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dissertation entitled

AN EVALUATION OF FORMICA EXSECTOIDES FOREL AS A
POTENTIAL BIOLOGICAL CONTROL AGENT OF INSECT PESTS
OF PINES

presented by

Nancy J. Campbell

has been accepted towards fulfillment
of the requirements for

Ph.D degree in Entomology

Major professor

Date 5/31/90

AN EVALUATION OF *FORMICA EXSECTOIDES* FOREL AS A POTENTIAL BIOLOGICAL CONTROL AGENT OF INSECT PESTS OF PINES

By

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A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Department of Entomology

1990

ABSTRACT

AN EVALUATION OF F. EXSECTOIDES FOREL AS A POTENTIAL BIOLOGICAL CONTROL AGENT OF INSECT PESTS OF PINES

By

Nancy J. Campbell

This study was designed to explore the potential of utilizing the predaceous ant, Formica exsectoides Forel as a biological control agent of insect pests of young pine plantations.

The effects of ants on the redheaded pine sawfly, jack pine budworm, gypsy moth and white pine weevil were examined. F. exsectoides readily preyed upon redheaded pine sawflies that were placed on small pine trees around ant mounds. The ants responded differentially to three instars of sawfly larvae.

F. exsectoides removed both second- and fourth-instar jack pine budworm from experimental trees. The budworm's silk chamber decreased ant predation. The ants also reduced the population of budworm larvae that were naturally occurring in mature jack pine stands. The amount of defoliation of jack pines in both the overstory and understory decreased as the number of ant mounds per hectare increased.

F. exsectoides preyed upon gypsy moth larvae, pupae, and adults but did not prey on eggs. Increasing the distance of pupae from the ant mound negatively affected ant predation.

The number of adult white pine weevils was reduced by ants foraging on small jack pine trees. The ants indirectly influenced adult weevils by disrupting their feeding behavior, causing the weevils to move to new feeding locations on the trees. The presence of aphids increased ant predation for all of the pests examined.

A pine-trefoil-ant simulation model was developed that predicted defoliation of pine trees in the presence and absence of ants. Model simulations showed that as the number of ant colonies per hectare increased, the amount of defoliation decreased. The model also showed that as the soil type improved, the maximum defoliation decreased independent of the number of ant colonies per hectare.

Portable ant nests were designed and field tested in a young stand of red pines located approximately 150 miles from the parent colonies. Several of the colonies survived in the artificial nests for over six weeks.

ACKNOWLEDGEMENTS

I am particularly indebted to Gary Simmons for his confidence, generosity and support. I am also grateful to Cathy Bristow and George Ayers for the encouragement and assistance they provided during my doctoral program.

I am also grateful to Louis Wilson and Leah Bauer for serving on my guidance committee.

In addition I wish to acknowledge Stuart Gage for his assistance in developing the simulation model. The simulation was part of the requirement for the Systems Science course, 843. In particular I wish to acknowledge several students from my class team who made the development of the model possible: Jim Seyler, Ruth Shultz, Kate Thompson, Angela Vandemehr and Martha Whitaker.

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General Thesis Introduction

This study represents the first steps in the process of exploring the potential of utilizing the predaceous ant, *Formica exsectoides* Forel, as a biological control agent of insect pests in young pine plantations.

Predaceous red wood ants, *Formica rufa* group, have been exploited in intensive forestry culture in Europe for over 150 years (Adlung, 1966). Five species of ants have been studied extensively, *F. polyctena* Foerst, *F. rufa* (L.), *F. lugubris* (Zett.), *F. aquilonia* (Yar.), and *F. nigricans* (Em.). Of the five, *F. polyctena* is considered to be the most valuable as a biological control agent.

Studies that have been conducted in North America have disclosed that carpenter ants in the genus *Camponotus* and mound-building ants in the genus *Formica* both feed on insects of economic importance in forestry (Finnegan et al., 1978; Campbell and Torgersen, 1982; Torgersen and Mason, 1987). Recently, ants in the genus *Solenopsis*, have proved to be valuable in the reduction of insect pests in agricultural systems (Tedders et al., 1990, Eskafi and Kolbe, 1990).

Predaceous ants are capable of removing a large number of insects from trees and shrubs in the forest ecosystem. Wellenstein (1952) counted eight million insects taken as prey by one medium sized nest of red wood ants during one season. Seventy-six percent of the scientists that were polled by Wellenstein (1954) regarded the merits of red wood ants as biological control agents to be positive. However, the remaining 24 percent regarded red wood ants to have a negative effect on the forest ecosystem as a whole. Three of the primary reasons of why the value of red wood ants as biological control agents continues to be disputed are: 1) for the ants to be effective they must be present in very large numbers which could result in damage to the ecosystem (Schrotter, 1959), 2) ant attendance of certain aphid species is known to increase the population of aphids to a level which is detrimental to the health of certain types of trees (Debach et al., 1951; Wellenstein, 1961), and 3) very little research has been done that encompasses more than one or two components of the ant-aphid-insect pest-tree ecosystem.

Mutualism between ants and homoptera is a common phenomenon (Way, 1963). The mutualism may have a positive or negative effect on the forest ecosystem as a whole depending upon the density of the aphids, the type of tree that is infested, and the effects of the ant attendance on the natural enemies of the aphids. Kloft (1959) and Bradley and Hinks (1968) found that aphid colonies were not randomly distributed but were more numerous near ant mounds. Whether the increase in the number of ants on trees resulted in higher ant predation on herbivores is not clear from these studies.

The jack pine budworm, *Choristoneura pinus* (Freeman), redheaded pine sawfly, *Neodiprion lecontei* (Fitch) and white pine weevil, *Pissodes strobi* (Peck) can be serious pests of young pine plantations (USDA, 1983). The gypsy moth, *Lymantria dispar* (L.), prefers to feed on deciduous trees such as oak and aspen, but will feed on conifers when growing with hardwoods. Ants have been recorded feeding on the larvae of jack pine budworm and western spruce budworm, *Choristoneura occidentalis* Free. (Allen et al. 1970; Jennings, 1971; Campbell and Torgersen, 1982). Goesswald (1940a) recorded ants preying on colonies of the redheaded pine sawfly, and found that trees closer to mounds of *F. polyctena* had less defoliation. Ants also prey on eggs and gypsy moth larvae (Weseloh, 1988; Brown and Cameron, 1982).

F. exsectoides is a native North American mound building ant occurring primarily in the eastern United States. It belongs to the *Formica exsecta* group which is a close relative to the *Formica rufa* group. Workers of *F. exsectoides* have been observed feeding on a variety of coniferous forest pests including certain species of beetles, flies, and Lepidoptera larvae. *F. exsectoides* foragers tend aphid colonies for honeydew, but will take dead or injured aphids back to the mounds as food (Andrews, 1929). Mounds of *F. exsectoides* are widely distributed in jack pine stands in the central part of the lower peninsula of Michigan. These jack pine stands support fluctuating populations of jack pine budworm and sawflies. Gypsy moths can be found in jack pine stands that have an oak and poplar component.

This study examined the interactions between the predaceous ant, *F. exsectoides*, aphids found on jack pine, *Cinara* sp., and four insect pests of pines: jack pine budworm, redheaded pine sawfly, white pine weevil, and the gypsy moth. The effects of ant protection of jack pines resulting from predation on the jack pine budworm was also measured.

In order to further explore the complex interactions between the ants, aphids, insect pests, and trees, a simulation model was developed. The model was used to identify several areas where additional research was needed, such as ant predation switching values. Very little information is available on the mechanisms underlying prey switching in ants between insect pests and honeydew produced by aphids and other homoptera. This prompted a study where the influence of internal colony conditions on prey selection was examined in both the laboratory and field during the following year. These studies are on going, and therefore are not included in this thesis.

The final portion of this study dealt with managing colonies of *F. exsectoides* in portable ant nests as a biological form of insect control. Fruit growers in China have been manipulating colonies of predaceous ants for many years by overwintering the nests and strategically placing them in the field in the spring (Huang and Yang, 1987). In North America, *Formica* spp. have been transplanted into forests to provide protection (Bradley, 1972; Finnegan, 1975; Kloft et al., 1979).

Literature Review

Among the insects, many ants are well known for their predatory habits. Ants are carnivorous and polyphagous, apparently inheriting their predatory nature from solitary wasp ancestors (Wilson, 1971). The predatory habits of ants were recognized thousands of years ago as ants are now thought to have been the first animals exploited for the control of insect pests (Huang and Yang, 1987). In 304 A. D., the benefits derived from the yellow citrus ant, *Oecophylla smaragdina* Fabr., for the protection of oranges was noted (Huang and Yang, 1987). The citrus ant, has been used to protect oranges, tangerines, lemons, and pomelos in parts of China. For a brief period of time during the rise of use in organic insecticides this practice was abandoned. Pesticide resistance and the rising cost of chemicals prompted orange growers in a Huangtien village of China to reestablish and once again expand colonies of the predaceous ant in citrus orchards. Today, ants are still utilized in China and other parts of the world in biological control and integrated pest management programs for a variety of insect pests in agriculture and forestry (Majer, 1986). Among the attributes ants possess as biological control agents are: 1) diversity and abundance, 2) responsiveness to spatial variations in prey density, 3) persistence in spite of fluctuations in their food supply, 4) effectiveness not limited by predator satiation, 5) in addition to predation, ants can indirectly reduce insect populations by disrupting feeding and oviposition, and 6) potential for manipulation to maximize contact with pests (Risch and Carroll, 1982). A recent surge in basic ecological research exploring mutualisms between ants and trees, and ants and their tended aphids has fueled a renewed interest in pursuing knowledge that could lead to further exploitation of ant species in plant protection programs, particularly in North America (Gotwald, 1986).

Ants have been recognized as performing a beneficial function in European forests for over 150 years (Adlung, 1966). Ants of the *Formica rufa* group, particularly *Formica polyctena* Foerst, have been propagated and distributed in artificial colonies in intensively managed European forest plantations (Goesswald, 1951). Large nests of *Formica* spp. have been reported to feed on from 65,000 to 100,000 caterpillars per day (Gotwald, 1986). Their feeding habits, aphid mutualisms and effects of aphid feeding on trees has been the focus of several European studies (Muller, 1956a, 1956b, 1958; Kloft, 1953, 1959).

Spurred by the successful exploitation of ants in European forests, several studies of native and introduced ant species have been conducted in North American forests. Perhaps the first direct reference to ants and forest insects is a note by Green and Sullivan (1950) that indicated predation by ants on the forest tent caterpillar, *Malacosoma disstria* Huebner. Later, a study by Sanders (1964) in New Brunswick forests explored the biology of three species of carpenter ants, *Camponotus herculeanus* (L.), *C. pennsylvanicus* (DeGeer), and *C. novaboracensis* (Fitch). Although much of the study was devoted to biology and gallery construction, mention was made of workers bringing caterpillars back to the nests. Bradley and Hinks (1968) studied ants and their attended aphids in Manitoba. They found three species of Myrmicinae, one species of Dolichoderinae, and 17 species of Formicinae which tended up to four species of aphids on jack pine, *Pinus banksiana* (Lambert). Two ant species were particularly common, *F.*

obscuripes Forel and *Dolochoderus taschenbergi* (Mayr). They tended several aphid species in the genus *Cinara.* The researchers noted how the trees benefitted from aphid tending through removal of defoliating insects by the ants. Bradley and Hinks (1968) observed that aphids were able to withdraw large amounts of sap from the jack pines without seriously injuring the trees, however, no direct measurements of the effects of aphids feeding on the trees was done. Subsequent studies showed these species of ants were present in areas of natural reproduction but absent in plantations.

In order to better exploit the predaceous activities of these ant species, Bradley (1972) explored the transplantation of nests and proximity of placement. He observed good establishment of nests and found little relocation of nests placed 20 m apart, while those placed within 5 m consistently moved apparently to accommodate the larger territory size of the colonies. The feeding and foraging behavior of *F. obscuripes* was further explored by Hill (1969) and Headings (1971) in jack pine plantations in Michigan. Hill (1969) found the ants preying on European pine sawfly, *Neodiprion sertifer* (Geoffroy) and the jack pine budworm, *Choristoneura pinus* Freeman, along with a broad group of insect families as they became available throughout the summer season. He further noted that humidity and distance from the nest or mound were influential in determining the number of ants foraging on a given tree. Headings (1971) showed that species of Aphididae and Miridae were more abundant on jack pine trees where *F. obscuripes* foraged; species of Cercopidae, Coccinellidae, Tortricidae (particularly jack pine budworm), Plutellidae, Psocoptera and Neuroptera were significantly fewer on trees where the ants did not forage. The general activity of *F. obscuripes* workers decreased with increased temperature and rainfall.

Several additional studies have dealt with the role ant predation plays in the population dynamics of budworm species: jack pine budworm, *C. pinus* Freeman, spruce budworm, *C. fumiferana* (Clem.), and western spruce budworm, *C. occidentalis* Freeman. Allen et al. (1970) and Jennings (1971) noted predation by *Formica* and *Camponotus* species on the jack pine budworm in Michigan and Wisconsin, respectively. McNeil (1978) observed reduction in spruce budworm populations by *F. lugubris* Zetterstedt, a species introduced from Italy, and that spruce budworm was the most common prey in Quebec. Campbell and Torgersen (1982) investigated 179 potential natural enemies of western spruce budworm in Oregon. Using "planted" pupae, they observed that 85% of the pupae were destroyed by foraging ant species from two genera: *Formica* and *Camponotus*. Youngs and Campbell (1984) investigated ant species feeding on western spruce budworm pupae in Oregon and Montana. A number of species of *Formica* and *Camponotus* were found to feed on budworm pupae. Related studies further disclosed the importance of ants in the population dynamics of budworm (Campbell et al. 1983, 1985). Campbell also studied ants in connection with spruce budworm in the east.

Recent studies have shown ants to be important in controlling leaf miner populations. Sato and Higashi (1987) showed that mine density on oaks was always lower on ant-rich trees than on trees where the ants were not as common. Faeth (1980) showed that ants contributed significantly to the mortality of the leaf-miner, *Ericraniella* sp.. These studies as well as several others showed consistently that smaller ants were the primarily responsible for the mortality of leaf miners. Wong et al. (1984) and Wong and Wong (1988) found that fire ants, *Solenopsis geminata* (F.), played an important role in reducing populations of Mediterranean Fruit Fly, *Ceratitis capitata* (Wiedemann), and the Oriental Fruit Fly, *Dacus dorsalis* Hendel. The fire ants preyed on fruit fly larvae in the laboratory and on pupae which were buried underneath the soil at the base of guava trees. *Solenopsis inivicta* Buren, has also been reported to be an important natural control of larval boll weevil (Sterling, 1979), and pecan weevil larvae, *Curculio caryae* (Horn), in Georgia (Dutcher and Sheppard, 1981).

The introduction of ant species into new habitats for the protection of forest trees has been tried in North America, but the success of such introductions has required some protection of the introduced colonies from predation by other ants and birds. Finnegan (1975, 1977) brought two species of *Formica* into Quebec one from Italy, *F. lugubris*, and one from Manitoba, *F. obscuripes*. In 1977, Finnegan concluded that the ant was well established and expanding in Quebec (Finnegan, 1977). In 1978, McNeil studied the seasonal predatory activity of several of the mounds that were transplanted into Quebec. Prey brought back to the nest by the ants included insects in the orders, Lepidoptera, Hymenoptera, Diptera, Coleoptera, and Hemiptera. Lepidopteran insects represented 58 percent of the total prey brought back with spruce budworm larvae being the most abundant insect in the sample. The estimated total number of larvae brought back to the nest was 2,175/day. A series of studies was also done with *F. integra* Nylander, a native "red wood ant" of oak-hickory forests of Georgia. This species was found to be polygenous (have multiple queens) and capable of feeding on a number of forest insect pests (Wilkinson et al. 1978; Kloft et al. 1979). Nest transplantation trials resulted in colonies persisting for up to 14 weeks with aphid tending and predation occurring on pest species. A native carpenter ant eventually killed out the colonies as was predicted in earlier laboratory experiments (Wilkinson et al. 1980). Room (1973) cautioned that attempts to exploit non-native species might not be as good as using native species primarily because of difficulties in establishment.

Relations Between Ants and Aphids and their Effect on Trees

Honeydew constitutes the most abundant type of food collected by many species of ants (Carol and Janzen, 1973; Skinner, 1980). However most ants also require protein usually in the form of insect prey to complete their diet. Homoptera benefit by ant attendance in a number of ways. Ants offer protection to homoptera from natural enemies and remove waste. Certain species of ants transport Homoptera to feeding sites (Way, 1963).

The effects of the interactions between ants and aphids in relation to biological control can be either positive or negative depending on a number of factors. Ant attendance of certain species of Homoptera interferes with the control exerted by the natural enemies (Flanders, 1943; Samways et al., 1982). Haney et al. (1987) monitored the activities of the Argentine ant, *Iridomyrmex humilis* (Mayr), in three citrus orchards for two years and found that the presence of the ant inhibited effective predation on the citrus red mite, *Panonychus citri* (McGregor). Fritz (1982) found significantly fewer predators of membracids on branches of black locust with ants than on branches where ants were absent. Protection of aphids by ants can negatively affect plant health and reproduction also when the potential prey are plant pollinators or parasitoids of insect herbivores. Bronstein (1988) found that ants readily attacked four species of wasps associated with fig trees. One of the species of wasps is an obligate pollinator of the fig and predation impacted successful pollination of the plant.

Other studies have shown that ant attendance of certain Homoptera does not interfere with the natural control of the Homoptera. Flanders (1943) found that the activities of the parasite, *Coccophaguss capensis* Comp., on black scale were not inhibited by ants. He later observed heavy infestations of the black scale, *Saissetia oleae* (Oliver), that were attended by ants that were completely parasitized (Flanders, 1951). Stary (1966) concluded from a study measuring aphid parasitism of several species of aphids, that aphid parasitism was not negatively effected by the presence of ants. He further suggested that in certain cases, the ant x aphid x parasite association effectively limited the population density of aphids.

Green and Sullivan (1950) suggested that ant predation is often a result of defence of aphid colonies. They observed ants removing a total of 1,800 forest tent caterpillar larvae, *M. disstria*. When young larvae passed through an aphid colony this immediately invoked an attack by the ants. They observed that when only one to two ants were tending aphids they would often kill the larvae and leave them or push them off the branch. When more than two ants were present they would kill the larvae and take them back to the nest. Goldenrod stems, *Solidago* spp., that contained membracids

Publilia concava, tended by ants, *Formica* spp., escaped defoliation by two species of beetles, *Trirhabda virgata* Leconte and *T. borealis* LeConte, and showed greater height increment and seed production than those stems that did not contain membracids (Messina, 1981). He suggested that plant protection may also be important for membracids because the ants insure host quality by driving away other defoliators. Colonies of Homoptera may also have positive effects on the plants by serving as a nucleus of food to attract natural enemies (Flanders, 1951).

Ant attendance of certain species of Homoptera is known to increase the population of Homoptera to economical injurious levels. Flanders (1951) suggested that when an ant-attended Homopteran population is large, it can be very destructive to the plant. Severe infestations of the black scale have been reported to be correlated with the presence of the Argentine ant (Compere, 1940). Increases in the brown soft scale, *Coccus hesperidum* L., due to ant attendance can cause the population of the scale to reach economically important outbreak numbers (Debach et al., 1951). Fruit growers will often band their trees with a sticky barrier substance such as grease to reduce infestations of aphids (Bremner, 1931). However, Samways et al. (1982) found that only 2 out of 123 species of ants recorded in South African citrus orchards were important in precipitating outbreaks of Homoptera. The other species of ants were relatively harmless and only caused isolated hompoteran outbreaks. They suggested that the recommendation to control ants in citrus orchards is probably unfounded in most situations because most ants are beneficial. An extensive survey of ant-aphid associations by Samways et al. (1982) showed that even when ant attendance elevated homopteran levels to economics importance, the predaceous activity of ants outweighed the occasional damage to shoots of citrus trees.

Determining if an ant-aphid association is positive or negative may also depend upon the type of tree affected. Dixon (1971a) suggested that with the exception of the spruce aphid, *Elatobium abietinum* (Walk.), aphids generally do not cause extensive defoliation of their host trees except when they are present in very large numbers. Bradley and Hinks (1968) observed that aphids are able to withdraw large amounts of sap from jack pines without seriously affecting the trees. They suggested that this relationship allowed the aphids to maintain themselves on the same trees or or in the ant's foraging territory for several years without depleting their food source. Ants had a positive influence on the survival of mountain birches, *Betula pubescens* spp. *tortuosa* (von Ledebour) Nyman), during an outbreak of the Lepidoptera, *Oporinia autumnata* (Borkhausen), despite the ant's association with the aphid, *Symydobius oblongus* (von der Heyden). Laine and Niemela (1980) suggested that the cost of the ants eating honeydew may limit the growth of individual birch trees for several years, but may perhaps insure its existence over defoliator outbreaks.

Banks and Macaulay (1967), found that bean plants without aphids yielded 56 seeds per plant, those with aphids but no ants yielded 17, and those with aphids and ants yielded only 8. Dixon (1971a) found that the aphid, *Drepanosiphum platanoides* (Schr.), reduced leaf size in sycamore by as much as 40 percent, and the production of stem wood by up to 62 percent. Feeding by aphids affected the growth of lime saplings, *Tilia vulgaris* Hayne, very little above ground but resulted in very poor root growth (Dixon, 1971b). The growth of the aphid infested lime saplings was limited by the reduced availability of photsynthate.

After reviewing the literature, conducting studies and performing experiments with ants, both Youngs (1983) and Majer (1986) encouraged further research on utilizing predaceous ants in forest ecosystems. Majer provides specific guidelines for studying potential ant species as biological control agents. Youngs suggests pursuing studies of both *Formica* species and *Camponotus* species to gain a better appreciation of their potential for exploitation in biological control under forest conditions.

APPROACH

Majer (1986) provided a formalized procedure for selecting and developing ants as suppression agents for pest insects. This is the approach we will follow. Stage 1 requires definition of the pest or the pest complex. To do this adequately, the biology of the pest insect(s) and the interaction of the pest insect(s) with the crop needs to be determined. Stage 2 is the process of identifying ant species that have potential as agents of pest insect suppression. Stage 3 is the investigation of whether or not an ant species identified in Stage 2 actually has some suppressing effect on the pest or pest complex identified in Stage 1. Stage 4 is entered if and when a beneficial ant species has been identified and involves the manipulation of the ant species to favor its utilization. Stage 5 is the point at which field trials are conducted to evaluate the practicality and efficacy of an ant species and the promising manipulations identified in Step 4. At this point it is possible for the ant-based biological suppression technique to be combined or integrated into a wider array of pest management methods. Lastly, grower recommendations are made with instruction about how to apply the ant-based suppression technique. This stage is implemented with the caution that following its incorporation in management, continued vigilance is needed to identify new pest problems that may require modification of the scheme (just as in any other approach to pest insect suppression). Further development of the "Approach" section will utilize the first 3 "stages" in Majer's (1986) procedure:

STAGE 1 - Identifying the Pest Complex.

Our focus in this program is on insect pest problems associated with young pines in the states and provinces of the Great Lakes Region. Red pine, *P. resinosa* Aiton., and jack pine are utilized for pulp and lumber and are planted extensively throughout the region. A third species, Scots pine, *P. silvestris* L., is the dominant conifer of an extensive Christmas tree industry. Scots pine Christmas trees are typically grown over a 7 to 10 year rotation, while jack pine and red pine are managed on rotations exceeding 50 years for pulp and longer for timber. Despite the differences in rotation lengths, the primary insect pests of these species affect the trees most when they are small, very commonly when trees are less than 10 to 15 years of age. The four insect pests used in this study were: 1) gypsy moth, *Lymantria dispar* (L), 2) jack pine budworm, *Choristoneura pinus* (Freeman), 3) redheaded pine sawfly, *Neodiprion lecontei* (Fitch), and 4) white pine weevil, *Pissodes strobi* (Peck).

Life Cycle, Impact and Control of the Gypsy Moth

The host complex of the gypsy moth includes over 300 kinds of trees and shrubs. The favored hosts of the gypsy moth are oak, aspen, apple and willow. The gypsy moth generally does not feed on pines when other favored host trees are readily available. However the gypsy moth can be a problem in stand of pines that are interplanted with hardwoods or near a stand of susceptible trees.

Hatch and larval activity are both strongly influenced by temperature (Leonard, 1981). As larvae emerge from egg masses they spin a silk thread. If the temperature is below 7^{o} C, the larvae will remain on the egg masses. When the temperature increases, they begin to move to the tops of the trees and disperse on wind currents. During the first three instars, the larvae remain on the leaves at all times and feed both during the day and night. During later larval development, they follow a daily migration pattern where they move down the trees during the day, and returns to feed only at night. The gypsy moth remains in the pupal stage for approximately 2 weeks (Leonard, 1981). The male moths emerge several days before the females. The males are strong fliers while the females are relatively flightless. Egg laying begins shortly after the females emerge.

The gypsy moth is considered not only to be a serious pest of forests, but can also be a serious nuisance to people. Control of this pest in Michigan is usually limited to areas that contain human dwellings or high-value timber. Tree mortality can occur after two to three years of repeated, heavy defoliation. Certain species of oaks, such as white oak, often incur the highest percentage of mortality; up to 50 percent of dominant and codominant trees (Leonard, 1981). People find it difficult to cope with the gypsy moth because of the large size of the mature caterpillars, constant droppings, and often high populations. This pest has the greatest impact on humans and their outdoor activities during the months of June and July.

The gypsy moth can be adequately controlled with properly timed applications of the bacterial insecticide, Bt., *Bacillus thuringiensis*. Other insecticides are also used to control this pest. Mechanical techniques such as removing the egg masses, are also recommended. Both native and introduced parasites can significantly impact gypsy moth populations. Predators such as ground beetles (Weseloh, 1988), birds (Brown and Cameron, 1982; Furuta and Koizumi, 1975) and small mammals are thought be effective at low population densities of gypsy moth. Campbell et al. (1975) found that the white-footed mouse, *Peromyscus leucopus*, was the major source of late-larval and pupal mortality. Parasitism from, *Parasetigena silvestris*, was a major mortality factor during the larval stage at low-density populations (Elkinton and Liebhold, 1990). At high population densities, the virus, NPV, Nucleopolyhedrosis virus, can cause the population of gypsy moths to collapse (Campbell, 1967; Doane, 1970).

Life Cycle, Impact and Control of the Jack Pine Budworm

The hosts of the jack pine budworm include, Scots, red, jack and Austrian pines. The jack pine budworm overwinters as first-instar larvae. Depending upon environmental conditions, the small larvae break diapause at the same time the male staminate flowers of jack pines begin opening. The larvae disperse before settling down to begin feeding. The larvae feed on the flowers and then move to new shoots to continue feeding (Dixon, 1961). Besides feeding on the foliage, the larvae also use it to build shelters. Larvae pupate in these shelters from early to mid summer. After approximately one week, the adults emerge. Mating and oviposition occur shortly afterward. In Michigan, adult jack pine budworms are present from late June to early August (Graham, 1935). The females lay egg masses, containing approximately 50 eggs on old growth needles throughout the crown.

The jack pine budworm can cause tree mortality, reduced growth and pollen production, and top kill (Elliot, 1985). High populations of budworm may result in up to 90 percent mortality of intermediate and suppressed trees, and 33 percent mortality of merchantable trees (Batzer and Millers, 1970). Tree mortality is more likely to occur when trees are stressed by other environmental or biological factors, such as drought or other defoliators (Batzer and Millers, 1970).

When larvae and pupae are concealed in their feeding shelters, they are difficult to control (USDA, 1983). Spraying with Bt. is recommended when the larvae disperse in the spring. Silvicultural techniques are also effective in controlling the jack pine budworm. Generally, young well stocked stands are resistant to heavy jack pine budworm attacks (Batzer and Jennings, 1980).

Natural enemies are thought to be important at low budworm densities. The parasites, *Apanteles fumiferanae* Viereck, and *A. morrisi* (Mason), commonly parasitize jack pine budworm larvae in Michigan (Elliot et al., 1986). Mortality of small larvae can also result from fall dispersal. Spring dispersal can significantly impact larger, third-instar budworm. The population of larger larvae and pupae can be reduced by parasites (Batzer and Jennings, 1980).

Life Cycle, Impact and Control of the Redheaded Pine Sawfly

The hosts of the redheaded pine sawfly are red, jack and other pines, and they occasionally attack spruce (USDA, 1983). Redheaded pine sawfly usually have one generation per year in Michigan. The sawfly overwinters as prepupae in cocoons in the duff or topsoil beneath its host. Some pupae may remain in diapause over several seasons. Pupation usually occurs after a period of warm weather and the adults emerge in approximately two weeks (MacAloney and Wilson, 1964). In Canada and the Lake states, adults emerge in June. The females lay approximately 120 eggs in clusters on the current or previous year's foliage. In three to five weeks, the larvae hatch and begin feeding in colonies of just a few to over 100 insects. The larvae feed for five to six weeks, during the months of July and early August in Michigan. Early instars feed on the outer tissue of the needles while mature larvae consume the entire needle (Averill et al., 1982). Mature larvae drop from the host tree and spin cocoons in the duff or topsoil.

The most susceptible hosts are trees less than 15 feet tall (MacAloney and Wilson, 1964). Jack and red pine are preferred hosts in Canada and the Lake states. When foliage is scarce, the larvae will consume the bark. Moderate to heavy defoliation usually results in reduced height. Complete defoliation will usually kill young jack and red pines especially when they are grown on poor sites (Averill et al., 1982). Many young trees are deformed or killed during an outbreak of this pest.

In the Lake states, the redheaded pine sawfly reaches outbreak levels approximately every five to eight years (Averill et al., 1982). Natural control factors that impact high population levels include, rodents, extreme temperatures, and disease. Hanski and Parviainen (1985) found that small mammals destroyed 70 percent of the population of European pine sawfly, *Neodiprion sertifer* (Geoffroy), cocoons at poor sites. A correlation between predation rate and the number of predators was not found at fertile sites. They suggested that this may have occurred because of the abundance of alternative prey.

In Southern Ontario, most outbreaks of sawflies are initiated by the discovery of a previously uninfested pine stand that contains few natural enemies (Lyons, 1977). Averill et al. (1982) suggested that the most effective method of controlling the sawfly is through prevention. The first step in this process is to avoid planting pines in high-risk areas, such as adjacent to hardwoods on poor soils.

When the population is scattered, mechanical removal of the entire colony is recommended (USDA, 1983). When the population is high, chemical control is often necessary.

Life Cycle, Impact and Control of the White Pine Weevil

The hosts of the white pine weevil include all pines, most species of spruce and occasionally fir (USDA, 1983). The adults overwinter in the duff layer beneath host trees. Adults emerge and begin to feed on the terminal growth, below the current year's bud usually in March and April (USDA, 1983). The females lay their eggs beneath the bark shortly after mating. Larvae emerge and feed on the cambium. As the number of larvae increase, they aggregate and form a ring around the terminal, causing girdling. The leader usually dies from a weevil attack and will curve over to one side. This "shepherds crook" is a good indicator of weevil damage in plantations or natural stands of pines. Larvae pupate in woody, chip cocoons in the xylem. The adults remain in these pupation chambers for several weeks before emerging. Adults feed on the new growth until environmental conditions force them into overwintering.

The white pine weevil can be an important insect pest in both plantations and natural stands of pines and occasionally spruce (USDA, 1983). In New York and New Hampshire, approximately 70 to 90 percent of all eastern white pines had been damaged by the weevil before reaching the age of 15 (Graham, 1926). Weevil damage often results in poor quality lumber that is not acceptable for sawlogs (Dirks, 1964). Weevils were found in every county in the Lower Peninsula of Michigan in 1979 (Michigan Forest Pest Report, 1979). In 1987, weevil damage in the lower peninsula continued to increase with an average of 43 percent of the leaders damaged (Michigan Forest Pest Report, 1987). Damage occurs as either a reduction in volume or quality of lumber (Plummer and Pillsbury, 1929). Weevils rarely kill mature trees.

Two of the more commonly recommended control methods for the white pine weevil are tip pruning and chemical control. Predation and parasitism are limited to insects that can mine in the cambium of shoots to locate weevils in the larval or pupal stage. Eggs of the parasite, *Lonchaea corticis*

Taylor, are laid in the feeding and oviposition punctures made by *P. strobi* and occasionally directly on the eggs (Harman and Wallace, 1971). Alfaro and Borden (1980) found that each *L. corticis* larva consumes almost 3 weevil pupae.

Silvicultural techniques such as the manipulation of the overstory or understory are very effective ways to control the weevils (Graham, 1926). Planting resistant stock is also recommended to control the white pine weevil (USDA, 1983).

1). STAGE 2 - Identifying Desirable Ant Species.

Finnegan (1971), while searching for potential ant species that might be exploited in forests, developed a list of desirable criteria: 1) *Size*. Large size of individual ants is helpful but can be offset by large colonies where additional workers can be recruited to help otherwise small workers; 2) *Food requirements and nest populations*. Those species that have large nests and developing broods with insect food needs are thought to place stronger demands per unit area of land on insect-based food items; 3) *Colonial nests*. Those species that have multidomous colonies or produce satellite colonies over adjacent areas are thought to be helpful from the point of view that they would increase in numbers and separate sub-colonies would be compatible; 4) *Queens*. Longer-lived colonies are thought to be those that have multiple queens or a queen replacement system; 5) *Ant-Homoptera relationships*. Those ant species that tend and encourage undesirable Homoptera such as aphids are considered less desirable. In addition to

Finnegan's set of desired criteria, Majer (1986) added: 6) *Species habitat range*. Those species with a broad habitat range might be more amenable to promotion in areas where they did not already exist. In addition to habitat range *per se*, broad tolerance of wide ranging physical factors such as temperature, moisture and solar radiation were also considered desirable, and 7) *Dominance hierarchy*. Useful species are those which are not likely to be outcompeted by other ants found in association with the crop.

Finnegan (1971) surveyed the existing literature and records of about 80 species of ants indigenous to Quebec and concluded that none of the species present possessed enough of the characteristics he considered desirable for exploitation against forest pest insects. In his discussion, however, he indicated species in the genera *Camponotus* and *Formica* possessed many of the desired characteristics except polygyny or the quality of having multiple queens. Finnegan stated "That the sole queen must always be included and kept in good condition, or the nest will perish." This prompted the importation of the non-native species, *F. lugubris* from Italy and *F. obscuripes* from Manitoba that possessed multiple queens.

Of the two species brought to Quebec, *F. obscuripes* seems to have established well. Later studies by Bradley (1972) indicated colonies of *F. obscuripes* could be transplanted, and after a period of reorganization lasting 2-4 days, colonies would re-establish without difficulty. Work by Hill (1969), Headings (1971) and Bradley (1972) provided additional information on general biology, colony size estimation, propagation techniques, aphid relationships and predator-prey relationships. Other studies done in other ecosystems have also shown *F. obscuripes* to prey on forest pests of interest

(Youngs 1983; Youngs and Campbell, 1984). Thus, a species from the genus *Formica*, would seem a logical choice to complete Stage 2 in Majer's selection procedure. The ant species used in this study is the Allegheny mound ant, *Formica exsectoides*.

The Life History of *F. exsectoides*

Pierson (1922) and Haviland (1947) described the life cycle and seasonal history of *F. exsectoides*. Depending upon seasonal cues and geographical location, *F. exsectoides* hibernates in burrows deep below the mound from approximately October to April (Haviland, 1947). Temperature appears to be the most important factor in determining the length of hibernation. Queens begin to appear in late April. A large number of small, white elliptical eggs can be found in the mound in April and egg laying continues throughout the warm season in the field (Pierson, 1922). The length of the egg stage in the field appears to be approximately 2 weeks. Larvae of all sizes were found in Maryland in the mound in May (Haviland, 1947). Large larvae develop into reproductives and smaller larvae become workers. Throughout the season, most of the colonies' activities occur within the top 6 inches of the mound proper. The adult workers move brood throughout the mound depending upon both the temperature and humidity. Pupae are present in the mound from approximately June through September. The mature larvae spin, white, papery cocoons and remain in this stage for about 2 weeks. The last reproductives are usually seen in mid-July in Maryland. In general, a large number of queens and kings swarm at the same time and the kings die soon after flight. Some of the queens are seized by workers who immediately start to build a new nest and begin colony formation (Pierson, 1922). There are several generations per season and queens of some species of ants have been known to survive for up to 15 years (Pierson, 1922). By August, colony activity has begins to decrease and by September some of the workers are down below the mound entering into hibernation. Only delated queens and workers are found in the mound during hibernation. The ants do not store food of any type, including live aphids or aphid eggs in the mound during this period.

Haviland (1947) reared *F. exsectoides* in the laboratory from the egg to the adult stage. In 30 artificial nests, eggs hatched anywhere from 10 to 27 days, with an average of 19.4 days at 70° F. In nine of the nests, it took 21 to 53 days, with an average of 37.1 days for complete larval development at 70° F. The pupal period lasted an average of 26.25 days at 70° F. The total time required from the egg to the callow stage ranged between 54 to 107 days, with an average of 75 days.

Growth of Mounds of *F. exsectoides*

Early work detailed the distribution and growth of mounds of *F. exsectoides* in pine plantations (Pierson, 1922; Andrews, 1925, 1926; Haviland 1938). The mounds occur in groups fairly close together and their size is a fairly accurate index to their age (Pierson, 1922). Examinations showed that galleries extended 20 feet or more from nests and penetrated to a depth of 6 feet. The mounds are built largely of coarse sand supported somewhat by pine needles and twigs and a one to two inch thatch covers the mounds and provides protection from the elements. The mounds in a group are usually connected to other mounds nearby by a network of tunnels. One of these mounds is usually the mother mound and the others are termed subsidiary mounds. Haviland (1938) showed that a mound 19 inches high contained 237,103 workers and 1,407 queens. They estimated that 12 million ants were present on 10 acres and averaged seven mounds per acre.

Andrews (1925) followed the growth of several mounds of *F. exsectoides* over 19 years. The growth of the mounds were not constant but fluctuated over this time. In the early years, growth is very slow and increases in rate in later years. However, Andrews concluded that the rate of growth of a mound of *F. exsectoides* is strongly influenced by the individual character of each community under its own complex environment.

In general, the survival and growth of *F. exsectoides* is dependent upon certain stages of forestation (Andrews, 1926). Shading by old growth trees appears to be an important factor in the survival of mounds of *F. exsectoides*. In the natural succession of forests, *F. exsectoides* thrives in areas in which the forest is temporarily interrupted or destroyed by fire or wind. Therefore the length of time mounds of *F. exsectoides* can be found in a forest appears to correlate well with the time required for a tree to reach maturity, 30 years or so. Haviland (1938) could not find a correlation between the dispersal of ant mounds and several factor she studied (distance from the trees, height of trees, presence of undergrowth, and the amount of sunlight). However, two out of the three locations where new mounds were found, were on the edge of a clearing where the light intensity was the greatest.

Relationship with Homoptera and Other Insects

Headley (1943) noted workers of *F. exsectoides* tending green aphids on trees. Haviland (1947) observed the ants tending treehoppers and aphids during two consecutive summers. No evidence was found that the workers feed on the aphids. In 1929, Andrews examined the relationship between membracids and ants. Membracids supply honeydew to the ants chiefly when they are young, but the ants eat injured or dead membracids. The ants tend membracids during the day and all through the night. *F. exsectoides* was found to make succursals (small mounds of sand) at the bases of small trees which were used by the membracids. The succursal provides both shelter and protection for the membracids and the ants benefit chiefly by limiting the freedom of the membracids. Andrews (1929) found that sugar flies associated with the membracids where effectively driven off by *F. exsectoides* in an attempt to monopolize the honeydew produced by the membracids. In this account of membracid-ant associations, Andrews mentions that this ant feeds on living and dead beetles, flies, bees, bugs and especially lepidoptera larvae. Workers of *F. exsectoides* were also noted preying on beetles, sowbugs, spiders, crickets, grasshoppers, termites, and unidentified Lepidoptera and Diptera from April through September (Haviland, 1947). Allen et al. (1970) observed the ants preying on budworm larvae that were on the ground or at other times when they were outside their protective silk chambers.

In Michigan jack pine stands where this ant species is frequently found, intensive management methods would not be cost-effective. However, manipulating this ant as a biological control agent in managed high value pine plantations may be worthwhile.

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MANUSCRIPT 1.

Predation of *Formica exsectoides* on four pine pests in Michigan.

Introduction

Predaceous red wood ants, *Formica rufa* group, have been exploited in intensive forestry culture for over 150 years (Adlung, 1966). European efforts have been aimed at encouraging the growth, mass rearing, and dispersal as well as protection of native ant species in forest ecosystems. Researchers in North America have tried introducing species from Europe to provide protection of forests from insect pests, such as the spruce budworm (Finnegan, 1975; McNeil et al., 1978).

Studies that have been conducted in North America have disclosed that native carpenter ants in the genus *Camponotus* and mound-building ants in the genus *Formica* both feed on insects of economic importance in forestry (Finnegan et al. 1978; Campbell and Torgersen, 1982; Torgersen and Mason, 1987). More recently, ants in the genus *Solenopsis,* have proved to be valuable in reducing insect pests in pecan and coffee and orange orchards, respectively (Tedders et al., 1990; Eskafi and Kolbe, 1990).

Many researchers have investigated utilizing predaceous ants because they are capable of removing a large number of insect prey. Wellenstein (1952) estimated eight million insects taken as prey by one medium-size mound of red wood ants during one season. In addition to preying on insects, many species of ants obtain honeydew by tending aphids (Way, 1963). The effects of the interactions between the ants and homoptera in relation to biological control can be either positive or negative, depending upon several factors. Ant attendance of certain species of aphids is known to increase the population of homoptera to economically injurious levels (DeBach et al., 1951; Flanders, 1951). In addition to damaging the host plant, ant attendance can negatively effect the natural enemy complex of aphids (Samways et al., 1982;

Haney et al., 1987). Other studies have shown that ant attendance of homoptera does not interfere with natural control but instead, increases predation (Stary, 1966). Flanders (1943) observed that heavy infestations of black scale that were attended by ants were completely parasitized.

Several North American studies have focused on the predatory behavior of the thatching mound ant, *Formica obscuripes* Forel, while the mound ant, *Formica exsectoides* Forel, has received little attention. Early studies examined the growth and distribution of mounds of *F. exsectoides* (Pierson, 1922; Andrews, 1925, 1926; Haviland, 1938). Haviland (1947) examined the life history and control of *F. exsectoides*. In the context of this study, she noted workers of *F. exsectoides* preying upon beetles, spiders and other insects.

F. exsectoides occurs primarily in the eastern United States but is also scattered throughout other parts of the country (Andrews, 1926). It can construct as many as 100 to 400 mounds per acre (Allen et al., 1970). It is a large, aggressive ant that will feed on both live and dead arthropods and tend aphids for honeydew (Andrews, 1929). Allen et al. (1970) observed *F. exsectoides* preying upon jack pine budworm larvae that were outside their feeding chambers. *F. exsectoides* possesses several other characteristics that Finnegan (1971) deemed important if a predaceous ant species were to be successful as a biological control agent in a forest ecosystem. It forages in all strata of the forest throughout the day and night and is polygynous (multiple queens), which increases the longevity of the mound.

F. exsectoides is frequently found in association with jack pine forests in parts of the lower peninsula of Michigan. This study examined the interactions between *F. exsectoides*, aphids, *Cinara* sp., and four potential insect pests of jack and red pines,: jack pine budworm, *Choristoneura pinus*

(Freeman), redheaded pine sawfly, *Neodiprion lecontei* (Fitch), white pine weevil, *Pissodes strobi* (Peck), and the gypsy moth, *Lymantria dispar* (L). Ant predation was examined on several developmental stages for each insect. Ant predation on the gypsy moth was included in this study because ant mounds were located near stands of hardwoods that were interspersed with jack and red pines. The effects of ant protection of jack pines resulting from predation of the jack pine budworm was also measured.

Materials and Methods

This study was conducted in a mature jack pine forest in the Huron-Manistee National Forest in Crawford County, Michigan. The overstory was predominantly jack pine, *Pinus banksiana* Lamb., interdispersed with both white pine, *Pinus strobus* L., and oak, *Quercus* spp. Mounds of *F. exsectoides* were scattered throughout the study area.

Ant predation was assessed by direct measurements of the number of insects removed from trial trees and indirectly through periods of observation. Ant predation was examined on several developmental stages for each insect. In 1987 and 1988, when these studies were conducted, the following pest conditions were reported for the Huron-Manistee forest: 1) Jack pine budworm populations were at low levels region wide with a trap catch of 23 male moths at a site in Crawford County; 2) In 1987, the median percent weeviling rate for the Lower Peninsula was 43 percent; 3) Redheaded pine sawflies were not detected at the study sites. Small sawfly larvae were collected at a mixed jack and red pine stand in Alpena County, Michigan and utilized in this study; and 4) The gypsy moth was present in Crawford County during 1987 but at levels below what is considered to cause significant defoliation (Michigan Forest Pest Report, 1987). However, the population of gypsy moth has increased 100-fold since 1987 and will cause some noticeable defoliation in Crawford County in 1990.

Experimental arenas were used for all of the experiments that examined ant predation on planted populations of insects. Large mounds of *F. exsectoides* that appeared very active, were selected non-randomly, to be the center of each experimental arena. The selected mounds were relatively free of plant growth on the surface which usually is a good indicator that a mound is active. Secondly, mounds that were selected had a minimum of two "major" foraging trails.

Eight or nine jack pines were planted 2.8 m from the edge of the nest, encircling the mound. Oak saplings were planted in the same pattern where ant predation was examined on the gypsy moth. The trees were planted equidistantly, except when a naturally occurring large tree interfered with this pattern (See Fig. 1). Trees that were > 2 m tall were removed from the experimental arenas. Control trees (three to four depending upon the experiment) were wrapped with a 8 cm sticky tape barrier to prevent ant foraging; trial trees were three to four trees where the ants foraged freely. The lowest whorl of branches of the trees were removed, making the trunk the only way the ants could access the trees.

Before the tests, the experimental trees were shaken vigorously and then carefully searched to remove foliage-feeding insects, predaceous insects and spiders. To prevent unwanted vertebrate predation, 1-cm hardware cloth cages were placed over the trees with a 5 cm clearance at the bottom, thus allowing the ants access to the trees.

A one-way analysis of variance was used to test for differences between the number of larvae remaining on trees after 24 h. Duncan's multiple range test and Fisher's PSLD were used to test for specific differences between treatments. Regression analysis was used to examine the relationship between the number of ants and insect pests on the trees.

Figure 1. Experimental arenas were used for all experiments where ant predation was examined on planted populations of insect pests. Cages were placed over the trees to prevent unwanted vertebrate predation.

Experiment 1. Ant Predation on the Redheaded Pine Sawfly (RHPS)

Ant predation was examined on larvae and pupae of the RHPS. The influence of aphids and larval size on ant predation was also examined.

A. Larval Stage:

Two colonies each with 30 fourth-instar RHPS were placed on opposite sides of the tree crown on each of the four trial trees for each experimental arena during July of 1987. The treatments were: 1) ants and JPBW; and 2) JPBW only. The parameters measured on each tree were the number of larvae and the number of ants found respectively every 12 hours for 3 days. Immediately after placing the larvae on the trees and then every 15 minutes, observations were made to determine how quickly the ants would discover the larvae. The experiment was conducted at three different ant mounds (experimental arenas) when fourth instar RHPS were naturally occurring in the field making a total of 12 trial and 12 control trees, each with 60 fourth-instar larvae.

B. Influence of Aphids:

Everything was done as in the above experiment except two small pine aphid colonies, *Cinara* sp., were transferred to the terminal leader of each of three trial trees for each experimental arena. This was done by field collecting pine shoots containing aphids tended by *F. exsectoides* nearby. The clipped shoots were attached to the terminal leader of the tree in such a way that as the twig dried out, the aphids moved to the live shoot. An aphid colony consisted of 30 to 50 individual aphids. The larvae were placed on the trees after the ants began tending the aphids. The treatments were: 1) ants and RHPS; and 2) ants, RHPS, and aphids. Control trees contained two colonies of RHPS and were banded with sticky tape to exclude ants. Each treatment was replicated on three jack pines and at four different ant mounds; making a total of 24 trial and 12 control trees, each with 60 fourth-instar larvae.

C. Influence of Larval Size:

Three distinct stages of RHPS larvae were placed on each of three trees for each experimental arena. The treatments were: 1) first instar RHPS and ants; 2) third instar RHPS and ants; and 3) fifth instar RHPS and ants. Controls were three trees containing larvae of the three respective sizes that were banded with sticky tape to prevent foraging by the ants. For the trial trees, the larvae were allowed to establish feeding sites before the ants were permitted to forage. Each treatment was replicated on three jack pines and at four different ant mounds; making a total of 12 trial and 12 control trees, each with 60 larvae.

Experiment 2. <u>Ant Predation on the Jack Pine Budworm (JPBW).</u>

Ant predation was examined on second and fourth instars and pupae of JPBW. The influence of aphids and the silk chamber of the JPBW on ant predation was also examined. JPBW larvae and pupae were obtained by collecting individual JPBW and their associated webbing from mature jack pine trees near the study sites.

A. Larval Stage:

Thirty, fourth-instar JPBW were placed on each of eight trees during June of 1987 for each experimental arena Four of the eight trees were banded with sticky tape and served as controls. The larvae were allowed 48 hours to establish before the ants accessed the trial trees. The parameters measured on each tree were the number of larvae and the number of ants found respectively every 12 hours for 3 days. This experiments was conducted at four different ant mounds; making a total of 16 trial and 16 control trees.

B. Influence of Aphids:

Ant predation on second instar and JPBW pupae was examined during the spring and summer of 1988.

Fifteen, second instar JPBW were placed on each of nine trial trees for each experimental arena. The treatments were: 1) ants and JPBW, 2) ants, JPBW, and aphids. The controls were three trees banded with sticky tape each containing 15 larvae. The parameters measured on each tree were the number of larvae and the number of ants found respectively every 12 hours for 3 days. In addition to direct measurements, a total of 26 hours of observations consisting of 15 minute blocks, were conducted on thourse interactions between thourse ants and JPBW. The following interactions were recorded: 1) ant made antennal contact with a larva or a silk chamber, 2) ant made mandibular contact with a larva or a silk chamber, 3) ant(s) carried a larva down a tree, 4) the JPBW dropped from the tree in response to ant(s), and 5) ant encountered a JPBW or its silk chamber and appeared to ignore it. Each treatment was replicated on 3 jack pines and at 3 different ant mounds; making a total of 18 trial and 9 control trees.

To examine ant predation on the pupal stage of the JPBW, 15 pupae and their associated webbing were placed on each of nine trees for each experimental arena. The treatments were the same as above except pupae were used instead of second instar JPBW. The parameters measured on each tree were the number of pupae and the number of ants found respectively every 12 h for 3 days. Ten hours of observations consisting of 15-minute blocks were conducted. The following interactions were recorded: 1) ant made antennal contact with a pupa or its silk chamber, 2) ant made mandibular contact with a pupa or its silk chamber, 3) ant(s) carried a pupa down the tree, and 4) ants removed fragments of a pupa. Each treatment was replicated on 3 jack pines and at 3 different ant mounds; making a total of 18 trial and 9 control trees.

C. The Influence of the Silk Chamber of the JPBW:

For this study the treatments were: 1) exposed; larvae without a silk chamber, and 2) intact (control); larvae that were protected inside their silk chambers. Fifteen larvae from the intact treatment were placed on each of four trees and 15 larvae from the exposed treatment were placed on each of four trees for experimental arena. Intact larvae were placed on the trial trees 2 days prior to placing the "exposed" larvae on trees. This was done to insure that the larvae had enough time to construct silk chambers. The trees were banded with sticky tape during this period to prevent ant predation. Exposed larvae were placed on the experimental trees approximately 1 h before the start of the study. The majority of the new silk produced by the exposed larvae was removed at 3 h intervals throughout the study. The parameters measured for each tree were the number of larvae and the number of ants found respectively at every 12 h for 3 days. Each treatment was replicated on 4 jack pines and at 3 different ant mounds; making a total of 12 trial and 12 control trees.

D. Protection of Jack Pine Trees by Ants from JPBW Defoliation:

The objectives of this study were to examine the influence of ant predation on field populations of JPBW and to determine the amount of protection resulting from the presence of ants on mature jack pine trees.

This study was conducted at three jack pine stands where there was considerable variation in the number of ant mounds per hectare. The characteristics of both the ant mounds and the stand were measured at 80 different sites within the jack pine stands. The sites were selected by walking a minimum distance of 12 m in any cardinal direction from the last ant mound sampled. The first mound encountered, was used as the base mound. All additional mounds found within an 8 m radius from the base mound also were evaluated for mound characteristics for that site. The following stand characteristics also were measured at each site: 1) stand basal area, 2) heights of all trees from which branch samples were collected, 3) the number of tips defoliated by the jack pine JPBW, and 4) the percent defoliation of the current year's growth due to JPBW feeding.

One branch sample was cut from the upper mid crown section of each of four trees at the 80 different sites. One hundred tips per branch were evaluated according to the Montgomery et al. (1982) method for assessing defoliation due to feeding by spruce budworm, *Choristoneura fumiferana* (Clemens). The number of pupae found in the branch samples was also recorded. The height of each tree that branch samples were taken from was visually estimated. Stand basal area was estimated using a 10-factor prism.

Three variables were measured for all of the trees (<0.1 m DBH) in the understory: 1) the number of pupae, 2) the number of tips that were defoliated by JPBW, and 3) the number of aphid colonies.

Both the number and the size of all ant mounds located within the 8 m radius from the base mound, were determined. Each mound was visually inspected and quantitatively rated for size from 1 to 3, with 3 being the largest. The values from the size of the mounds and the number of mounds were used to create a mound index for each site (mound size A + mound size B, etc). The values for the mound indices ranged from 0 to 13. Regression analysis was used to examine the relationships between stand and mound characteristics.

Experiment 3. Ant Predation on the Gypsy Moth (GM).

Ant predation was examined on egg masses, fourth instar larvae, pupae, and adult female GM. The influence of the setae of GM caterpillars on ant predation was also tested.

A. Adult Stage:

During the summer of 1987, 108 adult female GM were collected in the field and placed on oak saplings around ant mounds in the experimental arenas. Three GM adults were placed on each of nine trees for each experimental arena. The treatments were: 1) ants and GM; and 2) ants, GM, and aphids. Control trees were banded with sticky tape and each contained three female adult gypsy moths. The ants were allowed to access the trees only after all of the gypsy moth adults began depositing eggs. The parameters measured on each tree were the number of GM found every 2 h until there were no GM remaining. Each treatment was replicated on 3 jack pines and at 4 ant mounds; making a total of 24 trial and 12 control trees.

B. Egg Mass Stage:

After the ants had removed the majority of the adults from the trial trees, the remaining adults were removed while leaving the egg masses intact. The percent of individual egg masses that appeared to have been tampered with or removed by the ants was estimated every 6 h for a 24 h period.

C. Influence of the Setae of Fourth Instars:

The influence of the setae in deterring ant predation was examined by clipping back the setae of fourth instar GM. The treatments were: 1) caterpillars with clipped setae; and 2) caterpillars with setae intact. The control trees were banded with sticky tape and each contained 10 larvae. Three hundred sixty caterpillars were collected in the field and brought into the laboratory where they were anesthetized with carbon dioxide. The setae of one third of the caterpillars were clipped back to approximately one fourth of the original length with a razor blade. Ten larvae were placed on each of the trial trees in experimental arenas. Each treatment was replicated on 3 jack pines and at four different ant mounds; making a total of 24 trial and 12 control trees. The parameters measured for each tree were the number of caterpillars found respectively every 6 hours for a 24-hour period.

D. Pupal Stage:

During the summer of 1988, ant predation was examined on gypsy moth pupae. The influence of distance of the prey item from the mound was also examined. Jack pine trees that were less than 4 m tall were randomly selected at varying distances from mounds of *F. exsectoides* that appeared active. Four pupae were placed on each of 28 trees in hand-crafted pupation chambers constructed out of yarn and designed to mimic natural gypsy moth pupation sites. Approximately 60 percent of the trees were between 0 < 5 m, 25 percent were between 5 < 10 m, and 14 percent were > 10 m from the mound. The parameters measured for each tree were the number of pupae found respectively every 6 hours for a 48-hour period. Regression analysis was used to infer the influence of distance from the mound on ant predation of gypsy moth pupae.

Experiment 4. Ant Predation on the White Pine Weevil (WPW).

Ant predation was examined on adult WPW in the presence and absence of aphids. Two hundred forty adult WPW were collected from a nearby young jack pine plantation. Adult WPW were trapped in nylon bags as they emerged from pupation. On August 15, 1987, 20 WPW were placed on each of six trial trees. On two of the trees, aphid colonies were transferred to the terminal leaders before the WPW were placed on the trees. The treatments were: 1) ants and WPW; 2) ants, WPW, and aphids. Control trees were banded with sticky tape and each contained 20 weevils. To prevent unwanted vertebrate predation, nylon bags were placed over the trial trees. The bags were drawn closed by a cord underneath the bottom whorl of branches, thus allowing only a small opening at the trunk for the ants to access the trees. Each treatment was replicated on two trees and at two ant mounds; making a total of eight trial trees and four control trees.

The number of WPW remaining on the trees was recorded every 24 h for 3 days. In addition, 24 observation periods, consisting of 30-minute blocks, were conducted where the following interactions between the ants and WPW were recorded: 1) the WPW was feeding; 2) the ant made antennal contact with a WPW; 3) the ant made mandibular contact with the WPW; 4) the ant ignored the WPW (the ant walked on or by the WPW); 5) the WPW stopped feeding because of harassment from the ant(s); 6) the WPW stopped feeding on its own; and 7) the ant stopped tending aphids and responded aggressively toward the WPW. A series of interactions were classified as either persistent or non-persistent. A persistent interaction was one where the ant continued to harass the WPW until the WPW stopped feeding, moved to a new feeding location or the ant removed it from the tree. A non-persistent interaction was one in which the ant ignored the WPW even after walking on the weevil or nearby the weevil.

Results

Experiment 1. Ant Predation on the Redheaded Pine Sawfly (RHPS)

During the experiment, *F. exsectoides* was repeatedly seen attacking and removing fourth instar RHPS from the experimental trees (Fig. 2). *F. exsectoides* discovered the colonies of fourth-instar RHPS within 3 hours after they first ascended the trees. After 12 hours, control trees (without ants), showed an average of 57.67 ± 0.36 larvae per tree while trial trees had an average of 44.33 ± 2.60 larvae per tree. After 24 hours, the ants significantly reduced ($p<0.0005$) the number of RHPS larvae on trial trees to an average of 19.33 ± 4.94 while control trees retained an average of 55.42 ± 2.11 (Table 1). The average number of larvae remaining on trial trees after 36 hours was 0.46 ± 0.29 versus an average of 54.17 ± 0.72 on control trees.

The ants removed the RHPS larvae more quickly when aphids were present. *F. exsectoides* discovered the colonies of RHPS on trial trees containing aphids within 1 hour, while it took as long as 4 hours for the ants to discover RHPS on trial trees without aphids. Three times as many ants were observed foraging on trees with aphids present as compared to trees with RHPS larvae only.

After 12 hours, the ants reduced the number of larvae on trees with RHPS only to an average of 49.56 ± 1.81 while the average number remaining on trees with aphids present was 40.78 ± 4.23. The control trees retained an average of 56.11 ± 0.74 larvae. After 24 hours, the ants significantly reduced ($p<0.0001$) the number of RHPS larvae on trees with RHPS only to an average of

Figure 2. Workers of *F. exsectoides* readily preyed on fourth-instar redheaded pine sawfly.

Table 1. Mean number of fourth–instar RHPS remaining on experimental jack pine trees 24 h after placing them on the trees. Initially, each tree contained 60 larvae.

				t-test
	Mean	Std. Error	Count	P
Treatment	19.33	4.94	12	< 0.0005
Control	55.42	0.61	12	

42.42 ± 7.90, and on trees with RHPS and aphids to an average of 1.33 ± 2.31 (Table 2). There were significant differences between treatment means at 24 h ($p<0.05$) (Fig. 3).

Regression of ant numbers on sawfly numbers was significant ($p<0.0001$) on trees with RHPS only, while not significant ($p<0.50$) on trees with both RHPS and aphids present. On trees with RHPS only, the number of sawflies decreased as the number of ants increased (Fig. 4). There was not a direct relationship between the number of ants and the number of sawflies on trees when aphids were present. The number of ants on the trees remained relatively high throughout the experiment regardless of the density of sawflies (Fig. 5). Even after the majority of sawflies were removed from the trees, the ants remained on the trees tending aphids. The total number of ants found on trees that contained both aphids and RHPS was higher than on trees with RHPS only.

The ants preyed more readily on smaller sawfly larvae than on the larger fifth instars. Initially, the ants removed more fifth-instar RHPS than either first or third instars. After 6 h, the ants reduced the number of fifth-instar RHPS remaining on the trees to an average of 42.5 ± 6.65. The average number of third instar RHPS remaining was 46.0 ± 4.64 and the average number of first instar RHPS remaining was 49.0 ± 4.22. The average number of first instar RHPS remaining on trees was 38.67 ±6.00; the average number of third instar RHPS remaining was 37.67 ± 8.19; and the average number of fifth instar larvae remaining was 39.0 ± 8.54. However, after 24 h the trend reversed, there was an average of 32.0 ± 4.93 fifth instar RHPS remaining; 19.25 ± 0.75 third instar RHPS remaining; and an average of 22.75 ± 3.71 first instar RHPS remaining on the trial trees. After 36 h, an average of 29.25 ±

Table 2. Ant predation on fourth-instar RHPS in the presence and absence of aphids in Crawford County, Michigan during 1987. Mean number of larvae remaining on experimental trees after 24 h. Initially, each tree contained 60 larvae.

Group:	Count:	Mean:	Std. Error:	ANOVA F
With aphids	12	1.33	2.31	394.09
Without aphids	12	42.42	7.90	$p < 0.0001$
Control	12	55.17	2.17	

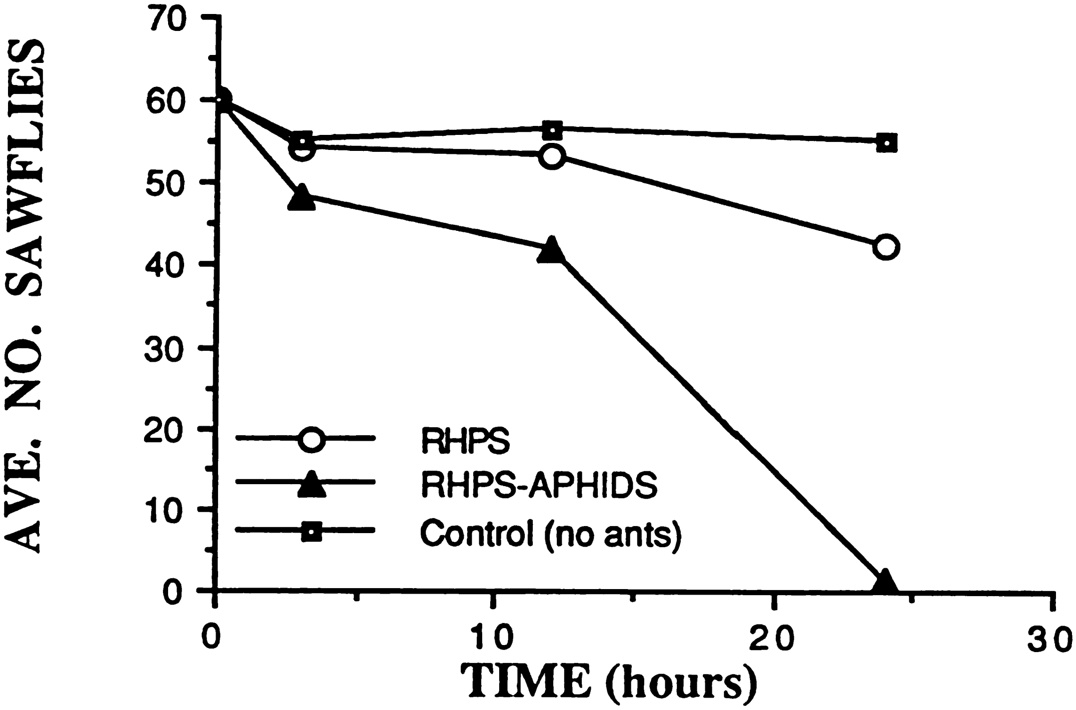


Figure 3. Mean number of sawflies on jack pines with RHPS only, RHPS and ants, and RHPS, ants and aphids. Differences between treatment means are significant at 24 h, n= 12 ($p < 0.05$).

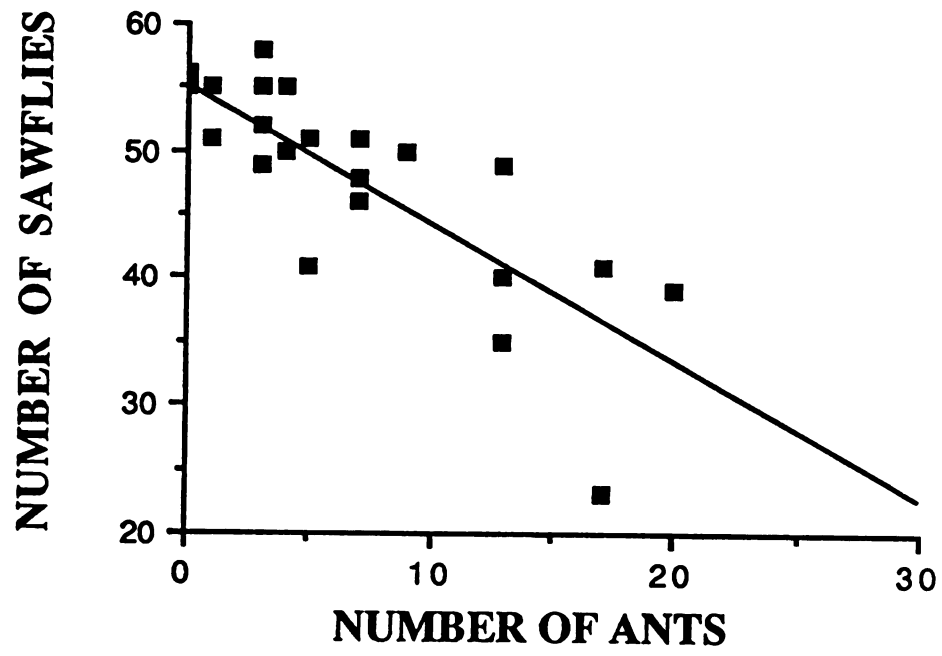


Figure 4. Regression of sawflies and ants on jack pines after 24 h. The regression was significant, $p < 0.0001$, ($y = 1.088 x + 55.180$, $r^2 = 0.63$).

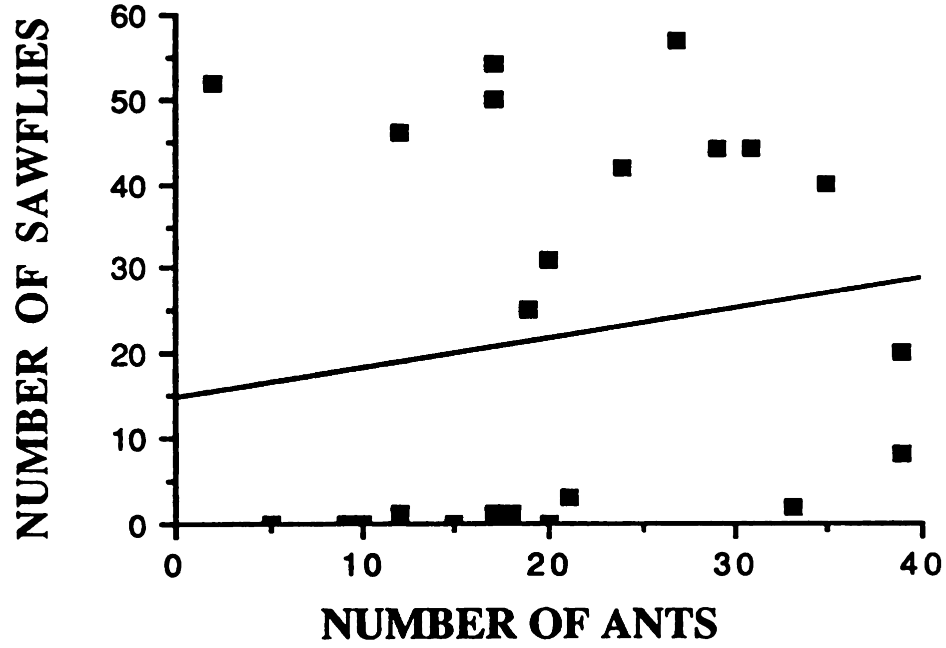


Figure 5. Regression of sawflies and ants in the presence of aphids on jack pine trees after 24 h. The regression was not significant, $p > 0.05$, ($y = 0.35x + 14.65$, $r^2 = 0.025$).

3.68 fifth instar RHPS were remaining on the trees while an average of 9.0 ± 3.58 third instar RHPS were remaining and 9.0 ± 4.10 first instar RHPS were remaining (Fig. 6).

Experiment 2. Ant Predation on the Jack Pine Budworm (JPBW)

F. exsectoides significantly reduced ($p<0.0001$) the population of fourth instar JPBW 72 h after placing them on trees. Trial trees contained an average of 10.19 ± 1.32 fourth instar JPBW while control trees retained on the average 20.63 ± 1.30 fourth instar JPBW (Table 3).

The ants removed second instar JPBW more quickly from trees that contained aphids than trees with JPBW only (Table 4). The JPBW population was significantly reduced ($p<0.0001$) by the ants 72 h after placing the second instar RHPS on trees. The trees that contained both aphids and JPBW had an average of 4.67 ± 0.76 larvae remaining as compared to trees that had JPBW only had an average of 8.44 ± 0.93. After 72 h, the control trees retained on the average 12.22 ± 0.52. There were significant differences ($p<0.05$) between treatment means after 72 h.

The ants significantly reduced ($p<0.0001$) the population of JPBW pupae (Table 5). There were significant differences between treatments ($p<0.05$) 72 h after stocking the pupae as inferred by Fisher's multiple comparison test (Statview 512, 1986). The average number of pupae remaining on trees with JPBW and aphids was 3.11 ± 1.24 while trees that did not contain aphids had 7.22 ± 1.43 pupae remaining after 72 h. The number of pupae on the control trees remained relatively high, 13.11 ± 0.51. During the study we observed 16 pupae being carried down the trees by foragers of *F.exsectoides*, 11 of the 16 were on

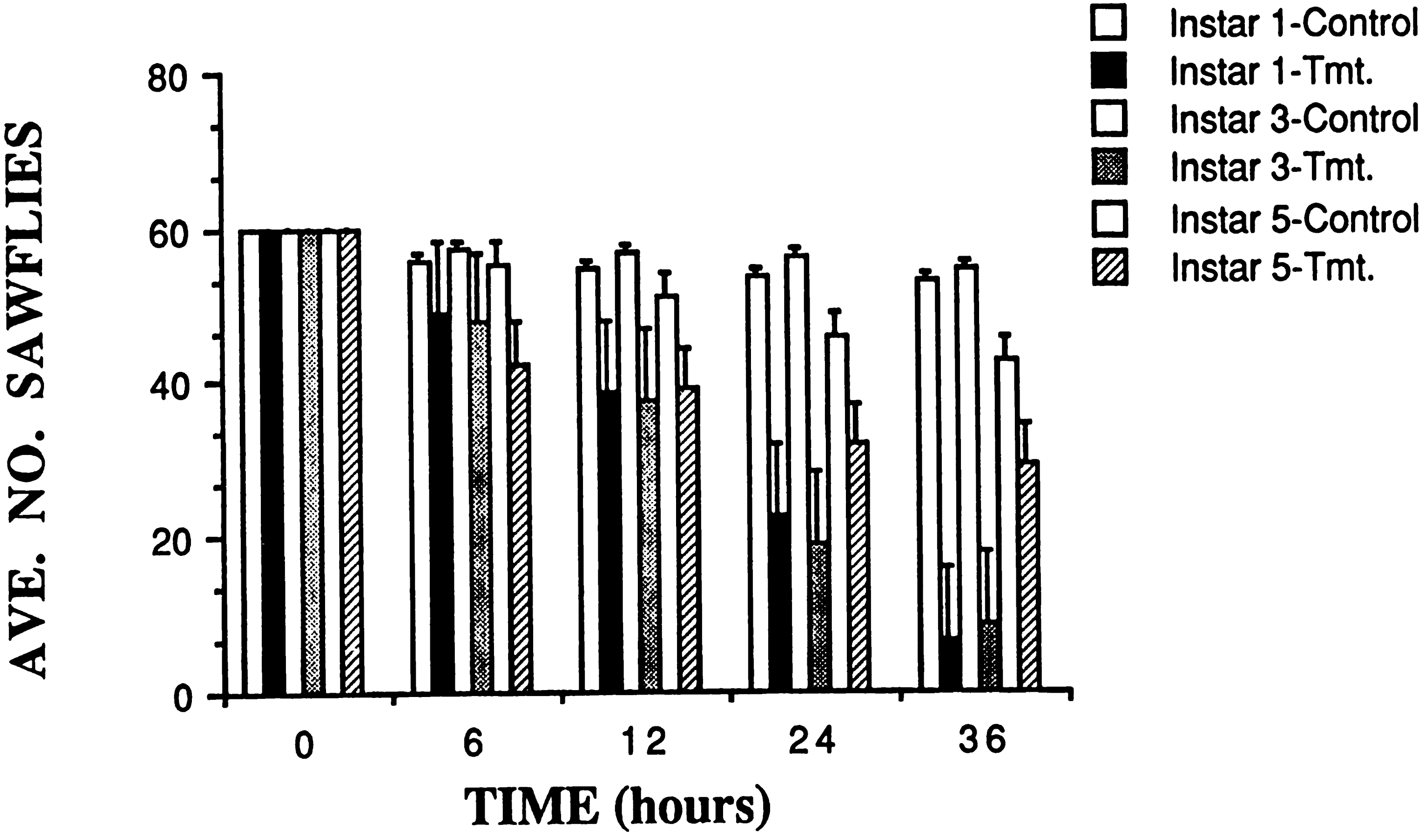


Figure 6. Effects of ant predation on three instars of sawflies over time. There were significant differences between means at 36 h, n= 4 ($p < 0.05$). Multiple comparison showed no differences in consumption between instars 1 and 3 but differences between instar 5 and instar 1, and instar 5 and instar 3, respectively.

Table 3. Ant predation on fourth-instar JPBW in Crawford County, Michigan during 1987. Mean number of larvae remaining on experimental jack pine trees 24 h after placing them on the trees.

	Mean:	Std. Error:	Count:	*t*-test P:
Treatment	10.19	1.31	16	0.0001
Control	20.63	1.30	16	

Table 4. Ant predation on second-instar JPBW in the presence and absence of aphids in Crawford County, Michigan. Mean number of larvae remaining on jack pine trees after 72 h.

Group:	Count:	Mean:	Std. Error:	ANOVA F:
with aphids	9	4.67	0.76	24.91
without aphids	9	8.44	0.93	$p < 0.0001$
control	9	12.22	0.52	

Table 5. Ant predation on JPBW pupae in the presence and absence of aphids in Crawford County, Michigan. Mean number of larvae remaining on trees after 72 h.

Group:	Count:	Mean:	Std. Error:	ANOVA F:
with aphids	9	3.11	1.24	19.68
without aphids	9	7.22	1.43	$p < 0.0001$
control	9	13.11	0.51	

trees where aphids were present. Besides removing whole pupae, the ants also returned to the mound with only fragments of pupae.

During the observation periods, a total of 157 ants were seen on trees with aphids, ants and JPBW compared to a total of only 56 ants seen on trees with ants and JPBW. The ants preyed readily upon both dislodged larvae and larvae that were protected inside their silk chambers. Only on one occasion did we see an ant encounter a budworm inside a silk chamber and ignore it. Ants were seen carrying larvae down trees on three separate occasions during the observation periods. Thirty five encounters were recorded between the ants and JPBW, and for nine of these the larvae dropped from branches on silk threads in response to the ants.

F. exsectoides preyed upon both dislodged larvae and those that are protected inside their silk chambers, however, the silk chambers did reduce ant predation. Significantly more ($p<0.0005$) larvae were removed by the ants that did not have silk chambers than those that were protected inside silk chambers within 72 h after stocking the larvae on the trees (Tables 6). The mean number of JPBW larvae remaining on trees that were protected by silk chambers was 7.67 ± 0.88 compared to a mean number of 3.08 ± 0.82 remaining on trees that did not have silk chambers.

During this study, 32 larvae were recorded dropping from branches in response to ants for the "exposed" treatment and 10 larvae were carried down the tree by the ants. For the "intact" treatment, only 15 larvae dropped from branches in response to ant probing and four larvae were seen being carried down trees by ants. A total of 369 ants were recorded on trees with "exposed" larvae during the 53 observation periods, while a total of 511 ants were seen on trees where the larvae were protected inside their silk chambers.

Table 6. The influence of the JPBW silk chamber on ant predation in Crawford County, Michigan. Mean number of larvae remaining on experimental jack pine trees 72 h after placing them on the trees.

	Mean	Std. Error	Count	*t*-test P
With chamber (control)	7.67	0.88	12	$p < 0.0005$
Without chamber	3.08	0.82	12	

Field Survey of Pupal Densities. The regression of mound index vs. number of pupae, $r^2 = 0.41$ (Fig. 7) and the regression of the number of mounds vs. the number of pupae, $r^2 = 0.35$ (Fig. 8), both were highly significant, but mound index was the better predictor of pupal densities. At the sites where there were no ant mounds, the number of pupae ranged from 7 to 53 per 400 branch tips. When the mound index was greater than 8, no pupae were found in the trees except in one instance.

The regression of mound index against average percent defoliation of jack pine tips was significant ($p<0.05$), $r^2 = 0.056$. As the value for the mound index increased, the percent defoliation in the overstory decreased. At sites where there were no ant mounds present the percent defoliation of jack pines ranged between 18 and 50% and averaged 33% of the current-year's growth. When the mound index was greater than 7, the percent defoliation ranged from 15 to 35% and averaged 27% of the current-year's growth.

More variation was explained ($r^2 = 0.08$) when the total number of tips defoliated by JPBW was regressed against mound index (Fig. 9). A trend was found similar to that for mound index vs. the number of pupae, suggesting that as mounds increased in number and size, predation on larvae increased resulting in reduced defoliation. Relative to the number of branches in the overstory that were at least partially defoliated due to JPBW feeding, few pupae were actually found. The regression was significant at ($p<0.0001$). When there were no ant mounds present at a site, the number of tips damaged ranged from 107 to 330, and averaged 209.58 ± 12.80 per 400 tips sampled. When the mound index was greater than 7, the number of tips damaged ranged from 57 to 247, and averaged 154 ± 12.52 per 400 tips sampled.

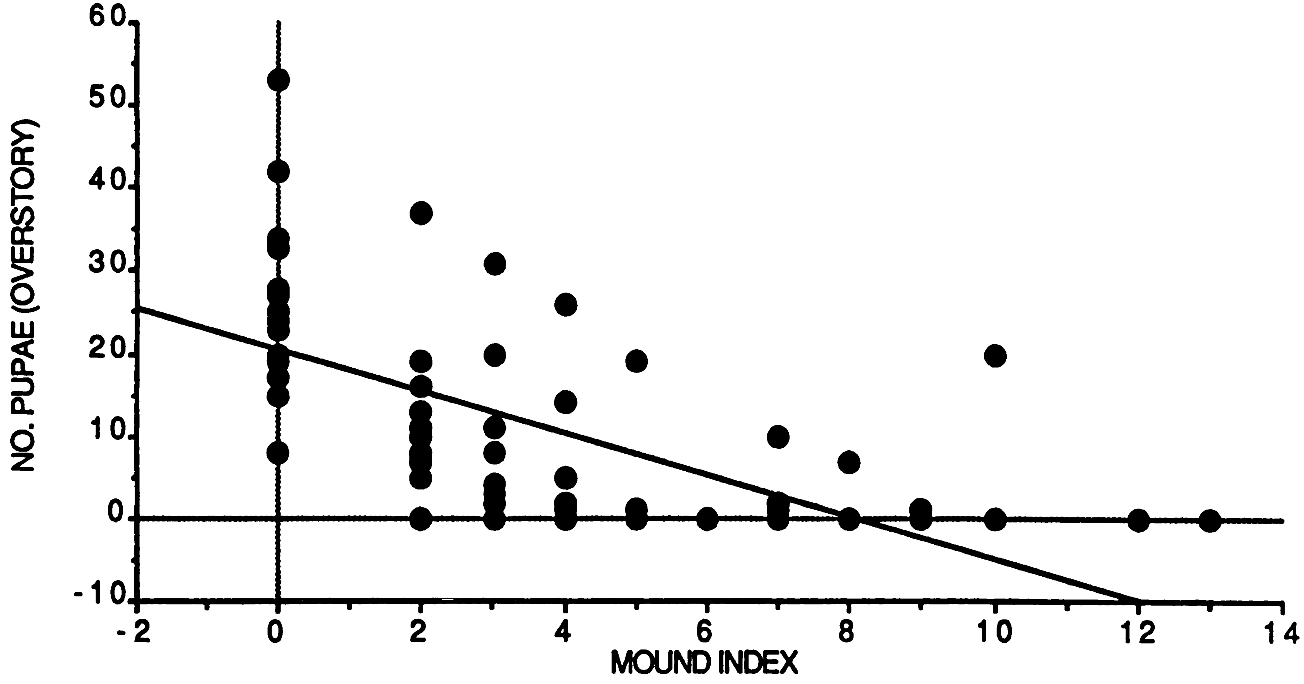


Figure 7. Relationship between mound index and the number of JPBW pupae on trees in the overstory, ($y = -2.54x + 20.39$, $r^2 = 0.42$). The regression is highly significant, $p < 0.001$; $n = 79$.

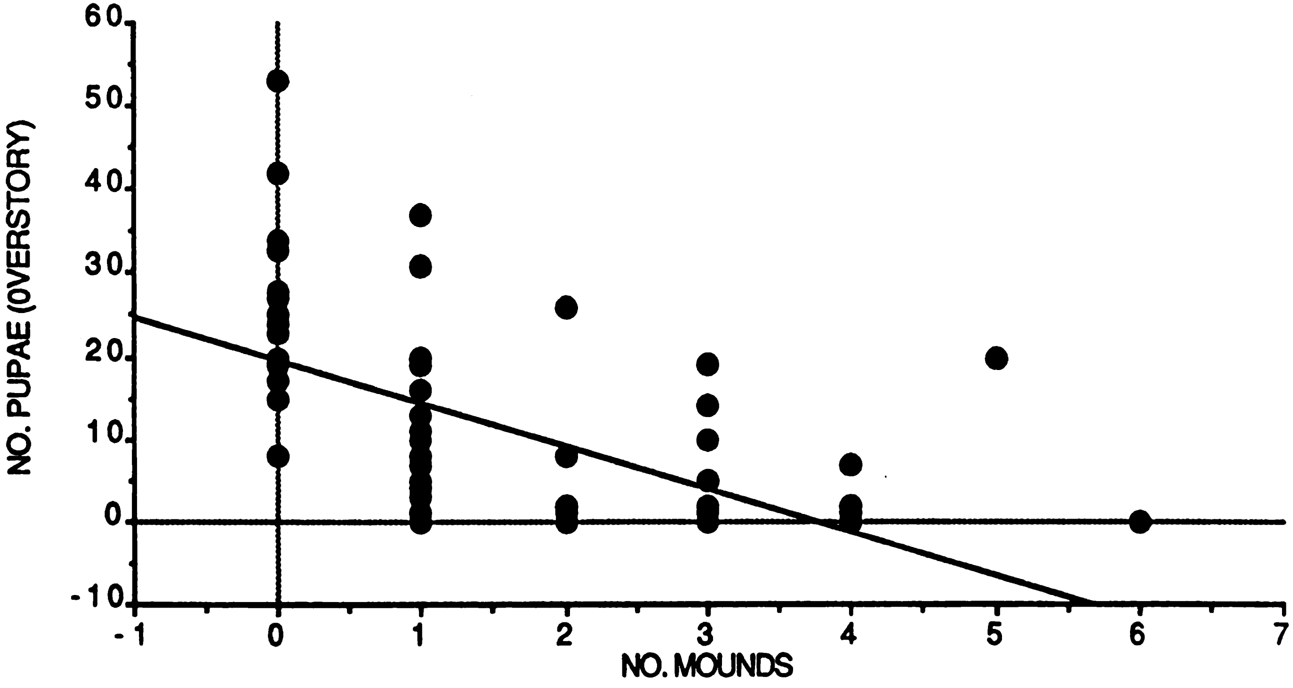


Figure 8. Relationship between the number of mounds and the number of JPBW pupae on trees in the overstory, ($y = -5.20x + 19.50$, $r^2 = 0.36$). The regression is highly significant, $p < 0.001$; $n = 79$.

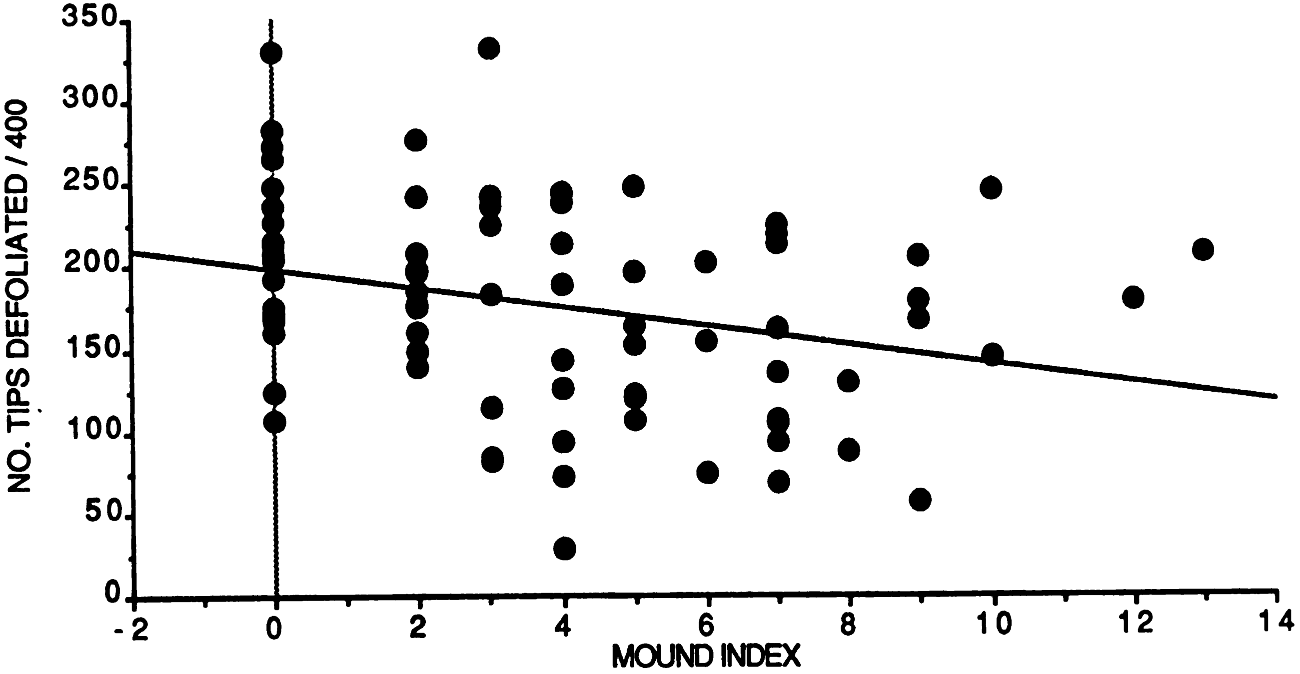


Figure 9. Relationship between mound index and the number of jack pine branch tips defoliated per 400 tips sampled ($y = -5.75x + 198.14$, $r^2 = 0.08$). The regression is significant, $p < 0.001$; $n = 79$.

Mound index was correlated with the number of pupae in the understory ($r^2 = 0.21$), but did not correlate as strongly with the percent defoliation in the understory due to JPBW feeding ($r^2 = 0.06$). However, there was considerable variability in defoliation of the understory, with a weak trend toward a decrease in defoliation as the value for the mound index increased (Fig. 10). Despite the large number of tips that were actually defoliated by JPBW, few pupae were actually found.

The basal area of the trees at the sites sampled in the jack pine plantations ranged from 0 to 110. The basal area of the stand did not appear to influence ant predation on JPBW ($r^2 = 0.002$). When pupal densities were regressed on basal area for only those sites where there were no ant mounds, the results were not significant at the ($p< 0.05$) even though a stronger linear trend was evident ($r^2 = 0.056$).

Tree height had no significant effect ($p<0.05$) on the density of JPBW pupae. These results suggest that *F. exsectoides* forages on trees of varying heights and height does not interfere with predation on JPBW larvae and pupae.

In the field experiments where we used planted JPBW, the presence of aphids increased ant predation. There was not a significant relationship between the regression of pupal densities vs. aphid densities in the field survey ($r^2 = 0.01$). However, because aphid colonies did not occur on many of the trees included in the survey, it is not certain whether the aphids actually influenced predation on JPBW pupae from this experiment.

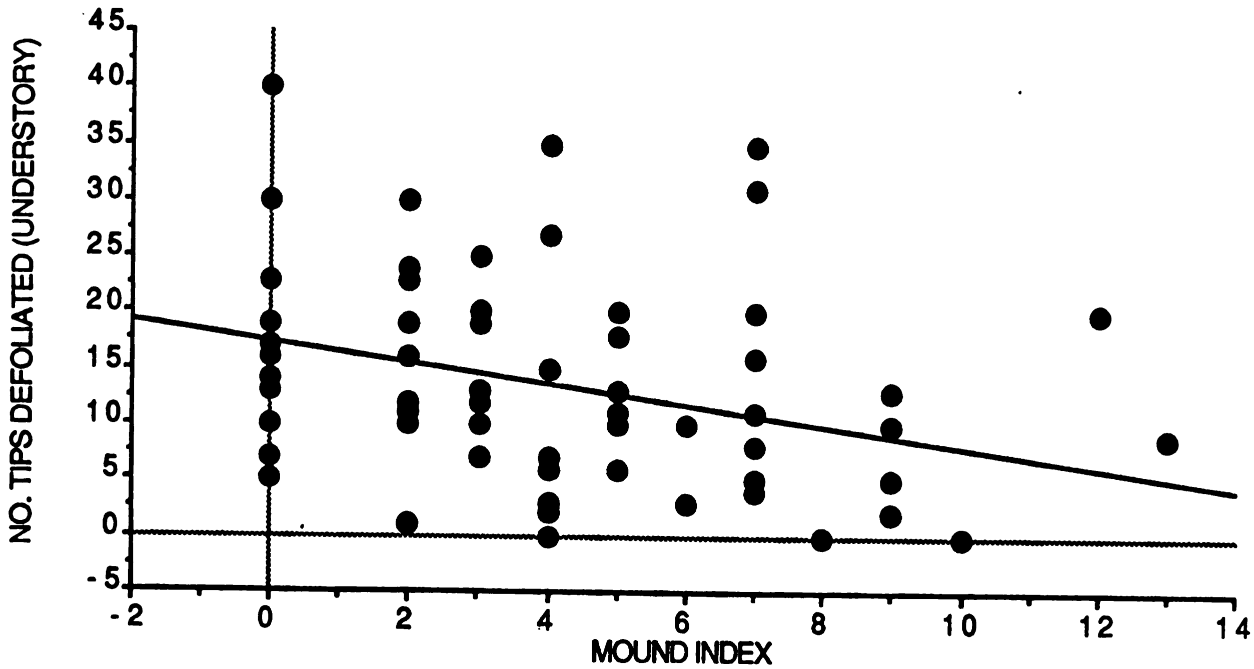


Figure 10. Relationship between mound index and the number of tips defoliated per 50 tips sampled in the understory ($y = -0.78x + 17.14$, $r^2 = 0.07$). The regression is significant, $p < 0.05$; $n = 64$.

Experiment 3. Ant Predation on the Gypsy Moth (GM)

F. exsectoides readily preyed upon adult female gypsy moths. Within 1 hour, the ants removed nearly all of the moths from the trees where aphids were present. The ants significantly ($p<0.05$) reduced the number of adults on trees both in the presence of aphids and on trees that contained only adult moths. The adult female moths remained on the control trees during this time and continued to deposit egg masses.

The ants forced gypsy moth adult females to drop from trees by repeatedly biting them. Moths dropping to the ground, were immediately seized by the ants and torn into pieces. Occasionally, the ants would drag an intact moth back to the nest.

The ants did not display much interest in the egg masses of the gypsy moth. Six hours after the ants were allowed to ascend the trees, the egg masses remained intact despite moderate to high numbers of ants on the trees. Even after 24 h, the ants continued to ignore the gypsy moth egg masses. During the observations, only a total of five ants were seen investigating egg masses and individual ants did not spend more than a few seconds on each egg mass.

The ants significantly ($p<0.0002$) reduced the population of fourth instar GM on trial trees after 24 h. However, there were no significant differences between the number of "intact" caterpillars and the number of caterpillars that had their setae mechanically reduced remaining on trial trees. The average number of caterpillars recorded on trees that were "intact" was 3.17 ± 0.91 while the number of caterpillars remaining on trees that had their setae reduced was 2.42 ± 2.43. The control trees where ants were not permitted to forage contained an average of 7.0 ± 0.52 fourth instar GM.

In this experiment, the caterpillars responded to an attack from an ant by moving to a different feeding place on the tree or dropping to the ground. *F. exsectoides* killed more gypsy moth caterpillars after they fell to the ground than when they were on the trees. Thirty nine interactions were recorded between ants and gypsy moth caterpillars. In 19 interactions, the caterpillars dropped from the trees in response to the ants. Twelve of these 19 caterpillars were captured by other ants that were foraging on the ground near the base of the trees.

As the distance from the mound increased, the percentage of pupae remaining on the trees also increased ($r^2 = 0.441$) (Fig. 11). This can be explained in part by the high concentration of ants occurring near the ant mounds. The ants removed 60 out of 112 pupae from the trial trees within 24 h after placing the pupae on the trees. Very few pupae were removed and few ants were found on trees that were more than 10 m from the mounds.

Gypsy moth pupae are large relative to *F. exsectoides*. Therefore, instead of removing an entire pupa, the ants would pierce a hole in the end of the pupal case and individual workers would remove pupal fragments (Fig. 12). After the initial discovery of a pupa, the ants would continue to forage on the pupa for up to 2.5 h. Only on two occasions did we see the ants remove an entire pupa from a tree.

Experiment 4. Ant Predation on the White Pine Weevil (WPW)

The ants significantly reduced the number of adult WPW on trial trees 72 h after placing the WPW on the trees. The average number of adult WPW remaining on trees with aphids was 2.00 + 0.91 while the average remaining on trees with WPW only was 6.25 ± 1.93 (Table 7). Control trees retained on the

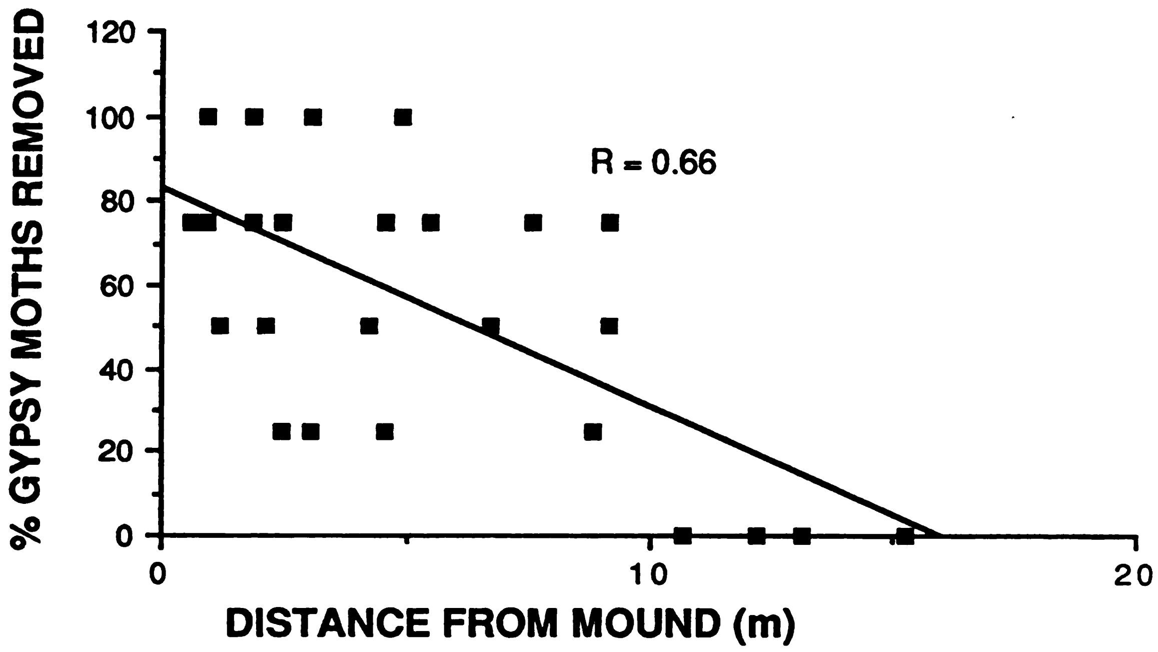


Figure 11. Regression results of the effect of the distance from the mound on the percent of adult female gypsy moths removed by ants from jack pine trees. The regression was significant, $P<0.0001$, ($y = -1.60x + 83.32$, $r^2 = 0.441$).

Figure 12. Workers of *F. exsectoides* entering a gypsy moth pupal case and removing fragments of a pupa.

Table 7. Ant predation on adult WPW in the presence and absence of aphids. Mean number WPW remaining on experimental trees after 72 h.

Group:	Count:	Mean:	Std. Error:	ANOVA F:
With aphids	4	2.00	0.91	22.16
Without aphids	4	6.25	1.93	p < 0.003
Control	4	13.75	0.50	

average 13.75 ± 0.58 adult WPW. Fisher's PLSD showed significant ($p<0.05$) differences between treatments after 72 h.

A total of 74 interactions were observed and recorded between the ants and WPW on the trial trees. An additional 22 observations were recorded on the feeding behavior of WPW adults on control trees (Table 8). Forty interactions were recorded between weevils and ants on trial trees with aphids present (Fig. 13). Out of the 40, there were 16 interactions in which the weevil stopped feeding because of persistent harassment from an ant(s). In six interactions, the weevil stopped feeding because of the ants and moved to a new location on the tree. In six other instances, we found that the weevil stopped feeding for a brief period following harassment from the ants but shortly afterwards relocated. In two out of the 16 persistent interactions, the ants captured the weevils and removed them from the experimental trees.

Frequently, even after an ant made antennal or mandibular contact with a weevil, the weevil did not relocate or discontinue feeding. We observed 21 non-persistent interactions in which the ants did not respond aggressively to weevils even after walking on or nearby the weevils. In five of these 21 non-persistent interactions, the weevils stopped feeding and moved to new locations on the tree.

On trees that did not contain aphids (weevils and ants only), we observed 34 interactions between ants and weevils (Fig. 14). Eighteen of 34 interactions were persistent in which the ant harassed the weevil until the weevil responded by discontinuing feeding or by moving. In five of the persistent interactions, the weevils stopped feeding and moved to new locations on the tree following repeated attacks by the ants. In 12 persistent

Table 8. Summary of 24, thirty-minute observation periods recording the interactions between *F. exsectoides* and white pine weevils on jack pines.

Treatment	# of Interact.	Antennal Contact	Mandibular Contact	Ant Ignores WPW	WPW Stops Feeding On Own	WPW Stops Feeding Due to Ant(s)
Without Aphids	34	26	16	13	3	18
With Aphids	40	31	20	21	0	16
Control (no ants)	22	--	--	--	13	--

I also observed and recorded six ants switch from tending aphids to preying on WPW.

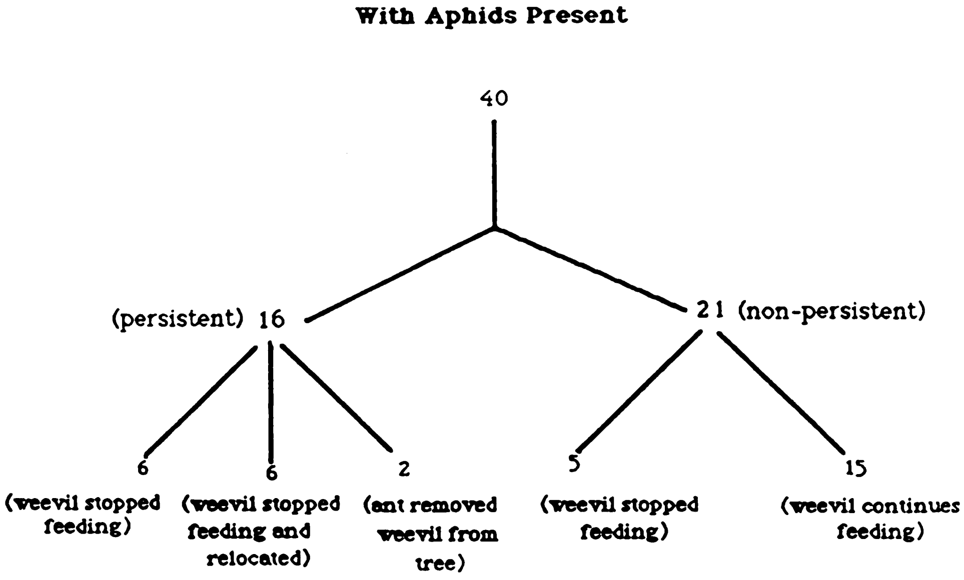


Figure 13. Persistent and non-persistent interactions between *F. exsectoides* and white pine weevils on trees that contained aphids.

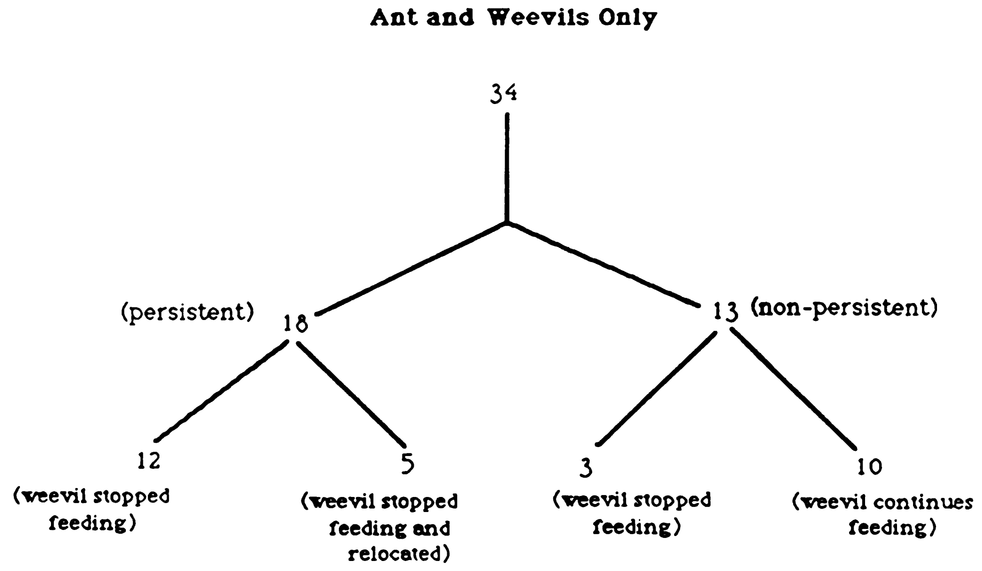


Figure 14. Persistent and non-persistent interactions between *F. exsectoides* and white pine weevils on trees that did not contain aphids.

interactions, the weevils did not relocate and resumed feeding shortly after the ant left the area.

Thirteen of the 34 interactions that were observed between the ants and weevils were non-persistent. These interactions were classified as non persistent because the ant walked on or near a weevil without responding to it. However, even though the ant did not respond aggressively, in three of these interactions, the weevils stopped feeding while the ants were in the immediate area. Ten of these interactions did not disrupt the weevil sufficiently enough to cause them to stop feeding or move to a new location on the tree.

Discussion

This study shows that *F. exsectoides* will prey on a wide variety of insect pests. This species of ant also can reduce the population density of adult WPW by disrupting their feeding and forcing them to move to new feedings locations (Summarized in Table 9) .

Ant Predation on the Larvae of RHPS, JPBW and GM

Little is known about predatory activity of *F. exsectoides* even though it is considered to be the most common mound building ant of North America (Wheeler, 1910). However, it is a close relative to the *Formica rufa* group where ant predation has been studied more extensively in both Europe and the United States for species in this group. In a study examining the relationship between *F. exsectoides* and membracids in the Eastern United States, Andrews (1929) observed that the ants preyed on beetles, flies, bugs and especially Lepidoptera larvae. Workers of *F. exsectoides* were also noted preying on beetles, sowbugs, spiders, crickets, grasshoppers, termites, and unidentified Lepidoptera and Diptera from April to September in Maryland by (Haviland, 1947).

In this study, *F. exsectoides* readily removed fourth-instar RHPS from trial trees. Despite the two obvious defense mechanisms of RHPS, the colonial feeding habit and the resin-rich substance that is stored in the sawflies diventricular pouch and discharged when they are disturbed by predators (Eisner et al., 1974), *F. exsectoides* removed 240 sawflies at one mound within 36 h. This represented only a small fraction of the total number of workers

Table 9. The Insects and Stages of Development that *F. exsectoides* Preyed Upon

Insect	Adult	Egg	Larvae	Pupae
RHPS			Y*	
JPBW			Y*	Y*
GM	Y*	N	Y*	Y*
WPW	Y*			

The asterisks indicate that the ants significantly reduced the insect pest population.

foraging in the forest during this time. Several European studies have shown that ants in the *Formica rufa* group significantly reduced populations of sawfly larvae (Wellenstein 1957a; Goesswald, 1940; Bruns and Schrader, 1955).

In the experiment comparing predation on the three stages of RHPS larvae, the ants initially removed fifth-instar sawflies more readily than either first or third instars. After 24 h, fewer first and third instar RHPS remained on the trial trees than fifth instars. Traniello (1987) found that when workers of *F. schaufussi* were given a choice between 50 and 400 mg prey, the ants selected the smaller prey. He suggested that smaller prey items have a greater net profitability because they do not require group retrieval and that there is less chance that smaller prey will be lost through interference from other predators, especially other ant species. A similar phenomenon may be true for *F. exsectoides* because individual workers were seen removing and carrying both first- and third-instar RHPS, while the removal of fifth instar RHPS usually required more than one and as many as seven workers of *F. exsectoides*. *F. exsectoides* may have discovered the larger fifth-instar lavae more quickly because of their relative size, but then removed the smaller instar RHPS more quickly because of the reduced handling time.

Bradley and Hinks (1968) observed workers of *F. obscuripes* carrying JPBW larvae back to their nests. Allen et al. (1970) observed workers of *F. exsectoides* attacking larvae of JPBW that fell from trees to the ground, however, they concluded that predation by *F. exsectoides* did not occur on JPBW larvae that were protected in their silk feeding chambers.

This study shows that *F. exsectoides* preys on JPBW larvae whether inside or outside their silk chambers. But those on the outside dropped from branches in response to ants more than twice as often. After a larva dropped from a branch the ants would either wait for the larva to climb back onto the branch via its silk thread before attacking or continue to pursue the larva down its silk thread (Fig. 15). The ants also responded aggressively to the silk chambers of the JPBW and repeated attacks would often result in the larvae backing out of its silk chamber and dropping on a silk strand. Often, ants were present at both ends of the silk chamber and the larva would be captured as it attempted to escape. These results suggest that the first line of defense for JPBW larvae is to remain in their protective silk chambers and drop from branches only when the ants continue to pursue them.

A few studies have been conducted where predation by ants, *Formica* spp., and ground beetles, *Calosoma* spp., have been recorded attacking GM larvae. In a recent study, Weseloh (1988) found that ants readily preyed on tethered GM larvae that occurred in the soil litter while small mammals consumed the majority of larvae that were on the boles of trees. Tethered larvae in the tree canopy were not preyed on as readily by invertebrates. The results of this study support Weseloh's findings in that more GM caterpillars were killed by ants that fell to the ground than those that remained on the trees.

My original hypothesis that the setae of fourth-instar GM is an effective deterrent against ant predation was not supported by the findings of this study. The direct measurements of predation and the observations suggest that it was not the setae that deterred ant predation but the large size of fourth-instar GM and their associated mobility. Sixty-three percent of the caterpillars that dropped to the ground were attacked by ants. The other caterpillars appeared to escape in the dense underbrush of the jack pine

Figure 15. Workers of *F. exsectoides* searching for a dislodged jack pine budworm larva.

forest. In the study area, ants were found covering much of the ground and foliage and the possibility that the caterpillars were captured later seems quite high.

Ant Predation on JPBW and GM Pupae

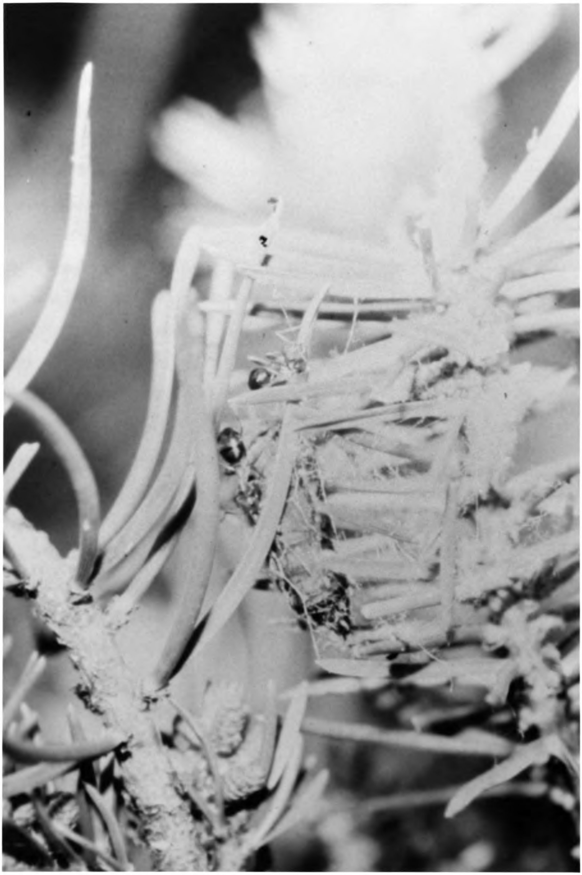
Several studies have suggested that predaceous ants may play an important role in the population dynamics of the western spruce budworm (Campbell and Torgerson, 1982; Youngs and Campbell, 1984). These studies examined ant predation on the pupae of the western spruce budworm.

F. exsectoides preyed on JPBW pupae that were placed on trees surrounding ant mounds in experimental arenas (Fig. 16). The field survey of JPBW pupal densities and ant mound densities indicated that moderate to high numbers of mounds of *F. exsectoides* have a significant negative effect on JPBW pupal densities.

The field survey also provided a measure of the effects of ant predation on defoliation due to JPBW feeding. At sites where the ants foraged, defoliation decreased 3 to 30 times compared to sites where the ants were not present. In a similar study, Warrington and Whittaker (1985) found that sycamore and ash trees suffered approximately 5 times as much defoliation in areas where ants (*Formica rufa* group) did not forage as compared to areas where ants foraged.

Although the presence of ants in the jack pines stands resulted in a significant decrease in the number of pupae found and defoliation of jack pines, there were still more tips defoliated than pupae actually found. One interpretation of this is that the ants removed budworm pupae more easily than budworm larvae, possibly due to the halt in silk production during the pupal stage of development. A second explanation could be that there was a

Figure 16. Workers of *F. exsectoides* removing a jack pine budworm pupa from its silk chamber.



source of alternative prey which was preferred by the ants available in the field during the time JPBW larvae were present. Perhaps the relationship between the number of pupae found and the amount of defoliation is simply a reflection of ant predation extending over the larval and pupal stages of development of the JPBW.

The ants readily preyed upon the pupae of the GM. Because the distance between the trial trees with pupae and the mound increased, the percentage of pupae remaining on the trees also increased suggesting that the pupae were outside the normal foraging range of the ants. Few ants were found on trees that were more than 10 m from the mounds, and thus few pupae were removed. Weseloh (1985) found that *Calosoma* larvae destroyed 70 percent of tagged gypsy moth pupae under burlap bands on trees near the ground. In this study, *F. exsectoides* destroyed 56 percent of the GM pupae within 24 h after placing them on trees. Smith and Lautenschlager (1981) also found that ants were responsible for removing a significant proportion of both healthy and parasitized gypsy moth pupae.

Ant Predation on Adult GM and WPW

The ants preyed on both adult GM and WPW, however, the GM were more readily removed from the trees than adult WPW. The ants had little difficulty preying on GM adults perhaps because the adult females are not capable of flight and can only escape predation by moving up the host tree. The ants caused the adults to drop from trial trees by repeatedly biting them.

F. exsectoides **directly reduced the density of WPW on trial trees shortly after the experiments began. The ants also negatively influenced the weevils indirectly by causing them to stop feeding and move to new feeding locations**

on the trees. This study was conducted in mid August when adult WPW spend most of their time feeding on pine shoots before overwintering (USDA, 1983). Ant predation may also disrupt WPW oviposition in the spring by directly reducing egg laying and interfering with adult males that are trying to locate females on the trees.

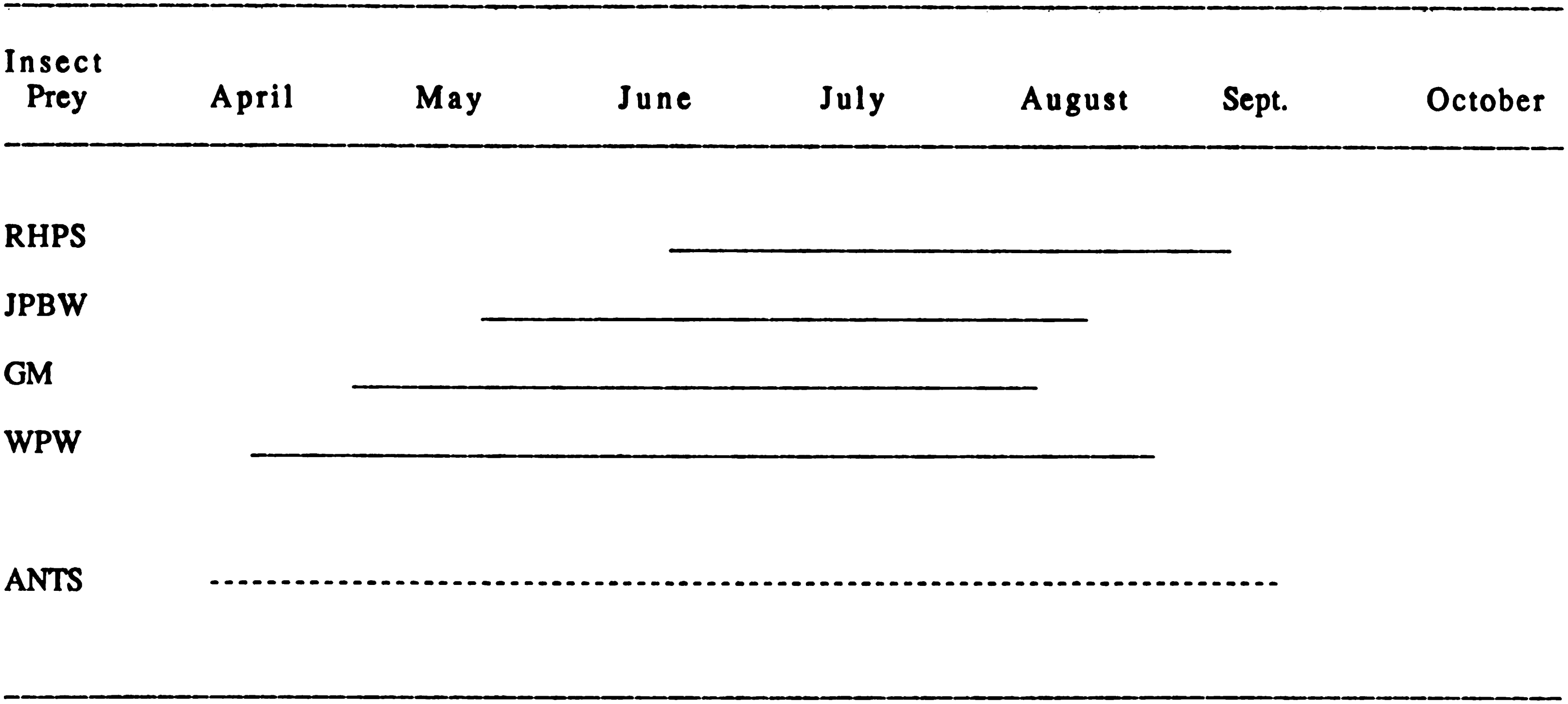
The ants removed the RHPS larvae more quickly than JPBW and GM larvae. After 24 h, the ants removed an average of 67 percent of the RHPS larvae as compared to an average of only 8.6 percent of JPBW larvae. Although RHPS larvae do have two mechanisms to deter predation, colonial feeding and the noxious fluid they dispel when approached by predators, they are relatively naked as compared to JPBW larvae that are protected inside silk chambers. *F. exsectoides* did reduce experimental populations of fourth-instar GM, but the results from this study showed that the setae were not a sufficient deterrent against ant predation. It appeared that it was the large size of the caterpillars and their mobility that allowed them to escape predation by *F. exsectoides*. Therefore, it seems likely that these ants would not be able to capture GM caterpillars that were beyond the fourth instar stage. This study may have overestimated predation on GM larvae because many of the caterpillars dropped from the trees in response to ants presence. However, disruption of the feeding of GM larvae should result in decreased defoliation of trees. The fate of individual caterpillars was not followed, but, instead predation was measured by the benefit the tree received by counting the number of caterpillars removed.

The only developmental stage that *F. exsectoides* showed no interest in was the egg stage of the gypsy moth. This may have occurred for two reasons: 1) the egg stage is sessile and movement may be necessary for initial recognition of a prey item by ants (Mathews and Mathews, 1978), and 2) the egg mass of the GM is protected by a thick layer of abdominal hair-like scales which the adult females deposits along with the eggs. The pupae of both the JPBW and the GM were readily preyed upon by the ants even though they are relatively motionless. This may suggest that GM egg masses were not acceptable prey because of the protective covering on the egg masses rather than the sessile condition. However, shortly after the JPBW and GM pupate and shortly before they emerge as adults slight movement does occur and may serve as a sufficient stimulus to elicit a predation response.

Relative abundance of each prey item in the field may also influence predation (Way, 1963). Colonies of *F. exsectoides* are active in the field from April to September (Haviland, 1947). The insect pests examined in this study were present at different times of the year, but many of the developmental stages of the insects overlap (Table 10). From late April to May, GM are in the early stage of development in Michigan (USDA, 1983), and were readily preyed upon by *F. exsectoides*. In the jack pine forest where this study was conducted, RHPS did not occur but a close relative, the European pine sawfly, *Neodiprion sertifer* (Geoffroy), were present as larvae during April and May. The European pine sawfly may offer a potential abundant food resource to the ants during this time and may be a more acceptable prey item to the ants then GM larvae if the ants prey on this sawfly as readily as they preyed on the RHPS larvae.

In May, the JPBW larvae hatch from egg masses in Michigan and may provide a relatively abundant source of food for the ants. *F. exsectoides* will prey on the JPBW through the pupal stage which usually lasts until August. In August WPW adults become available in the environment and may replace the

Table. 10. Seasonal Distribution of Insect Prey and *F. exsectoides*



The lines depict the times of the year that these insects are active.

JPBW as prey for the ants. At this time brood production in the ant mounds is beginning to decrease (Haviland, 1947) and the need for protein foods for the colony may decline as well (Edwards, 1951).

In conclusion, the JPBW would appear to offer the most stable food resource to *F. exsectoides* in the jack pine forest where this study was conducted because the ants will prey on small and large JPBW larvae and pupae. The JPBW also appeared to the most abundant insect pest in these jack pine forests. This may, in part, explain why the ants can prey on JPBW larvae and pupae despite their protective silk chamber.

The Influence of Aphids on Ant Predation

One of the most interesting findings of the study was that ants switched from tending aphids to attacking the insect pests when they wandered near a tended aphid colony. Green and Sullivan (1950) suggested that ant predation is often a result of defense of aphid colonies. They observed ants removing 1,800 forest tent caterpillar larvae, *Malacosoma disstria* Hbn. When young larvae moved on trees to feed or moult, they often passed through an aphid colony which immediately invoked an attack by the ants. During our observations we found that when an ant encountered a RHPS it would do one of the following: 1) antennate the larva and return to tending aphids, 2) attack and sometimes remove the larva from the tree, or 3) recruit other ants from the surrounding area by leaving the aphid it was tending and running up and down the tree trunk which appeared to excite other ants in the area. Many of the encounters between ants tending aphids and RHPS resulted in the ant attacking the larva or removing it from the tree.

Bradley and Hinks (1968) observed that ants protecting aphid colonies would chase away mirids. The mirids would escape further predation by running back an inch or two and remaining motionless. This is similar to our study in that an attack on a weevil by an ant that was tending an aphid colony did not always result in a capture, but would often force the weevil to find a new feeding location on trees.

In an omnivorous species such as *F. exsectoides*, individual workers tend homopterans to collect honeydew as well as forage for insects. However, Traniello (1989) found that workers of *Formica schaufussi* forage more persistently following a reward of sucrose than following a reward of insects. *F. exsectoides* preyed on WPW in both the presence of aphids and absence of aphids on trial trees. Although we recorded more interactions between the ants and the WPW on trees when aphids were present, the ants were more persistent in foraging on weevils when aphids were absent. On trees containing aphids, 52 percent of the interactions between the ants and the weevils were non-persistent. On trees that did not contain aphids, 38 percent of the interactions were non-persistent. Persistent foraging on a more constant food resource such as honeydew produced by the aphids may in part explain why, at times, the ants simply chase away the predators of the aphids. However, when individual workers switch from tending aphids to preying on insects, they may be just simply taking advantage of the prey item which is more abundant in the environment (Way, 1963).

The effects of the interactions between ants and aphids in relation to biological control can be either negative or positive depending upon a number of factors. Ant attendance of certain aphid species interferes with the control exerted by the natural enemies (Flanders, 1943; Samways et al., 1982).

Ant attendance of certain species of homoptera is known to increase the population of homoptera to economically injurious levels (Flanders, 1951; DeBach et al., 1951) and may reduce leaf size and stem wood production of certain types of trees (Dixon, 1971).

In this study, ant predation was positively influenced for each of the insect pests examined by the presence of aphids on the jack pines. Ant densities were always higher and more constant on trees that contained aphids as compared to trees that did not contain aphids. Whether the ants were searching for stray aphids or insect pests is not clear, but the results were always the same, fewer insect pests remained on trees that contained aphids. The effects of aphid feeding on the growth of jack pines was not examined, but, the trees did not appear to suffer from aphid feeding. The shoots of the jack pines that did contain aphid colonies were not discolored or brittle. However, before a conclusion can be made on the benefits to the trees derived from ant attendance of aphids in this system, the effects of aphid feeding on jack pine growth needs to be examined.

This study shows that *F. exsectoides* is a good candidate for biological control of certain forest insect pests. Finnegan (1974) suggests that ants combine certain qualities that make them ideal biological control agents. These characteristics include, that ants: 1) attain a high population density; 2) forage at all levels in the forest, from in the soil to the tree canopy; 3) have an extended period of activity; 4) are polygynous, assuring a prolonged nest life; 5) form colonial nests; 6) forage for and attack all stages in the life cycle of insect prey; and 7) specialize in foraging for those prey that explosively increase in total numbers of individuals. *F. exsectoides* can form as many as 400 mounds per acre (Allen et al., 1970). *F. exsectoides* preys on a wide variety of forest insect pests and on several developmental stages. Predation was not examined on all of the developmental stages of each insect, but the results of ant predation on the JPBW and GM suggest that their is great potential for this ant to prey on many developmental stages for similar types of insects. We also observed *F. exsectoides* bringing arthropods that dwell in the soil back to their nests. *F. exsectoides* forages over most of the spring and summer, (Haviland, 1947) when many important insect pests are present in jack pine forests. This species of ant is polygynous and queens from one colony were readily accepted when introduced to new colonies. *F. exsectoides* forms colonial nests that are connected by a series of underground tunnels. This enables the ants to share food and brood and thereby increases the stability and permanence in the ant colony over large areas and over an extended period of time. Although *F. exsectoides* preys on a wide variety of insect prey, JPBW larvae and pupae represented a large portion of the prey brought back to the nests. JPBW densities were at very low levels in the jack pine forest where this study was conducted during 1987 and 1988. *F. exsectoides* may prey exclusively on JPBW when it reaches outbreak levels. This would satisfy the last criteria Finnegan (1974) includes in his list of characteristics for biological control agents. The results of this study and information from the existing literature suggest that *F. exsectoides* would be an excellent biological control agent to incorporate into an integrated pest management programs in forest ecosystems.

The ability of colonies of *F. exsectoides* to prey on more than one type of insect and switch from preying on insect pests to collecting honeydew from aphids may aid in maintaining high and constant populations of this ant in forest ecosystems. Large and constant populations of predaceous ants may contribute to maintaining insect pest populations at levels below the economic thresholds. In addition to directly reducing insect pest populations, the disruption of feeding and oviposition of insect pests by ants should be considered by land managers. The ability of predaceous ants to disrupt the feeding of insect pests and therefore, reduce damage to trees would be especially beneficial for certain types of crops such as Christmas trees that are valued for their esthetic appearance as well as growth.

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MANUSCRIPT 2.

A Scots Pine Growth Simulation Model; A Focus on Ecological Management Strategies

Introduction

The long term nature of Christmas tree production as well as the rising costs and environmental effects associated with conventional practices, demands that we explore alternative and improved Christmas tree production technologies. Odum (1984) describes an "improved" agroecosystem as one that moves toward the reduction of one or more of the following factors: soil erosion, loss of biological diversity, and chemical pollution in agricultural or forest production. An example of such a system is a pine, birdsfoot trefoil and predaceous ant intercropping. This "improved" agroecosystem theoretically provides an ecologically sound alternative to existing practices. A simulation model was developed to test this hypothesis.

System Description. We have attempted to simulate an agroecosystem which includes the following components: Scotch pines trees, ***Pinus sylvestris*,,** birdsfoot trefoil, *Lotus corniculatus*, and colonies of the Allegheny mound ant, *F. exsectoides* Forel. The pines are grown on a short-term rotation and harvested for Christmas trees. A relatively low variety of birdsfoot trefoil, a leguminous ground cover, provides weed control and nitrogen through litter decomposition and nitrogen fixation, and is intercropped with the Christmas trees. Additionally, the trefoil provides both food and shelter to populations of aphids that are normally found on trefoil. The aphids in turn provide honeydew to the ants as an alternative food when insect prey is scarce. When the pests approach outbreak densities, the trefoil can be mowed forcing the ants to switch their foraging from honeydew to the insect pests of pines. An additional benefit of mowing the trefoil is a pulsed input of high nitrogen content organic matter to the soil. This input of nitrogen has the potential of increasing tree growth and leaf area by increasing soil nitrogen and cation exchange capacity over a period of time.

Components of the Simulation Model. The model is written in Fortran and is organized into eight subroutines: 1) a DRIVER to set the initial conditions; 2) WEATHER to generate typical seasonal temperatures; 3) TREE which selects leaf area for the trees at a given time, defoliation due to insect pests, as well as competition between the trees and the trefoil; 4) TREFOIL which provides an estimate of trefoil biomass; 5) NITROGEN which estimates rates of nitrogen application and site improvement; 6) PEST which estimates the number of prey available to the ants; 7) APHID which selects the amount of honeydew available to the ants; and 8) ANTS which selects a predation rate that determines the amount of insects removed from the trees. The overall system flowchart is represented by Fig. 17.

Driver. The driver calls the following subroutines at weekly iterations: tree, weather, trefoil, nitrogen, aphid, pest, and ant over an entire growing season. The season consists of a 31 week period. The driver also keeps a yearly account of the site improvement and the defoliation caused by the insect pests.

Temperature subroutine: The only weather parameter required for this model was temperature. The design of the weather generator was further simplified by taking advantage of the fact that temperatures for any particular climate can be roughly fit to a 'normal' distribution curve.

In the case of southeastern Michigan, the peak of this curve falls near July 22 with the lowest temperature falling near the last week in January. There is a flattening of the curve near the beginning of the year, thus the peak is shifted slightly towards the end of the cycle.

The equation used to generate the data shown in Fig. 18. is:

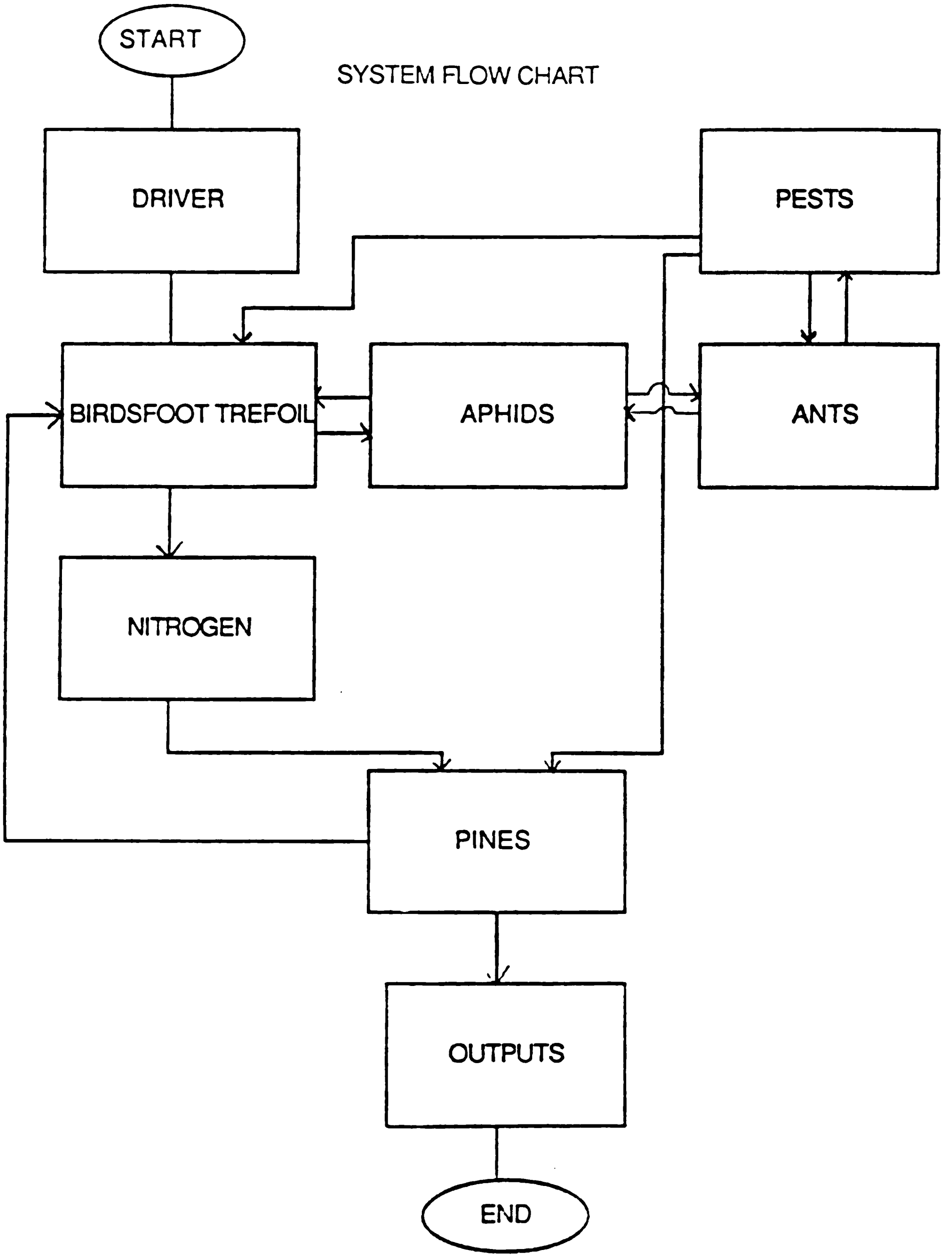


Fig. 17 System flow chart

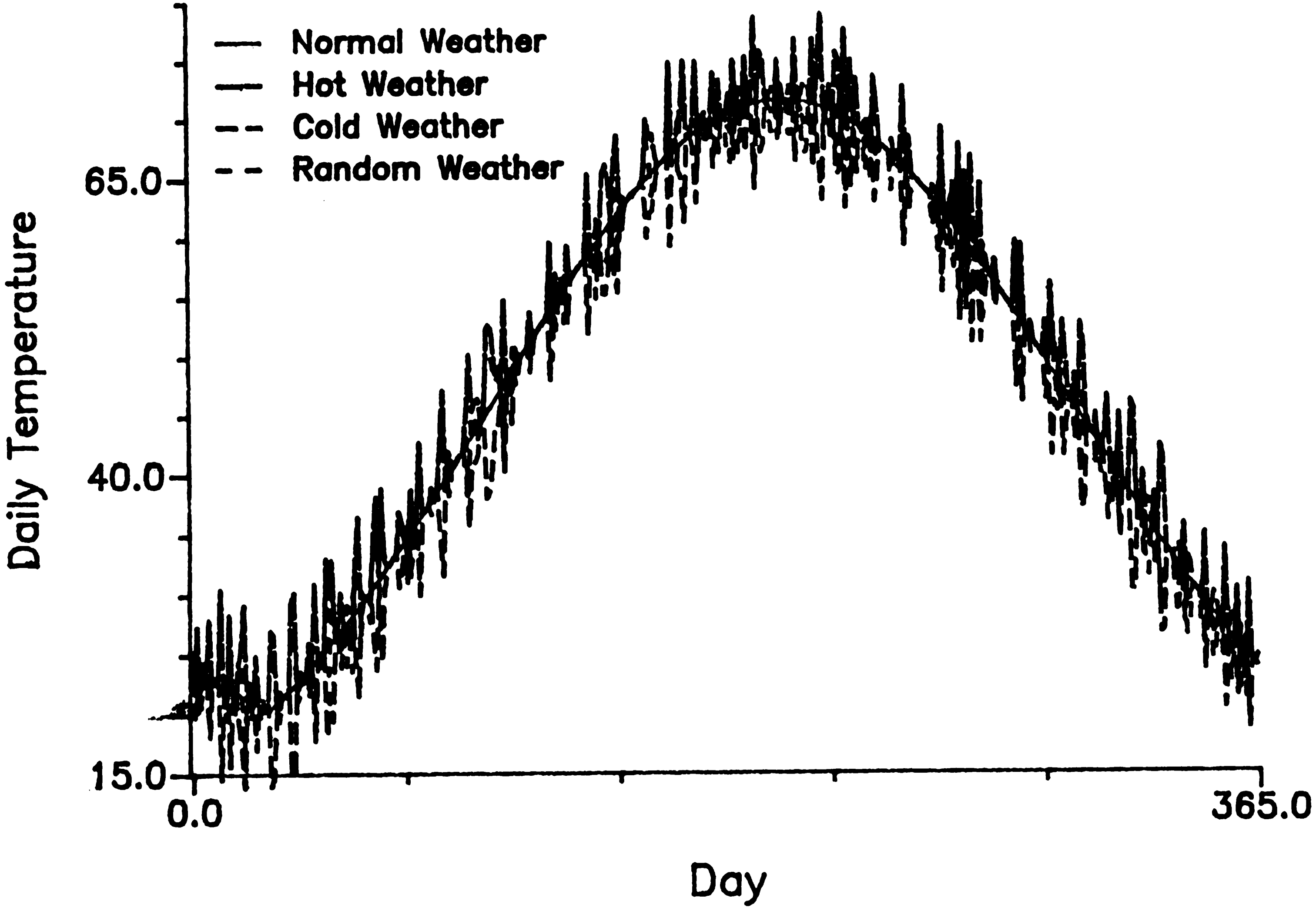
$$64.3*\exp[-(\text{Day}-203)^2 / 19280] = 7.4. \qquad [1]$$

It generates temperature, in degrees Fahrenheit that closely predicts the peak and valley and agrees with monthly averages obtained from the National Weather Service within 0.8^{o}. This curve is indicated by the solid green line shown in Fig. 18. The dashed lines signify randomized hot and cold years generated by the weather subroutine.

The subroutine allows the user to choose from four possible temperature regimes: hot, cold, normal and random. The normal was taken from a 30 year average from the First Order Noaa Weather Station. As depicted in the flowchart (Fig 19.), hot is a season that varies from the normal temperatures by -2^{0} to $+8^{0}$, cold is a season that inverts hot, and random more closely simulates normal weather patterns and varies from the normal by $+5^{0}$.

Since all random number generators on computers are 'pseudo-random' at best, the subroutine calculates daily temperatures and average weekly temperature to lessen the problem. The mean weekly temperature is then passed back to the main driver routine for distribution throughout the program.

Tree Subroutine: Scotch pine is capable of growing under almost any site conditions. On an average site, Scotch pines can be harvested for Christmas trees in 6 to 8 years. In attempting to model the growth of Scotch pine, we were looking for what is referred to as a "level 4" model (Landsberg, 1981) which would simulate growth as a function of radiant energy, water balance, and soil nutritional status. However, an extensive review of the literature indicated that previously developed models were lacking in two important criteria. First, most existing models are static in the sense that they employ the standard parameters of diameter at breast height (dbh), and site to predict biomass of



Temp = 64.3*exp(−(Day−203)²/19280)+7.4

$$\mathrm{Temp} = 64.3 * \exp(-(\mathrm{Day}-203)^2/19280)+7.4$$

MICHIGAN WEATHER

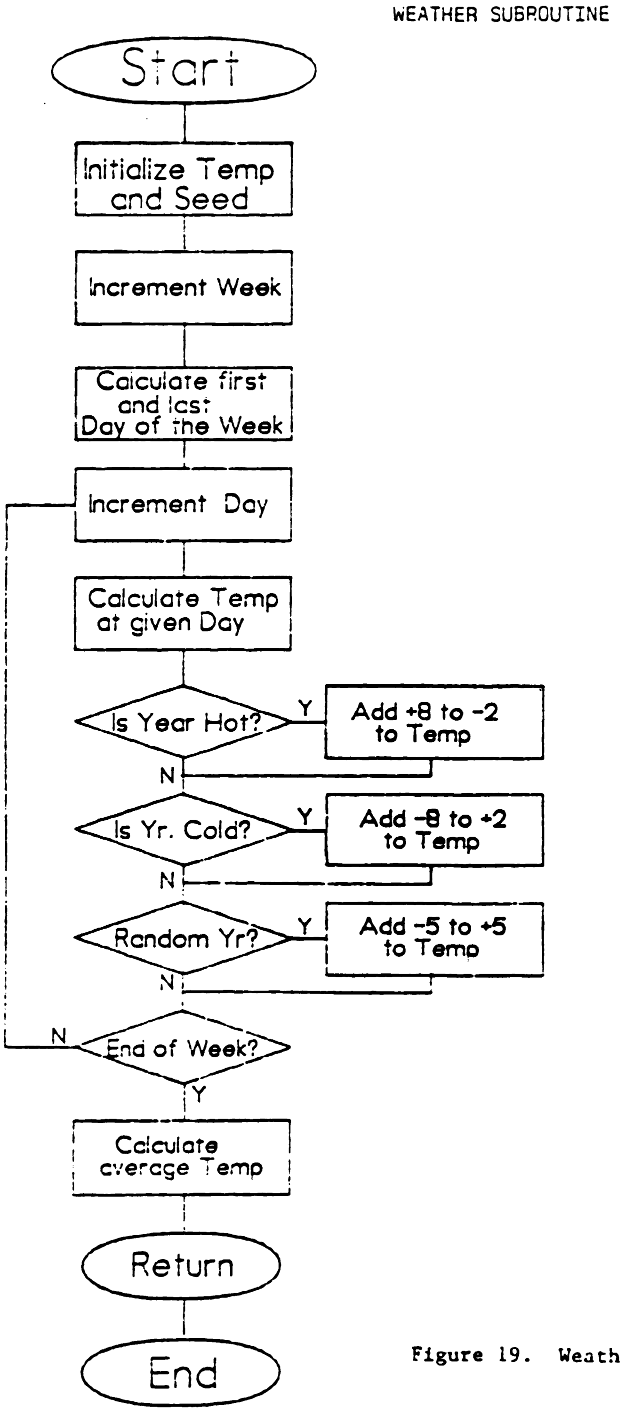


Figure 19. Weather Subroutine

wood volume· Moreover, these models are more suited for longer rotations/timber management than for Christmas tree culture. Second, these models only estimate above ground-biomass or wood volume and do not measure what Christmas growers "sell" which is leaf area and form (Pregitzer 1988).

The basis for our new TREE subroutine (Fig. 20) stems from what is referred to as a "pipe" model theory" (Waring et al., 1982). This theory maintains that a unit weight of tree foliage is serviced by a specific cross-sectional area of sapwood in the crown. Based on this relationship, Waring et al. (1982) citing Whitehead, provides an equation to determine leaf area of Scotch pine given the cross sectional area of sapwood directly below the crown. The equation is:

$$\text{Leaf area } (m^2) = 0.14 * \text{Cross-sectional sapwood area } (cm^2) \qquad [2]$$

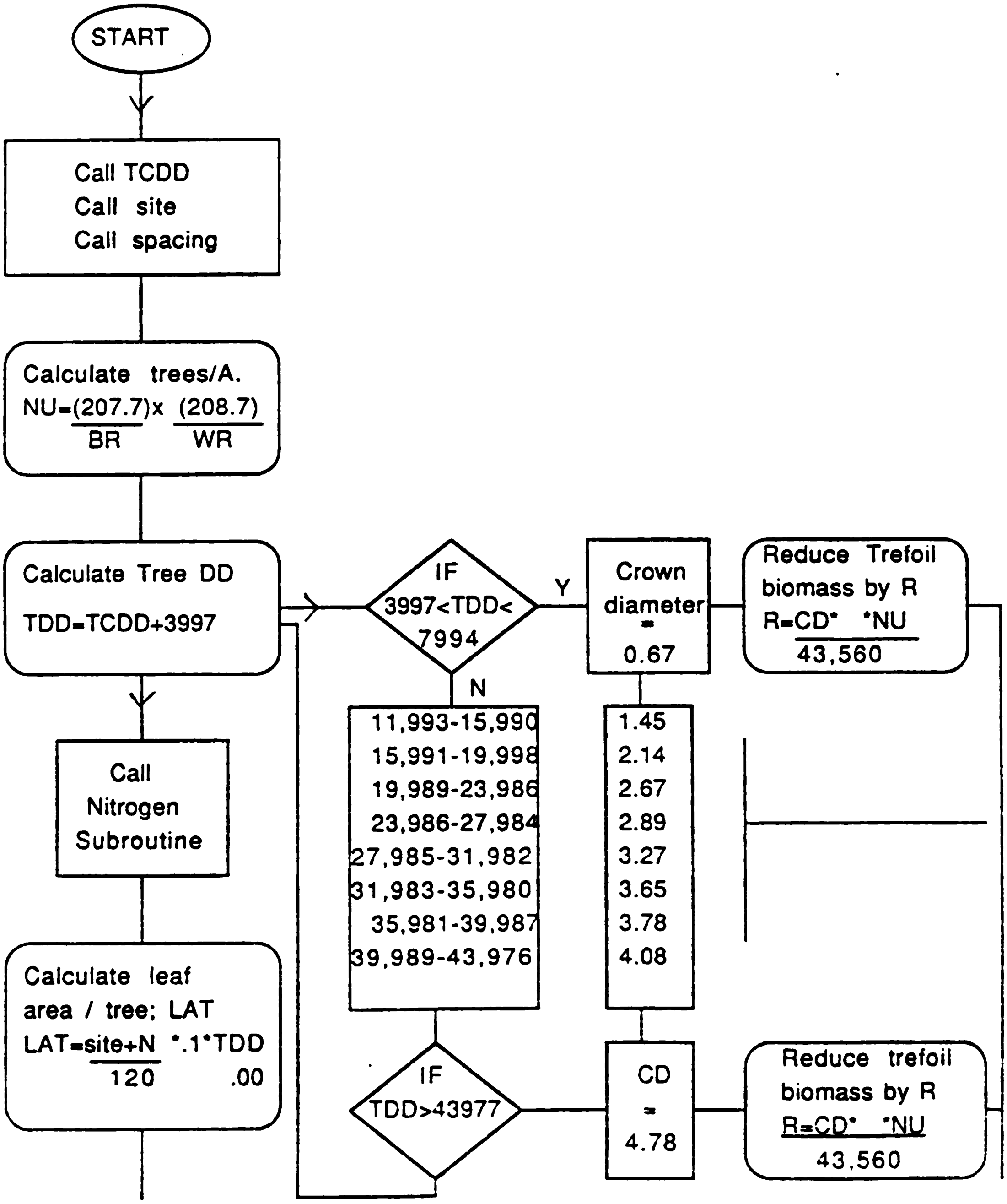
Data were then collected on sapwood area at ground level for different age classes of Scotch pines at the Tannenbaum Christmas tree farm located near the Michigan State University campus (Appendix 1). Total leaf area per tree was then estimated using equation [2] and regression analysis was used to predict leaf area as a function of cumulative degree days at base 45[2]. The resulting equation is:

$$\text{Leaf area/tree}(m^2) = 0.000104 * \text{Cumulative degree days} - 0.042 \qquad [3]$$

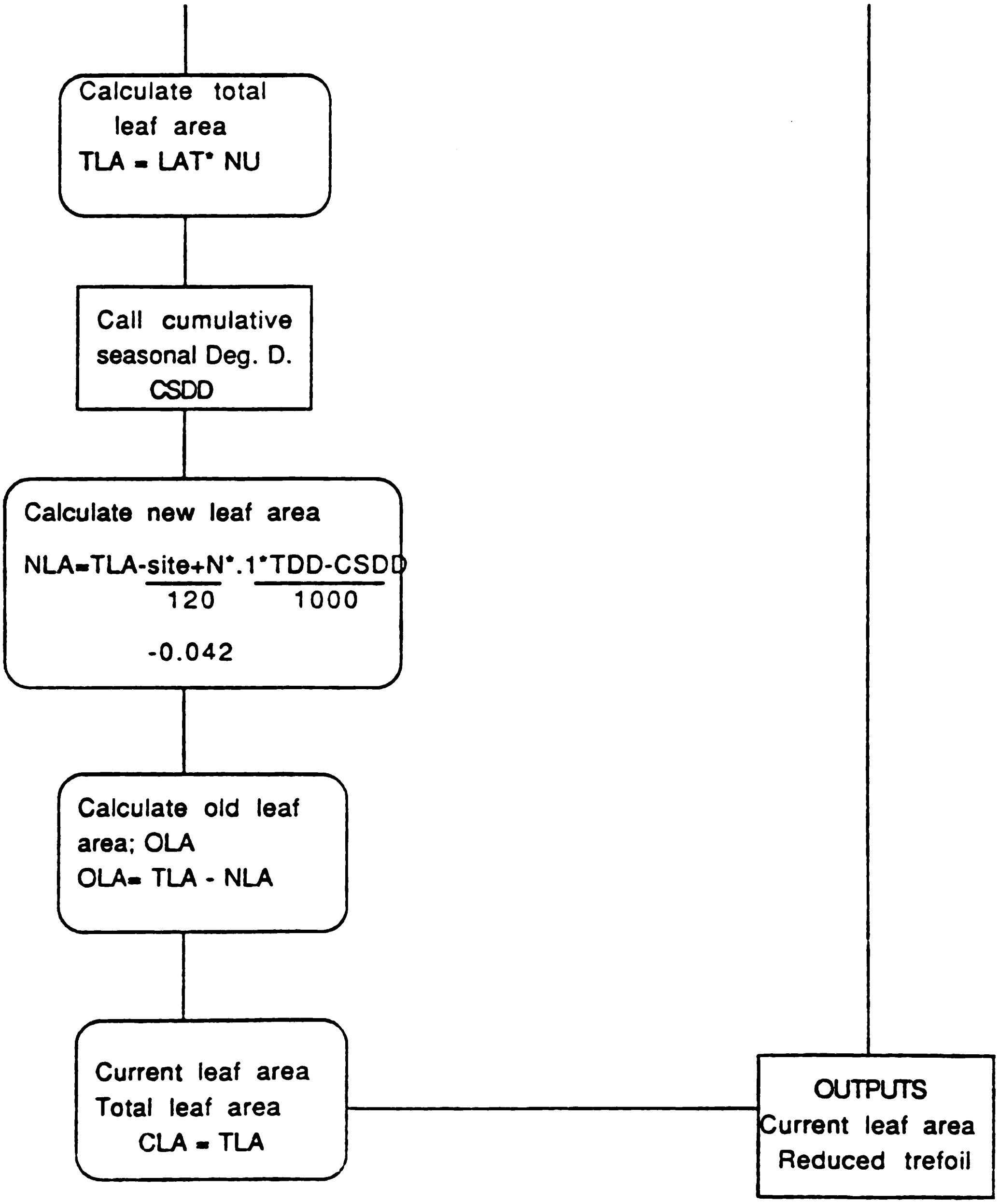
$$\text{Adjusted } r^2 = 0.838$$

It was also necessary to incorporate a site factor into this equation in order to quantify for the contribution of the trefoil nitrogen to increased leaf

Figure 20. TREE SUBROUTINE



Tree Subroutine Conti.



area. Unfortunately, time constraints did not permit sampling trees at representative sites. As a second best alternative, a site factor coefficient was developed for the leaf area equation. This coefficient is based on potential corn yield (corn equivalent yield) for various Michigan soil types. The soil type where the sapwood data was collected is one of the best in Michigan with a corn yield potential of 120 bushels per acre. The coefficient is based on the assumption that maximum leaf area is obtained on the best soil types. This coefficient is:

Original Site + Site Improvement Factor(from NITROGEN)/120 [3]

We assumed that any particular site could not be improved more than its maximum potential. Thus, in the model, this factor is always 1.0 or smaller.

The third major component of the tree subroutine attempts to account for reduced trefoil biomass as a result of competition for radiant energy between the trees and the trefoil. In order to incorporate competition, reduced trefoil planting density/biomass was considered to be a function of trees crown diameter. Data on tree crown diameter for different age classes were collected at the Tannenbaum farm and used to determine a trefoil reduction factor based on the following equation:

Trefoil Reduction Factor = (Crown Diameter*pi*No.Trees/Acre)/43560 [4]

The user of the simulation model is able to specify both between-row and within-row spacing as well as the original site factor (in corn yield equivalents) from the driver. Outputs of this subroutine are leaf area, adjusted by the site improvement coefficient and the pests; and the trefoil reduction factor.

Other assumptions in the development of this subroutine are:

1) there is a linear relationship between leaf area growth and time from 0 to 10 years. However, when actual data were plotted, same inflection is noted between 1-2 years and between 9-10 years.

2) crown diameter remains constant during any one growing season.

3) trefoil would eliminate all weeds and that any competition between trefoil and the trees is only for radiant energy.

4) total leaf area is directly related to site quality and that corn yield can be used as an indicator of site quality for Scotch pine.

TREFOIL SUBROUTINE: Birdsfoot trefoil, a perennial forage legume, has become the most frequently used plant in soil and water conservation projects. In addition to being a competitive plant, it provides weed control through the release of allelopathic chemicals. This in conjunction with its potential for nitrogen input, made it a prime candidate for the intercrop.

We had originally intended to model the growth of trefoil as a function of radiant energy, soil moisture and soil nutritional status, similar to the TREE subroutine. However, as development of the other subroutines progressed we found that only two points in the trefoil's development cycle were needed. The first is when the plant reaches a dry weight of approximately 10 g/plant and thus has sufficient leaf area and sap production to sustain aphid populations. This point is estimated to be at approximately 200 degree-days at base 45. The second point is when the trefoil reaches its maximum biomass potential (i.e. the top of the growth curve). This point is estimated to be at approximately 800 degree-days.

The flowchart describing this subroutine is presented in Fig. 21. The main input in this subroutine is planting density specified from the driver. The driver limits planting density between 10 and 30 plants m^2 and provides the user with an indication of the appropriate planting density which is dependent upon site quality. The system provides for harvesting the trefoil when the pest densities reach destructive levels. In addition, this subroutine allows for one mid-season management mow. If the ants adequately control the pests, then the mowing command again becomes an option. The output of this subroutine is biomass which is directed to the aphid and nitrogen subroutines.

Actual trefoil above-ground biomass yield is based on an equation developed by McGraw et al. (1986), employing planting density as the driving variable. The equation is:

$$\text{Biomass Yield } (g/m^2) = (654*\text{Planting Density})/3.54 + \text{Planting Density}) \quad [6]$$

This figure was then converted to biomass yield in pounds/acre.

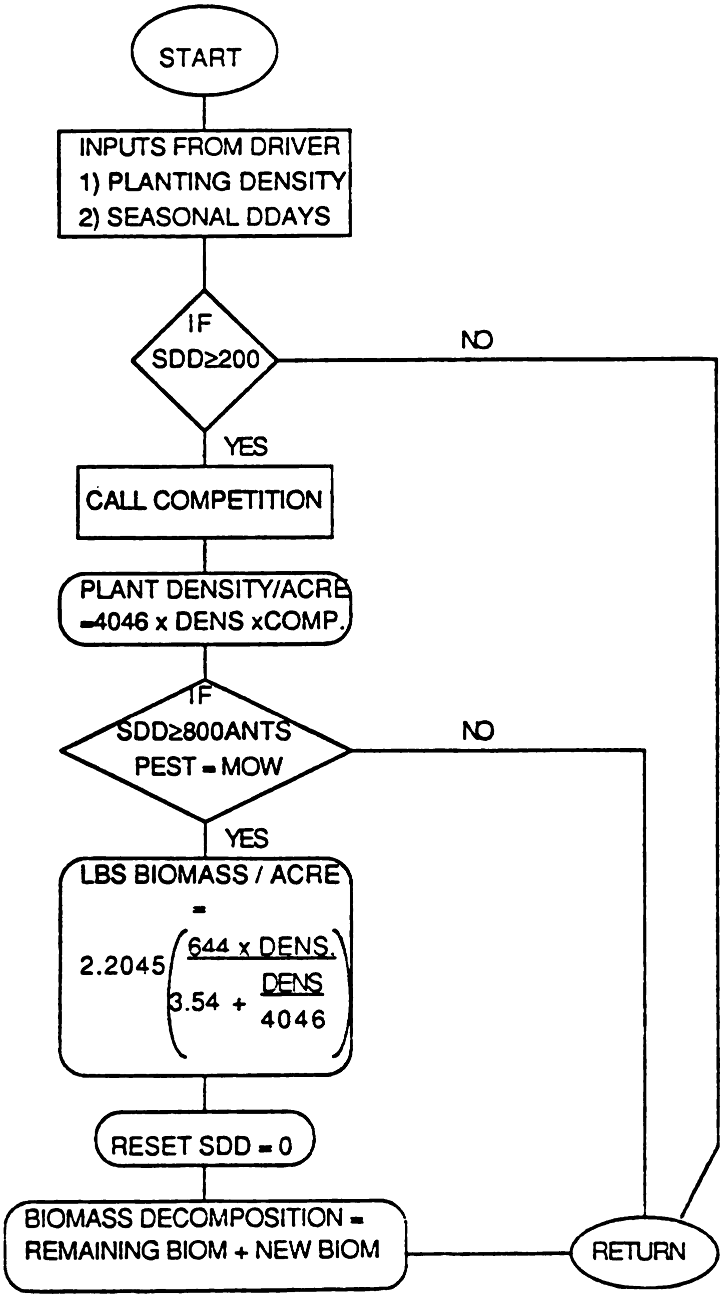
Other major assumptions in this subroutine are:

1) that there may be a maximum of three mowings per growing season and at least 800 degree days are required between mowings for trefoil to reach maximum biomass levels.

2) that biomass levels remain constant after 800 degree days until the trefoil is mowed.

3) that in the event that the trefoil is not mowed during the season (by the user or by the aphids), standing biomass at the end of the season is mowed and enters into the NITROGEN subroutine the following growing season.

Figure 21. TREFOIL SUBROUTINE (SIMPLIFIED)



NITROGEN SUBROUTINE: Nitrogen is a limiting factor in Scotch pine culture. While many tree-soil systems are deficient in nitrogen, there have been no attempts to model the cycling of the nitrogen in the tree-soil system. Instead the approach has been to model the behavior of the system based on expected performance using empirical and non-mechanistic equations.

The purpose of the nitrogen subroutine is to determine the nitrogen application rate due to the decomposition of the mowed trefoil in pounds/acre of organic material, and to calculate the subsequent site improvement due to the addition of nitrogen in bushels/acre. The site improvement value is a critical variable in the Scotch pine leaf area growth equation indicating the effect of site on leaf area growth.

The only input variable is the biomass of mowed trefoil. The output variable is the site improvement in terms of corn yield equivalent. Thus, when no mowing occurs and the biomass is zero, there is no subsequent site improvement. If the trefoil biomass is more than zero, mowing has occurred, and the site improvement due to the decomposing trefoil is calculated.

A negative exponential equation determined the rate of decomposition of organic matter as a pulsed input (Coleman et al. 1984).

$X/XO = e^{-kt}$ [7]

XO = the amount of trefoil at time 0

X = the amount of trefoil at time t

k = fractional loss rate

t = time interval

Equation [7] was modified to calculate the amount of mowed trefoil decomposed per week by solving for 'X' and subtracting this value from the total amount of trefoil mowed. The time interval 't' was set to be one week. The equation is:

$$\mathrm{Xdecomp} = \mathrm{XO} - \mathrm{XO}^{*}\, e^{-kt} \qquad [8]$$

where Xdecomp = the amount of decomposed trefoil biomass in one week.

The value of the decomposition rate constant 'k' has been examined in many ecosystems with low and high production rates and over a wide range of environmental conditions. A decomposition rate constant of 1.5 for a temperate grassland was used in the model. To obtain a rate per week, this value was divided by the number of weeks in our growing season.

The next step was to determine the amount of nitrogen applied to the system by the decomposed trefoil. Assuming an available nitrogen content of 3.6% of total trefoil biomass (Fribourg et al. 1956), the actual nitrogen application rate in pounds/acre/week is:

$$\mathrm{Napprate} = \mathrm{Xdecomp}/27 \qquad [9]$$

The site improvement factor in bu corn/acre is then calculated using a logarithmic equation that determines yield response of corn to the application of nitrogen in the form of alfalfa tops (Fribourg et al., 1956). It was assumed that this response is similar for trefoil litter application, because trefoil is closely related to alfalfa. Trefoil and alfalfa are both nitrogen fixing legumes (*Leguminacea)*.

$$\text{Site Improvement} = \{105.2[1-10 - 0.01484(N+35.2)] - 73.6\}/100$$

where N = nitrogen application rate. [10]

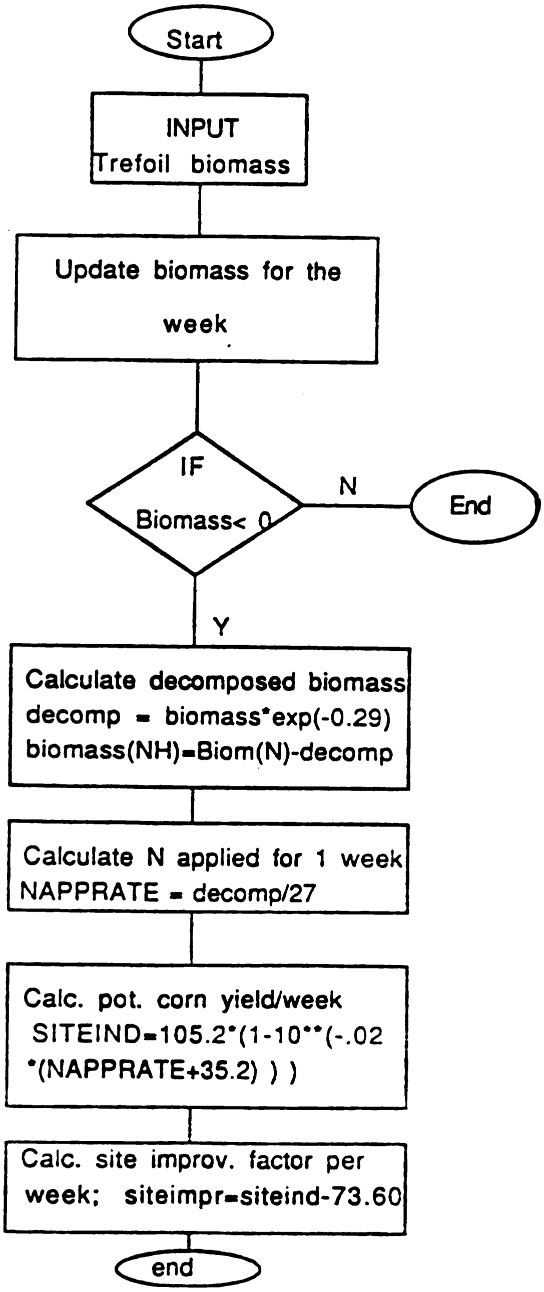
We modified the above equation in several ways. First, upon closer examination of the equation is was evident that the response of corn yield to nitrogen application in the form of alfalfa tops was unreasonably high. For example, the equation predicts that an application of only 6 pounds/acre of alfalfa nitrogen improved corn yields by 73 bu/acre to 80 bu/acre. To obtain a more realistic value a long-term availability of nitrogen of 1% was assumed for site improvements.

Finally, we assumed that all the nitrogen contained in the trefoil biomass is available to the Scotch pine for uptake after decomposition. Furthermore, nitrogen fixation and immobilization by microbes and leaching of available nitrogen from the soil were not incorporated in this subroutine because there was not enough time during the systems science course and it would be a very complex subroutine to develop. The difference in availability of nitrogen in sand, loam or clay was also not taken into consideration. The flowchart for the NITROGEN subroutine is represented in Fig. 22.

REDHEADED PINE SAWFLY SUBROUTINE: The redheaded pine sawfly is an important defoliator of young hard pines in eastern North America. The sawfly occurs in colonies of a few to more than 100 larvae, and just one or a few colonies can readily strip a small tree (1-5m) of its foliage (Averill et al. 1982; MacAloney & Wilson 1964). Even lightly defoliated Christmas trees are unfit for sale (USDA, 1983). Adult females prefer to lay their eggs on trees that are under stress.

The redheaded pine sawfly overwinters as pupae in the topsoil or duff. When degree-day accumulation surpasses 298, then the adults emerge. Below 298, ants are actively preying on the pupae. Between 298 and 500 degree days,

NITROGEN SUBROUTINE



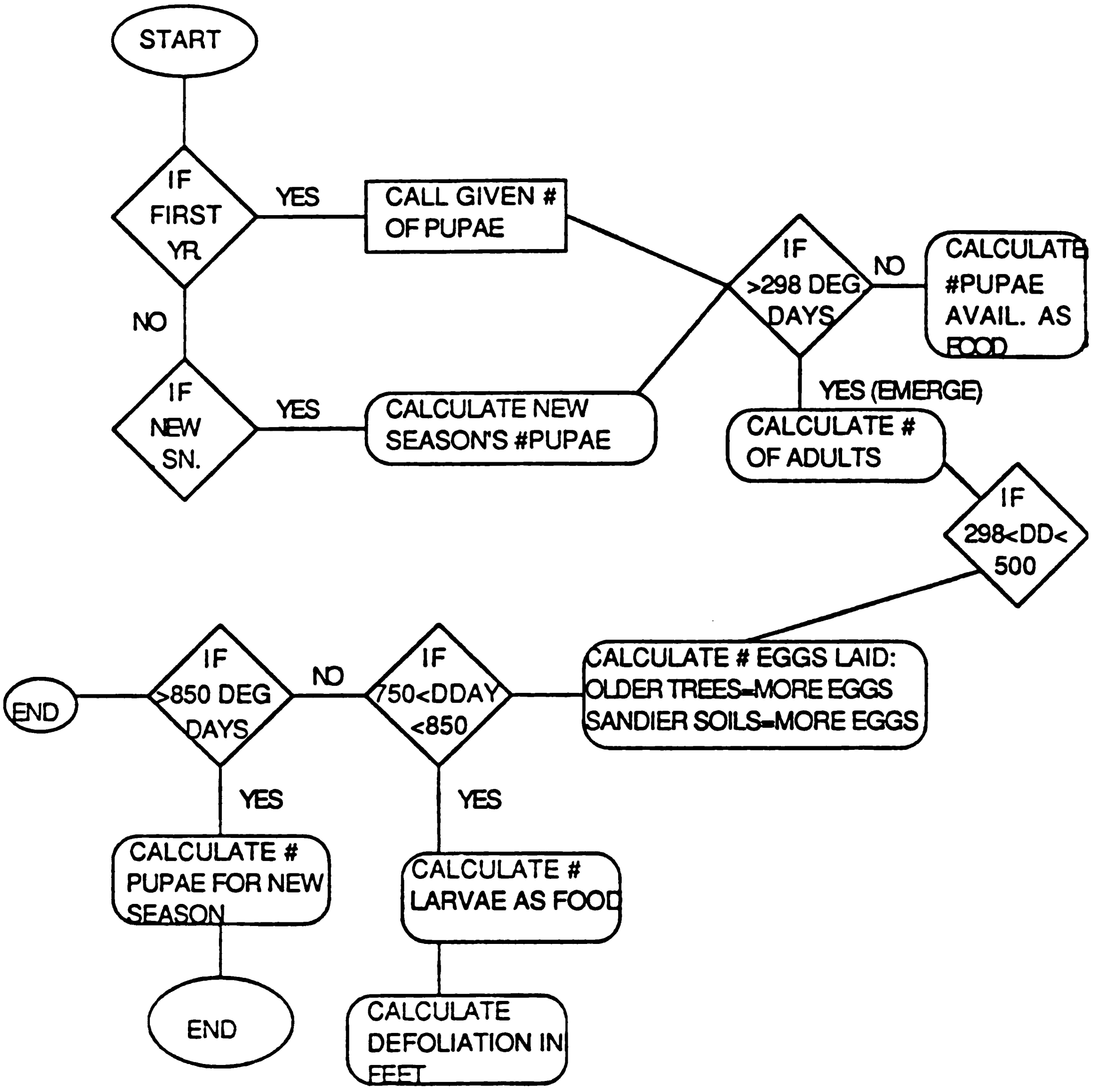
the females oviposit. If the trees are grown on a poor site or if the trees are older, it is assumed that the number of eggs laid reaches its maximum potential. Between 750 and 850 degree days the larvae hatch and start feeding immediately. By knowing the number of larvae, the amount of defoliation can be estimated. Studies showed that from the first to fifth instars, each larva can consume about 1.1 inches of foliated branch (Averill et al, 1982). The number of larvae used in the defoliation calculation equals the number of larvae available to the ants as food.

After 850 degree days pupation begins and defoliation tapers rapidly. The number of larvae that reach this stage and survive the winter, plus the number of pupae from the beginning of the season are used both for the number of sawflies available to the ants as prey and to determine the population density for the next year. This value is used to calculate the new season's pupae and reinitiates the cycle. The outputs of this subroutine are: 1) the number of larvae available to the ants as prey, and 2) the amount of defoliation. The subroutine is represented in Figure 23.

EUROPEAN PINE SAWFLY SUBROUTINE: The European pine sawfly, ***Neodiprion sertifer*** Geoff., larvae feed only on the older needles of pine trees. The trees usually recover and outgrow the injury in 2-3 years (USDA, 1983).

In the model, the season begins with calculating the number of eggs available. After the larvae hatch in mid- to late April, the number of larvae available to the ants as food is calculated and the defoliation caused by the larvae. The number of adults available to lay eggs is determined from the number of pupae. The total number of adults is the number that emerged from their cocoon in the current year and a small percentage of adults that did not eclose during the previous season. The outputs from this subroutine are: 1)

Figure 23. REDHEADED PINE SAWFLY SUBROUTINE



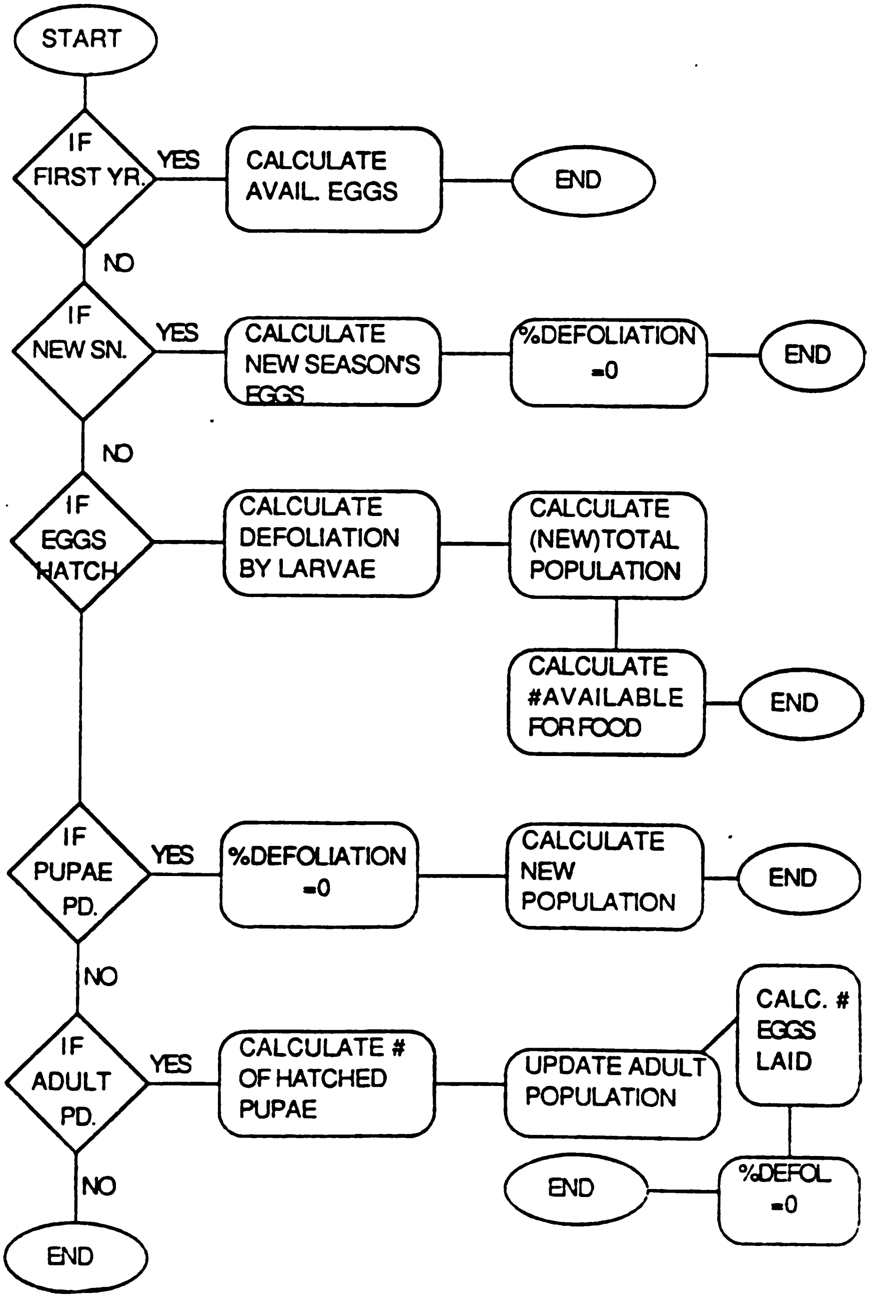
the number of larvae and pupae available to the ants as prey, and 2) the amount of defoliation caused by the larvae. The subroutine is represented in Figure 24.

APHID SUBROUTINE: Honeydew constitutes the most abundant type of food collected by many species of ants (Carol and Janzen, 1973: Skinner, 1980). However, most ants also require protein usually in the form of insect prey to complete their diet. The ant species used in this model, *F. exsectoides*, tends aphids for honeydew and preys on a wide variety of insect prey (Andrews, 1929; Headley, 1943; Haviland, 1947).

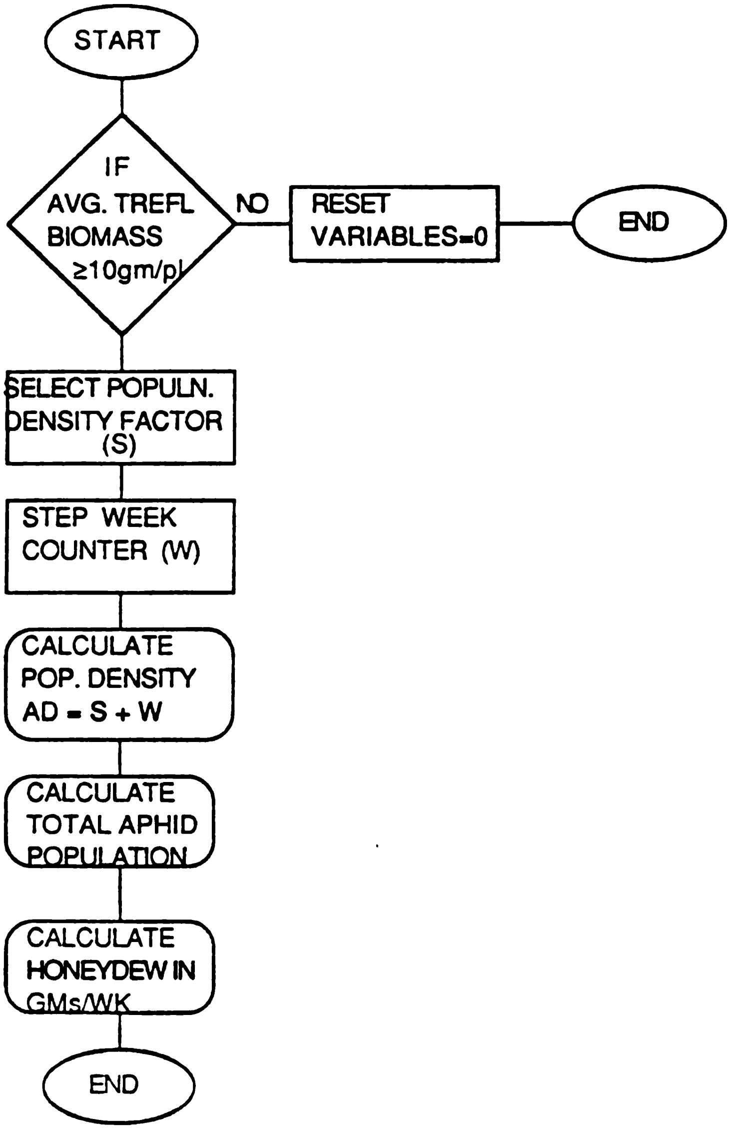
Biomass of trefoil is the only input for the APHID subroutine. If the average biomass of trefoil is less than 10 g/plant, the variables are reset to 0. If the average trefoil biomass is greater than 10 g/plant, we assumed that there was sufficient plant materials to support aphids and the subroutine is initiated. A population density for the aphids is randomly selected from one of two aphid population density series developed by Banks (1954). The density of aphids is determined at weekly intervals according to Taylor's method for estimating aphid densities on beans. Total honeydew produced (g/week) is determined based on the population density of aphids. This figure is input into the ANT subroutine. The subroutine is represented in Figure 25.

ANT SUBROUTINE: The ant species we've chosen to incorporate in the model is the Allegheny mound ant, *Formica exsectoides* Forel. This ant occurs primarily in eastern United States but is also scattered throughout other parts of the country as well (Andrews 1926). *F. exsectoides* is a predator of many forest insect pests, but also feeds on honeydew which is produced by aphids and other Homoptera. Because of this broad feeding habit, we assumed that *F.*

Figure 24. EUROPEAN PINE SAWFLY SUBROUTINE



APHID SUBROUTINE



exsectoides can maintain high and active populations in the absence of abundant insect defoliators by switching their foraging towards collecting more honeydew or perhaps soil dwelling arthropods.

In the ANT subroutine, manipulating this switching behavior is the key element in our biological pest management program. This is done by mowing the trefoil, thus significantly reducing the honeydew available to the ants. This obliges the ants to switch their foraging toward the insect pests of on pines. Mowing is done during the night when the number of ants foraging is reduced.

The amount of honeydew from the aphids subroutine is input into the ANT subroutine. If degree-day accumulation is less than 64, it is assumed that the ants are not actively foraging on either insect prey or honeydew. When degree day accumulation is greater than 64, a predation rate is selected. The predation rate is derived from published figures on the amount of prey/ day brought back to a mature nest of a closely related *Formica* spp. (Skinner, 1980), because values were not available for *F. exsectoides* . The maximum number of insects brought back to the nest in June is 3,600. This value correlates with the greatest need for protein to meet maximum brood production at this time. The minimum value of insects brought back to the nest is in September with a value of 500 insects/day and correlates with the decrease in protein needed because brood production has significantly declined (Haviland, 1947). When the ant colonies are younger then 4 years old, the predation rate is reduced by 0.9 due to the smaller foraging force that would be associated with smaller ant colonies. Although the demand for food increases during this phase of colony development, there is only a maximum amount of prey an individual forager can retrieve.

The subroutine is presented in Fig. 26. Next, the subroutine calculates the amount of prey eaten. This equation depends upon the amount of available honeydew and utilizes the predation rate previously selected.

The output from the ANT subroutine is: P = the number of prey eaten by the ants.

The assumptions of the subroutine are:

1) *F. exsectoides* will increase predation for a specific type of prey as it becomes available in the environment..

2) *F. exsectoides* can maintain and function as a colony in the absence of their main honeydew resource for relatively short periods of time (1-2 weeks), after harvesting the trefoil.

3) the ants will prey more heavily on insect prey in the absence of honeydew.

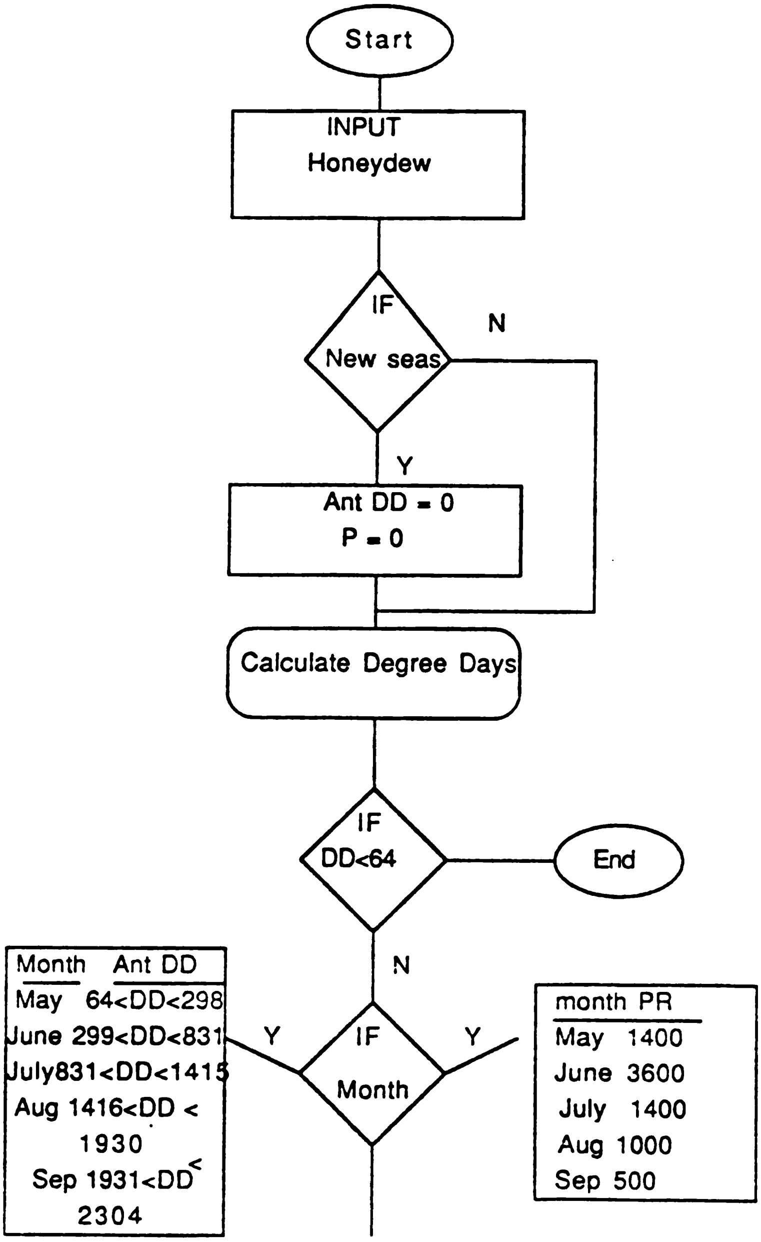
Analysis of Output

Simulations from this model addressed the more basic questions about the "improved" system including, trefoil, leaf area and defoliation, site improvement, and variations of defoliations as a functions of tree age, number of ant colonies and site quality.

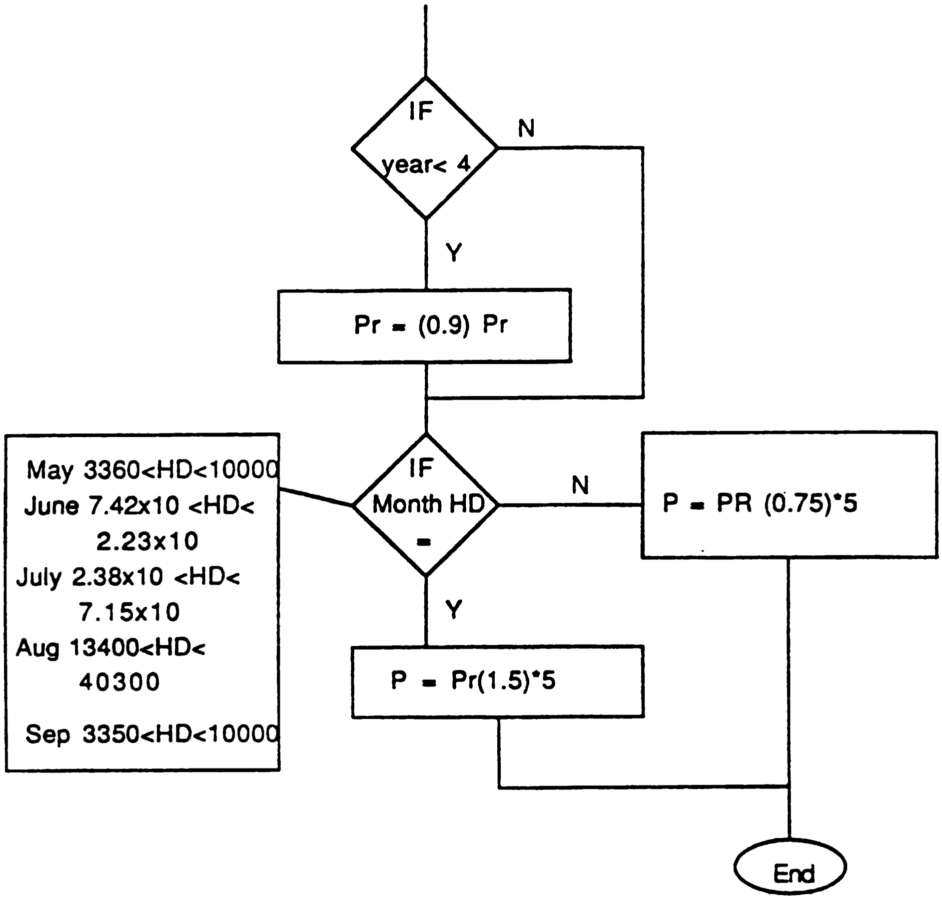
Trefoil vs. Leaf Area and Defoliation: The simulations showed that regardless of the original site classification, the improvement in terms of increased leaf area depends is influenced more by the number of mowings than the density of trefoil. To show the effect of trefoil density on leaf area for a given site classification, the leaf area generated by the site with no trefoil input was subtracted from all curves. The resulting curves are relative to this "constant" site (Figs. 27-30).

While all of the relationships are linear, the greatest site improvement occurs when the trefoil density is 10 plants/m^2. Only slight improvements

Figure. 26. ANT SUBROUTINE



ANT SUBROUTINE CONTINUED



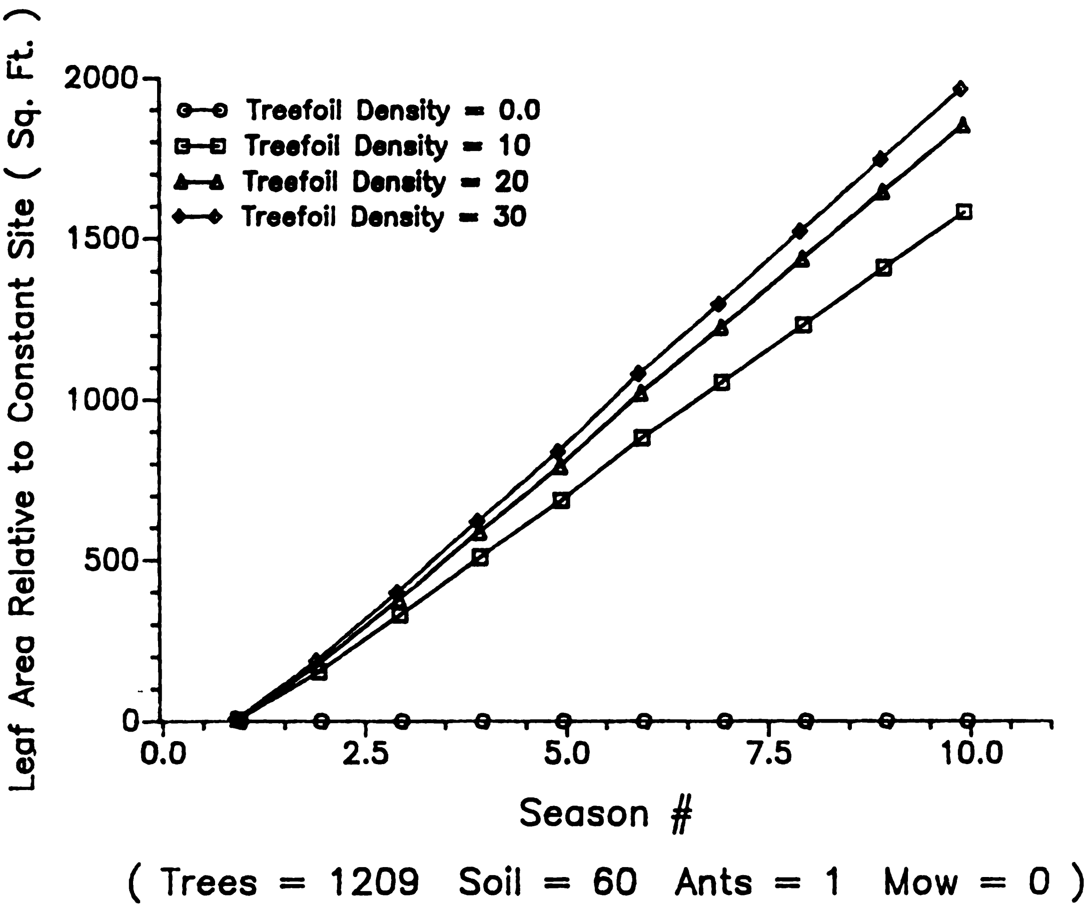
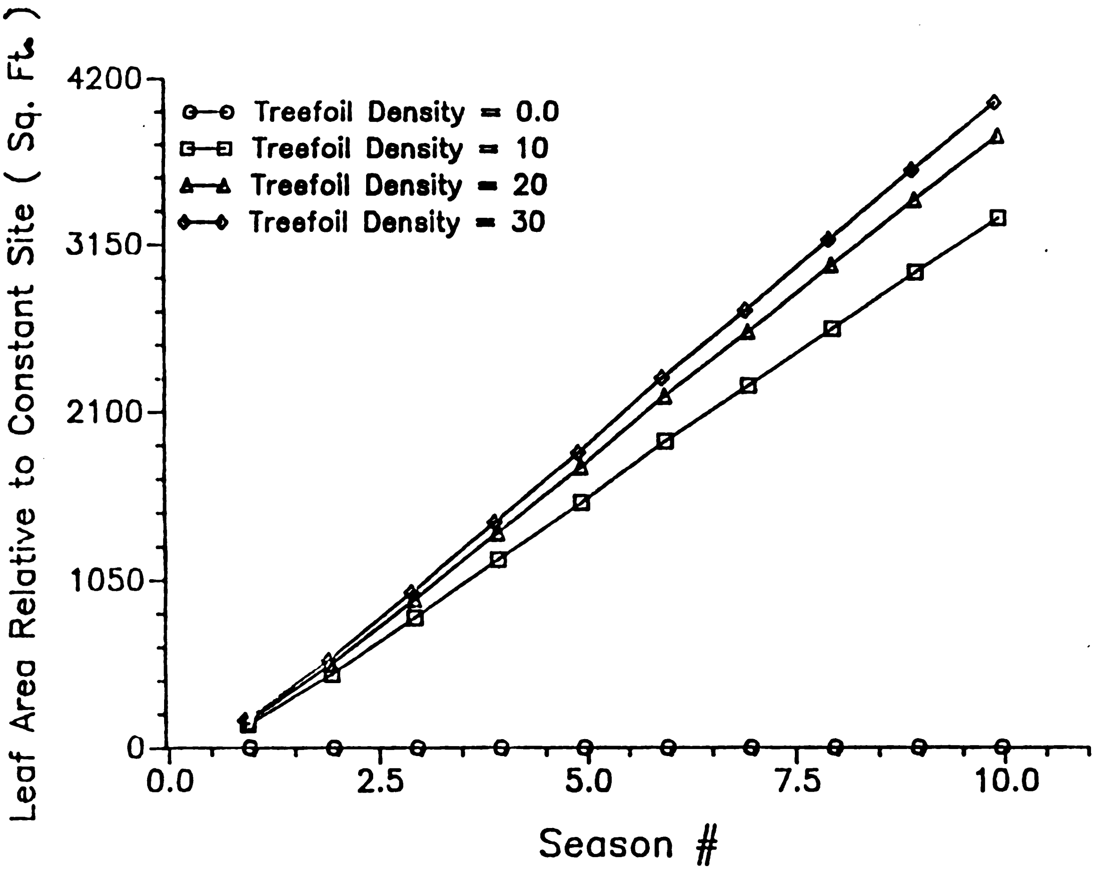
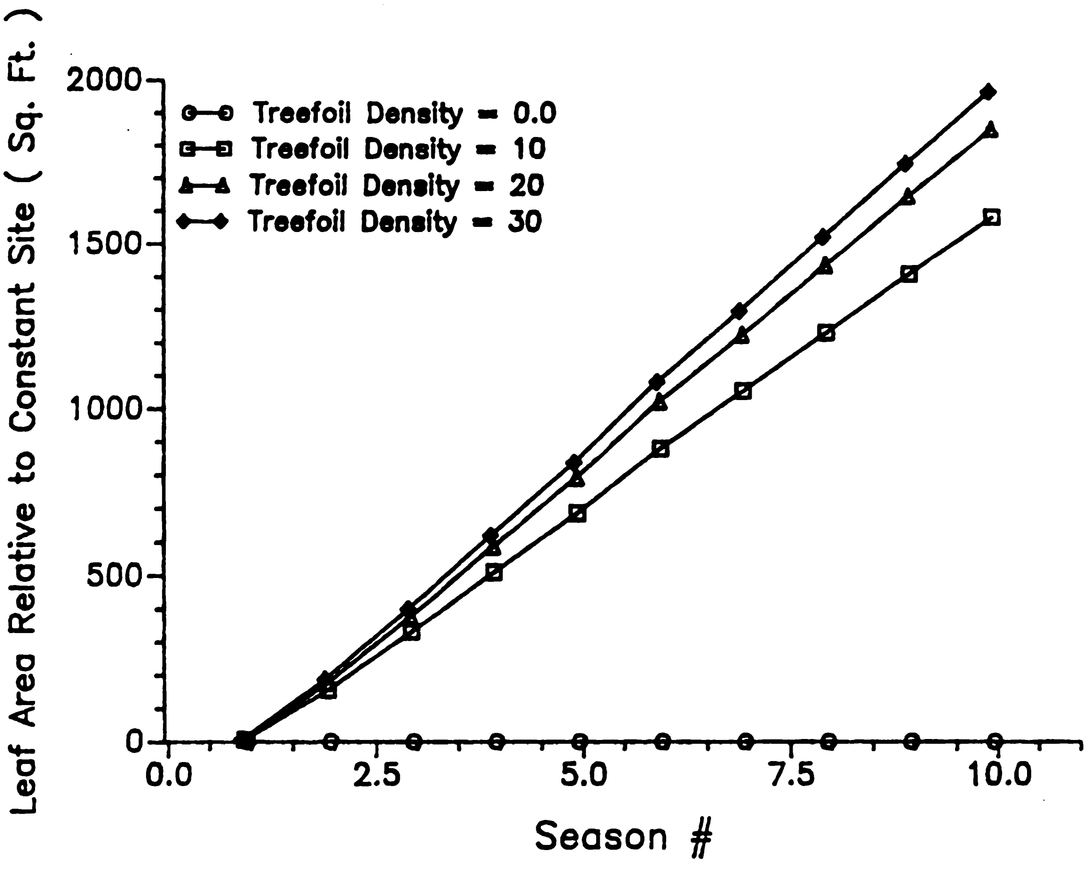


Figure 27. EFFECT OF TREEFOIL ON TREE GROWTH



(Trees = 1209 Soil = 60 Ants = 1 Mow = 1)

Figure 28. EFFECT OF TREEFOIL ON TREE GROWTH



(Trees = 1209 Soil = 100 Ants = 1 Mow = 0)

Figure 29. EFFECT OF TREEFOIL ON TREE GROWTH

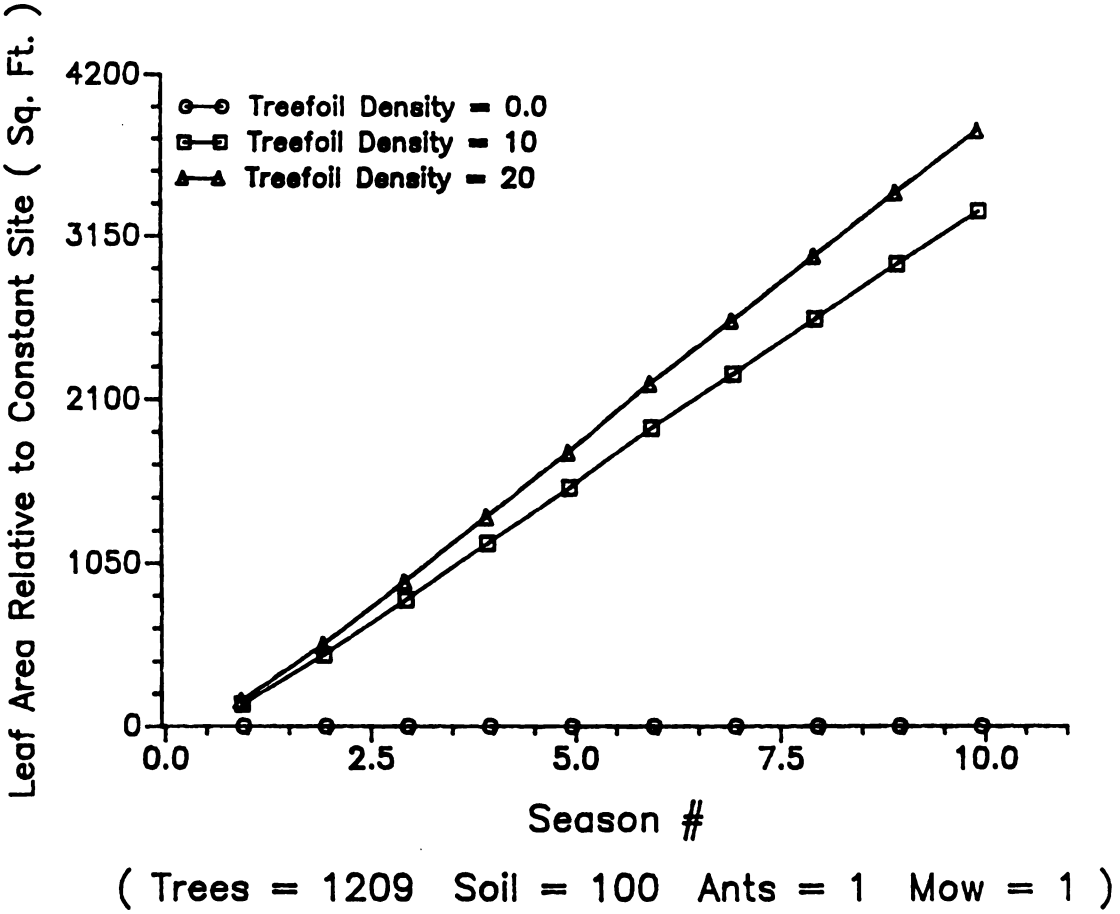


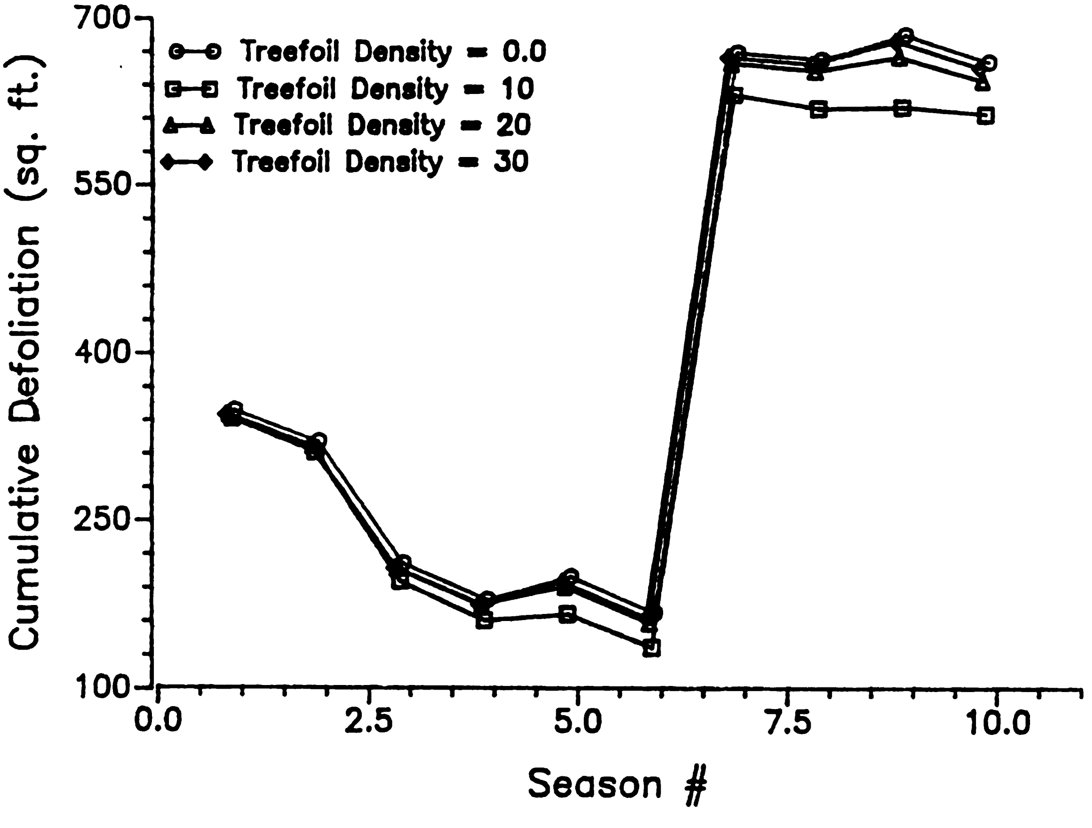
Figure 30. EFFECT OF TREEFOIL ON TREE GROWTH

occur when higher densities of trefoil are used. One mowing per season results in a maximum improvement of 4000 ft^2 over a 10 year period. If the trefoil is not mowed at least once per year, (allowing only decomposition at the end of the season) this figure is reduced by 50%.

If the primary objective is to increase leaf area and produce a high grade Christmas tree, then planting the trefoil at the highest density would seem to be the best strategy. The simulations showed that defoliation does not decrease proportionately to increases in the density of trefoil planted. In fact there is a slight trend toward a decrease in defoliation with lower densities of trefoil (Figs. 31 & 32). These results can be best understood by remembering that as the density of trefoil increases, the number of aphids and therefore available honeydew to the ants also increases. The model assumes that the ants will forage most readily on the food resource that is available in the greatest quantity, and, colony demands relative to brood production are also accounted for. Theses simulations suggest that the density of trefoil planted should be optimized, not maximized.

Site Improvement: One function of the trefoil is to supply nitrogen to the soil in an attempt to improve the site quality. This is especially relevant to Michigan Christmas tree production because pine plantations are usually established on marginally sandy soils. Site improvement is measured in terms of additional corn yields (corn equivalents) per acre. Thus, only site improvement for a site with a base rating of 60 corn equivalents was analyzed. The analyses was also limited to sites with 1 ant colony and mowing regimes of 0 (end of the season decomposition) and 1 (end of the year decomposition plus one management mow).

Although there is a carry-over each year of decomposing biomass in the soil, the decomposition rate and quantities of trefoil biomass are such that



(Trees = 907 Soil = 90 Ants = 2)

Figure 31. EFFECT OF TREEFOIL DENSITY ON DEFOLIATION

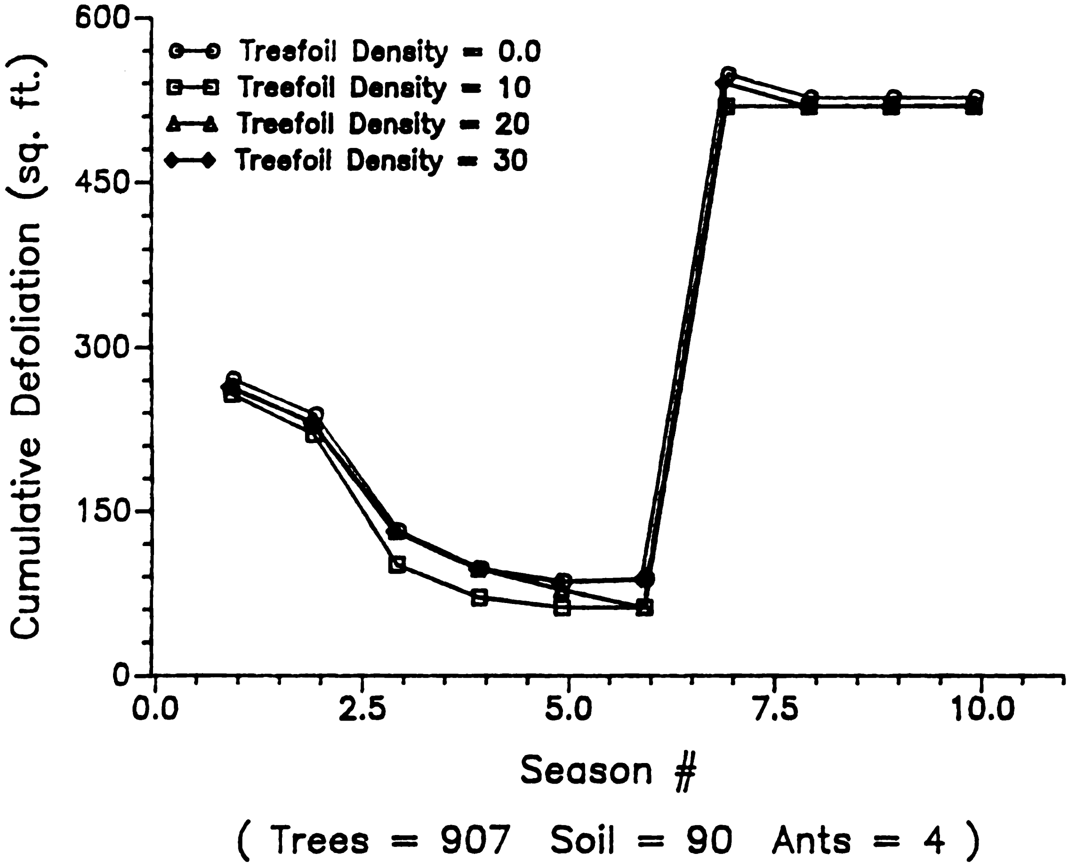


Figure 32. EFFECT OF TREEFOIL DENSITY ON DEFOLIATION

it is not possible to attain a maximum site improvement (to 120 corn equivalents) within the 10 year growing cycle used in the model. However, the simulations suggest that the 10 year time frame is enough time to significantly increase the quality of the site. This is best achieved by mowing the trefoil during the growing season as opposed to increasing the density of trefoil per acre (Figs. 33 & 34). Increasing the trefoil density per acre on sandy soil contributes only marginally to site improvement under either mowing regime. If the trefoil is not mowed once during the growing season, the site only realizes a maximum improvement of 15 corn equivalents over 10 years.

Mowing more than once during the growing season could significantly increase soil improvement, but because the model is based a low input sustainable system, only one mowing was incorporated in this model. Finally, tree density had little affect on site improvement. The competition factor is such that it did not significantly reduce site quality.

Variation in Defoliation as a Function of Tree Age, Number of Ant Colonies, and Soil Quality: The density of insect pests directly influences the quality and esthetic value of a Christmas trees. The main factor to influence the amount of defoliation due to insect pests was site quality. The differences in cumulative defoliation due to soil type and the number of ant colonies is shown in Figs. 35-37. As the soil type improves, the maximum defoliation decreases independent of the number of ant colonies. As the number of ant colonies per acre increases, there is also a decrease in defoliation. Potential defoliation may be due to the fact that female redheaded pine sawflies prefer to lay eggs on trees that are under stress, such as would be the case if the trees were growing on a poor site.

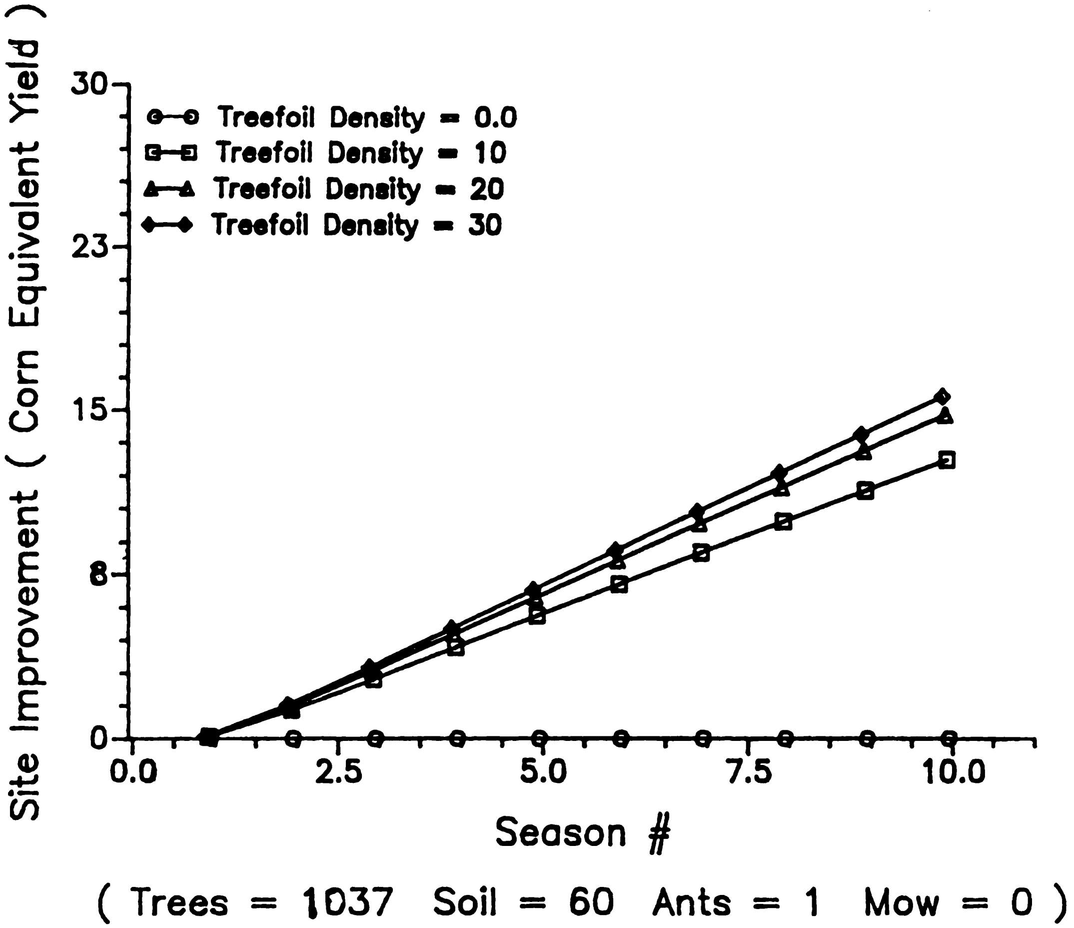
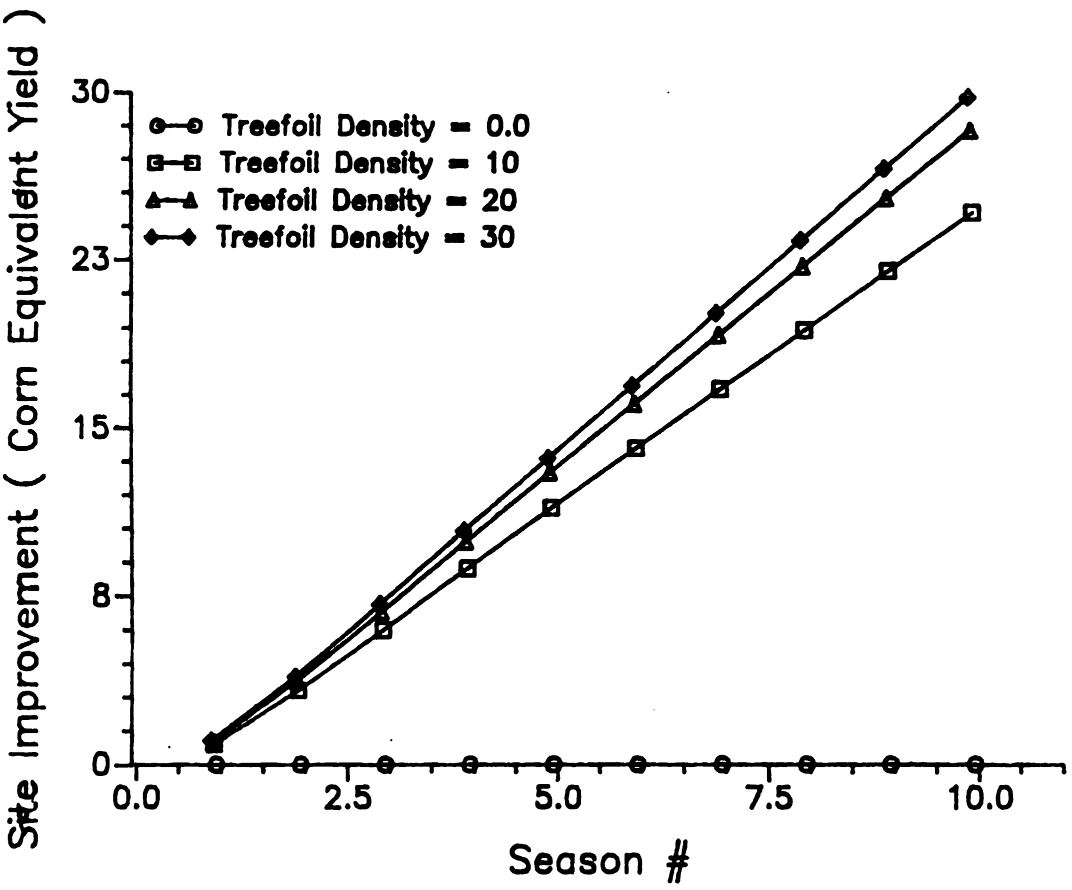


Figure 33. EFFECT OF TREEFOIL ON SITE CLASSIFICATION



(Trees = 1037 Soil = 60 Ants = 1 Mow = 1)

Figure 34. EFFECT OF TREEFOIL ON SITE CLASSIFICATION

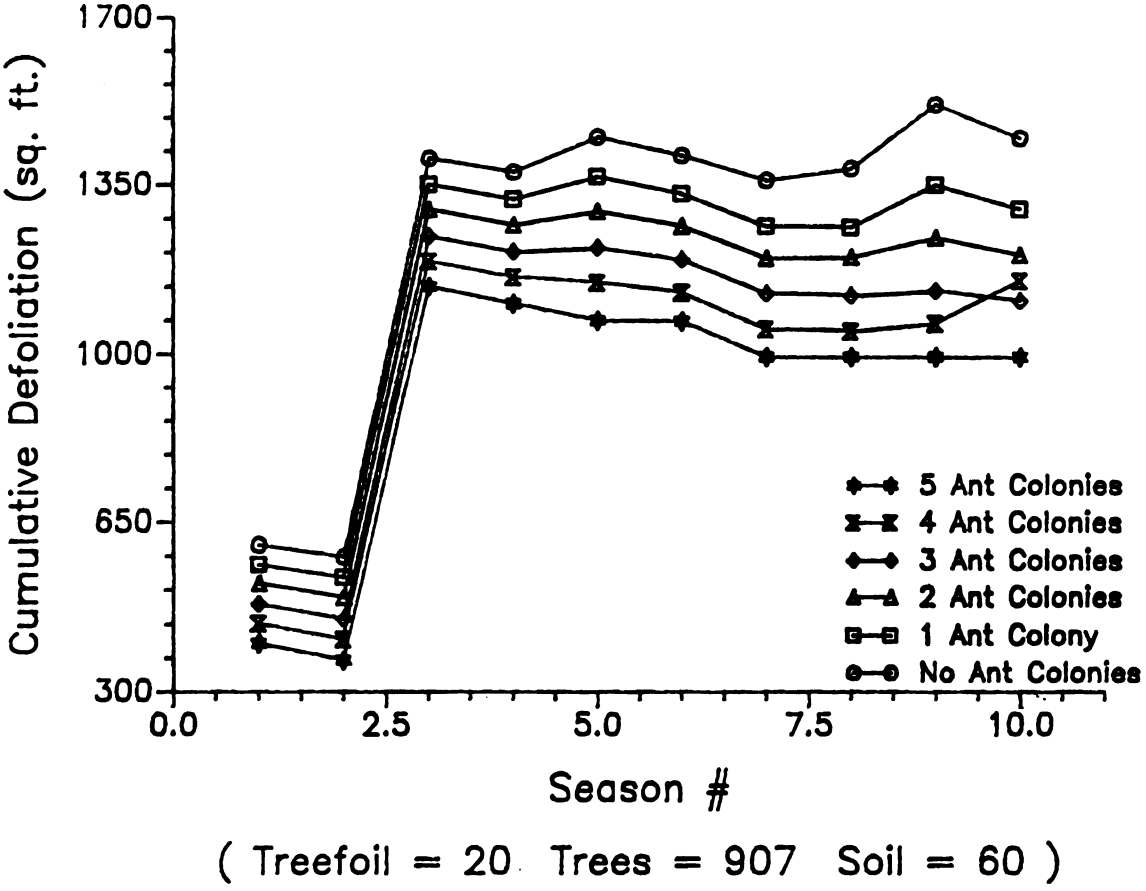


Figure 35. EFFECT OF SOIL TYPE AND ANTS ON DEFOLIATION

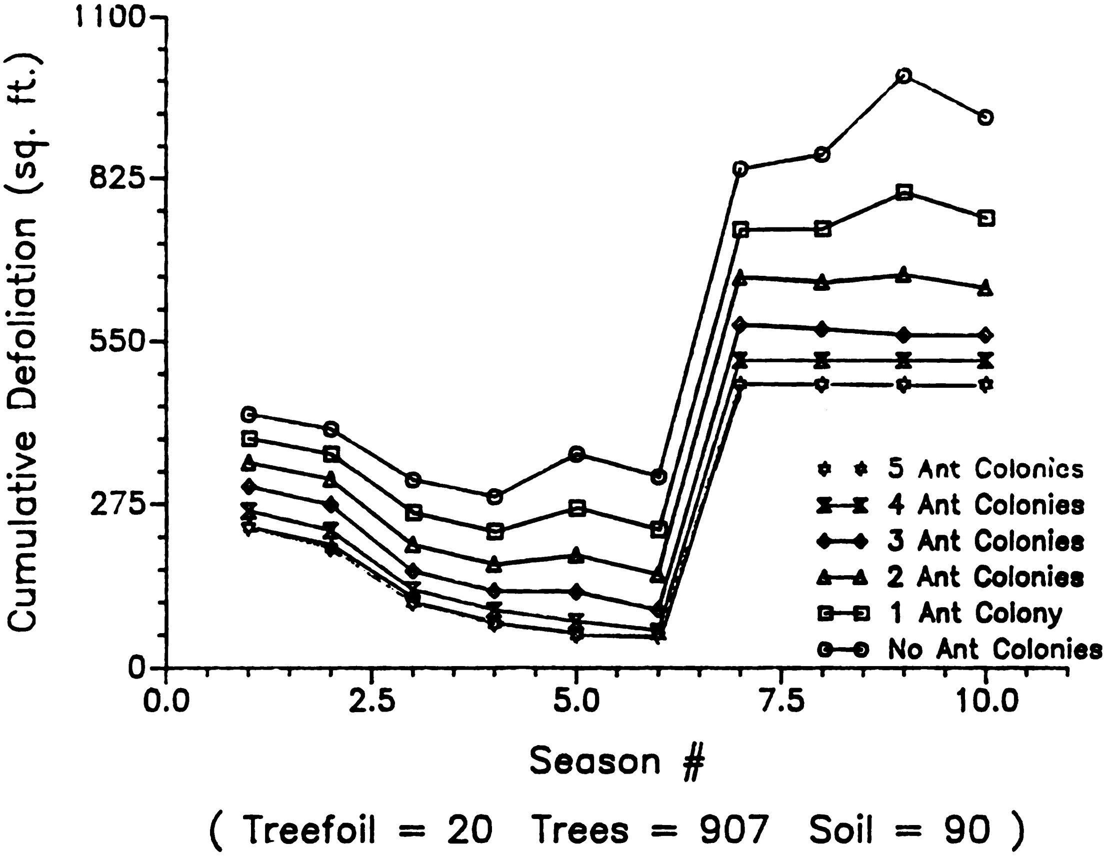


Figure 36. EFFECT OF SOIL TYPE AND ANTS ON DEFOLIATION

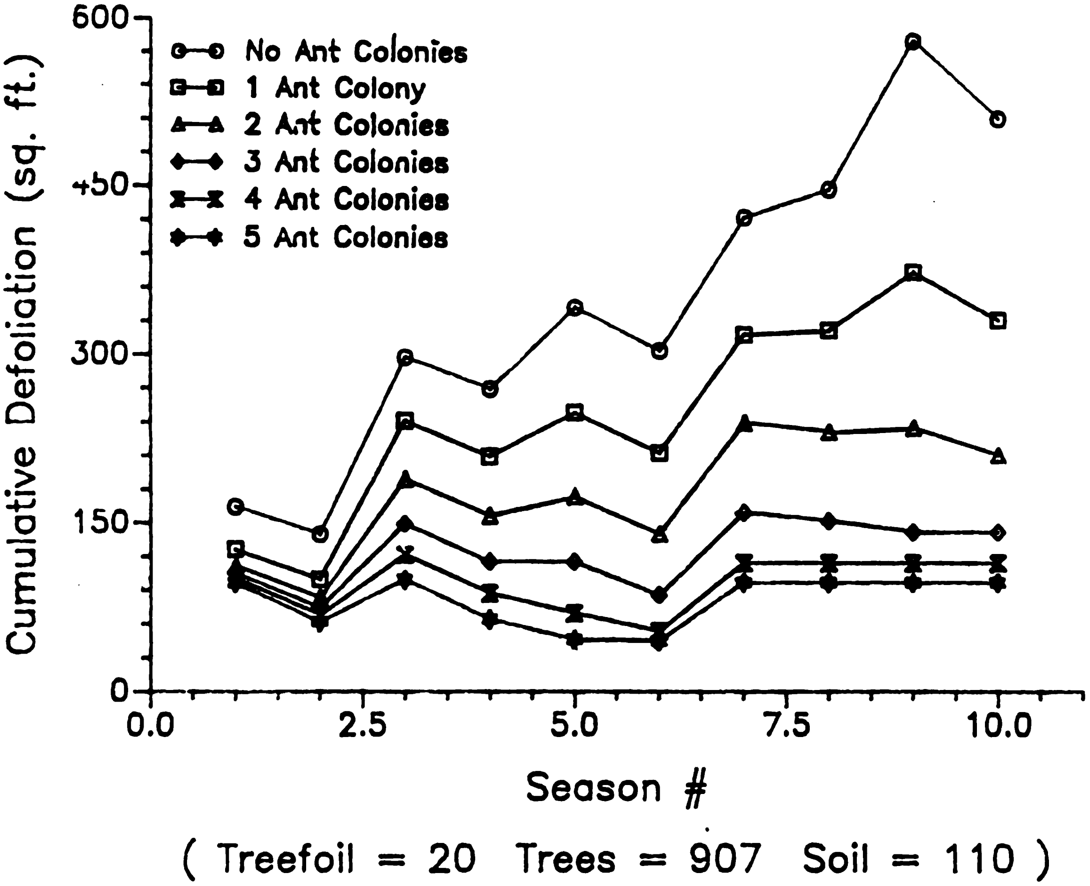


Figure 37. EFFECT OF SOIL TYPE AND ANTS ON DEFOLIATION

Figure 35 shows that 1200 ft^2 of defoliation per acre occurs by the third year even if there are five colonies of ants placed on each acre. However, the authors were very conservative for the values used in the predation rates of the ants. When ants are not employed as biological control agents, the simulations showed that potentially 1350 to 1490 ft^2 of foliage is defoliated. When ants are not present, a 37 percent decrease in defoliation can be expected if the trees are planted on a good site. When as many as five ant colonies are used per acre, defoliation on an ideal vs. a stressed site is reduced by 8 percent, indicating that less favorable sites potentially can produce good Christmas trees provided a form of pest management such as predaceous ants are employed.

Further Model Development

Based on the results of the analyses, we believe that the model warrants further development and fine tuning combined with additional research in order to better approximate the biology of the real system. Time did not permit a sensitivity analysis of all of the model's parameters to determine which ones had the greatest impact on the overall output. A first step in the fine tuning of the model would be to test the sensitivity of all parameters.

Similarly, the model only incorporated three of the several pests of Scotch pine in the Great Lakes region. While a subroutine and code for pales weevil was developed for this model, time did not permit it to be added to the model.

One additional area where the model requires some fine tuning is in the time horizon for long-term site improvement. As indicated in Fig. 38, the rate of leaf area production is fairly linear until about the year 8 at which time the rate begins to increase. This is more than likely due to the cumulative effects of the site improvement. Further work with this model should include a longer time horizon over several rotations in order to ascertain longer-term site improvement potential.

Finally, any new or revised versions of the model should begin to address the economics of the conventional and improved systems by attempting to quantify net returns. Financial and economic analysis of the system could be built into the model or addressed in a typical partial budget or benefit-cost framework.

Additional Research

While the model requires some additional sensitivity analyses, simulation results did point to certain priorities that should be addressed through research regarding the improved system. In particular, research is needed on ant predation switching values as leaf area lost is extremely sensitive to these values. However, literature on these values is virtually non-existent.

We also believe that a better leaf area growth model could be developed by incorporating site differences either by "corn equivalent" or by actual soil nitrogen content into the TREE regression equation. This would involve collecting data on a wider variety of sites where Scotch pines are known to grow. It would also be useful to validate any leaf area model by harvesting trees from representative age classes and removing and drying the leaves to determine total ovendry weight of leaf biomass. Conversion of leaf biomass to leaf area can be achieved though existing conversion factors.

While the NITROGEN subroutine provides a relative estimate of site improvement, additional research on trefoil decomposition rates and nitrogen contributions through organic matter decay and nitrogen fixation is needed to develop a more realistic model. Unfortunately there is currently very little information available on this subject. Moreover, to our collective knowledge, there has been no research on Scotch pine response rates to nitrogen. Currently, nitrogen fertilizer is applied to Christmas tree plantations only when the trees show signs on nitrogen deficiency. Research on the entire nitrogen cycling process in Scotch pine (organic and inorganic) appears to be sorely needed.

We assumed that due to the aggressive behavior and allelopathic effects of the trefoil, all of the weeds in the plantation would be eliminated. Further research is needed to determine if this in fact is true. Additionally, it was assumed that trefoil would make only a positive contribution to leaf area growth and the only competition between the trefoil and the trees would be for radiant energy. Below ground competition for nutrients and moisture as well as the allelopathic effects from the trefoil on the trees were assumed to be negligible. Additional research is required in order to determine whether this is indeed the case.

Finally, we assumed that the only biological control agent present in the plantations was one species of a predaceous ant. In most situations, there are many other natural enemies that negatively influence the pest complex; including predators other than ants, parasitoids, small mammals and disease. The addition of the trefoil to the system increases the potential number of food and shelter resources available for other biological control agents to utilize.

Conclusions

The model did predict that leaf area under the improved system would increase by 6037 m^2 over a 10-year period compared to a conventional system. A conventional system in the model is assumed to be one where there were no ants, no pests (due to the use of pesticides) and not long-term site improvement (due to the use of inorganic fertilizer). This amounts to a "savings" of approximately 80 degree days for a 10 year rotation (Fig. 38).

While these results do not seem spectacular, it should be noted that we were very conservative in many of the assumptions, believing that in this first approximation of the model, it was better to err on the side of caution. For example, published ant predation rates (Skinner, 1980), were reduced by a factor of 5 for the pests. Initially the published predation rates were used in the model and resulted in complete elimination of the pests. Similarly, the equation used to predict corn yields using nitrogen input from trefoil was reduced by a factor of 100. We believe the published figures for both ant predation and corn yields are very optimistic and possibly do not indicate the biology of the proposed system very well. This suggests that while models can be used to summarize existing information, this information may not always be correct.

Perhaps more importantly, the model predicted an increase in leaf area with very little inputs by the grower. While no attempts have been made to determine net margins of the conventional vs. the improved system, in the economist partial budget format, increased cost of the the improved system would be the one time trefoil planting and the cost of harvesting the trefoil. The cost incurred from mowing the trefoil could be offset by selling a portion of the trefoil for forage if more than one mowing per season occurred. The decreased costs associated with the improved system are less fertilizer and pesticides (if any) and fewer labor hours necessary for weed control. Benefits under the improved system (leaf area) would also increase slightly. In summary, the net benefits under the improved system appear to be greater than the benefits under the conventional system, While difficult to quantify,

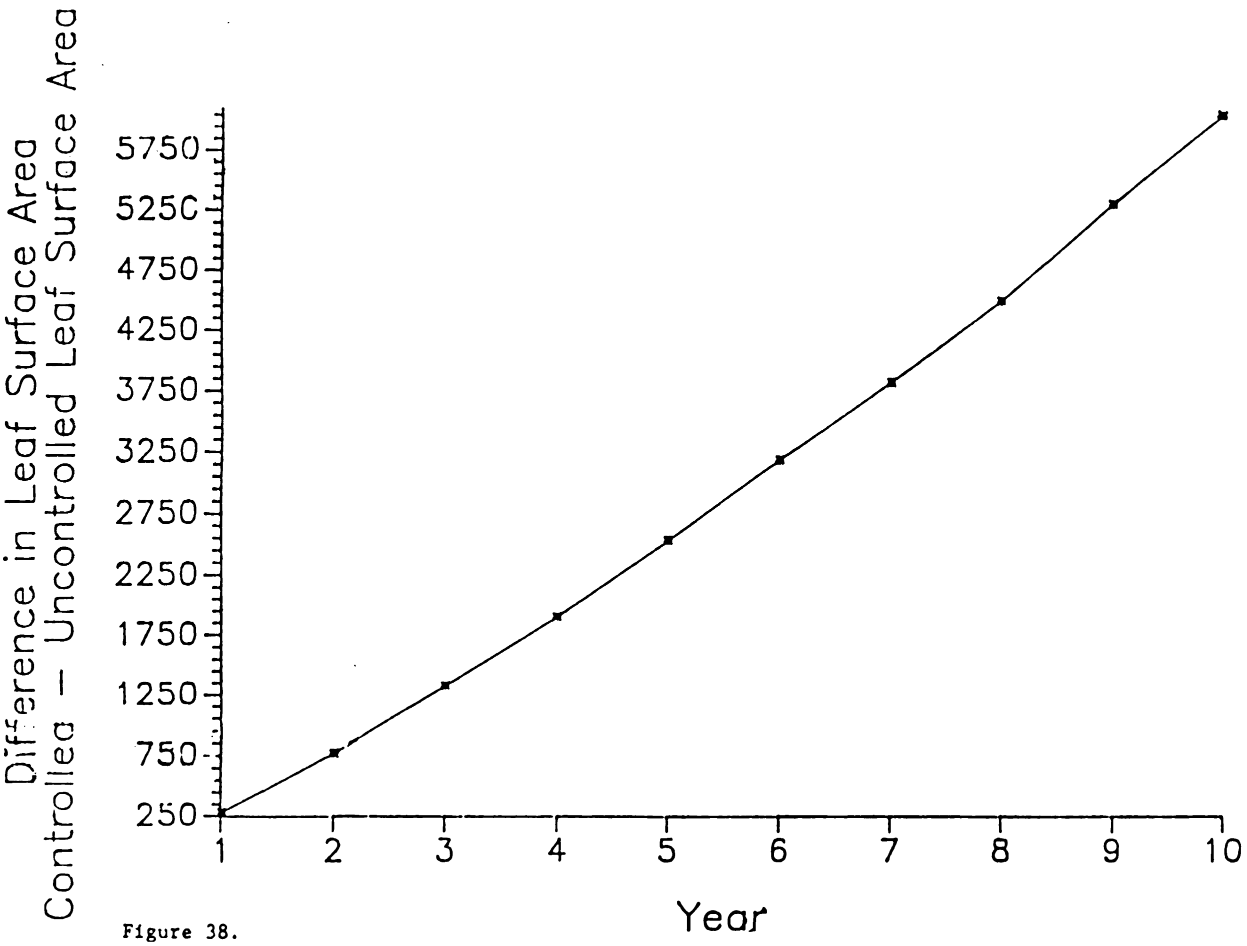


Figure 38.
Comparing conventional and 'improved system.

the improved system provides the additional social benefit of reduced ground water contamination and other chemical related problems.

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MANUSCRIPT 3.

Designing and Field Testing Portable Colonies of the Predaceous Ant, *Formica exsectoides* Forel

Introduction

This paper introduces a new technique for manipulating ants as biological control agents. Managing predaceous ants in portable nests could increase the potential for using a combination of pest management strategies in forest agroecosystems. The colonies could temporarily be removed or placed in optimal locations to meet specific management objectives such as chemical applications or harvesting. Many of the ideas that contributed toward the development of this technique are based on technologies successfully utilized by beekeepers.

The objectives of this study were to design, construct and test different portable ant nests and conditions that favoured colony survival. An additional objective was to determine how quickly the ants would begin to forage for insect prey after the transplant.

Material and Methods

Twelve portable nests of *Formica exsectoides* Forel, a native Michigan mound building ant, were constructed and transported to a 6-year old jack pine plantation in Alpena County, Michigan. On each of three dates beginning in late July, a cohort of four ant nests were transplanted into the jack pine plantation. The number of workers in the colonies increased and the nest design progressively changed over the 3-week period in accordance with our observations. Each cohort of nests was taken from the same parental colony. This was done for two reasons: 1) to have a larger force of nest siblings in one area (to eliminate intraspecific competition), and 2) to form a super-colony, if the individual colony size proved to be too small.

Portable Nest Design. The queens were placed in 15 x 8 x 5 cm plastic containers with 20 holes drilled in the side, top and bottom, large enough for the workers to utilize but small enough to restrain the queen. The workers and nest material from the parental colony were placed in 31 x 15 x 45 cm rectangular plastic waste baskets (portable nests). Small holes were made in the bottom of the nests for water drainage. The portable nests were placed in snug-fitting holes in the plantation with the lip of the nest approximately 3 cm above the surface of the ground. Small holes were drilled on the sides of the nests at ground level to allow the ants to enter and leave the portable nests.

The four colonies of the first cohort each consisted of 500 workers and one mated queen. The depth of the soil was 30 cm and the queen excluder was placed 10 cm below the soil surface. The ants were allowed to acclimate to the nests for 24 h prior to opening up the colonies in the new location. The colonies were fed honey-water and two crickets/day throughout this time. In addition, each colony was fed honey-water for 3 days following their release.

A small colony of 25 redheaded pine sawflies was placed on a tree approximately 1.5 m away from each nest to provide the ants with insect prey to improve the opportunity for the colonies to become established. Observations on ant predation on the sawfly colonies were made for two days following the transplant and thereafter weekly.

The second cohort consisted of four colonies each containing 1000 workers and one mated queen. The acclimation period was increased to 48 h and only two nests were left open. A flat lid was fitted over the top of the other two nests to protect them from possible rain damage. However, fifteen small holes were made in each lid to allow some moisture to enter the nests. One small colony of 25 sawflies was placed on each of three trees approximately 1.5 m from the nest.

In the third cohort, the number of workers per nest was increased to 1500 and one queen and each colony was covered with a lid. More nest material (soil and plant debris), was added, making the soil depth 40 cm and the queen excluder only 7 cm from the bottom. The ants were allowed to acclimate to their new nests for 5 days prior to release. The nests were placed 15 m apart in a row and each cohort was separated by 30 m. Each nest was provided with small colonies of sawflies, as described above.

We inspected each nest at weekly intervals for the following: 1) presence of a queen, 2) approximate number of workers, and 3) number of foraging trails established. Also, observations were made on the interactions between the ants and the sawflies. The queen excluders were removed from the portable nests with as little disturbance to the soil as possible. However, the soil around the queen excluder did cave in when the excluders were removed and had to be repacked around the excluder after returning the excluder to the nest.

Results and Discussion

Two days following the transplant of the first cohort of nests (each nest contained 500 workers), ants were seen moving nest material and nest mates to new locations within a 2 m radius of the nests. After 1 week no queens were found in any of the colonies and little activity was detected in the nests. The contents of the nests were sorted and only 5 to 19 workers were found. The sand throughout the nests was damp and and very few galleries were found.

Two days following the transplant of nests from the second cohort (each nest contained 1000 workers), ants from the two colonies without lids were seen moving both nest material and nest mates to new locations despite the noticeable increase in the number of galleries constructed during their acclimation period. Very few workers and no queens were found in the two colonies without lids after 1 week. A queen and approximately 50 workers were found inside of the excluder of the third nest, while the queen and many workers were near the excluder in the fourth nest. The surviving two colonies had established two foraging trails each. A foraging trail is defined as a steady flow of ants both entering and leaving the nests.

When the third cohort of nests (each nest contained 1,500 workers) were inspected after 1 week, many galleries were established in each of the four nests. In each excluder, a queen was found along with approximately 50 workers. The queen excluders were then carefully replaced and the colonies were monitored for 5 more weeks.

Three of the four colonies had established two foraging trails and the remaining colony established one. The ants were seen performing typical colony functions such as restructuring nest materials and carrying pupae to various chambers in the nest. A flow of ants was seen entering and leaving the two exit holes in each of the colonies. The colony with only one foraging trail exhibited the least activity overall. We observed four ants from the fourth cohort removing sawflies on nearby trees within 1 week following their release.

The survival time for two of the nests from the second cohort ranged from 3 to 7 weeks. The last cohort of nests survived in the portable nests for a period of 6 weeks. At this time the experiment was terminated.

Manipulating ants in portable nests should be useful when using an integrated approach to reducing pest populations. This study showed that the following factors positively influenced colony establishment: 1) the nest lid, 2) the queen excluder, and 3) the acclimation period. The next step in the development of the portable ant nests is to determine if the ants will remain in the portable colonies for more than 7 weeks and to increase the scale of introductions.

Figure 39. Portable nest of Formica exsectoides Forel