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Interactions of the Pine Shoot Beetle [Tomicus piniperda
(L.) (Coleoptera: Scolytidae)] with Native Pine Bark
Beetles and Their Associated Natural Enemies in Michigan

presented by

Amy Ann Kennedy

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Major professor

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INTERACTIONS OF THE PINE SHOOT BEETLE [*Tomicus piniperda* (L.) (COLEOPTERA: SCOLYTIDAE)] WITH NATIVE PINE BARK BEETLES AND THEIR ASSOCIATED NATURAL ENEMIES IN MICHIGAN

By

Amy Ann Kennedy

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Entomology

1998

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ABSTRACT

INTERACTIONS OF THE PINE SHOOT BEETLE [*Tomicus piniperda* (L.) (COLEOPTERA: SCOLYTIDAE)] WITH NATIVE PINE BARK BEETLES AND THEIR ASSOCIATED NATURAL ENEMIES IN MICHIGAN

By

Amy Ann Kennedy

The pine shoot beetle, *Tomicus piniperda* (L.) (Coleoptera: Scolytidae), native to Eurasia, was discovered in North America in 1992. Interactions of *T. piniperda* with native pine bark beetles and their natural enemies are not well-known in the Great Lakes region. The phenology of *T. piniperda* and native insects in red pine (*Pinus resinosa* Ait.) plantations were monitored in 1996 and 1997. Two species of phloem feeders and four species of predators were active as early in the spring as *T. piniperda*. The impacts of predators and parasitoids on the galleries and progeny of *T. piniperda* and of native *Ips* bark beetles were also quantified. There was a negative relationship between natural enemy density and the number of bark beetle progeny per parent female, but natural enemies did not significantly affect mean scolytid gallery density, gallery length, or progeny density. Interspecific competition between *T. piniperda* and native *Ips* bark beetles was studied in laboratory and field experiments. Mean *Ips* gallery density, gallery length, progeny density, and productivity were significantly reduced in the presence of *T. piniperda*, but *T. piniperda* was not affected by the presence of *Ips*.

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This work is dedicated to the memory of Dr. George B. Craig, Jr.,
of the Department of Biological Sciences at the University of Notre Dame.
He passed down his fascination with insects and enthusiasm for science
to hundreds of the students he mentored, including myself.

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I am grateful to my advisor, Dr. Deborah G. McCullough, for giving me the opportunity to work on this exciting project. I thank Deb for introducing me to the diversity of the field of forest entomology, and also for all of her assistance and expertise with the field work. She has been an excellent mentor and role model throughout this challenging project, and she has always encouraged me to do the best work possible.

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Funding for this study was primarily provided by the USDA Forest Service, North Central Research Station and the USDA Forest Service, National Center of Forest Health. I also would like to thank the MSU Department of Entomology for funding a portion of

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this research as well as funding my travel expenses to several regional and national entomological meetings through the Ray and Bernice Hutson Endowment.

Many thanks are also due to the student employees who assisted me in field work: Nathan Siegert, Kirsten Fondren, Angela Toma, Eric Black, and Philip Garvin. Without their help in the logistics of maintaining nine field sites and de-barking hundreds of red pine bolts, this research would not have been a success. The personnel at MSU's W.K. Kellogg Experimental Forest (Greg Kowalewski, Jim Curtis, John Vigneron, and Karen Bushouse) were especially helpful in providing red pine bolts, setting up the field sites, and checking the funnel traps during spring 1996 and 1997.

I would also like to thank the organizations and their staff who helped me locate the field sites, permitted me to work in their forests, and provided me with the stand history data: Maria Albright and John Lerg from the Allegan State Game Area; Dr. Carl Ramm and Greg Kowalewski of the W.K. Kellogg Experimental Forest; Matt Sands of the Huron-Manistee National Forest; Don Torchia of the AuSable State Forest; Roger Mech of the Department of Natural Resources; and Clara Ward of the Fenner Arboretum.

Deb Nelson of the USDA APHIS laboratory in Niles, Michigan and Drs. Robert Haack and Robert Lawrence of the USDA Forest Service assisted with scolytid identifications. Jim Zablotney of MSU assisted with identifications of cerambycid adults. Their help was greatly appreciated.

Finally, I would like to thank my family for all of their support and love throughout my education. My parents Jerry and Paula Christensen, sisters Becky, Erica, and Mary, brother Joey, and husband Chris all assisted me with field work when things were hectic. Their encouragement and love have been invaluable in my life.

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CHAPTER 1

Phenology of Parent and Progeny Pine Bark Beetles and their Natural Enemies

INTRODUCTION

The larger pine shoot beetle, *Tomicus* (*=Blastophagus =Myelophilus*) *piniperda* (L.) (Coleoptera: Scolytidae), is a well-known forest pest in Europe, Asia, and North Africa, where it infests several species of pine (*Pinus* spp.) (Langstrom 1980; Ye 1991). Established populations of *T. piniperda* were first discovered in North America in 1992 in a Scotch pine (*Pinus sylvestris* L.) Christmas tree plantation in Ohio (Haack and Kucera 1993). Haack and Lawrence (1995a) speculated that this bark beetle probably came to North America from Europe on cargo ships in wood packing material or dunnage (logs used to support cargo). As of September 1998, *T. piniperda* had been found in 243 counties in nine northeastern U.S. states, and 21 counties in the Canadian province of Ontario (NAPIS 1998).

With the introduction of an exotic insect comes the need to understand interactions between the new exotic insect and native insects with similar habits. *Tomicus piniperda* overwinters as adults, and early in spring, when temperatures reach 10-12°C, parent adults become active and fly to recently-cut pine stumps and logs for breeding (Langstrom 1980, Haack and Lawrence 1995b). *Tomicus piniperda* typically reproduce only in dead, recently cut, or severely weakened pines (Byers 1991, Schroeder 1992). Alpha-pinene and other monoterpene volatiles in pine oleoresin attract both sexes of *T. piniperda* to wounded and freshly cut or fallen pine trees (Byers 1991, Schroeder

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1988, Schroeder and Lindelow 1989, Vite et al. 1986), and a short range sex pheromone for *T. piniperda* has recently been identified (S. Teale, State University of New York Syracuse, personal communication). After locating a suitable host, females bore into the pine bark and begin excavating individual egg galleries. After a male enters the gallery and they mate, the female lays eggs along the sides of a long, straight gallery that parallels the grain of the wood (Langstrom 1980). After establishing one brood, the parents may emerge, excavate a new gallery, and produce a "sister" brood (Schroeder and Risberg 1989). Larvae feed and develop in the phloem for 6 – 12 weeks, then pupate. The progeny adults exit the bark and fly to the crowns of living pine trees. Each beetle bores into the distal tip of one to six current-year or one-year-old shoots, and tunnels toward the shoot tip, killing the shoot. This maturation feeding continues throughout the summer (Langstrom 1980, McCullough and Smitley 1995).

Many other Great Lakes insects also utilize the phloem of weakened or recently-killed pine trees. The pine engraver, *Ips pini* (Say) (Coleoptera: Scolytidae), is the most economically important and well-studied pine bark beetle of the Great Lakes region (Raffa 1991, Schenk and Benjamin 1969). This native bark beetle overwinters as an adult in the litter of pine stands, and initiates spring flight in late April or May in Michigan (Haack and Lawrence 1995b), when daily maximum temperatures are near 20°C (Schenk and Benjamin 1969). Like *T. piniperda, I. pini* is a secondary pest that breeds preferentially in recently-killed or damaged hosts, such as freshly cut pines, logging slash, or pines recently damaged by wind or ice (Coulson and Witter 1984, Schenk and Benjamin 1969). *Ips pini* is attracted to these host pines in large numbers via host volatiles and two aggregation pheromones that *I. pini* males produce: ipsdienol and

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lanierone (Lanier et al. 1980, Raffa and Klepzig 1989, Seybold et al. 1992). *Ips pini* males create nuptial chambers in the phloem and mate with 2 – 4 females (Schenk and Benjamin 1969). Each female excavates an egg gallery that leads away from the nuptial chamber, typically resulting in a "Y" or "H" shaped gallery that is distinct from *T. piniperda* galleries. *Ips pini* larvae and pupae develop under pine bark, but unlike *T. piniperda*, *I. pini* progeny adults do not require maturation feeding in shoots. Instead, newly emerged adults locate new host material to colonize, unless it is late summer or fall. In the Great Lakes region, *I. pini* typically completes three generations per year (Schenk and Benjamin 1969).

Other common pine bark beetles (Coleoptera: Scolytidae) in the Great Lakes region include *Ips grandicollis* (Eichhoff), *Orthotomicus caelatus* (Eichhoff), and *Dendroctonus valens* LeConte (Haack and Lawrence 1995b, Schenk and Benjamin 1969, Raffa 1991). Larvae of weevils (Coleoptera: Curculionidae) and long-horned beetles (Coleoptera: Cerambycidae) also compete with scolytids for pine phloem resources.

Red pine (*Pinus resinosa* Ait.), one of the most important and widely planted species for pulp, sawtimber, and poles in the Great Lakes region (Rudolf 1990), is a suitable host for *T. piniperda* and many native scolytids (Haack and Lawrence 1997b). Management of red pine plantations typically involves multiple thinnings or partial harvests during a rotation, each of which provides an abundance of suitable breeding material for bark beetles and related groups (Haack and Lawrence 1995b). To date, most of the research on *T. piniperda* in North America has taken place in Scotch pine Christmas tree plantations (Haack and Lawrence 1997a, Kauffman et al. 1998, McCullough and Smitley 1995, McCullough et al. 1998, McCullough and Sadof 1998).

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Red pine plantations represent a more stable ecosystem with no insecticide use, and, presumably, more natural enemies, and there is a need to learn more about the impacts and the interactions of *T. piniperda* in a forest ecosystem.

Pine phloem in dead and dying trees is an ephemeral resource in both space and time, and bark beetles must locate and colonize suitable brood material before the phloem becomes too dry for larval development. Because *T. piniperda* becomes active in the spring four to six weeks earlier than *Ips* spp. in the Great Lakes region (Haack and Lawrence 1995b, Haack and Lawrence 1997b), it may have an opportunity to colonize pine phloem for several weeks without interspecific competition from native bark beetles. Determining the spring emergence of both native and exotic bark beetle species is the first step in understanding the interactions between them and determining the degree to which competition for breeding material occurs.

Interactions between a newly established exotic insect and native natural enemies that may attack it are also important. Most predators can only prey upon one life stage or upon a certain size of an insect because of physical limitations. For example, *Anthocoris* spp. (Hemiptera: Anthocoridae) are egg predators of many pine bark beetles, but are too small to prey upon large larvae or adults (Schmitt and Goyer 1983). Most parasitoids are also stage- or size-specific (Jones and Stephen 1994, Kudon and Berisford 1980, Senger and Roitberg 1992). Therefore, the timing of emergence of a natural enemy in relation to its prey is vital to the natural enemy's success.

Most bark beetle natural enemies in the Great Lakes region are phenologically adapted to native bark beetles, becoming active in April or May (Raffa 1991). Haack and Lawrence (1995b) predicted that *T. piniperda* would encounter no native predators or ds an

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parasitoids until colonization and oviposition was mostly completed each spring. This concern was large enough to warrant consideration of importing the exotic predator *Thanasimus formicarius* (L.) (Coleoptera: Cleridae) to the United States soon after the discovery of widespread *T. piniperda* establishment (Haack and Lawrence 1995b, APHIS 1996). *Thanasimus formicarius* is the earliest of the major bark beetle predators in Europe to become active in the spring (Schroeder 1988). The native clerid predator *Thanasimus dubius* (F.) is known to be well-adapted to the later-emerging native *Ips* spp. bark beetles, and even uses *Ips* spp. aggregation pheromones as kairomones to locate their hosts (Herms et al. 1991; Raffa 1991; Teale et al. 1991). It was unclear whether *T. dubius* and other native natural enemies would emerge from overwintering early enough in the spring to prey upon *T. piniperda* parent adults or progeny.

In this study, I examined the phenology of pine bark beetles and their arthropod natural enemies in eight Michigan red pine plantations, using three methods: pheromone-baited funnel traps, observations of activity on red pine bolts, and rearing from red pine bolts. My objective was to compare the emergence of parent and progeny adults of the exotic *T. piniperda* with that of native pine phloem-feeding insects and native natural enemies.

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MATERIALS AND METHODS

Study Sites

In 1996, I monitored phenology of overwintering and progeny bark beetles, and their arthropod natural enemies at four red pine forest plantations in Michigan. Two plantations were in southwestern Michigan and were known to be infested with both *T. piniperda* and native *Ips* spp. These stands were located in Michigan State University's W.K. Kellogg Experimental Forest in Kalamazoo County (KAL1), and in the Allegan State Game Area in Allegan County (ALL1) (Figure 1). Two plantations in northern lower Michigan, where *T. piniperda* was not expected to be present, were also selected. One stand was in the Huron-Manistee National Forest in Wexford County (WEX1), and the other was in the AuSable State Forest in Roscommon County (ROS1). Although *T. piniperda* was later detected in these northern counties in regulatory surveys (NAPIS 1998), I did not observe any *T. piniperda* life stages or evidence of infestations in the northern plantations in either 1996 or 1997.

All four field sites shared the following characteristics: they were pole-sized red pine plantations of similar size, age, and basal area (Table 1) with some hardwood understory. Each field site was within 2 km of other red pine plantations, and each site had been thinned during the 1994-95 winter. An abundance of slash (for example, trunks, tops, large branches) was left on the ground from these thinnings and was expected to attract scolytids in 1995. Temperature, precipitation, and degree day accumulation (base 10°C) were monitored by Michigan State University weather stations near all four sites.

In 1997, I monitored the phenology of bark beetles and their natural enemies in the same four sites described above, which represented conditions two years after thinning. I also selected four additional red pine plantations, each one within 6.2 km of one of the original stands (KAL2, ALL2, WEX2, and ROS2). These sites had the same general characteristics of the original stands (Table 1), but were row-thinned during the 1995-1996 winter.

In both 1996 and 1997, the phenology of overwintering bark beetles and their natural enemies was also monitored at a mixed Scotch pine and red pine plantation in Lansing, Ingham County, Michigan (Figure 1). This stand, located in the Fenner Arboretum, was chosen because of its proximity to the Michigan State University campus and its intermediate location between the northern and southern sites. Observations of galleries in 1995 indicated that this plantation was infested with both *T. piniperda* and *Ips* spp. Brood material, consisting of dying and newly dead trees was available each year because the plantation suffers from annosus root rot (*Heterobasidion annosum* (Fr.) Bref.) and because of wind damage to trees and to tops.

Funnel Trapping

To monitor the spring flight activity of scolytids and their associates, two to four 12-unit Lindgren funnel traps (Lindgren 1983) (from PheroTech, Inc., Delta, British Columbia) were placed in each red pine stand, and seven funnel traps were placed in the Lansing Scotch/red pine stand. Traps were hung from metal poles to keep the trap bottoms approximately 1 m above the ground. Each trap was erected and baited in February of 1996 and 1997 with two α-pinene lures to attract *T. piniperda* (Byers 1991; Byers et al. 1985, Schroeder 1988, Schroeder and Lindelow 1989, Vite et al. 1986, Volz

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1988), and with one lure each of ipsdienol and lanierone. Ipsdienol and lanierone are aggregation pheromones of *I. pini* that are used as kairomones by predaceous clerid, tenebrionid, and histerid beetles (Herms et al. 1991; Raffa 1991; Teale et al. 1991).

All lures were manufactured by Phero Tech, Inc., and the following information came from the company. The α-pinene lures were made up of 15 ml polyethylene bottles with a release rate of 150 mg/day at 22°-24°C, and a 10:90 ratio of (+) and (-) enantiomers. The ipsdienol bubble-cap lures had a release rate of 100 μg/day at 25°C, and a 50:50 enantiomeric ratio. The lanierone bubble-cap lures had a release rate of 10 μg/day at 25°C. I placed insecticide strips in each trap, and collected insects from traps at weekly intervals from March through September in 1996 and 1997.

Progeny Rearing Study

A total of 204 red pine bolts in 1996, and 304 bolts in 1997, each approximately 61 cm long and 10 – 20 cm diameter, were cut from live red pine trees at the red pine field sites in February, April, and June of both years (Table 1). These times roughly corresponded to the initial activity of overwintering parent *T. piniperda*, initial activity of overwintering parent *Ips* spp., and emergence of the first *Ips* progeny adults. February-cut bolts were only placed in the southern sites because *T. piniperda* was not known to be present in the northern sites. The bolts were placed on the ground in a shady area of each plantation to reduce desiccation and were left for colonization by bark beetles and their associates. Bolts were returned to Michigan State University at two week intervals in 1996 and at one week intervals in 1997. The cut ends of the retrieved bolts were dipped in paraffin wax to reduce desiccation. Each bolt was placed in an individual emergence container consisting of a cardboard tube (15 – 25 cm diameter, 0.32 – 0.64 cm wall, 61 –

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71 cm overall length [Michigan Can and Tube, Inc., Saginaw, MI]) with opaque plastic endcaps and a clear plastic collection cup at one end. The emergence containers were stored on the Michigan State University campus in East Lansing in a screened outdoor insectary to expose the bolts to ambient temperature and humidity.

Bark beetle and natural enemy progeny adults emerging from the bolts were collected from emergence containers at least twice a week from June through October. When progeny emergence stopped in the winter, each log was de-barked and any insects still under the bark or dead on the bottom of the emergence container were collected. All insects reared from these bolts were assumed to be progeny adults, although it is possible that a few parent adults were inadvertently collected. The number of parent insects was assumed to be small and similar across all bolts and sites.

Field Observations

In addition to collecting insects from the funnel traps at regular intervals, I also examined the red pine bolts that had been left in the stands for the progeny rearing study in 1997. Each bolt was gently turned over to examine all sides. I recorded the presence and quantity of the following variables: frass from boring scolytids, exit holes of bark beetles, adult bark beetles or other phloem borers walking on the bolts, and adult and larval predators on the bolts. The bark was not peeled away because the bolts used for the observations were the same ones used to rear progeny, and I did not want to alter or destroy the phloem environment in those bolts.

Analysis

Phenology of the parent bark beetles and their natural enemies was examined by plotting the funnel trap collection (as proportion of total collected) of each species over

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time. Each year (1996 and 1997) was plotted separately. Phenology of the progeny bark beetles and their natural enemies was determined by plotting collections from the emergence tubes (as proportion of total reared) of each species over time, with each year analyzed separately. Progeny insects that were collected during the de-barking are not included in these graphs, since the date of emergence of these insects was not known.

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RESULTS

Phloem Feeders

Thirteen species of pine phloem feeders, including ten bark beetle species, one weevil, and two long-horned beetles, were collected in the pheromone-baited funnel traps. A total of 5296 adults were collected in 1996, and 2614 adults were collected in 1997 (Table 2). *Tomicus piniperda* was the first pine bark beetle to be found in the funnel traps at the southern sites (KF and ALL) and in Lansing in 1996 and in 1997 (Tables 3 and 4). Most native bark beetles, including *Ips pini*, *Hylurgops rugipennis pinifex* (Fitch), and *Ips grandicollis* were first collected in funnel traps approximately 45 days after *T. piniperda*'s first flight. Twelve species of pine phloem feeders were reared from the red pine bolts, including nine bark beetle species, *Pissodes nemorensis* Germar (Coleoptera: Curculionidae), *Monochamus scutellatus* (Say), and *M. carolinensis* (Olivier) (Coleoptera: Cerambycidae). In 1996, 19,045 progeny adults were reared, and 22,796 progeny were reared in 1997 (Table 5). *Tomicus piniperda* progeny were the first pine bark beetles to emerge in both years. *Ips perroti* Swaine (Coleoptera: Scolytidae) progeny emerged at the same time as *T. piniperda* progeny in 1996, but were four weeks later than *T. piniperda* in 1997. *Monochamus scutellatus* and *M. carolinensis* progeny were the last pine phloem feeders to emerge in both years; adults did not emerge until the following spring.

Flight of *T. piniperda* parent adults was early and quite brief; over 90% of all parent adults were collected in the first two weeks of activity in 1996 and in 1997 (Figure 2). Parent *T. piniperda* adults were observed on red pine bolts in the southern sites the same

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during the same two-week period that they were first collected in funnel traps. Both years, *T. piniperda* flew a few days earlier in Lansing than in KF or ALL (Tables 3 and 4). There were approximately 100 days between *T. piniperda* parent activity in funnel traps and *T. piniperda* progeny emergence. Emergence of *T. piniperda* progeny adults occurred during a brief period early in both summers; most of the progeny emerged by Julian date 200 (Figure 3).

Funnel trap collections of *I. pini* overwintering parent adults varied dramatically between 1996 and 1997. Parent *I. pini* adults initiated spring flight approximately six weeks after *T. piniperda* adults in both years. In 1996, the majority of the parent adults were collected in late summer, after Julian date 220 (Figure 2). But in 1997, half were collected within three weeks of first flight. In both years, there were three peaks of collection (Figure 2), reflecting the three generations of *I. pini* in Michigan. Observations of *I. pini* activity on red pine bolts coincided with the collection of *I. pini* in the funnel traps. There was little difference in dates of first *I. pini* flight between northern and southern sites in either year (Tables 3 and 4).

The first *I. pini* progeny adults were collected from emergence containers about 60 days after parent adults were first collected in funnel traps; progeny emergence began around Julian date 200 of 1996, and Julian date 180 in 1997 (Figure 3). *Ips pini* progeny adults continued to emerge throughout the summer and into the fall of both years. In 1996, *I. pini* progeny emergence peaked in early October, and in 1997, progeny adult emergence remained steady through the summer, with no discernible peaks. Red pine is not recorded as a host for *I. pini* by Wood (1982), but several studies report *I. pini* colonization in red pine (Raffa and Klepzig 1989, Raffa 1991, Teale and Lanier 1991).

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In both 1996 and 1997, the parent adult flight for *Ips grandicollis* peaked soon after flight began, and a second peak occurred seven weeks later (Figure 2) when F1 progeny adults emerged. Observations of *I. grandicollis* activity on the red pine bolts were consistent with the funnel trap collections and indicated that two generations of *I. grandicollis* occurred in both years. Flight of *I. grandicollis* parent adults occurred one or two weeks earlier in the southern sites than the northern sites (Tables 3 and 4). There were 50 – 60 days between flight of overwintering parents and flight of first generation progeny adults. *Ips grandicollis* progeny emergence occurred at the same time as *I. pini* in 1996, and a few weeks later than *I. pini* progeny in 1997 (approximately Julian date 200 of both years) (Figure 3). Progeny emergence began in late July of both years and continued through November with no distinct peaks of emergence.

Hylurgops rugipennis pinifex was not an abundant scolytid in funnel traps at any site (Table 2). However, I observed many parent adults actively colonizing the red pine bolts early in the spring when *T. piniperda* was also colonizing bolts. The few *Hylurgops* parent adults found in funnel traps were not collected until several weeks after they were first observed colonizing the bolts (Figure 4). As the snow was melting in the early spring, *Hylurgops* adults were found along the cool, damp bottom of nearly every red pine bolt at all four (1996) or eight (1997) sites, constructing galleries and laying eggs. In addition, *Hylurgops rugipennis pinifex* progeny adults were one of the first scolytids to be reared from the red pine bolts in 1997 (Figure 5). There were about 50 days between parent flight and progeny emergence in 1996, but only 20 days difference in 1997. In 1996, there were two distinct peaks of progeny adult emergence: around Julian date 190 and again after Julian date 300 (Figure 5). In 1997, *Hylurgops* progeny emerged from

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Julian date 160 through the rest of the summer (Figure 5). *H. rugipennis pinfex* was collected in funnel traps and reared from all nine field sites, which are new records in Michigan according to Wood (1982). This scolytid appears to have at least two generations per year, and since its generation time was only 20-50 days, a third generation appears possible in late summer.

Orthotomicus caelatus parent adults had one peak of flight activity in 1996, just after it was first collected (Figure 4). In 1997, however, this beetle had two peaks of flight, approximately seven weeks apart (Figure 4). This bark beetle was observed on red pine bolts only a few times, immediately after it was first collected in funnel traps, at the same time as *I. pini* and *I. grandicollis*. There was no difference in date of first activity between northern and southern sites (Tables 3 and 4). There were about 50 days between first parent flight and first emergence of progeny *O. caelatus* in both years. *Orthotomicus caelatus* progeny adults were first collected around Julian date 190 and emergence continued throughout the summer in both years (Figure 5). There were about seven weeks' difference between initial parent flight and initial progeny emergence, which concurs with the seven week separation of the first and second peaks in the 1997 funnel trap collection. There appear to be at least two generations of *O. caelatus* per year.

Ips perroti parent adults were not collected in funnel traps in either year, but progeny were reared from the red pine bolts from the northern sites in both years (Table 5). In 1996, most of the progeny adults emerged quite early in the season, before Julian date 200, similar to *T. piniperda* progeny (Figure 5). But in 1997, peak progeny emergence did not occur until mid-summer, coinciding with the other *Ips* species (Figure 5). In both years, *I. perroti* progeny emerged in mid-summer and again in

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September/October, suggesting at least two generations per year. This small bark beetle was not observed on the red pine bolts. Since overwintering parent adults were not collected in funnel traps, no estimate of generation time can be made. *Ips perroti* was reared from bolts from two of the northern sites (CAD1 and ROS2), and the CAD1 site is a new county record in Michigan (Wood 1982).

In both 1996 and 1997, overwintering parent adults of *Gnathotrichus materiarius* (Fitch) (Coleoptera: Scolytidae) were first found in funnel traps around the same time as the overwintering *I. pini* adults (Tables 3 and 4). *Gnathotrichus materiarius* parent adults had one main peak of activity soon after first flight in 1996 (Figure 6). In 1997, it had two peaks of activity: one immediately after first flight, and one six weeks later (Figure 6). I never observed this tiny bark beetle on the red pine bolts, so I do not know whether flight activity coincided with mating and gallery formation in this species. About 50 days separated the first parent flight and emergence of the first progeny adults. *Gnathotrichus materiarius* followed the same pattern as did *O. caelatus*: progeny emergence began just before Julian date 200, peaked in mid-summer, and continued throughout the summer (Figure 7). This scolytid appears capable of producing two or three generations per year. Red pine is a new host record for *G. materiarius* (Wood 1982).

In 1996, *Hylastes porculus* Erichson (Coleoptera: Scolytidae) parent adults flew much later in the northern sites than the southern sites (Table 3), but in 1997, there was no difference between northern and southern sites (Table 4). In both years, most of the *H. porculus* parent adults were collected soon after first flight, with a second smaller peak immediately after the first (Figure 6). This beetle was not observed on red pine bolts in either year. There were approximately 70 days between first parent flight and first progeny adult

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progeny adult emergence. In both 1996 and 1997, *H. porculus* progeny first emerged around Julian date 210. Another emergence peak occurred after Julian date 275 (Figure 7). As evidenced by the two peaks in progeny emergence and the 70 day generation time, *Hylastes porculus* appears to have two generations per year. This bark beetle was reared from all eight field sites and collected from funnel traps in Lansing, which are all new county collection records (Wood 1982).

The tiny beetle *Dryocetes autographus* (Ratzeburg) (Coleoptera: Scolytidae) was quite rare in the funnel traps; only two adults were collected in 1996 and three in 1997, all from the Lansing funnel traps (Table 2), and at the same time as *I. pini* (Figure 6). *Dryocetes autographus* was not observed on the red pine bolts in the field, but it was reared from bolts from the KF1 and KF2 sites (Table 5). Progeny adults of *D. autographus* began emerging in late June of both years, and emergence continued through September in 1996, and through August in 1997 (Figure 7). Forty days separated first parent flight and first progeny emergence in 1996; there was only 30 days' difference in 1997. Progeny of *Dryocetes autographus* had two distinct peaks of emergence in both years of the study, indicating two generations per year. Red pine is a new host record for this scolytid (Wood 1982).

Pissodes nemorensis, the eastern pine weevil, was not frequently found in funnel traps (Table 2), but parent adults were commonly observed feeding and ovipositing on the bottom of red pine bolts in KF1 and ALL1 early in the spring when *T. piniperda* and *H. rugipennis pinifex* were active. Progeny *P. nemorensis* adults emerged approximately 100 days after parent adults were collected. *Pissodes nemorensis* progeny emerged over the course of the entire summer, but peaked around Julian date 225 in both 1996 and

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The predominant cerambycid was *Monochamus scutellatus*, with *M. carolinensis* comprising only a small percentage of the funnel trap collections. The two cerambycids could not be distinguished in the field, so the numbers represent combined totals. Cerambycids were the last of the pine phloem feeders to be collected in funnel traps (Tables 3 and 4). Parent adult flight activity was irregular but lasted from mid- to late-summer of both years (Figure 8). *Monochamus* beetles were very conspicuous from mid-June through August on nearly all of the red pine bolts in both northern and southern sites. Though not many adults were collected in funnel traps (Table 2), they were frequently observed mating and ovipositing on the red pine bolts during this period. *Monochamus scutellatus* and *M. carolinensis* progeny adults were not collected in the emergence containers in either 1996 or 1997 until the bolts were de-barked the following winter and spring (Table 5). Progeny larvae were also collected from the bolts during de-barking; 523 larvae were collected in 1996, and 429 larvae were collected in 1997. These cerambycids take a full year for development, as evidenced by the single flight period and the large number of larvae that were collected during de-barking.

Overwintering parent adults of the red turpentine beetle, *Dendroctonus valens*, were fairly common in the funnel traps in both years (Table 2). *Dendroctonus valens* was collected in funnel traps from all nine sites, which are all new county records in Michigan (Wood 1982). Parent adults had one main peak of flight activity in both years, immediately after first flight (Figure 8), and were occasionally observed on red pine bolts during the same period. *Dendroctonus valens* became active at approximately the same in the sou

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time in the southern and northern sites (Tables 3 and 4). Although *D. valens* parent adults were commonly collected in funnel traps, *D. valens* progeny adults were not reared from red pine bolts in either year, probably because this beetle is larger than the other scolytids, and may prefer thicker bark or phloem, such as in pine stumps (Table 5).

Natural Enemies

Eight different species of bark beetle predators were collected in the pheromone-baited funnel traps. In 1996, a total of 957 adult predators were collected, and in 1997, 930 predators were collected. Bark beetle parasitoids were not collected in the funnel traps in either year. Staphylinid beetles (Coleoptera: Staphylinidae) and *Cucujus clavipes* F. (Coleoptera: Cucujidae) were the first arthropod natural enemies of bark beetles to be caught in funnel traps in both 1996 and 1997 (Tables 3 and 4), initiating spring activity within approximately a week after peak flight of *T. piniperda* parent adults in both years. Progeny of nine species of predators and six species of parasitic wasps were reared from the red pine bolts. A total of 1113 progeny adults were reared in 1996, and 2258 were reared in 1997.

The clerid predator *Thanasimus dubius* was among the most abundant and conspicuous of the scolytid natural enemies. In 1996, *T. dubius* adults were first collected in funnel traps less than three weeks after peak *T. piniperda* parent activity, and continued to be collected throughout the summer and into the fall (Figure 10). In 1997, *T. dubius* was not collected in funnel traps until about seven weeks after peak *T. piniperda* activity, corresponding to flights of native *Ips* spp. parent adults (Figure 10). The 1997 funnel trap collections of *T. dubius* only continued until the end of July (Figure 10).

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In contrast to the funnel trap catches, however, I observed *T. dubius* adults actively moving about on the red pine bolts early in the spring. In 1997, *T. dubius* was observed actively preying upon *T. piniperda* and *H. rugipennis pinifex* adults in the southern sites as early as April 18 (Julian date 108), only 2 ½ weeks after *T. piniperda* peak flight, again on April 25 (Julian date 115), May 7 (Julian date 127), and May 23 (Julian date 143), all before native *Ips* spp. flight activity began and before *T. dubius* was collected in funnel traps. My observations of lab colonies of *T. dubius* adults (maintained at 10°C) also show that *T. dubius* can be an active predator in cool weather, before it is warm enough to fly to funnel traps. *Thanasimus dubius* adults held at 10°C actively walked around the lab containers and would attack and consume any bark beetle adults placed into the container, but I did not observe them flying at this temperature.

Larvae of *T. dubius* were observed walking on the surface of the red pine bolts at the ROS2 and CAD2 sites on July 2, 1997 (Julian date 183). *Thanasimus dubius* progeny adults were the first predator species collected in emergence containers in both years, but these early individuals were probably parent adults. *Thanasimus dubius* progeny emergence lasted from mid- to late-summer of 1996, peaking around Julian date 250 (Figure 11). In 1997, progeny emergence began much later in the summer, after Julian date 225, and peaked nearly 50 days later (Figure 11). There were 90 days in 1996 and 60 days in 1997 between first collections of *T. dubius* parent adults in funnel traps and first emergence of progeny adults from red pine bolts. *Thanasimus dubius* adults that emerged from the rearing containers prior to August were probably not progeny, but parent adults that were on the bolts when they were collected from the field sites. Although *T. dubius* was active over several periods of the summer, it appears to only ave one gen

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The histerid predator *Platysoma* (=*Cylistix*) *cylindrica* (Paykull) (Coleoptera: Histeridae) was commonly collected in funnel traps at all sites (Table 2). In 1996, *P. cylindrica* was first collected only four weeks after peak *T. piniperda* flight (Table 3), and over 70% of the beetles were collected within three weeks of initial flight (Figure 10). In 1997, *P. cylindrica* began flight activity ten weeks after peak *T. piniperda* activity (Table 4), and over 80% of the beetles were collected within four weeks (Figure 10). This tiny predator was infrequently observed on red pine bolts in the summer months, and no conclusions can be drawn regarding flight activity and predation activity. Emergence of *P. cylindrica* progeny also differed greatly from 1996 to 1997. In 1996, progeny emergence continued throughout the entire summer, with no distinct peaks (Figure 11). In 1997, offspring emergence began in late summer, after Julian date 250, and peaked within 25 days (Figure 11). There were only 25 days between initial parent and progeny flights in 1996, and more than 100 days difference in 1997. As was the case with *T. dubius*, the emergence of *P. cylindrica* adults from the emergence containers throughout the summer of 1996 probably reflects numbers of parent adults that remained on the field-infested bolts when they were brought to the MSU rearing facility. The peak progeny emergence of this histerid occurred in September and October, and it probably only has one generation per year.

Corticeus parallelus Melsheimer (Coleoptera: Tenebrionidae) is another tiny predator that was frequently attracted to the funnel traps. In 1996, *C. parallelus* adults were collected in funnel traps two weeks after *T. piniperda* peak flight (Table 3). Although *C. parallelus* flight activity peaked early in the spring, adults were collected ghout t

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throughout the summer (Figure 10). In 1997, *C. parallelus* did not initiate spring flight until ten weeks after *T. piniperda* peak flight (Table 4), and was then collected until mid-July (Figure 10). *C. parallelus* was rarely observed on red pine bolts, and only during the warm summer months. In 1996, emergence of *C. parallelus* progeny adults began around Julian date 220, and peaked approximately 60 days later (Figure 11). Timing of emergence was similar in 1997, but there was a second emergence peak near Julian date 275 (Figure 11). There were approximately 75 days between first parent flight and first progeny emergence in both years. There were two peaks of progeny emergence in 1997: one in September and one in late October, which suggests that two generations per year are possible.

Two staphylinid species (Coleoptera: Staphylinidae) were active early in spring 1996; over 50% of these staphylinids were collected within two weeks of peak *T. piniperda* flight (Figure 12). In 1997, parent staphylinids had two main activity periods: early spring, near *T. piniperda* peak flight, and mid-summer, corresponding to flight of first generation *Ips* spp. progeny adults (Figure 12). Since I did not observe many staphylinids on the red pine bolts, nor did I observe any preying upon bark beetles, I cannot confidently connect the dates of first flight activity with the dates of first predatory activity. Staphylinids were collected earlier in southern sites than in northern sites, and there was no early flight of staphylinids in the northern sites in 1996 (Table 3). In 1996, staphylinid progeny adults emerged at three times: Julian dates 210 - 225, at 275, and again at 320 (Figure 13). In 1997, progeny adults emerged earlier; around Julian date 175, and continued to sporadically emerge until Julian date 240 (Figure 13). There were approximately 120 days separating first parent flight and first progeny

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emergence in 1996, and only 100 days difference in 1997. These predators appear to be univoltine, but the results in 1997 show that two generations per year are possible.

Medetera sp. (Diptera: Dolichopodidae) was not collected in funnel traps during either year, but was reared from the red pine bolts in both years. Timing of progeny emergence was quite similar in both years, with activity beginning around Julian date 200 and ending about 50 – 60 days later (Figure 13). Since no parent adults were collected in the funnel traps, I cannot estimate the length of time between generations. During de-barking, I collected hundreds of *Medetera* sp. larvae, so it appears that *Medetera* sp. produces two generations per year in Michigan: the first generation emerges in mid-summer, and the second generation emerges the following spring.

A second histerid predator, *Platysoma parallelum* Say (Coleoptera: Histeridae), began flying five weeks after peak *T. piniperda* parent flight in 1996 (Table 3), but was most commonly collected during peak *Ips* spp. parent flight (Figure 12). In 1997, *P. parallelum* was first collected ten weeks after peak *T. piniperda* flight, like many of the other scolytid predators that year (Table 4). In 1997, it was collected through the end of July (Figure 12). This predator was not observed on the red pine bolts. Progeny *P. parallelum* adults were reared from all sites in both years (Table 5). In 1996, *P. parallelum* progeny began emergence in September and continued through October (Figure 13). In 1997, no progeny were collected until the bolts were de-barked in the winter (Table 5). There were approximately 100 days separating first parent flight and first progeny emergence in 1996. Since progeny of this histerid were only collected late in the season of 1996, and not until de-barking in 1997, it appears that the funnel trap peaks represent activity, not different generations. *Platysoma parallelum* appears to be

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Cucujus clavipes was not a common predator in funnel traps, but it was among the earliest predators to become active in the spring (Tables 3 and 4). Over 80% of the 1996 total and over 50% of the 1997 total were collected within two weeks of peak *T. piniperda* parent flight in the corresponding years (Figure 14). In 1996 it was only collected in the southern sites and in Lansing, and in 1997 it was collected in all sites, but much later in the northern sites. *Cucujus clavipes* was not observed on the red pine bolts or preying upon bark beetles, and it was not reared from any of the red pine bolts.

Another clerid predator, *Enoclerus nigripes* Say (Coleoptera: Cleridae), was much less commonly encountered than *T. dubius*. *Enoclerus nigripes* was among the last of the scolytid predators to be collected in funnel traps in the southern sites; the first individual was collected in late July of both years (Tables 3 and 4). In the northern sites, *E. nigripes* initiated flight at approximately the same time as *Ips pini* (Tables 3 and 4). In 1996, *E. nigripes* was most often collected in July and August, whereas in 1997, it was mostly collected in June and July (Figure 14). *Enoclerus nigripes* was often observed actively searching for prey on the red pine bolts from all of the sites in the late summer months, but it was only reared from bolts from the northern sites (Table 5). In 1996, 110 days separated first parent flight and first progeny emergence; in 1997, there were 90 days difference. Since *E. nigripes* progeny adults were only collected in September of both 1996 and 1997 (Figure 15) and during de-barking the following winters, this clerid is probably univoltine in Michigan.

The anthocorid predator *Anthocoris* sp. was not collected in the funnel traps, but nymphs and adults were reared from the red pine bolts in both years. In 1996, *Anthocoris* progeny emer

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sp. progeny emerged from bolts three times between Julian dates 220 and 290 (Figure 15). In 1997, progeny were collected between Julian dates 185 and 275 (Figure 15). No estimates of generation time could be made since no parent adults were collected in the funnel traps.

Parasitic wasps (Hymenoptera: Braconidae, Ichneumonidae, and Chalcidoidea) were not collected in the funnel traps in either 1996 or 1997, but six species of parasitoids were reared from the red pine bolts throughout the summers (Julian dates 175 – 300) of both years (Figure 15). Since no parasitoids were collected in the funnel traps in either year, the length of time between generations cannot be estimated.

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DISCUSSION

As expected, *Tomicus piniperda* was the first bark beetle to initiate spring flight, but, surprisingly, it was not the first phloem feeder to begin colonizing the red pine bolts. *Hylurgops rugipennis pinifex* and *Pissodes nemorensis* were actively colonizing the bolts at the same time as *T. piniperda*, even though they were rarely collected in the pheromone-baited funnel traps early in the spring. The early spring activity of these phloem borers has not been previously recorded, and *T. piniperda* was not expected to have any competition for pine breeding material early in the season (Haack and Lawrence 1995b).

Four predators were also active early in the spring at the same time as *T. piniperda* adults were colonizing brood logs. *Thanasimus dubius* adults were actively walking on the bolts and preying upon *T. piniperda* and *H. rugipennis pinifex*, but were rarely found in funnel traps early in the spring. The predators *Cucujus clavipes* and two species of staphylinids were collected in the funnel traps soon after the start of *T. piniperda*'s flight, but neither were observed on the red pine bolts. Like *P. nemorensis* and *H. rugipennis pinifex*, these predators have not previously been observed to be active so early in the spring. Haack and Lawrence (1995b) speculated that *T. piniperda* would not encounter predators or parasitoids until most of its colonization was completed.

Most of the phloem feeders were collected in the funnel traps around the same time as *Ips pini* parent adults: *Ips grandicollis*, *Hylurgops rugipennis pinifex*, *Orthotomicus caelatus*, *Gnathotrichus materiarius*, *Hylastes porculus*, *Pissodes nemorensis*, and *Dendroctonus valens*. With the exceptions of *H. rugipennis pinifex* and

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P. nemorensis, which were active before they were collected in funnel traps, these native scolytids initiated both flight and colonization from mid- to late- spring of both years, as was expected. Schenk and Benjamin (1969) reported similar activity periods for several of these species during their study of *I. pini* parent adults.

Most native predators, including *T. dubius*, *P. cylindrica*, *C. parallelus*, and *P. parallelum*, were also first collected in funnel traps around the same time as *I. pini*. This activity was earlier than reported by Schenk and Benjamin (1969), who found that the highest predator populations on *I. pini*-infested jack pine (*Pinus banksiana* Lamb.) bolts occurred during the emergence of the first generation *I. pini* progeny.

Tomicus piniperda parent adults had an early and short spring flight in all southern sites in both years. This spring flight behavior has been well documented in Europe (Haack and Lawrence 1997b, Saarenmaa 1989, Salonen 1973) and in North America (Haack and Lawrence 1995b), and reflects *T. piniperda*'s comparatively low temperature threshold for flight (10 – 12 °C) (Langstrom 1980). Another explanation for *T. piniperda*'s early flight is that since it overwinters in crevices in the outer bark of standing pine trees, it is exposed to warm temperatures and solar radiation earlier than scolytids that overwinter under the snow layer and duff. *Tomicus piniperda* was probably collected first in Lansing because I checked the Lansing funnel traps more frequently than the traps at the southern sites. The generation time of 100 days was longer than the estimated 6-10 weeks described in Haack and Lawrence (1995a), and was likely due to the shaded, cool conditions of the emergence containers and rearing shed in Lansing. Emergence of progeny adults was characteristically brief, and earlier than most native scolytids. I found no evidence of sister broods, since *T. piniperda* parent flight and geny emer

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progeny emergence both occurred in short, discrete peaks of time.

Overwintering *I. pini* adults initiated spring flight six weeks after *T. piniperda* adults in both years of this study. Haack and Lawrence (1997 and 1995b) found that the first flight of *T. piniperda* ranged from three to six weeks earlier than the first flight of *I. pini* in Michigan from 1993 – 1996. The large funnel trap collections of *I. pini* late in the summer of 1996 paralleled the trends described by Teale and Lanier (1991) and Raffa (1991) in New York and Wisconsin, respectively: the highest funnel trap collections were obtained late in the flight season, and relatively few *I. pini* were collected in the spring and early summer. This late season peak is hypothesized to occur when *I. pini* adults stop colonizing new brood material, and begin a period of high-density feeding attacks, during which they continue to produce and respond to pheromones (Teale and Lanier 1991). Raffa (1991) also noted that the attraction of *I. pini* to ipsdienol seems to be activated by cool temperatures in the fall. The absence of a late-season peak in funnel trap catches in 1997 may be explained by the cool weather in the spring that delayed the initiation and development of the three generations. In 1997, degree-day (base 10°C) accumulations by Julian date were approximately one week behind 1996, and a total of 100 fewer degree-days were accumulated in 1997 compared with 1996 (Figure 16).

Ips pini progeny adults emerged about 60 days after initial parent flight; longer than the expected 42 days (Schenk and Benjamin 1969). Although there were three flight peaks for parent adults corresponding to the flight of the three generations of *I. pini*, progeny emergence did not occur in such discrete patterns. The constant yet irregular emergence of *I. pini* progeny throughout both summers may be due to the masking effect of the cool temperatures in the emergence containers, since the containers were not applied to

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Ips grandicollis parent adults were first collected in funnel traps at the same time as *I. pini*, not earlier than *I. pini* as reported in Wisconsin (Schenk and Benjamin 1969). Based on funnel trap collections, *I. grandicollis* appeared to have two generations per year, but the generation time of 50-60 days is similar to that of the trivoltine *I. pini*, so three generations per year could be possible.

Hylurgops rugipennis pinifex and *P. nemorensis* were exceptionally early colonizers of the red pine bolts; they were both observed frequently on the bottom and cut edges of nearly every bolt in March and April, as the snow was melting. The preference of these insects to colonize bolt sections that were in direct contact with the ground, suggests that this cool, moist environment is ideal for these species. *Tomicus piniperda* primarily colonized the sides of the bolts, not the underside, so competitive interactions between *T. piniperda* and these phloem feeders may be minimized by spatial partitioning. These were the only pine phloem feeders that were active as early in the spring as *T. piniperda*, and they could be important competitors of *T. piniperda* when pine breeding material is scarce.

Dendroctonus valens parent adults were first collected in funnel traps in mid-May of both years, a few weeks later than Haack and Lawrence's (1995b) first catch in Michigan in late April in 1993. In a Wisconsin study (Raffa 1991), *D. valens* had two peaks of collection in funnel traps: May-June and August-September, but I did not observe a second flight of *D. valens* in this study.

The clerid predator *Thanasimus dubius* was actively preying on *T. piniperda* and *H. rugipennis pinifex* adults for a few weeks in the spring before it was first collected in nnel

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the funnel traps. This was not anticipated, since *T. piniperda* was not expected to have predation pressure until colonization was complete (Haack and Lawrence 1995b). I speculate that *T. dubius* funnel trap collections occurred after I observed predaceous activity because *T. dubius* requires higher temperatures for flight than for walking. Another possible explanation is the temperatures were too cool for the ipsdienol baits to volatize sufficiently to attract *T. dubius*.

The first funnel trap catches of *T. dubius* occurred in late April 1996, and in early May 1997, which agrees with the 1993 Michigan study by Haack and Lawrence (1995b). *Thanasimus dubius* had several peaks of abundance: before *I. pini* parent adult emergence, during *I. pini* F1 progeny emergence, and in August, before *I. pini* F2 progeny emergence, which are all similar to *T. dubius* funnel trap catches by Raffa (1991). These collection peaks probably do not represent different generations of *T. dubius*, but rather differences in the activity of the adults. Since *T. dubius* adults prey upon *I. pini* adults, it makes sense that *T. dubius* would be active at the same time as *I. pini* adults are becoming active (i.e. overwintering adult emergence, F1 progeny emergence). *Ips pini* adults produce aggregation pheromones as they are colonizing their hosts, and *T. dubius* uses these pheromones as kairomones to locate *I. pini* prey (Hansen 1983, Raffa and Klepzig 1989).

These findings on the biology of *T. dubius* have many implications for the proposed introduction of the European clerid *Thanasimus formicarius*. The primary reasons for the consideration of *T. formicarius* were that it is the earliest of the major European bark beetle predators to become active in the spring (Schroeder 1988), and that *T. dubius* was not expected to be active early enough to prey upon *T. piniperda*. I have early demon

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clearly demonstrated that *T. dubius* is indeed active as early in the spring as is *T. piniperda*, and that it will prey upon the exotic scolytid. The introduction of *T. formicarius* or other biological control agents for the control of *T. piniperda* should be postponed until the biology and impact of North American natural enemies is better understood.

Platysoma cylindrica is another scolytid predator that has commonly been found in funnel traps baited with *I. pini* aggregation pheromones (Raffa and Klepzig 1989, Raffa 1991), although a field study in Georgia indicated that *P. cylindrica* is not attracted to ipsdienol, but is attracted to ipsenol, an aggregation pheromone of *I. grandicollis* (Turnbow and Franklin 1981). This histerid was first collected in funnel traps in late May of both years, nearly a month later than Haack and Lawrence's (1995b) 1993 Michigan study. *Platysoma cylindrica* was primarily collected in funnel traps during two periods; corresponding to *I. pini* overwintering parent adult flight, and *I. pini* F1 progeny adult flight, respectively, which is similar to a Wisconsin study (Raffa 1991).

Corticeus parallelus adults followed the same trends as *T. dubius* and *P. cylindrica*: the highest funnel trap catches occurred near peak *I. pini* parent adult catches and near peak *I. pini* F1 progeny adult catches. This tenebrionid is also suspected to use *I. pini* pheromones as kairomones (Raffa and Klepzig 1989, Raffa 1991), so this synchrony was expected. These tenebrionids were first collected in late May of both years, about a month later than reported in another Michigan study (Haack and Lawrence 1995b).

Medetera sp. parent adults were not collected in the funnel traps, suggesting that they are not attracted to α-pinene or the *I. pini* pheromone lures on the funnel traps.

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Fitzgerald and Nagel (1972) found that adults of *M. aldrichii*, a predator of *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae), responded to α-pinene as an ovipositional stimulant, but there are no references to whether any of the *Medetera* species have been collected in α-pinene-baited funnel traps. Since I do not have funnel trap or observational records, I could not determine when parent adults emerge and oviposit. Studies of *M. aldrichii* Wheeler in Washington and South Dakota (Hopping 1947, Schmid 1970) demonstrated initial parent activity in early June and early July, respectively. I first collected *Medetera* sp. progeny adults from late July through September. Numerous *Medetera* sp. larvae were collected from the de-barked bolts, which agrees with several studies of *M. aldrichii* and *M. dendrobaena* Kowarz that report that these predators overwinter as larvae (Hopping 1947, Nicolai 1995, Schmid 1970).

Cucujus clavipes, along with the staphylinids, were some of the earliest predators to become active in the spring. The majority of *C. clavipes* adults were collected in funnel traps within two weeks of peak *T. piniperda* parent flight, indicating that this predator either has a low temperature threshold for flight or that it overwinters in locations that warm up quickly in the spring. One such possible overwintering location is under the bark of standing trees, which receives solar radiation and warms up much earlier in the spring than does the snow-insulated forest litter layer. I did not observe the overwintering sites of either *C. clavipes* or the staphylinids.

The funnel trapping method and the observations on the red pine bolts were phenologically consistent for most of the phloem feeders: *Tomicus piniperda*, *Ips pini*, *Ips grandicollis*, *Dendroctonus valens*, *Monochamus scutellatus*, and *M. carolinensis*.

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Since these insects were attracted to the funnel trap baits, were present in large numbers, and were large enough to be visible, both the funnel traps and the observations were suitable for monitoring the initial spring activity of these species.

For two phloem feeders and one predator, however, the results of the funnel traps and the observations were not consistent: *H. rugipennis pinifex*, *P. nemorensis*, and *T. dubius*. These insects were observed on the red pine bolts several weeks before they were first collected in the funnel traps, which suggests that walking activity and flight activity are two separate events. A possible explanation is that insects require more heat for flight than for walking, so they do not fly until it gets warmer. Another explanation for the discrepancy between the two methods is that the funnel trap lures were not volatilizing sufficiently enough in the cool spring weather to be attractive to these species. For *P. nemorensis*, *H. rugipennis pinifex*, and *T. dubius*, direct observations of activity on pine slash provide the best means of determining initial spring activity.

Observations were not useful in determining spring activity of other species, though. Most of the smaller bark beetles and natural enemies were collected in the pheromone-baited funnel traps, but were too small or too rare to be observed on the red pine bolts: *Orthotomicus caelatus*, *Ips perroti*, *Gnathotrichus materiarius*, *Hylastes porculus*, *Dryocetes autographus*, *Platysoma cylindrica*, *Corticeus parallelus*, *Platysoma parallelum*, staphylinids, and *Cucujus clavipes*. In the cases of *Medetera* sp., *Anthocoris* sp., and parasitic wasps, neither observations nor funnel traps were useful as indicators of spring activity. These insects are not known to be attracted to α-pinene or pheromone-baited funnel traps, and they were probably too small to be seen during the observations.

Of the three methods utilized to study the phenology of bark beetles and their

natural enemies in this study, the pheromone-baited funnel traps were simple to use and collected the greatest number of species of pine phloem feeders, as well as eight species of their natural enemies. The funnel traps employed an effective pheromone/ kairomone system that was utilized by many bark beetles and natural enemies of varied sizes.

There were several problems associated with funnel trapping, however. Some bark beetle and natural enemy species were not attracted to α-pinene or the pheromones, including parasitoids, anthocorid predators, and dolichopodid predators. Because α-pinene, ipsdienol, and lanierone were deployed at the same time in all traps, I cannot determine which of the baits was most effective for each insect. Many incidental insects (neither phloem feeders nor natural enemies) were collected by this method – sometimes up to 50% of each catch was made up of incidental species of beetles, moths, and flies. Since I used insecticide in the collection cups, funnel trapping was a destructive sampling method, and could have potentially impacted the population dynamics of the phloem feeders or their natural enemies in my field sites (see Raffa 1991). Funnel traps are generally considered more of a qualitative than quantitative sampling method, since the effectiveness of the lures varies depending on the temperature, humidity, wind, and other factors (Lindgren 1983, Lindgren et al. 1983, Salom and McLean 1991). Finally, though funnel trapping was an effective means of determining first flight activity for many of these bark beetles and natural enemies, it did not determine first general activity (i.e. walking, mating, preying) for two abundant phloem feeders, *Hylurgops rugipennis pinifex* and *Pissodes nemorensis*, and for an important predator, *Thanasimus dubius*.

Observing insect activity on red pine bolts was useful for large, conspicuous, and numerous bark beetles and predators. Observations were an excellent means of

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determining the dates of the first walking and mating activity on the red pine bolts, the first predator activity, and the emergence of the progeny. The observations of insect activity were also useful when compared to the two other sampling methods – they provided a real-life check for the funnel trap and rearing results. Observations are an example of non-destructive sampling, and unlike the funnel trapping method, they weren't biased towards species utilizing host volatiles, pheromones, or kairomones.

However, this method underestimated activity of small, cryptic insect species and did not include activity such as most mating, gallery formation, development, and predation that occurred under the bark. The observations were also qualitative and difficult to standardize; activity on the bolts varied greatly depending on the temperature and weather.

Rearing pine phloem feeders and natural enemies from red pine bolts provided the best means for studying progeny emergence. The rearing method yielded slightly fewer numbers of phloem feeding species (twelve) than the funnel traps, but nearly twice as many natural enemy species (fifteen) were collected. Unlike the other two methods, rearing was not affected by insect size or utilization of lures. Very few incidental species were reared from the red pine bolts; nearly everything collected was either a phloem feeder or a natural enemy of phloem feeders. The rearing method was also the most quantitative of the three methods, since progeny abundance could be standardized across surface area measurements. Rearing provided an excellent insight on the number of generations of phloem feeders and natural enemies.

The rearing method had several disadvantages, though. It was the most time-consuming of the methods, since hundreds of emergence containers had to be checked several times a week. The red pine bolts were cumbersome to transport, and they required a large amount of room for storage. Because all of the bolts were subjected to the same (ambient) temperatures and humidity in the emergence containers, phenological differences between northern and southern sites were largely obscured. Also, the earliest collections of each of each species were likely re-emerging parent adults, and these parent adults confounded the actual date of first emergence of progeny. For the insects collected during de-barking, I could not determine when or why the insects had died. For some species, progeny were collected only during bolt dissection, so progeny emergence phenology could not be determined.

Conclusions

Overall, in the Great Lakes region, most pine bark beetles and their associates have not been well-studied (Raffa 1991). This paper has served to add phenological information and number of generations to the limited knowledge accumulated on Great Lakes pine bark beetles and their associates, but further research on the dynamics of this insect complex is needed. Funnel traps were effective for determining first flight activity of parent adults of bark beetles and coleopteran predators in the spring, but observations were the best means of determining actual activity (i.e. colonization, predation) for *H. rugipennis pinifex*, *P. nemorensis*, and *T. dubius*. *Tomicus piniperda,* despite its early spring flight, will face a number of natural enemies and competitors for pine breeding material in Michigan. I have demonstrated that two pine phloem feeders and four predators are active as early in the spring as is *T. piniperda*.

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Table 1. *General characteristics and number of red pine bolts placed at the 1996 and 1997 red pine plantation field sites.*

	KAL 1	KAL 2	ALL 1	ALL 2	WEX 1	WEX 2	ROS 1	ROS 2
Area (ha)	0.81	1.62	9.31	6.47	18.62	10.93	52.20	22.26

Table 1. General characteristics and number of red pine bolts placed at the 1996 and 1997 red pine plantation field sites.

	KAL 1	KAL 2	ALL 1	ALL 2	WEX 1	WEX 2	ROS 1	ROS 2
Area (ha)	0.81	1.62	9.31	6.47	18.62	10.93	52.20	22.26
Year planted	1937	1937	1939	1938	1937	1948	1937	1965
Basal area (m^2/ha) after thinning	30	18	21	23	28	28	21	21
Year(s) thinned	1995	1996	1987, 1995	1996	1975, 1995	1996	1995	1996
No. of batch 96-1 bolts (in field 6 March 1996)	30	—	30	—	0	—	0	—
No. of batch 96-2 bolts (in field 7 May 1996)	22	—	22	—	22	—	22	—
No. of batch 96-3 bolts (in field 20 June 1996)	14	—	14	—	14	—	14	—
No. of batch 97-1 bolts (in field 28 Feb. 1997)	28	28	28	28	0	0	0	0
No. of batch 97-2 bolts (in field 11 April 1997)	16	16	16	16	16	16	16	16
No. of batch 97-3 bolts (in field 2 July 1997)	8	8	8	8	8	8	8	8

Table 3. Total number of insects collected from pheromone baited funnel traps at either the southern ([illegible] and

Table 2. Total number of insects collected from pheromone-baited funnel traps at either the southern (1996: 4 traps each at KAL1 and ALL1; 1997: 2 traps each at KAL1, KAL2, ALL1, ALL2), or northern (1996: 4 traps each at WEX1 and ROS1; 1997: 2 traps each at WEX1, WEX2, ROS1, ROS2) Michigan red pine plantations, or in 7 funnel traps in a red and Scotch pine plantation in Lansing.

	Southern		Lansing		Northern	
	1996	1997	1996	1997	1996	1997
Phloem feeders						
Dendroctonus valens	93	52	0	6	145	171
Dryocetes autographus	0	3	2	0	0	0
Gnathotrichus materiarius	17	20	6	0	0	12
Hylastes porculus	79	2	5	0	1	5
Hylurgops rugipennis pinifex	5	18	0	4	17	22
Ips grandicollis	110	121	51	7	2	14
Ips perroti[1]	0	0	0	0	0	0
Ips pini	548	452	184	138	3474	672
Monochamus spp.	12	12	0	0	25	5
Pissodes nemorensis	25	5	0	3	1	1
Orthotomicus caelatus	37	62	12	3	2	26
Tomicus piniperda	14	297	429	481	0	0
Natural enemies						
Anthocoris sp.[1]	0	0	0	0	0	0
Corticeus parallelus	58	138	73	56	91	67
Cucujus clavipes	3	8	9	1	0	2
Enoclerus nigripes	2	3	0	0	4	13
Medetera sp.[1]	0	0	0	0	0	0
Parasitic wasps[1]	0	0	0	0	0	0
Platysoma cylindrica	40	53	7	8	375	132
Platysoma parallelum	0	5	0	2	1	15
Staphylinidae	27	59	56	14	28	32
Thanasimus dubius	23	164	52	24	61	134

[1] = These species were not collected in funnel traps, but were reared from red pine bolts.

Table 3. Julian dates (JD) and degree-days base 10°C (DD) (Baskerville-Emin method) in 1996 when insects were collected from pheromone-baited funnel traps in either southern (KAL1 and ALL1) or northern (WEX1 and ROS1) Michigan red pine plantations, or in a red pine and Scotch pine plantation in Lansing, Michigan.

	First collection			Last collection		
	Southern JD/DD	Lansing JD/DD	Northern JD/DD	Southern JD/DD	Lansing JD/DD	Northern JD/DD
Phloem feeders						
Dendroctonus valens	138/89	—	141/88	159/236	—	190/437
Dryocetes autographus	—	140/92	—	—	148/188	—
Gnathotrichus materiarius	137/89	127/74	—	159/236	140/92	—
Hylastes porculus	141/159	139/92	198/504	159/236	171/378	198/504
Hylurgops rugipennis pinifex	137/89	—	141/88	141/159	—	198/504
Ips grandicollis	134/89	139/92	152/109	159/236	185/449	152/109
Ips perroti	—	—	—	—	—	—
Ips pini	134/89	139/92	134/39	253/1230	264/1297	267/1038
Monochamus spp.	183/458	—	190/437	234/1084	—	253/949
Orthotomicus caelatus	138/89	139/92	141/88	176/458	252/1202	198/504
Pissodes nemorensis	103/29	—	134/9	197/673	—	134/39
Tomicus piniperda	90/10	87/8	—	206/756	127/74	—
Natural enemies						
Anthocoris sp.	—	—	—	—	—	—
Corticeus parallelus	103/29	75/0	138/39	197/673	199/642	253/949
Cucujus clavipes	103/29	103/22	—	103/29	140/92	—
Enoclerus nigripes	206/756	—	137/39	211/756	—	232/822
Medetera sp.	—	—	—	—	—	—
Parasitic wasps	—	—	—	—	—	—
Platysoma cylindrica	124/54	139/92	141/88	197/673	199/642	253/949
Platysoma parallelum	124/54	139/92	141/88	206/756	199/642	141/88
Staphylinidae	90/10	103/22	141/88	206/756	139/92	253/949
Thanasimus dubius	176/458	109/22	137/39	253/1230	243/1202	267/1038

Table 4. Julian dates (JD) and degree-days base 10°C (DD) (Baskerville-Emin method) in 1997 when insects were collected from pheromone-baited funnel traps in either southern (KAL1, KAL2, ALL1, ALL2) or northern (WEX1, WEX2, ROS1, ROS2) Michigan red pine plantations, or in a red pine and Scotch pine plantation in Lansing.

	First collection			Last collection		
	Southern JD/DD	Lansing JD/DD	Northern JD/DD	Southern JD/DD	Lansing JD/DD	Northern JD/DD
Phloem feeders						
Dendroctonus valens	149/125	150/103	154/111	204/712	217/812	203/559
Dryocetes autographus	156/170	—	—	156/170	—	—
Gnathotrichus materiarius	132/76	—	154/111	204/712	—	203/559
Hylastes porculus	156/170	—	155/111	156/170	—	177/295
Hylurgops rugipennis pinifex	127/66	195/586	155/111	204/712	195/586	203/559
Ips grandicollis	149/125	125/58	154/111	204/712	241/861	177/295
Ips perroti[1]	—	—	—	—	—	—
Ips pini	127/66	119/48	133/38	269/1218	276/1145	268/946
Monochamus spp.	176/381	—	177/354	232/997	—	203/559
Orthotomicus caelatus	156/170	150/103	154/111	204/712	157/139	177/295
Pissodes nemorensis	94/33	92/30	164/164	156/170	125/58	164/164
Tomicus piniperda	81/0	80/0	—	204/712	183/354	—
Natural enemies						
Anthocoris sp.[1]	—	—	—	—	—	—
Corticeus parallelus	156/170	105/30	154/111	204/712	282/1088	203/559
Cucujus clavipes	88/0	164/175	168/216	156/170	164/175	168/216
Enoclerus nigripes	204/712	—	155/111	204/712	—	203/559
Medetera sp.[1]	—	—	—	—	—	—
Parasitic wasps[1]	—	—	—	—	—	—
Platysoma cylindrica	156/170	150/103	154/111	204/712	269/1145	268/946
Platysoma parallelum	156/170	164/175	155/111	156/170	269/1145	203/559
Staphylinidae	88/0	80/0	109/15	204/712	269/1145	233/775
Thanasimus dubius	127/66	150/103	133/38	204/712	282/1088	233/775

Table 5. Total number of insects reared from red pine bolts from the southern (1996: KAL1 and ALL1; 1997: KAL1, KAL2, ALL1, ALL2), or northern (1996: WEX1 and ROS1; 1997: WEX1, WEX2, ROS1, ROS2) Michigan red pine plantations. A total of 204 bolts were used in 1996; 304 were used in 1997.

	Southern sites				Northern sites			
	1996		1997		1996		1997	
	Total Reared^1	No. left in bolts^2	Total Reared^1	No. left in bolts^2	Total Reared^1	No. left in bolts^2	Total Reared^1	No. left in bolts^2
Phloem feeders								
Dendroctonus valens^3	0	0	0	0	0	0	0	0
Dryocetes autographus	102	7	28	2	0	0	0	0
Gnathotrichus materiarius	249	92	211	114	138	27	6	1
Hylastes porculus	258	250	209	203	64	57	64	63
Hylurgops rugipennis pinifex	2705	1746	2133	1860	549	161	1557	1276
Ips grandicollis	1218	635	4287	1526	1033	193	508	147
Ips perroti	0	0	0	0	219	28	252	58
Ips pini	2716	824	3315	947	4553	1329	4941	1317
Monochamus spp.^{4}	203	203	102	102	464	464	338	338
Pissodes nemorensis	2067	809	1152	315	280	93	301	85
Orthotomicus caelatus	1230	918	420	311	333	124	31	14
Tomicus piniperda	1289	170	3438	627	0	0	0	0

Table 5 (cont'd).

	Southern sites				Northern sites			
	1996		1997		1996		1997	
	Total Reared[1]	No. left in bolts[2]	Total Reared[1]	No. left in bolts[2]	Total Reared[1]	No. left in bolts[2]	Total Reared[1]	No. left in bolts[2]
Natural enemies								
Anthocoris sp.[4]	5	3	147	59	2	1	40	27
Corticeus parallelus	186	182	362	346	33	26	162	144
Cucujus clavipes[3]	0	0	0	0	0	0	0	0
Enoclerus nigripes	0	0	0	0	11	5	13	1
Medetera sp.	225	50	405	38	96	32	23	2
Parasitic wasps	143	26	59	3	46	2	121	2
Platysoma cylindrica	83	70	330	218	30	16	116	89
Platysoma parallelum	64	50	49	49	18	14	28	28
Staphylinidae	51	47	38	26	11	9	20	17
Thanasimus dubius	67	23	287	79	135	28	142	46

[1] = Cumulative total number of insects reared from red pine bolts.

[2] = Number of insects collected during bolt dissection in the winter following the season.

[3] = These species were not reared from red pine bolts, but were collected in funnel traps.

[4] = Combination of adult and larval progeny.

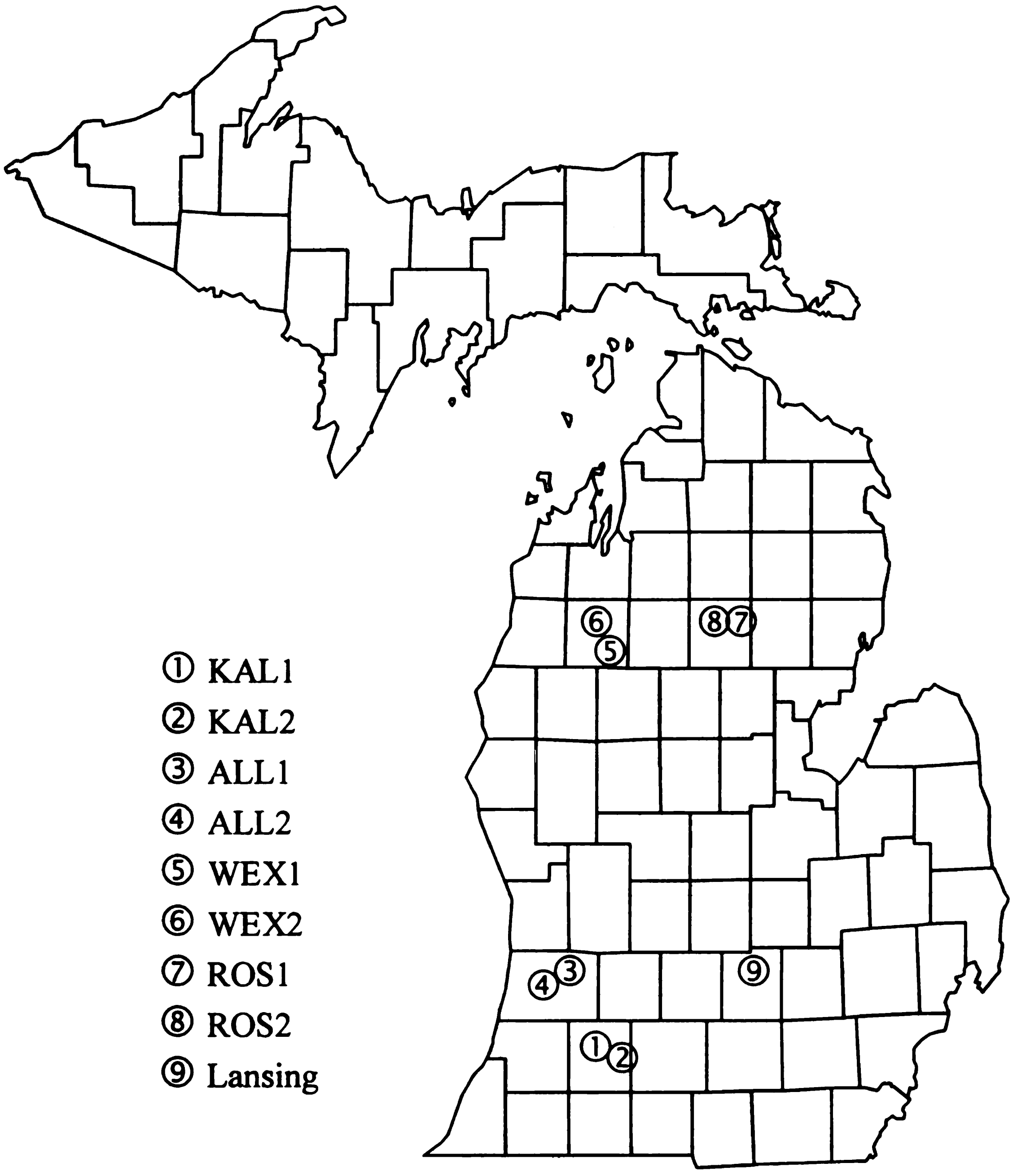


Figure 1. Location of red pine forest plantation field sites in Michigan. KAL1, ALL1, WEX1, ROS1, and Lansing were monitored in 1996; all stands were monitored in 1997.

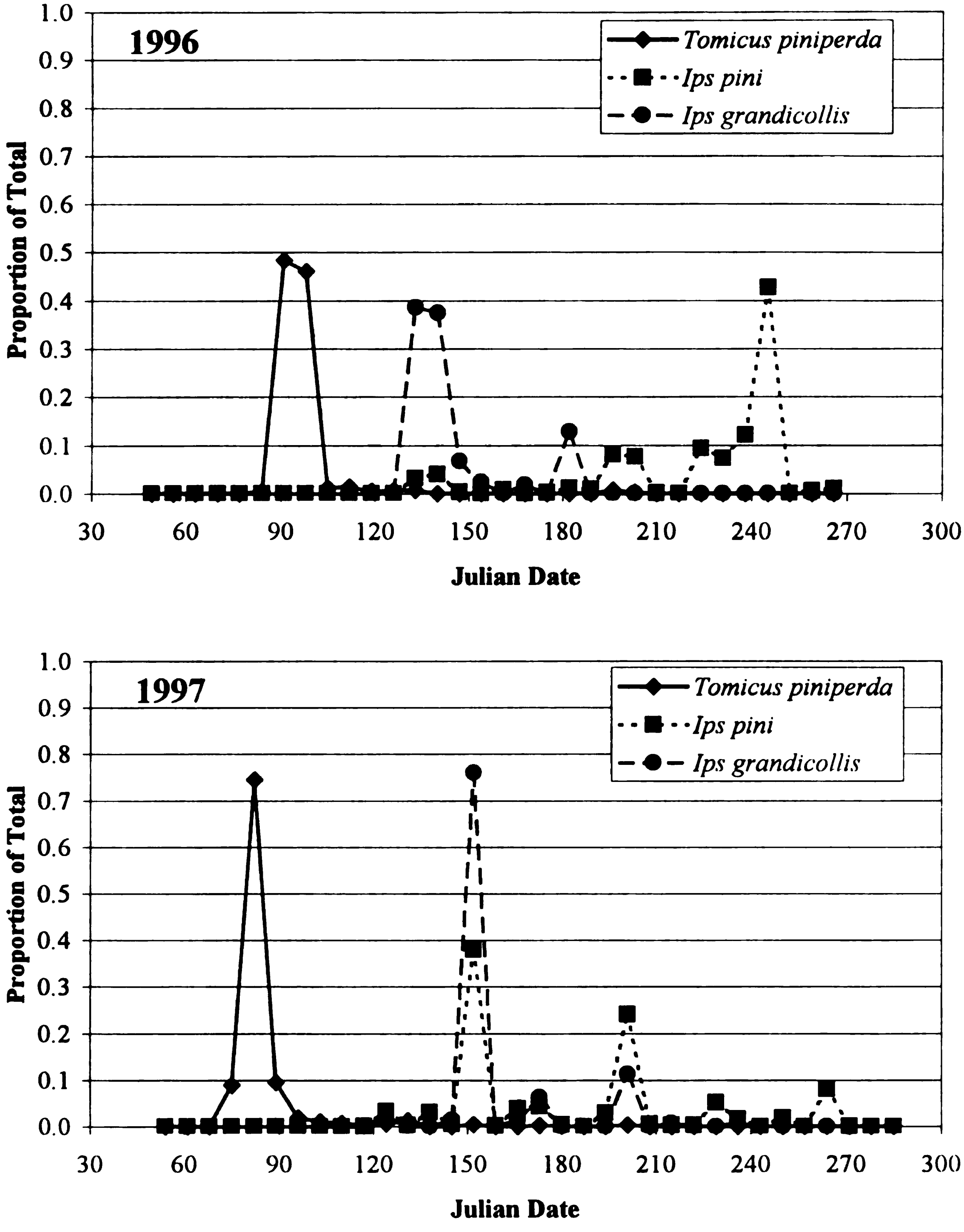


Figure 2. Seasonal distribution of scolytid adults collected in funnel traps baited with alpha-pinene, ipsdienol, and lanierone at five Michigan red pine plantations in 1996 and nine plantations in 1997.

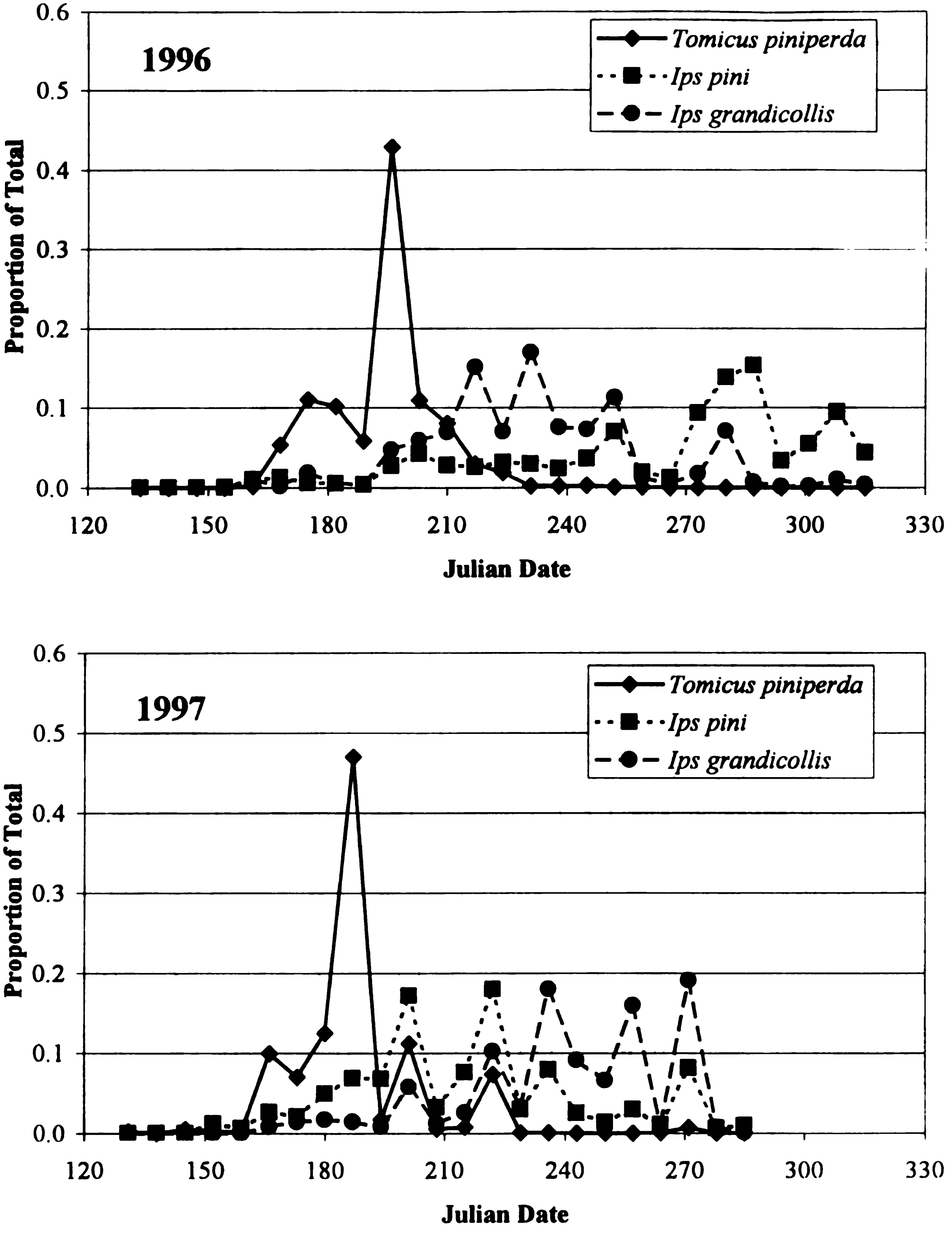


Figure 3. Seasonal distribution of scolytid progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.

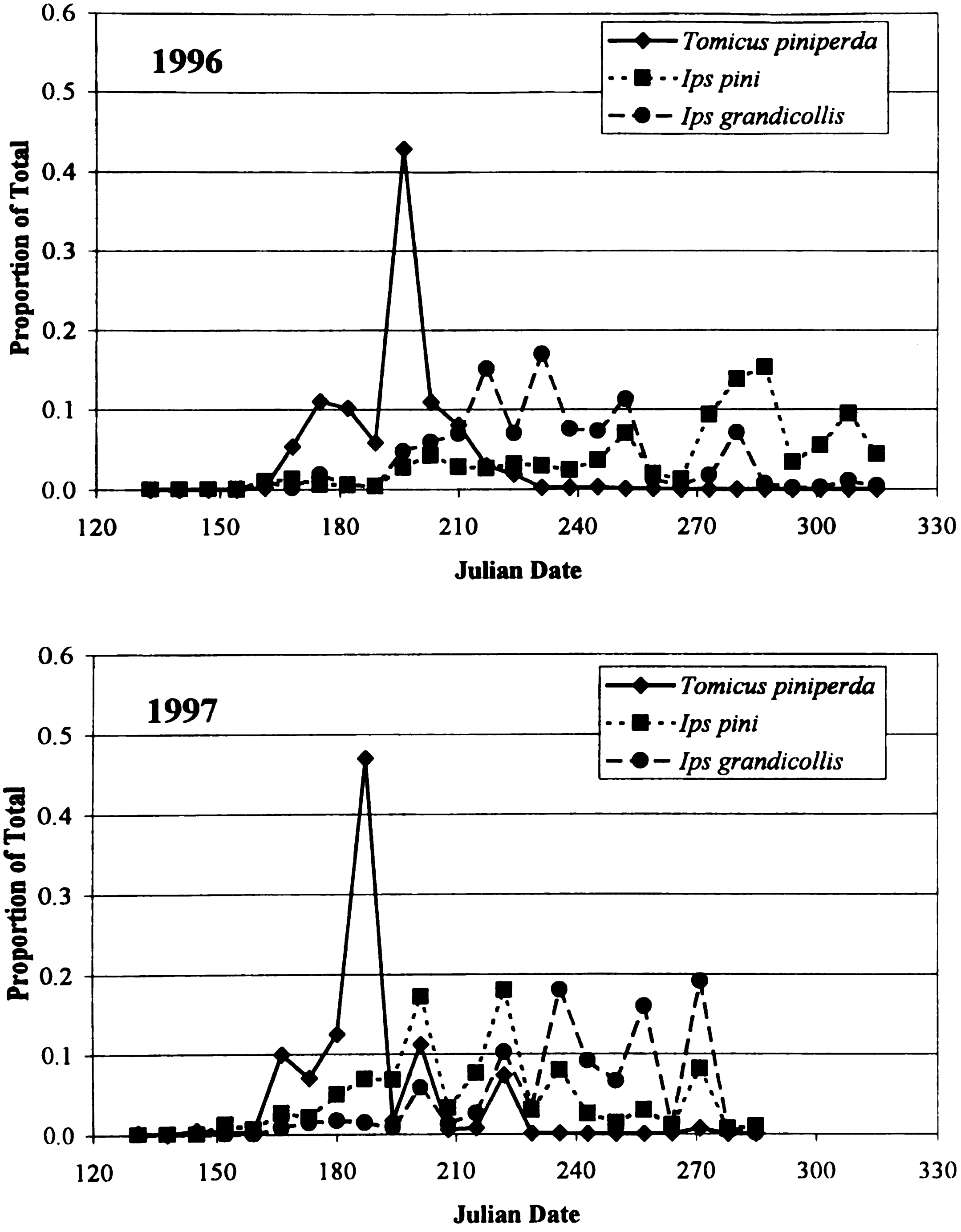
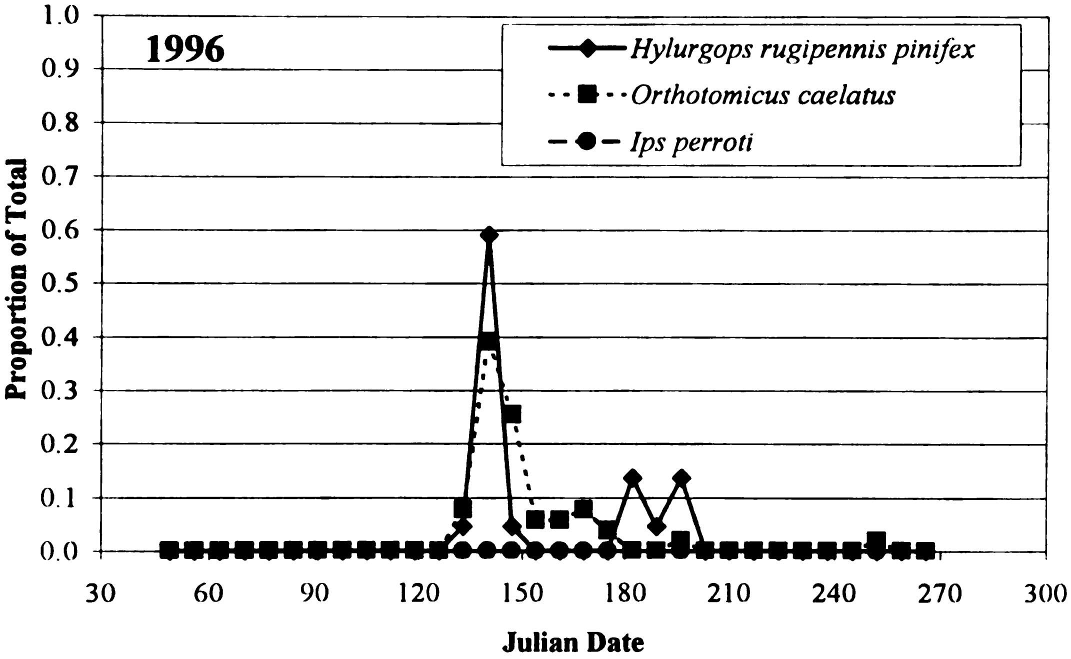


Figure 3. Seasonal distribution of scolytid progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.



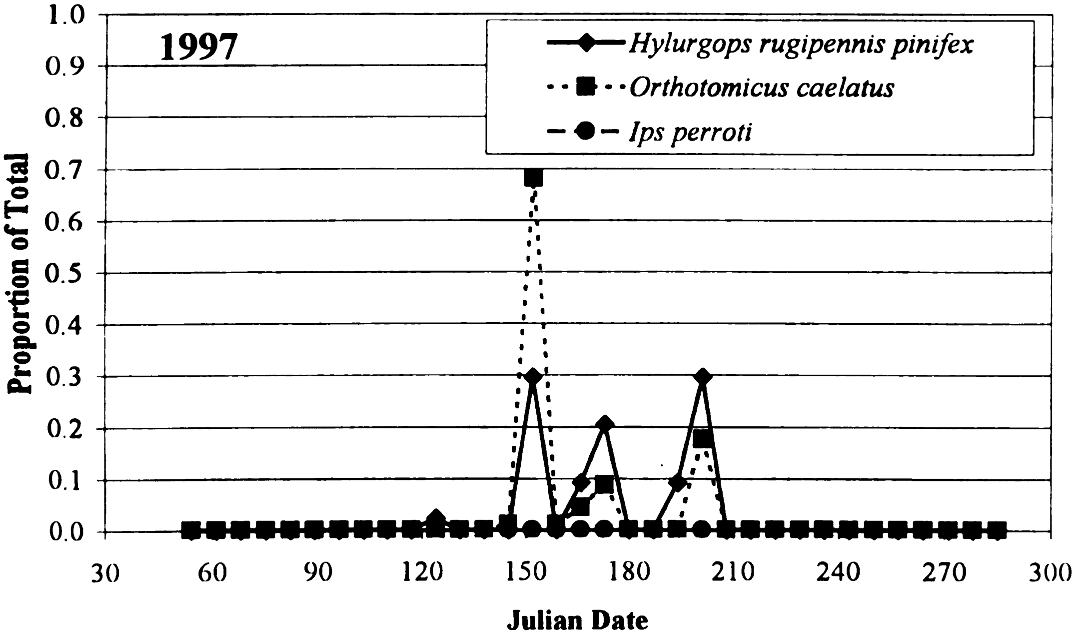
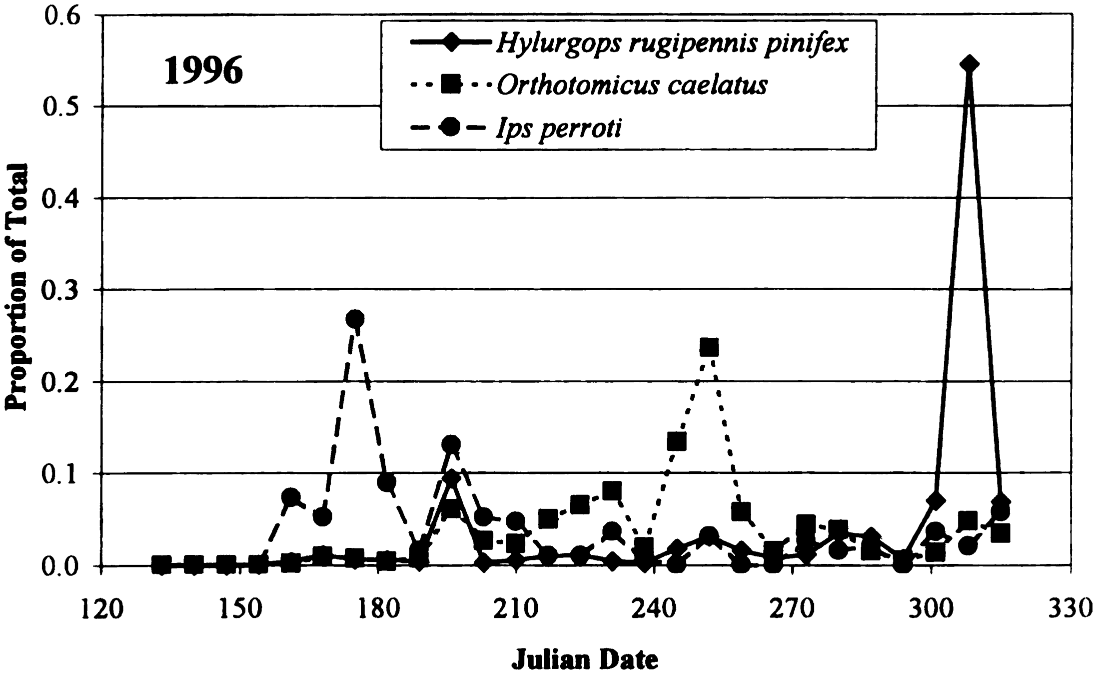


Figure 4. Seasonal distribution of scolytid adults collected in funnel traps baited with alpha-pinene, ipsdienol, and lanierone at five Michigan red pine plantations in 1996 and nine plantations in 1997.



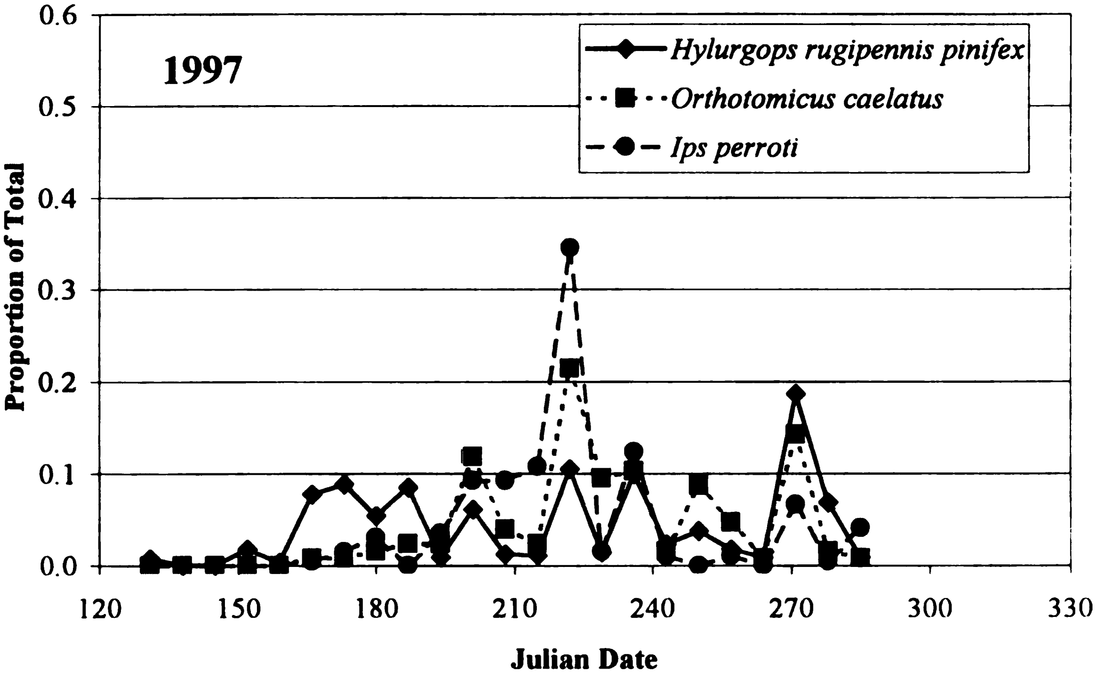


Figure 5. Seasonal distribution of scolytid progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.

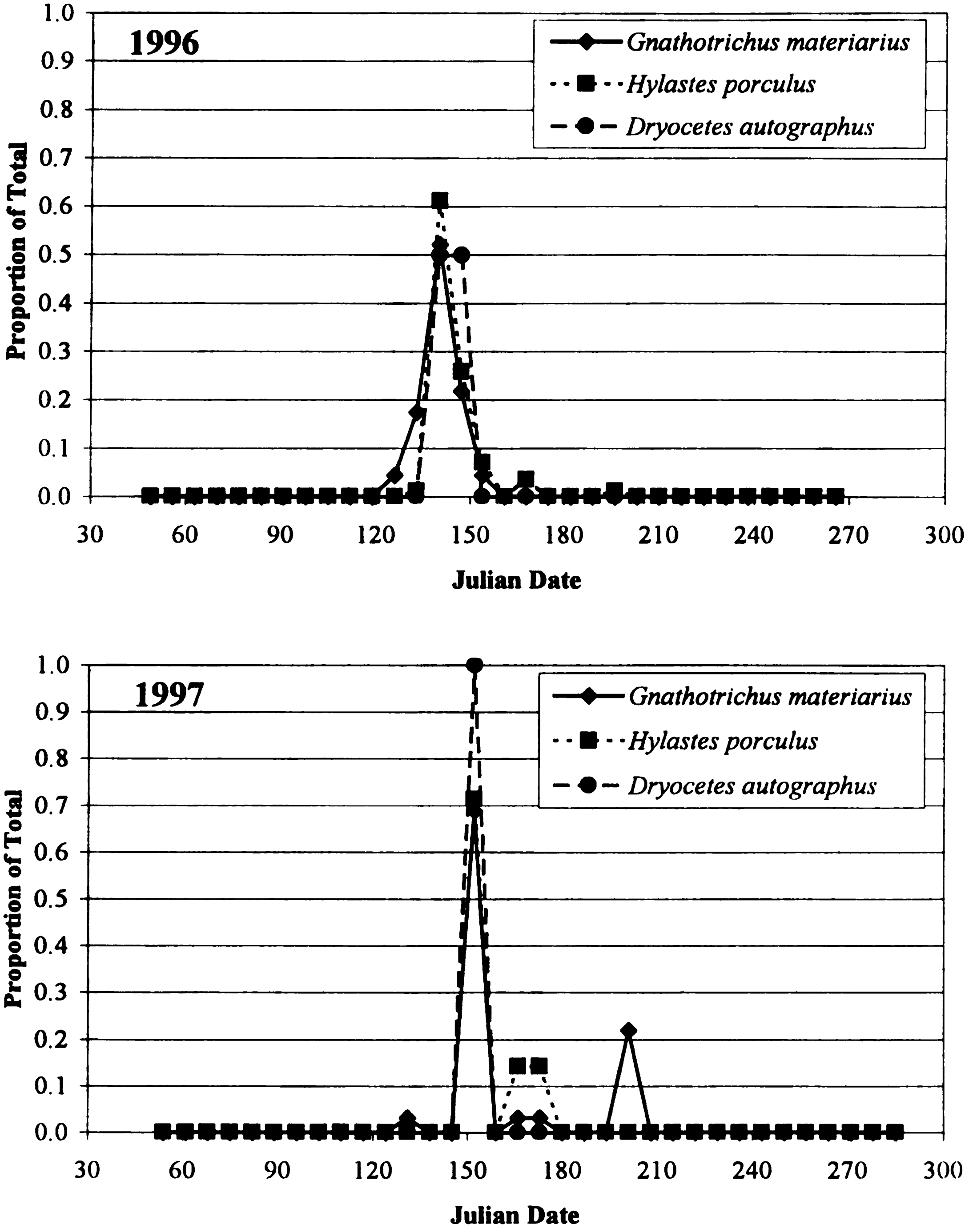


Figure 6. Seasonal distribution of scolytid adults collected in funnel traps baited with alpha-pinene, ipsdienol, and lanierone at five Michigan red pine plantations in 1996 and nine plantations in 1997.

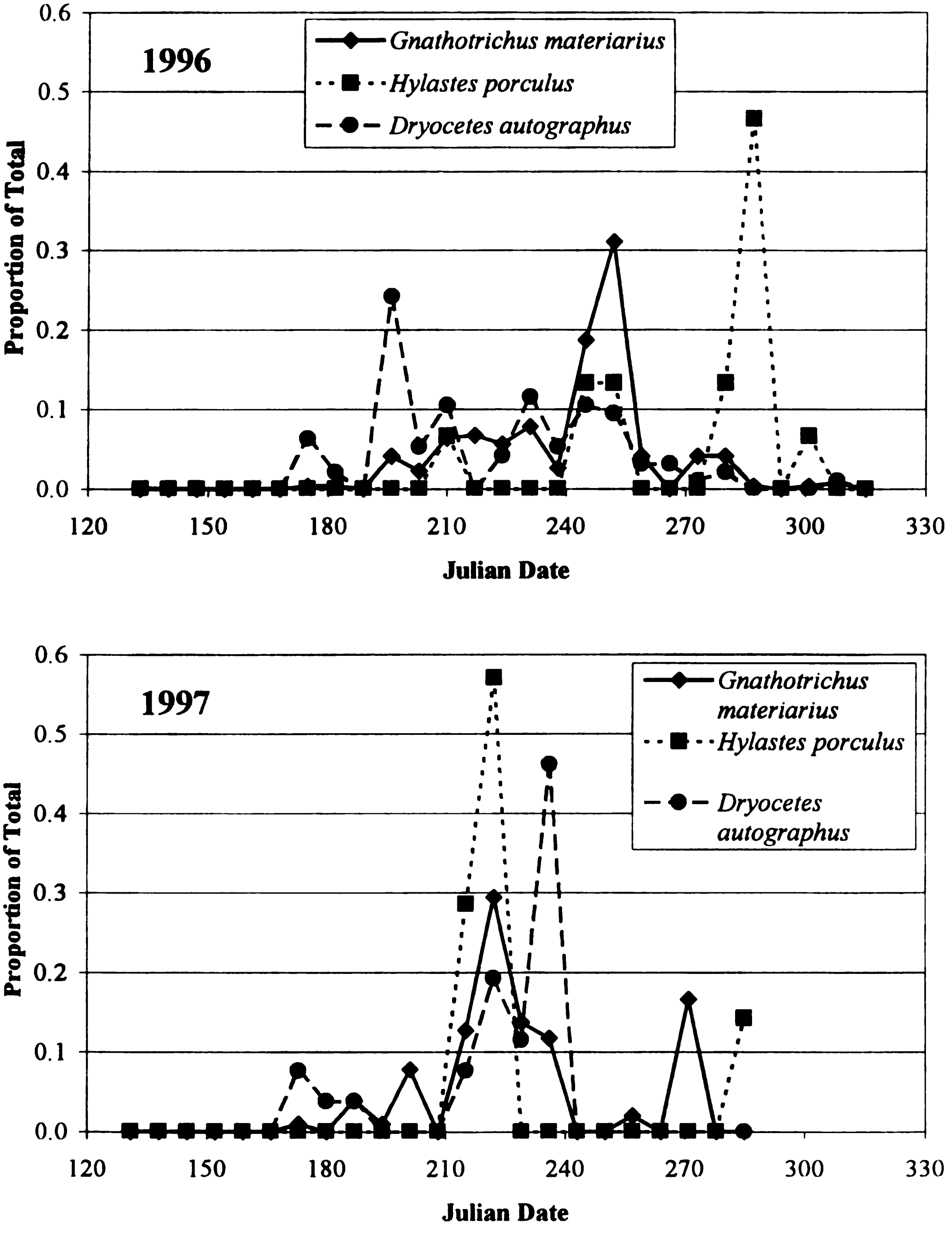


Figure 7. Seasonal distribution of scolytid progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.

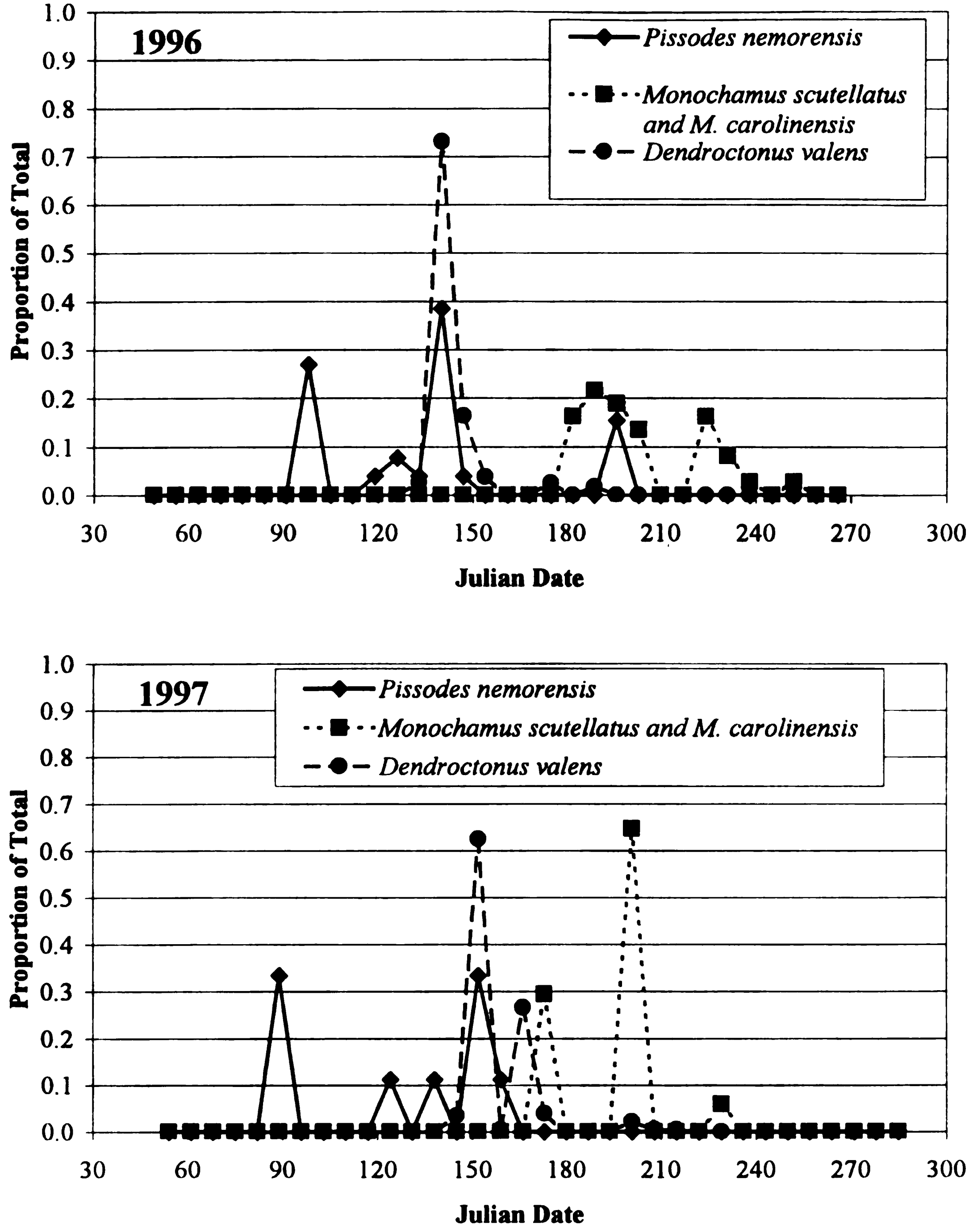
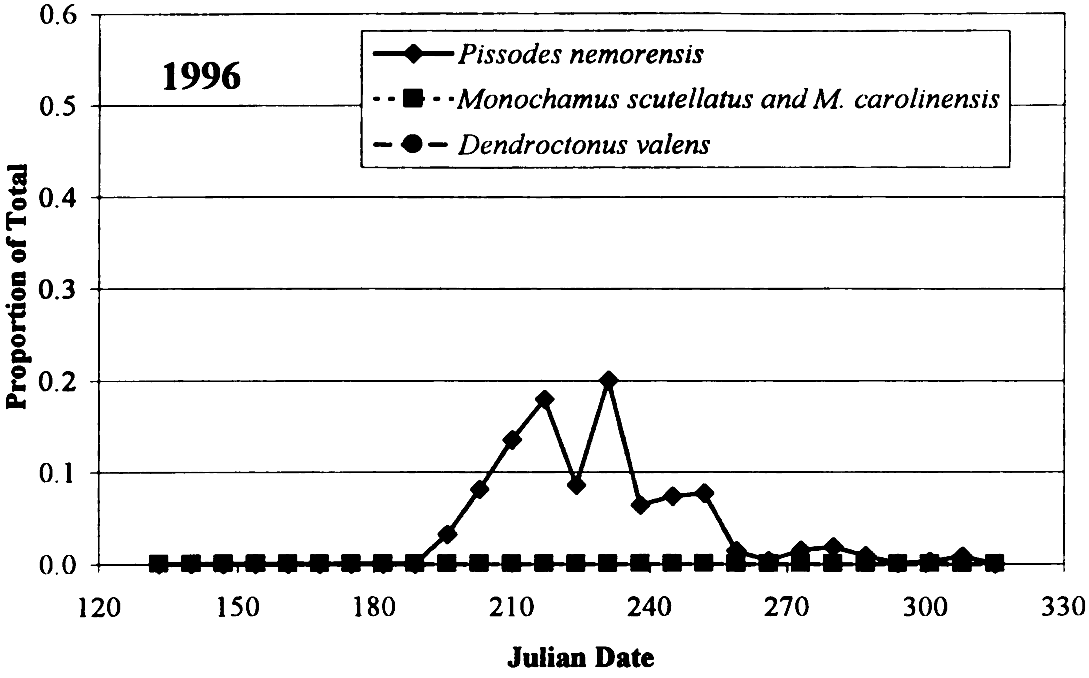


Figure 8. Seasonal distribution of adults collected in funnel traps baited with alpha-pinene, ipsdienol, and lanierone at five Michigan red pine plantations in 1996 and nine in 1997.



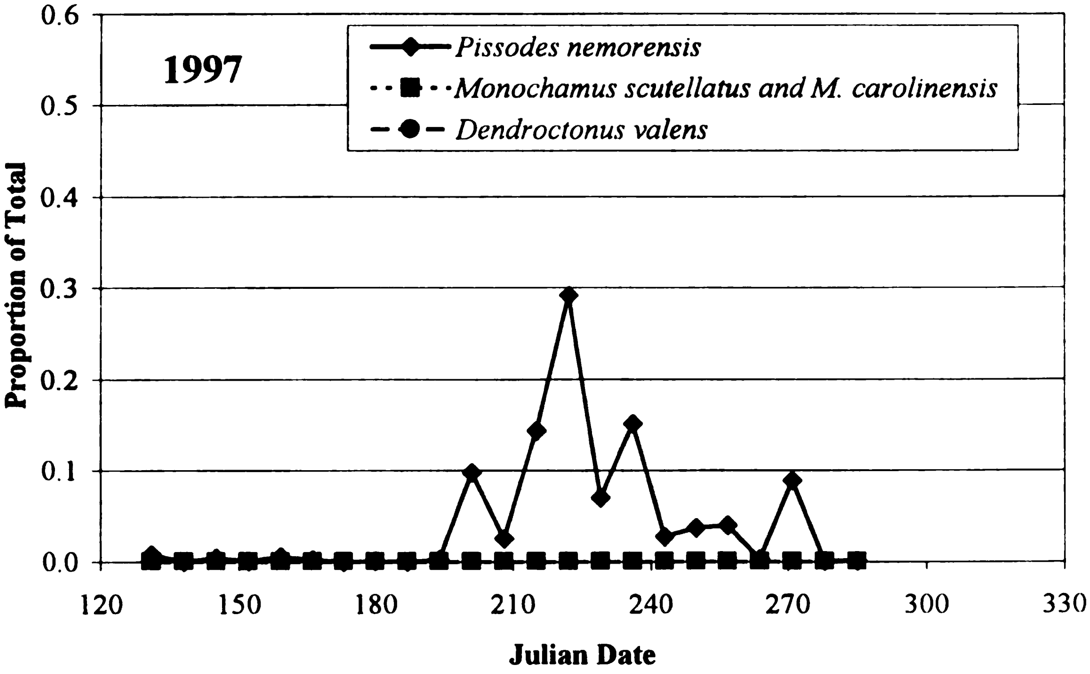


Figure 9. Seasonal distribution of progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.

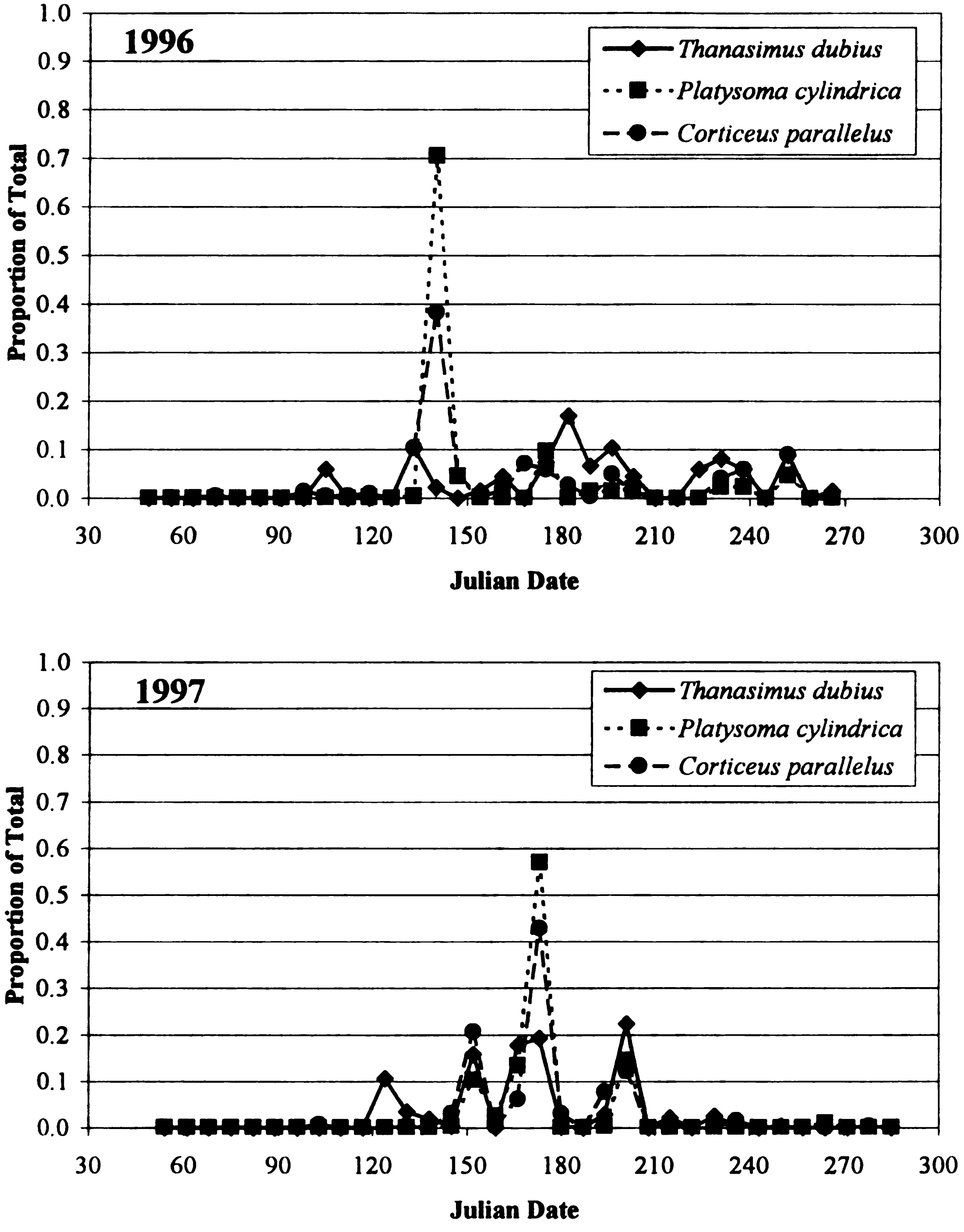
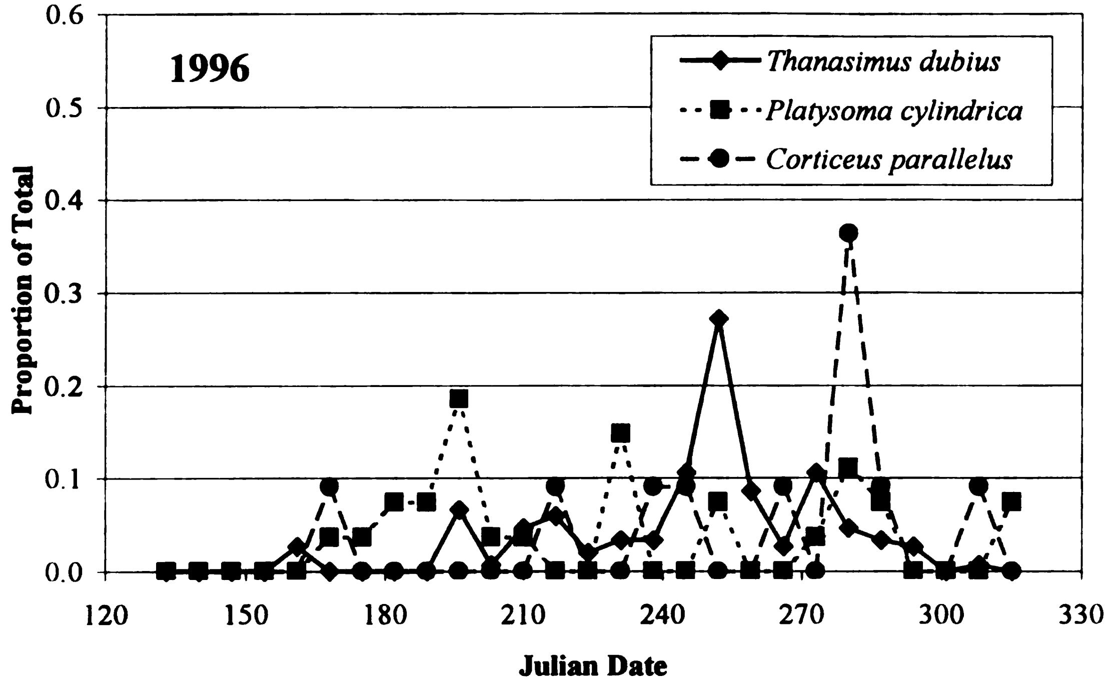


Figure 10. Seasonal distribution of parent adults collected in funnel traps baited with alpha-pinene, ipsdienol, and lanierone at five Michigan red pine plantations in 1996 and nine plantations in 1997.



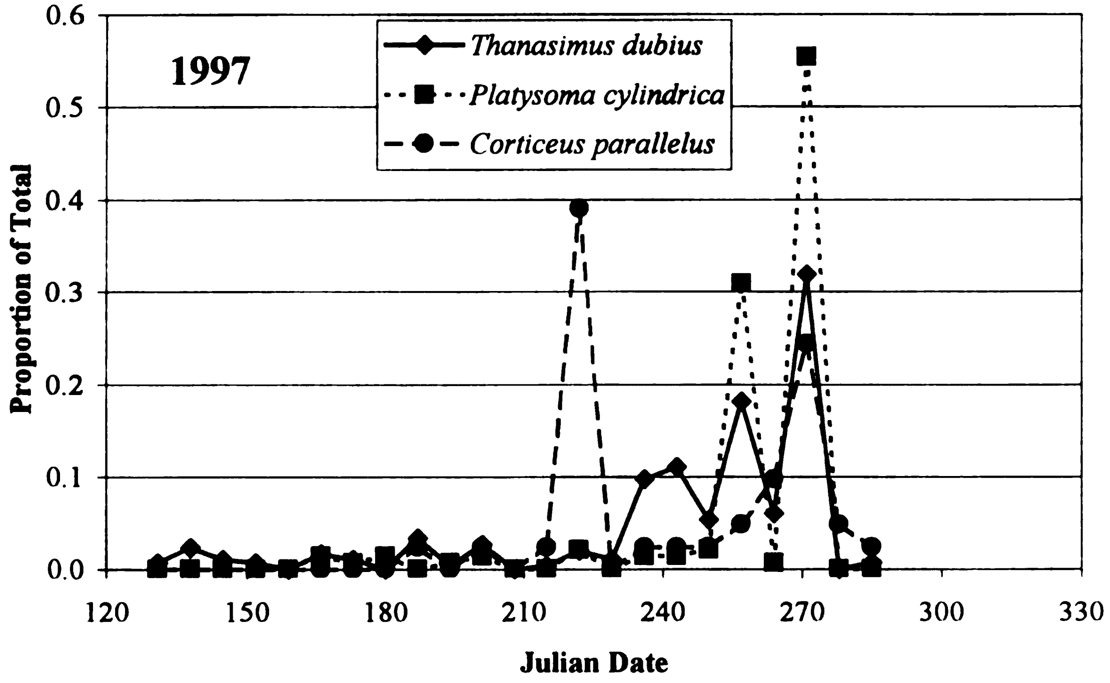


Figure 11. Seasonal distribution of predator progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.

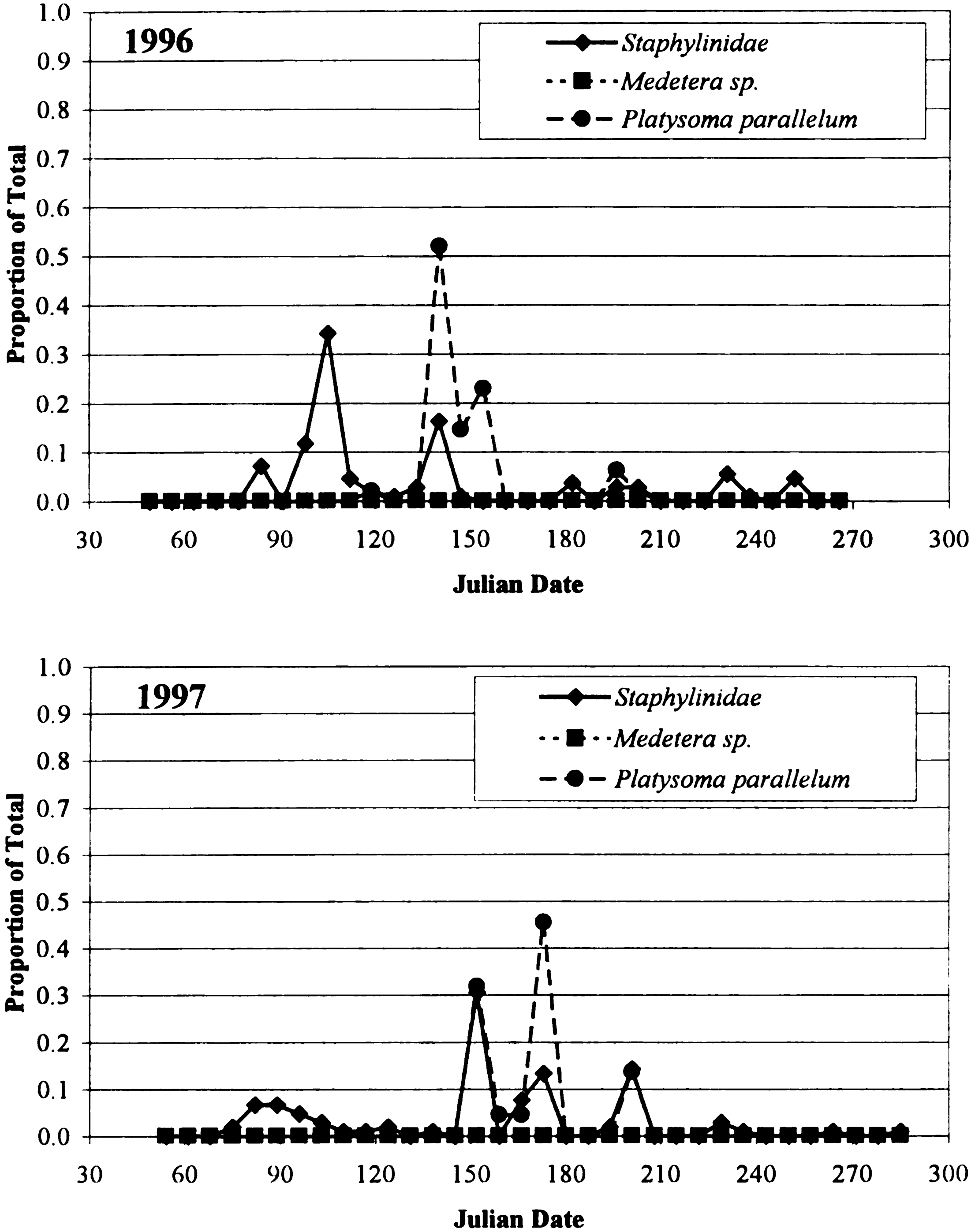


Figure 12. Seasonal distribution of predator adults collected in funnel traps baited with alpha pinene, ipsdienol, and lanierone at five Michigan red pine plantations in 1996 and nine plantations in 1997.

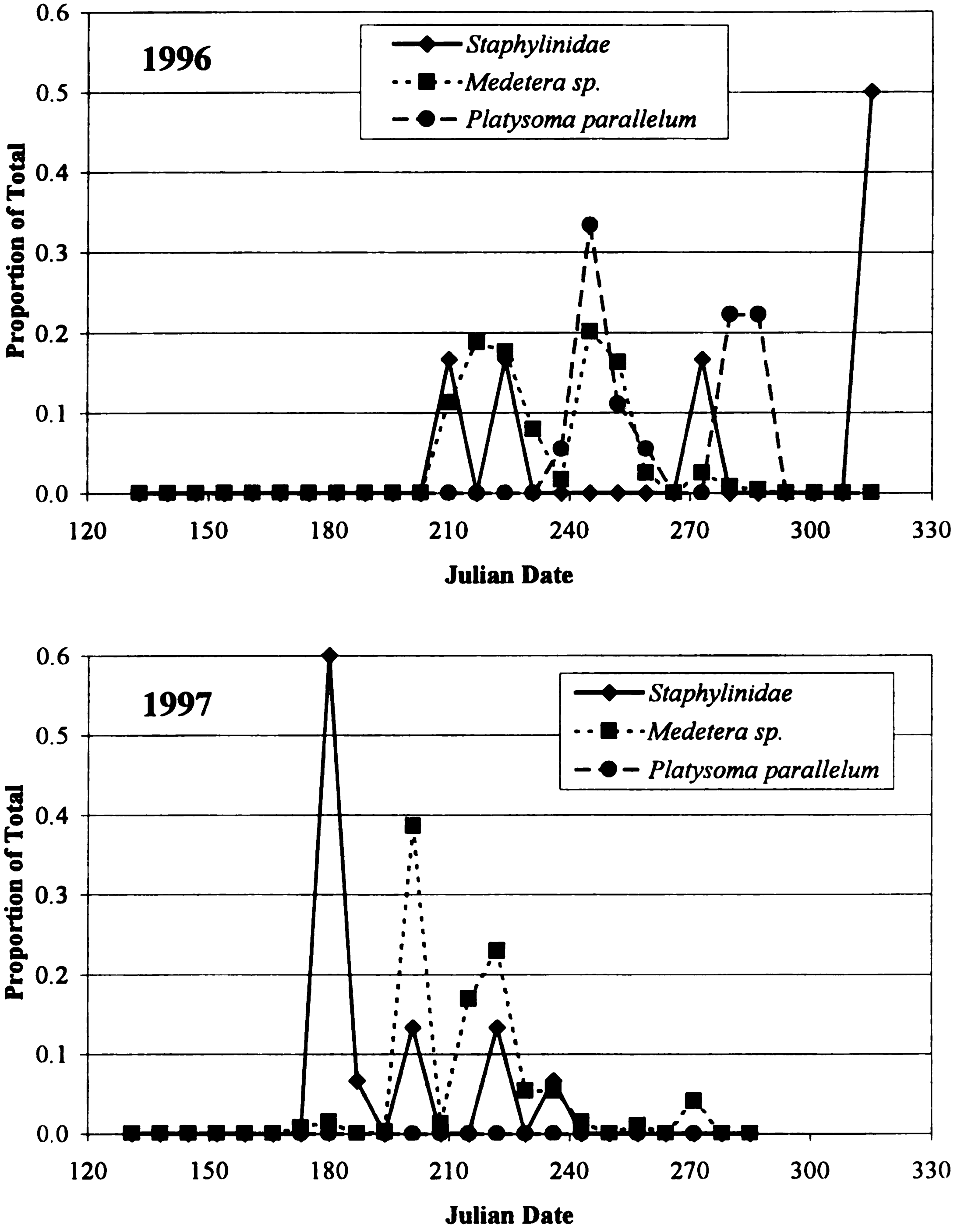
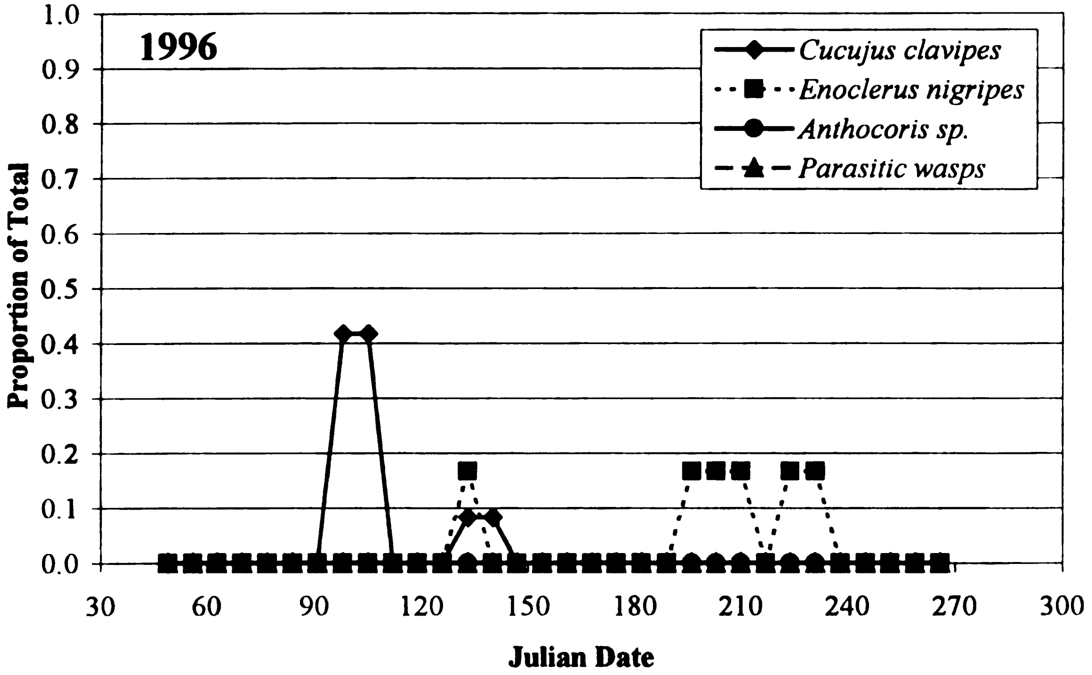


Figure 13. Seasonal distribution of predator progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.



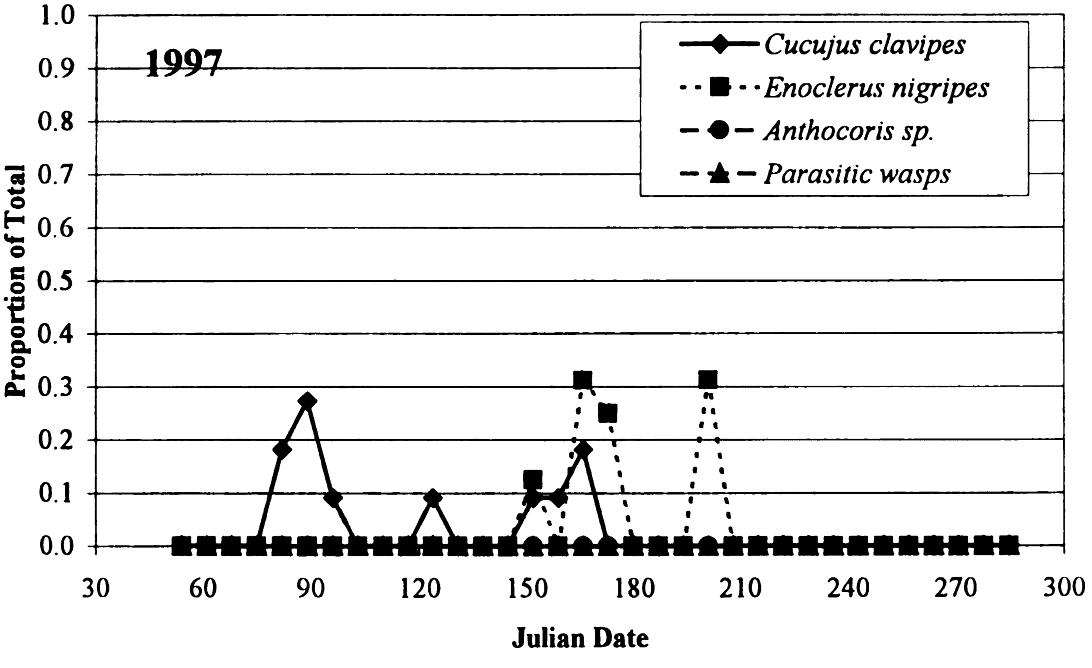
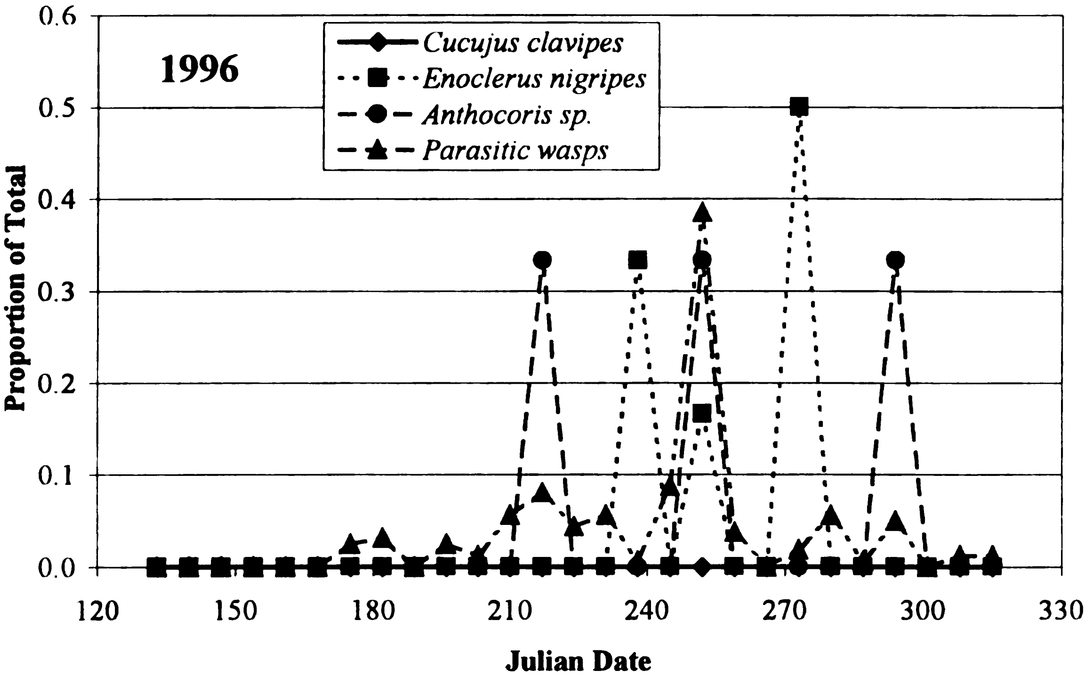


Figure 14. Seasonal distribution of predator and parasitoid adults collected in funnel traps baited with alpha-pinene, ipsdienol, and lanierone at five Michigan red pine plantations in 1996 and nine plantations in 1997.



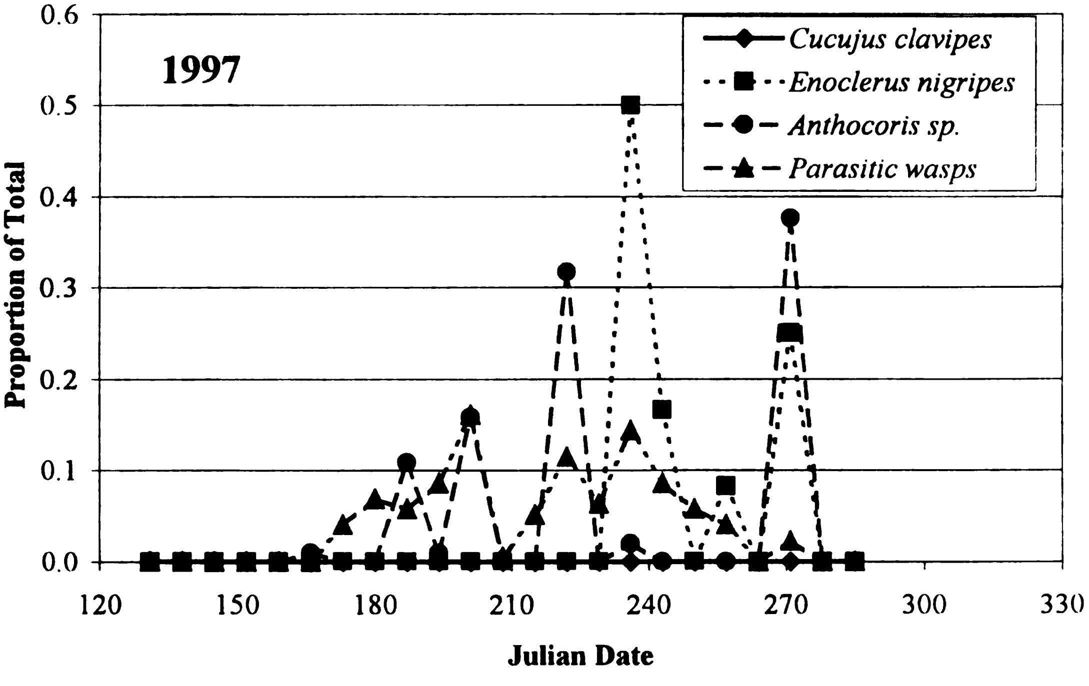
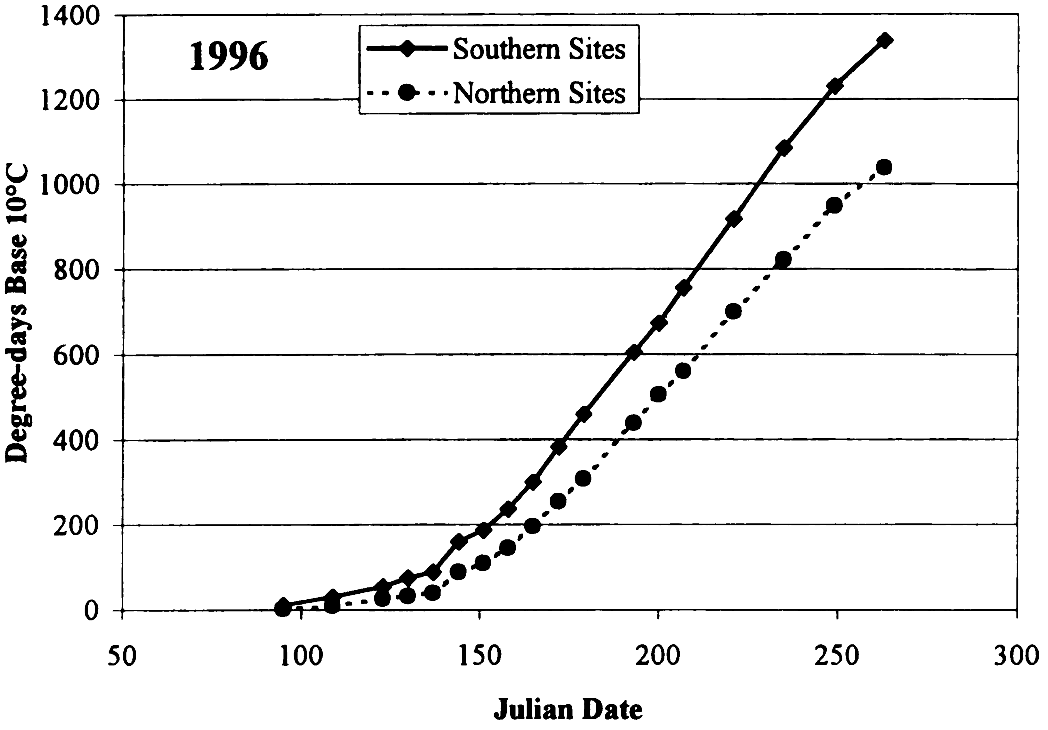


Figure 15. Seasonal distribution of predator and parasitoid progeny adults reared from 204 red pine bolts in 1996 and 304 bolts in 1997 in Michigan.



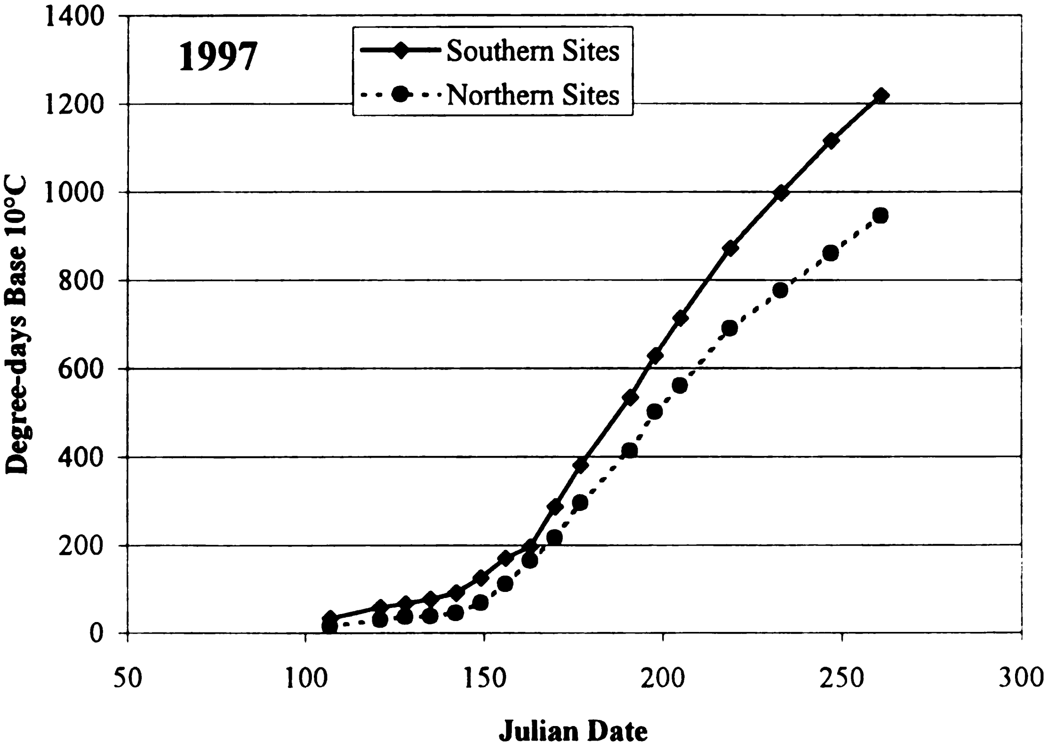


Figure 16. Average degree-day (base 10°C) accumulations from 1 March in the southern sites (KAL and ALL) and northern sites (WEX and ROS), by Julian date.

CHAPTER 2

Impacts of Natural Enemies on Native *Ips* spp. and Introduced *Tomicus piniperda* (Coleoptera: Scolytidae) Bark Beetles in Red Pine Plantations in Michigan

INTRODUCTION

The subcortical life stages of bark beetles (Coleoptera: Scolytidae) are attacked by many species of insect predators and parasitoids. Several studies in North America have evaluated the importance of predation and parasitism in pine bark beetle populations in the western (*Dendroctonus ponderosae* Hopkins) and southern U.S. (*Dendroctonus frontalis* Zimmermann) (Dahlsten and Stephen 1974, Smith and Goyer 1980), but there have been few quantitative studies on the influence of natural enemies on the pine bark beetles of the Great Lakes region. Bright (1996) and Reid (1957) listed the predators and parasitoids of *Tomicus piniperda* (L.) and *Ips pini* (Say), respectively, but did not examine their influence on the population dynamics of these bark beetles.

The recent establishment of an exotic pine bark beetle, *Tomicus piniperda*, in the Great Lakes region could potentially affect interactions between natural enemies and endemic bark beetle species. The larger pine shoot beetle, *T. piniperda*, a well-known pest of pines throughout much of Europe, Asia, and North Africa (Langstrom 1980, Ye 1991), was first discovered in 1992 in a Scotch pine (*Pinus sylvestris* L.) Christmas tree plantation in Ohio (Haack and Kucera 1993). As of September 1998, *T. piniperda* had been found in 243 counties in nine states, and in 21 counties in the Canadian province of Ontario (NAPIS 1998).

Although *T. piniperda* and several native bark beetles feed subcortically in pines, there are important differences in their life cycles that could affect interactions with natural enemies. For example, parent adults of the native scolytid *Ips pini* colonize phloem of stressed, dying, or recently-cut pine trees, and there can be three generations of *I. pini* per year in Michigan (Schenk and Benjamin 1969). *Tomicus piniperda* adults also colonize recently dead or dying pines, but *T. piniperda* is univoltine in Michigan (Haack and Lawrence 1995a). Teneral *T. piniperda* adults require maturation feeding, and spend most of the summer feeding in shoots of live pines. Both *I. pini* and *T. piniperda* overwinter as adults, but *T. piniperda* has a lower temperature threshold for spring flight (10-12°C) and can become active in the spring four to six weeks earlier than *I. pini* and many other native scolytids and natural enemies (Haack and Lawrence 1995b). These differences in the number of generations and the date of peak activity presumably influence the quantity and species diversity of the natural enemies encountered by these two scolytids.

Little is known about the impacts of predators and parasitoids on *I. pini* and other native scolytids in the Lake States region, and even less is known about how these natural enemies will interact with *T. piniperda* in North America. Previous studies of *I. pini* in the Great Lakes region list its most abundant predators as *Thanasimus dubius* (F.) (Coleoptera: Cleridae), *Corticeus* sp. (Coleoptera: Tenebrionidae), Histeridae (Coleoptera), and Staphylinidae (Coleoptera), but do not present actual mortality rates of *I. pini* due to these predators (Schenk and Benjamin 1969, Raffa and Klepzig 1989). A study in Ontario listed predators and parasitoids that emerged from a single Scotch pine tree infested by *T. piniperda*, but no mortality rates were presented (Bright 1996).

Information on interactions of *T. piniperda* and native scolytids with their natural enemies is needed to analyze scolytid population dynamics, predict population trends, and develop management guidelines for endemic and epidemic bark beetle populations (Riley and Goyer 1986). Knowledge of natural enemy biology is also needed to develop recommendations to conserve or enhance populations of natural enemies (Dahsten 1982).

Red pine, *Pinus resinosa* Ait., is one of the most extensively planted species for pulp, sawtimber, and poles in the Great Lakes region (Rudolf 1990), comprising over 364,000 hectares of Michigan's timberland (Leatherberry and Spencer 1996). Red pine is a suitable host for *T. piniperda* as well as *Ips* spp. and many other pine bark beetles (Lawrence and Haack 1995, Raffa 1991). During a typical rotation of red pine, multiple thinnings or partial harvests are performed, each of which generates an abundance of brood material for scolytid colonization. To date, most of the research conducted on *T. piniperda* in North America has taken place in Scotch pine Christmas tree plantations (Haack and Lawrence 1997a, Kauffman et al. 1998, McCullough and Smitley 1995, McCullough et al. 1998, McCullough and Sadof 1998). I chose to conduct this study in pole-sized red pine plantations because they represent a more stable ecosystem with no insecticide use, and, presumably, a more diverse complex of natural enemies.

I examined interactions among *T. piniperda*, *Ips* spp., and natural enemies in red pine forest stands in Michigan in 1996 and 1997. My objectives were to (1) identify and quantify natural enemies that were commonly associated with *T. piniperda* and *Ips* spp. in red pine plantations; (2) determine if these natural enemies affected bark beetle reproduction or survival; and (3) determine whether the presence of *T. piniperda* altered the impact of natural enemies on *Ips* spp.

MATERIALS AND METHODS

Field Sites

In 1996, I conducted field studies in four red pine forest plantations in Michigan. Two plantations were in southwestern Michigan and were known to be infested with both *T. piniperda* and native *Ips* spp. These stands were located in Michigan State University's W.K. Kellogg Experimental Forest in Kalamazoo County (KAL1), and in the Allegan State Game Area in Allegan County (ALL1) (Figure 1). Two red pine plantations in northern lower Michigan, where *T. piniperda* populations were not present (D. McCullough, unpublished data), were also selected. One stand was in the Huron-Manistee National Forest in Wexford County (WEX1), and the other was in the AuSable State Forest in Roscommon County (ROS1). Although *T. piniperda* was later detected in Wexford County in 1997 during regulatory surveys (NAPIS 1998), I did not observe any *T. piniperda* life stages or evidence of infestation in the northern field sites in 1996 or in 1997.

In general, all four research sites shared the following characteristics: they were pole-sized red pine plantations of similar size, age, and basal area (Table 1), with some hardwood understory; other red pine plantations were located within 2 km of the sites; and they were thinned during the 1994-1995 winter. An abundance of slash (for example, trunks, tops, large branches), suitable for scolytid colonization, was left on the ground in each stand from the thinnings, and was expected to attract scolytids in 1995. Temperature, precipitation, and degree day accumulation (base 10°C) from March 1were monitored by Michigan State University weather stations near all four sites.

In 1997, I used the same four sites described above, which represented conditions two years after thinning ("old" sites). I also expanded the study to include four additional red pine plantations (KAL2, ALL2, WEX2, and ROS2), each one within 6.2 km of one of the original stands. These "new" sites had the same general characteristics of the original stands (Table 1), but were row-thinned during the 1995-1996 winter.

Funnel Trapping

To monitor the flight activity of scolytids and their associates, two to four 12-unit Lindgren funnel traps (Lindgren 1983) (PheroTech, Inc., Delta, British Columbia) were placed in each stand. The traps were hung from metal poles to keep the trap bottoms approximately 1 m above the ground. Each trap was erected and baited in February of 1996 and 1997 with two α-pinene lures to attract *T. piniperda* (Byers 1991, Haack and Lawrence 1997b, Schroeder 1988) and with one lure each of ipsdienol and lanierone. Ipsdienol and lanierone are aggregation pheromones of *I. pini* that are used as kairomones by predaceous clerid, tenebrionid, and histerid beetles (Herms et al. 1991, Raffa 1991, Teale et al. 1991). Vapona insecticide strips were used in each trap, and insects were collected from traps at weekly intervals from March to September in 1996 and 1997.

Exclusion Study

In 1996, a total of 204 red pine bolts, and in 1997, a total of 304 bolts, each approximately 61 cm long and 10 – 20 cm diameter, were cut from felled red pine trees at each field site in February, April, and June of both years (Table 1). These times roughly corresponded to the initial activity of overwintering parent *T. piniperda*, overwintering parent *Ips* spp., and emergence of the F1 progeny *Ips* spp. adults. These times represented three batches, or groups, and the bolts in each batch were divided evenly among all field sites (Table 1), with the exception of batch 1. Batch 1 bolts were only placed in the southern sites since *T. piniperda* was not believed to be present in the northern sites. Bolts were placed on the forest floor at least 50 m away from the funnel traps, in a shady area of each plantation to reduce desiccation, just before the expected flight of *T. piniperda* or *Ips* spp. (Table 1). Two weeks after the bark beetles' peak flight (as determined by funnel trap collections), half of the bolts in each batch were moved to the floor of a nearby screened cage (1.8 x 3.7 x 1.8 m) constructed of 1 mm Lumite® amber screen (Synthetic Industries, Inc., Gainsville, GA) to exclude natural enemies. The other half of the bolts were left on the forest floor near the exclosure and remained exposed to natural enemies.

Beginning two weeks after the bark beetles' peak flight, two or three caged bolts and two or three exposed bolts from each batch were returned to Michigan State University. Bolts were retrieved at two week intervals in 1996 and at one week intervals in 1997. The cut ends of the retrieved bolts were dipped in paraffin wax to reduce desiccation. Each bolt was placed in an individual emergence container consisting of a cardboard tube (15 – 25 cm diameter, 0.3 – 0.6 cm wall, 61 – 71 cm overall length [Michigan Can & Tube, Inc., Saginaw, MI]) with opaque plastic endcaps and a clear plastic collection cup at one end. The emergence containers were stored on the Michigan State University campus in a screened insectary to expose the bolts to ambient temperatures and humidity.

Adult bark beetles and natural enemies were collected from the red pine bolts in the emergence containers at least twice a week until late October of both years. When progeny adult emergence stopped in the winter, I counted the number of scolytid exit holes per bolt, and then each bolt was debarked and any insects overwintering in the bark or dead on the bottom of the emergence container were collected. All insects that were reared from these bolts were assumed to be progeny adults. Although it is possible that a few parent adults were inadvertently collected, the number of parents was assumed to be small and similar across all bolts and sites.

For each debarked bolt, I determined the phloem surface area, calculated as a cylinder using the mean of two length measurements and the mean of four diameter measurements. I also measured the number and length of *Ips* spp. galleries (each egg gallery radiating from the nuptial chamber was counted), and the number and length of *T. piniperda* galleries for each bolt. *Tomicus piniperda* is monogamous, and its galleries are long and straight and parallel to the grain of the wood; *Ips* spp. are polygamous, and their galleries consist of a nuptial chamber with 2 – 4 radiating galleries, usually in the shape of a "Y" or "H." The number of scolytid egg galleries per bolt was used as an indicator of the density of female parent beetles (1 egg gallery = 1 female parent), and the number of scolytid progeny per gallery was used as a measure of productivity.

Data Analysis

For each bolt, I calculated the number of scolytid and natural enemy progeny reared per m^2 phloem surface area (progeny density), the number of scolytid progeny reared per gallery (productivity), the number of scolytid exit holes per m^2, the number of *T. piniperda* and *Ips* spp. galleries per m^2 (attack density), the total length of *T. piniperda* and *Ips* spp. galleries per bolt, and the average length of *T. piniperda* and *Ips* spp. galleries per bolt.

If fewer than five beetles of a particular scolytid species were reared from a bolt, it was considered a failed attack, and that species was excluded from that bolt's data set. Because the caging treatment did not effectively exclude all natural enemies, I instead evaluated the effect of the presence/absence of natural enemies on the number of scolytid offspring reared per m^2 of bolt surface area. A bolt with three or more natural enemy progeny was considered a successful attack (e.g. "with natural enemies"), and a bolt with two or fewer natural enemy progeny was considered a failed attack (e.g. "without natural enemies"). None of the natural enemy progeny data was excluded from the data set.

All variables were tested for normality with the Shapiro-Wilk W test, and were log transformed to increase homogeneity of variances and tested again for normality. None of the variables were normally distributed, even after log transformation, so the nonparametric Mann-Whitney test was used (SAS Institute 1996). Each batch of bolts was analyzed separately with the Mann-Whitney test to analyze the effects of exposure to natural enemies (0 – 2 natural enemies per bolt or 3+ natural enemies per bolt) on each of the variables. In addition, simple linear regression analysis was performed on the productivity data to evaluate the association between the actual natural enemy density and scolytid productivity.

RESULTS

In both 1996 and 1997, the mean phloem surface area per bolt did not differ significantly between bolts with natural enemies and bolts without natural enemies (Tables 9 and 10).

Scolytid Progeny Density – 1996

A total of 2294 scolytids were reared from 46 of the 60 bolts of batch 96-1, including 569 *Tomicus piniperda* and 404 *Ips* spp. (*I. pini* and *I. grandicollis*). From batch 96-2, 72 of 88 bolts were successfully colonized by a total of 3232 scolytids, with *Ips* spp. comprising nearly 70% of the total. From batch 96-3, 1292 bark beetles were reared from 38 of the 56 bolts, and over half of the bark beetles were either *I. pini* or *I. grandicollis*. The mean number of *I. pini* progeny per m^2 phloem surface area was highest in batch 96-3 (182 progeny/m^2) and lowest in batch 96-2 (130 progeny/m^2) (Table 2). *Ips grandicollis* densities were highest in batch 96-2 (156 progeny/m^2) (Table 2).

In batch 96-1, the mean number of *T. piniperda* progeny reared per m^2 phloem surface area was higher from bolts that also reared three or more natural enemies (referred to as "with natural enemies" from this point on) compared with bolts with two or fewer natural enemies ("without natural enemies" from this point on), but the difference was not significant at the 0.05 level (Table 3). *Ips pini* and *I. grandicollis* densities were higher from bolts without natural enemies, but the difference was not significant for *I. pini*, and there were not enough samples to test *I. grandicollis* (Table 3).

In batch 96-2, no *T. piniperda* progeny were reared. The mean number of *I. pini* reared per m^2 surface area was not significantly higher from bolts without natural enemies compared with bolts with natural enemies (Table 3). *Ips grandicollis* density was higher in bolts with natural enemies, but the difference was not significant (Table 3).

In batch 96-3, the mean number of *I. pini* reared per m^2 surface area was higher in bolts with natural enemies (Table 3). The results were the opposite for *I. grandicollis*: the density was higher in bolts without natural enemies (Table 3). In both cases, however, there were not enough colonized logs to test for significance.

Scolytid Progeny Density – 1997

From batch 97-1, a total of 7518 bark beetles were reared from 89 of the 112 bolts, including 3297 *T. piniperda* and 2656 *Ips* spp. (*I. pini* and *I. grandicollis*). A total of 7549 scolytids were reared from 119 of the 128 bolts of batch 97-2, including 6062 *Ips* spp. From batch 97-3, only 3140 bark beetles were reared from 52 of the 64 bolts, with *I. pini* and *I. grandicollis* comprising over 92% of this total. Mean *T. piniperda* density was highest in batch 97-1 (224.6 progeny/m^2) (Table 4). Mean *I. pini* density was highest in batch 97-3 (385.7 progeny/m^2), and *I. grandicollis* mean density was highest in batch 97-1 (138.7 progeny/m^2) (Table 4).

In batch 97-1, the mean number of *T. piniperda* and *I. pini* progeny reared per m^2 phloem surface area were both higher in bolts with natural enemies, but the differences were not significant (Table 5). *Ips grandicollis* followed the opposite trend: mean progeny per m^2 was higher in bolts without natural enemies, though not significantly (Table 5).

The results in batches 97-2 and 97-3 were similar. *T. piniperda* was reared from only three bolts in batch 97-2, and all three also had natural enemies (Table 5). In both batches, the mean number of *I. pini* progeny reared per m^2 phloem surface area was higher, but not significantly, from bolts with natural enemies (Table 5). And in both batches, mean *I. grandicollis* progeny per m^2 was higher in bolts without natural enemies, though not significantly (Table 5).

Scolytid Productivity – 1996

Scolytid productivity (mean number of scolytid offspring per gallery) varied widely between batches. *Tomicus piniperda* mean productivity in batch 96-1 was 8.7 progeny/gallery. *Ips pini* mean productivity was highest in batch 96-1 (28.5 progeny/gallery), and much lower in batch 96-2 (5.5 progeny/gallery) and batch 96-3 (6.7 progeny/gallery). The trend was similar for *I. grandicollis*: mean productivity was highest in batch 96-1 (21.0 progeny/gallery) and much lower in batch 96-2 (11.9 progeny/gallery) and batch 96-3 (9.4 progeny/gallery).

In batch 96-1, the mean number of *T. piniperda* progeny per gallery was higher in bolts without natural enemies (Table 6), and there was a weak negative relationship between natural enemy density and *T. piniperda* productivity (Figure 2a). For *I. pini*, the mean progeny per gallery was more than eight times higher in bolts without natural enemies, but the difference was not significant (Table 6). There was a negative but nonsignificant relationship between natural enemy density and *I. pini* productivity (Figure 2b). *Ips grandicollis* productivity was also higher in bolts without natural enemies, but there were not enough samples to analyze the data (Table 6).

No *T. piniperda* progeny were reared in batch 96-2. The mean number of *I. pini* progeny per gallery was again higher in bolts without natural enemies, but the difference was marginally insignificant (p = 0.0576) (Table 6). There was a negative but insignificant relationship between natural enemy density and *I. pini* productivity (Figure 3a). Mean *I. grandicollis* progeny per gallery was higher in bolts without natural enemies, but again, the difference was not significant (Table 6). The association between natural enemy density and *I. grandicollis* productivity was weakly positive, though not significant (Figure 3b).

In batch 96-3, no *T. piniperda* were reared. Mean number of *I. pini* offspring per gallery differed little between bolts with and without natural enemies, but there was a significant positive relationship between natural enemy density and *I. pini* productivity (p = 0.0124) (Figure 4a). This relationship may have been strongly influenced by one outlying point, though (Figure 4a). The mean number of *I. grandicollis* progeny per gallery was higher in bolts without natural enemies, but there was only one bolt with three or more natural enemies present (Table 6). The relationship between natural enemy density and *I. grandicollis* productivity was nonsignificant and negative (Figure 4b).

Scolytid Productivity – 1997

Scolytid productivity did not vary as widely between batches in 1997 as it did in 1996. Mean *T. piniperda* productivity in batch 97-1 was 10.5 progeny/gallery. For *I. pini*, mean productivity was again highest in the first batch (6.4 progeny/gallery), and lower in the later batches (97-2 mean: 3.4 progeny/gallery; 97-3 mean: 4.7 progeny/gallery). *Ips grandicollis* mean productivity was highest in batch 97-1 at 9.9

progeny/gallery, and lower in batch 97-2 (4.8 progeny/gallery) and batch 97-3 (5.3 progeny/gallery).

In batch 97-1, the mean number of *T. piniperda*, *I. pini*, and *I. grandicollis* progeny per gallery was higher in bolts without natural enemies for each species, but the differences were not significant (Table 7). There was a significant negative relationship between natural enemy density and *T. piniperda* productivity ($p = 0.0338$) (Figure 5a). There was a weakly negative relationship between natural enemy density and *I. pini* productivity, but it was not significant (Figure 5b). For *I. grandicollis*, the relationship between natural enemy density and productivity was negative and significant ($p = 0.0421$) (Figure 5c).

Tomicus piniperda was only reared from three bolts in batch 97-2, and all three bolts also had natural enemies (Table 7). Mean *I. pini* progeny per gallery was slightly higher in bolts with natural enemies (Table 7), and the relationship between natural enemy density and *I. pini* productivity was weakly negative (Figure 6a), but neither was significant. The mean number of *I. grandicollis* progeny per gallery was higher in bolts without natural enemies (Table 7), and there was a nonsignificant, negative relationship between natural enemy density and *I. grandicollis* productivity (Figure 6b).

Tomicus piniperda was not reared from batch 97-3. The mean number of progeny per gallery for *I. pini* was higher in bolts without natural enemies, but not significantly so (Table 7). The relationship between natural enemy density and *I. pini* productivity was negative, but nonsignificant (Figure 7a). For *I. grandicollis*, the productivity per gallery was significantly ($p = 0.0372$) higher in bolts without natural enemies (Table 7). There was a negative but nonsignificant relationship between natural enemy density and *I. grandicollis* density (Figure 7b).

Scolytid Egg Galleries and Exit Holes – 1996

The mean number of exit holes/m^2 phloem surface area was highest in batch 96-2, and lowest in batch 96-3 (Table 8). The mean number of *Ips* spp. galleries per m^2 and the total length of *Ips* spp. galleries per bolt were both highest in batches 96-2 and 96-3 (Table 8).

In batch 96-1, the mean number of scolytid exit holes per m^2 of phloem surface area, the total length and average length of *T. piniperda* galleries, and the average length of *Ips* spp. galleries were all higher in bolts with natural enemies, but the differences were not significant (Table 9). The mean number of *T. piniperda* galleries per unit area was also higher in bolts with natural enemies, and the difference was marginally significant ($p = 0.0539$) (Table 9). The mean number of *Ips* spp. galleries per unit area and the total length of *Ips* spp. galleries per bolts were both significantly higher in bolts with natural enemies ($p = 0.0266$ and $p = 0.0365$, respectively) (Table 9).

In batch 96-2, the trends were similar. The number of exit holes per m^2 of phloem surface area, the number of *Ips* spp. galleries per unit area, the total length of *Ips* spp. galleries per bolt, and the average length of *Ips* spp. galleries were all higher in bolts with natural enemies, but the differences were not significant (Table 9).

In batch 96-3, the number of exit holes per m^2 of phloem surface area and the average length of *Ips* spp. galleries were both higher in bolts without natural enemies, though not significantly (Table 9). The number of *Ips* spp. galleries per m^2 and the total length of *Ips* spp. galleries per bolt were both higher in bolts with natural enemies, but the difference was not significant (Table 9).

Scolytid Egg Galleries and Exit Holes – 1997

The mean number of exit holes/m^2 was much higher in batch 97-2 than in the other two batches (Table 8). In batch 97-1, the mean number of *T. piniperda* galleries per m^2 and total length of *T. piniperda* galleries per bolt were similar to the results in batch 96-1 (Table 8). The average length of *T. piniperda* galleries per bolt, however, was much lower in batch 97-1 than in batch 96-1 (Table 8). The mean number, total length, and average length of *Ips* spp. galleries were all highest in batch 97-2, and lowest in batch 97-1 (Table 8).

In batch 97-1, the mean number of scolytid exit holes per m^2, the mean number of *Ips* spp. galleries per m^2, the total lengths of *T. piniperda* and *Ips* spp. galleries per bolt, and the average lengths of *T. piniperda* and *Ips* spp. galleries were all significantly ($p < 0.0001$) higher in bolts with natural enemies (Table 10). The average number of *T. piniperda* galleries per m^2 was also significantly ($p = 0.0003$) higher in bolts with natural enemies (Table 10).

In batch 97-2, the number of exit holes per m^2 of phloem surface area was slightly higher in bolts without natural enemies, but the difference was not significant (Table 10). The mean number of *Ips* spp. galleries per m^2, the mean total length of *Ips* spp. galleries per bolt, and the average length of *Ips* spp. galleries were all significantly higher in bolts with natural enemies ($p = 0.0052$, $p = 0.0034$, and $p = 0.0252$, respectively) (Table 10). In batch 97-3, all of the variables were higher in bolts with natural enemies, but none of the differences were significant (Table 10).

Natural Enemies – 1996

The mean density of all natural enemy species combined was highest in batch 96-2, and lowest in batch 96-3 (Table 2). For *Corticeus parallelus* Melsheimer (Coleoptera: Tenebrionidae), *Medetera* sp. (Diptera: Dolichipodidae), parasitic wasps (Hymenoptera), and staphylinid beetles (Coleoptera: Staphylinidae), the mean densities of these species were highest in batch 96-2, and lowest in batch 96-3 (Table 2). *Platysoma cylindrica* (Paykull) (Coleoptera: Histeridae) density was highest in batch 96-1 and lowest in batch 96-3 (Table 2). *Thanasimus dubius* density was highest in batch 96-2 and lowest in batch 96-1 (Table 2).

In batch 96-1, a total of 96 arthropod natural enemies (94% predators, 6% parasitoids) were reared from 29 of the 60 bolts (Table 11). The most common predators reared from *T. piniperda*-infested bolts in batch 96-1 were *Thanasimus dubius*, *Medetera* sp, and *C. parallelus* (Table 12). These three predatory species, as well as *P. cylindrica* were the most common natural enemies in *Ips* spp. infested bolts (Table 12). Only one bolt from batch 96-1 was infested with both *T. piniperda* and *Ips* spp., and no natural enemies were reared from it. More predator species and slightly higher numbers of predators were reared from bolts infested with *Ips* spp. alone as compared with bolts with *T. piniperda* alone (Table 12).

A total of 458 arthropod natural enemies (90% predators, 10% parasitoids) were reared from 70 of the 88 bolts of batch 96-2 (Table 11). The most abundant natural enemies from this batch were *T. dubius, Medetera* sp., and *C. parallelus*. *Corticeus parallelus* and staphylinids were more common in the southern sites, but *T. dubius* was more abundant in bolts from the northern sites (Table 11).

For batch 96-3, I collected only 101 arthropod natural enemies, 85 of which were predators, from 40 of the 56 bolts (Table 11). *Medetera* sp., *T. dubius*, parasitic wasps, and *C. parallelus* were the most abundant natural enemies (Table 11). Once again, *C. parallelus* was more abundant in the southern sites, and *T. dubius* and *Medetera* sp. were more common in the northern sites (Table 11).

Natural Enemies – 1997

The mean density of all natural enemy species combined was highest in batch 97-2, and lowest in batch 97-3 (Table 4). *Anthocoris* sp. (Hemiptera: Anthocoridae) mean density was highest in batch 97-3, and *C. parallelus* and parasitic wasp mean densities were highest in batch 97-2 (Table 4). *Medetera* sp. and *T. dubius* densities were highest in batch 97-1 (Table 4). The mean densities of *P. cylindrica* and staphylinid beetles were similar across all batches (Table 4).

In batch 97-1, I collected a total of 665 arthropod natural enemies (97% predators, 3% parasitoids) from 68 of the 112 bolts (Table 13). Overall, natural enemies were twice as abundant from the "new" sites than the "old" sites (Table 13). The most common predators reared from *T. piniperda*-infested bolts were *T. dubius, P. cylindrica*, and *C. parallelus* (Table 14). From *Ips* spp.-infested bolts and from bolts infested with both *T. piniperda* and *Ips* spp., I found four more predator species in addition to the three listed above: two species of Staphylinidae (Coleoptera), *Medetera* sp., and *Anthocoris* sp. (Hemiptera: Anthocoridae) (Table 14). Predators were more common in bolts infested with *Ips* spp. alone or with both *Ips* spp. and *T. piniperda* than in bolts with *T. piniperda* alone (Table 14).

In batch 97-2, I collected nearly twice as many arthropod natural enemies, 1140, from 116 of the 128 bolts (Table 13). Parasitoids comprised 10% of the natural enemies, and predators made up the other 90%. Again, natural enemies were more abundant from new sites than old sites, with the difference most pronounced in the northern sites (Table 13). Overall, the most common natural enemies were *T. dubius*, *P. cylindrica*, *Medetera* sp., *C. parallelus*, and parasitic wasps (Table 13).

In batch 97-3, only 185 arthropod natural enemies (80% predators, 20% parasitoids) were reared from 46 of the 64 bolts (Table 13). Unlike the other batches, natural enemies in batch 97-3 were more abundant from the old sites than from the new sites (Table 13). The most common natural enemies were *Anthocoris* sp., *P. cylindrica*, *C. parallelus*, and parasitic wasps (Table 13).

DISCUSSION

When I compared the density of *T. piniperda*, *I. pini*, and *I. grandicollis* progeny reared from bolts with natural enemies to bolts without natural enemies, I found that there were no statistically significant differences, but the trends for each of these species were consistent. *Tomicus piniperda* progeny density was always higher in bolts with natural enemies, which may have been an artifact of the relatively small number of bolts colonized by this bark beetle. Another explanation for this trend is that natural enemies were more attracted to or had higher survival in bolts that had higher densities of *T. piniperda*. Though the natural enemies may have actually reduced *T. piniperda* progeny density, the difference could not be detected since the original density of *T. piniperda* parent adults (attack density) in those bolts was much higher than the bolts without natural enemies.

Ips pini progeny density was more complicated: in the first two batches of 1996, it was higher in bolts without natural enemies, suggesting that predators and parasitoids were reducing *I. pini* density. But in batch 96-3 and in all three batches of 1997, *I. pini* offspring density was higher in bolts with natural enemies. Several predators in the Coleopteran families Cleridae, Histeridae, and Tenebrionidae are known to use *I. pini* pheromones as kairomones (Herms et al. 1991, Raffa 1991, Teale et al. 1991), so it seems likely that these predators would be more attracted to bolts with higher densities of *I. pini* parent adults.

Ips grandicollis offspring density was higher in bolts without natural enemies in all batches except batch 96-2. In this case, it appears that natural enemies may have reduced bark beetle progeny density, although the low sample size and high variability resulted in insignificant differences.

The mean number of exit holes per m^2 of phloem surface area was used as a second measurement of scolytid progeny density, where one exit hole was assumed to correspond to emergence by one scolytid progeny adult. Occasionally, more than one bark beetle will emerge from a single exit hole (Hanson 1937, Salonen 1973), so the number of exit holes may slightly underestimate the number of progeny. In this study, the number of exit holes/m^2 was higher in bolts with natural enemies in four of the six batches, which was consistent with the results from actual progeny density for *T. piniperda* and *I. pini*.

In both years, *T. piniperda* productivity (progeny per gallery) was higher in bolts without natural enemies. In addition, the relationship between *T. piniperda* productivity and natural enemy density was significantly negative in 1997; the higher the density of natural enemies, the lower the productivity. Since *T. piniperda* galleries were longer in bolts with natural enemies, and gallery length is correlated with numbers of eggs laid (Anderbrant 1990, Foltz et al. 1976, Light et al. 1983), the number of eggs laid was not affected by natural enemies. Therefore, native natural enemies affected *T. piniperda* productivity by reducing survival of developing eggs, larvae, or pupae, but not by affecting parents.

In four of the six batches, *I. pini* productivity was higher in bolts without natural enemies, and in five batches, there was a negative relationship between productivity and natural enemy density. These findings for *I. pini* parallel the results for *T. piniperda*: natural enemies reduced productivity even though they did not reduce overall progeny density. And, like *T. piniperda*, *I. pini* productivity was likely affected by natural enemies during the egg, larval, and/or pupal stages, and not at the parent adult/oviposition stage because mean egg gallery lengths were not affected by the presence of natural enemies.

Ips grandicollis productivity was higher in bolts without natural enemies in all batches of both years, and with the exception of batch 96-2, there was a negative relationship between productivity and natural enemy density. Unlike *T. piniperda* and *I. pini*, more *I. grandicollis* progeny emerged from bolts without natural enemies. Therefore, natural enemies may have reduced productivity either by preying on parent adults before or during oviposition, or by causing mortality of the egg, larval, or pupal stages.

Scolytid productivity can be affected by more than just natural enemies; mortality due to intraspecific competition can also play an important role (Langstrom 1980, Schenk and Benjamin 1969). To determine whether the trend of reduced productivity in bolts with natural enemies was due to natural enemies or competition, I looked at the attack densities in bolts with and without natural enemies, and I compared these attack densities with other field studies where scolytid competition was documented.

Tomicus piniperda attack density (galleries per m^2 of phloem surface area) was higher in bolts with natural enemies in both years. One explanation is that natural enemies were either attracted to bolts with higher densities of parent adults or had higher survival rates in bolts with higher scolytid densities. Another explanation is that natural enemies simply did not reduce the number of attacks per bolt. *Tomicus piniperda* is one of the earliest bark beetles to colonize pine brood material in the spring (Haack and

Lawrence 1995b, Langstrom 1980), so large numbers of natural enemies were likely not active early enough in the spring to impact the number of parent adults colonizing logs.

Ips spp. attack densities were also higher in bolts with natural enemies in all six of the batches, and these differences were statistically significant in three of the batches. Again, natural enemies did not appear to reduce the number of colonizing parent adults; in fact, they may have been attracted to the bolts by the high numbers of adult beetles.

Since the number of eggs can be correlated with the length of scolytid egg galleries (Langstrom 1980, Salonen 1973), I looked at the effect of natural enemies on total gallery length (and indirectly on the number of scolytid eggs laid). I also wanted to determine if natural enemy presence affected the average gallery length excavated per female, which would also affect egg production. Natural enemies did not reduce the total or the mean gallery lengths for either *T. piniperda* or *I. pini*, rather, the galleries were longer in the bolts with natural enemies. Two inferences can be made: (1) natural enemies did not affect the parent adults constructing the egg galleries, and/or (2) natural enemies had higher survival in bolts where many scolytid prey were developing. These bark beetle parent adults were protected from most natural enemies while they were constructing galleries under the bark. *Thanasimus dubius*, the most abundant predator of adult scolytids, was likely too large to enter these bark beetles' galleries, and primarily preyed on adult scolytids on the outer bark surface.

Finally, to re-examine the question of whether competition or natural enemies caused the reduction in scolytid productivity, I compared the attack densities for *T. piniperda* and *I. pini* with those reported in the literature in this region (there were no findings for *I. grandicollis* in the Great Lakes region). The mean of about 21 *T.*

piniperda galleries/m^2 in this study was lower than Haack and Lawrence's (1995a) finding of 179 *T. piniperda* galleries/m^2 in Scotch pine bolts in Michigan. The finding of about 71 *Ips* spp. galleries/m^2 was much lower than a Wisconsin study, where mean *I. pini* attack densities of 186 galleries/m^2 on jack pine (*Pinus banksiana* Lamb.) were recorded (Schenk and Benjamin 1969). *Ips pini* attack densities in this study were comparable to Haack and Lawrence's (1995a) mean *I. pini* attack densities of 26 galleries/m^2 [number of nuptial chambers, not individual egg galleries, were counted; two to four females per male are typical (Schenk and Benjamin 1969)] in Scotch pine bolts.

It has been well documented that at high attack densities, the length of bark beetle galleries decrease, the number of eggs laid per gallery decrease, and the number of surviving progeny per gallery decrease as the phloem becomes more scarce (Langstrom 1980, Salonen 1973, Schenk and Benjamin 1969). At the relatively low attack densities observed in this study, however, it is unlikely that competition played such an important role. I hypothesize that the reduction in scolytid productivity in bolts with natural enemies was primarily due to predation and parasitism, not competition.

Several native bark beetle predators and parasitoids successfully reproduced in *T. piniperda*-infested red pine bolts. Three important scolytid predators had the highest densities in batch 1, bolts colonized by *T. piniperda*: *P. cylindrica* (batch 96-1), *Medetera* sp. (batch 97-1), and *T. dubius* (batch 97-1). But more species of predators and greater numbers of predators were reared from *Ips* spp.-infested bolts and from bolts infested with both *T. piniperda* and *Ips* spp. This suggests that natural enemies are (1) phenologically better timed with native *Ips* spp. than the exotic *T. piniperda*, (2) more attracted to bolts with *Ips* spp. than those with *T. piniperda* alone, or (3) can reproduce more successfully in bolts with *Ips* spp. than those with *T. piniperda*. Based on phenological data from a related study, I found that most native natural enemies are phenologically well-timed with native pine bark beetles, but that four predaceous species are active as early as *T. piniperda*.

Bright (1996) reared seven species of parasitoids and only four species of predators from a single *T. piniperda*-infested Scotch pine tree in Ontario. I reared six parasitoid species, but cannot be certain that they were from *T. piniperda* because other scolytids and weevils were also present in the *T. piniperda* bolts. Further research is needed to determine the relative effects of parasitoids on bark beetle populations.

Conclusions

Tomicus piniperda, *I. pini*, and *I. grandicollis* offspring density was not affected by predators and parasitoids, but productivity of these species was reduced in bolts with natural enemies compared to bolts without natural enemies. Attack density and gallery length of these species were higher in bolts with natural enemies, suggesting that natural enemies did not have an effect on colonizing parent adults. The field-imposed attack densities in this study were relatively low, so interspecific and intraspecific competition were likely not the important mortality factors; predation and parasitism appear to be the primary cause of reduced scolytid productivity. Natural enemies were more common in bolts with *Ips* spp. than with *T. piniperda* alone, but, in general, they were attracted to bolts with high numbers of colonizing adults of either species.

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Table 1. General characteristics and number of red pine bolts placed at the 1996 and 1997 red pine plantation field sites.

	KAL 1	KAL 2	ALL 1	ALL 2	WEX 1	WEX 2	ROS 1	ROS 2
Area (ha)	0.81	1.62	9.31	6.47	18.62	10.93	52.20	22.26
Year planted	1937	1937	1939	1938	1937	1948	1937	1965
Basal area (m^2/ha) after thinning	30	18	21	23	28	28	21	21
Year(s) thinned	1995	1996	1987, 1995	1996	1975, 1995	1996	1995	1996
No. of batch 96-1 bolts (in field 6 March 1996)	30	—	30	—	0	—	0	—
No. of batch 96-2 bolts (in field 7 May 1996)	22	—	22	—	22	—	22	—
No. of batch 96-3 bolts (in field 20 June 1996)	14	—	14	—	14	—	14	—
No. of batch 97-1 bolts (in field 28 Feb. 1997)	28	28	28	28	0	0	0	0
No. of batch 97-2 bolts (in field 11 April 1997)	16	16	16	16	16	16	16	16
No. of batch 97-3 bolts (in field 2 July 1997)	8	8	8	8	8	8	8	8

Table 2. Mean densities of scolytids and natural enemies per m^2 of phloem surface area from red pine bolts in 1996. There were a total of 60 bolts in batch 96-1; 88 bolts in batch 96-2; and 56 bolts in batch 96-3.

Insect	Batch 96-1		Batch 96-2		Batch 96-3	
	Mean ± SEM[a]	n[b]	Mean ± SEM[a]	n[b]	Mean ± SEM[a]	n[b]
Tomicus piniperda	115.7 ± 33.87	17	—	0	—	0
Ips pini	172.2 ± 101.72	10	130.0 ± 19.31	27	182.1 ± 65.52	11
Ips grandicollis	96.7 ± 23.91	4	155.9 ± 25.93	41	92.6 ± 18.99	8
All natural enemies	13.3 ± 2.87	29	30.7 ± 4.20	70	10.4 ± 1.41	40
Anthocoris sp.	—	0	—	0	4.7 ± 0.95	2
Corticeus parallelus	11.1 ± 4.64	6	30.0 ± 7.78	19	4.5 ± 0.74	10
Medetera sp.	9.6 ± 1.92	15	14.4 ± 2.11	31	8.9 ± 1.78	17
Parasitic wasps	7.4 ± 2.87	4	16.8 ± 8.10	14	6.1 ± 1.38	10
Platysoma cylindrica	13.8 ± 8.68	4	9.0 ± 1.77	22	8.7 ± 2.61	5
Staphylinid beetles	6.3 ± 3.39	3	6.4 ± 1.25	10	4.4 ± 0.54	7
Thanasimus dubius	6.0 ± 0.87	12	16.8 ± 3.49	37	7.7 ± 2.58	10

[a] SEM = standard error of the mean.

[b] n = number of red pine bolts that produced progeny.

for bolts with three or
88 bolts in batch

Table 3. Mean densities of scolytid progeny (number reared per m^2 of red pine phloem surface area) in 1996, for bolts with three or more natural enemies and bolts with two or fewer natural enemies (NE). There were a total of 60 bolts in batch 96-1; 88 bolts in batch 96-2, and 56 bolts in batch 96-3.

Scolytid species		Batch 96-1		Batch 96-2		Batch 96-3	
		Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE
Tomicus piniperda	Mean no./ m^2	85.4	214.3	—	—	—	—
	Standard error	22.84	122.44	—	—	—	—
	n (No. of bolts)	13	4	—	—	—	—
	χ^2 *	2.88					
	p *	0.09					
Ips pini	Mean no./ m^2	247.7	58.9	130.9	129.2	75.1	205.8
	Standard error	167.84	7.08	31.87	22.20	52.65	78.05
	n (No. of bolts)	6	4	14	13	2	9
	χ^2 *	0.046		0.12		Not enough samples	
	p *	0.83		0.73			
Ips grandicollis	Mean no./ m^2	137.6	55.7	131.7	186.7	101.1	32.8
	Standard error	5.86	6.44	22.71	51.48	19.58	—
	n (No. of bolts)	2	2	23	18	7	1
	χ^2 *	Not enough samples		0.20		Not enough samples	
	p *			0.66			

* Chi square and p-values obtained from the Mann-Whitney test.

Table 4. Mean densities of scolytids and natural enemies per m^2 of phloem surface area reared from red pine bolts in 1997. There were a total of 112 bolts in batch 97-1; 128 bolts in batch 97-2; and 64 bolts in batch 97-3.

Insect	Batch 97-1 Mean ± SEM[a]	n[b]	Batch 97-2 Mean ± `SEM[a]	n[b]	Batch 97-3 Mean ± SEM[a]	n[b]
Tomicus piniperda	224.6 ± 26.90	44	81.5 ± 22.59	3	—	0
Ips pini	140.0 ± 26.37	28	213.2 ± 23.96	77	385.7 ± 81.6	32
Ips grandicollis	138.7 ± 27.73	34	136.0 ± 26.73	53	126.4 ± 22.69	26
All natural enemies	31.7 ± 4.57	68	40.5 ± 3.97	116	20.8 ± 2.39	46
Anthocoris sp.	9.2 ± 2.59	18	8.8 ± 1.24	36	14.8 ± 3.79	18
Corticeus parallelus	12.5 ± 3.18	32	20.9 ± 3.05	65	11.1 ± 3.42	13
Medetera sp.	25.3 ± 3.65	24	17.2 ± 2.38	45	6.3 ± 0.71	4
Parasitic wasps	6.6 ± 1.53	10	18.6 ± 4.32	29	12.3 ± 4.32	16
Platysoma cylindrica	13.4 ± 2.37	25	13.2 ± 1.92	53	13.0 ± 2.95	19
Staphylinid beetles	4.6 ± 0.74	15	5.0 ± 0.56	16	5.0 ± 0.25	3
Thanasimus dubius	12.5 ± 2.41	38	11.7 ± 1.2	79	5.6 ± 0.43	11

[a] SEM = standard error of the mean.

[b] n = number of red pine bolts that produced progeny.

[illegible] 1997, [illegible] bolts with three or
[illegible] length 27-1; 1 3/8

Table 5. Mean densities of scolytid progeny (number reared per m^2 of red pine phloem surface area) in 1997, for bolts with three or more natural enemies and bolts with two or fewer natural enemies (NE). There were a total of 112 red pine bolts in batch 97-1; 128 bolts in batch 97-2; and 64 bolts in batch 97-3.

Scolytid species		Batch 97-1		Batch 97-2		Batch 97-3	
		Bolts With $\leq$2 NE	Bolts With $\geq$3 NE	Bolts With $\leq$2 NE	Bolts With $\geq$3 NE	Bolts With $\leq$2 NE	Bolts With $\geq$3 NE
Tomicus piniperda	Mean no./ m^2	201.2	261.8	—	81.5	—	—
	Standard error	26.35	55.68	—	22.59	—	—
	n (No. of bolts)	27	17	—	3	—	—
	χ^2 *	0.47		Not enough samples			
	p *	0.49					
Ips pini	Mean no./ m^2	91.0	166.1	188.0	220.8	304.7	466.7
	Standard error	29.70	33.22	43.71	28.41	71.04	146.94
	n (No. of bolts)	6	22	18	59	16	16
	χ^2 *	1.25		0.20		0.69	
	p *	0.26		0.66		0.41	
Ips grandicollis	Mean no./ m^2	204.3	111.3	142.2	134.3	142.3	112.8
	Standard error	77.68	21.64	54.87	30.84	34.51	30.72
	n (No. of bolts)	10	24	11	42	12	14
	χ^2 *	0.05		0.30		0.21	
	p *	0.82		0.58		0.64	

* Chi square and p-values obtained from the Mann-Whitney test.

Table 6. Scolytid productivity (number of scolytid progeny reared per parent female) in 1996, for bolts with three or more natural enemies and bolts with two or fewer natural enemies (NE). There were a total of 60 red pine bolts in batch 96-1; 88 bolts in batch 96-2; and 56 bolts in batch 96-3.

Scolytid species		Batch 96-1		Batch 96-2		Batch 96-3	
		Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE
Tomicus piniperda	Mean no./female[1]	9.0	7.6	—	—	—	—
	Standard error	5.33	5.56	—	—	—	—
	n (No. of bolts)	13	4	—	—	—	—
	χ^2*	0.37					
	p*	0.54					
Ips pini	Mean no./female[1]	43.9	5.3	8.3	2.6	5.8	6.8
	Standard error	26.01	2.30	2.60	0.92	5.55	2.69
	n (No. of bolts)	6	4	14	13	2	9
	χ^2*	2.93		3.60		0.22	
	p*	0.09		0.06		0.64	
Ips grandicollis	Mean no./female[1]	26.5	15.5	9.5	15.0	10.4	1.8
	Standard error	7.50	7.50	1.61	4.08	2.20	—
	n (No. of bolts)	2	2	23	18	7	1
	χ^2*	Not enough samples		0.11		Not enough samples	
	p*			0.74			

[1] = "Mean no./female" = average number of progeny per egg gallery (1 gallery = 1 female)

* = Chi square and p-values obtained from the Mann-Whitney test.

Table 7. Scolytid productivity (number of scolytid progeny reared per parent female) in 1997, for bolts with three or more natural enemies and bolts with two or fewer natural enemies (NE). There were a total of 112 red pine bolts in batch 97-1; 128 bolts in batch 97-2; and 64 bolts in batch 97-3.

Scolytid species		Batch 97-1		Batch 97-2		Batch 97-3	
		Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE
Tomicus piniperda	Mean no./female[†]	11.5	8.8	—	8.3	—	—
	Standard error	1.38	2.18	—	2.83	—	—
	n (No. of bolts)	27	17	—	3	—	—
	χ^{2*}	3.18		Not enough samples			
	p*	0.07					
Ips pini	Mean no./female[1]	9.2	5.7	2.6	3.6	7.2	2.2
	Standard error	6.85	1.70	0.73	1.32	4.49	0.69
	n (No. of bolts)	6	22	18	59	16	16
	χ^{2*}	0.20		0.03		0.006	
	p*	0.65		0.87		0.94	
Ips grandicollis	Mean no./female[1]	13.4	8.5	7.7	4.1	8.8	2.3
	Standard error	3.16	2.27	2.38	1.34	3.17	1.17
	n (No. of bolts)	10	24	11	42	12	14
	χ^{2*}	2.06		2.26		4.34	
	p*	0.15		0.13		0.0372	

[†] = "Mean no./female" = average number of progeny per egg gallery (1 gallery = 1 female).

* = Chi square and p-values obtained from the Mann-Whitney test.

Table 8. Mean number of scolytid exit holes and egg galleries per m^2 *of phloem surface area in 1996 and 1997*. There were a total of *60 red pine bolts in batch 96-1; 88 bolts in batch 96-2;* 56 bolts in batch 96-3; 112 bolts in batch 97-1; 128 bolts in batch 97-2; and 64 bolts in batch 97-3.

Variable	Batch 96-1 Mean ± SEM[a]	Batch 96-2 Mean ± SEM[a]	Batch 96-3 Mean ± SEM[a]	Batch 97-1 Mean ± SEM[a]	Batch 97-2 Mean ± SEM[a]	Batch 97-3 Mean ± SEM[a]
No. of exit holes/m^2	539.2 ± 44.31	667.6 ± 48.51	478.7 ± 50.9	574.6 ± 44.76	856.6 ± 30.88	590.9 ± 62.34
No. of *Tomicus piniperda* galleries/m^2	20.9 ± 2.57	—	—	21.5 ± 2.10	—	—
No. of *Ips* spp. galleries/m^2	16.8 ± 4.78	56.2 ± 8.07	48.1 ± 9.76	25.9 ± 4.38	110.3 ± 10.17	166.4 ± 29.93
Total length (cm) of *T. piniperda* galleries/bolt	49.3 ± 7.47	—	—	51.8 ± 5.94	—	—
Total length (cm) of *Ips* spp. galleries/bolt	33.1 ± 8.99	85.2 ± 9.46	60.8 ± 11.64	65.7 ± 11.86	200.6 ± 14.5	177.9 ± 29.17
Average length (cm) of *T. piniperda* galleries/bolt	7.2 ± 0.64	—	—	5.6 ± 0.36	—	—
Average length (cm) of *Ips* spp. galleries/bolt	2.8 ± 0.53	6.6 ± 0.52	2.7 ± 0.36	3.1 ± 0.41	7.4 ± 0.36	4.8 ± 0.44
Phloem surface area (m^2)	0.25 ± 0.001	0.23 ± 0.006	0.26 ± 0.006	0.30 ± 0.005	0.26 ± 0.004	0.20 ± 0.005

[a] SEM = standard error of the mean

Table 9. Number of scolytid exit holes and egg galleries per m^2 of phloem surface area in 1996, for bolts with three or more natural enemies and bolts with two or fewer natural enemies (NE). There were a total of 60 red pine bolts in batch 96-1; 88 bolts in batch 96-2; and 56 bolts in batch 96-3.

Variable		Batch 96-1		Batch 96-2		Batch 96-3	
		Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE
No. of exit holes/m^2	Mean no./m^2	510.5	654.0	619.9	724.8	502.1	451.8
	Standard error	52.54	63.14	54.14	84.60	71.51	73.43
	n (No. of bolts)	48	12	48	40	30	26
	χ^{2*}	2.95		0.57		0.43	
	p*	0.08		0.45		0.51	
No. of *Tomicus piniperda* galleries/m^2	Mean no./m^2	17.6	34.1	—	—	—	—
	Standard error	2.32	8.11	—	—	—	—
	n (No. of bolts)	48	12	—	—	—	—
	χ^{2*}	3.72					
	p*	0.0539					
No. of *Ips* spp. galleries/m^2	Mean no./m^2	11.9	36.2	50.3	63.2	32.1	66.6
	Standard error	5.00	11.93	9.48	13.69	8.06	18.42
	n (No. of bolts)	48	12	48	40	30	26
	χ^{2*}	4.92		1.26		0.47	
	p*	0.0266		0.26		0.49	
Total length of *T. piniperda* galleries/bolt	Mean cm/bolt	44.6	67.8	—	—	—	—
	Standard error	8.33	16.54	—	—	—	—
	n (No. of bolts)	48	12	—	—	—	—
	χ^{2*}	2.48					
	p*	0.12					

Table 9 (cont'd).

Variable		Batch 96-1		Batch 96-2		Batch 96-3	
		Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE
Total length of *Ips* spp. galleries/bolt	Mean cm/bolt	20.4	84.0	78.8	92.8	42.1	82.3
	Standard error	6.72	33.17	12.27	14.79	11.86	20.48
	n (No. of bolts)	48	12	48	40	30	26
	χ^2*	4.37		0.78		0.57	
	p*	0.0365		0.38		0.45	
Average length of *T. piniperda* galleries (cm)	Mean	7.0	8.0	—	—	—	—
	Standard error	0.76	0.97	—	—	—	—
	n (No. of bolts)	48	12	—	—	—	—
	χ^2*	1.41					
	p*	0.24					
Average length of *Ips* spp. galleries (cm)	Mean	2.3	4.6	6.2	6.9	2.7	2.7
	Standard error	0.56	1.40	0.78	0.68	0.47	0.55
	n (No. of bolts)	48	12	48	40	30	26
	χ^2*	2.86		0.84		0.003	
	p*	0.09		0.36		0.96	
Phloem surface area (m^2)	Mean (m^2)	0.26	0.25	0.23	0.23	0.26	0.26
	Standard error	0.01	0.002	0.01	0.01	0.01	0.01
	n (No. of bolts)	48	12	48	40	30	26
	χ^2*	0.28		0.06		0.01	
	p*	0.60		0.80		0.91	

* Chi square and p-values obtained from the Mann-Whitney test.

Table 10. Number of scolytid exit holes and egg galleries per m^2 of phloem surface area in 1997, for bolts with three or more natural enemies and bolts with two or fewer natural enemies (NE). There were a total of 112 red pine bolts in batch 97-1; 128 bolts in batch 97-2; and 64 bolts in batch 97-3.

Variable		Batch 97-1		Batch 97-2		Batch 97-3	
		Bolts With $\leq$2 NE	Bolts With $\geq$3 NE	Bolts With $\leq$2 NE	Bolts With $\geq$3 NE	Bolts With $\leq$2 NE	Bolts With $\geq$3 NE
No. of exit holes/m^2	Mean no./m^2	420.2	831.9	886.2	843.1	568.9	599.5
	Standard error	54.88	58.2	67.38	33.06	135.67	69.60
	n (No. of bolts)	70	42	40	88	18	46
	χ^{2*}	28.68		0.15		0.37	
	p*	<0.0001		0.70		0.54	
No. of *Tomicus piniperda* galleries/m^2	Mean no./m^2	15.7	31.2	—	—	—	—
	Standard error	2.14	3.90	—	—	—	—
	n (No. of bolts)	70	42	—	—	—	—
	χ^{2*}	13.35					
	p*	0.0003					
No. of *Ips* spp. galleries/m^2	Mean no./m^2	8.9	54.2	82.4	123.0	146.2	174.4
	Standard error	3.23	8.82	17.06	12.43	59.59	34.85
	n (No. of bolts)	70	42	40	88	18	46
	χ^{2*}	36.63		7.81		1.21	
	p*	<0.0001		0.0052		0.27	
Total length of *T. piniperda* galleries/bolt	Mean cm/bolt	32.8	83.7	—	—	—	—
	Standard error	4.90	12.14	—	—	—	—
	n (No. of bolts)	70	42	—	—	—	—
	χ^{2*}	17.82					
	p*	<0.0001					

Table 10 (cont'd).

Variable		Batch 97-1		Batch 97-2		Batch 97-3	
		Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE	Bolts With ≤2 NE	Bolts With ≥3 NE
Total length of *Ips* spp. galleries/bolt	Mean cm/bolt	18.1	145.0	146.3	225.2	156.7	186.2
	Standard error	6.25	25.70	24.37	17.43	59.37	33.63
	n (No. of bolts)	70	42	40	88	18	46
	χ^2*	38.23		8.60		1.00	
	p*	<0.0001		0.0034		0.32	
Average length of *T. piniperda* galleries (cm)	Mean	4.5	7.6	—	—	—	—
	Standard error	0.45	0.47	—	—	—	—
	n (No. of bolts)	70	42	—	—	—	—
	χ^2*	19.81					
	p*	<0.0001					
Average length of *Ips* spp. galleries (cm)	Mean	1.2	6.2	5.9	8.1	4.3	5.0
	Standard error	0.37	0.68	0.72	0.38	0.88	0.50
	n (No. of bolts)	70	42	40	88	18	46
	χ^2*	35.63		5.01		0.68	
	p*	<0.0001		0.0252		0.41	
Phloem surface area (m^2)	Mean	0.29	0.31	0.26	0.26	0.18	0.20
	Standard error	0.01	0.01	0.01	0.005	0.01	0.01
	n (No. of bolts)	70	42	40	88	18	46
	χ^2*	3.23		0.20		2.01	
	p*	0.0723		0.66		0.16	

* Chi square and p-values obtained from Mann-Whitney test.

Table 11. Total number of scolytid natural enemies reared from red pine bolts in 1996. There were a total of 60 bolts in batch 96-1; 88 bolts in batch 96-2; and 56 bolts in batch 96-3.

	Southern field sites[1]			Northern field sites[1]		
	Batch 96-1	Batch 96-2	Batch 96-3	Batch 96-1	Batch 96-2	Batch 96-3
All natural enemies	96	229	37	—	229	64
Anthocoris sp.	0	2	1	—	0	1
Corticeus parallelus	15	89	10	—	26	3
Medetera sp.	37	67	8	—	43	37
Parasitic wasps[2]	6	16	9	—	31	7
Platysoma cylindrica	12	23	3	—	16	6
Staphylinid beetles[3]	5	13	4	—	2	4
Thanasimus dubius	21	19	2	—	111	16

[1] Southern field sites included KAL1 and ALL1. Northern field sites included WEX1 and ROS1.

[2] Six species of parasitic wasps (Hymenoptera): 1 sp. Braconidae; 1 sp. Ichneumonidae; 4 spp. Chalcidoidea.

[3] Two species of staphylinid beetles (Coleoptera: Staphylinidae).

Table 12. Percentage of red pine bolts infested with *Tomicus piniperda* (Tp) or *Ips* spp. (Ip) from batch 96-1 that also reared natural enemies. Of the 60 bolts, 32 were not attacked by either scolytid.

Natural Enemy	Bolts infested with Tp only n = 15	Bolts infested with Ip only n = 12	Bolts infested with both Tp & Ip n = 1
Anthocoris sp.	0%	0%	0%
Corticeus parallelus	13.3%	25%	0%
Medetera sp.	20.0%	58.3%	0%
Parasitic wasps[1]	6.7%	8.3%	0%
Platysoma cylindrica	0%	16.7%	0%
Staphylinid beetles[2]	0%	8.3%	0%
Thanasimus dubius	26.7%	33.3%	0%
No natural enemies	40.0%	25%	100%

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[1] Six species of parasitic wasps (Hymenoptera): 1 sp. Braconidae; 1 sp. Ichneumonidae; 4 spp. Chalcidoidea.
[2] Two species of staphylinid beetles.

Table 13. Total number of scolytid natural enemies reared from red pine bolts in 1997. There were a total of 112 bolts in batch 97-1; 128 bolts in batch 97-2; and 64 bolts in batch 97-3.

	Southern field sites[1]						Northern field sites[1]					
	Old sites[2]			New sites[2]			Old sites[2]			New sites[2]		
	Batch 97-1	Batch 97-2	Batch 97-3	Batch 97-1	Batch 97-2	Batch 97-3	Batch 97-1	Batch 97-2	Batch 97-3	Batch 97-1	Batch 97-2	Batch 97-3
All natural enemies	223	285	54	442	364	35	—	121	59	—	370	37
Anthocoris sp.	5	10	26	40	40	14	—	4	2	—	26	8
Corticeus parallelus	20	56	5	96	137	4	—	19	11	—	112	13
Medetera sp.	71	72	1	119	111	1	—	9	2	—	12	0
Parasitic wasps (5 spp.)	9	23	6	12	4	2	—	42	29	—	47	1
Platysoma cylindrica	56	49	12	54	38	12	—	14	13	—	65	8
Staphylinidae (2 spp.)	11	8	0	10	1	0	—	1	1	—	10	2
Thanasimus dubius	43	67	4	106	33	2	—	32	1	—	98	5

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[1] = Southern field sites included KAL1, KAL2, ALL1, and ALL2. Northern field sites included WEX1, WEX2, ROS1, and ROS2.

[2] = Old sites were thinned during the 1994-1995 winter. New sites were thinned during the 1995-1996 winter.

Table 14. Percentage of red pine bolts infested with *Tomicus piniperda* (Tp) or *Ips* spp. (Ip) from batch 97-1 that also reared natural enemies. Of the 112 bolts, 34 were not attacked by either scolytid.

Natural Enemy	Bolts infested with Tp only n = 31	Bolts infested with Ip only n = 34	Bolts infested with both Tp & Ip n = 13
Anthocoris sp.	0%	25.0%	42.8%
Corticeus parallelus	4.5%	35.4%	57.1%
Medetera sp.	0%	33.3%	57.1%
Parasitic wasps[1]	4.5%	6.2%	21.4%
Platysoma cylindrica	6.8%	22.9%	57.1%
Staphylinid beetles[2]	0%	18.8%	21.4%
Thanasimus dubius	22.7%	37.5%	64.3%
No natural enemies	40.9%	6.2%	7.1%

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[1] Six species of parasitic wasps (Hymenoptera): 1 sp. Braconidae; 1 sp. Ichneumonidae; 4 spp. Chalcidoidea.

[2] Two species of staphylinid beetles.

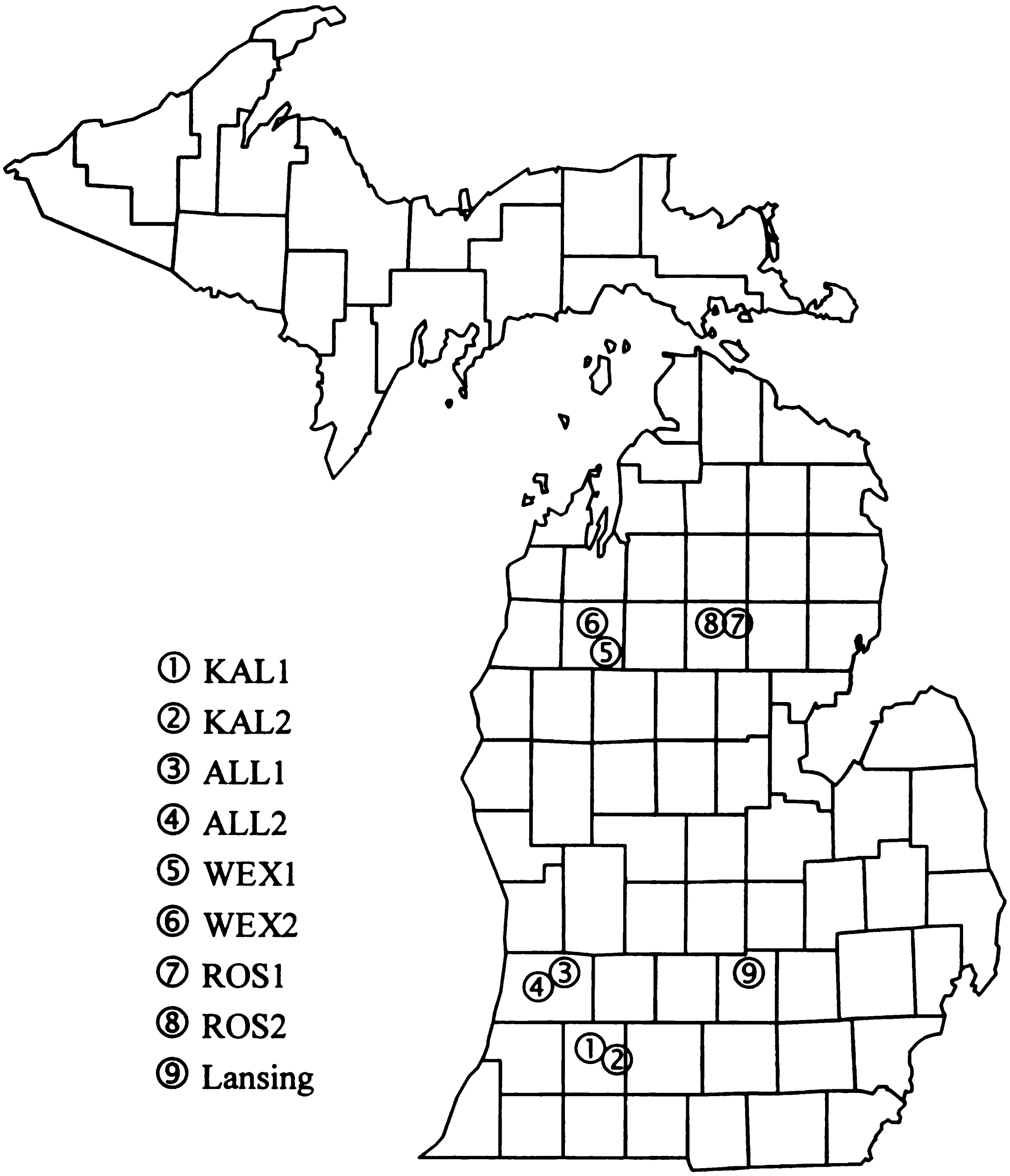

Figure 1. Location of red pine forest plantation field sites in Michigan. KAL1, ALL1, WEX1, ROS1, and Lansing were monitored in 1996; all stands were monitored in 1997.

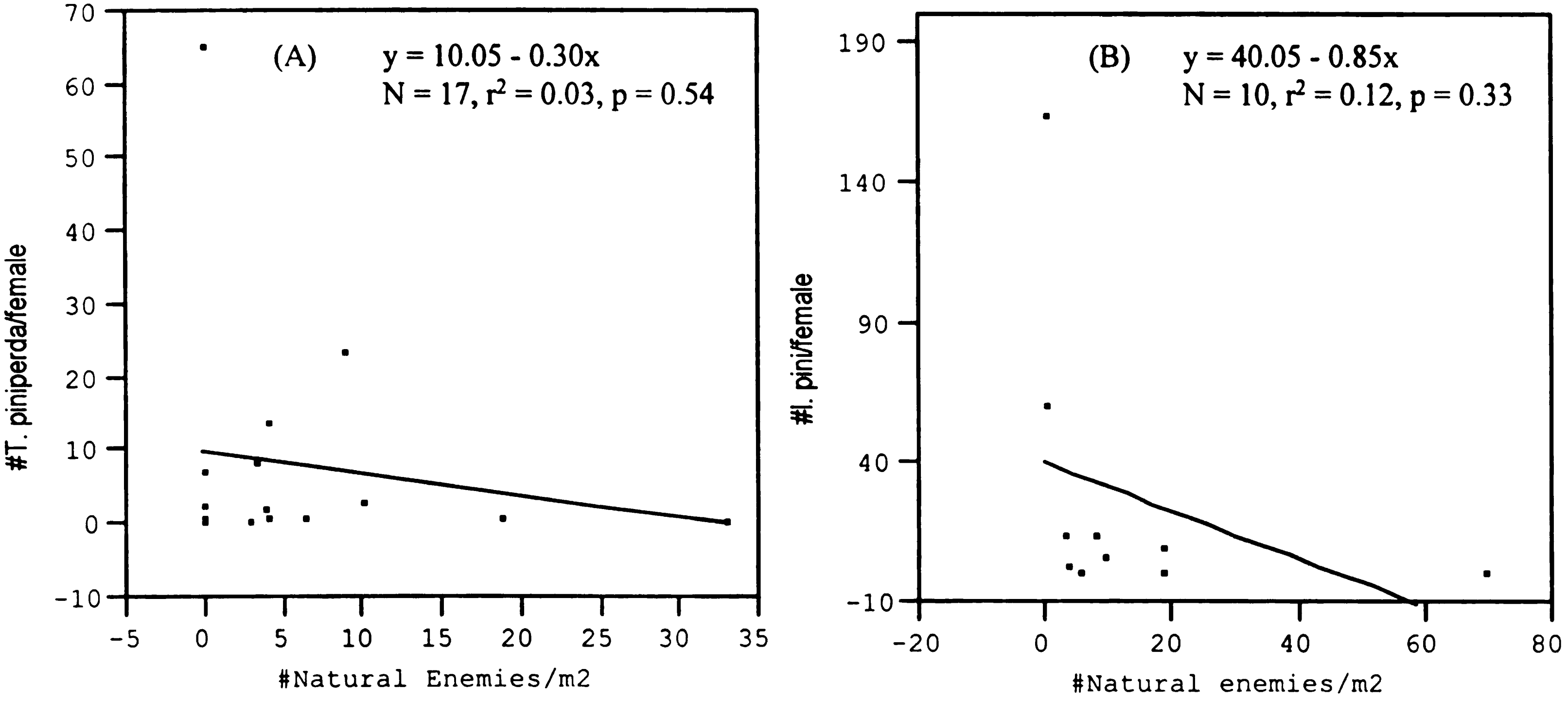

Figure 2. Relationships between natural enemy density and the productivity of (A) *Tomicus piniperda* and (B) *Ips pini*. All scolytid and natural enemy progeny adults were reared from batch 96-1. Note the different scales.

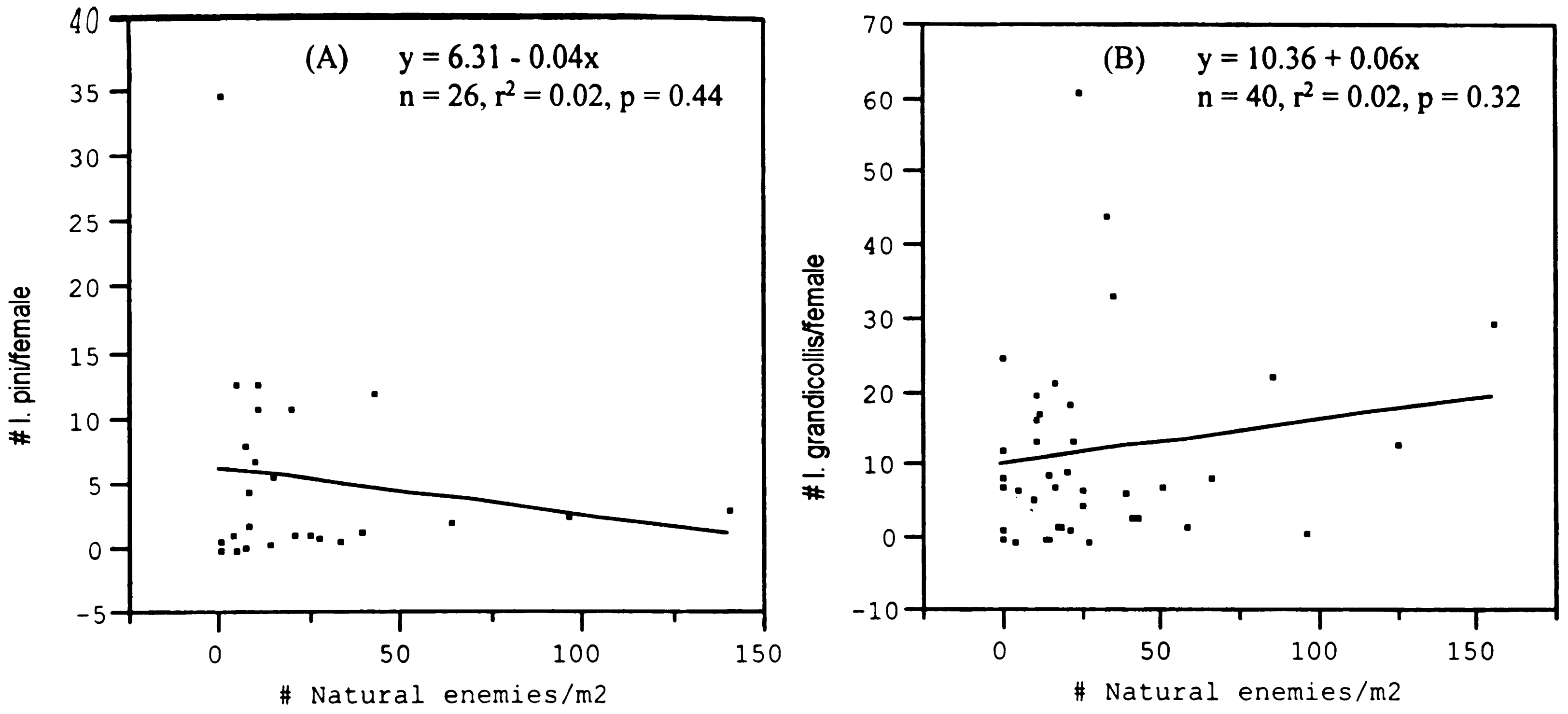

Figure 3. Relationships between natural enemy density and the productivity of (A) *Ips pini* and (B) *I. grandicollis*. All scolytid and natural enemy progeny adults were reared from batch 96-2. Note the different scales.

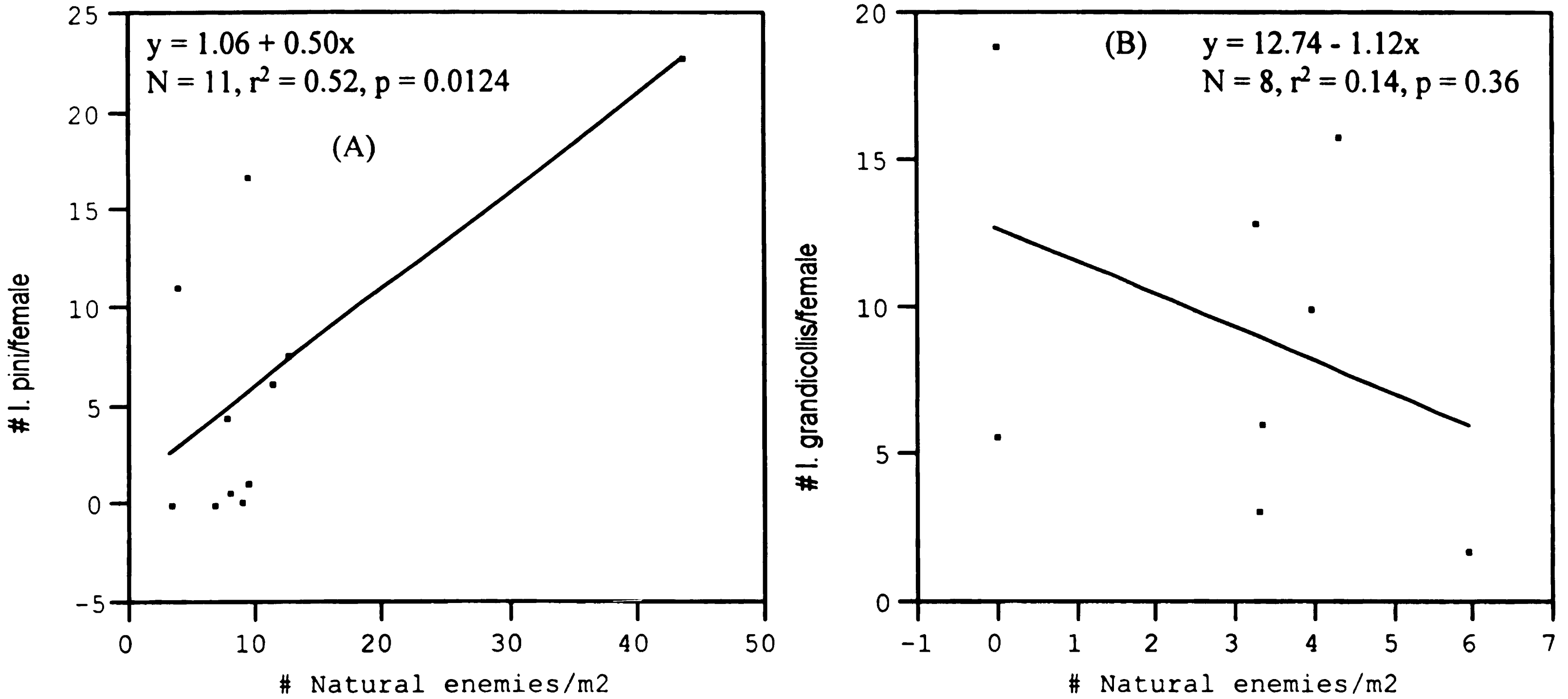

Figure 4. Relationships between natural enemy density and the productivity of (A) *Ips pini* and (B) *I. grandicollis*. All scolytid and natural enemy progeny adults were reared from batch 96-3. Note the different scales.

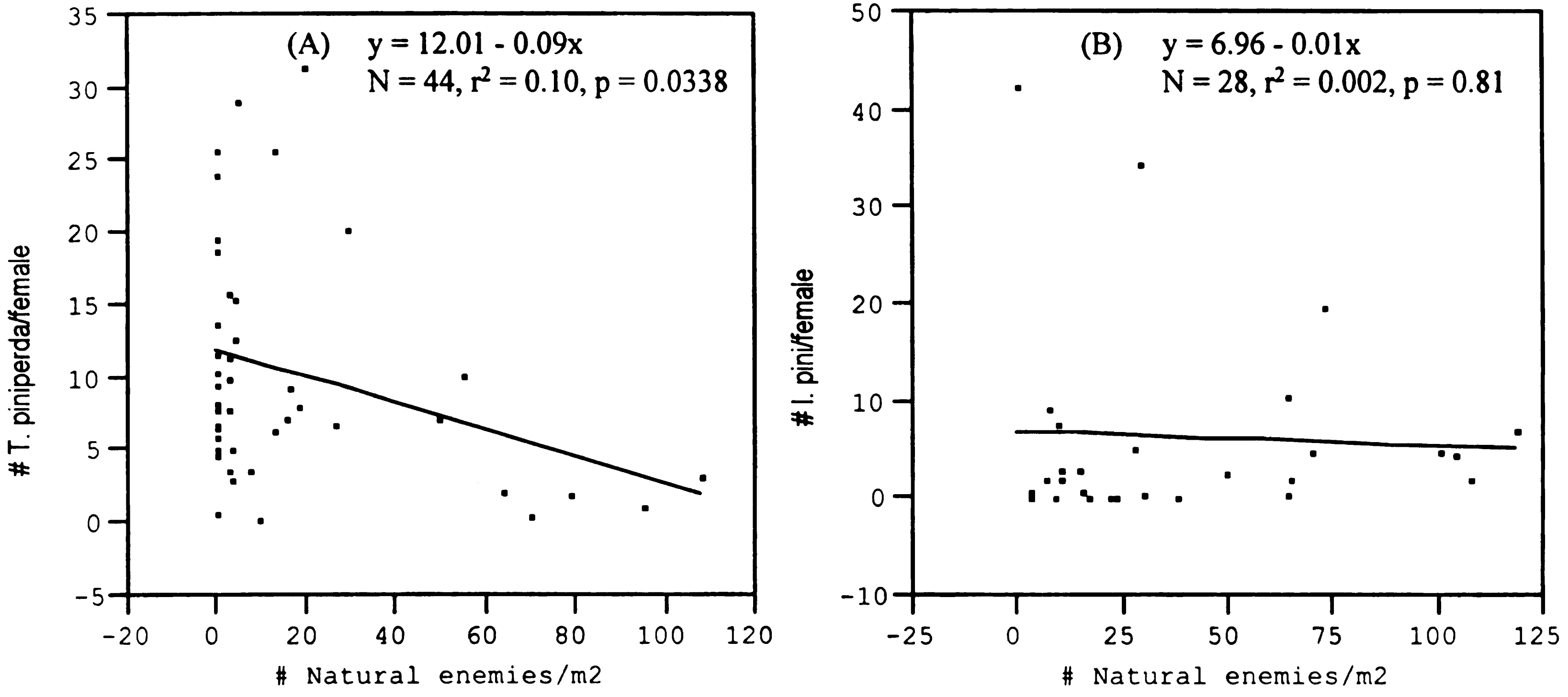

Figure 5. Relationships between natural enemy density and the productivity of (A) *Tomicus piniperda*, (B) *Ips pini*, and (C) *I. grandicollis*. All scolytid and natural enemy progeny were reared from batch 97-1. Note the different scales.

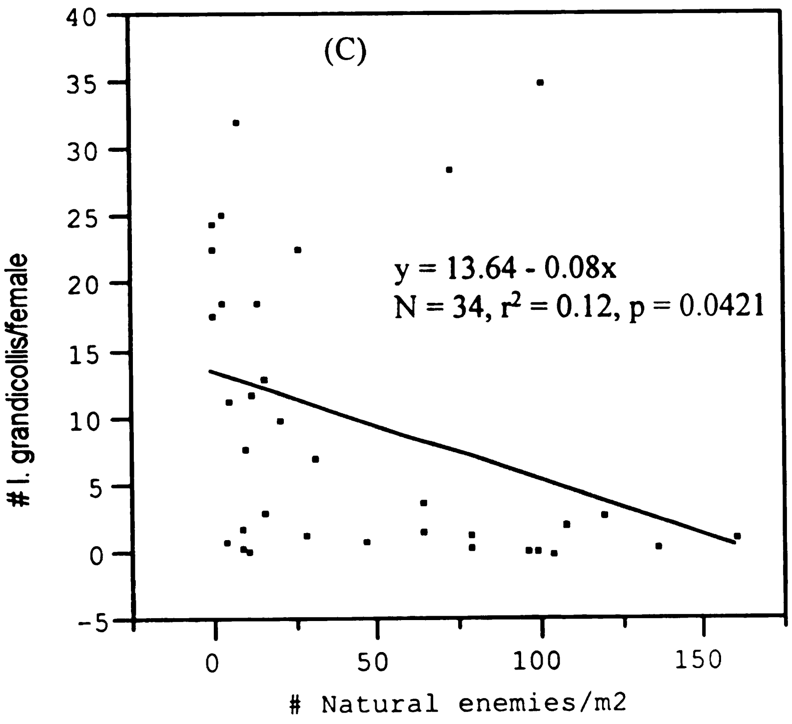

Figure 5 (cont'd).

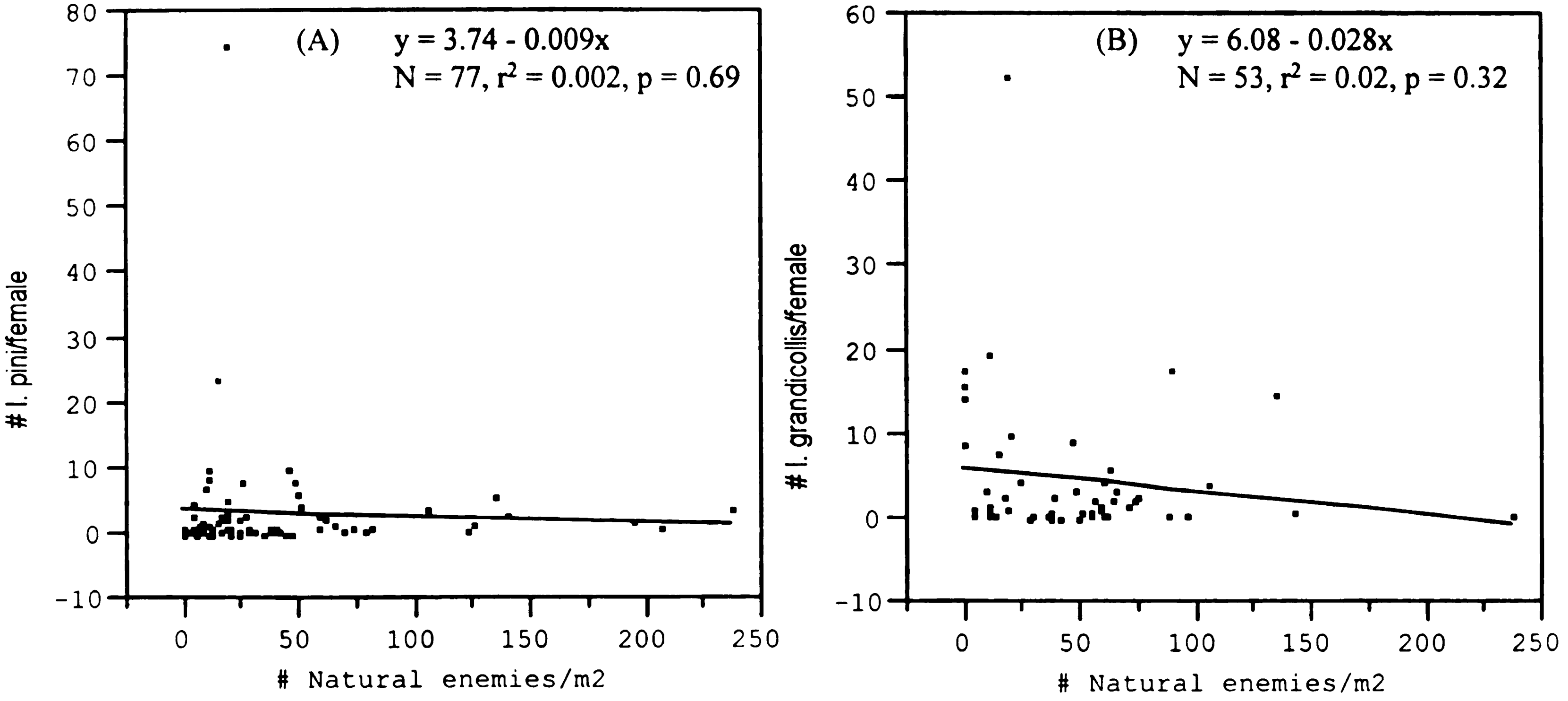

Figure 6. Relationships between natural enemy density and the productivity of (A) *Ips pini* and (B) *I. grandicollis*. All scolytid and natural enemy progeny adults were reared from batch 97-2. Note the different scales.

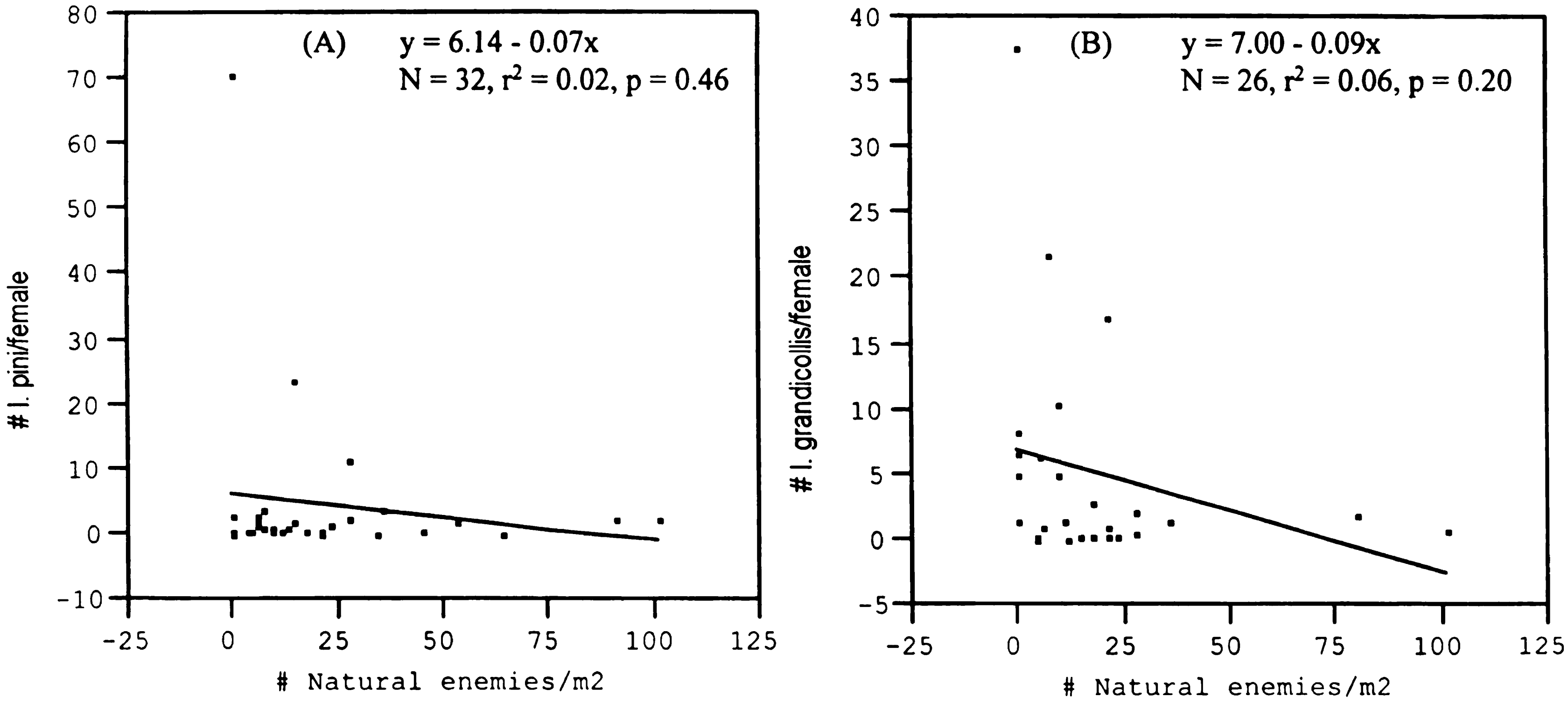

Figure 7. Relationships between natural enemy density and the productivity of (A) *Ips pini* and (B) *I. grandicollis*. All scolytid and natural enemy progeny adults were reared from batch 97-3. Note the different scales.

CHAPTER 3

Interspecific Competition Between Native *Ips pini* and Introduced *Tomicus piniperda* (Coleoptera: Scolytidae) Bark Beetles in Red Pine in Michigan

INTRODUCTION

Interspecific competition for food and space can be a major mortality factor when more than one bark beetle species attacks the same host tree species. Dead, weakened, and stressed trees are usually scarce and are distributed unevenly both temporally and spatially (Schroeder 1992). Weakened pines may be attacked simultaneously by several species of bark beetles, creating potential competition for food and breeding space. Interspecific competition has been demonstrated to increase mortality in numerous bark beetle species. For example, interspecific competition between *Ips pini* (Say) and *Dendroctonus ponderosae* Hopk. resulted in reduced success for both species when they infested the same host material (Rankin and Borden 1991). *Ips pini* and *I. paraconfusus* Lanier both had lower brood adult survival when the species were intermixed than when alone at the same densities (Light et al. 1983). Exploitative competition is believed to be the principal type of interspecific competition operating between bark beetles (Rankin and Borden 1991). This occurs when members of one species utilize common resources that are in short supply (i.e. larval breeding material) (Krebs 1994).

The recent establishment of an exotic pine bark beetle, *Tomicus piniperda* (L.), in the Great Lakes region allows us a rare opportunity to evaluate the interactions between native pine bark beetles and an exotic species that compete for the same resources. The larger pine shoot beetle, *T. piniperda*, a well-known pest of pines throughout much of Europe, Asia, and North Africa (Langstrom 1980, Ye 1991), was first discovered in 1992 in a Scotch pine (*Pinus sylvestris* L.) Christmas tree plantation in Ohio (Haack and Kucera 1993). As of September 1998, *T. piniperda* had been found in 243 counties in nine states, and in 21 counties in the Canadian province of Ontario (NAPIS 1998). *Tomicus piniperda* has a low temperature threshold for spring flight (10-12°), and is the first pine bark beetle to fly in the spring in Michigan (Haack and Lawrence 1995a). Adult beetles are attracted to stressed, dying, or recently-cut pine trees by host volatiles formed in the dying tissues of conifers (Volz 1988, Schroeder 1992, Schroeder 1987) and by short-range sex pheromones (S. Teale, State University of New York Syracuse, personal communication). *Tomicus piniperda* is univoltine (Langstrom 1980, Haack and Lawrence 1995b). Progeny adults feed in current-year or one-year pine shoots for the remainder of the summer (Langstrom 1980, McCullough and Smitley 1995).

The pine engraver, *Ips pini*, is the most economically important pine bark beetle in the Great Lakes region (Schenk and Benjamin 1969). Adults of this common scolytid also colonize dead or dying pines, but *I. pini* can produce three generations per year (Schenk and Benjamin 1969). Both *I. pini* and *T. piniperda* overwinter as adults, but *I. pini* typically becomes active in the spring four to six weeks later than *T. piniperda* (Haack and Lawrence 1995a). *Ips pini* adults are attracted in large numbers to host material by two aggregation pheromones that *I. pini* males produce: ipsdienol and lanierone (Raffa and Klepzig 1989, Seybold et al. 1992, Vite et al. 1972). These differences in the number of generations, the date of peak colonization activity, and the use of aggregation pheromones could presumably influence the interactions between these two scolytids.

Red pine (*Pinus resinosa* Ait.) is one of the most extensively planted species for pulp, sawtimber, and poles in the Great Lakes region (Rudolf 1990), comprising over 364,000 hectares of Michigan's timberland (Leatherberry and Spencer 1996). Red pine is a suitable host for *T. piniperda* as well as *I. pini* and many other pine bark beetles (Lawrence and Haack 1995, Raffa 1991). During a typical rotation of red pine, several thinnings or partial harvests may be performed, each of which generates an abundance of suitable brood material for scolytid colonization.

I examined interactions between *T. piniperda* and *I. pini* in laboratory and field experiments in red pine forest stands in Michigan in 1996 and 1997. The objective was to evaluate the effects of interspecific competition between *T. piniperda* and *I. pini* by comparing attack rates, gallery lengths, progeny density, and productivity in (1) red pine bolts artificially infested with one or both of these species, and in (2) red pine bolts naturally infested in the field by one or both of these species.

MATERIALS AND METHODS

Field Sites

In 1996, I conducted field studies in four red pine forest plantations in Michigan. Two plantations were in southwestern Michigan and were known to be infested with both *T. piniperda* and native *Ips* spp. These stands were located in Michigan State University's W.K. Kellogg Experimental Forest in Kalamazoo County (KAL1), and in the Allegan State Game Area in Allegan County (ALL1) (Figure 1). Two red pine plantations in northern lower Michigan, where *T. piniperda* populations were not known to be present, were also selected. One stand was in the Huron-Manistee National Forest in Wexford County (WEX1), and the other was in the AuSable State Forest in Roscommon County (ROS1). Although *T. piniperda* was later detected in Wexford County in 1997 during regulatory surveys, (NAPIS 1998), I did not observe any *T. piniperda* life stages or evidence of infestation in the northern field sites in 1996 or in 1997.

In general, all four research sites shared the following characteristics: they were pole-sized red pine plantations of similar size, age, and basal area (Table 1) with some hardwood understory; other red pine plantations were located within 2 km of the sites; and they were thinned during the 1994-1995 winter. An abundance of slash (for example, trunks, tops, large branches), suitable for scolytid colonization, was left on the ground in each stand from the thinnings, and was expected to serve as breeding material for scolytids in 1995. Temperature, precipitation, and degree day accumulation (base

10°C) were monitored after March 1 by Michigan State University weather stations near all four sites.

In 1997, I used the same four sites described above, which represented conditions two years after a thinning ("old" sites). I also expanded the study to include four additional red pine plantations (KAL2, ALL2, WEX2, and ROS2), each one within 6.2 km of one of the original stands. These "new" sites had the same general characteristics of the original stands (Table 1), but were row-thinned during the 1995-1996 winter.

Artificial Infestations

Red pine bolts, each approximately 61 cm long and 10 – 20 cm diameter, were cut from live red pine trees in the W. K. Kellogg Experimental Forest in Kalamazoo County in March 1996. A total of 120 bolts were used in the study: 40 bolts were infested with *T. piniperda*, 40 were infested with *I. pini*, and 40 were infested with both species. *Tomicus piniperda* and *I. pini* adults used in this study were collected live from Lindgren funnel traps in red pine stands at Kellogg Experimental Forest and in a mixed Scotch and red pine stand at the Fenner Nature Center in Lansing, in Ingham County. Additional *I. pini* adults were collected from galleries under the bark of red pine in a recently-thinned stand in Wexford County in late May. *Tomicus piniperda* were sexed on the basis of stridulation (Bakke 1968), and *I. pini* were sexed on the basis of the third spine on the elytral declivity (Wood, 1982).

Ips pini infestations took place six weeks after *T. piniperda* infestations, reflecting the average time difference in initial flight and colonization between these species in Michigan (Haack and Lawrence 1995a). Beetles were introduced into the bolts by making a small "starter" hole in the bark of the bolts with the point of a nail sterilized in

95% EtOH. One beetle of the initiating sex (female *T. piniperda* or male *I. pini*) was placed in the hole, and one half of a size 00 clear gelatin capsule was placed over the beetle and starter hole. The capsule was sealed to the bark with nontoxic clay. After 24 hours, the capsules were checked for the presence of boring dust as an indicator of a successful attack. If boring dust was present, a single beetle of the other sex (male *T. piniperda* or female *I. pini*) was added to the gelcap. If the beetle did not successfully bore into the phloem, it was removed, and another beetle was added to the same hole. For the polygamous *I. pini*, two females were added for each male; the second added 24 hours after the first. When only one species was introduced, five infestations were made on small (10 – 13 cm diameter) bolts (about 23 females/m^2), six infestations were made on medium (13 – 17 cm diameter) bolts (about 21 females/m^2), and seven infestations were made on large (17 – 20 cm diameter) bolts (about 20 females/m^2). When both species were introduced, a combined total of ten, twelve, and fourteen infestations (46, 42, and 40 females/m^2) were made, respectively, on small, medium, and large bolts. The points of infestation were picked at random and were spaced over the entire bolt.

These bolts were taken to the field sites immediately after all of the infestations were successfully completed. Bolts infested with *I. pini* were distributed equally to all four sites, and bolts with *T. piniperda* or *T. piniperda* + *I. pini* were distributed equally between the two southern (KF1 and ALL1) sites only. Bolts were placed in a shaded part of each stand to reduce potential desiccation. Four to six bolts from each group (*T. piniperda* alone, *I. pini* alone, and both species) were returned to Michigan State University at two week intervals to rear out the insects. Collected bolts were placed into emergence containers and reared as described below.

I was not able to repeat this experiment in 1997. Unfortunately, most *T. piniperda* beetles collected from the funnel traps in 1997 developed a fungal disease in the lab and died before the experiment began, and few live *I. pini* adults were collected in funnel traps.

Field Infestations

In 1996, a total of 204 red pine bolts, and in 1997, a total of 304 bolts, each approximately 61 cm long and 10 – 20 cm diameter, were cut from live red pine trees at the field sites in February, April, and June of both years (Table 1). These times roughly corresponded to the initial activity of overwintering parent *T. piniperda*, overwintering parent *Ips* spp., and emergence of the F1 progeny *Ips* spp. adults. These three times represented three batches, or groups, and the bolts in each batch were divided evenly among all field sites, with the exception of batch 1 (Table 1). Batch 1 bolts were only placed in the southern sites since *T. piniperda* was not present in the northern sites. Each batch of bolts was placed on the forest floor in a shady area of each plantation to reduce desiccation, just before the expected flight of *T. piniperda* or *Ips* spp. (Table 1).

Beginning two weeks after the bark beetles' peak flight, four to six bolts from each batch were returned to Michigan State University. Bolts were retrieved at two week intervals in 1996 and at one week intervals in 1997. The cut ends of the retrieved bolts were dipped in paraffin wax to reduce desiccation. Each bolt was placed in an individual emergence container consisting of a cardboard tube (15 – 25 cm diameter, 0.3 – 0.6 cm wall, 61 – 71 cm overall length [Michigan Can & Tube, Inc., Saginaw, MI]) with opaque plastic endcaps and a clear plastic collection cup at one end. The emergence containers were stored on the Michigan State University campus in a screened insectary to expose the bolts to ambient temperatures and humidity.

Bark beetle progeny adults emerging from the red pine bolts were collected from the emergence containers at least twice a week until late October. When progeny emergence stopped in the winter, I counted the number of scolytid exit holes per bolt, and then each bolt was de-barked and any insects overwintering in the bark or dead on the bottom of the emergence container were collected. All the insects that were reared from these bolts were assumed to be progeny adults. Although it is possible that a few parent adults were inadvertently collected, the number of parents was assumed to be small and similar across all bolts and sites.

For each debarked bolt, I determined the phloem surface area, calculated as a cylinder using the mean of two length measurements and the mean of four diameter measurements. I also measured the number and length of *Ips* spp. galleries (each egg gallery radiating from the nuptial chamber was counted), and the number and length of *T. piniperda* galleries for each bolt. *Tomicus piniperda* is monogamous, and its galleries are long and straight and parallel to the grain of the wood; *Ips* spp. are polygamous, and their galleries consist of a nuptial chamber with 2 – 4 radiating galleries in the shape of a "Y" or "H." All *Ips* spp. galleries in the artificially infested bolts were assumed to be those of *I. pini*. For the field-infested bolts, though, I was not able to distinguish which *Ips* species excavated each gallery; *Ips grandicollis* (Eichhoff) and *Ips perroti* Swaine were reared from the field bolts along with *I. pini*. Based on data from a related study, though, *I. pini* was the most abundant *Ips* species reared from the field-infested bolts. The number of scolytid egg galleries per bolt was used as an indicator of the density of female parent beetles (1 egg gallery = 1 female parent), and the number of scolytid progeny per female was used as a measure of productivity.

Data Analysis

For each artificially- and field-infested bolt, I calculated the number of *T. piniperda* and *Ips* spp. galleries per m^2 of phloem surface area (attack density), the average length of *T. piniperda* and *Ips* spp. galleries per bolt, the number of scolytid progeny reared per m^2 (progeny density), and the number of scolytid progeny reared per parent female (productivity). If fewer than five adults of a particular scolytid species were reared from a bolt, it was considered a failed attack, and that species was excluded from that bolt's data set.

All variables were tested for normality with the Shapiro-Wilk W test, and were log transformed to increase homogeneity of variances and tested again for normality. None of the variables were normally distributed, even after log transformation, so the nonparametric Mann-Whitney one-way test was used (SAS Institute 1996). The artificially infested bolts were analyzed with the Mann-Whitney test to compare these variables (attack density, gallery length, progeny density, and productivity) for *T. piniperda* and *I. pini* between bolts with one species and bolts with both species. Each of the three batches of field-infested bolts per year was analyzed separately with the Mann-Whitney test to analyze the effects of location (northern = without *T. piniperda* or southern = with *T. piniperda*) on these variables for *Ips* spp. For batches 96-1 and 97-1, which were placed only in the southern sites, I compared these variables between bolts with one species and bolts with both species.

RESULTS

Artificial Infestations

Ips pini attack densities (number of galleries/m^2 of phloem surface area), mean gallery length, progeny density (number of *I. pini* progeny adults reared/m^2 of phloem surface area), and productivity (number of *I. pini* progeny adults reared/gallery) were all significantly lower in the bolts infested with both *I. pini* and *T. piniperda* than in the bolts with *I. pini* alone (Table 2). An average of 43 *I. pini* females/m^2 (= attacks) were introduced into 80 of the laboratory bolts. In the bolts with *I. pini* alone, fewer than half of these attacks resulted in successful gallery completion, and in the bolts infested with both species, only 20% of the attacks were successful.

Tomicus piniperda attack densities, gallery length, and productivity were all slightly lower in bolts with both *T. piniperda* and *I. pini* than in the bolts with *T. piniperda* alone, but none of the differences were significant (Table 3). Significantly fewer *T. piniperda* progeny/m^2 emerged from bolts infested with both species than from bolts with *T. piniperda* alone (Table 3). In the laboratory, about 22 *T. piniperda* females/m^2 (= attacks) were introduced into each bolt. About two-thirds of these attacks resulted in successful gallery completion.

Field Infestations: Effect of Location on *Ips* spp.

In the field-infested bolts of batches 96-2 and 96-3, *Ips* spp. attack densities were lower in the southern sites than in northern sites, but differences were not significant (Table 4). In 1997, *Ips* spp. attack densities were significantly lower in southern sites in batch 97-3, and were lower in southern sites in batch 97-2, though not significantly

(Table 5). *Ips* spp. gallery lengths followed the opposite trend: galleries were significantly longer in the southern sites than in the northern sites in batches 96-2, 97-2, and 97-3 (Tables 4 and 5).

Ips spp. progeny density (number of progeny reared/m^2) did not differ between northern sites and southern sites in 1996 (Table 4), but in 1997, *Ips* spp. progeny density was significantly lower in the bolts from the southern sites in batches 97-2 and 97-3 (Table 5). Mean *Ips* spp. productivity did not significantly differ between northern and southern sites in either year (Tables 4 and 5).

Field Infestations: Single Species vs. Both Species

Only a single bolt was infested by both *T. piniperda* and *Ips* spp. in 1996. I could not statistically analyze the 1996 data, although the results indicate that each of the variables were fairly consistent from year to year when logs were only colonized by only one of the species (Tables 6 and 7).

In 1997, eight bolts were colonized by both *T. piniperda* and *Ips* spp. in the field. *Ips* spp. attack density, mean gallery length, and progeny density were lower in bolts attacked by both *T. piniperda* and *Ips* spp. than in the bolts with *Ips* spp. alone, but the difference was not significant (Table 6). Productivity for *Ips* spp., however, was significantly higher in bolts with both species (Table 6).

Tomicus piniperda attack density and progeny density were higher in bolts attacked by both *T. piniperda* and *Ips* spp., but the differences were not significant (Table 7). Average *T. piniperda* gallery length was significantly higher in bolts with both species (Table 7). *Tomicus piniperda* productivity was lower in bolts attacked by both species, though not significantly (Table 7).

DISCUSSION

Several field and laboratory studies have demonstrated that interspecific competition can occur between bark beetles, but the relative importance of interspecific competition in regulating population dynamics has been debated. Berryman (1973) found that *Scolytis ventralis* LeConte was a poor competitor against secondary bark beetles that attacked the trees killed by *S. ventralis*, especially during a period of outbreak decline. Light et al. (1983) demonstrated that the effects of interspecific competition between *I. paraconfusus* and *I. pini* were much greater than the effects of intraspecific competition in bolts with similarly high densities of single species. *Ips pini* has been found to reduce *Dendroctonus ponderosae* Hopkins progeny production in lodgepole pine, *Pinus contorta* var. *latifolia* Engelm. (Rankin and Borden 1991). Interspecific competition can also affect niche breadth and resource partitioning in bark beetles (Paine et al. 1981).

Although interspecific competition has been studied for several aggressive bark beetle species, it has not been thoroughly investigated in the Great Lakes region, where endemic pine bark beetles are secondary invaders of dying or cut trees. Schenk and Benjamin (1969) reported that both interspecific and intraspecific competition were major mortality factors for *I. pini* in Wisconsin, but that intraspecific competition was more important, since *I. pini* comprised 95% of the scolytid population. The recently-introduced bark beetle *T. piniperda* represents an additional competitor for *I. pini* in the Great Lakes region. Haack and Lawrence (1995b) found that at high densities, *T. piniperda* colonized all sides of Scotch pine logs including upper and lower surfaces, but at lower densities, *T. piniperda* preferred to colonize only the sides of logs. When *T. piniperda* was already present in a log, *I. pini* was restricted to colonizing the tops of the logs, which can be subject to extreme temperature fluctuations due to direct exposure to the sun. Haack and Lawrence's (1995b) results demonstrated that *T. piniperda* and *I. pini* partitioned the phloem resource, but there was likely not much direct interaction between the species.

In the lab portion of this study, the infestations of *T. piniperda* and *I. pini* were spaced over all sides of the bolts, so that the two species were not spatially segregated from each other. Overall, the artificial introductions of bark beetles to the red pine bolts were less successful than expected; 66% of the *T. piniperda* artificial introductions and only 30% of the *I. pini* artificial introductions resulted in successful galleries. There are several possible reasons for the poor success rates. I observed that the initiating sex of both species (male *I. pini*, female *T. piniperda*) usually began boring into the outer bark and phloem readily, but once the beetles were under the bark, some may have died. I also witnessed a few cases of beetles boring into the phloem, and then promptly chewing a second hole out of the bark, just a few centimeters away, suggesting that the region of bark or phloem was unsuitable to the parent beetles.

The lab-imposed attack densities were selected to represent low field populations and to reduce the chance of intraspecific competition. The artificial attack densities were comparable with those seen in the field-infested batch 1 red pine bolts: about 74 *Ips* spp. (primarily *I. pini*) attacks/m^2 and 30 *T. piniperda* attacks/m^2 (Tables 6 and 7). In another field study of *T. piniperda* and *I. pini* attack densities in Michigan, Haack and Lawrence

(1995b) found similar *I. pini* attack densities, but much higher *T. piniperda* attack densities (179 attacks/m^2) in field-infested Scotch pine bolts.

Compared with other scolytid competition studies, the lab-imposed attack densities in this study were much lower. In other interspecific competition studies with *I. pini*, densities of 300 and 600 *I. pini* galleries/m^2 (Rankin and Borden 1991) and densities of 200, 400, and 800 *I. pini* galleries/m^2 (Light et al. 1983) were used.

Even at relatively low gallery densities in the lab-infested bolts, *I. pini* galleries (attack densities and gallery lengths) and progeny (density and productivity) were significantly lower in bolts that were first infested with *T. piniperda* than in bolts infested with *I. pini* alone. The field-infested bolts showed similar trends for *Ips* spp., indicating that the lab study accurately represented the interactions taking place in the field. The only inconsistent result in the field-infested bolts was that *Ips* spp. productivity was higher in the bolts with both species. This finding may be an artifact of the small number of bolts infested with both species and lack of replication in the field-infested bolts. Further field and lab research on the interactions of these species is needed.

The most likely reason for *I. pini*'s lower attack densities, gallery length, progeny densities, and productivity was that *T. piniperda* parent adults, with their six week head start over *I. pini* (in the field and in the lab), colonized most of the available phloem in the red pine bolts. This is an example of exploitation competition, where the first species to arrive at the limited resource has better survival than the species that arrives later (Krebs 1994). Interference competition may also be taking place, where one species has the capabilitity to damage another; for example, through aggressive acts or cannibalism (Krebs 1994). By the time *I. pini* larvae hatch, *T. piniperda* larvae would likely be much larger, and would be capable of consuming any small *I. pini* eggs and larvae they encountered. A third possible explanation for *I. pini*'s poor success in the bolts with both species is that *T. piniperda* may have introduced fungi into the bolts that inhibited either *I. pini* parent adults or larvae (Paine et al. 1981, Yearian et al. 1972). Further research is needed to elucidate which, if any, of these interactions are causing the reduced success of *I. pini*.

Tomicus piniperda, in both the lab-infested and the field-infested bolts, fared much better than did *I. pini* in the bolts with both species. *Tomicus piniperda* progeny density in the lab-infested bolts was the only variable that was significantly decreased in the bolts with both species compared to the bolts with *T. piniperda* alone. In the field-infested bolts, all of the variables except *T. piniperda* productivity were actually higher in the bolts with both species. Having six weeks to colonize and begin development without competitive pressure from *I. pini* appeared to be the key to *T. piniperda*'s success in this study. In a related study, I found that two other pine phloem borers, *Pissodes nemorensis* Germar (Coleoptera: Curculionidae) and *Hylurgops rugipennis pinifex* (Fitch) (Coleoptera: Scolytidae), were actively colonizing the field bolts as early in the spring as *T. piniperda*. These beetles were primarily colonizing the cool, damp underside of the bolts, though, not the sides of the bolts, where *T. piniperda* was more prevalent. Interspecific competitive interactions are reduced when the phloem resource is partitioned, and when colonization occurs simultaneously (Paine et al. 1981, Rankin and Borden 1991), so it is not likely that severe competition was taking place between these early colonizers.

I took advantage of the fact that *T. piniperda* had not yet spread to northern Michigan, and compared *Ips* spp. galleries (attack density and gallery length) and progeny (density and productivity) in the northern Michigan sites with the southern sites. Although *Ips* spp. attack densities were lower in the southern sites, where *T. piniperda* was also present, than in the northern sites, this trend cannot solely be attributed to the presence of *T. piniperda*. Higher attack densities in the northern sites could be simply a result of the larger *Ips* spp. populations in northern Michigan, where pines are more abundant (Rudolf 1990). Although I can speculate that years of competition with *T. piniperda* may have reduced the *Ips* spp. populations in southern Michigan, this explanation was not likely, and it was not within the scope of this study to determine the basis for *Ips* bark beetles' regional population size.

Gallery length can be directly correlated with number of eggs laid by scolytids (Anderbrant 1990, Foltz et al. 1976, Light et al. 1983), with shorter galleries I expected to find fewer progeny per gallery (Anderbrant et al. 1985, Rankin and Borden 1991). *Ips* spp. gallery lengths were longer, on average, in the southern sites (where *T. piniperda* was also present) than in the northern sites. Although this seems to contradict the previous finding of lower attack densities in the southern sites, it can actually be explained by intraspecific or interspecific competition. At high densities, bark beetle galleries tend to be shorter, presumably because of the deterioration of the phloem, or because females stop gallery construction when they sense the presence of other females (Anderbrant 1990). At lower densities, such as in the southern sites, galleries tend to be longer. At the highest densities in the northern sites (279 attacks/m^2), densities were high enough to expect intraspecific competition to occur, since Schenk and Benjamin (1969) found intraspecific competition to be a major mortality factor at attack densities of only 186 *I. pini* attacks/m^2.

Conclusions

Even at the relatively low attack densities used in the lab study, *Ips pini* attack density, gallery length, progeny density, and productivity were significantly lower in bolts first attacked by *T. piniperda* than in bolts with similar densities of *I. pini* alone. *Tomicus piniperda* galleries and progeny were generally unaffected by the addition of *I. pini* later in the season. Studies on field-infested red pine bolts confirmed these findings. Interspecific competition, probably in the form of exploitation competition, is hypothesized as the primary reason for *I. pini*'s reduced success.

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Table 1. General characteristics and number of red pine bolts placed at the 1996 and 1997 red pine plantation field sites.

	KAL 1	KAL 2	ALL 1	ALL 2	WEX 1	WEX 2	ROS 1	ROS 2
Area (ha)	0.81	1.62	9.31	6.47	18.62	10.93	52.20	22.26
Year planted	1937	1937	1939	1938	1937	1948	1937	1965
Basal area (m^2/ha) after thinning	30	18	21	23	28	28	21	21
Year(s) thinned	1995	1996	1987, 1995	1996	1975, 1995	1996	1995	1996
No. of batch 96-1 bolts (in field 6 March 1996)	30	—	30	—	0	—	0	—
No. of batch 96-2 bolts (in field 7 May 1996)	22	—	22	—	22	—	22	—
No. of batch 96-3 bolts (in field 20 June 1996)	14	—	14	—	14	—	14	—
No. of batch 97-1 bolts (in field 28 Feb. 1997)	28	28	28	28	0	0	0	0
No. of batch 97-2 bolts (in field 11 April 1997)	16	16	16	16	16	16	16	16
No. of batch 97-3 bolts (in field 2 July 1997)	8	8	8	8	8	8	8	8

Table 2. *Ips pini* gallery densities, gallery lengths, progeny density, and productivity in artificially-infested red pine bolts in 1996, for bolts infested with *I. pini* only and bolts infested with equal densities of *I. pini* and *Tomicus piniperda*.

Variable		Bolts infested with *Ips pini* only	Bolts infested equally with *T. piniperda* and *I. pini*
No. of *I. pini* galleries/m^2	Mean no./ m^2	18.4	8.1
	Standard error	3.30	1.86
	n (No. of bolts)	40	40
	χ^2 *	6.94	
	p *	0.0084	
Average length (cm) of *I. pini* galleries	Mean length	4.5	2.0
	Standard error	0.60	0.42
	n (No. of bolts)	40	40
	χ^2 *	9.66	
	p *	0.0019	
No. of *I. pini* progeny adults reared/m^2	Mean no./ m^2	132.2	1.6
	Standard error	20.78	1.13
	n (No. of bolts)	40	40
	χ^2 *	45.08	
	p *	<0.0001	
No. of *I. pini* progeny adults reared/gallery	Mean no./ gallery	6.5	0.08
	Standard error	1.74	0.08
	n (No. of bolts)	40	40
	χ^2 *	29.91	
	p *	<0.0001	

* Chi square and p-values obtained from the Mann-Whitney test.

Table 3. *Tomicus piniperda* gallery densities, gallery lengths, progeny density, and productivity in artificially-infested red pine bolts in 1996, for bolts infested with *T. piniperda* only and bolts infested with equal densities of *T. piniperda* and *Ips pini*.

Variable		Bolts infested with *T. piniperda* only	Bolts infested equally with *T. piniperda* and *I. pini*
No. of *T. piniperda* galleries/m^2	Mean no./ m^2	14.8	14.6
	Standard error	1.51	1.72
	n (No. of bolts)	40	40
	χ^2 *	0.10	
	p *	0.75	
Average length (cm) of *T. piniperda* galleries	Mean length	6.8	5.4
	Standard error	0.88	0.45
	n (No. of bolts)	40	40
	χ^2 *	1.40	
	p *	0.24	
No. of *T. piniperda* progeny adults reared/m^2	Mean no./ m^2	48.3	10.9
	Standard error	14.15	3.71
	n (No. of bolts)	40	40
	χ^2 *	6.38	
	p *	0.0116	
No. of *T. piniperda* progeny adults reared/gallery	Mean no./ gallery	2.2	0.90
	Standard error	0.63	0.32
	n (No. of bolts)	40	40
	χ^2 *	3.30	
	p *	0.07	

* Chi square and p-values obtained from the Mann-Whitney test.

Table 4. *Ips* spp. gallery densities, gallery lengths, progeny density, and productivity in field-infested red pine bolts in 1996, for bolts from southern sites (KF and ALL), where both *T. piniperda* and *I. pini* were present, and from northern sites (WEX and ROS), where *T. piniperda* was absent. There were a total of 60 bolts in batch 96-1; 88 bolts in batch 96-2; and 56 bolts in batch 96-3.

		Batch 96-1		Batch 96-2		Batch 96-3	
Variable		Bolts from southern sites	Bolts from northern sites	Bolts from southern sites	Bolts from northern sites	Bolts from southern sites	Bolts from northern sites
No. of *Ips* spp. galleries/m^2	Mean no./ m^2	16.8	—	46.9	65.4	38.7	57.5
	Standard error	4.78	—	6.29	14.83	10.1	16.72
	χ^2 *			0.28		0.00	
	p *			0.60		1.00	
Average length (cm) of *Ips* spp. galleries	Mean length	2.8	—	8.1	5.0	3.2	2.3
	Standard error	0.53	—	0.80	0.61	0.53	0.47
	χ^2 *			9.28		1.31	
	p *			0.0023		0.25	
No. of *I.ps* spp. progeny adults reared/m^2	Mean no./ m^2	172.2	—	141.8	88.9	130.5	201.4
	Standard error	101.72	—	23.67	21.21	52.89	89.09
	χ^2 *			1.23		0.00	
	p *			0.27		1.00	
No. of *Ips* spp. progeny adults reared/gallery	Mean no./ gallery	28.5	—	4.1	10.1	9.8	5.5
	Standard error	16.31	—	0.92	5.49	6.80	2.17
	χ^2 *			0.075		0.17	
	p *			0.78		0.68	

* Chi square and p-values obtained from the Mann-Whitney test.

Table 5. *Ips* spp. gallery densities, gallery lengths, progeny density, and productivity in field-infested red pine bolts in 1997, for bolts from southern sites (KF and ALL), where both *T. piniperda* and *I. pini* were present, and from northern sites (WEX and ROS), where *T. piniperda* was absent. There were a total of 112 bolts in batch 97-1; 128 bolts in batch 97-2; and 64 bolts in batch 97-3.

Variable		Batch 97-1		Batch 97-2		Batch 97-3	
		Bolts from southern sites	Bolts from northern sites	Bolts from southern sites	Bolts from northern sites	Bolts from southern sites	Bolts from northern sites
No. of *Ips* spp. galleries/m^2	Mean no./ m^2	25.9	—	90.9	129.7	54.1	278.6
	Standard error	4.38	—	8.86	18.08	10.80	52.05
	χ^2 *			0.098		7.36	
	p *			0.75		0.0067	
Average length (cm) of *Ips* spp. galleries	Mean length	3.1	—	8.5	6.4	6.1	3.6
	Standard error	0.41	—	0.45	0.52	0.70	0.42
	χ^2 *			15.62		10.68	
	p *			<0.001		0.0011	
No. of *Ips* spp. progeny adults reared/m^2	Mean no./ m^2	140.0	—	142.6	269.0	168.7	499.3
	Standard error	26.37	—	25.82	35.76	33.30	116.42
	χ^2 *			9.92		4.18	
	p *			0.0016		0.0410	
No. of *Ips* spp. progeny adults reared/gallery	Mean no./ gallery	6.4	—	4.5	2.5	8.0	2.9
	Standard error	1.93	—	2.26	0.38	6.31	1.19
	χ^2 *			1.89		0.66	
	p *			0.17		0.42	

* Chi square and p-values obtained from the Mann-Whitney test.

Table 6. *Ips* spp. gallery densities, gallery lengths, progeny density, and productivity in field-infested red pine bolts in 1996 and 1997, for bolts infested with *Ips* spp. only and bolts infested with both *Ips* spp. and *Tomicus piniperda*.

Variable		Batch 96-1		Batch 97-1	
		Bolts with *Ips* spp. only (n = 9)	Bolts with *T. piniperda* and *Ips* spp. (n = 1)	Bolts with *Ips* spp. only (n = 20)	Bolts with *T. piniperda* and *Ips* spp. (n = 8)
No. of *Ips* spp. galleries/m^2	Mean no./ m^2	73.6	17.3	74.3	39.9
	Standard error	21.28	—	11.55	13.91
	χ^2 *			2.66	
	p *			0.10	
Average length (cm) of *Ips* spp. galleries	Mean length	6.7	2.0	7.7	6.1
	Standard error	1.15	—	0.84	1.46
	χ^2 *			0.44	
	p *			0.51	
No. of *Ips* spp. progeny adults reared/m^2	Mean no./ m^2	161.5	268.8	161.1	122.3
	Standard error	113.09	—	36.59	28.56
	χ^2 *			0.16	
	p *			0.68	
No. of *Ips* spp. progeny adults reared/gallery	Mean no./ gallery	13.6	62.0	3.5	13.7
	Standard error	6.80	—	1.02	5.70
	χ^2 *			4.78	
	p *			0.0288	

* Chi square and p-values obtained from the Mann-Whitney test.

Table 7. *Tomicus piniperda* gallery densities, gallery lengths, progeny density, and productivity in field-infested red pine bolts in 1996 and 1997, for bolts infested with *Tomicus piniperda* only and bolts infested with both *Ips* spp. and *T. piniperda*.

		Batch 96-1		Batch 97-1	
Variable		Bolts with *T. piniperda* only (n = 16)	Bolts with *T. piniperda* and *Ips* spp. (n = 1)	Bolts with *T. piniperda* only (n = 36)	Bolts with *T. piniperda* and *Ips* spp. (n = 8)
No. of *T. piniperda* galleries/m^2	Mean no./ m^2	30.3	17.34	24.1	47.1
	Standard error	4.55	—	2.55	11.91
	χ^2 *			3.33	
	p *			0.07	
Average length (cm) of *T. piniperda* galleries	Mean length	7.88	12.9	6.6	8.4
	Standard error	1.06	—	0.36	0.66
	χ^2 *			6.84	
	p *			0.0089	
No. of *T. piniperda* progeny adults reared/m^2	Mean no./ m^2	120.5	39.0	217.7	255.7
	Standard error	35.70	—	28.99	73.31
	χ^2 *			0.13	
	p *			0.72	
No. of *T. piniperda* progeny adults reared/gallery	Mean no./ gallery	8.7	3.0	11.3	6.8
	Standard error	4.15	—	1.36	2.18
	χ^2 *			2.75	
	p *			0.10	

* Chi square and p-values obtained from the Mann-Whitney test.

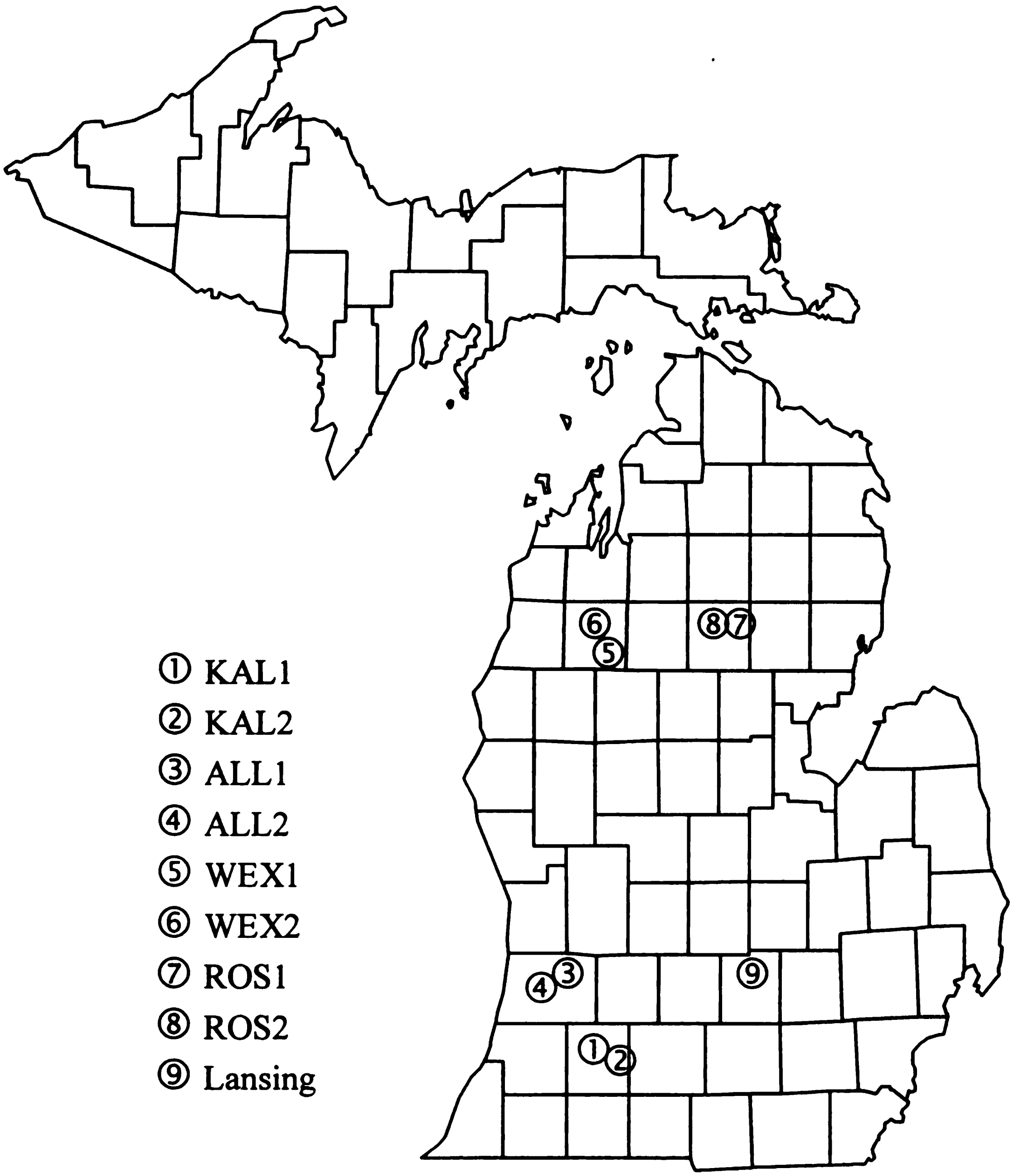

Figure 1. Location of red pine forest plantation field sites in Michigan. KAL1, ALL1, WEX1, ROS1, and Lansing were monitored in 1996; all stands were monitored in 1997.

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.: 1998-8

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

Interactions of the Pine Shoot Beetle [Tomicus piniperda (L.) (Coleoptera: Scolytidae)] with Native Pine Bark Beetles and Their Associated Natural Enemies in Michigan

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

Entomology Museum, Michigan State University (MSU)

Other Museums: none

Investigator's Name (s) (typed)
Amy Ann Kennedy

Date 16 December 1998

*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 3 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
Coleoptera: Scolytidae									
Ips grandicollis (Eichhoff)	Michigan: Allegan Co. (A), Wexford Co.(W) Roscommon Co. (R)					10			
Ips perroti Swaine	Michigan: W, R					10			
Tomicus piniperda (L.)	Michigan: A, Kalamazoo Co. (K)					10 10	parent teneral		
Ips pini (Say)	Michigan: A, W, R					10			
Orthotomicus caelatus (Eichhoff)	Michigan: K, A, R					10			
Dendroctonus valens LeConte	Michigan: K, A, R, W					5			
Dryocetes autographus (Ratzeburg)	Michigan: K					10			
Hylurgops rugipennis pinifex (Fitch)	Michigan: K, A, W					10			
Hylastes porculus Erichson	Michigan: A, K, W					10			
Gnathotrichus materiarius (Fitch)	Michigan: A, K					10			

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

Amy Ann Kennedy

Date 16 December 1998

Voucher No. 1998-8

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

17 Dec 1998

Curator Date

APPENDIX 1.1

Voucher Specimen Data

Page 2 of 3 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
Coleoptera: Curculionidae Pissodes nemorensis Germar	Michigan: Kalamazoo Co. (K), Allegan Co. (A), Roscommon Co. (R)					10			
Coleoptera: Cerambycidae Monochamus scutellatus (Say)	Michigan: Ingham Co. (I), K, A, R					5	5		
Monochamus carolinensis (Olivier)	Michigan: K					2			
Coleoptera: Cucujidae Cucujus clavipes F.	Michigan: K					5			
Coleoptera: Cleridae Thanasimus dubius (F.)	Michigan: A, K, R, Wexford Co. (W)					10			
Enoclerus nigripes Say	Michigan: I, W					3			
Coleoptera: Tenebrionidae Corticeus parallelus Melsheimer	Michigan: A, K, R, W					10			

(Use additional sheets if necessary)

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17 Dec 1998

Date

APPENDIX 1.1

Voucher Specimen Data

Page 3 of 3 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
Coleoptera: Staphylinidae									
Sp. 1	Michigan: Kalamazoo Co. (K), Allegan Co. (A), Wexford Co. (W)					5			
Sp. 2	Michigan: K, A, W					5			
Coleoptera: Histeridae									
Platysoma cylindrica (Paykull)	Michigan: K, A, W, Roscommon Co. (R)					10			
Platysoma parallelum Say	Michigan: K, A, R, W, Ingham Co. (I)					10			
Diptera: Dolichopodidae									
Medetera sp.	Michigan: K, A, R					10			
Hymenoptera: Braconidae	Michigan: K, A					5			
Hemiptera: Anthocoridae	Michigan: K, A					5			

(Use additional sheets if necessary)

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