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Evaluation of the Susceptibility of Four Scotch Pine Christmas Tree Varieties to Insect Pests

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EVALUATION OF THE SUSCEPTIBILITY OF FOUR SCOTCH PINE CHRISTMAS TREE VARIETIES TO INSECT PESTS

By

Eileen Amber Eliason

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ABSTRACT

EVALUATION OF THE SUSCEPTIBILITY OF FOUR SCOTCH PINE CHRISTMAS TREE VARIETIES TO INSECT PESTS

By

Eileen Amber Eliason

Four Scotch pine (*Pinus sylvestris* L.) Christmas tree varieties were tested for resistance to Zimmerman pine moth (Lepidoptera: Pyralidae), European pine sawfly (Hymenoptera: Diprionidae) and pine needle scale (Homoptera: Diaspididae). Insects were reared in 1994 and 1995 on trees at the Michigan State University Kellogg Experimental Forest, Kalamazoo County. Differences among tree varieties in sawfly and scale survival and fecundity were detected, but Zimmerman survival was too low to determine varietal differences. Multiple regressions predicted Zimmerman pupal weight, sawfly development and pupal weight, and scale survival and fecundity. In another study, trees at Kellogg Forest and a field in Montcalm County were monitored twice a month during each summer. Natural feeding guild infestations under observation differed in abundance and phenology, but sap-feeders were dominant. Inconsistent results of guild abundance among varieties implicated factors other than resistance affecting community structure. Alternatives to resistance acting on reared species and guilds are discussed.

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I am also grateful to my mom and grandmother for their encouragement and support, and to my dad, who now more fully respects my love of biology. I'll always be happy to check out their plant problems.

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INTRODUCTION

Scotch pine, *Pinus sylvestris* L., has been a valuable ornamental, forest and Christmas tree species in Michigan since its importation from Europe and Asia in the early nineteenth century (Bridgen and Hanover 1982, Giertych and Matyas 1991, Sowder 1966). It has long been a favorite Christmas tree species among growers and consumers. In Michigan, Scotch pine is grown on about 39,000 ac (15,783 ha), and over three million or 71% of Christmas trees harvested annually are Scotch pine (Mich. Agr. Stat. Serv. 1994).

Geographic and climatic conditions in Europe and Asia affected isolated populations of Scotch pine trees over time, exerting different selection pressures on each gene pool (Giertych and Matyas 1991). Over 30 varieties of Scotch pine have been recognized (Ruby and Wright 1976), differing in traits such as needle length, needle color and moisture content, cone production, stem form, growth rate and monoterpene composition (Carlisle 1958, Ruby and Wright 1976, Tobolski and Hanover 1971, Wright 1976). Varieties also vary in degree of resistance to insects and diseases (Squillace et al. 1975, Steiner 1974, Wright and Wilson 1972, Wright et al. 1975) and can be selectively bred to further decrease their susceptibility to insect damage (Bridgen and Hanover 1982).

In the first study, my objectives were to evaluate the resistance of four Scotch pine varieties to three insect pests caged on trees. In the second study, I monitored five arthropod feeding guilds on the same Scotch pine varieties and determined their phenology and seasonal abundance at two locations in southern Michigan.

The thesis is structured to include a comprehensive literature review, two chapters and final conclusions. The literature review discusses the geographic distribution of Scotch pine, traits of Christmas trees, Christmas tree management (e.g., planting, site preparation and maintenance, shearing, pesticide applications and harvesting), and integrated pest management (IPM) in Christmas tree production, including host plant resistance. Chapter one presents the results from all tree measurements made at Kellogg Forest, the life cycles, methods, results and discussions pertaining to the study of varietal resistance to three insect pests, including Zimmerman pine moth (*Dioryctria zimmermani* (Grote)), European pine sawfly (*Neodiprion sertifer* Geoff.), and pine needle scale (*Chionaspis pinifoliae* (Fitch)). This chapter will be submitted for publication to the Journal of Economic Entomology. Chapter two describes a study of the phenology of five naturally occurring feeding guilds on the four Scotch pine varieties, the methods, results and discussion. This chapter will be submitted to the journal Environmental Entomology. The most important conclusions are summarized in the final section.

LITERATURE REVIEW

Geographic Distribution. Scotch pine, *Pinus sylvestris* L., also known as Scots pine, is one of the most widely distributed conifers in the world (Skilling 1990), and has been grown for ornamental, windbreak, timber, and Christmas tree purposes (Bridgen and Hanover 1982, Giertych and Matyas 1991). Scotch pine has two-needle fascicles, is shade-intolerant, and is primarily monoecious (Giertych and Matyas 1991, Skilling 1990). Its natural distribution ranges from Scotland to the Pacific Ocean and from Scandinavia to the Mediterranean Sea (Giertych and Matyas 1991, Skilling 1990). This species has been widely planted in North America during the twentieth century (Sowder 1966, Wright et al. 1966). It can grow on a variety of soils, but well-drained sand and gravel soil types are preferred (Skilling 1990). Over 30 geographic varieties of Scotch pine have been recognized; varieties differ in needle length, color and moisture content, cone production, stem form, growth rate and monoterpene concentration (Carlisle 1958, Ruby and Wright 1976, Tobolski and Hanover 1971, Wright 1976). Varieties also vary in degree of resistance to insects and diseases (Squillace et al. 1975, Steiner 1974, Wright and Wilson 1972, Wright et al. 1967, 1975) and can be selectively bred to decrease susceptibility to damage (Bridgen and Hanover 1982).

Traits important to tree breeders and Christmas tree growers include winter needle color, needle length, stem form, and growth rate (Koelling and Heiligmann 1993, Sowder

1966). Variability among Scotch pine varieties from various geographic locations is readily apparent (Wright and Bull 1963). For example, Scandinavian varieties typically have yellow winter foliage, whereas varieties originating from central and southern Europe possess green needles year-round (Heit 1964, Wright and Bull 1963). Needle length is relatively short for northern varieties, intermediate for western European and southern Eurasian varieties, and relatively long for central European varieties (Ruby and Wright 1976). Although central and southern European varieties grow faster than Scandinavian varieties, factors such as soil quality, nutrient availability, and the presence of birds and phloem- and wood-boring insects can influence stem strength and straightness (Skilling 1990).

Christmas Tree Management. Scotch pine Christmas trees are grown on a 7- to 10-year rotation in Michigan and are usually managed intensively to minimize damage from insects and diseases (Leefers et al. 1988). In most Christmas tree operations, seedlings are placed in the soil using mechanical planters, a more efficient method than hand-planting (Koelling and Dornbush 1992). Seedlings are grown from nursery stock instead of natural reproduction (Skilling 1990), and using "certified seed" ensures the genetic purity and quality of varieties (Haverbeke 1981, Koelling and Heiligmann 1993). Stocking density averages 1,210 trees/ac (490 trees/ha), if trees are spaced 6 x 6 ft (1.8 x 1.8 m) apart (Koelling and Dornbush 1992). The Scotch pine varieties recommended for planting as Christmas trees in the northern United States include *iberica* (Spanish), *aquitana* (French Massif or Van's), *armena* (Lake Superior Blue), and *haguenensis* (Belgium) (Stadt and Hanover 1983). These varieties are valued as Christmas trees for

having fast growth rates, green winter needle color, straight stems, dense foliage, and durable branch strength (Koelling and Heiligmann 1993, Sowder 1966).

Site preparation and management in Christmas tree plantations include controlling competing vegetation before and after seedlings have been planted. Herbaceous vegetation growing around trees may provide habitat for small rodents, increase tree susceptibility to diseases and certain insect pests, compete for sunlight and increase competition for soil nutrients (Lantagne et al. 1990, Shick 1965). Methods of controlling vegetation include mowing, herbicide application or, less commonly, planting a cover crop (Koelling and Dornbush 1992). Fertilization may give other pine or non-pine conifers a competitive edge over herbaceous vegetation, but it does not significantly increase growth rates in Scotch pine (Lantagne 1988).

The process of shearing Christmas trees, or cutting off newly expanded shoots, reduces height growth and promotes the growth of adventitious buds near the cut end of shoots (Hill 1989, Skilling 1990). The purpose of shearing is to produce trees with one straight stem, a conical crown, and balanced, full foliage (Hill 1989, Johnson 1991). The amount and quality of shearing is determined by tree age, time until harvest, the tool used (e.g., machete, power clippers, hedge shears), and worker experience (Johnson 1991). Trees are sheared annually in early summer beginning the second or third year following planting until the year of harvest (Johnson et al. 1992, Koelling 1991). USDA grading standards recommend that the tree base be sheared to two-thirds as wide as the height of the tree (Koelling 1991).

Insecticides are widely used on Christmas trees against pests that damage stem form and foliage. Both major and minor pests in the Lake States, their life cycles and management are listed in several comprehensive Extension and USDA Forest Service bulletins (Benyus 1983, Kachadoorian et al. 1995, McCullough and Ellis 1995). Despite the short-term benefits of using chemical controls, sole dependence on insecticides can result in several negative effects. These effects can include loss of beneficial arthropods, secondary pest outbreaks, reinfestation of plants by surviving or newly invading arthropods requiring the reapplication of sprays, and pesticide residues and drift (Stern et al. 1959). Spraying on a regular, calendar basis is not the most effective means to manage pests (Ascerno 1991).

Christmas tree harvesting occurs annually from mid-October through December, and trees are either marketed wholesale or retail (Hill 1989). Prior to harvest, however, many trees are painted with a blue-green colorant (Johnson 1989). This is intended to hide some winter yellowing that occurs in certain varieties of Scotch pine and to make trees look healthier (Hill 1989). Once cut, trees are placed on shakers to remove dead needles, baled for transportation, inspected for quarantined pests, and shipped (Kidd 1993). Tree quality (grade) and price depend on taper, freshness, cleanliness, stem form, foliage density, and “handle” length (length from the bottom of the stem to the first whorl of branches) (Anonymous 1989). Trees are typically transported by truck to their intended destination.

Growing and marketing Scotch pine Christmas trees depends on consumer demand and the cost of managing trees throughout their rotation. The production of Scotch pine in Michigan peaked in the 1980’s, when about 70% of all Christmas trees harvested in Michigan were Scotch pine, costing consumers $8 to $15 per tree (Koelling et al. 1992, Mich. Agr. Stat. Serv. 1994, Riessen 1995). With increasing competition among growers, consumer demand for higher quality trees and increased management costs, fewer acres of Scotch pine have been planted in recent years in Michigan (Koelling and Heiligmann 1993, Koelling et al. 1992, Mich. Agr. Stat. Serv. 1994, Riessen 1995). Since over 40 insects and diseases attack Scotch pine Christmas trees in the Great Lakes region (Benyus 1983), growers have difficulty maintaining management standards to keep trees healthy and undamaged (Riessen 1995).

Integrated Pest Management (IPM). From planting monocultures, introducing exotic pests, and decreasing public tolerance for damage on plants, agricultural conditions have become ideal for pest outbreaks (Stern et al. 1959, Pedigo 1996). This set of conditions has resulted in growers spraying pesticides regularly in many agricultural systems to minimize pest damage (Leslie and Cuperus 1993). An alternative to a complete reliance on pesticides is "integrated pest management" or IPM, an approach that optimizes the combined effects of biological, cultural and pesticide controls in a more environmentally sound manner. An IPM program involves regular scouting or monitoring for pests, pest identification, evaluation of damage severity, determining and implementing a course of action, and evaluating the effectiveness of the strategy (McCullough and Ellis 1995, Turgeon and de Groot 1992). Instead of maintaining zero tolerance, the concept of economic injury levels is used to identify the threshold at which management efforts are implemented (Pedigo 1996, Stern et al. 1959).

Natural resistance to pests can be exploited in IPM to supplement other management strategies (Nielsen 1989). Beck (1965) defined resistance as "the collective heritable characteristics by which a plant species, race, clone, or individual may reduce the probability of successful utilization of that plant as a host by an insect species, race, biotype, or individual." This definition includes the concepts of "nonpreference" and "antibiosis," but not "tolerance" as defined by Painter (1951). Painter (1951) described resistance in five categories, ranging from immunity to high susceptibility. Host resistance against insects can be reflected in insect host selection and survival, developmental rate, fecundity and behavior (Beck 1965). Insects may respond to host plant resistance by death, reduced fecundity, weight loss, increased development period, or avoidance of the plant for feeding and/or ovipositing (Singh 1986).

Techniques used to evaluate plant varieties for insect resistance include controlled caging studies and observations of field populations of insects (Tingey 1986). Insect density, immigration, emigration, and presence of non-target organisms in the test environment can be controlled with caging procedures (Tingey 1986). However, monitoring natural pest populations provides data on pest ecology under normal conditions. In studies of host plant resistance, insect population levels, age structure, phenology and the effect on crop yield should be analyzed, while minimizing experimental error (Tingey 1986). In addition, traits in plants contributing to resistance need to be determined, whether they are morphological, chemical stimuli, or nutrients (Hanover 1975). After the preliminary step of evaluating varieties for degree of resistance to pests, more thorough genetic and chemical tests to determine inheritance and pathways are needed (Hanover 1975). Then selective breeding of varieties to maximize resistance against pests can begin.

CHAPTER 1

Resistance of Four Scotch Pine Varieties to Three Insect Pests in Michigan

INTRODUCTION

Michigan is one of the largest producers of Scotch pine Christmas trees in the United States (Riessen 1995). However, growers have been planting less Scotch pine during the past few years due to its overabundance, low value and high management costs (Koelling et al. 1992, Riessen 1995). If current management practices have contributed to the decreasing supply and demand of this Christmas tree species, then alternative management approaches should be considered. One such possibility is planting or breeding varieties of Scotch pine that are resistant to major insect pests and diseases. Some varieties have been observed to have higher or lower infestation levels of pests, indicating greater or less resistance to attack (Ruby and Wright 1976, Steiner 1974, Wright and Wilson 1972, Wright et al. 1967, 1975).

The objectives of this study were to: 1) determine if differences in tree growth traits varied significantly among four Scotch pine Christmas tree varieties in southern MI, 2) determine if the survival and fecundity of Zimmerman pine moth (*Dioryctria zimmermani* (Grote)), European pine sawfly (*Neodiprion sertifer* (Geoff.)) and pine needle scale (*Chionaspis pinifoliae* (Fitch)) differed significantly when reared on the four varieties, and 3) determine which tree growth traits may affect insect performance.

ZIMMERMAN PINE MOTH DAMAGE AND PHENOLOGY

Zimmerman pine moth (Lepidoptera: Pyralidae) is a native phloem-borer of pine trees in the North Central United States. It has become a significant pest of Scotch pine in southern Michigan and other states where Scotch pine was widely planted as a Christmas tree species (Rennels 1960, Schuder 1960). Other hosts in the Lake States include Austrian (*Pinus nigra* Arnold), red (*Pinus resinosa* Ait.), Japanese-red (*Pinus densiflora*), jack (*Pinus banksiana* Lamb.), eastern white (*Pinus strobus* L.) and mugho pines (*Pinus mugo*) (Carlson and Wilson 1967). Zimmerman pine moth is part of a phloem-boring complex that includes two other native species that occasionally occur together in Christmas trees, *D. abietivorella* Grote and *D. cambiicola* Dyar (Butcher and Carlson 1962, Carlson and Butcher 1967). Their taxonomy is described in Leidy and Neunzig (1989), Neunzig et al. (1964b), and Neunzig and Merkel (1967).

Zimmerman pine moth is univoltine in Michigan. Adults emerge from July to August, are active in late evening and night, and seem to be attracted to recently sheared or pruned trees (Ruby and Wright 1976, Wright et al. 1975). Eggs are laid singly beneath bark scales or in crevices on the main stem or branches of trees and hatch in about two weeks. First instars do not feed or disperse after emergence, but spin small hibernaculae in which to overwinter. In early April of the next year, larvae emerge, bore into the phloem near the oviposition site, and feed until early August (Carlson and

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Butcher 1967, Carlson and Wilson 1967). Pupation occurs in the larval tunnel behind the pitch mass in July and August, and adults emerge approximately two to three weeks later.

Typical attack sites are at the nodes of the upper three whorls of Christmas trees, on larger branches, or at the base of terminal shoots (Carlson 1965). In spring and early summer, soft, reddish pitch masses indicate larval feeding sites. The pitch mass is a mixture of tree resin and reddish frass that congeal together on the bark surface. Larvae clean their galleries by pushing pitch out one small hole they chew through the bark. Pitch masses are soft and shiny in early summer, but harden and fade to a dull whitish-yellow in late summer. The stem directly below the gallery may constrict or weaken from partial or complete girdling, while tissue above the wound may swell due to accumulation of photosynthates. Severe damage makes trees susceptible to windfall or breakage during harvest and baling, and dead branches or gaps in the foliage reduce Christmas tree grade and marketability (Butcher and Carlson 1962).

Managing this pest in Christmas tree plantations is difficult. Signs of infestation are hard to detect and infestations may go unnoticed until fall, when pitch masses and dead branches are more evident (Yonker and Schuder 1987). Persistent insecticides are typically applied during April, when larvae emerge from hibernaculae to bore into the phloem, but many growers also spray in the summer or fall (Appleby and Randell 1980, Butcher and Carlson 1962). Despite this management effort, dense foliage prevents the thorough pesticide coverage of stems and branches needed to kill larvae. In addition, Zimmerman pine moth dispersal and feeding preference have had no predictable pattern, other than certain trees seem to be attacked more often than others (Rennels 1960, Schuder 1960, Yonker and Schuder 1987). These trees are referred to as "brood trees."

The apparent attractiveness of certain trees to Zimmerman pine moth and the subsequent population build-up on those trees suggest that some varieties of Scotch pine may be more susceptible to attack than others (Harrell 1993, Wright et al. 1975). Given the genetic variability of Scotch pine (Ruby and Wright 1976), its varieties may vary in traits related to defense against phloem-borers like Zimmerman pine moth. Studies on conifer resistance to phloem-boring insects, primarily bark beetles, have shown that trees have several kinds of defense mechanisms. Defenses may include thick bark, a thin phloem layer, increased number and size of resin ducts, or a high rate of resin flow (Lorio 1994, Schroeder 1990, Stroh and Gerhold 1965). Trees also use chemical defenses, such as feeding deterrents or attractants (Dell and McComb 1979, Heikkenen and Hrutfiord 1965, Smith 1963). In addition, resistance may result from changes in tree phenology and nutritional status (Blais 1957, Hanover 1975, Painter 1966).

EUROPEAN PINE SAWFLY DAMAGE AND PHENOLOGY

European pine sawfly (Hymenoptera: Diprionidae) is a univoltine, exotic pest of pines in Michigan. It was introduced to the United States from Europe in 1925 and is now a pest in Christmas tree plantations, nurseries and ornamental trees (Schaffner 1939). Preferred hosts include Scotch pine, red pine, Japanese-red pine, jack pine and mugho pine (Wilson 1965).

Sawfly larvae hatch from eggs embedded in needles in late April or early May in Michigan (Lyons 1964). Shortly after hatching, larvae form feeding groups (colonies) and remain so until pupation. Early instars skeletonize one-year-old needles while older larvae consume entire one-to-three-year-old needles. Sawfly males pass through five larval stadia and females through six; the final instar is an active, non-feeding larva. Pupation typically occurs from mid- to late June when prespinning larvae drop to the ground and spin cocoons in the duff near the tree base. Extended pupal diapause may occur during unfavorable conditions or outbreaks, and may be influenced by hormonal secretions, length of photoperiod, weather and host quality (Kolomiets et al. 1979). Short-lived adults emerge from early September through October, mate and lay eggs in the needles. The crowns of open-grown trees are favored oviposition sites (Kolomiets et al. 1979).

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European pine sawfly feeding can cause both physical and aesthetic damage to Christmas trees. Gregarious feeding can create gaps in the foliage, reduce growth, and during severe outbreaks, cause tree mortality (Wilson 1965). Gaps in the foliage are considered defects and reduce a Christmas tree's appearance and marketability (Lyons 1964). While shearing may correct minor damage, hiding gaps is difficult. European pine sawfly management in Christmas tree production typically includes a foliar insecticide application in May. Although effective at killing sawflies, insecticide applications may not be cost-effective for growers (Kolomiets et al. 1979), and negatively affect beneficial or non-target organisms.

Resistance of certain Scotch pine varieties to European pine sawfly attack has been observed (Ghent 1959, Ruby and Wright 1976). Female sawflies cue in on certain traits when mating and ovipositing, which may contribute to a tree's overall susceptibility (Lyytikainen 1993b, Mopper et al. 1990). These traits may include needle length, width, toughness, twistiness, color, and nutrient or resin content (Hardy and Allen 1975, Olofsson 1989, Wilson 1965). High foliar resin acid concentrations, which vary among Scotch pine varieties, are known to reduce early instar survival (Larsson et al. 1986). Pschorn-Walcher (1991) detected variety-dependent differences in length of pupal diapause in cocoons and in adult emergence. Scotch pine varieties most resistant to attack tend to originate from Scandinavia, while the most susceptible varieties are from central Europe (Wright et al. 1967).

PINE NEEDLE SCALE DAMAGE AND PHENOLOGY

Pine needle scale (Homoptera: Diaspididae) is a serious pest of Scotch pine Christmas trees (*Pinus sylvestris* L.) in Michigan. It is native to North America and feeds on needles of Scotch pine, eastern white pine, mugho pine, spruce (*Picea* spp.) and other ornamental and nursery trees (Dekle 1976, McKenzie 1956, Nakahara 1982). The distribution of pine needle scale has been confused with the nearly identical scale *Chionaspis heterophyllae* (Cooley) (Shour and Schuder 1987, Takagi and Kawai 1967), and scale dispersal has been increased by transport of infested plants (Cumming 1953). Heavy infestations of pine needle scale cause trees to look grayish instead of green, cause premature needle drop, reduce tree vigor, reduce Christmas tree marketability (Cumming 1953, Turner 1930), and eventually cause tree mortality if needles are infested for more than one consecutive year (Johnson and Lyon 1988).

Pine needle scale has two generations per year in Michigan (Cumming 1953, Shour 1986). Overwintering eggs hatch in late May, or phenologically, when lilacs are in bloom (Beard and McLeod 1992). Hatching may occur over two to three weeks, and crawlers disperse by wind or by walking (Brown 1958). First instars, or crawlers, are mobile for up to four days, then settle and begin feeding. Males molt three times and females molt twice before becoming adults. In both generations, adult females remain sessile, and males develop wings as adults and fly to find a mate. Brown (1959) reported that equal numbers of males and females are typically found in populations of pine needle scale. Second generation eggs hatch in late July and develop to adults during late summer. Adults mate, females oviposit, and the eggs overwinter below the female "armor" or "tests" until the following May.

Scale damage to trees is both aesthetic and physical. Green winter foliage is an important trait in Christmas trees, but pine needle scale armor is white and easily visible on needles (Luck and Dahlsten 1974). Scales insert their long stylets through needle stomates and feed on mesophyll tissue, which causes needle discoloration (yellow bands), kills cells at the feeding site, and reduces net photosynthesis (Cumming 1953, Walstad et al. 1973). When many scales feed on the same needle, the needle dies and falls off the branch.

Management of this pest is difficult for Christmas tree growers because crawlers of both generations emerge over several weeks and individual crawlers are only vulnerable to insecticides for a few days (Beard and McLeod 1992, Burks 1994, Cumming 1953). However, dormant oils can be sprayed on overwintering scales to suffocate eggs (Nielsen 1990). Natural enemies regulate low populations, but are susceptible to pesticides sprayed on trees (Luck and Dahlsten 1975). The tinting that growers use to improve foliage color in the fall may also be intended to hide small scale infestations, but the white armor remains visible on foliage, and persists even after scales die (Beard and McLeod 1992).

Few studies have addressed potential host plant resistance to scale insects. Nielsen and Johnson (1973) suggested that tree varieties grown under identical conditions might have different levels of resistance to pine needle scale. Studies with a similar insect, the black pineleaf scale (*Nuculaspis californica* (Coleman)), indicated that populations could adapt to individual host trees, leading to the formation of genetically differentiated demes (Alstad et al. 1980, Edmunds 1973, Edmunds and Alstad 1978, 1981). A study in Israel showed that varieties of *Pinus halepensis* (Mill.) differed in resistance to the Israeli pine bast scale (*Matsucoccus josephi* Bodenheimer et Harpaz) (Mendel 1984). Another study testing the effect of location and age of *Euonymus* varieties on the euonymus scale (*Unaspis euonymi* (Comstock)), found one variety that was consistently more infested (Brewer and Oliver 1987).

MATERIALS AND METHODS

Study site

The field site located at the Michigan State University W. K. Kellogg Experimental Forest (Kalamazoo County, Michigan) was hand-planted with 27 Scotch pine varieties in 1987. The 0.8 ha field was bordered by mature white spruce (*Picea glauca* (Moench) Voss) and Scotch pine. Each variety was planted in two adjacent rows in a north-south direction with 6 x 6 ft (1.8 x 1.8 m) between trees. Spacing increased in some areas of the field as trees were sold or culled due to insect and disease damage. Trees were sheared each July and herbaceous vegetation was mowed monthly during the growing season. Pesticides were not sprayed on or near the field during this study.

Scotch Pine Varieties

Four Scotch pine varieties were chosen for this study: Pike Lake Improved (var. *aquitana*), Land O' Pine (var. *hercynica*), Belgium (var. *haguenensis*) and Riga (var. *rigensis*). These varieties were selected based on physical differences, range of geographic origin, and the results of previous research (Ruby and Wright 1976, Tobolski and Hanover 1971, Wright et al. 1975). Traits that differed among these varieties included needle length, winter needle color and growth rate (Table 1). Twelve trees of each variety were randomly chosen for the study.

Tree Characteristics

Measurements taken in 1994 included tree height, basal diameter, stem diameters between the top second and third whorls and the third and fourth whorls, percentage needle moisture, amount of needle twist, and percentage of total foliar nitrogen. In 1995, tree height, basal diameter, diameter at breast height (1.4 m), rate of stem resin flow, percentage needle moisture, amount of needle twist, and percentage of total foliar nitrogen were measured.

To test the rate of resin flow in each Scotch pine variety, each experimental tree was artificially wounded using methods of Lorio and Sommers (1986). Wounds were created by pushing a 1.3 cm arch punch into the phloem, twisting the punch to finish the cut and removing the bark. A small triangular notch was cut beneath the wound to direct resin flow. An aluminum tray was set into a horizontal cut below the notch and was secured to the tree with two push pins. The resin was channeled into a 15 ml polystyrene graduated conical tube held to the tree with electrical tape. All materials were removed from trees after the sampling was complete. Resin was sampled for 24 h on 26 May, 14 June and 18 July 1995. In May and June, only one wound was made on the middle south and south-east sides of each tree, respectively, to prevent interference with Zimmerman pine moth development. In July, after Zimmerman pine moth larvae had completed feeding, wounds were made on the east, northeast, north and northwest sides of each tree, and results were averaged per tree. Sampling occurred on days with no precipitation and began after 9 am for each sampling period.

Needle biomass and percentage moisture were calculated by collecting needles and measuring fresh and dry needle weights (40 one-year-old needles/tree on 30 July and 60 one-year-old needles on 6 September 1994; 20 one-year-old needles/tree on 12 May, 26 May, 8 June and 15 September 1995). Needles were removed from the upper half of the east side of the tree, placed in paper bags, transported in a cooler to the lab and weighed. Needles were dried to a constant weight for 48 h at 43 °C in a drying oven and weighed again. Percentage moisture was determined by dividing wet weight by dry weight and multiplying by 100. Length of 20 randomly selected needles collected from each tree in September was measured in both years, and 10 needles randomly selected from each tree were ranked for amount of twist (1/4 turn = 1, 1/2 turn = 2, 3/4 turn = 3, and 1 turn = 4).

To test the amount of total foliar nitrogen potentially available to herbivores, shoots were collected from trees in early November of both years (Leaf 1990). In 1994, current and one-year-old shoots on the east side in the upper third of the crown of each experimental tree were cut, placed in individual paper bags, transported to the laboratory in a cooler, then frozen at 4 °C. The analysis was conducted separately for both needle ages on each tree. In 1995, current-year needles were again cut from branches in the upper third of the crown on the east side of trees. Needles were oven-dried for over 48 h at 60 °C, then ground up and stored in vials until further testing. In 1995, three samples from each tree were analyzed, and results were averaged. Ms. Jill Fisher from the Forestry Department, Michigan State University analyzed total nitrogen by flash combustion using the Carlo Erba 1500 Series II Nitrogen Analyzer (Fisons Instruments, Massachusetts, USA).

Weather Monitoring

Personnel at Kellogg Forest maintained daily records of maximum and minimum temperatures and precipitation. Temperature was recorded with a Belfort hygrothermograph (company, city) and precipitation was measured with a Forest Service type rain gauge. Degree days were calculated by determining the mean temperature of the day and subtracting the base temperature (50 °F) (Agnello et al. 1993). The starting date was 1 January 1994 and 1995.

Insect Rearing

Zimmerman Pine Moth. Scotch pine trees infested with Zimmerman pine moth larvae were collected from five plantations in southern Michigan in April 1994 and May 1995 and transported to the laboratory. Stems and branches were examined for larval activityby removing bark from infested areas with a knife and forceps. Larval galleries were carefully excavated until the larvae were found. Single larvae were placed in plastic containers with small chunks of phloem and bark, and were transported to Kellogg Forest the following day. A piece of phloem with a larva on it was carefully placed next to the bark of the experimental tree and was secured to the main stem with thin nylon mesh. The mesh cage was wrapped around the tree between two whorls of branches and fastened firmly on both ends with electrical tape. In 1994, two larvae were caged on each tree between different whorls, and in 1995 one larva was caged per tree. Larval handling was minimized to reduce stress.

European Pine Sawfly. First instars were collected from wild populations in three areas in Ingham County, Michigan, and transported to Kellogg Forest on 1 May 1994 and

5 May 1995. Since European pine sawfly larvae are gregarious, 10 larvae were randomly selected and placed in a nylon mesh cage on each tree. One cage was positioned on the east side of each tree at mid-canopy, around a large branch containing old and new shoots. Cages were closed at both ends with electrical tape and larvae were allowed to develop. Adverse weather was not a problem in 1994, but in 1995 all caged sawfly larvae, larvae from overwintering eggs, and local populations of wild larvae under observation died on 10 May during a heavy rainstorm. A new cohort of second instars was located and placed in cages on 15 May, as previously described.

Pine Needle Scale. Before introducing scales to experimental trees at Kellogg Forest, I collected several Scotch pine branches infested with pine needle scale from three local Christmas tree fields and returned them to the laboratory. Using a dissecting scope and micrometer, I measured lengths and widths of the waxy armor and soft scale bodies, counted the number of eggs laid by each female, and the number of scales on each needle. The total number of scales measured was 205. I tried to determine if the number of scales feeding on a needle was related to scale fecundity, permitting me to estimate the number of crawlers hatching in the first generation.

Branches with female scale bodies were collected from Scotch pine trees at private Christmas tree plantations in Ingham County in early May 1994. In May, 20 fecund females of similar size still attached to needles were placed on foliage in nylon mesh cages located on the lower west side of each experimental tree. Crawlers hatched from the infested introduced needles and moved onto living needles on experimental trees in late May. This infestation process was repeated in 1995, but 40 female scales instead of 20 were fastened to foliage in mid-May to increase the sample size of scales on each tree.

Insect Survival

Zimmerman Pine Moth. After the initial infestation, larvae were checked on 8 June, 23 June, and 1 July 1994, and 12 June, 23 June, and 4 July 1995 for evidence of larval establishment on host trees. Since larval instars could not be identified in the field, larvae were classified as "early" at the time of the first check, "middle" at the second check and "late" at the last check. Caged larvae were considered alive when pitch or frass was present and dead when cadavers were found or in the absence of pitch masses. When cadavers or parasitoids were found within pitch masses, they were removed using forceps, placed in plastic containers and frozen. Specimens were later sent to specialists at the USDA-ARS for identification. Checks for pupae occurred twice a week until all caged Zimmerman pine moth were accounted for. Pupae were kept in plastic containers until adults emerged.

Scotch pine resistance to Zimmerman pine moth was evaluated by computing percentage larval survival at three stages, length of development period (days and degree days), growth rate (mg/degree day), percentage pupal survival (pupation to adult emergence), pupal fresh weight (mg), and adult fresh weight (mg). Survival among varieties was analyzed by hand using Cochran's Q test (Zar 1996), then pooled and organized into a cohort life table (Krebs 1985). To measure larval growth rate, the unit mg/degree day was used rather than mg/day to avoid possible confounding effects of increasing temperatures during the growing season.

Neuter values (sex effect standardized) were determined for development period, growth rate, pupal and adult weights by converting values for individual males to female-equivalent values (Haukioja and Neuvonen 1985). For example, the weight of an individual male was changed to its neuter value by multiplying the male's weight by the ratio of mean female weight to mean male weight on each Scotch pine variety. This procedure was done to minimize sex-based variability in the data analysis, and it resulted in larger sample sizes.

European Pine Sawfly. Larval survival was monitored weekly from May until pupation began, then survival was monitored daily until the end of pupation. Development period (day and degree day) from the time of caging until pupation was determined for larvae on each tree. Growth rate was determined by dividing pupal weight by the number of accumulated degree days. Neuter values (sex effect standardized) were computed for pupal weight, adult weight, development period and growth rate (Haukioja and Neuvonen 1985).

In 1994, pupae lying at the bottom of cages were vulnerable to parasitism and predation. In 1995, pupae were placed in a small nylon mesh pouch and hung inside the cage with a wire twist tie. Pupae were removed from pouches at the end of August, when little parasitism was expected, and left in the foliage or at the bottom of cages. After adult emergence, the remaining pupae were dissected to determine pupal fates. Parasitoid specimens were collected from cages and sawfly pupae, and were later identified to species by a specialist at the USDA-ARS.

Number of needles consumed and amount of frass produced in each cage were determined after pupation to minimize larval disturbance. One-year-old needles missing from the shoot with recent wounds at the fascicle were considered to be eaten by larvae. Frequent visits to each cage disturbed accumulated frass and occasionally caused a small amount to slip through the small mesh holes; I assumed that each cage lost a similar amount. The collected frass was sifted and all needles, dead insects and exuviae were removed. Frass was dried for 48 h at 43 °C, then weighed. Since the greatest amount of feeding occured in later instars, measurements of needle biomass consumption and frass production for each cage were divided by the number of larvae surviving through the final instar. This calculation allowed me to make comparisons among the amount of needle biomass consumed, pupal weight, development time and growth rate.

Pine Needle Scale. Surviving pine needle scales were counted once in June and July, twice in August, and once in October of both years. Live and dead scales were determined based on the color and condition of the scale armor, presence of fungus on scale bodies, and evidence of parasitism or predation (Luck and Dahlsten 1975). The accuracy of counting scales varied due to extended crawler emergence and sampling error, so only the data with a high degree of confidence are presented. One coccinelid found feeding on eggs was identified by a specialist at Michigan State University.

As second generation pine needle scale survival was determined in the lab, I also tried to quantify needle damage by scales. I recorded the number of female scales causing needle necrosis from their feeding, the location of the female on the needle surface (flat or round side), and whether needle necrosis was more prevalent depending on where females were located.

Insect Fecundity

Zimmerman Pine Moth. Checks for pupae were done twice a week from early July until late August. When live pupae were found, they were removed from pitch masses, weighed in the laboratory within 12 h and placed in plastic containers until adult emergence. Adults were kept alive in 1995 for 24 h to increase the likelihood of egg production, then were frozen until dissections could be made. Adults were weighed and sexed at the laboratory. Female adults were dissected and number of eggs was determined.

European Pine Sawfly. Cages were checked daily from the first day of pupation in late May to early July. New pupae were removed from cages, transported to the laboratory and weighed within 12 h. Pupae were returned to their cage after all larvae from that cage had pupated. Adults emerged in the fall, mated, oviposited and died in the cages. Several wild males were observed landing on cages, apparently attracted by female pheromones, but no mating through the mesh was observed. I assumed that virgin and mated females could produce similar numbers of eggs based on previous reports (Benjamin et al. 1955, Griffiths 1959, Hardy and Allen 1975). Number of eggs laid in each cage was counted and related to number of ovipositing females and number of needles with eggs. In 1994, sawfly eggs were left to overwinter on the trees, but branches were cut and brought to the laboratory in 1995.

Pine Needle Scale. After the initial infestation, scales were allowed to develop under field conditions. Branches were cut off the experimental trees in late October in both years and brought to the laboratory. Infested needles were removed from branches and stored in plastic bags in the freezer. During the winter, the number of eggs laid per female was counted under a dissecting scope. The number of females examined for fecundity varied, depending on survival on each tree. When possible, fecundity was determined for 20 females from each infested branch in 1994, and 30 females in 1995. To count eggs, an infested needle was held with forceps and the female armor was carefully pried up on one side with a probe. Number of live eggs laid under the armor was counted. Live eggs were oval and bright red, dead eggs were brown, and pieces of white chorion gave evidence of hatched or predated eggs. Evidence of parasitism and third generation egg hatch were noted for each adult female in 1995.

Statistical Analysis

Measurements of tree growth, insect survival and fecundity for each year were tested for homogeneity of variance with the Levene test (JMP for Windows, Version 3.1, SAS Institute 1995). The Shapiro-Wilk test was used to test for normality of data. A one-way analysis of variance (ANOVA) was used to determine if results differed by variety when data were normally distributed and variance was homogeneous (Zar 1996). Given non-homogeneous variances, the Welch statistic was used to test the significance of the ANOVA. The [log (x+1)] transformation was applied to all insect survival and fecundity data to adjust for non-normality, but tree measurements did not require transformation. All ANOVAs significant at the $p<0.05$ level were tested with Tukey's Honestly Significant Difference multiple comparisons test to further evaluate differences among varieties. When two variables were normally distributed, Pearson's product-moment test was used to analyze correlations. If one or both variables were not normally distributed, Spearman's nonparametric test was used to analyze the significance of correlations. The relationship between pupal weight and fecundity for Zimmerman pine moth and European pine sawfly was tested using regression analysis. Backward-stepping multiple regressions were used to predict insect survival and fecundity from tree growth variables in both years.

RESULTS

Tree Characteristics

From 1994 to 1995, Belgium and Riga trees had significantly greater basal diameter growth than Land O' Pine and Pike Lake Improved trees (F=9.43, df=3, *p*<0.001) (Table 2). For all trees, mean basal diameters ranged from 6.4 to 9.7 cm in 1994, and grew an additional 1.8 to 3.3 cm in 1995. Belgium and Pike Lake Improved trees had the largest stem diameters in 1994 (F=21.11, df=3, *p*<0.001), but Belgium trees were tallest (F=38.99, df=3, *p*<0.001). In 1995, stem diameters were significantly smaller in Riga trees than in the other three varieties (F=13.86, df=3, *p*<0.001), and tree height was significantly greater in Belgium trees (F=19.85, df=3, *p*<0.001). Mean tree height ranged from 192 to 260 cm in 1994, and trees grew in height between 12 to 20 cm during the following year. However, tree height was reduced by annual shearing, and height growth from 1994 to 1995 was not significantly different among varieties.

Rate of resin flow was variable both within and among varieties (Figure 1). No significant differences among varieties occurred on any of the three sampling dates, or when the results from all three sampling dates were averaged and analyzed. Basal stem diameter was significantly and negatively associated with the amount of resin flowing on 14 June 1995, indicating that smaller stem diameters had higher rates of resin flow (Table 3).

In 1994, needle length was significantly shorter for Riga and Pike Lake Improved than for Belgium and Land O' Pine (F=5.42, df=3, $p<0.01$) (Table 2). Percentage moisture in current-year needles on Riga was significantly lower than in needles from the other varieties (F=15.51, df=3, $p<0.001$), but moisture in one-year-old needles did not differ significantly among varieties. Percentage nitrogen in current-year needles and needle twist did not differ among varieties. However, percentage nitrogen in one-year-old needles was significantly higher in Belgium trees than in Land O' Pine trees (F=2.96, df=3, $p<0.05$) (Table 2). Significant correlations were found among tree height, stem diameter, basal diameter, percentage needle moisture, needle length, percentage nitrogen in needles and needle twist (Table 3).

In 1995, Riga and Pike Lake Improved had the shortest needles and Belgium had the longest needles (F=8.16, df=3, $p<0.001$) (Table 2). In terms of foliage density, Pike Lake Improved had significantly more needles on 5 cm of shoot than the other varieties (F=2.76, df=3, $p=0.05$). Percentage needle moisture was inconsistent among sampling dates. No significant differences were detected in early May, but in late May, percentage foliage moisture was significantly higher on Riga than on Land O' Pine trees (F=3.95, df=3, $p<0.05$). In early June, percentage foliage moisture was significantly higher on Land O' Pine than on Belgium trees (F=2.77, df=3, $p<0.05$). Percentage nitrogen in current-year needles and needle twist did not significantly differ among varieties (Table 2), and percentage nitrogen was not significantly correlated with any other tree measurement. Significant correlations were found among tree height, stem diameter, basal diameter, percentage needle moisture, length and density on shoots (Table 3).

Weather Monitoring

Winter and summer temperatures in 1994 were cooler than in 1995 at Kellogg Forest (Table 4). Extremely cold temperatures occurred from 15 January to 20 January 1994, when the maximum daily temperature was -12.2 °C and the minimum daily temperature dropped to -29.4 °C. Temperatures in 1995 warmed up quickly in the spring and remained hot all summer. Monthly precipitation totals were similar in both years.

Insect Survival

Zimmerman Pine Moth. I did not detect any significant differences in larval or pupal survival among Scotch pine varieties in 1994 (Figure 2). Percentage survival dropped uniformly in all varieties during the middle larval instars, then survival remained relatively constant from the last instar through adult emergence. Survival data from the varieties were pooled and organized into a cohort life table (Table 5). Only 27% of the larvae survived to the adult stage. Almost half of the mortality occurred before larvae reached the middle instars. Overall survival of Zimmerman pine moth during each life stage was not significantly different when varieties were pooled and when larvae caged between different whorls were tested (Table 6).

Again, in 1995, no significant differences in larval or pupal survival were detected among varieties (Figure 2). Although early larval survival was high, survival from the middle to late instars rapidly dropped and then stabilized through to adult emergence. After data from varieties were combined into a cohort life table, I determined that only 8% of the larvae originally caged on trees survived to the adult stage (Table 5). Over two-thirds of the mortality had occurred before larvae reached the late instars. Overall survival of Zimmerman pine moth during each life stage was again not significant when varieties were pooled (Table 6).

The factors causing mortality to Zimmerman pine moth larvae in 1994 included parasitism, fungal infection, and unknown factors. Some of the 21 early larval deaths categorized as "unknown" may have resulted from poor establishment after introduction to the trees (Table 5). The parasitoid wasps that attacked Zimmerman pine moth larvae were *Exeristes comstockii* (Cresson) (Hymenoptera: Ichneumonidae) and *Hyssopus rhyacioniae* (Gahan) (Hymenoptera: Eulophidae), as identified by Dr. John Luhman of the Minnesota Department of Agriculture, Plant Protection Division, and M. E. Schauff of the USDA Systematic Entomology Laboratory. Parasitized larvae were found within pitch masses as early as 22 June 1994. Of the 15 Zimmerman pine moth larvae known to be parasitized, *E. comstockii* killed 10 of the larvae and *Hyssopus rhycioniae* killed 5 larvae. *Exeristes comstockii* laid one to four eggs on Zimmerman pine moth larvae, which developed to the adult stage within the pitch masses. Those that attacked larvae later in the summer overwintered as adults inside pitch masses and emerged in the spring. I also found larvae infected with the fungus *Hirsutella nodulosa* (Petch), but had confused symptoms of infection with evidence that larvae had drowned in pitch in feeding tunnels. Dr. Richard Humber from the US Plant, Soil, and Nutrition Laboratory provided the species identification. The fungus accounted for eight larval deaths, in addition to some larvae not developing diagnostic symptoms and were considered "unknown." It is possible that Zimmerman pine moth larvae escaped from cages and re-entered the phloem in other areas on trees. Single exit holes were chewed through the mesh used for cages, and I observed several larvae from wild populations exiting fresh pitch masses and boring into new areas on stems of the experimental trees. Two pupae died from being injured during removal from host trees.

In 1995, factors causing mortality to Zimmerman pine moth again included parasitism, infection by *Hirsutella nodulosa* (Petch), and unknown factors. Parasitized Zimmerman pine moth larvae were found within pitch masses beginning 22 July 1995. *Hyssopus rhyacioniae* was the primary parasitoid throughout the summer, killing six of the seven parasitized Zimmerman pine moth larvae (Table 5), but *E. comstockii* did kill one Zimmerman pine moth larva. *Hyssopus rhyacioniae* had two or more generations during the year, and its offspring completed development within a month after hatching from eggs. I found 1 to 9 eggs laid on Zimmerman pine moth larvae by *H. rhyacioniae* adults during the summer of 1995. These adults mated, laid eggs, the pupae overwintered and finished development in early spring. Two larvae were obviously infected with the fungus *H. nodulosa* in 1995, but some larvae that died from "unknown" causes may have also been infected without the fungus being detected. Several unknown mites were found on or near Zimmerman pine moth larvae infected with *H. nodulosa*, but were not recognized at that time as being potential vectors of the fungus and were not identified. One pupa died from being injured during removal from its host tree.

In 1994, after being caged, larvae fed on phloem until pupation, which occurred between 15 June and 1 August. Adult emergence lasted from 26 June to 17 August 1994. Mean development of healthy larvae lasted from 81 to 95 days (861 to 1,094 degree days); means did not significantly vary among Scotch pine varieties (Table 7). Mean neuter pupal weights ranged from 85 mg to 95 mg, and mean adult weights ranged from

40 to 53 mg. Growth rate, pupal and adult weights also did not differ significantly among varieties. However, pupal weight was significantly and positively correlated with development period, indicating that larvae that fed longer had higher pupal weights (Table 8). Pupal length was significantly correlated with pupal weight. Stem diameter between the upper second and third whorls on trees was positively correlated with pupal weight and development period (days and degree days), which suggested that stem or phloem thickness in areas where larvae fed could affect larval growth and development (Table 8).

In 1995, larval development on experimental trees lasted 91 to 100 days, or 1682 to 1952 degree days until pupation (Table 7). Pupation lasted from 20 June to 1 August, and adults emerged from 6 July to 17 August. The time required for the development of each life stage appeared to be constant each year despite differences in degree day accumulation. No significant differences were found among varieties for development period (days or degree days), growth rate, pupal or adult weight in 1995 (Table 7). Pupal length was again significantly correlated with pupal weight (Table 8).

European Pine Sawfly. Survival of European pine sawfly larvae, pupae and adults varied among Scotch pine varieties, but differences were not always significant at each life stage. In 1994, sawfly larvae were present in the field from approximately 26 April to 12 June 1994, pupation began on 6 June, and adults were present from early September to mid-October. Percentage survival to the adult stage was significantly higher for sawflies reared on Land O' Pine or Pike Lake Improved than for larvae reared on Riga trees ($F=2.89$, $df=3$, $p<0.05$) (Figure 3). Overall survival did not significantly differ among Belgium, Land O' Pine and Pike Lake Improved; these three varieties were therefore pooled and compared to Riga in cohort life tables (Table 9). Percentage mortality was greatest during the period between the first and third instars and during pupation, but mortality was 21% higher for sawflies on Riga than on other varieties. Early larval mortality may have resulted from an inability to establish colonies or feeding sites. Only 39% of all pupae survived to become adults, while 2% emerged from pupae poorly developed, 30% were parasitized, 17% were preyed upon, 3% had entered extended diapause, and 9% died of unknown causes. The most common pupal parasitoid was *Pleolophus basizonus* (Gravenhorst) (Hymenoptera: Ichneumonidae), and only single parasitoids larvae were found developing within each sawfly cocoon.

In 1995, sawfly larvae began hatching from eggs on 1 May and were active in the field until 24 June 1995. Pupation began on 4 June, and adults were present from September to mid-October. Degree day accumulation as determined by Kellogg Forest personnel was more rapid in 1995 than in 1994 due to higher temperatures in early summer (Table 4). It has been shown that with higher summer temperatures, European pine sawfly eonymphal diapause in cocoons is intensified (Knerer 1983). This apparently resulted in more rapid sawfly larval development and may have contributed to later adult emergence.

In 1995, survival during the third instar was lowest for sawflies caged on Riga and highest on Belgium and Pike Lake Improved (F=3.32, df=3, $p<0.05$) (Figure 3). Survival to the last instar, pupal and adult stages did not significantly differ among varieties. Again, data on sawfly survival for varieties Belgium, Land O' Pine and Pike Lake Improved were pooled and compared to Riga in cohort life tables (Table 10).

Percentage mortality during the first through third instars and pupation was 9 to 13% higher on Riga than on the other varieties. By 27 October 1995, 76% of all pupae survived to become adults, while 2% emerged from pupae poorly developed, 5% had reached the adult stage and died in the cocoon, 2% had entered extended diapause, and 11% died of unknown causes. Overall survival was higher in 1995 than in 1994 because in 1995, first instars killed in a heavy rainstorm were replaced with second instars, and I protected pupae from parasitism by suspending them in mesh fabric within cages.

I expected to find differences in needle consumption and sawfly growth rate given the differences in survival. However, in 1994, there were no significant differences among varieties in needle biomass consumption or frass production (Table 11). Larval growth rate was significantly lower (F=5.56, df=3, $p<0.01$) and development period (days) (F=4.06, df=3, $p<0.01$) and (degree days) (F=4.68, df=3, $p<0.01$) was significantly longer for sawflies on Riga, which suggests that compensatory feeding occurred. Needle biomass consumed was positively correlated with development period (degree days); larvae that fed longer before pupation consumed more needles (Table 12). Percentage nitrogen and percentage moisture in needles were not significantly correlated with larval feeding or survival measurements. Backward-stepping multiple regressions were able to significantly predict larval development period using degree of twist of one-year-old needles and tree height as predictors in 1994 ($r^2=0.23$), but were unable to predict biomass consumption or survival (Table 13).

In 1995, sawflies caged on Riga consumed significantly more needle biomass than sawflies on Land O' Pine or Pike Lake Improved (F=4.35, df=3, $p<0.01$) (Table 11). This may indicate that larvae reared on Riga again did some compensatory feeding.

Frass production did not significantly differ among sawflies on the four varieties. Larval growth rate was significantly lower on Land O' Pine and Pike Lake Improved than on Belgium (F=5.73, df=3, $p<0.001$). Development period (degree days) was significantly longer for sawflies on Land O' Pine than on Belgium (F=2.82, df=3, $p<0.05$), indicating that compensatory feeding may have occurred on Land O' Pine. Larval development period lasted from 28 to 40 d. Larval development period (days and degree days) and percentage foliar nitrogen were positively correlated with pupal weight (Table 12). Percentage foliar nitrogen was not significantly correlated with other larval feeding or survival measurements. Backward-stepping multiple regressions were able to significantly predict larval development period using degree of twist of current-year needles and tree height as predictors in 1995 ($r^2=0.19$), but did not significantly predict needle biomass consumption or sawfly survival (Table 13).

Pine Needle Scale. Before beginning the main study, I measured armor of 205 female scales from wild populations to determine some basic information. On average, the soft female body was 1.06 mm (±0.02) long and 0.48 mm (±0.01) wide. Mean armor size was 2.27 mm (±0.03) long and 0.90 mm (±0.01) wide. Mean number of live eggs laid per female was 18.3 (±0.8). I found a strong positive association between female armor length and the number of eggs laid per female in 1994 (Table 14). Armor length was correlated with body length, needle width and needle length. Body length was negatively associated with scale density. Fecundity and scale density were not significantly correlated with needle length nor width.

Scale survival differed from the first to second generations, but was difficult to accurately determine in the field. Luck and Dahlsten (1975) also had difficulty in accurately assessing field scale densities, reducing the likelihood of detecting significant differences. In 1994, first generation pine needle scale survival did not significantly differ among varieties of Scotch pine (Table 15). From the twenty females originally used to infest experimental branches, only 15 to 28 crawlers per tree survived through June. The population increased in the second generation to between 77 and 293 scales per tree. Survival of second generation scales caged on Belgium trees was significantly lower than for scales caged on Pike Lake Improved trees (F=3.05, df=3, p<0.05) (Table 15). Using a backward-stepping multiple regression, I was unable to significantly predict scale survival using the tree traits measured in this study (Table 16). However, second generation survival was significantly correlated with percentage needle moisture in August and basal diameter, but not tree growth rate (Table 14). First and second generation survival were also correlated, indicating that if first generation survival was high, survival of the second generation should be high also. Rates of parasitism in the field and the species of parasitoids could not be determined.

In 1995, survival of first generation scales reared on Riga trees was significantly higher than for scales on Land O' Pine trees (F=3.67, df=3, p<0.05) (Table 15). Survival of second generation scales reared on Riga trees was significantly higher than on Belgium and Land O' Pine in early August (F=3.48, df=3, p<0.05) and mid-October (F=4.87, df=3, p<0.05). Only 48 to 71 percent of female scales still attached to needles in October had laid eggs. Using a backward-stepping multiple regression, basal diameter and percentage needle moisture in May significantly predicted second generation survival

(Table 16). Second generation survival was significantly correlated with tree height, stem diameter, basal diameter growth rate, and percentage needle moisture in May (Table 14). These associations suggested that tree vigor affected scale survival. However, first and second generation scale survival were not correlated, indicating that an external factor (e.g., predation, parasitism) was more critical to survival than host factors, or something I did not measure.

In 1995, causes of scale mortality included fungal infection, parasitism, or predation. Some of the females who were still alive in October, but had not laid eggs may not have been fertilized. Rates of parasitism in the field and parasitoid species were not determined. I found coccinelid larvae and adults, identified as *Coccidophilus marginatus* (LeConte) by Dr. Richard Leschen at Michigan State University, feeding on natural and study populations of pine needle scale. Adults chewed holes in female armor and fed on eggs and female bodies in early spring and late summer. When infested branches were removed from experimental trees and brought to the lab in October, *C. marginatus* larvae of several instars were found beneath female scale armor, consuming eggs.

I did not find any significant differences in location of scale feeding and damage among the four varieties in 1995. Between 71 and 88 percent of female pine needle scales were found on the flat side of needles (inner fascicle), while the rest were found on the round outer side of the needle. Yellow bands of necrotic tissue resulted from the feeding of 52 to 72 percent of the females examined. Of those females causing cell necrosis, 76 to 92 percent of the damage was from females feeding on the flat side, and 8 to 24 percent of the damage resulted from females feeding on the round side of needles.

Insect Fecundity

Zimmerman Pine Moth. Fecundity did not significantly differ among varieties in 1995 (Table 7). Of the 10 females dissected, the number of eggs per female ranged from 10 to 44. Female survival was too low under field conditions to determine differences among varieties. However, fecundity was positively correlated with adult weight (Table 8) and could be predicted by pupal weight (Figure 4). In 1994, pupal weight was positively correlated with development period. The significant correlation between pupal weight and tree stem diameter where larvae were caged in 1994 may also suggest that tree growth or vigor affected Zimmerman pine moth fecundity (Table 8). In addition, backward-stepping multiple regressions using tree variables as predictors significantly predicted pupal weight in both years (Table 17). In 1994, stem diameter, tree height and percentage foliar nitrogen were significant predictors (r^2=0.62), while in 1995, basal diameter, percentage foliar nitrogen, tree height and rate of resin flow from May to June predicted a significant proportion of Zimmerman pine moth pupal weight (r^2=0.95).

European Pine Sawfly. European pine sawfly pupal weight and fecundity on the four varieties were measured (Table 18), although few females survived to the adult stage. Sawflies caged on Riga had lower pupal weight than on Belgium and Pike Lake Improved (F=3.53, df=3, p<0.05), but other variables did not significantly differ among varieties. The number of eggs laid per female ranged from 14 to 59, and the number of eggs laid per needle ranged from 3 to 8. I found significant correlations between pupal weight and fecundity, needle biomass consumption and fecundity, and between tree growth and fecundity (Table 12). Backward-stepping multiple regressions did not significantly predict pupal weight using any of the measured tree characteristics in 1994.

In 1995, females caged on Riga laid fewer eggs compared to the other varieties (F=4.66, df=3, $p<0.01$) (Table 18). However, pupal weights were lower for females caged on Land O' Pine and were highest on Belgium (F=4.12, df=3, $p<0.01$). The number of eggs laid per female ranged from 3 to 114 in 1995. Similarly, the number of eggs laid per needle ranged from 1 to 8. I also detected significant correlations among pupal weight, development period (days and degree days), percentage foliar nitrogen, and fecundity (Table 12). A regression between pupal weight and number of eggs laid per female was statistically significant (Figure 5), indicating that heavier pupae were more fecund as adults. Backward-stepping multiple regressions did not significantly predict pupal weight using any of the measured tree characteristics.

Pine Needle Scale. I detected differences in scale fecundity among varieties in 1994 (Table 15). Number of eggs laid per female ranged from 15 to 48. Scales reared on Pike Lake Improved laid more eggs per female than scales on the other varieties (F=6.79, df=3, $p<0.01$). Using a backward-stepping multiple regression, I could not significantly predict second generation pine needle scale fecundity with the tree traits measured in this study. Fecundity was not correlated with percentage foliar nitrogen or percentage moisture content.

In 1995, females on Land O' Pine had significantly lower fecundity than females on the other varieties (F=4.97, df=3, $p<0.05$) (Table 18). The number of eggs laid per female ranged from 17 to 55 on trees. Using a backward-stepping multiple regression, I significantly predicted second generation pine needle scale fecundity with percentage needle moisture in May and September and percentage foliar nitrogen (Table 16).

DISCUSSION

Differences Among Varieties

The four Scotch pine varieties used in this study differed in traits potentially affecting susceptibility to insect pests, including tree height, stem diameter, needle length, needle density, percentage nitrogen and moisture in needles, and height and basal diameter growth rates. The faster basal diameter growth rate in both Riga and Belgium trees was unexpected. Riga trees typically had smaller stem diameters than the other three varieties, which suggested that growth rates would be slower as well. Perhaps in the reportedly faster growing varieties, like Belgium and Land O' Pine, growth rates had declined over time, which comparatively increased the relative growth rate in Riga. Greater needle density in Pike Lake Improved trees may have compensated for less leaf area in short needles (Mooney et al. 1988, Sadof and Raupp 1991).

Some other tree variables, including growth and differences in monoterpene concentration and resin acids, were previously studied in several Scotch pine Christmas tree varieties in Michigan. Among the four varieties, Pike Lake Improved (var. *aquitana*) and Riga (var. *rigensis*) were short and of similar heights, Land O' Pine (var. *hercynica*) was moderately tall, and Belgium (var. *haguenensis*) was the tallest variety with the fastest growth rate (Ruby and Wright 1976, Wright et al. 1966). From foliage color ranks, southern European varieties (e.g., Pike Lake Improved) were greenest, Scandinavian varieties (e.g., Riga) were yellowest and central European varieties had intermediate hues of green (Ruby and Wright 1976, Wright et al. 1966). Needles were longest in Belgium, moderately long in Land O' Pine, short in Riga, and shortest in Pike Lake Improved (Ruby and Wright 1976, Wright et al. 1966). In general, Scandinavian varieties (e.g. Riga) had lower concentrations of cortical monoterpenes (Tobolski and Hanover 1971), higher concentrations of resin acids, lower oleoresin pressure and smaller resin canal cross-sectional areas than the other varieties (Bridgen and Hanover 1982). Nutrient differences in foliage among varieties were apparent, but statistical significance was not reported (Ruby and Wright 1976).

The correlations among tree variables indicated that most of the traits measured were interrelated. For example, shearing may reduce tree height growth rate by removing shoots and promoting lateral bud growth (Hill 1989, Langstrom et al. 1989), but it does not eliminate the genetic effects contributing to varietal differences in growth rate, considering the strong correlations among stem diameter, basal diameter and tree height. Foliar moisture and nitrogen content are known to be correlated (Mattson 1980), but I also found strong correlations between stem diameter and both foliar moisture and nitrogen content. A negative correlation between basal diameter and rate of resin flow in June suggested that resin flow decreased in trees with larger diameters, although this association was not consistent. Even needle length was associated with tree height, stem diameter and needle density. Understanding the interrelatedness of these tree variables may contribute to understanding relationships between insect performance and variety differences.

Differences in Variety Resistance to Zimmerman Pine Moth

Wright et al. (1975) suggested that fast-growing Scotch pine varieties from central Europe (e.g., Belgium and Land O' Pine) were most susceptible to Zimmerman pine moth infestation, northern European varieties (e.g., Riga) were moderate and southern European varieties (e.g., Pike Lake Improved) were most resistant in mixed plantings. These conclusions were based on observations of natural attack rates without considering the survival or fecundity of Zimmerman pine moth reared on trees of each variety. Our results did not indicate that Zimmerman pine moth survival and fecundity differed significantly among the four varieties. Therefore, we hypothesized that host selection may be primarily determined by females during oviposition. Adults may be influenced by cues such as volatiles emitted from resin at the site of larval feeding or shearing wounds. Once adults deposit eggs and larvae develop in trees, parasitism and fungal infection become important factors in larval survival, apparently outweighing potential host plant differences.

Primary host selection by adult moths attracted to recently sheared or pruned trees has been proposed by researchers studying other *Dioryctria* species (Asher 1970, Jactel et al. 1994, Wright et al. 1975). Branch wounds on sheared Christmas trees need several weeks to heal, and I suspect (but have no data for) that volatiles from sheared trees may attract Zimmerman pine moth females searching for an oviposition site. I also suspect that emerging adults may be affected by host stimuli (Jaenike 1988), such as volatiles in pitch masses, which later attract adults to previously infested or wounded trees. If adults still inside the pitch masses were forced to leave through the small exit hole made by larvae, and were sensitive to the volatiles upon emergence, it seems possible that adults would return to similar conditions when mating and ovipositing. Examples of early adult host learning behavior in several insect orders are cited by Jaenike (1988). This could pose problems for Christmas tree growers who continue to plant the same varieties of Scotch pine and do not destroy infested trees.

In 1995, I tested whether larvae could have been "pitched out" by excessive stem resin flow when white crystallized resin-like specks were found on larval cadavers during the previous summer. Due to low rates of resin flow and low Zimmerman pine moth survival from other factors, I could not determine a critical rate of resin flow at which larvae could be killed, but I suspected that resin flow may be more effective against small Zimmerman pine moth larvae in May than later in the summer. Some level of resin flow must be acceptable to larvae because I observed several larvae pushing frass out of exit holes in the bark to create pitch masses. In timber trees, southern pine beetle (*Dendroctonus frontalis* Zimm.; Coleoptera: Scolytidae) success is negatively affected by resin flow in four southern pine species (Hodges et al. 1979). Lorio (1994) and Blanche et al. (1992) found correlations between rates of resin flow in loblolly pine (*Pinus taeda* L.) and soil water storage, maximum temperature and cumulative water deficit when studied in relation to bark beetle attack, indicating important environmental effects on tree susceptibility. It may be possible that the amount of resin annually lost by Christmas trees due to shearing could reduce stem resin flow and temporarily increase susceptibility to phloem-borers, but this has not been studied. However, Jactel et al. (1994) demonstrated that the level of attack by *Dioryctria sylvestrella* (Ratz.) of pruned maritime pine (*Pinus pinaster*) in France increased with the intensity of branch pruning.

Larval choice of feeding sites may be limited to areas on individual trees near the oviposition site (Carlson and Butcher 1967). The multiple regression predictions of pupal weight using stem diameter, tree height, percentage foliar nitrogen, and rate of resin flow suggest that an optimum stem size, bark or phloem thickness, whorl age, or tree growth rate may exist for larval development (Carlson 1965, Jactel et al. 1994), but adult oviposition preferences may not directly correspond to larval feeding preferences (Fatzinger and Merkel 1985). Percentage nitrogen may be one of the most limiting factors of development since its concentration in phloem is low (Mattson 1980). Highest concentrations of nitrogen occur in young, actively growing tissues (Mattson 1980). For other phloem-feeders (e.g., bark beetles in slash pine, *Pinus elliottii* Engelm.), phloem thickness affects the proportions of xylem, phloem and outer bark encountered while insects tunnel (Haack et al. 1984). Thicker phloem may contain relatively more nutrients, provide larvae adequate space to excavate tunnels, and increase stem tissue thickness to minimize chances of parasitism. In addition, if vigorous tree growth results in thinner outer bark or greater bark cracking in younger whorls, larvae may more easily enter the phloem in those areas (Carlson 1962, Mauge 1987, Wright et al. 1975).

Zimmerman pine moth larval survival was reduced by parasitism and fungal infection in both years. The parasitoids *Exeristes comstockii* (Cresson) and *Hyssopus rhyacioniae* (Gahan) have been previously reported as natural enemies of Zimmerman pine moth (Carlson and Butcher 1967, Carlson and Wilson 1967, Krombein et al. 1979, Neunzig et al. 1964a) and other *Dioryctria* species (Hainze and Benjamin 1985, Neel and Sartor

1969, Wong 1972), but this is the first record of *Hirsutella nodulosa* (Petch) infection on Zimmerman pine moth larvae. Both parasitoids and fungus attacked multiple instars of Zimmerman pine moth and killed larvae inside their tunnels.

The following life cycle for *E. comstockii* is from the life history study by Arthur (1963). This ichneumonid parasitoid is native to North America and is distributed throughout the United States. First generation adults become active in mid-May, the second generation is present in late June and a partial third generation occurs during the fall. Females can live up to 100 days if a food source is available, and males live up to a month. Most females paralyze larval prey with their ovipositors before laying one or more eggs on or near the larvae. Each female may be capable of laying up to 153 eggs, and can lay 15 eggs per day. Eggs hatch in about two days, and development to adult emergence may last up to one month. When temperatures drop in the fall, *E. comstockii* larvae develop to the mature larval stage and remain protected in the host tunnel until spring. Other hosts include *Dioryctria disclusa* Heinrich, *Eucosma monitorana* Heinrich, *Argyresthia laricella* Kft., *Laspeyresia caryana* (Fitch), and other coleopterous and lepidopterous hosts (Eidt and Sippel 1961, Lyons 1957a,b, Townes and Townes 1960).

The life cycle and specific habits of *Hyssopus rhyacioniae* have not been determined. Its taxonomy as reared from the pine tip moth, *Rhyacionia frustrana* (Comstock), was described by Gahan (1927). *Hyssopus rhyacioniae* is native to North America, gregarious as larvae, and adults lay from 3 to 12 eggs on mature host larvae (Cushman 1927). Its mating behavior was described by Greenbaum (1976). Other known hosts for this eulophid parasitoid include *Dioryctria resinosella*, *Dioryctria taedae* Schaber and

Wood, *D. abietella* (D. & S.), *D. amatella* (Hulst), and *D. cambiicola* (Dyar) (Hainze and Benjamin 1985, Krombein et al. 1979, Schaber 1981).

H. nodulosa is an entomopathogenic fungus previously found on the coffee borer (*Zeuzera coffeae)* in Sri Lanka and on the strawberry mite (*Tarsonemus fragariae)* in England (Minter and Brady 1980). It has recently been found infecting spruce budworm (*Choristoneura fumiferana* (Clemens)) larvae in New Brunswick, Canada (Strongman et al. 1990). Symptoms of infection include cessation of larval feeding, larval color change, powdery white spores on larvae, hardened cadavers, elongated and slender phialides, and slender synnemata (Poinar and Thomas 1984). The life cycle of this species is uncertain, but like many entomopathogens, it may begin infecting a larva with a germinating spore, which penetrates the larva's cuticle (Poinar and Thomas 1984). The invasive hypha enters the host's tissues, then partially breaks apart and distributes throughout the larva. When the dead larva is filled with mycelium, emergence hyphae grow through the larva's integument, produce conidia, which disperse externally. Samples of conidia and synnemata are necessary for species identification.

How compatible are current methods of Zimmerman pine moth control with the biology of the previously described parasitoids and fungus? Early spring pesticide applications to control Zimmerman pine moth larvae while they bore into the phloem may not interfere with parasitoid or fungal life cycles. However, if insecticides are sprayed in May or late June to control other Christmas tree pests, the parasitoids may be active and could be killed. In addition, fungicides sprayed to manage needlecast and gall rust diseases could kill any *Hirsutella nodulosa* present on trees, and insecticides or miticides may kill mites if they vector the fungus. Hand removal of pitch masses in early summer may expose larvae to greater parasitism, predation and pathogenic infection, but this is labor-intensive and impractical in large fields. Another alternative would be to keep flowering plants near or in fields to provide nectar sources for parasitoids. Syme (1975) demonstrated that *E. comstockii* adults lived up to seven times longer when provided with flowers than when given no food. An optimal management system for Zimmerman pine moth would combine the use of host plant resistance, management for natural enemies, and selective use of pesticides.

Differences in Variety Resistance to European Pine Sawfly

Foliar resin acid concentration, nutrient and moisture content may be the most limiting factors in European pine sawfly development (Larsson et al. 1986, Lyytikainen 1994). Unexpectedly, percentage foliar nitrogen and needle moisture in my study were not significantly related to sawfly performance. However, resin acid concentration can influence by the amount of nitrogen available to trees, which changes resin duct size (Bjorkman and Larsson 1991). Other studies have shown that large concentrations of resin acids and chemical deterrents in needles increase sawfly larval development time and early instar mortality (Bjorkman and Larsson 1991, Larsson et al. 1986, Niemela et al. 1982), without affecting pupal survival (Bjorkman and Gref 1993). Bridgen and Hanover (1982) determined that Scandinavian varieties of Scotch pine (eg., Riga) had the highest resin acid concentrations, which may indicate why sawflies reared on Riga had lower survival, needle consumption and pupal weight, and longer development period than sawflies reared on the other varieties.

Alternatively, tree height and vigor may be important factors in oviposition site preference by adult sawflies. Wright et al. (1967) showed that European pine sawfly attack corresponded to tree height in different Scotch pine varieties, and I found that as tree height and stem diameter increased, so did the number of eggs laid per female. Females are known to search for taller trees or more exposed branches on which to lay eggs (Hardy and Allen 1975), but Olofsson (1989) explained that this behavior could result from females seeking optimal temperatures for oviposition or early egg and larval development. Adult females do not travel far from larval host trees to mate and oviposit (Henson 1964), except during outbreaks and heavy competition for oviposition sites (Olofsson 1989); potential fecundity may be primarily determined by factors that affected their larval development. In addition, resin duct size was found to be significantly larger on needles bearing eggs (Hardy and Allen 1975).

A small percentage of pupae in my study entered an extended diapause, but differences were not significant among varieties. In 1994, two pupae in extended diapause were found on Riga, two on Belgium and three on Pike Lake Improved. In 1995, four were found on Riga, one on Land O' Pine and three on Pike Lake Improved. This is not an uncommon occurrance for this species, but occurs more frequently during outbreak or unfavorable conditions (Kolomiets et al. 1979). Pschorn-Walcher (1965) reported that in Europe, between 5% and 100% of European pine sawfly cocoons enter extended diapause, depending on climate and altitude, and emerge as adults up to five years from the beginning of diapause (Kolomiets et al. 1979). Extended or prolonged diapause may be further influenced by hormonal secretions, length of photoperiod, high cocoon temperatures, and host quality (Knerer 1983, Kolomiets et al. 1979).

The greatest mortality of European pine sawfly from factors other than varietal resistance occurred during the pupal stage in 1994. The exotic ichneumonid *Pleolophus basizonus* (Gravenhorst) parasitized about 30% of the 400 caged pupae. However, under normal conditions, female parasitoids search for sawfly pupae on the ground, and rarely search tree foliage (Kolomiets et al. 1979, Price 1970). Percentage parasitism did not vary among the varieties on which sawflies were reared.

By protecting sawflies from pupal parasitism in 1995, I demonstrated the importance of parasitism in reducing numbers of adult sawflies able to reproduce. Although pupal parasitism occurs too late to prevent larval feeding damage in one year, a population reduction in sawfly numbers the following year could result. By allowing natural enemies and host plant resistance to manage sawfly populations in Christmas trees, most damaged shoots could be sheared off without reducing tree value. Sawfly larvae can be easily killed by an insecticide application in May or early June (McCullough and Ellis 1995, Wilson 1965), but this could be expensive on an annual basis. Pesticide applications could also kill the first generation *Pleolophus basizonus* adults emerging in late May from overwintering alternate host pupae. Thus, by combining host plant resistance, providing adequate habitat for natural enemies, and using pesticides judiciously, European pine sawfly populations and the damage they cause can be maintained below economic threshold levels.

Differences in Variety Resistance to Pine Needle Scale

Survival and fecundity of pine needle scale reared on Belgium and Land O' Pine tended to be low, indicating that these varieties were more resistant than Riga and Pike

Lake Improved. The most important factors potentially contributing to resistance in these varieties were percentage needle moisture and percentage nitrogen in needles. Previous studies have shown that low water availability in trees limits the movement of minerals through phloem sap, affecting sap-feeding insect feeding efficiency, survival and fecundity (Hanks and Denno 1993). Foliage moisture content and nitrogen content are known to be correlated (Mattson 1980), but I also found strong correlations between stem diameter and both foliage moisture and nitrogen content. Stem diameter and percentage moisture significantly predicted second generation scale survival, while percentage moisture and percentage nitrogen significantly predicted second generation scale fecundity in 1995. Stem diameters were smallest in Riga trees, but percentage needle moisture was not consistently significant among varieties. However, foliage nitrogen concentration and scale survival were not correlated, despite other studies demonstating this association (Kidd 1985, McClure 1977, 1980, Sheffer and Williams 1987). This could indicate that needle nitrogen content in the four varieties was adequate for scale development, or that percentage nitrogen did not vary enough among varieties to strongly affect scale survival and fecundity.

The increased scale survival on all varieties from the first generation to the second in 1994 could be interpreted in several ways. One hypothesis could be that scales began to adapt to each variety's natural defenses. Edmunds and Alstad (1978) suggested that scales form highly localized populations, and when scales from one population are transferred to another tree, crawler survival is reduced, supposedly because scales are not adapted to the new tree's defenses. However, it is unlikely that selection favoring genetic differentiation in scales would be strong enough to occur in less than hundreds of generations (Unruh and Luck 1987). Evidence both supporting and refuting the controversy of local adaptation or deme formation in sessile insects has been discussed (Unruh and Luck 1987). A deme is a group of interbreeding individuals adapted to local conditions (Krebs 1985, Unruh and Luck 1987), and one of the main requirements for deme formation includes a long-lived host plant with sessile herbivores feeding on it (Edmunds and Alstad 1978). Given that pine needle scale typically has two generations each year in Michigan and Scotch pine Christmas tree have rotation times of 7- to 10-years (Leefers et al. 1988), it seems unlikely that demes would have time to form.

In 1994, low first generation scale survival and higher second generation survival on all varieties may have been due to weather. Wind, rain and extreme temperatures can facilitate crawler dispersal, dislodge scales or affect rate of development (McClure 1989), and periods of cold temperatures in winter (-14° to -4° C) can cause mortality in overwintering scales (Struble and Johnson 1964). I suspect that the mild 1994-1995 winter and hot summer in 1995 provided good conditions for scale survival and fecundity (Sheffer and Williams 1987), but six days of -18° C (0° F) or below temperatures in January 1994 may have increased egg mortality, resulting in lower first generation survival. Despite weather effects, pine needle scale fecundity was highest in Pike Lake Improved trees in 1994, and scales on Land O' Pine trees had the lowest fecundity in 1995. Fecundity in 1994 averaged 28 to 39 eggs per female, and 30 to 45 eggs per female in 1995, both somewhat lower than egg counts in New York (42 eggs per female) (Nielsen and Johnson 1973) or in Saskachewan (47 eggs per female) (Cumming 1953).

Where pine needle scale crawlers establish feeding sites on a needle may be an important factor in scale survival (Brown 1958, Luck and Dahlsten 1975). Several studies have shown that scales prefer feeding on the inner side of needles, and that most female crawlers move to new needles, while most males remain on older needles (Cumming 1953, Luck and Dahlsten 1974, Walstad et al. 1973). I also found that female scales primarily fed on the flat, inner side of needles in all four varieties. Luck and Dahlsten (1974) suggested that scale survival may be higher on the less exposed, flat side of needles, near the fascicle. Parasitoids and predators may have more difficulty finding scales in this area.

Christmas tree shearing may not strongly affect pine needle scale survival or fecundity. When trees are sheared in early summer (Hill 1989), first generation scales are still feeding on older needles, and second generation crawlers do not emerge until July (Nielsen and Johnson 1973). Contact between densely stocked trees may facilitate second generation wind-dispersal to uninfested trees, but crawler dispersal by walking is limited to less than 11cm from the parent scale (Brown 1958). In addition, the greater density of foliage caused by shearing may provide scales better access to other branches within the same tree. Dispersing crawlers may fall onto lower branches and become established there.

Greater parasitism and predation of scales in late summer 1995 may explain why second generation survival decreased. I found immature parasitoids developing within adult pine needle scale and coccinelid larvae were observed feeding on eggs, although their precise impact on the population could not be determined. The increased scale population size may have attracted more density-dependent parasitoids and predators (Luck and Dahlsten 1975). Parasitoids known to attack pine needle scale include *Achrysocharis phenacapsia* Yoshimoto, *Aphytis chilensis* Howard, *Aphytis diaspidis* (Howard), *Aphytis mytilaspidis* (LeBaron), *Aspidiotiphagus citrinus citrinus* (Craw.), *Coccobius varicornis* (Howard), *Coccophagus flavifrons* Howard, *Marietta mexicana* (Howard), *Marietta pulchella* (Howard), *Physcus howardi* Compere, and *Prospaltella bella* Gahan. Known predators include *Chilocorus stigma* (Say), *Chilocorus orbus* Casey var. *monticolus* Drea, *Cryptoweisia atronitens* (Casey), *Microweisia misella* LeConte (Burden and Hart 1990, Krombein et al. 1979, Luck and Dahlsten 1974, Nielsen and Johnson 1973). In this study, I found both larvae and adults of the coccinelid *Coccidophilus marginatus* (LeConte) feeding on scale eggs. Several natural enemies may be able to regulate scale populations at low levels, but are susceptible to pesticide applications (Clarke et al. 1992, Luck and Dahlsten 1975, Negron and Clarke 1995).

Some variation in resistance to pine needle scale was demonstrated in this study, but results were not always consistent. I would recommend that host plant resistance be used in comination with biological and chemical control to reduce populations of pine needle scale to low levels. Other cultural methods besides shearing could also be developed to reduce crawler survival in both generations, which would enhance the management of this pest.

Table 1. Characteristics of four Scotch pine varieties according to Wright et al. (1966) and Ruby and Wright (1976).

	Riga	Belgium	Land O' Pine	Pike Lake Imp.
Country of origin	Sweden	Belgium	Germany	France
Range of needle lengths (mm)[a]	56 - 77	79 - 111	66 - 99	47 - 56
Winter needle color[b]	2.5	6.2	5.1	7.9
Average height (% of mean for all varieties)[c]	95	126	118	104

[a] On six-year old trees

[b] Color ranks: 1 = yellow-green, 9 = blue-green

[c] On 13-year old trees

Table 2. Mean tree growth measurements (±SE) of four Scotch pine varieties in 1994 and 1995 (n = 12 trees per variety).[1]

Variable	Riga	Belgium	Land O'Pine	Pike Lake I.
1994				
Needle length (mm)	55.3 (2.2)^{a}	68.9 (2.7)^{b}	70.4 (3.2)^{b}	57.0 (4.9)^{a}
Percentage moisture				
current-year foliage	48.7 (1.06)^{a}	52.7 (0.93)^{b}	55.9 (1.84)^{b}	55.6 (0.81)^{b}
1-year old foliage	47.5 (1.42)^{a}	47.4 (1.26)^{a}	49.2 (1.14)^{a}	46.8 (1.09)^{a}
Needle twist				
current-year foliage	3.5 (0.15)^{a}	3.7 (0.14)^{a}	3.6 (0.22)^{a}	3.8 (0.19)^{a}
1-year old foliage	3.9 (0.17)^{a}	3.8 (0.15)^{a}	3.7 (0.17)^{a}	3.5 (0.17)^{a}
Percentage nitrogen				
current-year foliage	1.7 (0.16)^{a}	2.0 (0.07)^{a}	1.9 (0.05)^{a}	1.8 (0.04)^{a}
1-year old foliage	1.6 (0.04)^{ab}	1.7 (0.05)^{b}	1.5 (0.05)^{a}	1.6 (0.04)^{ab}
Tree height (cm)	192.2 (4.2)^{a}	260.3 (4.0)^{d}	230.6 (4.7)^{c}	210.5 (5.6)^{b}
Basal diameter (cm)	6.35 (0.23)^{a}	8.84 (0.34)^{b}	9.58 (0.37)^{b}	9.70 (0.39)^{b}
Stem diameter (cm)				
whorls 2 to 3	2.82 (0.12)^{a}	3.51 (0.16)^{b}	3.40 (0.23)^{ab}	3.77 (0.18)^{b}
whorls 3 to 4	4.34 (0.22)^{a}	4.57 (0.23)^{a}	4.39 (0.20)^{a}	5.14 (0.22)^{b}
1995				
Needle length (mm)	52.7 (1.9)^{a}	66.7 (2.8)^{b}	59.4 (2.9)^{ab}	51.6 (1.9)^{a}
No. fascicles/5cm shoot	36.0 (1.8)^{ab}	34.4 (1.9)^{a}	35.2 (2.0)^{a}	41.3 (1.8)^{b}
Percentage moisture				
May 12	41.6 (0.55)^{a}	41.0 (0.55)^{a}	40.7 (0.55)^{a}	41.1 (0.55)^{a}
May 26	45.1 (0.40)^{b}	44.2 (0.40)^{ab}	43.2 (0.40)^{a}	43.9 (0.40)^{ab}
June 8	43.4 (1.17)^{ab}	41.7 (1.17)^{a}	46.2 (1.17)^{b}	42.8 (1.17)^{ab}
Needle Twist (current-year)	3.5 (0.1)^{a}	3.8 (0.1)^{a}	3.7 (0.2)^{a}	3.7 (0.2)^{a}
Percentage nitrogen				
current-year foliage	1.68 (0.03)^{a}	1.71 (0.03)^{a}	1.67 (0.03)^{a}	1.64 (0.03)^{a}
Tree height (cm)	212.2 (5.5)^{a}	272.8 (4.9)^{c}	249.9 (5.3)^{b}	226.6 (7.8)^{a}
Basal diameter (cm)	9.27 (0.29)^{a}	12.09 (0.21)^{b}	11.40 (0.32)^{b}	11.51 (0.46)^{b}
Diameter at breast ht (cm)	3.16 (0.25)^{a}	5.09 (0.27)^{b}	4.85 (0.25)^{b}	4.46 (0.34)^{b}
Height growth: 1994-1995	20.0 (2.7)^{a}	13.0 (2.8)^{a}	19.8 (2.4)^{a}	18.8 (2.8)^{a}
Basal diameter growth (cm)	2.91 (0.17)^{b}	3.25 (0.26)^{b}	1.84 (0.19)^{a}	1.82 (0.32)^{a}

[1] Means followed by the same letter did not significantly differ at the $p<0.05$ level.

Table 3. Pearson's product-moment (r) and Spearman rank (r_s) correlations among Scotch pine tree characteristics.[1]

Variable	Variable	Correlation coefficient	*p*<	Correlation coefficient	*p*<
		1994		**1995**	
Tree height	Basal diameter	$r = 0.43$	0.01	$r = 0.68$	0.001
Tree height	Stem diameter	$r = 0.41$	0.01	$r = 0.77$	0.001
Basal diameter	% needle moisture (6 Sept.)	$r = 0.60$	0.001	[2]	[2]
Stem diameter	% needle moisture (6 Sept.)	$r = 0.47$	0.001	[2]	[2]
Stem diameter	% needle moisture (26 May)	[2]	[2]	$r = -0.34$	0.05
Basal diameter	Needle twist	$r_s = -0.30$	0.05	[2]	[2]
Needle length	Tree height	$r = 0.50$	0.001	$r = 0.52$	0.001
Needle length	Basal diameter	$r = 0.31$	0.05	$r = 0.35$	0.05
Tree height	% N in current yr foliage	$r = 0.27$	0.05	[2]	[2]
Stem diameter	% N in 1-year old foliage	$r = 0.36$	0.01	[2]	[2]
Needle length	Needle density	[2]	[2]	$r = -0.43$	0.01
Basal diameter	Rate of resin flow in June	[2]	[2]	$r_s = -0.58$	0.05

[1] Varietal data were pooled

[2] Correlations were not significant between the two variables

Table 4. Mean monthly temperature and precipitation accumulation in 1994 and 1995 at Kellogg Forest near Kalamazoo, MI.

Year	Month	Mean Maximum Temperature (°C)	Mean Minimum Temperature (°C)	Total Precipitation (cm)
1994	January	-6.8	-15.6	5.3
	February	-6.2	-14.4	4.4
	March	2.7	-5.7	4.5
	April	11.8	1.6	10.0
	May	17.1	4.0	3.2
	June	23.5	11.4	14.9
	July	23.9	14.3	11.1
	August	25.6	14.9	15.7
	September	22.4	12.8	3.0
	October	17.8	9.0	4.6
	November	12.2	4.9	11.5
	December	6.8	1.7	3.6
1995	January	3.1	-1.4	5.6
	February	0.3	-6.1	2.5
	March	10.3	1.4	3.4
	April	14.4	5.3	9.5
	May	22.1	8.5	10.4
	June	29.1	14.6	8.4
	July	30.7	17.2	7.2
	August	30.7	19.3	12.8
	September	20.8	8.3	5.4
	October	16.9	5.6	9.5
	November	3.6	-3.3	12.0
	December	-0.6	-7.8	2.8

Table 5. Cohort life table analysis for Zimmerman pine moth caged on Scotch pine trees at Kellogg Forest in 1994 and 1995 (n = 48 trees).[1]

Year	Age interval (x)	No. insects alive at each stage (n_x)	% alive at start of age interval x (l_x)	No. dying in age interval x to x+1 (d_x)	Percent mortality ($100q_x$)	Mean expectation of further life for insects alive at start of age x (e_x)	Mortality Factor		
							Fungus	Paras.	Unkn.
1994	Caging date	96	100.0	23	24.0	2.59	2	0	21
	Early larvae	73	76.0	22	30.1	2.25	2	7	13
	Middle larvae	51	53.1	15	49.0	2.01	1	5	9
	Late larvae	36	37.5	8	22.2	1.64	3	3	2
	Pupae	28	29.2	2	7.1	0.96	0	0	0
	Adults	26	27.1	-	-	-	-	-	-
1995	Caging date	48	100.0	6	12.5	2.38	0	0	6
	Early larvae	42	87.5	6	14.3	1.64	0	0	6
	Middle larvae	36	75.0	31	86.1	0.83	2	7	22
	Late larvae	5	10.4	0	0.0	1.90	0	0	0
	Pupae	5	10.4	1	20.0	0.90	0	0	1
	Adults	4	8.3	-	-	-	-	-	-

[1] Data from the four Scotch pine varieties were pooled.

Table 6. Analysis of Zimmerman pine moth survival during 1994 and 1995 using the Cochran's Q test, $X^2_{0.05,3}$ (n = 48 trees).[1]

Year	Life Stage	Whorl	Q	Probability
1994	Early larvae	2	5.1	$0.1 < p < 0.2$
	Middle larvae		3.3	$0.4 < p < 0.3$
	Late larvae		2.6	$p > 0.3$
	Pupae		1.3	$p > 0.3$
	Early larvae	3	1.2	$p > 0.3$
	Middle larvae		0.2	$p > 0.3$
	Late larvae		0.2	$p > 0.3$
	Pupae		1.0	$p > 0.3$
1995	Early larvae	3	3.3	$0.3 < p < 0.4$
	Middle larvae		5.6	$0.1 < p < 0.2$
	Late larvae		4.4	$0.2 < p < 0.3$
	Pupae		4.4	$0.2 < p < 0.3$

[1] Data from the four Scotch pine varieties were pooled.

Table 7. Mean growth and fecundity (±SE) of Zimmerman pine moth when caged on four Scotch pine varieties in 1994 and 1995 (n = 12 trees per variety).[1]

Year	Variable	Riga	Belgium	Land O' Pine	Pike Lake Imp.
1994	Development period (days)	83.3 (9.12)	81.1 (10.17)	82.7 (8.04)	94.9 (7.65)
	Development period (°DD)	905.0 (152.1)	861.4 (168.2)	892.2 (132.1)	1093.9 (126.8)
	Growth rate (mg/°DD)	0.109 (0.022)	0.111 (0.015)	0.102 (0.012)	0.096 (0.014)
	Pupal fresh weight (mg)	88.5 (2.34)	85.5 (5.74)	85.1 (3.38)	94.7 (2.93)
	Adult fresh weight (mg)	49.5 (3.04)	40.4 (6.23)	44.5 (3.69)	52.5 (2.31)
1995	Development period (days)	99.6 (3.59)	100.4 (4.60)	90.8 (5.55)	91.7 (6.65)
	Development period (°DD)	1928.3 (101.4)	1952.2 (131.1)	681.5 (149.5)	1709.0 (181.0)
	Growth rate (mg/°DD)	0.039 (0.004)	0.042 (0.004)	0.054 (0.008)	0.048 (0.005)
	Pupal fresh weight (mg)	78.6 (5.45)	81.2 (8.46)	92.5 (21.79)	82.3 (0.58)
	Adult fresh weight (mg)	33.6 (4.49)	44.0 (3.78)	49.0 (17.17)	39.8 (1.77)
	Fecundity (number of eggs)	21.7 (7.51)	21.0 (9.20)	-[2]	18.0 (13.01)

[1] Differences among varieties were not significant for any variable ($p<0.05$)

[2] No female survived to lay eggs

Table 8. Pearson's product-moment (r) and Spearman rank (r_s) correlations among Zimmerman pine moth and tree variables with varietal data pooled.

Year	Variable	Variable	Correlation coefficient	$p<$
1994	Adult weight (mg)	Pupal weight (mg)	$r = 0.811$	0.001
	Pupal length (mm)	Pupal weight (mg)	$r_s = 0.902$	0.001
	Pupal weight (mg)	Development period (days)	$r_s = 0.630$	0.01
	Pupal weight (mg)	Tree diameter, whorls 2-3	$r = 0.511$	0.01
	Development (days)	Tree diameter, whorls 2-3	$r_s = 0.581$	0.01
	Development (days)	Tree diameter, whorls 3-4	$r_s = 0.537$	0.02
1995	Adult weight (mg)	Pupal weight (mg)	$r = 0.948$	0.01
	Pupal length (mm)	Pupal weight (mg)	$r_s = 0.96$	0.001
	Adult weight (mg)	Fecundity (number of eggs)	$r_s = 0.396$	0.05
	Basal diameter (cm)	Rate of resin flow in June	$r_s = -0.58$	0.05

Table 9. Cohort life table analysis for European pine sawfly in 1994.

Variety	Age interval (x)	Observed no. insects alive at each stage (n_x)	Percent alive at start of age interval x (l_x)	No. dying within age interval x to x+1 (d_x)	Percent mortality ($100q_x$)	Mean expectation of further life for insects alive at start of age x (e_x)
Pooled[1]	1st instar	360	100.0	123	34.2	2.29
	3rd instar	237	65.8	48	20.3	2.21
	Ultimate instar	189	52.5	11	5.8	1.65
	Pupae	178	49.4	101	56.7	1.66
	Adults	77	21.4	-	-	-
Riga	1st instar	120	100.0	67	55.8	1.63
	3rd instar	53	44.2	13	24.5	2.07
	Ultimate instar	40	33.3	1	2.5	1.58
	Pupae	39	32.5	31	79.5	0.60
	Adults	8	6.7	-	-	-

[1] Pooled varieties included Belgium, Land O' Pine and Pike Lake Improved (n = 12 trees per variety).

Table 10. Cohort life table analysis for European pine sawfly in 1995.

Variety	Age interval (x)	Observed no. insects alive at each stage (n_x)	Percent alive at start of age interval x (l_x)	No. dying within age interval x to x+1 (d_x)	Percent mortality ($100q_x$)	Mean expectation of further life for insects alive at start of age x (e_x)
Pooled[1]	1st instar	360	100.0	15	4.2	3.57
	3rd instar	345	95.8	21	6.1	2.71
	Ultimate instar	324	90.0	10	3.1	1.85
	Pupae	314	87.2	68	21.7	0.89
	Adults	246	68.3	-	-	-
Riga	1st instar	120	100.0	21	17.5	3.01
	3rd instar	99	82.5	10	10.1	2.54
	Ultimate instar	89	74.2	5	5.6	1.77
	Pupae	84	70.0	26	31.0	0.85
	Adults	58	48.3	-	-	-

[1] Pooled varieties included Belgium, Land O' Pine and Pike Lake Improved (n = 12 trees per variety).

Table 11. Mean values for European pine sawfly development (±SE) on four varieties of Scotch pine in 1994 and 1995 (n=12 trees per variety).[1]

Year	Variable	Riga	Belgium	Land O' Pine	Pike Lake Imp.
1994	Needle biomass consumed (g)	0.40 (0.06)^{a}	0.26 (0.05)^{a}	0.30 (0.05)^{a}	0.23 (0.04)^{a}
	Frass per larva (mg dw)	0.20 (0.04)^{a}	0.18 (0.03)^{a}	0.16 (0.03)^{a}	0.13 (0.03)^{a}
	Development period (days)	39.4 (0.6)^{b}	37.2 (0.4)^{a}	37.6 (0.4)^{a}	37.7 (0.4)^{a}
	Development period (°DD)	237.7 (5.9)^{b}	215.0 (3.0)^{a}	218.3 (4.2)^{a}	220.5 (4.0)^{a}
	Growth rate (mg/100 °DD)	27.0 (0.7)^{a}	31.6 (0.8)^{b}	30.0 (0.8)^{b}	30.7 (0.6)^{b}
1995	Needle biomass consumed (g)	0.40 (0.03)^{b}	0.40 (0.03)^{b}	0.32 (0.03)^{ab}	0.27 (0.03)^{a}
	Frass per larva (mg dw)	0.33 (0.02)^{a}	0.29 (0.02)^{a}	0.29 (0.02)^{a}	0.34 (0.02)^{a}
	Development period (days)	30.9 (0.3)^{a}	29.9 (0.3)^{a}	30.7 (0.3)^{a}	30.5 (0.3)^{a}
	Development period (°DD)	620.1 (5.5)^{ab}	602.6 (5.3)^{a}	623.5 (6.7)^{b}	614.0 (4.3)^{ab}
	Growth rate (mg/100 °DD)	12.4 (0.2)^{ab}	12.9 (0.2)^{b}	11.9 (0.002)^{a}	12.1 (0.2)^{ab}

[1] Means followed by the same letter did not significantly differ at the $p<0.05$ level.

Table 12. Pearson's product-moment (r) and Spearman rank (r_s) correlations among European pine sawfly and tree variables with varietal data pooled together.

Year	Variable	Variable	Correlation coefficient	$p<$
1994	Pupal weight (mg)	Development period (days)	$r_s = -0.367$	0.05
	Pupal weight (mg)	Number of eggs laid/female	$r_s = 0.447$	0.01
	Needle biomass eaten	Development period (°DD)	$r_s = 0.685$	0.05
	Tree height (cm)	Development period (°DD)	$r_s = -0.282$	0.05
1995	Pupal weight (mg)	Development period (days)	$r_s = -0.494$	0.001
	Pupal weight (mg)	Development period (°DD)	$r_s = -0.492$	0.001
	Pupal weight (mg)	% nitrogen in needles	$r = 0.272$	0.05
	Pupal weight (mg)	Number of eggs laid/female	$r_s = 0.292$	0.05
	No. eggs laid/female	Tree height (cm)	$r_s = 0.577$	0.001
	No. eggs laid/female	Diameter at breast height (cm)	$r_s = 0.460$	0.001
	No. eggs laid/female	Basal diameter (cm)	$r_s = 0.385$	0.001

Table 13. Backward-stepping multiple regression predictions of European pine sawfly development period (day), pupal weight and percentage nitrogen in one-year old needles in 1994 (n=39) and 1995 (n=42).

Year	Response variable	Predictor variable	Coefficients of predictors	SS	F	$p<$	r^2
1994	Development period (days)	1-yr old needle twist	2.265	48.56	6.82	0.05	0.229
		Tree height	-0.037	43.24	6.08		
1995	Pupal weight (mg)	% N in current-year needles	16.337	146.77	5.49	0.06	0.220
		% needle moisture - May	0.905	103.78	3.88		
		% needle moisture - June	-0.385	97.35	3.64		
	Development period (days)	Tree height	-0.018	11.90	6.10	0.05	0.194
		Current-year needle twist	1.141	11.06	5.67		

Table 14. Pearson's product-moment (r) and Spearman rank (r_s) correlations among pine needle scale and tree variables.[1]

Variable	Variable	Correlation Coefficient	$p<$
Preliminary study			
Armor length (mm)	Number of eggs laid per female	$r_s = 0.581$	0.001
Armor length (mm)	Body length (mm)	$r = 0.303$	0.05
Body length (mm)	Scale density on each needle	$r_s = -0.356$	0.01
Armor length (mm)	Needle width (mm)	$r = -0.377$	0.01
Armor length (mm)	Needle length (mm)	$r = -0.229$	0.01
1994			
2nd generation survival	% needle moisture (28 Aug.)	$r_s = 0.307$	0.05
2nd generation survival	Basal diameter (cm)	$r_s = 0.372$	0.05
2nd generation fecundity	Basal diameter (cm)	$r_s = 0.350$	0.05
1st generation survival	2nd generation survival	$r_s = 0.573$	0.001
2nd generation survival	Number of eggs laid per female	$r_s = 0.312$	0.05
1995			
2nd generation survival	Tree height	$r_s = -0.347$	0.05
2nd generation survival	Diameter at breast height	$r_s = -0.413$	0.05
2nd generation survival	Basal diameter	$r_s = -0.371$	0.01
2nd generation survival	Basal diameter growth rate	$r_s = 0.337$	0.05
2nd generation survival	% needle moisture (12 May)	$r_s = 0.335$	0.01
1st generation survival	2nd generation survival	$r_s = 0.272$	0.061

[1] Varietal data were pooled in 1994 and 1995.

Table 15. Mean realized survival and fecundity (±SE) of pine needle scale on four varieties of Scotch pine in 1994 and 1995 (n = 12 trees per variety).[1]

Year	Variable	Riga	Belgium	Land O' Pine	Pike Lake Imp.
1994	First generation scale survival	14.7 (5.6)^{a}	22.4 (6.3)^{a}	28.2 (9.6)^{a}	24.6 (6.5)^{a}
	Second generation scale survival	164.8 (67.0)^{ab}	76.7 (29.3)^{a}	222.8 (77.5)^{ab}	293.3 (74.9)^{b}
	No. eggs/egg-laying female	28.9 (2.27)^{a}	29.6 (3.46)^{a}	30.2 (2.42)^{ab}	39.3 (1.48)^{b}
1995	First generation scale survival	223.3 (29.0)^{b}	197.5 (33.7)^{ab}	119.9 (19.6)^{a}	142.3 (28.6)^{ab}
	Second generation scale survival				
	12 August	172.2 (82.0)^{b}	43.1 (9.7)^{a}	15.9 (6.7)^{a}	60.0 (21.0)^{ab}
	15 October	90.8 (22.0)^{b}	31.5 (7.2)^{a}	12.5 (3.7)^{a}	35.9 (12.1)^{ab}
	No. eggs/egg-laying female	45.1 (1.5)^{b}	41.8 (3.1)^{b}	30.5 (4.3)^{a}	42.4 (1.9)^{b}

[1] Means followed by the same letter did not significantly differ at the $p<0.05$ level.

Table 16. Backward-stepping multiple regression predictions of pine needle scale survival and second generation fecundity in 1994 and 1995 (n=48 trees).

Year	Response variable	Predictor variable	Coefficients of predictors	SS	F	$p<$	r^2
1994	2nd generation fecundity	1-yr old needle twist	-6.108	556.824	7.479	0.08	0.214
		Diameter bet. whorls 3-4	7.167	235.938	3.169		
1995	2nd generation survival	Tree basal diameter	-56.617	55554.2	11.867	0.05	0.286
		% needle moisture - early May	377.080	19728.4	4.214		
	2nd generation fecundity	% needle moisture - late May	80.848	717.771	7.662	0.05	0.305
		% needle moisture - Sept.	21.558	668.632	7.137		
		% N in current-year needles	29.067	514.817	5.495		

Table 17. Backward-stepping multiple regression predictions of Zimmerman pine moth pupal weight in 1994 (n=19) and 1995 (n=10).

Year	Response variable	Predictor variable	Coefficients of predictors	SS	F	*p*<	r^2
1994	Pupal weight	Diameter between whorls 2-3 (cm)	17.877	388.394	11.407	0.05	0.617
		Tree height (cm)	-0.146	292.059	8.578		
		% N in 1-year old needles	23.541	257.178	7.553		
1995	Pupal weight	Basal diameter (cm)	-68.192	1420.961	43.747	0.05	0.950
		% N in current-year needles	-242.918	1074.857	33.092		
		May resin flow (ml/24 h)	-1803.464	1026.373	31.599		
		Tree height (cm)	2.239	950.647	29.268		
		Early June resin flow (ml/24 h)	106.583	941.532	28.987		
		Late June resin flow (ml/24 h)	-233.070	471.770	14.524		

Table 18. Mean values for European pine sawfly fecundity (±SE) on four varieties of Scotch pine in 1994 and 1995 (n = 12 trees per variety).

Year	Variables	Riga	Belgium	Land O' Pine	Pike Lake Imp.
1994	No. egg-laying females	1.0 (0.0)^{a}	2.2 (0.4)^{a}	2.2 (0.6)^{a}	2.4 (0.3)^{a}
	No. eggs/egg-laying female	53.0 (0.0)^{a}	43.3 (4.8)^{a}	38.2 (6.7)^{a}	43.3 (3.0)^{a}
	Number eggs/needle	6.0 (0.0)^{a}	5.2 (0.58)^{a}	3.8 (1.11)^{a}	4.9 (0.64)^{a}
	Pupal weight (mg)	62.2 (1.40)^{a}	67.1 (1.30)^{b}	64.6 (1.58)^{ab}	67.0 (1.20)^{b}
1995	No. egg-laying females	3.6 (0.6)^{a}	5.4 (0.6)^{a}	4.5 (0.6)^{a}	4.1 (0.6)^{a}
	No. eggs/egg-laying female	40.0 (7.8)^{a}	76.7 (7.0)^{b}	64.9 (6.7)^{b}	71.3 (6.7)^{b}
	Number eggs/needle	4.5 (0.38)^{a}	6.1 (0.35)^{a}	5.4 (0.33)^{a}	5.6 (0.33)^{a}
	Pupal weight (mg)	76.0 (1.26)^{ab}	77.2 (0.85)^{b}	73.1 (0.97)^{a}	74.0 (0.80)^{ab}

[1] Means followed by the same letter did not significantly differ at the $p<0.05$ level.

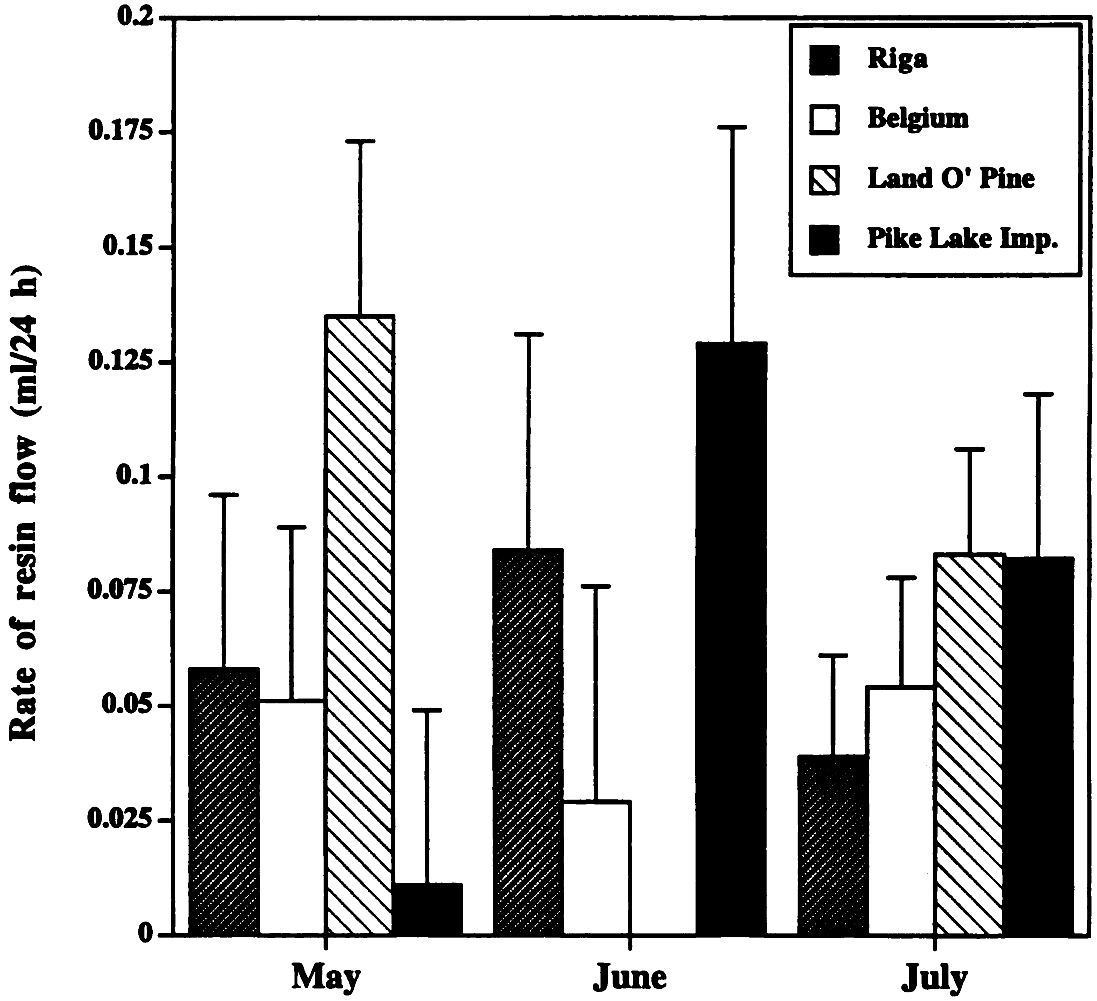

Figure 1. Mean rate of resin flow (±SE) (ml/24 h) for four varieties of Scotch pine measured in May, June and July 1995 (n = 12 trees per variety).

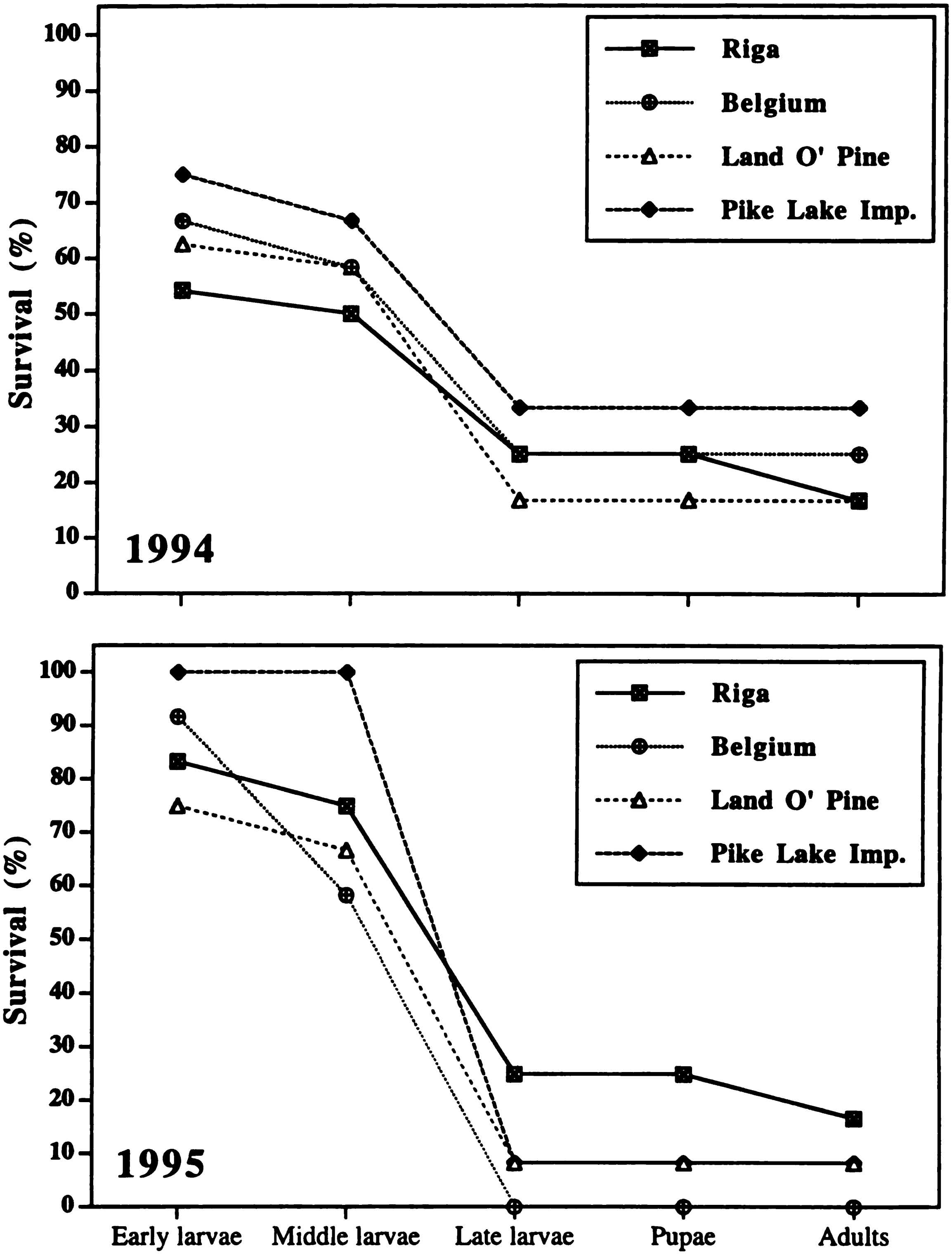

Figure 2. Mean percentage survival of Zimmerman pine moth in 1994 and 1995 when reared on four varieties of Scotch pine.

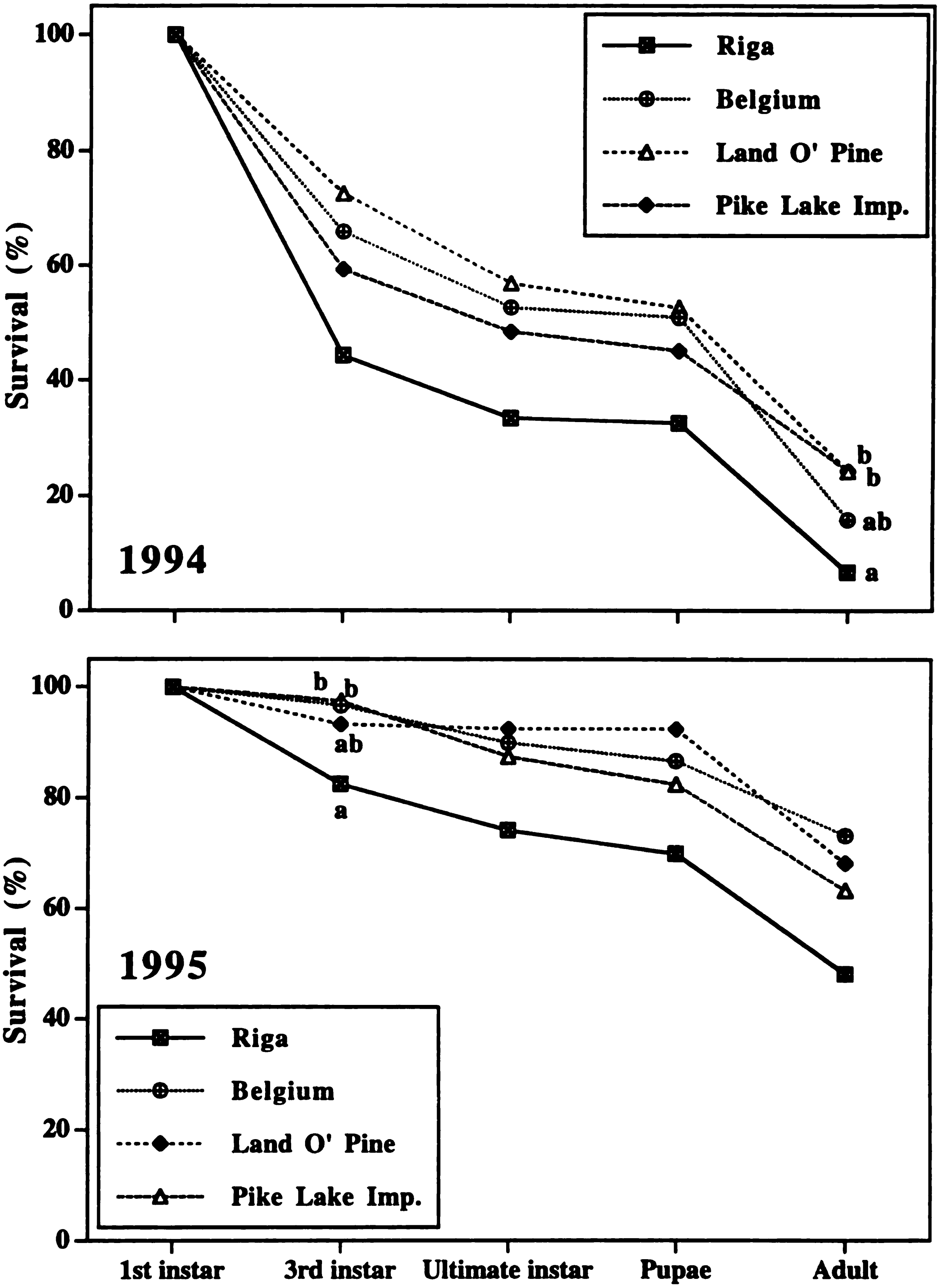

Figure 3. Mean percentage survival of Eurpean pine sawfly in 1994 and 1995 when reared on four varieties of Scotch pine.

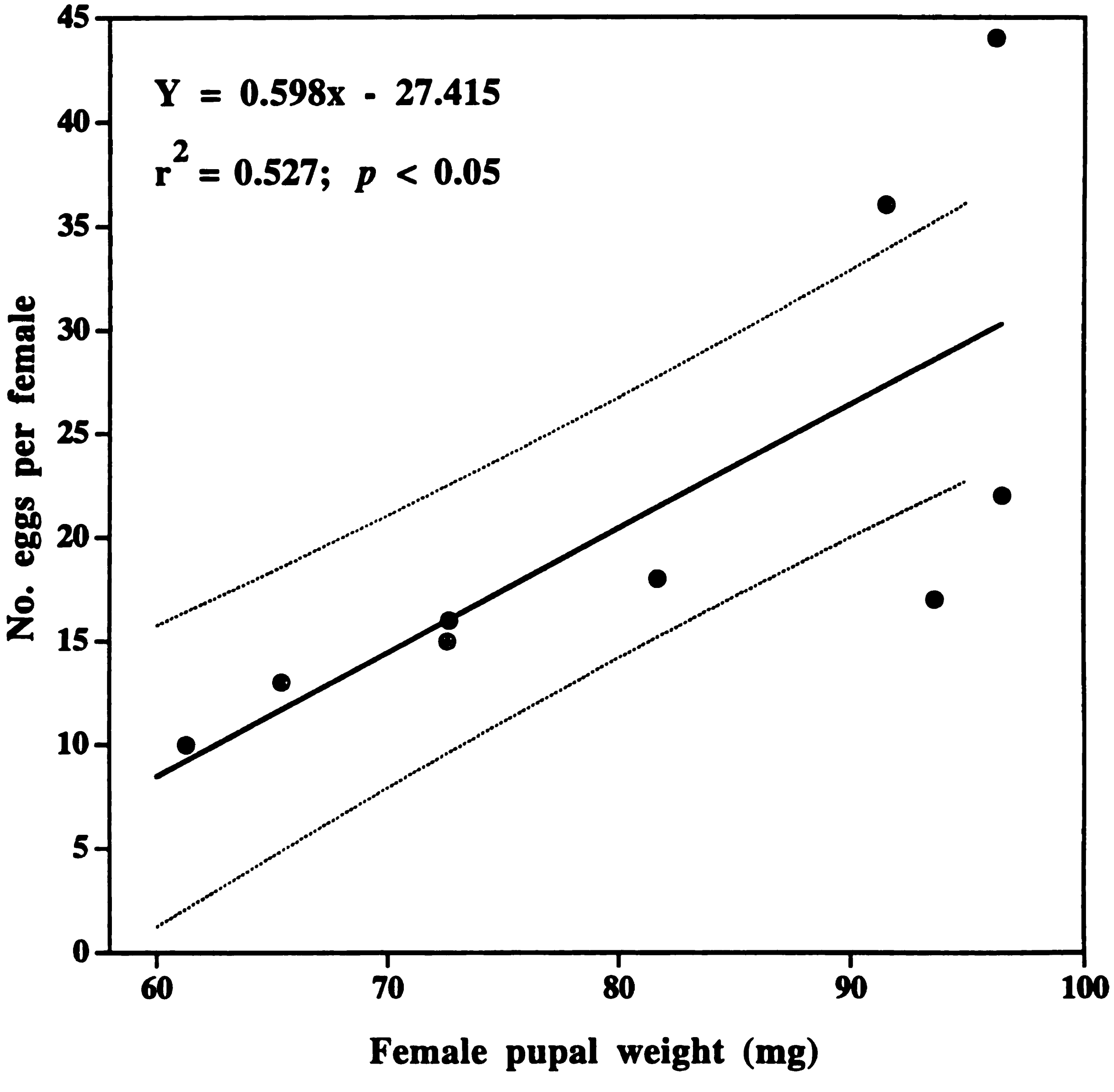

Figure 4. Linear regression and 95% confidence interval of Zimmerman pine moth female pupal weight and number of eggs produced per female in 1995 (n=9 females).

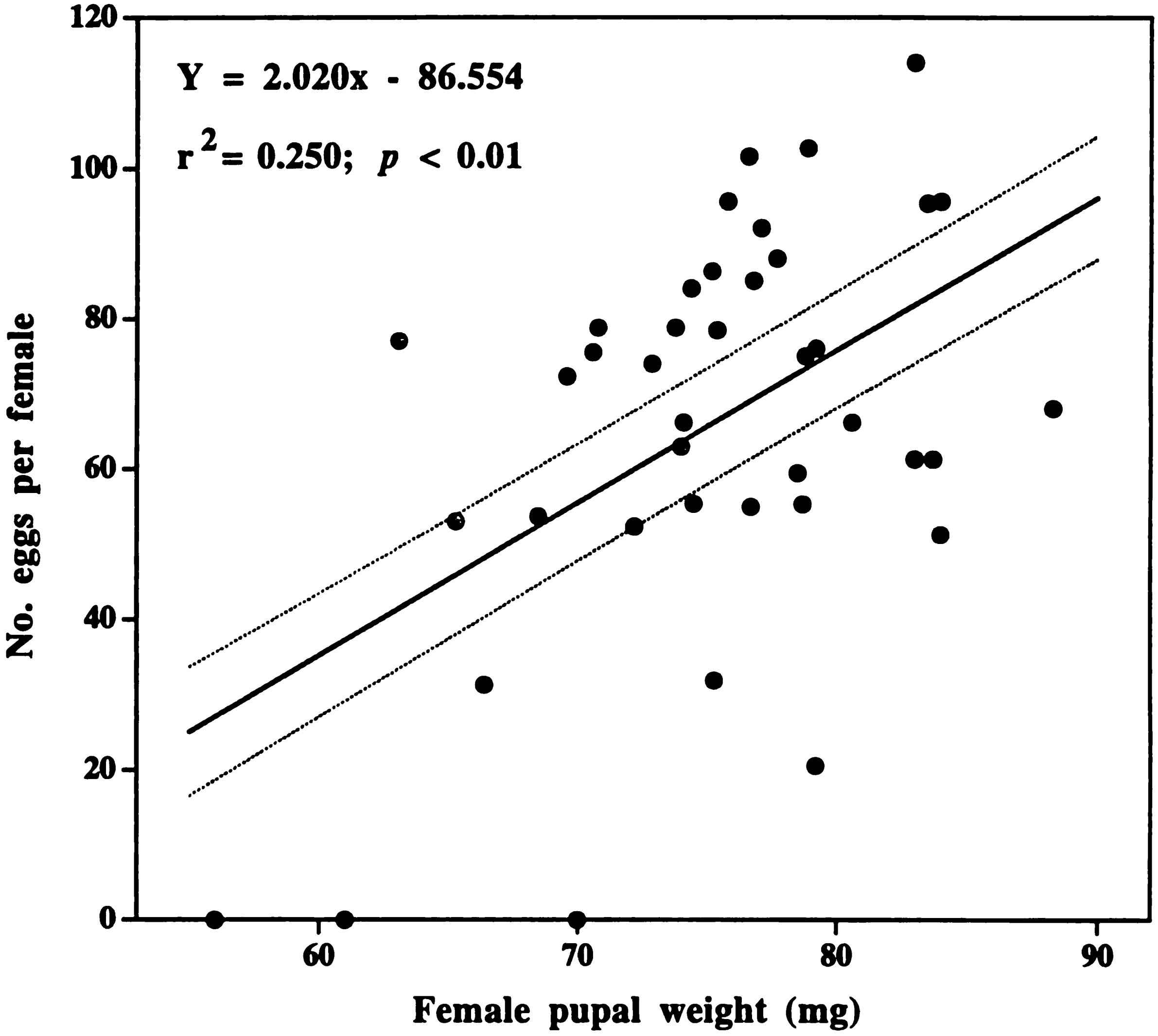

Figure 5. Linear regression and 95% confidence interval of European pine sawfly female pupal weight and number of eggs laid per female in 1995 (n=40).

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CHAPTER 2

Phenology and Species Composition of Pest and Beneficial Arthropods in Four Varieties of Scotch Pine Christmas Trees in Southern Michigan

INTRODUCTION

Scotch pine, *Pinus sylvestris* L., has been a valuable ornamental, forest and Christmas tree species in Michigan since it's importation from Europe and Asia during the twentieth century (Sowder 1966, Wright et al. 1966). It is grown for timber, as a windbreak, and as a tree to decorate both outdoors and indoors at Christmas (Bridgen and Hanover 1982, Giertych and Matyas 1991). Scotch pine has long been a favorite Christmas tree species among growers and consumers. In Michigan, Scotch pine is grown on approximately 39,000 acres, over three million trees are harvested annually, and 71% of all Christmas trees cut are Scotch pine (Mich. Agr. Stat. Serv. 1994).

Geographic and climatic conditions in Europe and Asia affected isolated populations of Scotch pine trees over time, exerting different selection pressures on each gene pool (Giertych and Matyas 1991). Over 30 separate varieties of Scotch pine have been recognized (Ruby and Wright 1976). Varieties differ in traits such as needle length, color and moisture content, cone production, stem form, growth rate and monoterpene concentration (Bridgen et al. 1979, Carlisle 1958, Ruby and Wright 1976, Tobolski and Hanover 1971, Wright 1976). Varieties also vary in degree of resistance to insects and

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diseases (Squillace et al. 1975, Steiner 1974, Wright and Wilson 1972, Wright et al. 1975) and could be selectively bred to further decrease their susceptibility to damage (Bridgen and Hanover 1982).

As with most agricultural commodities, growers and consumers tolerate only minimal damage to Christmas trees. Scotch pine is grown on a 7- to 10-year rotation and many fields are intensively managed to minimize damage from pests (Leefers et al. 1988). Traits that can be affected by insect pests include growth rate, fullness and color of foliage, stem and branch strength, and aesthetic qualities of Christmas trees (Koelling and Heiligmann 1993, Sowder 1966). Insect pests can be grouped according to the type of feeding damage they cause (Root 1967). Sap-feeding insects, such as scales, aphids and adelgids create necrotic spots on needles and premature needle drop or provide entry points for disease (Walstad et al. 1973). Defoliating insects, such as sawflies and some chafer beetle adults, form gaps in the foliage, which can reduce tree growth rate and detracts from a tree's symmetrical shape (Dunn and Kennedy 1983). Phloem-borers, such as weevils and *Dioryctria* spp. can weaken tree stems and branches, causing the stem or limbs to break in the wind or during harvest (Jactel et al. 1994). Insects feeding inside shoots, such as some bark beetles and some lepidopterans, cause shoots to bend, redden and die (McKeague and Simmons 1978). Many of these types of insects are difficult to control in Christmas tree fields.

Knowledge of insect phenology and seasonal abundance is important for planning scouting, management activities, and estimating potential damage. Over 30 insect species are known to infest Scotch pine in Michigan, but not all of them are considered major pests (Benyus 1983). Given the different life cycles and feeding habits of each species, growers may overuse pesticides as a control method (Ascerno 1991, Benyus 1983). Pesticide applications kill parasitoids and predators of pests, as well as non-target arthropods, sometimes resulting in pest resurgence (Clarke et al. 1992, Luck and Dahlsten 1975, Negron and Clarke 1995, Stern et al. 1959). An improved understanding of whether pest management can be timed to avoid negatively impacting beneficials and non-targets and whether varietal differences affect beneficial arthropod abundance is needed. In addition, research is needed to determine if various pest species or feeding guilds selectively attack certain Scotch pine varieties.

The objectives of this study included identifying the phenology and species composition of beneficial and pest arthropods and determining if differences existed among four varieties of Scotch pine throughout the growing season in 1994 and 1995.

MATERIALS AND METHODS

Study Sites

Phenology and species composition of pest and beneficial arthropods were monitored at two field locations. In the W. K. Kellogg Experimental Forest (Augusta, Kalamazoo County, Michigan), a 0.8 ha field with 27 Scotch pine varieties was hand-planted in 1987. Each variety was planted in two adjacent rows in a north-south direction, with 6 x 6 ft (1.8 x 1.8 m) between trees. Spacing increased as trees were sold or culled due to insect and disease damage. Trees were sheared each July and herbaceous vegetation was mowed monthly. Pesticides were used to control major pests before this project began, but were not applied on or near trees during 1994 and 1995. The field was bordered by mature white spruce (*Picea glauca* (Moench) Voss) and Scotch pine.

The other field site was in a private, 1.6 ha Christmas tree field near Greenville, Montcalm County, Michigan. In 1986, 19 varieties were planted in rows from north to south with 6 x 6 ft (1.8 x 1.8 m) spacings between trees. The field was adjacent to agricultural land and a small woodlot. Trees were sheared annually and herbaceous vegetation was mowed monthly. Pesticides were not applied to these trees in 1994 or 1995, and were only used once previously in the field during a pine root collar weevil (*Hylobius radicis* Buch., Coleoptera: Curculionidae) infestation in 1992.

Scotch Pine Varieties

The four varieties chosen for this study were Pike Lake Improved (var. *aquitana*), Land O' Pine (var. *hercynica*), Belgium (var. *haguenensis*) and Riga (var. *rigensis*). They were selected based on their physical differences, range of geographic origin and the results of previous research (Ruby and Wright 1976, Tobolski and Hanover 1971, Wright et al. 1975). Primary differences among varieties were in origin, needle length, winter needle color, and relative growth rate (Chapter 1, Table 1) (Tobolski and Hanover 1971, Wright et al. 1966).

In 1994, 18 trees per variety were randomly selected from Riga, Land O' Pine and Pike Lake Improved at Kellogg Forest. Only 13 trees were selected in Belgium because other trees had been cut and sold as Christmas trees within the variety. At the Greenville site, 36 trees per variety were randomly selected. Height, basal diameter, and stem diameter between the top second and third whorls and the third and fourth whorls were measured on all trees in 1994. In 1995, 13 trees per variety were selected at Kellogg Forest, and 16 trees per variety were randomly selected at the Greenville site. Tree size in 1995 was standardized at both locations by choosing trees of similar heights.

Species Composition and Phenology

Several insect pests and beneficial arthropod groups were monitored on the experimental trees (Table 1). Arthropod populations were counted twice a month on the selected trees from early May to late August. Each tree was examined from top to bottom from three directions (N, SE, SW) and total numbers of pests and beneficials according to species (when possible), feeding guild and date were determined. At the time of each sampling occasion, arthropods were not removed from their feeding sites, but tree damage was assessed and marked (flagging tape or paint) or dead shoots were removed to prevent subsequent recounting. Results for mobile arthropods (e.g., beneficials, Lepidoptera, Coleoptera) varied in each sample, but sessile or non-dispersing arthropods (e.g., scales) were recounted. Tree shearing each summer removed most early summer shoot-boring damage.

Statistical Analysis

Before analysis, species and damage data were pooled into feeding guilds by month. Results were transformed [log (x+1)] to adjust for non-normal distributions and heterogeneous variances, then analyzed using a parametric two-factor ANOVA with repeated measures to test for effects of field location (Kellogg Forest vs. Greenville) and variety (JMP for Windows, Version 3.1, SAS Institute 1995). Species differences among varieties in each month at both locations were tested with the nonparametric Kruskal-Wallis test since the assumptions of a parametric ANOVA were not met, and Chi-square values are reported. Associations among arthropod abundance, tree height, basal diameter and upper whorl diameters in 1994 were examined using the nonparametric Spearman's rank correlation test (Zar 1996). All analyses were conducted with an alpha level of $p<0.05$.

RESULTS

Scotch Pine Varieties

Tree characteristics potentially relevant to arthropod feeding guilds differed among varieties. Tree heights at Kellogg Forest ranged from 193 cm to 268 cm, while at Greenville, tree heights ranged from 209 cm to 236 cm (Table 2). At Kellogg Forest, Riga trees were the shortest (F=59.12, df=3, $p<0.001$), had the smallest basal diameter (F=26.16, df=3, $p<0.001$), diameter at breast height (F=4.07, df=3, $p<0.05$), and the shortest needles in 1994 (F=5.42, df=3, $p<0.01$), while Belgium trees were the tallest, and the stem diameters were nearly identical in the other three varieties. At Greenville, Riga trees were again the shortest (F=9.88, df=3, $p<0.001$), had the smallest basal diameter (F=11.96, df=3, $p<0.001$) and diameter at breast height (F=8.21, df=3, $p<0.001$), while Land O' Pine had the tallest trees, and stem diameters were nearly identical in the other three varieties (Table 2).

Arthropod Communities in Scotch Pine Fields

Feeding guild abundance was dominated by sap-feeding insects at both Kellogg Forest and Greenville in 1994 and 1995 (Figure 1). The beneficial arthropod guild represented 42% of the community at Kellogg Forest in 1994, but decreased slightly to 37% in 1995 as the percentage of sap-feeders increased. In addition, the percentage of shoot-borers, defoliators and phloem-borers decreased from 9.5% in 1994 to 2.6% in 1995 at Kellogg Forest. Sap-feeders at Greenville in 1994 comprised 91% of the community and increased to 99.6% in 1995.

Seasonal Changes in Feeding Guild Abundance

Arthropod abundance in each feeding guild varied throughout the summer at Kellogg Forest and Greenville in 1994 (Tables 3, 4). At Kellogg Forest, the number of sap-feeders and phloem-borers declined over time, but not significantly. In contrast, at Greenville, the number of sap-feeders was significantly higher during August and the number of phloem-borers was higher in May than in other months. At Kellogg Forest, defoliator abundance was higher during July than in the other months sampled (Tables 3, 4), but Greenville had a small, declining defoliator population. Shoot-borer abundance was highest in June, and the abundance of beneficial arthropods was highest in August at both locations (Tables 3, 4).

In 1995, numbers of arthropods in each feeding guild varied from May through August at both locations (Table 4, 5). At Kellogg Forest, numbers of sap-feeders and shoot-borers were highest in June (Table 5). In contrast, at Greenville the number of sap-feeders was highest in August and the number of shoot-borers did not vary significantly during the summer (Table 5). Defoliator abundance was highest in August at Kellogg Forest, but numbers did not vary significantly at Greenville (Table 5). Phloem-borer abundance did not vary significantly at either location in 1995, but the abundance of beneficial arthropods was highest in August at both locations (Table 5).

Feeding Guild Abundance Among Four Scotch Pine Varieties

Differences in total feeding guild abundance among the four Scotch pine varieties were more apparent at Kellogg Forest than at Greenville in 1994 (Table 6). Shoot-borer abundance was lowest on Riga at both Kellogg Forest ($X^2=33.40$, df=3, $p<0.001$) and Greenville ($X^2=9.27$, df=3, $p<0.05$) compared to other varieties. Total numbers of sap-feeders and defoliators were not significantly different among varieties at either location. Although the number of phloem-borers was highest on Belgium at Kellogg Forest ($X^2=24.74$, df=3, $p<0.001$), differences among varieties were not significantly different at Greenville. Similarly, the abundance of beneficial arthropods was higher on Riga at Kellogg Forest ($X^2=34.08$, df=3, $p<0.001$) (Table 6), but differences in beneficial arthropod numbers among varieties at Greenville did not significantly differ.

The ratio of beneficial to pest arthropods was significant at both Kellogg Forest and Greenville in 1994 (Table 7). From one to two beneficials per pest arthropod were present on trees at Kellogg Forest, and this ratio was significantly higher on Riga trees than on the other varieties (F=4.61, df=3, $p<0.01$). Pine needle scale abundance may have lowered this ratio, so if pine needle scale numbers were excluded, the ratio increased to up to five beneficials for every one pest arthropod in Riga (F=11.09, df=3, $p<0.001$) (Table 7). At Greenville, pest arthropods outnumbered beneficials, except in Belgium trees (F=3.12, df=3, $p<0.05$) (Table 7). If pine needle scale numbers were excluded, one to two beneficials per pest arthropod were found on varieties, but the ratio was significantly higher in Belgium trees (F=4.58, df=3, $p<0.01$).

Fewer differences in total feeding guild abundance among the four varieties were observed in 1995 than in 1994 at Kellogg Forest and Greenville (Table 8). Sap-feeder abundance was highest on Belgium at Kellogg Forest (F=2.91, df=3, $p<0.05$), but did not differ significantly among varieties at Greenville. Shoot-borer abundance was highest on Pike Lake Improved and lowest on Belgium at Greenville (F=3.44, df=3, $p<0.05$), but differences were not significant at Kellogg Forest. Number of beneficial arthropods was highest on Riga at Kellogg Forest (F=10.52, df=3, $p<0.001$), but did not differ among varieties at Greenville.

The ratio of beneficial to pest arthropods was significant at Kellogg Forest, but not at Greenville in 1995 (Table 7). Less than one beneficial per pest arthropod was present on most trees at Kellogg Forest, but the ratio was significantly higher on Riga trees than on the other varieties (F=3.07, df=3, $p<0.05$). If pine needle scale numbers were excluded, the ratio increased only slightly, although it was still statistically higher in Riga trees (F=3.53, df=3, $p<0.05$) (Table 7). At Greenville, pest arthropods greatly outnumbered beneficials, but differences did not significantly differ among varieties (Table 7). Ratios were increased if pine needle scale numbers were excluded, but again did not significantly differ among varieties.

Species Composition of Feeding Guilds

Sap-feeding Guild. The insects monitored in this guild were pine spittlebug, pine needle scale, pine tortoise scale and aphids (Table 1). At Kellogg Forest and Greenville in 1994, pine needle scale was the predominant sap-feeder (Tables 9, 10). Pine needle scale numbers were higher on Riga than on Belgium at Greenville in August (Table 10). Pine tortoise scale abundance was highest on Riga at Kellogg Forest in May and June (Table 9). At Kellogg Forest, spittlebug abundance was highest on Belgium and lowest on Land O' Pine and Pike Lake Improved in June and July (Table 9). However, at Greenville in July and August, spittlebug numbers were highest on Land O' Pine and lowest on Belgium and Pike Lake Improved in July and August (Table 10). Numbers of aphids in May at Greenville were highest on Riga and lowest on Belgium, but in July abundance was highest on Pike Lake Improved and lowest on Riga (Table 10).

In 1995, pine spittlebugs were the primary sap-feeders at Kellogg Forest (Table 11), but at Greenville, pine needle scales were most abundant (Table 12). Pine needle scale numbers were higher on Riga and Pike Lake Improved than on Land O' Pine at Kellogg Forest in May, but did not significantly differ the following months. Abundance of pine tortoise scale was higher on Belgium than on Land O' Pine in June at Kellogg Forest (Table 11). Numbers of pine spittlebug were higher on Riga than on Pike Lake Improved in July and August at Kellogg Forest. Pine aphid abundance was higher on Pike Lake Improved than on other varieties at Kellogg Forest in May and June (Table 11). Significant differences in species abundance in the sap-feeding guild were not detected at Greenville in 1995 (Table 12).

Defoliating Guild. The defoliators monitored were sawflies, chafer beetles, grasshoppers and jack pine budworm (Table 1). In 1994, chafer beetles were predominant at Kellogg Forest (Table 9), while jack pine budworm was the major defoliator at Greenville (Table 10). More grasshoppers were found on Riga trees at Kellogg Forest than on other varieties from June through August in 1994 (Table 9). There were no significant differences in species abundance in the defoliating guild at Greenville in 1994 (Table 10). In general, fewer defoliators were found at Greenville than at Kellogg Forest.

In 1995, chafer beetles were the most abundant defoliator at Kellogg Forest, while there were more pine sawflies than other defoliators at Greenville (Tables 11, 12). Significant differences among varieties were not detected at the species level at either location.

Shoot-boring Guild. The shoot-boring species monitored were eastern pine shoot borer and the pine shoot beetle (Table 1). In June 1994, eastern pine shoot borer abundance at Kellogg Forest was significantly lower on Riga trees than on the other three varieties, and lower on Land O' Pine trees in July (Table 10). At Greenville, eastern pine shoot borer abundance was lower on Riga during June and July, but was higher on Riga in May than on other varieties (Table 11). Pine shoot beetle abundance was higher on Belgium than on Riga in June at Kellogg Forest, but numbers of pine shoot beetle were not significantly different among varieties at Greenville for any month (Table 11). Tree shearing that occurred in late June removed most shoot-boring damage on trees, so the numbers of shoot-borers on study trees dropped in July.

In 1995, the eastern pine shoot borer comprised more of the shoot-borer guild than the pine shoot beetle at both locations (Tables 12, 13). Eastern pine shoot borer abundance was not significantly different among varieties at Kellogg Forest, but was higher on Pike Lake Improved than on Riga and Belgium in July at Greenville. Pine shoot beetle abundance was not significantly different among varieties at either location during the summer.

Phloem-boring Guild. The phloem-boring guild consisted of Zimmerman pine moth and weevils, such as pales weevil (*Hylobius pales* Herbst.), pine root collar weevil (*Hylobius radicis* Buch.) and white pine weevil (*Pissodes strobi* (Peck)) (Table 2).

Zimmerman pine moth was found in greater proportions than the weevils at both Kellogg Forest and Greenville in 1994 (Tables 10, 11). At Kellogg Forest in May and July 1994, higher numbers of Zimmerman pine moth were found on Belgium than on other varieties. At Greenville in May 1994, Land O' Pine had higher numbers of Zimmerman pine moth than Riga, but Zimmerman pine moth was more abundant on Belgium than on other varieties in June, according to the number of pitch masses found. Significant differences in weevil abundance among varieties were not detected at either location in any month.

In 1995, there were proportionally more Zimmerman pine moth than weevils at both locations (Tables 12, 13). No significant differences in Zimmerman pine moth and weevil abundance among varieties at either location for any month could be detected.

Beneficial Arthropod Guild. The beneficial arthropod guild consisted of sheet and funnel web spiders, ladybird beetles, lacewings and parasitic wasps (Table 2). In 1994, spiders represented most of the beneficial arthropod guild at both Kellogg Forest and Greenville (Tables 10, 11). At Kellogg Forest, numbers of spiders were higher on Riga than on the other varieties from June through August. At Greenville in June, spider abundance was higher on Belgium than on Pike Lake Improved. No significant differences for lacewings or parasitic wasps were detected at either location, but ladybird beetle abundance was higher on Land O' Pine than on other varieties in May.

In 1995, spiders were again the most abundant species in the beneficial arthropod guild at Kellogg Forest and Greenville (Tables 12, 13). At Kellogg Forest, spider abundance was higher on Riga than on the other varieties from May through August. At

Greenville in May, spider abundance was higher on Belgium than on Pike Lake Improved. Spiders were an important source of scale mortality because I observed webs covered with crawlers during peak emergence periods. In August at Kellogg Forest, lacewing abundance was higher on Belgium than on Land O' Pine and Pike Lake Improved. Parasitic wasp and ladybird beetle abundance did not significantly differ at either location.

DISCUSSION

The four Scotch pine varieties used in this study differed in traits potentially affecting susceptibility to the different feeding guilds. Belgium and Land O' Pine had the tallest trees, Pike Lake Improved was moderate, and Riga had the shortest trees and smallest stem diameters at both locations. Although trees at Greenville were planted a year earlier than at Kellogg Forest, varieties had similar stem diameters and tree height at both locations. Variation in monoterpene concentration (Tobolski and Hanover 1971) and resin acids (Bridgen and Hanover 1982) for these and other varieties have been studied in Michigan. In addition to the environmental and genetic factors affecting tree growth rates, the cultural practice of shearing reduces height growth and promotes lateral bud growth (Hill 1989, Johnson 1991). If shearing is timed appropriately, in addition to improving tree shape, it can also remove early shoot-feeding damage.

Some other tree variables, including differences in monoterpene concentration and resin acids, were previously studied in these and other Scotch pine Christmas tree varieties in Michigan. Among the four varieties, Pike Lake Improved (var. *aquitana*) and Riga (var. *rigensis*) were short and of similar heights, Land O' Pine (var. *hercynica*) was moderately tall, and Belgium (var. *haguenensis*) was the tallest variety with the fastest growth rate (Ruby and Wright 1976, Wright et al. 1966). From foliage color ranks, southern European varieties (e.g., Pike Lake Improved) were greenest, Scandinavian varieties (e.g., Riga) were yellowest and central European varieties had intermediate hues of green (Ruby and Wright 1976, Wright et al. 1966). Needles were longest in Belgium, moderately long in Land O' Pine, short in Riga, and shortest in Pike Lake Improved (Ruby and Wright 1976, Wright et al. 1966). In general, Scandinavian varieties (e.g., Riga) had lower concentrations of cortical monoterpenes (Tobolski and Hanover 1971), higher concentrations of resin acids, lower oleoresin pressure and smaller resin canal cross-sectional areas than the other varieties (Bridgen and Hanover 1982). Nutrient differences in foliage among varieties were apparent, but statistical significance was unknown (Ruby and Wright 1976).

Tree characteristics contributing to resistance to different arthropod feeding guilds and species vary. Previous studies have shown that water availability in trees limits the movement of minerals through phloem sap, affecting sap-feeding insect feeding efficiency, survival and fecundity (see Hanks and Denno 1993). Resin acid concentration, nutrient and moisture content of needles, and tree vigor may be important factors in defoliator survival (Larsson et al. 1986, Lyytikainen 1994, Mopper et al. 1990). Shoot phenology, tree size and shoot diameter may be critical to shoot-boring arthropods (Lawrence and Haack 1995, McCullough and Smitley 1995, McKeague and Simmons 1978). Phloem-borer success may be associated with rate of resin flow, phloem thickness, monoterpene concentration or intensity of branch pruning (Hodges et al. 1979, Jactel et al. 1994, Wilson et al. 1975). Beneficial arthropods need a stable food supply and shelter from pesticide applications and other management methods (Arthur 1963, Clarke et al. 1992, Luck and Dahlsten 1975, Negron and Clarke 1995).

The communities of arthropods in the two Christmas tree fields differed in diversity. Total numbers of sap-feeders and beneficial arthropods were higher at Greenville than at Kellogg Forest, but more shoot-borers, phloem-borers and defoliators were found at Kellogg Forest. This variation between locations may have resulted from differences in the density of Scotch pine Christmas trees in the area. The site at Kellogg Forest was surrounded by mature deciduous and coniferous trees which may have harbored low populations of several minor pests. Kellogg Forest was also isolated from other Christmas tree fields; there were only 18 other Christmas tree operations in Kalamazoo County (158 ha) (Mich. Agr. Stat. Serv. 1994). In contrast, the site near Greenville was surrounded mostly by agricultural and Christmas tree fields; about 30 other Christmas tree operations were located near Greenville (2,145 ha) (Mich. Agr. Stat. Serv. 1994). The greater production of Christmas trees near Greenville may have contributed to higher populations of arthropod pests in that experimental field.

It was expected that the abundance of each feeding guild would vary throughout the summer months, given the diverse life cycles of species within the guilds. Arthropods most active in early summer were the phloem-borers and shoot-borers. By late summer, numbers of defoliators, sap-feeders, and beneficial arthropods had increased. Most of the phloem-borer activity monitored was of the Zimmerman pine moth, which began feeding in the spring and created visible pitch masses on the bark. Eastern pine shoot borer was the primary species monitored in the shoot-boring guild. Larval activity of this insect in shoots was completed by late June, and subsequent shearing removed damaged shoots. Defoliator numbers had increased by the end of the summer because of the increasing chafer beetle presence on trees. Sap-feeder abundance also rose through the summer because of the multiple generations of the monitored species, such as aphids and pine needle scale. In the beneficial arthropod guild, numbers of ballooning spiders increased gradually in agricultural systems and reached a peak in late summer (Nyffeler et al. 1994). The slower increase on Christmas trees in early summer may have been due to the disruption of webs caused by shearing.

Total feeding guild abundance on the four Scotch pine varieties indicated resistance in some varieties, but results were not always consistent. There were fewer shoot-borers on Riga trees than on the other varieties, but previous studies on resistance to eastern pine shoot borer noted that Pike Lake Improved was most heavily attacked, while Belgium was more resistant (King 1971, Steiner 1974). Studies on resistance to sawflies found that Scotch pine varieties from central Europe (e.g., Belgium and Land O' Pine) were more susceptible to defoliation than Scandinavian varieties (e.g., Riga) (Ghent 1959, Wright et al. 1967), but differences were not detected in my study. My results also suggest that phloem-borers and sap-feeders may have preferred Belgium trees as hosts. However, sap-feeder abundance varied between years, months and locations, making results less reliable. Others also suggested the presence of resistance in varieties against phloem-borers (e.g., Zimmerman pine moth), where Belgium was considered one of the most susceptible varieties (Harrell 1993, Wright et al. 1975).

The ratio of beneficial arthropods to pest abundance was higher on Riga trees at Kellogg Forest and higher on Belgium trees at Greenville than on other varieties. Pests were more abundant than beneficial arthropods due to the number of scales present. If scales were excluded from the analysis, differences among varieties remained similar, but the ratios increased. It was interesting to note that the ratios at Kellogg Forest and

Greenville were somewhat similar, although the Greenville field had more pests than beneficials. The nearly 1:1 ratio of beneficials to pest arthropods in unsprayed Christmas tree fields suggests that for every pest killed by a pesticide spray, one beneficial could be killed. At Greenville, pesticide applications on neighboring agricultural fields may have increased the emigration of beneficials from those fields onto the unsprayed Christmas tree field.

Varietal resistance to sap-feeding, defoliating, shoot-boring, phloem-boring and beneficial arthropod feeding guilds may not provide enough justification for initiating new tree breeding programs in the Christmas tree industry. I found very little evidence of resistance to entire feeding guilds, although I did find some resistance to individual pest species. Of the feeding guilds studied, shoot-borers and defoliators were minor pests in terms of their abundance and the amount of damage that they caused. Varieties may have some resistance against phloem-borers, which have the potential to be major pests, but numbers were too low in this study to detect strong differences. However, sap-feeders were abundant and major pests, and it seems evident that the large numbers of beneficials present in fields were unable to regulate their population. If further studies investigating varietal resistance are conducted, efforts should be concentrated on those pests capable of causing the greatest economic injury.

Table 1. Arthropod pests and beneficials monitored at Kellogg Forest and Greenville in 1994 and 1995.

Common name	Scientific name	Order: Family
Sap-feeders:		
Pine needle scale	*Chionaspis pinifoliae* (Fitch)	Homoptera: Diaspididae
Pine tortoise scale	*Toumeyella parvicornis* (Cockerell)	Homoptera: Coccidae
Pine spittlebug	*Aphrophora parallela* (Say)	Homoptera: Cercopidae
Pine aphids	*Cinara* spp.	Homoptera: Aphididae
Defoliators:		
Grasshoppers	*Melanoplus* spp.	
Chafer beetles	*Anomala oblivia* (Horn) and *Popillia japonica* Neum.	Coleoptera: Scarabaeidae
Pine sawflies	*Diprion similis* (Hartig), *Neodiprion sertifer* (Grote), *Gilpinia frutetorum (F.)*	Hymenoptera: Diprionidae
Jack pine budworm	*Choristoneura pinus* (Freeman)	Lepidoptera: Tortricidae
Shoot-borers:		
Eastern pine shoot borer	*Eucosma gloriola* Heinrich	Lepidoptera: Tortricidae
Pine shoot beetle	*Tomicus piniperda* (L.)	Coleoptera: Scolytidae
Phloem-borers:		
Weevils		Coleoptera: Curculionidae
Zimmerman pine moth	*Dioryctria zimmermani* (Grote)	Lepidoptera: Pyralidae
Beneficial arthropods:		
Ladybird beetles	-	Coleoptera: Coccinellidae
Lacewings	-	Neuroptera: Chrysopidae, Hemerobiidae
Parasitic wasps	-	Hymenoptera: Ichneumonidae, Brachonidae
Spiders	-	Arachnidae: Agelenidae, Linyphiidae

Table 2. Mean tree measurements (±SE) on four varieties of Scotch pine at Kellogg Forest and Greenville in 1994 (n = 18 trees per variety).[1]

Location	Variable	Riga	Belgium	Land O' Pine	Pike Lake Imp.
Kellogg Forest	Needle length (mm)[2]	55.3 (2.2)^{a}	68.9 (2.7)^{b}	70.4 (3.2)^{b}	57.0 (4.9)^{a}
	Tree height (cm)	192.9 (4.5)^{a}	267.8 (4.5)^{c}	226.0 (3.7)^{b}	205.3 (3.3)^{a}
	Basal diameter (cm)	6.6 (0.2)^{a}	9.0 (0.3)^{b}	9.8 (0.3)^{b}	9.3 (0.4)^{b}
	Diameter at breast height (cm)	2.9 (0.2)^{a}	3.6 (0.1)^{b}	3.1 (0.1)^{ab}	3.2 (0.1)^{ab}
Greenville	Tree height (cm)	209.1 (3.4)^{a}	227.8 (4.2)^{bc}	236.1 (4.0)^{c}	222.4 (2.7)^{b}
	Basal diameter (cm)	8.1 (0.2)^{a}	9.0 (0.2)^{b}	9.7 (0.2)^{b}	9.4 (0.2)^{b}
	Diameter at breast height (cm)	3.6 (0.2)^{a}	4.4 (0.2)^{b}	4.6 (0.2)^{b}	4.3 (0.1)^{b}

[1] Means followed by the same letter did not differ significantly at the $p < 0.05$ level.

[2] Needle lengths were measured at Kellogg Forest as part of a related study; needle length was not measured at Greenville.

Table 3. Mean number of arthropods per tree (±SE) in each feeding guild at Kellogg Forest and Greenville in 1994 (varieties were pooled).[1]

Arthropod guild	May	June	July	August
Kellogg Forest				
Sap-feeders	311.8 (54.8)^{a}	288.3 (64.3)^{a}	210.5 (50.8)^{a}	202.8 (107.2)^{a}
Defoliators	0.0^{a}	17.5 (7.4)^{ab}	44.3 (8.3)^{c}	30.8 (4.7)^{bc}
Shoot-borers	3.0 (1.7)^{a}	59.3 (16.9)^{b}	6.8 (2.6)^{a}	1.3 (0.8)^{a}
Phloem-borers	12.0 (8.4)^{a}	6.5 (1.0)^{a}	4.8 (2.2)^{a}	0^{a}
Beneficials	89.0 (10.2)^{a}	134.0 (30.2)^{a}	197.8 (46.9)^{a}	469.0 (100.4)^{b}
Greenville				
Sap-feeders[2]	1,900 (206)^{a}	4,420 (846)^{a}	1,799 (422)^{a}	27,216 (10,727)^{b}
Defoliators	6.88 (5.00)^{a}	0.38 (0.26)^{a}	0^{a}	0^{a}
Shoot-borers	4.3 (0.9)^{a}	21.6 (3.9)^{b}	4.8 (1.5)^{a}	0.6 (0.4)^{a}
Phloem-borers	7.50 (3.57)^{b}	0.88 (0.48)^{ab}	2.00 (1.02)^{ab}	0.13 (0.13)^{a}
Beneficials	243.8 (21.0)^{a}	305.4 (31.3)^{a}	980.1 (64.6)^{b}	1,769.8 (238.7)^{c}

[1] Guild means followed by the same letter did not significantly differ at the $p<0.05$ level.

[2] Field measurements were estimated due to high population sizes.

Table 4. Results of two-factor analysis of variance with repeated measures for feeding guilds at Kellogg Forest and Greenville in 1994 and 1995.[1]

Year	Anova table	df	Sap-feeders	Defoliators	Shoot-borers	Phloem-borers	Beneficials
1994	Location	1	29.18 **	5.19	1.18	3.15	13.61 *
	Variety	3	0.70	0.52	1.28	1.66	1.02
	Loc*Var	3	1.39	0.72	1.26	1.71	4.34 **
	Tree (Loc, Var)	131	2.18 ***	2.51 ***	1.19	1.94 ***	4.27 ***
	Month	3	5.75	0.83	4.05	6.39	16.29 *
	Month*Loc	3	3.09	43.29 ***	9.00 **	0.65	27.52 ***
	Month*Var	9	0.28	1.29	3.32 *	1.02	1.29
	Month*Loc*Var	9	2.15 **	2.62 **	4.24 ***	7.58 ***	1.02
1995	Location	1	15.08 *	0.70	3.54	5.51	11.98 *
	Variety	3	0.79	1.57	1.84	1.21	0.87
	Loc*Var	3	1.42	0.77	0.96	0.84	4.04 *
	Tree (Loc, Var)	108	4.58 ***	1.21	1.27	3.87 ***	5.79 ***
	Month	3	0.32	0.32	1.65	1.88	34.3 *
	Month*Loc	3	143.25 ***	37.29 ***	16.23 ***	1.93	4.24 *
	Month*Var	9	1.24	1.67	3.17 *	1.20	0.60
	Month*Loc*Var	9	0.55	1.01	0.65	1.83	1.88

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[1] * = significant at $p<0.05$; ** = significant at $p<0.01$; *** = significant at $p<0.001$.

Table 5. Mean number of arthropods per tree (±SE) in each feeding guild at Kellogg Forest and Greenville in 1995 (varieties were pooled).[1]

Arthropod guild	May	June	July	August
Kellogg Forest				
Sap-feeders	294.3 (23.0)^{a}	1,841.5 (171.4)^{b}	258.3 (35.6)^{a}	135.5 (119.3)^{a}
Defoliators	9.3 (8.6)^{a}	4.3 (1.5)^{a}	22.5 (3.9)^{ab}	36.0 (5.0)^{b}
Shoot-borers	0.75 (0.48)^{a}	13.25 (4.48)^{b}	7.75 (1.80)^{ab}	0.25 (0.25)^{a}
Phloem-borers	1.00 (0.41)^{a}	2.75 (1.25)^{a}	7.75 (3.33)^{a}	3.00 (1.29)^{a}
Beneficials	225.0 (59.6)^{a}	228.8 (43.7)^{a}	382.5 (43.0)^{a}	689.0 (71.9)^{b}
Greenville				
Sap-feeders[2]	29,080 (2,930)^{a}	54,840 (13,490)^{a}	112,650 (26,600)^{a}	677,830 (252,800)^{b}
Defoliators	61.3 (52.9)^{a}	33.0 (10.7)^{a}	2.3 (0.8)^{a}	3.5 (1.3)^{a}
Shoot-borers	0^{a}	1.00 (0.41)^{a}	2.75 (2.43)^{a}	0^{a}
Phloem-borers	0^{a}	1.25 (0.95)^{a}	1.75 (1.11)^{a}	0.50 (0.29)^{a}
Beneficials	667.0 (57.6)^{a}	547.5 (33.9)^{a}	874.3 (25.3)^{b}	1,441.0 (39.1)^{c}

[1] Guild means followed by the same letter did not significantly differ at the $p<0.05$ level.

[2] Field measurements were estimated due to high population sizes.

Table 6. Mean number of arthropods per tree (±SE) in each feeding guild at Kellogg Forest and Greenville in 1994 (n=18 trees per variety).[1]

Arthropod guild	Riga	Belgium	Land O' Pine	Pike Lake Imp.
Kellogg Forest				
Sap-feeders	72.4 (26.3)^{a}	103.4 (41.2)^{a}	29.9 (10.5)^{a}	48.2 (12.6)^{a}
Defoliators	4.8 (0.7)^{a}	4.2 (0.8)^{a}	6.4 (1.5)^{a}	6.3 (2.1)^{a}
Shoot-borers	0.9 (0.3)^{a}	6.6 (1.0)^{b}	5.7 (0.8)^{b}	4.3 (0.7)^{b}
Phloem-borers	0.5 (0.3)^{a}	4.1 (0.9)^{b}	1.3 (0.5)^{a}	0.4 (0.4)^{a}
Beneficials	80.3 (5.7)^{b}	50.5 (3.6)^{a}	39.2 (2.3)^{a}	41.7 (3.3)^{a}
Greenville				
Sap-feeders[2]	3,302 (1090)^{a}	587.3 (185)^{a}	904.8 (235)^{a}	3058 (1075)^{a}
Defoliators	0^{a}	1.5 (1.1)^{a}	0.1 (0.1)^{a}	0.03 (0.03)^{a}
Shoot-borers	0.8 (0.2)^{a}	2.0 (0.4)^{ab}	2.2 (0.4)^{b}	2.0 (0.4)^{ab}
Phloem-borers	0.1 (0.1)^{a}	0.8 (0.4)^{a}	0.9 (0.3)^{a}	0.5 (0.2)^{a}
Beneficials	164.0 (13.9)^{a}	221.3 (18.4)^{a}	180.5 (15.5)^{a}	167.3 (13.6)^{a}

[1] Guild means followed by the same letter did not significantly differ at the $p<0.05$ level.

[2] Field measurements were estimated due to high population sizes.

Table 7. Mean ratios of beneficial to pest arthropod numbers per tree (±SE) among varieties at Kellogg Forest and Greenville in 1994 and 1995.[1]

	Riga	Belgium	Land O' Pine	Pike Lake Imp.
Kellogg Forest 1994				
Ratio including all pests:	2.76 (0.61)^{b}	1.35 (0.29)^{ab}	1.47 (0.20)^{ab}	1.02 (0.12)^{a}
Ratio excluding pine needle scale:	5.12 (0.77)^{b}	1.82 (0.27)^{a}	2.12 (0.23)^{a}	2.26 (0.27)^{a}
Kellogg Forest 1995				
Ratio including all pests:	1.52 (0.42)^{b}	0.53 (0.10)^{a}	0.72 (0.21)^{ab}	0.74 (0.14)^{ab}
Ratio excluding pine needle scale:	1.68 (0.41)^{b}	0.66 (0.12)^{a}	0.74 (0.21)^{a}	0.87 (0.15)^{ab}
Greenville 1994				
Ratio including all pests:	0.66 (0.17)^{a}	1.36 (0.24)^{b}	0.66 (0.14)^{a}	0.84 (0.18)^{ab}
Ratio excluding pine needle scale:	1.18 (0.17)^{a}	2.44 (0.49)^{b}	1.14 (0.16)^{a}	1.43 (0.19)^{ab}
Greenville 1995				
Ratio including all pests:	0.08 (0.06)^{a}	0.09 (0.05)^{a}	0.10 (0.05)^{a}	0.06 (0.05)^{a}
Ratio excluding pine needle scale:	0.30 (0.05)^{a}	0.41 (0.09)^{a}	0.36 (0.05)^{a}	0.63 (0.25)^{a}

[1] Means followed by the same letter did not significantly differ at the $p<0.05$ level.

Table 8. Mean number of arthropods per tree (±SE) in each feeding guild at Kellogg Forest and Greenville in 1995 (n=13 trees per variety at Kellogg Forest; 16 trees per variety at Greenville).[1]

Arthropod guild	Riga	Belgium	Land O' Pine	Pike Lake Imp.
Kellogg Forest				
Sap-feeders	158.2 (24.4)^{a}	266.5 (38.1)^{b}	177.9 (23.2)^{ab}	175.7 (26.0)^{ab}
Defoliators	4.1 (0.7)^{a}	7.9 (2.8)^{a}	6.6 (0.9)^{a}	3.5 (0.8)^{a}
Shoot-borers	0.9 (0.3)^{a}	1.5 (0.5)^{a}	1.4 (0.5)^{a}	3.0 (1.1)^{a}
Phloem-borers	1.2 (0.9)^{a}	2.2 (1.1)^{a}	0.4 (0.4)^{a}	0.7 (0.3)^{a}
Beneficials	163.8 (14.1)^{b}	114.4 (12.0)^{a}	89.1 (4.7)^{a}	100.0 (6.2)^{a}
Greenville				
Sap-feeders[2]	49,747 (9590)^{a}	32,151 (8430)^{a}	30,189 (9230)^{a}	106,512 (44,400)^{a}
Defoliators	4.4 (2.5)^{a}	15.6 (9.5)^{a}	1.9 (0.6)^{a}	3.1 (1.8)^{a}
Shoot-borers	0.1 (0.1)^{ab}	0.0^{a}	0.1 (0.1)^{ab}	0.8 (0.4)^{b}
Phloem-borers	0.1 (0.1)^{a}	0.4 (0.4)^{a}	0.1 (0.1)^{a}	0.3 (0.2)^{a}
Beneficials	216.3 (26.4)^{a}	229.1 (29.4)^{a}	229.4 (18.8)^{a}	206.1 (25.8)^{a}

[1] Guild means followed by the same letter did not significantly differ at the $p<0.05$ level.

[2] Field measurements were estimated due to high population sizes.

Table 9. Percentage of species within each guild and Chi-square values from the Kruskal-Wallis analysis of variance to determine if species abundance varied among four varieties of Scotch pine at Kellogg Forest in 1994.

Arthropod	Percentage of guild	Sampling period May	 June	 July	 August
Sap-feeders:					
Pine needle scale	75.6	ns	ns	ns	ns
Pine tortoise scale	4.2	8.20*	8.11*	ns	ns
Pine spittlebug	18.3	ns	9.69*	21.43***	ns
Pine aphids	1.9	8.43*	ns	ns	ns
Defoliators:					
Grasshoppers	13.1	-	10.17*	10.36*	12.41**
Chafer beetles	86.9	-	ns	ns	ns
Pine sawflies	0.0	-	-	-	-
Jack pine budworm	0.0	-	-	-	-
Shoot-borers:					
Eastern pine shoot borer	67.3	-	24.11***	8.36*	ns
Pine shoot beetle	32.7	ns	21.95***	ns	ns
Phloem-borers:					
Weevils	7.5	ns	ns	ns	-
Zimmerman pine moth	92.5	27.91***	ns	11.23*	-
Beneficial arthropods:					
Ladybird beetles	1.2	ns	ns	ns	ns
Lacewings	0.2	-	ns	ns	-
Parasitic wasps	0.1	-	ns	-	-
Spiders	98.5	ns	18.10***	33.46***	28.98***

[a] * = significant at $p<0.05$; ** = significant at $p<0.01$; *** = significant at $p<0.001$.

- = Individuals of the species were not observed at the time of sampling.

Table 10. Percentage of species within each guild and Chi-square values from the Kruskal-Wallis analysis of variance to determine if species abundance varied among four varieties of Scotch pine at Greenville in 1994.

Arthropod	Percentage of guild	Sampling period			
		May	June	July	August
Sap-feeders:					
Pine needle scale	90.1	ns	ns	ns	8.93*
Pine tortoise scale	0.1	ns	ns	-	-
Pine spittlebug	8.8	ns	ns	16.40***	17.94***
Pine aphids	1	11.25*	ns	8.47*	ns
Defoliators:					
Grasshoppers	7.8	-	ns	ns	ns
Chafer beetles	2.2	-	ns	-	-
Pine sawflies	30.4	ns	ns	-	-
Jack pine budworm	59.6	-	8.83*	-	-
Shoot-borers:					
Eastern pine shoot borer	96.4	12.32**	8.54*	10.08*	ns
Pine shoot beetle	3.6	ns	ns	-	-
Phloem-borers:					
Weevils	11.9	ns	ns	ns	ns
Zimmerman pine moth	88.1	11.00*	9.13*	ns	-
Beneficial arthropods:					
Ladybird beetles	1.1	8.73*	ns	ns	ns
Lacewings	0.1	ns	ns	ns	8.83*
Parasitic wasps	0.1	ns	-	-	-
Spiders	98.7	ns	8.87*	ns	ns

[a] * = significant at $p<0.05$; ** = significant at $p<0.01$; *** = significant at $p<0.001$.

- = Individuals of the species were not observed at the time of sampling.

Table 11. Percentage of species within each guild and Chi-square values from the Kruskal-Wallis analysis of variance to determine if species abundance varied among four varieties of Scotch pine at Kellogg Forest in 1995.

	Percentage	Sampling period			
Arthropod	of guild	May	June	July	August
Sap-feeders:					
Pine needle scale	18.0	9.34*	ns	ns	ns
Pine tortoise scale	1.3	ns	14.23**	ns	ns
Pine spittlebug	79.1	ns	ns	13.24**	7.78*
Pine aphids	1.6	14.61**	14.43**	3.82	-
Defoliators:					
Grasshoppers	25.3	-	ns	ns	ns
Chafer beetles	61.8	-	ns	ns	ns
Pine sawflies	12.9	ns	-	-	-
Jack pine budworm	0.0	-	-	-	-
Shoot-borers:					
Eastern pine shoot borer	62.5	ns	ns	ns	ns
Pine shoot beetle	37.5	ns	ns	ns	-
Phloem-borers:					
Weevils	10.3	ns	ns	ns	ns
Zimmerman pine moth	89.7	ns	ns	ns	ns
Beneficial arthropods:					
Ladybird beetles	1.2	ns	ns	-	-
Lacewings	0.4	-	ns	ns	9.42*
Parasitic wasps	0.2	ns	ns	ns	ns
Spiders	98.2	26.10***	14.30***	14.23***	10.93*

[a] * = significant at p<0.05; ** = significant at p<0.01; *** = significant at p<0.001.

\- = Individuals of the species were not observed at the time of sampling.

Table 12. Percentage of species within each guild and Chi-square values from the Kruskal-Wallis analysis of variance to determine if species abundance varied among four varieties of Scotch pine at Greenville in 1995.

Arthropod	Percentage of guild	Sampling period May	June	July	August
Sap-feeders:					
Pine needle scale	98.5	ns	ns	ns	ns
Pine tortoise scale	0.2	ns	ns	ns	ns
Pine spittlebug	1.2	ns	ns	ns	ns
Pine aphids	0.1	ns	ns	ns	ns
Defoliators:					
Grasshoppers	3.4	-	ns	ns	ns
Chafer beetles	0.1	-	-	-	-
Pine sawflies	74.5	ns	ns	-	ns
Jack pine budworm	22.0	-	ns	ns	-
Shoot-borers:					
Eastern pine shoot borer	86.7	-	ns	9.41*	-
Pine shoot beetle	13.3	-	ns	-	-
Phloem-borers:					
Weevils	35.7	-	ns	-	-
Zimmerman pine moth	64.3	-	-	ns	ns
Beneficial arthropods:					
Ladybird beetles	6.5	ns	ns	ns	ns
Lacewings	0.2	ns	ns	ns	ns
Parasitic wasps	0.2	ns	ns	ns	ns
Spiders	93.1	8.4*	ns	ns	ns

[a] * = significant at p<0.05; ** = significant at p<0.01; *** = significant at p<0.001.

- = Individuals of the species were not observed at the time of sampling.

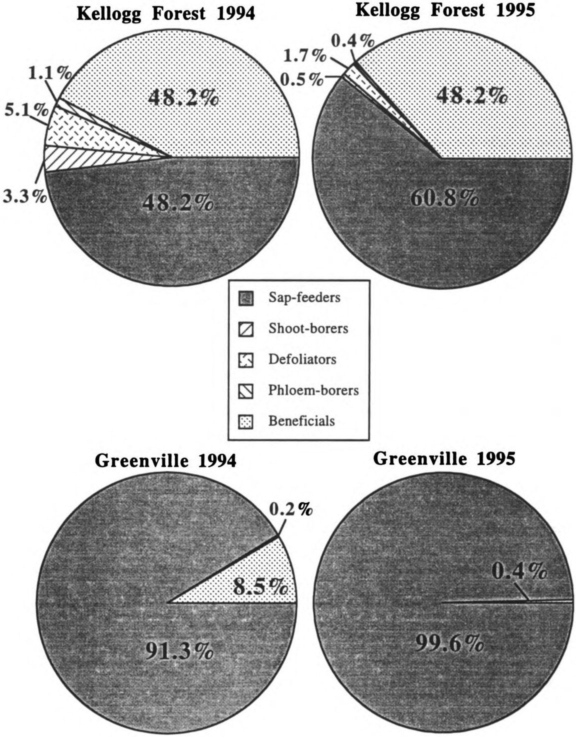

Figure 1. The proportion of arthropod feeding guilds on Scotch pine trees at Kellogg Forest and Greenville in 1994 and 1995.

FINAL CONCLUSIONS

The four varieties of Scotch pine used in this study differed from each other in height, stem diameter, basal diameter growth rate, needle length, percentage of moisture in needles, needle density and in percentage of nitrogen in one-year-old needles when grown under identical environmental conditions. These traits may contribute to greater genetic resistance against one or more major insect pests. Percentage nitrogen and/or percentage moisture in foliage were important traits in relation to Zimmerman pine moth, European pine sawfly and pine needle scale success.

These varieties of Scotch pine did not exhibit any obvious resistance to Zimmerman pine moth, a native pyralid in the Lake States. If it existed, the effects of host plant resistance were not strong enough to detect, perhaps because many larvae were killed by parasitism and disease. Conditions for larval development were influenced by tree stem diameter, tree height, percentage nitrogen in foliage and rate of resin flow. I could not determine the impact of resin flow on larvae, but suspected that it may be a source of early larval mortality. Other important mortality factors included parasitism by *Exeristes comstockii* (Hymenoptera: Ichneumonidae) and *Hyssopus rhyacioniae* (Hymenoptera: Eulophidae) and fungal infection by *Hirsutella nodulosa.*

Differences in European pine sawfly survival, development and fecundity were found among varieties. Sawfly performance was poor on Riga, slightly better on Land O' Pine, and fairly good on Belgium and Pike Lake Improved. I suspect that resin acid concentration, although not measured in this study, combined with nutrient and moisture content of foliage may have contributed to varietal resistance against larvae, while tree height and vigor may have been important traits to ovipositing adult females. Pupal parasitism by *Pleolophus basizonus* (Hymenoptera: Ichneumonidae) did not differ among varieties, but reduced sawfly survival in 1994.

Differences in pine needle scale performance were found among varieties. Scale survival and fecundity were higher on Pike Lake Improved and Riga than on Belgium and Land O' Pine. Percentage needle moisture and tree stem diameter predicted scale survival, and percentage nitrogen in needles and percentage needle moisture significantly predicted second generation scale fecundity. However, percentage nitrogen was not correlated with survival, perhaps because nitrogen content did not vary enough among varieties or was not limiting to scale performance. Deme formation was probably not applicable for scales living on Christmas trees, but scale performance may be affected by weather, dispersal mortality, and parasitism and predation. Evaluation of variety effects on pine needle scale would be more accurate under more controlled environmental conditions and over more than two scale generations.

Differences among varieties in resistance to natural infestations of arthropod guilds, and the phenology and species composition of beneficial and pest arthropods were also evaluated. In general, numbers of arthropods increased throughout the summer, primarily due to increasing numbers of scales and spiders on trees. Sap-feeders were more abundant than other guilds at both locations, but higher percentages of defoliators, shoot-borers, phloem-borers and beneficials were present at Kellogg Forest than at Greenville. Riga was more resistant than the other varieties to shoot-borers, while Belgium was more susceptible to phloem-borers. No strong significant differences among varieties in numbers of defoliators or sap-feeders were detected. Number of beneficial arthropods was highest on Riga trees at Kellogg Forest, but ratios of beneficials to pests indicated close to a 1:1 correspondence on all varieties. Ratios of beneficials to pests were slightly higher in 1994 than in 1995.

From these results, I suggest that Land O' Pine was not a strongly preferred host for any of the insects in this study, it had a moderate growth rate, moderate green needle color, and it originated from a climate similar to the Lake States. This variety may require less management for insect pests, and thus be an acceptable variety to grow as a Christmas tree. Alternatively, Riga trees could be grown as windbreaks in areas where foliage color and aesthetics are not as critical as in a Christmas tree field. Further studies to identify the specific mechanisms of resistance to these pests need to be conducted before breeding programs for improved varieties can begin.

APPENDIX 1

APPENDIX 1

Record of Deposition of Voucher Specimens*

The specimens listed on the following sheet(s) have been deposited in the named museum(s) as samples of those species or other taxa which were used in this research. Voucher recognition labels bearing the Voucher No. have been attached or included in fluid-preserved specimens.

Voucher No.: 1996-5

Title of thesis or dissertation (or other research projects):

Evaluation of the Susceptibility of Four Scotch Pine Christmas Tree Varieties to Insect Pests

Museum(s) where deposited and abbreviations for table on following sheets:

Entomology Museum, Michigan State University (MSU)

Other Museums:

Investigator's Name (s) (typed)

Eileen A. Eliason

Date 15 July 1996

*Reference: Yoshimoto, C. M. 1978. Voucher Specimens for Entomology in North America. Bull. Entomol. Soc. Amer. 24:141-42.

Deposit as follows:

Original:	Include as Appendix 1 in ribbon copy of thesis or dissertation.
Copies:	Included as Appendix 1 in copies of thesis or dissertation. Museum(s) files. Research project files.

This form is available from and the Voucher No. is assigned by the Curator, Michigan State University Entomology Museum.

APPENDIX 1.1

APPENDIX 1.1

Voucher Specimen Data

Page 1 of 1 Pages

Species or other taxon	Label data for specimens collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Pleolophus basizonus (Gravenhorst)	Mich: Kalamazoo Co., Kellogg Forest T1S R9W S22, June-Oct. 1994, 6 Oct. 1995					2	3		
Neodiprion sertifer (Geoff.)	Mich: Kalamazoo Co., Kellogg Forest T1S R9W S22, Sep.-Oct.1994, Oct.1995		20			10	10		
Gelis tenellus (Say)	Mich: Kalamazoo Co., Kellogg Forest T1S R9W S22, 13 Oct. 1994					1			
Dioryctria zimmermani (Grote)	Mich: Kalamazoo Co., Kellogg Forest T1S R9W S22, 8 Aug.1994, July-Aug.1995		2			3	3		
	Mich: Montcalm Co., Korson's Tree Farm Sidney, near Greenville, July 1995					3	1		
Exeristes comstockii (Cresson)	Mich: Kalamazoo Co., Kellogg Forest T1S R9W S22, 22 June 1994, 25 June 1995					3	2		
Hyssopus rhyacioniae (Gahan)	Mich: Kalamazoo Co., Kellogg Forest T1S R9W S22, 25 June 1994	specimens in vial							
Chionaspis pinifoliae (Fitch)	Mich: Kalamazoo Co., Kellogg Forest T1S R9W S22, 15 Oct. 1995	specimens in vial							

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Eileen A. Eliason

Date 15 July 1996

Voucher No. 1996-5

Received the above listed specimens for deposit in the Michigan State University Entomology Museum.

Curator

15 July 1996

Date

LIST OF REFERENCES

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