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Impact of Coccinellids on the Asparagus Aphid
In Comparison to Other Natural Enemies

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By

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ABSTRACT

IMPACT OF COCCINELLIDS ON THE ASPARAGUS APHID IN COMPARISON TO OTHER NATURAL ENEMIES

BY

David Robert Prokrym

Three studies were conducted during 1983-1985; each emphasized some aspect of coccinellid biology:

A) Flight traps and visual counts were used to identify potential natural enemies of asparagus aphid, *Brachycorynella asparagi* (Mordvilko). Anthocorids, coccinellids and chrysopids were most numerous. An aphidiid parasitoid and entomophthoralean fungus were also important beneficial organisms.

B) Two field experiments assessed the impact of a pathogen, parasitoid and coccinellid predators on the asparagus aphid through exclusion-inclusion techniques. A combination of pesticides and cages were employed to enhance or limit the effect of one natural enemy over another.

The physical barrier experiment used a cage-fungicide combination to include and exclude natural enemies. The fungal pathogen was most effective in lowering aphid growth rates as compared with the introduced parasitoid and coccinellid. Results suggested that aphidiids and coccinellids also had the potential to influence the aphid's rate of increase. The chemical exclusion trial used fungicide and insecticide to control natural enemies. Chemical treatments did not produce differences as well defined as those demonstrated for the cage study.

Of the three natural enemies, only the pathogen substantially reduced aphid numbers.

C) Eggs and newly-emerged larvae of four coccinellid species were monitored to determine the impact of cannibalism.

Between 72-89% of the eggs hatched for all four species. In one trial cannibalism was prevented by removing newly-emerged larvae. This revealed that viable eggs normally cannibalized ranged from 5.4-20.8%, while 7-29% were nonviable (all 4 species).

Larvae that consumed one egg survived from 1.6-2.1 days longer than unfed individuals, but did not molt. Larvae that consumed two eggs did not appreciably increase their life span beyond that gained from one egg, but a large number of them molted to the second instar (49-87%, over all 4 species).

Cannibalism did not greatly delay mean time to dispersal for *H. convergens* larvae. Departure times from batches with moderate cannibalism rates, up to 0.5 eggs/larva, were not substantially later than from batches without cannibalism (21.5 vs 18.0 h). *H. convergens* larvae hatching from clustered eggs (no cannibalism) left the egg batch later than those emerging from single, isolated eggs (15.2 vs 4.0 h).

Parents often worry about doing the right things for their children.
Thank you, mom and dad, for having the courage to send your teenager
away to college when many around you chose
not to educate in this manner.
You did good!

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The Ph.D. experience reinforced one axiom of life, "you can't do it alone". In retrospect, almost everyone in the Department of Entomology gave me advice, answers or encouragement at one point in my graduate career. I would like to acknowledge some of them here.

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TABLE OF CONTENTS

LIST OF TABLES..... x

LIST OF FIGURES..... xii

I. INTRODUCTION

THE ASPARAGUS COMPLEX..... 1

ASPARAGUS.

The crop..... 4
The plant..... 4

THE ASPARAGUS APHID.

Overview..... 7
General appearance..... 9
Biology..... 9
Damage to plant..... 11
Hosts..... 11
Pest status..... 11
Michigan and Washington State--a comparison..... 12

NATURAL ENEMY COMPLEX.

General composition..... 16
Predators..... 16
Parasitoids..... 17
Fungal pathogen..... 17

PRELIMINARY SURVEY..... 20

OBJECTIVES..... 21

II. ARTICLE 1

A survey of natural enemies of the asparagus aphid, *Brachycorynella asparagi* (Homoptera: Aphididae), in Michigan with an emphasis on coccinellids (Coleoptera: Coccinellidae).

ABSTRACT, KEY WORDS..... 23

INTRODUCTION..... 24

MATERIALS AND METHODS.

EXPERIMENTAL PLOTS..... 26
SAMPLING..... 28
PRESENTATION OF DATA..... 32

RESULTS.

SPECIES COMPOSITION AND ABUNDANCE.
Predators..... 33
Parasitoids..... 36
Fungal pathogen..... 36

POPULATION TRENDS.
Anthocoridae..... 39
Aphidiidae..... 39
Chrysopidae..... 40

TRENDS FOR COCCINELLIDAE BY YEAR AND SPECIES..... 40
1983 season..... 44
1984 season..... 46
1985 season..... 53

DISCUSSION..... 59

III. ARTICLE 2

The impact of coccinellids, aphidiid parasitoid and entomophthoralean fungus on the asparagus aphid, *Brachycorynella asparagi* (Mordvilko), assessed with exclusion-inclusion techniques.

ABSTRACT, KEY WORDS..... 63

INTRODUCTION..... 64

MATERIALS AND METHODS.

PLOTS..... 66
EXPERIMENTAL UNITS..... 66
PESTICIDE SELECTION AND TESTING..... 69
CHEMICAL EXCLUSION EXPERIMENT, PLOT A..... 70
PHYSICAL EXCLUSION EXPERIMENT, PLOT B..... 75
SAMPLING METHODS.
OVERVIEW..... 78

Aphids.
FINITE RATE OF INCREASE (FRI)..... 79
MEAN APHIDS PER COLONY..... 82
PLANT RATING..... 82

Parasitoid and pathogen.
COLONY COUNT..... 82
PARASITISM & DISEASE DETERMINATION..... 83

Predators.
VISUAL COUNT..... 83

Plant injury assessment..... 84

RESULTS.

EFFECTIVENESS OF TREATMENT APPLICATIONS.
CAGES..... 85
APHIDS..... 88
PARASITISM..... 89
DISEASE..... 90
PREDATION..... 90

RESULTS--PHYSICAL BARRIER EXPERIMENT.

Comparison I, physical barrier trial..... 92
OVERVIEW..... 95
Comparison II, physical barrier trial..... 96
OVERVIEW..... 98
Plant injury assessment..... 99

RESULTS--CHEMICAL BARRIER TRIAL.

Comparison I, chemical barrier trial..... 116
Comparison II, chemical barrier trial..... 118
OVERVIEW..... 119
Plant injury assessment..... 120
Coccinellid abundance by species..... 120

DISCUSSION.

PHYSICAL BARRIER STUDY..... 135
CHEMICAL BARRIER STUDY..... 137
SAMPLING TECHNIQUES AND METHODOLOGY..... 138

IV. ARTICLE 3

Egg cannibalism by newly-emerged coccinellids (Coleoptera: Coccinellidae)--its impact on viable eggs, larval survival and time spent on the egg mass.

ABSTRACT, KEY WORDS..... 140

INTRODUCTION..... 141

MATERIALS AND METHODS..... 142

FATE OF EGGS..... 144
LARVAL SURVIVAL..... 146
TIME SPENT ON EGG MASS..... 149

RESULTS.

FATE OF EGGS.
Mean eggs per batch..... 150
Percent hatch
Level I..... 152
Level II..... 154
Level III..... 156

LARVAL SURVIVAL.
Trial I..... 158
Trial II..... 160
Trial III..... 161
Trial IV..... 165

TIME SPENT ON EGG MASS.
Trial I..... 165
Trial II..... 165

DISCUSSION..... 167

V. CONCLUSION

OVERVIEW..... 171
SURVEY OF NATURAL ENEMIES..... 171
EXCLUSION-INCLUSION STUDY..... 173
LABORATORY TRIAL ON CANNIBALISM..... 175

VI. APPENDICES

A. PRELIMINARY CHEMICAL EXCLUSION EXPERIMENT (1983).

INTRODUCTION..... 177

MATERIALS AND METHODS..... 178

RESULTS..... 180

DISCUSSION..... 181

B. PRELIMINARY PHYSICAL BARRIER EXPERIMENT (1983).

INTRODUCTION..... 183

MATERIALS AND METHODS..... 183

RESULTS AND DISCUSSION..... 184

C. PESTICIDE SELECTION AND DETERMINATION OF FIELD DOSE LEVEL.

INTRODUCTION..... 187

MATERIALS AND METHODS..... 188

RESULTS.

RESULTS OF LABORATORY TRIALS--MANEB..... 191
RESULTS OF LABORATORY TRIALS--CARBARYL..... 192
SELECTION OF EXPERIMENTAL FIELD RATE..... 193
RESULTS OF FIELD TRIALS..... 194

LITERATURE REVIEW.

CARBARYL--IMPACT ON TARGET ORGANISMS..... 195
CARBARYL--IMPACT ON NON-TARGET ORGANISMS..... 197
MANEB--IMPACT ON TARGET ORGANISMS..... 198
MANEB--IMPACT ON NON-TARGET ORGANISMS..... 199

DISCUSSION..... 200

D. VOUCHER SPECIMENS..... 202

VII. BIBLIOGRAPHY..... 205

LIST OF TABLES

1. Major factors influencing the asparagus cropping system..... 2

2. Asparagus production statistics for the top three growing states..... 5

3. Chronology of dates for the discovery of the asparagus aphid by state..... 8

4. Developmental threshold temperatures for natural enemies of the asparagus aphid..... 34

5. Natural enemies of the asparagus aphid collected in Michigan by three sampling techniques (sticky can, FIP, and visual counts)..... 35

6. Seasonal and overall totals for (A) sticky-can traps and (B) flight interception panels by family and species..... 37

7. Seasonal and overall totals for visual counts by family and species for 1984 and 1985..... 38

8. Toxicity of pesticides to the asparagus aphid and several of its natural enemies..... 71

9. Treatments for CHEMICAL EXCLUSION experiments (Plot A) and mortality agents promoted by the treatment..... 74

10. Treatments for PHYSICAL EXCLUSION experiments (Plot B) and mortality agents promoted by the treatment..... 74

11. Examples of colony counts and their respective values for finite rate of increase (FRI) over a sampling interval of four days..... 80

12. Cage conditions: mean (±SEM) temperatures, relative humidity and differences (inside minus outside cage) over six time periods for 1984 and 1985. Data recorded with micrologger probes (Model CR-21, Campbell Scientific Inc., Logan, Utah) located inside and outside cages..... 86

13. Relative humidity readings from inside and outside of a physical exclusion cage as recorded by three devices: CR-21 micrologger (CR-21), sling psychrometer (PSYCH) and hygrometer (HYGRO). Comparative means (±SEM) included..... 87

14. Mean finite rate of increase (±SEM) by Julian date for 1984 physical barrier experiment..... 101

15. Mean finite rate of increase (±SEM) by Julian date for 1985 physical barrier experiment..... 102

16. Mean finite rate of increase (±SEM) by Julian date for 1984 chemical barrier experiment..... 122

17. Mean finite rate of increase (±SEM) by Julian date for 1985 chemical barrier experiment..... 123

18. Number of eggs per batch for field-collected and laboratory -reared coccinellids..... 151

19. Fate of eggs by category (mean percent ± SEM) and ranges for egg masses of field-collected and laboratory-reared coccinellids..... 153

20. The number of eggs per batch that synchronously darkened as a percentage of the total eggs and percent darkened eggs per batch that produced viable larvae (mean ± SEM) for egg masses of field-collected and laboratory-reared coccinellids..... 155

21. Fate of eggs by category (mean percent ± SEM) for egg masses where cannibalism was prevented by removing newly-emerged larvae..... 157

22. Survival time for newly-emerged coccinellid larvae for three feeding treatments..... 159

23. Survival time for newly-emerged coccinellid larvae for four feeding treatments (larvae of laboratory-reared adults only)..... 162

LIST OF FIGURES

1. Michigan counties that produce asparagus, 1977 acreage (Michigan Dept. of Agriculture 1977)..... 6

2. Comparison between (A) the green peach aphid and (B) the asparagus aphid (from Peterson & Cone 1982). (C) Generalized life cycle of asparagus aphid (from Tamaki et al. 1983)..... 10

3. (A) Maximum and (B) minimum temperatures (30-year means) for representative areas from the major asparagus growing regions of the United States: Yakima, Washington (U.S. Dept. of Commerce 1965); Hart, Michigan (Dept. of Commerce 1971); and Wilmington, Delaware (Dept. of Commerce 1959)..... 14

4. (A) Precipitation (30-year means) for representative areas from the major asparagus growing regions of the United States: Yakima, Washington; Hart, Michigan; and Wilmington, Delaware. (B) Morning and evening values (30-year means) for relative humidity in Yakima, Washington and Muskegon, Michigan. See Figure 3 for references..... 15

5. Developmental process of *E. planchoniana* (from Brobyn & Wilding 1977)..... 19

6. Sticky-can trap (Hayakawa 1985). A) Placement of transparent plastic strip covered with adhesive Tangle-trap on yellow can. B) Arrangement of Velcro tabs that facilitated easy removal... 29

7. A) Flight interception panel (FIP). B) Placement of 16 sticky-can traps within rows and 4 flight interception panels along plot perimeter for 1984-1985 season..... 31

8. Percent occurrence for anthocorids caught in (A) flight interception panels and (B) sticky-can traps, and (C) for aphidiids caught in can traps, 1984-1985..... 41

9. Percent occurrence for chrysopids, all species combined, for (A) flight interception panels in 1984-1985 and (B) sticky-can traps in 1983-1985..... 42

10. Percent occurrence for coccinellids, all species combined, for (A) flight interception panels in 1984-1985 and (B) sticky-can traps in 1983-1985..... 43

11. (A) Daily rainfall and maximum-minimum temperatures during the study period, and (B) coccinellid catch of most common species for 1983. For 11B: The vertical bars mark the placement of exclusion cages or introduction of aphids. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. KEY: TOTAL, all 9 species combined; *H.c., H. convergens; C.m., C. maculata;* and *H.p., H. parenthesis*..... 45

12. (A) Daily rainfall and maximum-minimum temperatures during the study period, and coccinellid catch of most common species for (B) flight interception panels and (C) sticky-trap cans during 1984. For 12b-c: The three vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation. KEY: TOTAL, all 9 species combined; *H.c., H. convergens; C.m., C. maculata;* and *H.p., H. parenthesis*.... 48

13. Visual counts of coccinellids for (A) 1984 and (B) 1985; all species and sampling times combined to produce seasonal overview. The vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation..... 50

14. Visual counts of coccinellids for 1984 for three sampling times: A) 0730-1030 h, B) 1130-1300 h and C) 1530-1900 h. The two vertical bars mark the placement and removal of exclusion cages. KEY: TOTAL, all 9 species combined; *H.c., H. convergens; C.m., C. maculata*..... 52

15. (A) Daily rainfall and maximum-minimum temperatures during the study period, and coccinellid catch of most common species for (B) flight interception panels and (C) sticky-trap cans during 1985. For 12B-C: The four vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation. KEY: TOTAL, all 9 species combined; *H.c., H. convergens; C.m., C. maculata;* and *H.p., H. parenthesis*..... 56

16. Coccinellid catch of less abundant species (see Table 7) for (A) flight interception panels and (B) sticky-trap cans during 1985. The vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation. KEY: TOTAL, all 9 species combined; OTHER, 4 miscellaneous species combined (see Table 7); *H.t., H. tredecimpunctata; C.t., Coccinella transversoguttata*..... 57

17. Visual counts of coccinellids for 1985 for three sampling times: (A) 0930-1100 h, (B) 1300-1500 h and (C) 1600-2000 h. The three vertical bars mark the placement and removal of exclusion cages. KEY: TOTAL, all 9 species combined; OTHER, 4 miscellaneous species combined, see Table 7; *H.c., H. convergens; C.t., C. transversoguttata*..... 58

18. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: CG-NONE, NOCG-NONE, NOCG-ALL; and (C) Comparison-II treatments: CG-DIS, CG-PAR, CG-COCC. The vertical dashed lines demarcate August 1-September 1, 1984. For C, the bold letters indicate introductions of aphidiids ("B") and coccinellids ("C")..... 104

19. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Mean number of aphids per experimental colony (A) for Comparison-I treatments: CG-NONE, NOCG-NONE and NOCG-ALL, and (B) Comparison-II treatments: CG-DIS, CG-PAR and CG-COCC. (C) Mean number of coccinellid adults per plant for: NOCG-ALL, NOCG-NONE and CG-COCC. The vertical dashed lines demarcate August 1-September 1, 1984..... 105

20. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Mean percent PARASITISM (A) for Comparison-I treatments: CG-NONE, NOCG-NONE, NOCG-ALL; and (B) for Comparison-II treatments: CG-DIS, CG-PAR, CG-COCC. Mean percent DISEASE for (C) Comparison-I and (D) Comparison-II treatments. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M"). The vertical dashed lines demarcate August 1-September 1, 1984..... 106

21. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (A) CG-COCC, (B) NOCG-NONE and (C) NOCG-ALL. The letters "C" indicate an application of carbaryl insecticide. The vertical dashed lines demarcate August 1-September 1, 1984..... 107

22. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Percent relative humidity from inside and outside of an exclusion cage for four time periods: (A) 0800, (B) 1200, (C) 1600 and (D) 2000 hrs. The vertical dashed lines demarcate August 1-September 1, 1984..... 108

23. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: CG-NONE, NOCG-NONE, NOCG-ALL; and (C) Comparison-II treatments: CG-DIS, CG-PAR, CG-COCC. The vertical dashed lines demarcate August 1-September 1, 1985. For C, the bold letters indicate introductions of aphidiids ("B") and coccinellids ("C")..... 110

24. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. Mean aphid rating (A) for Comparison-I treatments: CG-NONE, NOCG-NONE and NOCG-ALL; and (B) for Comparison-II treatments: CG-DIS, CG-PAR and CG-COCC. Mean number of aphids per experimental colony (C) for Comparison-I treatments and (D) for Comparison-II treatments. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "A" indicate aphid introductions..... 111

25. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. Mean percent PARASITISM for Comparison-I treatments (CG-NONE, NOCG-NONE, NOCG-ALL) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-I treatments from two sources: C) colony counts and D) PDD. The vertical dashed lines demarcate August 1-September 1, 1985. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M")..... 112

26. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. Mean percent PARASITISM for Comparison-II treatments (CG-DIS, CG-PAR and CG-COCC) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-II treatments from two sources: C) colony counts and D) PDD. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "M" indicate applications of maneb fungicide..... 113

27. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. (A) Mean number of coccinellid adults per plant for: CG-NONE, NOCG-NONE and CG-COCC. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (B) CG-COCC, (C) NOCG-ALL and (D) NOCG-NONE. For D, the letter "C" indicates an application of carbaryl insecticide. The vertical dashed lines demarcate August 1-September 1, 1984..... 114

28. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: NONE+W, NOCHEM; and (C) Comparison-II treatments: PRED&PAR, DIS. The vertical dashed lines demarcate September 1-October 1, 1984... 124

29. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. Mean number of aphids per experimental colony (A) for Comparison-I treatments: NONE+W, NOCHEM; and (B) Comparison-II treatments: PRED&PAR, DIS. (C) Mean number of coccinellid adults per plant for: NONE+W, NOCHEM, PRED&PAR, DIS. The vertical dashed lines demarcate September 1-October 1, 1984. The letters "A" indicate aphid introductions..... 125

30. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. Mean percent (A) PARASITISM and (B) DISEASE for Comparison-I treatments: NONE+W, NOCHEM. (C) Mean percent parasitism and (D) disease for Comparison-II treatments: PRED&PAR, DIS. The vertical dashed lines demarcate September 1-October 1, 1984..... 126

31. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. Mean number of coccinellids per plant by stage (adult, larva and egg) for the following treatments: (A) NOCHEM, (B) NONE+W, (C) PRED&PAR, and (D) DIS..... 127

32. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: SHELTER, NONE+W, NOCHEM; and (C) Comparison-II treatments: DIS, NONE+W, PRED&PAR. The vertical dashed lines demarcate August 1-September 1, 1985..... 128

33. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. (A) Mean aphid rating and (B) mean number of aphids per experimental colony for Comparison-I treatments: SHELTER, NONE+W, NOCHEM. (C) Mean aphid rating and (D) mean number of aphids per colony for Comparison-II treatments: DIS, NONE+W, PRED&PAR. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "A" indicate aphid introductions..... 129

34. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean percent PARASITISM for Comparison-I treatments (SHELTER, NONE+W, NOCHEM) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-I treatments from two sources: C) colony counts and D) PPD. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M"). The vertical dashed lines demarcate August 1-September 1, 1985..... 130

35. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean percent PARASITISM for Comparison-II treatments (DIS, NONE+W, PRED&PAR) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-II treatments from two sources: C) colony counts and D) PPD. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M"). The vertical dashed lines demarcate August 1-September 1, 1985..... 131

36. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean number of coccinellid adults per plant (A) for Comparison-I treatments: SHELTER, NONE+W, NOCHEM; and (B) Comparison-II treatments: DIS, NONE+W, PRED&PAR. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "C" indicate applications of carbaryl insecticide..... 132

37. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (A) SHELTER, (B) NONE+W, and (C) NOCHEM. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "C" indicate applications of carbaryl insecticide..... 133

38. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (A) PRED&PAR and (B) DIS. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "C" indicate applications of carbaryl insecticide..... 134

39. Mean survival times for field-collected *H. convergens* larvae versus the number of eggs consumed per larva. A) Mean times for isolated larvae fed 0, 1 and 2 eggs per larva (N = 190 larvae from 8 batches). B) Mean times for larvae that were allowed to remain undisturbed on the egg mass until all unhatched eggs were eaten (N = 53 larvae, 8 batches). Regression equations are significant at $P < 0.05$; y, survival time in hours; x, eggs consumed per larva (REG program, pp 655-710, SAS Institute, 1985)..... 163

40. Mean survival times for laboratory-reared *H. convergens* larvae as related to the number of eggs consumed per larva. A) Mean times for isolated larvae fed 0, 1 and 2 eggs per larva (N = 256 larvae from 21 batches). B) Mean times for larvae that were allowed to remain on the egg mass until all unhatched eggs were eaten (N = 131 larvae, 22 batches). Regression equations are significant at $P < 0.05$; y, survival time in hours; x, eggs consumed per larva (REG program, pp 655-710, SAS Institute, 1985)..... 164

41. Mean time spent on egg mass for two species of laboratory-reared beetles as related to the number of eggs consumed per larva. A) Mean times for *H. convergens* larvae that were allowed to remain on the egg mass until all unhatched eggs were eaten (N = 175 larvae from 20 batches). B) Similar data for *C. transversoguttata* (N = 237 larvae from 18 batches). Regression equations are significant at $P < 0.05$; y, time on batch in hours; x, eggs consumed per larva (REG program, pp 655-710, SAS Institute, 1985)..... 166

42. Mean time spent on egg mass for two groups of *H. convergens* larvae, those isolated as single eggs and those clustered as small groups, as related to the number of eggs per batch. Regression equations are significant at $P < 0.05$; y, time on batch in hours; x, eggs per batch (REG program, pp 655-710, SAS Institute, 1985)..... 168

INTRODUCTION

THE ASPARAGUS COMPLEX.

This study investigated the relationships and interactions between the asparagus aphid and its natural enemies. However, it was necessary to first obtain a general understanding of the system in which the interactions take place before examining specific topics. The asparagus plant served as the central reference point because of its importance as the managed commodity. Without reducing the asparagus cropping system down to its most finite parts, the following major categories of inputs were recognized: soil factors, cultural practices, pests (diseases, weeds, insects), chemicals (pesticides & fertilizers), abiotic factors and beneficial organisms (parasitoids, insect predators, and fungal pathogens).

The resulting overview was a combination of agricultural and biological inputs (Table 1). It included elements common to most commercial plantings while incorporating factors important to scientific research. This exercise was not executed solely to define the boundaries and components of the asparagus system. The overview also provided the basis for identifying biological relationships too numerous to document in this study, i. e. entomological topics such as the importance of herbivores as alternate food sources for predators, weeds as refugia, chemical applications harmful to beneficial organisms, and management practices that promoted or hindered the increase of pest populations.

Table 1. Major factors influencing the asparagus cropping system[a].

A. PESTS.

1) Diseases:

asparagus rust, *Puccinia asparagi* D.C.
fusarium crown rot, *Fusarium oxysporum* f. sp. *asparagi* & *F. moniliforme*
purple spot, *Stemphyllium vesicarium*

2) Weeds:

perennial weeds:
horsenettle, *Solanum carolinense* L.
common milkweed, *Asclepias syriaca* L.
field bindweed, *Convolvulus arvensis* L.
swamp smartweed, *Polygonum coccineum* Muhl.
yellow nutsedge, *Cyperus esculentus* L.
quackgrass, *Agropyron repens* (L.) Beauv.

annual weeds:
yellow foxtail, *Setaria lutescens* (L.) Beauv.
barnyardgrass, *Echinochloa crusgalli* (L.) Beauv.
fall panicum, *Panicum dichotomiflorum*
common lambsquarters, *Chenopodium album* L.
redroot pigweed, *Amaranthus retroflexus* L.

3) Insects:

asparagus beetles: common, *Crioceris asparagi* L., and spotted, *C. duodecimpunctata* L.
asparagus miner, *Ophiomyia simplex* (Loew)
cutworms, eg. *Euxoa scandens* (Riley), *E. messoria* (Harris)
asparagus aphid, *Brachycorynella (=Brachycolus) asparagi* (Mordvilko)
plant bugs: tarnished, *Lygus lineolaris* (Palisot de Beauvios), alfalfa, *Adelphocoris lineolatus* (Goeze).

B. CHEMICALS USED (pesticides & fertilizers):

insecticides (carbaryl, permethrin, fonofos, methomyl, methoxychlor)
fungicides (maneb, mancozeb)
herbicides (glyphosate, linuron, simazine, terbacil, metribuzin)
fertilizers (N, P_2O_5, K_2O)

Table 1. (cont'd).

C. SOIL FACTORS:

soil type, well-drained sands and sandy loams
pH, basic, 5.0-6.8

D. CULTURAL PRACTICES:

selection of varieties
crown beds vs production fields
duration of harvest
fern management, minimum vs no-tillage
processing vs fresh market
irrigation vs non-irrigation

E. ABIOTIC FACTORS:

maximum & minimum temperatures for soil and air
precipitation (rainstorms)
wind (windstorms)
relative humidity
leaf wetness

F. BENEFICIAL ORGANISMS THAT ATTACK THE ASPARAGUS APHID.

1) Insects:

Coccinellidae: *Hippodamia* spp., *Coccinella* spp., *Coleomegilla maculata lengi* Timberlake, *Adalia bipunctata* (L.), *Cycloneda munda* (Say)
Chrysopidae, *Chrysoperla* spp.
Anthocoridae, *Orius* spp.
Nabidae, *Nabis* spp.
Hemerobiidae
Syrphidae
Cecidomyiidae

2) Parasitoids:

Aphidiidae, *Diaeretiella rapae* (M'Intosh)

3) Diseases:

Entomophthoraceae, *Entomophthora planchoniana* Cornu

* Sources for information on components related to asparagus production: Grafius et al. 1985, Zandstra et al. 1986, Putnam et al. 1983, Zandstra & Putnam 1985, Thornton et al. 1982 and 1985 Farm Chemicals Handbook.

ASPARAGUS.

The crop. As the third largest asparagus producer, Michigan ranks well behind California and Washington State (Table 2). In 1981, asparagus made up about 7.4% of the $135 million total vegetable production in Michigan and 10.0% of U.S. output for this crop (Michigan Dept. of Agriculture 1982). The average yield in Michigan is 589.6 kg/0.405 ha with 907.0 kg/0.405 ha considered as a good yield. About 80% of the Michigan crop is sold to processors and 20% to fresh market (Zandstra et al. 1986).

Three-fourths of the acreage planted to asparagus in Michigan is located in Oceana, Van Buren and Berrien counties (Figure 1). Harvest usually begins in late April to early May and ends in late June. The most active picking occurs around May 1 to June 20 (U.S. Dept. of Agriculture 1977)

The plant. Asparagus, *Asparagus officinalis* L. (Family Liliaceae) is a dioecious perennial, grown in a variety of environments and soil types. Simplistically, the plant can be divided into three parts: crown, spear and fern. The crown can be thought of as an underground rhizome stem that includes the fibrous and storage roots. Buds elongate from the crown to form spears, initiating when the soil temperatures reach above 11°C. If the spear is not harvested, it will lengthen and produce a fern with primary and secondary branches. The secondary branches have whorls composed of needle-like leaves called cladophylls.

Decreased spear production can result from damage to the crown-root system or to the fern. Carbohydrates produced during photosynthesis are translocated to the root system and stored. This

Table 2. Asparagus production statistics for the top three growing states[a].

STATE BY RANKING:	YEAR[b]	AREA (HA)	PRODUCTION (METRIC TONS)	VALUE ($1000)
CALIFORNIA	1985	14,292	44,725	74,666
	1984	13,846	38,783	59,796
	1981	11,053	37,150	51,962
WASHINGTON	1985	12,551	36,832	42,443
	1984	12,551	32,886	37,454
	1981	9,595	26,898	29,268
MICHIGAN	1985	8,097	10,433	13,423
	1984	8,097	10,433	13,318
	1981	8,097	7,757	10,690

[a] References: U.S. Department of Agriculture, Statistical Reporting Service, 1985; USDA National Agricultural Statistical Service, 1986.

[b] Survey discontinued from 1982-1983.

Figure 1. Michigan counties that produce asparagus, 1977 acreage (Michigan Dept. of Agriculture 1977).

reserve is redistributed during budding and realized as spear or fern growth. Therefore, any destruction of the storage site or disruption of photosynthesis can create a net reduction in spear production in the next harvest. Two fungal pathogens, *Fusarium oxysporum* f. sp. *asparagi* and *F. moniliforme*, damage the vascular system of the crown and stems below ground. Phytophagous pests, like the common asparagus beetle (*Crioceris asparagi* L.), damage fern foliage.

Asparagus plantings are similar to orchards in that each plant is long-lived and has the potential of producing a crop for 10-20 years. In Michigan, young plants are transplanted from nurseries at 1-2 years of age. Only after the third year is limited picking nondestructive to plant vigor (Zandstra et al. 1986).

THE ASPARAGUS APHID.

Overview. A. K. Mordvilko (1928) described the asparagus aphid, *Brachycorynella (=Brachycolus) asparagi* (Mordvilko), from *Asparagus* sp. and gave Astrakhan on the Caspian Sea as the type locality in the Soviet Union. Szelegiewicz (1961) reported that its geographic distribution also included Southern Poland (Pinczow) and areas around Kiev and Khrahov in the Ukraine.

Angalet & Stevens (1977) provided the best recount of the appearance of the asparagus aphid in North America with its first discovery in 1969 on Long Island, New York. However, a number of sources were required to assemble a chronology of dates that illustrated the movement of this aphid to the west coast (Table 3). Capinera (1974) commented that the aphid may have been established in the United States for some time because of the short periods between the initial discovery

Table 3. Chronology of dates for discovery of the asparagus aphid by state[a].

YEAR	STATE
1969	New York, New Jersey
1970	Pennsylvania, Virginia
1971	Maryland
1972	Massachusetts
1973	North Carolina
1977	Illinois
1979	Missouri, Washington
1980	Michigan, Oregon, Indiana, Georgia
1981	Ohio, Oklahoma, Idaho
1984	California

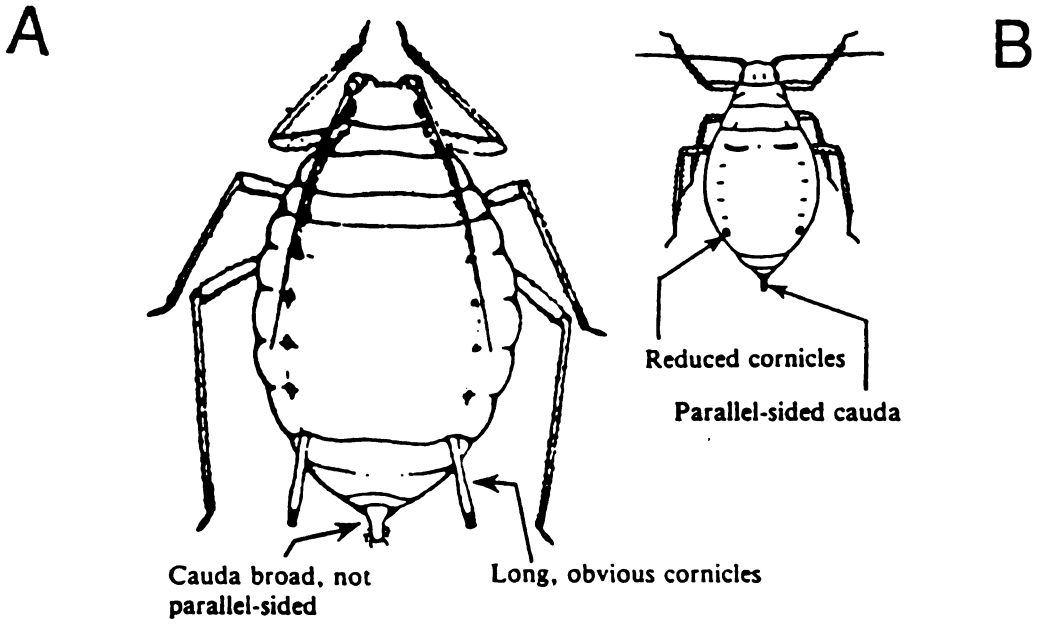
[a] Sources: Angalet & Stevens 1977, Grafius 1980, Stozel 1981, Peterson & Cone 1982, and Ball 1986.

dates. This remark probably applied to individual states as well. Although the aphid was reported in Washington State in 1979 (Peterson & Cone 1982) and in British Columbia, Canada in 1981 (Forbes & Chan 1981), Forbes (1981) noted that this aphid was caught in water traps in British Columbia several years before its presence on asparagus became apparent.

General appearance. The asparagus aphid is blue-green to powdery gray in color. The body is oval, elongate and about 1 mm long or one-third the size of the green peach aphid, *Myzus persicae* (Sulzer) (Figure 2). Two distinguishing features are its parallel-sided cauda and very small, mammiform cornicles (Forbes 1981). Szelegiewicz (1961) provided detailed morphological description and diagrams.

Biology. Until the study by Tamaki et al. (1983), almost no detailed information on asparagus aphid biology was available. Their study detailed the general life cycle (Figure 2c). There are four larval instars and a number of morphs. Eggs oviposited on the asparagus fern in the fall hatch the next spring to establish the fundatrices or stem mothers. In summer, alate or apterous virginoparae are prevalent in dense colonies. Toward autumn, the sexuparae occur. These individuals produce the sexual morphs--wingless oviparae and winged males. Upon mating, the oviparae lay shiny green eggs that turn black within 1-2 days. Capinera (1974) observed the overwintering eggs on nodes and under bracts of the asparagus plant.

Tamaki et al. (1983) reported that the net reproduction rate (R_o), i.e. the number of offspring produced by the average female in a generation, was 54.4 for virginoparae and 18.0 for stem mothers at 24.1°C and photoperiod of 16:8 (L:D). The generation and doubling times for virginoparae were 14.8 and 2.57 days, respectively.



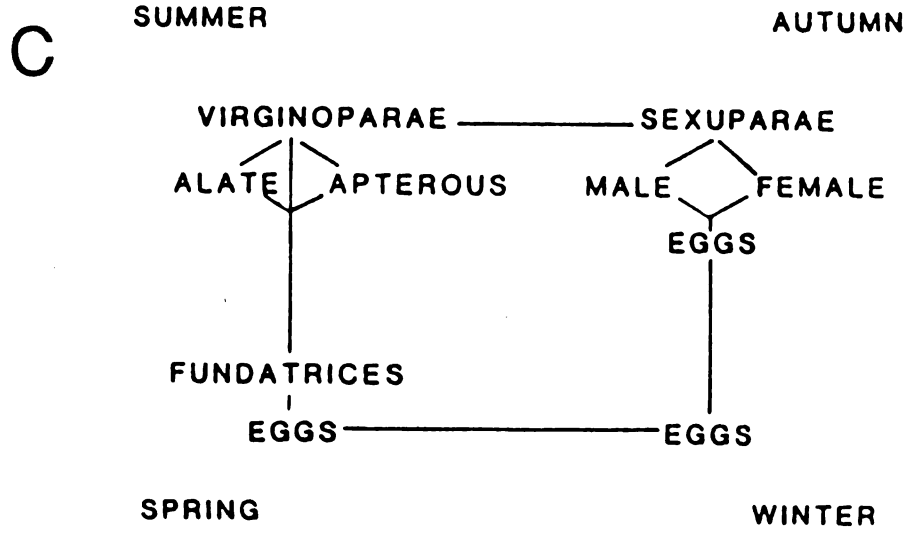


Figure 2. Comparison between (A) the green peach aphid and (B) the asparagus aphid (from Peterson & Cone 1982). (C) Generalized life cycle of asparagus aphid (from Tamaki et al. 1983).

Damage to plant. Aphid feeding causes growth abnormalities in the asparagus plant, but the mechanisms are unclear. Affected ferns developed a witches'-broom condition or rosetting in which the internodes and cladophylls are severely shortened and blue-green in color (Forbes 1981). Capinera (1974) reported that aphid feeding not only caused a reduction in the growth of the top of seedlings but it also inhibited root development. Morse (1916) suggested that damage to the top interfered with synthesis of sugar and translocation to the roots. Forbes (1981) concluded that the rosetting was a result of feeding and not related to a pathogenic infection. The aphid probably injects some substances into the plant that induces abnormal growth.

Hosts. The asparagus aphid is reported to be specific on asparagus (Blackman & Eastop 1984). Noting that there are about 150 species and more than 200 cultivars of asparagus, Halfhill (1987) determined the suitability of some ornamental asparagus varieties as hosts for the aphid. The findings indicated that all ornamentals were significantly less suitable then edible asparagus. From 1-5% of the aphids tested were adapted to either *Asparagus densiflorus* (Kunth) CV Meyeri or CV Sprengeri and could produce sexual morphs and eggs on these cultivars.

Pest status. The asparagus aphid is an acknowledged pest on the West coast (Thornton et al. 1982, Peterson & Cone 1982). A reduction in spear size and yield for the Washington asparagus industry in the spring of 1980 and 1981 was attributed to this aphid (Wildman & Cone 1986). Emergency exemptions were granted in Washington for the use of the systemic insecticide disulfoton as a foliar spray from 1981-1983. In 1984 approval for disulfoton use was given under a special local needs

registration in Washington State.

By comparison to Washington State, the aphid is not a problem in eastern growing regions--Maryland, Delaware, New Jersey--or Michigan (Grafius 1986, Hendrickson 1986). This seems to be the situation in Europe as well. Quarterly Reports for 1970 and 1971 by the European Parasite Laboratory stated that surveys in France and Turkey found no asparagus aphids on the crop (European Parasite Laboratory 1971, 1970). Furthermore, an exhaustive bibliography on asparagus with over 2400 references did not list any entries for the aphid under the pest section (Hung 1975). This book provided 50 references on the asparagus fly (*Platypareae poecilopterа* Schrank), 46 for the common and spotted asparagus beetles (*C. asparagi* and *C. duodecimpunctata*) and 15 for the asparagus miner (*Ophiomyia simplex* [Loew]).

During a vacation in Europe in September 1983, I casually sampled three asparagus plots and discovered moderate asparagus aphid infestations as follows: 1) France, several km north of Erstein on Strasbourg-Colmar road, Route 83; 90% of the plants supported aphid colonies in a small plot (15 rows by 50 m) intercropped between corn and an apple orchard. 2) Italy, several km south of Trento on Route A22; small colonies discovered on every plant inspected in a large plot with rows of asparagus intercropped between grapes. 3) West Germany, near the Wunnenstein-Beilstein exit on Stuttgart-Heilbronn Highway, Route 81; 1 of 30 plants inspected had a heavy infestation in a large plot intercropped with corn and forage crops.

Michigan and Washington State--a comparison. The pest status of the aphid is markedly different for Michigan and Washington State. A comparison of the components that make up the cropping system (Table 1)

in both locations would be required to adequately explain this situation. Although a detailed analysis at the system level was beyond the scope of this study, a brief comparison of climatic conditions and cultural practices in each state was possible.

The largest difference between Washington State and Michigan is the climate. I compared 30-year averages for several parameters (maximum and minimum temperatures, precipitation, and relative humidity) for asparagus growing areas in both states to illustrate this point. Yakima was chosen as the representative location for Washington; Hart (Oceana County) and Muskegon (Muskegon County) for Michigan. Wilmington, Delaware was included as an example of conditions in the eastern growing regions comprised of Delaware, New Jersey and Maryland.

A plot of the 30-year means of maximum and minimum temperatures (Figures 3a&b) reveals that Yakima displayed a greater range between the upper and lower values; its average maximum temperatures not too dissimilar from Hart, Michigan. However, precipitation and relative humidity at Yakima are distinctly lower (Figures 4a&b). Overall, the climate of the Yakima Valley growing region is hot and dry in the summer; winters are cool with only light snowfall. In Michigan, the influence of Lake Michigan on the climate of Hart and Muskegon is quite strong throughout most of the year. Spring and early summer temperatures are cooler than would normally be expected at this latitude; fall and winter temperatures are correspondingly milder.

Cultural practices are somewhat influenced by the weather. For example, Washington growers usually irrigate their fields because of the low rainfall (Thornton et al. 1982). This negative aspect may be offset by the comparatively longer picking season. Another difference is in

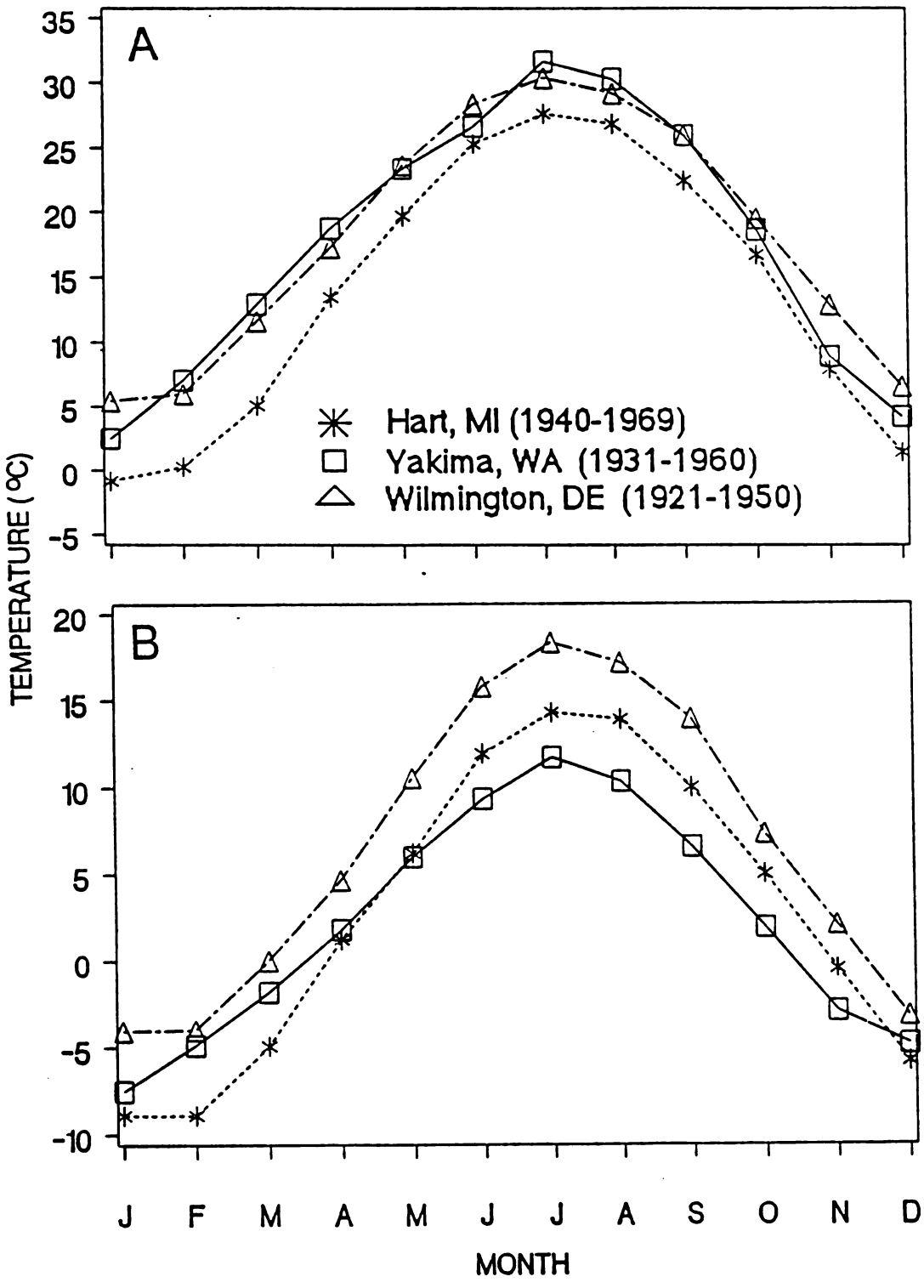


Figure 3. (A) Maximum and (B) minimum temperatures (30-year means) for representative areas from the major asparagus growing regions of the United States: Yakima, Washington (U.S. Dept. of Commerce 1965); Hart, Michigan (Dept. of Commerce 1971); and Wilmington, Delaware (Dept. of Commerce 1959).

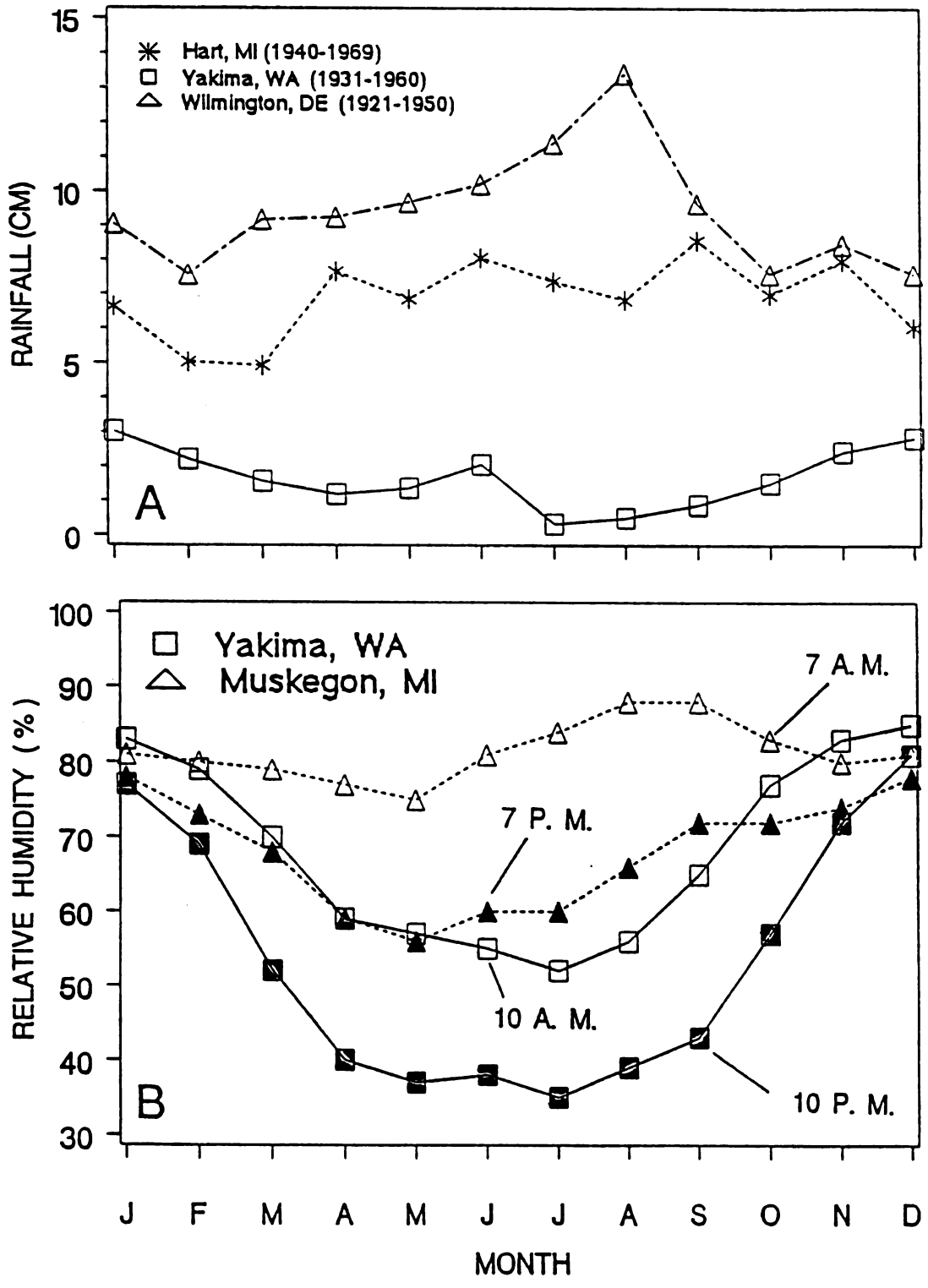


Figure 4. (A) Precipitation (30-year means) for representative areas from the major asparagus growing regions of the United States: Yakima, Washington; Hart, Michigan; and Wilmington, Delaware. (B) Morning and evening values (30-year means) for relative humidity in Yakima, Washington and Muskegon, Michigan. See Figure 3 for references.

the selection of asparagus varieties. "Washington" strains (Mary, Martha and Waltham) and "Viking" strains are recommended for use in Michigan (Zandstra et al. 1986). For Washington, Thornton et al. (1982) recommend variety 500 W or "WSU 1 & WSU 2" developed by Washington State University. Mary Washington strains are suggested only if they were selected in Washington State.

NATURAL ENEMY COMPLEX.

General composition. The survey of asparagus plots in New Jersey and Delaware by Angalet & Stevens (1977) provided the basis for identifying natural enemies of the asparagus aphid in Michigan. Their listing indicated that predators, parasitoids and pathogens were all important mortality agents. The most abundant aphid predators in that study were coccinellids and the parasitoid most often recovered was *Diaeretiella rapae* (M'Intosh). Angalet & Stevens also reported that 50-95% of the aphids were killed by a fungal disease (*Entomophthora* sp.) in some fields. Based on this data, I expected to find the same composition of natural enemies in Michigan (Table 1F) with differences occurring at the species level.

Predators. Aphid predators occur in many insect orders but are mostly found in the families already listed (Table 1F). However, aphidophagous coccinellids were considered to be the most important predator group in the Michigan asparagus system. Much of the information on general coccinellid biology and ecology (i.e. life history, distribution, habitat, food preferences, diapause, voltinism, synchrony with prey, and aggregation behavior) was already organized by Hodek (1967, 1973) and Hagen (1962). Gordon (1985) complemented their

efforts with an extensive document on coccinellid taxonomy. Since my study dealt with a complex of coccinellid species, an overview was not done for this group. Instead of listing general points, pertinent facts were noted from selected studies when applicable.

Parasitoids. The most important aphid parasitoids belong to the hymenopterous families Aphidiidae and Aphelinidae (Hagen & van den Bosch 1968). In the Michigan asparagus system the impact of the aphidiid *Diaeretiella rapae* (M'Intosh) on the asparagus aphid was significant enough to warrant separate study (Hayakawa 1985).

Since Hayakawa covered parasitoid biology, the following general comments on its life cycle were condensed from her work. First, the parasitic wasp is tiny (about 2 mm) and a solitary endoparasitoid that attacks all host stages but the egg. The female typically oviposits a single egg per host. While the egg, first and second instar may not adversely affect the host or host feeding, the third instar effectively halts aphid feeding. The internal organs are consumed by the fourth instar parasitoid and the already distended aphid cuticle becomes papery thin forming the mummy. Before pupation, the larva cuts a hole in the aphid venter and attaches the host to the substrate with silk. The adult chews a hole through the aphid skin to emerge. The wasp can have from 5-11 generations per year, overwintering as a late instar or pupa. *D. rapae* parasitizes other aphid hosts like the cabbage aphid, *Brevicoryne brassicae* L., and green peach aphid, *Myzus persicae* Sulzer.

Fungal pathogen. Humber (1984a) noted that the majority of species in the order Entomophthorales are entomopathogenic and have been included by most authors in a heterogeneous assemblage as *Entomophthora* Fresenius. To avoid such errors, I took samples of infected asparagus

aphids to Dr. Humber (Boyce Thompson Institute at Cornell University, Ithaca, New York) for identification. The fungus was identified as *Entomophthora planchoniana* Cornu, Subdivision Zygomycotina, Class Zygomycetes, Order Entomophthorales, Family Entomophthoraceae (Humber 1984b). Humber also explained that there was only one report of successful culture of this species (Holdom 1983) and that he was repeatedly unable to isolate the pathogen.

Brobyn & Wilding (1977) described the developmental process of *E. planchoniana* in three parts (Figure 5):

1) *Conidium germination and host penetration.* Conidium adheres to host cuticle, germ-tube forms from conidium and penetrates the cuticle.

2) *Invasion of host tissue.* The fungal tube grows rapidly through the epidermis and fat body, passing into the hemocoel, and multiplying as branched hyphal filaments. The filaments fragment into hyphal bodies that disperse throughout the hemocoel. The hyphal bodies elongate, filling the hemocoel and invading the solid tissues.

3) *Development of rhizoids and conidiophores.* These two structures develop from elongating hyphal bodies. Conidiophores develop in the abdominal area, converging into well-defined groups before rupturing the cuticle. Emerging through the dorsal and lateral regions, conidiophores form a felt-like hymenium. In contrast, rhizoids emerge mid-ventrally along the abdomen. Comprised of 4-10 bundles of undifferentiated hyphae, rhizoids secret a viscous fluid that attaches the host firmly to the substrate.

One of the more interesting aspects of *Entomophthora* biology is the mechanism for bringing conidia into contact with a host. As the developing conidial bud matures, its contents and that of the

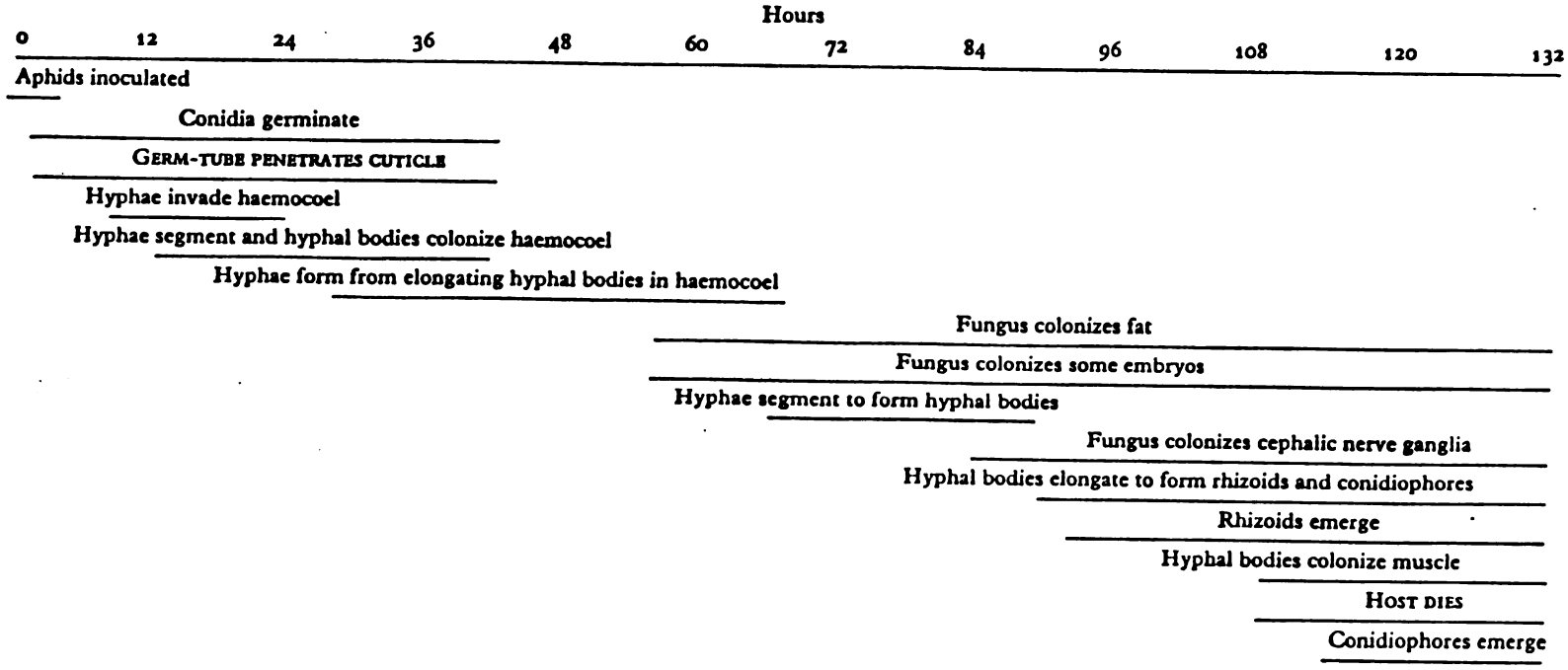


Figure 5. Developmental process of *E. planchoniana* (from Brobyn & Wilding 1977).

conidiophore absorb water. The resulting osmotic pressure breaks the attachment, and the mature conidium is explosively discharged into the air. The conidia have sticky walls that aid in adhering to a new host. If the conidium contacts a suitable host and the environmental conditions are favorable, it germinates and produces a germ-tube. When no host is contacted, the conidium may produce a new bud that fills with cytoplasm from the original conidium thus forming a secondary conidium. The new conidium has the same infection potential as the primary conidium. This process may repeat, forming tertiary conidia, or until the succeeding conidia becomes exhausted (Bell 1974). A more precise description of these details is provided by Humber (1981, 1984a).

PRELIMINARY SURVEY.

Oceana and Berrien counties are the largest producers of asparagus in Michigan (Michigan Dept. of Agriculture 1977). In August 1980, commercial plots in these two counties were surveyed for the asparagus aphid. Of the 17 plots visited in Oceana county, only 2 fields were classified as having "abundant" numbers in comparison to the remaining fields that had "none" or "few". In Berrien county, the aphid was termed as "common" in two of the six fields surveyed.

In June 1982 I started sampling 5-7 fields in Oceana county every 2-3 weeks. Plants in the border rows were usually selected; the fern beat into a white enamel pan (46 by 26 by 10 cm deep). Aphids were rare in all plots. However, a dozen plants with moderate aphid numbers were located in an abandoned field (20 by 70 m) in Oceana county. Numerous colonies were tagged and reexamined after 10 days. Within that time period all aphids were destroyed by various natural enemies. This was

determined by the evidence located in and around the decimated colonies, such as diseased and mummified aphid bodies, hatched coccinellid and lacewing eggs, and lacewing and coccinellid pupae. A similar tagging effort was executed in a research plot (12 by 34 m) at the Horticulture Research Center, MSU campus from July-August 1983. Again, the colonies disappeared within 1-2 weeks, but there was even greater evidence of the fungal pathogen, less so for the parasitoids and predators.

These findings were used to formulate the working suppositions that shaped my experiments: 1) The aphid was relatively rare in Michigan fields and therefore hard to consistently find in large numbers; 2) in addition to predators and parasitoids, a fungal pathogen was attacking the aphid; and 3) since the natural enemies were quickly destroying the colonies, daily observations were needed to accurately understand population trends. The observed diversity of mortality agents discovered in Michigan corroborated the findings of Angalet & Stevens (1977). The speed with which the beneficial organisms acted required that any field experiments be conducted at a local site on campus in artificially infested plots.

OBJECTIVES.

The goals for this dissertation were the same as the objectives stated in the three proposed articles (Sections II-IV). In order of their presentation in this document, the objectives were:

1) Survey Michigan asparagus plots for the potential natural enemies of the asparagus aphid.

2) Compare the impact of selected coccinellid species to that of two other important natural enemies--the aphidiid parasitoid and entomophthoralean pathogen--through inclusion-exclusion techniques.

3) Investigate aspects of coccinellid biology that could negatively affect their impact as biological control agents, such as egg cannibalism by newly-emerged larvae.

ARTICLE 1

A survey of natural enemies of the asparagus aphid, *Brachycorynella asparagi* (Homoptera: Aphididae), in Michigan with an emphasis on coccinellids (Coleoptera: Coccinellidae).

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ABSTRACT

Sticky-can traps, flight interception panels and walking visual counts were used to identify potential natural enemies of the asparagus aphid, *Brachycorynella asparagi* (Mordvilko), in Michigan asparagus. Anthocorids, coccinellids and chrysopids, in this order, were the predators most commonly caught during 1983-1985. An aphidiid parasitoid, *Diaeretiella rapae* (M'Intosh), and entomophthoralean fungus, *Entomophthora planchoniana* Cornu, were also noted as important beneficial organisms. The natural enemies were similar to those reported for New Jersey and Delaware by Angalet and Stevens (1977).

Seasonal population trends were similar for anthocorids, less so for coccinellids and chrysopids (all species combined). Monitored as individual species, the yearly catches for coccinellids revealed differences between sampling methods. Each sampling technique indicated a different beetle species to be dominant in the 1985 season. Also, visual counts showed no specific time interval (A.M., noon or P.M.) as

best for sampling coccinellids. Instead, temperature exerted more influence on coccinellid counts.

KEY WORDS: asparagus, *Brachycorynella asparagi* (Mordvilko), natural enemies, Coccinellidae, Anthocoridae, Chrysopidae, *Entomophthora*, Aphidiidae, flight traps, visual counts.

INTRODUCTION

A.K. Mordvilko described the asparagus aphid, *Brachycorynella (=Brachycolus) asparagi* (Mordvilko), in a key to aphids from Eastern Europe (Szelegiewicz 1961). The aphid was first reported in eastern North America in 1969 from New York State (Capinera 1974). By 1979 it was discovered on asparagus in Washington State and British Columbia, Canada (Forbes 1981, Thornton et al. 1982). Forbes (1981) revealed even earlier catches of winged asparagus aphids from water traps located in Summerland, British Columbia in 1975 and 1976.

Although this aphid now occurs in 27 states and in Canada (Halfhill 1987), it is not always an economic pest on its preferred host, *Asparagus officinalis* L. The aphid achieved major pest status in western U.S., causing an estimated $10-12 million damage to Washington asparagus plantings in 1980 (Anonymous 1980). The current status of this aphid in the major asparagus-growing regions of the United States is: 1) requires chemical control in Washington State (Cone 1986); 2) discovered in 1984, now present in 10 counties of California and requiring treatment where large populations develop (Ball 1986); and 3) aphid causes no significant damage in Michigan (Grafius 1986), Maryland, Delaware or New Jersey (Hendrickson 1986). With respect to the international status of this aphid, Prokrym found moderate infestations

on asparagus in Italy, Germany and France during a brief trip to these countries in September 1983 (see Section I).

The most recent articles on the aphid come from Washington State researchers and concern aspects of its biology (Tamaki et al. 1983, Wright and Cone 1986a), the impact of cultural practices (Halfhill et al. 1984, and Wildman and Cone 1986), and sampling (Halfhill et al. 1983, 1987; Wright and Cone 1983, 1986b). Angalet and Stevens (1977) reported that native natural enemies and diseases seem to control asparagus aphid numbers in eastern United States, but few other researchers have investigated natural enemies from areas where the aphid is considered a nonpest. A majority of the cited articles stress pest control as their objective.

In 1982 and 1983, preliminary surveys of commercial plots in Michigan revealed several observations that would shape subsequent studies: 1) the aphid occurred in low numbers in Michigan plantings, 2) marked colonies disappeared within 5-10 days, and 3) monitored colonies showed evidence that three groups of natural enemies were utilizing the aphid resource--predaceous coccinellids, aphidiid parasitoids and a fungal pathogen (See Section I).

The first objective of this study was to survey Michigan asparagus plots and list potential natural enemies of the asparagus aphid. This effort complemented the work of Angalet and Stevens (1977). Since no single method was adequate to sample all beneficial organisms, several techniques were used: sticky traps, flight interception traps, and walking visual counts. We also listed the most abundant groups, i.e. those natural enemies most commonly detected by the sampling methods, and graphed their seasonal population trends for 1983-1985. The trap

catches for the lady beetle predators were analyzed in detail because, of all natural enemy groups, only coccinellids were easily identified to species in the field. Finally, we discussed the positive and negative aspects of each sampling method.

MATERIALS AND METHODS

EXPERIMENTAL PLOTS.

The research plots were two 5-year-old asparagus plantings (variety Mary Washington), measuring 10 rows by 38 m, and situated 50 m apart. The plots were located at Michigan State University Botany & Plant Pathology Field Laboratory, about 2 km south of the main campus in East Lansing, Michigan. One plot was sampled in 1983 and the other in 1984 and 1985. Both study sites, situated in a 10 ha block of the agricultural research facility (ca. 660 ha), were bordered by small plots of vegetable and field crops as well as fallow areas. Larger plantings of alfalfa and corn occurred within a 1 km radius of the plots. Alfalfa (57 ha total within 1 km) was cut three times a year for hay, usually in June, July and August. Corn (74 ha total within 1 km) was cut for silage once a year in September or October.

The primary source of asparagus aphids in the research plots came from artificial infestations because the aphid naturally occurred in very low numbers during most of the season. An earlier attempt to uniformly infest a plot by placing ca. 200 aphids per plant on 100 of the 350 plants failed to create suitable densities. Subsequent infestations were restricted to a smaller number of selected plants. About 5-10 heavily infested branches were placed in the foliage; as the

branch dried the aphids moved onto the fern. This method not only produced high-density concentrations, but it better utilized the limited number of cultured aphids to firmly establish the host in the plot. Later in the season we supplemented the cultured aphid source reared in the greenhouse or in growth chambers with colonies taken from another asparagus plot.

Another important reason for infesting selected plants pertained to the exclusion experiments that were concurrently conducted during the abundance survey (see Section III). The infested plants constituted a small group that were randomly chosen as experimental units and caged for varying periods to eliminate the impact of natural enemies on the introduced aphids. The exclusion cages not only influenced access to aphids by natural enemies, but they also created potential barriers to insect movement while in place.

Since the placement and removal of exclusion cages could affect the trapping and arrestment of beneficial organisms in the plot, a brief description of the infestation procedure is necessary. In 1983 six of 18 treatment plants (plot total, 360) remained uncaged throughout the experiment and during all infestations. In 1984 only half of the 16 experimental plants were initially caged during infestation while the remaining eight plants were uncaged and exposed to natural enemies. These eight uncaged plants were treated with the insecticide carbaryl and a maneb fungicide to reduce aphid mortality by natural enemies (See Section III). These uncaged plants were eventually caged because their aphid populations failed to increase as rapidly as those on the covered plants. In 1985 all experimental plants (20 of 350) were caged for infestation. Cage placement and infestation occurred twice in 1985

because the exclusion trial was conducted two times that season. In 1983 the cages measured 1.83 tall by .914 by .914 m and essentially enclosed a single plant. The larger cages (1.83 by 1.83 by 1.83 m) used in 1984 and 1985 could cover one or two additional plants adjacent to the experimental plant selected for infestation. This meant that a large group of nonexperimental plants also supported sizeable aphid populations. In 1984 and 1985 all plants were uncaged when the exclusion experiment began.

SAMPLING.

The sampling methods used in 1983 included: sweep-netting along borders, beating fern into a pan, whole-plant removal, sticky-can trap, modified window pane trap, and walking visual count of plot. The first three techniques were rejected during the 1984-1985 surveys because of their destructive nature, unrepresentative low counts on the most common natural enemies, or inability to adequately sample the bushy asparagus plant (See Appendix A).

The main collection methods for flying insects were sticky traps and flight interception panels. The sticky traps were constructed from coffee cans (12.7 cm diameter by 16.5 cm tall) painted with safety-yellow enamel (Krylon #1813, Borden Inc., New York, New York), mounted atop a one meter stake (Figure 6). A transparent plastic strip (16.5 by 43.1 cm) covered with an adhesive substance (Tangle-trap, The Tanglefoot Co., Grand Rapids, Michigan) was attached around the outside of the can with Velcro tabs for easy removal of the entrapped insects.

The detachable sticky strips were changed every two weeks in 1983 and at monthly intervals in 1984 and 1985. In all years the larger

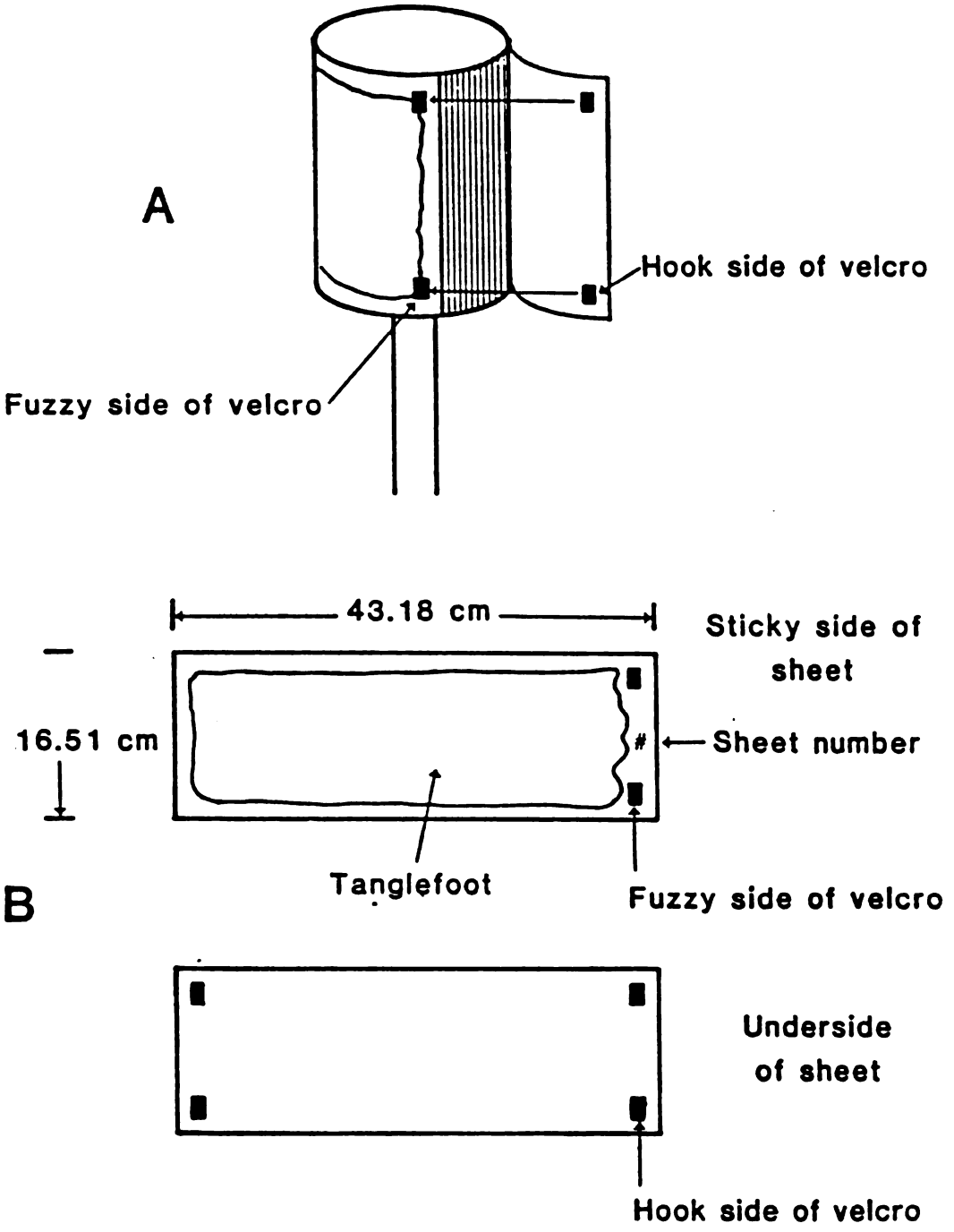
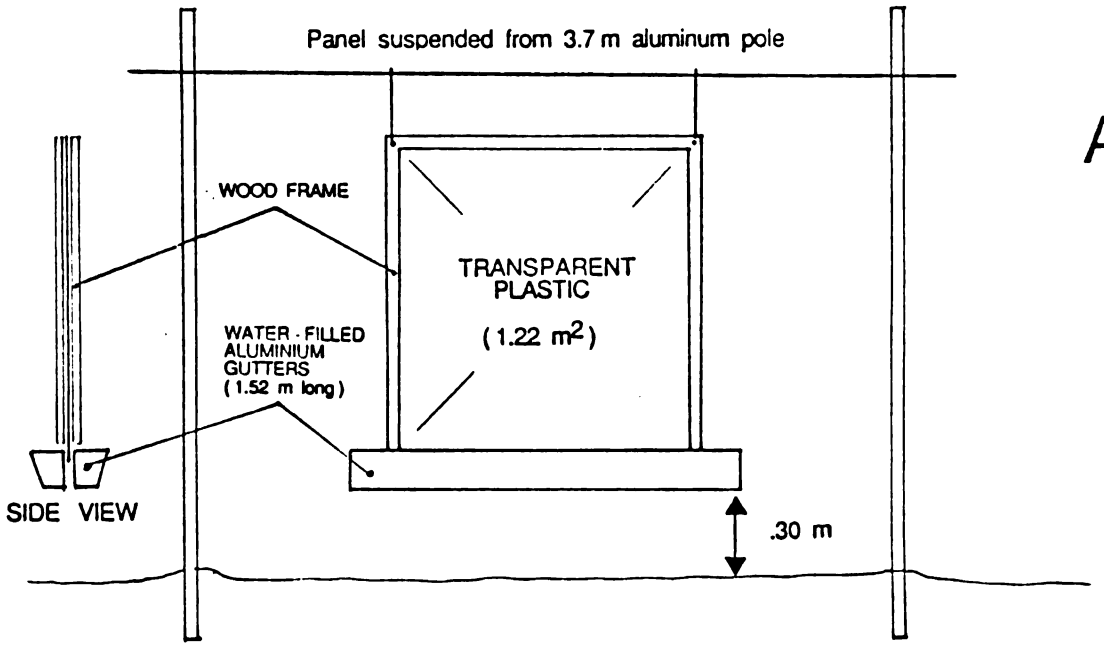


Figure 6. Sticky-can trap (Hayakawa 1985). A) Placement of transparent plastic strip covered with adhesive Tangle-trap on yellow can. B) Arrangement of Velcro tabs that facilitated easy removal.

aphidophagous insects (Coccinellidae and Chrysopidae) were counted in the field and then removed from the sticky strips every 1-3 days. The smaller entrapped specimens (Anthocoridae and Aphidiidae) were counted in the laboratory on the removed strips under a stereomicroscope. The cans were placed in the rows, the location adjusted to fall in the open spaces that frequently occurred between plants. Sixteen can traps were placed inside each plot, four to a row within the inner six rows (Figure 7b). In 1983 there were an additional eight traps along the perimeter, two to a side (Hayakawa 1985). This technique was the only sampling method used in 1983.

In addition to sticky traps, flight interception panels (FIP) were also positioned inside the perimeter of the plot in 1984 and 1985 (Figure 7b). This trap was a modification of the window-pane trap described by Peck et al. (1980) and Masner et al. (1981). Each FIP was constructed from transparent plastic (0.254 mm thick Flex-o-pane) fastened to a wooden frame (1.2 by 1.2 m) and suspended one meter above the ground (Figure 7a). Water-filled aluminum gutters attached to the bottom of the frame caught insects that hit both sides of the plastic barrier. In 1984 the gutter water was filtered weekly to isolate the water-trapped specimens. Although the frame was hung in a way that permitted it to sway, the large panels were especially susceptible to strong winds. A daily collection scheme was initiated on August 20, 1984 to prevent the loss of specimens during windy weather. Then, a small-meshed net was used to scoop the floating insects from the water.

Visual counts were conducted in 1984 and 1985. In 1984 counts were made by walking diagonally across the entire plot over a 15-minute period. This was done three times a day, during the periods of 730-



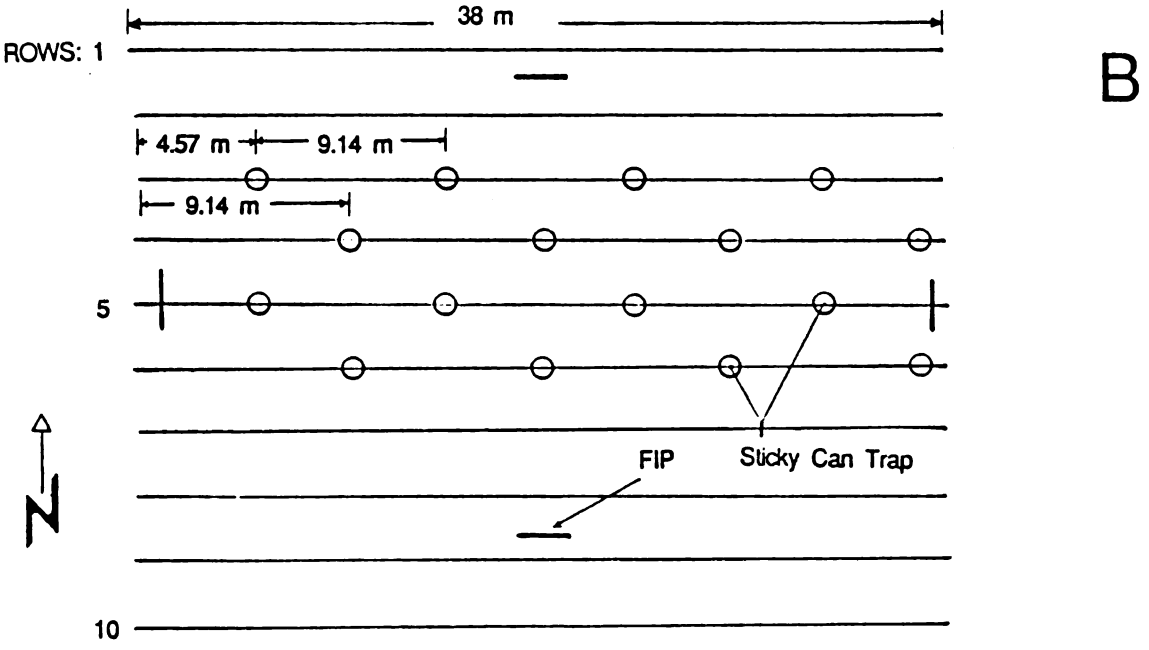


Figure 7. A) Flight interception panel (FIP). B) Placement of 16 sticky-can traps within rows and 4 flight interception panels along plot perimeter for 1984-1985 season.

1030, 1130-1300, and 1530-1900 hours. In 1985 the plot was divided in half, each sampled by 15-minute walks during the periods of 930-1100, 1300-1500 and 1600-2000 hours. The 1985 visual counts were conducted only after cages for the exclusion experiment were removed.

Aphid mummies and cadavers were the primary source for identifying the specific parasitoid and fungal agents. The parasitoids were identified as part of a separate study by Hayakawa (1985). Since the taxonomy of entomophthoralean species is complex, we enlisted the services of Dr. Richard A. Humber (USDA-ARS, Boyce Thompson Institute, Cornell University, Ithaca, New York) to identify the fungal disease.

PRESENTATION OF DATA.

To emphasize population trends and provide a basis for comparing the three different sampling techniques, the data were transformed into percentages. The value for a trapping interval was divided by the total seasonal count and multiplied by 100, and assigned to the last day of the interval when graphed. However, the trapping interval varied for each method. As the simplest case, the interval for visual counts was one day. Therefore, each day's catch was divided by the season total.

The interval for the sticky cans depended on the species trapped. The larger predators could be easily identified and were removed from the sticky strips in the field. Counts of coccinellids and chrysopids were made every 1-3 days over the calendar week and aggregated into a weekly interval value. The strips were then collected every month and inspected for anthocorids and aphidiids--a monthly interval value.

We initially planned weekly collections for the interception panels, but these traps could not be operated during high winds.

Therefore, specimens were removed from the water-filled gutters daily. These daily catches were summed over periods that varied from three to seven consecutive trapping days. Due to its variable length, the trapping interval was calculated as an average daily value, i.e. the number of specimens caught divided by the days in the trapping period. The total of the daily averages was used when calculating precentages.

Weather data collected at the Michigan State University Horticultural Research Center, 2 km south of the plot, were used to calculate accumulated degree days by the Baskerville-Emin method (1969). A base temperature of 10°C (DD_{10}) was chosen as a reasonable compromise for the species sampled. Developmental threshold temperatures ranged from 8.3°C for lacewing larvae to 12.2°C for the total preimaginal development of coccinellids (Table 4).

RESULTS

SPECIES COMPOSITION AND ABUNDANCE.

The composition of natural enemies detected by our sampling techniques was similar to that reported by Angalet and Stevens (1977) for New Jersey and Delaware. Unlike Angalet and Stevens, we did not identify all specimens to species (Table 5). Individuals that occurred infrequently in our samples were only categorized to family level.

Predators. Of the predatory families, both studies produced a representative list of coccinellid species (Table 5). Two Michigan lady beetles not listed by Angalet and Stevens (1977) were *Coccinella transversoguttata richardsoni* Brown and *C. trifasciata* (L.). Our list lacked two of their species: *Olla abdominalis* (Say) and *Coccinella*

Table 4. Developmental threshold temperatures for natural enemies of the asparagus aphid.

TAXA	TEMPERATURE (°C) (STAGE)[a]	REFERENCE[b]
COCCINELLIDAE:		
H. convergens	9.0 (L)	BD 1972 [c]
"	12.0 (TP)	OT 1982
C. maculata	11.3 (TP)	OT 1978
C. transversoguttata	12.2 (TP)	OT 1981
C. septempunctata	12.1 (TP)	OT 1981
A. bipunctata	9.0 (TP)	OT 1981
CHRYSOPIDAE:		
Chrysopa carnea	8.3 (L)	BR 1970[c]
ANTHOCORIDAE:		
Orius insidiosus	10.0 (T)	MH 1986
"	10.2 (T)	KH 1981
"	13.7 (T)	IY 1981

[a] Stages: L, larvae; T, total--eclosion to adult; TP, total preimaginal development.

[b] Abbreviations for references: BD, Butler & Dickerson 1972; BR, Butler & Ritchie 1970; IY, Isenhour & Yeargan 1981; KH, Kingsley & Harrington 1981; MH, McCaffrey & Horsburgh 1986; OT, Obrycki & Tauber 1978, 1981, 1982.

[c] Threshold temperature calculated by Neuenschwander (1975) from data cited in authors' paper.

Table 5. Natural enemies of the asparagus aphid collected in Michigan.

PREDATORS:

Coccinellidae
- *Hippodamia convergens* Guerin*
- *Hippodamia parenthesis* (Say)*
- *Hippodamia tredecimpunctata tibialis* (Say)*
- *Hippodamia glacialis* (F.)*
- *Coleomegilla maculata lengi* Timberlake*
- *Coccinella transversoguttata richardsoni* Brown*
- *Coccinella septempunctata* L.
- *Coccinella novemnotata* Herbst*
- *Coccinella trifasciata* (L.)*
- *Adalia bipunctata* (L.)*
- *Cycloneda munda* (Say)*

Chrysopidae
- *Chrysopa plorabunda* Fitch*
- *Chrysopa oculata* Say*

Hemerobiidae
- *Micromos subanticus* (Walker)*
- *Hemerobius stigmaterus* Fitch*

Anthocoridae
- *Orius insidiosus* (Say)*

Nabidae
- *Nabis* spp.

Syrphidae
- *Syrphus* spp.*

Cecidomyiidae

Pemphridinidae
- *Diodontus minutus* (Fabricios)*

PARASITOID:

Aphidiidae
- *Diaeretiella rapae* (M'Intosh)

PATHOGEN:

Entomophthorales
- *Entomophthora planchoniana* Cornu

* Voucher specimen deposited in Entomology Museum, Michigan State University, E. Lansing, Michigan; Voucher No. 1988-02.

undecimpunctata (L.). We also recorded different lady beetle species as most common. Angalet & Stevens (1977) reported *Hippodamia convergens* Guerin-Meneville, *Coleomegilla maculata* (DeGeer), *Coccinella novemnotata* Herbst and *Cycloneda munda* (Say) as abundant whereas we ranked *Hippodamia parenthesis* (Say), *H. convergens* Guerin, *Coleomegilla maculata lengi* Timberlake and *Coccinella transversoguttata* as the top four species in this order (Tables 6 & 7).

Coccinellids and chrysopids were found to be abundant by both studies, but our sampling methods indicated minute pirate bugs (Anthocoridae) as the most numerous predator (Table 6). Aphidophagous families represented by relatively low numbers or frequency in both studies were: Syrphidae, Cecidomyiidae, Hemerobiidae, and Nabidae. In our research plots an aphid wasp (Hymenoptera: Pemphridinidae) was probably a numerous and active predator on the aphid over all years but it was only recognized as a predator late in the 1985 season. These wasps provision their ground nests with aphids.

Parasitoids. Both studies listed *Diaeretiella rapae* (M'Intosh) as the most common parasitoid. Hayakawa (1985) reported *Aphidencyrtus aphidivorus* Mayr (Encyrtidae) as the hyperparasitoid of *D. rapae*. *D. rapae* parasitizes other aphid hosts like the cabbage aphid, *Brevicoryne brassicae* L., and green peach aphid, *Myzus persicae* Sulzer.

Fungal pathogen. Angalet & Stevens (1977) reported that 50-95% of the aphids had been killed by *Entomophthora aphidis* Hoffman in some fields. Humber (1984a) noted that the majority of species in the order Entomophthorales are entomopathogenic and have been included by most authors in a heterogeneous assemblage as *Entomophthora* Fresenius. To avoid such errors, we took samples of infected asparagus aphids to Dr.

Table 6. Seasonal and overall totals for (A) sticky-can traps and (B) flight interception panels by family and species.

A. STICKY-CAN TRAPS	1985	1984	1983	TOTALS
Anthocoridae	1900	332	--	2232
Coccinellidae, all species	198	120	122	440
H. convergens	40	41	41	122
C. maculata	21	32	54	107
H. parenthesis	27	8	13	48
C. transversoguttata	24	15	2	41
H. tredecimpunctata	25	9	7	41
Other: (*C. septempunctata*, *C. novemnotata*, *A. bipunctata*, *C. munda*)	61	15	5	81
Chrysopidae	73	127	17	217
Aphidiidae	74	117	--	191
Nabidae	7	0	--	7
Syrphidae	20	30	--	50
Hemerobiidae	15	16	--	31
Cecidomyiidae	--	--	--	--

B. FLIGHT INTERCEPTION PANEL (FIP)	1985		1984		TOTALS	
Anthocoridae	570	(90.9)	1424	(295.5)	1994	(386.4)*
Coccinellidae:						
All species	301	(49.3)	334	(84.3)	635	(133.6)
H. convergens	23	(3.7)	60	(13.9)	83	(17.6)
C. maculata	1	(.1)	66	(17.5)	67	(17.6)
H. parenthesis	193	(31.0)	107	(27.0)	300	(58.0)
C. transversoguttata	28	(4.7)	28	(6.8)	56	(11.5)
H. tredecimpunctata	11	(1.7)	41	(10.5)	52	(12.2)
Other (see above):	44	(8.1)	32	(8.7)	76	(16.8)
Chrysopidae	13	(2.1)	29	(5.0)	42	(7.1)
Nabidae	29	(5.3)	20	(4.3)	49	(9.6)
Syrphidae	9	(1.5)	1	(.2)	10	(1.7)
Aphidiidae	--		--		--	
Hemerobiidae	--		--		--	
Cecidomyiidae	--		--		--	

* The average daily total in parentheses was calculated by dividing the interval count by the number of days (4-7) in the sampling period. These average values were used to graph the seasonal trends for the interception panels.

Table 7. Seasonal and overall totals for visual counts by family and species for 1984 and 1985.

A. VISUAL COUNTS FOR 1984[a]	A.M.	NOON	P.M.	TOTALS
Coccinellidae, all species.....	98	94	119	311
H. convergens.....	38	29	44	111
C. maculata.....	37	41	46	124
H. parenthesis.....	0	2	0	2
C. transversoguttata.....	10	14	20	44
H. tredecimpunctata.....	2	5	3	10
Other (*C. septempunctata*, *C. novemnotata*, *A. bipunctata*, *C. munda*).....	11	3	6	20
Chrysopidae.....	34	66	95	195
Anthocoridae.....	0	0	0	0
Syrphidae.....	9	1	3	13
Hemerobiidae.....	0	0	0	0
Cecidomyiidae.....	-	-	-	-

B. VISUAL COUNTS FOR 1985[b]	A.M.	NOON	P.M.	TOTALS
Coccinellidae, all species.....	153	145	142	440
H. convergens.....	37	33	27	97
C. maculata.....	10	16	7	33
H. parenthesis.....	11	5	3	19
C. transversoguttata.....	52	57	76	185
H. tredecimpunctata.....	6	3	2	11
Other (see above):.....	37	31	27	95
Chrysopidae.....	7	2	2	11
Anthocoridae.....	0	0	0	0
Nabidae.....	1	0	0	1
Syrphidae.....	4	4	5	13
Hemerobiidae.....	0	0	0	0
Cecidomyiidae.....	-	-	-	-

[a] Sampling times for 1984: A.M., 0730-1030; NOON, 1130-1300; and P.M., 1530-1900 h.

[b] Sampling times for 1985: A.M., 0930-1100; NOON, 1300-1500; and P.M., 1600-2000 h.

R.A. Humber at Boyce Thompson Institute. The fungus was identified as *Entomophthora planchoniana* Cornu, Subdivision Zygomycotina, Class Zygomycetes, Order Entomophthorales, Family Entomophthoraceae (Humber 1984b). Humber also explained that there was only one report of successful culture of this species (Holdom 1983) and that he was repeatedly unable to isolate the pathogen.

POPULATION TRENDS.

Anthocoridae. The trends for anthocorids caught by interception panels followed a similar pattern over the two years sampled (Figure 8a). Numbers stayed around the 5% level through most of August (835-1185 DD_{10} for 1984; 872-1158 DD_{10}, 1985) and then peaked on 1325 DD_{10} (September 21, 1984) and 1252 DD_{10} (September 7, 1985). Here, the 10°C base temperature for accumulated degree day calculation was arguably more appropriate than for other species (Table 4). Also, cage removal may not have greatly influenced the trends in either year. In 1984 the curve moved upward on 1249 DD_{10}, 17 days after cage removal on 1103 DD_{10}. In 1985 numbers started to increase at 1088 DD_{10}, four days before the cages came off on 1130 DD_{10}.

As monthly values, the sticky-can counts for anthocorids did not include enough points for detailed comparisons between the two trapping methods (Figure 8b). Weekly or bimonthly collections were needed. However, these curves revealed a similar pattern of population increase towards September.

Aphididae. As for anthocorids, the sticky-can counts based on monthly values did not represent parasitoid population trends with any detail (Figure 8c). In general terms, aphidiids were more abundant in

can traps during September, after 1175 DD_{10}. We anticipated that the interception panels would provide better information on aphidiid numbers than the cans because of their larger trapping area. However, the small parasitoid was not detected or could not be distinguished from other hymenopterans of similar size and shape.

Chrysopidae. The population curves for adult lacewings caught by panel traps (Figure 9a) were less similar between years when compared with the plot for anthocorids (Figure 8a). However, the 1985 peak occurred earlier in the season than the 1984 peak for both families. In 1984 chrysopid numbers were highest on 1178 DD_{10} (August 30), and on 969-1037 DD_{10} in 1985 (August 10-17).

Trends for sticky-can traps closely agreed with those from panel counts for the same year (Figures 9a&b). The interception panel data indicated a peak in activity slightly before the increase detected by the sticky cans. This phenomenon would be expected due to the location of the panels on the edge of the field where the initial influx of animals occurs. Also, data for both traps suggested that there may be two periods of activity with a small peak occurring in late-July to early-August. This hypothesis was supported by the 1983 can counts with two distinct peaks at 907 DD_{10} (August 7) and 1389 DD_{10} (September 21).

TRENDS FOR COCCINELLIDAE BY YEAR AND SPECIES.

Analyzing population trends based on total numbers was valid for families Anthocoridae and Aphidiidae because only one species was involved, less so for Chrysopidae with 2-3 species (Table 5). However, curves for total numbers probably masked variable seasonal phenologies for the 11 coccinellid species (Figure 10). Data collected for these

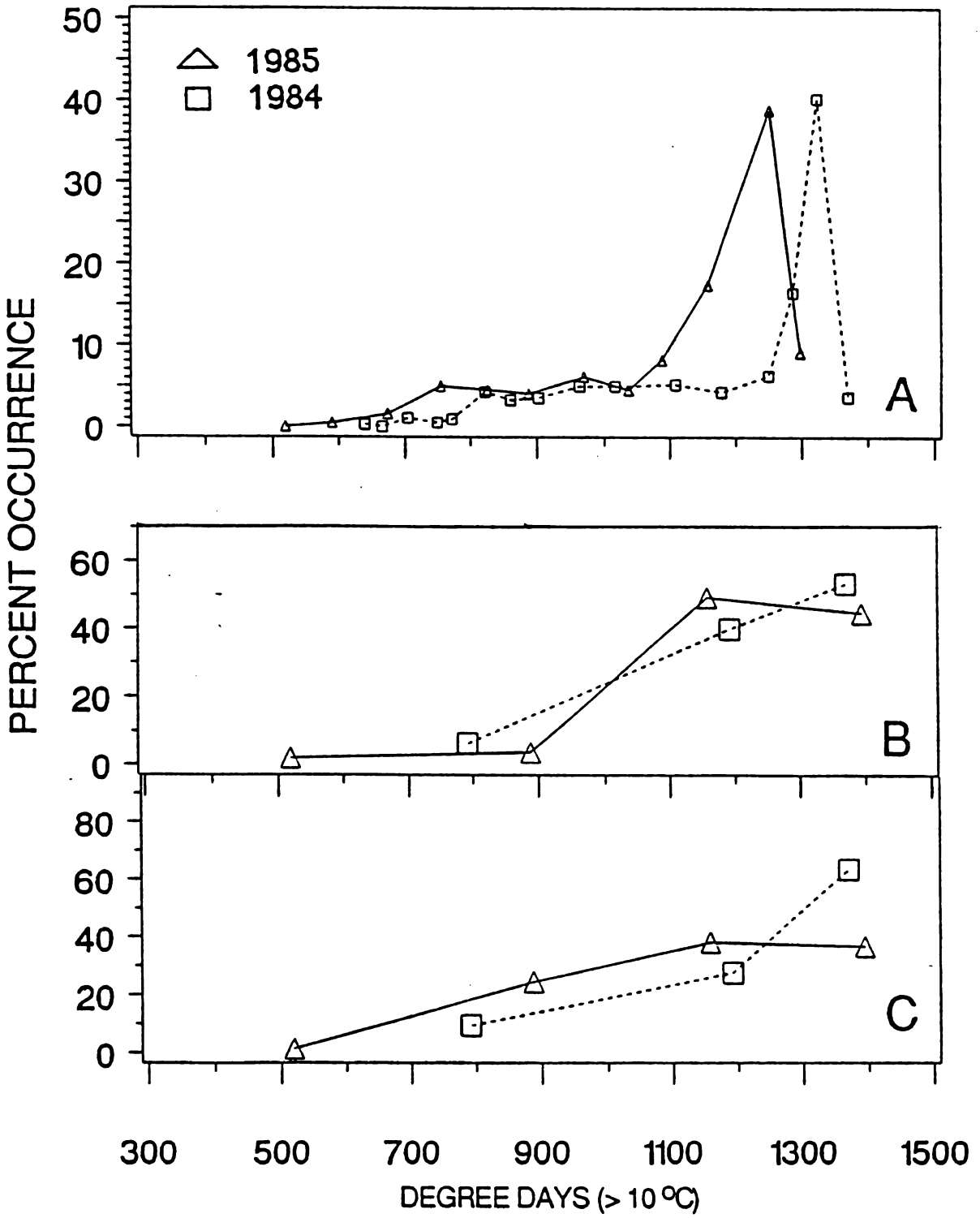


Figure 8. Percent occurrence for anthocorids caught in (A) flight interception panels and (B) sticky-can traps, and (C) for aphidiids caught in can traps, 1984-1985.

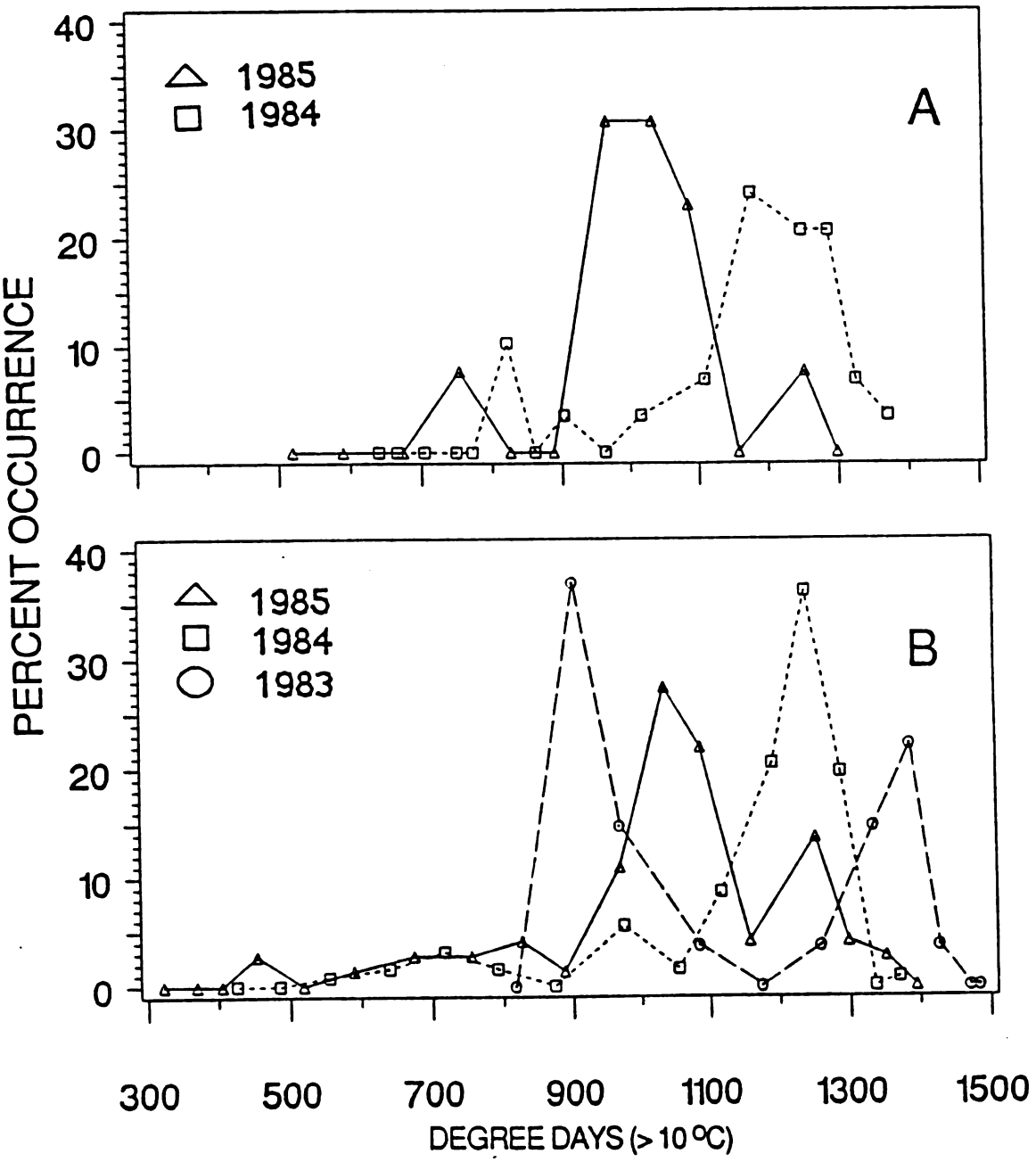


Figure 9. Percent occurrence for chrysopids, all species combined, for (A) flight interception panels in 1984-1985 and (B) sticky-can traps in 1983-1985.

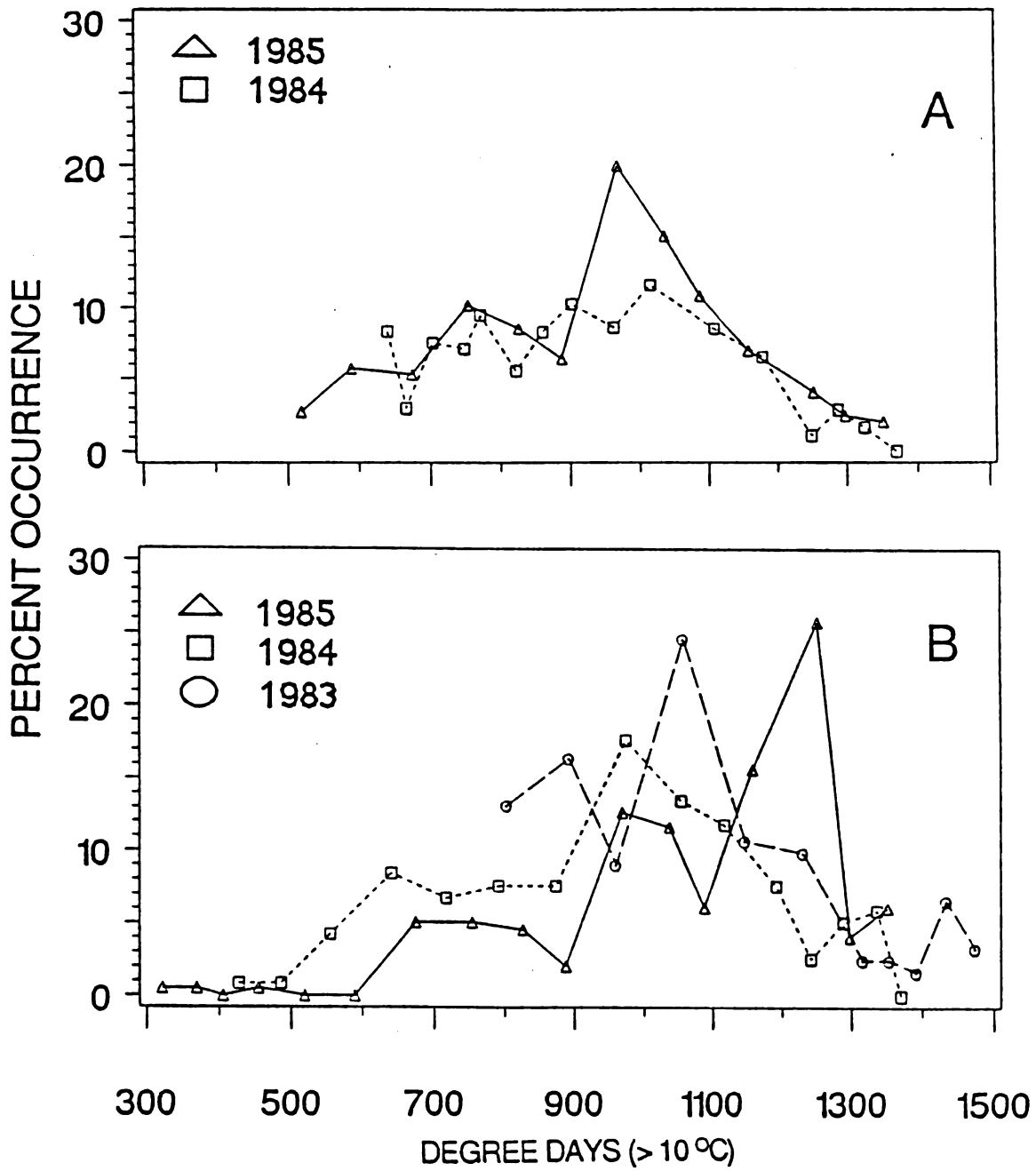


Figure 10. Percent occurrence for coccinellids, all species combined, for (A) flight interception panels in 1984-1985 and (B) sticky-can traps in 1983-1985.

predators offered the best opportunity to demonstrate individual trends because lady beetles were abundant in all years and easily identified to species in the field. Therefore, we discussed the trends for abundant species by year.

To emphasize the impact of influences internal and external to the plot, other parameters were indicated on selected graphs. Internal factors included the placement and removal of exclusion cages as well as aphid infestations of selected experimental plants; both events introduced significant food resources at specific intervals. External factors were the daily maximum and minimum temperatures, rainfall, and the dates when adjacent plots of alfalfa and corn were cut.

Due to the small size of the plots, external circumstances might influence the in-migration of aphidophagous insects. The cutting of large alfalfa and corn plantings near the plots could create such a condition as insects leave the disturbed areas. However, no casual connection to cutting dates could be linked to higher trap catches. Only counts of mirids, primarily *Lygus lineolaris* (Palisot de Beauvois) (Hemiptera: Miridae), seemed to increase after alfalfa was cut in July and August.

1983 season.

Only sticky-can traps provided data for this year (Figure 11b). Three other sampling methods (whole-plant removal, sweep-netting and beating fern into a pan) were employed in a second plot and discarded as suitable techniques (See Appendix A). After the 12 exclusion cages were erected (830 DD_{10}) only six plants remained uncaged during the entire period of aphid infestations (beginning 893 DD_{10}). The high and low values for trap catches, especially during 900-1100 DD_{10}, seemed to be

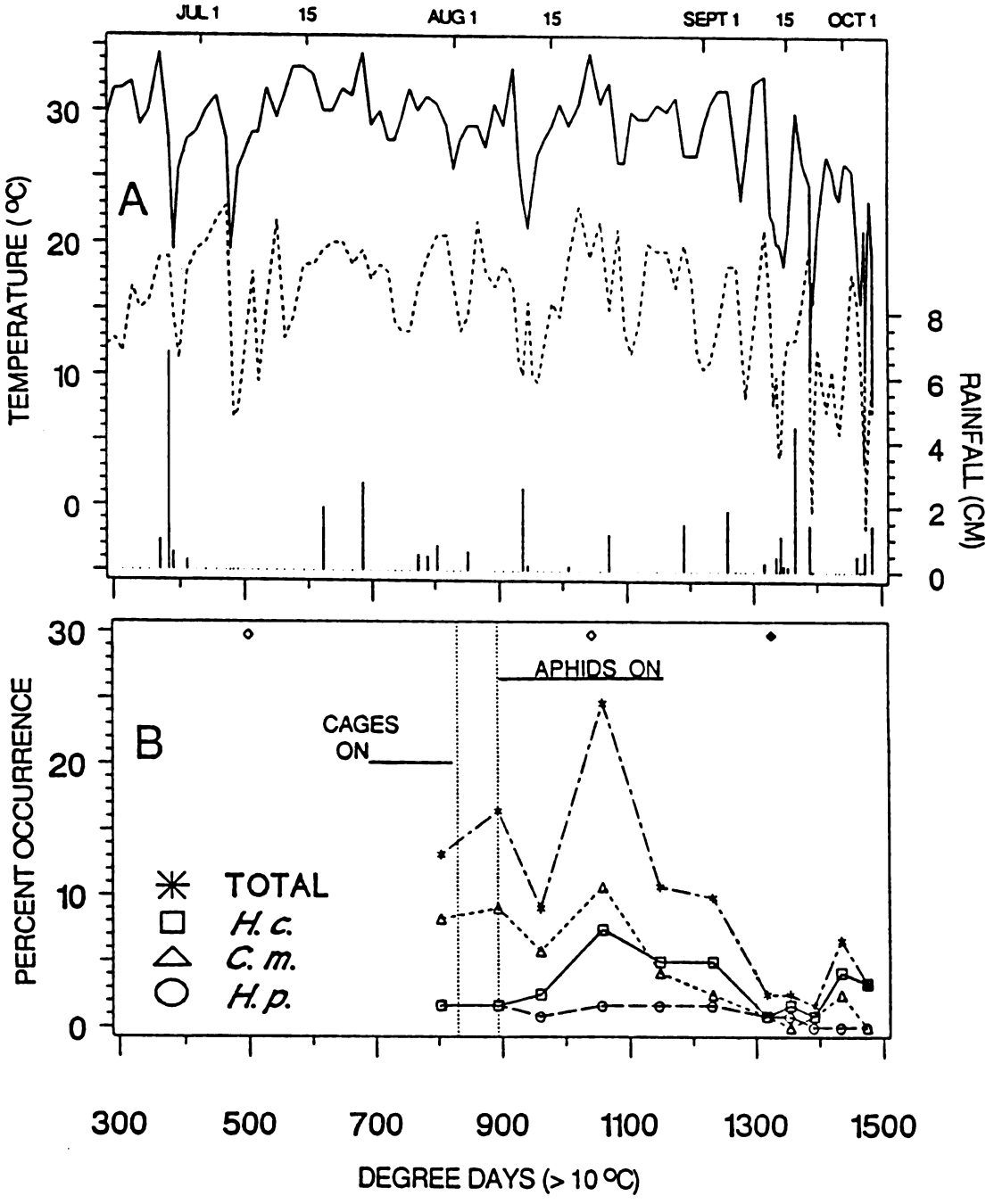


Figure 11. (A) Daily rainfall and maximum-minimum temperatures during the study period, and (B) coccinellid catch of most common species for 1983. For 11B: The vertical bars mark the placement of exclusion cages or introduction of aphids. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. KEY: TOTAL, all 9 species combined; *H.c., H. convergens; C.m., C. maculata;* and *H.p., H. parenthesis.*

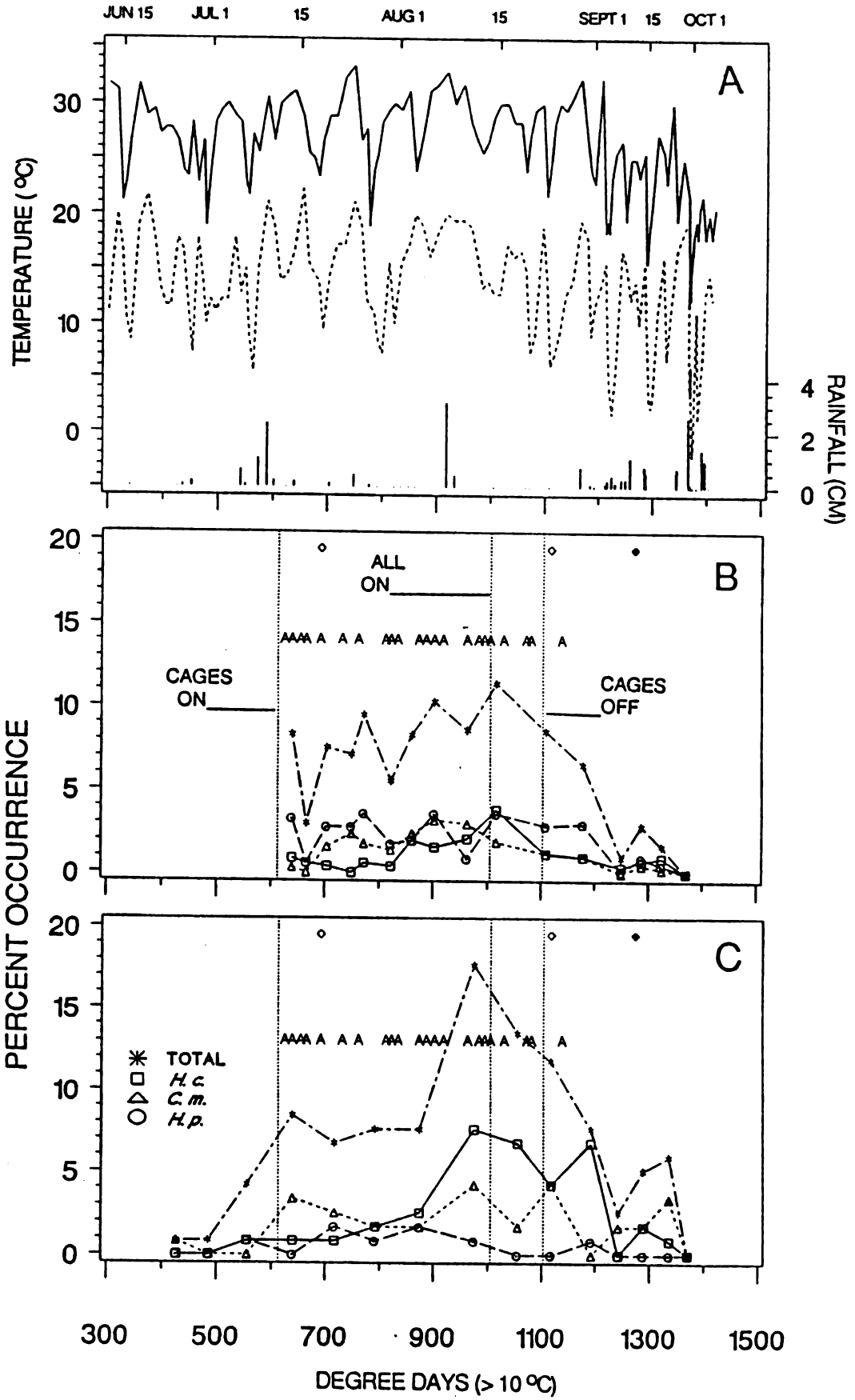
closely associated with weather fluctuations as revealed by the maximum-minimum curves (Figure 11a). Ives (1981) noted that daily maximum temperature had a significant effect on coccinellids caught in flight traps. Moreover, the author stated that this effect was much stronger for *Coccinella californica* Mannerheim than for *C. trifasciata* Mulsant. The beetles *H. convergens* and *C. maculata* were the two most abundant species in this trap (Table 6a), comprising about 61% of the total seasonal catch.

1984 season.

The overall trend for total coccinellids caught by interception panels, i. e. all species combined, slightly resembled its counterpart for sticky-can traps (TOTAL, Figures 12b&c). Examination of species composition revealed the differences between traps. The variable portion of the TOTAL curve for interception panels (638-1000 DD_{10}, Figure 12b) was essentially shaped by the catch of *H. parenthesis*, the most abundant species for this trap (64% of total catch, Table 6b). In contrast, the general shape of the TOTAL curve for the can counts reflected the combined presence of *H. convergens* and *C. maculata*. Though *H. parenthesis* was included in Figure 12c for comparison, *C. transversoguttata* actually ranked as the third most common coccinellid trapped by the cans (Table 6a).

The counts for interception panels and sticky cans dropped slightly as the exclusion cages were first erected (613 DD_{10}). However, beetle numbers showed a gradual increase during 614-1000 DD_{10}; a time when 8 of the 16 experimental plants were still uncaged and being regularly infested ("A" on Figures 12b&c). Percent occurrence did not markedly increase after all cages were removed at 1100 DD_{10}. Catches

Figure 12. (A) Daily rainfall and maximum-minimum temperatures during the study period, and coccinellid catch of most common species for (B) flight interception panels and (C) sticky-trap cans during 1984. For 12b-c: The three vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation. KEY: TOTAL, all 9 species combined; *H.c., H. convergens; C.m., C. maculata;* and *H.p., H. parenthesis*.


JUN 15
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ALL ON
CAGES ON
CAGES OFF
C
TOTAL
H. c.
C. m.
H. p.
PERCENT OCCURRENCE
20
15
10
5
0
300
500
700
900
1100
1300
1500
DEGREE DAYS (> 10 °C)

Figure 12.

were probably negatively influenced by the rainy period that followed (1160-1250 DD_{10}, Figure 12a). The small peak toward the end of the trapping period (1250-1330 DD_{10}) coincided with a period of moderately high temperatures and low rainfall.

The visual count data for all species and time periods (A.M., NOON, & P.M.) were combined to produce a seasonal overview (Figure 13a). This graph did not readily complement the TOTAL curves for panel or can counts, because the latter represented mean catches over longer intervals. However, the visual overview revealed that the placement of 18 exclusion cages had a pronounced impact on this sampling method. Beetle numbers markedly dropped when all aphid-infested plants were caged and sharply rose after all plants were uncaged.

When plotted individually, trends for the three periods of the visual count did not differ greatly in general shape (Figures 14a-c). This similarity in trends suggests that the counts were not influenced by time of day. This was further supported by nonsignificant correlations of the counts with time of day ($p < 0.05$). In contrast to time of day, temperature had a slight influence on counts of *C. maculata* during the afternoon ($r^2 = 0.16$, $y = 0.24x - 4.9$) and evening hours ($r^2 = 0.16$, $y = 0.19x - 3.6$, where y = beetle numbers, x = temperature, °C). Overall, neither factor really demonstrated a significant association ($p < 0.05$) with beetle counts when analyzed for a single species or over all species combined.

The visual and can counts both ranked the same three beetle species as the most abundant: *H. convergens*, *C. maculata* and *C. transversoguttata* (Tables 6a & 7a). Although *H. parenthesis* frequently flew into the panel traps located at the edge of the plot, this species

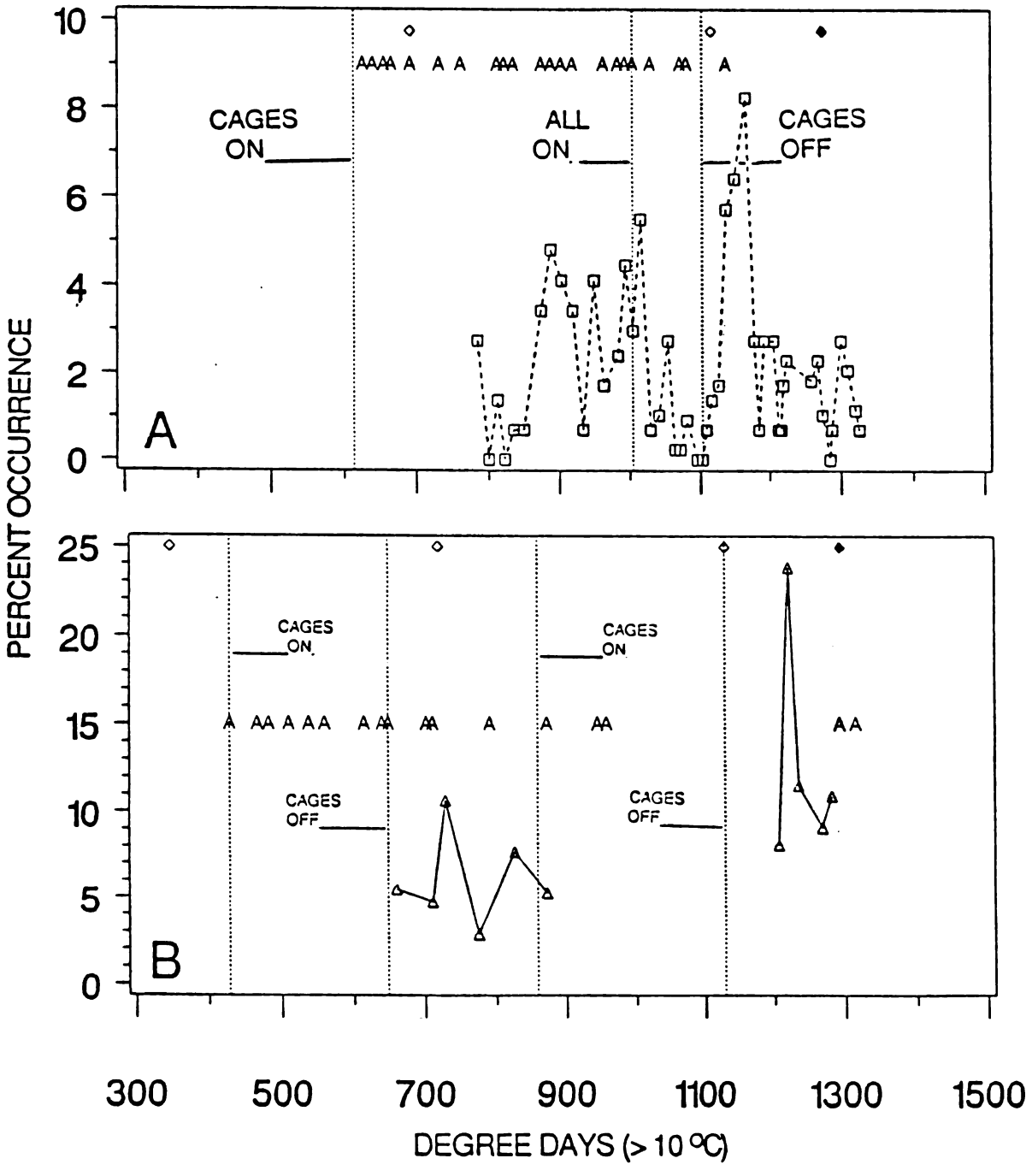

Figure 13. Visual counts of coccinellids for (A) 1984 and (B) 1985; all species and sampling times combined to produce seasonal overview. The vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation.

Figure 14. Visual counts of coccinellids for 1984 for three sampling times: A) 0730-1030 h, B) 1130-1300 h and C) 1530-1900 h. The two vertical bars mark the placement and removal of exclusion cages. KEY: TOTAL, all 9 species combined; *H.c.*, *H. convergens*; *C.m.*, *C. maculata*.

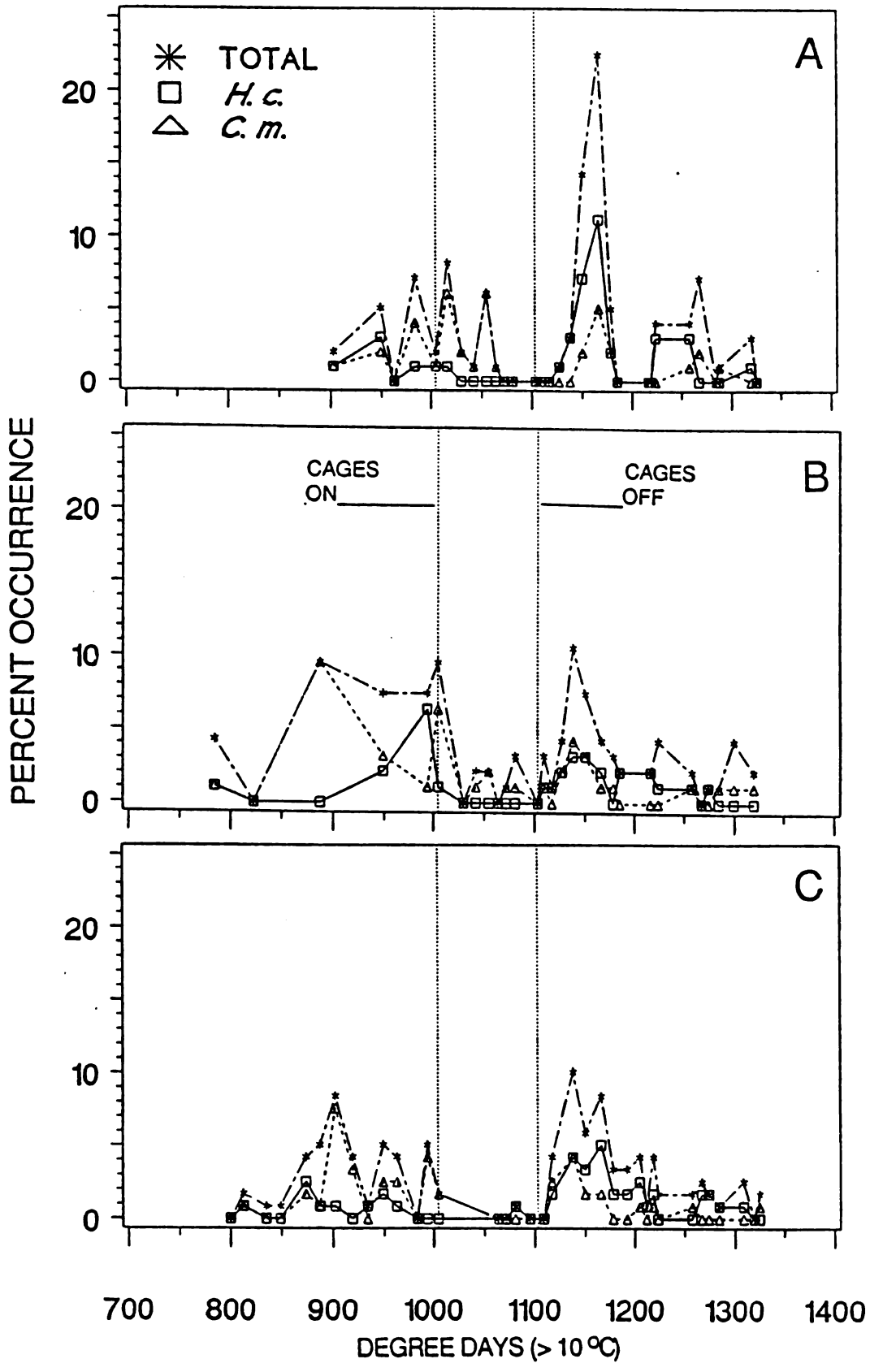
TOTAL
H. c.
C. m.
A
B
C
CAGES ON
CAGES OFF
PERCENT OCCURRENCE
0
10
20
700
800
900
1000
1100
1200
1300
1400
DEGREE DAYS (> 10 °C)

Figure 14.

was hardly present in samples that monitored beetle activity within the plot (cans) and on the asparagus fern (visual). This observation was supported by data from the exclusion trial (see Section III). Visual examinations of the 18 experimental plants showed that *C. maculata* and *H. convergens* were overwhelmingly the most abundant beetles on the aphid-infested plants (77.3% of total), followed by *C. transversoguttata* (10.8%). By comparison, *H. parenthesis* was rare--less than 1.0% of beetles observed.

1985 season.

Data for this season dramatically demonstrated how different the three sampling methods were in monitoring coccinellids as a group and by species. Though each method exhibited a unique seasonal trend for all species combined, comparisons of overall abundance were complicated by the influence of cage placement and removal (TOTAL, Figures 13b, 15, 16). In the extreme case, the walking visual counts were discontinued while the 20 cages were up because the structures partitioned the plot in a way that prevented a representative visual count (Figure 13b). For sticky-can curves, two of the three peaks occurred after the removal of exclusion cages (TOTAL, Figure 15c). Although cage manipulation regulated the availability of aphid prey and subsequently effected beetle movement in the plot, trap catches for cans and panels also increased while the predator barriers were in place during 900-1100 DD_{10} (TOTAL, Figures 15b&c). By selecting and caging a new group of plants for the second exclusion trial, we left exposed a large aphid population that was previously protected with pesticides and hand-removal of predators.

In addition to the association between cage manipulations and trap

counts, overall trends for total coccinellid catches were often shaped by the presence of 1 or 2 species. For example, the curve for FIPs reflected the appearance of a single species, *H. parenthesis* (TOTAL, Figure 15b). Other species added little to the dimensions of the curve (TOTAL, Figure 16a). The overall shape of the sticky-can curve was defined by the catch-all category "other" (Figure 16b). However, *H. convergens* was the single most common species for can traps because of its large presence late in the season (1250 DD_{10}, Figure 15c). Lastly, the trend for visual counts in all three time periods mirrored the abrupt appearances of *C. transversoguttata* during 650-850 DD_{10}, and was also dominated by the upsurge of *H. convergens* later in the season from 1200-1300 DD_{10} (Figures 17a-c).

Overall, a different species was indicated as the most abundant by the three survey techniques (Tables 6 & 7). This outcome strongly suggests that each method was sampling a different environment or habitat preference of individual species: interception panel--edge of plot; sticky can--between plants; and visual--within plant. In spite of a bias towards actively flying or crawling beetles, the methods adequately defined which beetle species were exploiting the aphid resource in the asparagus habitat. The 1984 and 1985 panel counts showed that *H. parenthesis* was abundant in the area but the sticky can and visual surveys indicated that this beetle was not equally active in or around the asparagus plants. This observation was also supported by visual counts of aphid-infested plants associated with the 1985 exclusion experiments (see Section III). *H. convergens* and *C. transversoguttata* were the most abundant species, making up 68% of the observations, followed by *C. maculata* at 12%. *H. parenthesis* comprised

Figure 15. (A) Daily rainfall and maximum-minimum temperatures during the study period, and coccinellid catch of most common species for (B) flight interception panels and (C) sticky-trap cans during 1985. For 12B-C: The four vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation. KEY: TOTAL, all 9 species combined; *H.c., H. convergens; C.m., C. maculata;* and *H.p., H. parenthesis.*

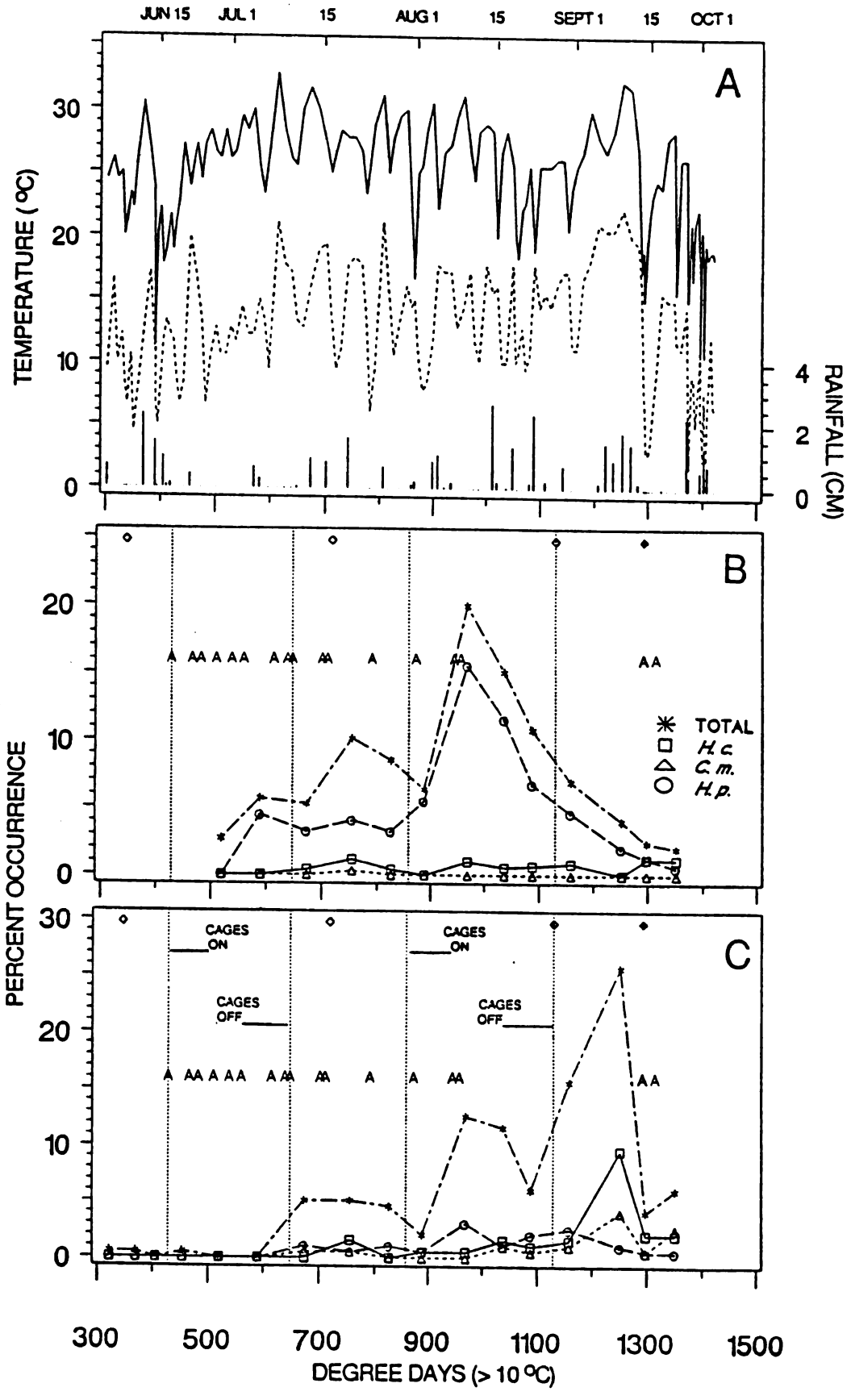
JUN 15
JUL 1
15
AUG 1
15
SEPT 1
15
OCT 1
A
TEMPERATURE (°C)
RAINFALL (CM)
B
PERCENT OCCURRENCE
TOTAL
H.c.
C.m.
H.p.
C
CAGES ON
CAGES OFF
CAGES ON
CAGES OFF
DEGREE DAYS (> 10 °C)

Figure 15.

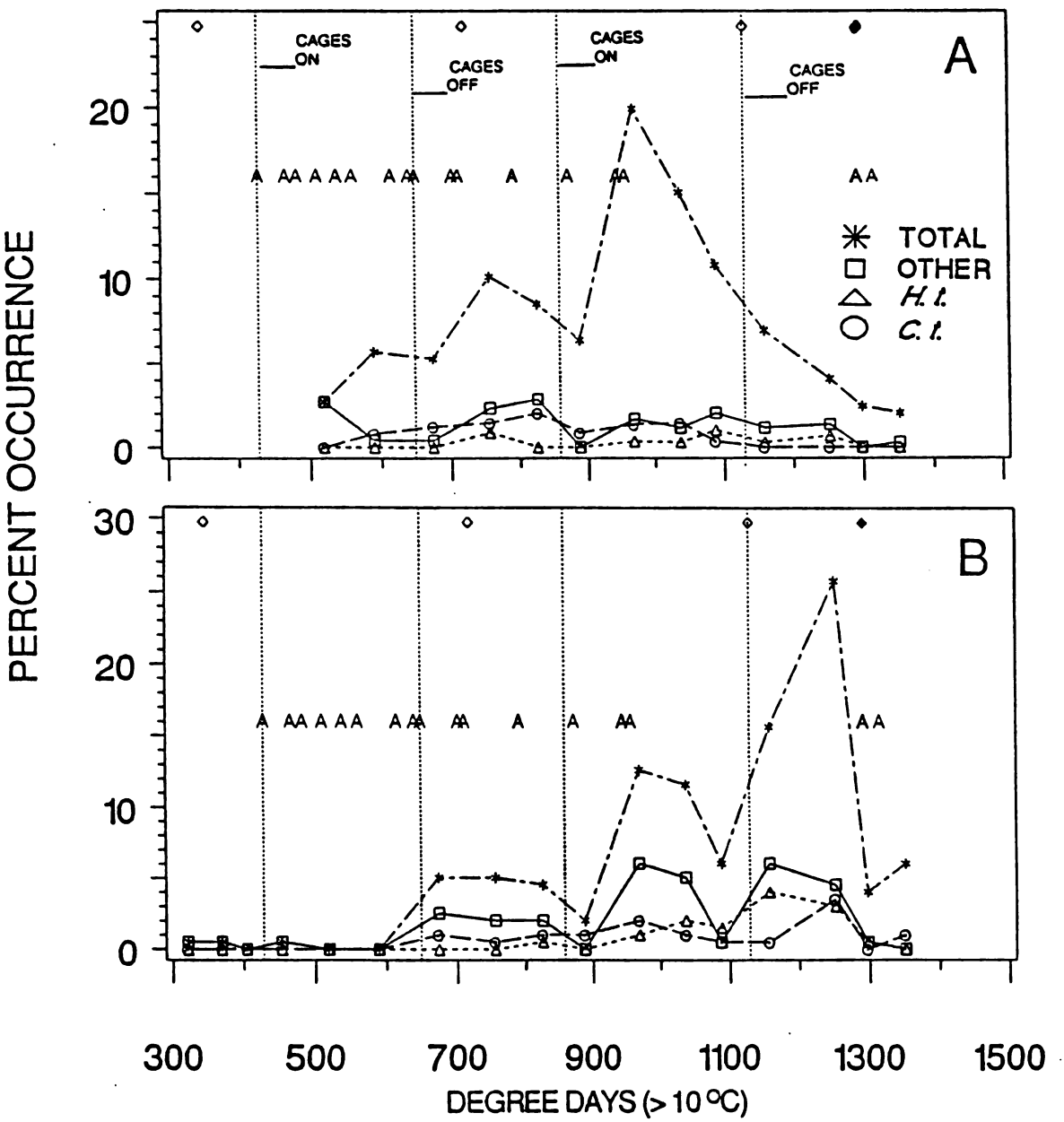

Figure 16. Coccinellid catch of less abundant species (see Table 7) for (A) flight interception panels and (B) sticky-trap cans during 1985. The vertical bars mark the placement and removal of exclusion cages. The small diamonds at the top indicate cutting times for alfalfa (open) and corn (shaded) plantings near the plot. The symbol "A" indicates time of aphid infestation. KEY: TOTAL, all 9 species combined; OTHER, 4 miscellaneous species combined (see Table 7); *H.t., H. tredecimpunctata; C.t., Coccinella transversoguttata.*

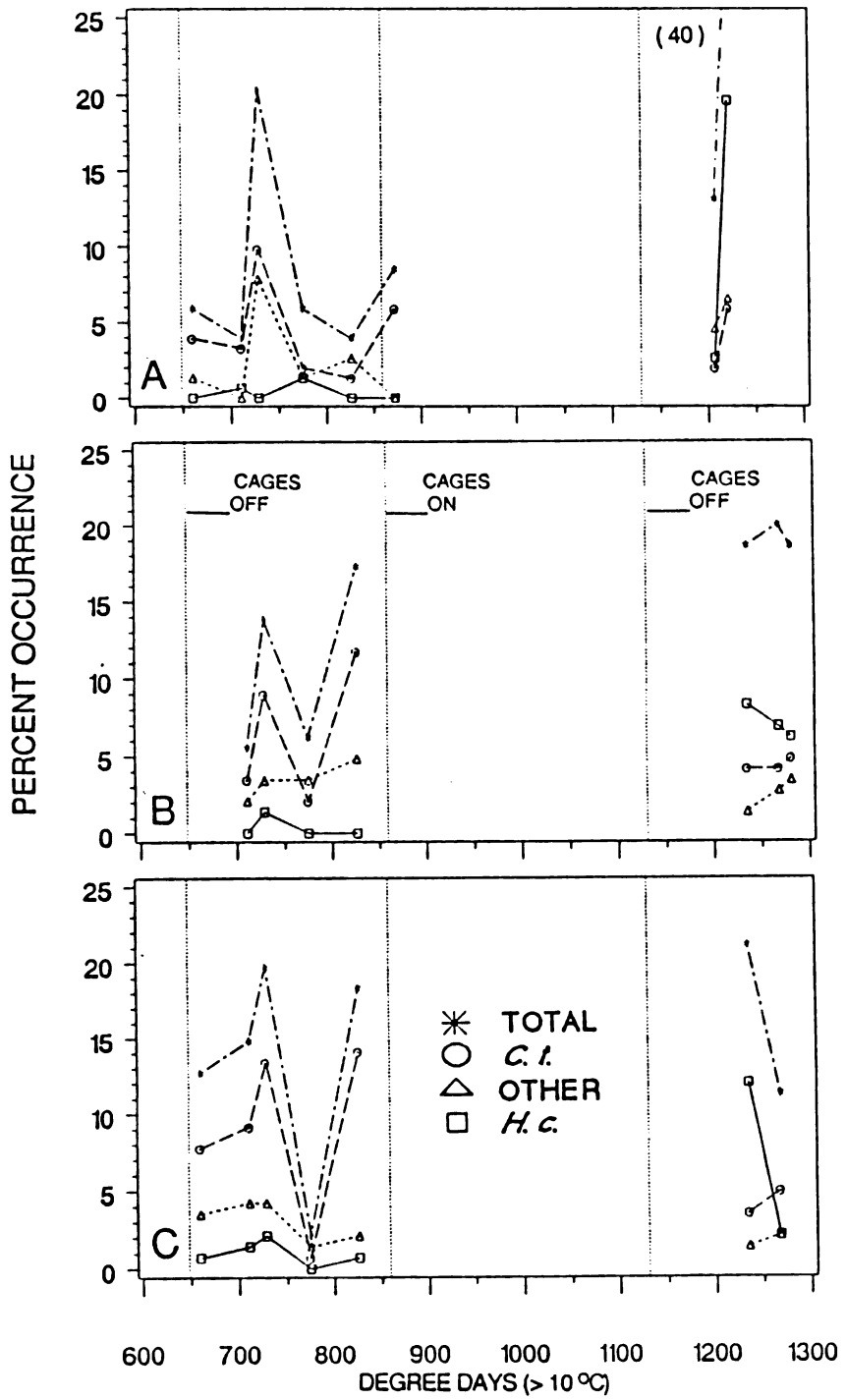

Figure 17. Visual counts of coccinellids for 1985 for three sampling times: (A) 0930-1100 h, (B) 1300-1500 h and (C) 1600-2000 h. The three vertical bars mark the placement and removal of exclusion cages. KEY: TOTAL, all 9 species combined; OTHER, 4 miscellaneous species combined, see Table 7; *H.c., H. convergens; C.t., C. transversoguttata.*

about 3.6% of the total beetles sighted.

As suggested for the 1984 visual counts, temperature, and not time of day, exerted some influence on numbers observed. Significant correlations of counts with time of day varied by species: *C. maculata* in A.M. ($r^2 = 0.65$, $y = 0.20x - 3.5$) and *C. transversoguttata* at noon ($r^2 = 0.34$, $y = 0.74x - 15.4$, where y = beetle numbers, x = temperature, °C, $p < 0.05$). When compared to August, the higher temperatures experienced in September probably increased beetle activity and, therefore, encounters with sticky-can traps (1150-1300 DD_{10}, Figure 15a).

Note. Several authors have noted the expanding North American distribution of the introduced lady beetle *Coccinella septempunctata* L. (Angalet et al. 1979, Cartwright et al. 1979, Hoebeke & Wheeler 1980, Tedders & Angalet 1981). Due to its initial rarity in our asparagus plots, it was lumped into the catch-all category "other" with five other beetles species (Tables 6&7). Sighted about 5 times in 1983, *C. septempunctata* was relatively common in Ingham Co. by 1985 with over 30 beetles showing up in a visual count of individual plants--a survey connected to the exclusion study (See Section III). This observation was included in the most recent article on this beetle's range (Schaefer et al. 1987).

DISCUSSION

Angalet & Stevens (1977) commented that no natural enemies of *B. asparagi* were introduced into the United States with the aphid. Therefore, the nonpest status of this aphid in New Jersey, Delaware and Michigan can be attributed to the impact of native beneficial organisms.

While our study and that of Angalet & Stevens agreed on the basic components of the natural enemy complex in asparagus, there were differences in species abundance and composition.

Much of the discussion on abundance, composition and population trends was closely linked to sampling methodology. First, the results suggest that the survey techniques were redundant because all three primarily detected flying or actively moving adult predators. However, we selected each method to monitor a specific group of natural enemies: flight interception panels to catch parasitoids more effectively than sticky cans; walking visual counts to reveal immature stages in a nondestructive manner; and yellow can traps to monitor winged asparagus aphids. In practice none of the procedures sampled immature insects or the fungal pathogen, and all three methods were inadequate in detecting parasitoids or winged asparagus aphids. A recent study indicated that yellow pan traps were ineffective for monitoring asparagus aphid activity in the field in spite of the apparent attractiveness of yellow demonstrated in a color preference test (Halfhill et al. 1987). This fact may have explained the lack of asparagus aphids on our yellow can traps.

The underlying theme of this sampling effort was to efficiently and accurately characterize the most abundant natural enemies of the asparagus aphid. We noted the substantially different information each sampling technique provided on coccinellid abundance and population trends by species. Comparisons of sampling schemes in other crops have demonstrated specific methods to be more efficient in sampling predator groups, i.e. nabids, chrysopids and coccinellids, but little information was provided at the species level (Bechinski & Pedigo 1982, Garcia et

al. 1982, Herbert & Harper 1983 and Shepard et al. 1974).

The ability to equally monitor all members of a predatory family becomes important when the sampling method fails to detect the most abundant species of that group. For example, flight traps like our sticky cans are a common sampling method. Using this technique alone we could argue that *H. convergens* and *C. maculata* were consistently the most numerous and active beetles in the plot during 1983-1985 and subsequently list them as the primary coccinellid predators of the asparagus aphid. Based on the data from flight interception panels, *H. parenthesis* was convincingly the most abundant beetle during 1984-1985. However, visual observations indicated that *C. transversoguttata* was also a major aphid predator of greater significance than revealed by either flight trap.

The concept of sampling a natural enemy "group" or family rather than species within that group has certain applications and limitations. The differences detected in this study resulted from the fact that coccinellids were relatively easy to count and identify, and some species displayed different behaviors and habitat preferences. Individuals of other families, like Syrphidae, are more difficult to trap and identify to species even with the appropriate taxonomic aids. The effort may not be warranted when the group is not important to biological control or is represented by a few species.

As another factor for consideration, several studies have examined the best time of day for sampling coccinellids. Mack & Smilowitz (1979) found that *C. maculata* and *C. transversoguttata* were captured in greatest abundance by sticky traps in potato fields during two sampling periods; 0900-1300 and 1300-1700 hours. Mack & Smilowitz (1980)

recommended 0900-1115 hours as the least variable period for sampling *C. maculata* with sweep net or groundcloth in potatoes. Dumas et al. (1962) reported that *C. maculata* numbers in soybean were not significantly different at various times of day either with sweep-netting or plant examinations; but results were inconsistent. No correlation with temperature, cloud cover or humidity could be discovered in that study. In agreement with Dumas, no time stood out as best for visual counts in our study.

Rather than time of day, our data suggested that temperature could be a more important factor when surveying certain species. This observation attains greater meaning when temperature corresponds to beetle movement, especially for traps that specifically catch actively flying insects or visual methods that rely on motion for meaningful detection in dense foliage. Frazer & Gilbert (1976) showed that the number of *C. trifasciata* observed moving during visual counts in alfalfa increased steadily with temperature. After establishing and sampling known quantities of beetles in field cages, the authors also stated that their visual sampling techniques never revealed more that 25% of the true numbers, even at high temperatures (>28°C). Beetles spent most of their time down in the stubble, unobserved. Frazer & Gill (1981) linked beetle movement to other factors such as hunger and circadian rhythm. They determined that beetles encountered in samples like a visual count are mainly hungry; satiated beetles are not encountered. In a study that estimated coccinellid numbers and movement in the field, Ives (1981) concluded that the predominant controller of beetle movements, besides prey density, was temperature. For flight traps, the author reported a positive relationship between numbers caught and temperature.

ARTICLE 2

The impact of coccinellids, aphidiid parasitoid and entomophthoralean fungus on the asparagus aphid, *Brachycorynella asparagi* (Mordvilko), assessed with exclusion-inclusion techniques.

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ABSTRACT

This study assessed the impact of individual natural mortality factors on the asparagus aphid, *Brachycorynella asparagi* (Mordvilko), through exclusion-inclusion techniques. A combination of pesticides and cages were employed in the field to enhance or limit the effect of one group of natural enemies over another. The mortality agents included coccinellids *Hippodamia convergens* Guerin and *Coccinella transversoguttata richardsoni* Brown, aphidiid parasitoid *Diaeretiella rapae* (M'Intosh) and fungal pathogen *Entomophthora planchoniana* Cornu. The nondestructive sampling strategy associated fluctuations in aphid numbers with the presence of the pathogen, parasitoid and predators at the plant and colony level. Aphid mortality was determined by counting tagged aphid colonies *in situ* and calculating their finite rate of increase.

The physical barrier experiment used a cage-fungicide combination to include and exclude natural enemies. The fungal pathogen was most effective in lowering aphid population growth rates in the cages as

compared with the introduced parasitoid and coccinellid. High aphid numbers occurred when the maneb fungicide was used to suppress the pathogen. Results suggested that, after a gradual build-up of their own numbers, aphidiids and coccinellids also had the potential to influence the rate of increase of even very high aphid populations.

For the chemical exclusion trial, maneb fungicide and carbaryl insecticide were used to control specific groups of natural enemies. The chemical treatments did not produce differences as well defined as those demonstrated for the cage study. Of the three agents, only the pathogen substantially reduced aphid numbers. Plants receiving both pesticides consistently supported high aphid numbers while untreated plants had low aphid populations and high levels of each mortality agent. A clear distinction between the impact of abiotic (wind and rain) and biotic factors was not provided by the treatments in this experiment.

KEY WORDS: *Brachycorynella asparagi* (Mordvilko), cage exclusion-inclusion methods, chemical exclusion methods, finite rate of increase, Coccinellidae, Aphidiidae, *Entomophthora*.

INTRODUCTION

The asparagus aphid, *Brachycorynella (=Brachycolus) asparagi* (Mordvilko), was first reported in Michigan in 1980 (Grafius 1980). It is not considered a pest in commercial plantings of asparagus (*Asparagus officinalis* L.) in this state or several eastern states--New Jersey, Delaware and Maryland (Hendrickson 1986). The aphid is a pest in Washington State (Cone 1986) and California (Ball 1986), causing substantial damage (Anonymous 1980) and requiring chemical control

(Thornton et al. 1982).

Angalet and Stevens (1977) surveyed New Jersey and Delaware for natural enemies of the asparagus aphid; we conducted a similar study in Michigan (See Section II). Both studies listed a diverse number of predators as well as a parasitoid and fungal disease, and concluded that the native natural enemies were responsible for the control of this introduced aphid. Our work suggested that a complex of four coccinellid species (*Hippodamia convergens* Guerin, *H. parenthesis* [Say], *Coleomegilla maculata lengi* Timberlake and *Coccinella transversoguttata richardsoni* Brown; Coleoptera: Coccinellidae), a parasitoid (*Diaeretiella rapae* [M'Intosh]; Hymenoptera: Aphidiidae) and a fungal disease (*Entomophthora planchoniana* Cornu; Entomophthorales: Entomophthoraceae) were the most important natural enemies of this aphid. Other predators included members of the following families: Anthocoridae, Chrysopidae, Hemerobiidae, Nabidae, Syrphidae and Cecidomyiidae.

The objective of this study was to assess the impact of individual natural mortality agents on the asparagus aphid through exclusion-inclusion techniques. A combination of pesticides and cages were employed to enhance or limit the effect of one group of natural enemies over another. We also used a nondestructive sampling method so that tagged aphid colonies could be followed over time. Instead of assessing aphid populations with measurement criteria such as aphids per unit area (leaf or plant) or unit effort (50 sweeps of net), the finite rate of increase (Tamaki et al. 1981a) for individual aphid colonies was used to detect the impact of mortality factors.

MATERIALS AND METHODS

PLOTS.

The study was conducted in two 5-year-old asparagus plantings (variety Mary Washington) located at Michigan State University (MSU) Botany & Plant Pathology Field Laboratory, about 2 km from the main campus in East Lansing, Michigan. The plots, A and B, measured 14.6 by 38.0 m with 10 rows of 30-45 plants per row and were situated 50 m apart. Located in a 10 ha block of the agricultural research facility (ca. 660 ha), these test fields were bordered by small plots of vegetable and field crops as well as fallow areas. Large plantings of alfalfa and corn occurred within a 1 km radius of the plots.

Both plots were fairly weedy, with grasses being predominant. Herbicide (sethoxydim or glyphosate) was applied once before the spears emerged in May-early June. Thereafter, weed control was done with rototiller and hoe. Plant debris from the previous year was not removed from the plots to preserve any overwintering aphid eggs that occurred on the stems. The plot was lightly harvested (1-2 weeks) and then the spears were allowed to elongate and fern out.

EXPERIMENTAL UNITS.

Several qualitative and quantitative assessments were made for each asparagus plant in the plots after plants ferned out in mid- to late-June. Based on factors of height, number of stems per crown, sex, and degree of fern bushiness, 25-40 of the most uniform plants were identified. To reduce the edge effect, no plants were selected if they were located within 2 m of the perimeter. This procedure excluded the

outside two border rows and the first 3-4 plants on the row ends. Treatments were randomly assigned to plants from this uniform group.

Experimental plants were artificially infested to produce suitable populations because the asparagus aphid was relatively rare in the plots. Aphids were reared in a greenhouse and in growth chambers. Later in the season aphids were also taken from another asparagus plot. Aphid-laden branches were placed in the fern of experimental plants, forcing aphids to disperse as the branch dried. Except where noted below, the experimental plants were caged to promote aphid buildup by reducing or eliminating the impact of natural enemies.

Occasions arose when new plants were selected and infested as replacement experimental units. In some cases aphids reached such high numbers that they substantially reduced plant vigor. Other times aphid numbers dropped to such low levels that the plant was useless as a treatment replicate. Additional infestations were conducted throughout the season to maintain aphid populations at suitable levels.

When aphid populations reached moderately high densities on all the experimental plants, aphid colonies were tagged. The selection of a colony was not statistically randomized in the strictest sense. Only colonies located on the tips of branches and possessing between 20-100 individuals were selected. Since aphids were counted *in situ*, colonies located on the growing tips were the most accessible to counting and manipulation without great disturbance. The acceptable size for initial selection was based on considerations for: counting errors associated with colony size above 100 aphids; unaccountable dispersal of alates that results with crowded conditions; theoretical threshold level when colony becomes "visible" to natural enemies; immigration; and assorted

incongruities associated with colonies below 20 individuals.

Aphids were only counted along a 6 cm stem length, and each colony distinctly labelled and numbered. A new replacement colony was selected for the following reasons: 1) when no living aphids were present to be counted, 2) when colony numbers moved out of the theoretical working range of 10-150 aphids, 3) when all or a majority of the living aphids died due to parasitism or disease, 4) when the branch broke or became overly stunted from aphid feeding as to hinder the ability to see aphids in the twisted growth and 5) when counter disturbed the colony to the point where a majority of the individuals began to leave the stem.

Data on daily maximum and minimum temperatures and precipitation were collected at the MSU Horticultural Research Center, located 2.25 km from the test plots. Since the limitations associated with the use of cages to exclude natural enemies include microhabitat modification (Smith & DeBach 1942), temperature and relative humidity readings were also compared. A micrologger (model CR-21, Campbell Scientific Inc., Logan, Utah) was used to record these conditions over six time periods for both years. In 1984 temperature and relative humidity (RH) probes were situated inside and outside of a selected cage. The RH probes were placed inside a ventilated white can (20.3 by 28 cm) that was elevated (25 cm) on a stake because the device required protection from rain. Temperature probes were located at the base of the protective cans. In 1985 additional measurements were taken with a sling psychrometer (Bacharach Instruments, Pittsburgh, PA) and hygrometer (Watrous, Garden City, NY) to check against the micrologger RH readings.

PESTICIDE SELECTION AND TESTING.

We required pesticides that demonstrated the potential to reduce or eliminate the impact of predators, parasitoids or disease without harming the asparagus aphid. Two chemicals, maneb and carbaryl, were chosen from those recommended for common asparagus pests (Grafius et al. 1983). The fungicide maneb is used to control rust (*Puccina asparagi* D.C.) while the insecticide carbaryl is applied for the common asparagus beetle, *Crioceris asparagi* (L.), and 12-spotted asparagus beetle, *C. duodecimpunctata* (L.).

Carbaryl is not recommended as a good material for aphid control in vegetable crops (Grafius et al. 1983), but was reported as toxic to most natural enemies at field rates (Bartlett 1963, 1964). A review of the product label revealed that very few aphid species are listed as potential targets for this compound in vegetable crops (1983 Chemical Guide, 1983). The specific impact of maneb on target and nontarget organisms is unclear. Several authors demonstrated its activity against entomopathogenic fungi that attack aphids (Boykin et al. 1984, Hall & Dunn 1959, Nanne & Radcliffe 1971 and Soper et al. 1974). Others reported maneb and related products (zineb and mancozeb) as nontoxic to nontarget animals (Bartlett 1963, 1964 & 1968, Boykin et al. 1984, Felton & Dahlam 1984, McMullen & Jong 1971).

Test solutions of commercial grade carbaryl (80% wettable powder) and two maneb products (flowable formulations with 0.479 kg [AI]/l) were developed around the recommended field rates for asparagus pests (0.907 kg and 1.09 kg [AI]/0.405 ha, respectively) and an application rate of 113.55 l/0.405 ha (30 gpa). The 50% lethal concentrations (LC_{50}) for both compounds were initially determined in the laboratory for target

and nontarget organisms with subsequent field evaluations of the selected dose level. We used a residual method on adult coccinellids and parasitoids and the slide-dip method for the aphid (see Appendix C). Pesticides were not screened against the pathogen because the fungus could not be cultured on artificial media.

Laboratory tests produced LC_{50} values in terms of percent solutions that originally corresponded to recommended field rates in units per hectare (Table 8). These concentrations were not directly applicable because we were using a hand-held sprayer to treat individual plants (see Appendix C). Therefore, selected rates were adjusted to maintain the dose relationship at the plant level based on a volume of liquid that adequately covered the dense fern (150 ml) and the approximate area of a single plant (0.8364 m^2). The resulting percent solutions in the sprayer were: 0.0156% for carbaryl (0.0907 kg [AI]/0.405 ha) and 0.156% for maneb (0.545 kg [AI]/0.405 ha).

CHEMICAL EXCLUSION EXPERIMENT, PLOT A.

In 1984, plot A received the first four treatments listed in Table 9. Four plants were assigned to a treatment and seven colonies per plant were tagged. In 1985, plot A received all five treatments and the experiment was run twice. The first run was conducted with four plants per treatment and the second with three plants, each with seven marked colonies per plant.

As the primary deterrent to natural enemies, cages (1.83 by 1.83 by 1.83 m with 20 mesh per 2.54 cm) were used only on the plants designated to receive the nonchemical control treatment. Selected pesticide doses were used to exclude the natural enemies from the other

TABLE 8. Toxicity of pesticides to the asparagus aphid and several of its natural enemies.

Pesticide[a]	Insect[b] (source)	*n*[c] (ctrl)	Time[d]	LC_{50}[e] (% sol)	95% CL[f] (upper-lower)	Slope±SE
carbaryl	aphid(L)	687(197)	24	0.49	0.33-0.79	1.025±0.165
maneb(M)	aphid(L)	311(101)	24	NSM[g]	--	--
maneb(M)	aphid(F)	311 (90)	24	NSM	--	--
maneb(D)	aphid(L)	367(108)	24	0.55	0.375-0.72	2.82±0.525
maneb(D)	aphid(F)	316 (91)	24	9.50	2.30-**	0.65±0.355
carbaryl	beetle-1(F)	231 (61)	12	NSM[h]	--	--
carbaryl	beetle-2(F)	50 (10)	12	0.003	0.00025-0.01	1.65±0.631
maneb(M)	beetle-2(F)	90 (15)	12	NSM	--	--
carbaryl	braconid(F)	210 (60)	12	0.0475	0.02-0.081	1.632±0.344
maneb(D)	braconid(F)	240 (71)	24	NSM	--	--

[a] Carbaryl, Sevin 80S, Union Carbide; maneb(M), Manex 4F from Griffin Ag Products Co. Inc.; maneb(D), Dithane FZ from Rohm & Haas Co.

[b] Insect: aphid, *B. asparagi*; beetle-1, *C. maculata* and *H. tredecimpunctata*; beetle-2, *H. convergens*; aphidiid, *D. rapae*. Source: L, laboratory, i.e. specimens reared in a growth chamber or greenhouse; F, field-collected specimens.

[c] Total individuals and number in control treatment.

[d] Hours from start when mortality data was collected.

[e] LC_{50} expressed as percent solution. A 1.0% carbaryl solution equalled recommended field rate of 0.907 kg (AI)/0.405 ha; 2.0% maneb solution--1.09 kg (AI)/0.405 ha. Application rate of 113.55 l water/0.405 ha (30 GPA).

[f] LC_{50} calculated by a computer program (PROBITANALYSIS) that employed Abbott's correction.

[g] NSM, no significant mortality at highest dose tested.

[h] Coccinellid mortality was 92.5% at lowest dose level--0.01%.

treatment plants during infestation. Since the uncaged plants did not develop high populations when compared to the caged plants, all plants were caged. After aphids reached suitable levels, all cages were removed and treatments were applied.

Pesticides were applied to individual treatment plants with a hand-held, six-liter sprayer. Each plant received 150 ml of liquid, a 16-17 second spray at 1.37 kg/cm^2 (20 psi), which corresponded to a field rate of 725.8 l/0.405 ha (192 gal/A). The entire plant could be covered with this quantity without reaching the point where the excess dripped off. For maximum effectiveness, the fungicide was applied every 4-5 days while the insecticide was applied every 2-3 days. This schedule was often altered by severe weather conditions and pesticides were reapplied within one day after a heavy rain. White cloth sheets were placed on the ground below the fern to detect the presence of aphids or natural enemies dislodged after pesticide applications, and to control weeds. Natural enemies were also removed every 1-2 days by hand from treatments that received carbaryl. Field doses were sufficient to incapacitate adults and larvae of beneficial insects, knocking them from the fern, but they were too low to provide significant residual protection against later immigration.

The shelter treatment was added in 1985 (SHELTER, Table 9). A metal frame (1.2 by 1.2 m) was erected around the plant and a large screen cage was placed over the frame, leaving the two downwind sides open. The cage (1.83 by 1.83 by 1.83 m, 20 mesh per 2.54 cm) was doubled over onto itself so that the top and two sides provided protection from heavy rain and wind. This treatment also received both pesticides.

We theorized that high, artificially-induced aphid numbers would decrease due to predation, parasitism and disease. Extremes in weather were also recognized as important mortality factors. However, climatic events, specifically heavy windstorms and rainstorms, are difficult to control or evaluate. For the chemical exclusion experiment, pesticide applications subtracted or reduced specific mortality agents, allowing others to operate at normal levels. For example, the fungicide treatment reduced disease, leaving predators and parasitoids as the major mortality agents (PRED&PAR). Conversely, the insecticide treatment promoted disease as a factor by removing the predator-parasitoid complex (DIS). The combination of fungicide and insecticide eliminated all biotic agents so that any aphid mortality could be attributed to weather extremes (NONE+W). Untreated plants were the control upon which all mortality agents acted without chemical interference (NOCHEM). Since weather could exert a substantial impact on aphid numbers, treatment SHELTER was added to detect the effect of an abiotic agent that included many components: temperature, relative humidity, wind, rain, light and others. [NOTE: Treatment abbreviations emphasized the mortality factors active and not the chemical applications; see Table 9 for abbreviations.]

We anticipated that treatments NONE+W and SHELTER would produce the highest aphid numbers while aphids on the untreated control, NOCHEM, would be decimated by all mortality agents combined. Treatments that employed fungicide (PRED&PAR) or insecticide (DIS) alone would fall in between these two groups depending on the occurrence of predators, parasitoids and pathogen. If a mortality agent was not present at a given time, then the treatment selected to reduce its impact had little

Table 9. Treatments for CHEMICAL EXCLUSION experiments (Plot A) and mortality agents promoted by the treatment.

TREATMENT	MORTALITY AGENTS ACTIVE	CODE[a]
1. Untreated control	ALL NATURAL ENEMIES & WEATHER	NOCHEM
2. Fungicide[b]	PREDATORS, PARASITOIDS & WEATHER	PRED&PAR
3. Insecticide[c]	FUNGAL PATHOGEN & WEATHER	DIS
4. Fungicide & Insecticide	WEATHER ONLY	NONE+W
5. Fungicide & Insecticide & Shelter[d]	NONE (WEATHER REDUCED)	SHELTER

[a] Abbreviations for terms that were used in text.
[b] 150 ml/plant of a 0.156% maneb solution (0.545 kg [AI]/0.405 ha).
[c] 150 ml/plant of a 0.0156% carbaryl solution (0.0907 kg [AI]/0.405 ha)
[d] The shelter was a mesh cage suspended over the plant on a frame; two sides were left open.

Table 10. Treatments for PHYSICAL EXCLUSION experiments (Plot B) and mortality agents promoted by the treatment.

TREATMENT[a]	MORTALITY AGENTS ACTIVE	CODE[a]
1. Uncaged & Untreated	ALL AGENTS & WEATHER	NOCG-ALL
2. Uncaged & Fungicide & Insecticide	NONE, WEATHER ONLY	NOCG-NONE
3. Caged & Fungicide	NONE, WEATHER ONLY	CG-NONE
4. Caged & Untreated	FUNGAL PATHOGEN & WEATHER	CG-DIS
5. Caged & Fungicide & Coccinellids	COCCINELLIDS & WEATHER	CG-COCC
6. Caged & Fungicide & Aphidiids	APHIDIIDS & WEATHER	CG-PAR

[a] See Table 9 for detailed explanations of treatments and code.

comparative meaning.

PHYSICAL EXCLUSION EXPERIMENT, PLOT B.

In 1984 and 1985, plot B received six treatments (Table 10). Three plants were randomly assigned to a treatment for a total of 18 plants. Twelve colonies were tagged per plant in 1984, eight--in 1985.

The chemical exclusion experiment relied upon pesticides to control natural enemies. This study employed both exclusion approaches, but physical barriers were the most important method. Cages were custom made from material that prevented all types of natural enemies from penetrating from outside or escaping after introduction--Saran (52 mesh per 2.54 cm) on top and two sides, and nylon organdy on the other two sides. Cages (1.83 tall by 0.914 by 0.914 m) were supported by aluminum frames erected around plants. Access was achieved through two corner flaps secured with velcro strips. The two uncaged treatments (NOCG-ALL and NOCG-NONE, Table 10) were handled similar to NOCHEM and NONE+W of the chemical exclusion trial (Table 9). Pesticides were applied to treatment NOCG-NONE as described for the chemical barrier study. [NOTE: Treatment abbreviations emphasized the presence or absence of cages (CG-, NOCG-) and mortality factors active (-ALL, -NONE, -DIS, etc) and not the chemical applications. See Table 10 for abbreviations.]

The cage mesh did not exclude the fungal pathogen. Resting spores of *Entomophthora* species are often the overwintering stage of the fungus and can be present in the soil or aphid cadavers (Wallace et al. 1976, Payandeh et al. 1978). Since spores were probably present throughout the entire plot, no inoculum of the pathogen was introduced into the cages. Therefore, untreated plants served as the disease

treatment (CG-DIS, Table 10) whereas the pathogen was regulated in other treatments with the fungicide maneb.

Aphidiid parasitoids, *D. rapae*, were reared from aphid mummies collected in the field. In 1984, newly emerged adults were sexed and groups of each sex were introduced into the aphidiid treatment cages (CG-PAR), placed at the base of the fern. The introductions per cage for 1984 were: 18 of both sexes on August 6 (Julian Date 219), 8 of both sexes on September 1 (JD 245), and 7 males and 10 females on September 4 (JD 248).

In 1985, the parasitoids were introduced in larger numbers without consideration for sex ratios. One hundred aphidiids per cage were introduced on July 30, August 1 and 6 (JD 211, 213 & 218), and 200 per cage on August 12 (JD 224). The random assignment of treatments was violated in 1985 because two cages already contaminated with modest numbers of *D. rapae* were deliberately assigned to the parasitoid treatment. Therefore, parasitoids were considered active in these treatments from the onset of the experiment.

Based on our 1983 flight trap survey, *H. convergens* was one of the most abundant coccinellid in asparagus (see Table 6a, Section II). In 1984 we collected *H. convergens* adults from nearby alfalfa (*Medicago sativa* L.) fields for introduction onto the coccinellid treatment plants (CG-COCC). For the first two introductions on August 6 and 15 (JD 219 & 228) five beetles of each sex were placed in a cage at the fern base. Attempts to mark the elytra with paint proved unreliable because the spots regularly fell off. Since the sexes could not be marked and it was difficult to capture and replace all beetles in a cage, we no longer emphasized equal sex ratios. Instead, beetles were added to maintain a

specific population level. On August 25 (JD 238) six beetles were added to two plants to reset the total observed number for this treatment at ten per plant. On September 2 (JD 246) ten beetles were added to one plant so that each plant had 15 adults. Also, all beetle larvae were removed up to August 15 (JD 228) because they could not be specifically attributed to the introduced coccinellids.

The beetle *H. convergens* occurred in relatively low numbers during July and August of the 1985 season (see Figures 15b-c, 17a-c, Section II). Since this species could not be collected in adequate quantities to start the exclusion experiment, the comparatively more abundant *C. transversoguttata* was substituted as the introduced species. Initially, 15 beetles of mixed sex were put in each coccinellid treatment cage on July 30 (JD 211). Beetles were removed and added to produce a variable sex ratio and relatively similar population level across all plants. Subsequent introductions were made to maintain population levels between 20-40 individuals per cage, as follows: August 3 (JD 215)--20 in one cage, 5 in the other two for 20 per cage; August 8 (JD 220)--10 in one cage, 20 in the others for 20 per cage; August 12 (JD 224)--20 in all cages for 20 per cage; August 18 & 23 (JD 230, & 235)--30 in all cages for 40 and 30 per cage, respectively.

There were other differences in experimental procedure by year in addition to the variations on quantity or species placed in the cages. For example, in both years natural enemies were removed by hand from cages where they did not belong. Emerged mummies were also removed daily from tagged colonies in the aphidiid treatment (CG-PAR) in 1984 and percent parasitism was determined by counting only 'intact' mummies, i.e. adult not yet emerged. No mummies were removed in 1985; all were

included in the calculation. Also in 1984, the mean number of aphids and mummies per growing tip were estimated with a stratified destructive sampling scheme. Thirty tips were selected for counting on August 14 and 21, and September 5, 14 and 27 (JD 227, 234, 249, 258, and 271). The data was analyzed and reported elsewhere by Hayakawa (1985).

By comparison to the chemical barrier experiment, this study relied upon both additive and subtractive treatment effects. The combination of cages and fungicide subtracted predators, parasitoids and pathogens. Starting with an aphid-infested plant devoid of natural enemies, we then added or permitted the expression of specific agents so that any reduction in aphid numbers could be attributed to the agent. Plants of the caged & fungicide treatment were protected from all three biotic agents (CG-NONE) while a caged & untreated plant was only exposed to the omnipresent spores of the fungal pathogen (CG-DIS). Cages forced the introduced aphidiids (CG-PAR) and coccinellids (CG-COCC) to utilize the monitored aphid population within as a resource. The two uncaged treatments, NOCG-ALL and NOCG-NONE, were expected to produce results similar to NOCHEM and NONE+W of the chemical exclusion experiment. We also assumed that the weather component was comparable for each cage.

SAMPLING METHODS.

OVERVIEW. The objective of this study was to assess the impact of individual mortality factors on the asparagus aphid. This goal required a sampling strategy that could associate fluctuations in aphid numbers with the presence of the pathogen, parasitoid and predators. As an additional constraint, the process had to preserve scarce plant and aphid resources, i.e. be nondestructive. Our methods were developed

around the following biological properties of the sampled populations: 1) asparagus aphids remained very near the spot where they were larviposited to form well defined colonies, usually located on branch tips; 2) parasitoids produced conspicuous mummies; 3) pathogen produced brown cadavers and 4) predators left almost no trace of consumption, therefore we had to associate their numbers with predatory activity.

Only a small number of the growing tips with aphid colonies could be monitored because of the time involved with counting aphids *in situ*. To ensure that colony counts detected real trends for all groups, i.e aphid, predator, pathogen and parasitoid, we also monitored these populations at the plant level. Except for predators, we effectively had two sampling techniques for each group. The descriptive methods were as follows:

Aphids.

FINITE RATE OF INCREASE (FRI). The primary sampling statistic for determining the impact of natural enemies on aphids comes from the work of George Tamaki and his fellow researchers. The use of exclusion techniques, especially cages, and the search for a method of describing the impact of the predator complex on prey populations were major themes in many of Tamaki's articles (Tamaki & Weeks 1972, 1973; Tamaki 1973; Tamaki et al. 1974; Tamaki & Long 1978; Tamaki et al. 1981a; and Tamaki et al. 1981b). The equation and term, finite rate of increase (q), were utilized to evaluate the population growth of the green peach aphid, *Myzus persicae* (Sulzer) (Tamaki et al. 1981a). The formula,

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

where A_x = first count on day x and A_n = later count on day n, was more

thoroughly explained in an earlier article (Tamaki et al. 1974) as a modification of Bremer's equation [$A_n = A_o q^n$ (Bremer 1929) where A_n = number of aphids on day n, A_o = initial maternal population, and q = daily rate of increase].

Tamaki et al (1981a) counted insects on the same plants 2-3 times per week. That study only provided a single rate for periods ranging from 9 to 29 days, possibly a mean figure. By comparison, we reported rates of increase for each sampling interval and attempted to follow the same populations throughout the entire season without interruption. This procedure yielded more data points for evaluation and expressed trends in terms of finite rate of increase (FRI) rather than more familiar units like the number of individuals per plant, per leaf or per row-foot. Here, a value of 1.0 indicates no net change in colony size over the sampling period and FRI means above 1.0 generally correspond to increasing populations, below 1.0--decreasing. Large changes in aphid numbers may only produce small movements in the rate above and below 1.0 because of the time factor. Therefore, rate differences of $\pm$0.10-0.25 are often meaningful (Table 11).

Table 11. Examples of colony counts and their respective values for finite rate of increase (FRI) over a sampling interval of four days.

A_1	A_4	FRI
25	75	1.44
25	50	1.26
25	25	1.00
50	25	0.79
75	25	0.69

To satisfy the rate equation, each tagged colony was counted on two consecutive dates. The number of healthy, diseased and parasitized aphids was recorded for each colony as well as the number and type of beneficial insects present on the plant. For calculation purposes the number of healthy aphids was adjusted to account for the death of aphids by mortality factors that were supposed to be excluded from the plant. For example, the number of diseased aphids on a plant where the fungus was being controlled with maneb fungicide (CG-NONE, Table 10) would be included with the healthy aphids for that interval calculation. Although this procedure did not account for diminished reproduction, it was considered sufficient over short time intervals. If a colony was destroyed or lost before the second count, then the FRI value was impossible to calculate for that colony.

The time period between counting dates, referred to here as the sampling interval, varied from 2-10 days. All colonies were usually counted in one day between 0900-2000 hours. The count required from 5-8 hours depending on the weather. One person counted a plot throughout the season. Hayakawa conducted the survey in plot B in 1984 (Hayakawa 1985). Prokrym counted colonies in plot A for both years and in plot B during 1985.

Experiments were organized as a completely randomized design. Treatment means were analyzed by each Julian date interval. Bartlett's test for homogeneity of variance showed that transformation of FRI values was not necessary. The analysis of variance was done with the general linear models program by SAS (GLM program, pp. 433-506, SAS Institute, 1985). Treatment means were separated in each interval with Duncan's multiple comparison test ($p < 0.10$, p. 448, SAS Institute,

1985) when the F test indicated significance.

MEAN APHIDS PER COLONY. In addition to the FRI calculation, colony counts were used to determine the mean number of aphids per colony for each treatment. Though the experimental colonies were not chosen randomly, an average colony count indirectly reflected aphid density. Plants experiencing high mortality pressure from natural enemies usually presented a choice of colonies with lower numbers than ferns protected with chemical and physical barriers.

PLANT RATING. In 1985 a rating system was initiated to better express the number of aphids per plant. Instead of estimating aphids numbers by collecting subsamples, we visually rated each plant on the scale of 0-10. A rating of 10 indicated that 100% of the branches and growing tips had aphids on them, whereas a 0-1 rating indicated a 0-10% infestation. Any value above 5 described an enormous aphid population that could potentially kill the plant.

Parasitoid and pathogen.

COLONY COUNT. Two procedures were used to assess the pressure of parasitism and disease as mortality agents and evaluate the effectiveness of the chemical and physical barriers. First, the number of diseased and parasitized aphids on each experimental colony was recorded during colony counts. The number of dead aphids, i.e. parasitized or diseased, was divided by the sum of dead and healthy aphids to produce a percentage: $(Dead_{T+N} / (Dead_{T+N} + Healthy_{T+N})) * 100$. However, this calculation over-estimated mortality when there was a high incidence of parasitism or disease and the number of healthy and dead aphids at the later time, *T+N*, was substantially lower than the original colony number at time *T*. To compensate for those unaccountable

aphids that may have moved or fallen off the branch when killed or attacked, we used the following equation: $(Dead_{T+M} / Healthy_{T}) * 100$. When a colony remained in the data base for several counts, this statistic became cumulative in nature. Also, empty mummies were removed from tagged colonies during the 1984 physical barrier experiment, thus changing the nature of this calculation for that year.

PARASITISM & DISEASE DETERMINATION (PDD). The above calculation produced a crude estimate of disease and parasitism at the colony level. A second measurement was added in 1985 to assess the presence of pathogen and parasitoid at the plant level--the parasitism and disease determination (PDD). Small numbers of aphids from outer portions of each plant were beaten into a pan, while avoiding marked colonies. About 40-60 of the collected aphids were mounted on a microscope slide as described for pesticide testing (See Appendix C). The slides were placed in a growth chamber at 22°C, photoperiod of 16:8 h (L:D) and 60-85% RH. As fungal hyphae developed within its host, the aphid body color changed from green to brown. Formation of a pearl-colored, papery mummy was positive indication of parasitism. Developing parasitoid larvae could also be seen through the aphid integument with a stereomicroscope (25x). Therefore, parasitism was detected in apparently healthy aphids 3-5 days before the mummy formed. Diseased and parasitized aphids were counted after 24 and 48 hours.

Predators.

VISUAL COUNT. The presence of predators was regularly recorded while counting the aphid colonies. An additional survey was conducted during the chemical exclusion trial because more and detailed information was required on predator numbers. Each experimental plant

was visually inspected for 5-10 minutes, 1-2 times per week. Predators were often removed at this time as a supplemental means of excluding natural enemies from treatments DIS, NONE+W and SHELTER. Data from both sampling efforts were combined to produce an experimental plant visual count (EPV) of the major predators over the season. Due to the small size and cryptic coloration of predators like chrysopid larvae and anthocorids, the visual survey essentially tracked the number of coccinellid morphs (adults, larvae and eggs) and identified the abundant beetle species. The intent was to link any reduction of aphid numbers on specific treatments to recorded predator activity on the plant. While visual counts usually underestimate coccinellid numbers (Frazer & Gilbert 1976), this method sampled predators without removing them or greatly disturbing the aphid colonies.

Plant injury assessment.

We avoided using the same plant twice because of the potentially negative impact on plant health from prolonged exposure to high aphid numbers. Injury from aphid feeding is known to cause abnormalities like stunted growth and bushy rosetting of fern (Grafius 1980, Capinera 1974), but the exact reasons for plant death are speculative. Therefore, it was necessary to mark experimental plants from the previous year. Using the same criteria for selecting test plants, we evaluated previously exposed plants by height, stems per crown and overall vigor. The survey was conducted during June-July after most spears emerged and started to fern out.

Many factors probably influence the number of stems produced from year to year. Since no single index can adequately express the specific impact of aphids on growth the next season, we selected a simple

calculation based upon the original stem count (S_1) and the number of stems that emerged the next season (S_2): $((S_1-S_2)/S_1)*100$. This approach was complicated by the fact that some plants died during the experiment and were replaced with new plants. Therefore not all plants within a treatment experienced the same aphid pressures. A reduction in stem number per crown was thought to be a significant impact of prolonged aphid infestations of the past season.

RESULTS

EFFECTIVENESS OF TREATMENT APPLICATIONS.

CAGES. Cage temperatures were slightly cooler than the outside conditions during early morning and late evening hours with a mean difference range of 0.1-0.19°C in 1984 and 0.03-0.08°C in 1985 (Table 12). Predictably, this trend was reversed during the day and the cage was warmer; mean difference ranging between 0.26-0.84°C in 1984 and 0.46-1.32°C in 1985. While cage temperatures varied slightly from the outside environment, the relative humidity (RH) for 1984 had a seasonal mean difference of 14-21%. When compared to the micrologger data, RH readings made with a hygrometer and sling psychrometer in 1985 showed smaller, negligible differences between the cage and outside conditions (Table 13). This second data set also suggested that the cage promoted slightly lower humidity. We concluded that the accuracy of the micrologger RH probes used in 1984 was questionable and that the cages did not grossly alter temperature or RH levels.

Since there are many more aspects to weather than temperature and RH, we included treatments that attempted to address the overall

Table 12. Cage conditions: mean (±SEM) temperatures, relative humidity and differences (inside minus outside cage) over six time periods for 1984 and 1985. Data recorded with micrologger probes (Model CR-21, Campbell Scientific Inc., Logan, Utah) located inside and outside cages.

HOUR	N	INSIDE	OUTSIDE	DIFFERENCE
1984 MEAN TEMPERATURES (°C).				
0400	53	14.91±0.66	15.10±0.65	-0.19±0.02
0800	53	14.68±0.64	14.77±0.64	-0.10±0.02
1200	52	23.97±0.64	23.71±0.61	0.26±0.08
1600	54	27.26±0.68	26.42±0.63	0.84±0.14
2000	53	24.13±0.62	23.65±0.62	0.47±0.10
2400	53	17.01±0.57	17.18±0.57	-0.17±0.02
1984 RELATIVE HUMIDITY (%)				
0400	55	86.06±0.97	65.34±1.05	20.72±1.12
0800	55	89.22±0.55	68.67±1.08	20.55±1.00
1200	54	56.48±2.83	37.61±2.80	18.87±1.14
1600	56	42.23±3.08	28.34±2.75	13.89±1.27
2000	55	51.67±2.92	37.92±2.73	13.75±1.17
2400	55	81.46±1.17	61.62±1.56	19.85±1.25
1985 MEAN TEMPERATURES (°C).				
0400	41	16.02±0.58	16.00±0.56	-0.03±0.03
1200	41	23.93±0.54	23.47±0.60	0.46±0.23
1600	41	27.44±0.67	26.37±0.67	1.07±0.23
2000	41	24.79±0.66	23.47±0.56	1.32±0.22
2400	41	17.80±0.51	17.87±0.51	-0.08±0.04
1985 RELATIVE HUMIDITY (%)				
0400	41	97.66±0.36	---	---
0800	41	98.43±0.29	---	---
1200	41	73.80±2.66	---	---
1600	41	59 76±2.83	---	---
2000	41	65 10±3 33	---	---
2400	41	93 61±0.91	---	---

Table 13. Relative humidity readings from inside and outside of a physical exclusion cage as recorded by three devices: CR-21 micrologger (CR-21), sling psychrometer (PSYCH) and hygrometer (HYGRO). Comparative means (±SEM) included.

JULIAN DATE	HOUR (2400)	REP	PSYCH IN	PSYCH OUT	CR-21 IN	CR-21 OUT	HYGRO IN	HYGRO OUT
240	1011	1	78	79	83.0	NR*	81	76
240	1640	1	69	69	67	NR	72	74
241	1126	1	86	87	84	NR	82	81
241	1126	2	NR	84	NR	NR	NR	NR
241	1600	1	63	61	64	NR	64	63
241	1600	2	NR	64	NR	NR	NR	63
246	1315	1	67	70	65	NR	67	68
246	1315	2	68	70	64	NR	67	68
246	1700	1	62	57	54.8	NR	61	60
246	1700	2	57	58	55	NR	62	62
247	1645	1	74	74	71.6	72	77	76
247	1645	2	73	80	71.7	73	79	75
254	1015	1	77	83	75.8	75.9	82	86
254	1015	2	77	83	74.8	71.2	75	87
261	1045	1	63	70	66.5	69.5	50	68
261	1045	2	66	71	65.3	68.6	58	65
	N =		14	16	14	6	14	15
	MEAN =		70.0	72.5	68.8	71.7	69.8	71.5
	±SEM =		2.10	2.37	2.35	1.07	2.68	2.23

* NR, no recording.

potential of a cage to reduce abiotic mortality factors. We were especially interested in weather of a more catastrophic nature such as heavy windstorms and rainstorms. Each experiment had two treatments to address this concern--for the physical barrier experiment in both years there were treatments CG-NONE and NOCG-NONE (Table 10), and treatments NONE+W and SHELTER (Table 9) for the chemical experiment in 1985. These treatments were expected to produce similar mean FRI values unless the total weather component was an important mortality agent for the aphid.

For the physical barrier experiment, it was clear that CG-NONE and NOCG-NONE displayed very different seasonal trends. Trends for treatment NOCG-NONE more closely resembled the other uncaged treatment, NOCG-ALL (Figures 18b, 23b). However, other factors could account for the discrepancies between CG-NONE and NOCG-NONE, such as alate emigration from the uncaged plants and failure of the pesticides to completely control natural enemies.

An indication of cage influence was revealed during the chemical exclusion experiment. The treatment SHELTER was specifically aimed at assessing weather modification by a cage structure. Here, mean FRI values for NONE+W remained below SHELTER and only resembled it toward the end of the experiment (Figure 32b). The downward trend for NONE+W from JD 246-253 and later upswing from JD 258-262 seemed to fluctuate around rainstorms as indicated by precipitation levels (Figure 32a). Since our selected experimental plants had sparse fern and few stems per crown, it could be argued that denser foliage would simulate the protection afforded by cages and potentially promote increased aphid numbers.

APHIDS. The successful execution of the carbaryl treatment

required that the insecticide substantially curtail the activity of predators and parasitoids without harming the aphid or drastically altering aphid behavior. On a casual basis we estimated the numbers of aphids that dropped onto the white ground sheets after an application. This survey revealed that aphids did fall from the fern after applications of insecticide and fungicide. In most cases the drop was minimal, i.e. 20-1000 aphids, in comparison to the populations that these plants supported. Plants with the highest populations (i.e. plant rating > 5.0, see SHELTER, Figure 33a) exhibited substantial aphid drop (ca. 5,000-10,000) at the beginning of the experiment with minimal impact after several applications. In spite of this acclimation, the pesticides probably contributed to aphid mortality.

PARASITISM. The cage and carbaryl applications were relatively effective in controlling parasitism. According to the number of mummies recorded during colony counts, cages kept aphidiid-related mortality below 6% in the physical exclusion experiment. Exceptions occurred for treatment CG-COCC in 1984 (Figure 20b) and 1985 (Figure 26a). Treatment CG-NONE also experienced elevated levels during two intervals in 1984 (Figure 20a). Parasitoids probably entered cages when the side panels were opened for counting and by the introduction of parasitized aphids during infestation. In the chemical exclusion experiment, aphidiids produced higher mortality on plants protected only with carbaryl. In 1985 parasitism moved above 6% at times for treatments SHELTER and NONE+W (Figure 34a).

The parasitism and disease determination (PDD) data for 1985 revealed parasitism contamination levels about two times higher than colony counts indicated (Figures 25b, 26b, 34b, 35b). The PDD data

better represented mortality at the plant level. When accumulative, the colony counts slightly overestimated parasitoid activity.

DISEASE. Data collected during the FRI colony counts indicated that disease was effectively controlled by the fungicide. Disease incidence remained below 6% for all maneb-treated plants in both experiments (Figures 20c&d, 25c, 26c, 30b&d, 34c, 35c). The application schedule did fail for one treatment--NONE+W, 1985 chemical exclusion trial--allowing a 10-20% increase (Figure 34c). As for parasitism, the 1985 PDD data provided a different perspective. While the disease data for the two sampling procedures (colony counts and PDD) were complementary for the physical barrier trial (Figures 25c&d, 26c&d), they were contradictory for the chemical exclusion study (Figures 34c&d, 35c&d). The low number of points for the latter data set may have contributed to the discrepancies by obscuring the real trend.

Weather data from the micrologger also revealed RH and temperature levels, both inside and outside of the cages, that could support conidial germination of the fungal pathogen (Table 12). In addition to free water, species in the genus *Entomophthora* require high moisture levels and temperatures within the 15-24°C range for optimum germination (Carruthers and Haynes 1986; Hall and Bell 1960, Kramer 1980; and Yendol 1968). Conditions above 70% RH regularly occurred in the early- to late-morning hours (2400-0800 hr; Figure 22a) while RH fluctuated to lower levels during the day time (1200-2400 hrs; Figures 22b-d). On the microclimate level, free moisture was often trapped and retained by the whorls of cladophyls after rainstorms and more commonly as dew.

PREDATION. The diversity and phenology of predators in the chemical trial plot were recorded by several relative sampling methods:

sticky-can traps, flight interception panels and walking visual count of plot. These surveys indicated that, in addition to coccinellids, anthocorids and chrysopids were also common aphid predators (See Tables 6 & 7, Section II). Anthocorids consistently attained high levels in late August-September (September 9-28 in 1984 and August 24-September 14 in 1985; See Section II, Figure 8a). However, the adults and larvae of anthocorids and chrysopids were not detected in significant numbers by the visual count of experimental plants. The size or cryptic coloration of these predators made visual observation in the dense fern less reliable.

Though carbaryl was very toxic to coccinellids, the applied concentrations were not sufficient to completely eliminate the presence of beetle adults on treated plants. The insecticide performed well on beetles in treatments DIS and NONE+W for the 1984 chemical exclusion study (Figure 29c), but it allowed some isolated buildups for these treatments in 1985 (Figure 36b).

The combination of insecticide and daily hand removal of all predators proved sufficient in reducing predatory pressures on uncaged treatments. For the 1984 chemical trial, the visual count indicated that numbers of lady beetle eggs and larvae were kept lower than those of the highly mobile adults on carbaryl-treated plants (NONE+W, DIS; Figures 31b&d). In 1985 this count again showed lower levels of eggs and larvae for the three treatments receiving carbaryl (SHELTER, DIS and NONE+W; Figures 37a&b, 38b) in comparison with the non-insecticide group (NOCHEM, PRED&PAR; Figures 37c, 38a). In the physical exclusion experiment this situation only pertained to treatment NOCG-NONE (Figures 21b, 27d), since the cages effectively eliminated predators.

Undesired mortality by disease and parasitoids could be partially compensated for in the FRI calculation by adding the number of mummies or cadavers to the healthy aphid count, but losses due to predation produced an unaccountable error. Like the parasitism and disease determination, the visual plant count monitored predator activity at the plant level and did not provide a good indication of predatory impact on the experimental colonies. Also, the attempt to filter out undesired mortality from FRI values with adjusted colony counts did not permit exact cause-and-effect comparisons between mean rates of increase and their corresponding contamination levels of percent parasitism and disease. Contamination mortality above 10% for prolonged periods probably resulted in lowered FRI means as the adjustment technique failed to adequately compensate for lost aphid reproduction.

RESULTS--PHYSICAL BARRIER EXPERIMENT.

Treatment means were separated into two groupings for comparison and presentation. First, we combined three treatments where we expected the greatest differences. Aphid colonies receiving protection with cages and pesticides (CG-NONE, NOCG-NONE) should have lower mortality than colonies on uncaged, untreated plants (NOCG-ALL, Table 10). The second comparison was between the caged treatments that enhanced the influence of the three natural enemies: disease (CG-DIS), aphidiids (CG-PAR) and coccinellids (CG-COCC). In this second group, the fungus was expected to produce the greatest aphid mortality.

Comparison I, physical barrier trial.

Treatment CG-NONE allowed the asparagus aphid to demonstrate its potential growth rate in Michigan by excluding all mortality agents and

reducing the impact of rain and wind. In 1984 disease was totally controlled by the fungicide for this treatment (Figure 20c) and predators did not penetrate the cage. The occurrence of an elevated parasitoid incidence (2-6%, Figure 20a) was associated with a sharp drop in mean FRI at JD 214 and the slight decline in mean FRI values over JD 235-249 (Figure 18b). The fall of FRI means below 1.0 after JD 233 could also be attributed to deteriorating plant health caused by high aphid populations from JD 217-230. We interpreted the yellowing of ferns as reduced plant vigor because the average number of aphids per experimental colony also declined during JD 235-249 (Figure 19a). This situation required the replacement of two plants at JD 249 and 252 which then resulted in higher FRI values after JD 252.

In 1985 data from the colony counts suggested that both disease and parasitism were controlled for CG-NONE (Figures 25a&c). The parasitism & disease determination (PDD) indicated parasitism levels approaching 8% at the plant level (Figure 25b), while confirming the absence of the pathogen (Figure 25d). Impact of the parasitoids was minimal in view of the tremendous aphid buildup over JD 210-219 (aphid rating 5.5-7.0, Figure 24a). Aphid numbers were so high that two plants were replaced very early in the study on JD 219 to offset the influence of reduced plant vigor. Subsequent resurgence to outbreak proportions on the new plants was documented by the plant rating survey and average aphids per colony (Figures 24a&c) as well as by mean FRI values above 1.0 (Figure 23b).

The uncaged treatments (NOCG-NONE and NOCG-ALL) represented the other end of the spectrum for aphid growth. In both years the mean FRI levels plunged below 1.0 to decreasing growth rates within two weeks of

start (Figures 18b, 23b). For 1984 these lower values could not be adequately explained by the presence of natural enemies. Percent parasitism and disease at the colony level were low for these treatments over most of the 1984 season (Figures 20a&c). Only counts of adult coccinellids could be considered slightly elevated at times (> 5 beetles per plant, Figure 19c), assuming that visual counts were often underestimations of these predators (Frazer & Gilbert 1976). Levels of beetle larvae were reduced for NOCG-NONE by insecticide sprays and NOCG-ALL supported modest populations (Figures 21b&c).

An FRI value was not calculated for treatment NOCG-ALL for one interval in 1984 (JD 235, Figure 18b) because no colonies were found on those plants. Six new plants were caged, infested, and introduced on JD 235 as replacements for both uncaged treatments. The higher levels after JD 243 for average colony size (Figure 19a) and mean FRI (Figure 18b) resulted in part from plant replacement. From JD 243 onward, FRI means for the new plants of both uncaged treatments dropped and then swung toward 1.0 as the pressure from all three mortality agents diminished (Figures 19c, 20a&c). The slight drop in FRI values for NOCG-ALL after JD 262 could be attributed to increased disease mortality during this same interval (Figure 20c).

One argument for the extreme differences between the uncaged and caged treatments in 1984 was the "cage effect". In spite of the pronounced absence of biotic mortality agents on uncaged plants, it was difficult to discern the action of a prominent abiotic mortality factor. The uncaged colonies maintained relatively high FRI values during a prolonged period of rainy weather (JD 247-258). Also, the downward trend observed from JD 220-235 occurred over a calm period with few

rainstorms (Figure 18a).

The downward trends for uncaged plants during 1985--mean FRI, rating index and colony size--were more closely linked to the presence of mortality agents (Figures 23b, 24a&c). Although data from the colony counts indicated modest parasitoid and pathogen levels (Figures 25a&c), the PDD survey suggested a greater impact from these two agents (Figures 25b&d). Beetle numbers for adults and larvae were comparable to the 1984 levels during JD 210-235 (Figures 27c&d). The FRI curve for NOCG-NONE went up at JD 234 because two plants were replaced on JD 232. The curve for treatment NOCG-ALL leveled off at JD 234 with only one plant being replaced on JD 232.

OVERVIEW. The cage-fungicide combination (CG-NONE) consistently produced significantly higher FRI means than the two uncaged treatments (NOCG-NONE and NOCG-ALL) in both seasons (Tables 14 & 15). There was little difference between these three treatments over the first three to five sampling intervals, but then their trends markedly separated (Figures 18b, 23b). The uncaged treatments dropped well below 1.0, while the CG-NONE treatment continually remained near or above the 1.0 level.

In 1984 the introduction of new plants essentially produced two series of data for comparison: JD 212-233 and 243-264 (Figure 18b). Means for treatment CG-NONE (Table 14) were often significantly different from the uncaged treatments during the first part of this experiment (JD 224-235) when mortality agents were active. The data on mean aphids per colony also demonstrated this trend (Figure 19a).

The 1985 experiment ran approximately half the duration of its 1984 counterpart. Trends for both trials were very similar through

August (JD 210-240) which was delineated on the graphs by the two dashed lines (Figures 18b, 23b). As in 1984, 1985 mean FRI values for treatment CG-NONE significantly differed from both uncaged treatments soon after the experiment started (Table 15). Although interrupted by new plant introductions, the trend of increased aphid growth rates for CG-NONE was further revealed by data on aphids per colony and plant rating (Figures 24a&c).

Treatment NOCG-NONE more closely resembled NOCG-ALL than CG-NONE for both seasons; a demonstration that the pesticides alone were not as efficient at reducing the impact of selected mortality agents as the cage-fungicide combination. The NOCG-NONE treatments experienced higher parasitoid, disease and coccinellid densities than CG-NONE. Although high levels of adult coccinellids occurred on NOCG-NONE, hand removal kept larvae and eggs numbers low.

Comparison II, physical barrier trial.

In 1984 the impact of the introduced aphidiids (CG-PAR) never significantly differed from the mortality produced by caged coccinellids (CG-COCC, Table 14). The graphed trends for both treatments (Figure 18c) closely resembled CG-NONE (Figure 18b). Parasitism rates were low in treatment CG-PAR and similar to the contamination levels recorded for CG-COCC (Figure 20b). Disease was not an important contamination factor in either treatment (Figure 20d). The gradual declines in aphid numbers and growth rate for CG-PAR were probably associated more with decreased plant vigor than the parasitoid (Figures 18c, 19b). One plant was replaced at JD 252 for an aphidiid treatment.

Visual counts for 1984 showed that beetle densities from JD 212-230 (Figure 19c) were not much higher on treatment CG-COCC than those

observed for the uncaged plants (NOCG-NONE and NOCG-ALL). While the coccinellid population for CG-COCC was artificially maintained, the number of adult beetles per plant did not attain high levels (5-15 per plant) until the third and fourth introductions (JD 238 & 246, Figure 19c). The potential to generate new adults was not realized through increased egg and larvae production (Figure 21a). Slight downward trends in mean FRI and aphids per colony after JD 228 occurred during an upsurge of adult and larval numbers (Figures 18c, 19b). This trend was interrupted by the replacement of two plants at JD 249 and 257 that required the transfer of all coccinellid life stages from the original units to the new plants. Fortunately, oviposition had stopped by that time.

In sharp contrast to coccinellids and parasitoids, the fungal pathogen (CG-DIS) markedly reduced 1984 FRI means during JD 226-246 (Figure 18c). This period coincided with a disease incidence of 18-88% (Figure 20d). The overall trends for FRI means and average aphids per colony followed the fluctuations of disease quite well (Figure 19b), but the number of diseased aphids did not increase during rainy periods (Figure 18a). Instead, the dew and humidity present in early morning and late evening probably provided the free water needed for high germination rates by the naturally-occurring fungal spores (Figures 22a&d). Disease decimated the colonies to the point where two replacement plants were needed at JD 249 and 252. As a consequence, mean FRI moved above 1.0 at JD 252 only to drop again with a resurgence of the pathogen.

In 1984 we did not introduce sufficient numbers of parasitoids or coccinellids in proportion to the tremendous aphid populations produced

by the cage conditions. Consequently, 1984 FRI means did not drop due to these two mortality agents. For 1985, substantially more natural enemies were put in the cages. Again, treatments CG-PAR and CG-COCC were very similar to each other in 1985 except that their FRI values clearly dropped below 1.0 and remained there (Figure 23c). Disease was not a significant contamination factor for these two treatments (Figures 26c&d), but parasitism did remain above 10% for treatment CG-COCC after JD 232 (Figures 26a&b). Surveys of parasitoid and coccinellid numbers indicated that these two agents were present at high levels in their respective treatments (Figures 26a&b, 27b).

Similar to 1984, the 1985 disease treatment (CG-DIS) displayed high mean values until the pathogen became established on the colonies. As percent disease moved above 10% at JD 225-226 (Figures 26c&d) the rate of increase, rating index and aphids per colony for CG-DIS dropped below the 1.0 level at JD 230 (Figures 23c, 24b&d). The PDD survey revealed a slightly higher level of aphidiid contamination for CG-DIS at the plant level (Figure 26b) than recorded for the test colonies (Figure 26a).

OVERVIEW. Unlike the results for 1984, the 1985 experiment allowed us to better evaluate the impact of these three mortality agents because each natural enemy produced a slightly different trend. Both seasons documented the potential of the pathogen, but a comparison of percent parasitism and coccinellid numbers per plant revealed that the 1985 treatments experienced substantially higher levels of these two agents than in 1984. Although the 1985 FRI means were not significantly different when analyzed by Julian date, treatment CG-PAR showed a seasonal trend of values lower than CG-COCC (Table 15). Further,

aphidiids seemed as capable of reducing aphids numbers as the pathogen.

The data for these three treatments suggested that the parasitoid, coccinellid and pathogen were able to influence aphid growth rates in 1985. However, estimates of aphid numbers--rating index and aphids per colony--revealed that plants in these treatments experienced very high aphid populations (Figures 24b&d). Therefore, reduced plant vigor could also contribute to the observed decline in aphid numbers.

The expanded sampling effort conducted in 1985 permitted us to better associate the occurrence of natural enemies with lower FRI means. Just as the 1985 plant rating data (Figures 24a&b) complemented information on FRI means and aphids per colony (Figures 23b&c, 24c&d), the parasitism and disease determination (PDD, Figures 25b&d) confirmed the magnitude of these two mortality agents at the plant level. Additional sampling may have altered the interpretation of the 1984 results. For example, in both years data on parasitism and disease collected during colony counts indicated low values for treatment CG-NONE while the uncaged plants experienced low to moderate levels. Contrary to these colony counts, the 1985 PDD data showed substantially elevated levels for uncaged treatments. It is quite possible that the 1984 plants had significantly higher rates of parasitism and disease than the colony counts indicated.

Plant injury assessment, physical barrier trial.

The survey of experimental plants did not produce stem count data that could be rigorously analyzed. We grouped plants into caged and uncaged treatments (Table 10), and then categorized them by the percent reduction in stem growth from season to season: no growth/dead (100% reduction), greatly reduced (30-99% reduction), reduced (6-29%

reduction) and no change (0-5% reduction). Of the 18 uncaged plants 5.5% exhibited no growth, 27.8%--greatly reduced, 11.1%--reduced and 55.6%--no effect. Of the 35 caged plants 42.9% showed no growth, 25.7%--greatly reduced, 14.3%--reduced and 17.1%--unchanged. It seems that the extremely high aphid populations on the caged plants produced greater plant mortality than the comparatively reduced aphid numbers on the uncaged plants.

Table 14. Mean finite rate of increase (±SEM) by Julian date for 1984 physical barrier experiment.

JULIAN DATE	212		214		217		219		222		224		226	
TMT[a]	N[b]	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM
CG-NONE	28	1.137±0.089 NS[c]	27	0.943±0.077 NS	27	1.101±0.070 NS	30	1.270±0.067 NS	30	0.946±0.048 ABC	30	1.130±0.062 A	30	1.111±0.045 A
CG-COCC	31	1.091±0.072 NS	29	1.186±0.052 NS	32	1.152±0.048 NS	33	1.196±0.045 NS	35	1.171±0.066 A	33	0.990±0.106 A	32	1.051±0.067 A
CG-PAR	26	1.239±0.066 NS	27	1.046±0.092 NS	26	1.130±0.096 NS	30	1.103±0.054 NS	33	1.035±0.038 AB	27	1.034±0.055 A	27	1.113±0.050 A
CG-DIS	29	1.206±0.073 NS	30	1.307±0.082 NS	30	1.139±0.057 NS	35	1.289±0.071 NS	34	1.080±0.066 A	32	0.950±0.050 A	31	0.866±0.058 AB
NOCG-NONE	30	1.127±0.046 NS	30	1.032±0.057 NS	28	1.177±0.048 NS	31	1.258±0.079 NS	31	0.738±0.045 C	25	0.517±0.070 B	22	0.884±0.105 AB
NOCG-ALL	33	1.169±0.096 NS	28	0.893±0.089 NS	24	1.275±0.064 NS	30	1.065±0.121 NS	29	0.791±0.075 BC	25	0.620±0.080 B	23	0.637±0.091 B
F (*df*)[d]	0.21(5,12) p <.95		1.75(5,12) p <.198		0.89(5,12) p <.517		0.59(5,12) p <.705		2.54(5,12) p <.086		5.59(5,12) p <.007		2.26(5,12) p <.114	

JULIAN DATE	228		230		233		235		243		246		249	
CG-NONE	29	1.144±0.066 A	29	1.055±0.041 A	29	0.947±0.037 A	28	1.002±0.051 A	27	0.940±0.025 B	21	0.946±0.064 NS	28	0.914±0.032 AB
CG-COCC	32	0.994±0.046 AB	29	1.111±0.031 A	27	0.947±0.040 A	27	0.936±0.040 A	29	0.981±0.019 AB	27	0.977±0.032 NS	28	0.882±0.035 ABC
CG-PAR	29	0.910±0.036 B	29	1.127±0.079 A	30	1.041±0.036 A	32	1.051±0.041 A	32	0.972±0.019 AB	29	0.931±0.039 NS	29	0.956±0.041 AB
CG-DIS	28	0.658±0.043 C	28	0.879±0.063 B	25	0.675±0.042 B	18	0.537±0.061 B	23	0.701±0.033 C	24	0.956±0.073 NS	21	1.033±0.059 A
NOCG-NONE	23	0.551±0.066 C	22	0.547±0.105 C	16	0.486±0.066 C	4	0.157±0.010 C	35	1.040±0.027 AB	35	0.880±0.044 NS	33	0.736±0.051 C
NOCG-ALL	21	0.537±0.069 C	17	0.577±0.094 C	7	0.573±0.178 BC	0	——	34	1.067±0.027 A	35	0.812±0.051 NS	33	0.864±0.043 BC
F (*df*)	10.2(5,12) p <.0005		13.64(5,12) p <.0001		24.7(5,10) p <.0001		27.9(4,9) p <.0001		7.68(5,12) p <.002		0.74(5,12) p <.61		2.81(5,12) p <.066	

JULIAN DATE	252		255		258		261		264	
CG-NONE	21	1.077±0.087 AB	33	1.079±0.031 A	31	1.074±0.052 A	30	0.940±0.043 NS	31	1.099±0.031 A
CG-COCC	29	0.926±0.048 B	31	1.021±0.064 AB	30	0.873±0.049 B	32	0.897±0.037 NS	23	0.943±0.039 B
CG-PAR	20	0.865±0.049 B	29	0.945±0.037 B	28	0.930±0.036 B	30	0.951±0.038 NS	29	1.005±0.021 AB
CG-DIS	22	1.269±0.100 A	32	1.069±0.037 A	30	1.092±0.031 A	30	0.999±0.024 NS	31	0.927±0.030 B
NOCG-NONE	31	0.936±0.056 B	32	0.838±0.045 C	30	1.074±0.045 A	30	0.941±0.018 NS	30	0.941±0.030 B
NOCG-ALL	31	0.833±0.052 B	32	0.978±0.036 B	33	1.061±0.045 A	32	0.945±0.032 NS	31	0.880±0.022 B
F (*df*)	2.27(5,9) p <.134		8.68(5,12) p <.001		5.02(5,12) p <.01		0.28(5,12) p <.917		2.70(5,12) p <.073	

[a] Treatment abbreviations described in Table 10.
[b] N, aphid colonies per treatment.
[c] Means within columns followed by the same letter are not significantly different (p < 0.10, Duncan's multiple range test; pg 448, SAS Institute, 1985). NS, nonsignificant result.
[d] The data were analyzed by Julian date; the F test, degrees of freedom and probability level were produced by the general linear models program (GLM program, pp 433-506, SAS Institute, 1985), plants treated as a replicate.

Table 15. Mean finite rate of increase (±SEM) by Julian date for 1985 physical barrier experiment.

JULIAN DATE	210		214		219		225	
TMT[a]	N[b]	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM
CG-NONE	24	1.304±0.064 NS[c]	23	1.019±0.030 B	24	1.049±0.026 B	22	1.104±0.032 B
CG-DIS	23	1.264±0.044 NS	23	1.126±0.025 A	21	1.240±0.045 A	22	1.237±0.037 A
CG-COCC	24	1.347±0.033 NS	23	1.132±0.029 A	23	1.055±0.028 B	24	1.078±0.040 B
CG-PAR	24	1.482±0.059 NS	21	1.054±0.033 AB	23	1.036±0.024 B	22	0.897±0.017 C
NOCG-NONE	24	1.177±0.057 NS	23	1.001±0.033 B	24	0.975±0.031 B	24	0.824±0.030 C
NOCG-ALL	24	1.295±0.049 NS	22	1.012±0.040 B	22	0.995±0.026 B	24	0.734±0.027 D
F (*df*)[d]	2.25(5,12) p <.116		2.97(5,12) p <.057		4.20(5,12) p <.019		21.39(5,12) p <.0001	

JULIAN DATE	230		234		239		247	
CG-NONE	23	1.093±0.035 A	23	1.069±0.031 A	23	1.074±0.022 A	21	1.070±0.021 A
CG-DIS	23	0.922±0.024 B	24	0.798±0.032 C	23	0.802±0.040 BC	15	0.731±0.049 C
CG-COCC	23	0.897±0.023 B	23	0.921±0.025 B	22	0.932±0.034 AB	21	0.901±0.029 B
CG-PAR	22	0.905±0.014 B	24	0.888±0.023 BC	24	0.812±0.029 BC	14	0.758±0.042 BC
NOCG-NONE	22	0.550±0.042 C	22	0.926±0.028 B	21	0.739±0.049 C		
NOCG-ALL	22	0.627±0.035 C	24	0.575±0.044 D	14	0.576±0.062 D		
F (*df*)	16.4(5,12) p <.0001		20.3(5,12) p <.0001		6.44(5,11) p <.005		7.46(3,6) p <.019	

[a] Treatment abbreviations described in Table 10. [b] N, aphid colonies per treatment.
[c] Means within columns followed by the same letter are not significantly different (p < 0.10, Duncan's multiple range test; pg 448, SAS Institute, 1985). NS, nonsignificant result.
[d] The data were analyzed by Julian date; the F test, degrees of freedom and probability level were produced by the general linear models program (GLM program, pp 433-506, SAS Institute, 1985), plants treated as a replicate.

Figure 18. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: CG-NONE, NOCG-NONE, NOCG-ALL; and (C) Comparison-II treatments: CG-DIS, CG-PAR, CG-COCC. The vertical dashed lines demarcate August 1-September 1, 1984. For C, the bold letters indicate introductions of aphidiids ("B") and coccinellids ("C").

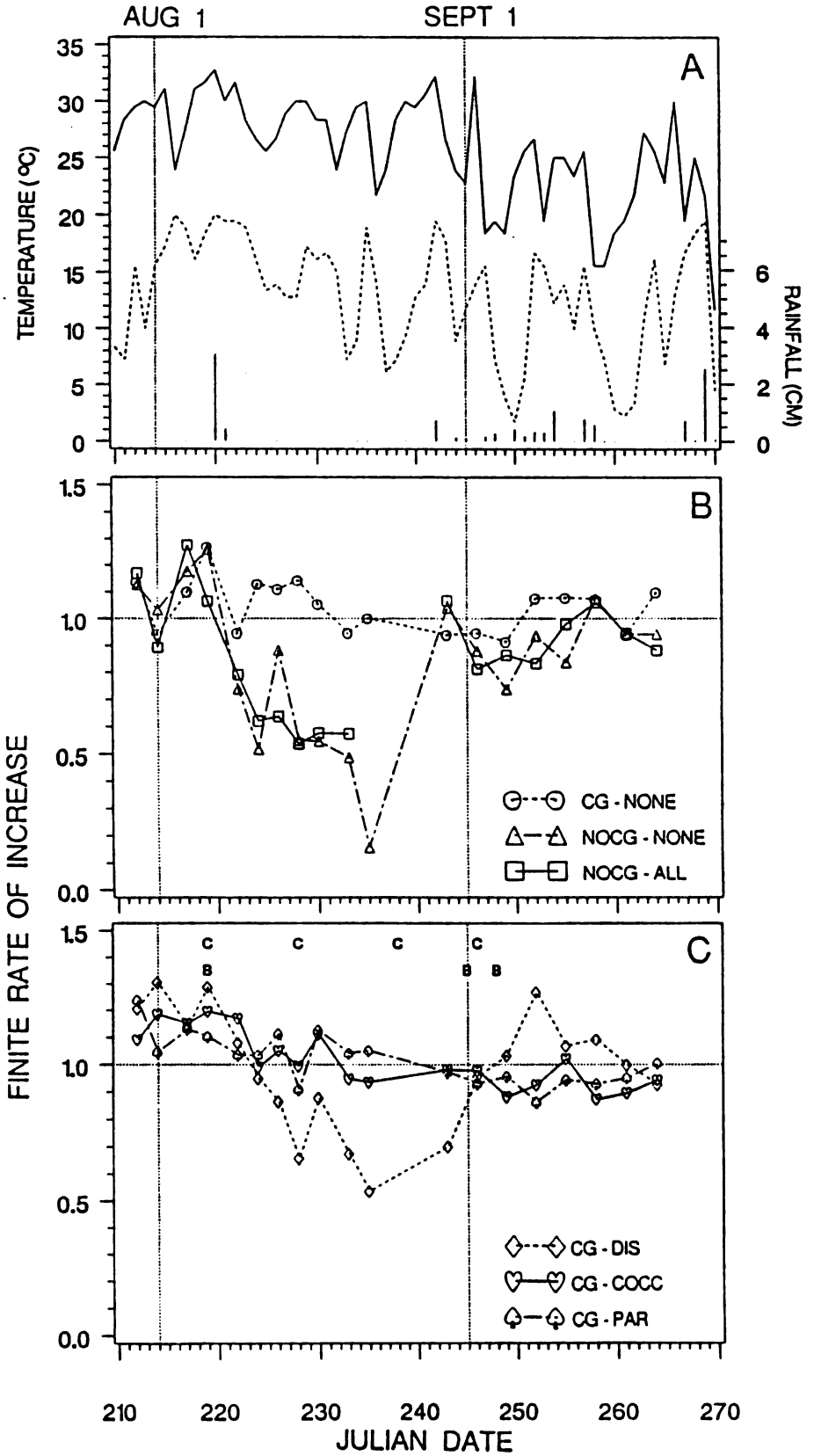
AUG 1
SEPT 1
A
TEMPERATURE (°C)
RAINFALL (CM)
B
CG - NONE
NOCG - NONE
NOCG - ALL
C
CG - DIS
CG - COCC
CG - PAR
FINITE RATE OF INCREASE
JULIAN DATE

Figure 18.

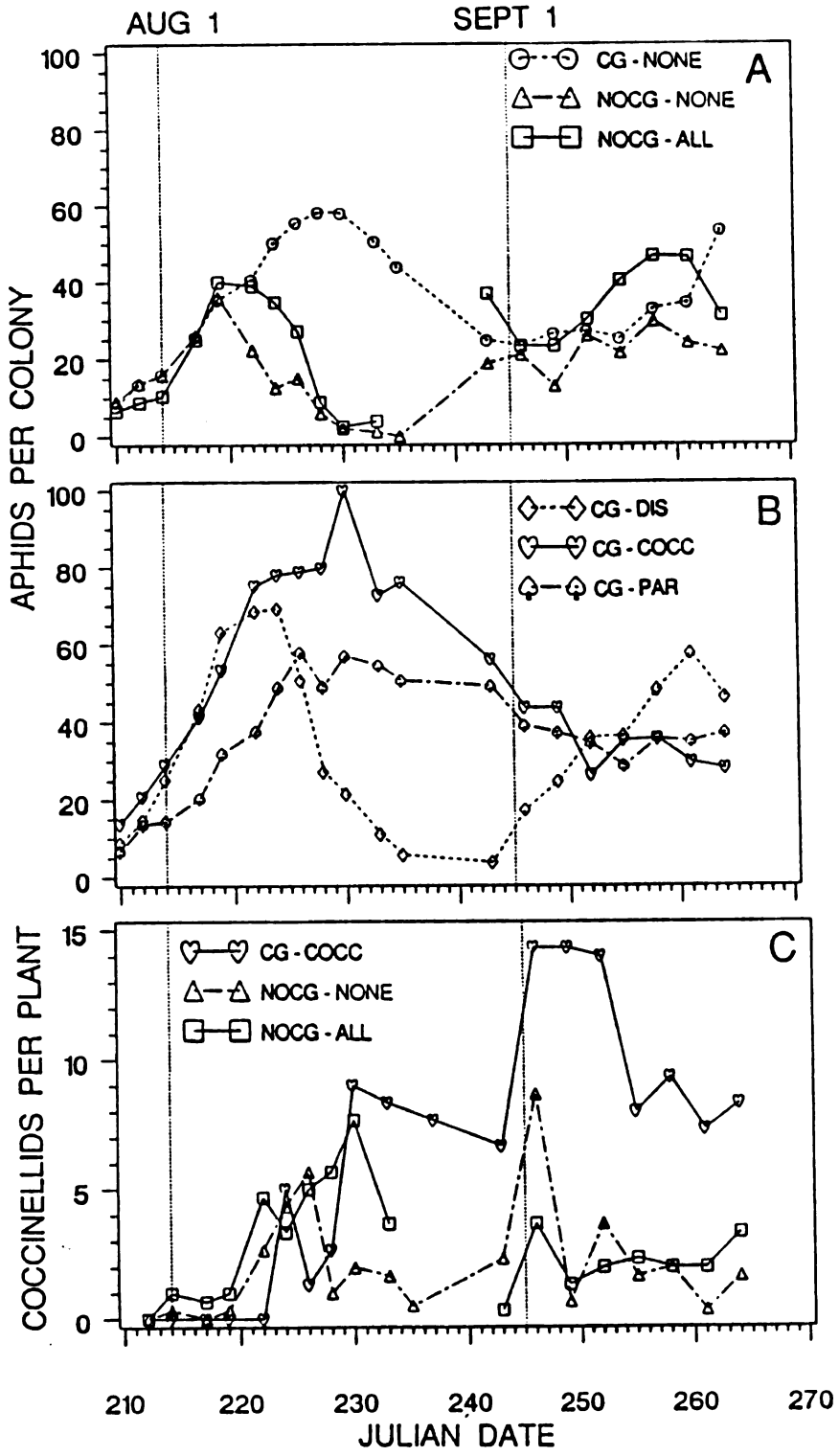

Figure 19. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Mean number of aphids per experimental colony (A) for Comparison-I treatments: CG-NONE, NOCG-NONE and NOCG-ALL, and (B) Comparison-II treatments: CG-DIS, CG-PAR and CG-COCC. (C) Mean number of coccinellid adults per plant for: NOCG-ALL, NOCG-NONE and CG-COCC. The vertical dashed lines demarcate August 1-September 1, 1984.

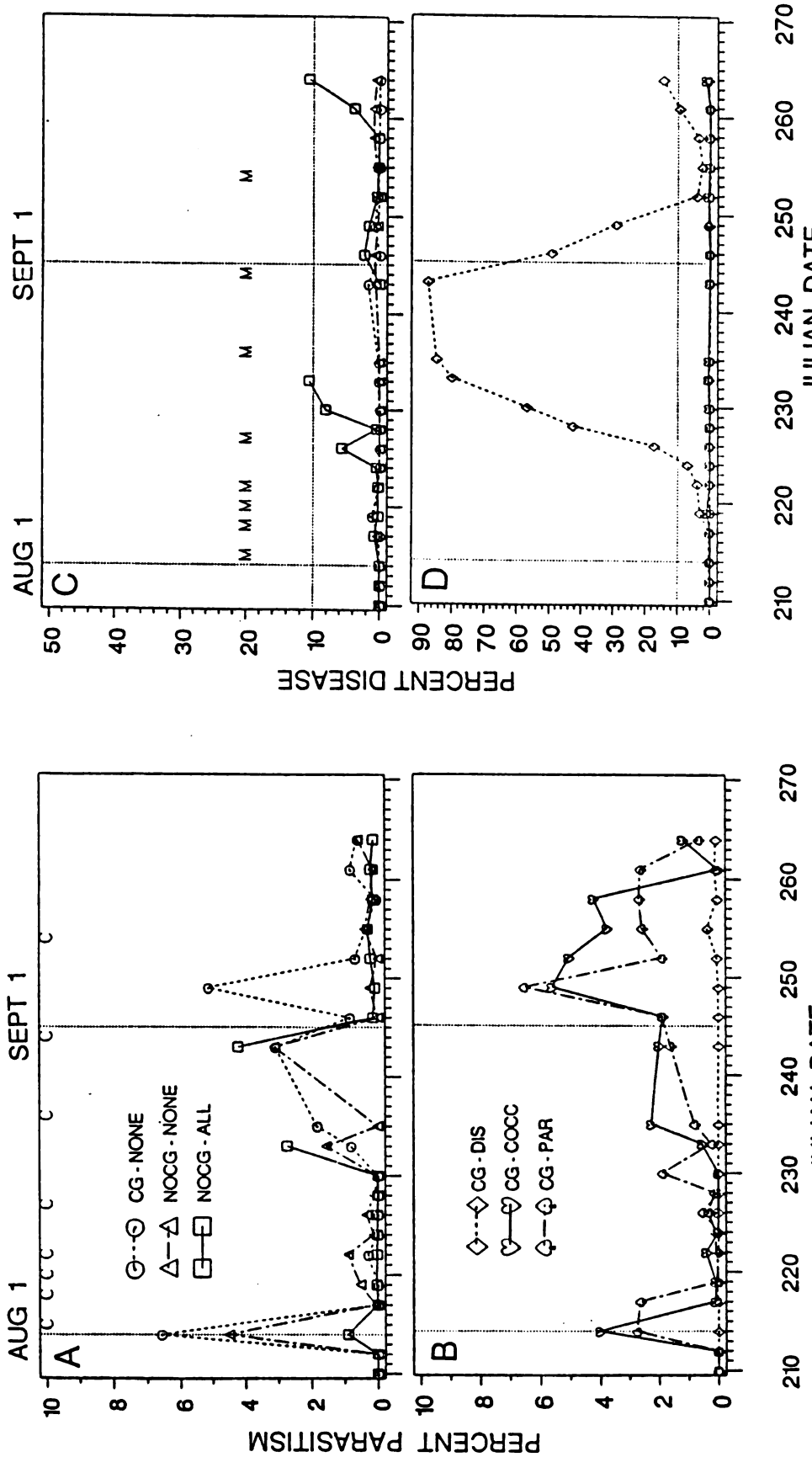

Figure 20. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Mean percent PARASITISM (A) for Comparison-I treatments: CG-NONE, NOCG-NONE, NOCG-ALL; and (B) for Comparison-II treatments: CG-DIS, CG-PAR, CG-COCC. Mean percent DISEASE for (C) Comparison-I and (D) Comparison-II treatments. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M"). The vertical dashed lines demarcate August 1-September 1, 1984.

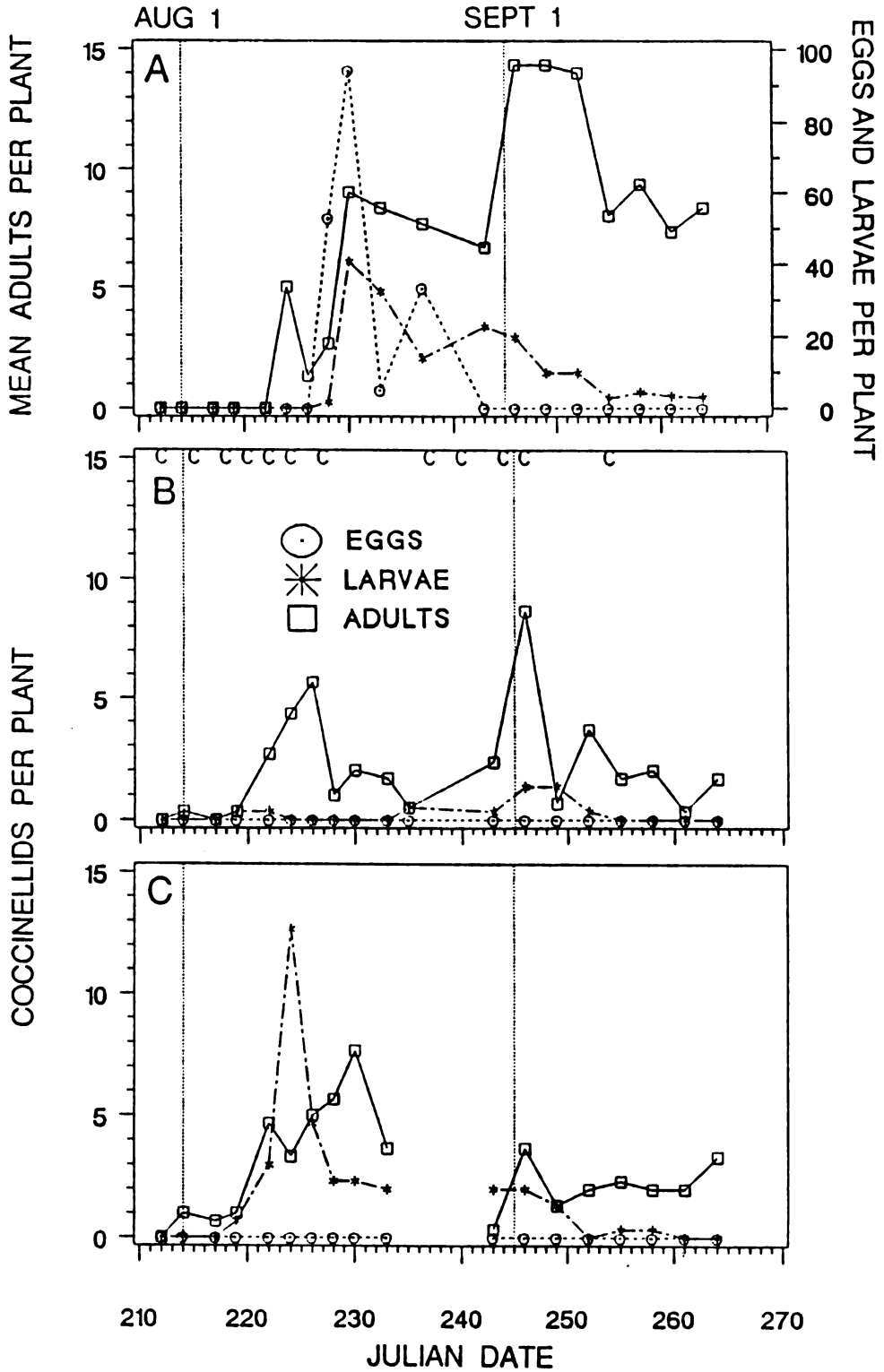

Figure 21. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (A) CG-COCC, (B) NOCG-NONE and (C) NOCG-ALL. The letters "C" indicate an application of carbaryl insecticide. The vertical dashed lines demarcate August 1-September 1, 1984.

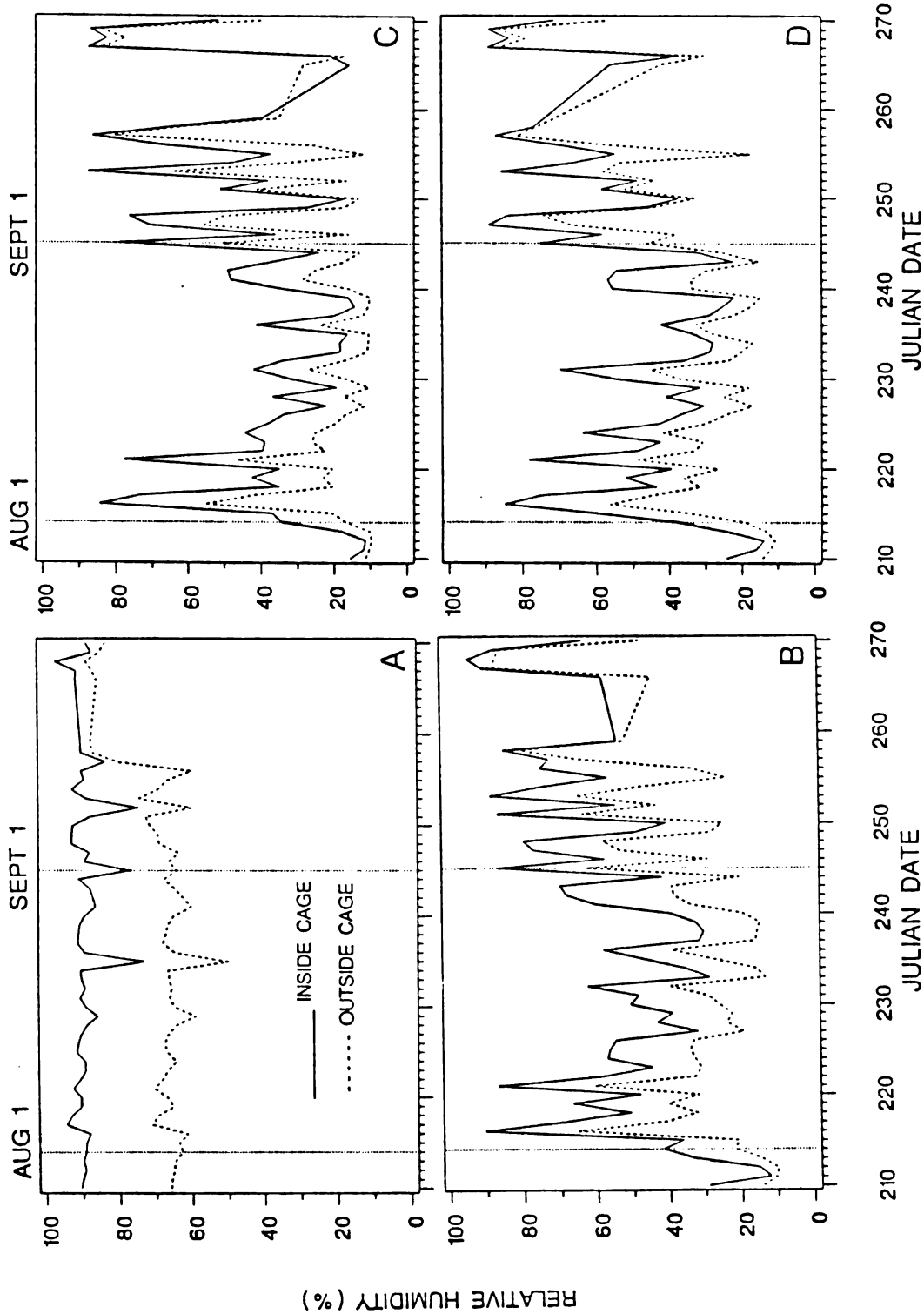

Figure 22. PHYSICAL BARRIER EXPERIMENT (Plot B), 1984. Percent relative humidity from inside and outside of an exclusion cage for four time periods: (A) 0800, (B) 1200, (C) 1600 and (D) 2000 hrs. The vertical dashed lines demarcate August 1-September 1, 1984.

Figure 23. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: CG-NONE, NOCG-NONE, NOCG-ALL; and (C) Comparison-II treatments: CG-DIS, CG-PAR, CG-COCC. The vertical dashed lines demarcate August 1-September 1, 1985. For C, the bold letters indicate introductions of aphidiids ("B") and coccinellids ("C").

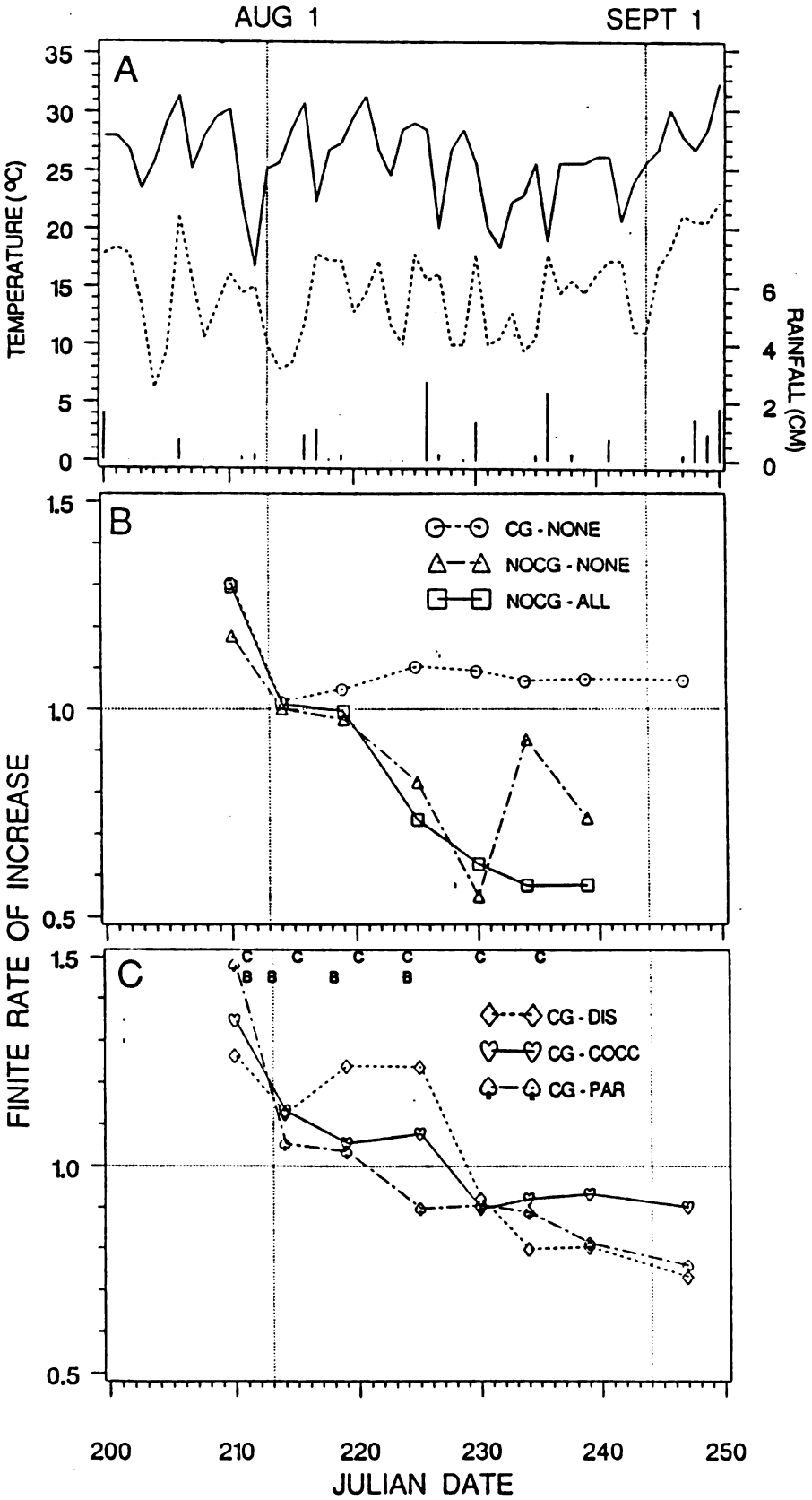
AUG 1
SEPT 1
A
TEMPERATURE (°C)
RAINFALL (CM)
B
CG - NONE
NOCG - NONE
NOCG - ALL
FINITE RATE OF INCREASE
C
CG - DIS
CG - COCC
CG - PAR
JULIAN DATE

Figure 23.

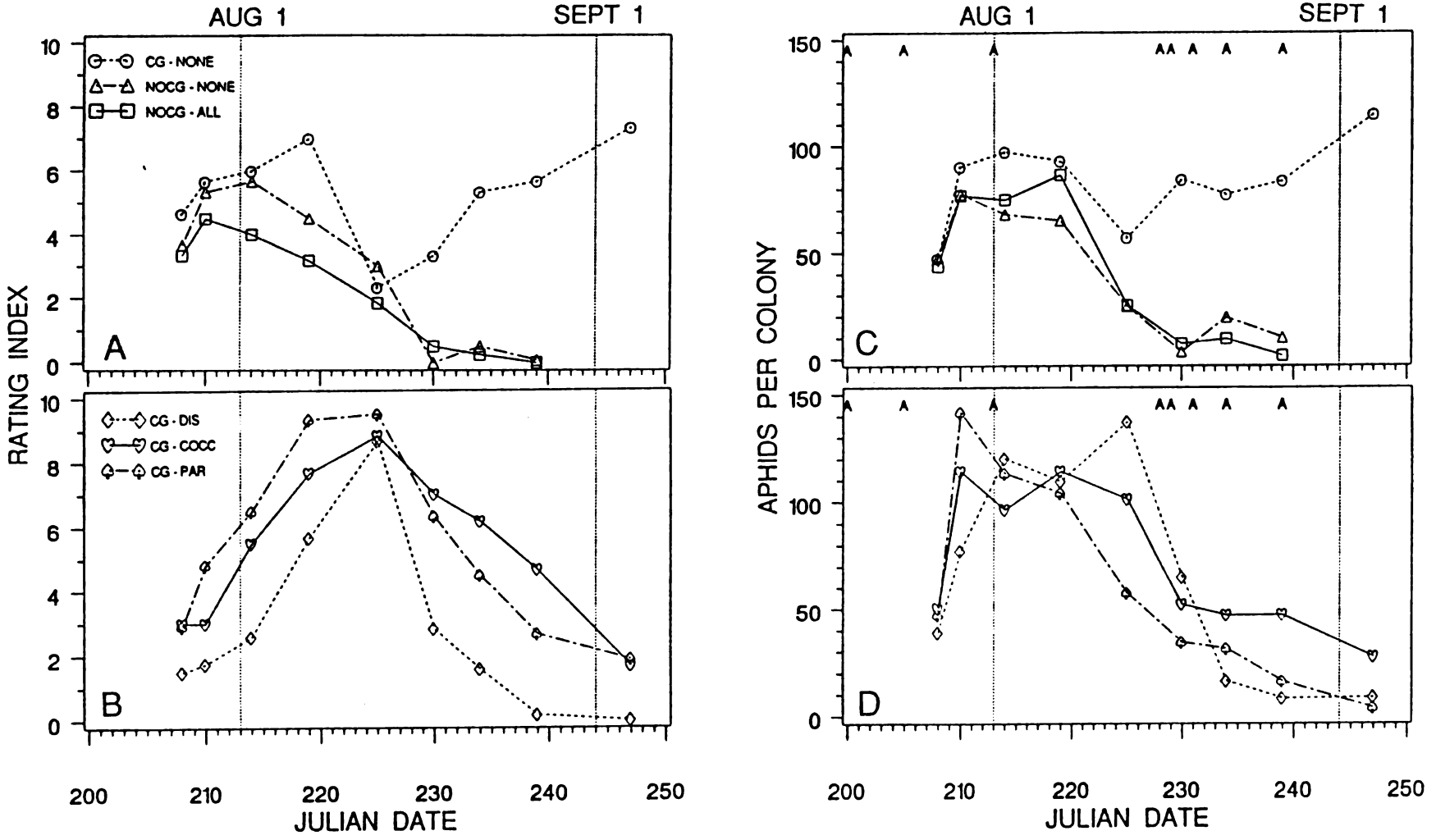

Figure 24. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. Mean aphid rating (A) for Comparison-I treatments: CG-NONE, NOCG-NONE and NOCG-ALL; and (B) for Comparison-II treatments: CG-DIS, CG-PAR and CG-COCC. Mean number of aphids per experimental colony (C) for Comparison-I treatments and (D) for Comparison-II treatments. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "A" indicate aphid introductions.

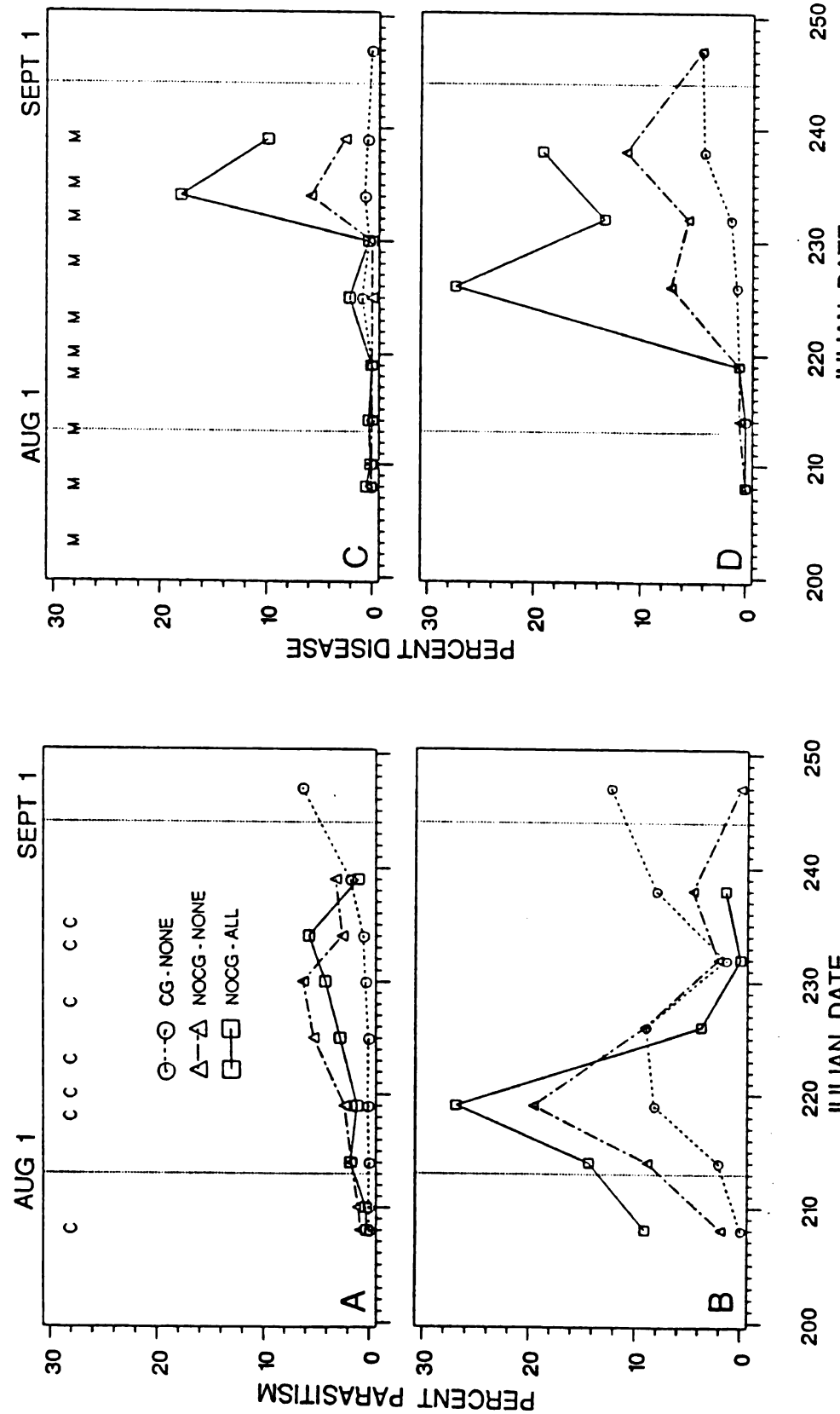

Figure 25. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. Mean percent PARASITISM for Comparison-I treatments (CG-NONE, NOCG-NONE, NOCG-ALL) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-I treatments from two sources: C) colony counts and D) PDD. The vertical dashed lines demarcate August 1-September 1, 1985. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M").

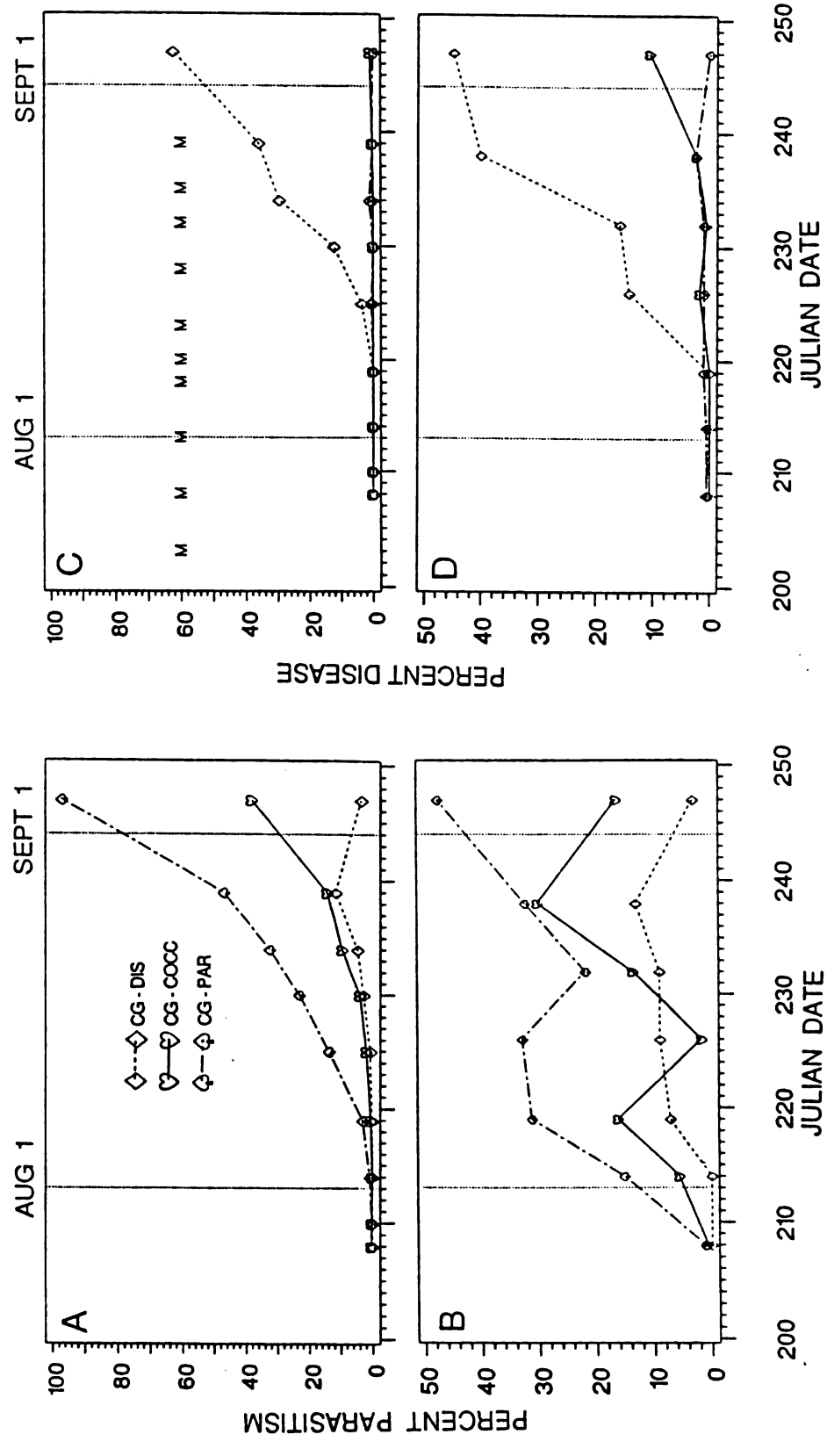

Figure 26. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. Mean percent PARASITISM for Comparison-II treatments (CG-DIS, CG-PAR and CG-COCC) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-II treatments from two sources: C) colony counts and D) PDD. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "M" indicate applications of maneb fungicide.

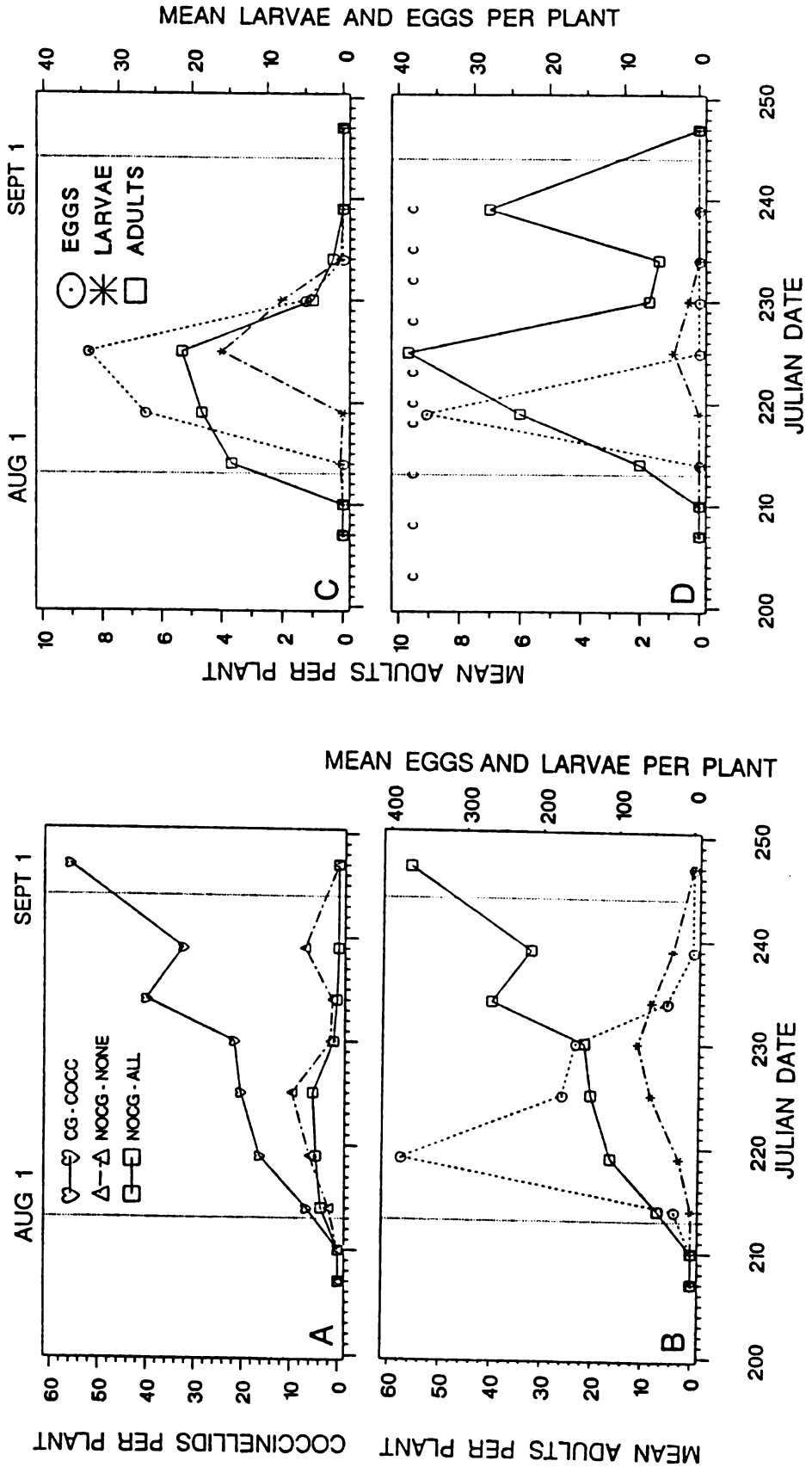

Figure 27. PHYSICAL BARRIER EXPERIMENT (Plot B), 1985. (A) Mean number of coccinellid adults per plant for: CG-NONE, NOCG-NONE and CG-COCC. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (B) CG-COCC, (C) NOCG-ALL and (D) NOCG-NONE. For D, the letter "C" indicates an application of carbaryl insecticide. The vertical dashed lines demarcate August 1-September 1, 1984.

RESULTS--CHEMICAL BARRIER TRIAL.

Again, the treatments were separated into two groupings for presentation. In 1984, comparison I graphs included two treatments expected to produce the high and low extremes: plants sprayed with fungicide and insecticide (NONE+W) and those that received no chemical applications (NOCHEM, Table 9). Comparison II for this year combined treatments that favored disease with the application of insecticide (DIS), and those that promoted the predator-parasitoid complex with fungicide sprays (PRED&PAR).

The groupings were altered slightly for 1985 to accommodate the addition of a fifth treatment, SHELTER (Table 9). In comparison I, NOCHEM was displayed with SHELTER and NONE+W. We modified NONE+W to produce SHELTER by placing a cage over sprayed plants and expected these two treatments to be similar if weather was not an important mortality agent. For comparison II, NONE+W was included with DIS and PRED&PAR curves as a reference.

Due to the time requirements for counting colonies by one person, only one experiment could be properly executed over a given period. Therefore, the physical barrier experiment described above was sandwiched between two runs of the chemical barrier experiment in 1985. From the viewpoint of seasonal variability, the 1984 experiment is more similar to the second 1985 run. The short duration eliminated the need for replacement plants in either year.

Comparison I, chemical barrier trial.

In 1984 treatment NOCHEM produced many of the lowest means (Table 16). The high and low points on the FRI curve (Figure 28b) coincided closely with the fluctuations in disease (Figure 30b) and beetle numbers (Figure 29c). Though overall beetle numbers (Figure 31a) and mortality from parasitism (0-2%, Figure 30a) was low, the uncaged plants experienced a relatively high incidence of disease (6-28%, Figure 30b). Since all of the mortality agents were present to some degree, any reduction in aphid growth rate was attributed to their combined impact.

Pesticide applications were relatively effective in reducing the impact of natural enemies on treatment NONE+W in 1984. However, lowered FRI means at JD 244 and 276 (Figure 28b) occurred during rises in pathogen and parasitoid counts for this treatment (Figures 30a&b). The combination of insecticide and hand-removal of predators was needed to keep all coccinellid stages at acceptable levels (Figure 31b). We cannot explain the sharp drop at JD 258 (NONE+W, Figure 28b), except to note that it was also revealed on the plot of aphids per colony (Figure 29a). It is possible that heavy rainstorms preceding the count (Figure 28a) caused a drop in aphid numbers since FRI mean values for all treatments showed a slight downturn at this point.

Of the four trials conducted, this 1984 study went the latest into the fall months. Tamaki et al. (1983) noted that sexual morphs were produced in late September in Washington State; an occurrence that marked a definite transition from larviposition to oviposition. Since the FRI counts measured aphid numbers, the shift to egg production would produce declining means. Egg counts for all 1984 experimental colonies revealed 1, 15 and 237 eggs on September 19 & 22 and October 2 (JD 263,

266, 276), respectively. For 1985, total counts were 7, 10, and 26 on September 15, 19 and 23 (JD 258, 262 and 266), respectively. Therefore, the last count in the 1984 chemical barrier trial was probably lower because of egg production while the other three trials were not greatly influenced because of earlier termination dates.

Statistical tests indicated that the 1985 means for NOCHEM and NONE+W were rarely significantly different at $p < 0.10$ (Table 17). However, some comments can be made concerning the seasonal trends for both uncaged treatments. During the first run disease was nonexistent (Figures 34c&d), but parasitism was moderate (Figures 34a&b) and coccinellid numbers per plant exhibited low levels of adults (Figure 36a). The untreated plants supported higher levels of beetle eggs and larvae (Figure 37c). Nonetheless, the trends for mean FRI, plant rating and aphids per colony were very similar for both treatments (Figures 32b, 33a&b). We attributed the similarities to poor control over parasitoids and beetle adults by the insecticide. Only the number of beetle eggs and larvae were lower for NONE+W, possibly due to a more intensive hand-removal effort than in 1984 (Figure 37b).

Treatment SHELTER seemed to maintain slightly higher levels than NONE+W for mean FRI, plant rating and average aphids per colony over the first part of 1985 (Figures 32b, 33a&b). The trend difference between SHELTER and NONE+W suggests that the cage structure afforded some protection to the aphid colonies from detrimental weather conditions, like the numerous rainstorms of that season (Figure 32a).

The second run in September 1985 conflicted with the interpretation of results from the first part. Trends for SHELTER and NONE+W were now more alike while NOCHEM fluctuated at even lower mean

values (Figures 32b, 33a&b). Contamination by the pathogen was indicated as a problem on NONE+W according to the FRI colony count data (Figure 34c), but the parasitism & disease determination (PDD) suggested that all three treatments experienced similar levels (Figure 34d). For NOCHEM, the up and down oscillations of the FRI curve seemed to result from the impact of disease and coccinellids (Figures 34c, 36a). When superimposed, the two curves for disease (Figures 34c&d) illustrated that they were in agreement in spite of the few data points for the PDD survey. Treatment NOCHEM also supported high levels of all beetle stages (Figure 37c).

Comparison II, chemical barrier trial.

In 1984 the impact of disease (DIS) produced lower values than the combined effects of predators and parasitoids (PRED&PAR). The trend differences recorded by mean FRI and aphids per colony resulted from the effective exclusion of natural enemies by pesticides (Figures 28c, 29b). The fungicide practically eliminated the pathogen from PRED&PAR (Figure 30d) while the insecticide severely limited populations of parasites (Figure 30c) and coccinellids (Figure 29c) for DIS. The largest coccinellid populations (Figure 31c) and highest overall parasitism trend (Figure 30c) were found on fungicide treated plants (PRED&PAR); the highest incidence of disease occurred on treatment DIS (Figure 30d). Assuming that weather produced an equal impact on all treatments, it seems that the destructive potential of these three agents was clearly revealed.

Similar conclusions could not be readily made for treatments PRED&PAR and DIS based on the 1985 data. These two treatments were similar to NONE+W during the first run (Figure 32c). This outcome is

not surprising because percent disease was close to zero for this period (Figures 35c&d) and all three treatments experienced similar parasitism rates (Figures 35a&b). This condition essentially created three identical treatments with PRED&PAR showing the lowest trend. Although the number of adult coccinellids per plant was the same for these treatments (Figure 36b), PRED&PAR probably had more undetected beetle larvae in view of the high numbers of eggs observed (Figure 38a).

Treatment means for PRED&PAR and DIS were not significantly different from each other on the second run (Figures 32c, 33c&d). Separating the trends was complicated by the disease surveys. The increasing levels of disease detected during the colony counts (Figure 35c) did not agree with the parasitism & disease determination (Figure 35d). PRED&PAR did support substantially higher numbers of coccinellid larvae and eggs than DIS to produce a modestly lower seasonal trend (Figures 38a&b). Parasitism was very low for both treatments (Figures 35a&b). Aphid introductions (see Figure 35c), meant to keep the declining aphid populations at a level where the experiment could continue, may have overshadowed the impact of mortality agents on FRI values.

OVERVIEW. In spite of the extra effort to sample mortality agents and rate aphid numbers at the plant level during 1985, results for that year were more difficult to interpret than those for the 1984 season. Several general comments can be made for both years when considering the data collected only in September of both seasons: 1) treatment NONE+W consistently produced high FRI means with pesticide protection while NOCHEM supported low aphid populations and high levels of each agent; 2) the pathogen alone did substantially reduce aphid numbers; and 3) it

seems that a protective covering over the plant enhanced increased aphid growth.

Plant injury assessment, chemical barrier trial.

The criteria used to describe the percent reduction in stem growth from season to season in the physical barrier trial were applied here. Three treatment groups were created based upon the degree of exclusion produced by the pesticides. Of the 12 plants that had all agents active (NOCHEM); none died, 58.3% showed greatly reduced growth, 16.7%--reduced growth and 25%--no difference. Of the 22 plants with some agents active (PRED&PAR, DIS); 91% died or had substantially reduced stem numbers and 9% were relatively unaffected. The 18 plants with all agents excluded (NONE+W, SHELTER) had 83.3% dead or severely reduced and 16.7% with reduced growth. The untreated plants still had a high number of negatively affected plants in spite of lower aphid populations. The remaining treatments that promoted aphid growth produced bare spots where plants once grew.

Coccinellid abundance by species.

Data from visual counts of experimental plants emphasized only coccinellids, and had two applications: 1) to link reductions in aphid numbers with elevated predator densities and 2) to verify the impact of pesticides on the beetles. However, easy field identification also allowed us to list the most abundant species in the plot. For comparative purposes, the relative ranking was expressed as a percent of the combined total of all beetle species observed in two treatments--PRED&PAR and NOCHEM. Coccinellids on these treatments were not subjected to insecticides or hand removal. In 1984 *C. maculata* was the most abundant comprising 46.2% of the seasonal total (823), followed by

H. convergens (31.2%) and *C. transversoguttata* (10.9%). In 1985 *H. convergens* was the most common (42.8%), followed by *C. transversoguttata* (23.4%), and *C. maculata* (14.2%); total, 691.

From the perspective of biological control, visual plant counts revealed which coccinellid species were actively searching the fern for asparagus aphids, especially when compared to counts from an abundance survey that sampled the entire plot with three relative methods (see Section II). For example, flight interception panels used in the survey trapped *H. parenthesis* most often; 32.0% of the total trap catch (334) in 1984 and a massive 64.1% in 1985 (total, 301). In 1984 sticky-can flight traps ranked the beetles as follows: *H. convergens* (34.2%), *C. maculata* (26.7%), *C. transversoguttata* (12.5%); total, 120. With minor differences in percentages the 1984 visual counts for the plot agreed with those observed on the plant. In 1985 can traps caught five beetle species with regularity, but top-ranked *H. convergens* made up 20.2% of the total (198). *C. transversoguttata* (42.0% of 440) was most often observed in the 1985 visual plot count followed by *H. convergens* (22.0%). Of the four methods, a walking visual count permitted an easy and accurate listing of the most common beetles, but examinations of aphid-infested plants revealed the coccinellids that were using the aphid resource to the detriment of the prey species.

Table 16. Mean finite rate of increase (± SEM) by Julian date for 1984 chemical barrier experiment.

JULIAN DATE	238		241		244		248		254	
TMT[a]	N[b]	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM
DIS	24	0.941±0.048 NS[c]	25	0.704±0.074 BC	25	0.610±0.065 AB	27	1.037±0.036 NS	26	0.936±0.035 B
NONE+W	27	0.957±0.066 NS	28	0.825±0.053 B	26	0.735±0.057 A	28	0.940±0.041 NS	28	1.037±0.030 A
PRED&PAR	28	1.141±0.026 NS	28	1.032±0.054 A	24	0.784±0.040 A	26	0.922±0.026 NS	28	1.027±0.034 A
NOCHEM	28	0.964±0.070 NS	28	0.574±0.067 C	28	0.528±0.065 B	27	0.850±0.060 NS	27	0.945±0.034 B
F (*df*)[d] :	2.15(3,12) p <.147		6.22(3,12) p <.009		2.72(3,12) p <.09		1.40(3,12) p <.29		3.2(3,12) p <.062	

JULIAN DATE	258		263		266		276	
TMT[a]	N[b]	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM
DIS	26	0.905±0.040 NS	27	0.847±0.030 NS	27	0.721±0.049 B	27	0.705±0.022 D
NONE+W	27	0.857±0.043 NS	28	1.016±0.022 NS	28	1.022±0.019 A	27	0.950±0.016 A
PRED&PAR	28	0.979±0.054 NS	27	1.012±0.031 NS	28	1.025±0.035 A	26	0.860±0.022 B
NOCHEM	28	0.889±0.044 NS	28	0.864±0.047 NS	28	0.803±0.057 B	27	0.788±0.030 C
F (*df*) :	0.53(3,12) p <.67		1.89(3,12) p <.185		9.32(3,12) p <.002		15.2(3,12) p <.0002	

[a] Treatment abbreviations described in Table 9.
[b] N, aphid colonies per treatment.
[c] Means within columns followed by the same letter are not significantly different (p < 0.10, Duncan's multiple range test; pg 448, SAS Institute, 1985). NS, nonsignificant result.
[d] The data were analyzed by Julian date; the F test, degrees of freedom and probability level were produced by the general linear models program (GLM program, pp 433-506, SAS Institute, 1985), plants treated as a replicate.

Table 17. Mean finite rate of increase (± SEM) by Julian date for 1985 chemical barrier experiment.

JULIAN DATE	195		198		202		205		213	
TMT[a]	N[b]	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM	N	MEAN ± SEM
SHELTER	28	1.032±0.054 NS[c]	28	1.078±0.022 A	28	0.970±0.029 NS	27	0.967±0.038 A	25	0.839±0.025 A
DIS	24	0.874±0.042 NS	25	0.983±0.067 A	26	0.944±0.041 NS	26	0.762±0.047 AB	28	0.818±0.032 A
NONE+W	25	0.937±0.037 NS	26	0.852±0.040 B	27	0.930±0.033 NS	25	0.651±0.069 B	24	0.778±0.036 AB
PRED&PAR	26	0.841±0.084 NS	28	0.780±0.059 B	28	0.944±0.042 NS	28	0.513±0.069 B	20	0.710±0.036 B
NOCHEM	28	1.137±0.066 NS	26	0.894±0.051 AB	28	0.828±0.050 NS	27	0.589±0.071 B	22	0.703±0.030 B
F (*df*)[d]		1.41(4,15) p <.277		2.32(4,15) p <.104		1.38(4,15) p <.286		2.24(4,15) p <.113		2.51(4,14) p <.089

JULIAN DATE	246		253		258		262		266	
SHELTER	16	0.940±0.054 NS	18	1.009±0.049 A	21	0.961±0.018 NS	20	0.930±0.028 AB	21	0.912±0.032 NS
DIS	19	0.807±0.068 NS	18	0.801±0.050 B	21	0.812±0.040 NS	20	0.773±0.046 ABC	21	0.838±0.049 NS
NONE+W	13	0.986±0.066 NS	20	0.791±0.046 B	19	0.900±0.038 NS	20	0.977±0.041 A	21	0.929±0.019 NS
PRED&PAR	19	0.696±0.067 NS	16	0.668±0.039 BC	19	0.863±0.035 NS	21	0.733±0.056 BC	20	0.760±0.034 NS
NOCHEM	28	0.800±0.050 NS	21	0.511±0.033 C	21	0.808±0.059 NS	21	0.620±0.067 C	21	0.769±0.055 NS
F (*df*)		0.96(4,11) p <.464		7.04(4,10) p <.005		2.06(4,10) p <.161		3.62(4,10) p <.045		1.66(4,10) p <.234

[a] Treatment abbreviations described in Table 9.
[b] N, aphid colonies per treatment.
[c] Means within columns followed by the same letter are not significantly different (p < 0.10, Duncan's multiple range test; pg 448, SAS Institute, 1985). NS, nonsignificant result.
[d] The data were analyzed by Julian date; the F test, degrees of freedom and probability level were produced by the general linear models program (GLM program, pp 433-506, SAS Institute, 1985), plants treated as a replicate.

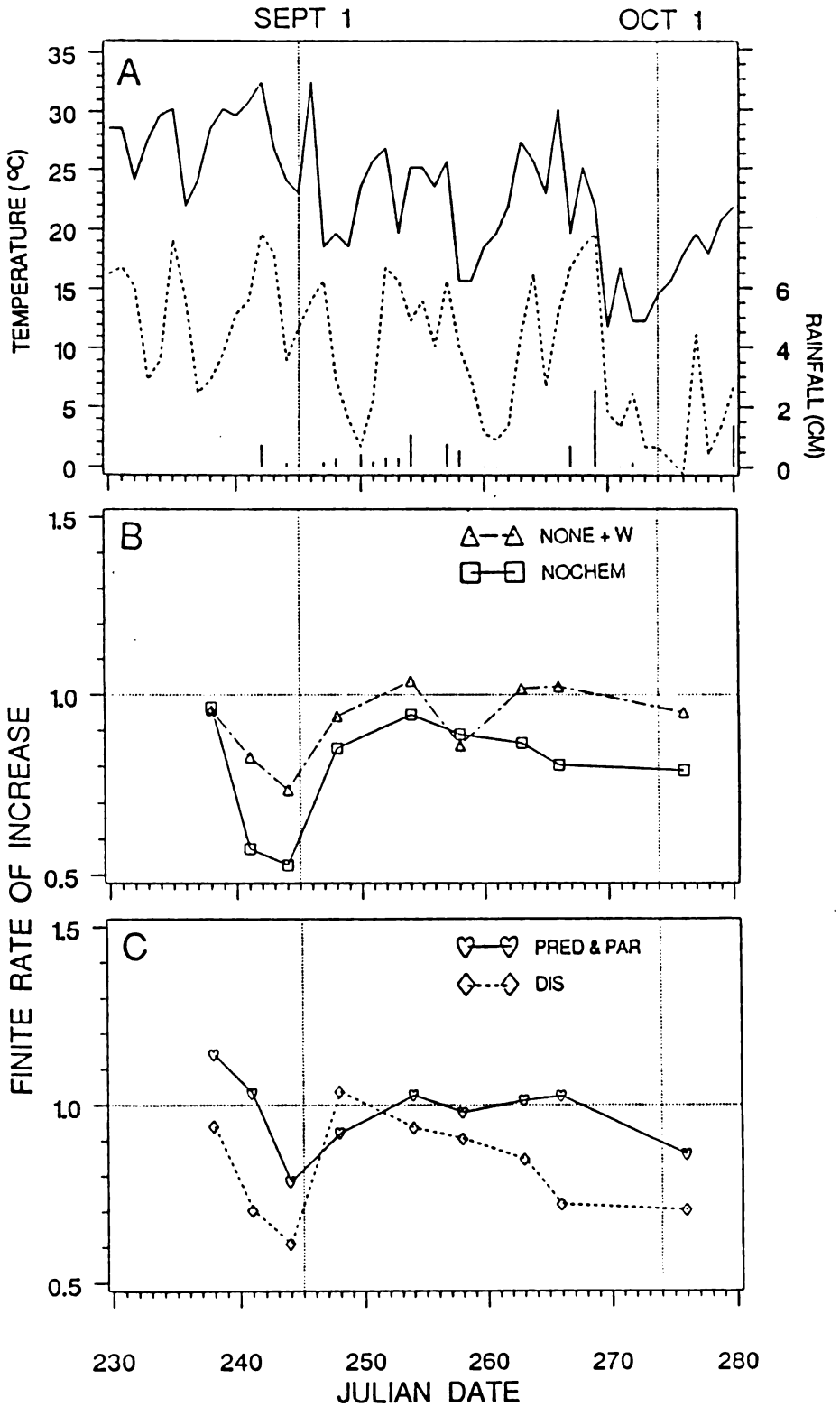

Figure 28. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: NONE+W, NOCHEM; and (C) Comparison-II treatments: PRED&PAR, DIS. The vertical dashed lines demarcate September 1-October 1, 1984.

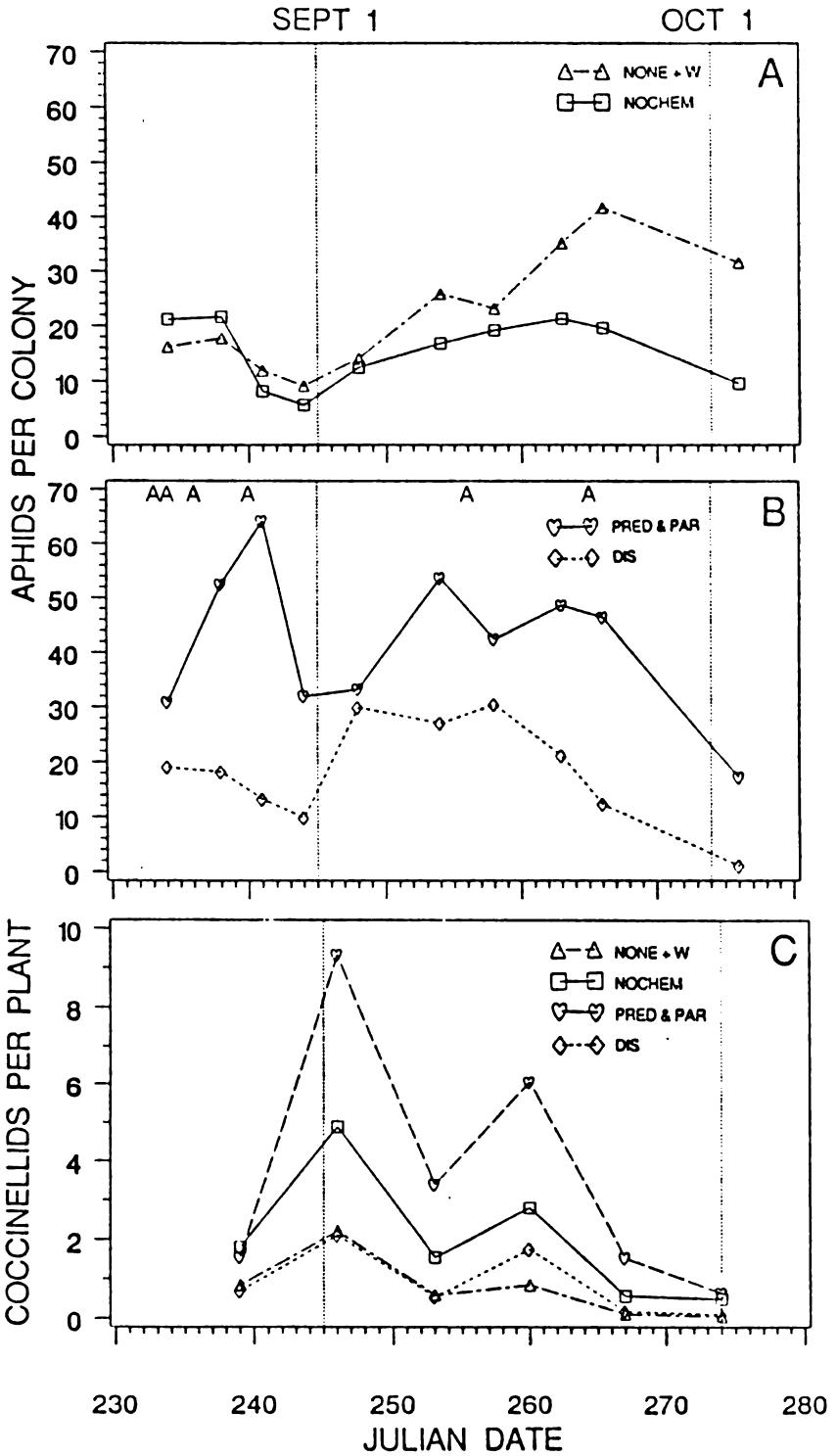

Figure 29. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. Mean number of aphids per experimental colony (A) for Comparison-I treatments: NONE+W, NOCHEM; and (B) Comparison-II treatments: PRED&PAR, DIS. (C) Mean number of coccinellid adults per plant for: NONE+W, NOCHEM, PRED&PAR, DIS. The vertical dashed lines demarcate September 1-October 1, 1984. The letters "A" indicate aphid introductions.

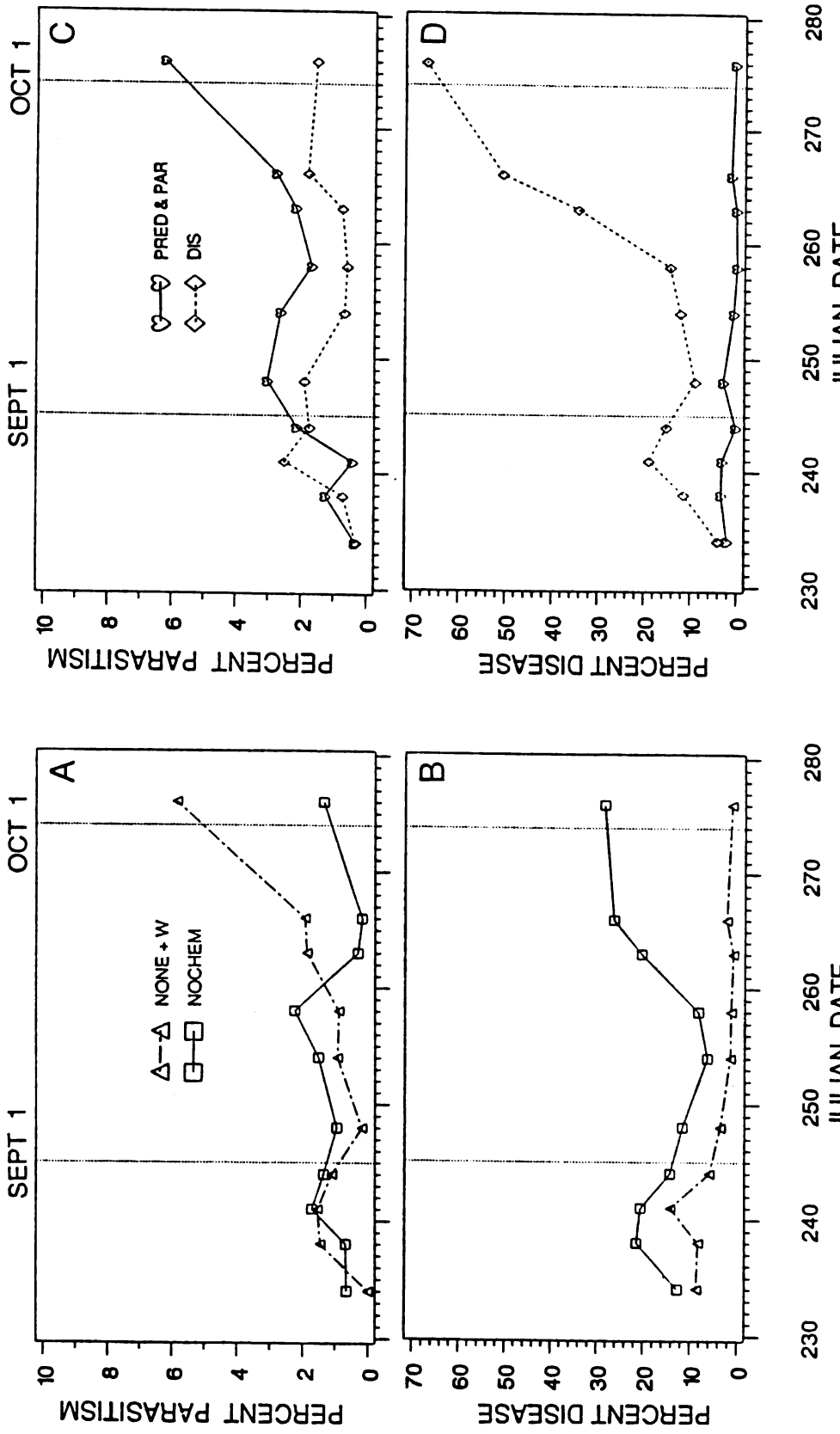

Figure 30. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. Mean percent (A) PARASITISM and (B) DISEASE for Comparison-I treatments: NONE+W, NOCHEM. Mean percent (C) PARASITISM and (D) DISEASE for Comparison-II treatments: PRED&PAR, DIS. The vertical dashed lines demarcate September 1-October 1, 1984.

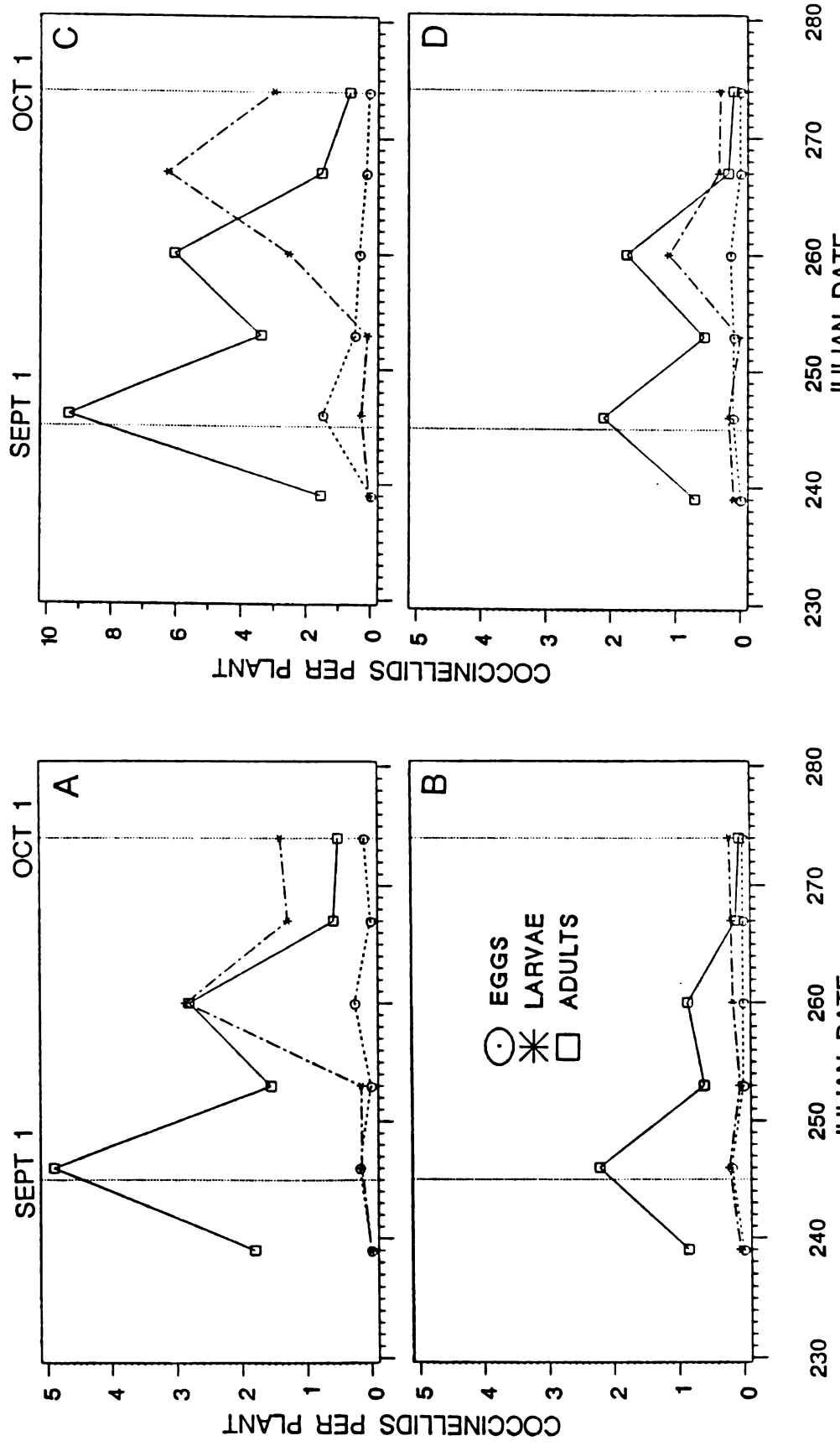

Figure 31. CHEMICAL BARRIER EXPERIMENT (Plot A), 1984. Mean number of coccinellids per plant by stage (adult, larva and egg) for the following treatments: (A) NOCHEM, (B) NONE+W, (C) PRED&PAR, and (D) DIS.

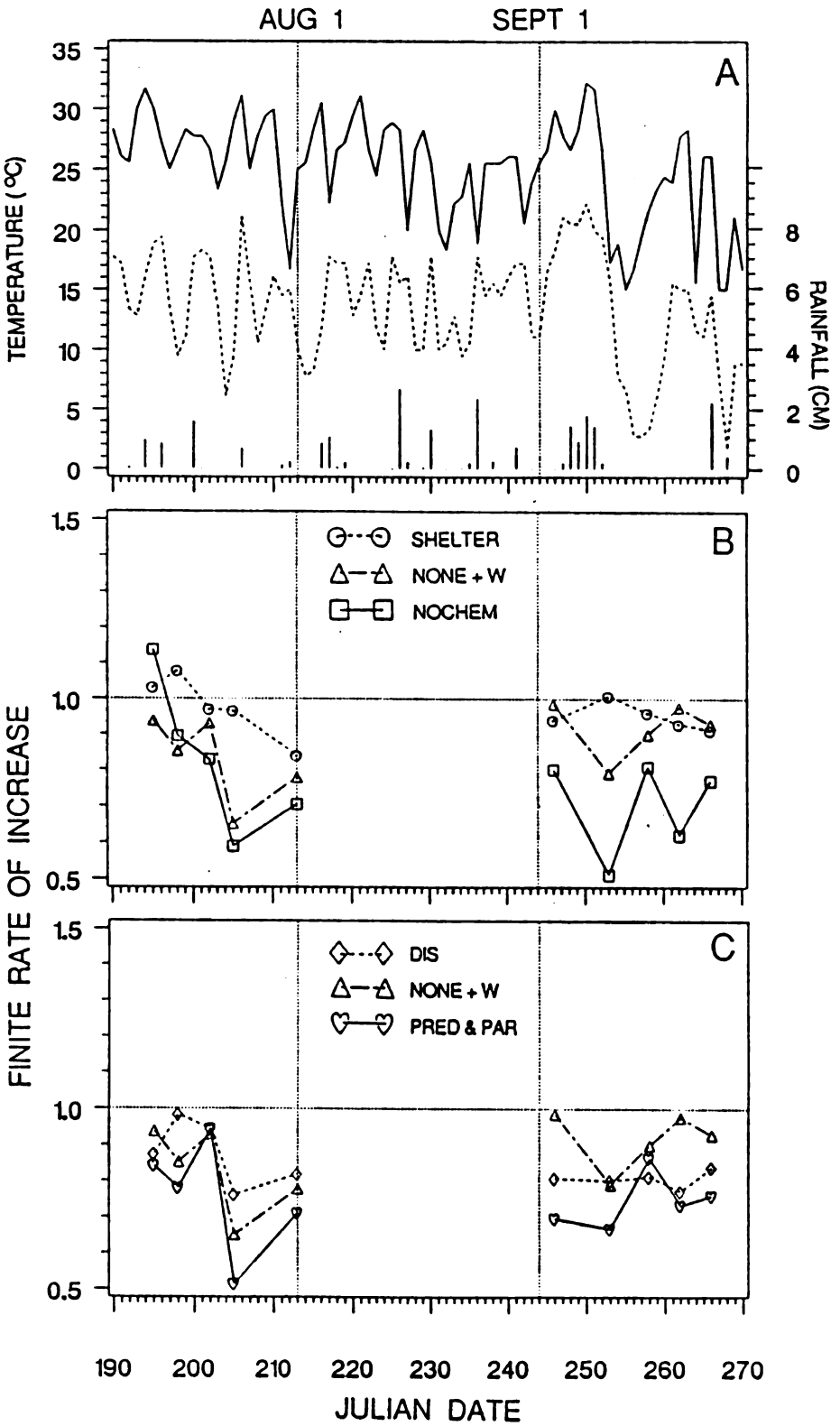

Figure 32. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. (A) Daily rainfall and maximum-minimum temperatures during the study period. Mean finite rate of increase (B) for Comparison-I treatments: SHELTER, NONE+W, NOCHEM; and (C) Comparison-II treatments: DIS, NONE+W, PRED&PAR. The vertical dashed lines demarcate August 1-September 1, 1985.

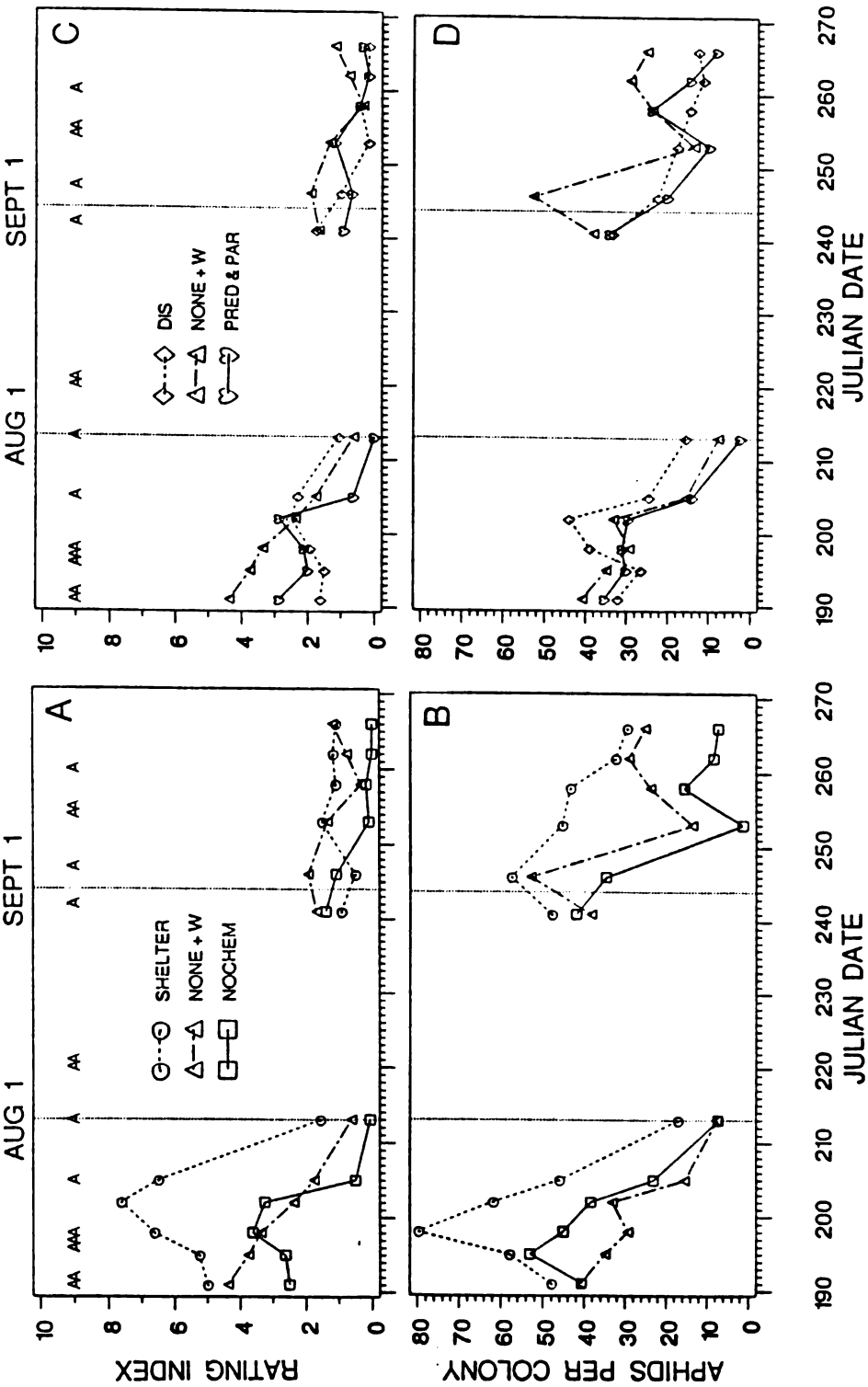

Figure 33. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. (A) Mean aphid rating and (B) mean number of aphids per experimental colony for Comparison-I treatments: SHELTER, NONE+W, NOCHEM. (C) Mean aphid rating and (D) mean number of aphids per colony for Comparison-II treatments: DIS, NONE+W, PRED&PAR. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "A" indicate aphid introductions.

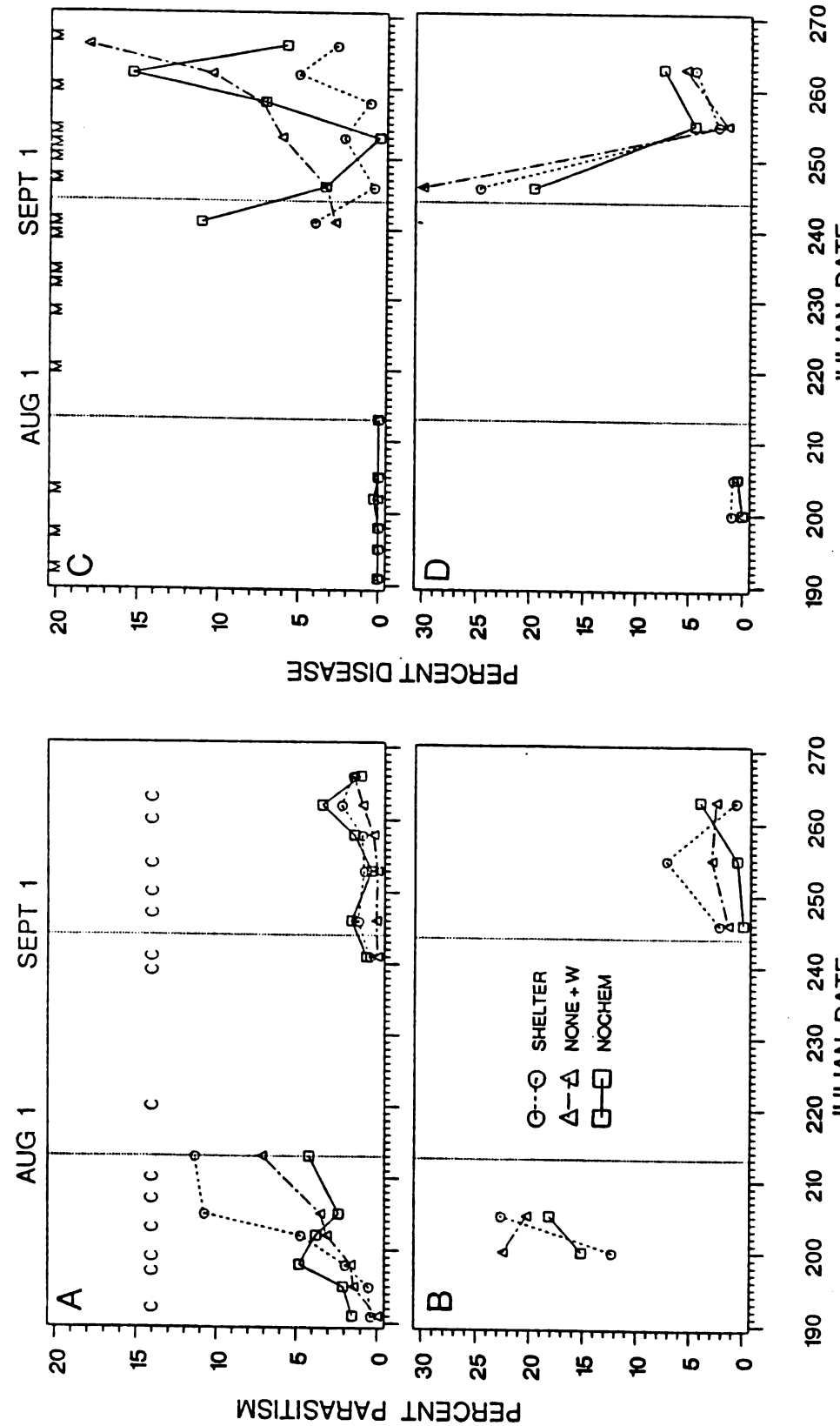

Figure 34. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean percent PARASITISM for Comparison-I treatments (SHELTER, NONE+W, NOCHEM) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-I treatments from two sources: C) colony counts and D) PPD. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M"). The vertical dashed lines demarcate August 1-September 1, 1985.

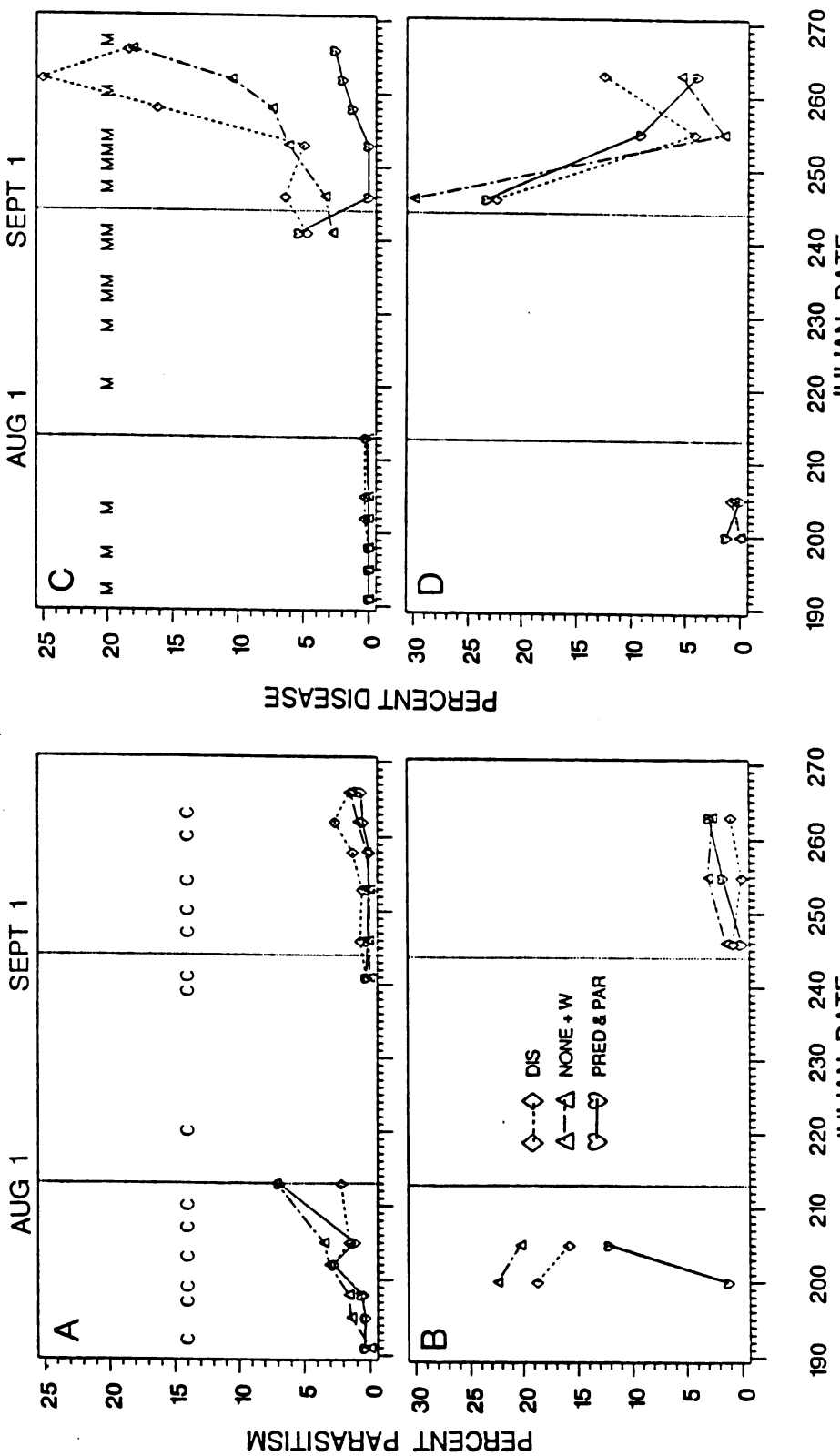

Figure 35. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean percent PARASITISM for Comparison-II treatments (DIS, NONE+W, PRED&PAR) from two sources: A) FRI experimental colony counts and B) the parasitism and disease determination (PDD). Mean percent DISEASE for Comparison-II treatments from two sources: C) colony counts and D) PPD. The letters indicate applications of carbaryl insecticide ("C") and maneb fungicide ("M"). The vertical dashed lines demarcate August 1-September 1, 1985.

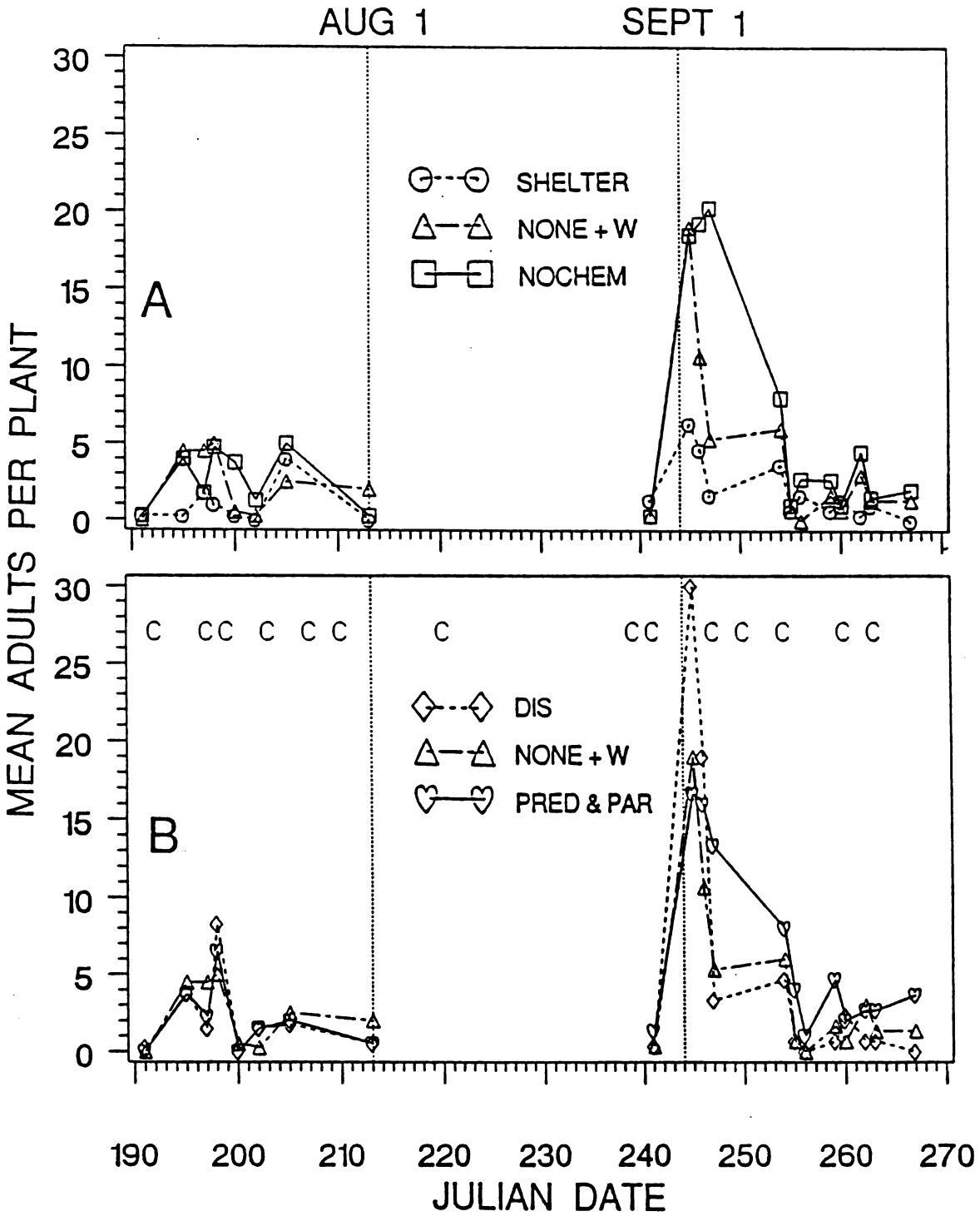

Figure 36. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean number of coccinellid adults per plant (A) for Comparison-I treatments: SHELTER, NONE+W, NOCHEM; and (B) Comparison-II treatments: DIS, NONE+W, PRED&PAR. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "C" indicate applications of carbaryl insecticide.

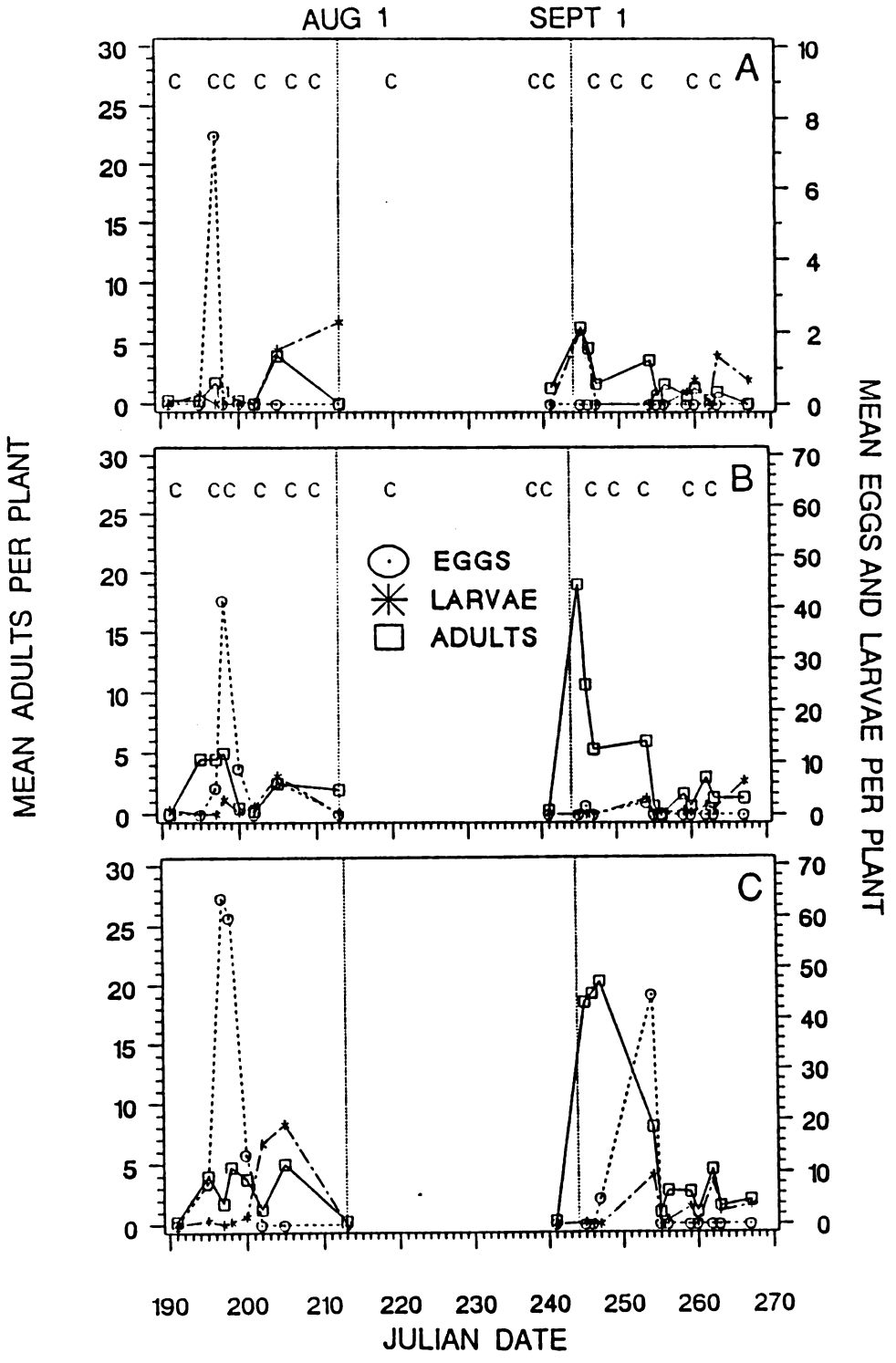

Figure 37. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (A) SHELTER, (B) NONE+W, and (C) NOCHEM. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "C" indicate applications of carbaryl insecticide.

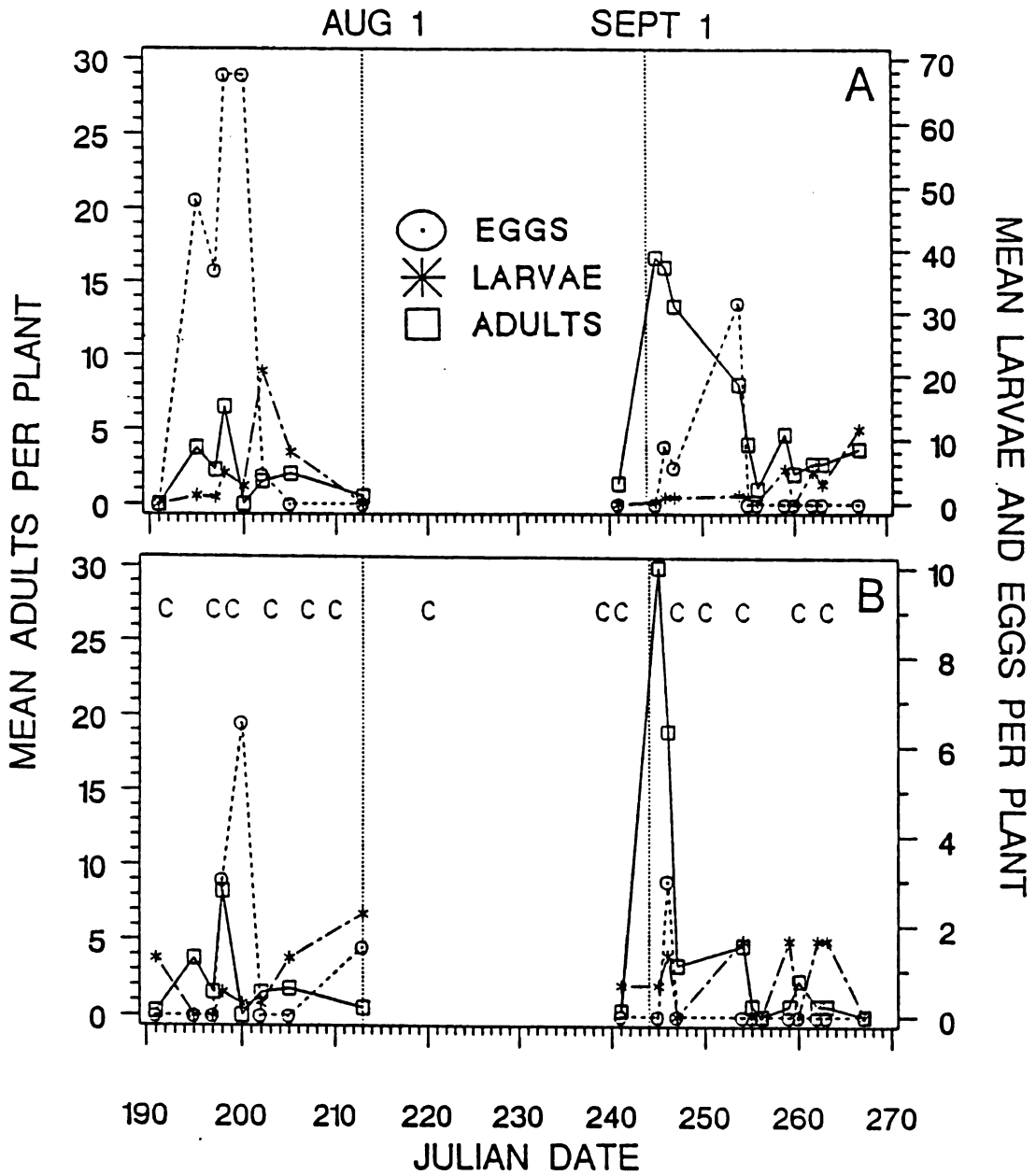

Figure 38. CHEMICAL BARRIER EXPERIMENT (Plot A), 1985. Mean number of coccinellids per plant by stage (adult, larva and egg) for: (A) PRED&PAR and (B) DIS. The vertical dashed lines demarcate August 1-September 1, 1985. The letters "C" indicate applications of carbaryl insecticide.

DISCUSSION.

PHYSICAL BARRIER STUDY.

This experiment permitted the association of fluctuations in aphid numbers with the presence of a specific mortality agent. Of the three biotic agents, the fungal pathogen was most efficient in lowering aphid growth rates for both seasons. However, the 1985 data suggested that, after a gradual build-up of their own numbers, aphidiids and coccinellids also had the potential to reduce the growth rates of even very high aphid populations. The difference between years was probably related to the greater numbers of parasitoids and predators introduced into the cages in 1985. Since it was not introduced, only the pathogen was able to naturally regulate its response to aphid densities.

Overall, caged aphids reached and maintained higher mean levels than uncaged populations. Under the proper conditions the aphid can build up tremendous numbers in Michigan asparagus plantings. This outcome suggests that the local climate, i.e. temperature and relative humidity, is not a limiting factor for this introduced species. A dense, bushy fern that simulates the caged conditions may also promote aphid growth by reducing the impact of rain and wind to create a favorable microhabitat.

The maneb fungicide demonstrated its influence on the pathogen. This compound promoted the build-up of extremely high aphid numbers in cages by prohibiting the fungal pathogen from fully expressing its potential. Without successive applications the pathogen quickly increased to become a major mortality factor. From the perspective of treatment execution, the parasitoid was also a persistent threat to the

aphid. It often introduced unwanted mortality by penetrating the cage barriers and reducing aphid reproduction. The season-long presence of both agents subjected the aphids to constant mortality pressures.

Recent exclusion studies both support and refute the ability of natural enemies to control other aphid species. Obrycki et al. (1983) compared an uncaged or "open"-cage treatment to a situation where aphids on potatoes, primarily the green peach aphid (*Myzus persicae* [Sulzer]) and potato aphid (*Macrosiphum euphorbiae* [Thomas]), were protected by an exclusion cage. Obrycki et al. reported that aphid densities were reduced >65% in open cages compared to closed cages. The authors attributed the decrease to naturally-occurring aphid predators (mainly Coccinellidae and Chrysopidae) and parasitoids (primarily Aphidiidae). Diseased aphids occurred in such low numbers that the authors discounted the impact of entomopathogenic fungi.

Carroll & Hoyt (1984) also used exclusion cages, but in an apple orchard. This study also showed lower trends for uncaged apple aphid (*Aphis pomi* DeGeer) colonies than those caged. However, the authors commented on the lack of synchrony between this aphid and its most effective predators during the summer months. Most of the eight identified coccinellid species were rare and only contributed to early-season control.

Kring et al. (1985) and Liao et al. (1985) introduced natural enemies into cages as well as evaluated opened- and closed-cage situations. Liao et al. stated that populations of the blackmargined pecan aphid (*Monellia caryella* [Fitch]) in the opened cages declined faster than those in the closed cages, or never attained levels observed in closed cages. Though the coccinellid populations in our cages had an

impact on the asparagus aphid, Liao et al. reported that chrysopid or coccinellid larvae were able to eliminate aphid populations in caged situations. Kring et al. indicated that coccinellids possessed the potential to reduce greenbug, *Schizaphis graminum* (Rondani), populations but the beetles demonstrated no suppressive capacity during the early portion of the growing season.

Frazer et al. (1981) modified cages to ascertain weather effects. When comparing pea aphid (*Acyrthosiphon pisum* Harris) densities in cages that lacked walls or a roof to densities in closed cages, the authors stated that their experiments eliminated the possibility that the cages merely protected the aphids from wind and rain. Their study also demonstrated a clear association between the low rate of aphid increase in the open field and the aggregation of predators. The overall conclusion was that pea aphid densities in alfalfa at Vancouver, Canada were normally held down by a complex of predator species, each responding to changes in aphid density.

CHEMICAL BARRIER STUDY.

The degree of protection offered by the chemical applications did not produce differences as dramatic as the physical barrier experiment. Similar to the other study, the uncaged, untreated plants consistently had the lowest mean growth levels. Native natural enemies were always present at some level and used the introduced aphid as a food resource when available.

A clear distinction between the impact of abiotic and biotic factors was not provided by this experiment. We assumed that the SHELTER treatment would reduce the negative effects of wind and rain

enough to produce a treatment difference. The shelter and cages probably influenced other undetermined abiotic factors, as well as behavior, to produce their effects. The sparseness of the experimental ferns in comparison to plants often encountered in commercial plots may have exaggerated the outcome.

Walker et al. (1984) reported that natural enemies did not control potato aphid, *M. euphorbiae*, populations in Ohio but rainfall in combination with high winds appeared to be the major mortality factor. He also noted that carbaryl applied at 0.1782 kg (AI)/0.405 ha did not seem to affect aphid populations. These results would relate to our untreated and insecticide-treated plants.

SAMPLING TECHNIQUES AND METHODOLOGY.

The decision to study each mortality agent in an integrated experiment, rather than as an isolated component of the larger system, required the implementation of a comprehensive sampling scheme. The quantity and variety of information needed to positively implicate a natural enemy in the reduction of large aphid populations often poorly translated into two-dimensional graphics or narrative script. Therefore, the presentation of this multidimensional data set did not make for quick reading nor yield unearned insights on cause-and-effect relationships.

In spite of the difficulties associated with presentation, this study offered some innovative approaches for monitoring and recording the impact of beneficial insects on their hosts. First, the finite rate of increase was a flexible calculation that expressed the growth of dissimilar starting units, both in time and magnitude, as a single index

that did not require elaborate transformations for statistical analysis. The nondestructive nature of this approach preserved scarce resources of aphids and plants, as well as the mortality agents, that would be removed by frequent stem samples. The finite rate of increase calculation also demanded that the researcher follow the biological fate of selected colonies thus preserving the continuity of their fluctuations.

The finite rate of increase statistic was not without limitations, especially concerning its underlying assumptions such as: stable or uniform age distribution, unlimited food and space, no emigration, no dispersal of alates, no oviposition of overwintering eggs, no loss due to factors other than the active mortality agent of the treatment, and the requirement that each aphid experiences the same environmental conditions (temperature, RH, wind, rain, etc). In spite of potential incongruities, additional measurements to determine mean aphids per colony and plant infestation ratings both complemented and verified the trends revealed by mean rates of increase. When these data were combined with multiple surveys of the active mortality agents, the real trends became evident.

Improvements to our methodology would include the following: 1) starting the experiments with smaller aphid populations so that the natural enemies could influence the rate of increase before the aphid reached levels that damaged the plant; 2) reducing the time between colony counts to a maximum of 4 days; 3) increasing the number of colonies per plant and plants per treatment; and 4) including treatments that better assessed the "cage effect" and the impact of weather on aphid growth rates.

ARTICLE 3

Egg cannibalism by newly-emerged coccinellids (Coleoptera: Coccinellidae)--its impact on viable eggs, larval survival and time spent on the egg mass.

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ABSTRACT

The eggs and larvae of four coccinellid species (*Hippodamia convergens* Guerin, *Coleomegilla maculata lengi* Timberlake, *Coccinella transversoguttata richardsoni* Brown, and *Coccinella septempunctata* L.), from field-caught and laboratory-reared cultures, were used to determine the impact of cannibalism.

Egg masses were monitored to determine mean hatch rates. Data for the 4 species in both groups showed that 72-89% of the eggs produced larvae. In one trial cannibalism was prevented by removing newly-emerged larvae. The proportion of viable eggs normally consumed ranged from 5.4% (*C. transversoguttata*) to 20.8% (*H. convergens*). This trial also revealed that many eggs were nonviable, ranging from 7-29% over all species.

Newly-emerged larvae that consumed one egg survived from 1.6-2.1 days longer than unfed individuals, but did not molt. Larvae that consumed two eggs did not appreciably increase their life span beyond that gained from one egg, but a large number of them molted to the second instar (49-87%, over all 4 species).

Cannibalism did not greatly delay mean time to dispersal for *H. convergens* larvae. Departure times from batches with cannibalism rates of up to 0.5 eggs consumed per larva were not substantially later than from batches without cannibalism (21.5 vs 18 hours). The number of eggs per batch may influence the dispersal process. *H. convergens* larvae hatching from eggs that were clustered (no cannibalism) left the egg batch later than those emerging from single, isolated eggs (15.2 vs 4.0 hours).

Key words: Coccinellidae, cannibalism, percent hatch, larval survival, time on egg mass, egg batch size.

INTRODUCTION

The contribution of the predaceous larval stage cannot be ignored when evaluating the impact of aphidophagous coccinellids on a prey population. Factors that influence abundance, survival or behavior of coccinellid larvae can also effect the overall predatory response by these predators. Egg cannibalism, i.e. newly-hatched larvae feeding on unhatched eggs in their own egg mass, is such a factor that can have both negative and positive results. For example, larval numbers are reduced when viable eggs are destroyed. Pienkowski (1965) reported the effective reduction of larvae due to cannibalism was 12.7% for *Coleomegilla maculata lengi* Timberlake after adjusting for the number of nonviable eggs. Pienkowski also calculated a 11.8% reduction for *Adalia bipunctata* (L.) using Banks' (1956) data and estimated a 2.9% decrease for *A. decempunctata* (L.) based upon Dixon's (1959) study.

Cannibalistic behavior can have a positive impact on larval survival. Banks (1956) and Dixon (1959) stated that cannibalism

produces an increased life span for larvae that do not encounter prey. Pienkowski (1965) acknowledged this outcome but also found that cannibalism extended the time interval between eclosion and dispersal, and resulted in larvae which were less active after leaving the egg mass.

Our first objective was to determine the number of viable eggs destroyed by cannibalistic larvae. This involved monitoring the fate of all eggs in a batch. To distinguish between viable and nonviable eggs, newly-emerged larvae were removed before they ate any unhatched eggs. The mean number of eggs per batch could also be calculated at this point. Second, we assessed the benefit a larva gained by eating an egg. Since increased survival was a major advantage of cannibalism, the longevity of unfed and egg-fed larvae was measured. In addition, comparisons between egg-fed and aphid-fed individuals were made. Coccinellid larvae usually spend some time on the egg mass before dispersing. Our last objective was to evaluate if cannibalism increased the predispersal interval. This entire effort was conducted for several beetle species from both field-caught and laboratory-reared sources.

MATERIALS AND METHODS

Adult coccinellids were collected from asparagus plants (*Asparagus officinalis* L.) during September 14-October 4, 1985. Three species commonly found in asparagus were selected: *Hippodamia convergens* Guerin, *Coleomegilla maculata lengi* Timberlake, and *Coccinella transversoguttata richardsoni* Brown (see Section II). We included a fourth beetle, *Coccinella septempunctata* L., that was introduced into the U.S. and recently reported in Michigan (Schaefer 1987, Section II).

Adult beetles were segregated by species into large petri dishes (150 by 15 mm). Once copulation began, females were separated into smaller petri dishes (60 by 15 mm) and assigned a number while the males were left aggregated in the larger dishes. Atallah (1966) noted that maximum egg production for *C. maculata* was obtained by confining mated females singly while satisfactory production occurred with one male and one female in an oviposition cage. Using this method, we separated mating beetle pairs after 24 hours. If oviposition did not begin within 48 hours, a male was reintroduced until eggs were produced. The dishes were kept in a growth chamber at 22°C, photoperiod of 16:8 (L:D), and 60-80% relative humidity (RH).

To create a favorable substrate for oviposition, small pieces of paper towel (4 by 8 cm) were folded in half and loosely placed in petri dishes containing females. Female coccinellids more often oviposited on the underside of the folded paper towel than on the filter paper fitted into the dish bottom or on the plastic sides. Egg masses were removed daily and fresh toweling and filter paper were inserted. We cut the excess paper from around the egg mass before inserting it into a transparent zip-lock plastic bag (6.5 by 9.0 cm). To minimize damage from handling while in the bag, egg batches were loosely placed on filter paper (7 cm dia.) that was folded in a way to contain them. The oviposition date and female's identifying number were recorded for each egg mass. Collection bags were placed in the same growth chamber as the adults.

The beetles were fed asparagus aphids, *Brachycorynella asparagi* (Mordvilko), and pea aphids, *Acyrthosiphon pisum* (Harris). Each isolated female was provided an overabundance of aphids, approximately

20-30 pea aphids or 75-150 asparagus aphids per day. Hagen & Sluss (1966) reported a daily consumption rate of 14-19 pea aphids per day for *H. convergens* during its preoviposition period.

Only the larvae of field-collected beetles were reared out to produce the laboratory-reared adults. These adults were treated similarly to the field-collected adults with respect to feeding and rearing conditions.

FATE OF EGGS.

The hatching process, described by Banks (1956) and Brown (1972), begins 3-5 days after oviposition (22°C, 16:8 L:D, 60-80% RH). Prior to hatching the egg darkens; the eyes and segmented embryo are discernible through the chorion. Soon thereafter, the larva ruptures the egg near the top and squeezes out. Upon emerging, it rests on the egg shell anchored to the inside of the empty shell by the tip of the abdomen. Except for flexing movements, the larva remains stationary for about an hour until its cuticle hardens and darkens. As both Banks and Brown noted, the larva remains on or near the egg mass for 12-24 hours after eclosion and it is during this time that the destruction of unhatched eggs takes place.

To prevent cannibalism of unhatched eggs, the newly-emerged larvae had to be removed within 1-2 hours of eclosion. Since it was difficult to observe an egg mass at this precise stage of development, many batches were evaluated after cannibalism occurred. This situation produced three levels of assessment and three to five categories for the fate of eggs.

The first assessment level occurred well after larvae emerged and

often after dispersal from the egg mass. Eggs were categorized as: 1) those producing viable larvae (EMERGED), 2) unhatched eggs which remained yellow without the yolk undergoing differentiation (EGG-NONVIABLE), 3) darkened eggs containing developed embryos that failed to emerge (DARK-NONVIABLE), and 4 & 5) the cannibalized counterparts of categories 2 & 3 (EGG-EATEN & DARK-EATEN). Although shriveled and collapsed, the two kinds of consumed eggs could be distinguished by the traces of yellow yolk for EGG-EATEN, or the darkened remains within the shell for DARK-EATEN. However, viability could not be determined for eaten eggs.

At *level II* the egg mass was observed 2-4 hours before hatching and the number of eggs that synchronously darkened (DARKENED) were recorded. Failing to remove the larvae before cannibalism started, we counted the number of larvae that emerged from the synchronously darkened eggs (EMERGED) and then categorized the remaining eggs as described for *level I*. As an expression of synchronous hatching, the number of emerged larvae was divided by the number of eggs that synchronously darkened.

The third level of observation produced a unique data set with categories that were similar but more comprehensive than at the other two levels. As for *level II*, the number of synchronously darkened eggs (DARKENED) was noted. Larvae that emerged from darkened eggs (EMERGED1) over a 1-2 hour period were removed to prevent cannibalism. This procedure eliminated two categories, DARK-EATEN and EGG-EATEN, and created a second class of darkened eggs (DARKENED2) that often produced viable larvae (EMERGED2). Since the second group of larvae emerged over an extended period, it was difficult to control cannibalism and produce

batches that could be included at this level.

The effort to collect data at *level III* was needed because observations at *level I* suggested that the second group of darkened eggs was usually cannibalized by larvae that synchronously emerged. By excluding all cannibalism, we could then separate the truly nonviable eggs (EGG-NONVIABLE and DARK-NONVIABLE) from viable eggs that matured later and were at risk of being destroyed.

LARVAL SURVIVAL.

Four experiments were conducted to determine the impact of egg cannibalism on larval survival. In *trial I* of this series, egg masses were collected and handled as described above. An experimental batch was selected if: 1) the approximate time of emergence could be determined within 2 hours, and 2) all cannibalism was prevented by removing the emerged larvae. Larvae of *H. convergens* from both source groups were employed, but only egg masses from laboratory-reared beetles were used for the other three species.

The newly-emerged larvae were allowed to darken and harden for 24 hours before being isolated singly in small petri dishes (35 by 10 mm) lined with filter paper. The isolated larvae from a single egg mass were randomly assigned a feeding treatment per larva: 1) no food, 2) one coccinellid egg (*H. convergens*) from a freshly oviposited egg mass or 3) two such eggs. To ensure consumption, the eggs were placed in close proximity to the larva which was usually actively searching its environment after the 24-hour pretest period. The treatment dishes for all trials of this series were placed in the same growth chamber conditions as the adults.

A larva was considered dead if it did not respond to prodding with an artist's brush by crawling 1-2 cm. This determination was revised for *C. transversoguttata* larvae because they responded to prodding with inactivity, i.e. 'playing dead'. In this case, a larva that did not attempt to right itself after being maneuvered onto its dorsum with the brush was deemed dead after 30 seconds of observation.

Larval survival was monitored every 4 hours except from 2400 to 0800 hours. The median value between the two observation periods when a larva was last seen alive was used as the survival time, i.e. $(T_2 - T_1)/2$. Larvae that escaped or were injured during counting were eliminated from the data base. The number of larvae that molted to the second instar was also noted in each treatment by batch.

Execution of the second experiment was similar to *trial I*. Here, treatments were: 1) no food, 2) one *H. convergens* egg from a newly oviposited mass, 3) three adult, apterous asparagus aphids and 4) one beetle egg and three aphids. Larvae provisioned with eggs and aphids were monitored to ensure that they consumed everything. In treatments 2 and 3 the single egg and the aphid group were usually eaten within 24 hours of introduction. The egg and aphids combined (treatment 4) were all located within 48 hours. Aphids were replaced with fresh, healthy individuals if they were not eaten after 24 hours. Only larvae from laboratory-reared adults were used.

Since egg masses from different females were used, a randomized block design was employed to analyze these two experiments, blocking on female. Also, the difficulty in obtaining an equal number of batches from each female or equal number of larvae for each treatment produced an unbalanced data set. The data was analyzed with the SAS general

linear models program due to its unbalanced nature (GLM program, pp. 433-506, SAS Institute, 1985). The treatment means were separated by Duncan's multiple comparison test, $p < 0.05$ (p. 448, SAS Institute, 1985).

When hatch rates are well above 50%, the majority of cannibalistic larvae probably do not consume an entire egg, and rarer yet--two eggs. Therefore, the third trial allowed for a range of egg consumption levels. Again, individual egg batches were observed to fix the time of emergence. Larvae were allowed to remain on the egg mass until all unemerged eggs were eaten and dispersal began. We did not monitor consumption by individual larvae. A subsample of the larvae (ca. 2/3) was randomly selected from a batch, placed singly into small petri dishes, and followed until death. The number of eggs potentially available for consumption by each larva in the egg mass was calculated as the number of unhatched eggs divided by emerged larva. Mean survival time was calculated for each egg mass. The relationship between mean survival times and the number of eggs available per larva was analyzed by regression (REG program, pp. 655-710, SAS Institute, 1985). Data from *trial I* of this series were also analyzed this way to provide a basis for comparison.

The eggs of *H. convergens* were used as the food source for all species tested in *trials I* and *II*. In *trial IV* we tested the hypothesis that the egg source was not a factor in these experiments by comparing the longevity of *C. transversoguttata* on its own eggs and on the eggs of *H. convergens*. Larvae from two egg masses of *C. transversoguttata* were isolated as described in *trial I* and fed either one *H. convergens* or *C. transversoguttata* egg.

TIME SPENT ON EGG MASS.

Two experiments were conducted to determine the factors that influenced the time larvae remained on their egg mass before dispersing. For the first trial of this series the emergence time was fixed and larvae were permitted to consume all unhatched eggs. We monitored the larvae every 2-4 hours until all had dispersed from the batch. Similar to the calculation for larval survival, the average departure time for each larva was determined from the last time it was observed on the mass: $(T_2 - T_1)/2$. The mean time spent on the egg mass by all larvae was regressed against the eggs available per larva (REG program, pp. 655-710, SAS Institute, 1985). Larvae that left the batch were removed from the petri dish. The treatment dishes for all trials of this series were placed in the same growth chamber conditions as the adults.

Some coccinellids oviposit eggs singly rather than in batches (Hagen 1962). To test the hypothesis that larvae postpone departure from the oviposition site when grouped in an egg mass, we compared the time a larva spent on a single egg with times for batches. Eggs in a mass were divided so that half remained clustered while the other half were separated as single eggs. By slightly moistening the paper towel from the bottom, the adhesive substance holding the eggs to the towel was dissolved to the point where eggs could be easily removed. Eggs were singly spaced on filter paper in the proper up-down orientation, the adhesive drying and affixing the egg back in place with no apparent damage. Unhatched eggs were removed from the massed eggs to prevent cannibalism. An *F* test was conducted to determine treatment differences (GLM program, pp. 433-506, SAS Institute, 1985).

The data collected in this second experiment also allowed us to

analyze the relationship of batch size and the time spent on the egg mass (REG program, pp. 655-710, SAS Institute, 1985). Since the larvae in *trial I* of that series were allowed to cannibalize, the regression model for this data included variables for both batch size and eggs consumed per larva.

RESULTS

FATE OF EGGS.

The quantity of eggs masses selected from each species was sufficient to produce representative means for percent hatch and batch size. However, the experimental design was not rigorous enough to make statistical comparisons between field-collected and laboratory-reared groups. Only percentages for *H. convergens* and *C. septempunctata* included an adequate number of adults to discuss potentially significant differences between the two groups.

Mean eggs per batch.

Within species, the mean number of eggs per batch differed for the two groups of adults (Table 18). Field-collected adults produced higher mean batch counts than the laboratory-reared beetles with the exception of *C. maculata*. This trend was supported by the range of means for individual beetles. For *H. convergens*, the 17 field-collected females exhibited means from 11-25 eggs while the 31 laboratory-reared beetles ranged from 8-20. Similarly, the 7 field-collected *C. septempunctata* adults varied between 15-39; the 3 laboratory-reared beetles, 18-24.

Beetle fecundity has often been measured in terms other than eggs per batch, such as eggs per day per female (Hagen & Sluss 1966, Smith &

Table 18. Number of eggs per batch (mean±SEM) for field-collected and laboratory-reared coccinellids.

	FIELD-COLLECTED			LABORATORY-REARED		
SPECIES	EGG BATCHES (FEMALES)[a]	EGGS/BATCH (±SEM)	RANGE (MIN-MAX)	EGG BATCHES (FEMALES)	EGGS/BATCH (±SEM)	RANGE (MIN-MAX)
H. convergens	280(17)	17.16±0.43	3-40	638(31)	13.98±0.24	2-39
C. transversoguttata	21(1)	28.14±2.45	13-47	87(5)	22.83±1.05	6-47
C. maculata	7(1)	7.00±1.36	3-13	9(2)	10.33±1.42	4-16
C. septempunctata	174(7)	27.80±1.11	4-84	18(3)	21.78±2.63	4-58

[a] Number of females producing egg masses.

Williams 1967) or total eggs per female (Balduf 1935, Hodek 1976). Our data for *C. maculata* were lower than that recorded by researchers who reported their findings as eggs per cluster. For example, Wright & Laing (1982) reported a mean of 13.6 for 77 egg clusters collected from corn plants. This figure agreed with their earlier field observations (Wright & Laing 1980). Pienkowski (1965) noted 11.8 eggs per mass for *C. maculata* based on 200 batches collected from alfalfa. Smith (1965) got this species to oviposit 13.2 eggs per cluster on an artificial diet of beef, and 11.0 on a liver diet. Furthermore, when three generations of this beetle were fed on a desiccated liver diet, the number of eggs per cluster for the first and second generation dropped off when compared to the field-collected beetles: 8.7, 6.9, and 11.2, respectively. For *C. septempunctata*, Banks (1956) reported a mean batch size of 32 for 16 clusters collected from beans while Shands et al. (1970) got this species to produce 25.7 eggs per batch in the laboratory. Both values are higher than those yielded in this study.

Percent hatch.

Level I--assessment after dispersal. The data for all four species and both groups indicated that a large number of larvae successfully emerged (72-89%, EMERGED, Table 19). Eggs that were unfertilized or slow in developing and subsequently cannibalized by the newly-emerged larvae varied from 5.2% for *C. maculata* (n = 7) to 22.1% for *C. septempunctata* (n = 18) (EGG-EATEN + DARK-EATEN, Table 19). The remaining eggs that were not eaten and could be clearly classified as nonviable also exhibited a wide range of values over all species and groups (0-11.1%, EGG-NONVIABLE + DARK-NONVIABLE).

Due to the limited number of female beetles that contributed egg

TABLE 19. Fate of eggs by category (mean percent ± SEM) and ranges for egg masses of field-collected and laboratory-reared coccinellids.

SOURCE:	FIELD-COLLECTED		LABORATORY-REARED	
CATEGORY[a]	PERCENT ±SEM	RANGE (MIN-MAX)	PERCENT ±SEM	RANGE (MIN-MAX)
Hippodamia convergens Guerin				
EMERGED	78.9±1.4	6-100	86.3±0.7	11-100
EGG-EATEN	12.0±1.0	0-87	5.8±0.4	0-50
DARK-EATEN	3.6±0.4	0-33	4.7±0.3	0-43
EGG-NONVIABLE	3.8±0.8	0-78	1.7±0.3	0-78
DARK-NONVIABLE	1.8±0.4	0-47	1.5±0.3	0-65
N (batches, females)[b]	237, 17		594, 31	
Coccinella transversoguttata richardsoni Brown				
EMERGED	74.3±4.9	38-100	71.9±1.9	25-100
EGG-EATEN	12.8±3.7	0-52	8.2±1.1	0-50
DARK-EATEN	1.7±0.8	0-10	12.9±1.6	0-47
EGG-NONVIABLE	7.0±3.4	0-40	3.5±0.9	0-35
DARK-NONVIABLE	4.1±2.0	0-21	3.6±0.9	0-33
N (batches, females)	16, 1		74, 5	
Coleomegilla maculata lengi Timberlake				
EMERGED	83.6±7.2	50-100	86.5±5.0	60-100
EGG-EATEN	5.2±3.7	0-25	11.3±4.5	0-40
DARK-EATEN	0.0±0.0	0-0	2.2±1.5	0-13
EGG-NONVIABLE	11.2±7.6	0-50	0.0±0.0	0-0
DARK-NONVIABLE	0.0±0.0	0-0	0.0±0.0	0-0
N (batches, females)	7, 1		9, 2	
Coccinella septempunctata L.				
EMERGED	89.1±0.9	32-100	75.3±3.7	50-100
EGG-EATEN	6.2±0.6	0-44	12.2±3.3	0-42
DARK-EATEN	3.7±0.5	0-44	9.9±2.8	0-40
EGG-NONVIABLE	0.7±0.4	0-58	2.0±2.0	0-36
DARK-NONVIABLE	0.4±0.2	0-25	0.6±0.5	0-7
N (batches, females)	156, 7		18, 3	

[a] EMERGED, egg produced viable larva; DARK-, egg that began maturation process by darkening; EGG-, egg that remained yellow, undifferentiated; -EATEN, egg that was cannibalized by emerged larvae; -NONVIABLE, egg that was not cannibalized, but did not produce a viable larva.
[b] The number of females and their egg batches used to calculate means.

masses to the calculations, descriptive comparisons between field and laboratory groups by species seemed valid only for *H. convergens* and *C. septempunctata*. For *H. convergens* the percent hatch was higher for laboratory-reared beetles than field-collected adults (86.3 vs 78.9%, Table 19). This difference could be attributed to the higher percentage of eggs that were nonviable or eaten in the field group. This situation was reversed for *C. septempunctata*. The percentage of cannibalized eggs, i.e. categories EGG-EATEN & DARK-EATEN, for laboratory-reared beetles was twice that of the field-collected group resulting in a lower hatch rate (75.3 vs 89.1%, EMERGED, Table 19). The larvae of these two species were very efficient in consuming unhatched eggs. Only 1.1-5.6% of them remained uneaten to be recorded as nonviable (EGG-NONVIABLE & DARK-NONVIABLE, Table 19).

Level II--synchronously darkened. The data summarized in Table 20 is actually a subset of the eggs masses from *level I* because only two more observations were recorded for selected batches: 1) the number of synchronously darkened eggs and 2) the number of larvae to emerge from these eggs. At this second level of observation, the means showed that 73-96% of the eggs darkened for all species and source groups (DARKENED, Table 20). This meant that a large proportion of the eggs contained developing embryos. Also, a substantial proportion of the eggs that synchronously darkened completed development and hatched (85-100%, EMERGED/DARKENED, Table 20). The lowest percentage in this range occurred for laboratory-reared *C. transversoguttata*, a species that also exhibited a high percentage of cannibalized darkened eggs (12.9%, DARK-EATEN, Table 19).

Only data for *H. convergens* were comprehensive enough to be

TABLE 20. The number of eggs per batch (mean ± SEM) that synchronously darkened as a percentage of the total eggs and percent darkened eggs per batch that produced viable larvae for egg masses of field-collected and laboratory-reared coccinellids.

SOURCE:	FIELD-COLLECTED		LABORATORY-REARED	
CATEGORY BY SPECIES	PERCENT ±SEM	RANGE (MIN-MAX)	PERCENT ±SEM	RANGE (MIN-MAX)
Hippodamia convergens Guerin				
DARKENED	83.7±1.9	25-100	92.6±0.8	29-100
EMERGED/DARKENED	94.6±1.3	15-100	95.2±0.6	50-100
N (batches, females)*	111, 17		212, 30	
Coccinella transversoguttata richardsoni Brown				
DARKENED	73.3±12.6	49-90	80.7±2.3	64-100
EMERGED/DARKENED	98.5±1.9	95-100	85.3±3.6	55-100
N (batches, females)	3, 1		18, 5	
Coleomegilla maculata lengi Timberlake				
DARKENED	85.7±14.3	71-100	96.2±3.9	92-100
EMERGED/DARKENED	100±0.0	100	100±0.0	100
N (batches, females)	2, 1		2, 2	
Coccinella septempunctata L.				
DARKENED	92.1±2.1	37-100	95.5±2.7	89-100
EMERGED/DARKENED	96.8±0.8	78-100	96.0±1.6	92-100
N (batches, females)	40, 7		4, 2	

* The number of females and their egg batches used to calculate means.

complementary between the two assessment levels. For example, the percent darkened eggs from *level II* (DARKENED, Table 20) should be comparable to the combined percentages of emerged and darkened eggs at *level I* (EMERGED, DARK-EATEN and DARK-NONVIABLE, Table 19). The sum of these three *level-I* categories for both source groups of this species (field, 84.3%; laboratory, 92.5%) agreed with the percent observed to synchronously darken (83.7 and 92.6%, Table 20). Except for field-collected *C. septempunctata*, samples were too small to convincingly reflect relationships of this nature for other species.

Level III--cannibalism prevented. In contrast to the high number of eggs that successfully emerged (EMERGED, Table 19) or synchronously darkened (DARKENED, Table 20) in the first two observation levels, percentages in these two categories were lower for *level-III* egg masses. Over all species and groups, the number of larvae to first emerge as a group comprised 57-74% of the total eggs (EMERGED1, Table 21). Any eggs that matured after the first group of larvae emerged were at risk of being cannibalized. This late group varied from 5.4% for field-collected *C. transversoguttata* (n = 5) to 20.8% for laboratory-reared *H. convergens* (n = 44) (EMERGED2, Table 21). Since the newly-emerged larvae had to be removed as soon as they were discovered to prevent cannibalism, the distinction between the two emerged groups was sometimes arbitrarily determined. However, this intervention revealed that a high percentage of the remaining darkened eggs were viable--from 46% for *C. transversoguttata* (n = 5) to 84% for *C. septempunctata* (n = 18) (EMERGED2/DARKENED2, Table 21). Also, nonviable eggs were often quite numerous; 7.2% for *C. septempunctata* (n = 18) to 29.3% for *C. transversoguttata* (n = 5) (DARK-NONVIABLE + EGG-NONVIABLE, Table 21).

TABLE 21. Fate of eggs by category (mean percent ± SEM) for egg masses where cannibalism was prevented by removing newly-emerged larvae.

SOURCE:	FIELD-COLLECTED		LABORATORY-REARED	
CATEGORY[a]	PERCENT ±SEM	RANGE (MIN-MAX)	PERCENT ±SEM	RANGE (MIN-MAX)
Hippodamia convergens Guerin				
EMERGED1	67.4±3.7	10-96	66.4±3.4	7-96
EMERGED2	9.1±1.3	0-41	20.8±3.4	0-93
DARK-NONVIABLE	9.5±1.9	0-56	7.3±1.3	0-46
EGG-NONVIABLE	14.0±2.6	0-80	5.5±1.2	0-31
DARKENED	80.9±2.8	20-100	87.2±2.3	23-100
EMERGED/DARKENED	81.4±3.1	25-100	77.7±3.7	7-100
EMERGED2/DARKENED2	67.9±6.3	0-100	70.4±6.5	0-100
N (batches, females)[b]	43, 13		44, 19	
Coccinella transversoguttata richardsoni Brown				
EMERGED1	65.3±3.5	53-74	57.2±5.2	23-84
EMERGED2	5.4±2.3	0-13	16.4±4.0	0-38
DARK-NONVIABLE	9.9±4.5	2-27	11.8±2.9	0-32
EGG-NONVIABLE	19.4±3.7	7-30	14.4±3.8	0-41
DARKENED	68.3±3.0	60-77	78.7±4.1	60-100
EMERGED/DARKENED	95.5±1.8	89-100	73.3±6.4	39-100
EMERGED2/DARKENED2	46.0±16.0	0-100	51.6±9.8	0-100
N (batches, females)	5, 1		13, 5	
Coccinella septempunctata L.				
EMERGED1	74.2±4.5	13-94	---	---
EMERGED2	18.6±4.3	0-73	---	---
DARK-NONVIABLE	3.9±1.0	0-12	---	---
EGG-NONVIABLE	3.3±1.1	7-13	---	---
DARKENED	90.2±4.2	27-100	---	---
EMERGED/DARKENED	81.2±3.3	50-100	---	---
EMERGED2/DARKENED2	84.0±6.6	0-100	---	---
N (batches, females)	18, 6			

[a] EMERGED1, first group of larvae to synchronously emerge; EMERGED2, larvae that emerged after removal of first group; DARK-, egg that began maturation process by darkening; EGG-, egg that remained yellow, undifferentiated; -NONVIABLE, egg did not produce a viable larva; DARKENED, eggs that synchronously darkened; DARKENED2, darkened eggs remaining after emergence of EMERGED1; EMERGED/DARKENED, percent darkened eggs that produced viable larvae. Except where noted, percents were calculated by dividing the number in each category by the total eggs in the egg batch.

[b] The number of females and their egg batches used to calculate means.

Pienkowski (1965) was also interested in egg cannibalism and its impact on viable eggs in *C. maculata*. He reported a 77.2% hatch rate for 141 batches taken from alfalfa, attributing the remainder to cannibalism (21.1%) and nonviability (1.7%). By monitoring separated eggs from 30 egg masses, Pienkowski adjusted the apparent cannibalism to account for nonviable eggs and stated that only 12.7% of the viable eggs are destroyed by newly-emerged larvae. Our small data set (n = 7 batches) indicated an 83.4% hatch for *C. maculata*; 5.2%--cannibalized and 11.2%--nonviable (Table 19). While investigating the influence of food quality on this same beetle, Smith (1965) reported hatch rates of 45, 63 and 71% for three aphid species. For *H. convergens*, Kirby & Ehler (1977) reported a 91.8% hatch rate for 837 eggs taken from grain sorghum. Our observed rates were lower for *H. convergens* (field-collected, 78.9%; laboratory-reared, 86.3%, Table 19).

LARVAL SURVIVAL.

Trial I--eggs only. Over all species and groups, larvae that consumed one egg survived between 1.6-2.1 days longer than unfed individuals (Table 22). Furthermore, larvae receiving two eggs only increased their life span by 0.32-0.85 days when compared with the one-egg group. (NOTE: Due to low sample size, these overall ranges do not include species *C. maculata* with 3.12 and 1.72 days, respectively.) The small incremental increase in life span between the one- and two-egg groups was probably related to the high percentage of larvae that molted to the next instar after eating two eggs. The advantages gained by molting, i.e. the ability to handle larger prey items or higher mobility, could be more important than increased life span under

TABLE 22. Survival time for newly-emerged coccinellid larvae for three feeding treatments.

A. LARVAE FROM FIELD-COLLECTED BEETLES:

**_Hippodamia convergens_ (8 egg batches, 4 females)[a].

EGGS FED PER LARVA	LARVAE TESTED	MEAN SURVIVAL TIME IN HOURS±SEM (DAYS)	MOLT (%±SEM)
2	64	144.3 ± 2.3A[b] (6.01)	48.7±9.4[c]
1	63	124.0 ± 2.2B (5.17)	0
0	63	75.2 ± 1.1C (3.13)	0

B. LARVAE OF LABORATORY-REARED BEETLES:

**_Hippodamia convergens_ (21 egg batches, 11 females).

2	116	114.1 ± 1.3A (4.75)	83.0±3.4
1	121	106.5 ± 1.3B (4.44)	0
0	139	54.9 ± 0.8C (2.29)	0

**_Coccinella transversoguttata_ (10 batches, 5 females)

2	67	122.6 ± 1.6A (5.11)	78.6±6.2
1	64	108.8 ± 1.6B (4.53)	0
0	71	70.0 ± 1.5C (2.92)	0

**_Coleomegilla maculata_ (1 egg batch, 1 female).

2	3	181.6 ± 2.9A (7.57)	66.6±0.0
1	3	140.4 ± 6.6B (5.85)	0
0	3	65.5 ± 10.1C (2.73)	0

**_Coccinella septempunctata_ (4 egg batches, 2 females.)

2	25	109.8 ± 1.3A (4.58)	86.5±7.1
1	27	101.6 ± 1.8B (4.23)	0
0	28	59.7 ± 0.8C (2.49)	0

[a] The number of egg batches and females from which the larvae were selected and assigned to the three treatments.
[b] Means within columns followed by the same letter are not significantly different ($p < 0.05$, Duncan's multiple range test; p. 448, SAS Institute, 1985).
[c] Percent that molted to the second instar for each egg mass.

conditions of high prey density.

Only *H. convergens* was represented in both source groups for this study (Table 22A&B). Larvae from field-collected females survived longer in each treatment level than those of laboratory-reared beetles, but they had a lower molting rate--48.7 vs 83.0%.

The unfed larvae in our small sample of *C. maculata* survived 65.5 hours (n = 3). Although the environmental conditions were not stated, Pienkowski (1965) recorded survival times of 70 hours (n = 13 larvae) and Smith (1961) stated 77 hours for unfed larvae of this species. Pienkowski also reported that larvae receiving one egg survived 88.1 hours (n = 9), a value considerably below our findings of 140.4 hours. However, Banks (1956) discovered a considerable increase in longevity between the unfed and one-egg treatments for *Adalia bipunctata* (L.); 60 and 100 hours, respectively (n = 5). In that study larvae also molted after eating 2-3 eggs. Brown (1972) conducted a similar trial with two species from South Africa. The coccinellid *Lioadalia flavomaculata* (De Geer) lived 38.0, 68.0 and 92.0 hours from time of dispersal on 0, 1, and 2 eggs respectively, while *Cheilomenes lunata* (F.) survived 48.6, 127.4 and 167.6 hours (n = 4, at 19-21°C).

Trial II--eggs and aphids. The introduction of aphids as food in the second trial produced some interesting results on larval survival (Table 23). First, two treatments--UNFED and 1 EGG--were identical to those executed in the first trial (Table 22B) and consequently exhibited very similar survival times. Second, there was no significant difference in survival when larvae were fed three aphids or the combination of one egg and three aphids. The one-egg and three-aphid treatments for *C. septempunctata* could not be declared different at $p <$

0.05 (Table 23). However, the egg-aphid group had a higher percent that molted to the second instar, a possible benefit from eating the nutrient-rich egg. The combination of molting and searching for a mobile prey may have contributed to lower incremental increases in longevity with the aphid and egg-aphid treatments. These times were not dramatically different than those calculated for the two-egg treatment in *trial I* (Table 22).

Trial III--uninterrupted cannibalism. This trial was only conducted on *H. convergens* larvae from both field and laboratory sources. For comparative purposes, the batch means produced by *trial I* for these two source groups were regressed against the number of eggs consumed per larva, i. e. 0, 1 and 2 eggs per larva. The regression line and data points for *trial I* suggest that the relationship between larval survival time and eggs consumed per larva was not truly linear (Figures 39a & 40a). Also, the regression equations for field-collected ($y = 79.6 + 34.1x$) and laboratory-reared beetles ($y = 63.1 + 29.7x$) suggested higher survival times for zero eggs consumed (y-intercept, Figures 39 & 40) than revealed by the mean survival times for unfed *H. convergens* larvae (Table 22).

The data for *trial III* also showed that newly-emerged larvae did not often consume an entire egg per larva (Figures 39b & 40b). The mean ($\pm$SEM) and range of eggs consumed per larva was 0.56 ± 0.12 (0.31-1.33) for the field group and 0.42 ± 0.07 (0.08-1.2) for the laboratory group. In comparison to the data from *trial I*, regressions for the field-collected group of *trial III* indicated a weaker relationship and shallower slope (Figure 39a&b). The laboratory source of *trial III* had a lower r^2 value than *trial I* but a similar slope (Figure 40a&b).

TABLE 23. Survival time for newly-emerged coccinellid larvae for four feeding treatments (larvae of laboratory-reared adults only).

TREATMENT	LARVAE TESTED	MEAN SURVIVAL TIME IN HOURS±SEM (DAYS)	MOLT (%±SEM)
**_Hippodamia convergens_ (12 egg batches, 5 females)[a].			
1 EGG & 3 APHIDS	56	122.2 ± 1.7A[b] (5.09)	95.8±2.8[c]
3 APHIDS	55	120.8 ± 2.5A (5.03)	72.6±9.5
1 EGG	57	113.6 ± 1.7B (4.73)	8.3±4.7
UNFED	58	59.8 ± 1.4C (2.50)	0
**_Coccinella transversoguttata_ (8 batches, 5 females)			
1 EGG & 3 APHIDS	46	120.2 ± 1.9A (5.01)	94.2±3.0
3 APHIDS	45	114.3 ± 2.0A (4.76)	70.8±6.6
1 EGG	45	107.1 ± 1.9B (4.46)	2.5±2.5
UNFED	45	67.2 ± 1.3C (2.80)	0
**_Coccinella septempunctata_ (2 egg batches, 2 females.)			
1 EGG & 3 APHIDS	18	109.6 ± 2.9A (4.57)	100±0.0
3 APHIDS	17	103.8 ± 1.0AB (4.35)	95.8±4.2
1 EGG	17	99.1 ± 2.6B (4.13)	0
UNFED	14	58.9 ± 1.1C (2.45)	0

[a] The number of egg batches and females from which the larvae were selected and assigned to the three treatments.
[b] Means within columns followed by the same letter are not significantly different ($p < 0.05$, Duncan's multiple range test; p. 448, SAS Institute, 1985).
[c] Percent that molted to the second instar for each egg mass.

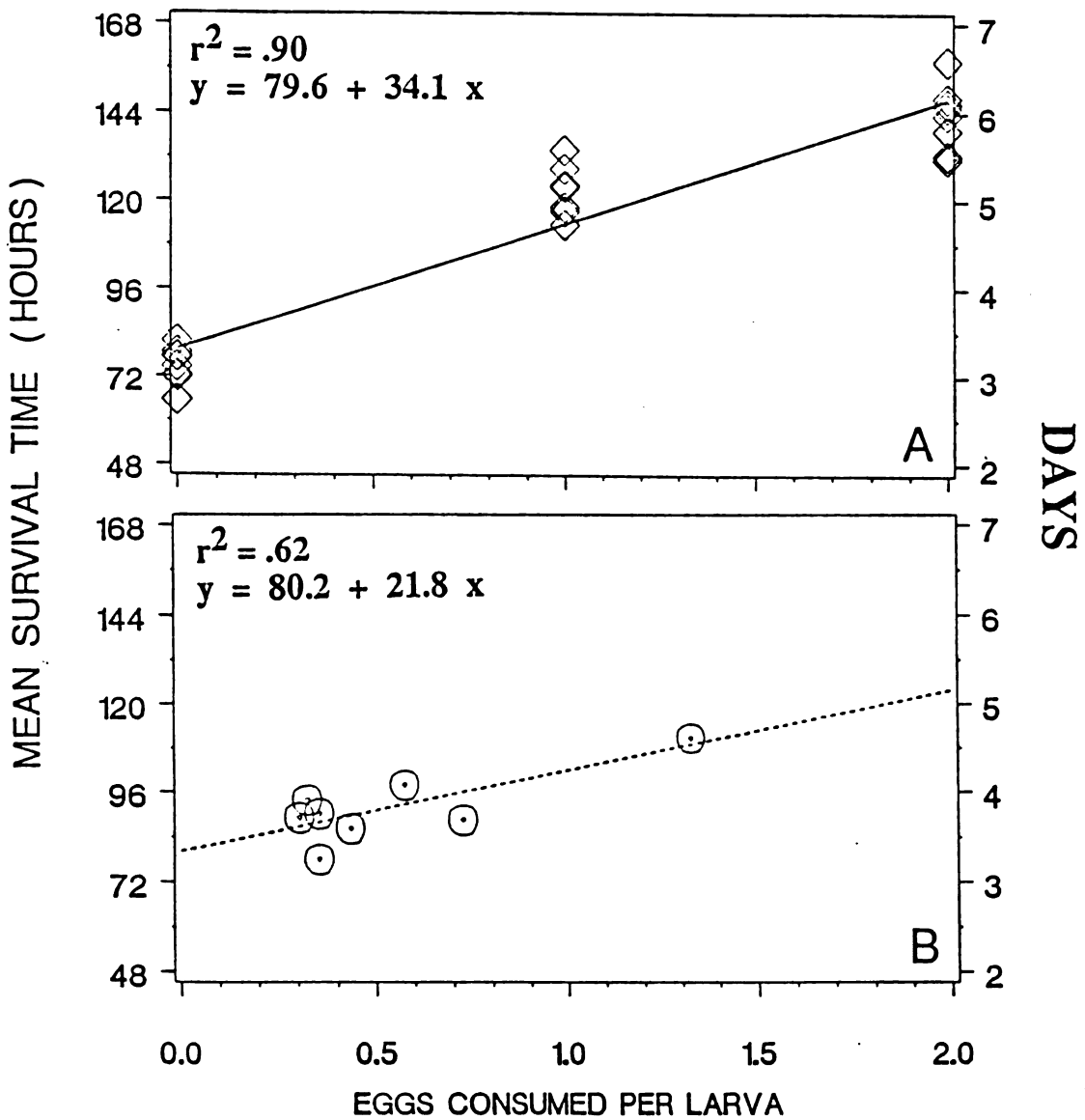

Figure 39. Mean survival times for field-collected *H. convergens* larvae as related to the number of eggs consumed per larva. A) Mean times for isolated larvae fed 0, 1 and 2 eggs per larva (N = 190 larvae from 8 batches). B) Mean times for larvae that were allowed to remain on the egg mass until all unhatched eggs were eaten (N = 53 larvae, 8 batches). Regression equations are significant at $P < 0.05$; y, survival time in hours; x, eggs consumed per larva (REG program, pp 655-710, SAS Institute, 1985).

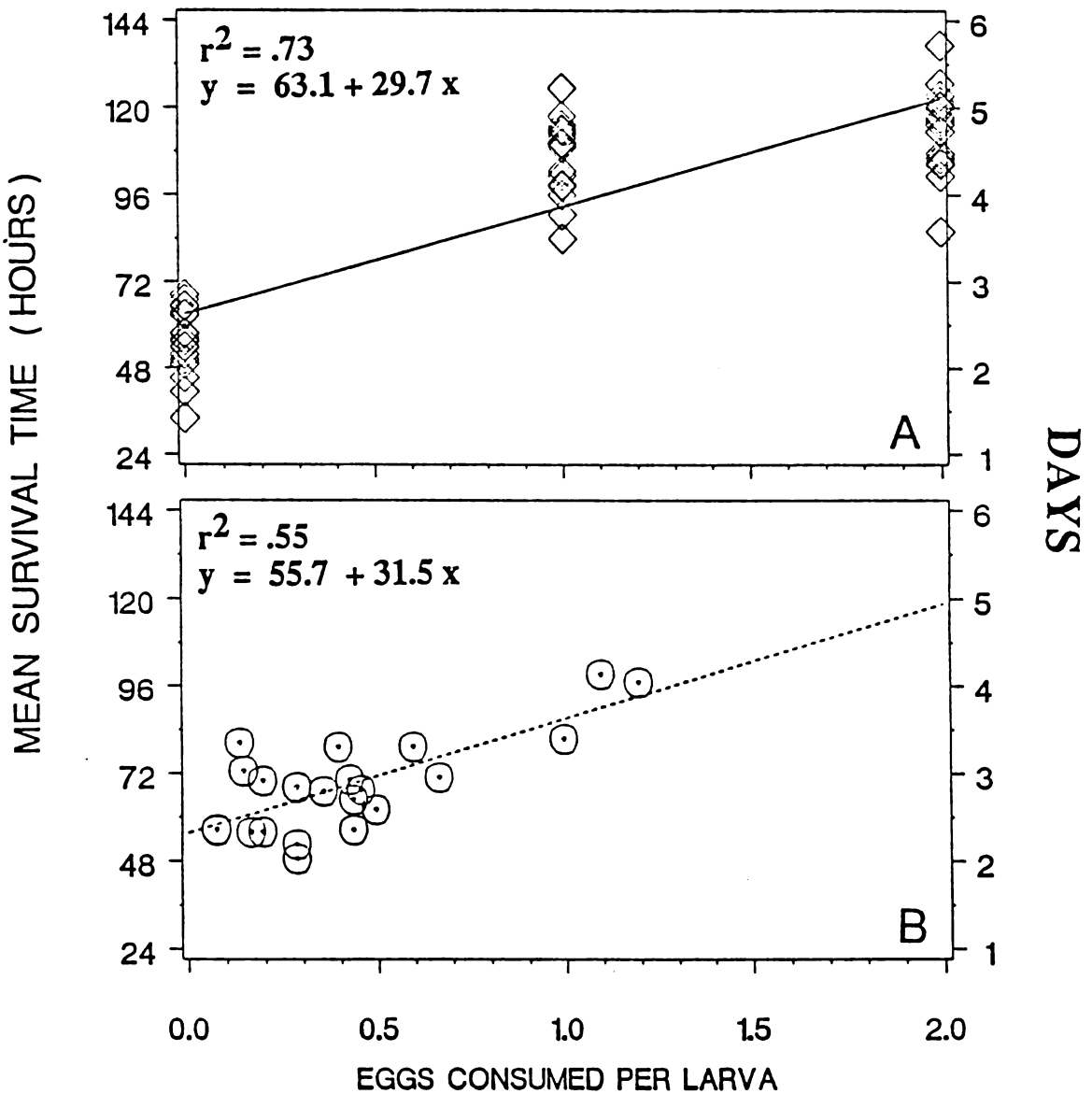

Figure 40. Mean survival times for laboratory-reared *H. convergens* larvae as related to the number of eggs consumed per larva. A) Mean times for isolated larvae fed 0, 1 and 2 eggs per larva (N = 256 larvae from 21 batches). B) Mean times for larvae that were allowed to remain on the egg mass until all unhatched eggs were eaten (N = 131 larvae, 22 batches). Regression equations are significant at $P < 0.05$; y, survival time in hours; x, eggs consumed per larva (REG program, pp 655-710, SAS Institute, 1985).

Trial IV--H. convergens eggs. There was no difference in survival times for larvae of *C. transversoguttata* when fed on its own eggs or those of *H. convergens* ($F = 0.25$; $df = 1,2$; $p < 0.05$; $n = 33$ larvae).

TIME SPENT ON EGG MASS.

Trial I--dispersal after cannibalism. As for *trial III* on larval survival, *trial I* of this series revealed that the mean number of eggs consumed per larva was low for the batches tested: 0.22±0.08 (ranging from 0-1.3; $n = 175$ larvae, 20 batches) for *H. convergens* and 0.25±0.06 (0-0.86; $n = 237$ larvae, 18 batches) for *C. transversoguttata*. When time spent on the batch was regressed against egg consumption, the data for both species produced significant results but the relationship was poorly described by the regression curve (Figures 41a&b). The scatter of the data points and the regression equations suggest that cannibalism did not greatly delay dispersal. The mean time to dispersal for batches that consume up to 0.5 eggs per larvae was not substantially longer than that of unfed larvae--21.5 vs 18.0 hours for *H. convergens* and 26.5 vs 17.4 for *C. transversoguttata*; where x = 0 and 0.5 in the regression equation.

Trial II--single and clustered eggs. The comparison of departure times for larvae from single eggs with those larvae left as a cluster was significant ($F = 112.79$; $df = 1,8$; $p < 0.05$; $n = 77$ larvae). The mean (±SEM) for the 5 groups of single eggs was 4.0±0.62 hours, with means ranging from 2.5-6.6 hours. Departure times were considerably higher for the 5 groups of clustered eggs--15.2±1.1 hours, ranging from 12.4-22.9 hours. *Trial I* for *H. convergens* somewhat duplicated this experiment when there was no cannibalism. The regression equation of

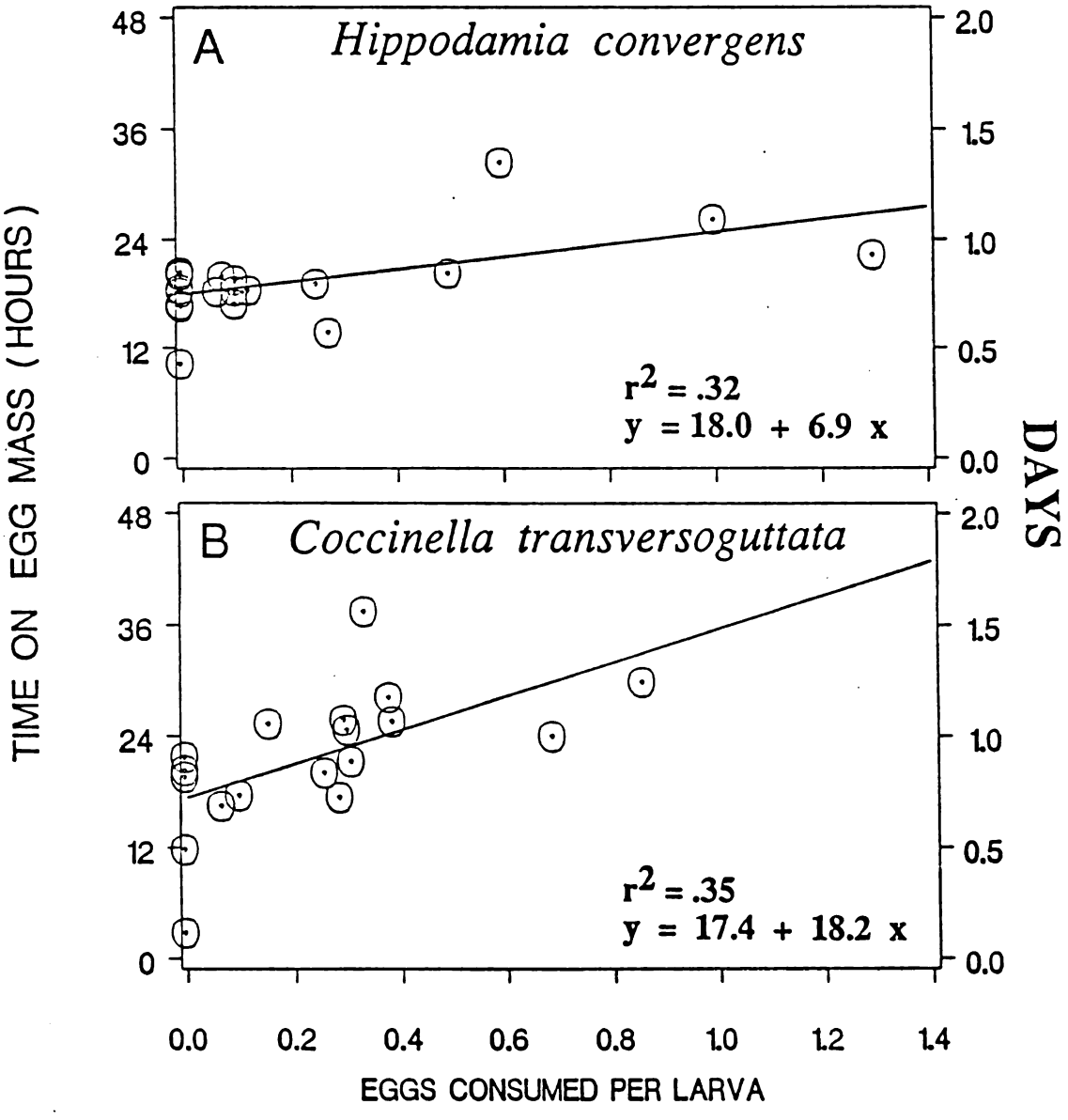

Figure 41. Mean time spent on egg mass for two species of laboratory-reared beetles as related to the number of eggs consumed per larva. A) Mean times for *H. convergens* larvae that were allowed to remain on the egg mass until all unhatched eggs were eaten (N = 175 larvae from 20 batches). B) Similar data for *C. transversoguttata* (N = 237 larvae from 18 batches). Regression equations are significant at $P < 0.05$; y, time on batch in hours; x, eggs consumed per larva (REG program, pp 655-710, SAS Institute, 1985).

trial I provided a value of 18.0 hours at zero eggs consumed per larva (Figure 41a), a time close to the 15.2 hours for the clustered eggs in *trial II*.

The significant difference between time spent on single eggs and egg batches supported the theory that the number of eggs in a batch might influence the dispersal process. The regression of departure time on the number of eggs produced a strong relationship ($r^2 = 0.77$, Figure 42). However, similar regressions on the *trial-I* data set produced nonsignificant results for both species. Since egg consumption was a major difference between these two trials, the regression model was modified for the analysis of *trial-I* data to include total eggs per batch and eggs consumed per larva. Then the results were significant with marginally higher r^2 values than reported for eggs consumed as a single variable: $r^2 = 0.48$, $y = 21.7 + 9.0x - 0.4z$ for *H. convergens*; and $r^2 = 0.40$, $y = 15.2 + 15.0x + 0.18z$ for *C. transversoguttata*; where y = time spent of egg mass, x = eggs consumed and z = eggs per batch.

DISCUSSION

In spite of the attempt to include field-collected beetles in the experiments, this was a laboratory study. As such the results may apply only to the laboratory conditions. Mills (1982) supported this view because observations of 42 egg masses of *A. bipunctata* on lime trees showed little cannibalism from the first larvae to hatch. With this conclusion Mills considered cannibalism a laboratory phenomenon resulting from infertility, an outcome common in eggs laid by adults under artificial conditions.

Our study indicated that about 75% of the eggs from field-

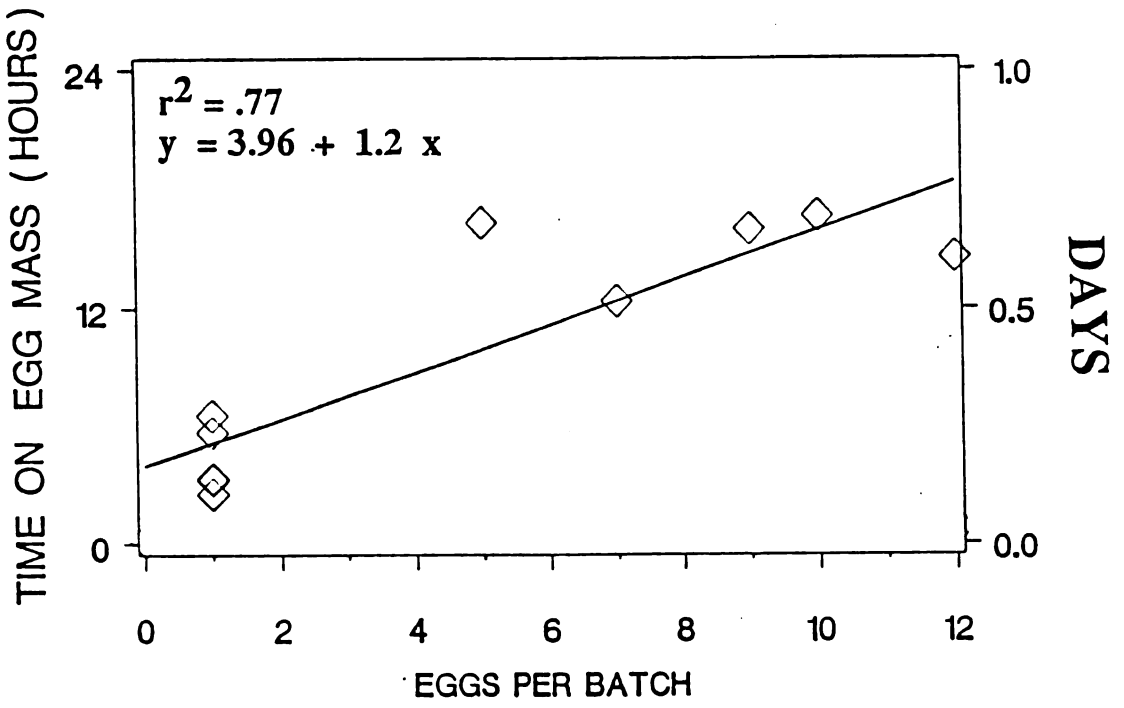

Figure 42. Mean time spent on egg mass for two groups of *H. convergens* larvae, those isolated as single eggs and those clustered as small groups, as related to the number of eggs per batch. Regression equations are significant at $P < 0.05$; y, time on batch in hours; x, eggs per batch (REG program, pp 655-710, SAS Institute, 1985).

collected beetles successfully hatched. Of the remaining 25%, a substantial number were nonviable. Thus, newly-emerged larvae could cannibalize any unhatched eggs in the same cluster without greatly influencing the larval population. For example, in the field group of *H. convergens* only 1.5 viable eggs per batch were at risk of cannibalism assuming a mean of 17 eggs per batch and a 9% secondary emergence rate. For *C. transversoguttata* 1.5 eggs were at risk (28 eggs per batch * 5.4%). The situation for laboratory-reared individuals was slightly different with about 3.0 and 3.75 eggs at risk for *H. convergens* and *C. transversoguttata*, respectively.

The differences between the field-collected and laboratory-reared groups could be attributed to many factors. We feel that the rearing conditions in the growth chamber, i.e. environmental parameters and feeding, were relatively consistent for each group. However, the genetic diversity of the laboratory-reared adults was diluted as they were the progeny of a smaller population of field-collected individuals. Since the laboratory-reared group was only one generation removed from its source, this outcome may be important to researchers using laboratory cultures or to commercial enterprises that mass-produce coccinellids.

Cannibalistic larvae benefited through increased life span and the acquisition of resources necessary to molt to the second instar. Our study also showed that the difference in longevity between aphid-fed and egg-fed larvae was not that great. The energy expended in consuming adjacent eggs was less than that needed to locate prey through random search patterns. However, the time larvae spent on the egg mass could delay their predatory influence on the prey population. For *H.*

convergens the time to dispersal was not greatly lengthened for cannibalistic individuals, although the proximity of other eggs or larvae influenced the time spent on the egg mass even in the absence of cannibalism. Overall, the consumption of unhatched eggs could be highly adaptive with few negative features, especially under conditions of low prey populations.

CONCLUSION

OVERVIEW.

The common element throughout this work was the emphasis placed on coccinellids. First, the survey for potential natural enemies of the asparagus aphid identified coccinellids as a major component of the predator complex. Though the survey reported the presence of other beneficial organisms, lady beetles were sampled with enough detail to be discussed at the species level. Then, the exclusion-inclusion trials compared the impact of coccinellid predation on the aphid with mortality from parasitism and disease. The experimental approach was narrowed, proceeding from a broad survey of all natural enemies to a more defined field experiment involving representatives of the three natural enemy groups. Continuing this trend, the objectives of the laboratory study were more focused and concerned specific aspects of coccinellid biology.

SURVEY OF NATURAL ENEMIES.

Sampling. Sampling the asparagus cropping system was the greatest challenge and the largest obstacle to understanding interactions between the aphid and its natural enemies. The optimum situation was to employ a nondestructive method that did not remove the finite plant resource, nor the natural enemies that would eventually impact the aphid colonies. Almost all sampling schemes currently employed by entomologists consume the habitat (plant, plant products, hosts) or remove the target organism (Southwood 1966). Methods that proved simple and efficient in other field crops (sweep-netting, whole-plant removal, beating foliage into a

pan) were not suitable in asparagus because of the dense fern.

Sampling coccinellids. Although coccinellids were just one of the many beneficial organisms in asparagus, the primary sampling techniques--visual counts, can traps and interception panels--were best suited for monitoring these large flying predators rather than the minute parasitoids or elusive fungal pathogen. This bias was more important during the exclusion experiments because predation was difficult to determine in the field. Unlike the parasitoid and pathogen that left behind mummies and diseased cadavers for counting, the activity of predators could only be inferred from their presence and close association with the aphid colonies.

Ideally, I expected that seasonal trends for coccinellids, as a group and by species, would be similar across all three sampling methods and only differ in magnitude. This assumption seemed especially valid for the sticky cans and interception panels since they both effectively caught actively flying adults. The survey results demonstrated the potential for sampling errors. In one season any of the sampling techniques would have accurately revealed coccinellid activity, but next season these same methods each indicated a different species as the most abundant. This outcome was satisfactory for creating species lists but it was misleading for determining seasonal trends or relating abundance to vacillations in prey densities.

Other studies have also been hampered by counting problems. In deriving an empirical formula for coccinellid predation rates Frazer and Gilbert (1976) lamented:

"Although we have a good estimate of the predation rate, we still have no sure way of sampling beetle numbers in the field. Standard methods using sweep nets, walking counts, or suction machines, are hopelessly inaccurate. Our intensive counts find only a fraction of the numbers

actually present, and that fraction must vary with aphid density, temperature, and probably the time of day. The adult coccinellid, at first sight so conspicuous an animal, is in fact very cryptic."

Their colleague, P. M. Ives specifically attacked this problem by using Jolly's capture-recapture method to estimate beetle numbers (Ives 1981). Due to the labor-intensive nature of mark-recapture techniques, Ives supplemented this survey with walking counts and added sticky traps to monitor the beetles' flight activities. In spite of these determined efforts, Ives commented that one or two of the basic assumptions of the estimation method were not met, so that individual population estimates of that study cannot necessarily be trusted. The author also stated that a series of such estimates could provide useful information on population levels, especially when supported by trap catches and other data on predator movements.

Overall, the sampling techniques presently available to most field entomologists seem very inadequate. After several seasons in the field, I feel that my ability to understand the interactions between aphids and their natural enemies was limited by the ability to accurately sample the system. Without the technology to characterize populations over larger areas and longer periods, most studies like mine provide results that are not applicable beyond the boundaries of the small research plot in which they were conducted. This dilemma may well apply to other ecological studies. Our imperfect knowledge of complex natural systems seems inextricably linked to our primitive methods of description.

EXCLUSION-INCLUSION STUDY.

The physical and chemical barrier experiments were designed around the idea that one could "bump" a system and then follow its rebound to

normalcy. The "bump" was the large and continued introduction of aphids into the small research plots. However, the same mortality factors that often depressed asparagus aphid numbers also prevented me from successfully infesting an entire plot. Barriers against mortality were needed. The late Dr. George Tamaki suggested the season-long use of cages to selectively include or exclude mortality agents, permitting evaluation of a specific agent as it responded to elevated aphid numbers. Therefore, individual plants were temporarily caged to create sustainable concentrations of aphids that could be followed over the season. Based upon the characteristic scarcity of aphids in the plots, I expected that the native beneficial organisms would quickly reduce aphid numbers to low levels after cage removal.

Again, sampling was a problem. Unlike the abundance survey, this study demanded accurate assessments of the parasitoid and pathogen. The two methods selected for monitoring these mortality agents--noting mummies and cadavers during colony counts, and the parasitism and disease determination--provided a compromise between accuracy and minimum disturbance to the system. When evaluating aphid numbers, the laborious procedure of counting aphids *in situ* was balanced by the relatively simplistic plant rating index to provide an acceptable means for tracking population fluctuations. This sampling scheme had the potential to deliver precise information on aphid mortality when executed with sufficient replications (plants per treatment and colonies per plant) and short sampling intervals. The requirement of more replicates was a limiting factor because the time-consuming counting of aphids would have precluded all other activities.

LABORATORY TRIAL ON CANNIBALISM.

Huffaker et al (1971) provided four criteria for assessing an insect's potential as a biological control agent. Insect predators and parasitoids should possess the following traits: 1) adaptability to the varying physical conditions of the environment, 2) searching capacity, including general mobility, 3) capacity to increase relative to prey reproduction and consumption of prey items, and 4) other intrinsic properties such as synchronization with prey, prey specificity, degree of discrimination and ability to survive during periods of low prey densities. Based on this list, one can study and evaluate aspects of coccinellid behavior and biology that potentially detract from their usefulness to man as efficient biological control organisms. As a survival strategy, egg cannibalism could benefit newly-emerged larvae during periods of low prey densities. At high prey densities cannibalism could potentially reduce the overall predatory impact by destroying viable larvae and increasing the time that larvae spend on the egg mass rather than consuming prey.

The results of this study provide some basis for further study of the hatching process. Differences between field-collected and laboratory-reared individuals, i.e. a lower hatch rate and reduced eggs per batch for laboratory cultures, could have important implications. For example, commercial operations that rear coccinellids for biological control applications may not want to keep the same beetles in culture too long as to avoid diminished batch sizes. Also, decreased reproduction is sometimes used as an indication of the impact of pesticides and microbial agents on a nontarget organism, specifically natural enemies. Laboratory cultures are recommended for toxicity

testing in order to produce a physiologically uniform group of experimental animals. Therefore, the control group should contain enough individuals to detect a drop in fecundity not related to the treatments.

APPENDICES

APPENDIX A

Preliminary Chemical Exclusion Experiment (1983).

INTRODUCTION

The nonpest status of the asparagus aphid in Michigan created an excellent opportunity to study a system in which an introduced insect was being naturally controlled. Were aphid numbers low because of the climate, or due to the substantial influence of native natural enemies, or a combination of both? These questions gained weight as the asparagus industry in Washington State experienced aphid populations at destructive levels. The objectives seemed clear: 1) identify the mortality agents at work in Michigan and estimate their abundance, and 2) once identified, determine which agent is the most important one in reducing aphid numbers.

To achieve these objectives the asparagus system had to be sampled and manipulated in a way that illustrated the presence and impact of individual mortality agents. However, methods commonly employed with pest insects or in other field crops were not suitable for this aphid and plant. Therefore, the two preliminary exclusion studies represent initial attempts to conduct tightly controlled experiments in the asparagus system. The results were often more important for what they did not show than for what they revealed.

The first study was a chemical exclusion experiment. Pesticides

were applied to selectively exclude certain groups of natural enemies while permitting another to operate at normal levels. Fluctuations in the artificially increased aphid populations were theoretically related to the action of the active mortality agent. The objective was to evaluate the impact of selected natural enemies on the asparagus aphid. The seasonal occurrence and diversity within the groups of beneficial organisms were also monitored. Although predatory coccinellids were known to be abundant in the New Jersey system (Angalet & Stevens 1977), the specific species and timing of their impact were still unknown for Michigan.

MATERIALS AND METHODS

The test site was a 5-year-old asparagus field (10 rows by 38 m) located at the Botany & Plant Pathology Field Laboratory, 2 km south of main campus in East Lansing, Michigan. The plot was divided into four equal sized quadrants, each 5 rows by 19 m. The entire field had about 350 plants, 87 in each quadrant.

Since the natural aphid numbers were very low, the field was artificially infested. Aphids reared in the greenhouse were weighed to create approximately equal groupings of 100 individuals. Clinging to pieces of filter paper, aphids were placed on randomly selected plants in each of the four quadrants of the field. The process was repeated until 25 plants in each quadrant received about 200 aphids per plant (Hayakawa 1985).

A pesticide treatment was randomly assigned to each quadrant, as follows: 1) the insecticide carbaryl that was toxic to predators and parasitoids (see Appendix C), 2) the fungicide maneb that prevented

pathogen germination, 3) the maneb-carbaryl combination that eliminated all natural enemies and 4) no sprays, as the control. The chemicals were applied with a specially fabricated boom sprayer that treated two rows at a time. The sprayer was pulled down the rows by a small garden tractor. Maneb (flowable formulation with 0.479 kg (AI)/l product, Rohm & Haas Co.) was applied at 544.0 g (AI)/0.405 ha; carbaryl (80% wettable powder, Union Carbide) at 90.8 g (AI)/0.405 ha with 113.55 l of water per 0.405 ha. The field was sprayed 11 times between July 23-October 17, 1983 (Hayakawa 1985).

The sampling techniques fulfilled two purposes: to provide a basis for estimating aphid population trends, and to collect beneficial organisms for identification and timing of their peak abundance. The methods included: sweep-netting along borders, beating fern into a pan, whole-plant removal, and interception of flying adults with sticky-can traps. These methods were judged on several levels: efficiency in detecting the species of interest in a timely and uncomplicated manner, the degree that the method preserved the limited number of plants and introduced aphids, and how it disturbed the system by its execution.

Sweep net. The net could only be used along the weedy borders of the plot. The asparagus was too bushy--individual plants varied from 3-50 stems, ranging 1-1.5 m tall--for a continuous sweeping motion to be effective. Sets of 25 sweeps with a 38 cm net were done once a week.

Beating fern with pan. About 5 stems per plant, from a selected series of plants, were beat into a white enamel pan (46 by 26 by 10 cm deep) (Hayakawa 1985). Dislodged insects and fern pieces were quickly poured into a plastic bag. The contents were examined with a stereomicroscope; specimens identified to family and counted. This

method was conducted weekly.

Whole-plant removal. Fern of an entire plant was quickly stuffed into a dark plastic garbage bag (113.55 l capacity) and then cut off at soil level. The bag was tied closed and stored at 5°C until processed. The collected fern was placed into giant Berlese funnels lighted by 500 watt heat lamps. Trapped insects moved down the funnel, falling into soap-filled dishes. This sample consumed 24 plants, 6 per quadrant, every two weeks.

Sticky-can traps. Sticky traps were constructed from coffee cans (12.7 cm diameter by 15.9 cm tall) painted with safety-yellow enamel (Krylon #1813, Borden Inc., New York, New York), mounted atop a one meter stake (Figure 6). A transparent plastic sheet (15.2 by 43.1 cm) covered with an adhesive substance (Tangle-trap, The Tanglefoot Co., Grand Rapids, Michigan) was attached around the outside of the can with Velcro for easy removal of the entrapped insects. The detachable sticky sheets were changed weekly at first, then every two weeks toward the end of the season. The sheets were examined with a stereomicroscope; specimens identified to family and counted (Hayakawa 1985).

RESULTS

The sweep net did not provide any meaningful numbers on predators or parasitoids. Improved weed control practices at the research facility later eliminated the weedy border areas around the plot. This method was no longer applicable.

The beat samples only captured aphids; all other swift-flying adults easily escaped once dislodged into the pan. However, fluctuations in aphid counts were difficult to interpret without

information on the level of activity for each mortality agent by treatment. For example, any decrease in aphid numbers in the control quadrant could not be correlated to parasitoids or pathogen because the numbers of diseased aphids or mummies were not recorded. If the agent was not active, then the use of selected pesticides had little effect in enhancing aphid population trends in the other treatments. The distinction between treatments was further weakened by low aphid populations and difficulties in creating effective chemical barriers. Therefore, treatment comparisons were not justified.

The whole-plant removal method produced nonsignificant differences between the four treatments (Hayakawa 1985). Like the beat sample, it only adequately recorded aphid numbers. This technique also violated the stated criteria for acceptability since it was very labor intensive, highly disruptive to the system and destructive to the limited plant resources.

The sticky-can traps offered the only source of data that effectively monitored predators and parasitoids. Except for Anthocoridae, representatives of other families--Aphidiidae, Syrphidae, Coccinellidae and Chrysopidae--occurred in low numbers. Of the seven coccinellid species collected, *H. convergens* was the most numerous, followed by *C. maculata* and *H. parenthesis*.

DISCUSSION

This trial revealed a number of deficiencies in the methods. First, the chemical barrier was a workable technique but it could not be created for the whole plot. The disruption and destruction caused by the sprayer and tractor was reason enough to abandon the method.

However, individual plants could be treated and inspected on a regular basis to ensure that the pesticide treatment was effective. The use of individual plants rather than fields as the experimental unit also permitted replication of treatments. An added benefit was the greater ability to infest individual plants since the uniform introduction of aphids over the entire plot was not possible.

A different set of sampling methods was needed to assess the impact of mortality agents at the colony level for each treatment. Fluctuations in aphid populations had to be linked with the documented absence or presence of specific beneficial organisms. This required the implementation of several monitoring approaches since no single method was suitable to record the impact of predators, pathogen and parasitoid. The whole-plant, beat sample and sweep net techniques were summarily dropped.

Sticky-can traps were effective at monitoring predators in the plot. However, Hayakawa (1985) listed several deficiencies. First, the trap information was strictly qualitative, indicating relative abundance. Second, these traps were biased toward catching actively flying adults that did not avoid the sticky surface. Also, it was difficult to manipulate small insects (Aphididae, Anthocoridae) for identification purposes once they became embedded in the tanglefoot.

APPENDIX B

Preliminary Physical Barrier Experiment (1983).

INTRODUCTION

The physical exclusion experiment was a more refined version of the chemical barrier trial, because it investigated the impact of specific mortality agents rather than their combined effects. In agreement with reported information (Angalet & Stevens 1977), a preliminary survey suggested that the hymenopteran parasitoid *D. rapae*, fungal pathogen *E. planchoniana*, and coccinellid predators were important mortality agents of the asparagus aphid. The objective of this exclusion method was to exclude all beneficial organisms from an enclosed plant and include only one of the three designated natural enemies. Any trends in the aphid population could then be attributed to the introduced agent.

MATERIALS AND METHODS

The study plot was similar in dimensions and age to the one used in the chemical trial, located 50 m away. Excluding plants along the borders, approximately 200 of the 360 total plants were labelled and categorized by the number of stems per crown and height. About 25-40 of the most uniform plants were identified. Eighteen plants were randomly

selected from the uniform group and assigned to six treatments. The treatments were the combination of physical and chemical barriers with a cage as the primary deterrent to natural enemies (Table 10, and Hayakawa 1985). While cages effectively eliminated predators and parasitoids, a fungicide was required to suppress the pathogen. Since natural aphid populations were practically nonexistent even in mid-August, all plants were infested from greenhouse cultures. The cages promoted high numbers to quickly develop within 2 weeks.

Two sampling methods were employed. First, sticky-can traps were used to determine species composition as described for the chemical barrier trial. The second technique was nondestructive, aimed at monitoring aphid colonies *in situ*. For this approach, individual colonies were selected on each treatment plant and all the aphids on a 6 cm length of a branch were counted. Of 15 preselected colonies per plant, 5 were randomly tagged and counted over the season. The finite rate of increase (Tamaki et al. 1981a) was calculated from two consecutive counts of the same colony (See Section III). Hayakawa (1985) counted the colonies for this trial.

RESULTS AND DISCUSSION

In the attempt to follow the same colony over the season, some data was lost as colonies decreased to zero. Calculation of the finite rate of increase (FRI) required consecutive counts. When a colony could not be found due to a lost tag or broken stem, the data was also lost. Aphid numbers dropped suddenly after the trial started so that the rate of increase value could not be determined for many of the colonies. Therefore, the mean number of aphids per colony was calculated for each

treatment as a substitute statistic.

The experiment was not designed to produce mean colony counts, but this data revealed several valuable points. First, cages created conditions that allowed the aphid to quickly reach outbreak proportions. Although cages can alter the microclimate, it seemed possible that the cage decreased the impact of natural enemies more than it reduced detrimental weather factors. Therefore, the general climatic conditions in Michigan were not considered to be the limiting factor on aphid growth in this experiment.

The pathogen reached epizootic levels, producing substantial mortality on the elevated aphid populations (Hayakawa 1985). Since the fungus was not actively introduced into the cages, it was considered as present throughout the plot. The other two agents were not as impressive. The introduced beetle, *H. convergens*, did not produce colony counts that were significantly different from the control means. This was probably a result of the small numbers introduced per cage as well as the time of season when the experiment was conducted (September 9-October 17). No data was collected for the parasitoid, because it was not found in the plot until the experiment terminated and could not be included in this trial.

Hayakawa (1985) attributed the declining aphid numbers to other reasons. First, the sexuparae became more numerous in September. This morph produces eggs not larvae, thereby creating a drop in actual numbers. Populations were also influenced by the physiological state of the host as plant senescence began. Finally, the fall conditions, cooler temperatures and hard rainfall, probably negatively influenced aphid growth.

Again, the can traps proved useful in tracking species composition. Although this trial had 6 uncaged plants, most of the aphids were excluded as a potential food source for predators by the cage barriers. Before aphid numbers dropped, anthocorids, coccinellids and aphidiids were trapped in moderate quantities. The beetle species caught were similar to those found in the chemical trial. Of the seven coccinellid species collected, *C. maculata* was the most numerous, followed by *H. convergens* and *H. parenthesis*.

APPENDIX C

Pesticide Selection and Determination of Field Dose Level.

INTRODUCTION

The objectives of the pesticide screening procedure were in opposition to the principles of biological control. Successful implementation of the exclusion experiments required pesticides that were toxic to natural enemies but not toxic to the pest species. Such compounds were essential to the creation of a chemical barrier that favored the pest over the beneficial species.

Pesticides were chosen from those recommended for common asparagus pests in Michigan (Grafius et al. 1983). Two chemicals that demonstrated the potential to reduce or eliminate the impact of predators, parasitoids and entomopathogenic fungi without causing high mortality to the asparagus aphid were maneb and carbaryl. The fungicide maneb (manganese ethylenebisdithiocarbamate) is used to control rust (*Puccina asparagi* D.C.) while the insecticide carbaryl (1-naphthyl *N*-methylcarbamate) is suggested for the common asparagus beetle, *Crioceris asparagi* (L.), and 12-spotted asparagus beetle, *C. duodecimpunctata* (L.).

The intent was to find an insecticide that was highly toxic to a

diverse group of natural enemies but relatively nontoxic to aphids. Carbaryl is not recommended as a good material for aphid control in vegetable crops (Grafius et al. 1983), but was reported as toxic to most natural enemies at field rates (Bartlett 1963, 1964). A review of the product label (1983 Chemical Guide, 1983) revealed that very few aphid species are listed as potential targets for this compound in vegetable crops. Susceptible aphids were listed mostly for tree fruit and nut crops: apple aphid, *Aphis pomi* DeGeer; rosy apple aphid, *Dyaphis plantaginea* (Passerini); filbert aphid, *Myzocallis coryli* (Goetze); and blackmargined pecan aphid, *Monellia caryella* (Fitch).

A fungicide with high specificity was also required. It had to selectively eliminate the fungal disease without harming any nontarget organisms. It was important to define the effects of maneb on nontarget species because this fungicide and related compounds (mancozeb and zineb) had already demonstrated activity against entomopathogenic fungi that attack aphids (Boykin et al. 1984, Carruthers 1981, Hall & Dunn 1959, Nanne & Radcliffe 1971, Soper et al. 1974). [NOTE: Mancozeb is a coordination product of zinc ion and manganese ethylenebisdithiocarbamate and is related to both maneb and zineb, while zineb is another dithiocarbamate with the formula: zinc ethylenebisdithiocarbamate [[1,2,-ethane diylbis[carbamodithioato]](2-)] zinc complex (1985 Farm Chemicals Handbook, 1985).]

MATERIALS AND METHODS

The 50% lethal concentrations (LC_{50}) for both pesticides were initially determined in the laboratory for target and nontarget organisms with subsequent field evaluations of the selected dose level.

I used a residual method on adult coccinellids and parasitoids and the slide-dip method for the aphid. The pesticides were not screened against the pathogen in the laboratory because the fungus could not be cultured on artificial media.

For the residual method, about 30 ml of a pesticide solution was poured into a 0.946 liter glass canning jar and swished around until the walls were uniformly coated with the suspension. The excess was poured out and the residue allowed to dry before the natural enemies were introduced into the container. An untreated screen covered the jar mouth to prevent escape and promote ventilation. For the slide-dip technique, asparagus aphids were affixed onto transparent cellophane tape placed sticky-side-up on a microscope slide. With the aid of a stereomicroscope (25X) and a camel's-hair artist brush, adult apterous aphids were positioned dorsal-side-down on the tape. The slide was dipped into a test solution and then allowed to drip dry at an angle to facilitate runoff. Distilled water was used for the control treatment in both techniques; no food was supplied.

Field trials complemented the laboratory screening. In one evaluation, aphids and lady beetles were attached to microscope slides as described for the slide-dip technique. The test animals were then placed on ice in a styrofoam cooler during transportation to the asparagus plot. The slides were rapidly situated inside the foliage of an asparagus plant and treated. Test solutions were applied with a 6-liter hand-held sprayer. The maneb solution was sprayed until runoff, somewhat simulating the immersed condition created by the slide-dip technique. About 150 ml of carbaryl solution was applied per plant in 16-17 seconds at 1.37 kg/cm^2 (20 psi). The control was an application

of water. The treated slides were tapped to remove excess solution and placed back in the cooler for transport to the laboratory and subsequent observation.

Test solutions of commercial grade carbaryl (80% wettable powder, Union Carbide) and maneb (flowable formulations with 0.479 kg (AI)/l product) were developed around the recommended field rates (0.907 kg (AI)/0.405 ha and 1.09 kg (AI)/0.405 ha, respectively) and an application rate of 113.55 l/0.405 ha. For carbaryl, 1.0 g of commercial product suspended in 100 ml water constituted a 1.0% solution, equivalent to the recommended field rate of 1133.97 g of product in 113.55 l of water. Similarly, 2 ml of commercial maneb in 100 ml water produced a 2.0% solution comparable to the suggested field rate of 2.27 l of product per 113.55 l of water. Various combinations of the following solution concentrations were tested for both chemicals; carbaryl: 1.0, 0.5, 0.1, 0.05, 0.01, & 0.001%; and maneb: 8.0, 4.0, 2.0, 1.0, 0.05, 0.01, & 0.001%. (NOTE: As a reference point, all percent solution values will also be listed as a percent of their stated recommended field rate or RFR. The 1% carbaryl and 2% maneb solutions equal 100% RFR.)

Test animals. Three species of field-caught coccinellids were tested: *H. convergens, H. tredecimpunctata* and *C. maculata.* The beetles were held and fed asparagus aphids for three days before the trial. The aphidiids, *D. rapae,* were obtained from asparagus aphid mummies collected from the field. Parasitoids were exposed to the pesticide within 24 hours of emergence from mummies. Adult apterous asparagus aphids were reared in growth chambers. Aphids collected from the experimental plots were also used in several tests.

Treated specimens were maintained in a growth chamber at 22°C, photoperiod of 16:8 h (L:D), and approximately 60-85% relative humidity (RH). Mortality was recorded at 12, 24, 36 and 48 hours. Test organisms were considered dead if they did not respond with leg or antennal movement when being probed with an artist brush. Since I used two control replicates for each trial, mortalities from both were pooled and used to adjust each chemical treatment replicate for natural mortality (Abbott 1925). The dose-response data was analyzed by a computer program (BNPGPROBIT ANALYSIS, Michigan State University) that calculates probits using the maximum-likelihood approximation after Finney (1971). This program listed LC_{50} and LC_{95} values with 95% confidence limits for each level.

RESULTS

RESULTS OF LABORATORY TRIALS--MANEB.

Asparagus aphid. Preliminary laboratory experiments done to perfect the slide-dip method indicated that maneb (Manex 4F from Griffin Ag Products Co. Inc.) was nontoxic to the asparagus aphid at the concentrations tested. Based upon this data I selected the 1.0% maneb solution (50% RFR) to run in a preliminary field trial. However, another maneb product (Dithane FZ by Rohm & Haas Co.) was substituted. When compared to the water control, Dithane produced a corrected mortality of 56.25% (Abbott 1925) after 24 h (n = 140).

This result prompted a more extensive laboratory test to compare the two maneb products. Aphids collected from two sources--individuals reared in growth chambers or field-collected--were tested over five

concentrations of the two products: 4.0, 2.0, 1.0, 0.5, & 0.1%. Two replications (four for the control), each with about 22 aphids, were tested. Manex had little measurable impact on aphids from either source after 24 hours at the highest dose level (Table 8). However, Dithane did produce mortality for laboratory-reared aphids over the same concentrations and time; LC_{50} = 0.55% solution (27.5% RFR). The field-collected aphids experienced lower mortality from Dithane; LC_{50} = 9.5% solution (475% RFR). The different mortality for the two formulations was attributed to the carrier component because visual inspection revealed an oily deposit covering each aphid dipped in Dithane. The difference between aphid sources may be due to the previous exposure of the field aphids to Dithane.

Coccinellids. Lady beetles (*H. convergens*) were exposed to five concentrations of Manex 4F; 15 per dose level: 2.0, 1.0, 0.1, 0.01 & 0.001%. No beetles died in any of the treatments when exposed to the fungicide for 24 hours (Table 8).

Aphidiids. *D. rapae* were exposed to five concentrations of maneb (Dithane FZ); 34 per dose level: 4.0, 2.0, 1.0, 0.5 & 0.1%. The residual test indicated that the fungicide had no measurable impact after 12 hours when compared to the control. Although data was also collected at 24, 36 and 48 hours, the control mortality was too high (30-62%) to consider the results meaningful (Table 8).

RESULTS OF LABORATORY TRIALS--CARBARYL.

Asparagus aphid. Aphids reared in a growth chamber (25°C, 16:8 h L:D, 70-85% RH) were exposed to five concentrations of carbaryl: 1.0, 0.5, 0.1, 0.05, and 0.01%. Four replications (8 for control), each with

about 24 aphids, were tested. The slide-dip test produced a 24-hour LC_{50} of 0.499% (49.9% RFR) (Table 8). I used the regression equation to extrapolate a LC_{10} of 0.028% (2.8% RFR), an acceptable field dose for the exclusion experiments.

Coccinellids. Three species of coccinellids were tested in two laboratory experiments. In the first trial two species, *H. tredecimpunctata* and *C. maculata*, were exposed to five concentrations of carbaryl: 1.0, 0.5, 0.1, 0.05, and 0.01%. About 15 individuals of each species were tested per dose; 30 in the control. No valid dose-response could be determined because all concentrations killed 100% of the beetles except the lowest with 92.5% mortality (Beetle I, Table 8). The second trial exposed fifteen *H. convergens* per treatment to four concentrations: 1.0, 0.1, 0.01 & 0.001%. The LC_{50} was 0.003% (95% CL = 0.00025-.01; 0.3% RFR) while the LC_{95} was 0.031% (95% CL = 0.01-8.34; 3.1% RFR) (Table 8).

Aphidiids. Parasitoids were exposed to five concentrations of carbaryl; 30 per dose level: 1.0, 0.5, 0.1, 0.05, and 0.01%. As with the maneb test for these specimens, the control mortality was acceptably low only at the 12-hour period. This trial produced a LC_{50} of 0.0475% (95% CL = 0.02-0.08; 4.75% RFR) and the LC_{95} was 0.48% (95% CL= 0.26-1.68; 48% RFR) (Table 8).

SELECTION OF EXPERIMENTAL FIELD RATE.

It was difficult to translate LC values obtained in the laboratory into field rates that adequately covered the dense fern. However, 150 ml of liquid was sufficient to penetrate the asparagus foliage and the 1.0% (50% RFR) maneb solution seemed suitable as a nonlethal dose level.

Based on the application rate of 113.55 l water/0.405 ha, the 1.0% fungicide concentration was equivalent to 544.31 g (AI)/0.405 ha (1.2 qts product/A). If 150 ml of this solution was sprayed on individual asparagus plants, the dose per unit area would really be equal to 3477 g (AI)/0.405 ha or 6.38 times the desired rate. I scaled the region to be sprayed from hectares to the plant area (0.8364 m^2). The resulting 0.156% solution, when applied at 150 ml per plant, produced the appropriate amount of active ingredient per unit area.

Similarly, a 0.1% carbaryl solution (10% RFR) was selected for field use. This dose was equivalent to the reduced rate of 90.72 g (AI)/0.405 ha (0.25 lbs product/A), assuming 113.55 l water/0.405 ha. If sprayed on individual asparagus plants in this concentration, a 15-second application of 150 ml per plant equaled 580.63 g (AI)/0.405 ha or 6.4 times the selected rate. This dose was adjusted to a 0.0156% solution by scaling the chosen solution from hectares to the plant area (0.8364 m^2).

RESULTS OF FIELD TRIALS.

Asparagus aphids. Carbaryl was field tested at two adjusted rates, as 0.0156% (10% RFR) and 0.0312% (20% RFR) solutions. At the lower 0.0156% dose level, 22.22% of the aphids died within 24 h (n = 36) as compared to 18.75% mortality in the control group (n = 32). This result produced a corrected value of 4.27% (Abbott 1925). Two trials were conducted at the 0.0312% level. The adjusted mortalities after 24 h were 13.88% (n = 64) and 31.15% (n = 123) (Abbott 1925).

The 0.0156% carbaryl dose was also applied to a moderately infested plant that had a white ground sheet at its base. Since some

aphid drop was noticed within 2 hours after an application, a more rigorous field evaluation of the insecticide was conducted. An asparagus plot located in the MSU Horticultural Research Center served as the test site. The plot had a high level of natural aphid infestation. Six plants with greater than 100 colonies per plant were selected, and ten aphid colonies were tagged and counted per plant. Two plants each got 150 ml of a 0.0156% (10% RFR) or 0.00156% (1% RFR) carbaryl spray. Water was used as the control treatment. White sheets were placed under each plant to catch fallen aphids and indicate the overall level of aphid drop for individual plants. Although the plants were moderately infested, no aphids fell to the sheets from any of the plants after 8 hours. This outcome suggested that the 0.0156% dose was still acceptable for the exclusion experiments.

Coccinellids. A group of mixed species (*H. convergens, H. parenthesis, C. maculata, C. transversoguttata richardsoni* Brown, *Coccinella novemnotata* Herbst and *Adalia bipunctata* [L.]) were exposed to the adjusted 0.0156% carbaryl concentration. The corrected 24- and 48-hour mortalities were 85.7% and 90.0%, respectively (n = 40).

No field trials were conducted with maneb for any species. No field trials were conducted for the *D. rapae* with carbaryl or maneb.

LITERATURE REVIEW

CARBARYL--IMPACT ON TARGET ORGANISMS.

Bartlett (1963) demonstrated that carbaryl (Sevin 50% WP, 0.5 lb (AI)/100 gal) was highly toxic to coccinellids, specifically *Hippodamia* spp. He later demonstrated its toxicity to lacewing (*Chrysopa carnea*)

adults and larvae, but not the eggs (Bartlett 1964, 1968).

Boykin et al. (1984) investigated the impact of pesticides on the natural enemies of the twospotted spider mite (*Tetranychus urticae* Koch, Acari: Tetranychidae) in the field. They found no evidence that carbaryl at 1.4 kg/ha reduced the predators below that found in the check plot. The most abundant predator was *Orius insidiosus* (Say) (Hemiptera: Anthocoridae); representatives of the families Coccinellidae, Nabidae, and Chrysopidae were also present.

Grafton-Cardwell & Hoy (1986) reported that the dose-response for susceptible lacewings, *Chrysoperla carnea* (Stephens), to carbaryl in the field was LC_{50} = 0.55 g (AI)/liter (95% CL = 0.43-0.83, slope = 3.34$\pm$ 0.53, *n* = 240) based on a recommended field rate of 18 g (AI)/liter.

Martinez & Pienkowski (1983) reported the LC_{50} for the nabid *Reduviolus americoferus* (Carayon) after a 2-sec immersion in a solution of carbaryl 50WP: LC_{50} = 2.9% of recommended rate of 1.12 kg/ha or 6.57 g (AI)/0.405 ha.

Moffitt et al. (1972) exposed *Hippodamia convergens* adults to carbaryl in a laboratory spray chamber. No survival occurred after 6 hr when diapausing adults were directly sprayed or exposed to residues of 0.125 or 0.25 lb (AI)/100 gal. [NOTE: 0.25 lb (AI)/100 gal = 0.00429 g/100 ml, a 0.0043% solution].

Pree & Hagley (1985) found concentrations of technical grade carbaryl to be toxic to both chrysopid larvae and adults (*Chrysopa oculata* Say). A 0.2% solution killed 100% of the larvae and adults tested when sprayed from a Potter tower.

Tipping and Burbutis (1983) showed that carbaryl (Sevin 50WP) residues at 1.4 kg (AI)/ha dosage rate inhibited emergence of

Trichogramma nubilale Ertle and Davis (Hymenoptera: Trichogrammatidae), an egg parasitoid of the European corn borer, *Ostrinia nubilalis* (Hubner), in both a greenhouse study and field test.

Travis et al. (1978) showed the effect of carbaryl (Sevin 50W) against *Coccinella novemnotata* (Herbst): LC_{50} = 0.07% concentration (AI), slope = 1.62±0.43, 95% FL = 0.114-**, *n* = 96.

Wilkinson et al. (1975) applied carbaryl (50% WP) dilutions as a 1 ml solution to filter paper. After air drying, the insects were exposed to the treated filter paper. The LC_{50} responses were determined (g (AI)/0.405 ha, *n* = 30 per dose) for the following: coccinellid *Hippodamia convergens*, 13.6; lacewing *Chrysopa carnea*, adults 68.1, larvae 1362; braconid, *Chelonus blackburni* (Cameron), 286; and braconid, *Meteorus leviventris* (Wesmael), 18.2.

CARBARYL--IMPACT ON NON-TARGET ORGANISMS.

By exposing 3rd- and 4th-instar nymphs of the filbert aphid, *Myzocallis coryli* (Goetze), to filbert leaves dipped in aqueous solutions of carbaryl, Aliniazee (1983) produced the following data on aphid mortality after 48 hours: LC_{50} = 0.02 g (AI)/liter (95% CL = 0.013-0.030, *n* = 50) for a susceptible strain; or a 0.002% solution. A resistant strain revealed a LC_{50} = 1.55 g (AI)/liter (95% CL = 0.489-4.78); or a 0.155% solution.

Soper et al. (1974) tested carbaryl against four entomophthoraceous fungi: *Entomophthora exitialis* Hall & Dunn, *E. virulenta* H.& D., *E.* nr. *thaxteriana* Petch and *E. culisis* (Braun), the first three known to attack aphids. Carbaryl allowed 0-33.7% growth at 0.5 pt/A.

Stern et al. (1960) in a field study showed that Sevin (probably Sevin 4F with 4 lbs (AI)/ gal product) applied at 19 oz/A (269.32 g (AI)/0.405 ha) markedly reduced the immature and adult coccinellids and nabids but was not quite as effective on the spotted alfalfa aphid, *Therioaphis maculata* (Buckton).

MANEB--IMPACT ON TARGET ORGANISMS.

Boykin et al. (1984) investigated the impact of pesticides on natural enemies of the twospotted spider mite (*Tetranychus urticae* Koch, Acari: Tetranychidae) in the field. The entomopathogenic fungus *Neozygites floridana* Weiser and Muma (formerly *Entomophthora floridana* Weiser and Muma) was suppressed in plots that were treated with the fungicide mancozeb.

Carruthers (1981) showed that maneb completely inhibited conidial germination of *Entomophthora muscae* (Cohn) at the lowest rate tested--0.0057%. This solution would be comparable to my 0.02% test solution.

Hall and Dunn (1959) exposed five entomophthoralean fungi--*Entomophthora exitialis* Hall & Dunn, *E. virulenta* H.& D., *E. obscura* H.& D., *E. ignobilis* H.& D. and *E. coronata* (Cost.) Kevorkian--of the spotted alfalfa aphid, *Therioaphis maculata* (Buckton), to technical grade zineb (Dithane Z-78). This fungicide had a varied impact, stopping the growth of *E. exitialis* and *E. obscura*, but not affecting growth of *E. virulenta* or *E. coronata* on treated substrate.

Nanne & Radcliffe (1971) did a field trial that suggested that mancozeb (Dithane M-45 at 1.25 lbs (AI)/A) may protect aphids from fungal diseases.

Soper et al. (1974) tested maneb against four entomophthoraceous

fungi: *Entomophthora exitialis* Hall & Dunn, *E. virulenta* H.& D., *E.* nr. *thaxteriana* Petch and *E. culisis* (Braun), the first three known to attack aphids. At 1 lb/A maneb allowed from 0-18.4% growth of the four fungi when added to the agar medium.

Wilding (1982) conducted field trials with mancozeb and maneb and showed that the proportions of infected *Aphis fabae* Scop. were little affected by weekly applications of these fungicides. *E. planchoniana* was a dominant or abundant during the tests.

MANEB--IMPACT ON NON-TARGET ORGANISMS.

Bartlett (1963) demonstrated that the fungicide zineb (75% WP, 1.3 lb (AI)/100 gal) was not harmful to coccinellids, specifically *Hippodamia* spp. He later demonstrated its low toxicity to lacewing (*Chrysopa carnea*) adults, larvae, and eggs (Bartlett 1964, 1968).

Boykin et al. (1984) investigated the impact of pesticides on natural enemies of the twospotted spider mite (*Tetranychus urticae* Koch, Acari: Tetranychidae) in the field. They found no evidence that mancozeb at 1.68 kg/ha reduced the predators below that found in the check plot.

Carruthers (1981) showed that maneb produced significant mortality to the braconid *Aphaereta pallipes* (Say) (LD_{50} = 13.10%, 95% CL = 4.6-37.4). However, the 13.10% solution is 23 times the recommended field rate, 0.57%, a level at which the parasitoid experienced lower mortality.

Felton & Dahlam (1984) emphasized maneb's current status by noting that ethylene bisdithiocarbamate fungicides are registered for use in 271 crops and 1,296 diseases. Maneb exerts its main effects on cellular

metabolism by inhibiting enzymes with active sulfhydryl groups. They showed that topical applications of maneb to adult *Microplitis croceipes* (Hymenoptera: Braconidae) failed to produce mortality significantly higher than the control.

McMullen and Jong (1971) demonstrated in field trials that spray residues of maneb (Maneb 80% WP at 0.5kg/100 l water, 9.0 kg/ha) and mancozeb (Mancozeb 80% WP at 0.5kg/100 l, 11.2 kg/ha) were toxic to newly hatched nymphs of the pear psylla, *Psylla pyricola* Foerster (Homoptera: Psyllidae) and ineffective against adults. Mancozeb had a low impact on predaceous insects like *Chrysopa* spp. and *Anthocoris* spp.

DISCUSSION

The literature both supported and refuted my selection of pesticides and rates. It was difficult to interpret the reported lethal doses since the authors did not always express the data in terms of kg (AI)/ha or any transformable equivalent. Research did reveal that carbaryl is toxic to many natural enemies and maneb can affect the growth of entomophthoralean fungi. However, both compounds also affect non-target organisms. Since the application techniques and organisms varied, these reports provided the basic guidelines for chemical and dose selection.

Based upon the results of the pesticide trials, I chose the 0.0156% carbaryl solution (10% RFR) and the 0.156% maneb solution (50% RFR) for the exclusion experiments (See Section III). The screening procedure suggested that the fungicide maneb (Manex 4F) was not toxic to nontarget organisms at any of the test doses, specifically not at the selected level. I anticipated excellent control over the disease with

little affect to other organisms. The insecticide carbaryl was extremely toxic to natural enemies and only slightly toxic to the asparagus aphid at the 0.0156% concentration. However, the real capacity for this insecticide to reduce predator and parasitoid numbers under field conditions was not fully proven by these trials, and the potential for unwanted aphid mortality was recognized.

I also noted that the two maneb formulations differed in toxicity to the asparagus aphid. The fungicide Dithane FZ was used during the initial infestation of the experimental plants in 1984 before its slightly toxic properties were known. The less toxic product, Manex 4F, was substituted before the 1984 exclusion experiment started and used exclusively during the 1985 season.

APPENDIX D

Record of Deposition of Voucher Specimens*

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

Voucher No.: 1988-02

Title of dissertation: Impact of Coccinellids on the Asparagus Aphid in Comparison to Other Natural Enemies.

Museum where deposited: Entomology Museum, Department of Entomology, Michigan State University, E. Lansing, Michigan 48824.

Investigator's Name: David R. Prokrym

Date: July 11, 1988

* Reference: Yoshimoto, C.M. 1978. Voucher specimens for entomology in North America. Bull. Entomol. Soc. Amer. 24:141-142.

Deposit as follows:

Original: Include as Appendix in ribbon copy of dissertation.

Copies: Included as Appendix in copies of dissertation; museum files; and research project files.

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

APPENDIX D

Voucher Specimen Data

Page 1 of 2 Pages

Species or other taxon *	Label data for specimens ** collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Hippodamia convergens Guerin	Lansing, MI; 12 Sept. 1985							19	MSU
Hippodamia parenthesis (Say)	Lansing, MI; 25 Aug. 1985							9	MSU
Hippodamia tredecimpunctata tibialis (Say)	Lansing, MI; 12 Sept 1985							6	MSU
Hippodamia glacialis (F.)	Lansing, MI 12 Sept. 1985							1	MSU
Coleomegilla maculata lengi Timberlake	Lansing, MI; 12 Sept. 1985							6	MSU
Coccinella transversoguttata richardsoni Brown	Lansing, MI; 11-28 July 1985							12	MSU
Coccinella novemnotata Herbst	Lansing, MI; 24 Aug & 12 Sept 1985							14	MSU
Coccinella trifasciata (L.)	Lansing, MI; 29 July 1985							1	MSU
Adalia bipunctata (L.)	Lansing, MI; 11 July & 12 Sept 1985							2	MSU
Cycloneda munda (Say)	Lansing, MI; 11&26 July 1985							2	MSU
* Determined by Dr. R. Fischer	**Collected by S. Armbrust								

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

David Robert Prokrym

Date July 11, 1988

Voucher No. 1988-02

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

Edward N. Fischer 11 July 1988

Curator Date

APPENDIX D

Voucher Specimen Data

Page 2 of 2 Pages

Species or other taxon *	Label data for specimens ** collected or used and deposited	Number of: Eggs	Larvae	Nymphs	Pupae	Adults ♀	Adults ♂	Other	Museum where deposited
Brachycorynella asparagi (Mordvilko); Det: D. Prokrym	Lansing, MI; 6 April 1984			100		25			MSU
Chrysopa oculata Say	Lansing, MI; 29 & 31 July 1985							2	MSU
Chrysopa plorabunda Fitch	Lansing, MI; 31 July 1985							8	MSU
Micromos subanticus (Walker)	Lansing, MI; 31 July-25 Aug, 1985							6	MSU
Hemerobius stigmaterus Fitch	Lansing, MI; 21 Jyly 1985							1	MSU
Orius insidiosus (Say)	Lansing, MI; 25 Aug, 1985							2	MSU
Diodontus minutus (Fabricios)	Lansing, MI; 6 Aug. 1985					2	2		MSU
Syrphus sp.	Lansing, MI; 31 July-28 Aug 1985							5	MSU

* Determined by Dr. R. Fischer

** Collected by S. Armbrust

(Use additional sheets if necessary)

Investigator's Name(s) (typed)

David Robert Prokrym

Date July 11, 1988

Voucher No. 1988-02

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

Roland L. Fischer 11 July 1988

Curator Date

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