Tolerance To Tip Moth Attack In Loblolly Pine Families

Roy Hedden[1], Scott Cameron[2], Mike Cunningham[2], and C. Dana Nelson[3]

[1]*Department of Forestry, Clemson University, Clemson, SC*
[2]*Forest Health Research and Eastern Tree Improvement, International Paper Company, Savannah, GA*
[3]*Genetic Marker Development, International Paper Company, Bainbridge, GA*

rhddn@clemson.edu

ABSTRACT
Two distinct factors characterize resistance to insect attack in trees. The first is true resistance and it is defined as the ability of the tree to reduce successful insect attack. The second type of resistance is called tolerance. Tolerance is the ability of the tree to grow better than expected for a given level of infestation. We examined resistance (defined as the proportion of infested pine buds per insect generation) and tolerance (defined as the difference between predicted and observed pine family mean heights at two-years of age) to tip moth attack in 60 loblolly pine families at two locations in southeast Georgia. The predicted family mean height was the average of the predicted heights for each tree from a regression model of height at age two years as a function of the observed infestation levels for the four tip moth generations of the second year in the field. Differences among families in proportion of infested buds were significant in three of eight generations, suggesting that observed levels of resistance contain a genetic component. Analysis of the tolerance values revealed seven families with values significantly greater than zero. These families are considered tolerant in that they grew taller in the presence of tip moth attack than would be expected given their observed infestation levels. Eight families had tolerance values that were significantly less than zero and thus are considered intolerant. Levels of tolerance exceeded plus or minus 6% of the average second-year height for some families. These results have implications for the design of field tests in loblolly pine tree improvement programs and for the deployment of loblolly families on sites where high levels of tip moth attack are expected.

INTRODUCTION
Pine tip moth (*Rhyacionia frustrana* Zimm.) causes damage to the terminal and lateral buds of young loblolly pine (*Pinus taeda* L.) trees, resulting in reduced growth and loss of photosynthetic area (Hedden 1998). In coastal Georgia, the insect has four generations per year, and constitutes an economic problem for at least the first two years of plantation life (Berisford 1988). Numerous insecticides have been shown to effectively control tip moth. Their use in pine plantations has been limited, though, due to the relatively small economic margins available for reducing damage (Cade and Hedden 1987). However, many industrial forest managers are establishing plantations in large blocks, using seedlings with selected genetic backgrounds. If different genetic sources (e.g., pine families) could be shown to possess sufficient variability in their resistance to tip moth attack, resistant families could be allocated to known high hazard sites. In this manner, damage could conceivably be reduced at virtually no cost to the forest manager or environment.

To further investigate the genetic variation in loblolly pine resistance to tip moth attack, we evaluated infestation and height growth in 60 half-sib families growing at two locations in southeast Georgia. Host resistance to insect attack can be characterized by two distinct factors. The first is true resistance and it is defined as the ability of the tree to reduce successful insect attack. The second factor is called tolerance and it is defined as the ability of the tree to grow better than expected for a given level of infestation. In the present paper, we report results on a genetic analysis of both true resistance and tolerance and offer suggestions for developing progeny tests designed to identify tip moth resistant and tolerant families of loblolly pine.

METHODS

A study was installed at two locations in southeastern Georgia in 1997 to test loblolly pine for resistance to pine tip moth attack. At both locations, containerized seedlings from 60 open-pollinated families of loblolly pine were planted in 25 randomized single-tree plots. Numbers of tip moth infested and uninfested buds in the terminal and top whorl of each tree were assessed at the end of each insect generation for the first two years in the field (for a total of eight generations). These data were used to calculate the proportion of infested buds for each tree and generation. Tree height was measured at the end of each of the first two growing seasons.

Resistance was defined as a significant difference in family mean infestation levels. It was evaluated using a two-factor ANOVA separately for each generation. The dependent variable was the proportion of infested buds for the individual trees. The main effects were location and family. The location x family interaction was also evaluated.

Tolerance was defined as the difference between predicted and observed height as a function of tip moth infestation. This process involved two steps. First, simple linear regression was used to generate an equation expressing tree height at the end of the second growing season as a function of tree height at the end of the first growing season. The adjusted height, calculated as the observed minus predicted height for each tree, was then used as the dependent variable in a second regression analysis. This height adjustment was necessary to remove inherent differences in growth rate among the pine families. For this second analysis, the independent regression variables were the proportion of infested buds for each of the four tip moth generations during the second growing season. The tolerance level for each tree (defined as the difference between the observed adjusted height and predicted adjusted height) was calculated using the observed infestation levels for each tree and the second regression equation.

Tolerance levels were evaluated using a two-factor ANOVA, with family and location as main effects and location x family as an interaction effect. Families were classified for tolerance using simple t-tests. Families with family mean tolerance levels significantly greater than zero were classified as tolerant. Conversely, families with mean tolerance levels significantly less than zero were classified as intolerant.

RESULTS AND DISCUSSION

Resistance

Table 1 lists the F-test significance values from the ANOVA of the proportion of infested pine buds in each tip moth generation.

Table 1. Significance levels for main effects and interaction F-tests in the ANOVA of proportion of infested buds in each generation.

Tip Moth Generation	Growing Season	Location	Family	Loc x Fam
1	1	<0.0001	0.1325	0.0645
2	1	<0.0001	0.2147	0.1254
3	1	<0.0001	0.9342	0.3065
4	1	<0.0001	0.7568	0.8326
5	2	<0.0001	0.0041	0.7301
6	2	<0.0001	0.0675	0.7174
7	2	<0.0001	0.0017	0.0106
8	2	<0.0001	0.0074	0.8388

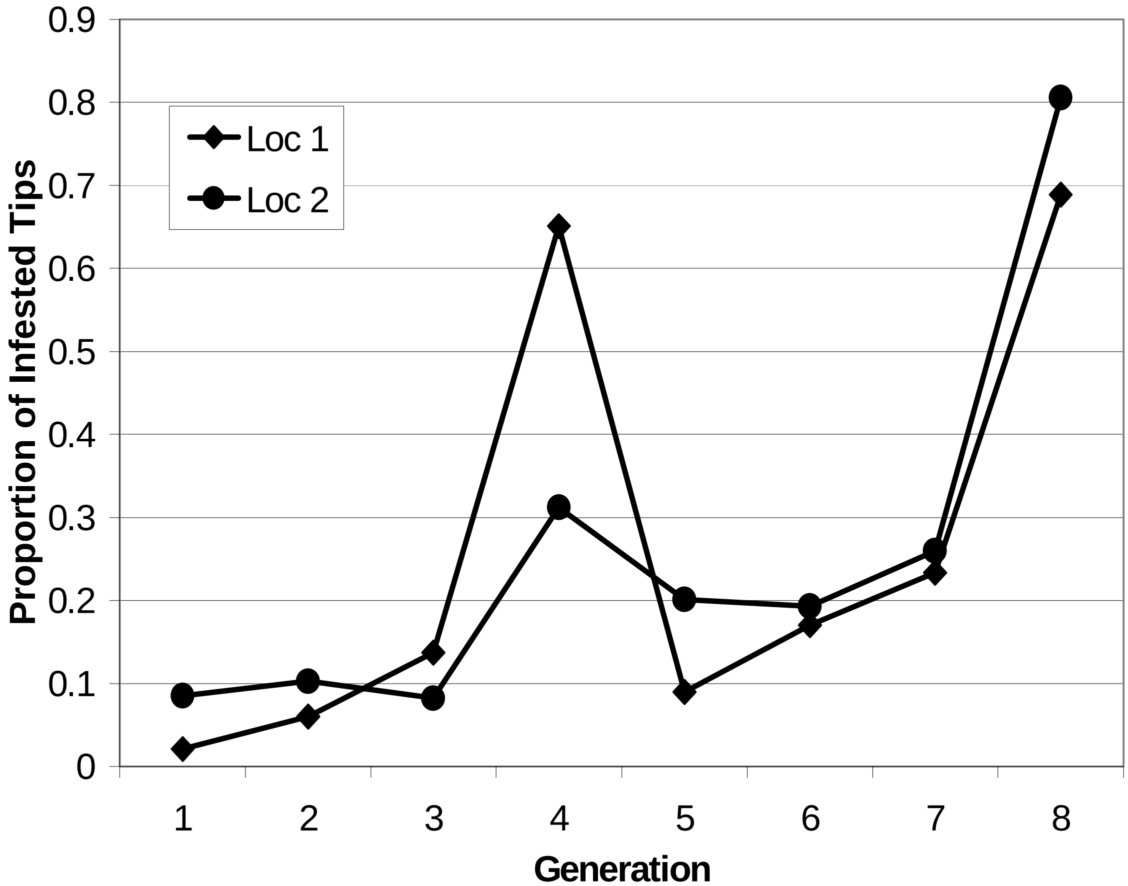

Figure 1. Tip moth infestation level by generation at two locations (Loc) in southeast Georgia.

Although the seasonal patterns of infestation were similar at both locations, differences in the mean proportion of infested buds between the locations in each generation were significant (Figure 1). Families were significantly different in three of four generations in the second growing season (generations 5, 7 and 8), but not in any generation during the first season. Even from generation to generation. This lack of consistency appears to make selection for tip moth resistance difficult at best. though there were significant family differences in the second year, the correlation of infestation level between generations was uniformly low at each location in the second year. The family mean correlation coefficients ranged from -0.17 to 0.24, and none of them were significantly different from zero (p=0.05). Therefore, in spite of evidence of family differences in infestation level in certain generations in the second growing season, these differences were not consistent

Tolerance

Tolerance is the ability of a family to grow better than expected when subjected to tip moth attack. The first step in this analysis was to remove the effect in tree heights due to the genetic differences between pine families. This adjustment was made by generating a simple linear regression equation using tree height at the end of the second year as the dependent variable and height at the end of the first year as the independent variable, and then calculating adjusted tree height by subtracting the predicted from the observed height:

$$ADJHT = (OHT - PHT) = OHT - (b_0 + b_1 IHT)$$

where ADJHT = adjusted tree height (ft)
OHT = observed tree height (ft) at the end of the second year
PHT = predicted tree height (ft) at the end of the second year
IHT = tree height (ft) at the end of the first year
b_0 = regression intercept
b_1 = regression coefficient

Regression equations were generated separately for each location. The estimated regression parameters for Location 1 were b_0=1.70638 and b_1=1.51863 (R^2=0.63), while at Location 2 the estimates were b_0=2.3116 and b_1=1.42414 (R^2=0.63). Adjusted tree heights (ADJHT) were then used as the dependent variable in the following regression equation:

$$ADJHT = b_0 + b_1 I1 + b_2 I2 + b_3 I3 + b_4 I4$$

where ADJHT = adjusted tree height (ft) and I1, I2, I3 and I4 are the proportion of infested buds in the first through fourth tip moth generations in the second year while b_0, b_1, b_2, b_3 and b_4 are regression coefficients. The estimated values for the intercepts and regression coefficients are provided in Table 2.

The tolerance level (TL) for each tree was calculated as the observed ADJHT minus predicted ADJHT. Family mean TLs (FMTLs) were derived by averaging individual tree TLs in each family. The ANOVA of TLs showed significant variation among families (p<0.0001), but not between locations (p=0.9754) or the interaction between location and family (p=0.5657). The correlation of FMTLs between locations was r=0.46 (Figure 2). FMTLs at Location 1 ranged

Table 2. Regression parameter estimates and significance test results for the equation ADJHT = $b_0 + b_1I1 + b_2I2 + b_3I3 + b_4I4$ modeled at both locations.

Variable	**Parameter Estimate (b_i)**	**Standard Error**	**T-value**	**Pr > |t|**
LOCATION 1				
Intercept	0.51166	0.04703	10.88	<0.0001
I1	-0.45196	0.09982	-4.54	<0.0001
I2	-0.66648	0.0893	-7.46	<0.0001
I3	-0.65017	0.078	-8.34	<0.0001
I4	-0.29919	0.05553	-5.39	<0.0001
LOCATION 2				
Intercept	0.60935	0.0712	8.56	<0.0001
I1	0.19008	0.09321	2.04	0.0416
I2	-0.70885	0.09222	-7.69	<0.0001
I3	-0.70347	0.08444	-8.33	<0.0001
I4	-0.40807	0.07549	-5.41	<0.0001

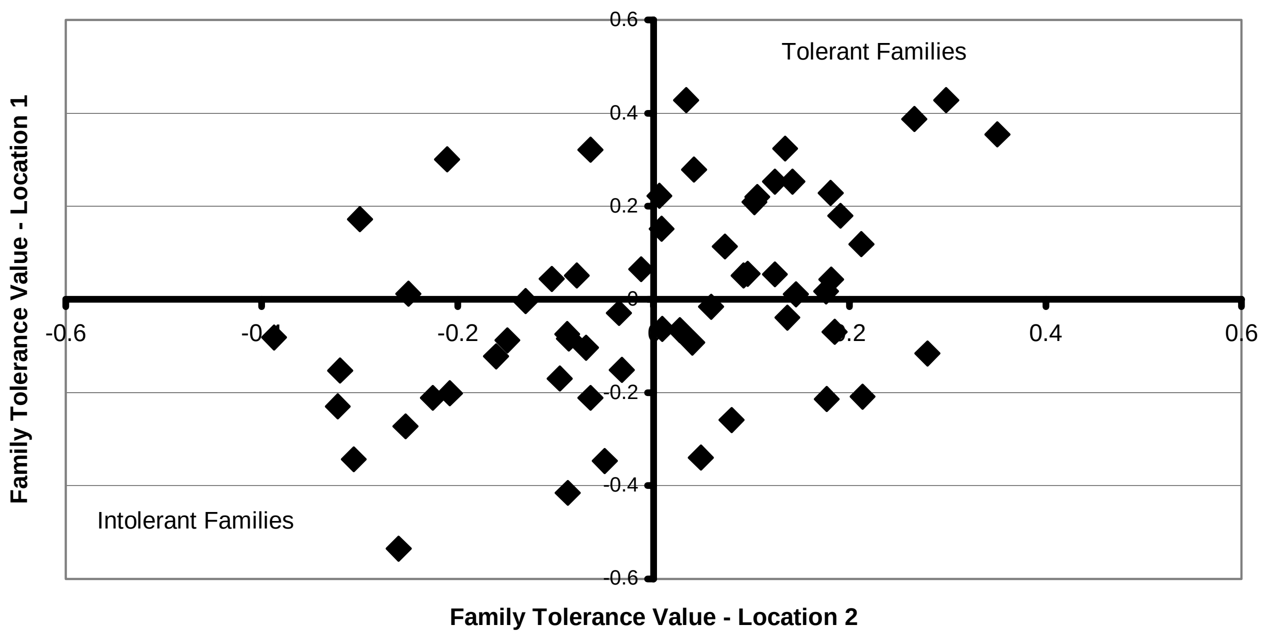

Figure 2. Relationship between family mean tolerance level at two locations in southeast Georgia.

from -0.39 ft to +0.35 ft or about -6.6% to +5.5% of the family mean height. The range of FMTLs was greater at Location 2, ranging from -0.54 ft to +0.43 ft or about -9.3% to +6.2% of family mean height. Overall, we classified seven families as tolerant, with an average FMTL value of +0.26 ft (sd=0.08), and eight families as intolerant, with an average FMTL of -0.28 ft (sd=0.06).

The biological characteristics that result in insect tolerance and intolerance are not known. The most tolerant families tended to be among the fastest growing families in these tests. Fast growth might result in asynchrony between tree growth and tip moth attack behavior. Thus, faster growing trees may have growth cycles that escape tip moth attack. There are other possibilities as well, such as tolerant trees having fewer multiple infested shoots than intolerant trees. This might result in less loss of photosynthetic area in tolerant trees. However, the actual mechanisms of tolerance will need to be assessed in future studies. Regardless of the biological basis for tolerance, the results of this study suggest that significant gains can be made in reducing growth impact from pine tip moth attack by planting tolerant families.

Identification of Tolerant and Resistant Families

The results of this and other studies (Cade and Hedden 1989) suggest procedures that might be useful in designing tests for identifying pine families that are tolerant and/or resistant to pine tip moth attack. The ideal test would replicate families at two or more locations and years, because tip moth infestation can vary by location, year, and generation. A split-plot design would be appropriate with family whole-plots and insecticide-treatment (treated and untreated) sub-plots. For every two insecticide-treated trees we recommend three untreated trees, since the variability in tree growth is greater in untreated trees. The total number of trees tested per family per location should be at least 50. Tip moth infestation and height growth data should be collected for at least the first two growing seasons.

Comparison of family performance of insecticide-treated and untreated trees would facilitate the identification of tolerant and intolerant genetic sources, in addition to identifying families that perform significantly different in the presence of tip moth infestation than in its absence. For instance, in a study reported by Cade and Hedden (1989), the loblolly pine family most intolerant to tip moth infestation was one that grew extremely well when it was insecticide-treated. These "change-in-rank" families may be common. For instance, there was considerable overlap in this study between the family growth performance index for families with the highest and lowest FMTLs (Figure 3). This performance index was derived from independent genetic tests that received treatments for tip moth control. The minimum information collected for each tree should include height at planting and at the end of the first two growing seasons, and tip moth infestation level in each generation during the first two seasons. A study with these characteristics should provide adequate information to select appropriate families for planting on high-hazard tip moth sites.

Finally, we would like to make a comment regarding insecticide treatment for pine tip moth control in progeny tests. Traditionally, tip moth populations have been controlled in young progeny tests. The rationale for this strategy is to reduce the environment caused variability in tree growth in these tests. It assumes that tip moth infestation is "noise" or error variance. This strategy makes good sense under two scenarios. First, when pine families selected for rapid growth will be screened for tip moth tolerance in tests similar to the one just described, or second, where the operational silvicultural regime will include tip moth control during most

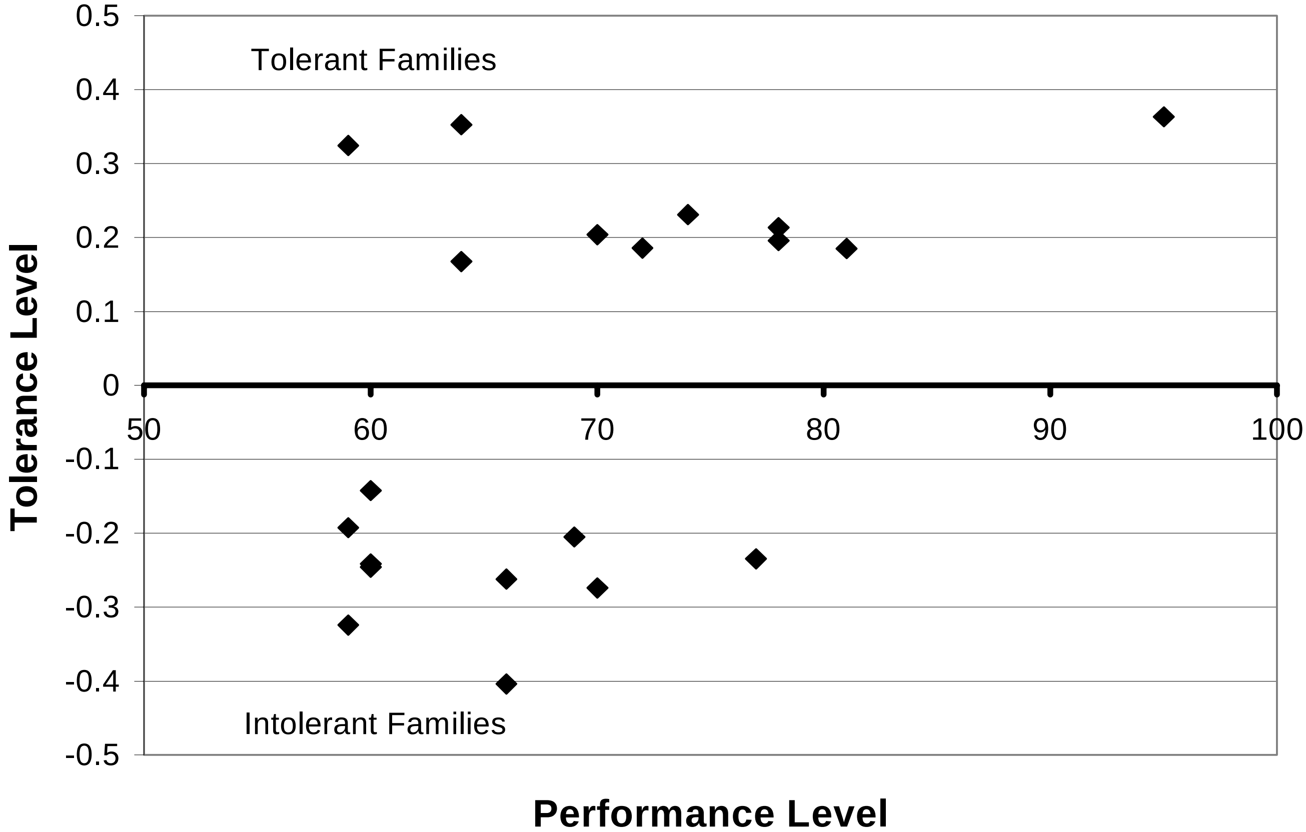

Figure 3. Relationship between family mean tolerance level and family performance level for the ten most tolerant and intolerant families.

insect generations in the first two years. It might also make good sense in the absence of genetic interaction between pine growth and tip moth attack, or when the potential loss in growth of intolerant families is less than that to be gained by tolerant families or insecticide treatments. However, both of these last two assumptions are questionable. Ultimately, well-implemented progeny tests, where the trees are subjected to pine tip moth infestation, and proper data collection and analysis will result in the selection of families tolerant to tip moth attack.

LITERATURE CITED

Berisford, C.W. 1988. The Nantucket pine tip moth. Chapter 6 In A.A. Berryman, ed. Forest insect outbreaks: patterns, causes, and management strategies. Plenum.

Cade, S.C., Hedden, R.L. 1987. Growth impact of pine tip moth on loblolly pine plantations in the Ouachita Mountains of Arkansas. Southern J. Appl. For. 11(3):128-133.

Cade, S.C., Hedden, R.L. 1989. Evidence for tip moth (Rhyacionia frustrana) resistance in loblolly pine (Pinus taeda). pp. 137-144. In: R.I. Alfaro and S.G. Glover, eds. Insects affecting reforestation: biology and damage. Forestry Canada, Victoria, B.C., Canada.

Berisford, C.W. 1988. The Nantucket pine tip moth. Chapter 6 In A.A. Berryman, ed. Forest insect outbreaks: patterns, causes, and management strategies. Plenum.

Hedden, R.L. 1998. Impact of Nantucket pine tip moth attack on loblolly pine-- A southwide summary. pp 569-573. In: T.A. Waldrop, ed. Proceedings of the 10th biennial southern silvicultural conference, USDA For. Serv., So. Res. Sta., Asheville, NC, Gen. Tech. Rep. SO-20.