Nantucket Pine Tip Moth Development and Population Dynamics: Influence of Nitrogen Fertilization and Vegetation Control

John T. Nowak, Timothy B. Harrington, and C. Wayne Berisford

ABSTRACT. It is commonly believed that Nantucket pine tip moth (Rhyacionia frustrana [Comstock]) feeding damage on loblolly pine (Pinus taeda L.) increases in relation to the intensity of silvicultural practices. Some studies have produced contrary or inconclusive data regarding this issue. This study was designed to examine the relationships between tree growth rates and tip moth development by enhancing growth with nitrogen (N) fertilizer and herbicide applications. The four treatments were N fertilizer, herbicide, herbicide+fertilizer, and untreated control. These treatments were monitored for tip moth damage levels, tip moth pupal numbers per pine shoot, insect population dynamics, and tree growth. Pine growth was significantly greater in the herbicide treatments than in the other treatments. There was a significant increase in diameter related to the fertilizer treatments, but no differences in tree height or volume were detected. Pupal weight was significantly lower in the herbicide treatment in the second year. Tip moth population fluctuations were greater in the herbicide treated plots than in the untreated control, and there were significant linear relationships between these fluctuations in the treatments versus percent parasitism, pupal weight, and diameter growth. This study shows that tip moth populations are not necessarily increased or decreased by intensive management practices, but can be less stable due to these practices. For. Sci. 49(5):731–737.

Key Words: Rhyacionia frustrana, Pinus taeda, glyphosate, silviculture.

The Nantucket pine tip moth (Rhyacionia frustrana [Comstock]) is a common pest of recently regenerated loblolly pine (Pinus taeda L.) plantations. Feeding damage by this insect has been shown to decrease tree volume growth (Cade and Hedden 1987, Fettig et al. 2000, Nowak and Berisford 2000). Tip moth larvae decrease tree height and volume growth by feeding inside shoots and buds of loblolly, shortleaf (P. echinata Mill.), and Virginia pines (P. virginiana Mill.) (Berisford 1988). Cade and Hedden (1987) showed that tip moth control, applied at stand ages of 3–5 yr, increased stand volume at age 12 from 10.49 m$^3$/ha (150 ft$^3$/ac) to 14.9 m$^3$/ha (213 ft$^3$/ac). Tip moths have 3–4
generations per year in most of Georgia (Fettig et al. 2000). Benedict and Baker (1963) considered the tip moth to be a minor pest that had little impact on forest growth, but as they predicted, intensive forest management practices that improve tree growth, such as weed control and fertilization, have been shown to exacerbate its damage (Hedden and Nebeker 1984, Ross and Berisford 1990, Ross et al. 1990, Sun et al. 1998). Tip moth damage may also become more important because increased tree production costs lead to a lower economic pest control threshold (National Academy of Sciences 1975). Other studies on tip moths have produced contrary or inconclusive data regarding the effects of herbicide applications on damage levels. Several studies have shown an increase in tip moth damage associated with reductions in competing vegetation (Berisford and Kulman 1967, Hertel and Benjamin 1977, Hood et al. 1988, Ross et al. 1990). However, McCravy and Berisford (2001) showed significantly lower tip moth damage in plots with vegetation control than in untreated plots, and Miller and Stephen (1983) concluded that vegetation levels were not a major factor in determining tip moth damage levels. Changes in vegetation levels could affect tip moth damage levels by changing the habitat and thereby reducing parasitism rates or by changing the physiological status of the host. Nowak and Berisford (2000) suggested that tip moth populations fluctuated more in stands with very low levels of competing vegetation compared to those with moderate levels of herbaceous and woody vegetation, possibly due to reduced activities of natural enemies. It has been shown that removing competing vegetation in loblolly pine plantations can reduce total parasitism (McCravy and Berisford 2001), which could therefore lead to greater instability in prey populations (Price 1997).

There is a similar disparity in the literature regarding the effects of fertilization on tip moth damage. Ross and Berisford (1990) predicted that tip moth damage levels would increase with increased use of fertilizer in young forest plantations. Nowak and Berisford (2000), however, found no significant differences in tip moth damage related to fertilization treatments. Pritchett and Smith (1972) showed significant reductions in tip moth damage levels related to phosphorous (P) and potassium (K) fertilization, but not related to nitrogen (N) fertilization. These studies focused only on tip moth damage; however, and did not examine the effects of fertilization on larval and pupal development.

Many herbivorous insects, including tip moth, perform better on faster growing seedlings. Pupal weight and development of Western spruce budworm (Choristoneura occidentalis Freeman) can increase with the N content of Douglas-fir (Pseudotsuga menziesii [Mirb.] foliage (Brewer et al. 1987, Clancy 1992). It is believed that increasing N availability to plants is beneficial to herbivorous insects not only because of the increased N available to the herbivore, but also because of a decrease in the plant’s production of defensive compounds (Bryant et al. 1987, Kainulainen et al. 1996, Stout et al. 1998). In a greenhouse study, Ross and Berisford (1990) found that the most vigorous loblolly pine seedlings supported the highest number of tip moth pupae, and that concentrations of plant defensive compounds (total phenolics and condensed tannins) were inversely related to seedling growth. Similar field studies examining the effects of N fertilization on tip moth pupal development have not been conducted.

The objectives of this study were to examine the effects of N fertilization and weed control on tip moth damage, number of pupae per shoot, population dynamics, and tree growth. Foliar analyses of nutrients and plant defensive compounds were also performed to assess treatment effects.

Materials and Methods

This study was conducted in the Piedmont physiographic region near Powelton, Georgia (Hancock Co.) in 1999 and 2000 on a recently harvested site that had been replanted by hand in 1997 with approximately 1300 1+0 bareroot loblolly pine seedlings per hectare. Prior to planting, the site was ripped, bedded, and treated with banded applications of hexazinone (Velpar® L) and sulfometuron (Oust®) herbicides.

The experiment was designed as a randomized complete block with 3 replications and 4 treatments for a total of 12 plots (0.04 ha/plot). The 4 treatments were N fertilizer only, herbicide only, herbicide+fertilizer, and untreated control. In the herbicide treatments, glyphosate (Accord®) was applied twice a year (May and July) with backpack sprayers (Solo®, Newport News, VA) at 5.0 kg ai/ha with a 0.5% surfactant by volume. Since glyphosate, a non-soil-active herbicide, would not be absorbed by pine roots, it would not be present in the tree’s vascular system where it could potentially influence tip moth feeding. The trees were bagged with large white plastic bags during herbicide application to protect trees from exposure in 1999. Trees were only covered for about 15 min during application, and applications were timed to limit any potential damage to tip moth eggs on the pine shoots at the time of applications. Trees were not covered in 2000 because only spot herbicide applications were performed. In the fertilizer treatments, a broadcast application of urea was applied twice in 1999 (May and July) and three times in 2000 (March, May, and July) at a rate of 56 kg of N per ha per application.

The percentage of shoots with Nantucket pine tip moth damage was determined three times annually after the first, second, and third generations. There are three tip moth generations per year in this region of Georgia (Fettig et al. 2000). The first tip moth evaluation was taken prior to treatment initiation to provide background data. Evaluation dates were timed to coincide with the tip moth pupal stage or immediately follow adult emergence. The terminal shoot and shoots in the top whorl were examined for tip moth damage on each evaluation date in 1999 and 2000 and whole tree evaluations were performed the first year. The number of damaged shoots was expressed as a percentage of the total number of shoots. Damage counts were confined to the top whorl in the second year because there is a strong linear relationship between top whorl and whole tree infestations (Fettig and Berisford 1999).

After the third generations in 1999 and 2000, 135 tip moth-damaged shoots per treatment were clipped, placed in plastic
bags, and returned to the laboratory on ice for examination. The shoots were dissected, and the number and life stage of tip moths present were recorded. Larval instars were determined by measuring head capsule width (Fox et al. 1971) using a dissecting microscope fitted with an ocular micrometer. Pupal weight was determined using an electronic analytical balance (Brinkmann Instruments Co., Westbury, NY). Only female pupae were weighed, which were identified as *R. frustrana* and were separated from males using the methods of Yates (1967, 1969). The number of parasitic hymenopteran and dipteran larvae, pupae, and adults in each collected pine shoot were also counted in the third generation of 2000. These data are reported as the proportion of parasites found per tip moth larva and pupa.

During the winter of 1999 and 2000, 96 undamaged shoots (8 per treatment per block) were collected as described above and returned to the laboratory for foliar analysis. For each collected shoot, 100 needle fascicles (=3 needles/fascicle) were removed and placed in paper bags. Foliar nutrient analysis was conducted by the University of Georgia Soil Testing Laboratory (Athens, GA). The samples were also tested for total phenols and condensed tannins present in 1999 by the University of Georgia Crop and Soil Sciences Department (Athens, GA).

Within each treatment plot, basal stem diameter (mm) (taken at ground level) and total height (cm) were measured for 60 planted pine trees immediately after each tip moth generation, except the first generation of 1999. Average basal area growth for each plot was calculated by subtracting the average basal area for trees in each plot at the beginning of the study from the average basal area at the end of the study. For comparative purposes, a stem volume index was calculated by multiplying the square of the diameter by height (*D*^2^*H*). This volume index has been shown to correlate well with aboveground biomass (Tiarks and Haywood 1981, Hatchell et al. 1985) and is commonly used in tip moth literature (Ross et al. 1990, Nowak and Berisford 2000). Percentage cover and average height of competing vegetation were quantified in September 1999 and October 2000 within each of four 1 m^2^ quadrats per treatment plot following the methods of Daubenmire (1959).

Tip moth damage percentages were arcsine square-root (angular) transformed and subjected to an analysis of variance (ANOVA) (Sokal and Rohlf 1995). The coefficient of variation (CV) of tip moth damage was determined for each treatment plot and was used as a measure of the variability in percent tip moth damage over time for the treatments. Coefficient of variation for each treatment were subjected to ANOVA and separated with Tukey’s Studentized Range Test. The treatment with the highest CV has the greatest fluctuation in the population over time (Sokal and Rohlf 1995). Numbers of pupae and larvae per shoot were transformed using the natural logarithm of the square root of each observation plus one (log (square-root [X + 1])) prior to ANOVA. Tree growth and vegetation data were also subjected to ANOVA. Percentage of damaged shoots, number of insects per shoot, tree growth, pupal weight, and vegetation data were analyzed as a 2 × 2 factorial randomized complete block design with the main effects being fertilizer and herbicide treatments. Means were separated using PROC GLM and the Tukey studentized range test (SAS Institute 1989) if there was a significant (*P > 0.05*) interaction between the two main effects. Correlation analysis (SPSS 1997) was used to examine relationships among variables. Treatment means for each plot were used as variables in correlation analyses (*n* = 12).

### Results and Discussion

Woody and herbaceous vegetation were significantly less abundant in herbicide treated plots than in untreated plots in 1999 (*F* = 35.14; *df* 3,6; *P* = 0.0001) and 2000 (*F* = 62.14; *df* 3,6; *P* = 0.0001). Vegetation cover averaged 4 and 9% in 1999 and 2000 in the herbicide treated plots, respectively, while in nonherbicide treated plots it averaged 67 and 66%. Tree height ranged from 214 to 259 cm, and diameter ranged from 5.0 to 6.8 cm at the end of the second year of the study (2000; third growing season) for all treatments. Pine height, diameter, and volume were significantly greater in the herbicide treatments (*P <0.01*) (Table 1). Tree diameter was significantly higher in the fertilizer treatments, and increased by 3.1, 3.8, 4.4, and 4.8 cm in the control, fertilizer, herbicide and herbicide+fertilizer treatments, respectively, from the first sample period to the last sample period (through two growing seasons).

Mean percentage of shoots with tip moth damage for each treatment ranged from 3 to 51%, but significant treatment effects were only observed in the third tip moth generations of 1999 and 2000 (Table 2). Tip moth damage levels were significantly lower in the untreated control than in the herbicide treatments in the third generation of 1999 (*P* = 0.025).

<table>
<thead>
<tr>
<th>TRT</th>
<th>Height (cm)</th>
<th>Diameter (cm^2^)</th>
<th>Volume (cm^3^)</th>
<th>Pupal weight (mg) 1999</th>
<th>Pupal weight (mg) 2000</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>214 (5.4)</td>
<td>5.03 (0.1)</td>
<td>6553 (442)</td>
<td>8.72 (0.55)</td>
<td>9.06 (0.19)</td>
</tr>
<tr>
<td>Fert</td>
<td>239 (4.4)</td>
<td>5.76 (0.12)</td>
<td>8887 (457)</td>
<td>8.56 (0.89)</td>
<td>8.75 (0.21)</td>
</tr>
<tr>
<td>Herb</td>
<td>259 (4.0)</td>
<td>6.60 (0.0)</td>
<td>11882 (432)</td>
<td>7.45 (0.49)</td>
<td>7.95 (0.18)</td>
</tr>
<tr>
<td>Herb + Fert</td>
<td>253 (4.6)</td>
<td>6.80 (0.1)</td>
<td>12666 (586)</td>
<td>9.29 (0.31)</td>
<td>8.14 (0.1)</td>
</tr>
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<td>Main effects 1</td>
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<tr>
<td>Fertilizer</td>
<td>NS</td>
<td>0.046</td>
<td>0.130</td>
<td>N/A^2</td>
<td>N/A</td>
</tr>
<tr>
<td>Herbicide</td>
<td>0.006</td>
<td>0.0001</td>
<td>0.002</td>
<td>N/A</td>
<td>N/A</td>
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1 *P*-values for main effects of ANOVA for each tip moth generation (NS: *P > 0.05*).

2 There was a significant interaction between the main effects for the pupal weight data, therefore these means were separated using Tukey’s test. Means within columns (years) followed by the same letter are not significantly different (*P > 0.05*).
Table 2. Percentage (± SE) of loblolly pine, Pinus taeda L., top whorl shoots damaged by Nantucket pine tip moth, Rhyacionia frustrana (Comstock), in a study conducted in the Piedmont physiographic region of Georgia.

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<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Control</td>
<td>25.0 (2.6)</td>
<td>10.2 (±1.9)</td>
<td>21.0 (±3.2)</td>
</tr>
<tr>
<td>Fert</td>
<td>25.0 (2.6)</td>
<td>11.1 (±1.9)</td>
<td>37.1 (±3.6)</td>
</tr>
<tr>
<td>Herb</td>
<td>34.1 (±3.6)</td>
<td>6.0 (±1.2)</td>
<td>50.7 (±4.3)</td>
</tr>
<tr>
<td>Herb + Fert</td>
<td>20.7 (±2.3)</td>
<td>7.4 (±1.6)</td>
<td>50.6 (±4.1)</td>
</tr>
</tbody>
</table>

1 P-values for main effects of ANOVA for each tip moth generation (NS: P > 0.05).
2 Mean (of three blocks) coefficient of variation (%, standard deviation divided by the mean x 100) for tip moth damage for each treatment over the six generations. The CV is a measure of the degree of population fluctuation over time. The CVs were compared using ANOVA and means followed by the same letter are not significantly different (P > 0.05).

but significantly higher in the third generation of 2000 (P = 0.0001) (Table 2). The 1999 data support the findings of several other studies that have demonstrated increased levels of tip moth damage associated with lower levels of competing vegetation (Beresford and Kulman 1967, Hertel and Benjamin 1977, White et al. 1984, Ross et al. 1990). Studies in other plant systems have predicted that removing competing vegetation tends to increase pest insect outbreaks because of a reduction in natural enemies (Pimentel 1961, Russell 1989). Root (1973) concluded that pest populations were higher in pure stands due to a concentration of host plants that selected for a few pests that were adapted to those plant hosts. Ross et al. (1990) showed that tip moth damage increased in areas with reduced vegetation during the first half of a 3-year study. However, in the second half of their study, tip moth damage levels were lower or unchanged in the areas with less vegetation, which is similar to our data from 2000. Two other studies concluded that tip moth damage decreased after herbicide applications (Sun et al. 2000, McCravy and Berisford 2001). However, McCravy and Berisford (2001) only sampled for 1 year and conducted the study when tip moth populations were low (i.e. <10%). Sun et al. (2000) only reported data from one generation, in which there was not a significant difference between the untreated control and the herbicide treatments. Sun et al. (2000) may have based their conclusions on the lower damage in the herbicide+fertilizer treatment compared to the fertilizer-only treatment. However, damage levels were again <10%, and the fertilizer-only treatment led to significant increases in vegetation competition over the nontreated control.

Our study corroborates the findings of Nowak and Berisford (2000), who suggest that vegetation control does not simply increase or decrease tip moth damage, but leads to a destabilization in tip moth populations and to more variability in these populations. To determine if variability in tip moth damage was greater in the herbicide treatments than in the untreated control, the coefficient of variation (CV) for each treatment was determined using tip moth damage levels pooled for the 6 successive generations (2 yr). Coefficient of variation values averaged 72% in the nonherbicide treated plots, but averaged 100% in the herbicide treated plots (Table 2). Our results indicate that tip moth population levels fluctuate more over successive generations in herbicide treated plots than in untreated plots. The CV of the tip moth damage levels in the herbicide-only and the herbicide+fertilizer treat-

ments was significantly higher than the CV for the control treatment. Miller and Stephen (1983) concluded that vegetation height did not determine tip moth damage levels, but a reexamination of their data reveals that the variability in tip moth populations over 7 successive generations was inversely related to the vegetation level. Abundance of competing vegetation cover could affect tip moth population dynamics by regulating the abundance of tip moth natural enemies or the food resource of tip moth (Price 1997). Russell (1989) reported that plant communities of greater species diversity tend to have higher predation and parasitism rates than less diverse systems. Predators and parasites tend to have a stabilizing effect on herbivore populations (Price 1997), and Pimentel (1961) concluded that less diverse plant communities tend to support less stable herbivore communities. We found a significant correlation between the treatment CV and percent parasitism, indicating that the tip moth population fluctuated less in treatments with higher parasitism rates (r = -0.52; P = 0.0079) (Figure 1a).

Growth in pine stem basal area was highly correlated with tip moth population fluctuations (r = 0.89; P = 0.001) (Figure 1b). This indicates that as trees are grown at a faster rate with silvicultural treatments such as vegetation control, tip moth population fluctuations will increase. This might result in part because the fastest growing trees were in the herbicide treatments which led to a decrease in natural enemies, but it could also be that greater production of shoots led to a more rapid increase in tip moth populations. Populations with higher rates of increase tend to have the most extreme fluctuations between generations (May 1976).

Pupal weight was also significantly related to intensity of tip moth fluctuations (r = -0.93; P = 0.0001) (Figure 1c). There was a significant interaction (P < 0.05) between the two main effects for pupal weight in 1999 and 2000; therefore, the means were separated with Tukey’s test. Female pupal weight was significantly lower in the herbicide-only treatment than in the other treatments in 1999 at the 0.1 significance level (F = 3.74; df 3; 6; P = 0.079), and lower in the herbicide+fertilizer treatment compared to the untreated control in 2000 (F = 7.01; df 3; 6; P = 0.0219) (Table 1). There were no significant correlations between pupal weight and condensed tannin or total phenolic production, however. There were also no significant differences due to treatment for either total phenols or condensed tannins (Table 3). The lower pupal weights in the herbicide treatments may be
associated with higher levels of resin production. Dunn and Lorio (1993) showed that resin production was higher in more vigorous trees. This was not tested in our study, however, and Dunn and Lorio (1993) studied more mature trees, which may make comparisons difficult.

Nitrogen fertilization did not affect percent tip moth damage ($P > 0.1$), foliar N levels in 1999 ($P > 0.1$), or tree growth ($P > 0.1$). However, there were significant changes in the N:P ratio of pine foliage in 1999 ($P = 0.002$) and 2000 ($P = 0.045$) (Table 3). This ratio is considered a better indicator

Figure 1. Correlations for the coefficient of variation versus percent parasitism, loblolly pine basal area, and tip moth pupal weight in a 2 yr study in the Piedmont of Georgia. Data points represent treatment means for each of the 3 blocks used in the study ($n = 12$).
of N deficient sites than percent N (Comerford and Fisher 1984, Adams and Allen 1985). Other studies have shown no difference in tip moth damage related to N fertilization (Pritchett and Smith 1972, Berisford et al. 1989, Nowak and Berisford 2000).

There were significantly more pupae per shoot related to the fertilizer ($P = 0.009$) and herbicide treatments ($P = 0.002$) in 1999 (Table 1), but no significant differences in tip moth (larvae and pupae combined) number per shoot were detected in 1999 ($P > 0.05$) or 2000 ($P > 0.05$). The number of tip moth (larvae and pupae) in 1999 ranged from 0.86 to 1.44 per shoot in 1999. The faster growing trees were able to support a higher number of pupae when tip moth damage reached moderate levels in 1999. These data support the previous discussion on population dynamics, showing that in 1999 the number of tip moth (percent shoots damaged and number of pupae per shoot) was higher in the more intensive treatments, but lower or not different in 2000. Ross and Berisford (1990) found that the most vigorous seedlings supported the most pupae in a greenhouse study. The higher number of pupae per shoot in 1999 herbicide and fertilizer treatments could be due to earlier egg deposition on those shoots, or it could be that pupal development was faster in those treatments. The ratio of pupae:larvae was significantly higher in the herbicide+fertilizer treatment than in the other treatments ($P = 0.021$). This suggests that pupal development was faster in the herbicide+fertilizer treatment, possibly due to more nutritious food resource. Brewer et al. (1987) showed that larval and pupal development varied due to the level of foliar N in Douglas-fir seedlings. The more vigorous seedlings also produced heavier pupae in their study, but this was not the case in our study.

## Conclusions

Our results demonstrate that tip moth population stability is likely to decrease in intensively managed stands. This decrease in stability is related to reduced parasitism and increased tree growth. It was clear in this study that the fastest growing trees had the most erratic tip moth damage over the six generations. Because populations may fluctuate wildly, decisions to implement tip moth control are more difficult in intensively managed stands. However, if the dramatic increases in tip moth damage could be predicted, such as with pheromone baited traps (Asaro and Berisford 2001), then there is a potential to reduce losses associated with tip moth infestations with chemical control (Fettig et al. 2000, Nowak et al. 2000).

## Literature Cited


**ASARO, C., AND C.W. BERISFORD.** 2001. Predicting infestation levels of the Nantucket pine tip moth (Lepidoptera:Tortricidae) using pheromone traps. Environ. Entomol. 30:776–784.


