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Pine Tip Moth (Lepidoptera: Tortricidae) Infestation Rates as Influenced by Site and Stand Characteristics in Loblolly Pine Plantations in East Texas

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ABSTRACT Three young loblolly pine plantations grown on contrasting soil types produced quantitatively and qualitatively different host material for pine tip moths during 1985 and 1986. Amounts, periodicity, and availability of soil moisture regulated internal moisture conditions within host trees. Host xylem moisture potential in conjunction with soil nutrient status governed tree growth and influenced pine tip moth infestation rates. Pines on a sandy site exhibited the poorest growth with lowest infestation rates, indicative of low-quality hosts with little if any tolerance to damage. A clayey site produced vigorous plant growth with moderate infestation rates. The less apparent hosts appeared capable of withstanding pine tip moth attack and overcoming damage. Pines on a loamy site grew at moderate rates and received the highest infestation rates. This moderate growth indicated susceptible stand conditions.

KEY WORDS Insecta, *Rhyacionia frustrana*, site–stand influences, host quality

PINE TIP MOTHS, notably Nantucket pine tip moths, *Rhyacionia frustrana* (Comstock), are important insect pests of young pines in the southeastern United States, New Mexico, Arizona, and central California. Tip moths cause serious damage to young pine plantations, seed orchards, nurseries, Christmas tree plantations, and ornamental pines (Lashomb et al. 1978). Larval feeding severs the conductive tissue of growing tips, causing shoot dieback. Repeated infestations cause losses in height growth, stem deformation, losses in wood quality, bushy appearance, reduced cone crops, lower aesthetic value, and in severe instances, tree mortality (Yates et al. 1981).

Industrial forest management, in an effort to maximize fiber and timber production, has increasingly favored the establishment of large acreages of pine plantations. With the advent of high-yield forestry, management practices on these larger areas have become more intensified. Correspondingly, increases in tip moth numbers and intensity of infestations have occurred (Stephen 1984).

Three common species of *Rhyacionia* tip moths occur in the southeastern United States. These are the Nantucket pine tip moth; the pitch pine tip moth, *R. rigidana* (Fernald); and the subtropical pine tip moth, *R. subtropica* Miller. In East Texas, little if anything is known of the occurrence and life habits of the latter two species. Berisford (1987) indicated the natural range of *R. rigidana* extended westward into southeastern Texas, whereas *R. subtropica* was found only as far west as Mississippi. In samples collected by Miller & Wilson (1964), the Nantucket pine tip moth was always present in greater numbers, and all three species never occurred together. The Nantucket pine tip moth is prevalent across East Texas and was of primary concern in this study.

In the eastern United States, all species of native and exotic pines are attacked by the Nantucket pine tip moth except eastern white pine, *Pinus strobus* L., and longleaf pine, *P. palustris* Mill. Slash pine, *P. elliottii* Engelm., is highly resistant to attack. Loblolly pine, *P. taeda* L., and shortleaf pine, *P. echinata* Mill., are the favored hosts of Nantucket pine tip moth in the southern and southeastern United States (Yates et al. 1981).

Site and stand factors influence the amount of tip moth damage. Generally, the more suited the host trees are to the site, the less severe the damage (Wakeley 1928). Intensive vegetation management, which tends to reduce the diversity of an ecosystem, results in increased Nantucket pine tip moth infestation rates (Berisford 1987). Site preparation intensity, site index, and a number of other site–stand variables have been correlated with levels of tip moth infestations (White et al. 1984, Wilson 1984, Hood et al. 1988, Kulhavy & Meeker 1989, Ross & Berisford 1990).

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Rapid growth enables host trees to reach a threshold height (≈4.5 m) sooner, beyond which trees become less susceptible (Lashomb & Steinhauer 1974, Berisford 1987). Fertilizing with nitrogen has resulted in slight reductions in tip moth attack, whereas applications of phosphorus resulted in significantly decreased infestation rates (Pritchett & Smith 1972; W. G. Ross & D.L.K., unpublished data). In response to fertilization, Ross & Berisford (1990) alternatively showed that Nantucket pine tip moth egg density, number of pupae per seedling, and pupal weight were directly related to host tree nutrient status, although larval survival was negatively correlated. In their study, nutrient and moisture conditions were controlled carefully in potted seedlings in a greenhouse before hosts were subjected to wild populations of adult tip moths. Berisford (1987) postulated that the increased general health of trees grown on better sites may lead to higher resin flow and increased resinosus of young tip moth larvae.

In part, findings of Ross & Berisford (1990), Ross et al. (1990), and W. G. Ross & D.L.K. (unpublished data) together supported the following theory. Increased water and nutrient availability causing vigorous growth of host trees, as well as competing vegetation, produces a desirable high-quality host for Nantucket pine tip moths, but also affords hosts better protection against tip moths because of increased masking and improved defense mechanisms such as increased resin production. In addition, vigorous growth promotes host tolerance and recuperative capacity. Nantucket pine tip moth infestation rates and resulting damage on highly productive sites may therefore, in some instances, be substantially lower than that experienced on less productive sites.

The objectives of this study were to correlate moisture and nutrient conditions on three contrasting sites–stands with stand development and pine tip moth infestation rates.

Materials and Methods

The study was conducted during 1985 and 1986 on three loblolly pine plantations planted during 1983 on contrasting soil types. These sites were chosen to reflect droughty, wet, and more favorable soil moisture conditions for plantation growth in East Texas (Brady 1974, SCS 1980). Host tree species, age of host trees, and intensity of site preparation were similar across sites.

Site 1, located 40 km N of Nacogdoches, is an excessively drained, sandy soil (Typic Quartzipsamments) of the Tonkawa series and has a site index of ≈55 (SCS 1980). Regeneration survival was sparse and patchy, containing ≈250 trees per ha. Efforts to regenerate the site have met with repeated failure (Kulhavy et al. 1987). Ground cover was sparse.

Site 2, located ≈48 km SE of Nacogdoches on State Highway 103, is a moderately well-drained clayey soil (Vertic Hapludalfs) of the Woodtell series with a site index of ≈70 (SCS 1980). Ground cover was abundant and dense. Pine stocking was ≈1,837 trees per ha.

Site 3, located ≈45 km SW of Nacogdoches on State Highway 103, is a well-drained loamy soil (Arenic Plinthic Paleudults) of the Lilbert series. Site index for the soil type is ≈80 (SCS 1980). Ground cover was sparse, with pine stocking of ≈1,136 trees per ha.

On each site, three experimental plots at least 40 m apart were established. Each plot consisted of 25 loblolly pines >0.6 m in height. Total tips and apparently infested tips were used to calculate whole-tree infestation rates for each sample tree. Apparently infested tips were those exhibiting browning, curling, dieback, and resin globules. Apparent end-of-year infestation rates were determined during November 1985 and November 1986. Generations of Nantucket pine tip moth during 1986 were timed using Pherocon traps (Zoecon, Palo Alto, Calif.) and pheromone dispensers (Trece, Inc., Salinas, Calif.). Two Nantucket pine tip moth traps, one *R. rigidana* trap (pheromone lures from C. W. Berisford, University of Georgia) and one *R. subtropica* trap (European pine shoot moth, *R. buoliana* (Denis & Schiffermüller), pheromone lures from Trece) were placed at each site at a distance not influencing field plot populations. Tip moth counts were recorded from the traps on a weekly or semiweekly basis.

Soil moisture measurements were taken using a nuclear hydroprobe, a neutron-scattering moderation instrument, in conjunction with 1.83-m seamless aluminum access tubing (5.03 cm outside diameter, 0.245 cm thick). Three access tubes were installed to a depth of 1.65 m at each field plot during the summer of 1985. Tubes were placed equidistant from each other, from plot edges, and from neighboring trees along a line bisecting each plot. Soil moisture measurements began during February of 1986 and were recorded semimonthly through the end of the 1986 growing season (in conjunction with xylem moisture potential [XMP] measurements). Readings were taken at six different depths from the soil surface: 15, 30, 60, 90, 120, and 150 cm. Calibration equations for conversion of count ratios were calculated for each of the three soil types, based on soil texture and moisture-holding capacity.

Host tree xylem moisture potential (XMP) was measured directly using the pressure chamber technique (Scholander et al. 1965). A portable pressure apparatus (Plant Moisture Stress Instrument Company, Corvallis, Ore.) along with a portable nitrogen gas tank were used for the field experiment. XMP was determined on host trees from twigs located in the upper one-third of the

Table 1. One-way ANOVA on end-of-year pine tip moth infestation rates for 1985 and 1986 by plot and site and resulting change between years

Site and plot	Sample size[a]	1985, $\bar{x}$ ± SD	1986, $\bar{x}$ ± SD	% Change
Tonkawa				
1	25 (24)	8.62 ± 8.19bc	5.49 ± 3.95c	−3.13
2	21 (20)	6.66 ± 6.21bc	7.02 ± 4.76c	+0.36
3	25 (25)	4.60 ± 5.35c	8.55 ± 5.84bc	+3.95
Total	71 (69)	6.62 ± 6.83c	7.42 ± 5.03b	+0.42
Woodtell				
1	25	11.29 ± 5.99b	6.74 ± 3.55c	−4.55
2	25	9.94 ± 6.17b	6.83 ± 4.92c	−3.11
3	25	11.30 ± 7.68b	8.70 ± 5.26bc	−2.60
Total	75	10.84 ± 6.60b	7.42 ± 4.66b	−3.42
Lilbert				
1	25	18.42 ± 10.75a	11.07 ± 7.29ab	−7.35
2	25	19.46 ± 14.43a	13.40 ± 5.95a	−6.06
3	25	21.15 ± 9.56a	13.69 ± 6.84a	−7.46
Total	75	19.68 ± 11.66a	12.77 ± 6.73a	−6.96

Among rows, means followed by the same letter are not significantly different ($P > 0.05$, Duncan's multiple range test). Rate is the percentage of total tips infested per tree.

[a] Values in parentheses represent mortality of sample trees during 1986 growing season.

crown (excluding the terminal), where tip moth infestations are concentrated and exposure to sunlight is greatest. Samples consisted of hardened-off branch segments ≈15 cm in length containing fully developed needles. Sample size at each plot for each sampling interval consisted of five twigs, one from each of five different trees located in the area immediately surrounding each plot. Measurements were recorded in pounds per square inch (psi) (g/cm^2) required to force water to the cut surface of the severed twig. XMP was characterized diurnally at each site six times: once at the commencement of the growing season, at four intervals throughout the growing season, and once again at the end of the growing season. Diurnal XMP was determined at four times throughout the day: (1) before sunrise, (2) between 0930 and 1030 hours (CDT), (3) between 1300 and 1400 hours, and (4) between 1600 and 1700 hours. Beginning at the end of June 1986, XMP was measured semimonthly at all three sites during the peak daily stress period between 1300 and 1400 hours.

Soil samples were collected at depths of 15, 30, 60, 90, 120, and 150 cm during installation of soil access tubes. Composite samples were made for each plot from the three sampling points per plot. Nutrient analysis was conducted on the 15-, 30-, 60-, and 120-cm samples. Total nitrogen was determined using the micro-Kjeldahl method. Concentrations of phosphorus, potassium, magnesium, iron, manganese, zinc, copper, and calcium were determined by emission spectroscopy. All soil nutrient analyses were conducted in the Soils Testing Laboratory by the Agriculture Department, Stephen F. Austin State University. A texture analysis using the Bouyoucos method was conducted on all soil samples.

Eight tree growth parameters measured during the winter of 1985 and 1986 included: (1) total tree height, (2) diameter at base of tree, (3) length of terminal leader from cessation of previous year's growth, (4) number of flushes of growth during each year, (5) diameter of terminal five cm down from tip, (6) diameter at base of current season's terminal leader, (7) length of most dominant three laterals originating from the base of the current season's terminal leader, and (8) diameter at the base of those laterals.

Analysis of variance (ANOVA) was used to test for differences among pine tip moth infestation rates, soil texture, soil moisture, XMP, soil nutrition, and tree growth parameters among sites using SPSS–X (Norušis 1983) statistical software. When F tests were significant, Duncan's multiple range tests were conducted to determine where significant differences occurred.

Results and Discussion

Pine tip moth infestation rates varied in intensity among stands, among individual trees within stands, and between years (Table 1). An examination of contrasting site–stand characteristics and accompanying climatic conditions in the three study sites showed quantitative and qualitative differences among hosts and associated vegetation which corresponded to observed tip moth infestation rates according to the proposed theory.

Three species of pine tip moths were trapped at each site: *R. frustrana*, *R. rigidana*, and *R. subtropica*. The Nantucket pine tip moth was the most prevalent and occurred with the greatest regularity across all sites, exhibiting five generations during 1986.

End-of-year pine tip moth infestation rates during 1985 were significantly different among all sites, averaging approximately 20, 11, and 7% for Lilbert, Woodtell, and Tonkawa sites, respectively (Table 1). Infestation rates were expected to be even higher in tops of trees (Berisford & Kulman 1967). Andersen (1980) found that an 8% whole-tree infestation rate corresponded to a terminal leader infestation rate of ≈50%. Therefore, the whole-tree infestation rates reported here, which were similar to those noted by others (Miller & Stephen 1983, Hood et al. 1988, Ross et al. 1990), suggested substantial differences in tip moth incidence. At Tonkawa, where the mean tree infestation rate was the lowest, individual tree infestation rates exhibited the narrowest range (0–23%), with the greatest number of trees (18) escaping infestation. The Woodtell site, which was moderate in mean tree infestation rate, showed a greater range in individual infestation rates (0–35%), with fewer trees (3) escaping infestation. The Lilbert site, which had the highest mean tree infestation rate, exhibited the largest range in individual tree infestation rates (0–52%).

During 1986, mean end-of-year pine tip moth infestation rates generally decreased, presumably due to mortality caused by a substantial freeze during March and increased host tree vigor. Infestations declined to 13% at Lilbert, 7% at Woodtell, and 7% at Tonkawa (Table 1); however, the number of trees escaping infestation also decreased at each site during 1986. Maximum ranges in individual tree infestation rates also declined to highs of 34, 22, and 11% for Lilbert, Woodtell, and Tonkawa trees, respectively.

The three different soil types produced contrasting moisture regimes (Brady 1974), which resulted in distinctive stands of host type and competing vegetation with correspondingly different levels of pine tip moth infestation. Soil textural analyses indicated that the Tonkawa soil consisted of >94% sand for all depths combined. This soil is characteristically deep and excessively drained, having rapid permeability. Among study sites, the extremely poor moisture-holding capacity of the Tonkawa soil (Brady 1974) resulted in soil moisture contents (SMC) (averaged for all depths combined) that were generally at the lowest levels throughout the year, maintained for the longest period at yearly lows, exhibited declines earlier and recoveries later, and showed moderate rates of decline and increase over the shortest range in levels (Fig. 1). Although relatively little moisture is held in unavailable forms in this soil, the range of moisture available to plants is small because water is easily lost to gravitational forces at low levels (Brady 1974).

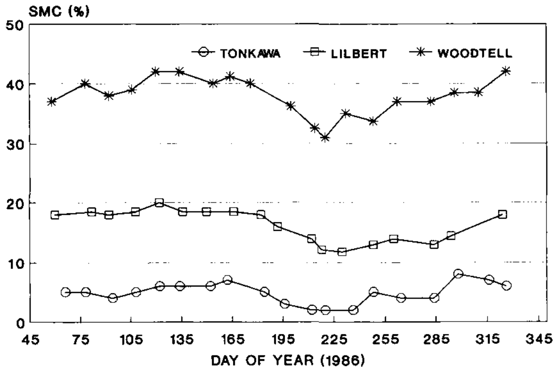

Fig. 1. Average percentage moisture content of the soil (SMC) down to 150 cm during 1986 for three contrasting sites. Each data point represents an average of 54 measurements from nine sampling points.

The high sand content leading to low SMCs indicated that soil–plant moisture conditions were poorest at the Tonkawa site. This was evidenced by Tonkawa host trees generally exhibiting longer and additional seasonal moisture stresses to lower levels of XMP than at the other two sites (Fig. 2). XMP results also indicated that longer and more severe diurnal moisture stresses occurred in the Tonkawa trees (data not shown). During the early spring and midsummer of 1986 when periods of relatively high moisture stress occurred, trees at Tonkawa reached significantly lower levels of XMP. Average diurnal XMP at the beginning of March in Tonkawa trees reached −0.91 MPa. Peak stresses recorded during early August at Tonkawa reached an average diurnal XMP low of −1.39 MPa. Even by early October, when moisture stresses were relatively less, Tonkawa host trees still maintained the lowest average diurnal XMP at −0.76 MPa.

Concentrations of most nutrients sampled were generally lowest at the Tonkawa site (Table 2). Because of the combined effects of the poorest soil–plant moisture conditions and the lowest

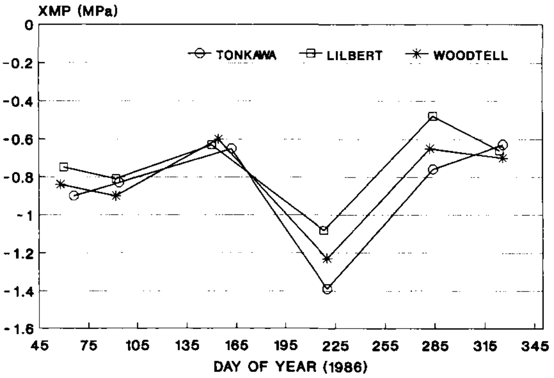

Fig. 2. Average diurnal xylem moisture potential (XMP) of loblolly pine host trees from three contrasting sites during 1986. Averages are based on four sampling periods per day. Each data point represents an average of 60 measurements from 15 trees.

Table 2. One-way ANOVA on macro- and micronutrients sampled in the soil at 15 cm depth on three contrasting soil types in eastern Texas by site

Element	Site[a]		
	Tonkawa	Woodtell	Lilbert
N	352.00 ± 93.006b	748.67 ± 109.02a	321.00 ± 63.596b
P	4.00 ± 0.00a	3.33 ± 2.08a	2.33 ± 0.58a
K	21.67 ± 4.51b	125.67 ± 26.54a	44.33 ± 7.77b
Ca	350.00 ± 195.25b	971.00 ± 346.87a	350.00 ± 132.75b
Mg	41.67 ± 6.35b	221.67 ± 72.47a	58.33 ± 10.21b
Fe	11.40 ± 7.21b	63.90 ± 11.96a	28.97 ± 10.13b
Mn	4.29 ± 4.77b	21.90 ± 4.91a	11.58 ± 9.77ab
Zn	0.31 ± 0.33b	1.84 ± 0.73a	0.68 ± 0.24b
Cu	0.20 ± 0.08b	1.36 ± 0.08a	0.95 ± 0.50a

Among columns, means followed by the same letter are not significantly different ($P > 0.05$, Duncan's multiple range test).

[a] Values represent $\bar{x}$ ± SD ppm.

soil nutritional levels, resulting host trees at the Tonkawa site generally were significantly smaller, thinner, and of less volume than trees at the other two sites after their third and fourth growing seasons (Table 3). Severe site conditions similarly affected competing vegetation, which was minimal and mostly herbaceous. Poor growth of Tonkawa host trees corresponded to low infestation rates. Although host tree tips apparently were overcome easily by attacks, populations remained low because of the lack of sufficient host type.

In contrast, the Woodtell site contained soil consisting primarily of clay, averaging 64% for all depths combined. This created an excellent soil moisture-holding capacity (Brady 1974). Accompanied by substantially smaller amounts of sand and silt, the Woodtell soil is only moderately

Table 3. One-way ANOVA on end-of-year growth parameters for loblolly pine host trees grown on three contrasting soil types in eastern Texas by site, and resulting changes between years

Variable	Site[a]		
	Tonkawa	Woodtell	Lilbert
Total height, cm			
1985	94.89 ± 26.46c	139.97 ± 35.55a	119.20 ± 37.09b
1986	166.93 ± 44.93c	247.15 ± 43.83a	204.71 ± 99.27b
Change	+72.04	+107.18	+85.81
Diameter at base, cm			
1985	1.92 ± 0.62b	2.40 ± 0.66a	1.98 ± 0.82b
1986	3.55 ± 1.15b	4.79 ± 1.08a	3.59 ± 1.35b
Change	+1.63	+2.39	+1.61
Leader volume, cm^3			
1985	7.03 ± 7.58c	79.24 ± 56.79a	36.39 ± 39.28b
1986	122.50 ± 97.42b	343.57 ± 168.43a	158.89 ± 134.14b
Change	+115.47	+264.33	+122.50
Lateral volume, cm^3			
1985	1.27 ± 2.17c	11.06 ± 9.07a	6.93 ± 7.24b
1986	18.75 ± 16.21c	51.05 ± 29.85a	22.31 ± 21.63b
Change	+17.48	+39.99	+15.38
Tip diameter, cm			
1985	0.42 ± 0.11b	0.53 ± 0.12a	0.46 ± 0.13b
1986	0.54 ± 0.16c	0.76 ± 0.14a	0.63 ± 0.16b
Change	+0.12	+0.23	+0.17
Flushes			
1985	2.15 ± 0.47c	4.01 ± 0.69a	2.97 ± 0.70b
1986	4.08 ± 0.74b	4.69 ± 0.70a	4.28 ± 0.91b
Change	+1.93	+0.68	+1.31
Total tips			
1985	30.03 ± 16.18b	36.39 ± 11.46a	22.21 ± 11.00c

Among columns, means followed by the same letter indicate no significant difference ($P > 0.05$, Duncan's multiple range test).

[a] Values represent $\bar{x}$ + SD.

well drained and has slow permeability. Compared with the Tonkawa and Lilbert sites, SMCs on the Woodtell site were generally highest throughout the year, maintained the shortest period of seasonal decline during the summer, and exhibited the most rapid increases and decreases with the largest range in recorded values (Fig. 1). Although the Woodtell site had the highest SMC, the majority of that water was probably held in forms unavailable for plant use because of the high clay content of the soil (Brady 1974). Second, soil moisture content in the top 15 cm fluctuated drastically, dropping to almost 0.00% during summer.

Because precipitation was supplied in amounts and occurrences substantially greater than that of the long-term average during both 1985 and 1986 (32 cm greater on 16 more d during 1985 and 34 cm greater on 27 more d during 1986), nutrition became more limiting to plant growth during both years. The Woodtell soil generally contained the highest concentrations of most elements and at substantially higher levels than in the other sites (Table 2). Moderate soil–plant moisture conditions and high nutrient levels in the soil resulted in Woodtell trees being significantly larger than those at the other sites for all tree growth parameters during both years (Table 3). Similar to results found by W. G. Ross & D.L.K. (unpublished data), these site conditions also promoted relatively high levels of competing vegetation. Zutter et al. (1986) showed that increased levels of competing vegetation were associated with lower levels of XMP in young loblolly pines. Moisture status of host trees at the Woodtell site appeared to be similarly affected because XMPs were relatively moderate despite the obviously superior growth.

At the Woodtell site, values of average diurnal XMPs for host trees were between those of the other two sites during moisture stress periods (Fig. 2). Woodtell trees also incurred long seasonal moisture stresses like those on Tonkawa but with later initiation and reduction of those stresses compared with the other two sites. Seasonal moisture stresses exhibited at the Woodtell site during peak periods and diurnal samplings were, however, at lower levels relative to Tonkawa trees (data not shown). Shorter ranges in XMPs and higher daily as well as higher seasonal XMPs at the Woodtell site showed that trees had consistently better moisture conditions for growth versus those at the Tonkawa site.

Vigorous growth of host trees and competing vegetation corresponded to moderate and low infestation rates during 1985 and 1986, respectively. In accordance with findings of Ross & Berisford (1990), a desirable host was produced through vigorous growth, but end-of-year infestation rates and damage appeared limited. A similar scenario was found for host trees receiving fertilizer treatments without control of competing vegetation (W. G. Ross & D.L.K., unpublished data). Increased levels of competing vegetation on a given site reduces crop tree growth and survival and has been linked to lowering the incidence of tip moth infestations (Zutter et al. 1986). Ross et al. (1990), however, showed that the incidence of infested tips in untreated check plots varied above and below those in plots receiving herbicide treatments. More important, they noted that when tip moth damage was higher in plots receiving vegetation control, the greater growth of host trees therein more than compensated for losses and was consistently greater than in untreated check plots. Among sites differing in productivity, the rapid growth of host trees and competing vegetation at Woodtell enabled hosts to outgrow pine tip moth attacks without noticeable damage, to recover from successful attacks, and reduced the apparency of host trees. Rapid growth would also enable host trees to escape susceptible stages sooner.

The Lilbert site contained soil consisting of less sand and more clay than the Tonkawa soil and had the greatest amount of silt (22%) of the three sites. The soil is characteristically deep and well drained, having moderately slow permeability. These factors create good moisture-holding capacities within the Lilbert soil (Brady 1974). Relative to the other sites, the Lilbert site exhibited SMCs that were typically at moderate levels throughout the year; moderate in duration of period of declining SMCs to a yearly low, reached at the latest date; and exhibited the most gradual rates of increasing and decreasing SMCs (Fig. 1). The Lilbert site was between Tonkawa and Woodtell sites in moisture-holding capacity (Brady 1974). Given the favorable availability of water to plants provided by the textural makeup of the Lilbert soil, soil–plant moisture relationships were conditionally the best.

At the Lilbert site during the summer drying cycle and subsequent recharge, SMCs at 15 and 30 cm were maintained at substantially higher levels than those at 60 cm (data not shown). Occurrence of light, periodic summer rains supplied moisture in amounts adequate to replenish SMCs above 30 cm, resulting in only slightly changing levels at these depths, but not enough to prevent the rapid and continual loss in soil moisture at 60 cm. As a result, significantly higher SMCs were observed relative to the other sites in the surface levels of the soil during summer. Most feeder roots occur in these upper soil levels. Therefore, soil–plant moisture relationships were distinctly improved at the Lilbert site. Increased amounts of available water for trees on the Lilbert site are reflected in the generally higher XMPs recorded for host trees (Fig. 2).

The Lilbert site produced host trees having the lowest seasonal moisture stresses for the shortest period of time of all sites (Fig. 2). Daily

XMPs were also higher and at physiologically hindering lower levels for the shortest periods of time among sites (data not shown). The highest average diurnal XMPs were exhibited by host trees at the Lilbert site for periods of relatively high moisture stress and during the recovery stage in early October. During peak stress in the summer, Lilbert host trees averaged −1.102 MPa. During October, average daily XMP on Lilbert host trees was −0.469 MPa and was at the highest level measured during the study period.

Concentrations of essential elements were usually higher on the Lilbert site compared with Tonkawa but were markedly lower than those on the Woodtell site (Table 2). The superior internal moisture conditions combined with limiting low nutritional levels resulted in host trees of only moderate growth (Table 3) and low levels of associated herbaceous vegetation. Moderate growth of host trees at the Lilbert site corresponded to the highest tip moth infestation rates. Moderate growth produced a desirable, readily apparent host flushing in synchrony with emergence of successive generations of Nantucket pine tip moths.

These results indicated that moisture and nutrient conditions promoting vigorous plant growth throughout the stand produces a highly desirable host but supports only moderate tip moth infestations, presumably due to increased internal defense mechanisms, the ability to withstand successful attacks without noticeable damage, and greater associated protection. Highly productive sites also promote rapid host recovery from damage and reduced time spent in susceptible stages. Cultural practices aimed at reducing competing vegetation to increase growth and survival of host trees may realize greater gains on less productive sites with regard to minimizing tip moth damage. In commercial forestry, little else can be done to improve soil moisture conditions. Where soil–plant moisture conditions are favorable for rapid host tree growth and nutrients are limiting, fertilization may increase pine growth as well as lower tip moth susceptibility. Marginal sites, such as Tonkawa with poor moisture and nutrient conditions leading to low host productivity, should be planted to a more suitable species such as longleaf pine, which is immune to Nantucket pine tip moth.

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