# The Nantucket Pine Tip Moth (Lepidoptera: Tortricidae): A Literature Review with Management Implications[1]

Christopher Asaro, Christopher J. Fettig,[2] Kenneth W. McCravy,[3] John T. Nowak[4] and C. Wayne Berisford

Department of Entomology, University of Georgia, Athens, GA 30602 USA

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**Abstract** The Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock), an important pest of intensively-managed loblolly pine, *Pinus taeda* L., was first noted in the scientific literature in 1879. This pest gained notoriety with the establishment of loblolly pine monocultures throughout the southeastern United States during the 1950s. Current intensive forest management practices have led to increasing interest in managing this insect. Herein we review all Nantucket pine tip moth literature (1879–2002) by addressing the following subjects: biology and life history, natural enemies, sampling methodologies, site and stand influences, economic impact, and management strategies. Further, we provide management recommendations in the form of a decision chart that is based upon the best available information to date and our collective experience.

**Key Words** *Rhyacionia frustrana, Pinus taeda,* loblolly pine, intensive forestry, integrated pest management

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The Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae), is a common pest of pine plantations throughout the eastern United States. In recent years, perhaps as a result of more intensive forest management, renewed interest has developed in the ecology and management of *R. frustrana,* particularly in the southeastern United States. S. H. Scudder first reported *R. frustrana* as a pest of pine in 1879 during the Annual Meeting of the Entomological Club of the American Association for the Advancement of Science (Saunders 1879). Scudder spoke of an undescribed microlepidopteran that, since 1876, had been causing significant damage to pitch pine, *Pinus rigida* Mill. (Coniferales: Pinaceae), planted on Nantucket Island, MA, to reforest stands harvested for firewood during the War of 1812. At the same meeting, J. H. Comstock commented that he had observed a similar insect infesting the tips of scrub pines in northern Virginia near Washington, DC (Saunders 1879, Comstock 1880). Comstock described the species as *Retinia* (= *Rhyacionia*) *frustrana* or "the frustrating Retinia," which was subsequently determined to be iden-

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[2] Current address: USDA Forest Service, Pacific Southwest Research Station, 1107 Kennedy Place, Suite 8, Davis, CA 95616.

[3] Current address: Dept. of Biological Sciences, Western Illinois University, 1 University Circle, Macomb, IL 61455.

[4] Current address: USDA Forest Service, Forest Health Protection, 200 WT Weaver Boulevard, Asheville, NC 28802.

tical to the species described in Scudder's manuscript (Comstock 1880). Scudder (1883) published the first definitive study on *R. frustrana,* describing its life history based on his observations from Nantucket Island.

*Rhyacionia frustrana* was not mentioned again in the scientific literature until Swenk (1910). During that year, the Nebraska state entomologist described the insect as a significant pest of young ponderosa, *P. ponderosa* Dougl. Ex. Laws., jack, *P. banksiana* Lamb., and Scots, *P. sylvestris* L., pine planted in the Nebraska National Forest (Swenk 1910). Seedlings used to afforest this naturally treeless region were transplanted from other areas, and it is thought that *R. frustrana* was accidentally introduced by the planting of infested nursery stock. Swenk (1910) feared that *R. frustrana* infestations would interfere with the establishment of the Nebraska National Forest and, therefore, in cooperation with the Bureau of Entomology and U.S. Forest Service, he coordinated studies of the pest's life history (Howard 1925, Graham and Baumhofer 1927, 1930, Swenk 1927). Other investigators searched for biological control agents (Cushman 1927a, b, Gahan 1927, Wakeley 1928) and explored the possibility of breeding resistant tree species (Graham and Baumhofer 1930).

*Rhyacionia frustrana* was initially placed in the family Olethreutidae by Heinrich (1923). Powell and Miller (1978) reclassified the Olethreutidae as the subfamily Olethreutinae (Tortricidae). Forbes (1923) studied the Lepidoptera of New York and surrounding states, and provided the first definitive key to the known species of *Rhyacionia,* including *R. frustrana.* Miller (1967a) reviewed the taxonomy of the *R. frustrana* group and established *R. bushnelli,* currently recognized as the western pine tip moth, as a distinct species from *R. frustrana.* The two species are allopatric, although their respective ranges overlap slightly in Missouri (Powell and Miller 1978). The primary biological difference between the two species is that *R. bushnelli* overwinters in the duff; whereas, *R. frustrana* overwinters in infested shoots. Because *R. bushnelli* had not yet been distinguished as a separate species, the tip moth population noted by Swenk (1910) in the Nebraska National Forest may indeed have been *R. bushnelli* rather than *R. frustrana.*

*Rhyacionia frustrana* is frequently a significant pest of pine plantations throughout its native range, which includes most of the eastern United States (Fig. 1). Disjunct populations exist in southern California, where *R. frustrana* was accidentally introduced in 1967 by a nursery stock shipment of infested seedlings from Georgia (Powell and Miller 1978), and throughout much of New Mexico (pers. commun., Robert Cain, New Mexico State University, Forestry Division, Santa Fe, NM) and Arizona (pers. commun., J. McMillin, USDA Forest Service, Forest Health Protection, Flagstaff, AZ) (Fig. 1). The species is also found in the Dominican Republic (Etheridge 1971), Cuba (Hochmut 1972), Jamaica (Powell and Miller 1978), Mexico (Oaxaca State) (Powell and Miller 1978), Guatemala (Schwerdtfeger 1962), Honduras (Powell and Miller 1978) and Nicaragua (Becker 1973) (Fig. 1). Presumably, *R. frustrana* exists throughout most of Mexico, Central America, and the Caribbean. The natural range overlaps that of several other common species of *Rhyacionia* including *R. rigidana* (Fernald), *R. subtropica* Miller, and *R. buoliana* (Denis & Schiffermüller). *Rhyacionia frustrana* and *R. rigidana* can often be found simultaneously on the same host (Berisford 1974b, Canalos and Berisford 1981), although *R. frustrana* is usually much more abundant where these species co-occur (Baer and Berisford 1975).

Most species of native and exotic pines are susceptible to attack (Friend 1934, Polivka and Houser 1936, Berisford 1988), and preference varies by region. Loblolly, *P. taeda* L., shortleaf, *P. echinata* Mill., and Virginia, *P. virginiana* Mill., pines are

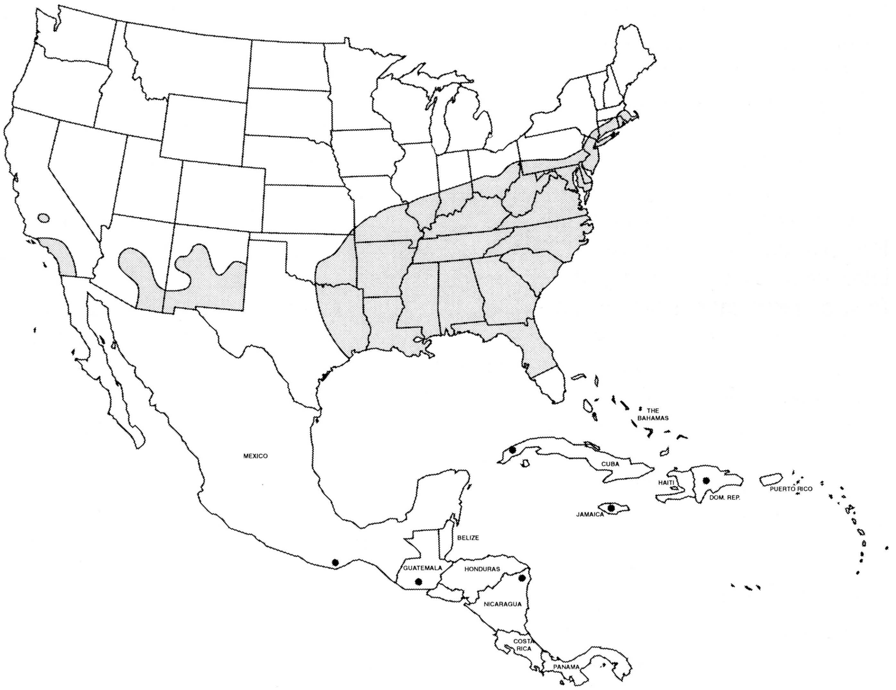

Fig. 1. The known distribution of the Nantucket pine tip moth, *Rhyacionia frustrana.* Shaded areas indicate contiguous distributions while dots denote isolated collection locations. The range indicated for the western United States is based on collection records from specific counties within each state but probably does not conform to the actual distribution, which may be contiguous through Texas, New Mexico, Arizona, California, and Mexico.

preferred hosts in the southeastern United States. In the Northeast, preferred hosts include Scots and pitch pine, but red, *P. resinosa* Ait., and Mugo, *P. mugo* Turra., pines are also attacked (Gibson 1968). In the Southwest, Ponderosa pine is a common host while most infestations in California occur in Monterey pine, *P. radiata* D. Don (Scriven and Luck 1980). In general, slash, *P. elliottii* Engelm., longleaf, *P. palustris* Mill., and eastern white, *P. strobus* L., pine are resistant to attack, although infestations do occur on these species (Wakeley 1928, 1935a, b, Smith et al. 1930). It has been reported that Japanese black pine, *P. thungbergii* Parlatore, is highly resistant to attack and, therefore, was planted extensively on Nantucket Island and along the North Atlantic Coast during the 1930s (Jones 1930, Littlefield 1942). Damage is most severe on seedlings and saplings less than 5 yrs old (Berisford 1988).

Adults of *R. frustrana* are covered with light gray scales over the head, body, and appendages. The forewings are 4 to 7.5 mm long and covered with patches of scales that are brick red, rust, orange, and copper colored, separated by irregular bands of gray and white scales (Powell and Miller 1978). The eyes are copper colored or olive green. Male moths are attracted to females via a sex pheromone (Berisford and Brady

1972). Once mating occurs, the female deposits eggs singly on the needles and shoots. Following eclosion, first-instar larvae mine within the needles. Mid-instar larvae begin feeding at the needle and bud axils and later enter the lateral and terminal shoots, which severs the vascular tissue and kills the apical meristem. Fifth-instar larvae pupate and overwinter within these damaged shoots. Multiple infestations are common with up to 15 individuals per shoot in stands with extremely high populations (Berisford 1988).

Larval feeding can cause shoot mortality and tree deformity (Berisford and Kulman 1967), height and volume reductions (Fettig et al. 2000b), compression wood (Hedden and Clason 1980), and occasional tree mortality (Yates et al. 1981). Simulated tip moth attacks have been shown to decrease root growth of newly-planted shortleaf pine seedlings (Coyne 1968). Attacks may also reduce cone crops by injuring conelets and killing potential seed bearing cones (Yates and Ebel 1972). Form loss is of particular importance in ornamental plantings and Christmas tree plantations. Growth loss may be permanent or transitory and partially or completely regained as stands approach crown closure. Studies on growth impacts, particularly height, have often produced contradictory results (Berisford 1988), suggesting that genetics, site, and edaphic factors may play important roles.

While the worldwide demand for paper products is growing, the acreage available for fiber production is declining. Some forest industry analysts predict that continued land conversions for urban and suburban development as well as societal pressures to conserve forest land for non-timber objectives will require that most of the nation's fiber supply come from intensively managed plantations (Fosgate 1996). Herbaceous and woody weed control, fertilization, and irrigation have been the cornerstone of this effort (Nowak and Berisford 2000). It is also believed that the vast majority of fiber in the United States will be produced from loblolly pine plantations in the Southeast (Ince and Durbak 2002). With the establishment of pine plantations under intensive management, *R. frustrana* has become more abundant and has forced forest managers to become more concerned with the associated impacts. Consequently, the 1990s saw a resurgence of research on this insect with an emphasis on developing new tools for monitoring and control. Previous works published by Yates (1960) and Berisford (1988) provided thorough reviews of the most important *R. frustrana* literature. This work summarizes all of the literature on *R. frustrana* published from 1879 to 2002. In addition, we synthesize the latest research and provide management recommendations via a decision flow chart that we hope will be a useful tool for researchers and natural resource professionals.

## Biology and Life History

**Phenology.** Throughout its range, the life cycle of the Nantucket pine tip moth is roughly synchronized with its primary hosts to produce a new generation of egg-laying adults with each new growth flush (Berisford 1988). This synchrony maximizes host tissue quality for early developing larvae. The moth has two to five generations annually, depending on climate (Fettig et al. 2000a). Two generations are found in most locations north of Maryland and Delaware (Yates 1960, Lashomb and Steinhauer 1974, Powell and Miller 1978). Throughout the South, two generations predominate in the mountainous regions of the Appalachians, three in most locations of the Piedmont and Ozarks, and four in the Coastal Plain (Ross et al. 1989, Berisford et al. 1992, Moreira et al. 1994, Fettig et al. 2000a). Five generations per year are seen in Florida and extreme southern regions of Georgia, Alabama, Mississippi, Louisiana, and Texas (Meeker and Kulhavy 1992, Fettig et al. 2000a). Yates (1960) speculated that six generations may occur at the extreme southern edge of the range during a very warm season, but this has never been documented. Four generations occur in southern California, where the moth was accidentally introduced (Malinoski and Paine 1988). Transition zones between patterns of voltinism are not precise, and variation in annual weather patterns and associated shifts in heat unit accumulation may cause slight phenological shifts (Kudon et al. 1988, Canalos 1989, Ross et al. 1989).

**Adult emergence and mating.** Adult emergence from shoots containing overwintering pupae begins in late December or January in the southernmost portions of its range in the United States (Berisford 1988), and as late as April in northern regions (Yates 1960). Adults are crepuscular, although late afternoon flights may precede evening temperatures that fall below a flight threshold of 9.5°C during spring (Webb and Berisford 1978). Daytime temperatures just above the threshold may trigger such early flight behavior. Males emerge several days before females and are quite numerous when the first females appear (Berisford and Brady 1972, Canalos et al. 1984).

Wray and Farrier (1963) first demonstrated pheromone-mediated attraction in *R. frustrana* using virgin females as bait to attract males. The two-component sex pheromone is produced in a gland located under the eighth abdominal tergite of females, and is released through an external opening in the inter-segmental membrane between the eighth and ninth abdominal tergites (Baer et al. 1976). The major component of this pheromone blend, E-9-dodecenyl acetate, and the minor component, E-9,11-dodecadienyl acetate, occur in a ratio of approximately 20:1 (Hill et al. 1981, Asaro et al. 2001). This ratio appears to be consistent throughout much of *R. frustrana*'s range and among generations (Asaro et al. 2001). However, these ratios are based on pheromone gland extraction and not actual release rates. The latter have not been determined for this species because it is difficult to induce female calling and mating under artificial conditions (Richmond and Thomas 1977) and *R. frustrana* lacks a distinctive calling posture, unlike many other Lepidoptera (C. Asaro, pers. obs.). Males appear equally attracted to pheromone blend ratios within a range of 20:1 to 40:1 (Hill et al. 1981). Estimates of the quantity of stored pheromone at any one time are approximately 10 to 20 ng for the major component and 0.5 to 1 ng for the minor component (Asaro et al. 2001).

Virgin females and crude extracts from female abdominal tips can be used to attract males to traps (Berisford and Brady 1972, Hill et al. 1981). Pheromone extracts from adult females reared on artificial diet were comparable to those of wild females, and both were equally attractive to wild males in field tests (Richmond and Berisford 1980). Rubber septa loaded with pheromone in the proper ratio are as attractive as virgin females and crude tip extracts (Hill et al. 1981). There are several effective traps and commercial bait dispensers currently available. Debarr et al. (2002) studied the influence of trap design, color, and lure type on trap catch and found that Pherocon 1C® (Trecé Inc., Salinas, CA) wing traps baited with rubber septa lures caught the greatest number of moths. Traps painted white, black, orange, or green caught significantly more moths than those painted red, yellow, blue, or gray during one test, while in another test only blue and gray traps caught significantly fewer moths (Debarr et al. 2002). Traps baited with synthetic pheromone loaded on rubber septa are currently used to monitor this pest and initiate a spray-timing model based on degree-day accumulation (Gargiullo et al. 1985, Fettig and Berisford 1999b). Synthetic-baited traps may also be used in certain situations to predict future damage by *R. frustrana* (Asaro and Berisford 2001a). Trap catches for the Nantucket pine tip moth generally decrease precipitously from the first (spring) generation through subsequent (summer) generations, regardless of changes in population density (Asaro and Berisford 2001a). This is thought to be due, in part, to reduced male longevity during warmer portions of the year (Asaro and Berisford 2001b), although other factors may be involved. *Rhyacionia frustrana* adult males also have been shown to be attracted to blacklights (Manley and Farrier 1969).

*Rhyacionia frustrana* shares part of its range with three other common *Rhyacionia* species: the pitch pine tip moth, *R. rigidana* (Fernald), the subtropical pine tip moth, *R. subtropica* Miller, and the European pine shoot moth, *R. buoliana* (Denis & Schiffermüller), the latter introduced to the United States in 1914 (Miller 1967b). Of the three, *R. rigidana* is most sympatric with *R. frustrana* (Berisford et al. 1979), and the two species may emerge at the same time during spring (Berisford 1974b, Canalos and Berisford 1981). The sex pheromones of these two species are mutually inhibitory (Berisford and Brady 1973, Berisford et al. 1974, Berisford 1977), although interference is further minimized by calling at different times (Berisford 1974a). *Rhyacionia rigidana* begins calling about 1 h after dark when *R. frustrana* generally ceases (Berisford 1974a), releasing the single-component pheromone, E, E-8, 10-dodecadienyl acetate (Hill et al. 1976). The ranges of *R. subtropica* and *R. buoliana* overlap with that of *R. frustrana* only at the southern and northern extremes, respectively (Berisford et al. 1979). All pheromones thus far identified from *Rhyacionia* spp. are straight-chain 12-carbon acetates or alcohols (Berisford 1982, Skillen et al. 1997). The same single-component pheromone, E-9 dodecenyl acetate, is produced by both *R. subtropica* (Roelofs et al. 1979) and *R. buoliana* (Smith et al. 1974). It is only weakly attractive to *R. frustrana* (Berisford et al. 1979) and has been shown to suppress male *R. frustrana* response to live females (Berisford and Hedden 1978). Pheromone cross-attraction among *Rhyacionia* spp. appears to decrease with greater species sympatry, although other species isolating mechanisms exist (Berisford 1974a). Wing color pattern, wing length, and genital characters can be used to differentiate sympatric species of adult tip moths (Miller and Wilson 1964, Miller 1967a, Powell and Miller 1978).

**Oviposition.** Shortly after mating, oviposition on needles and shoots occurs. The internal anatomy of the male and female reproductive system has been described and illustrated (Richmond and Tomescu 1987). If *R. frustrana* and *R. rigidana* are active at the same time, it is not uncommon to find eggs of both species on the same shoot (Berisford 1988). However, *R. frustrana* eggs are laid singly while *R. rigidana* deposit their eggs in clusters (Gargiullo and Berisford 1983). Females can discriminate between susceptible and resistant hosts and preferentially lay eggs on susceptible hosts such as loblolly pine even though resistant hosts such as slash pine may be more numerous (Yates 1966b, Hood et al. 1985). The mechanism by which hosts are chosen for oviposition has been investigated but remains unknown (Ross et al. 1995). The eggs are initially opaque white when laid, but turn yellow to medium orange upon maturity, are convex and approximately 0.8 mm in diam (Yates et al. 1981). Development of all life stages, including eggs, occurs above a temperature threshold of 9.5°C (Haugen and Stephen 1984, Richmond and Becheler 1989). The development rate curves for each life stage are the characteristic sigmoid shape of other insect development rate curves (Haugen and Stephen 1984). Humidity has a relatively small effect on development time compared to temperature (Haugen and Stephen 1984). During cool spring weather, eggs may take as long as 30 d to hatch, although later in the summer eclosion typically occurs within 5 to 10 days (Yates et al. 1981).

**Larvae.** Larvae chew their way out of the egg, leaving the egg chorion still secured to the plant (Yates 1960). Young larvae are cream colored with a black head while later instars are yellow to orange, with mature larvae measuring about 9 to 10 mm long (Yates et al. 1981). Fox et al. (1971), using Dyar's (1890) method, showed that the Nantucket pine tip moth has five instars. Average head capsule widths for each successive instar were 0.200, 0.266, 0.371, 0.517, and 0.723 mm, respectively. Setal characters are used for differentiation of sympatric species of tip moth larvae (Miller and Wilson 1964). Newly-enclosed larvae mine needles, shoots, or buds and often produce evidence of attack via small resin drops exuding from needle bases where they have bored in. Second and third instars feed within needle or bud axils where they construct a silken tent that becomes covered in resin, the first really visible evidence of attack. Subsequent instars feed within buds and shoots, severing the vascular cambium and killing the apical meristem. Fully developed larvae pupate within the dead shoots (Berisford 1988). This cycle is repeated from two to five times per year, depending on location and weather conditions.

The Nantucket pine tip moth also will attack conelets (Yates and Ebel 1972, Ebel and Yates 1974, Yates et al. 1981). In this case, larvae will feed on the surface tissues then migrate to the axil formed by the shoot and conelet stalk. Conelet mortality can occur when larvae bore into the stalk and continue into the conelet. The larva will either move to the shoot tip or a healthy conelet to continue feeding. This type of feeding and damage generally occurs during the first generation of the year (Yates et al. 1981).

**Pupae and diapause.** Pupae overwinter inside damaged shoots of the host tree. As many as 17 pupae have been found in a single shoot during extremely heavy infestations, but more commonly there are less than five (Waters and Henson 1959, Warren 1963, Berisford 1988). Pupae are light to dark brown in color and approximately 6 mm long. Male and female pupae can be distinguished by their size, shape, the number of abdominal segments containing a finely textured band on the lower third of their surfaces, and the location of the genital opening (Yates 1969). Male and female pupal weights overlap slightly, with males averaging 5 to 7 mg and females 7 to 10 mg across all generations (Asaro and Berisford 2001b). Pupae of *R. frustrana* can be distinguished from those of other sympatric species by the size, shape of the frontal horn, and size of the cuticular spines on the abdomen (Yates 1967b, Dickerson and Kearby 1972). Pupae are able to partially maneuver out of infested tips by circular movements of the abdomen, which contains rows of abdominal spines (Yates 1960). Subsequently, the adult is able to emerge without injury while the empty pupal case is left behind projecting from the pine tip.

There appears to be a facultative diapause mechanism for the last generation that remains uninterrupted even when temperatures are artificially kept above the development threshold (Wallis and Stephen 1980). However, rearing *R. frustrana* through three generations on artificial diet produced a non-diapausing third generation in the laboratory (Richmond and Thomas 1976). Moths reared from these non-diapausing pupae did produce eggs (85 eggs from 4 females), although egg viability was not reported (Richmond and Thomas 1976). It is not known what factors led to this lack of diapause, although diet and altered photoperiod are likely contributors (Richmond and Thomas 1976). Generally, greater larval mortality and reduced pupal weight occur with tip moths reared on artificial diets (Cresswell et al. 1971, Richmond and Thomas 1976).

Little is known about how overwintering temperatures affect survivorship and fecundity. Asaro and Berisford (2001b) found no significant difference in weight between pupae collected before and after the overwintering period. However, this study was conducted in Georgia where winter temperatures are relatively mild. Gibson (1968) observed a widespread *R. frustrana* population collapse in Ohio and suggested that severe winter weather, among other factors, may have been important in the mortality of the overwintering generation. This phenomenon has never been adequately studied, however.

**Hypothesis for population behavior.** Little is known about tip moth population dynamics and dispersal at the landscape level, and only one study has addressed genetics. Gargiullo and Berisford (1983) constructed life tables for *R. frustrana,* identifying key mortality factors and estimating life stage recruitment. Key factor analysis showed that most mortality occurred during the egg and pupal stages. Namkoong et al. (1982) examined five polymorphic loci from populations in Georgia, Louisiana, Maryland, North Carolina, and California. They found considerable genetic variation between collection sites and suggested that many disjunct, non-interbreeding populations occur within the moth's range.

*Rhyacionia frustrana* typically invades stands shortly after establishment with most rapid colonization occurring in stands with relatively little competing vegetation. However, trees planted in old pastures with well-developed sod are also quickly infested and often develop very high populations (C. W. Berisford, pers. obs.). Establishment and population expansion are often rapid and possibly aided by generally low rates of parasitism (Lashomb et al. 1980). Tree resistance to tip moth attack is apparently lower in newly-established seedlings, but increases rapidly with age. For example, slash pine is susceptible to attack at planting but is generally immune to attack after the first year in the field (Yates 1966b, Hood et al. 1985). Yates (1962) speculated that the relatively slow crystallization rate of slash pine oleoresin might account for the decreased success of tip moth on this species.

Populations usually level off in 3 to 5 yrs, gradually decline and then rapidly diminish as trees approach crown closure (Berisford 1988). As stands become older, competing vegetation may mechanically disrupt access to pine shoots by ovipositing females (Warren 1963), and other vegetation may provide alternate hosts and nectar for parasitic insects. The more complex environment provided by vertical stratification of older stands may also favor natural enemies.

Older trees appear to be more resistant to *R. frustrana* attack. This phenomenon may be related to the following: (1) higher resin flow from the needles of older trees may repel or encapsulate boring larvae. Loblolly pine resin is also known to be toxic to first-instar larvae (Yates 1962); (2) the percentage of shaded shoots increases in older stands as crown closure occurs. Shaded loblolly pines have low tip moth infestations but attacks increase dramatically if the shade is removed. This is apparently at least partly a physical phenomenon unrelated to the physiology of the trees since it can occur immediately following removal of shade (Berisford and Kulman (1967); (3) as crown closure approaches, competition for available shoots between the Nantucket pine tip moth and the pitch pine tip moth increases. The pitch pine tip moth is the more successful invader at this time and occupies a greater proportion of available shoots, so that progressively fewer susceptible shoots are available for the Nantucket pine tip moth; (4) as trees become older, the frequency of flushing decreases and the flushes are less in synchrony with *R. frustrana,* possibly decreasing the success of attacking larvae which may not have access to the soft meristematic tissue in new shoots (Berisford 1988).

## Natural Enemies

The Nantucket pine tip moth is attacked by a variety of natural enemies, some of which can cause substantial mortality. Several synoptic lists and keys have been published for arthropod natural enemies, particularly parasitoids. Nowak et al. (2001a) provide a guide to identification of common arthropod natural enemies of the Nantucket pine tip moth. A world survey of parasitoids and predators of the genus *Rhyacionia* also is available (Harman and Kulman 1973), and Frank and Foltz (1997) provide a list of resident parasitoids of the Nantucket pine tip moth. Yates (1967a) provides a key to Nearctic parasitoids of the genus *Rhyacionia,* and Yates (1967d) describes a radiographic technique for detecting *Rhyacionia* immatures and their arthropod natural enemies within pine shoots.

**Pathogens.** There is a paucity of information on pathogens of the Nantucket pine tip moth. Stephen et al. (1982b) and McLeod et al. (1983) evaluated codling moth granulosis virus for tip moth suppression. They found that the virus reduced tip moth population levels when applied to 3-yr-old loblolly pines at $2.5 \times 10^{13}$ granules per ha. Their results also suggested that virus applications can have an effect on subsequent tip moth generations. Nash and Fox (1969) showed that the nematode DD-136 will kill *R. frustrana* larvae under natural conditions, with highest mortality achieved in spring (first) generation larvae. However, the authors concluded that the nematode did not provide sufficient control to recommend its use.

Mihelcic (1998) examined tip moth larvae collected from Georgia, Alabama, South Carolina, Virginia, and Texas and identified only two diseased larvae from thousands of specimens. Each larva was infected with one of two common fungi, *Beauveria bassiana* (Balsamo) Vuillemin and *Aspergillus parasiticus* Speare. It could not be determined whether these fungi were entomopathogenic or saprophytic, although larval mortality was induced by treatment with a high density of spore inoculum isolated from each fungus (Mihelcic 1998). It seems clear from this and other surveys of tip moth larvae from the western United States (J. L. Hanula, USDA Forest Service, Southern Research Station, Athens, GA, pers. comm.) that pathogens are not an important natural source of mortality among tip moth populations.

**Predators.** Numerous arthropod predators have been associated with the Nantucket pine tip moth, but little work has been done to evaluate the impacts of these predators on tip moth populations. Of these predators, clerid beetles (*Phyllobaenus* spp.) (Coleoptera: Cleridae) and various spiders appear to be the most important. Eikenbary and Fox (1968a) found *Phyllobaenus singularis* (Walcott) and *P. lecontei* (Wolcott) to be especially abundant in the spring generation in the South Carolina Piedmont, with roughly one-third of tip moth-infested loblolly pine shoots containing clerid larvae. *Phyllobaenus singularis* is also a common predator of *R. frustrana* in Arkansas. It is bivoltine in the southern part of the state and univoltine, with a partial second generation, in the northwest. It overwinters as a larva within the pine tip, and larvae are active in the field from June to mid-August (Wingfield and Warren 1968). *Phyllobaenus* sp., along with *Hemerobius* sp. (Neuroptera: Hemerobiidae), were also reared from tip moth-infested loblolly pine shoots in central Mississippi (Harlan and Neel 1967). The black imported fire ant, *Solenopsis richteri* Forel (Hymenoptera:

Formicidae), was found to have little impact on tip moth populations in southeastern Louisiana (Wilson and Oliver 1970).

Eikenbary and Fox (1968a) found spider populations to be highest in the early and late summer in their South Carolina study. *Metaphidippus galathea* (Walckenaer) (Araneae: Salticidae), *Misumenops asperatus* (Hentz) (Araneae: Thomisidae), and *Peucetia viridans* (Hentz) (Araneae: Oxyopidae) appeared to be the most important spider predators in the field. Bosworth et al. (1971), in studies of spiders in Oklahoma loblolly pine plantations, found *Cyclosa conica* (Pallas) (Araneae: Argiopidae) and *Paraphidippus marginatus* (Walckenaer) (Araneae: Salticidae) to be most important. In general, web-building argiopid spiders appeared to be more efficient in trapping adult tip moths than did the hunting spiders (Bosworth et al. 1970). However, Wilson and Oliver (1970) found little relationship between spider counts and tip moth population levels in their Louisiana study.

Other groups of predators may be important tip moth mortality agents as well. *Zethus spinipes* (Say) (Hymenoptera: Eumenidae) has been observed extracting tip moth larvae from loblolly pine shoots, with as many as 10% of terminal and large lateral tips showing wasp foraging activity (Lashomb and Steinhauer 1980). Woodpeckers (Piciformes: Picidae) have also been observed foraging for tip moth immatures in infested shoots (C. W. Berisford, pers. obs.). More work is needed to determine the important predators of tip moths and to clarify the role that they play in tip moth population regulation.

**Parasitoids.** The bulk of work dealing with natural enemies of the Nantucket pine tip moth has involved larval/pupal parasitoids. The great majority of these studies detail parasitoid species reared from tip moth-infested shoots in various regions, including Arkansas (Warren 1985), Florida (McGraw et al. 1974), Georgia (Freeman and Berisford 1979, McCravy and Berisford 2000), Maryland (Harman 1972, Lashomb et al. 1980), Mississippi (Harlan and Neel 1967), Missouri (Kearby and Taylor 1975), Nebraska (Cushman 1927a), South Carolina (Eikenbary and Fox 1965), Virginia (Lewis et al. 1970), and the northeastern United States (Schaffner 1959). Approximately 64 species of parasitoids in 11 families have been associated with *R. frustrana* (Frank and Foltz 1997), but only a few of these appear to be abundant enough to cause substantial tip moth mortality.

Among larval/pupal parasitoids, *Campoplex frustranae* Cushman (Hymenoptera: Ichneumonidae), *Lixophaga mediocris* Aldrich (Diptera: Tachinidae), and *Eurytoma pini* Bugbee (Hymenoptera: Eurytomidae) have been the most commonly collected parasitoids in rearing studies. *Campoplex* constituted 24% of all parasitoids reared over four generations in the Georgia Piedmont (Freeman and Berisford 1979), 31 to 54% of parasitoids reared in southwestern Virginia (Lewis et al. 1970), 11% and 17% of parasitoids reared in Maryland (Harman 1972, Lashomb et al. 1980), and 31% of parasitoids reared in South Carolina (Eikenbary and Fox 1965). However, *C. frustranae* was not found in a study that included over 4,000 parasitoid rearings from the Georgia Coastal Plain (McCravy and Berisford 2000).

*Campoplex frustranae* is a primary, internal, solitary parasitoid that pupates in a white silken cocoon inside *R. frustrana* pupae (Eikenbary and Fox 1968c, Freeman and Berisford 1979). Eikenbary and Fox (1968c) studied *C. frustranae* biology and ecology. They observed *C. frustranae* ovipositing in first through fourth instars, although all first and second instars died when stung by *Campoplex.* The greatest numbers of *C. frustranae* in the field were observed when most tip moths were third instars. Optimum *C. frustranae* flight occurred between 19 and 35°C, with frequent and prolonged resting above 32°C, and parasitism was greatest in the upper one-fourth of the crown.

*Lixophaga mediocris* is by far the most common dipteran parasitoid of *R. frustrana.* It is a primary, internal, solitary, larval parasitoid that develops within *R. frustrana* larvae and pupates externally (Freeman and Berisford 1979). *Lixophaga mediocris* has three larval instars (DuRant and Hyche 1967) and apparently overwinters as an adult because few puparia and many empty pupal cases were recovered from shoots sampled in winter (McCravy and Berisford 2000). It comprised 45% of parasitoids reared in the Georgia Piedmont (Freeman and Berisford 1979) and 36% of rearings in the Georgia Coastal Plain (McCravy and Berisford 2000). It accounted for 44% of parasitoids found in Maryland (Lashomb et al. 1980) and 20% of parasitoids recovered in South Carolina (Eikenbary and Fox 1965). *Lixophaga mediocris* was the most abundant parasitoid found in all except the South Carolina study, where it was second most abundant. It is also a common parasitoid in central Alabama, sometimes parasitizing 20 to 30% of late-instar tip moth larvae (DuRant and Hyche 1967).

*Eurytoma pini* is an internal, solitary parasitoid that attacks late instar tip moth larvae (Freeman and Berisford 1979). First described by Bugbee (1958), it has been recorded as a cleptoparasitoid on *Rhyacionia buoliana* (Schiffermuller) (Arthur 1961), and as a hyperparasite on other primary parasitoids of *R. frustrana*. Hyperparasitism was observed in 13 of 15 *E. pini* recovered directly from hosts in Georgia, with secondary hosts including *C. frustranae, L. mediocris,* and *Macrocentrus ancylivorus* Rohwer (Hymenoptera: Braconidae) (Freeman and Berisford 1979, McCravy and Berisford 2000). An inverse relationship between abundances of *E. pini* and *L. mediocris* raises the possibility that *E. pini* has detrimental effects on *L. mediocris* populations (McCravy and Berisford 2000).

Eikenbary and Fox (1968b) and Kulman and Auld (1970) also investigated various aspects of the ecology and parasitic habits of *R. frustrana* larval/pupal parasitoids. The former study involved investigations of the responses of parasitoids to tree level, orientation, and hosts per pine tip. The authors found that percent parasitism of tip moths in the top whorl of shoots was significantly higher than in lower tree levels. Tree orientation and *R. frustrana* density per pine tip had no effect on parasitism. Kulman and Auld (1970) examined duff taken from under tip moth-infested loblolly pines for overwintering parasitoids. Forty-one species of parasitoids belonging to families known to contain species parasitic on *R. frustrana* emerged from the duff. None, however, were known parasitoids of *R. frustrana.*

Larval/pupal parasitoids have been shown to cause substantial tip moth mortality. As pine plantation management increases in intensity, there is concern that practices such as chemical weed control and insect pest control may have negative effects on parasitoid populations. In a study of the effects of vegetation control on tip moth parasitoids, McCravy and Berisford (2001) found no difference in rates of tip moth larval/pupal parasitism between herbicide-treated and untreated loblolly pine stands, although total parasitism was greater in the untreated plots, which had higher tip moth densities. There is evidence, however, that certain insecticides commonly used for tip moth control can have detrimental effects on parasitoids. Applications of the organophosphate acephate, for instance, lowered parasitism rates significantly in a central Georgia study (McCravy et al. 2001). Effects were species specific, with relatively little effect on *L. mediocris,* but substantial effects on the chalcidid *Haltichella rhyacioniae* Gahan (Hymenoptera: Chalcididae). *Bacillus thuringiensis* var. *kurstaki* Berliner and the insect growth regulator tebufenozide had little or no effect on parasitism. In a laboratory study, the pyrethroids permethrin and lambda-cyhalothrin caused 33% and 49% average mortality, respectively, among tip moth parasitoids exposed for 1 h, and 55% and 66%, respectively, after a 24 h exposure (Nowak et al. 2001b). Spinosad, a derivative of a soil actinomycete bacterium, produced only 7% average mortality after exposure for 1 h but 81% after 24 h. Indoxacarb, the first available product in a new class of insecticides, the oxadiazines, did not produce mortality significantly greater than the untreated control for either exposure period. Overall, the braconid *M. ancylivorus* suffered higher mortality than did the chalcidoids *E. pini* and *H. rhyacioniae* (Nowak et al. 2001b). Tip moth suppression efforts that incorporate the use of insecticides should consider the effects of these compounds on the tip moth parasitoid community.

Egg parasitoids in the genus *Trichogramma* (Hymenoptera: Trichogrammatidae) can also cause substantial tip moth mortality. Yates (1966a) found 64.5% parasitism of *Rhyacionia* eggs by *Trichogramma minutum* Riley in central Georgia. Gargiullo and Berisford (1983) found tip moth egg mortality to be temporally density-dependent over six consecutive generations in the Georgia Piedmont, with 48% egg parasitism by *Trichogramma* spp. in the summer generation. Spring generation egg parasitism was lowest (13%). McCravy and Berisford (1998) also found high tip moth egg parasitism in the Georgia Piedmont, with 37% and 43% of eggs parasitized in spring and summer generation eggs, respectively. In the latter study, rearings of *Trichogramma* adults from parasitized tip moth eggs produced primarily (over 90%) *T. pretiosum* Riley and *T. exiguum* Pinto and Platner, with the remainder being *T. marthae* Goodpasture. Experimental manipulations of tip moth egg densities produced inversely density dependent egg parasitism in the top whorl of shoots and also at the needle fascicle level. Eggs laid on shoots suffered significantly higher parasitism than eggs on needles (66% vs 21%) (McCravy and Berisford 1998).

Despite the evidence that parasitoids cause high tip moth mortality, few attempts at tip moth control via parasitoid releases or manipulation have been made. *Campoplex frustranae* has twice been successfully introduced into epidemic tip moth populations. A release in 1924 against *Rhyacionia bushnelli* in Nebraska ponderosa pine stands was accompanied by an 80% reduction in tip moth numbers (Wadley 1932). *Lixophaga mediocris* and *C. frustranae* were released against *R. frustrana* infesting Monterey pine in California (Scriven and Luck 1978, Wallis et al. 1980). No evidence for establishment of *L. mediocris* was found. However, *C. frustranae* was established and populations increased rapidly, coinciding with a concomitant decrease in the number of dead pine tips over a 4-yr period.

Experimental inundative releases of approximately 330,000 female *T. exiguum* females per ha in eastern North Carolina loblolly pine plantations resulted in significant increases in tip moth egg parasitism (Orr et al. 2000). Mean parasitism rates were increased from 42% in the control plots to 54% in the release plots. Percentage of shoots attacked and length of tunneling were reduced in release plots. Parasitoid emergence from release capsules and predation on parasitoids were affected by temperature, microhabitat, and length of exposure to field conditions prior to emergence. Lower parasitoid emergence occurred in response to increasing numbers of hours above 35°C. Predation rates increased with increasing number of days of capsule exposure. With regard to microhabitat, predation of *Trichogramma* parasitoids was highest in second-year plantations at the soil surface with herbaceous cover. Currently, inundative releases of encapsulated *T. exiguum* are not practical for tip moth management due to the high mortality rates encountered (D. Orr, Dept. of Entomology, N.C. State Univ., Raleigh, NC, pers. comm.).

## Sampling Methodologies

The pine shoot is the unit on the tree that is both inhabited and damaged by tip moth immatures and is, therefore, the most desirable sampling unit. However, questions arise as to how many shoots should be sampled and from what portions of the tree they should be collected to obtain various levels of accuracy and precision. A number of methods are available with varying degrees of complexity and reliability. The method chosen depends on the specificity of the information required, such as the level of precision and accuracy and whether one desires relative or absolute estimates of population density. One complicating factor is the uncertain relationship between damaged or 'apparently infested' shoots on a tree and the proportion of those shoots that are actually infested. Damaged shoots have a characteristic mass of crystallized oleoresin, usually on or near the bud, along with browning of adjacent needles. However, dissection of these damaged shoots often reveals no tip moths, either because they have already emerged as adults or have been killed by parasitism or some other agent. Furthermore, multiple larvae can infest a single shoot. Warren (1963) found as many as 17 immatures within a single pine shoot, although more commonly one finds 1 to 5 immatures per shoot in heavy infestations. Therefore, if precise population estimates are desired, dissection of damaged shoots is necessary.

Waters (1959) and Waters and Henson (1959) discussed some sampling attributes of the negative binomial distribution with reference to the Nantucket pine tip moth. Frequency of larvae in individual damaged tips followed a Poisson distribution, indicating that a small number of moths per infested shoot are most common. However, with each whorl as the sampling unit, damage distribution had a negative binomial distribution. The authors point out that insect sampling data rarely meet the assumptions of the Poisson distribution that all sampling units are equal and that individuals are distributed randomly and independently of one another among the sampling units. Rather, one should expect insects to exhibit a "contagious" or aggregative distribution as described by the negative binomial. Indeed, a consistent stratification by whorl levels was detected, with the top whorl showing the greatest aggregation of tip moth damage. They further explained that the apparent randomness of the individual tip counts is due to the limited size of the sampling unit. Only 4 tips out of 798 contained more than four insects. Thus, there is a general limit to the number of immatures contained within any shoot tip, even under heavy populations, so the larger numbers expected in an aggregated distribution will not occur. A Poisson, binomial, or approximate normal distribution would then most often be observed with an individual shoot as the sampling unit.

Very little is known about the spatial distribution of tip moths within a plantation and their patterns of dispersal, immigration, and emigration. Stephen and Wallis (1980) found that tip moth populations were aggregated within 2 to 5-yr-old plantations when whole trees were used as the sampling unit. Clarke et. al (1990) provide the only study to date that addresses this issue in detail. They examined the spatial distribution of the Nantucket pine tip moth in newly-established loblolly pine stands and found that infestations are distributed throughout the first year plantations by the end of the second tip moth generation. Furthermore, the distribution of infested trees was generally random in the first generation, with increasing aggregation in subsequent generations. This finding supports the hypothesis that in later generations adult tip moths do not disperse far from where they were deposited as eggs. It was further speculated that vegetation levels and other factors might alter this pattern of aggregation. Coody et al. (2000) showed that previous tip moth infestations predispose trees to heavier attacks in subsequent generations, suggesting that tip moths generally re-infest areas where they are already abundant.

Fox and King (1963) did not consider whole tree sampling because they sought a sampling system that was adequate for control decisions only, and it is the infestation of shoots in the tip and top whorl of the tree that is most likely to cause economic damage. They found that by examining only terminal shoots rather than terminals and laterals in the top whorl, they saved 80% in time and lost only 10.2% in accuracy. Hedden (1979) further elaborated on this sampling scheme by describing a method of ranking plantations by infestation level using only terminals. He also discussed a double sampling technique that estimates the proportion of infested terminals over a large number of plantations.

Other studies attempted to address the relationship between terminal, top whorl, and whole-tree infestations in an attempt to find the best compromise between sampling efficiency and accuracy. Berisford and Kulman (1969) found that top whorl populations were poorly correlated with whole tree populations at the extreme ranges of infestation, concluding that one was not a sensitive indicator of the other. Anderson et al. (1984) reached a similar conclusion when they employed a sequential sampling scheme (Waters 1955) for the Nantucket pine tip moth and used radiographic detection (Yates 1967d) to count moths within shoots.

However, Stephen and Wallis (1978) presented a regression model in which whole tree populations explained 88% of the variation in top whorl populations, provided the trees were young (2 to 3 yrs) and tip moth density was low. Older trees with greater densities provided poorer regressions ($r^2 = 0.42$). They reported that the variation among groups of trees with respect to the percent of damaged shoots that were actually infested ranged from less than 15% to greater than 70%. Some reasons proposed for why damaged tips were often uninfested include: (1) maturation of pupae and adult emergence, (2) damage was from an earlier generation, (3) removal of the tip moth immature by predators, (4) external feeding by larvae which subsequently migrated to a different shoot or tip (Yates 1967c), or (5) damage by a different agent. The inability of field personnel conducting sampling operations to accurately specify which tips were currently infested created the need for a shoot damage index as a measure of actual tip moth density. Therefore, other types of regressions reported were the relationship between apparently infested and actually infested shoots ($r^2 = 0.74$), actually infested shoots and tip moth density (number of immatures per tree) ($r^2 = 0.97$), and apparently infested shoots and tip moth density ($r^2 = 0.71$) (Stephen and Wallis 1978).

Fettig and Berisford (1999a) concluded that top whorl damage estimates were the best compromise between accuracy and labor. They reported correlations between the terminal and top whorl ($r = 0.87$), terminal and whole tree ($r = 0.71$), and top whorl and whole tree ($r = 0.86$). Regression of top whorl infestation levels against whole tree infestation levels produced an $r^2$ of 0.73. Although there have been some conflicting reports regarding the efficiency of top whorl damage estimates, the evidence thus far seems to justify their widespread use by forest managers.

Asaro and Berisford (2001a) found a very strong association between tip moth density (number of immatures per whole tree) and the number of damaged shoots (per whole tree) ($r^2 = 0.93$), density and the percent of damaged shoots (per whole tree) ($r^2 = 0.93$), and the number of damaged shoots (whole tree) and percent of damaged shoots (whole tree) ($r^2 = 0.92$). They concluded that, for control decisions, the percent of damaged shoots is a sufficient surrogate for density estimates.

For precise population estimates of tip moths during any life stage (including when damage is not visible), the two-stage cluster-sampling scheme of Gargiullo and Berisford (1981) and Gargiullo et al. (1983a) is the most comprehensive. This scheme involves division of a tree into multiple strata and destructively sampling shoots at random from within each stratum. Shoots are subsequently returned to the lab, dissected, and the number of each life stage is reported, along with the presence or absence of parasitoids and the level of tip moth mortality. Mathematical formulae (Gargiullo et al. 1983a) and a Fortran program (Gargiullo and Berisford 1981) are presented for determination of precise population estimates on a per tree and unit area basis. Using this methodology, one can make reasonably accurate statements regarding population density without being concerned with distinguishing apparently infested versus actually infested shoots. This method is considerably more labor intensive, however.

Asaro and Berisford (2001a) used moth counts from pheromone-baited traps to predict whole tree damage and tip moth population density as determined by the method of Gargiullo et al. (1983a). They found that trap catch predicted damage and density equally well, despite changes in trap efficiency between generations and considerable variation in parasitism rates among stands, which can lead to significant variability in the association between apparently and actually infested shoots. Therefore, due to the relative simplicity and reasonable accuracy of damage estimates, they suggested that traps should be used to predict tip moth damage rather than density. Reasonably informed control decisions could thus be made on a widespread basis by simply trapping moths from the generation prior to that which one wishes to control. Further work is required on the relationship between terminal, top whorl, and whole tree damage and long term stand volume reduction.

## Site and Stand Influences

Tip moth populations can vary in relation to site and stand characteristics. Benedict and Baker (1963) considered the Nantucket pine tip moth a minor pest, but predicted that its pest status would increase because of more intensive and widespread pine plantation management. Warren (1964) concluded that the pest status of the Nantucket pine tip moth in Arkansas had indeed increased, confirming the predictions of Baker (1963). In Virginia, Berisford and Kulman (1967) found that tip moth infestations were heavier in plantations compared to naturally-seeded pine with similar stocking densities. Thomas et al. (1982) found that planted seedlings had higher damage levels than directly seeded pines in all 3 yrs of a study in the Georgia Piedmont; tip moths damaged less than 7% of the seedlings grown from seed in the second year of the study compared to 29% of the planted seedlings. Site preparation, such as disking, plowing, and roller chopping to reduce competing vegetation has been shown to exacerbate tip moth damage levels (Warren 1964, Hertel and Benjamin 1977, Thomas et al. 1982). Hertel and Benjamin (1977) found that tip moth damage levels followed a gradient that increased with the intensity of site preparation. In eastern Texas, higher tip moth populations were associated with higher site indices (White et al. 1984). However, low site index was associated with higher tip moth levels in the Piedmont of Georgia and South Carolina (Hood et al. 1988).

**Weed control.** It has been suggested that tip moth damage increases with the intensity of site preparation due to reduced vegetation levels, which can increase nutrient and water availability to residual plants or decrease local populations of natural enemies (Pimentel 1961). Several studies have shown an increase in tip moth damage associated with reductions in competing vegetation (Warren 1964, Berisford and Kulman 1967, Warren et al. 1974, Hertel and Benjamin 1977, Nelson and Cade 1984, Hood et al. 1988, Ross et al. 1990). Ross et al. (1990) found that herbicide-treated plots had significantly more damage from *R. frustrana* than check plots in the first two growing seasons in a study conducted in the upper coastal plain of Georgia. However, by the third growing season, the damage in the control treatment was not significantly different than the herbicide treated areas. Other studies on *R. frustrana* have produced contradictory or inconclusive data regarding herbicide applications. For example, McCravy and Berisford (2001) showed significantly lower tip moth damage in plots with vegetation control than in untreated plots. Nowak et al. (2003) found that damage levels were significantly greater following herbicide treatments during the first year of a 2-yr study in the Georgia Piedmont. During the second year, however, damage levels were significantly lower following herbicide treatments. Miller and Stephen (1983) concluded that vegetation levels were not a major factor in determining tip moth damage. Sun et al. (2000) reported that tip moth infestation levels were inversely related to herbicide treatments. However, their results may have been confounded by nitrogen and phosphorous fertilization, and their data were collected for only one generation.

Nowak and Berisford (2000) suggested that such inconsistencies may be due to highly fluctuating and unpredictable tip moth populations in stands with very low levels of competing herbaceous and woody vegetation, possibly due to reduced regulation by natural enemies. Nowak et al. (2003) found that more rapid tree growth and reduced parasitism were significantly correlated with greater variability in tip moth infestation levels over six generations. Although Miller and Stephen (1983) concluded that vegetation level is not a good predictor of tip moth damage, their data show that tip moth damage levels fluctuated more prominently within stands having less competing vegetation. It has been observed that decreases in total parasitism are associated with reductions in competing vegetation (McCravy and Berisford 2001), which can lead to greater instability of insect herbivore populations (May 1976, Price 1997).

**Fertilization.** Several studies on insect herbivores have shown that greater plant nutrient levels can increase palatability and subsequently lead to greater insect survivorship and fecundity (Brewer et al. 1987, Bryant et al. 1987, Clancy 1992). Sun et al. (2000) concluded that nitrogen fertilization increased *R. frustrana* infestation levels and pupal weights. In a greenhouse study, Ross and Berisford (1990) tested the hypothesis that increased forest fertilization at the time of planting can increase tip moth populations. They irrigated and fertilized (N-P-K + micronutrients) loblolly pine seedlings in pots, exposed them to ovipositing tip moth females in a 4 yr-old pine plantation, and subsequently returned seedlings to the greenhouse. Seedlings receiving a high water, high fertilizer treatment grew most vigorously, had the lowest concentration of total phenolics and condensed tannins, and the highest proportion of infested shoots. They concluded that forest management practices that increased nutrient and water availability also increases tip moth infestation levels. Other field studies do not support the above conclusions, however. Pritchett and Smith (1972) observed significant reductions in tip moth damaged associated with phosphorous and potassium fertilization, but no differences were observed after nitrogen fertilization. In a 3-yr study, Berisford et al. (1989) showed significantly less tip moth damage in fertilizer-herbicide-tip moth control treatments than in herbicide-tip moth control treatments during one year, and no statistical differences in the other two years. Nowak and Berisford (2000) found no significant differences in tip moth damage levels associated with a complete fertilizer (N-P-K + micronutrients) and irrigation treatment and Nowak et al. (2003) found that nitrogen applied five times over 2 yrs at a rate of 56 kg of N per ha as urea did not have a significant effect on tip moth damage levels. Coyle et al. (unpubl. data) found that a complete fertilizer treatment was associated with reduced tip moth damage levels. Therefore, the response of *R. frustrana* to fertilizer treaments appears complex and remains poorly understood, particularly when confounded by weed control and additional intensive treatments.

## Economic Impact

The Nantucket pine tip moth generally causes growth reduction and tree deformity. Widespread stagnation and tree mortality is quite rare, with one of the few accounts of this coming from Nantucket Island in 30-yr-old pitch pine (Scudder 1883). Trees that are heavily attacked by tip moths tend to have poor, bush-like growth form (Berisford and Kulman 1967, Lashomb et al. 1978). This bushy appearance is due to significant branching from codominant shoots following destruction of the terminal shoot and reduced internodal growth between the stem and branches (Lashomb et al. 1978). In addition to impacts on tree growth and form, tip moth damage has been implicated in causing increased compression wood (Hedden and Clason 1980) which can cause a significant reduction in pulp yield (Panshin and DeZeeuw 1964). It has also been suggested that tip moth feeding may increase the incidence of two tree diseases afflicting southern pines, fusiform rust (Powers and Stone 1988, Hedden et al. 1991) and pitch canker disease (Matthews 1962, Cade et al. 1986, Runion et al. 1993). Powers and Stone (1988) found that fusiform rust infection, caused by the fungus *Cronartium quercuum* (Berk.) Miyabe ex Shirai f. sp. *fusiforme,* was significantly lower in carbofuran-treated trees than in trees unprotected from tip moth attack. Runion et al. (1993) found that the number of loblolly pine terminals that were infected with the fungus *Fusarium circinatum* Nirenberg and O'Donnell, the causal agent of pitch canker, was positively correlated with the number of terminals damaged by the Nantucket pine tip moth in a study in North Carolina. However, this relationship does not appear to be a widespread phenomenon in loblolly pine plantations.

**Short-term growth impact.** The most widespread and deleterious effect of tip moth infestations is its impact on growth. Since the 1950s there have been numerous attempts to determine if tip moth damage leads to short-term growth loss. One such study from Maryland (Somes and McIntyre 1963) found that tip moth control did not significantly increase tree growth 3 yrs after treatment. However, the majority of research indicates that tip moth damage can lead to significant reductions in height and diameter growth of loblolly pine. Several studies have demonstrated that tip moths reduce early tree growth (Warren 1964, Beal 1967, Lashomb et al. 1978, Stephen et al. 1983, Berisford et al. 1989, Fettig et al. 2000b, Nowak and Berisford 2000). Lashomb et al. (1978) found that 30 to 60% whole tree tip moth damage led to a 2 m difference in height growth after the third growing season. Nowak and Berisford (2000) showed that tip moth control accounted for a 27% increase in tree volume in a maximum growth study of loblolly pine (vegetation control, irrigation, fertilization), although tip moth damage was moderate (40%) to very low (<10) for the first 3 yrs of the study.

**Long-term growth impact.** Although there is considerable, conclusive evidence that even modest tip moth population levels are capable of causing short-term growth losses, there is still debate about whether these growth losses are sustained through stand rotation. Beal (1967) was the first to attempt a study of long-term growth impacts caused by *R. frustrana* infestations. This study began in 1959 using loblolly and shortleaf pine to determine the impact of tip moth damage on a stand through one rotation. Nine study sites were established in seven states, including Alabama, Arkansas, Florida, Louisiana, Mississippi, Tennessee, and Texas. The trees were protected from tip moth damage with insecticide for 5 to 6 yrs depending on the site. Tip moth damage severity was estimated at the end of each growing season by computing the percentage of terminals damaged and recorded in one of the following categories: very light (1-10%), light (11-40%), medium (41-70%), and heavy (71-100%). Three of the nine study sites had extremely low tip moth populations and are, therefore, excluded from this discussion because there was no significant difference in tip moth damage between the untreated and control plots. Of the remaining 6 sites, four had significant height gains from tip moth control. The author concluded that trees protected from tip moth attack significantly outgrew unprotected trees after the sixth growing season.

These same sites were re-measured at year 16 (Williston and Barras 1977) and year 23 (Thomas and Oprean 1984). At year 16, only 1 of the 4 sites with significant height differences at year 6 still showed a significant height difference corresponding to tip moth protection. Of the six sites that had medium to heavy tip moth damage, the protected trees produced an average of 40.3 $m^3$ per ha more wood volume at age 16 than the unprotected trees. However, the authors concluded that insecticide treatments would not have been economically feasible given the market price for pulpwood at the time of the study. Thomas and Oprean (1984) re-measured three of the four sites that had significant differences at year 7 again at year 23 and found significant height differences at one of the sites. The authors concluded that (1) early height gains from tip moth control might persist through a rotation, (2) pines on good quality sites showed less impact from tip moth infestation, and (3) pines grown on medium sites with high tip moth damage may benefit from control. However, because damage was only recorded for the last tip moth generation of each year early in the study, it is difficult to fully evaluate these results and conclusions.

Other long-term studies show significant volume differences between insecticide-treated plots and untreated plots (Burns 1975, Young et al. 1979, Hedden et al. 1981, Stephen et al. 1982a, Cade and Hedden 1987). In a 10-yr-old loblolly pine plantation in Maryland, 55 carbofuran-treated trees had 280% more volume than 47 unprotected trees (Hedden et al. 1981). Cade and Hedden (1987) showed significant volume differences of 62 $m^3$ per ha versus 48 $m^3$ per ha between carbofuran treated and untreated trees, respectively, following the twelfth growing season in a loblolly plantation in Arkansas. They then used growth and yield models to estimate the long-term growth impact of tip moth damage. According to these models, tip moth control was marginally cost effective if the stands were grown to sawtimber size after one thinning. They concluded that tip moth control would not have been cost effective for pulpwood production, but contended that tip moth control would have been more economically feasible if populations were greater and the study sites had higher site indices.

Berisford et al. (1989) began an ongoing study in 1985 in the upper Coastal Plain of Georgia examining the impact of pine tip moth control, weed control, and fertilizer on loblolly pine growth and form. During the first three years of this study, the average annual percentage of top-whorl infested shoots in the check treatment (no tip moth control, herbicide or fertilizer) was 35%, 78%, and 75%, respectively. After 15 yrs (unpubl. data), trees with tip moth control averaged approximately 12,650 $cm^3$ (1.5 $ft^3$) greater volume per stem than the check trees. Tip moth control in combination with herbicide and fertilizer produced greater differences. Differences in tree volume between the check and other treatments continue to diverge as this study continues into its eighteenth year.

Additional long-term studies that accurately measure tip moth damage for each generation during the first 3 to 5 yrs of stand rotation are necessary before a consensus can be reached on the long-term growth impacts of *R. frustrana*. Unfortunately, due to the extensive time and effort involved, few researchers are willing to make the necessary commitments for such an undertaking. Such attitudes may change as conventional pulpwood rotations continue to shorten. The impact of tip moth could be significantly greater during a short rotation because trees do not have as much time to outgrow initial damage and tip moth affects stand growth for a proportionally longer part of the rotation. Furthermore, greater investments in short rotation forestry (site preparation, fertilizer, herbicide) may make tip moth control more economical.

## Management Strategies

In the late 1800s, *Rhyacionia* spp. populations were causing significant damage to regeneration efforts on both the Nebraska National Forest and Nantucket Island, MA. Therefore, most of the early control techniques were developed in these locations. Comstock (1880) was the first to suggest collecting and burning infested twigs during winter. Scudder (1883) added two additional remedies including the building of bonfires at night to attract and kill gravid females, and the removal of all pines from Nantucket Island to eliminate potential hosts. Today, management strategies include the integration of silvicultural, chemical, and biological control methods.

**Silvicultural control.** Wakeley (1928) stated that the control methods recommended by Comstock (1880) and Scudder (1883) were impractical for use in timber production. In addition, he also concluded that the feasibility of chemical control was greatly limited by the technology of available spray equipment in the 1920s. Wakeley, a silviculturalist by training, recognized the importance of proper forest management to minimize stand risk and hazard from insect epidemics. He suggested several silvicultural techniques to minimize *R. frustrana* impacts including confining plantations to favorable sites, starting seedlings among brush, utilizing a shelterwood cut, or planting more resistant species when applicable (Wakeley 1928).

Silvicultural techniques are recommended that maintain some competing vegetation, increase stand vigor, and enhance biodiversity on the premise of increasing natural plant defenses (Wakeley 1928), or reducing the apparency of preferred hosts (Graham and Baumhofer 1927, Wakeley 1928, Huckenpahler 1951, 1953, Beal et al. 1952, Wenger 1955a, 1955b, Hansbrough 1956). It is thought that maintaining shade adversely affects *R. frustrana* development (Yates 1960, Bersiford and Kulman 1967), but earlier research has suggested otherwise (Harrington 1955). The highest tip moth populations tend to occur in even-aged stands with wide spacings and little competing vegetation (Berisford and Kulman 1967). Several studies have shown that *R. frustrana* densities are inversely correlated with the amount of competing vegetation (see above). To date, we still have a very poor understanding of the mechanisms at work here, however, they are thought to be unrelated to changes in the physiological status of the tree (Berisford 1988).

Other investigators have searched for *R. frustrana*-resistant tree species and seed sources. Japanese black pine, *P. thungbergii* Parlatore, is highly resistant to *R. frustrana* attack and, therefore, was extensively planted along the North Atlantic Coast during the 1930s (Jones 1930, Littlefield 1942, Afanasiev 1949). Afanasiev (1949) reported that of the six pine species he studied in Oklahoma, Japanese black pine was first in overall survival, second in growth (to shortleaf pine), and least susceptible to *R. frustrana* infestation. With the exception of newly-planted seedlings, slash pine is virtually immune to *R. frustrana* attack throughout its native range (Williston 1958, Williston and Huckenpahler 1960). Operationally, today's resource managers may give little thought to planting tip moth resistant tree species, and most frequently base selections on other criteria.

Crow (1956, 1958) looked at different geographic seed sources of loblolly pine in Louisiana, and found no differences in the amount of *R. frustrana* damage among the four sources. Significant interest has since developed in selective breeding of pines that are naturally resistant or tolerant of tip moth infestation (Holst and Heimnurger 1955, Henry and Hepting 1957, Harris 1960, Yates 1962, Holst 1963, Warren and Young 1972, Hertel and Benjamin 1975, Hood et al. 1985). In one of the more robust studies, significant differences were found among 12 half-sib families of loblolly pine planted in eastern North Carolina (Cade and Hedden 1989). Each family was from genetically-improved parents, and all were representative of operational plantings occurring within the region. Lopez-Upton et al. (2000) were unable to find any family differences in the attack frequency of loblolly pine in Florida, and heritability for tip moth resistance was very low. Nowak and Berisford (2000) detected no significant differences in damage among four genetically-improved loblolly pine seed sources. Unfortunately, most progeny tests routinely involve treatment with insecticides and, therefore, provide little or no opportunity for selecting and promoting insect resistance mechanisms. Currently, selection of planting stock is made without consideration to *R. frustrana* resistance and tolerance levels.

Silvicultural control recommendations include less intensive site preparations, natural or direct seeding in lieu of planting, promoting stand diversity, and reducing the size of regeneration blocks (Berisford 1988). All silvicultural controls are, therefore, preventative in nature. Unfortunately, most of these recommendations conflict with preferred silvicultural treatments that promote rapid juvenile growth and simplified harvest and regeneration schedules. In recent years, the use of silvicultural controls for managing *R. frustrana* infestations has received little, if any, attention by resource managers. This trend is likely to continue in the future with the increasing intensity of pine silviculture.

**Chemical control.** Baumhofer (1936) first documented the importance of preplant seedling dips to destroy *R. frustrana* eggs prior to shipment. Underhill (1943) recommended inspecting nursery stock before planting, and rejecting any material that contained dead or dying shoot tips. Beal et al. (1952) reported satisfactory control by fumigation with sodium cyanide. Today, it is common for seedlings to be insecticide-treated in the nursery prior to shipment for control of both *R. frustrana* and pine regeneration weevils.

Numerous studies have been published on the efficacy of various classes, active ingredients, and formulations of insecticides for controlling *R. frustrana* populations. (Howard 1925, Smith et al. 1930, Baumhofer 1936, Hall 1936, Moritimer 1941, Fenton and Afanasiev 1946, Afanasiev and Fenton 1947, Bieberdorf 1959). Many of these data are now obsolete because registrations have been cancelled or the products themselves are no longer manufactured. Specific detailed references will not be made to all studies (Beal 1958, Neel 1959a, b, Donley 1960, Williston and Huckenpahler 1960, Foil et al. 1961, 1962, Warren 1964, Burns 1966, Beal 1967, Grano and Grigsby 1968, Warren 1968, Scheer and Johnson 1970, Shepard 1973, Appleby 1975, Brown and Eads 1975, Burns 1975, Dupree and Davis 1975, Overgaard et al. 1975, Chatelain et al. 1977, Nord 1978, Brown and Eads 1980). Howard (1925) first reported that a 2% nicotine dust was highly effective in killing *R. frustrana* adults. In the 1940s, dichlorodiphenyltrichloroethane (DDT) became available and was determined to be highly effective for controlling *R. frustrana* infestations (Fenton and Afanasiev 1946, Afanasiev and Fenton 1947, Beal 1958). It was used extensively until banned by the U.S. Environmental Protection Agency in 1973. Stearns (1953) tested the efficacy of Blackleaf 40, lead arsenate, benzenehexachloride (BHC), parathion and DDT, and found only DDT and parathion to produce satisfactory results. Recommendations commonly called for spraying 14 d before peak emergence, at peak emergence, and 14 d after peak emergence. In Kansas, adequate control was achieved by spraying 10 to 14 d after peak adult emergence with diazinon and azinphosmethyl (Dick and Thompson 1971). Today, pyrethroids are most commonly used in tip moth management (Fettig et al. 2000a, b, Nowak et al. 2000), although other compounds may be effective, including botanicals such as neem, biological insecticides such as *B. thuringiensis* var. *kurstaki* and more host-specific chemicals which may preserve natural enemies (Dalusky and Berisford 2002).

In the 1960s, it was recognized that 3 to 9 applications of DDT in a single growing season could not be justified economically (Thor and Beavers 1964, Boyd et al. 1968). Consequently, investigators began examining the potential of systemic insecticides for managing *R. frustrana* populations. Systemics are generally applied to the soil as granular or liquid formulations, or as pre-plant root dips. Uptake and translocation within plant tissues usually provides favorable and prolonged control. Unfortunately, efficacy is highly dependent on appropriate soil moisture levels. Insufficient soil moisture prevents absorption by roots while too much moisture can cause leaching into groundwater systems. Thor and Beavers (1964) determined that, although phytotoxic effects were observed, disulfoton was highly effective at controlling *R. frustrana* infestations during the first and second years following application. Cade and Heikkenen (1965) applied granules of disulfoton and phorate at rates of 27.5 and 82.5 kg per ha prior to sowing. Phorate was efficacious; however, disulfoton provided no control. When treatments were applied to the roots of seedlings in a clay slurry, strong phytotoxic effects were observed with phorate, although disulfoton provided adequate control (Cade and Heikkenen 1965, Barras et al. 1967, Yates 1970). Merkel and Hertel (1976) showed that carbofuran provided excellent late season control in northern Florida. Carbofuran served as the standard in tip moth management for several years (Kerr and Owebs 1973, Overgaard et al. 1976, 1978). Powers and Stone (1988) demonstrated that carbofuran also reduced the number of fusiform rust infections, although the insecticide is not known to have any fungicidal properties. The registration of carbofuran was cancelled, and the product is no longer available for use in *R. frustrana* management.

A listing of insecticides currently registered for use in pine plantations can be obtained in the most recent edition of the pest control handbook distributed by State Cooperative Extension offices. Today, insecticides are most commonly used to protect high-valued stands such as Christmas tree plantations, seed orchards, progeny tests, and/or short-rotation sawtimber and pulpwood stands. Initial interest in developing more reliable methods for controlling *R. frustrana* infestations came from Christmas tree growers unsatisfied with the efficacy of biweekly calendar sprays. Accordingly, Richmond et al. (1983) developed a method for predicting spring flight using heat unit accumulation, while Gargiullo et al. (1983b) developed a degree-day spray-timing model for dimethoate insecticides in the Georgia Piedmont, where *R. frustrana* has three generations annually. The procedure involves accumulating degree-day summations commencing on the date of first catch in pheromone-baited traps for each generation, and continuing until an experimentally determined sum is attained. This sum indicates the optimal spray date. Insecticide treatments are applied once during each generation on or about the optimal date. Spraying at 30 to 80% egg hatch maximizes control and corresponds with an abundance of first and second instars (Berisford et al. 1984). These stages appear most susceptible to control due to their small size, presence on the tree surface, and movement over sprayed areas when in search of new feeding sites. Subsequently, Gargiullo et al. (1985) developed similar models for esfenvalerate insecticides in the Georgia Coastal Plain where *R. frustrana* completes four generations annually. Each of these models has since been refined to increase their utility (Kudon et al. 1988, Fettig et al. 1998). Currently, spray timing values are only available for three and four generation phenologies. It has been suggested that a model should be developed for areas where five generation phenologies are observed because an increasing amount of loblolly pine production is occurring in these regions. A complete listing of spray timing models is provided (Table 1).

In the early 1980s, several forest product companies in the Southeast began managing loblolly pine plantations using silvicultural techniques including intensive site preparation, herbaceous and woody weed control, fertilization, irrigation, and, in rare cases, insect control. Some companies began using spray timing models to control *R. frustrana* infestations, but improper use frequently led to errors in spray date predictions and, therefore, yielded unsatisfactory results. The spray timing models are not complex, but require a detailed knowledge of *R. frustrana* biology and identification, proper pheromone-baited trap deployment, intensive trap monitoring, and knowledge of degree-day calculations, conversions and utility. Collection of phenology and degree-day data is costly and laborious, and provides only short-term advanced notice of optimal spray dates.

Fettig et al. (2000a) developed a simplified system using long-term historical temperature data to predict optimal spray intervals based on 5-day periods for 354 locations throughout the southeastern United States. These optimal spray period predictions can be obtained from the original publication or associated website (http://www.forestpests.org/nptm). Resource managers applying contact insecticides, such as pyrethroids, can simply locate the nearest weather station, and then reference the associated table to determine the corresponding optimal spray period predictions for that location. Fettig et al. (2000a) have suggested that in most cases their predictions will meet spray-timing objectives with the same effectiveness as the more labor intensive degree-day spray timing models. Validation studies comparing optimal

**Table 1. Papers published 1980-2002 on the timing of insecticide applications for controlling *Rhyacionia frustrana* populations**

| Application topic | Citation |
|---|---|
| Degree-day based spray timing model for a 3 generation phenology in the Georgia Piedmont | Gargiullo et al. 1983b |
| Non-systemic chemical control must be directed toward early developmental stages | Berisford et al. 1984 |
| Degree-day based spray timing model for a 3 generation phenology in the Georgia Piedmont and validated and refined in Oklahoma and North Carolina | Gargiullo et al. 1984 |
| Degree-day based spray timing model for a 4 generation phenology in the Georgia Coastal Plain | Gargiullo et al. 1985 |
| Two insecticide applications may be necessary for adequate control of the third generation in the Georgia Piedmont | Kudon et al. 1988 |
| Prediction of optimum spray dates using trap catch data and a degree-day flight model for a 4 generation phenology in southern California | Malinoski and Paine 1988 |
| Automated computer system that provided daily predictions of optimal spray dates for 70 weather stations in Georgia (not in use) | Pickering et al. 1989 |
| A spray timing model developed for North Carolina based on thermal units | Richmond 1992 |
| Refined spray timing values are reported for data initially provided by Gargiullo et al. 1985 | Fettig et al. 1998 |
| Spray timing model for a 3 generation phenology in eastern North Carolina and Virginia | Fettig and Berisford 1999b |
| Optimal spray period predictions provided for 354 locations throughout the southeastern USA | Fettig et al. 2000a |
| An optimal insecticide spray schedule is identified that eliminates four sprays over a two-year period when compared to standard applications | Fettig et al. 2000b |
| Optimal spray timing values are provided for permethrin, lambda-cyhalothrin, spinosad, and *Bacillus thuringiensis* Berliner in the Georgia Piedmont | Nowak et al. 2000 |
| Validation of spray timing and schedules in areas with extremely high *R. frustrana* populations | Fettig and Berisford 2002 |

spray period predictions with those determined on site by monitoring moth phenology and accumulating degree-day summations exceeds 48% agreement. Recently, additional studies were conducted to provide optimal spray period predictions for Arkansas, Louisiana and East Texas (C. J. Fettig, unpubl. data). These data will allow resource managers throughout the southern pine belt to time *R. frustrana* insecticide applications accurately with minimal effort.

Frequent and prolonged insecticide applications are likely to be impractical and uneconomical for commercial timber production. Fettig et al. (2000b) evaluated all possible combinations of spray schedules for three annual tip moth generations. The most economically feasible spray schedule was found to be a single spray during the first generation of the first and second years following stand establishment. Relative to conventional applications, this schedule eliminates four sprays over the 2-yr period. Fettig et al. (2000b) have suggested that applying a single first generation spray during the initial 2 yrs following planting may be sufficient in yielding favorable returns. However, similar studies should be conducted in stands with higher tip moth populations than were observed (Fettig et al. 2000b) and in those areas with four or five generations.

Fettig and Berisford (2002) subsequently evaluated their optimal spray period predictions and optimal spray schedules in eastern North Carolina. Insecticide treatments timed according to the optimal spray periods were highly effective. Mean whole-tree damage levels averaged 47.0% and 0.6% in untreated and treated plots, respectively. In many agricultural systems, prolonged insecticide applications have caused secondary pest outbreaks, insect resistance, and resurgence. Similar outbreaks have occurred in Christmas tree plantations where frequent insecticide applications were made. Therefore, efforts should be made toward minimizing the frequency and extent of treatments, maximizing efficacy by precise timing of applications, and conserving natural enemies. An overall growth increase of 52.0% was observed by controlling the first generation only, and 88.5% by treating each of three generations (Fettig and Berisford 2002). In the simplest of cases, conventional timing schedules would cost three times that of treating only the first generation, assuming costs were fixed throughout the year. Therefore, limiting insecticide applications to the first *R. frustrana* generation may be a viable technique for tree protection, resistance and resurgence management, and conservation of natural enemies.

Recently, there has been some interest in examining the potential of attract-and-kill technologies in tip moth management. This technique utilizes an attractive bait or pheromone (in the case of *R. frustrana*) to draw insects toward an insecticide-treated substrate (Krupke et al. 2002). The strategy reduces non-target mortality because theoretically only the pest species is attracted to these sites. Studies are currently being conducted in Georgia and California to determine the effectiveness of this tool for tip moth management.

**Biological control.** The Nantucket pine tip moth has a rich compliment of natural enemies that are important regulators of population density. Some pathogens and parasitioids have been examined as potential biological control agents, the most successful of which are insecticides containing the soil bacterium *B. thuringiensis* var. *kurstaki* Berliner. *Bacillus thuringiensis* is activated in the midgut of susceptible caterpillars and, therefore, must be ingested while feeding. In a recent study, *B. thuringiensis* was the least effective insecticide evaluated, yielding only 34% control (Nowak et al. 2000). Other studies have examined the potential of viruses and nematodes as biological control agents and have yielded limited success. A codling moth granulosis virus applied at $2.5 \times 10^{11}$ granules/g at 100g/ha using a backpack sprayer provided sufficient control, but additional studies have not been conducted (Stephen et al. 1982b, McLeod et al. 1983). The application of nematode DD-136 (*Neoaplectana* sp.) to *R. frustrana* larvae caused mortality in the laboratory, but no significant differences between nematode-treated and untreated shoots were observed in the field (Nash and Fox 1969). The USDA Forest Service is currently screening field populations for pathogens that may later have potential for use in a biological control program.

Two native parasitoid species have been successfully introduced into epidemic tip moth populations (Swenk 1927, Wadley 1932, Scriven and Luck 1978), and at least one release produced a dramatic decrease in tip moth damage (Scriven and Luck 1978). Recently, inundative releases of an egg parasitoid *Trichogramma exiguum* (Hymenoptera: Trichogrammatidae) has been evaluated in eastern North Carolina. Each of three releases were separated by 7 days at rates of 328,238 ± 88,379 females/ha in capsules hand-placed at 100 release points within each 0.4-ha plot. Egg parasitism rates were significantly increased by 29%, and hatch significantly reduced by 46% (Orr et al. 2000). Both the percentage of infested shoots and the length of damage along the shoots were significantly reduced in the release plots.

Questions remain about the most effective ways in which to conserve or enhance natural enemies, and if any such techniques will be compatible with other forest management objectives. Operational releases of biological control agents into pine plantations are unlikely at this time due to economics, but conservation approaches are less likely to be hampered by costs.

**Mating disruption.** Several efforts have been made to use synthetic pheromones for tip moth control. Berisford and Hedden (1978) demonstrated that air permeation with the major component of the *R. frustrana* pheromone significantly reduced attraction to female-baited traps whereas the pheromone of *R. rigidana* did not affect catch. There was no reduction in tip moth damage, however. Subsequent large scale disruption attempts did not reduce infestation levels where populations were sufficient to cause significant damage (C. W. Berisford, unpubl. data).

**Hazard rating and damage prediction models.** A hazard-rating model for *R. frustrana* has been developed from vegetative, physiographic, and soil characteristics in loblolly pine stands in the Piedmont (Hood et al. 1988). However, tip moth management in the Piedmont is likely to be less economical than in the Coastal Plain and there is currently no operational use of hazard rating systems for *R. frustrana* in this latter (or any other) region. Some of the variables identified as indicators of high hazard (i.e., intensity of site preparation) are integral components of silvicultural prescriptions. Hood et al. (1988) reported that tip moth damage was higher on sites with higher levels of soil calcium. Sun et al. (1998) developed regression equations predicting whole tree tip moth damage levels from foliar nutrient levels ($r^2 = .54$), concluding that percent foliar nitrogen and calcium were good indicators of future tip moth damage.

There is some potential for predicting tip moth infestation levels from pheromone-baited trap catches (Asaro and Berisford 2001a). Strong associations between damage and trap catch within a generation were demonstrated for each of three generations in the Georgia Piedmont. Ideally, damage levels for the next generation might be predicted using trap catches from the current generation that occur prior to the optimal spray date. The ability to do this has shown some promise, particularly when using trap catch from the overwintering generation to predict subsequent first generation damage (Asaro and Berisford 2001a). Validation of these techniques throughout the Southeast is warranted.

**An integrated pest management system.** Integrated pest management programs attempt to reduce insect associated losses to acceptable levels using multiple techniques that are effective, economically viable, and ecologically compatible. It is unlikely that silvicultural and biological controls will be incorporated into an IPM program for *R. frustrana* in intensively managed stands in the near future. Damage prediction models and insecticide treatments are likely to be the cornerstone of efforts to manage tip moth populations in these systems. Decisions to manage *R. frustrana* infestations will be based on many factors, but costs versus benefits, usually expressed as increased volume or wood quality, will dominate.

The following decision chart (Fig. 2) is designed to assist foresters in managing Nantucket pine tip moth infestations in the southeastern United States. These results may not be applicable to other portions of the moth's range, such as southern California, Arizona and New Mexico. Every attempt has been made to include the most current and reliable information available. However, some of the recommendations may be subject to change based on additional research. Furthermore, certain aspects of tip moth IPM that are not currently practical (i.e., parasitoid augmentation), but which may become feasible in the future were not included in the chart. We recognize the challenges of adapting research results to operational programs, and therefore we were fairly conservative in the absence of more complete data. For example, the designations for hazard ratings being 'high' or 'low' indicates our current knowledge base does not allow for such precision when dealing with intermediate population levels. This chart should not be thought of as a precise protocol for tip moth management, but rather, as a general guide that should be supplemented by good judgment based on practical experience.

**The future.** It seems likely that management practices in the southeastern United States and elsewhere will continue to elevate the pest status of the Nantucket pine tip moth. The use of fertilizer, herbicides, and insecticides can have highly complex and interactive effects on tree growth rates and the population dynamics of tip moths and their extensive complement of natural enemies. Increased acreage and/or intensified management of industrial forest plantations will further facilitate tip moth population buildup and spread over large areas. Control measures are likely to become more widely used.

Further concerns about *R. frustrana* at the international level are warranted. Extensive areas of intensively managed loblolly pine and other highly susceptible hosts such as Monterey pine are widely planted throughout South America, South Africa, Australia, and New Zealand. The accidental introduction and establishment of *R. frustrana* into these areas in the absence of their natural enemies could have potentially devastating economic impacts. Given the widespread native distribution of *R. frustrana* in the eastern United States, Mexico, Central America and the Caribbean, as well as its apparent success in establishing itself in the western United States, it appears to be a highly adaptable insect when it comes to colonizing new areas. Increased globalization and international trade will only increase the risk of such an occurrence.

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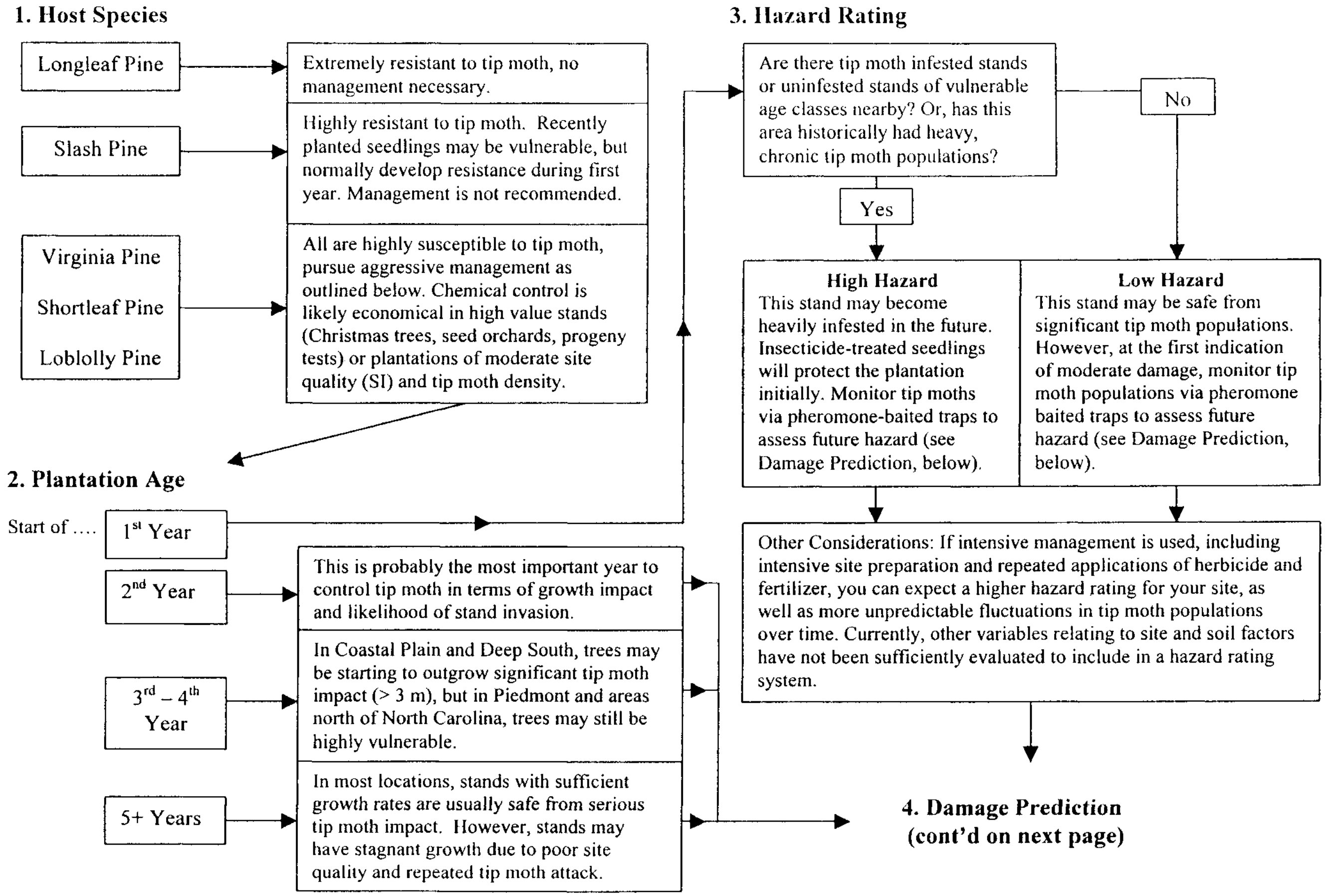
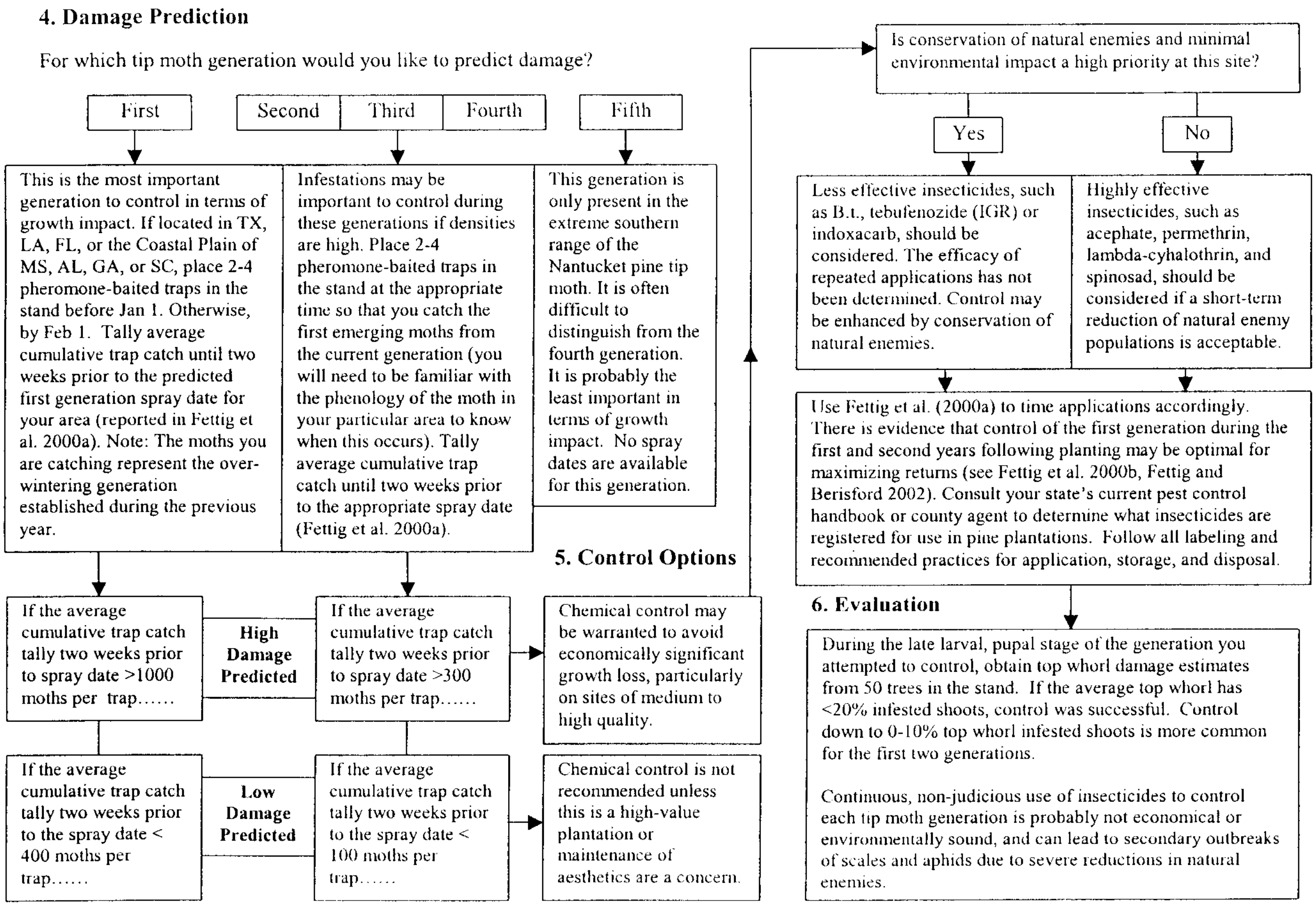


Fig. 2. A decision flow chart for management of the Nantucket pine tip moth in the southeastern United States.



4. Damage Prediction

For which tip moth generation would you like to predict damage?

This is the most important generation to control in terms of growth impact. If located in TX, LA, FL, or the Coastal Plain of MS, AL, GA, or SC, place 2-4 pheromone-baited traps in the stand before Jan 1. Otherwise, by Feb 1. Tally average cumulative trap catch until two weeks prior to the predicted first generation spray date for your area (reported in Fettig et al. 2000a). Note: The moths you are catching represent the over-wintering generation established during the previous year.

Infestations may be important to control during these generations if densities are high. Place 2-4 pheromone-baited traps in the stand at the appropriate time so that you catch the first emerging moths from the current generation (you will need to be familiar with the phenology of the moth in your particular area to know when this occurs). Tally average cumulative trap catch until two weeks prior to the appropriate spray date (Fettig et al. 2000a).

This generation is only present in the extreme southern range of the Nantucket pine tip moth. It is often difficult to distinguish from the fourth generation. It is probably the least important in terms of growth impact. No spray dates are available for this generation.

If the average cumulative trap catch tally two weeks prior to spray date >1000 moths per trap……

**High Damage Predicted**

If the average cumulative trap catch tally two weeks prior to spray date >300 moths per trap……

If the average cumulative trap catch tally two weeks prior to the spray date < 400 moths per trap……

**Low Damage Predicted**

If the average cumulative trap catch tally two weeks prior to the spray date < 100 moths per trap……

5. Control Options

Chemical control may be warranted to avoid economically significant growth loss, particularly on sites of medium to high quality.

Chemical control is not recommended unless this is a high-value plantation or maintenance of aesthetics are a concern.

Is conservation of natural enemies and minimal environmental impact a high priority at this site?

Less effective insecticides, such as B.t., tebufenozide (IGR) or indoxacarb, should be considered. The efficacy of repeated applications has not been determined. Control may be enhanced by conservation of natural enemies.

Highly effective insecticides, such as acephate, permethrin, lambda-cyhalothrin, and spinosad, should be considered if a short-term reduction of natural enemy populations is acceptable.

Use Fettig et al. (2000a) to time applications accordingly. There is evidence that control of the first generation during the first and second years following planting may be optimal for maximizing returns (see Fettig et al. 2000b, Fettig and Berisford 2002). Consult your state's current pest control handbook or county agent to determine what insecticides are registered for use in pine plantations. Follow all labeling and recommended practices for application, storage, and disposal.

6. Evaluation

During the late larval, pupal stage of the generation you attempted to control, obtain top whorl damage estimates from 50 trees in the stand. If the average top whorl has <20% infested shoots, control was successful. Control down to 0-10% top whorl infested shoots is more common for the first two generations.

Continuous, non-judicious use of insecticides to control each tip moth generation is probably not economical or environmentally sound, and can lead to secondary outbreaks of scales and aphids due to severe reductions in natural enemies.

Fig. 2. Continued.

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