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The Bionomics and Interactions of the Parasitoid, Diaeretiella rapae (M'Intosh) (Hymenoptera: Braconidae), And the European Asparagus Aphid, Brachycolus asparagi Mordvilko (Homoptera: Aphididae)

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THE BIONOMICS AND INTERACTIONS OF THE PARASITOID, *DIAERETIELLA RAPAE* (M'INTOSH) (HYMENOPTERA: BRACONIDAE), AND THE EUROPEAN ASPARAGUS APHID, *BRACHYCOLUS ASPARAGI* MORDVILKO (HOMOPTERA: APHIDIDAE)

By

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ABSTRACT

THE BIONOMICS AND INTERACTIONS OF THE PARASITOID, *DIAERETIELLA RAPAE* (M'INTOSH) (HYMENOPTERA: BRACONIDAE), AND THE EUROPEAN ASPARAGUS APHID, *BRACHYCOLUS ASPARAGI* MORDVILKO (HOMOPTERA: APHIDIDAE)

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The European asparagus aphid is a severe asparagus pest in Washington State but not in Michigan, where natural enemies were believed primarily responsible for low aphid populations. Efficacy of *Diaeretiella rapae* (M'Intosh) (parasitoid), *Hippodamia convergens* Guérin-Méneville (predator) and *Entomophthora planchoniana* Cornu (fungal pathogen) was assessed: high aphid populations were propagated by excluding mortality factors with cages and pesticides; natural enemies were introduced. Temperature effects on aphid and parasitoid biology were investigated in the laboratory. High populations produced in the absence of mortality factors demonstrated the aphid's potential for destruction. *E. planchoniana* regulated aphids most effectively. Abiotic factors affected aphids more than hypothesized; they caused physical injury and influenced aphid biology, plant physiology and natural enemy abundance. Moderate temperatures (23°C) and higher temperatures (30°C) were favorable to aphid and parasitoid

biology, respectively. Biological similarities between Michigan and Washington aphids suggest that dissimilar pest status was not attributable to aphid biotype differences.

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OVERALL INTRODUCTION

Most insects possess high potential rates of increase because of their high fecundities and short generation time. However, these rapidly breeding insects do not increase over successive generations or for extended periods, but rather only increase periodically and to a limited extent because of natural controls present in their environment (van den Bosch and Messenger 1973).

Natural control regulates numbers and prevents a population from becoming too high or eases certain suppressive factors when the population is low. According to van den Bosch and Messenger (1973), "This long-term maintenance of the population at a characteristic level of abundance relative to other organisms in the community is the demonstration of the 'balance of nature.' The mechanisms and interactions between the population and its environment which bring about the relative balance of numbers constitute the natural control of populations." Natural control includes all factors of the environment which keep a given population in check against its own ability for numerical growth. These work primarily through mortality factors, but also through factors affecting natality or reproduction. Natural controls include limited

resources (food, space, shelter), climate factors (especially heat and cold), intraspecific and interspecific competition, and natural enemies (predators, parasitoids, pathogens). This last group is especially important for many pest species in monocultures, for while resources are usually abundant, weather may be continuously favorable and competition scarce or absent, natural enemies are almost always present and of some significance (van den Bosch and Messenger 1973).

Biological control is a major component of natural control. Van den Bosch et al. (1982) use the term biological control to "encompass both the introduction and manipulation of natural enemies by man to control pests (applied biological control) and control that occurs without man's intervention (natural biological control). Van den Bosch et al. use the term pest here to imply that the species' activities cause "damage" to man. From an ecological standpoint, the species may be just occupying its evolved niche. Biological control, as used in the latter definition, is a natural ecological phenomenon and a dynamic process which results from the natural association of different kinds of organisms (natural enemies, prey and hosts). It is affected by other factors such as changes in the environment, and the adaptations, properties and limitations of the organisms involved in each case (van den Bosch and Messenger 1973).

In agricultural systems, natural enemies are often absent due to several factors. Specialization in only one or a few crops has led to a reduction in plant diversity and consequently in faunal diversity, which in turn leads to instability within the system. This, coupled with the fact that a monoculture is grown extensively over a large area, provides conditions conducive to pest proliferation and subsequent crop damage. If the resulting control measures involve application of pesticides, this may further compound the problem by eliminating nontarget organisms such as natural enemies.

Often a potentially damaging pest may occur in an agricultural system at such low population levels that it does not require control measures. This low pest incidence may result from natural controls. This may be the case for the European asparagus aphid on asparagus in Michigan. Despite its presence in most fields in Michigan (Grafius 1980), the aphid appears to be regulated by natural control factors since it almost never occurs in damaging numbers. Thus far, no economic injury level has been established in Michigan (Grafius 1980). Natural biological control may be the major mechanism responsible; consequently, it is the focus of this study.

ASPARAGUS

Asparagus officinalis L. is a dioecious perennial crop which occurs in temperate regions. It grows well in all

parts of Michigan, and the average yield is 1300 lb. per acre, with a good yield being about 2000 lb. per acre. Eighty percent of the crop in Michigan is processed and 20% is sold in fresh market (Zandstra et al. 1984).

The asparagus spear is an elongated bud with an apical meristem which originates from the crown (Brian Benson, University of California at Davis, pers. comm.). The ferns, or stalks, are elongated spears which are produced when lateral meristems at the base of the bud scale along the side of the spear differentiate into primary and secondary branches and flower primordia. Once harvest ceases, spear maturation occurs and the lateral buds start to develop and grow. Primary branches arise from these buds, and in turn, secondary branches arise from the primary branches. Secondary branches consist of whorls of cladophylls located at nodes along the branch length. Cladophylls are needle-like leaves which serve as the main regions of photosynthesis. Tertiary branches are rarely produced.

In the fall, frost kills the fern. The fern is chopped to 10-12 inches in the fall or left standing throughout the winter to trap snow (Zandstra et al. 1984). This fern debris provides an overwintering refuge for aphid eggs and mummies containing immature parasitoids.

THE EUROPEAN ASPARAGUS APHID

The European asparagus aphid, Brachycolus asparagi Mordvilko, is native to the Mediterranean area and Eastern Europe, where it is a significant economic pest (Anonymous, 1980). It appears to be host specific to asparagus, even though the initial sighting in North America (July, 1969; Orient, Long Island) was a single alate on redtop, Agrostis album. Within three years of this sighting, the aphid had been reported on asparagus throughout much of the Eastern U.S. (Angalet and Stevens 1977). It was found in Illinois in 1977 and, in 1979, the aphid was recorded in lower British Columbia and in Washington, where it caused severe economic losses to the asparagus industry. By 1980 it had become established in Oregon (Anonymous 1980) and was recorded in many fields in Michigan. Its widespread distribution suggests that it may have been established in Michigan for many years prior to these sightings (Grafius 1980). The aphid was found in California in 1984 (Larry Bezark, State of California, Department of Food and Agriculture, pers. comm.).

The European asparagus aphid is small (adult ca. 0.16 cm in length), bluish-green to gray and most are apterous. Two distinguishing characteristics are the minute cornicles, only visible under high magnification (50X), and the parallel-sided cauda (Grafius 1980).

Asparagus aphids overwinter as eggs. Oviposition begins in mid-September and continues until late November.

When first laid, eggs are shiny green but turn black within a few hours. Most eggs are deposited on the nodes and beneath the bracts of the asparagus plant. Hatching begins in April in the Northeast, and peak populations occur in July and August (Angalet and Stevens 1977).

Damage to asparagus consists of a rosetting of newly emerged spears and a tufting of the fern at the base of the plants. This bushy growth is blue-gray-green and results form a shortening of the internodes between the whorls of cladophylls. Only branches which aphids are feeding on are affected. Toxins injected by the aphid during feeding are believed to be responsible for the abnormal growth (Forbes 1981). It is postulated that these toxins are translocated from the fern down to the crown. This may cause an imbalance or alteration of the hormones responsible for growth in the crown, resulting in release of the lateral buds at the fern base and initiation of spear elongation. Premature release of buds in summer and fall may be lethal to the plant (Brian Benson, University of California at Davis, pers. comm.). Other indicators of aphid presence are honeydew deposits at aphid feeding sites and the presence of predaceous coccinellids (Anonymous 1980).

Damage to plants three years or younger is most severe (Anonymous 1980). Capinera (1974) found that a single aphid and its progeny can greatly suppress asparagus seedling growth in the greenhouse and the field. Damage on older plants varies, depending on the size of the aphid

infestation. Moderately infested plants are relatively unaffected (Brian Benson, University of California at Davis, pers. comm.).

NATURAL ENEMIES AND *DIAERETIELLA RAPAE* (M'INTOSH)

Variation in the amount of the infestation may be partially attributable to the presence or absence of natural enemies. In New Jersey and Delaware, numerous natural enemies were found associated with the aphid, and populations were so low that insecticides were unnecessary (Angalet and Stevens 1977). Plants suffered very little damage. Twenty-six species of predators from eight families were reported: Coccinellidae (Coleoptera), Chrysopidae and Hemerobiidae (Neuroptera), Syrphidae (Diptera), Nabidae (Hemiptera), Pentatomidae (Hemiptera), Anthocoridae (Hemiptera) and Cecidomyiidae (Diptera). In addition, four species of hymenopteran parasitoids from two families, Braconidae and Aphelinidae, as well as one disease, *Entomophthora aphidis* Hoffman were present.

A comparable situation appears to exist in Michigan. The asparagus aphid is present in a number of Michigan fields, however, no serious damage has been reported (Grafius 1980). The natural enemy complex in Michigan is similar to that reported in New Jersey and Delaware and it may be responsible for the low aphid populations.

One natural enemy of interest is the parasitoid, *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Braconidae).

This tiny (approximately 2 mm long) wasp is a solitary endoparasitoid which attacks all host stages except the egg. The female normally lays a single egg per aphid host but superparasitism may occur under low host densities. If it does, only one larva will survive and reach maturity; other larvae within the same aphid are killed by biochemical inhibition (Spencer 1926).

Couchman and King (1979) studied the effects of developing D. rapae on the feeding rate of the cabbage aphid (Brevicoryne brassicae L.), concluding that the presence of a parasitoid egg in the aphid hemocoel has no effect on host feeding rate. The mandibulate first instar larva, however, adversely affects host tissues and hormonal balance, resulting in changes in external morphology of the parasitized aphid and a decrease in its feeding rate. The amandibulate second larval instar feeds on liquid or semi-liquid material obtained from the surrounding hemolymph and does not adversely affect host feeding rate. The third instar larva also lacks mandibles, and its body distends the abdomen of its host. There is a significant decrease in aphid food intake, culminating in the host's death within 24 hours. Parasitized aphids are sluggish and show little response to mechanical stimulation. They may even stay on leaves which are no longer suitable for feeding and have been abandoned by non-parasitized aphids. The mandibulate fourth instar larva consumes the internal organs of the aphid, and the aphid cuticle becomes

pearl-colored and thin (a mummy). Before the aphid skin dries, the larva cuts a hole in the venter of the aphid, and spins a silken cocoon that attaches the aphid to the substrate through the opening. Parasitized aphids may also be attached to their substrate by a "death grip" of the tarsal claws, or by a sticky fluid exuded through the pores of the aphid (Spencer 1926). Once this is accomplished, the larva voids the meconium, which consists of 10-20 black cigar-shaped pellets, and pupates (Hafez 1961). The adult chews a circular hole through the aphid skin and exits. When adults emerge it takes about five minutes for their wings to expand and dry and the body to become compact. At this time, they are ready to mate (Spencer 1926). Since the species is arrhenotokous, unmated females will produce only male progeny (Hafez 1961). In The Netherlands, D. rapae has from 5-11 generations per year (Hafez 1961). Parasitoids may overwinter as either late instar larvae or pupae (Vater 1971).

D. rapae commonly occurs in a number of agricultural systems on various aphid hosts, such as the cabbage aphid (Brevicoryne brassicae L.) on cabbage (Askari and Alishah 1979) and brussel sprouts (Chua 1978), the green peach aphid (Myzus persicae Sulzer) on potatoes, aphids on cruciferous crops (Read et al. 1970) and the mustard aphid (Lipaphis erysimi Kaltenbach) on mustard (Pandey et al. 1984). It is present in a number of asparagus systems,

including those of New Jersey, Delaware, Washington and Michigan (Angalet and Stevens 1977, Anonymous 1980).

D. rapae is just one of a number of naturally occurring biotic components in the asparagus system and, consequently, its presence does not necessarily mean that it is a principal factor in maintaining low aphid populations. Additionally, abiotic factors may play a major role in regulating aphid populations. Favorable weather conditions may be conducive to increasing aphid numbers while unfavorable conditions may physically injure aphids, affect host plant quality and/or adversely affect aphid biology. Also, abiotic factors may favor natural enemy increases, thereby reducing aphid populations.

OBJECTIVES

The goal of this study was to determine the impact of D. rapae on the European asparagus aphid in Michigan. It consisted of two parts.

1) Determine the natural enemy composition and assess the impact of selected natural enemies on the aphid, with special emphasis on the parasitoid, D. rapae.

2) Investigate the effect of temperature on asparagus aphid and D. rapae biology.

MANAGEMENT OF ASPARAGUS PLANTS, ASPARAGUS APHIDS, AND D. RAPAE

The success of this study depended in part, on an abundant supply of asparagus plants, asparagus aphids and parasitoids. The parasitoids required aphids for their reproduction, growth and development, and the aphids relied on the asparagus plants for their nutritional and reproductive requirements.

Asparagus plant and seedlings were reared in the greenhouse. All insect cultures were maintained on plants started from Mary Washington variety crowns. Seedlings of a closely related variety (Viking KB III) were used for all experiments, since varietal differences could result in differential aphid responses and thus contribute to experimental error.

Aphids were reared in the laboratory at room temperature (22-26°C) and photoperiod LD 16:8 on caged asparagus plants. The wooden cages were 61.0 cm tall x 63.5 cm wide x 45.7 cm deep and were covered with 52 x 52 (52 mesh per 2.54 cm) Saran® mesh screens on three sides, Warp's Flex-O-Glass® flexible window material on top, and a sliding plexiglass door on the front. Pots fit snugly into six 15.4 cm wide holes in the cage floor. The lower edge of the pot lip was flush with the cage floor and the lower portion of the pot was suspended below the cage bottom; thus only fern occupied the interior of the cage and excess water drained through the bottom of the pots into a

collecting tray below. In order to insure that the aphid colonies remained parasitoid-free, they were maintained in a separate room from the parasitoid cultures. These aphids were used in laboratory experiments and for parasitoid rearing.

Parasitoids were reared in the same type of cage on asparagus plants infested with asparagus aphids. A 50% honey solution served as a nutritional source for the adults and increased their longevity and fecundity. In the case of synovigenic parasitic Hymenoptera, egg production is dependent upon the nutrition of the adult female rather than on the food reserves retained from the immature stages. For many parasitoids, protein required for egg production is provided by aphid honeydew deposits or plant nectaries, both of which have been shown to contain free amino acids (Doutt 1964). Honey has been shown to be a suitable substitute for these food sources (Hagen and van den Bosch 1968).

PRELIMINARY STUDIES

1983

PRELIMINARY STUDIES - 1983

INTRODUCTION

One of the objectives of the first study (Morrow Field) was to determine the natural enemies of the European asparagus aphid in Michigan and their impact on the aphid population. Another was to assess the impact of an insecticide and a fungicide commonly used by commercial asparagus growers for the control of the common asparagus beetle (Crioceris asparagi (L.)), the spotted asparagus beetle (C. duodecempunctata (L.)) and asparagus rust (Puccinia asparagi D.C.) on these natural enemies.

The objectives of the second study (DD Field) were to evaluate the impact of selected artificially-introduced natural enemies on asparagus aphid populations, and to examine the role that weather plays in regulation of insect populations.

Climatic factors, such as heavy rain and wind, in the Michigan system may function as a major source of mortality for both the asparagus aphid and D. rapae. Extremes in temperature and humidity may also act directly on insects to cause mortality. Additionally, these abiotic factors may indirectly result in aphid or parasitoid death by creating conditions favorable to the development of other

natural mortality factors such as fungal diseases, Entomophthora spp. These pathogens cause striking epizootics in aphid populations and attack all stages except possibly the overwintering egg. Several scientists conclude that "it is the simultaneous occurrence of certain physical and biotic environmental factors acting on both the host aphid and the fungus that permits the epizootic" (Hagen and van den Bosch (1968).

Among the physical factors responsible for disease outbreaks are temperature, relative humidity, rainfall, and light. High relative humidity is required for both sporulation and germination of resting spores. Free water is also a requisite for the latter process. Rainfall plays a major role in initiating an epizootic by providing the free water necessary for germination. Biotic factors which influence Entomphthora spp. epizootics include aphid density (density-dependent mortality) and the density of fungal spores in the environment (Hagen and van den Bosch 1968).

In addition to causing aphid mortality, the fungal pathogen has also been shown to interfere considerably with the activity of the parasitoid, Aphidius smithi Sharma and Subba Rao on Acyrthosiphon pisum (Harris) (van den Bosch et al. 1966). The fungus attacks the internal wasp larvae, reducing the parasitoid population and decreasing its ability to control the host (Hagen and van den Bosch 1963). Consequently, the fungal pathogen, Entomophthora

planchoniana Cornu, common on Michigan asparagus aphids, was studied as one of the selected mortality factors in this system.

MATERIALS AND METHODS

MORROW FIELD 1983

These studies were conducted on the MSU Botany Farm. The experimental plot, the Morrow Field, was 62.18 m X 23.77 m and consisted of 10 rows, each with from 31 to 43 plants (Figure 1). Each plant was labelled alphabetically and numerically to correspond to its row and position within the row.

Asparagus spears in the field were harvested until early June. Once picking ceased, the field was checked weekly until the first week of July, but no natural populations of asparagus aphids were located. The following procedure was used to infest the field with greenhouse populations: Samples of 100 aphids of various stages were weighed (mean weight of .0081 gm per 100 aphids) and 90 samples of .0081 gm of aphids each were weighed onto filter paper, each paper was placed in a small numbered petri dish and stored in an ice chest with ice until all 90 samples were weighed. The ice chest was stored uncovered in a growth chamber at 12.8°C until the following morning. One hundred plants (25 per quadrant) in

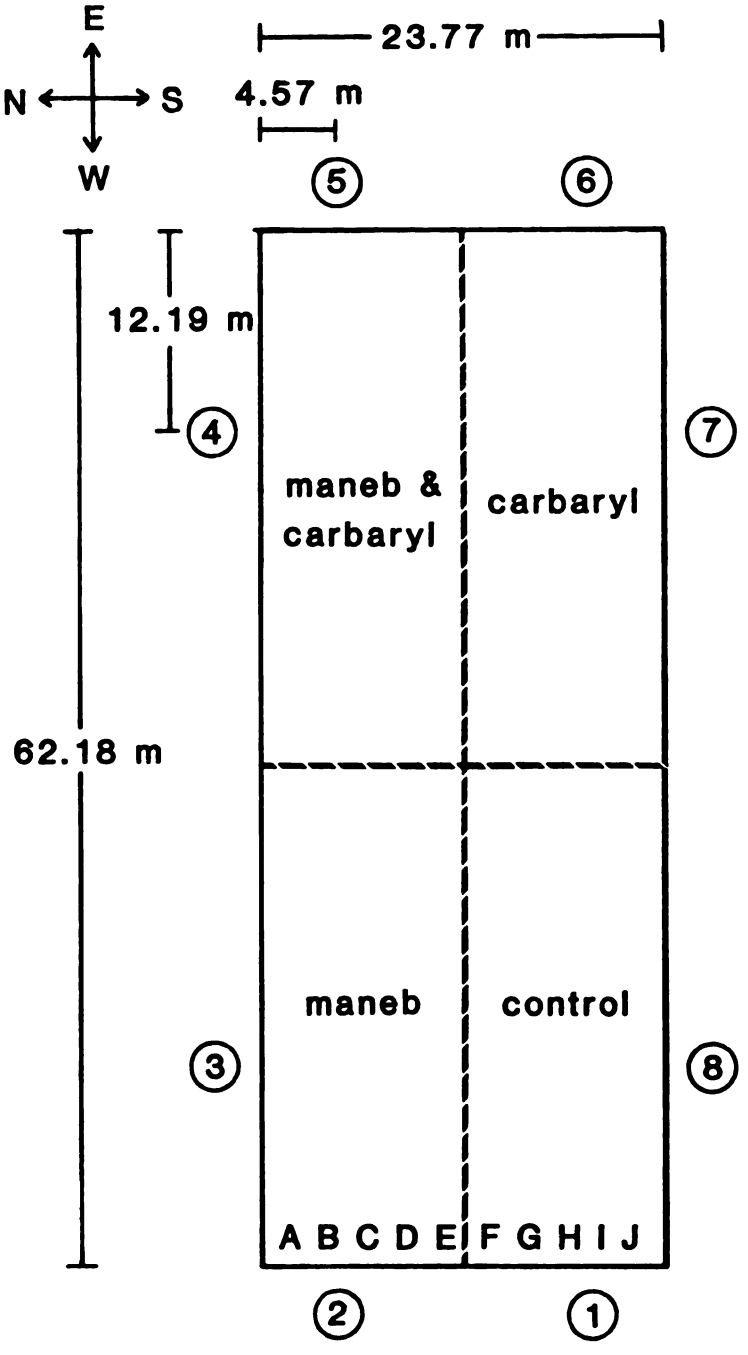


Figure 1. Morrow Field showing plot dimensions, location of treatments and location of cylindrical sticky traps (circled numbers).

the field were randomly chosen to be infested. Ten randomly selected plants from these 25 per quadrant were infested with aphids from the first batch of 90 dishes. Prior to release, a 10 dish sample was randomly selected from the 90 dishes. This sample was taken back to the lab for counting, as a double check on how many aphids were in each dish.

Aphids in the 80 remaining dishes were released in the field by placing the aphid-covered filter papers in the fern. This allowed the aphids to crawl onto the surrounding branches. Two dishes of aphids were placed on each plant. This procedure was repeated the second day with 90 groups of aphids and the third day with 50 groups, giving a total of approximately 200 aphids for each of the 100 plants over a three day period. Aphids were always released during the morning hours so that they would have an opportunity to become active and establish themselves during the warmest part of the day.

Due to the small size of the field, the experiment could not be set up with replications. Instead, the field was divided into four quadrants. Each quadrant received a different treatment as follows: 1) the fungicide maneb (Dithane FZ), 2) a combination of maneb and the insecticide carbaryl (Sevin 80S), 3) carbaryl and 4) a control (no spray) (Figure 1).

The pesticide used (1352.98 gm a.i. maneb/hectare, and 228 gm a.i. carbaryl/hectare) were determined from

laboratory toxicology tests (David Prokrym, Department of Entomology, Michigan State University, pers. comm.). The results indicated that these rates would effectively reduce natural enemy populations without affecting asparagus aphid populations. Sprays were applied with a boom sprayer with six nozzles arranged so that two rows were sprayed at a time.

The field was sprayed on the following dates in 1983: July 22, 31; August 9, 12, 20, 24, 31; September 7, 15, 26; October 17.

It was necessary to assess different sampling methods in this study. Four different sampling methods were employed in the Morrow Field: cylindrical yellow sticky traps, visual counts, beat samples, and destructive samples. All sampling methods except for the first were not initiated until after inoculation of the field with asparagus aphids.

The cylindrical yellow sticky trap consisted of a 2-lb coffee can (12.7 cm in diameter by 16.5 cm tall) painted with OSHA safety yellow enamel (Krylon 1813). The can was screwed onto the top of a 5.1 cm x 5.1 cm x 1 m tall wooden post (Figure 2A). Eight of these cans were placed around the perimeter of the field, 4.57 m from the corners of the narrow ends of the field and 12.19 m in from the corners of the sides of the field (Figure 1). Insects were collected on 16.5 cm x 43.2 cm x .005 mm thick acetate sheets secured around the can via velcro fasteners which were stapled to

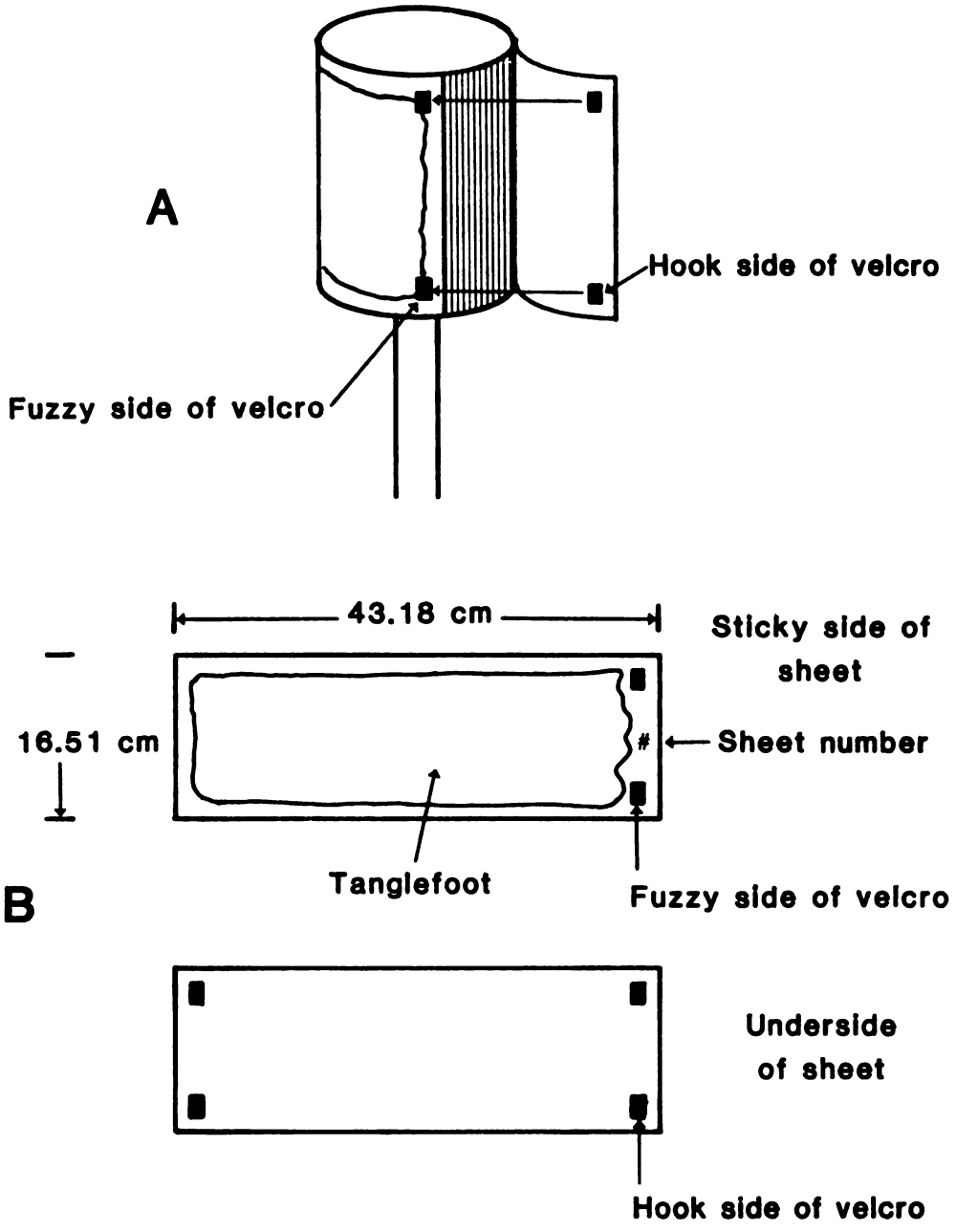


Figure 2. Cylindrical sticky trap showing (A) placement of sticky sheet on yellow can and (B) sticky side and underside of same sheet showing arrangement of velcro pieces.

and glued to the acetate with a hot glue gun (Figure 2B). Each sheet was labelled with a number corresponding to its position in the field and then sprayed with Tanglefoot® Tangletrap aerosol adhesive. There were two cans per quadrant, and these caught airborne insects active in the field. Traps were changed weekly for the first part of the season and biweekly toward the end of the season. To facilitate collecting and changing of the traps, the following method was used: Each acetate sheet was mounted on a piece of cardboard in such a way that the hooked pieces of velcro on the back of the acetate sheet would match up to fuzzy pieces of velcro mounted on the board (Figure 3A). As a result, sheets could be attached and peeled off easily. Each board fit into a numbered slot in a box (Figure 3B). When traps were changed, clean, newly sprayed sheets were removed from the cardboard and replaced with used sheets from the traps. All cans had numbers painted on them for easy identification and location. Sheet counts were made using a checkerboard grid method (Figure 3C). Alternate squares in the grid were counted so that half of the total surface area of the trap was evaluated. All insects were examined and those pertinent to the study were identified and recorded. Used sheets were cleaned with paint thinner and washed with soap and water. These were resprayed and reused two to three times each.

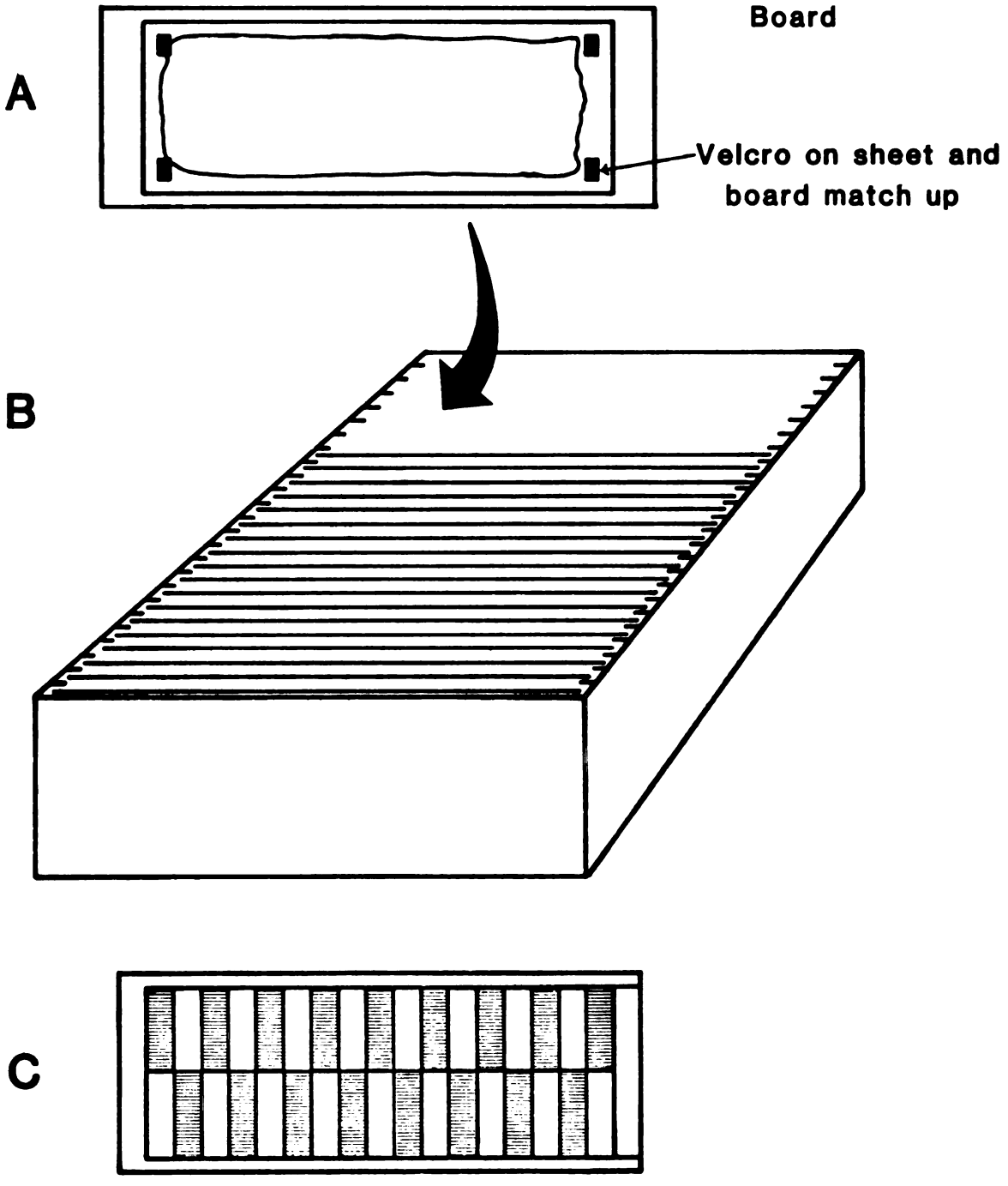


Figure 3. Sticky sheet mounted on cardboard (A) which fits into a numbered slot in the box (B). Sheet is evaluated on checkerboard counting grid (C).

A visual count was the second sampling method employed. The sampler spent 15 minutes per quadrant, slowly walking up and down each row and noting any insects. No plants were touched, and each plant was examined only once during the period (i.e. the sampler did not walk down the same row twice). Thus, the sampler spent about three minutes per row. This method was effective for spotting large insects but not for aphids and parasitoids. Consequently, it was terminated after a few trials.

The third sampling technique entailed beating the asparagus fern against a white enamel pan to dislodge any insects present. The two center rows of each quadrant (rows B, C, H and I) were sampled on each sampling date; border rows on the outer edges and inner edges of each quadrant were not used since these may have received spray drift from an adjacent quadrant. Plants were numbered and sampling alternated between sets of odd and even numbered plants for each sampling date. Approximately five stems for each fern were grasped with the hand and vigorously beaten against the enamel pan. The contents were immediately placed in a labelled plastic bag. These were later examined under a microscope and all insects of interest recorded. Initially, this sampling method was done twice a week but, in the latter part of the season collection by this method was done once a week.

The final sampling procedure was a biweekly destructive sample, which was the most time consuming and

labor intensive. A ground cloth was placed at the base of the fern to catch any insects which might be dislodged. A large garbage bag was placed over the foliage so that it encompassed the entire plant, and then the stems of the fern were cut at the base. An aspirator was used to suck up any dislodged insects on the ground cloth. Each bag was labelled and kept at 5°C until processing. A total of 24 randomly selected plants (six plants per quadrant, two plants each for three rows) were collected at each sampling date.

These samples were processed in garbage can-size Berlese funnels and collected in soapy water. Samples were left in the funnels for a day, bottled in 75% EtOH and examined when time permitted.

Samples were taken throughout the growing season to provide information on population fluctuations. Also, the data were used to examine the synchronization between aphid and parasitoid populations, an important aspect of population regulation by a natural enemy.

DD FIELD 1983

In this experiment the impact of selected artificially-introduced natural enemies of the asparagus aphid was examined. The study was conducted on the MSU Botany Farm. The experimental plot, the DD Field, was 14.63 m x 36.58 m with 10 rows of 31 to 43 plants each. The two outer rows on each side and the first and last two

plants in each row were designated as guard rows and were not used (Figure 4).

Daily temperature and precipitation readings were taken at the MSU Horticulture Farm, located 2.253 km from the MSU Botany Farm. This daily monitoring provided data on seasonal weather fluctuations which could be correlated with seasonal insect population fluctuations. Preliminary weather data on the cages were taken with a CR21 Micrologger (Campbell Scientific Inc.). Temperatures inside the cage were 2-3°C greater than those outside of the cage.

Asparagus spears were picked until early June in the experimental field. The field was monitored for asparagus aphids and natural enemies. At this time, the fern was small, and the only insects observed were common (Crioceris asparagi (L.)) and spotted (C. duodecimpunctata (L.)) asparagus beetle adults and larvae.

In the second week of July (July 13), all plants (except guard rows) were labelled, number of stems per crown were counted and the height of the tallest stem was measured. Fifteen plants with similar measurements from the original 214 were selected. These experimental units were used to assess the impact of specific natural enemies

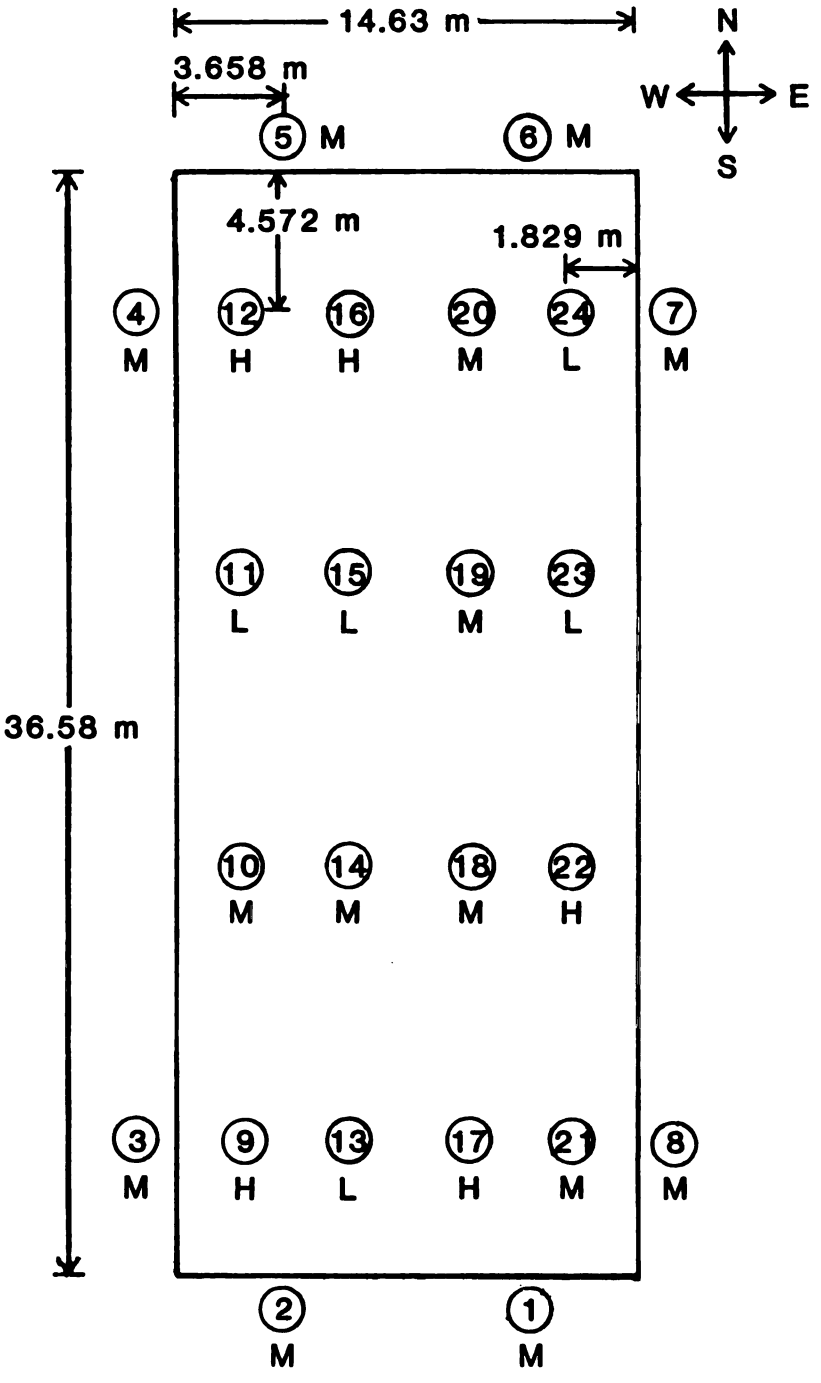


Figure 4. 1983 DD Field showing plot dimensions and arrangement and heights of sticky traps (L = low, M = medium and H = high).

on the European asparagus aphid. The experiment consisted of five treatments:

Tmt	Caged	Maneb	Primary Mortality Factors
1	No	No	All natural enemies, weather
2	No	Yes	Predators, parasitoids, weather
3	Yes	No	Entomophthora planchoniana Cornu
4	Yes	Yes	Hippodamia convergens Guérin-Méneville
5	Yes	Yes	Nothing (control)

A sixth treatment with D. rapae as the primary mortality factor had been planned, but since parasitoids were not observed in the field until fall, it was not used.

The caged treatment plants were enclosed with .914 m x .914 m x 1.829 m cages made of aluminum frames and covered with Saran® mesh (52 mesh per 2.54 cm) on two sides, and nylon organdy on the other two sides. The use of two different materials was necessary due to an insufficient amount of either one, and a desire to keep all experimental units as uniform as possible. Access to the cage was via two velcro secured flaps on opposite corners of the cage.

In all caged treatments, the cage excluded predators and parasitoids. It also lessened the effects of weather within the cage. Since the cages did not exclude the fungal pathogen, E. planchoniana, a 1% solution of maneb (Dithane FZ) was applied to the nonfungal treatment plants

with a hand sprayer on the following dates: August 19 and 29, September 7, 18 (one plant each from treatments 1, 2 and 5 were not sprayed on this date) and 26.

Since natural aphid populations were not detected by mid-August, the experimental units were infested with aphid-covered asparagus stems from greenhouse colonies. One 21.5 cm long cutting was taped to each experimental unit and aphids were allowed to crawl off. Within two weeks, all experimental units were infested with large aphid populations.

Two sampling techniques were used in the field. Cylindrical yellow sticky traps were employed to assess the general insect species composition in the field. Eight 1-m high traps were placed along the perimeter of the field. An additional 16 traps were distributed at various heights (five .305 m, six 1 m, and five 1.676 m) within the field (Figure 4). Sampling began prior to infesting the field and traps were changed on July 22, 31, August 14, 22, 29, September 5, 13, 21, 30 and October 17, with the last set being collected on October 24.

The second sampling method involved monitoring specific colonies on each plant through time without removal. A colony was defined as the aphids inhabiting the terminal 6 cm of fern. Any aphids proximal to this point were not counted. On September 7 and 8, 15 colonies per experimental unit were tagged and marked and five of the 15 colonies were randomly selected to follow throughout the

season. Colony counts were initiated after plants were inoculated with asparagus aphids and counts were taken on September 9-10, 17, 23-25, 30, October 7 and 17. A small cosmetic mirror was used to count aphids on the underside of the colony, since Tamaki et al. (1970) had shown that use of a dental mirror reduced disturbance to colonies and increased accuracy of counts. All parasitized and diseased aphids were noted.

On October 19, all cages were removed and the fern was cut down. A ground cloth was placed under each plant to catch any dislodged insects, which were sucked up with an aspirator. Older asparagus aphid eggs were observed all over the fern and on the ground at the base of the plant, and newly laid eggs were on the ground at the base of the fern.

RESULTS AND DISCUSSION

MORROW FIELD 1983

Cylindrical Sticky Traps

Total insects trapped over the four treatments were summed for each sampling period but, except for anthocorids and aphid species other than B. asparagi, all insects were trapped in low numbers along the periphery of the field. Other aphid species and anthocorids exhibited a declining trend over the season (Table 1). These other aphid species may have come from weeds in and/or around the field or from plants in adjacent plots. Since the asparagus aphid is an

Table 1. 1983 Morrow Field cylindrical sticky trap counts totalled over all treatments within a sampling period.

Insects	Total Insects Trapped/Sampling Period Sampling Periods								
	7/22-7/31	7/31-8/14	8/14-8/22	8/22-8/29	8/29-9/5	9/5-9/13	9/13-9/21	9/21-9/30	9/30-10/17
Common asparagus beetle	0	0	0	3	0	0	0	0	0
Asparagus aphid	0	0	0	4	0	0	2	1	0
Other alate aphids	7316	999	306	142	223	159	303	512	210
Coccinellidae	9	11	9	10	5	2	1	7	2
Anthocoridae	8	54	30	47	15	7	4	4	4
Syrphidae	3	4	1	1	1	0	0	0	1
Chrysopidae	0	1	1	1	0	2	0	0	0
D. rapae	0	0	1	0	0	0	0	0	0

introduced pest and the natural enemies are native, these other aphids may have served as the primary food source in the absence of the asparagus aphid and as an additional source during low asparagus aphid abundance.

Sticky traps are more qualitative than quantitative; hence, they mainly provide information on insect species composition and activity in the field. They can indicate relative abundance of a particular species over the season but cannot be used to make quantitative comparisons between species.

Since the sticky trap preferentially catches insects which are active and do not avoid the trap, it is a measure of insect activity. It only traps airborne insects (those actively flying or passively blown by the wind) or those which crawl onto the trap. Thus, it will not provide data on wingless insects such as apterous aphids, unless they are dislodged from the plant and blown onto the sticky trap. Another drawback is that small insects, such as parasitoids and aphids, may become embedded in the tanglefoot and cannot be manipulated for identification.

Beat Samples

Mean asparagus aphids per plant were so low that total number of asparagus aphids per sampling date were plotted by treatment over the season (Figure 5). Aphids in the maneb treatment experienced the largest population fluctuations during the season. Maneb did not seem to

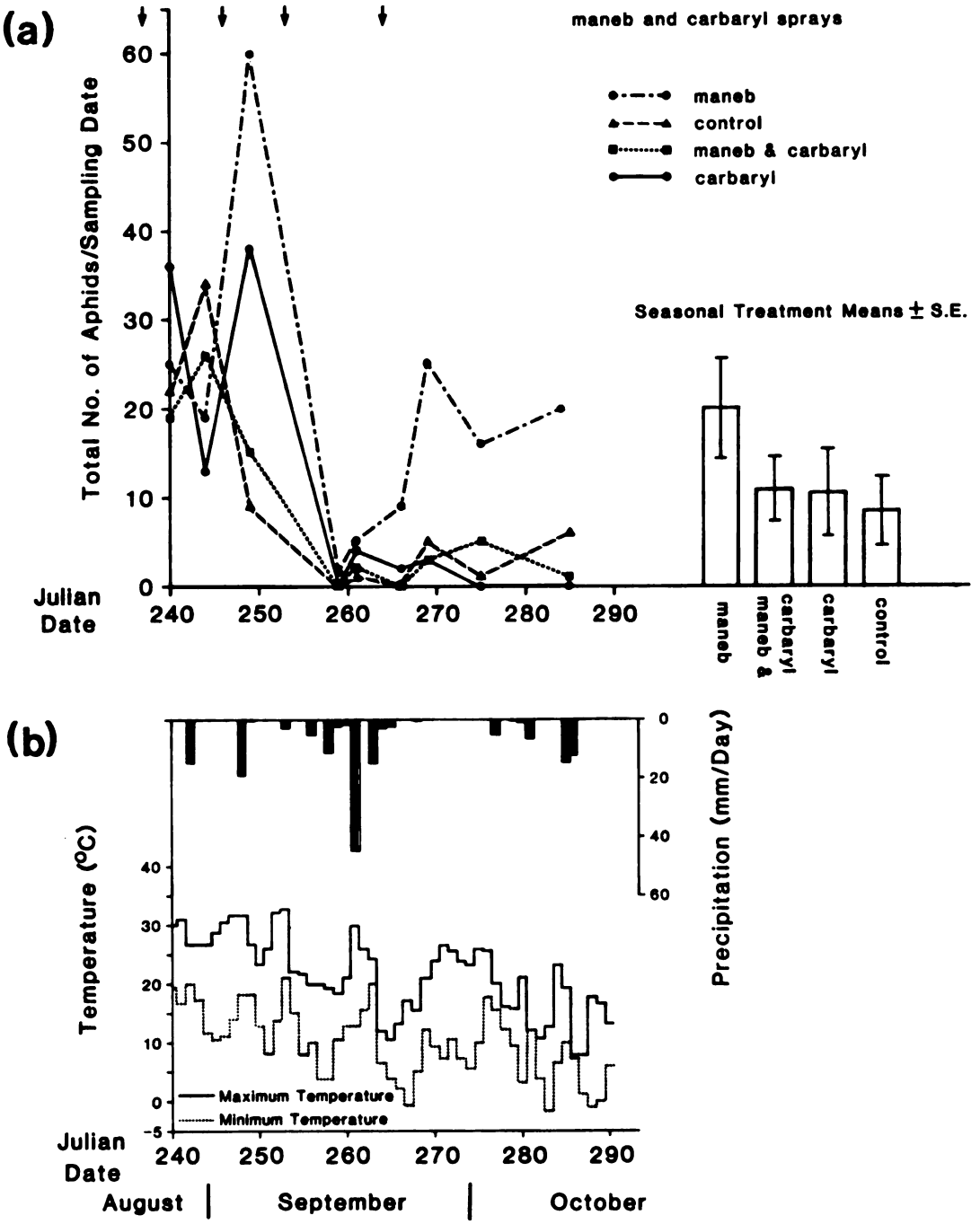


Figure 5. (a) 1983 Morrow Field beat samples showing occurrence of asparagus aphids by treatment; seasonal treatment means are given in bar graph to the right. (b) Daily weather data.

adversely affect aphid populations since fluctuations and directional changes in the population curve were independent of fungicide spray dates. In general, when maneb was applied regularly (first half of the season), aphid populations for the control tended to increase while maneb-treated aphid populations decreased and vice versa. However, during the latter half of the season when maneb applications became irregular, both population curves exhibited similar trends, but the maneb-treated aphid populations still showed higher numbers than the control. This probably resulted because aphid populations were initially higher in the maneb treatment, and aphids were able to produce more progeny and thus attain higher levels than the control populations in the latter part of the season.

Aphid numbers in the maneb + carbaryl treatment and control exhibited similar trends for the first half of the season. In the second half, however, aphid populations in the maneb + carbaryl treatment peaked after the Sept. 26 spray, but as residues wore off and spraying ceased, the populations decreased. During this same time the control behaved inversely. Decrease in the maneb + carbaryl aphid populations could be attributed to the invasion of natural enemies once spraying ceased.

Aphid numbers in the carbaryl treatment fluctuated similarly to those in the maneb treatment for the first half of the season, but declined and remained low in the

latter half of the season. Comparisons of aphid numbers between the maneb + carbaryl and carbaryl treatments after the September 26 spray demonstrates the protection afforded by maneb. Aphids in the maneb + carbaryl treatment peaked immediately after spraying while aphids in the carbaryl treatment remained low. As chemical protection wore off, however, the maneb + carbaryl populations decreased to a level similar to the carbaryl treatment for the remainder of the season.

Reduction in aphid populations for all treatments on Sept. 21 may be attributed to abiotic factors. Figure 5b shows daily maximum and minimum temperatures and precipitation (mm) for the entire season. During this same period, there was a large amount of rainfall which could have caused direct mortality to the aphids and/or indirectly by providing conditions favorable to natural enemies.

The decline of aphid populations over the season for all treatments may have resulted from plant senescence and aphid egg production, both which began in early September. In addition, abiotic factors became less favorable for aphids in the fall. Also, natural enemies may have had a greater impact on aphid populations.

Destructive Samples

Due to time constraints, only three of the six samples taken per sampling date per treatment were examined. A

tremendous amount of variability occurred within treatments for each sampling date, and it was necessary to transform the data (log10(x + 1)). None of the treatment means were significantly different for the first three sampling dates (Duncan's multiple range test, $p < 0.05$) (Table 2). In the last sampling period, however, aphid numbers for the maneb + carbaryl treatment were significantly higher than those for the control.

Despite nonsignificance in most cases, the data did show some trends. Aphid numbers for the maneb and carbaryl treatments varied for each sampling date, which could have resulted from effects of the different natural enemies. On all sampling dates, either the maneb or carbaryl treatments had the most aphids while the control had the lowest or the second lowest number. The maneb + sevin treatment was intermediate. This trend suggests that in treatments in which natural enemies were excluded, aphids attained higher populations levels.

DD FIELD 1983

Cylindrical Sticky Traps

In general, counts were low for most insects, with the exception of various other aphid species, anthocorids, common asparagus beetles, coccinellids and Chalcidoidea (Table 3). The common trend exhibited by all of the insects with larger populations was a decline in numbers

Table 2. Asparagus aphid population densities for Morrow Field destructive samples.

Treatment	Aphids per Plant ± S.E.[a]			
	Sept. 12	Sept. 20	Sept. 26	Oct. 24
Maneb	121.0 ± 116.5	46.0 ± 28.5	45.7 ± 32.3	1.7 ± 1.2ab
Maneb + Carbaryl	349.0 ± 288.2	5.0 ± 2.9	11.3 ± 4.26	20.7 ± 9.0a
Carbaryl	327.3 ± 324.8	19.3 ± 2.0	2.3 ± 0.7	27.7 ± 27.7ab
Control (no spray)	37.0 ± 25.9	5.0 ± 4.0	8.3 ± 7.8	0.0 ± 0.0b

[a]Values within a column which are followed by different letters are significantly different at the 5% level, Duncan's multiple range test.

Table 3. 1983 DD Field cylindrical sticky trap total insect counts.

Insects	No. of Insects Totalled Over 24 Traps/Period Trapping Periods								
	7/22-7/31	7/31-8/14	8/14-8/22	8/22-8/29	8/29-9/5	9/5-9/13	9/13-9/21	9/21-9/30	9/30-10/17
Common asparagus beetle	40	52	16	11	1	1	0	0	0
Asparagus aphid	0	0	0	0	0	0	0	4	4
Other alate aphids	17152	4446	1479	425	523	541	1125	1439	709
D. rapae	14	3	0	0	0	0	0	0	4
Chalcidoidea	660	704	378	195	250	313	360	115	102
Coccinellidae	23	33	27	16	11	4	2	8	4
Anthocoridae	103	165	69	31	24	9	20	28	17
Chrysopidae	0	9	1	0	0	5	2	0	0
Syrphidae	8	9	3	1	0	0	0	0	0
Cecidomyiidae	8	9	4	4	0	1	1	1	9

over the season. Low asparagus aphid numbers could be attributed to several factors. Unlike populations on caged plants (which had high aphid numbers), populations on uncaged plants crashed shortly after they were established and remained low to nonexistent for the remainder of the season. Thus, there was no crowding stimulus for any asparagus aphid populations on uncaged plants to produce alates and disperse. Also, since asparagus aphids occur predominantly in the lower one third of the plant (Wright and Cone 1983) and often may be located within the dense fern canopy, they may be less likely to become airborne.

Numbers of other aphids species were inversely related to trap height, with populations decreasing with ascending height (low, medium within the field, medium on the perimeter and high) - sticky traps closer to the ground (and the weeds) caught more aphids. Significant differences existed among trap heights in all but the last sampling period (Duncan's multiple range test, $p < 0.05$) (Table 4). The low traps had significantly higher numbers of aphids than the other traps in all of the first eight sampling periods; they also had significantly higher aphid numbers than either type of medium height trap (perimeter or within-the-field) in seven of the first eight sampling periods. It was suspected that other aphid species were more abundant on lower traps because they came from weeds within the field. These other aphids may have served as alternate hosts for natural enemies.

Table 4. 1983 DD Field cylindrical sticky trap counts for other aphid species.

Trap Height	No. of Non-asparagus Aphids/Sampling Period ± S.E.[a]								
	7/22-7/31	7/31-8/14	8/14-8/22	8/22-8/29	8/29-9/5	9/5-9/13	9/13-9/21	9/21-9/30	9/30-10/17
Low	1278.8 ± 311.5a	537.8 ± 92.6a	136.8 ± 21.8a	45.0 ± 8.7a	61.5 ± 11.4a	38.3 ± 13.2a	93.3 ± 24.0a	118.8 ± 38.4a	42.3 ± 16.3a
Medium (Within)	734.0 ± 64.0b	198.0 ± 46.9b	56.7 ± 8.0b	12.4 ± 3.0b	25.7 ± 6.0b	22.4 ± 4.9ab	55.4 ± 6.7b	47.9 ± 9.4b	22.6 ± 2.3a
Medium (Perimeter)	640.6 ± 81.4bc	90.4 ± 7.9bc	53.6 ± 19.9b	16.4 ± 2.6b	22.5 ± 3.8b	22.9 ± 3.6ab	41.4 ± 7.4bc	64.6 ± 9.8b	34.3 ± 4.7a
High	253.3 ± 37.3c	55.2 ± 2.9c	21.2 ± 3.5b	5.4 ± 1.4b	4.2 ± 1.8c	9.6 ± 0.9b	17.4 ± 3.2c	22.4 ± 2.8b	21.6 ± 3.2a

[a]Values within a column which are followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

Colony Counts

For the first two sampling dates, uncaged treatment means were significantly lower than caged ones (Duncan's multiple range test, $p < 0.05$) (Table 5). This was assumed to result from a combination of biotic and abiotic mortality factors. By the third sampling date, the E. planchoniana infection was beginning to reach epizootic proportions, and it was causing severe mortality (Fig. 6a); for this date and subsequent ones, aphid populations in the two uncaged and the caged, E. planchoniana infected treatments were significantly lower than the two remaining caged treatments (Table 5).

In the two remaining caged treatments, the one with H. convergens introduced differed significantly from the control on only two dates (Sept. 17 and 30). Thus, coccinellids may have regulated the aphids only sporadically during the season. Figure 7a compares aphid populations for the three caged treatments and illustrates the rapid reduction of aphids in the E. planchoniana treatment in a very short time.

All populations declined over the season due to several factors. First, aphids began to produce eggs instead of nymphs in early September. Secondly, plants started to senesce with the approach of fall, as well as from being stressed by high aphid populations. By influencing the physiological state of the host, climatic factors can indirectly affect the potential reproductive

Table 5. 1983 DD Field asparagus aphid colony counts.

Treatment	Mean aphids/treatment ± S.E.[a] Sampling Date 9/9	9/17	9/24	9/30	10/7	10/17
Uncaged, no spray	15.9 ± 4.9b	13.6 ± 12.2c	0.9 ± 0.5b	7.3 ± 4.5c	1.9 ± 1.3b	1.5 ± 1.0b
Uncaged, maneb	2.8 ± 1.4b	1.4 ± 1.0c	0.3 ± 0.2b	0.1 ± 0.1c	0.0b	0.1 ± 0.1b
Caged, no spray (*E. planchoniana*)	235.9 ± 54.7a	197.7 ± 37.2b	19.5 ± 8.9b	13.3 ± 4.8c	0.0b	0.0b
Caged, maneb + *H. convergens*	296.4 ± 34.0a	226.53 ± 37.0b	145.7 ± 17.0a	59.1 ± 10.4b	31.1 ± 9.7a	15.6 ± 3.7a
Caged, maneb (Control)	269.2 ± 39.1a	330.0 ± 47.0a	175.3 ± 27.5a	116.5 ± 21.6a	37.4 ± 9.4a	13.8 ± 5.8a

[a]Values followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

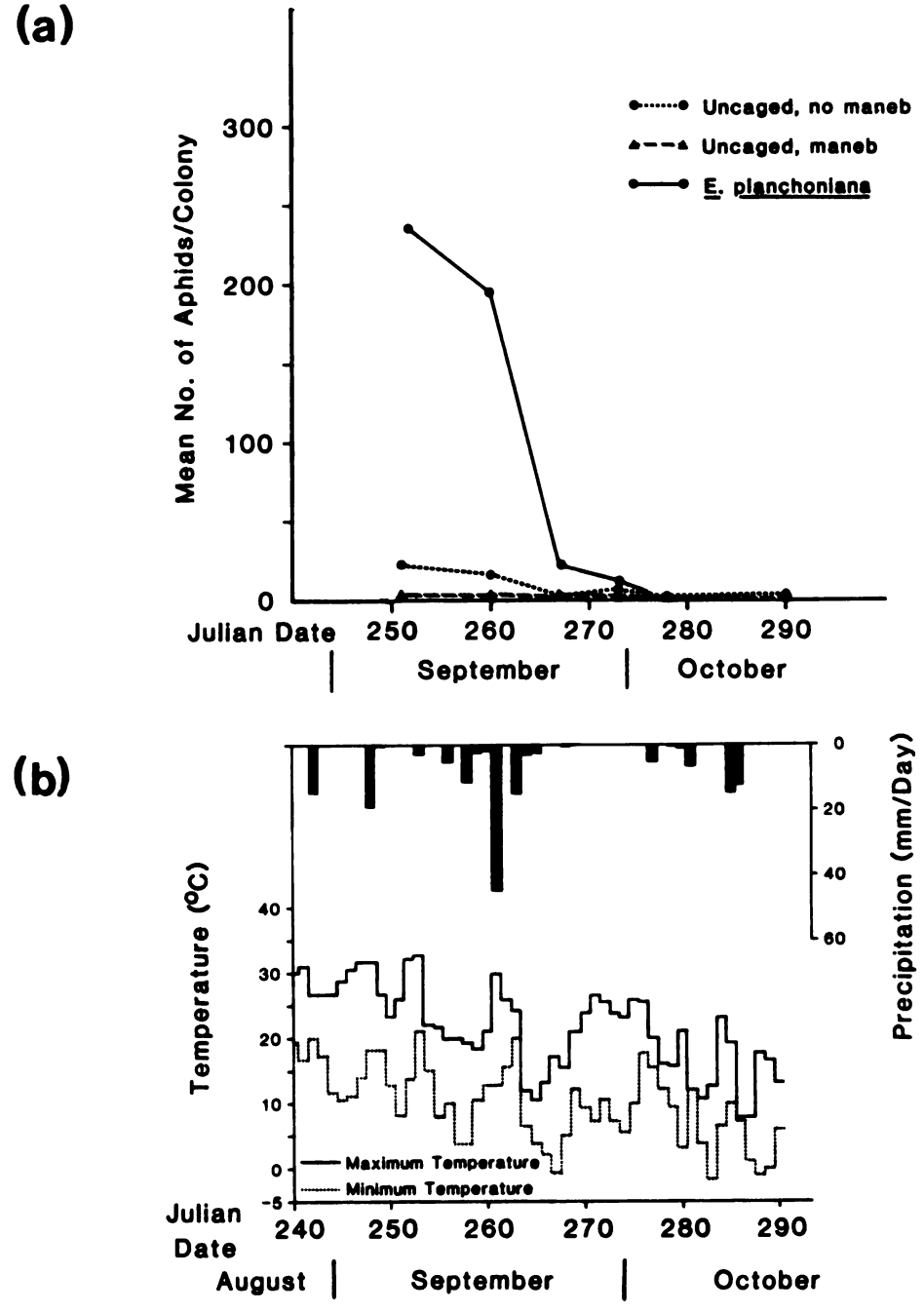


Figure 6. (a) 1983 DD Field asparagus aphid colony counts comparing the uncaged (with and without maneb) and the caged, E. planchoniana treatments. (b) Daily weather data.

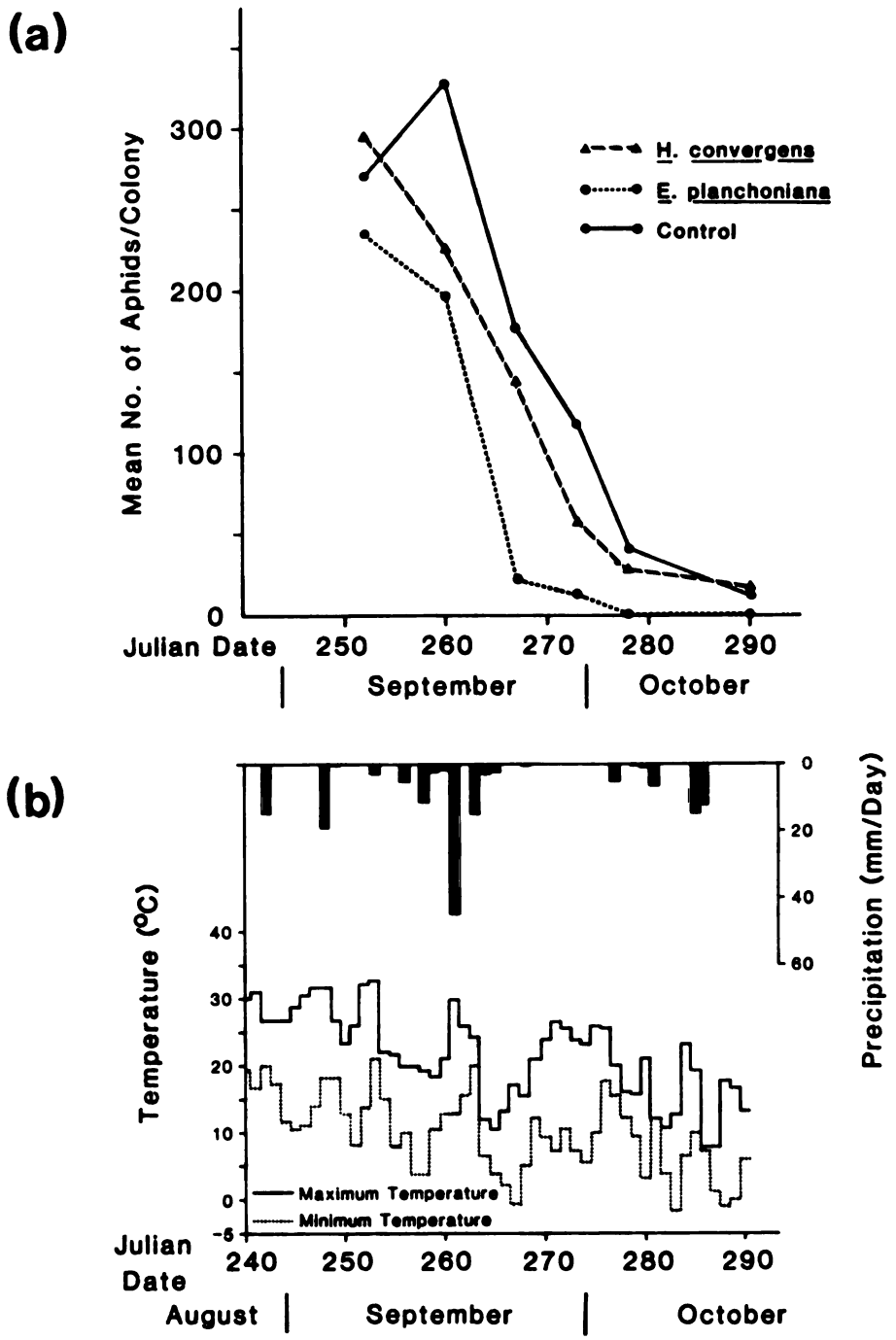


Figure 7. (a) 1983 DD Field asparagus aphid colony counts comparing caged treatments with E. planchoniana, H. convergens, or nothing (control) as the selected mortality factor. (b) Daily weather data.

rate of the aphid (Tomiuk and Wohrmann 1980). Cooler temperatures may have also directly affected aphids to reduce reproductive and developmental rates, and rainfall may have dislodged aphids from the fern and subsequently drowned them (especially day 261, see Figure 7b).

CONCLUSIONS

In the Morrow Field study, data suggested trends of increased asparagus aphid numbers for treatments in which natural enemies were thought to be reduced. Thus, pesticides commonly used by commercial asparagus growers to control asparagus pests may be detrimental to natural enemies of the asparagus aphid.

Very few statistically significant differences were obtained in this study. One problem was that most insects occurred in low numbers throughout the entire field. In the case of the asparagus aphid, initial populations on each plant varied and, once established, populations did not last for very long. Secondly, although spray applications were quite frequent in the first part of the season, there were several days of rain which may have washed off or at least diluted the effect of the pesticides. Spraying ceased in the latter half of the season due to the poor weather. Thirdly, sampling dates were not coordinated with spray dates, so that the number of days between application and sampling varied. Spray rates used may not have been as effective as expected,

since laboratory test conditions were rather artificial compared to field conditions and rates were purposely kept low to minimize the effect on the asparagus aphid.

The most useful results obtained from these studies were comparisons of different sampling techniques. Each of the four sampling methods had limitations, only sampling certain types of insects or requiring too much time and labor. In order to obtain the maximum amount of information about the field, a combination of sampling techniques is indicated.

While examining sticky sheets, it was observed that different groups of insects were caught in larger numbers at certain heights. For instance, chalcidoid parasitoids occurred in the largest numbers on the high traps, while aphids were most numerous on the lowest traps. Different species seemed to be preferentially caught at different heights in the DD Field, suggesting that a variety of trap heights should be used in order to effectively sample for all airborne insect species in a field. Also, traps can be arranged to sample for specific insects if one knows where they are likely to occur.

Asparagus aphid counts on the sticky traps may have been low throughout the season because aphids may have occurred in low numbers and were less active flyers. Also, it is difficult to draw conclusions since it is not known how effective the sticky traps would be with high asparagus aphid populations.

The abundance of other aphid species in the field suggests that weather alone could not be responsible for mortality, since, theoretically all aphids in the field experienced the same environmental conditions. It is unlikely that weather selectively caused greater mortality to asparagus aphids than other species. Of course, plant structure of weed hosts may have afforded these other aphids better protection against the elements, but it still does not completely account for the tremendous differences in numbers between asparagus aphids and other species. Thus, natural enemies probably were a major source of mortality for the asparagus aphids. Of the two introduced natural enemies, it appears that the fungal pathogen E. planchoniana had the greatest impact on asparagus aphid populations. The devastating effect of epizootics was demonstrated by the rapid decline of aphid populations in a very short period. Also, once the populations decreased, they remained low for the rest of the season.

In the DD colony count experiment, it was apparent that the cages provided conditions conducive to asparagus aphid population outbreaks. The cages seemed to exclude most natural enemies and many of the more severe weather effects and enabled artificially high aphid populations to be produced, a situation which is uncommon in Michigan asparagus fields.

This preliminary information on sampling techniques and the natural enemy complex in Michigan asparagus fields

is applicable to future field studies. Knowledge of the effects of weather and natural enemies will provide information to help answer the question of why the asparagus aphid is not an economic pest in Michigan.

JOURNAL ARTICLE 1

BIONOMICS AND INTERACTIONS OF THE PARASITOID, *DIAERETIELLA RAPAE* (M'INTOSH) (HYMENOPTERA: BRACONIDAE), AND THE EUROPEAN ASPARAGUS APHID, *BRACHYCOLUS ASPARAGI* MORDVILKO (HOMOPTERA: APHIDIDAE). 1. THE EFFECTS OF TEMPERATURE ON APHID AND PARASITOID LONGEVITY, FECUNDITY, REPRODUCTIVE RATE AND DEVELOPMENTAL RATE.

Dana L. Hayakawa and Edward J. Grafius

ABSTRACT

The effects of various constant temperatures on longevity, fecundity, reproductive rate and developmental rate of the European asparagus aphid and its parasitoid, *Diaeretiella rapae* (M'Intosh), were investigated. Moderate temperatures (23°C) were optimal for aphid survival and reproduction. Similarities in aphid biology between Michigan and Washington State, where the aphid is a severe pest, suggest that the variation in pest status between the two states was not attributable to biotype differences. *D. rapae* reproductive and developmental rates were highest at 30°C, but longevity was reduced considerably. Information concerning the role of temperature on aphid and parasitoid biology will be useful when examining their seasonal occurrence and host-parasitoid interactions in the field.

INTRODUCTION

The European asparagus aphid, Brachycolus asparagi Mordvilko, is an introduced pest from the Mediterranean area and Eastern Europe (Angalet and Stevens 1977). It is host specific to asparagus and was first sighted in North American in 1969, at Long Island, New York. Since then, the aphid has spread throughout much of the Eastern U.S. (Angalet and Stevens 1977), lower British Columbia (Forbes 1981), Michigan (Grafius 1980), Illinois, Oregon, Washington (Anonymous 1980) and California (Larry Bezark, State of California, Department of Food and Agriculture, pers. comm.).

Damage to asparagus consists of a rosetting of newly emerged spears and a tufting of the fern at the base of the plants. This bushy growth is blue-green and results from a shortening of the internodes between the whorls of cladophylls. Damage only occurs on fern branches where aphids are feeding. Plants are weakened and spear production may be affected by aphid feeding and the resulting abnormal growth (Forbes 1981).

In several states, the aphid appears to be under good natural control due to native natural enemies (Angalet and Stevens 1977). This may be the case in Michigan, where the aphid is present in a number of fields, but no serious damage has been reported (Grafius 1980).

Unlike the situation in Michigan, natural enemies do not appear to be regulating the asparagus aphid well in

Washington State, where populations were very high and economic losses were severe in 1980 (Anonymous 1980). Since Washington has many of the same natural enemies as Michigan, it was hypothesized that differences in aphid infestations in the two states might be a result of insect biotype and/or climatic differences which affect the aphid and/or its natural enemies differently.

One natural enemy of interest which is present in both states is the parasitoid, Diaeretiella rapae (M'Intosh). This solitary primary endoparasitoid attacks many different aphid species (Starý 1976, Vater 1971). The wasp's distribution is almost cosmopolitan and it is particularly common in Europe and throughout temperate North America (Read et al. 1970).

In the field, both biotic and abiotic factors influence the natural enemy and its host. Of the abiotic factors, it was hypothesized that temperature would have the greatest impact on D. rapae, since temperature has been shown to greatly influence parasitoid biology (Doutt 1959, Hafez 1961, Messenger 1968, Smith 1935). Temperature can also indirectly influence parasitoid abundance by affecting aphid host's biology and abundance (Campbell and Mackauer 1977; Tamaki et al. 1980, Woods 1974).

The objective of this study was to assess the impact of selected temperatures on asparagus aphid and D. rapae longevity, fecundity, oviposition rate and developmental rate. The effects of temperature on aphid biology were

then compared with data from Washington State to determine whether biotype differences exist.

MATERIALS AND METHODS - ASPARAGUS APHID

Data on aphid biology were obtained by the following procedure. An apterous fourth instar or adult female was placed on an asparagus seedling (10 replicates per temperature) and held at 14, 23 or 32.5°C and photoperiod LD 16:8. Relative humidity varied with temperature: 100% at 14°C, 50-75% at 23°C and 50-85% at 32.5°C. Every 24 hours each seedling was examined until nymph production began, at which time all progeny except one were removed. The remaining nymph was allowed to mature on the seedling, which was checked daily to determine when the nymph began to produce offspring (at the time of offspring production, the aphid was considered an adult). Progeny were removed daily and the number recorded. This was continued until the adult female died. The length of time the female survived indicated aphid longevity. The number of progeny produced per day gave the reproductive rate, and the total number of offspring represented fecundity. The amount of time that it took for a nymph to mature to a reproductive adult indicated developmental time.

RESULTS AND DISCUSSION - ASPARAGUS APHID

Longevity

Both mean adult and mean total apterous aphid longevity at 14°C were significantly different from that at 23 and 32.5°C (Table 6). Total longevity at 14°C was about twice as long as that at the higher temperatures. These results contradict those of Grafius and Morrow (1982) in which longevity was greatest at 20°C, second highest at 10°C and slightly less at 17.5 and 25°C.

Fecundity and Reproductive Rate

Fecundity differed significantly with temperature; highest at 23°C (55.11 nymphs/female), about half as much at 14°C (27.20 nymphs/female) and about one-seventh as much at 32.5°C (8.50 nymphs/female) (Table 7). Tamaki et al. (1983) obtained a similar mean fecundity (54.38 nymphs/female) for apterous virginoparae at 24.1°C. In contrast, Grafius and Morrow (1982) obtained results which were lower (25.2 nymphs/female at 25°C and 44.0 nymphs/female at 20°C).

Daily reproductive rates at 14°C and 32.5°C were significantly different from rates at 23°C but not from each other (Duncan's multiple range test, $p < 0.05$), but aphids at 14°C had a higher fecundity because of greater longevity and greater duration of the nymphal production period. At 14°C nymphs were produced for almost 40 days, whereas at 32.5°C they were only produced for 9 days.

Table 6. Asparagus aphid longevity at three constant temperatures.

Temp. (°C)	N	Mean age of first reproduction ± S.E. (days)[a]	Mean adult longevity ± S.E. (days)[a]	Mean total longevity ± S.E. (days)[a]
14	10	21.9 ± 0.9a	47.6 ± 3.9a	69.5 ± 3.6a
23	9	7.7 ± 0.7b	30.6 ± 2.8b	38.2 ± 3.0b
32.5	10	8.5 ± 0.9b	29.3 ± 2.5b	37.8 ± 2.8b

[a]Values within a column which are followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

Table 7. Asparagus aphid fecundity and reproductive rates at three constant temperatures.

Temp. (°C)	N	Range of nymphs per female	Mean no. of nymphs ± S.E.[a]	Range of nymphs per female per day	Mean nymphs per day ± S.E.[a]
14	10	5-44	27.2 ± 3.8b	0.2-0.9	0.6 ± 0.1b
23	9	9-76	55.1 ± 6.4a	0.9-2.5	1.8 ± 0.2a
32.5	10	1-19	8.5 ± 1.5c	0.03-0.7	0.3 ± 0.1b

[a]Values within a column which are followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

Mean number of days before production of the first nymph at 23 and 32.5°C were not significantly different and were similar to results obtained by Grafius and Morrow (1982) (8.0 days at 25°C, 9.9 days at 20°C, and 24 days at 10°C) and Tamaki et al. (1983) (7.3 days at mean temperature of 24.1°C, and 8.1 days at 17.9°C).

The importance of evaluating longevity and fecundity together is evident in Figure 8, which shows age-specific fecundity and survival rates at each temperature. DeLoach (1974) and Campbell and Mackauer (1977) stress the importance of the reproductive pattern over time, particularly the time when the largest proportion of offspring are contributed to the population. In this study, reproductive rates at all three temperatures were greatest during the first half of the reproductive period. The difference in reproductive rate between the first and last half of the reproductive period was more pronounced at 23°C (5x) than at 14°C (2x) or 32.5°C (2.5x). Nymph production ceased while a minimum of 70% of the adult aphids were still alive. In general, these results are in agreement with those of Tamaki et al. (1983), except that nymph production began three days later and reproductive period and longevity were each about seven days longer in their study.

These findings indicate that longevity may not be a major factor in aphid reproduction since most of the offspring are produced early in the adult's lifetime. It

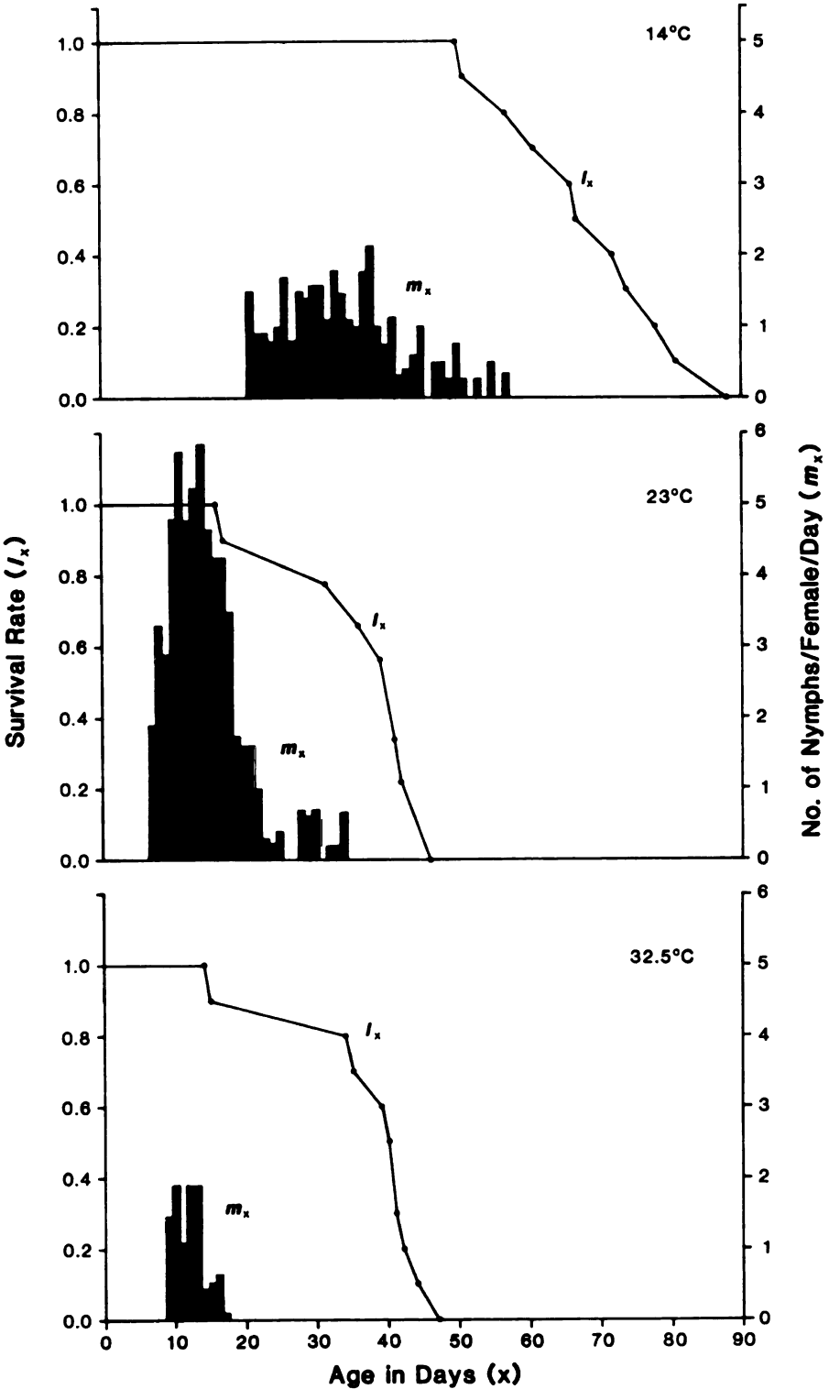


Figure 8. Asparagus aphid age-specific fecundity and survival rates at three constant temperatures.

is advantageous for the aphid to produce progeny early in its lifetime since it will probably die prematurely from external mortality factors.

Timing of the reproductive period is also important when comparing efficacy of various biological control agents. Some predators may feed on all life stages of prey (rather than preferentially on less vigorous aphids), and many of the adult aphids which are consumed may be in the post-reproductive phase. In the same manner, some insect pathogens are nonselective with regard to host stages which they infect, and many of these hosts may no longer be reproductively active. Thus, a large portion of the aphids affected by predators and pathogens may no longer be contributing progeny to the population. In contrast, if a parasitoid selectively attacks a first or second instar nymph, the aphid will not mature. If later instars are parasitized, they will produce offspring but their fecundity is reduced (Hagen and van den Bosch 1968). This is the case with D. rapae, which preferentially parasitizes second and third instars (Hafez 1961), although it can parasitize all stages of the host except the egg (Lyon 1968). The parasitoid thus reduces the proportion of potentially reproductive adults and future progeny. Therefore, from a theoretical standpoint, of the three types of natural enemies, parasitoids may disproportionately affect fecundity in relation to overall mortality or attack rate.

Developmental Rate

Developmental time of the asparagus aphid to reproductive maturity at 14°C (21.9 $\pm$ 0.9 days) was approximately 3x longer than at 23°C (7.7 $\pm$ 0.7 days) or 32.5°C (8.5 $\pm$ 0.9 days) (significance $p < 0.05$) (Table 8). These times are slightly shorter than those obtained by Grafius and Morrow (1982) (9.9 days at 20°C and 8.0 days at 25°C). Tamaki et al. (1983) obtained a mean developmental period of 7.5 days at 24.1°C.

Figure 9 shows developmental time for each temperature plotted with percent development per day for each temperature. According to DeLoach (1974), adverse effects of high temperature on developmental rate is indicated by longer developmental time at higher temperatures than at moderate ones. In this study, developmental time increases for aphids at 32.5°C, which suggests that the optimum developmental threshold had been exceeded. A lower optimum developmental threshold could not be obtained by extrapolation to the x-axis because of too few data points.

Results from this study indicate that moderate temperatures, in this case 23°C, seem to be better for aphid survival and reproduction. At 14°C aphids lived longer, but they had a much lower fecundity, reproductive rate and developmental rate. At 23°C and 32.5°C the aphids reached reproductive maturity at about the same rate and had about the same longevity, but fecundity and daily reproductive rates were much greater at 23°C than at

Table 8. Asparagus aphid developmental time and percent development per day at three constant temperatures.

Temp. (°C)	N	Mean developmental time to adult ± S.E.	Mean % development per day ± S.E.
14	10	21.9 ± 0.9a	4.6 ± 0.2b
23	9	7.7 ± 0.7b	13.1 ± 0.4a
32.5	10	8.5 ± 0.9b	12.6 ± 0.9a

[a]Values within a column which are followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

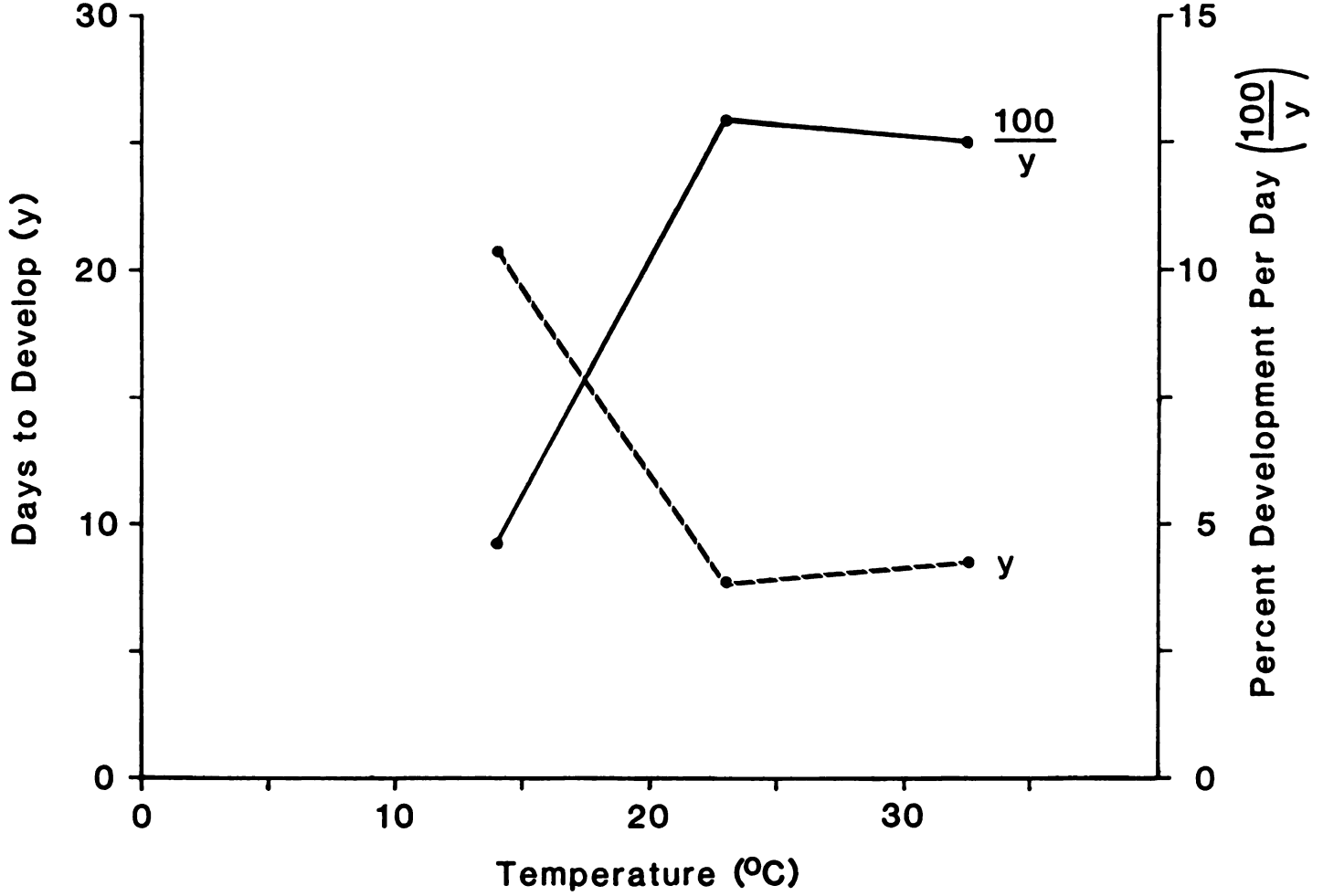


Figure 9. Asparagus aphid developmental time and percent development per day at three constant temperatures.

32.5°C. In addition, high temperatures may be detrimental since they can directly affect aphid somatic tissue, including the developing embryos within in its body, and indirectly affect the nutritional quality of the host plant (Campbell and Mackauer 1977).

The effects of temperature on alate aphid biology were not evaluated; however, this information is important since, while apterous aphids are primarily reproductive in function, transportation of developing parasitoid larvae within alate aphids is a primary means of passive parasitoid dispersal (Hafez 1961, van den Bosch et al. 1966, Vater 1971). Further studies should also be conducted to determine the role of alates in aphid and parasitoid larvae dispersal in asparagus fields.

MATERIALS AND METHODS - D. RAPAE

Longevity

In order to examine temperature as a sole mortality factor, other conditions were optimized for parasitoid survival. Percival 1-30BL growth chambers were kept constant at three temperatures with RH between 55-85%. Photoperiod was kept at LD 16:8 with fluorescent lights. A 50% honeywater solution was provided for the adults.

The experiment was carried out with parasitoids from field-collected mummies or laboratory cultures (two to four generations after field collection). Laboratory

populations experienced fairly constant temperatures while the field populations experienced fluctuating temperatures.

Parasitoids (0-48 hours old) were reared from mummies held in petri dishes at room temperature. Longevity was recorded as the lifespan of the adult parasitoid after the initial 0-48 hours. Once parasitoids emerged from the mummies, they were collected with an aspirator. A piece of tissue was placed in the bottom of the collecting vial to minimize the chance of injury as they were aspirated. Parasitoids were placed individually in shell vials (25 mm x 75 mm) which were covered with nylon organdy and secured with tape. Parasitoids were randomly assigned to each of the three temperatures, with each temperature receiving equal numbers of a particular sex. The number of males and females for each experiment depended upon the number of each sex which emerged. Once vials were numbered and a drop of honeywater placed on the organdy top they were stored sideways on a tray in their respective growth chambers. Vials were examined once or twice daily, the status of the parasitoid (alive or dead) was recorded and a fresh drop of honeywater was provided.

In Trial 1, 0-24 hour hold parasitoids from field collected mummies were used. Sets of nine females and 23 males were held at 14, 21.5 and 32.5°C. Vials were checked twice daily for the first two days and once a day thereafter.

Laboratory reared parasitoids were used for Trial 2. The parasitoids were 0-24 hours old when placed in individual vials, and they were held overnight in a refrigerator (2°C) before the experiment. Sets of 15 males and 15 females were held at 10, 20 and 30°C. Vials were checked twice a day (12 and 18 hours after the experiment was initiated).

Fecundity and Reproductive Rate

Aphid mummies were held individually in glass vials at 20°C, LD 16:8 in a growth chamber. Newly emerged (0-24 hours old) males and females were paired up in vials, provided with honeywater and held for an additional 24 hours at 20°C for mating. According to El-Minshawy and Hegazi (1980), 24 hours is considered sufficient time for parasitoids to mate.

In Trial 1, each mated female was introduced onto a lantern globe-covered, aphid-infested seedling (Figure 10). Aphid numbers on each seedling ranged from 27-1,370 with a mean of 374.9 $\pm$ 30.1 aphids. These seedlings were 12.7-18.0 cm tall and were heavily infested with aphids to insure that oviposition rate was not reduced by the female searching for hosts. A 50% honeywater solution was provided for food.

Seedlings were held at 10, 20 or 30°C for 24 hours. The female was then removed with an aspirator and placed on a new aphid-infested seedling for the next 24 hour period.

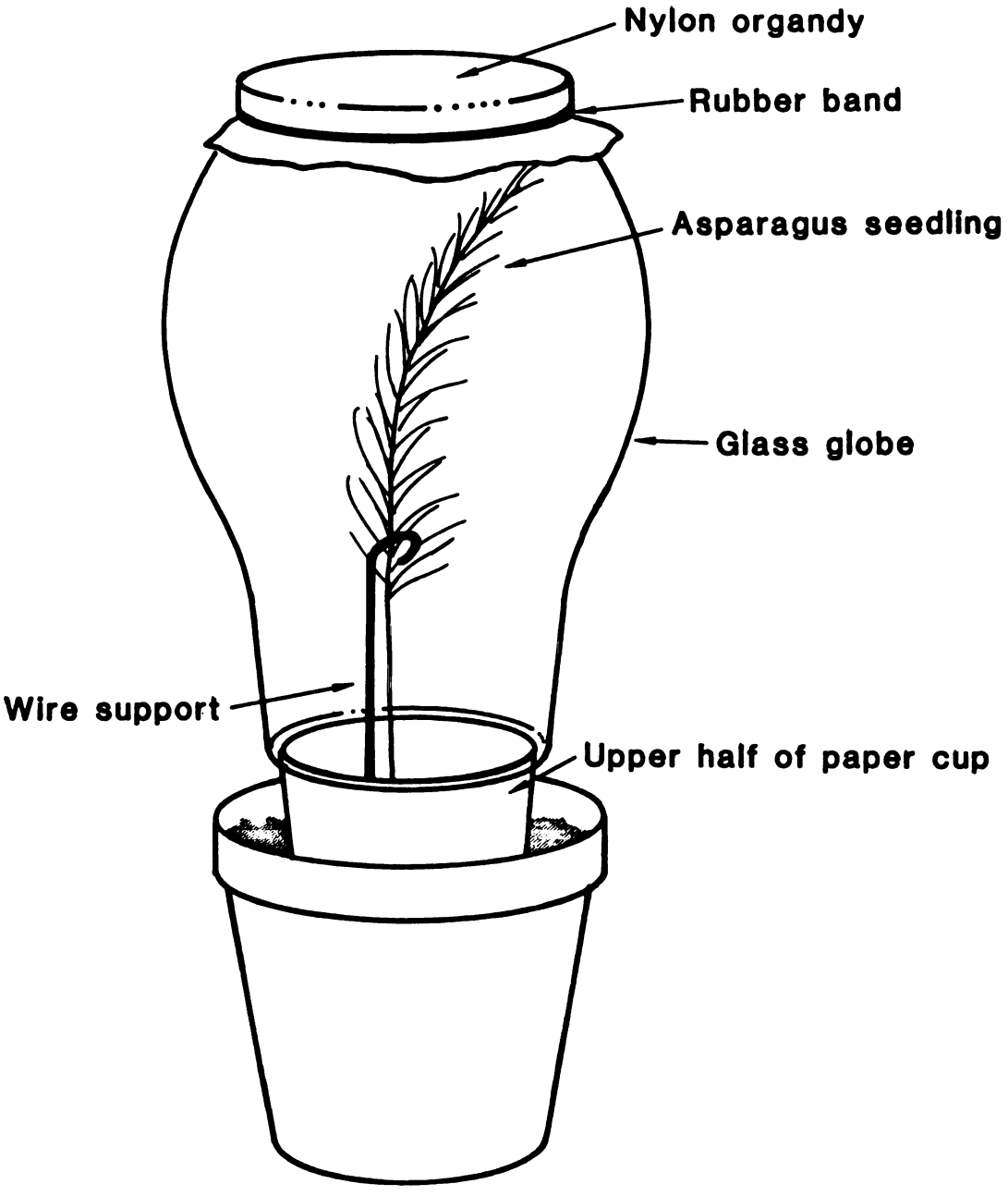


Figure 10. Trial 1 D. rapae fecundity and reproductive rate experimental set-up.

The previously exposed seedlings were maintained for an additional 48 hours at 22-27°C and LD 16:8 to allow the parasitoid eggs to hatch and the larvae to develop. Seedlings were then placed in mini-Berlese funnels and all aphids were collected in 70% ethyl alcohol. Each original sample was run through a plankton sample splitter twice to obtain a quarter of the total sample for dissection and larval parasitoid counting.

In Trial 2, a different arena was used. This consisted of a 52 x 52 Saran® mesh cage (15 cm x 17 cm tall) which was wrapped around the seedling to form a cylinder. Flexible electrical wire glued along the upper rim provided rigidity and enabled the cage to retain its cylindrical shape. The cage was further secured shut with twist ties. A sponge cork glued to the cage bottom bore a slit which allowed it to be slipped around the base of the seedling. Another sponge cork plugged the top of the cage. Stiff wire supports held up both seedling and cage. The narrow sides of the cage contacted the seedling so that a wasp on the cage sides would have a greater chance of encountering the plant.

Other than the enclosure, the only difference in experimental procedure between this trial and Trial 1 was that upon removal of the female from the caged seedling, the cage was replaced with a lantern globe for the next 48 hour period. Each seedling had from 25-868 aphids with a mean of 330.2 $\pm$ 20.9 aphids each.

Developmental Rate

Adults were reared from mummies held individually in glass vials at room temperature. A newly emerged (0-24 hours old) female was introduced into a lantern globe covered with nylon organdy on one end, and the globe was placed over a 3-stemmed, aphid-infested seedling approximately 17-23 cm tall. Seedlings were held at 10, 20 or 30°C and RH 55-80% for 24 hours, after which the female was removed and the seedling maintained uncovered at its proper temperature.

Seedlings were checked daily for mummies, which were placed in labelled petri dishes at the respective temperatures and checked daily for adult emergence.

RESULTS AND DISCUSSION - D. RAPAE

Longevity

Longevity was inversely related to temperature, that is, as temperature increased, longevity decreased (Table 9). In both trials, wasps at 10 and 14°C lived over twice as long as those at 20 and 21°C and over 24x longer than those at 30 and 32.5°C (Figure 11).

The short lifespan of D. rapae at 30 and 32.5°C indicates that it does not survive well at higher temperatures and may not live long enough to have an impact on its host. However, the experimental conditions under which these results were obtained were highly artificial and, given a more natural microhabitat, the parasitoid

Table 9. *D. rapae* adult longevity at various constant temperatures.

Temperature (°C)	Number tested	Mean adult longevity[a] ± S.E. (days)	Time to 50% mortality (days)
Trial 1:			
14	32	19.5 ± 1.4a	20.5
21	32	8.8 ± 0.8b	8.6
32.5	32	0.8 ± 0.0c	0.5
Trial 2:			
10	30	21.1 ± 2.2a	20.0
20	30	6.4 ± 0.7b	5.5
30	30	0.9 ± 0.1c	0.7

[a]Values with different letters are significantly different at the 5% level, by Duncan's multiple range test.

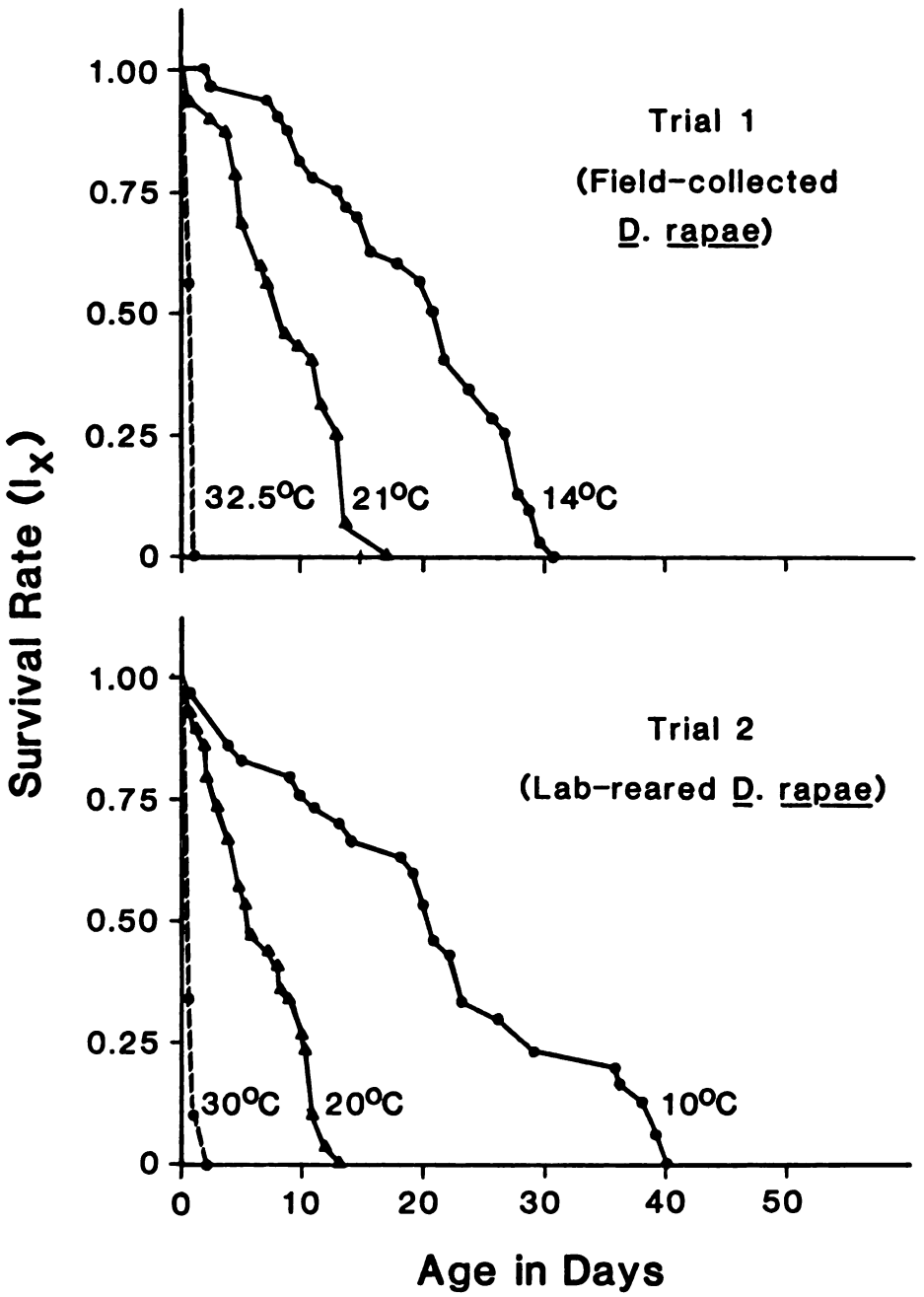


Figure 11. D. rapae survival rate at three constant temperatures for Trials 1 and 2.

would probably survive longer. This was demonstrated in the fecundity studies (see next section), in which females lived up to three days at 30°C when maintained on an enclosed, aphid-infested asparagus seedling.

Fecundity

In Trial 1, mean fecundity and daily oviposition rate at 10°C differed significantly from values at 20 and 30°C, but the two higher temperatures were not significantly from each other. While overall fecundity for 20 and 30°C were very close, daily oviposition rate for 30°C was almost twice as great as that at 20°C (Table 10).

Trial 2 mean fecundity and daily oviposition rate at 10 and 30°C were significantly different, but neither differed significantly from results at 20°C (Duncan's multiple range test, $p < 0.05$). Fecundity and oviposition rate were directly related to temperature, that is, as temperature increased, fecundity and daily oviposition rate also increased (Table 10). Overall mean fecundity at 30°C was about 6.3x greater than at 10°C and about 1.7x greater than mean fecundity at 20°C. Oviposition rate for 30°C was 16x greater than at 10°C and about 2.4x the rate at 20°C.

Fecundity results of this study were low compared to those of Hafez (1961), who conducted extensive studies of D. rapae on the cabbage aphid (Brevicoryne brassicae (L.)). He obtained a range of 25-175 eggs per female, with a mean fecundity of 83 eggs per female at 25°C. Reproductive rate

Table 10. D. rapae fecundity and oviposition rates on the asparagus aphid at three constant temperatures in two different enclosures.

Temperature (°C)	N	Range of Eggs per Female ± S.E.	Mean Eggs per Female ± S.E.[a]	Range of Eggs per Female per Day ± S.E.	Mean Egg per Female per Day ± S.E.[a]
Trial 1 (Globes):					
10	7	0-2	0.3 ± 0.3b	0-2	0.04 ± 0.04b
20	7	0-60	25.9 ± 8.7a	0-48	9.6 ± 3.0a
30	7	0-70	25.7 ± 11.2a	0-70	17.9 ± 9.7a
Trial 2 (Cages):					
10	8	0-28	4.5 ± 0.9b	0-8	0.9 ± 0.6b
20	8	0-52	17.1 ± 7.7ab	0-52	6.9 ± 3.4ab
30	8	0-48	28.5 ± 6.6a	0-52	16.3 ± 5.6a

*Values within a column which are followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

ranged from 0-55 eggs per day with a mean of 10.3 eggs per day per female. In almost all of the 25 replicates, the female was able to oviposit from the first day of emergence. After a few days of ovipositing, the female completely stopped or only laid one or two eggs per day for one or more days, then resumed oviposition of large numbers again. In general, oviposition was greater early in the female's life, with 8-13 eggs being laid during the first nine days.

The host stage most frequently parasitized in the current study at 20 and 30°C were third and fourth instar pre-alate (nymphs with visible wing pads) and apterous nymphs (Table 11). Oviposition was so low at 10°C that no conclusions could be made about preferred host stage. Parasitism also occurred in alate adults, which supports that idea that this stage is a means of passive parasitoid dispersal.

Fecundity and longevity of females in this experiment were evaluated together in age-specific fecundity and survivorship curves for both trials. In Trial 1 (Figure 12) oviposition began on the first day that parasitoids were introduced onto the seedlings. Parasitoids died fairly rapidly at all three temperatures, the longest survival being 10 days at 20°C. Parasitoids survived for the least amount of time at 30°C but produced the most offspring. In contrast, fecundity and oviposition rate

Table 11. D. rapae fecundity experiment - host stage preference at three constant temperatures for Trials 1 (globes) and 2 (cages).

	Parasitoid larvae/aphids							
Temp. (°C)	Alate adults Para.[b]	SP[b]	Apterous adults Para.	SP	Apterous nymphs[a] Para.	SP	Pre-alate nymphs[a] Para.	SP
Trial 1 (globes):								
10	0/2080	0/0	0/223	0/0	0/9670	0/0	2/2566	0/0
20	39/1840	0/0	14/198	0/0	93/5457	8/4	77/1316	0/0
30	20/957	8/4	2/94	0/0	110/4151	0/0	32/906	4/2
Trial 2 (cages):								
10	8/728	0/0	0/142	0/0	24/4690	0/0	12/1205	0/0
20	32/792	0/0	0/86	0/0	72/4425	0/0	28/1306	2/1
30	32/664	0/0	8/40	0/0	140/3652	4/2	64/1156	2/1

[a]All nymphal stages are included in these categories, but parasitoid larvae were found only in the third and fourth stage nymphs.

[b]Para. = parasitized by a single larva; SP = superparasitized by two larvae.

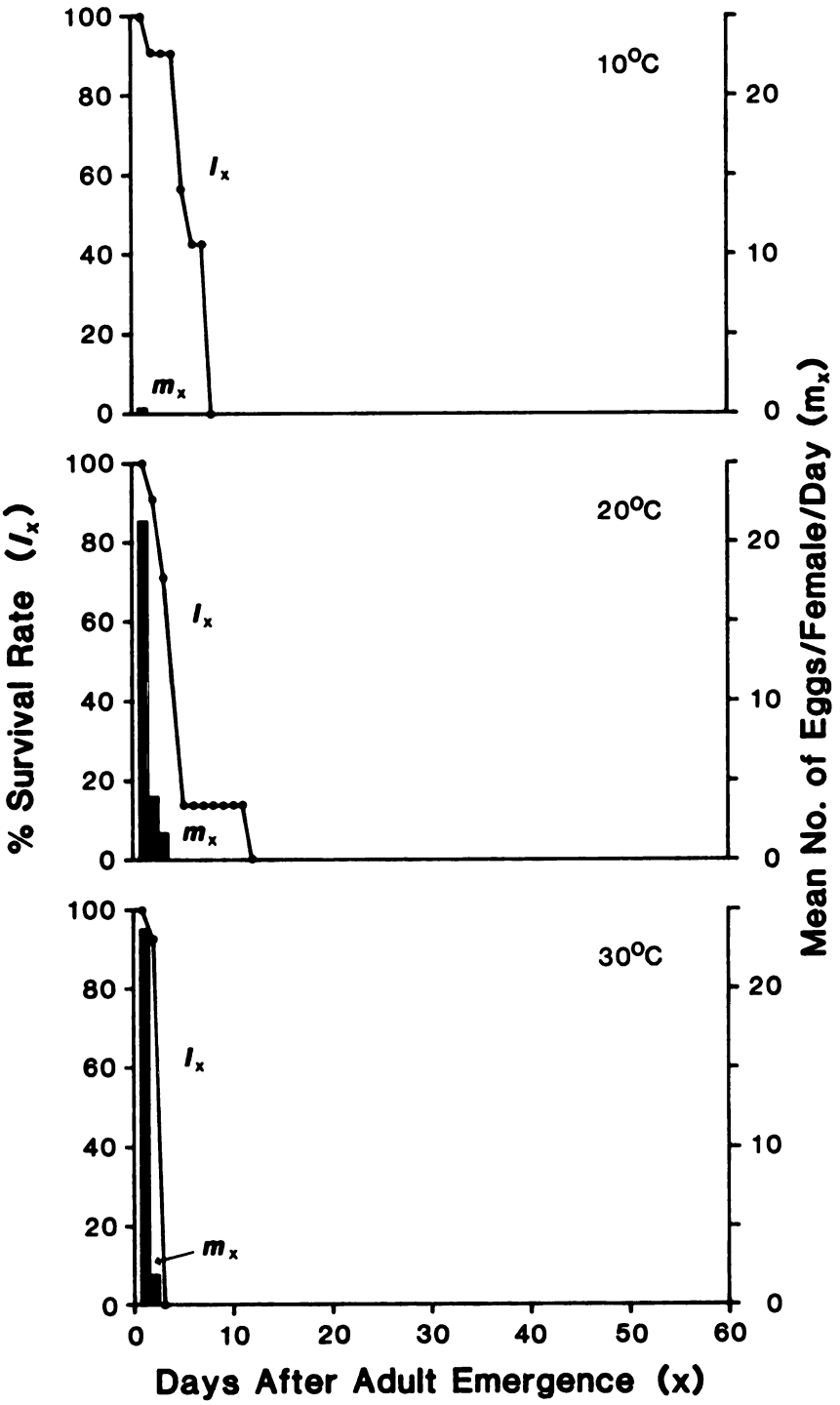


Figure 12. Trial 1 D. rapae age-specific fecundity and survival rates on the asparagus aphid at three constant temperatures.

were lowest at 10°C but longevity was highest. Reduced oviposition rate with greater fecundity is a less desirable situation in terms of affecting the host population, since premature death may prevent the female from laying her full compliment of eggs. A more desirable situation occurred at 20°C, where the reproductive period ceased before 50% of the population had died. This demonstrates the importance of timing of the reproductive period being early in the parasitoid's adult life.

In terms of the fecundity-survivorship curves for Trial 2, oviposition occurred almost up to the point of death at all three temperatures (Figure 13). Survival rate curves for all three temperatures exhibited about the same rate of decline.

D. rapae fecundity may have been lower than that determined by Hafez (1961) for several reasons. Ahmad et al. (1983), working with Apanteles galleriae Wilkinson (Braconidae), a parasitoid of the greater wax moth (Galleria melonella L.), found that fecundity was lowered as a consequence of inbreeding. In the current study, parasitoid cultures had been maintained in the laboratory for 4-6 months prior to the fecundity experiments. This would be approximately 7-11 generations.

Low parasitism may also have resulted from the experimental arena. In Trial 1, lantern globes were used to cover seedlings. Resulting numbers were low, and it was hypothesized that this was due to a modification of the

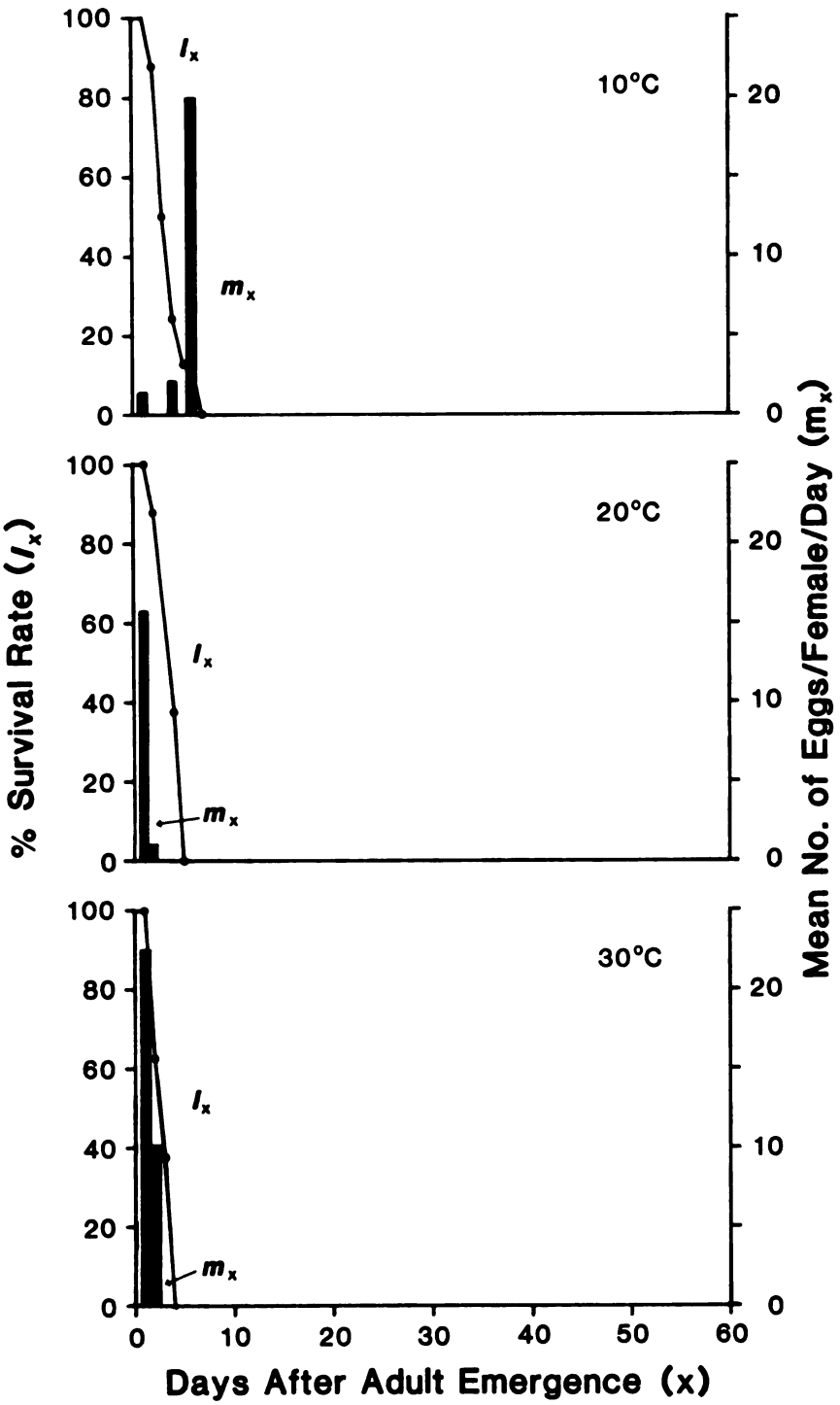


Figure 13. Trial 2 D. rapae age-specific fecundity and survival rates on the asparagus aphid at three constant temperatures.

parasitoid's behavior by the enclosure. The female appeared to spend more time on the glass sides and organdy top rather than searching on the seedling. Gage (1974) cites a similar problem with the lantern globes. He found that the universe which gave the most satisfactory results was a 15.24-cm cylindrical cage made of Lumite® screen with a 2.54-cm diameter and removable sponge plugs on both ends. Since the objective of the present study was to determine parasitoid fecundity and not her behavior away from the aphids, a cage similar to Gage's was used (Trial 2) to "force" the female onto the seedling to reduce her searching time. Once on the seedling, it was still up to the female to locate and oviposit in the aphids on her own.

Reduced fecundity at 10°C may have resulted from temperature effects. According to Messenger (1968), who looked at the impact of temperature on ovipositional activity of Praon exsoletum (Nees) (Braconidae), high and low temperature extremes can inhibit or depress oviposition in three distinct ways. First by changing the proportion of ovipositional to non-ovipositional activities of the adult female. For example, at certain temperatures a female spent proportionally more time resting and preening herself than searching and ovipositing. Secondly, the proportion of successful to total strikes was reduced, i.e. the oviposition behavior was not altered but the ability to insert eggs was greatly reduced. Finally, temperature can inhibit the actual ovipositional strike.

Messenger found that low temperatures greatly decreased the rate of behavioral activities. Also, the occurrence of false strikes (no eggs laid) increased greatly. In contrast, at high temperature extremes the rate of all activities was much greater than at the more favorable temperatures. However, the incidence of false strikes was very high. As the temperature approached the upper thermal limit for oviposition, attacks stopped completely.

In the current study, it appeared that the higher temperature threshold had not been reached, since D. rapae was not inhibited by 30°C, and in fact reproductive and developmental rates were highest at 30°C.

Developmental Rate

Mean developmental time for all stages (egg to mummy, mummy to adult and egg to adult) were significantly different at 10, 20 and 30°C and were inversely related to temperature; as temperature increased, developmental time decreased (Table 12). Mean developmental time from egg to mummy for 10°C was approximately 2.2x more than for 20°C and about 3.2x more than for 30°C. Developmental time at 20°C was about 1.5x more than at 30°C. Mean developmental time from mummy to adult showed a similar relationship. At 10°C it was 2.7x greater than at 20°C and almost 3.8x greater than at 30°C. At 20°C it was approximately 1.5x greater than at 30°C. Total developmental time for 10°C was 2.3x longer than at 20°C and about 3.4x longer than at

Table 12. *D. rapae* developmental time and percent development per day on the asparagus aphid at three constant temperatures.

Temperature (°C)	N	Mean developmental time (Days ± S.E.)[a] E to M[b]	M to A[c]	Total	% Development per day[a]
10	78	30.5 ± 0.5a	16.4 ± 0.3a	46.9 ± 0.7a	2.2 ± 0.0a
20	196	13.8 ± 0.3b	6.1 ± 0.1b	19.9 ± 0.3b	5.2 ± 0.1b
30	57	9.4 ± 0.1c	4.3 ± 0.2c	13.7 ± 0.3c	7.5 ± 0.1c

[a]Values within a column which are followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

[b]E to M represents developmental time from egg to appearance of the mummy.

[c]M to A represents developmental time from mummy to adult emergence.

30°C; 20°C was about 1.5x greater than at 30°C. In contrast, Vater (1971), working with D. rapae on the cabbage aphid, obtained a mean developmental time from egg to mummy of 9 days at 20°C and a total developmental time from egg to adult of 15 days.

Percent development per day was directly related to temperature; as temperature increased, percent development per day also increased. Wasps developed approximately 3.4x faster at 30 than at 10°C and approximately 1.4x faster than at 20°C. Although 30°C was not the upper developmental threshold for D. rapae, the decreasing slopes of both curves in Figure 14 suggest that they may be approaching an upper limit.

Hafez (1961) discussed the importance of temperature in influencing D. rapae both before and after mummification. Because it is an internal parasitoid, the effect of temperature before mummification may be indirect due to the effect of the host. Hafez found that developmental rate showed the same trends in both the host and parasitoid. He estimated the lower temperature threshold to be the same for both, about 6.5°C. Optimal parasitoid development was 10 days at approximately 25°C. High temperatures decreased survival rate. When 90 parasitized nymphs were reared at an average of 30.6°C, only 16 mummies developed and the remainder of the hosts died. Most of the 16 mummies failed to emerge. Therefore, Hafez concluded that high temperatures are detrimental to

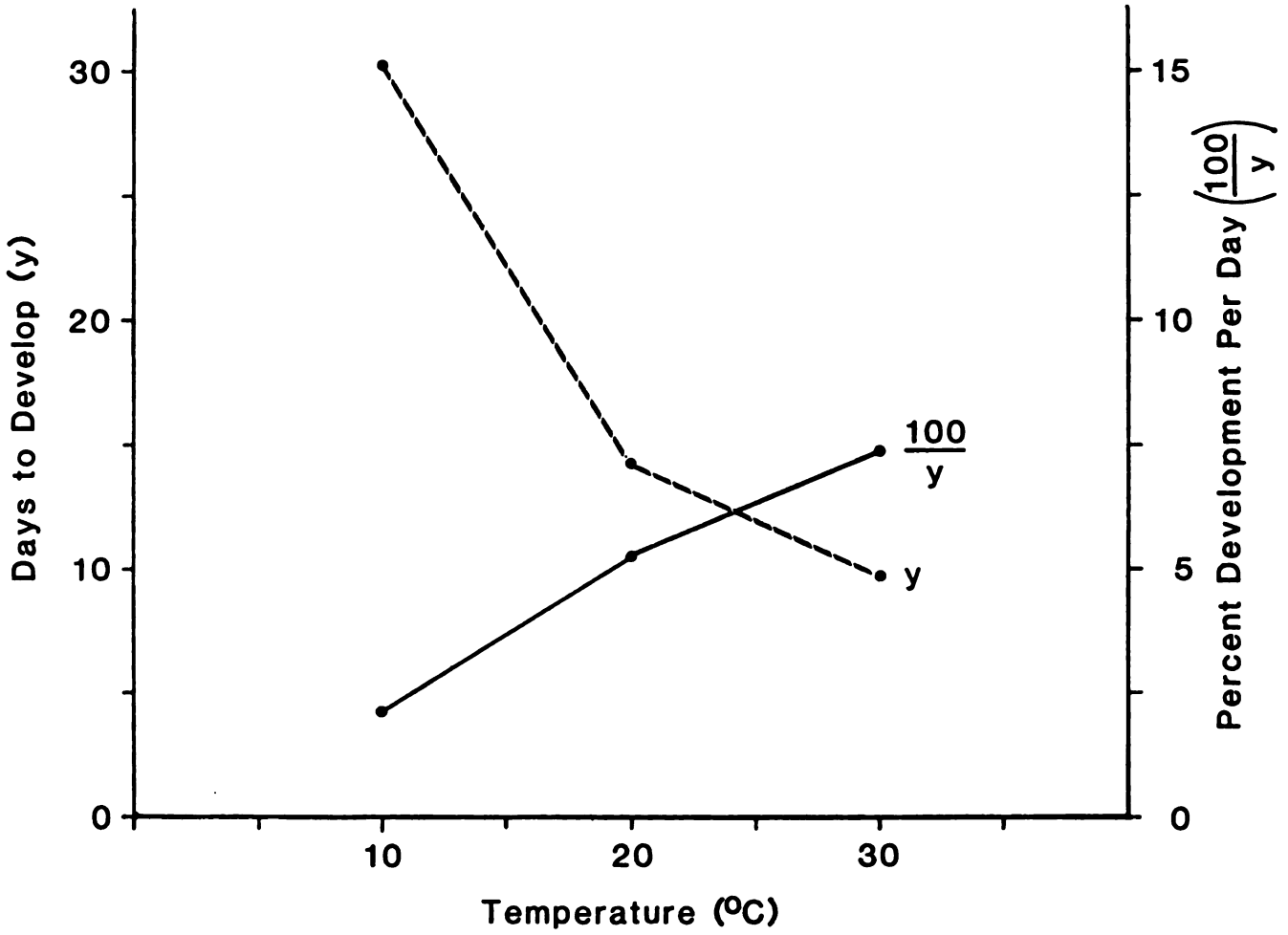


Figure 14. D. rapae developmental time and percent development per day at three constant temperatures.

parasitoids in the last larval stage, but this stage is very tolerant to low temperatures, and in fact is the stage which overwinters.

In contrast, 57 out of 97 mummies emerged at 30°C in the present study. In addition, parasitoids developed the fastest at 30°C, which suggests that different biotypes of D. rapae may exist between Michigan and The Netherlands.

CONCLUSIONS

Comparisons between this study and the ones by Tamaki et al. (1983) and Grafius and Morrow (1982) suggest that asparagus aphids in Michigan and Washington State possess some similar biological attributes. Hence, the difference in aphid abundance and damage between the two states are probably attributable to differences in other factors such as natural enemies and/or environmental factors.

Results from D. rapae biology studies indicate that 30°C was detrimental to adult longevity but was better for reproduction and development. This was unexpected, since studies by other authors on D. rapae indicated that it survives and reproduces best under moderate temperatures. In the field, temperatures slightly less than 30°C are probably optimal for D. rapae, since they would be conducive to high reproductive and developmental rates, yet enable the parasitoid to survive through its reproductive period. Dissimilarities in results among the other

authors's studies suggest that biotype differences in D. rapae may exist.

Differential responses of the aphid and parasitoid to different temperatures are important when examining population regulation in the field. At moderate temperatures the aphid, with its high reproductive and developmental rates, should be able to increase rapidly and attain high population levels before the parasitoid can have an impact. At temperatures at or slightly below 30°C, parasitoids may have a greater impact on the aphid population if survival rates are high enough to permit oviposition. However, high temperatures may indirectly and negatively influence parasitoids by affecting aphid biology and abundance.

High temperatures appear to be conducive to higher parasitoid fecundity, but fecundity may not play that large a role in regulating host populations in the field. According to Hopper (1984), fecundity and larval competitive ability of parasitoids are not well correlated with field abundance. Parasitoids are much more likely to be limited by their ability to find hosts than by fecundity. Thus, it is important to look at search time relative to when the parasitoid is reproductively active and its adult longevity.

Knowledge of temperature effects on both aphid and parasitoid is applicable to field studies. Although these experiments were done under constant temperatures which are

unrealistic when compared to field conditions, the results still provide an indication of the effects of various temperatures relative to each other on aphid and parasitoid biology. Seasonal abundance and occurrence of the insects can be better assessed by knowing how the parasitoid and its host respond to different temperatures.

JOURNAL ARTICLE 2

THE BIONOMICS AND INTERACTIONS OF THE PARASITOID, *DIAERETIELLA RAPAE* (M'INTOSH) (HYMENOPTERA: BRACONIDAE), AND THE EUROPEAN ASPARAGUS APHID, *BRACHYCOLUS ASPARAGI* MORDVILKO (HOMOPTERA: APHIDIDAE). 2. THE ROLE OF THE PARASITOID IN REGULATING APHID POPULATIONS IN THE FIELD.

D. L. Hayakawa, D. R. Prokrym and E. J. Grafius

ABSTRACT

The impact of various native natural enemies on an introduced pest, the European asparagus aphid, were assessed with special emphasis on the parasitoid, *Diaeretiella rapae* (M'Intosh). Artificially high asparagus aphid populations were propagated in the field, and different treatments were used to selectively exclude or include specific natural enemies. Results indicated that *D. rapae* and the coccinellid, *Hippodamia convergens* Guérin-Méneville, stabilized aphid population fluctuations but were unable to reduce populations to low levels, whereas the fungal pathogen, *Entomophthora planchoniana* Cornu, maintained aphid populations at low levels. Each natural enemy appeared to play a role in the overall regulation of the pest, thereby preventing the aphid from being a problem in Michigan asparagus fields.

INTRODUCTION

Many insects with high reproductive rates are capable of attaining high numbers, but fail to do so because they are regulated by natural controls. According to van den Bosch and Messenger (1973), natural control encompasses all the factors of the environment which keep a given population in check against its own ability for numerical growth. These include limited resources, climatic factors, intra- and interspecific competition and natural enemies. In an agricultural situation, particularly a monoculture, resources and competition are usually not the limiting factors for an insect pest, and weather and natural enemies may take on a greater role in insect mortality.

The European asparagus aphid is an introduced pest on asparagus which is present in most asparagus fields in Michigan (Grafius 1980), but almost never occurs in damaging numbers. Since this pest is known to be well controlled by natural enemies in New Jersey and Delaware (Angalet and Stevens 1977), it was hypothesized that this might also be the situation in Michigan. Particular emphasis was given to Diaeretiella rapae (M'Intosh), a primary endoparasitoid in the family Braconidae. This wasp attacks many different aphid species (Starý 1976, Vater 1971), and its distribution is almost cosmopolitan (Read et al. 1970).

Weather was also considered as a control factor in this system. Temperature and rainfall can affect both

insects species directly, either by causing physical injury or by affecting their biological processes. These factors can also operate indirectly by affecting the physiology of the host plant which in turn affects aphid reproduction and development. Any detrimental effects on the aphids will subsequently affect the parasitoid. Temperature and rainfall can also create conditions favorable to other natural enemies, such as the fungal pathogens, Entomophthora spp., which can cause striking epizootics in aphid populations.

The objective of this study was to assess the impact of selected natural enemies on the asparagus aphid. Special emphasis was placed on the role of D. rapae.

MATERIALS AND METHODS

This study was conducted on the MSU Botany Farm. The experimental plot was 14.6 m x 36.6 m with 10 rows of 31 to 44 plants each. Asparagus spears were not harvested in the spring so they would fern out and produce lush and healthy plants suitable for aphid infestation by early June. Plant residues left in the field from the 1983 season contained overwintering asparagus aphid eggs and served as a source of inoculum. Daily weather readings were taken at the MSU Horticulture Farm, 2.253 km from the MSU Botany Farm.

In selecting experimental units, asparagus plants were evaluated in terms of their height, number of stems and

sex. Twenty-three plants with similar specifications were selected from the 203 usable plants in the field. The two outer rows on each side of the field and the two plants at both sides of each row were designated as guard rows to eliminate edge effects. Eighteen plants were randomly selected from the 23 and assigned to the six treatments, making sure that all plants of a single replicate were of the same sex. Two replicates had all males and one replicate all females.

Prior to the experiment, all experimental plants were covered with 1.83 m x 1.83 m x 1.52 m Saran® mesh cages (20 mesh per 2.54 cm) and infested with field-collected aphids (first observed in the field on June 18). Visible natural enemies were removed by hand and plants were sprayed with maneb (1% solution of Dithane FZ) to reduce the occurrence of Entomophthora planchoniana Cornu. It was suspected that inoculum came from the soil or plant debris, where species of Entomophthora are generally thought to overwinter as thick-walled spores (Brandenburg and Kennedy 1981). After aphid populations became established and increased, the large cages were removed and plants were assigned to the six treatments. The six treatments consisted of two uncaged treatments and four caged treatments. Preliminary studies suggested that the cage enhanced aphid survival by creating a favorable and relatively natural enemy-free environment. Also, temperatures within the cage were 2-3°C higher than those outside the cage. In order to determine

whether the cage effect was due to exclusion of natural enemies or to moderation of severe weather conditions, two uncaged treatments were used. One uncaged treatment was designed to assess the impact of both weather and natural enemies on aphids. In the second uncaged treatment, carbaryl (Sevin 80S) was used to exclude predators and pathogens and maneb (Dithane FZ) was used to exclude E. planchoniana, so that weather was the primary mortality factor. Predators and mummies were also removed daily by hand. Three of the caged treatments were designed to evaluate the impact of specific introduced natural enemies on aphid populations. These were the parasitoid, D. rapae; a coccinellid predator, Hippodamia convergens Guérin-Méneville; and a fungal insect pathogen, E. planchoniana. The fourth caged treatment was a control (all natural enemies excluded). The caged treatment plants were enclosed with .914 m x .914 m x 1.829 m cages made of aluminum frames and covered with Saran® mesh (52 mesh per 2.54 cm) on two sides and nylon organdy on the other two sides. Access to the plant was via two velcro-secured flaps on opposite corners of the cage.

The cage acted as a physical barrier against entry by unwanted natural enemies as well as emigration by the introduced natural enemies. In addition, the cage lessened the impact of severe weather on the insects (e.g. dislodging by wind or rain). Since the cage could not prevent the movement of fungal spores, all plants

except those in which E. planchoniana was the primary mortality factor were sprayed with the fungicide maneb every five days except when it rained, in which case spraying was as soon thereafter as possible.

Application of maneb (Dithane FZ) was as a 1% solution via a hand sprayer. The main goal in application was to achieve total coverage to insure exclusion of the fungus, so plants were sprayed until runoff occurred (about 25 seconds per plant). Carbaryl (Sevin 805) was applied at a rate of one gram per six liters of water also for about 25 seconds per plant. Laboratory tests indicated that rates used would kill natural enemies without harming the aphids.

Introduction of D. rapae and H. convergens was as follows. Parasitoid mummies were held individually in vials until adults emerged, at which time they were sexed. Uncovered vials were then placed at the base of the fern for selected experimental units and the parasitoids were allowed to crawl out. Eighteen parasitoids of each sex were introduced from Aug. 6-10 (time span due to nonsynchronous emergence of parasitoids), eight males and eight females were introduced on Sept. 1 and seven males and 10 females were introduced on Sept. 4. Five male and five female coccinellids were introduced into selected cages on Aug. 6, and again on Aug. 19. These were placed at the fern base and allowed to climb up on the fern on their own.

Aphid Colony Samples

This sampling method was nondestructive, since aphids were counted on the fern without removal. For all plants, colonies of approximately five to 20 aphids were labelled and followed throughout the season. Selection of initially small colonies ensured that aphid populations would have an opportunity to increase, and lessened the possibility of emigration as a result of overcrowding. A colony was defined as the aphids occupying the terminal 7 cm of a growing tip. The 7-cm length was selected since it represented average length of a typical colony. Only the aphids on this part of the fern were counted, even if the rest of the population occupied the fern proximal to this length. A "twist tie," marked in 1-cm increments, was used to measure the length of the growing tip, since its flexible nature enabled it to conform to the shape of the fern, and thus provide an accurate measure of length. Labels consisted of a twist tie bearing a piece of tape with a number. Twelve colonies per plant, three plants per treatment, for a total of 216 colonies, were monitored over the season. Colonies which were lost due to senescence of the fern or a decline of the aphid population were replaced with new colonies. Colony counts were conducted every two to four days (with one eight day interval) depending upon the weather (20 sample dates over the 58 day sampling period. A randomized complete block design was used for sampling, and replicates were blocked over time during the

sample day. Time can contribute to error in terms of fatigue of the sampler as well as the behavior of the insects (insects may be more active during certain times of the day due to photoperiod and temperature).

The index used to measure healthy aphids (nonparasitized or nondiseased) in the colony counts was a finite rate of increase (FRI). Aphids in a particular colony were counted on two consecutive sampling dates, and the change in the population that occurred during that time interval was determined by using a formula developed by Tamaki et al. (1981):

$$q = \sqrt[n-x]{\frac{A_n}{A_x}}$$

where A = early count on day x and A = succeeding count or later count at day n.

If the FRI value is equal to 1.0, this indicates a stable population experiencing no change. Any value greater than 1.0 indicates a population which is increasing; conversely, any value less than 1.0 represents a decreasing population. When plotted on a graph, the slope of the line connecting consecutive dates indicates the acceleration of the increase or decrease.

The FRI method was preferred over using absolute aphid numbers, since it was impossible to start with the same initial population size for all experimental units. With

the FRI method, all that was needed were aphid colony counts on two consecutive dates and the time interval between the two dates to obtain a standardized index of population change. An added advantage of this method is that the equation has a time component, which compensates for different time intervals, so that sampling dates do not have to be equally spaced. This was especially useful when sampling intervals became irregular due to poor weather conditions.

In sampling for mortality factors, parasitism was determined by counting only unemerged mummies on the marked colonies. Mummies found in the non-braconid treatments were removed to reduce unwanted mortality. Viable mummies were left on braconid treatment plants since the emerging wasps served as the primary mortality factor. Percent disease was determined by counting all aphids which appeared pinkish-brown, indicating infection by the fungus.

Whole Plant Samples

Mean number of aphids per growing tip were estimated via a stratified destructive sampling procedure. A stratified method was used because the asparagus aphids are distributed with the greatest numbers and highest variability at the bottom of the plant (Wright and Cone 1983).

The experimental units was sampled on August 14, 21, September 5, 14 and 27. Five growing tips were randomly

selected from the top third of the plant, 10 from the middle third and 15 from the bottom third. Each tip was individually bagged and taken to the laboratory for counting. Total numbers of each life stage of the aphid, as well as parasitized and diseased aphids were recorded.

Once destructive samples were counted, the means and variances were calculated for the three levels (top, middle and bottom) within the plant. Prior to the experiment, 30 asparagus stems had been examined to estimate mean number of growing tips per stem at each of the three levels of the plant. The mean number of stems for each plant was then multiplied by the mean number of growing tips per stem for each level to get the mean number of growing tips per level within the plant. These numbers, along with the means and variances per level obtained from each sample were used to obtain the mean number of insects per tip $\pm$ S.E. (Cochran 1963).

Hyperparasitism

To assess hyperparasitism, colonies of mummified aphids were taken from the various treatment plants in the field on two occasions. It should be noted that this was a nonrandom sample, since only heavily-parasitized colonies were selected. Thirty-nine to forty mummies were collected from each treatment, placed individually in vials and held at room temperature. Daily checks were made to determine

whether a parasitoid or hyperparasitoid emerged and, in the case of D. rapae, the sex.

RESULTS AND DISCUSSION

Aphid Colony and Whole Plant Samples

A few problems arose in the aphid colony counts. First, immigration and emigration of the aphids could not be regulated or measured. However, it was assumed that all plants experienced the same amount of aphid emigration, and thus aphid numbers on each plant relative to each other would not be affected. The second factor was the disappearance of aphids due to being dislodged from the plant. Again, it was assumed that all caged plants experienced the same phenomenon.

Aphid populations in the two uncaged treatments appeared to track fairly closely (Figure 15a), which suggested that both were being influenced by similar mortality factors. Daily maximum and minimum temperatures and precipitation for the entire season are shown in Figure 15b. The occurrence of E. planchoniana corresponded well with periods of heavy or prolonged rainfall, which is evident in the two large and rapid decreases in aphid FRI values after the rainfall (Figure 15a). This supports the fact that rainfall is conducive to Entomophthora spp. outbreaks (Hagen and van den Bosch 1968). In this case, weather may have been the major factor causing both

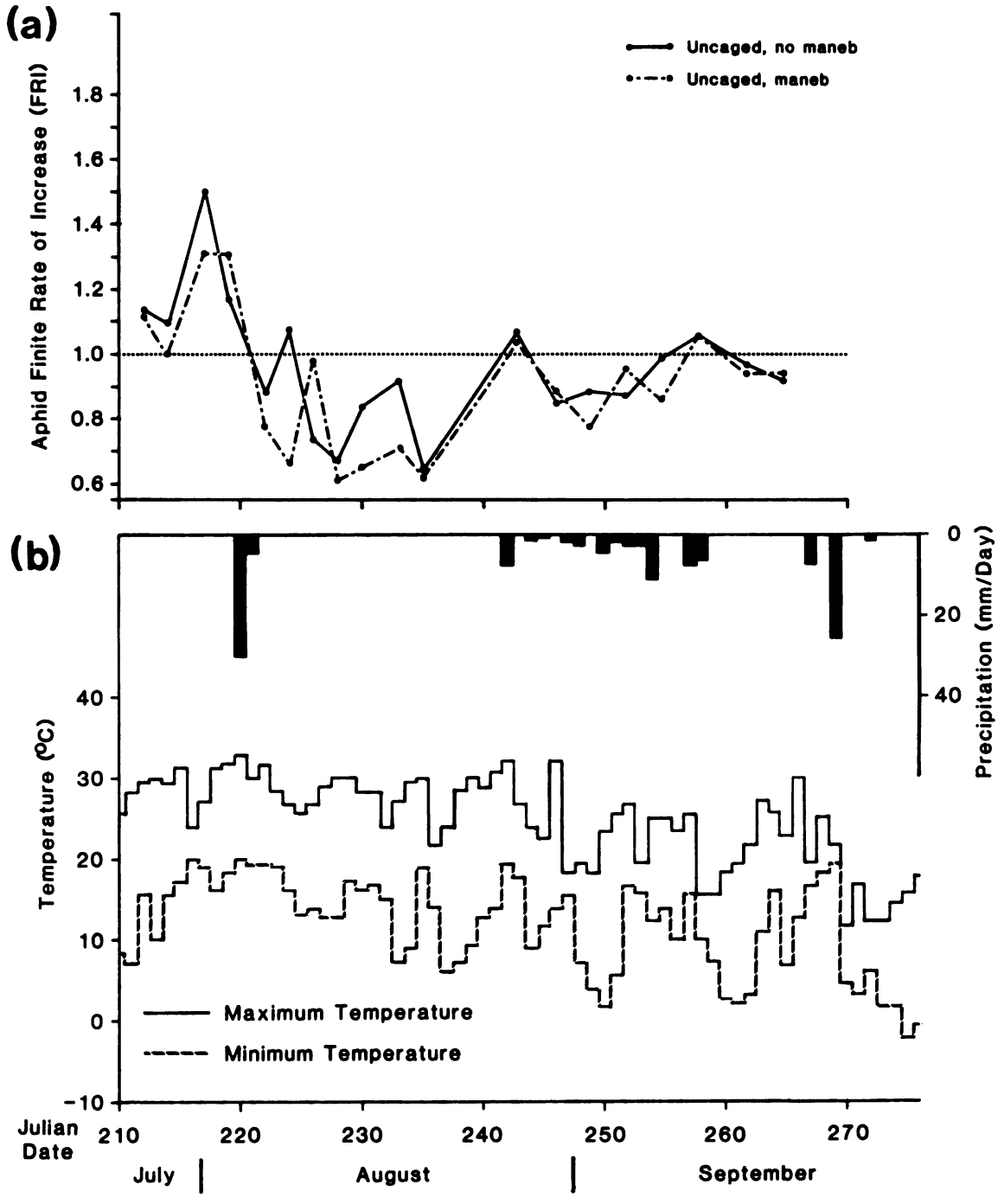


Figure 15. (a) Asparagus aphid FRI values comparing weather + natural enemies (uncaged, no spray) to weather alone (uncaged, maneb + carbaryl) as the primary mortality factors. (b) 1984 daily weather data.

direct mortality to the aphids, as well as enabling the fungal pathogen to cause epizootics.

All aphids in marked colonies, including those that were parasitized or diseased, were counted on each sampling date. The number of viable mummies and diseased aphids represents mortality for that sampling date due to E. planchoniana and D. rapae, respectively (Tables 13 and 14). Percent mortality due to the fungal pathogen in the E. planchoniana treatment (caged, no spray) started low, then experienced a rapid increase to 90% mortality in late August, and finally dropped to low levels in September (Figure 16a). In contrast percent parasitism in the D. rapae treatment never exceeded 10% throughout the entire season, although it did show an increasing trend toward the fall (Figure 16a). This trend is similar to that found in New Jersey and Delaware, where parasitism was low until late August, when it increased up to 29% in some samples (Angalet and Stevens 1977). D. rapae was the most common parasitoid in those states, and it was found to be active until mid-November.

Comparisons of aphid FRI values (Table 15) in the E. planchoniana and D. rapae treatments show quite a difference in the behavior of aphid populations (Figure 17a). Populations in the E. planchoniana treatment experienced a series of abrupt increases and decreases throughout the season. These extreme fluctuations are typical of epizootics, where the host population is allowed

Table 13. Mean percent asparagus aphid mortality due to *E. planchoniana*

	Mean percent diseased asparagus aphids by treatment					
Sampling Interval	Uncaged, no spray	Uncaged, maneb + carbaryl	Caged, no spray	Caged, maneb, *D. rapae*	Caged, maneb, *H. convergens*	Caged, maneb (control)
1	0	0	0	0	0	0
2	0	0	0	0	0	0
3	0	0.64	0	0.40	0	0
4	0	0	3.59	0	0	0
5	0	0	2.79	0	0	0
6	0	0	5.54	0	0	0
7	6.28	0	14.96	0.07	0.19	0
8	2.58	0	45.40	0	0	0
9	6.70	0	54.62	0	0.05	0
10	7.30	0	82.16	0.24	0.39	0.17

Table 13 (cont'd.).

Sampling Interval	Mean percent diseased asparagus aphids by treatment					
	Uncaged, no spray	Uncaged, maneb + carbaryl	Caged, no spray	Caged, maneb, *D. rapae*	Caged, maneb, *H. convergens*	Caged, maneb (control)
11	0	0	87.84	0	0	0
12	2.74	0	89.90	0	1.04	0
13	2.29	1.00	43.58	0	0	0
14	1.84	0.39	41.76	0.69	0.06	0.66
15	0.46	0	6.97	0.50	0.81	0.68
16	0.15	3.32	2.64	0	0.39	0
17	0.04	0.84	4.15	0	0	0.06
18	3.83	1.21	9.71	0.09	0	0
19	11.19	0.79	14.63	0.64	1.36	0.03

Table 14. Mean percent asparagus aphid mortality due to D. rapae.

Sampling Interval	Mean percent parasitized asparagus aphids by treatment					
	Uncaged, no spray	Uncaged, maneb + carbaryl	Caged, no spray	Caged, maneb, D. rapae	Caged, maneb, H. convergens	Caged, maneb (control)
1	0	0	0	0	0	0.12
2	0	0.17	0	0	0	0
3	0	0.05	0	0	0	0
4	0	1.89	0.05	0	0	0
5	0.02	1.11	0	0.07	0.40	0.57
6	0.02	0	0	0.08	0.01	0
7	0.01	1.05	1.61	2.75	0	0
8	0	0.27	3.45	0.12	0	0
9	0.58	0	0.14	0.47	0	0
10	0.84	4.76	0	0.32	1.04	0.76

Table 14 (cont'd.).

Mean percent parasitized asparagus aphids by treatment						
Sampling Interval	Uncaged, no spray	Uncaged, maneb + carbaryl	Caged, no spray	Caged, maneb, *D. rapae*	Caged, maneb, *H. convergens*	Caged, maneb (control)
11	3.42	0.53	0	0.79	5.67	1.72
12	2.37	4.29	0	1.03	2.37	9.06
13	0.14	0	0	2.09	2.34	1.72
14	0.07	0.33	0	6.11	7.99	10.30
15	0.19	0	0.05	5.49	11.03	0.99
16	2.81	0.10	0.37	2.45	6.56	0.33
17	0.13	0.20	0.04	2.75	3.70	0.04
18	0.20	0.14	0.04	2.35	0	3.74
19	0.12	0.40	0.11	0.76	4.67	0.48

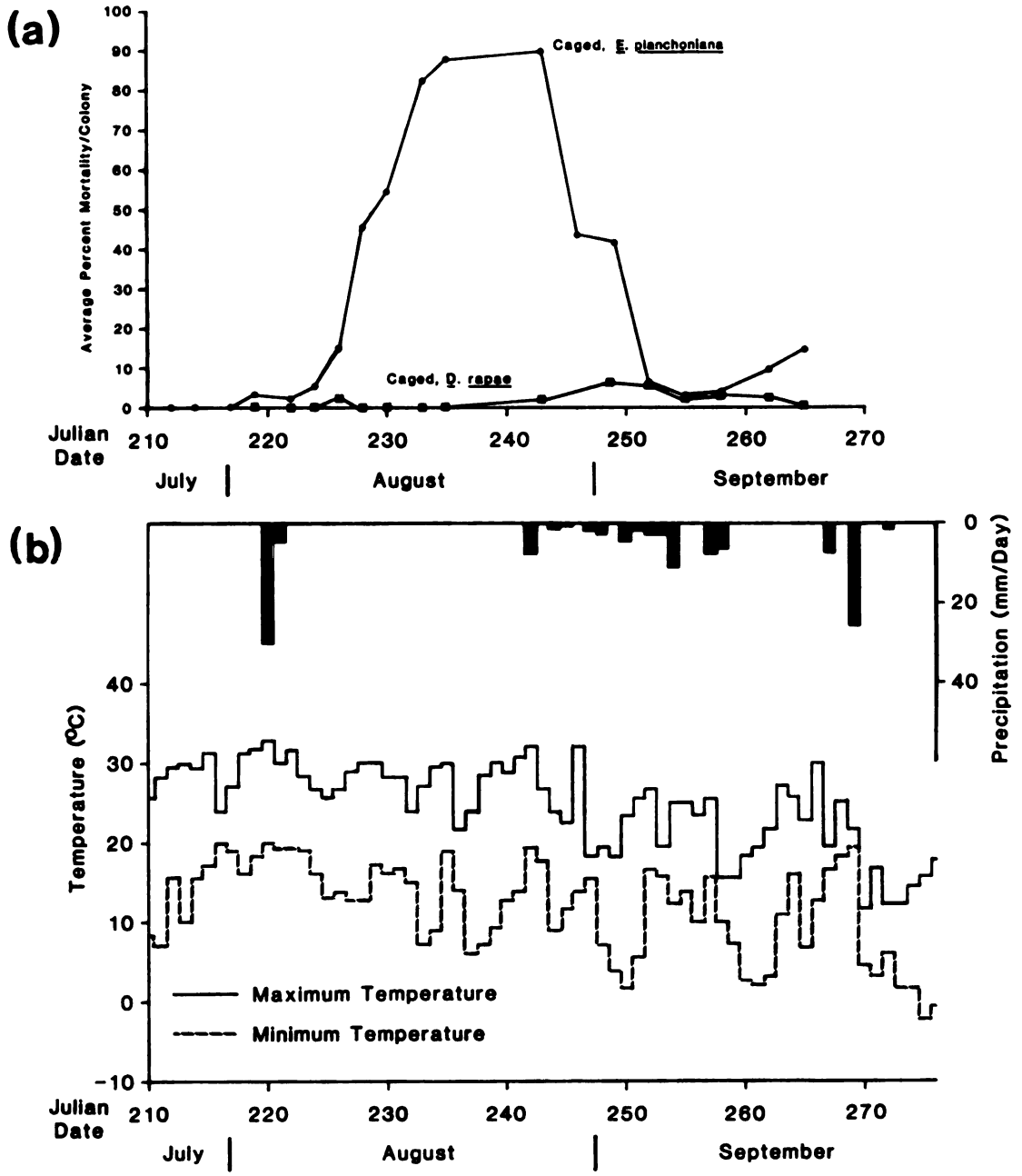


Figure 16. (a) Percent asparagus aphid mortality in the D. rapae and E. planchoniana treatments. (b) Daily weather data.

Table 15. Asparagus aphid mean FRI values ± S.E. for the 1984 season.

Sampling Interval	Mean FRI value ± S.E. by treatment[a]					
	Uncaged, no spray	Uncaged, maneb + carbaryl	Caged, no spray	Caged, maneb, *D. rapae*	Caged, maneb, *H. convergens*	Caged, maneb (control)
1	1.134 ± 0.069a	1.127 ± 0.038a	1.186 ± 0.052a	1.202 ± 0.60a	1.107 ± 0.067a	1.118 ± 0.065a
2	0.997 ± 0.069a	1.001 ± 0.048a	1.262 ± 0.066a	1.122 ± 0.081a	1.188 ± 0.054a	1.150 ± 0.130a
3	1.508 ± 0.093a	1.310 ± 0.093a	1.308 ± 0.093a	1.650 ± 0.0281a	1.362 ± 0.0126a	1.244 ± 0.086a
4	1.177 ± 0.093a	1.308 ± 0.061a	1.309 ± 0.047a	1.073 ± 0.037a	1.270 ± 0.066a	1.211 ± 0.043a
5	0.878 ± 0.059bc	0.780 ± 0.036c	1.076 ± 0.062ab	1.049 ± 0.034ab	1.161 ± 0.062a	0.951 ± 0.038abc
6	1.068 ± 0.152a	0.664 ± 0.052b	0.973 ± 0.045ab	1.042 ± 0.058a	0.983 ± 0.094ab	1.126 ± 0.057a
7	0.731 ± 0.046b	0.974 ± 0.058b	0.963 ± 0.039ab	1.098 ± 0.031a	1.042 ± 0.040a	1.098 ± 0.028a

Table 15 (cont'd.).

Sampling Interval	Mean FRI value ± S.E. by treatment[a]					
	Uncaged, no spray	Uncaged, maneb + carbaryl	Caged, no spray	Caged, maneb, *D. rapae*	Caged, maneb, *H. convergens*	Caged, maneb (control)
8	0.671 ± 0.044c	0.621 ± 0.041c	0.909 ± 0.051b	0.970 ± 0.042ab	1.000 ± 0.043ab	1.126 ± 0.058a
9	0.842 ± 0.066cd	0.668 ± 0.060d	1.390 ± 0.093a	1.177 ± 0.072ab	1.113 ± 0.030abc	1.067 ± 0.038bc
10	0.919 ± 0.050c	0.715 ± 0.035d	1.279 ± 0.053a	1.089 ± 0.051b	0.946 ± 0.038bc	0.954 ± 0.030bc
11	0.647 ± 0.034b	0.624 ± 0.027b	1.762 ± 0.182a	1.056 ± 0.040b	0.996 ± 0.065b	0.989 ± 0.047b
12	1.070 ± 0.022ab	1.044 ± 0.021b	1.173 ± 0.032a	0.980 ± 0.018b	0.982 ± 0.018b	0.949 ± 0.020b
13	0.851 ± 0.044b	0.894 ± 0.039b	1.321 ± 0.078a	0.947 ± 0.038b	1.024 ± 0.055b	1.010 ± 0.057b
14	0.881 ± 0.039b	0.774 ± 0.040b	1.324 ± 0.089a	0.985 ± 0.032b	0.892 ± 0.033b	0.909 ± 0.031b

Table 15 (cont'd.).

Sampling Interval	Mean FRI value ± S.E. by treatment[a]					
	Uncaged, no spray	Uncaged, maneb + carbaryl	Caged, no spray	Caged, maneb, *D. rapae*	Caged, maneb, *H. convergens*	Caged, maneb (control)
15	0.878 ± 0.040b	0.959 ± 0.042ab	1.257 ± 0.084a	0.880 ± 0.46b	0.970 ± 0.049ab	1.058 ± 0.069ab
16	0.984 ± 0.033ab	0.862 ± 0.039c	1.074 ± 0.036a	0.955 ± 0.034b	1.021 ± 0.060ab	1.068 ± 0.029a
17	1.065 ± 0.040ab	1.064 ± 0.039ab	1.178 ± 0.087a	0.943 ± 0.034bc	0.893 ± 0.043c	1.068 ± 0.049ab
18	0.965 ± 0.028a	0.943 ± 0.017a	1.031 ± 0.021a	0.967 ± 0.032a	0.912 ± 0.030a	0.986 ± 0.069a
19	0.923 ± 0.021b	0.942 ± 0.029b	0.990 ± 0.029ab	1.009 ± 0.021ab	0.947 ± 0.032b	1.093 ± 0.030a

[a]Values within a row which are followed by the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

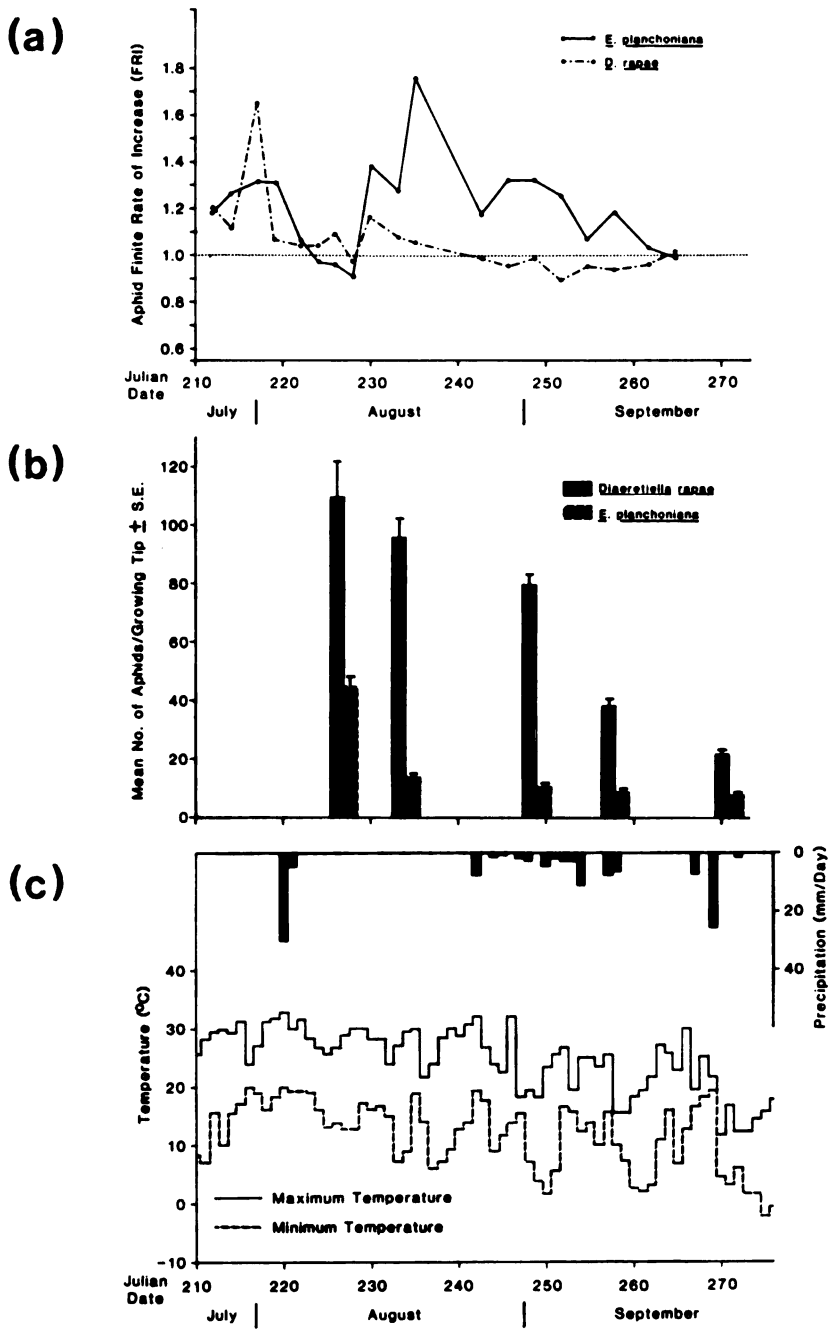


Figure 17. E. planchoniana and D. rapae treatments: (a) asparagus aphid FRI values, (b) mean no. of aphids/growing tip ± S.E. and (c) daily weather data.

to build up, crashes due to the microorganism and then repeats the cycle.

Aphid populations exposed to D. rapae also experienced fluctuations, but these were much less dramatic. It may be that the braconids stabilized the aphid population fluctuations or, the aphid populations may have reached the carrying capacity of the system and the asparagus fern could not support any more aphids. In either case, a conclusion cannot be drawn unless one knows about the normal fluctuations in the availability of resources to which the species are adapted.

Mean aphids per growing tip obtained from the destructive samples (mean values given in Table 16) indicate that aphids in the braconid treatment remained high throughout much of the season, while populations exposed to E. planchoniana experienced an initial reduction and remained fairly low throughout the rest of the season (Figure 17b). From an ecological standpoint, D. rapae may have lended stability to aphid populations during the season, but from an economical standpoint, it was unable to reduce aphid populations to low levels. In contrast, E. planchoniana caused unstable aphid population fluctuations, but these oscillations occurred around a lower mean population level. Thus, the fungal pathogen appears to be a more effective biocontrol agent.

Table 16. Asparagus aphid destructive sample counts for the 1984 season.

Treatment	Mean aphids/growing tip ± S.E.[a] Sampling Date				
	Aug. 14	Aug. 21	Sept. 5	Sept. 14	Sept. 27
Uncaged, no spray	7.0 ± 1.3a	0.4 ± 0.1a	29.5 ± 3.0b	24.9 ± 2.3b	9.9 ± 0.7a
Uncaged, maneb + carbaryl	10.8 ± 1.1a	1.1 ± 0.2b	20.2 ± 3.0b	14.3 ± 2.1a	18.2 ± 1.5b
Caged, no spray	45.3 ± 4.0b	14.0 ± 1.1c	11.5 ± 0.9a	9.0 ± 0.9a	8.0 ± 0.9a
Caged, maneb, *D. rapae*	110.2 ± 11.9d	96.5 ± 6.3e	80.7 ± 3.8c	38.6 ± 2.4c	22.4 ± 1.2b
Caged, maneb, *H. convergens*	136.0 ± 8.2d	107.4 ± 5.8e	118.6 ± 7.3d	21.6 ± 1.5b	18.0 ± 1.2b
Caged, maneb (control)	61.0 ± 3.1c	54.7 ± 3.7d	66.6 ± 3.5c	26.7 ± 1.4b	20.7 ± 1.7b

[a]Values with the same letter are not significantly different at the 5% level, by Duncan's multiple range test.

FRI values for the control, D. rapae, and H. convergens treatments (Figure 18a) appeared to track fairly closely throughout the season. This probably resulted because non-braconid treatments accidentally became infested with parasitoids early in the season (mummies were found in non-braconid treatments on August 9). It was suspected that this occurred when the experimental plots were initially inoculated with field aphids. At the time of infestation, some of the aphids which appeared healthy may actually have been parasitized. Since these aphids would not become mummified until at least a week later, they went unnoticed. Also, even though plants were checked regularly, some of the mummies may have been overlooked because of the size and denseness of the fern.

The fact that parasitoids were so abundant in the control treatment meant that it was actually another D. rapae treatment. Both treatments are plotted in Figure 19a and b with their FRI values and mean number of aphids per growing tip, respectively. Aphid populations in the D. rapae treatment are higher than those in the control throughout most of the season, but this resulted because braconids in the D. rapae treatment lagged behind those in the control by at least one generation (mummies were found in the control about the same time that adults were introduced into the braconid treatment). This lag is evident in Figure 19c, where D. rapae treatment braconids

Figure 18. Control, D. rapae and H. convergens treatments: (a) asparagus aphids FRI values; control and H. convergens treatments: (b) mean no. of aphids and (c) mean no. of D. rapae mummies/growing tip ± S.E. and (d) daily weather data.

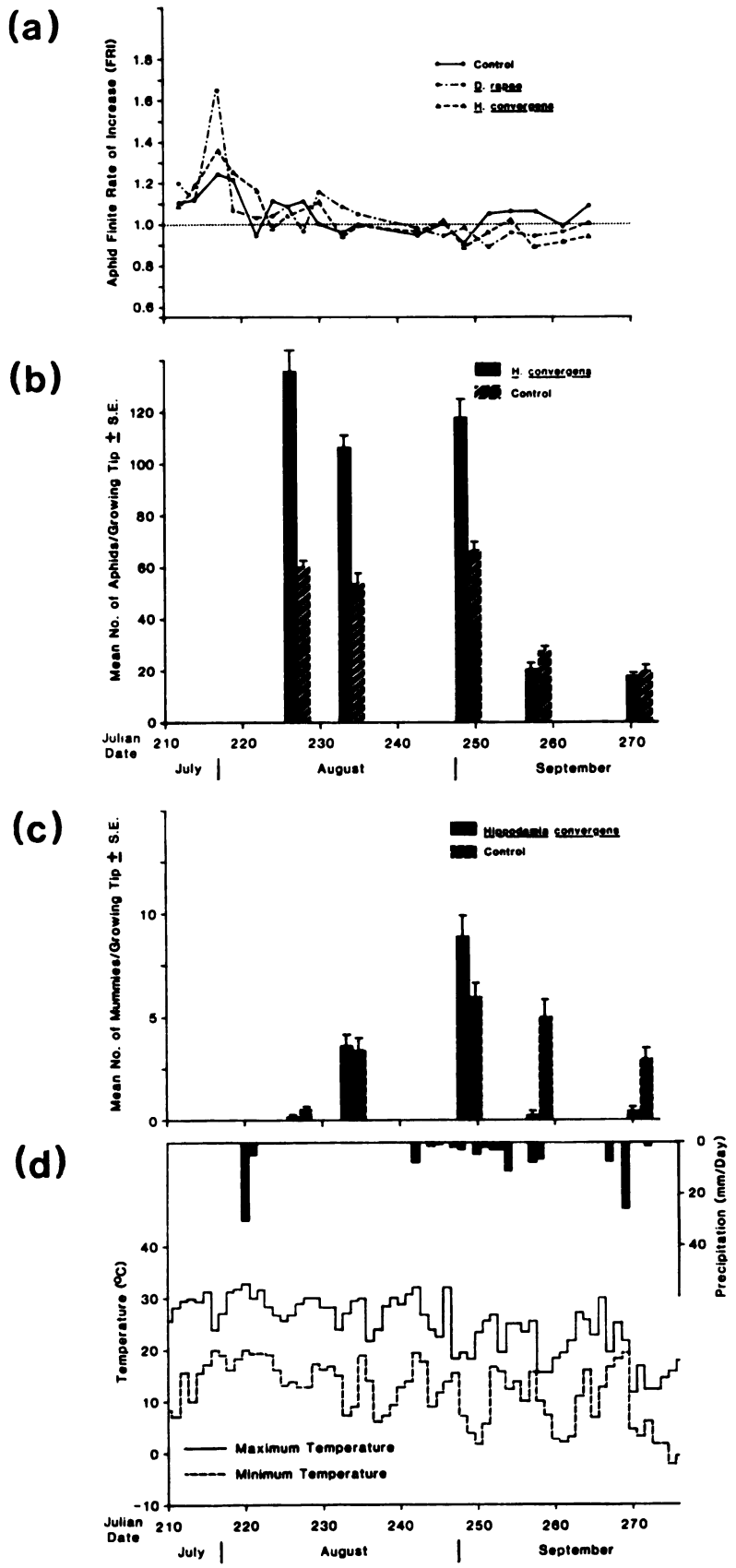
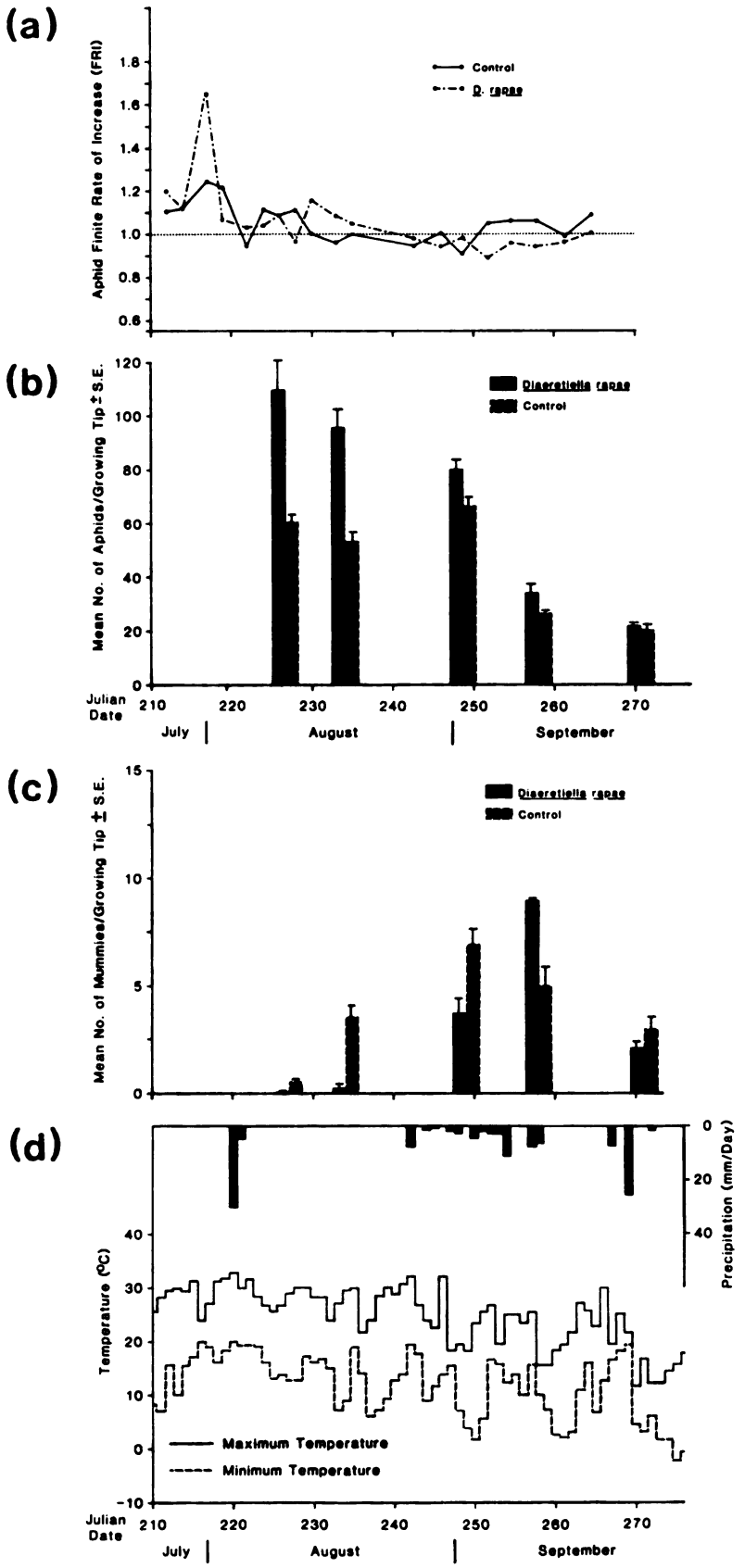

(a)
Aphid Finite Rate of Increase (FRI)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
Control
D. rapae
H. convergens
(b)
Mean No. of Aphids/Growing Tip ± S.E.
120
100
80
60
40
20
0
H. convergens
Control
Julian Date
210
220
230
240
250
260
270
July
August
September
(c)
Mean No. of Mummies/Growing Tip ± S.E.
10
5
0
Hippodamia convergens
Control
(d)
Temperature (°C)
40
30
20
10
0
-10
Precipitation (mm/Day)
0
20
40
Maximum Temperature
Minimum Temperature
Julian Date
210
220
230
240
250
260
270
July
August
September

Figure 19. D. rapae and control treatments: (a) asparagus aphid FRI values, (b) mean no. of aphids and (c) mean no. of D. rapae mummies/growing tip ± S.E. and (d) daily weather data.


(a)
Aphid Finite Rate of Increase (FRI)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
Control
D. rapae
(b)
Mean No. of Aphids/Growing Tip ± S.E.
120
100
80
60
40
20
0
D. rapae
Control
Julian Date
210
220
230
240
250
260
270
July
August
September
(c)
Mean No. of Mummies/Growing Tip ± S.E.
15
10
5
0
D. rapae
Control
(d)
Temperature (°C)
40
30
20
10
0
-10
Precipitation (mm/Day)
0
20
40
Maximum Temperature
Minimum Temperature
Julian Date
210
220
230
240
250
260
270
July
August
September

are about one sampling date behind the control braconids. The decline in braconids in both treatments corresponds to a decrease in available aphid hosts in the fall.

A similar situation exists in the H. convergens treatment (Figure 18a), except that aphid numbers per growing tip (Figure 18b) were higher in the coccinellid treatment than in the control and braconid treatments for the first three destructive samples (Table 16). Both aphid and parasitoid numbers in the coccinellid treatment crashed rather rapidly in the last two samples, and this was probably due to senescence of the fern.

Braconids also infested the caged treatment which had E. planchoniana as its primary mortality factor but never attained high numbers because of interference from the fungal pathogen. The pathogen is known to attack developing parasitoid larvae within aphids (Hagen and van den Bosch 1968) and reduce their ability to regulate aphid populations.

In all treatments there was a decline in aphid numbers which can be attributed to the following factors: 1) The cessation of nymph production in early September and the beginning of aphid egg production, 2) decreasing temperatures adversely affect aphid biology and physiology directly, 3) plants beginning to senesce, thereby affecting the survival, reproduction and development of the aphids and, 4) natural enemies were beginning to have an impact on the aphids.

Hyperparasitism

Emergence of parasitoids from mummies for all treatments was high, ranging from 82.5-92.3% for the Sept. 19 samples and 65-95% for the October 2 samples (Table 17). Both D. rapae and its hyperparasitoid, Aphidencyrtus aphidivorus Mayr (Hymenoptera: Encyrtidae), emerged from mummies in all three treatments, but hyperparasitism was lowest in the braconid treatment. This same species was found associated with D. rapae in New Jersey and Delaware asparagus systems (Angalet and Stevens 1977).

Occurrence of hyperparasitism in the uncaged treatment was not surprising, since aphid mummies containing developing D. rapae larvae were exposed to natural enemies. However, incidence of hyperparasitism in the caged plants was unexpected. It is possible that A. aphidivorus entered cages during sampling, since they were open for an extended period of time.

Incidence of hyperparasitism was much lower in the October 2 samples. This decrease may have resulted from the fact that the braconid populations were increasing at a faster rate than the encyrtids and thus, proportionally, hyperparasitism was lower. Also, the hyperparasitoid population may have been on the downward slope of its population fluctuation. Mummies which failed to emerge may have been in diapause, or they may have just died from natural causes.

Table 17. 1984 DD Field incidence of hyperparasitism by *Aphidencyrtus aphidivorus* (Mayr) on *Diaeretiella rapae* (M'Intosh).

Sampling Date & Tmt	Total Mummies	No. Emerged	% Emerged	No. and % of each			
				D. rapae		*A. aphidivorus*	
Sept. 19							
2	39	36	92.3	15	41.7	21	58.3
4	39	34	87.2	26	76.5	8	23.5
6	39	33	82.5	18	56.3	14	43.7
Oct. 2							
2	40	34	85.0	26	76.5	8	23.5
2	40	32	80.0	28	87.5	4	12.5
4	40	38	95.0	37	97.4	1	2.6
4	40	29	72.5	29	100.0	0	0
6	40	26	65.0	23	88.5	3	11.5

Treatments:

2 = Uncaged, maneb + carbaryl

4 = Caged, *D. rapae* introduced

6 = Caged, control

Hyperparasitism may have greatly interfered with the ability of D. rapae to regulate the asparagus aphid. Chua (1978) found that percent parasitism of the cabbage aphid by D. rapae was low and the parasitoid did not appear capable of regulating aphid populations, perhaps partially due to the activities of five hyperparasitoids.

Hyperparasitism may also be beneficial to the primary parasitoid. According to Flanders (1963) hyperparasitism is a type of mutualism which prevents the primary parasitoid from eradicating its phytophagous host and consequently itself. Thus, the hyperparasitoid may maintain D. rapae at a level which insures that some aphids are left to be parasitized late in the fall for the overwintering population.

CONCLUSIONS

Regulation of asparagus aphid populations in Michigan asparagus fields appeared to result from a combination of abiotic and biotic mortality factors. Weather influenced the biology of both the aphid and its natural enemies, caused physical injury, affected host plant physiology, and provided conditions which were conducive to fungal disease outbreaks. These effects also indirectly influenced the abundance and efficacy of other natural enemies.

Evaluation of the three types of natural enemies indicates that H. convergens and D. rapae were able to stabilize aphid population fluctuations, but were unable to

reduce aphid numbers to low levels. The fungal pathogen, E. planchoniana caused a series of erratic fluctuations in aphid populations which reduced numbers to much lower levels than either H. convergens or D. rapae. Consequently, of the three natural enemies, it had the greatest impact.

This study suggests that, by itself, D. rapae does not appear to have much impact on the pest population. However, it may be able to fill in gaps where other natural enemies are scarce or absent from the system due to adverse or suboptimal conditions. Consequently, its presence in the system may help stabilize aphid populations so that other natural enemies, when more abundant, may effectively regulate the pest.

OVERALL CONCLUSIONS

Laboratory studies indicated that asparagus aphid biotype differences did not appear to exist between Michigan and Washington State. Consequently, the disparity in aphid population levels and damage between the two states is probably attributed to differences in natural enemy composition, efficacy and/or environmental factors. In addition, the asparagus aphid and D. rapae exhibited different responses to similar temperatures. Since each species had different optimum and threshold temperatures, knowledge of the influence of temperature on these insects could aid in predicting their seasonal abundance.

This study demonstrates the importance of natural control in insect population regulation. Results indicated that the natural enemies, D. rapae, H. convergens and E. planchoniana, had some impact on the asparagus aphid in Michigan. D. rapae, by itself, was unable to reduce aphid populations appreciably. However, it may contribute to aphid regulation by causing aphid mortality during parts of the season when other natural enemies are at low levels or absent. The parasitoid may suppress aphid population increases sufficiently to enable other natural controls to have a greater impact on the pest than if D. rapae was

absent. Although all three natural enemies commonly occurred in Michigan asparagus fields, E. planchoniana affected the aphid most markedly. The pathogen's striking impact was made possible by weather conditions conducive to fungal epizootics. Thus, while natural biological control was an integral part of this system, its effectiveness depended greatly upon abiotic factors.

Weather influenced the asparagus aphid much more than hypothesized at the onset of this study. In addition to providing conditions necessary for fungal outbreaks, weather also influenced insect biology, affected host plant physiology and caused physical injury by dislodging insects. These factors subsequently affected the abundance and efficacy of the natural enemies.

The large role of weather in regulating Michigan asparagus aphids may partially account for the difference in the pest problem between the two states. Even if the natural enemy species composition is similar in both states, Michigan weather may be more favorable to natural enemies, thereby enabling them to be more effective. This is especially true for the fungal pathogen which may not do well in the hot, arid asparagus growing regions of Washington.

The impact of biotic and abiotic natural controls was especially apparent in their absence. Physical and chemical barriers in the form of cages and pesticides lessened the impact of natural controls. In their absence,

asparagus aphid populations proliferated, limited mainly by intraspecific competition and a depletion of resources. High aphid numbers caused asparagus fern decline and eventual senescence. The ability of aphid populations to build up to such large numbers and damage the fern demonstrated the potential destruction these insects could cause, were it not for the natural controls which exist in Michigan.

The present level of aphid abundance in Michigan poses little threat to the commercial asparagus industry. However, as the study suggested, the use of selected pesticides for the control of various asparagus pests can be detrimental to nontarget species, particularly natural enemies. This could lead to aphid outbreaks and subsequent economic losses in the future.

Further studies should be conducted to more thoroughly assess the impact of pesticides on the asparagus aphid's natural enemies. These should determine lethal rates for the organisms and make spray recommendations which will be less detrimental to natural enemies and incorporate more natural controls. Comparative biology studies should be carried out on D. rapae and other natural enemies from Michigan and Washington to determine whether biotype differences are partially responsible for the dissimilarity in aphid abundance and damage between the two states. A better understanding of the role of natural controls in the asparagus system will help to avoid pest problems now and

in the future for Michigan asparagus, as well as provide insight into the pest problem in other states.

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