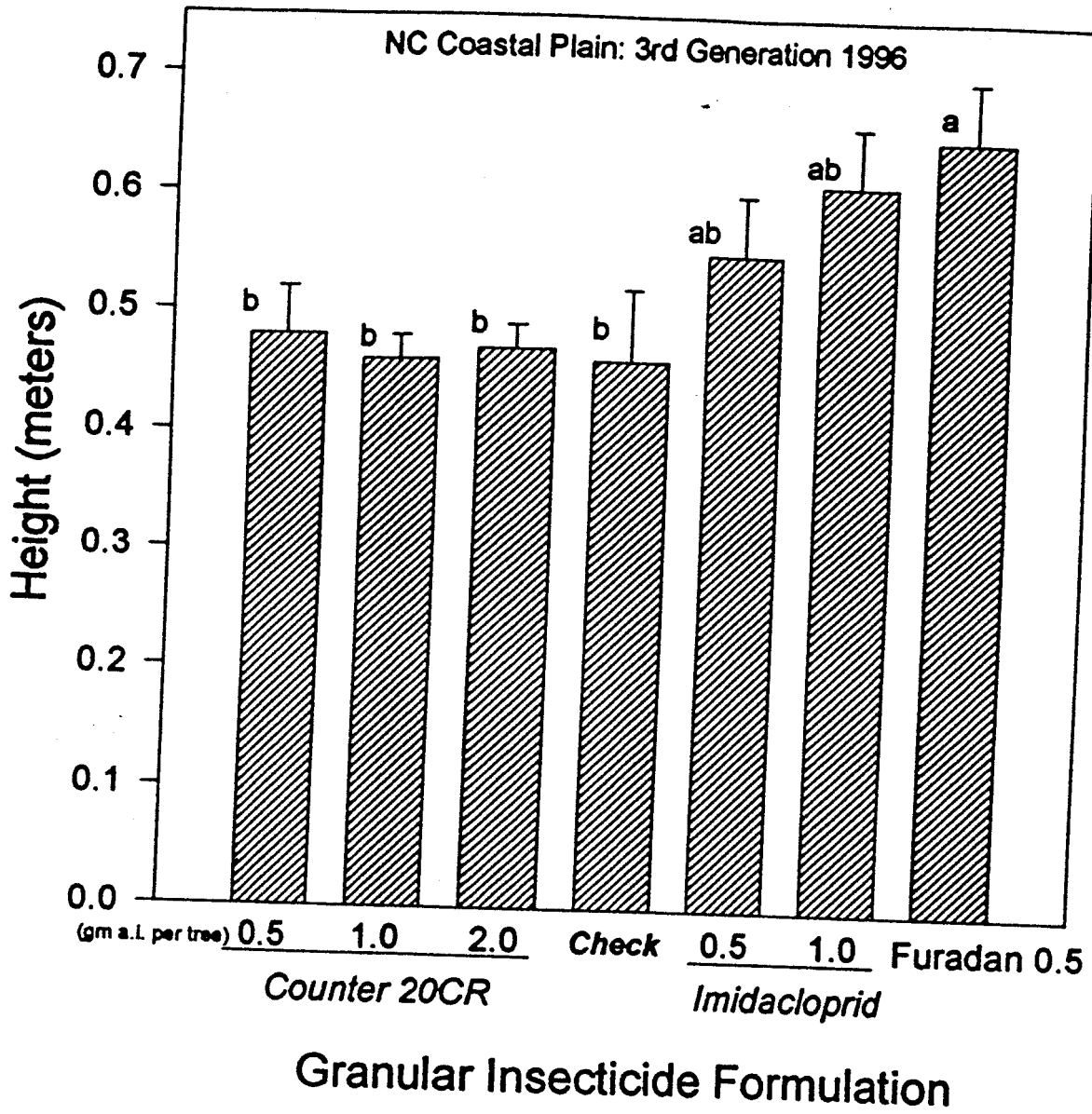


Figure 9.

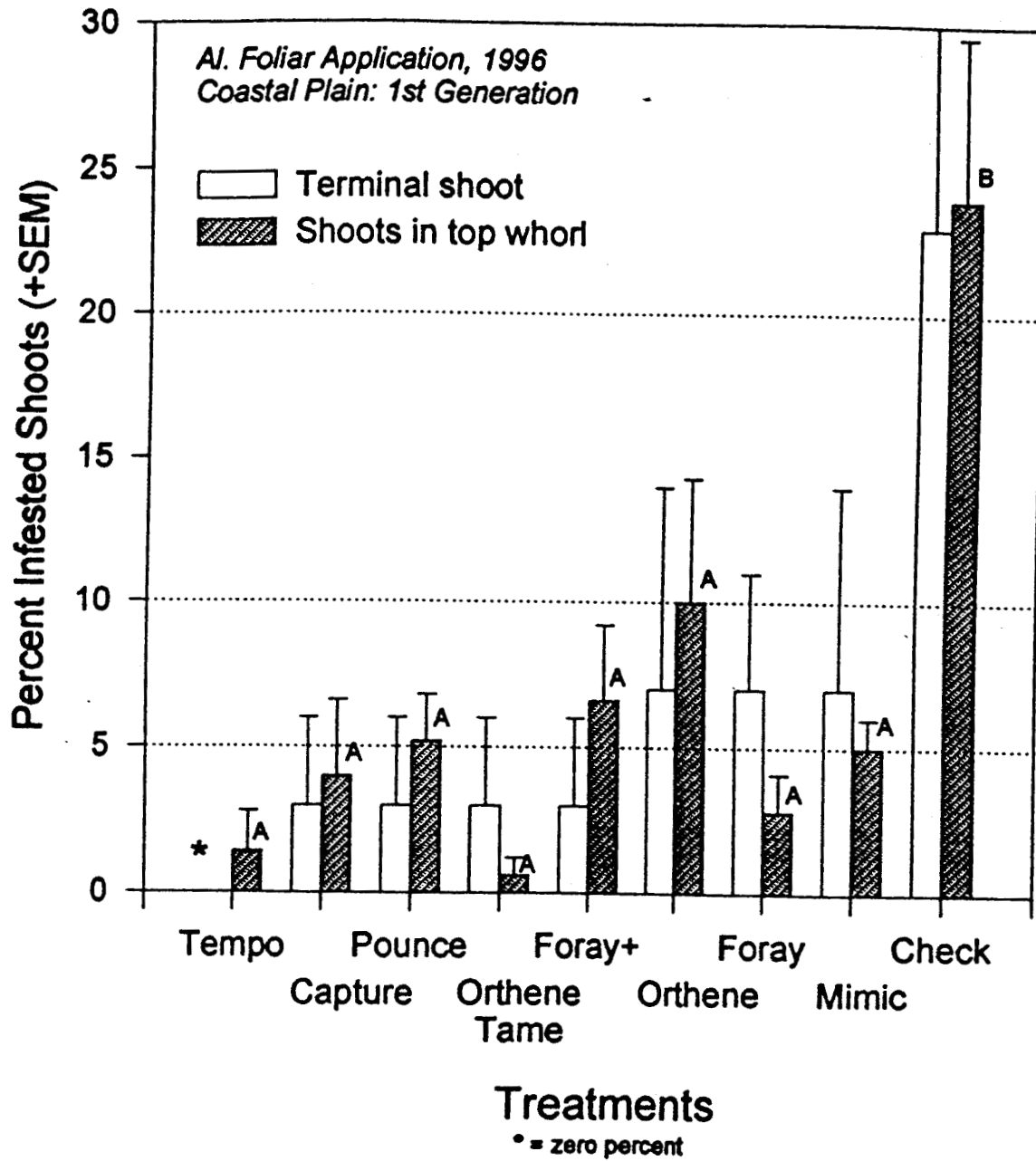


Figure 10.

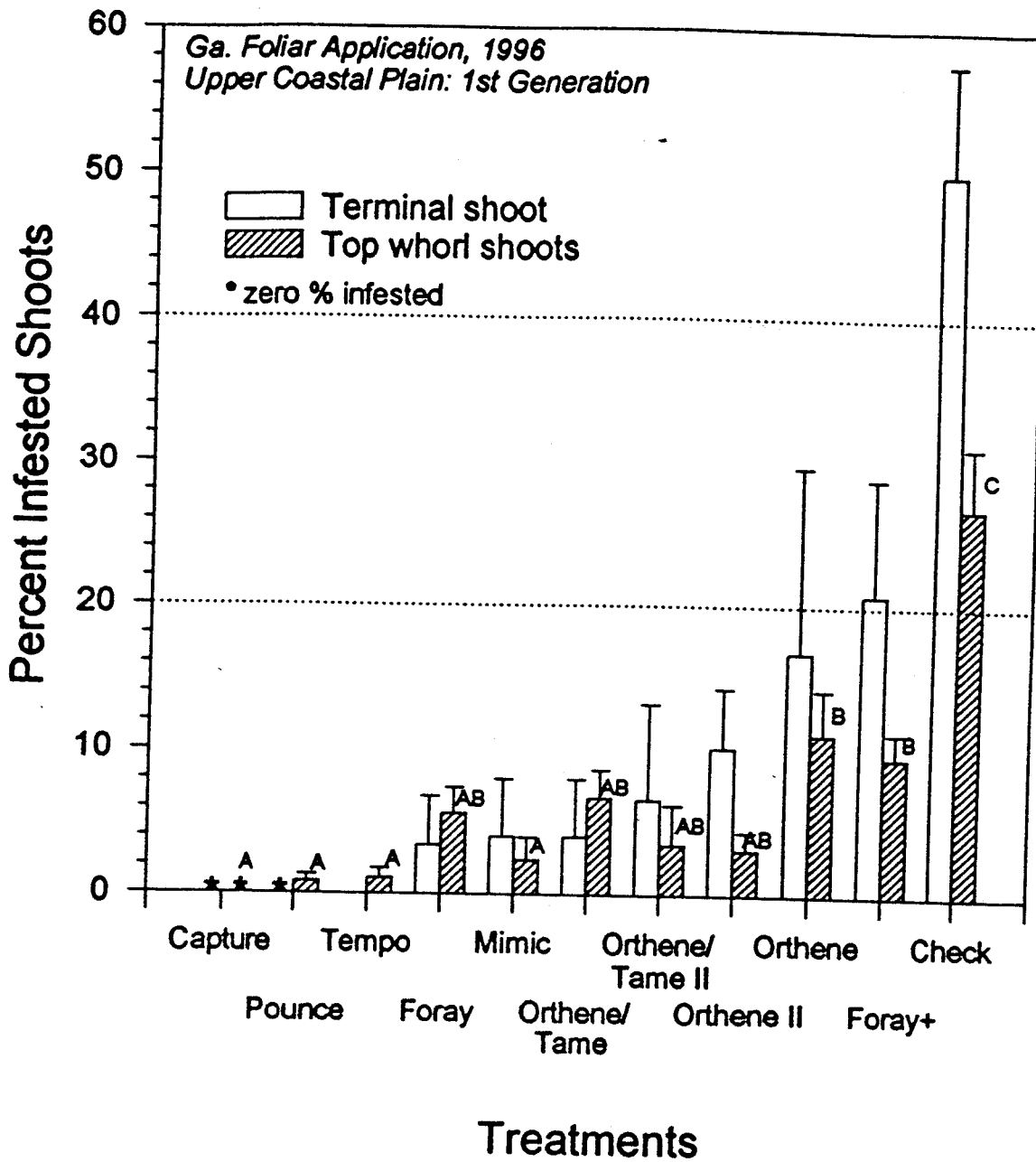
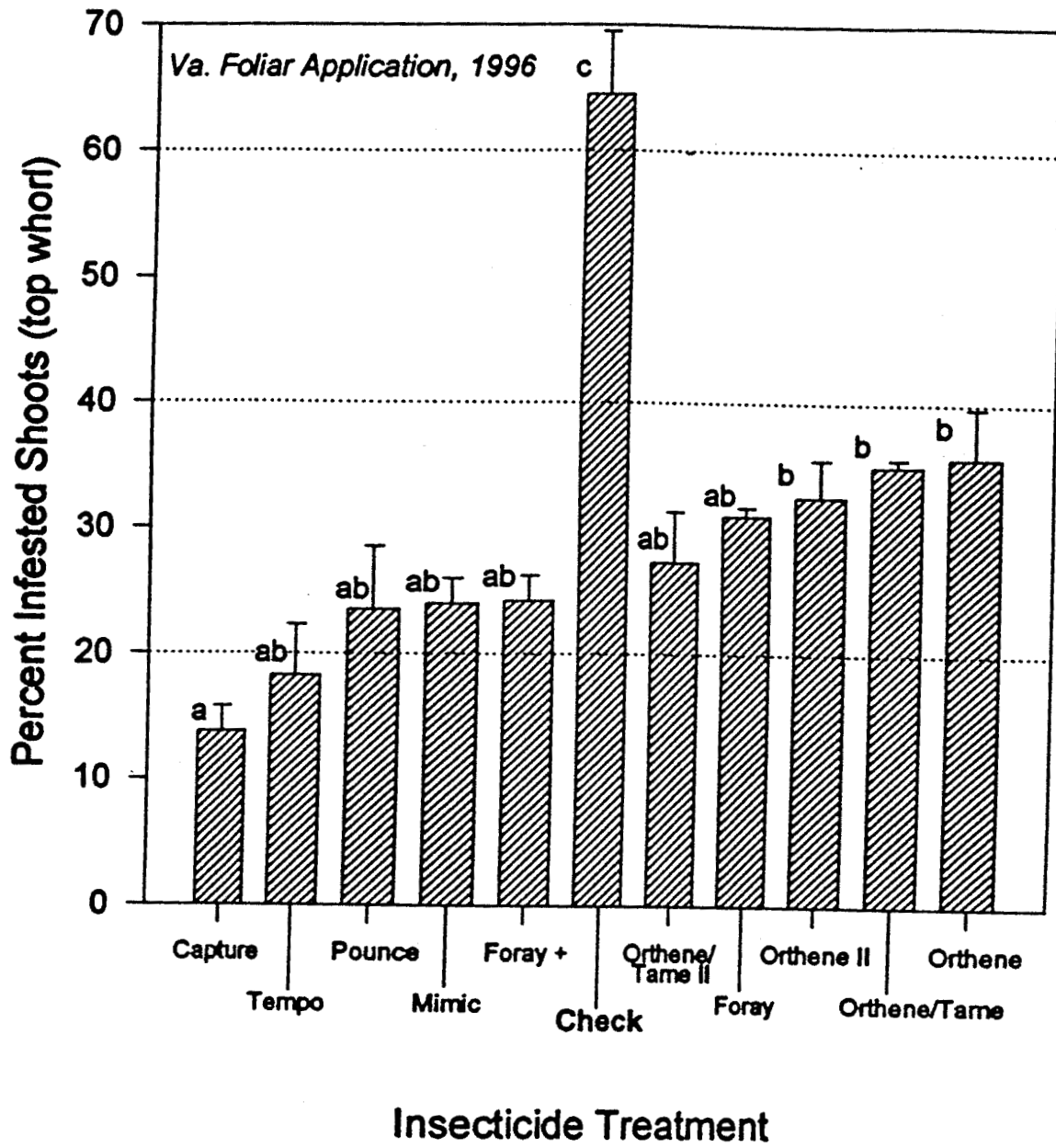


Figure 11.



Studies On Natural Enemies

Research on natural enemies at the University of Georgia has continued along three primary fronts. One objective is simply to better define the natural enemies complex in the coastal plain, since much of the heavy tip moth damage occurs there. Work at Georgia Southern University under the direction of Dr. Dan Hagan is also being done on the same objective. A second objective in the UGA studies by Ken McCravy as part of his dissertation research is to determine how the presence and/or quantities of herbaceous vegetation affects the abundance, diversity and efficacy of tip moth parasitoids. His progress report is included here. A third objective is to determine the identity of egg parasites and to assess their contribution to tip moth mortality. Three egg parasites have been identified (all *Trichogramma* Spp.) and Ken has prepared a manuscript on the impact of egg parasitism relative to egg density.

Effects of Herbaceous Vegetation Control on Parasitoids of the Nantucket Pine Tip Moth

Introduction

Populations of tip moths are generally higher in stands under intensive site management and with little competing vegetation. One possible reason for this is a decline in populations of tip moth natural enemies due to loss of food sources, habitat, or changes in microclimate. In this study, the effects of vegetation control on parasitoids of tip moths were examined at three study sites in the coastal plain of Georgia.

Materials and Methods

This study was done at two sites near Waynesboro, GA and a third site near Statesboro, GA. Sites ranged from 80 to 120 acres. Each site was divided into two large treatment plots, with one plot receiving broadcast herbicide treatment and the other no herbicide treatment. At the two Waynesboro sites, the untreated plots were augmented with commercial wildflower seed in an attempt to provide additional pollen and nectar sources, but this experiment failed due to a general failure of the seeds to germinate.

Vegetation was sampled at each site in June, August, and October, 1996. Twenty one meter square quadrats were randomly located within each plot. For each quadrat, vegetation was quantified, and samples of all plants were collected for later identification.

Tip moth populations were assessed for each generation (second, third, and fourth or overwintering) at each site by counting infested and uninfested shoots on 50 randomly selected, permanently marked sample trees per plot. Data were expressed as percentage of shoots attacked. The study was not initiated in time to estimate first generation damage.

In order to measure parasitism rates of tip moths, parasitoids and adult tip moths were reared in the laboratory from field-collected infested shoots. For each site and each tip moth generation, 2000 infested shoots were randomly collected in each treatment plot when moths were in the late larval/pupal stages. Shoots were returned to the laboratory, placed in rearing containers, and emerging parasitoids and adult moths were collected. Parasitism rates were determined by dividing the number of parasitoids by the total number of parasitoids and adult moths that emerged. Parasitoids were stored in 70% EtOH for later identification.

Malaise traps, which are designed to intercept flying insects, were used to collect adult parasitoids in the field. Two traps, one in each treatment plot, were installed at the

Statesboro site and at one of the Waynesboro sites. Insects were collected every five days, preserved in 70% EtOH, and returned to the laboratory for sorting and removal of parasitic hymenoptera and diptera.

Results and Discussion

For all tip moth generations and all sites, the quantities of competing vegetation were significantly less in the herbicide-treated than in the untreated plots. Percent ground cover ranged from 9.8% to 54.8% for treated plots over all sites and generations, while the range for untreated plots was 36.0% to 78.3%. Attempts at augmentation of flowering vegetation by sowing wildflower seed was largely unsuccessful, as very few proceeded to germinate and flower. Blackberry (*Pubus* spp.), greenbrier (*Smilax* spp.), maypops (*Passiflora incarnata*), prickly pear (*Opuntia compressa*), and muscadine (*Vitis rotundifolia*) were the most common plants found.

Tip moth infestation rates, expressed as percentage of shoots infested, are shown in Figure 1. These are combined data for three generations for each study site, as well as the totals for all sites and generations. In all cases, the untreated plots had significantly greater infestation rates than did the herbicided plots. This finding is contrary to most of our previous data which show that infestations are generally higher in stands where competing vegetation has been controlled. It may be that the trees in the herbicide-treated plots had greater resistance to tip moth attack due to increased vigor resulting from the decrease in competing vegetation.

Rearings of tip moth parasitoids from infested shoots yielded a total of 2389 instances of parasitism for the three study sites combined (Figure 2). Three species of parasitoids were responsible for over three-quarters of this parasitism. *Eurytoma pini*, a eurytomid wasp, was the most common parasitoid, accounting for 32.1% of tip moth parasitism.

Hyssopus rhyacioniae, a gregarious eulophid wasp, was responsible for 25.9% of parasitism. It should be noted that the mean brood size for *H. rhyacioniae* in this study was about seven per tip moth larva. Therefore, data on parasitism rates for this parasitoid represent actual numbers of adults reared divided by seven. *Lixophaga mediocris*, a tachinid fly, showed 19.0% of parasitism, and braconid wasps, mostly *Macrocentrus ancylivorus*, accounted for 11.1%. One interesting feature of these rearing data is the lack of ichneumonid wasps, particularly *Campoplex frustranae*, in the coastal plain. *Campoplex frustranae* was the most common hymenopteran parasitoid reared from piedmont collections in studies by Eikenbary and Fox (1965) and Freeman and Berisford (1979).

Overall tip moth parasitism rates for all sites and generations were 64.9% for herbicide-treated plots and 62.4% for untreated plots (Figure 3). Differences between treatment plots were statistically significant only for the Statesboro site. Among the most abundant species, *Eurytoma pini* showed no significant difference in parasitism rates between treatments (Figure 4). *Lixophaga mediocris* showed increased parasitism in the untreated plots, but this result was borderline nonsignificant. Braconids caused significantly greater parasitism in the untreated plots, while parasitism by *H. rhyacioniae* was much greater in the herbicide-treated plots. This latter result is surprising, and could possibly reflect a lack of predators and/or competitors in the less vegetated plots. At any rate, the lack of overall differences in parasitism between the herbicided and untreated plots seems to mask an interesting assortment of vegetation control effects at the species level.

Sorting and identification of malaise trap samples is an ongoing process. Figure 5 shows mean numbers of parasitoids captured during six five-day trapping periods in each treatment plot at the Statesboro and Waynesboro 1 study sites are given. These numbers show a very slight increase in hymenopterous parasitoids in the untreated plots, while

thereverse was true for tachinids. These data should be regarded as preliminary at this point.

References Cited

Eikenbary, R. D. and R. C. Fox. 1965. The parasites of the Nantucket pine tip moth in South Carolina. S. C. Agric. Expt. Sta. Tech. Bull. 1017.

Freeman, B. L. and C. W. Berisford. 1979. Abundance and parasitic habits of some parasitoids of the Nantucket pine tip moth (Lepidoptera: Tortricidae). Can. Entomol. 111: 509-514.

Parasitism of Tip Moth Eggs by *Trichogramma* Spp. Wasps

The manuscript prepared by Ken McCravy on egg parasitism is appended as part of this report. The paper shows that once *Trichogramma* females find and parasitize one or more tip moth eggs on individual needle fascicles, parasitism of other eggs in the vicinity increases. However, when eggs reach high densities, the percentage of parasitism decreases even though the total number of parasitized eggs increases. This study provides additional data which show that egg parasitism is an important factor in tip moth population dynamics. The *Trichogramma* wasps are the only natural enemies identified so far which kill tip moths before they inflict any damage on their hosts.

Tip Moth Infestation Rates

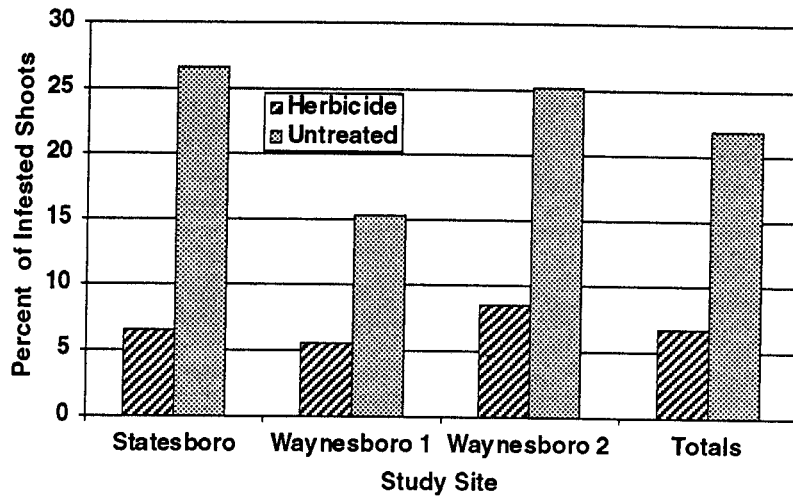


Figure 1. Tip moth infestation rates in herbicide-treated and untreated plots at three study sites. All differences were statistically significant.

Relative Abundance of Tip Moth Parasitoids

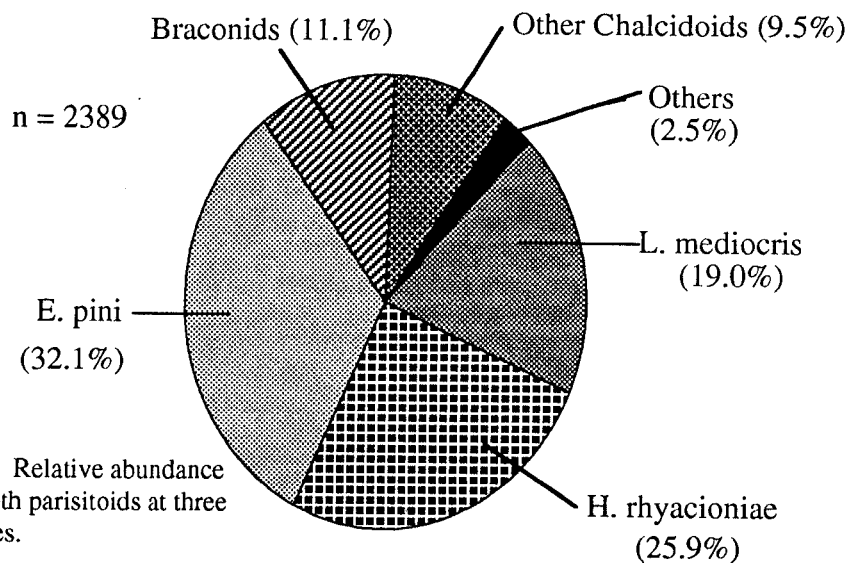


Figure 2. Relative abundance of tip moth parasitoids at three study sites.

Parasitism in Treated vs. Untreated Plots

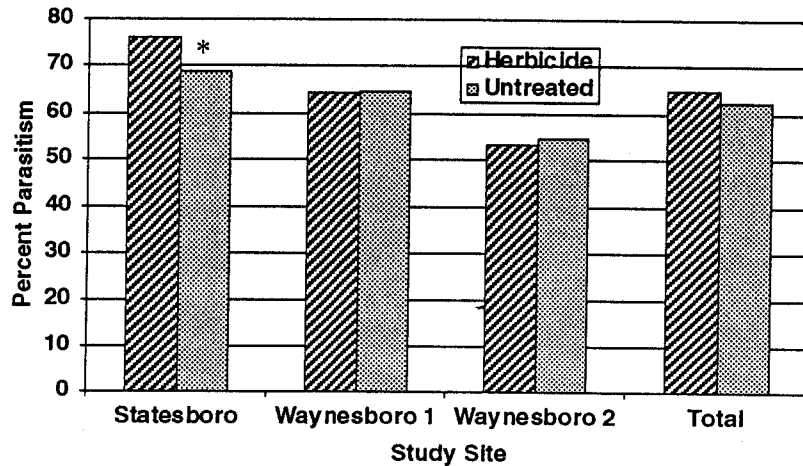


Figure 3. Tip moth parasitism rates in herbicide-treated and untreated plots at three study sites. * = statistically significant difference.

Parasitism by Common Tip Moth Parasitoids

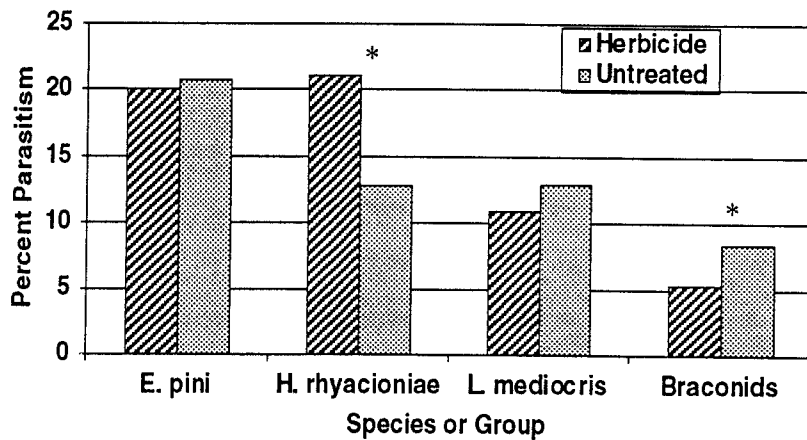


Figure 4. Parasitism rates by the most abundant tip moth parasitoids in herbicide-treated and untreated plots. * = statistically significant difference.

Malaise Trapping of Parasitoids

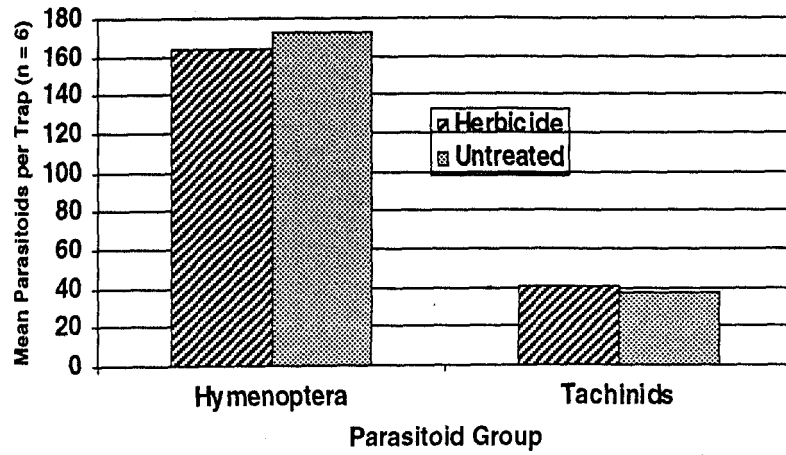


Figure 5. Mean numbers of parasitoids captured by malaise traps in six five-day trapping periods at two study sites.

APPENDIX

Tip Moth Egg Parasitism by *Trichogramma* Spp. Wasps

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**Parasitism by *Trichogramma* spp. (Hymenoptera: Trichogrammatidae) in
Relation to Nantucket Pine Tip Moth (Lepidoptera: Tortricidae)
Egg Density and Location**

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Running head: *Rhyacionia* egg parasitism by *Trichogramma*

ABSTRACT Patterns of parasitism by *Trichogramma* spp. in relation to density and location of Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock), eggs were examined during 1994 in a 13 ha, two year old *Pinus taeda* L. plantation in northeastern Georgia. Egg densities were adjusted by enclosing trees in fine mesh screen cages and introducing differing numbers of tip moths temporarily. After exposing eggs to naturally occurring parasitism, all shoots were removed, and eggs were counted and evaluated for parasitism. Tip moth egg densities ranged from 203 to 2579 per tree for the spring generation, and one to 89 per tree for the summer generation. Tip moths deposited significantly greater numbers of eggs on needles than shoots on high vs. low egg density trees. Overall parasitism rates were 37.2% and 43.3% for spring and summer generation eggs, respectively. Parasitism was density-independent at the whole-tree level in both generations, but spring generation parasitism was strongly inversely density-dependent in the top whorl. Numbers of eggs per needle fascicle ranged from one to 15 for spring generation trees. Actual numbers of parasitized eggs per "discovered" fascicle (one on which parasitism occurred) increased with egg density, but the percentage of parasitized eggs decreased. Egg density had no effect on fascicle discovery. These factors produced an inversely density-dependent relationship between egg parasitism and density at the fascicle level. Eggs located on shoots suffered significantly greater parasitism rates than eggs on needles. Implications of these results are discussed.

KEY WORDS *Rhyacionia frustrana*, Nantucket pine tip moth, *Trichogramma* spp., egg parasitism, egg location, egg density

The Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock), is one of the most common pests of some commercially important southern pines, attacking seedlings and saplings under 5 m tall. It has three generations per year in the Georgia Piedmont Plateau. Its eggs are laid primarily on the surface of growing shoots and the inner surface of needles, near the fascicle sheath. Early instar larvae mine the needles and shoots, whereas later instar larvae bore into the shoot, killing it and often causing loss of growth, form, and wood quality (Berisford 1988). However, tip moth densities, and therefore extent of damage, vary considerably among stands, for reasons that are poorly understood (Berisford and Kulman 1967).

Egg parasitism has been shown to be an important mortality factor for tip moths. Gargiullo and Berisford (1983), in a key factor analysis, found highest *R. frustrana* mortality among the egg and pupal stages, with up to 87 percent egg mortality and 47 percent egg parasitism by *Trichogramma* sp. Similarly, Yates (1966) found 64.5 percent egg mortality due to *Trichogramma minutum* Riley in central Georgia. It might be expected that, as tip moth egg densities increase, parasitism rates would also increase, because of increased chance of location of other host eggs nearby. Egg mortality in *R. frustrana* has been shown to be temporally density-dependent with most mortality caused by *Trichogramma* parasitism (Garguillo and Berisford 1983). However studies of parasitism in relation to spatial variation in egg density have been inconclusive. Responses of *T. minutum* to varying European pine shoot moth, *R. buoliana* (Schiffermuller) egg mass sizes have indicated that once *T. minutum* locates an egg mass it tends to oviposit in all the eggs contained in that mass (Haynes and Butcher 1962; Kulman 1965). However, Kulman also found that the rate of parasitism was greatest in egg masses containing four eggs, and decreased in larger and smaller masses. Among studies of *Trichogramma* parasitism of other lepidopteran pests, density-dependent (Edwards 1961; Gross 1981), density-independent (Pak et al. 1989; Pena and Waddill 1983), and inversely density-dependent (Hirose et al. 1976; Morrison et al. 1980) relationships have been found.

The objective of our study was to determine the effects of *R. frustrana* egg density and location on *Trichogramma* spp. parasitism rates.

Materials and Methods

This study was conducted during February - July, 1994 in a 13 ha, two year old loblolly pine (*Pinus taeda* L.) plantation ca. 32 km southwest of Athens in Walton Co., Georgia. In late February, seven trees, between 1.4 and 1.6 m tall and similar in form, were chosen for study. All were located at least 15 m from the plantation edge and from each other. Six of these were enclosed in fine mesh (0.35 mm) Lumite^R screen cages, 1.8 m³ in size. Approximately 5250 tip moth-infested shoots, with overwintering pupae inside, were placed in the cages at this time in the following amounts: 2000, 1500, 1000, 500, 250, and 0. Approximately 2100 reared tip moth adults were also allocated over a seven day period in late March: 800, 600, 400, 200, 100, and 0. The remaining tree was left uncaged to get an approximation of the normal number of eggs laid on a tree. After allowing three additional days for mating and oviposition, cages were removed to allow attack by parasitoids. In late April, trees were divided into terminal, subterminal (the next four highest shoots after the terminal), middle (upper half of the remainder of the crown), and bottom (lower half of the remainder of the crown) strata. All shoots from each tree were removed, kept separate by tree and stratum, and returned to the lab for examination for parasitized and unparasitized eggs, the former being evident due to the blackening of the vitelline membrane that occurs when parasitism has taken place (Flanders 1937). Viable, parasitized eggs were held for rearing of *Trichogramma* adults for species identification. When a tip moth egg was located, the tree number, stratum, and egg location (shoot or needle) were recorded. Similar methods were used for the summer tip moth generation, beginning in early May. Because of much lower tip moth populations in this generation, fewer infested shoots containing pupae were collected. They were placed in the enclosure cages in the following amounts: 400, 300, 200, 100, 50, and 0. In early June, cages were

removed to allow attack by parasitoids. All shoots were collected from the study trees in late June and data were taken as for the spring generation.

Least squares regression was used to analyze relationships between egg density (per tree and per fascicle) and parasitism (Velleman 1995). Comparisons involving egg location and parasitism were made by contingency table analysis using the chi-square test for independence (Abacus Concepts 1986).

Results and Discussion

Identification of *Trichogramma* adults. Forty-five adult male wasps were reared for identification. Male genitalia are required for identification of *Trichogramma* spp. (Nagarkatti and Nagaraji 1971), so females were not identified. Of these, 23 (51.1%) were identified as *T. pretiosum* Riley, 20 (44.4%) as *T. exiguum* Pinto/Platner, and 2 (4.4%) as *T. marthae* Goodpasture. The latter species is commonly used as a biological control agent of the European corn borer (*Ostrinia nubilalis* Hbn.) in Europe, but has not been previously reported from Georgia. Earlier works reporting *T. minutum* Riley as the sole egg parasitoid of *R. frustrana* should be viewed with caution, based on these results.

Patterns of tip moth oviposition. For the spring generation, tip moth egg densities ranged from 203 to 2579 eggs per tree for the seven study trees (Fig. 1a). The unenclosed tree, which was included in the analyses, contained 241 eggs, indicating that we successfully increased egg densities with the enclosure technique. Because of dramatically lower tip moth populations in the summer generation, egg densities ranged from one to 89 per tree, with the uncaged tree containing 11 eggs.

For the spring generation, 63.8% of eggs were laid on needles vs. 36.2% on shoots, and egg deposition was similar in the summer generation with 67.9% and 32.1% of eggs on needles and shoots, respectively. The proportion of eggs laid on shoots in this study was somewhat higher than the 20.5% and 6.0% found by Hood et al. (1985) for two tip moth generations in the Georgia Coastal Plain. Preferred oviposition sites varied dramatically with egg density in our study. In the spring generation, the four trees with

lower egg densities had significantly greater numbers of eggs on shoots vs. needles compared to the three trees with higher egg densities ($X^2 = 107.38$; $P = 0.0001$). These data suggest that tip moth females preferentially oviposit on shoots vs. needles at low to moderate densities even though parasitism is higher among eggs placed on shoots (Fig. 3). It may be that the shoot surface is a much more accessible location for female tip moths to oviposit, or perhaps shoots provide superior nutrition for feeding early instar larvae.

Parasitism and egg density. For the spring generation, egg parasitism rates ranged from 25.1% to 66.5%, with an overall rate of 37.2%. There was no correlation between egg density per tree and parasitism rate (Fig. 1a). The overall parasitism rate for the summer generation was 43.3%, ranging from 6.3% to 55.6%. There was no significant correlation between egg density and parasitism rate. Patterns of parasitism for the spring generation varied among tree levels. Parasitism of eggs located in top level whorls (terminal and subterminal) showed a strong negative correlation with egg density (Fig. 1b), whereas parasitism of eggs in the middle and bottom levels was density-independent. In the summer generation, which had much lower egg densities, eggs in the upper tree levels had significantly greater parasitism rates than eggs in the middle and bottom levels ($X^2 = 12.28$; $P = 0.0005$).

Numbers of eggs per needle fascicle ranged from zero to 15 for the spring generation study trees. Because there were relatively few fascicles with higher egg densities, data for fascicles with 10 to 15 eggs were combined for this analysis. There was a significant increase in the number of parasitized eggs per "discovered" fascicle with increasing egg density (Fig. 2a), a discovery being a fascicle on which at least one instance of parasitism occurred (Morrison et al. 1980). However, there was a significant decrease in the probability of parasitism with increasing egg density per fascicle among discovered fascicles (Fig. 2b). This pattern, combined with the lack of response of *Trichogramma* discoveries to increasing egg density (Fig. 2c), resulted in a negative response of *Trichogramma* parasitism to egg density (Fig. 2d). These results are similar to those of

Morrison et al. (1980) and may reflect *Trichogramma* egg depletion at high host densities, increased rate of encounter with previously parasitized hosts, or both.

Parasitism and egg location. Tip moth eggs on shoots had significantly higher parasitism than eggs on needles for both generations (Fig. 3). Host location has been shown to be an important factor in host-finding by parasitoids, and differences in parasitism rates have been found for the same insect host on different plant structures. For example, Pimentel (1961) showed that *Pieris rapae* (L.) suffered greater parasitism on open leafed than curly leafed varieties of *Brassica oleracea* L., and Yu et al. (1984) found greater parasitism by *Trichogramma* spp. on upper surfaces of apple leaves than lower surfaces. In a study of host-finding in relation to plant structural complexity, Andow and Prokrym (1990) found that *T. nubilale* located hosts 2.4 times faster, searched 1.2 times longer, and produced a 2.9 times higher parasitism rate among *Ostrinia nubilalis* eggs on simple than complex surfaces. Structural complexity could be a factor in the low parasitism rates of eggs on needle fascicles in our study. Tip moth eggs are usually laid on the inner, slightly concave surface of needles near the fascicle sheath, where the egg is enclosed by (usually) three needles, a more complex and inaccessible location than the relatively flat and open surface of a shoot.

We found no evidence of a spatial density-dependent response of *Trichogramma* spp. to tip moth egg densities. At the very high densities of the spring generation, inverse density-dependent parasitism occurred at both the tree and fascicle levels. It may be that parasitoid egg depletion becomes a factor only at high egg densities, or that increased chance of encountering a previously parasitized host causes the parasite to leave the area before most eggs are attacked. The apparent preference of tip moth females for ovipositing on shoots rather than needles at low to moderate egg densities is somewhat surprising given the much greater probability of parasitism of eggs on shoots. Perhaps there is some nutritional advantage to first instar larvae feeding on shoots rather than needles, or there

could be time and energy constraints that make oviposition on shoots, a very apparent and accessible resource, advantageous despite the higher risk of parasitism.

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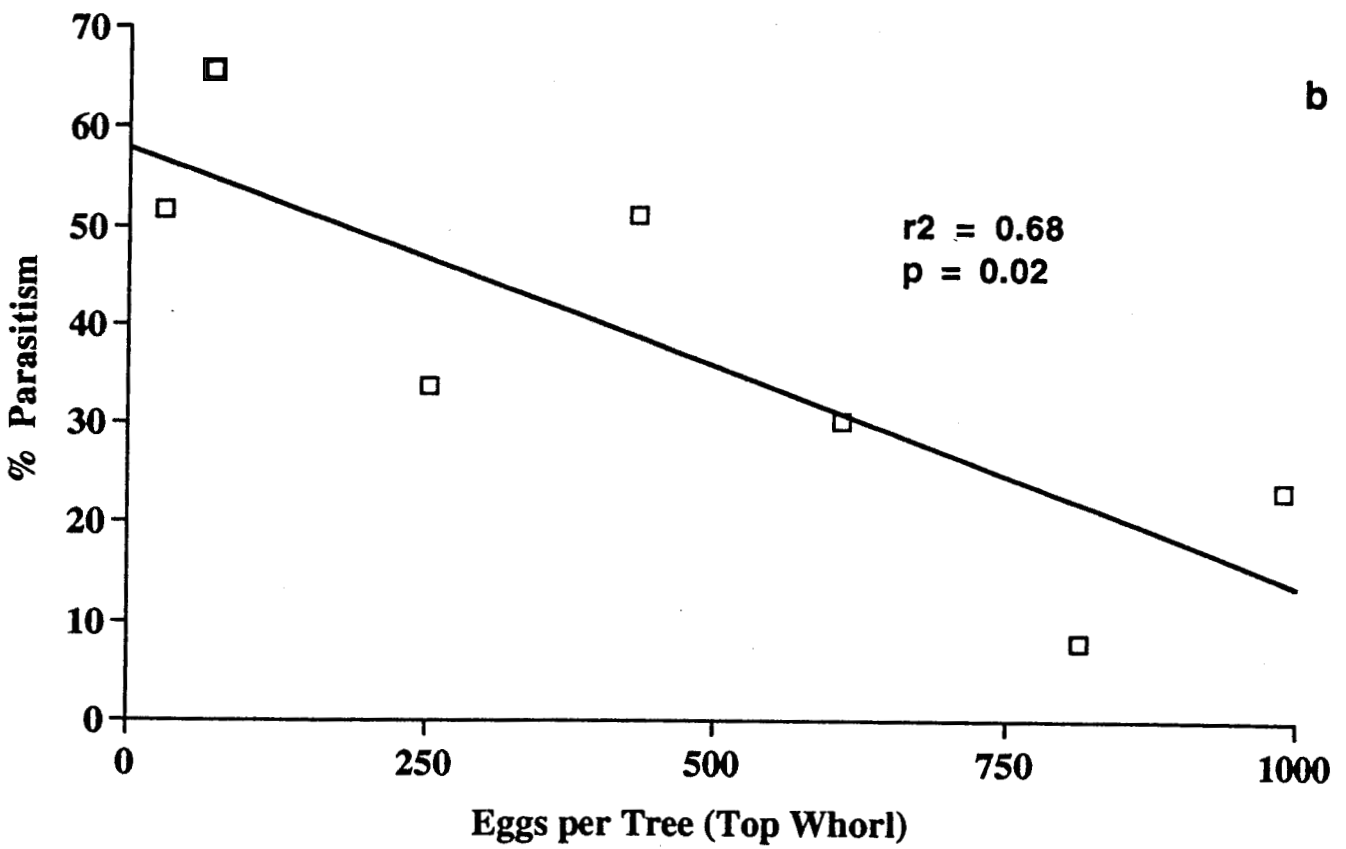
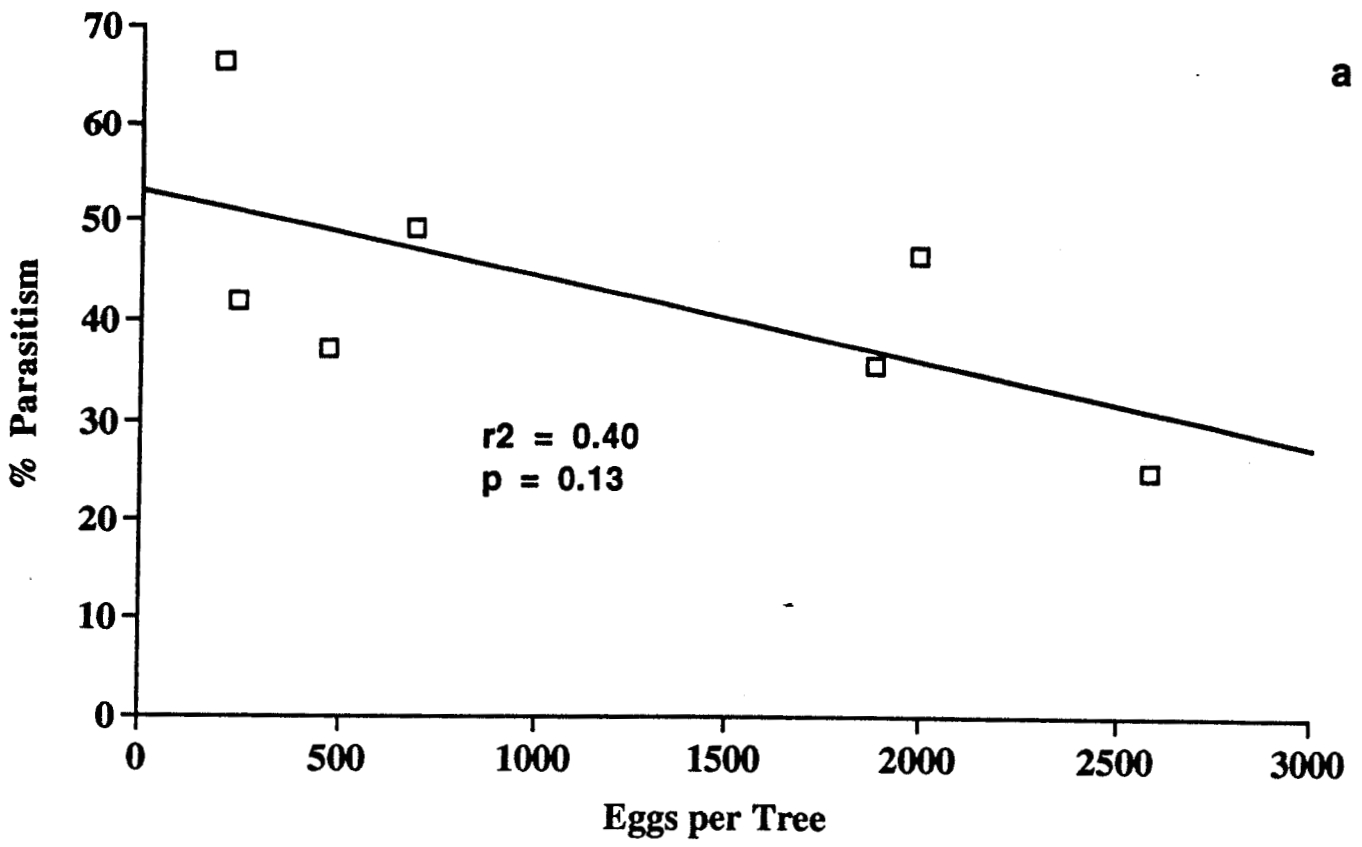
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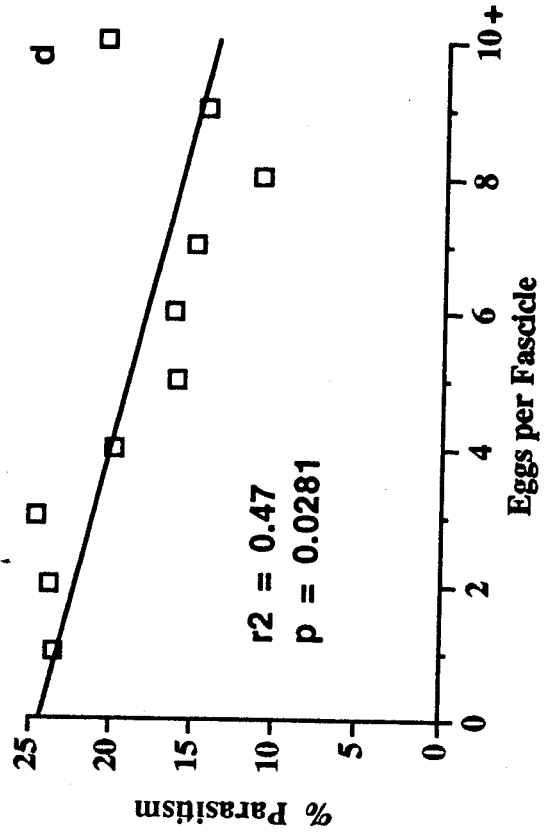
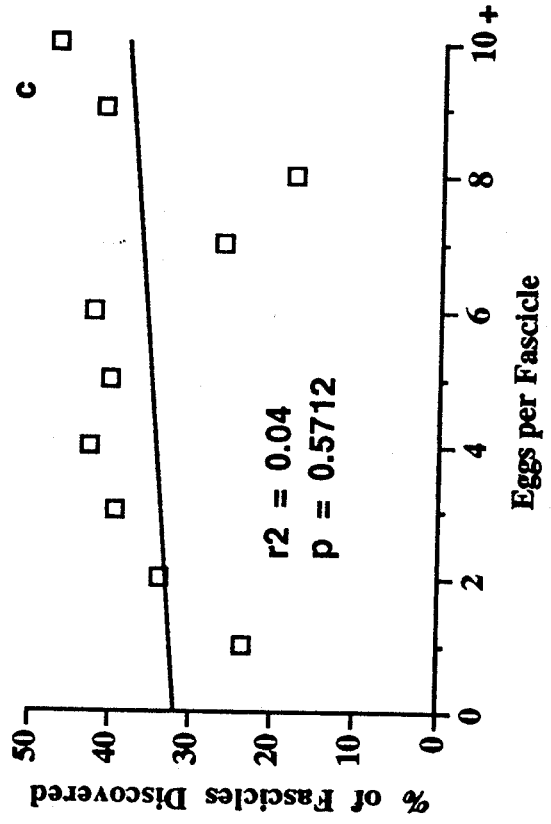
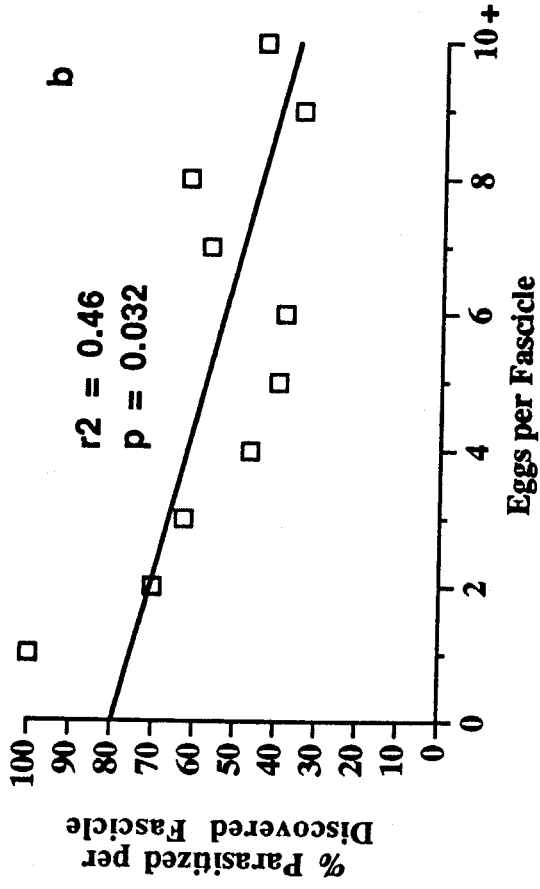
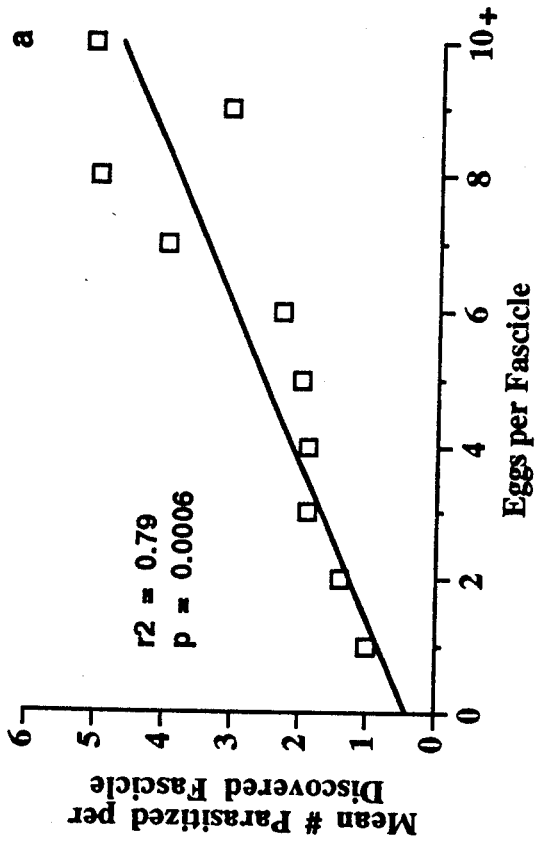
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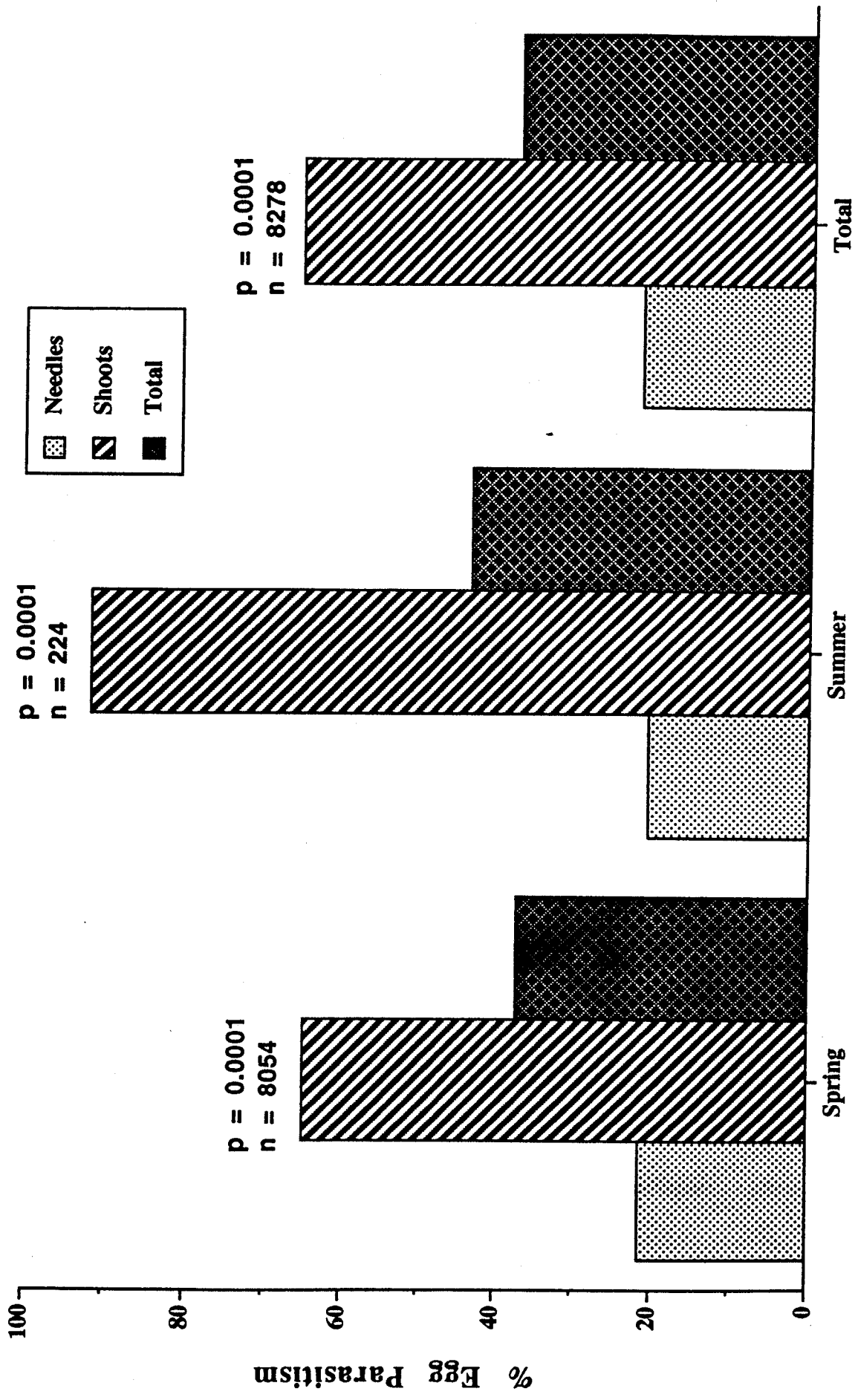
Fig. 1. Parasitism rates of *R. frustrana* eggs in relation to egg density (a) per tree and (b) per top whorl only.

Fig. 2. Parasitism rates of *R. frustrana* eggs in relation to egg density per fascicle.

Fig. 3. Parasitism rates of *R. frustrana* eggs on needles vs. shoots for each generation and total for all generations.







Tip Moth Generation