EFFECTS OF CULTURAL TREATMENTS AND GENETICS ON TIP MOTH INFESTATION OF LOBLOLLY PINE, SLASH PINE, AND SOME SLASH PINE HYBRIDS

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ABSTRACT

Seven taxa, including open-pollinated families of improved *Pinus taeda* (PTA), improved (PEE) and unimproved *P. elliottii* var. *elliottii* (PEU) and four hybrid families, PEE × PTA, PEE × *P. caribaea* var. *bahamensis* (PEE × PCB), PEE × *P. caribaea* var. *hondurensis* (PEE × PCH), and the backcross PEE to PEE × PCH, were tested in 11 field tests in the lower Coastal Plain of the southeastern USA. Each field test included 16 families per taxon and two silvicultural treatments, intensive (fertilizer, weed control and insecticide applications) and less intensive. Tip moth attacks were less frequent in the intensive treatment. In both treatments, tip moth incidence was highest during the first year, declining to a very low level after the third growing period. The Nantucket pine tip moth, *Rhyacionia frustrana*, was the most commonly encountered species.

PTA and its hybrid with slash pine (PEE × PTA) were more frequently attacked than other taxa. All other taxa showed few tip moth attacks. Family differences in frequency of attack were not detected in PTA. Estimated heritability for tip moth resistance was very low.

Key words: *Pinus taeda*, *Pinus elliottii*, *Pinus caribaea*, hybrids, *Rhyacionia*, tip-moth resistance

INTRODUCTION

Pine tip moths, *Rhyacionia* spp., are major pests of young pines in the eastern United States. They are of major concern in pine plantations, especially loblolly pine (*Pinus taeda* L.), where they have become increasingly abundant and destructive in recent years (YATES 1960, YATES *et al.* 1981; BERISFORD *et al.* 1992). Larvae of pine tip-moths inhabit the growing tips of pines, where their feeding habits may produce deformation of the host tree, and loss or retardation of growth (CADE & HEDDEN 1987; BERISFORD 1988). In addition, it is thought that tip moths create wounds or alter growth habits, favoring the occurrence of diseases such as pitch canker (RUNION & BRUCK 1985) or fusiform rust (POWERS & STONE 1988; HEDDEN *et al.* 1991). Pine tip moths affect even-aged plantations more severely than natural stands (LASHOMB *et al.* 1980; BERISFORD 1988). Increased damage from pine tip moth is frequently associated with increased intensity of forest management (BERISFORD & KULMAN 1967; HOOD *et al.* 1988).

Two of the 23 Neartic species of *Rhyacionia* are commonly found in the lower Coastal Plain (LCP) of the southeastern USA (POWELL & MILLER 1978). The Nantucket tip moth (*R. frustrana* Comstock) is commonly associated with loblolly pine, while the subtropical pine tip moth (*R. subtropica* Miller) appears to prefer slash pine (*Pinus elliottii* var. *elliottii*) (MCGRAW 1975; HERTEL & BENJAMIN 1977; HOOD *et al.* 1988). However, no testing to provide further evidence of the preferences of tip moths has been conducted in the LCP when improved loblolly and slash pine are growing in the same locations.

Current strategies to control damage from tip moths include the use of slash pine, a more resistant species than loblolly pine (YATES 1960; BERISFORD 1988) and the use of insecticides after planting (LASHOMB *et al.* 1980; STEPHEN *et al.* 1982). However, insecticide applications could lead to the selection of loblolly pine trees that are susceptible to pine moth and tests protected by insecticides cannot be used to select for resistance to tip moth (BERISFORD 1988). HOLST (1963) concluded that individual tree selection and interspecific hybridization with slash pine would be required to improve resistance in loblolly pine. In fact, some family differences in tip moth incidence may be found in loblolly pine (YOUNG *et al.* 1979; CADE & HEDDEN 1989), but almost no heritability estimates have been reported for tip moth resistance.

Improved loblolly, improved slash and the slash × loblolly pine hybrid were included in 11 field trials to allow comparisons for their relative resistance to the moth attack. The excellent performance of some slash × Caribbean hybrids in other parts of the world motivated the Cooperative Forest Genetics Research Program (CFGRP) at the University of Florida to assess the growth potential of these hybrids in the LCP. Commercial market value in the southeastern USA requires that these hybrids not suffer negative impacts from tip moth.

The primary objectives of this research were: 1) to evaluate tip moth resistance among seven taxa planted across eleven sites in the LCP; 2) to assess the effect of hybridization of slash pine and loblolly pine on tip moth resistance; and 3) to determine if family differences in resistance could be useful for selection.

MATERIALS AND METHODS

Taxa

Seven different pine taxa were tested: improved loblolly pine (PTA), improved slash pine (PEE), unimproved slash pine (PEU), the slash × loblolly F_1 hybrid (PEE × PTA), and three slash × Caribbean pine hybrids (PEE × *P. caribaea* var. *hondurensis* Barret *et.* Golfari (PEE × PCH), PEE × *P. caribaea* var. *bahamensis* Barret *et.* Golfari (PEE × PCB) and the backcross of PEE to PEE × PCH.

The improved slash taxon consisted of open-pollinated seed from 18 slash pine trees which are outstanding in terms of volume growth or resistance to fusiform rust. The PEE seed came from 11 seed orchards in southeastern USA. There are all possible combinations of clones in these orchards, but no more than five parents were from the same orchard. Since these families are open-pollinated, the average breeding values for the seedlots were calculated considering the breeding values of the clones (females parents) and all trees in the seed orchard (assuming 30 % pollen contamination). The PEE seedlot was estimated to have means of 18.3 % for volume gain and 37.1 % for rust (R50), as predicted by the CFGRP (LÓPEZ-UPTON 1999). The 18.3 % volume gain is expressed for 15-yr volume above unimproved material. Lower R50 values indicate more resistance to fusiform rust (WHITE & HODGE 1988; WHITE *et al.* 1988). For example, a breeding value of 37 % means that on a given site where unimproved material exhibit 50 % rust infection, the PEE families are predicted to average 37 % infection.

The unimproved slash pine families consisted of open-pollinated seed from 17 parents representative of slash pine as it existed in 1955, before domestication.

The PEU seed came from 9 seed orchards in southeastern USA. All orchards contain plus and unimproved clones and some orchards had been rogued one time, so we tried for PEU to compensate for the slight average superiority of the pollen cloud by choosing females that were slightly below average based on their breeding values. For comparison, the PEU seedlot was estimated to have a 4.9 % volume gain and an R50 of 51.3 %. All PEE and PEU trees are from the CFGRP. The improved loblolly taxon consisted of open-pollinated seed from 17 superior parents located in seed orchards with materials mostly from the Atlantic Coastal Plain of Florida and Georgia (LÓPEZ-UPTON 1999). Details are not available on breeding values of these parents.

Thirty superior slash pine clones from the CFGRP were used as female parents for all hybrid combinations. Each slash parent (PEE) was control pollinated with four different pollen mixes: 1) a 30-parent polymix of *P. caribaea* var. *hondurensis* (PCH) to produce the PEE × PCH; 2) a 25-parent polymix of the hybrid PEE × PCH to create the PEE × (PEE × PCH) backcross; 3) a 24-parent polymix of *P. caribaea* var. *bahamensis* (PCB) to produce the PEE × PCB; and 4) a 30-parent polymix of superior clones of *P. taeda* to make the PEE × PTA. All three sources of Caribbean pine pollen were obtained from the Queensland Forest Service in Australia. The loblolly pine pollen was obtained mainly from Atlantic Coastal Plain sources (Florida and Georgia). Slash pine was always used as the female parent. Seven PEE mother trees were used in all hybrid crosses and within the PEE taxon across all sites and hybrid taxa.

The number of families in each taxon planted in the 11 field trials is indicated in Table 1. However, sixteen families in each taxon were planted per location. Some of the 30 hybrid crosses did not yield sufficient seeds or seedlings for planting as a single family in all sites as initially designed. Thus, for the hybrids PEE × PCH and PEE × PCB only three sites have 16 "single" families (Table 1).

Field Implementation

Pollination for all hybrids was conducted in February of 1991 and 1992, with subsequent seed collection in 1992 and 1993. Open-pollinated seeds of PEE, PEU and PTA were collected in 1992. Both years' seed harvests were combined, cleaned and cold-stored at 5°C. Germination was done in June 1994 in greenhouse conditions, and plants were moved outdoors after transplanting and seedling establishment. The eleven field test locations were planted in December 1994 across the lower Costal Plain, including north Florida and the southern portions of Georgia and Alabama (8, 2 and 1 locations, respectively). These sites covered a wide range of soil groups,

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Table 1. Taxa and number of families tested across 11 field trials.

Female taxon	Male taxon (pollen)					
	PEE	PEU	PTA	PCH	PEE × PCH	PCB
PEE	PEE 18		PEE × PTA 19	PEE × PCH[1] 18 + (6)	PEE × (PEE × PCH) 20	PEE × PCB 17 + (5)
PEU		PEU 17				
PTA			PTA 17			

[1] Due to the lack of seedlings, this taxon was planted in eight sites. The more northern sites on Alabama and Georgia were not planted. Due to an insufficient number of seeds or seedlings, bulks lots of two or three families were formed. These are indicated in parenthesis.

from well to poorly drained and site index from 16 to 21 (meters at base age of 25 years). At each site, two cultural management intensities were established as: intensive, designated as High, and less intensive, designated as Low.

Site preparation included weed control, chopping, raking, burning, and bedding as needed for each location. For the Low treatment, no fertilization was used except for one location where phosphorus was added at establishment. Weed control was not used during the first three growing seasons, except for mowing prior to the winter measurement to facilitate data recording. For the High treatment, Asana, sometimes Diomethorate or Pyridine were the insecticides used for the control of tip moth. Applications were made in 1995, 1996 and 1997 at different rates among sites. In some locations pest traps were used to determine the timing of insecticide application, which varied from none to six times per year according to the presence of tip moth damage or the number of moths in the traps. Insecticide was not applied in the Low treatment, except for two locations, which received one insecticide application during the second and third growing seasons (1996 & 1997). Due to their low tip moth incidence, these two locations were not used in most analyses.

Variables Measured

Height was assessed at one, two and three years of age in the winters of 1995–96, 1996–97 and 1997–98, respectively. Height was measured as height to the highest terminal bud. Tip moth attacks on terminal buds were assessed in the 1995–96 winter (1 year after planting) and were scored as number of attacks in that year to each tree's terminal shoot. These measurements were not taken in the second and third years because

tree height precluded accurate measurements. Tip moth attacks on lateral buds were assessed at one, 2 and 3 years of age. It was recorded as percentage of lateral branches with evidence of tip moth attacks. The recorded percentage was the mean value of estimates by two independent observers for each tree. For the first year, all lateral branches were observed on each tree (each observer scored half the tree). Measurements of attacked tips at 2 and 3 years of age were taken from a sample of 10 branches evaluated by each observer. The score for each tree was converted to the percentage of lateral buds showing evidence of attacks. Terminal or lateral tips were considered as attacked if they exhibited browning, curling tips, die back, or resin globules typical of tip moth injury. Terminal attack was not counted as lateral attack.

Tip Moth Identification

To determine the species of tip moths attacking PEE, PTA, and their F_1 hybrid PEE × PTA, pupae were collected from four sites with high infestation rates. Species of *Rhyacionia* are distinguishable by several characteristics in its adult, larvae and pupae stages (MILLER 1960; YATES 1960, 1967a). Since large quantities of pine tip moths are in the readily identifiable pupae stage during the winter (MILLER & WILSON 1964), all samples were collected at the end of second growing season from the Low intensity sites. Five families per tree taxon were sampled from each site. The goal was to sample seven pupae per family-block, but the absence of successful attacks in some sites necessitated some samples being smaller than initially planned. A successful attack was defined according to the presence of a pupa inside a pine tip. On average, less than two damaged branch tips were needed to

obtain one pupa in PTA or PEE × PTA, while four to five damaged terminals were needed to obtain one pupa in PEE. Therefore, 15 or more apparently infested tips were collected for each family in each block. For PEE, the pupa collection was smaller since many larvae did not successfully progress to the pupal stage.

After collection, pine tips were dissected to detect the presence of pupae. Species identification was according to YATES (1967a) in which the size of the pupae, the shape of the frontal horn and the texture of the surface area between the eyes were used as key features for identification.

Statistical Analysis

Management effects on tip moth incidence

A series of single-site analyses of variance (ANOVAs) were performed to compare the efficiency of insecticide application to reduce tip moth attacks, i.e. treatment differences. These ANOVAs were performed in sites where tip moth incidences were high in the Low management treatment in which no insecticide was applied, and where cooperators made several insecticide applications in the High treatment (from 2 to 7 applications across sites and years). Four sites satisfied these criteria and were used for first-year lateral data and one site was suited for second-year lateral attack data. Lateral attacks were used because they may have represented more appropriately the incidence of tip moth attacks, and no terminals attacks were recorded during second year. Phenotypic variances among all six blocks nested in treatments were similar in each of these sites. Consequently, individual tree raw data were used for analyses, with a default probability value of 0.05 to show significance. Treatment, taxon and treatment by taxon interaction were fixed effects and tested per each site with a model based on the model:

$$Y_{ijkmn} = \mu + \alpha_i + b_{j(i)} + \tau_k + \alpha\tau_{ik} + b\tau_{ijk} + f_{m(k)} + \alpha f_{im(k)} + bf_{ijm(k)} + e_{ijkmn} \quad [1]$$

where: Y_{ijkmn} = is the nth observation of the mth family of the kth taxon in the jth block at the ith treatment; μ is the population mean; α_i is the fixed effect for treatment (High *vs.* Low); $b_{j(i)}$ is the random variable for block within treatment ~ *NID* $(0, \sigma^2_b)$; τ_k is the fixed effect for taxon (PEE, PEU or PTA); $\alpha\tau_{ik}$ is the fixed effect for the interaction of treatment by taxon; $b\tau_{ijk}$ is the random interaction block within treatment by taxon ~ *NID* $(0, \sigma^2_{b\tau})$; $f_{m(k)}$ is the random variable for family within taxon ~*NID* $(0, \sigma^2_f)$; $\alpha f_{im(k)}$ is the random interaction treatment by family ~*NID* $(0, \sigma^2_{f\alpha})$; $bf_{ijm(k)}$ is the random interac-

tion block within treatment by family within taxon ~*NID* $(0, \sigma^2_{bf})$; e_{ijkmn} is the error term ~*NID* $(0, \sigma^2_e)$, where $i = 1, 2$ treatments; $j = 1, 2, 3$ blocks; $k = 1, 2, 3$ taxa; $m = 1,...16$ families (taxon); and $n = 1,..5$ trees.

Taxon comparisons and hybrid vigor

A series of analyses of variance (ANOVAs) using only data from the Low cultural treatment were performed to compare taxon differences for terminal attacks and lateral attacks. Trees in the High treatment presented low tip moth attacks. To accomplish this objective, data across sites (pooled analyses) and single-site analyses were performed. For all ANOVAs individual tree and untransformed data were used. Since less than 1.4 % of the trees had more than 3 attacks on the same terminal, these values were converted to 2. Thus, 0, 1 and 2 terminal attacks represented 54 %, 31 % and 15 % of the observations during the first year, respectively.

To test the main effects of site, taxon and site by taxon interactions, pooled analyses were performed for sites where the most susceptible taxon had more than 20 % of the laterals attacked. Data from seven sites were pooled for analyses for terminal and lateral attacks during the first year, and four sites for second-year lateral attacks. No ANOVA is reported for the third year since no taxon had more than 20 % attacks during that time. The model used for the pooled analyses was:

$$Y_{tjkmn} = \mu + s_t + b_{j(t)} + \tau_k + s\tau_{tk} + b\tau_{tjk} + f_{m(k)} + sf_{tm(k)} + bf_{tjm(k)} + e_{tjkmn} \quad [2]$$

where: Y_{tjkmn} is the nth observation of the mth family of the kth taxon in the jth block at the tth site; μ is the population mean; s_t is the random variable for site ~*NID* $(0, \sigma^2_s)$; $b_{j(t)}$ is the random variable for block within site ~ *NID* $(0, \sigma^2_b)$; τ_k is the fixed effect for taxon (PEE, PTA, PEE × PTA, PEE × [PEE × PCH], PEE × PCH, PEE × PCB, or PEU); $s\tau_{tk}$ is the random interaction site by taxon ~*NID* $(0, \sigma^2_{s\tau})$; $b\tau_{tjk}$ is the random interaction block (site) by taxon ~ *NID* $(0, \sigma^2_{b\tau})$; $f_{m(k)}$ is the random variable for family within taxon ~*NID* $(0, \sigma^2_f)$; $sf_{tm(k)}$ is the random interaction site by family within taxon ~*NID* $(0, \sigma^2_{sf})$; $bf_{tjm(k)}$ is the random interaction block within site by family within taxon ~*NID* $(0, \sigma^2_{bf})$; e_{tjkmn} is the error term ~*NID* $(0, \sigma^2_e)$; where $t = 1,...7$ or 4 sites; $j = 1, 2, 3$ blocks; $k = 1,...7$ taxa; $m = 1,...16$ families (taxon); and $n = 1, ...5$ trees.

The model for the single-site analyses was derived from the complete model (2), where the number of sites (s_t) equals one. The model used is obtained by dropping all terms from (2) relating to site (i.e., dropping all terms with subscript t):

$$Y_{jkmn} = \mu + b_j + \tau_k + b\tau_{jk} + f_{m(k)} + bf_{jm(k)} + e_{jkmn} \qquad [3]$$

where: Y_{jkmn} is the nth observation of the mth family of the kth taxon in the jth block. All other terms were described in model (2).

For all single-site and pooled analyses, PROC GLM (SAS INSTITUTE 1988) was used to test the significance of random effects. Significance levels and estimated means (using LSMEANS option) for the fixed effect taxon were obtained from PROC MIXED with the Satterthwaite option (LITTELL et al. 1996). A default probability value of 0.05 was established to show significance, unless otherwise specified.

To compare taxa differences on the basis of tip moth attacks, single degree-of-freedom contrasts were computed for both single site and pooled analyses. For example, a specific null hypothesis for contrasts was: there is no difference between taxon a and taxon b. Two contrasts were also done to determine whether or not hybrid vigor was expressed in the hybrid taxa for all traits measured. These contrasts were calculated based on the formula:

$$\text{Hybrid vigor} = H / [(P_1 + P_2) / 2] \qquad [4]$$

Thus, the single degree-of-freedom compared each hybrid mean (H) to the mean of the two parental taxa (P_1 and P_2). A significant contrast indicated that H was not linearly intermediate to P_1 and P_2, and was taken as evidence of hybrid vigor. If the hybrid value was above midpoint this was taken as negative hybrid vigor and if the hybrid value was below midpoint this was taken as positive hybrid vigor. Less tip moth attacks was the goal in the breeding strategy for resistance.

Family level analyses

The goal was to determine the level of genetic control for tip moth resistance in all taxa. These analyses were conducted separately for each taxon using only data from the Low treatment. Thus, estimates of variance components for family, site by family, site by block and error were calculated for each taxon with a pooled analysis across sites. The model was derived from the complete model [2], where the number of taxa (τ_k) equals one. The model used was obtained by dropping all terms from [2] relating to taxon (i.e., dropping all terms with subscript k):

$$Y_{tjmn} = \mu + s_t + b_{j(t)} + f_m + sf_{tm} + bf_{tjm} + e_{tjmn} \qquad [5]$$

where: Y_{tjmn} is the nth observation of the mth family in the the jth block at the tth site. All other terms were described in model [2], but site and block effects were

considered as fixed effects.

Variance components were estimated by PROC MIXED, with the restricted maximum likelihood method, REML (LITTELL et al. 1996). For pooled analyses, lateral attack was standardized by dividing each observation in a site-treatment-block combination by the corresponding square root of the phenotypic variance for that block to remove the effects of scale (VISSCHER et al.1991; HODGE et al. 1996).

Single-site analyses were also performed to get estimates of variance components for each taxon-site combination. The model used was derived from the model [5], where the number of sites (s_t) equals one. The model used was obtained by dropping all terms from [5] relating to site (i.e., dropping all terms with subscript t):

$$Y_{jmn} = \mu + b_j + f_m + bf_{jm} + e_{jmn} \qquad [6]$$

where: Y_{jmn} is the nth observation of the mth family in the jth block. All terms are described in model [2], but block effect was considered as a fixed effect.

Heritabilities

The goal was to estimate pooled heritabilities (h^2) and single-site heritabilities (h^2_b) for first-year terminal, and first- and second-year lateral attacks, for each taxon, as a measure of the genetic control for tip moth resistance. All analyses were performed with standardized data for moderate to heavily attacked sites. Seven and four sites were used for first and for second-year lateral attacks, respectively. Estimates of variance components were used from pooled analyses with model [5] to estimate h^2 and from single-site analyses with model [6] to estimate h^2_b.

The open-pollinated families in the PEE, PEU and PTA taxa were assumed to be half-sib families; hence, the variance component for families (σ^2_f) can be interpreted as an estimate of one quarter of the additive genetic variance (σ^2_A) (FALCONER & MACKAY 1996). For the hybrids, a hybrid heritability (h^2_h), was calculated as the proportion of 4 times the hybrid family variance (σ^2_{fh}) over the total phenotypic variance. These h^2_h values for hybrids may be bigger than those of pure species because, in the hybrids, additive and non-additive variance are confounded in σ^2_{fh} and gene frequencies in parental species may be different (WEI et al. 1991). Therefore, estimates of heritability (h^2 or h^2_h) for each taxon were calculated as:

$$h^2 \text{ or } h^2_h = 4^* \sigma^2_f / \sigma^2_f + \sigma^2_{sf} + \sigma^2_p + \sigma^2_w \qquad [7]$$

where values were obtained from model [5], and $\sigma^2_p = \sigma^2_{bf}$ and $\sigma^2_w = \sigma^2_e$.

Lastly, biased heritabilities (h^2_b or h^2_{bh}) were estimated for each taxon-site combination with the following model:

$$h^2_b \text{ or } h^2_{bh} = 4* \sigma^2_f / \sigma^2_f + \sigma^2_p + \sigma^2_w \qquad [8]$$

where values were obtained from model 6, and $\sigma^2_p = \sigma^2_{bf}$ and $\sigma^2_w = \sigma^2_e$.

RESULTS

Efficiency of control of tip moth attack

Single-site analyses revealed that the frequency of tip moth attacks was significantly lower in the insecticide-treated plots in areas highly affected by tip moth ($p <$ 0.05). When averages are combined across all seven taxa in each site where the low treatment had high incidence of tip moth damage and several insecticide applications were done in the high treatment this tendency was more clear (Figure 1). Both lateral and terminal attacks were lower in the High treatment for all five sites analyzed (at least $p < 0.05$). The effectiveness of the insecticide application may be confounded with effects of other cultural treatments (fertilizer, weed control) that accelerate stand development and move the trees into taller height classes that are commonly less impacted by tip moth than are shorter trees. The likelihood of stand development effects masking insecticide treatment effects seems small, especially when increased tip moth attacks have been recorded in sites which received intensive management and weed control, but lacked insecticide treatment (BERISFORD & KULMAN 1967; HOOD *et al.* 1988). Increased tip moth attacks in intensively managed situations may be due to increased tree exposure, a decreased habitat for parasites or tip moth's predators or the increased pine biomass providing more feeding sites (NELSON & CADE 1984). Our results support the efficiency of insecticide application for tip moth control (STEPHEN *et al.* 1982). This approach should be especially efficacious when using a spray-timing model for pesticide applications that targets the most vulnerable life stages of pine tip moth (BERISFORD *et al.* 1984, *et al.* 1989; GARGIULLO *et al.* 1985).

In some of the highly affected areas, treatment by taxon interactions were significant ($p <$ 0.05), but overall, no taxon rank changes where detected across treatments. Improved loblolly pine (PTA) and the PEE × PTA hybrid were the most attacked taxa with (High treatment) or without (Low treatment) insecticide
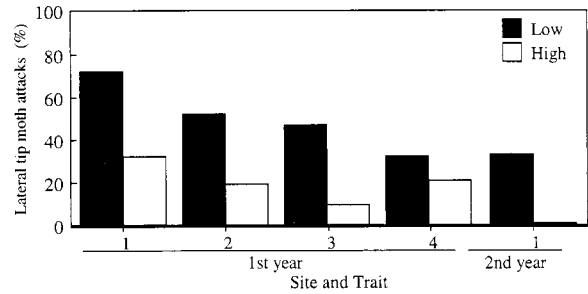

Figure 1. Percentage of lateral tips attacked by tip moth in the high and low cultural treatments. Averages are combined across all seven taxa in each site where the low treatment had high incidence of tip moth damage and several insecticide applications were done in the high treatment.
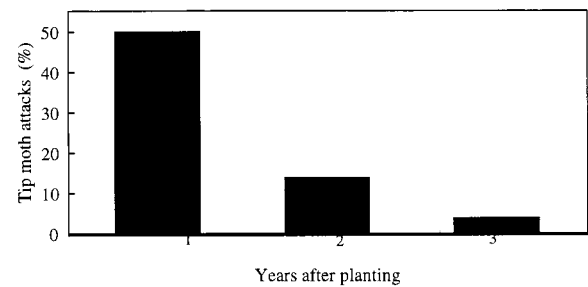

Figure 2. Average lateral tip moth attacks in percentage in the low treatment across years. Mean values are averaged of all seven taxa for the seven sites highly infected with tip moth.

application (see results below).

Taxon comparisons for tip moth incidence

Incidence of tip moth attacks decreased with age for High and Low treatments (see Figure 1 and 2 for Low treatment). Mean percentage of lateral attacks in the Low treatment was highest during the first growing season. For the seven most tip-moth affected sites, 50 %, 14 % and 4 % of lateral tips were attacked after the first, second and third growing season, respectively (Figure 2). The inverse relationship of stand age and the frequency of tip moth attacks is well known (CROSS *et al.* 1981; THOMAS *et al.* 1982) although the mechanisms responsible for this relationship have not been fully elucidated.

Highly significant differences for first-year attacks were found among sites. The reasons for different stands having radically different tip moth populations and/or damage are not fully understood (BERISFORD 1988), but they are related to tree species, weather, site quality, cultural practices, and natural enemies.

The pooled analysis using only sites with moderate to heavy incidence levels showed significant differ-

Table 2. Analysis of first- and second-year data pooled across sites in the Low treatment for lateral and terminal tip moth attacks[a].

Source	First year					Second year		
	Terminal			Lateral		Lateral		
	DF	F value	Pr > F	F value	Pr > F	DF	F value	Pr > F
Site	6	11.79	0.0001	12.65	0.0001	3	1.45	N.S.
Taxon	6	35.61	0.0001	20.49	0.0001	6	4.46	0.0075
Hybrid vigor in PEE × PTA	1	8.84	0.0049	9.17	0.0036	1	4.84	0.0425
Hybrid vigor in PEE × (PEE×PCH)	1	1.95	N.S.	0.04	N.S.	1	0.07	N.S.
PEE vs. PTA	1	101.80	0.0001	40.66	0.0001	1	12.53	0.0027
PEE vs. PEE × PCH	1	7.12	0.0120	1.01	N.S.	1	2.02	N.S.
PEE vs. PEE × PCB	1	1.03	N.S.	3.90	0.0528	1	0.08	N.S.
PEE × PCH vs. PEE × PCB	1	12.91	0.0009	7.49	0.0081	1	0.40	N.S.
Site × Taxon	35	1.73	0.0224	6.12	0.0001	16	6.50	0.0001
Family (Taxon)	130	1.66	0.0001	1.39	0.0057	129	1.52	0.0024
Site * Family (Taxon)	588	0.99	N.S.	1.27	0.0002	261	0.93	N.S
Error	8749					4580		

[a] ANOVA of first-year data was for the seven sites with moderate to high tip moth incidence. In the second year, later attacks were analyzed pooling four sites.

[b] Hybrid vigor of the PEE × PTA hybrid was analyzed by: PEE × PTA / (0.5 PEE + 0.5 PTA).

[c] Hybrid vigor of the PEE × (PEE × PCH) backcross hybrid was analyzed by using the contrast: PEE × (PEE × PCH) / (0.5 PEE + 0.5 PEE × PCH).

ences for taxon and site by taxon interaction for all traits (Table 2). Lateral attacks ranged across all taxa from 10 % to 72 % in the first year and from 8 % to 21 % in the second year. The most attacked taxon had in each site from 21 % to 93 % of and from 21 % to 90 % of lateral attacks, first year and second year, respectively. However, for first-year terminal, and for first- and second-year lateral attacks, no major rank changes were detected across sites. PTA and PEE × PTA were consistently the taxa most attacked by tip moth across all sites; there were smaller differences among the other five taxa (Figures 3 and 4).

Even though the frequency of terminal attacks on the PEE × PTA hybrid was less than on the PTA ($p = 0.02$, Figure 3), negative hybrid vigor was detected since the mean value was closer to the susceptible taxon, PTA. Further, the hypothesis that the PEE × PTA would be intermediate to parental taxa was rejected ($p < 0.005$, Table 2). First- and second-year evaluations indicated a negative hybrid vigor for lateral attack in PEE × PTA, with values across sites being similar to PTA (Table 2, Figure 4). Therefore, crossing loblolly by slash pine did not reduce tip moth attacks in loblolly pine. GRIGSBY (1959) using few crosses, found that hybrids between loblolly and slash pines were more resistant to tip moth than was loblolly pine. This was not the case here for lateral and terminal attacks. This difference may be by
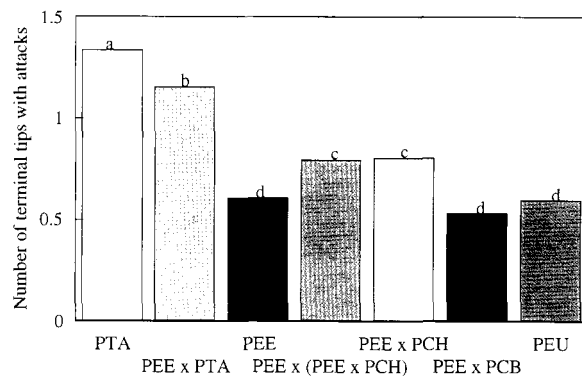

Figure 3. Average number of terminal tips attacked by tip moth after the first-year growing season for the tested taxa. Taxon was highly significant and some specific contrast are presented in Table 2. Taxon means with the same letter are not significantly different at least at the 0.05 level.

the sampling effect or differences in the genetic quality of both pines.

No significant differences were detected between improved and unimproved slash pine, i.e., PEU was as tip moth resistant as PEE. In general, the PEE × PCB hybrid was somewhat less attacked by tip moth than PEE × PCH hybrid or the PEE × (PEE × PCH) back-cross hybrid. For lateral tip moth attacks, PEE × PCB
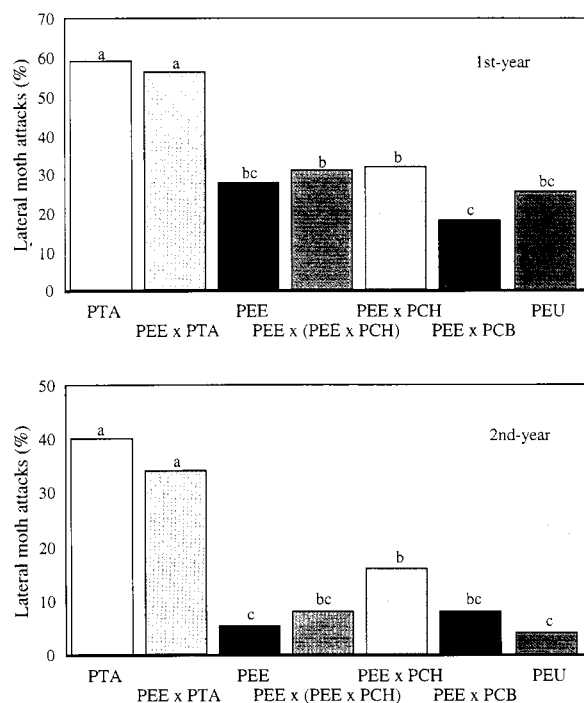
Figure 4. Average lateral tip moth attacks in percentage in the low treatment for the first-year and second-year after planting. First year results included seven sites highly infected with tip moth. Some specific contrasts are presented in Table 2. Taxon means with the same letter not significantly different at least at the 0.05 level.

hybrid was the least attacked of all taxa during the first year and was amongst the least attacked in the subsequent year (Figure 4).

Tip Moth Identification

Five hundred and sixty-five pupae were obtained at the end of the second-year from two of the study locations in north Florida and two locations in south Georgia. Overall, ninety-six percent of the pupae collected were Nantucket tip moth (R. frustrana), 2 % were subtropical tip moth (R. subtropica) and 2 % were Pitch-pine moth

pupae (R. rigidana Fernald). There were no differences among tip moth taxa across tree taxa (Table 3). Subtropical and Pitch-pine moths are scarce in Georgia and north Florida (MILLER 1960; BERISFORD et al. 1992). Other studies have indicated that the Nantucket tip moth prefers loblolly pine, while the subtropical prefers slash pine (McGRAW 1975; HERTEL & BENJAMIN 1977; HOOD et al. 1988). For example, HERTEL & BENJAMIN (1977) studying three locations in north-central Florida found that all tip moth attacks on loblolly pine were done by Nantucket tip moth, whereas more than 95 % of such attacks on slash pine were done by subtropical tip moth. This was not the case here.

Family Level

In general, no significant differences among families in tip moth attacks were found in any single-site analysis performed for any taxon (Model 6, results not presented). Pooled analyses [5] for PTA, PEU and the PEE × PCB hybrid indicated no significant differences among families in any year for terminal or lateral attacks. For PEE and the PEE × PCH hybrid, family differences were found for first-year terminal attack and second-year lateral attack. The other two hybrids, the PEE × PTA and the PEE × (PEE × PCH) backcross hybrid, showed family differences for one of the three traits (first-year terminal attack for PEE × (PEE × PCH) and second-year lateral attack for PEE × PTA, results not presented).

The small differences among families results in the estimates of heritability being quite low for all measures of tip moth incidence (Tables 4 and 5). The estimates of unbiased heritabilty (h^2) for loblolly pine indicated little if any genetic resistance to tip moth (at family level), at least for the traits measured. The hybrid PEE × PTA showed a little more family variation for tip moth resistance, since hybrid heritabilities were higher than heritability in PTA. However, additive and non-additive variance may be confounded, inflating the size of hybrid heritabilities (WEI al. 1991).

Table 3. Number and percentage (in parentheses) of pupae collected on each taxon. Insect identification was made according to the procedures of YATES (1967a) from samples collected after the second growing season on four sites.

Pine taxa	Tip moth taxa						Total	
	Nantucket		Subtropical		Pitch-pine			
PTA	265	(95%)	5	(2%)	8	(3%)	278	(49%)
PEE × PTA	207	(96%)	4	(2%)	5	(2%)	216	(38%)
PEE	70	(98%)	1	(2%)	0	(0%)	71	(13%)
Total	542	(96 %)	10	(2 %)	13	(2 %)	565	(100%)

Table 4. Mean and range (in parentheses) of single-site heritability estimates (h^2_b) and pooled-site heritabilities (h^2) bor terminal tip month attack for the pure taxa and the hybrids (hybrid heritability, h^2_h).

Taxon	h^2_b or h^2_{hb}	h^2 or h^2_h
PTA	0.05 (0.0–0.21)	0.01
PEE × PTA	0.06 (0.0–0.30)	0.02
PEE	0.04 (0.0–0.10)	0.03
PEE × (PEE × PCH)	0.14 (0.0–0.27)	0.05
PEE × PCH[a]	0.15 (0.0–0.55)	0.17
PEE × PCB	0.08 (0.0–0.31)	0.02
PEU	0.10 (0.0–0.40)	0.01

[a] Analyses with 6 sites.

Slash pine showed some degree of genetic control for second-year lateral attack (h^2 = 0.20), as did the PEE × PCH hybrid for terminal attack (h^2_h = 0.17). A few sites yielded estimates of single-site heritabilities (h^2_b or h^2_{hb}) that indicate moderate genetic control; however, there was no a clear relationship between the amount of tip moth attacks and the heritability estimates from each site, and those estimates ranged from 0 to 0.60. A lower bound of zero for individual heritability is not uncommon for traits which may have a true low heritability when based on a minimal number of families (little information). The primary limitations of our heritabiity estimates for tip moth resistance are (1) the low number of families in the study for a precise estimate and (2) the uncooperative tip moth populations which provided a low incidence at most evaluations.

DISCUSSION AND CONCLUSIONS

Tip moth attacks were the highest in the first year, then declined in the subsequent years to an insignificant level after the third growing period. This behavior was detected in both the High and the Low treatments. In the High treatment, tip moth incidence was drastically reduced. Insecticide application was also used during the second year, but the effects of treatments in accelerating stand development may change the rate of reduction of tip moth attacks across years. YATES (1966) and HOOD et al. (1985) found that slash pine was most susceptible to tip moth during the first year. Others have found under operational culture that tip moth attacks were relatively high in the second year, and either stabilized or declined in the third and following years (CROSS et al. 1981; THOMAS et al. 1982). Site and experimental conditions may explain differences in population size.

The Nantucket tip moth was the primary tip moth species found in the four sites sampled. Nantucket tip moth can cause more damage than the subtropical because it has more generations in a single season. For example, in northern Florida, Nantucket tip moth has five or six generations, double the number of generations of subtropical or Pitch-pine moth (MILLER 1960; MCGRAW 1975; HEDDEN et al. 1980). Nantucket tip moth will most likely need special control regimes such as those for other tip moth because the amount and accurate timing of the insecticide applications vary according to tip moth generation (YATES 1967b; GARGIULLO et al. 1983; BERISFORD et al. 1984).

Slash pine was significantly less attacked by tip moth than loblolly pine, supporting conclusions from other studies (e.g., YATES 1960; HERTEL & BENJAMIN 1977; BERISFORD 1988). The frequency of tip moth attacks on pure loblolly pine (PTA) and the PEE × PTA hybrid were significantly higher than those on slash pine or any slash × Caribbean hybrid. Approximately four to five developing shoot tips were required to obtain one pupa, while fewer than two pine tips were needed to collect one pupa for loblolly pine and the PEE × PTA hybrid. If this differential in successful

Table 5. Mean and range (in parentheses) of single-site heritability estimates (h^2_b) and pooled-site heritabilities (h^2) for lateral tip month attacks for the pure taxa and the hybrids (hybrid heritability, h^2_h).

Taxon	First-year lateral attack		Second-year lateral attack	
	h^2_b or h^2_{hb}	h^2 or h^2_h	h^2_b or h^2_{hb}	h^2 or h^2_h
PTA	0.14 (0.0–0.44)	0.01	0.07 (0.0–0.18)	0.00
PEE × PTA	0.10 (0.0–0.49)	0.02	0.07 (0.0–0.27)	0.07
PEE	0.12 (0.0–0.28)	0.04	0.11 (0.0–0.42)	0.20
PEE × (PEE × PCH)	0.15 (0.0–0.49)	0.04	0.09 (0.0–0.24)	0.05
PEE × PCH[a]	0.13 (0.0–0.60)	0.02	0.22 (0.0–0.44)	0.03
PEE × PCB	0.05 (0.0–0.20)	0.02	0.12 (0.0–0.32)	0.00
PEU	0.09 (0.0–0.40)	0.04	0.01 (0.0–0.03)	0.01

[a] Analyses with 6 and 2 sites for first and second-years respectively.

attacks (i.e, insect survives and matures to pupal stage) reflect differences in survival, they are consistent with the finding of YATES (1966) who determined that rates of larval mortality are higher on slash pine than in loblolly pine.

The frequency of tip moth attacks on slash pine might have been altered if slash pine had been grown in a single species plantation. The nature of the experimental design used in this study may have facilitated spread of the insects from the more susceptible loblolly into the surrounding slash pine. When insect population density is very high (as in outbreaks), the insect can spread into the surrounding healthy trees (SCRIVEN & LUCK 1980; SPEIGHT & WAINHOUSE 1989).

Family differences in tip moth attacks were all but absent in loblolly pine. Estimated heritability for tip moth resistance was very low, indicating almost no genetic control to resist tip moth attacks. All 17 loblolly pine families seemed to be equally susceptible to tip moth attack. The absence of evidence of genetic control may be influenced by the relatively low number of families sampled or it may in part reflect the way the traits were measured. In our study, most of the PTA families were from Florida sources. Evidence in one test in Georgia indicated that this provenance is susceptible to tip moth, while Livingston Parish provenance showed resistant to tip moth attacks (SCHMIDTLING & NELSON 1996). Also, other studies with non-Florida provenances found family differences in loblolly pine for tip moth infestation levels or for percent of growth loss (HERTEL & BENJAMIN 1975; CADE & HEDDEN 1989), and they may be useful to obtain resistance by interprovenances crosses of loblolly pine (SCHMIDTLING & NELSON 1996).

Proximity to heavily infested trees and synchrony between the emergence of adult moths and the availability of susceptible pine tips accentuate the apparent susceptibility of an individual (SCRIVEN & LUCK 1980). Thus, resistant families or individual trees may appear less resistant if grown in the proximity of susceptible trees. A small amount of genetic variation was detected among the PEE × PTA families tested, but this hybrid cross does not seem useful for increasing tip moth resistance as an F_1 hybrid since incidence of tip moth attacks were quite similar to those on pure loblolly pine.

A small amount of genetic control of tip moth attacks was detected among the slash pine and the slash × Caribbean hybrid families. In this study, a pine tip with tip moth attack was considered as any tip with evidence of tip-moth induced resin globules, or browning or dead tips. Most of the observed attacks in slash pine and the slash × Caribbean pine hybrids were of the resin globule type. Tips damaged by tip moth in loblolly pine and the PEE × PTA hybrid families were of the

browning or dead tips. The evidence here and in the literature suggested that resistance to tip moths in slash pine seems both quantitative and qualitative in nature. This study only measured the quantitative resistance.

Even with a high incidence of tip moth attack, loblolly pine height at three years of age was greater than slash pine (LÓPEZ-UPTON *et al.* 2000). PRICE (1991) found ample evidence that many shoot-borer insects prefer plants that have grown vigorously, because larvae survive better in larger buds on long shoots. However, fast-growing species can compensate for damage with vigorous growth. Apparently extremely rapid growth of host trees to some extent enables them to recover from successful attacks and to escape the susceptible stage sooner (ROSS & BERISFORD 1990; SUN 1990). At the same time however, rapid growth means more and succulent shoots that may favor increased frequency of attacks.

The apparent tip moth resistance of slash pine and the slash × Caribbean hybrids may reflect their ability to avoid or reduce the probability of being a host (antixenosis or non-preference, PAINTER 1951; KOGAN & ORTMAN 1978) and kill larvae (antibiosis). Antibiosis may explain why many buds on slash pine were found with an abandoned mine full of resin without a living larva. On the other hand, loblolly pine may present tolerance to tip moth damage, as WAKELEY & COYNE (1973) and SUN (1990) have found that loblolly pine has the ability to recover from the tip moth damage. Thus, selecting trees with asynchronous growth flushes (SCRIVEN & LUCK 1980), inter-provenance crosses (HERTEL & BENJAMIN 1975; SCHMIDTLING & NELSON 1996) and quick recovery after tip moth attacks (STEPHEN *et al.* 1982; ANDERSEN *et al.* 1984) have been mentioned as possible strategies to reduce impacts of tip moth in loblolly pine. Unlike antixenosis and antibiosis, tolerance is not part of an insect-plant interaction and involves only plant characteristics (SPEIGHT & WAINHOUSE 1989). Tolerance to tip moth damage is potentially stable, because it produces a weak selection pressure on the insect population (SPEIGHT & WAINHOUSE 1989). Therefore, selection for tolerance on loblolly pine may be useful by breeding tree with the ability to recover from the tip moth damage.

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