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Title:  A Three-Trophic-Level Perspective on Factors Influencing

Herbivore Abundance on Collard.

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Abstract approved: _____

Jeffrey C. Miller

The influence of natural enemies and plant apparency in
determining the abundance of the cabbage aphid Brevicoryne brassicae L.
and the imported cabbageworm Pieris rapae L. was examined on collards
grown in a collard monoculture and in a collard-alfalfa biculture.
This design was used to examine the factors affecting collard-
herbivore abundance from a three-trophic-level perspective.

Colonization rates of B. brassicae, the aphid parasite Diaeretiella
rapae M'Intosh and the syrphid Sphaerophoria sulphuripes Thom. onto
collards were higher in the monoculture, while P. rapae females laid
more eggs on collards grown in the biculture.

The abundance and diversity of foliar predators was greater in
the biculture, while the ground predator fauna did not vary as a
whole relative to the habitat modification.

Predators most commonly observed on the collard plants were the
harvestman Phalangium opilio L., the orb-weaver Tetragnatha laboriosa
Hentz and the dwarf spider Erigone dentosa O.P. Cambridge in the
biculture and Coccinella trifasciata L. and E. dentosa in the monoculture.

Serological analysis and natural enemy exclusion experiments
indicated that D. rapae and S. sulphuripes were associated with
significant mortality of B. brassicae in the monoculture while P.
opilio was associated with significant mortality of both P. rapae
and B. brassicae in the biculture.

These results argue for including plant properties as parameters in models of herbivore-natural enemy relations:

A. Plant apparency may influence the relation between herbivores and their natural enemies if both use the same cues for host location.

B. Changes in plant apparency over time may have substantial effects on local population dynamics of herbivores and natural enemies.

C. When herbivores respond differentially to plant apparency, relative abundance of herbivores on the host plant will change; this may cause switching of generalist predators from one herbivore to another, depending on the location of the host plant.

D. Since plant apparency may often be inversely related to plant species diversity, decreases in plant apparency may be correlated with increased establishment of generalist predators that respond to plant species diversity.

A three-trophic-level approach to theories on plant defense and predator-prey relations would add to our understanding of patterns of herbivore abundance in nature and would offer a theoretical framework for the design of multiple cropping systems.

A Three-Trophic-Level Perspective on Factors
Influencing Herbivore Abundance on Collard

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# A Three-Trophic-Level Perspective on Factors Influencing Herbivore Abundance on Collard

## CHAPTER I : GENERAL INTRODUCTION

The factors behind patterns of insect herbivore abundance have been studied from several perspectives. Among biotic factors, plant-herbivore and herbivore-natural enemy relations have received most of the attention. The theory of plant defense (Root 1973; Feeny 1975, 1976; Rhoades and Cates 1976) takes an evolutionary perspective in explaining the characteristics of plant-herbivore relations. Theory on arthropod predator-prey relations has been derived from a considerable body of empirical evidence from a variety of systems (Murdoch 1969; Paine 1977; Hassell 1978). Each theory considers the response of herbivores (or prey) to factors arising from the trophic level below (plants) or the trophic level above (natural enemies) and almost all studies to date have followed the theoretical framework by decoupling the herbivore from one trophic level or another and then examining the remaining interaction.

An example of how the theories have developed comes from the literature on diversified cropping systems. It has often been observed that insect herbivores attain higher densities on their host plants when grown in monoculture in comparison to when plants are grown in a more diverse setting. Two hypotheses have been proposed to explain this pattern: the resource concentration and natural enemy hypotheses.

Root (1973) suggested that a crop monoculture represents a concentrated resource that attracts and retains greater numbers of specialized herbivores per host plant when compared to the same host plant grown at the same density in a weedy or non-host background. The attractiveness of a host plant patch to specialized herbivores is equivalent to its apparency and the retention time of a patch is equivalent to its acceptability as a food source. The apparency of a plant is defined in terms of spatial or temporal dominance in the plant community. A brief review of plant defense theory will clarify this definition.

Plant defense theory draws a dichotomy between unapparent and apparent plant species as regards their evolutionary and ecological

relation to herbivores. Unapparent plant species are typically short-lived and tend to invest a large percentage of available energy in reproduction. Selection thus favors low-cost qualitative (all or none) defenses against herbivores in the form of poisons that function at low concentration. These poisons are an effective defense against generalist herbivores that may find the plant through feeding activity on neighboring plants; theory suggests that generalists cannot simultaneously overcome the specific qualitative defenses of several members of a plant community. But specific toxic defenses may select for herbivores that can detoxify or sequester qualitative poisons of particular species. These herbivore specialists may even evolve the means to locate their host plants through recognition of qualitative host plant chemicals. The tendency for short-lived plant species with qualitative defenses to rapidly colonize early successional, diverse communities is thought to be a counter-adaptation against specialist herbivory. Unapparency results from an associational resistance whereby specific host plant cues used by specialist herbivores are masked by the presence of non-host plants (Root 1975).

Apparent plant species are long-lived and invest a lower proportion of available energy in reproduction, and a higher percentage of energy in growth and maintenance. Long-lived species usually are large, persistent plants living in communities of relatively low diversity. These species are classified as apparent because specialized herbivores (especially insects) are very likely to locate the plant sometime during its long life span. Since herbivores on apparent plants have much shorter life spans than their hosts, the probability that qualitative poisons will remain effective for long periods of time is low. Thus, apparent plants have evolved high-cost, quantitative defenses (such as tannins) that serve to reduce digestibility for broad classes of herbivores, including both specialists and generalists.

Of these two classes of plants, unapparent species are typically ancestors of annually grown cultivars: this is the connection between plant defense theory (Feeny 1975) and the resource concentration hypothesis (Root 1973). According to theory, unapparent cultivars grown in monoculture will attract and retain greater numbers of specialist herbivores than cultivars grown in diverse settings.

The occurrence of epidemic herbivore population growth in monocultures has also been explained by hypotheses involving the role of habitat diversity in stabilizing the relation between pest and natural enemy (Pimentel 1961a). The natural enemy hypothesis proposes that biological control of herbivorous insects by natural enemies breaks down in simplified monocultures due to a decrease in alternate prey, host, other food item or elimination of favorable microhabitats for natural enemies (Flaherty 1969; Dempster 1969). This hypothesis proposes that natural enemies switch feeding preferences from alternate, non-economic prey to the pest species before densities of the pest reach economic threshold levels. The natural enemy hypothesis may be interpreted to predict that generalist natural enemies will better regulate insect pest populations because of the existence of alternate prey or habitat (Leius 1967; Vlijm et al. 1974; Sunderland 1975). Theory suggests that switching by generalist predators may stabilize prey populations if the abundance of the predator(s) does not fluctuate greatly through time (Hassell 1978).

The resource concentration hypothesis concerns the response of specialist herbivores to changes in plant apparency or plant quality or both; pest densities are decreased by breaking the tightly coupled, coevolved link between plant and herbivore. The natural enemy hypothesis concerns the strength of the interaction between herbivore and natural enemy; a stronger interaction is assumed to cause lower and more stable herbivore abundances through time. Clearly, each hypothesis is primarily concerned with interactions between two trophic levels, either plant-herbivore or herbivore-natural enemy. Yet, if it can be shown that changes in host plant factors (e.g. host plant quality or spatial pattern) modifies not only the relation between plant and herbivore but also the relation between herbivore and natural enemy, the argument for coupling the two theories is strengthened.

There is some basis for the idea that host plant factors can influence the third trophic level. Price et al. (1980) cite numerous examples where natural enemies are affected by properties of individual plants (van Emden 1966; Vinson 1976), of plant populations (Pimentel 1961b) and of plant communities (van Emden 1963; Read et al. 1970).

The purpose of this research was to demonstrate how a three-trophic-level perspective can contribute to a better understanding of the factors affecting herbivore abundance and distribution.

I chose collard (<u>Brassica oleracea acephala</u> L.: Cruciferae) as a cultivar derived from an unapparent ancestor and planted it either in  monoculture or in biculture with alfalfa.  This design was effective at establishing gradients in collard plant apparency and in microhabitat conditions (for generalist natural enemies) so that I could look at how each factor contributed to collard herbivore abundance.  This approach allowed me to examine the interactions between collard herbivores and their natural enemies and then to determine how these interactions were influenced by changes in collard plant apparency and changes in the plant community where the collards were grown (microhabitat conditions).  I could thus take a three-trophic-level perspective toward understanding herbivore abundance and distribution in this system.

The selection of collard for this study was based on the following criteria: collard ⚹ has broad, flat leaves that are easy to sample • is a bienniel, which provides a degree of stability over the sampling season • and has a well known , fairly distinct assemblage of arthropod associates.  This latter characteristic is largely due to the fact that collard foliage contains mustard oils that serve as attractants to a complex of specialized insect species, particularly herbivores and parasitoids (Kjaer 1963).  Root (1973) divided the herbivorous associates into three guilds: pit feeders, primarily flea beetles (<u>Phyllotreta</u> spp.); the strip feeders <u>Pieris rapae</u> L. and <u>Plutella</u> spp.; and several species of hemipterous sap feeders including <u>Brevicoryne brassicae</u> L. and <u>Myzus persicae</u> (Sulzer).

Several parasitoids are also known to be crucifer associates, some of which are also attracted to mustard oils (Gornitz 1957; Read et al. 1970).  Although the more dominant herbivores and parasitoids are typically associates of crucifers, most of the predators are foliar generalists of the families Syrphidae, Anthocoridae, Coccinellidae and Chrysopidae, ground dwelling predators such as carabids and

opilionids and several species of foliar and ground dwelling spiders
(Blunck 1957; Smith 1969; Root 1973; McIver pers. obs.).

In Root's terminology, the specialist herbivores and parasitoids
together form the collard 'component community', species that
are dependent on crucifers as a resource base. The generalist
predators link the collard component community with other such
components by being associated in time and space. Several studies
have examined various internal aspects of the collard component
community as well as the role of generalist predators in determining
abundances of Brassica associates. Since my research has focused
primarily on the colonization patterns and natural enemies of B.
brassicae and P. rapae, I will briefly review the literature on
the biology and ecology of these two species.

The most common aphid associated with cultivated crucifers in
North America is the cabbage aphid, B. brassicae. The cabbage aphid
has a typical temperate aphid life cycle -- fertilized eggs overwinter
on wild crucifers and hatch in early spring into fundatrices  (Hughes
1963). The fundatrix produces the first generation of apterous,
parthenogenetic, viviparous females and successive generations of
viviparae are produced throughout the growing season. A greater
percentage of alate parthenogenetic females are produced later in
the season, which may disperse to other patches of wild or cultivated
crucifers. In cold temperate regions, apterous, oviparous males and
females are produced at the approach of winter -- these mate to produce
the overwintering eggs to complete the life cycle. In warmer regions,
such as in the Willamette Valley, Oregon, viviparae may also overwinter
and both eggs and viviparae may occur in the same area (Pretherbridge
and Mellor 1936).

The cabbage aphid is primarily a specialist on Brassica spp.,
although viviparae can develop on other wild crucifers (Markkula 1953;
Root and Olsen 1969). Cabbage aphids may use a combination of visual
and olfactory cues to locate their host plant, though it is not clear
whether they can distinguish a suitable host plant without physically
sampling it (Kennedy et al. 1959, 1961). There is some evidence that
cabbage aphids respond to host plant tissue toughness (Trumble 1982)

and nutrient levels (van Emden 1966), but the primary attractant of
Brassica plants to aphids is their high concentration of the mustard
oil allyl isothiocyanate (Wensler 1962). This volatile mustard oil,
in combination with visual factors (A'Brook 1973) may explain the
common pattern of significantly higher alate arrival and persistence
on Brassica plants grown in monoculture when compared to host plants
grown in weedy or non-host backgrounds (Smith 1969; O'Donnell and
Coaker 1975; Theynissen and Den Ouden 1980). The effect of allyl iso-
thiocyanate has also been linked to host finding capabilities of the
cabbage aphid parasite Diaeretiella rapae M'Intosh. Smith (1976b)
reported lower D. rapae parasitism rates of B. brassicae on plants in
bare soil than on those surrounded by a weedy background, and Read et. al.
(1970) have demonstrated a laboratory response of D. rapae to allyl
isothiocyanate.

Other natural enemies of B. brassicae are not so dependent on
mustard oils for host location -- syrphid species differ in their use of
host plant and aphid cues (Bombosch 1958; Peschken 1965; Chandler 1968a,
b; Smith 1976a) while more generalized predators are typically not attract-
ed to B. brassicae or its host plant from great distances.

The degree of attractiveness of B. brassicae colonies to their
various natural enemies is related to their functional role in the collard
component community. The parasite D. rapae, its hyperparasites and some
species of syrphids (e.g., Platycheirus sp. (Smith 1969)) -- species that
locate their host by specific stimuli -- are members of the collard comp-
onent community, while most species of syrphids (e.g., Syrphus balteatus
DeGeer (Smith 1969)), foliar predators (Coccinellidae, Anthocoridae,
Chrysopidae), and generalist ground predators are links to other
component communities.

Clearly, if B. brassicae, along with its specialized natural enemies
locates the collard resource through host plant cues, changes in plant
apparency will influence the resultant component community at both trophic
levels. Furthermore, if changes in plant apparency are associated with
changes in microhabitat diversity, the role of resident generalist predators
in structuring the component community may also be modified. Thus, the
theory of plant-herbivore relations should include the effects of plant
apparency not only on the entire component community, but on its relevant

linkages to other component communities.

The imported cabbageworm, _Pieris rapae_ L., is an important world-wide pest of cultivated crucifers. The imported cabbageworm overwinters on wild crucifers as a diapausing pupa from which the cabbage white butterfly emerges to mate and lay eggs from early April to mid-May. The larvae develop through five instars with the total development time from egg to adult being 24 to 30 days at $22^{o}C$ (Richards 1940). As the summer progresses, an increasing percentage of pupae become dormant in preparation for overwintering. There are from three to five generations per year, depending on climate.

The response of ovipositing adult females to changes in host plant apparency is different from that observed in _B. brassicae_. Dempster (1969) found no significant differences in eggs laid by _P. rapae_ on Brussells sprouts grown in weedy backgrounds when compared to those grown in monoculture, while Root (1973) reported no significant difference in biomass of _P. rapae_ on collards grown in weedy and weedless plots. Companionate cropping may actually increase oviposition rates by _P. rapae_ onto interplanted cabbages when compared to monocultural situations (Latheef and Irwin 1979). Strong flying and mobile _P. rapae_ females are thus able to discriminate their host plant from diverse and variable non-host backgrounds, an ability which eliminates the plants's advantages conferred by decreased host plant apparency. Causes for pierid ovipositional behavior are unknown, though various hypotheses have been proposed. Harcourt (1961) observed that _P. rapae_ females intersperse ovipositional activity with feeding activity at blooms of non-host plants, suggesting that increased egg laying in diverse settings is an indirect consequence of feeding activity. An evolutionary explanation for the behavior has been offered by Root and Kareiva (pers. comm.), who suggest that placing eggs in diverse habitats serves to spread the risk of mortality in unpredictable environments. Finally, Hovanitz and Chang (1964) reported that _P. rapae_ laid fewest eggs on agar containing the highest concentrations of allyl isothiocyanate, indicating that females may be repelled by areas of high mustard plant density.

The two most important parasites of _P. rapae_ are the congeners

Apanteles rubecula Marsh (primarily in Europe) and A. glomeratus L.
(common in North America). Neither parasite is considered as an
important mortality factor of P. rapae in England (Dempster 1969),
New Zealand (Ashby and Pottinger 1974) or North America (Blunck
1957; Oatman and Platner 1969). Other important natural enemies
of P. rapae are several species of syrphids, foliar predators
(Coccinellidae, Nabidae and Chrysopidae) and generalist ground pred-
ators (Dempster 1967, 1969; Ashby 1974; Ashby and Pottinger 1974).
Both Dempster and Ashby have identified generalist predators as the
major mortality factors of juvenile pierids. Since these predators
are typically more numerous in diverse habitats (when compared to
monocultures), pierid ovipositional behavior would seem to place
more eggs at risk in terms of generalist predation.

The collard-herbivore system was useful in addressing two
primary research objectives, corresponding to the two chapters in
this thesis. Objective 1 will be addressed in the first chapter,
entitled, "A Three-Trophic-Level Perspective on Factors Influencing
Herbivore Abundance on Collard". I will first determine the major
species interactions between collard herbivores and their natural
enemies in the collard monoculture and in the biculture with alfalfa.
I will then discuss these interactions as they are modified by changes
in host plant properties and in plant community properties. Objective
2 will be addressed in the second chapter, entitled, "Generalist Predators
and Collard Herbivores: a Test of the Natural Enemy Hypothesis".
Here I will demonstrate how a crop diversification can change the
influence of a single species of natural enemy and will also describe
a fruitful approach of assessing the impact of natural enemies on
herbivore species in multiple cropping systems.

CHAPTER II

A Three-Trophic-Level Perspective on Factors
Influencing Herbivore Abundance on Collard

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INTRODUCTION

The biotic factors influencing the abundance and distribution of insect herbivores can be studied by examining herbivore relations with the host plant, with other herbivores or with natural enemies. Most research to date has dealt either with herbivore-plant or with herbivore-natural enemy relations. The result has been the independent development of two separate perspectives on factors affecting herbivore abundance and distribution: plant defense theory (Root 1973; Feeny 1975, 1976; Rhoades and Cates 1976) and the theory of predator-prey (or parasite-host) relations (Hassell 1978). Each of the two theories considers the response of herbivores arising from the trophic level below (plants) or the trophic level above (natural enemies) and most studies have followed the theoretical framework by decoupling the herbivore from one trophic level or another and then examining the remaining interaction (Benson 1973; Buranday and Raros 1975; Cromartie 1975b; Ralph 1977; Altieri and Whitcomb 1979b; Cates 1980; but see Ryan et al. 1980).

A good example of how the theories have developed comes from the literature on diversified cropping systems. It has often been observed that insect herbivores attain higher densities when host plants are grown in monoculture than when the same plant is grown in a more diverse setting (Dempster and Coaker 1974; Pimentel and Goodman 1978). Two hypotheses have been proposed to explain this pattern. The "resource concentration" hypothesis (Root 1973) argues that specialist herbivore densities on host plants grown in monoculture are higher because the plants are easier to find (more apparent) and the herbivores remain in the area for longer periods of time. This hypothesis suggests that cues utilized by specialist herbivores for host location are disrupted by the presence of non-host plants and that host plants grown in diverse settings are less acceptable as a resource base (Tahvanainen and Root 1972; Bach 1980a). Several studies have supported one or both aspects of this hypothesis (Smith 1969; Ralph 1977; Bach 1980a,b; Risch 1980, 1981).

The "natural enemy" hypothesis (Pimentel 1961a) proposes that herbivores are less abundant in diverse settings because natural enemies (parasites, predators) are more effective at reducing their numbers under these conditions. This hypothesis suggests that natural enemies are more capable of regulating herbivore populations in diverse settings because they maintain higher densities due to a greater availability of alternate prey (hosts), supplemental food such as pollen and nectar, a greater number and variety of hunting substrates and more favorable environmental conditions. Increases in abundance of natural enemies in diversified cropping systems has often been observed (Dempster 1969; Ashby 1974; Altieri et al. 1977; Altieri and Whitcomb 1980; Horn 1981), though data are limited that demonstrate that natural enemies are the cause for observed decreases in herbivore densities.

Each hypothesis is primarily concerned with interactions between two trophic levels, either herbivore-plant or herbivore-natural enemy. A need for coupling the two theories would be evident if it could be shown that changes in host plant factors (e.g., host plant quality or spatial pattern) modifies not only the relation between herbivore and plant but also the relation between herbivore and natural enemy. Host plant factors do influence the third trophic level. Price et al. (1980) cite numerous instances where herbivore-natural enemy relations are modifed by properties of individual plants (van Emden 1966; Vinson 1976), of plant populations (Pimentel 1961b; Tamaki et al. 1981), and of plant communities (Montieth 1960; van Emden 1963; Read et al. 1970). For instance, many of the models describing arthropod predator-prey relations incorporate a parameter respresenting enemy searching efficiency. Searching efficiency is considered to be an aspect of predator behavior that is important in stabilizing the relation between predator and prey (Hassell 1978). If searching efficiency is modified by changes in host plant properites (i.e., plant apparency) then a realistic model of predator-prey relations should incorporate the influence of these plant properties. In this case, a three-

trophic-level approach would provide essential information on the nature of searching efficiency, which would in turn allow more accurate predictions of the outcome of the predator-prey interaction. Any theory on factors affecting herbivore abundance should therefore consider the herbivore as part of a three-trophic-level hierarchy, where models describing interaction between any two levels include parameters arising from the third level.

The purpose of this research was to demonstrate how a three-trophic-level perspective can contribute to a better understanding of the factors affecting herbivore abundance and distribution. I chose to study the fauna of collard (Brassica oleracea acepahala L.: Cruciferae) because both Pimentel (1961a,b) and Root (1973) proposed their hypotheses after studying the Brassica-arthropod system. My aim was first to examine how collard herbivores interacted with their host plant and with their natural enemies. I could then look at how the herbivore-natural enemy interactions were modified by changes in host plant properties. These changes were brought about by studying the fauna on collards planted either in a monoculture habitat or in a biculture habitat with alfalfa. The effect of the plant community property (the alfalfa background) was then examined by comparing the nature of herbivore-natural enemy relations on collards in each habitat. I tested the hypothesis that the alfalfa plant background would change plant apparency and microhabitat conditions for natural enemies and thereby determine the form and strength of interaction between collard herbivores and their natural enemies. My approach was to identify and compare species composition of the collard-arthropod communities in the two habitats and to determine the extent to which these communities differed due to changes in the alfalfa background. If no differences in herbivore-natural enemy relations between habitats were detectable, I could reject the hypothesis.

The study was carried out by addressing three objectives: 1) Determine the effect of microhabitat conditions as modified by alfalfa on abundance and diversity of local natural enemies in the

alfalfa habitat and on their occurrence on the interplanted collards.
2) Determine the effect of alfalfa on plant apparency by examining
colonization patterns of collard specialists onto collards grown in
monoculture and in biculture. Collard specialists include both
herbivores and natural enemies that are typically associated with
Brassica spp.. Plant apparency is defined in terms of the spatial
and temporal dominance of the collards in relation to the background
community. When planted in monoculture, collards were considered
apparent; when grown among mature alfalfa plants, the collards were
considered unapparent. 3) Document the influence of natural enemies
on collard herbivores given differences in alfalfa plant background.
While objectives 1 and 2 identify the common arthropod species found
on collards in the two habitats, the third objective compares the
strength and form of herbivore-natural enemy interactions among those
species.

## METHODS AND MATERIALS

### Study Organisms and Habitats

The research was conducted between May and October 1980, 1981 and 1982 on a 0.69 ha plot at the Oregon State University Entomology farm, Corvallis, Oregon. I chose to study the fauna of collard (Brassica oleracea acephala L.: Cruciferae) because it is a cultivar derived from an unapparent ancestor, is easy to sample and has a well known, distinct group of arthropod associates--both herbivores and natural enemies. Several studies have described the colonization dynamics of the collard component species, including the cabbage aphid Brevicoryne brassicae L. (O'Donnell and Coaker 1975), the imported cabbageworm Pieris rapae L. (Dempster 1969; Latheef and Irwin 1979), and the cabbage aphid parasite Diaeretiella rapae M'Intosh (Read et al. 1970). Although there are other important component species on collard (Root 1973), I chose to study these species because they are common in western Oregon and have fairly distinct responses to changes in crop diversification. I also examined the colonization dynamics of the syrphid Sphaerophoria sulphuripes Thom., an aphidophagous predator that I found to be predictably associated with the collard component community.

Since collard is a typical unapparent plant species, theory would predict that the colonization dynamics of its component species would be modified by changes in collard plant background. My work focused on growing collards in two different background types and comparing colonization patterns of component species; collards grown in one background type (bare soil or recently planted alfalfa) were expected to be relatively apparent, while those grown in the other background type (2-3 year old alfalfa field) were expected to be relatively unapparent. I also assumed that alfalfa plant height was directly related to habitat complexity, which I define as the suite of biotic, environmental and physical factors on which generalist natural enemies depend for maintenance and reproduction. By

establishing this gradient in alfalfa plant height, I could look at how both plant apparency and habitat complexity modified the role of specialist and generalist natural enemies in determining abundances of B. brassicae and P. rapae on collards.

Alfalfa was sown over the 0.69 ha plot on 12 May 1980. No experiments were conducted during 1980, though I took extensive ground level and foliar arthropod samples throughout the season. On 16 June 1981, the 0.69 ha plot was divided into a 0.40 ha plot that remained in alfalfa (plot B) and a 0.29 ha plot that was plowed and replanted in alfalfa (plot A) (Figure II.1). The adjacent plots represented a dichotomy in alfalfa plant development throughout the summer of 1981, since plot B was cut only once (22 July), while the newly planted plot A was cut on 31 July and 12 August (Figure II.2). On 18 May 1982, plot A was again plowed and replanted in alfalfa, while plot B was allowed to develop normally. The purpose of repeatedly replanting the tilled plot A in alfalfa was to reduce colonization and persistence of wild Brassica weeds, since it was assumed that the presence of alternate hosts for collard component species would effect their colonization patterns. I used this procedure for the first three time periods (Figure II.2); in the fourth time period, I left plot A fallow and removed any colonizing or sprouting wild Brassica individuals by hand. Thus, for all experiments in the four time periods, plots A and B differed significantly in alfalfa plant height (Figure II.2).

## Objective 1

I examined the relation between alfalfa plant height (i.e., habitat complexity) and arthropod predators by following abundance and species richness of predators through time as the alfalfa grew (1980, 1981) and by comparing predator abundance and species richness in the two adjacent study plots at the same time in 1982. A grid of 52 pitfall traps (400 ml plastic containers spaced 3 meters apart) was established in the newly sown alfalfa field on 31 May 1980.
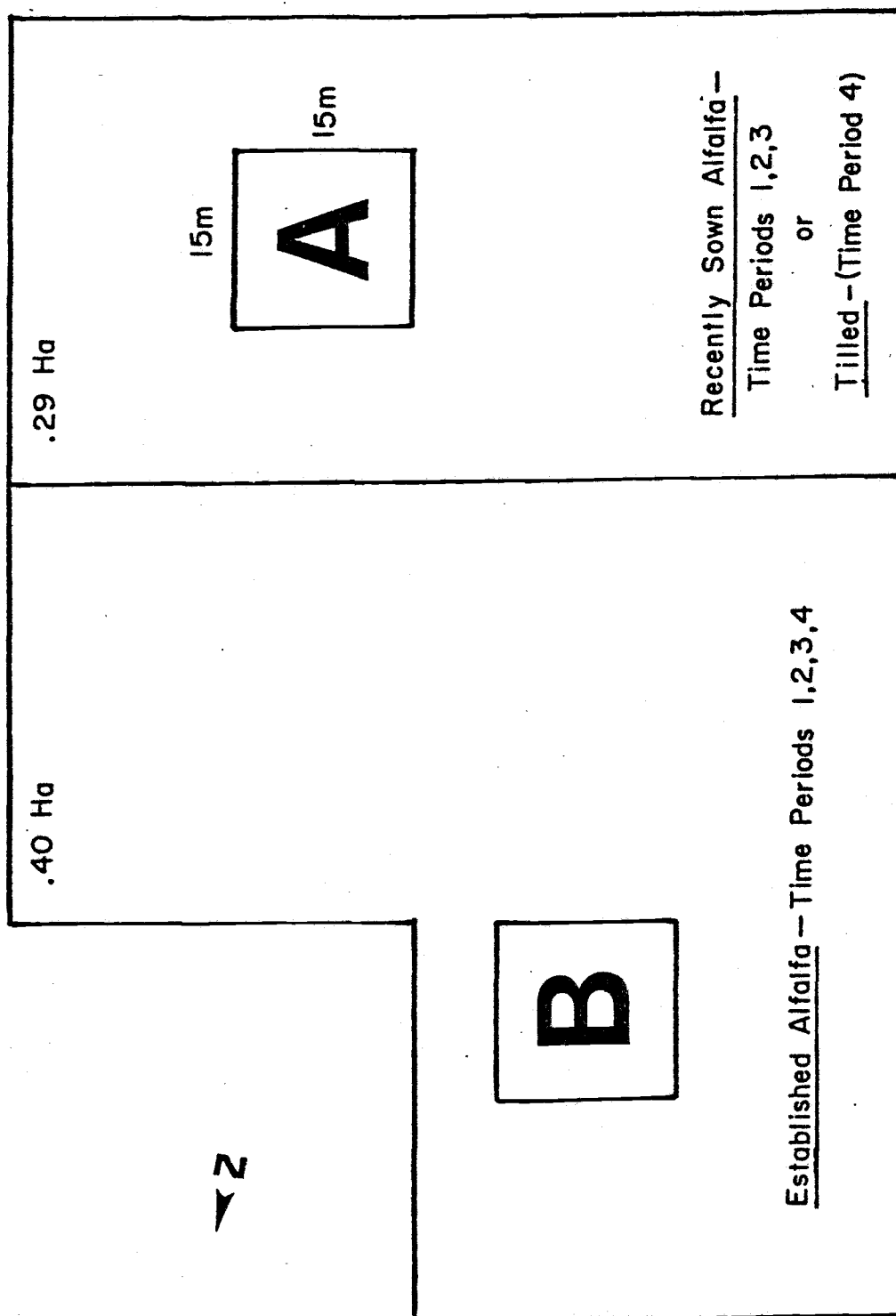
Figure II.1. The study site at the Entomology Farm,
Corvallis, Oregon; June 1980 -- September 1982.
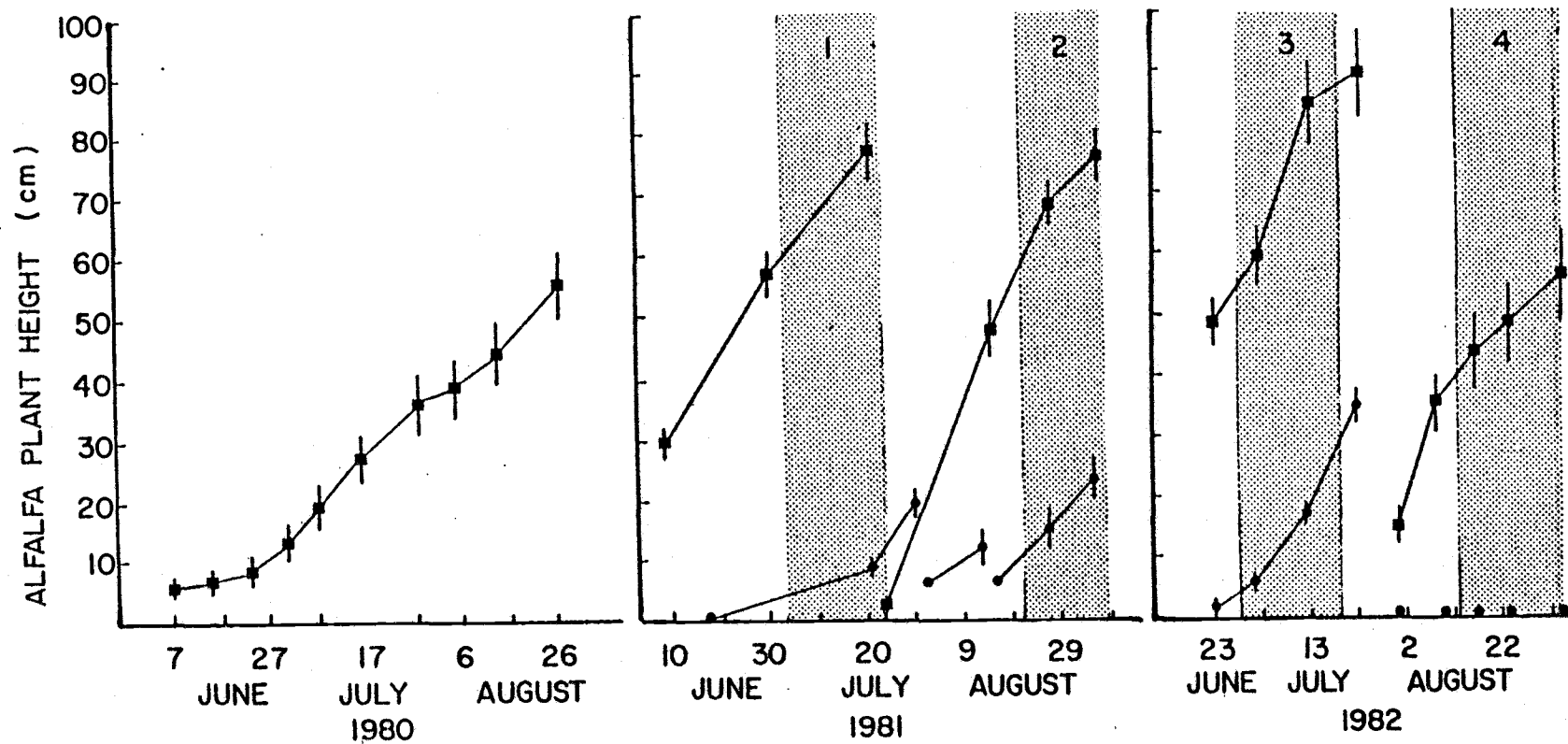
Figure II.2. History of alfalfa growth for 1980, 1981 and 1982 in plots A (●——●) and B (■——■); experimental time periods 1, 2, 3 and 4 indicated by shaded areas; OSU Entomology Farm, Corvallis, Oregon.

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Species richness and relative abundance of ground-dwelling predators was estimated by emptying the traps at 7-10 day intervals between June and September 1980. Specimens were sorted and the most abundant predators identified to species. Species richness, total abundance and abundance of each major species or species group were then related to alfalfa plant height.

Foliar predator abundance and species richness were estimated by sweep-netting. A 400-sweep sample was taken in plot B every two weeks from 4 June -- 19 August 1981. Predators were sorted, the most abundant species identified and both abundance and species richness related to alfalfa plant height.

Since the relation between alfalfa plant height and predator richness and abundance is confounded by the effect of time, I made direct comparisons of the predator fauna in plots A and B during the 1982 field season. The predator ground fauna was sampled daily: in the center of each plot, sixteen pitfall traps (2000 ml plastic containers spaced 3 meters apart) were arrayed in a 4 X 4 grid (Figure II.1). Sweep net samples (50 sweeps per sample) were also taken in the grid area of each plot at frequent intervals throughout the field season. I then related the abundance of important predator species sampled in each plot by the two sampling methods with their prevalence on or around collard plants spaced at two meter intervals throughout each grid area.

## Objective 2

Plant apparency was examined by comparing colonization rates of B. brassicae, P. rapae, D. rapae and the syrphid S. sulphuripes onto greenhouse-raised, 5-week-old collards planted in plots A and B during time periods 1 and 3 (Figure II.2). Colonization patterns of B. brassicae and P. rapae were studied by using collards raised in the absence of herbivores; colonization of D. rapae and S. sulphuripes was studied by providing a 25 aphid (apterous B. brassicae) inoculum per plant as a resource for these two natural

enemy species. Alate B. brassicae, P. rapae eggs, adult D. rapae and larval S. sulphuripes were taken as evidence of host-finding ability; I defined these stages as propagules.

Colonization rates onto collard plants were examined in two ways: by examining five plants in each plot every 2-4 days throughout each time period for evidence of colonization, and by counting the number of propagules of the four species that had arrived on plants in each plot on three separate sampling occasions (Table II.1a). I then tested the null hypothesis that alfalfa plant height or background had no effect on arrival of propagules of the four component species by comparing colonization rates onto collards in plots A and B for each sample date (Table II.1a; experiment a and c). I used one-way ANOVA for each comparison.

The same procedure was used to test the same hypothesis on sampling dates during time period 3 (Table II.1a; experiments a and c). In addition to planting collards at the ground surface in plots A and B, I placed a number of potted plants on 0.9 m stakes throughout plot B. This height maintained collards above the highest alfalfa plants during time period 3 -- I could then test the null hypotheses that alfalfa plant height alone had no effect on colonization rates of component species by comparing propagule arrival onto plants at the ground surface versus those on 0.9 m stakes on plot B (Table II.1a; experiments b and d; one-way ANOVA). Observations of propagule arrival onto plants in both treatments were also made at 2-4 day intervals throughout experiments b and d.

## Objective 3

The influence of natural enemies on the abundance of collard herbivores was studied by exclusion experiments supported by serololgical analysis. Four types of experiments were conducted to examine how habitat complexity and plant apparency modified the influence of natural enemies.

Table II.1a. Experimental methodology for addressing objective 2; (C=control; T=treatment; A=plot A; B=plot B; O=plants not inoculated with aphids; 1=plants inoculated with aphids; M=plants placed on 0.9m stakes).

| EXP. | TIME PERIOD | HYPOTHESIS | TEST CONTROL | TREATMENT |
|------|-------------|------------|--------------|-----------|
| a | 1,3 | Alfalfa plant height or back- ground had no effect on colon- ization rates of B. brassicae or P. rapae. | COA - 5-week-old collards planted in plot A. | TOB - 5-week-old collards planted in plot B. |
| b | 3 | Alfalfa plant height had no effect on colonization of B. brassicae or P.rapae. | COB- see experiment a. | TOM - 5-week-old collards planted in pots on .9 meter stakes in plot B. |
| c | 1,3 | Alfalfa plant height or back- ground had no effect on colon- ization rates of D. rapae or S. sulphuripes. | CIA - 5-week-old collards inoculated with 25 cabbage aphids and planted in plot A. | TIB - 5-week-old collards inoculated with 25 cabbage aphids and planted in plot B. |
| d | 3 | Alfalfa plant height had no effect on colonization rates of D. rapae or S. sulphuripes | CIB - same as experiment c. | TIM - 5-week-old collards inoculated with 25 cabbage aphids and planted in pots on .9 meter stakes in plot B. |

To determine the total influence of natural enemies on collard herbivores, a simple exclusion experiment was conducted during time periods 1 and 3 in plot A and during time period 1, 2 and 3 in plot B (Table II.1b; experiments e and f). In each case, I tested the null hypothesis that natural enemies as a group had no effect on populations of B. brassicae and P. rapae. Controls for each experiment were greenhouse-raised 5-week-old collards that had been inoculated with 25 apterous cabbage aphids at the start of the experiment. The inoculation procedure effectively decreased inter-plant variance in cabbage aphid population size, so that fewer replicates were needed to test the null hypothesis for cabbage aphids. Since P. rapae females tended to uniformly distribute eggs throughout each plot, no such inoculation was needed for this species. The same inoculation procedure for cabbage aphids was used for plants assigned to the natural enemy exclusion treatment, which differed from the control in that all natural enemies were manually removed on a daily basis throughout each experiment. Control and natural enemy exclusion treatments were compared with one-way ANOVA (except where otherwise noted, comparisons between control and treatment for all experiments were made with one-way ANOVA). Predator-prey interactions and general herbivore population fluctuations were observed by inspecting five plants in each treatment group at regular intervals during each experiment.

The influence of local natural enemies on B. brassicae populations was examined with a caging experiment in time periods 2 and 3 (Table II.1b; experiment g and h). In each plot, plants were either enclosed by a fine-mesh nylon bag-cage 0.5 m high and 0.3 m wide (control -- including only the plant) or enclosed by a wooden framed cage measuring 1.8 X 1.8 X 0.9 meters with 1 mm diameter nylon netting (predator-inclusion treatment). Each plant was inoculated with 25 cabbage aphids at the beginning of each trial, and the total number of cabbage aphids alive at the end of the experiment was compared for control and treatment plants in each plot (Table II.1b;

Table II.1b. Experimental methodology for addressing objective 3. (C=control; T=treatment; A=plot A; B=plot B; O=plants not inoculated with aphids; I=plants inoculated with aphids; M=plants placed on 0.9m stakes; PX=natural enemy exclusion treatment; LE=local enemy inclusion treatment; C+=bag-cage treatment; Cyl-6"=6" raised aluminum cylinder treatment; X-A= aluminum cylinder treatment; Cocc+=coccinellid addition treatment; S+=syrphid addition treatment).

| EXP. | TIME PERIOD | HYPOTHESIS | CONTROL | TEST TREATMENT |
|------|-------------|------------|---------|----------------|
| e | 1,3 | Total natural enemies had no effect on abundance of either B. brassicae or P. rapae in plot A. | C1A (see Table 1a) | TPXA-same as C1A except all natural enemies removed daily by hand. |
| f | 1,2,3 | Total natural enemies had no effect on abundance of either B. brassicae or P. rapae in plot B. | C1B (see Table 1a) | TPXB- same as C1B except all natural enemies removed daily by hand. |
| g | 2,3 | Local natural enemies had no effect on abundance of B. brassicae in plot A. | C+A- 5-week-old collards seeded with 25 cabbage aphids and enclosed in fine-mesh bag-cages in plot A. | TLEA- 5-week-old collards seeded with 25 cabbage aphids and enclosed in 1mm mesh 1.8 m X 1.8 m X .9m wooden cages in plot A. |
| h | 3 | Local natural enemies had no effect on abundance of B. brassicae in plotB. | C+B - same as C+A except in plot B. | TLEB - same as LEA except in plot B. |

Table II.1b. continued.

| EXP. | TIME PERIOD | HYPOTHESIS | CONTROL | TEST TREATMENT |
|---|---|---|---|---|
| i | 4 | Ground predators had no effect on B. brassicae abundance or P. rapae abundance or survivorship in plot A. | C-Cyl-6" - 5-week-old collards inoculated with 25 cabbage aphids and enclosed by aluminum cylinders raised 6" above ground in plot A. | TCyl-X-A - 5-week-old collards inoculated with 25 cabbage aphids and enclosed by aluminum cylinders resting on the ground surface in plot A. |
| j | 4 | Ground predators had no effect on B. brassicae abundance or P. rapae abundance or survivorship in plot B. | C1B (see Table 1a) | TCyl-X-B - same as Cyl-X-A except in plot B. |
| k | 2 | Coccinella trifasciata had no effect on B. brassicae abundance with controlled alate immigration. | C+A - same as experiment g. | TCocc+-A - same as C+A except one C. trifasciata added per bag-cage. |
| l | 2 | Sphaerophoria sulphuripes had no effect on B. brassicae abundance in plot B with controlled immigration. | C1B (see Table 1a) | TS+B - same as C1B except one S. sulphuripes added per plant. |

experiment g and h). I tested the null hypothesis that natural enemies from within the wooden caged area had no effect on B. brassicae abundance.

The influence of ground dwelling predators on collard herbivore abundance in each plot was examined in the fourth time period only (Table II.1b; experiment i and j). A total of 48 collards were planted in the center of plots A and B in a 7 X 7 array (empty center) at 2 m intervals. The array was nested within a 6 X 6 pitfall trap grid (3 m spacings) so that I could relate ground predator activity to their prevalence on the associated collard plants and to their influence on collard herbivore abundance. The original experimental design for each plot was the same: the 48 plants were divided into two groups of 24 and assigned to either a control treatment (unenclosed plants) or a ground predator exclusion treatment. Ground predator exclusions were achieved by enclosing each plant within an aluminum cylinder 30 cm high by 30 cm in diameter. This proved to be an effective barrier excluding ground dwelling predators. All plants in both treatments were inoculated with 25 apterous B. brassicae as in previous experiments. On the second day of the experiment, I noticed that alate cabbage aphids were preferentially colonizing unenclosed plants in plot A and avoiding plants enclosed by cylinders (this did not occur in plot B, because no alates were observed to locate any of the plants during the experiment, regardless of treatment). Since differential within-plot host plant selection would bias the results of the experiment, I divided the 24 enclosed plants in plot A into 2 groups: 12 were left intact and 12 were elevated 6 cm above the ground surface on wooden supports, which effectively allowed access to ground dwelling predators, while still inhibiting colonization by alate B. brassicae. All plants in both plots were censused on four occasions during the 18 day experiment (15, 19, 29 August and 1 September 1982). Numbers of B. brassicae and P. rapae were recorded on these four sample

dates, while P. rapae egg and larval survival was estimated by dividing the total number of pierid eggs and larvae alive on each plant at the end of the experiment by the total number of eggs observed to have been oviposited on each plant during the experiment. Since variances were not homogeneous between control and treatment, aphid counts (on the four sample dates) were compared with the Wilcoxon 2-sample test, while arcsine-transformed P. rapae % survivorships were compared for control and treatment in each plot with one-way ANOVA.

The effects of natural enemies on B. brassicae populations given controlled aphid immigration were examined for two different predator species: the coccinellid Hippodamia convergens Guerin-Meneville and the syrphid S. sulphuripes (experiments k and 1; Table II.1b). A single H. convergens adult was confined with 25 apterous cabbage aphids in collard bag-cages identical to those used in the local . enemy experiment. The number of cabbage aphids alive in the bags at the end of the experiment was then compared to the control, which had received 25 aphids but no coccinellids. The influence of the syrphid under controlled immigration of B. brassicae was examined by innoculating plants with 25 cabbage aphids only (control) and comparing the numbers on these plants at the end of twelve days with plants that had initially received 25 aphids plus a single 2nd instar S. sulphuripes larva. Aphid immigration was controlled by conducting this experiment in plot B; no alates were observed on any of the experimental plants during the experiment.

The final part of objective 3 was to identify the principal generalist predators on B. brassicae and P. rapae. A serological technique (the precipitin test) was used to determine the feeding habits of the common predators. Antigens for B. brassicae and P. rapae were each prepared by homogenizing one gram of whole insect in 50 ml 0.9% saline solution (Frank 1967). Filtered extract combined with complete Freund's adjuvant (1:1 ratio) were initially injected at ten sites subcutaneously (0.1 ml per site) into separate rabbits.

Booster injections of a 1:1 ratio of antigen to incomplete Freund's were administered at 2, 3 1/2 and 5 weeks post-initial injection. At week six, whole blood was removed and centrifuged to obtain the serum. Serum containing antibodies (antiserum) was frozen at -20° until needed.

Predators used in the serological analysis were collected in the field in four ways: by hand removal from enemy-exclusion plants in the various experiments; by removal from collard plant samples taken at the end of each experiment; by sweep netting alfalfa and; by pitfall trapping in alfalfa. All predators collected in the field were immediately brought back to the laboratory and frozen at -20°C.

Thawed, saline reconstituted, macerated predators were reacted with antiserum to both B. brassicae and P. rapae by double diffusion Ouchterlony (1958). Fifty plexiglas masks were prepared by drilling holes in the pattern of a 6-member rosette with a central well. These were laid on 0.60 mm thick supports over a film of Bacto agar. Antiserum of either B. brassicae or P. rapae was pipetted into the central well of each rosette and each macerated predator was pipetted into two of the six peripheral wells; this procedure was repeated for both antisera. After about three days in a humidifier, masks were gently removed and reactions observed under indirect light. The presence of a white precipitin line between central and peripheral well indicated a positive reaction; if both replicates showed pre-ipitin lines, the predator was scored positive and was judged to have fed on that prey species. If only one line was positive, the reaction was repeated for that predator. Data served as a qualitative determination of a trophic link between predator and prey (Boreham and Ohiagu 1978).

Since any given antiserum used in the precipitin test is not necessarily specific to the prey species used in its production (e.g., B. brassicae may cross-react with pea aphid antigens) results must be interpreted with caution. For instance, a generalist predator collected on a collard plant may already contain antigen in its gut that will cross-react with antisera against one or both of

the collard herbivore species. Given this consideration, however, one would still expect to find a higher percent of positive reactions for predators collected in association with cabbage aphids and cabbageworms (i.e., on collard plants) when compared to those predator individuals collected away from collard plants (in sweep net or pitfall trap samples). Thus, the percentage of positive reactions for predator individuals was compared for those collected on and off of collard plants; if the precipitin test was an accurate reflection of true trophic relations between B. brassicae, P. rapae and potential predator species, I expected that the percent positive reactions would be higher for those predators collected in association with the collard plants. The serological analysis was supported by direct field observations of predation of B. brassicae and P. rapae throughout the study.

RESULTS

## Objective 1

There was no clear relation between alfalfa plant height and ground predator abundance or species richness in 1980 (Figure II.3). Most of the ground predator species were already present in the field when the alfalfa was only 5 cm high. Species richness peaked at 37 on 28 June and declined thereafter to a low of 20 in late August. Seven predaceous taxa contributed between 68.7 and 90.6% of the total abundance of all predators on each sample date (Figure II.4). It is evident that the activity of these seven taxa were primarily responsible for the observed pattern of abundance of the ground fauna during the summer of 1980. For instance, the pattern of catch/unit effort for staphylinids and Pterostichus vulgaris L. closely parallels the pattern for all predator species; the influence of alfalfa plant height on these patterns, however, is not clear.

The relation between alfalfa plant height and foliar predator abundance and species richness is more direct (Figure II.5). Both species richness and total abundance increase with time and alfalfa plant height after the 17 May and 22 July cuttings in plot B to approximately the same level of 250-300 individuals/400 sweeps represented by 25-30 species. Eight species comprise between 61.3 and 72.7% of the abundance of all foliar predator species at each sample date (Table II.2). In general, the catch of each species increases with time and alfalfa plant height up to the time of each cutting.

A comparison of ground and foliar predator species richness and abundance in plots A and B at the same time in 1982 clarifies the influence of alfalfa plant height (Table II.3). Total abundance and richness of ground predators was higher in the biculture; a large part of this difference is due to the greater abundance of the most commonly collected predator, Phalangium opilio L. (Opiliones: Phalangiidae). When the abundance of P. opilio is subtracted from
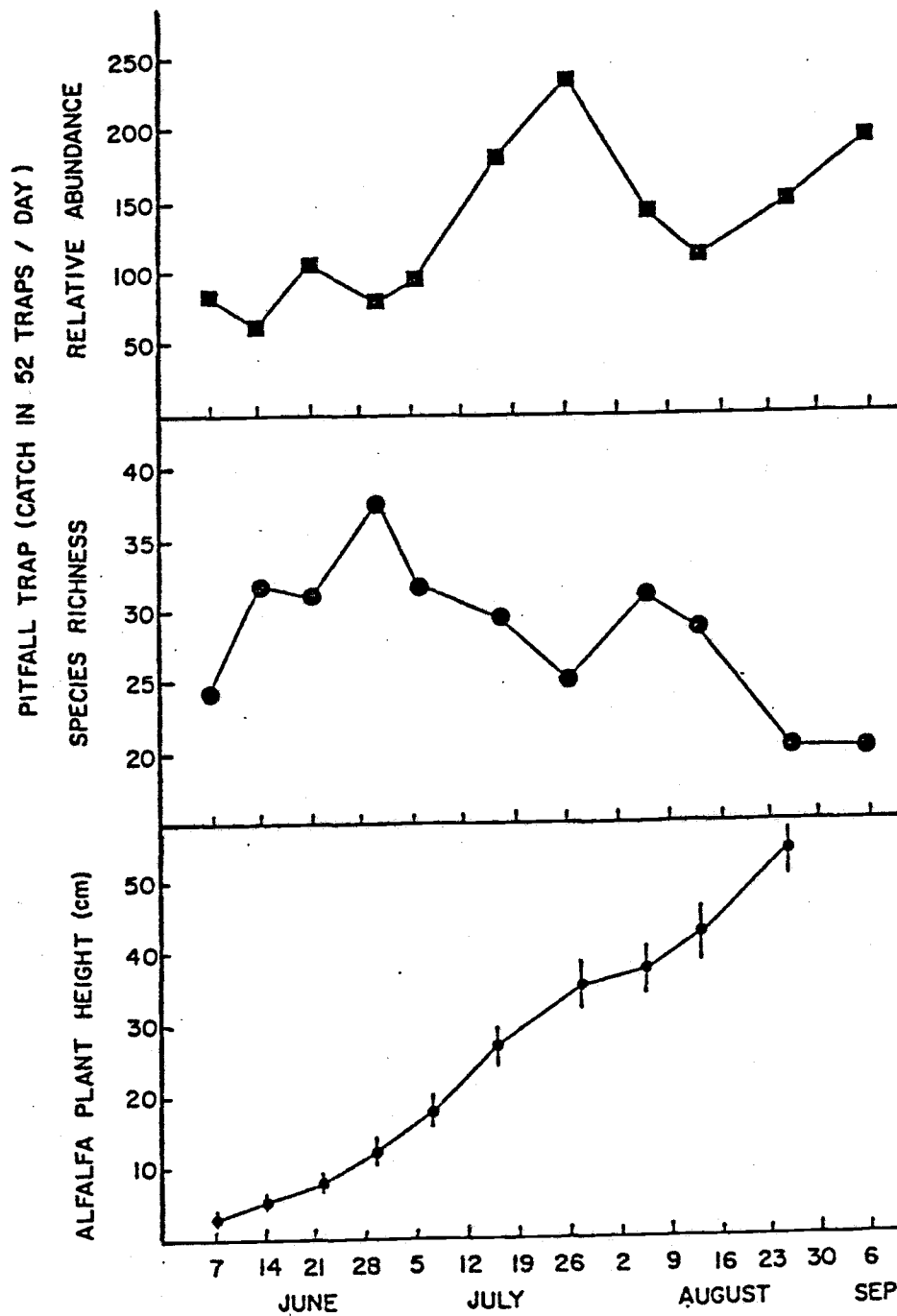
Figure II.3.  Predator abundance and species richness in
pitfall trap samples within alfalfa and alfalfa plant
height between 7 June and 6 September 1980; OSU Entomology
Farm, Corvallis, Oregon.
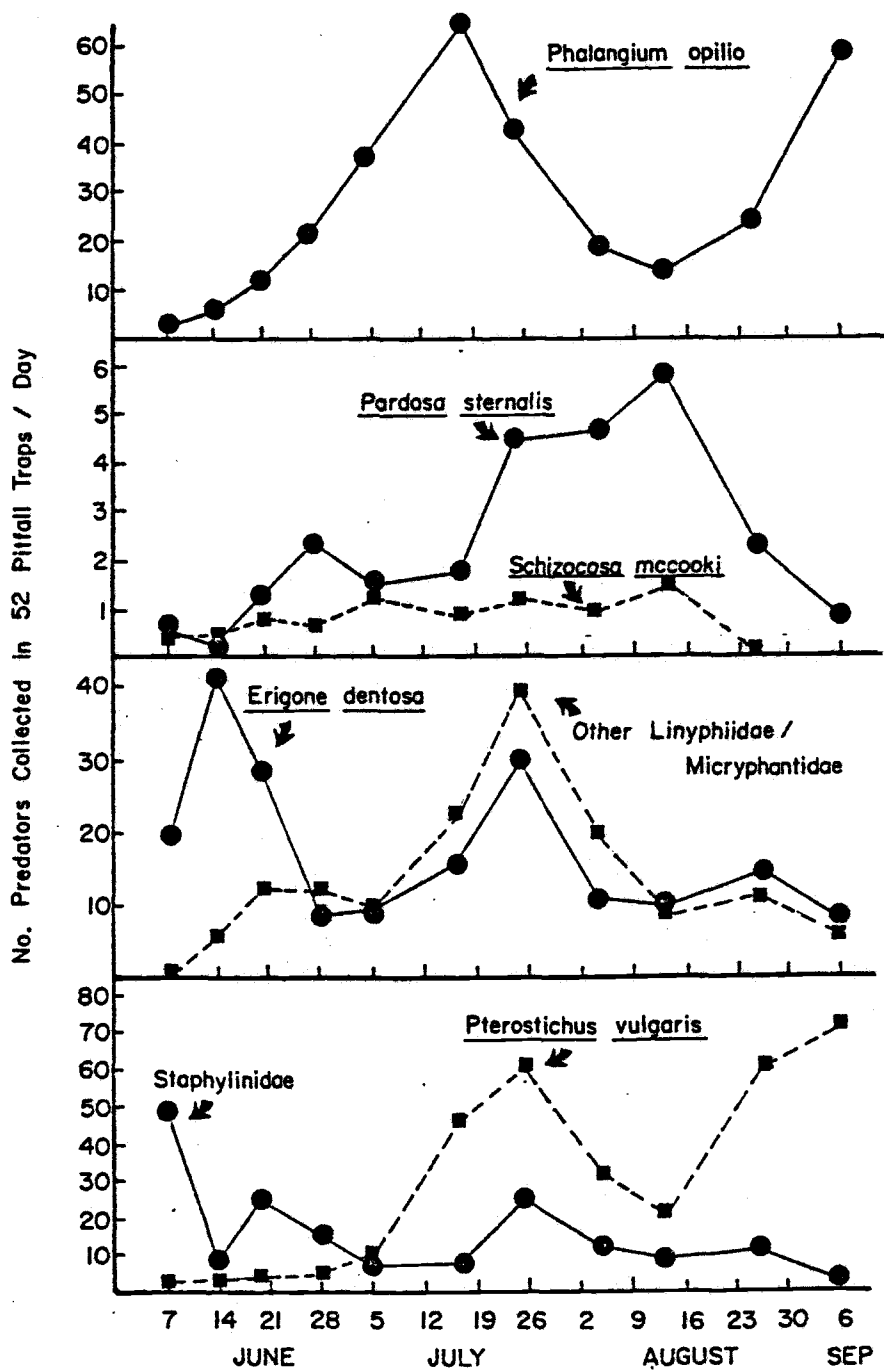
Figure II.4. Relative abundance of principal species of ground predators caught by pitfall trapping in alfalfa between 7 June and 6 September 1980; OSU Entomology Farm, Corvallis, Oregon.
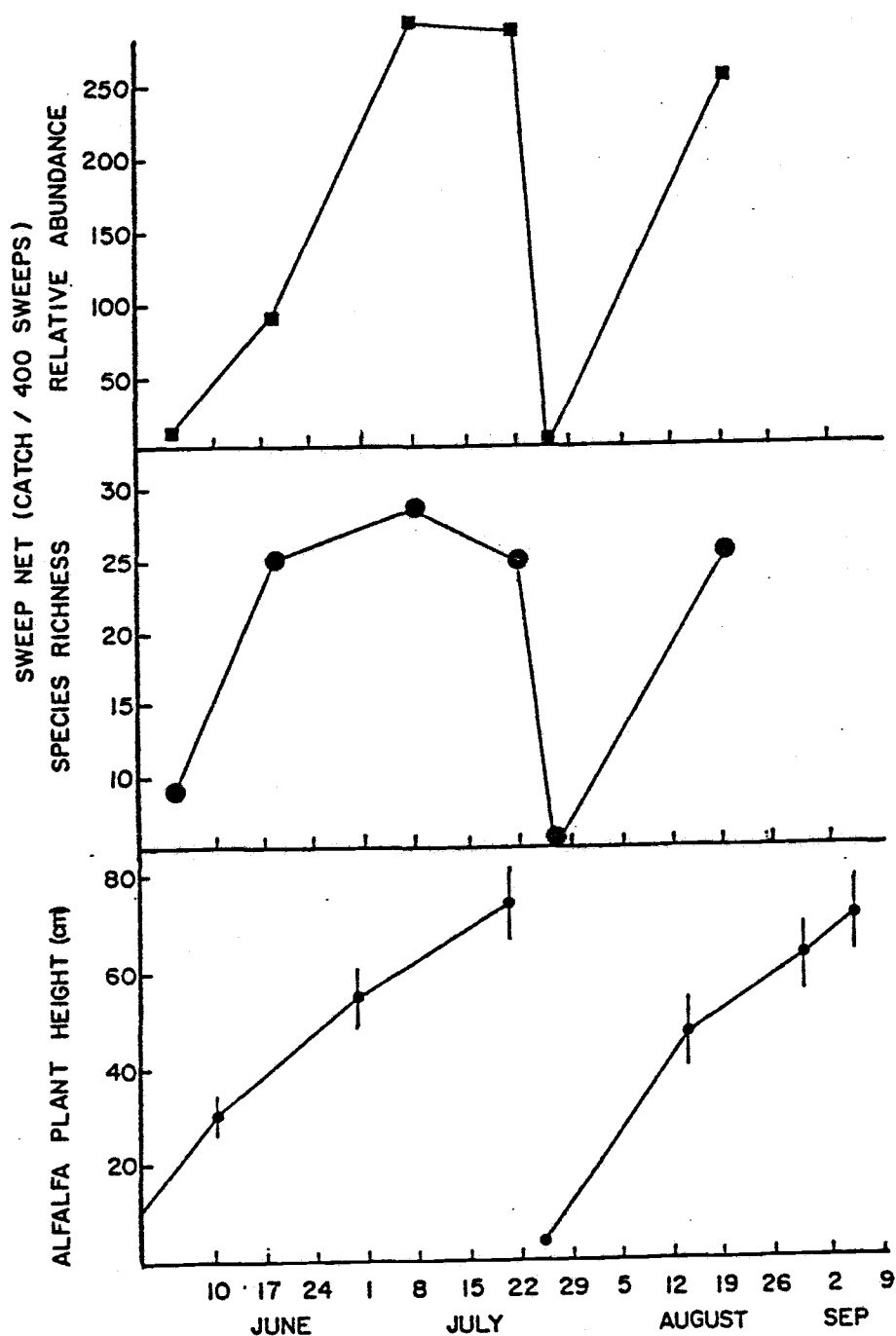
Figure II.5. Relative abundance and species richness of foliar arthropod predators caught by sweep netting alfalfa and alfalfa plant height between 10 June and 2 September 1981; OSU Entomology Farm, Corvallis, Oregon. Alfalfa was cut to 3 cm on 17 May and 25 July 1981.

Table II.2. Catch per 400 sweeps of principal predator species in alfalfa between 4 June and 19 August 1981. Alfalfa was cut on 17 May and 25 July 1981; OSU Entomology Farm, Corvallis, Oregon.

| SPECIES | 4 June | 19 June | 8 July | 22 July | 25 July | 19 August | TOTAL |
|---|---|---|---|---|---|---|---|
| Phalangium opilio L. | 0 | 8 | 33 | 11 | 0 | 4 | 56 |
| Misumenops celer (Hentz) | 6 | 6 | 0 | 21 | 0 | 23 | 56 |
| Tibellus oblongus (Walckenaer) | 2 | 6 | 6 | 2 | 0 | 4 | 20 |
| Tetragnatha laboriosa Hentz | 0 | 2 | 5 | 53 | 0 | 10 | 70 |
| Orius insidiosus (Say) | 0 | 4 | 29 | 33 | 0 | 43 | 109 |
| Nabis spp. | 2 | 2 | 52 | 13 | 0 | 56 | 125 |
| Coccinella trifasciata L. | 0 | 26 | 62 | 38 | 0 | 7 | 133 |
| Coccinella undecempunctata L. | 0 | 0 | 0 | 14 | 0 | 10 | 24 |
| TOTAL -- 8 principal species | 10 | 54 | 187 | 185 | 0 | 157 | 599 |
| TOTAL -- ALL PREDATORS | 11 | 88 | 292 | 278 | 0 | 256 | 928 |
| SPECIES RICHNESS | 8 | 25 | 28 | 25 | 0 | 25 | 53 |
| ALFALFA PLANT HEIGHT (cm $\pm$ 95% CL) | 28.1 $\pm$ 3.2 | 43.7 $\pm$ 4.8 | 63.0 $\pm$ 5.8 | 73.1 $\pm$ 7.3 | 3.0 | 47.9 $\pm$ 3.8 | --- |

Table II.3. Mean abundance + 95% confidence limits of the principal predator species collected by pitfall
trap (15 samples expressed as abundance / 100 traps / day) and sweep net (10 samples: 50 sweeps / sample)
and occurrence on collard plants in plots A and B, 10 June -- 25 July 1982. * Indicates significant
difference in abundance between plots (P<.05; one-way ANOVA); Plots located at OSU Ent. Farm, Corvallis, Ore.

| PREDATOR | PLOT A | PLOT B | F | PREVALENCE ON COLLARD PLANTS | |
| | | | | PLOT A (1215 plants) | PLOT B (1715 plants) |
| --- | --- | --- | --- | --- | --- |
| **PITFALL TRAP SAMPLES : GROUND PREDATORS** | | | | | |
| Phalangium opilio L. | 11.0 + 7.0 | 130.0 + 46.2 | 36.97* | .007 | .030 |
| Pardosa sternalis (Thorell) | 2.0 + 1.1 | 33.8 + 10.9 | 35.17* | 0 | .004 |
| Staphylinidae | 9.7 + 5.6 | 46.2 + 20.6 | 6.32* | 0 | 0 |
| All Micryphantidae | 12.2 + 10.0 | 7.2 + 7.1 | 0.65 | .002 | .002 |
| Lepthyphantes tenuis (Blackwall) | 10.0 + 3.6 | 6.0 + 4.8 | 1.76 | 0 | 0 |
| Erigone dentosa O.P.-Cambridge | 4.0 + 2.9 | 1.0 + 1.0 | 4.42* | .049 | .052 |
| Pterostichus vulgaris L. | 53.8 + 16.3 | 3.0 + 2.1 | 20.86* | 0 | 0 |
| Total ground predators | 116.9 + 33.8 | 241.9 + 45.6 | 19.39* | .060 | .107 |
| Species richness | 25 | 30 | ---- | 5 | 6 |
| **SWEEP NET SAMPLES : FOLIAR PREDATORS** | | | | | |
| Phalangium opilio L. | 0 | 6.6 + 6.6 | 3.96 | ---- | ----- |
| Sphaerophoria sulphuripes Thoms. | 2.7 + 4.0 | 6.7 + 1.9 | 3.19 | .139 | .045 |
| Orius insidiosus (Say) | 6.9 + 11.8 | 18.6 + 11.1 | 2.10 | .004 | .001 |
| Nabis spp. | 1.9 + 1.9 | 7.7 + 4.6 | 5.49* | .001 | .009 |
| Coccinella trifasciata L. | .7 + .8 | 8.6 + 7.8 | 4.04 | .059-(All Cocc.)-.005 | |
| Total foliar predators | 14.0 + 19.0 | 63.4 + 27.6 | 8.76* | .148 | .080 |
| Species richness | 13 | 25 | ---- | 14 | 17 |
| Alfalfa Plant Height | 18.6 + 1.2 | 72.3 + 7.8 | | | |

each total, each plot supported equivalent numbers of ground
predators (plot A = 33.3 individuals/trap/day; plot B = 32.9
individuals/trap/day). Species that exhibited a clear preference for
plot B included P. opilio, Pardosa sternalis (Thorell) and
staphylinids, while P. vulgaris, Erigone dentosa O.P. Cambridge and
Lepthyphantes tenuis (Blackwall) were more abundant in plot A. Of
the ground-dwelling predators, P. opilio and E. dentosa were most
commonly found associated with the interplanted collards. Phalangium
was more often observed on collards in plot B, reflecting its greater
abundance there, while E. dentosa was found to be equally common on
collards planted in the two habitats. The prevalence figures for P.
opilio, as well as any other active, vagrant ground predator, are
probably underestimates of prevalence relative to more sedentary
predators like E. dentosa, because the probability of observing an
active predator on a collard plant in a brief period of time is low
relative to the probability of observing a sedentary predator.

The nearly four-fold difference in mean alfalfa plant height
between plots A and B in June and July of 1982 had a significant
influence on foliar predator abundance and species richness (Table
II.3). Of the 13 species collected from plot A, only four species
comprised 91.2% of the total abundance of all predators collected.
These same four species were also present in plot A representing
76.3% of the total abundance of the 25 species collected there. For
each species, the trend is for greater abundance in plot B. Among
predators colected by sweep netting, S. sulphuripes was most commonly
observed on collard plants. I would classify S. sulphuripes as a
collard component species, since female syrphids are probably
attracted to cabbage aphids or the collard host plant from afar. Of
the typical foliar predators found in alfalfa, Coccinella trifasciata
L. was most often observed on the collard plants, although almost all
individuals were observed on collards in plot A, where few C.
trifasciata were collected out of alfalfa. The general lack of a
strong association between foliar predator abundance in alfalfa and

occurrence on the interplanted collards suggests that the alfalfa habitat did not serve as a useful reservoir of foliar predator species.

Comparisons of ground predator fauna between plots A and B when plot A was plowed and left fallow in early August 1982 yielded results similar to the comparisons for June and July 1982 (Table 11.4). Although species richness was the same for both plots (21 species), the patterns of abundance for each species were equivalent to those observed earlier in the summer. Phalangium opilio, P. sternalis and staphylinids were more abundant in plot B, while E. dentosa and P. vulgaris were more abundant in plot A. Also, when the abundance of P. opilio is subtracted from each total, plot A supported a greater abundance of ground predators than plot B (plot A = 37.9 individuals/trap/day; plot B = 28.0 individuals/trap/day).

For both comparisons between plots A and B in 1982, the overall effect of alfalfa plant height on ground predators varied with species, while increased plant height generally supported a greater abundance and species richness of foliar arthropod predators. Although increased habitat complexity was associated with higher prevalence of some species of ground predators on the interplanted collards, foliage predator occurrence on collards declined with increased alfalfa plant height.

## Objective 2

Both B. brassicae alates and P. rapae females exhibited clear patterns in colonization of collards planted against varying background type (Table II.5). In experiment a, I found significantly higher numbers of alate cabbage aphids on collards grown in the recently planted alfalfa field (plot A) when compared to the biculture (plot B) on five out of five sample dates. General observations during time period 1 confirmed this pattern (Figure II.6). The pattern also held in comparison of collards placed on 0.9 m stakes in plot B versus those planted at the ground surface in

Table II.4. Mean ± 95% confidence intervals of the principal ground predators caught / 100 pitfall traps / day in 36 pitfall traps on 10 sample dates in the collard monoculture (plot A) and in the collard/alfalfa biculture (plot B) (13 August -- 1 September 1982; OSU Entomology Farm, Corvallis, Oregon) and the degree to which each taxa was observed on the collard plants. * Indicates significant difference in abundance for plot comparisons (P <.05; one-way ANOVA).

| PREDATOR | COLLARD MONOCULTURE | COLLARD / ALFALFA | F | PREVALENCE ON COLLARD PLANTS |
|---|---|---|---|---|
| Phalangium opilio (Adults) | 3.0 ± 2.0 | 31.9 ± 10.0 | 32.20* | Common |
| Phalangium opilio (Juveniles) | 98.9 ± 30.0 | 165.1 ± 33.1 | 8.84* | Common |
| Pardosa sternalis | 0 | 23.9 ± 8.9 | 29.34* | Rare |
| Staphylinidae | 14.7 ± 3.6 | 29.5 ± 16.4 | 3.05 | Rare |
| Erigone dentosa | 31.1 ± 15.0 | 6.9 ± 3.1 | 9.97* | Common |
| Pterostichus vulgaris | 53.1 ± 10.8 | 16.9 ± 6.1 | 30.08* | Rare |
| TOTAL -- GROUND PREDATORS | 221.3 ± 50.0 | 286.1 ± 53.9 | 3.06 | ------ |
| PREDATOR SPECIES RICHNESS | 21 | 21 | ------ | ------ |
| ALFALFA PLANT HEIGHT (cm) | 0 | 50.1 ± 6.2 | ------ | ------ |

Table II.5. Mean Abundance ± 95% confidence intervals of B. brassicae alatae and P. rapae eggs on collards grown in plot A (control) versus plot B (alfalfa background treatment) (Experiment a) and on collards planted on the ground (control) versus on .9 meter stakes (alfalfa height treatment) in plot B (Experiment b). * Indicates significant difference (P < .05); one-way ANOVA: Plots A and B located at OSU Entomology Farm, Corvallis, Oregon.

| EXPERIMENT | TIME PERIOD | SAMPLE DATE | B. brassicae | | | | P. rapae | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | CONTROL | TREATMENT | df | F | CONTROL | TREATMENT | df | F |
| a | 1 | 11 Jl 81 | 47.0 ± 15.5 | .12 ± .25 | 1,16 | 29.1* | 0.1 ± 0.2 | .88 ± .70 | 1,16 | 5.5* |
| (A vs. B) | 1 | 20 Jl 81 | 20.0 ± 9.6 | .38 ± .47 | 1,16 | 13.1* | 0.5 ± 0.5 | 1.88 ± .92 | 1,16 | 6.9* |
| | 1 | 27 Jl 81 | 10.8 ± 4.4 | .15 ± .63 | 1,28 | 25.1* | 0.4 ± 0.4 | .16 ± .21 | 1,28 | 1.5 |
| | 3 | 13 Jl 82 | 5.0 ± 1.8 | 0 | 1,33 | 16.3* | 1.5 ± .6 | 1.64 ± 1.51 | 1,33 | 0.3 |
| | 3 | 22 Jl 82 | 2.8 ± 2.2 | 0 | 1,40 | 3.2 | 1.0 ± .7 | 2.30 ± 2.35 | 1,40 | 1.7 |
| b | 3 | 13 Jl 82 | 0 | 1.3 ± .85 | 1,24 | 7.8* | 1.6 ± 1.5 | .07 ± .14 | 1,24 | 5.0* |
| (B vs. .9 m) | 3 | 22 Jl 82 | 0 | .8 ± .36 | 1,36 | 12.0* | 2.3 ± 2.4 | .17 ± .20 | 1,36 | 5.5* |

37
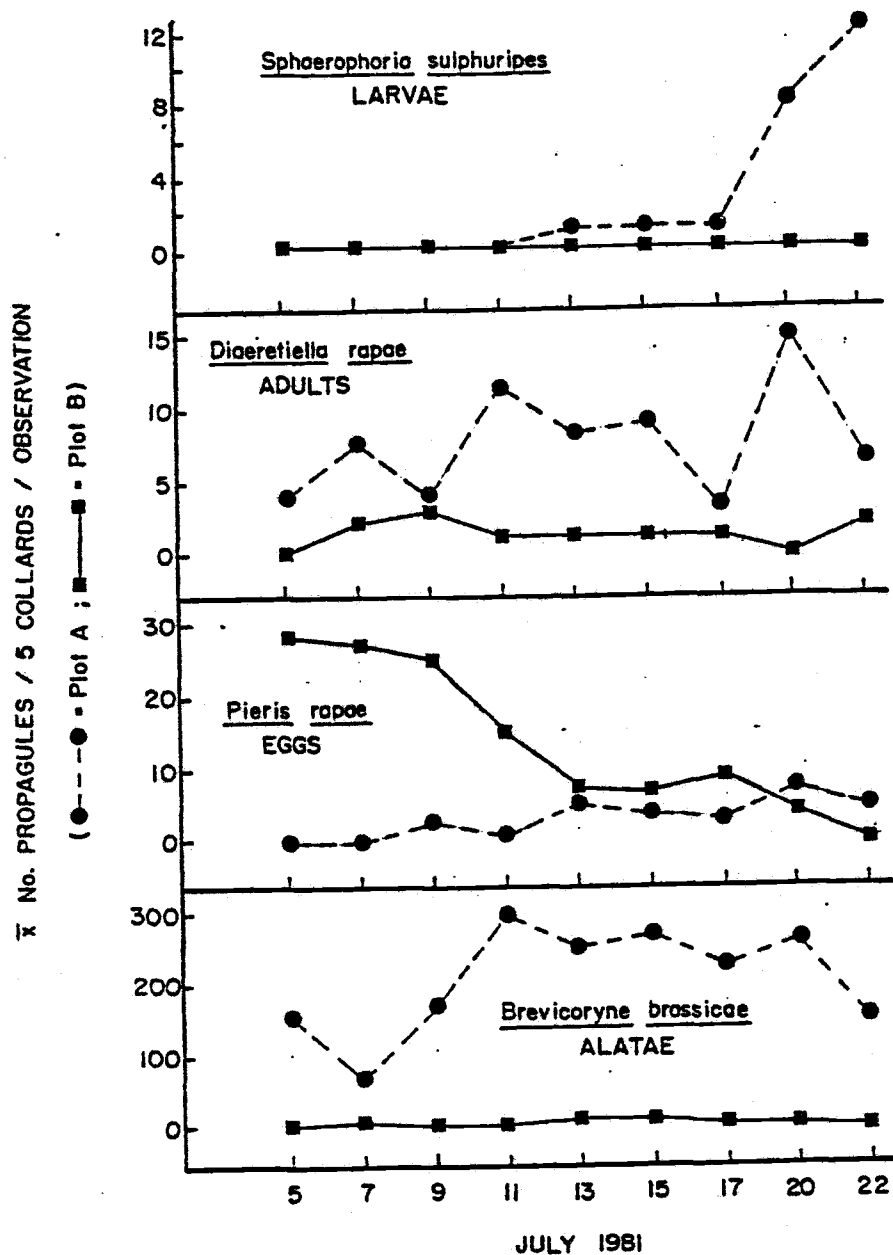
Figure II.6. Number of collard component species propagules
arriving on five (5) collard plants grown either in plot A
(●——●) or plot B (■——■) between 5 July and 22 July 1981.
OSU Entomology Farm, Corvallis, Oregon.

plot B (Table II.5). Significantly more alates were also observed over time on plants raised above the highest alfalfa plants when compared to those planted at the ground surface (Figure II.7).

The colonization pattern exhibited by P. rapae females was the reverse of that for B. brassicae (Table II.5). In experiment a, greater numbers of P. rapae eggs were counted on collards grown in plot B when compared to plot A on two out of five sample dates; observations during time period 1 indicated that greater numbers of eggs were initially oviposited on plants in plot B, with oviposition rates becoming equivalent after about 10 days (Figure II.6). The same result was obtained in experiment b when oviposition rates onto plants placed on 0.9 m stakes were compared with those planted at the ground surface (Table II.5). Female P. rapae showed a clear propensity to place their eggs on plants at the ground surface when compared to those raised above the alfalfa throughout the third time period (Figure II.7).

The natural enemy species of the component community, D. rapae and S. sulphuripes, exhibited colonization patterns similar to those shown by B. brassicae (Table II.6). In experiment c, the number of adult D. rapae found on plants in plot A was significantly higher than those found on plants in plot B on all three sample dates during time period 1. Percent B. brassicae mummy formation by D. rapae was also higher in plot A when compared to plot B on two of five sample dates in experiment c. This pattern was confirmed by observations of D. rapae colonization of plants in the two plots during time period 1 (Figure II.6). Although S. sulphuripes females tended to place more eggs on plants in plot A (Figure II.6), no significant difference in number of syrphid larvae was observed on any of the five sample dates in experiment c (Table II.6). There was no clear colonization pattern of either D. rapae or S. sulphuripes onto raised 0.9 m collards when compared to collards planted at the ground surface in plot B (Table II.6).
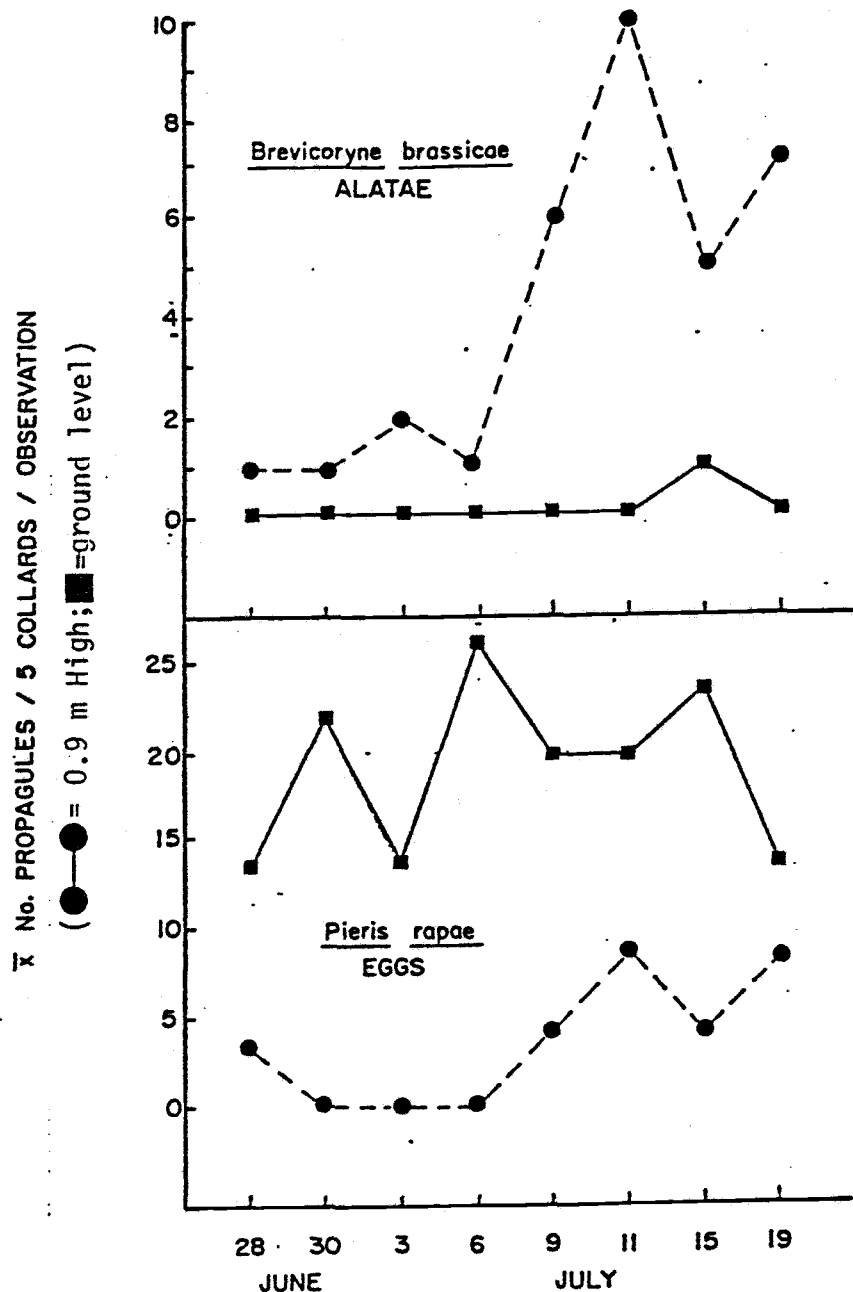
Figure II. 7. Number of <u>Brevicoryne brassicae</u> alatae and <u>Pieris rapae</u> eggs observed on five (5) collard plants placed either at the ground surface in plot B (■——■) or raised on .9 m high stakes in plot B (●——●) between 28 June and 19 July 1982. OSU Entomology Farm, Corvallis, Oregon.

Table II.6. Number of D. rapae adults, S. sulphuripes larvae, and arcsine % B. brassicae mumm-
ies on collards grown in plot A (control) versus plot B (alfalfa background treatment)
(experiment c) and on collards grown on the ground (control) versus on 0.9 m stakes (alfalfa
height treatment) in plot B (experiment d). * Indicates significant difference (p < 0.05; ANOVA)
for comparison of means ± 95% confidence limits.

| EXPER. | TIME PERIOD | SAMPLE DATE | D. rapae | | | % Mummies | | | S. sulphuripes | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | CONTROL | TREATMENT | F | CONTROL | TREATMENT | F | CONTROL | TREATMENT | F |
| c (A vs. B) | 1 | 11 Jl 81 | 1.20 (.57) | .13 (.22) | 5.68* | 0 | 0 | --- | .22 (.26) | 0 | 1.45 |
| | 1 | 20 Jl 81 | .93 (.57) | .22 (.44) | 3.05 | 12.9 (4.7) | 12.9 (10.2) | 0 | .20 (.29) | 0 | 1.00 |
| | 1 | 27 Jl 81 | .56 (.36) | .08 (.17) | 2.91 | 26.4 (4.6) | 19.9 (7.2) | 1.07 | 1.00 (.89) | 0 | 2.35 |
| | 3 | 13 Jl 82 | --- | --- | --- | 12.4 (5.9) | 0 | 8.27* | .14 (.14) | .20 (.20) | .57 |
| | 3 | 22 Jl 82 | --- | --- | --- | 19.0 (5.6) | 0 | 30.38* | .35 (.20) | .13 (.25) | .52 |
| d (B vs. .9 m) | 3 | 13 Jl 82 | --- | --- | --- | 0 | 7.1 (6.3) | 3.23 | .20 (.20) | 0 | 2.20 |
| | 3 | 22 Jl 82 | --- | --- | --- | 0 | 0 | --- | .13 (.16) | 0 | 2.06 |

Of the four collard component species studied, B. brassicae, D. rapae and S. sulphuripes tended to colonize apparent plants, while P. rapae exhibited a tendency to place more eggs on relatively unapparent plants.

## Objective 3

The hand removal exclusion technique produced significant effects on collard herbivore populations in 4 of 21 possible comparisons (control vs. treatment; Table II.7). All seven comparisons of mean P. rapae individuals per plant for plots A and B were statistically equivalent. One comparison of mean % mummy formation and three comparions of mean number of cabbage aphids were significantly different; three of these differences occurred in plot A and one in plot B. In the plot A comparison on 20 July 1982, there were significantly more aphids and significantly less percent mummy formation on natural enemy exclusion plants than on control plants. The implication that the aphid parasite D. rapae was responsible for the greater mortality of cabbage aphids on control plants is supported by data on the natural enemies removed from exclusion plants during that experiment (Table II.8). Clearly, the most commonly removed natural enemy during the experiment ending on 20 July 1982 was D. rapae, followed by the syrphid S. sulphuripes, the coccinellid C. trifasciata and the dwarf spider E. dentosa. That D. rapae also had some impact on B. brassicae populations in the other two comparisons in plot A (27 July 1981, 13 July 1982) is indicated by the trend of higher % mummy formation and lower aphid numbers on control plants for 3 out of 4 of these comparisons (Table II.7). One comparison (13 July 1982) is part of the same experiment as the comparison on 20 July 1982, so the similar results are not surprising. The other comparison, on 27 July 1981, is independent of the other two and numbers of D. rapae removed from exclusion plants during this experiment are comparable to those removed during time period 3 (Table II.8).

Table II.7. Number of B. brassicae, P. rapae and arcsine % B. brassicae mummies for control versus enemy-exclusion treatments in plot A (experiment e) and plot B (experiment f) at O.S.U. Entomology Farm, Corvallis, Oregon. * Indicates significant difference ($p < 0.05$; ANOVA; 95% confidence limits in parentheses).

| EXPER. | TIME PERIOD | SAMPLE DATE | df | B. brassicae CONTROL | TREATMENT | F | % Mummies CONTROL | TREATMENT | F | P. rapae CONTROL | TREATMENT | F |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| e (plot A) | 1 | 27 Jl 81 | 1,45 | 78.5 (28.6) | 184.1 (87.4) | 6.25* | 26.4 (4.6) | 24.2 (3.3) | .57 | 2.66 (1.86) | 2.24 (.85) | .14 |
| | 3 | 13 Jl 82 | 1,34 | 35.3 (18.0) | 50 3 (18.5) | 1.30 | 12.4 (5.9) | 14.5 (7.1) | .23 | 2.24 (.85) | 2.10 (1.20) | .06 |
| | 3 | 20 Jl 82 | 1,48 | 36.3 (14.2) | 71.5 (22.9) | 6.53* | 19.0 (5.6) | 8.9 (3.5) | 11.71* | 2.81 (.63) | 2.90 (1.47) | .00 |
| f (plot B) | 1 | 27 Jl 81 | 1,25 | 11.8 (7.9) | 13.7 (9.4) | .08 | 19.9 (7.2) | 16.9 (7.7) | .28 | 3.30 (1.90) | 2.80 (1.70) | .19 |
| | 2 | 5 Sep 81 | 1,72 | 4.5 (2.0) | 12.5 (6.3) | 8.88* | 0 0 | 0 0 | --- | 2.10 (.64) | 2.70 (1.10) | .40 |
| | 3 | 13 Jl 82 | 1,20 | 36.9 (39.2) | 3.8 (1.40) | 4.17 | 0 0 | 0 0 | | 3.80 (1.90) | 5.50 (1.60) | 2.38 |

Table II.8. Number of natural enemies removed per plant for exclusion treatments in plot  A (time periods 1 & 3) and plot B (time periods 1, 2 & 3); OSU Entomology Farm, Corvallis, Oregon.

| NATURAL ENEMIES | PLOT A | | PLOT B | | |
|---|---|---|---|---|---|
| | 1 (216 plants) | 3 (300 plants) | 1 (192 plants) | 2 (120 plants) | 3 (300 plants) |
| Diaeretiella rapae (M'Intosh) | 215-.995 | 233-.777 | 12-.062 | 7-.058 | 21-.070 |
| Sphaerophoria sulphuripes Thomp. | 6-.028 | 9-.030 | 1-.005 | 2-.016 | 13-.043 |
| Coccinellidae | 9-.042 | 3-.010 | 3-.016 | 3-.025 | |
| Chrysopa spp. | 0 | 0 | 0 | 0 | 1-.003 |
| Orius insidiosus (Say) | 1-.005 | 0 | 0 | 0 | 0 |
| Deraocoris spp. | 1-.005 | 0 | 0 | 0 | 0 |
| Lygus spp. | 3-.014 | 0 | 1-.005 | 2-.016 | 0 |
| Tetragnatha laboriosa Hentz | 3-.014 | 1-.003 | 11-.057 | 2-.016 | 1-.003 |
| Enoplognatha ovata (Clerck) | 3-.014 | 1-.003 | 2-.010 | 0 | 0 |
| Oxyopes salticus Hentz | 0 | 0 | 2-.010 | 0 | 2-.007 |
| Other foliar spiders | 3-.014 | 1-.003 | 5-.028 | 2-.016 | 2-.007 |
| Phalangium opilio L. | 0 | 0 | 0 | 0 | 18-.060 |
| Erigone dentosa O.P.-Cambridge | 10-.046 | 6-.020 | 10-.052 | 4-.033 | 7-.023 |
| Pardosa sternalis (Thorell) | 0 | 0 | 2-.010 | 0 | 2-.007 |
| TOTAL PREDATORS | 39-.181 | 21-.070 | 37-.193 | 13-.108 | 46-.153 |
| TOTAL NATURAL ENEMIES | 254-1.18 | 254-.847 | 49-.255 | 20-.167 | 67-.223 |

Comparatively few natural enemies were removed from exclusion plants in plot B during any of the hand-removal experiments (Table II.8). The significant results on 5 September 1981 for B. brassicae is not explained by data on hand removal during time period 2 (Table II.8).

The experiments on the influence of local natural enemies on B. brassicae populations gave some interesting results (Table II.9). For each of the three comparisons in the two plots, mean number of B. brassicae alive at the end of the experiment was significantly higher on control plants (enclosed by fine-mesh bag-cages) than on predator-inclusion plants (enclosed by large wooden cages; 1 mm mesh). For plot A, mean percent B. brassicae mummy formation was also significantly higher on the inclusion plants than on control; after these experiments had been completed, I discovered that adult D. rapae (but not alate B. brassicae) could penetrate the 1 mm mesh of the large inclusion cages, but not the fine mesh of the bag-cages. Apparently this caused the difference in percent mummy formation and probably contributed to the decline in aphid numbers under the wooden cages. For plot B, no mummies were formed on any of the plants in either treatment during the experiment, so the decline in aphid numbers on the inclusion plants was due to some other factor, such as local predation.

The influence of ground predators on B. brassicae and P. rapae populations differed for plots A and B (Table II.10). For plot A, mean number of B. brassicae and mean percent pierid survival on control and treatment plants were statistically equivalent for each comparison made, although aphid numbers on control plants declined slightly while number on treatment plants increased slightly over the sample dates. For plot B, aphid numbers on unenclosed control plants decreased from a mean of 25.2 on 15 August to 6.9 on 1 September, while for the exclusion treatment plants, mean aphid number increased from 16.1 to 53.7 over the course of the experiment. Of the four possible paired comparisons, the pairs on 15 August and 1 September were significantly different with higher aphid numbers on control

Table II.9. Mean ± 95% confidence limits of number of B. brassicae and arcsine % B. brassicae mummies for control (fine mesh bag-cages) versus enemy inclusion treatments (1 mm mesh wooden cages) in plot A and plot B at O.S.U. Entomology Farm, Corvallis, Oregon.  * Indicates significant difference (p <0.05; ANOVA).

| EXPERIMENT | TIME PERIOD | SAMPLE DATE | B. brassicae | | | | %Mummies | | | |
| | | | CONTROL | TREATMENT | df | F | CONTROL | TREATMENT | df | F |
| g (plot A) | 1 | 27 Jl 81 | 168.1 + 90.0 | 33.5 + 30.0 | 1,27 | 8.36* | 0 | 54.1 + 5.7 | 1,27 | 338.6* |
| | 3 | 20 Jl 82 | 170.2 + 86.4 | 25.3 + 13.1 | 1,17 | 6.36* | 0 | 33.0 + 6.5 | 1.17 | 218.3* |
| h (plot B) | 3 | 20 Jl 82 | 91.4 + 58.9 | 17.5 + 9.3 | 1,30 | 12.37* | 0 | 0 | 1,30 | ---- |

Table II.10. Mean number of B. brassicae and P. rapae on 3 sample dates in plot A (control = 6" raised cylinders, n=12; exclusion treatment =ground level cylinders, n=12) and on 4 sample dates in plot B (control = unenclosed plants, n=23; treatment = ground level cylinders, n=14) and mean arcsine % P. rapae survivorship on the final sample date in each plot for control and treatment plants, O.S.U. Entomology Farm, Corvallis, Oregon. * Indicates significant difference (p < 0.05; Wilcoxon 2-sample test for B. brassicae comparisons; ANOVA for P. rapae comparisons).

| EXPER. | TIME PERIOD | SAMPLE DATE | df | Brevicoryne brassicae | | | Pieris rapae | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | Numbers | | | % Survivorship | | |
| | | | | CONTROL | TREAT. | $t_s$ | CONTROL | TREAT. | F | CONTROL | TREAT. | F |
| i (plot A) | 4 | 15 Ag 82 | 1,22 | 27.3 (10.2) | 25.2 (19.4) | .07 | 1.83 (1.62) | 3.27 (1.84) | .94 | ----- | ---- | --- |
| | | 23 Ag 82 | 1,22 | 30.3 (8.2) | 34.2 (29.8) | .07 | 17.90 (2.8) | 16.90 (5.8) | .08 | ---- | ---- | --- |
| | | 27 Ag 82 | 1,22 | 24.8 (12.1) | 39.7 (42.0) | .66 | 15.30 (3.6) | 11.60 (6.0) | 1.28 | 63.60 (12.20) | 46.00 (12.00) | 2.96 |
| j (plot B) | 4 | 15 Ag 82 | 1,35 | 24.8 (7.4) | 16.5 (8.10) | 2.26 | 7.86 (2.92) | 6.05 (2.58) | 1.29 | ---- | ---- | --- |
| | | 23 Ag 82 | 1,35 | 20.3 (8.2) | 28.8 (17.4) | .55 | 24.91 (5.8) | 25.20 (7.50) | .004 | ---- | ---- | --- |
| | | 27 Ag 82 | 1,35 | 13.4 (5.4) | 32.4 (26.6) | 3.07 | 18.42 (5.0) | 22.40 (8.2) | .420 | ---- | ---- | --- |
| | | 1 Sep 82 | 1,35 | 7.2 (2.1) | 56.6 (60.6) | 4.37* | 13.30 (2.92) | 19.60 (6.40) | 4.13* | 38.60 (1.60) | 51.70 (4.60) | 10.23* |

plants at the beginning of the experiment and increased numbers on treatment plants at the end of the experiment (Table II.10; Wilcoxon 2-sample test). Pierid egg and larval survivorship on 1 September was also significantly higher for treatment plants in plot B, although no differences were observed for any paired comparison on the four sample dates. These data suggest that both aphids and pierids were signficantly influenced by the treatment effects in plot B, but not in plot A. The most common ground predator in plot B was the harvestman P. opilio; this species was significantly less common in the collard monoculture. Harvestmen were also commonly collected on the collard plants, suggesting that this species contributed to the results in Table II.10.

The addition of one C. trifasciata per bag-cage significantly reduced B. brassicae numbers relative to control plants (Table II.11). The addition of one S. sulphuripes per plant in plot B had no significant effect on mean B. brassicae numbers. Results of these two brief experiments on the influence of natural enemies under conditions of controlled immigration can be supplemented by viewing results of another experiment from a different perspective (Figure II.8). In two separate experiments (ending dates: 27 July 1981 and 20 July 1982), the mean number of B. brassicae per plant on collards that had been enclosed by the fine-mesh bag-cages was significantly higher than the mean number on collards enclosed by the large inclusive 1 mm mesh wooden cages. Mean numbers of cabbage aphids on bag-caged plants was also signifcantly higher than mean numbers on unenclosed collards (both treatments in plot A) on 20 July 1982 and nearly significantly different on 27 July 1981. The opposite pattern was observed for mean percent B. brassicae mummy formation for the two sample dates (Figure II.8). Since I observed that D. rapae adults but not B. brassicae alatae could penetrate the 1 mm mesh of the large cages, these data may represent another example of the influence of a natural enemy under conditions of controlled herbivore immigration.

Table II.11. Mean ± 95% confidence limits of B. brassicae numbers for control and predator-inclusion treatments in experiments k and l; Experiment k: control = plants inoculated with 25 B. brassicae apteri within fine-mesh bag-cages; treatment = same as control except one (1) Coccinella trifasciata adult added per bag-cage. Experiment l: control = plants inoculated with 25 B. brassicae apteri and left unenclosed in plot B; treatment = same as control except one (1) Sphaerophoria sulphuripes added per plant. * Indicates significant difference (P < .05; one-way ANOVA).

| EXPERIMENT | TIME PERIOD | SAMPLE DATE | df | CONTROL | TREATMENT | F |
|---|---|---|---|---|---|---|
| k | 2 | 5 Sep 81 | 1,33 | 166.6 ± 90.9 | 41.8 ± 26.1 | 9.89* |
| l | 2 | 5 Sep 81 | 1,55 | 4.5 ± 1.9 | 2.4 ± 1.9 | .81 |
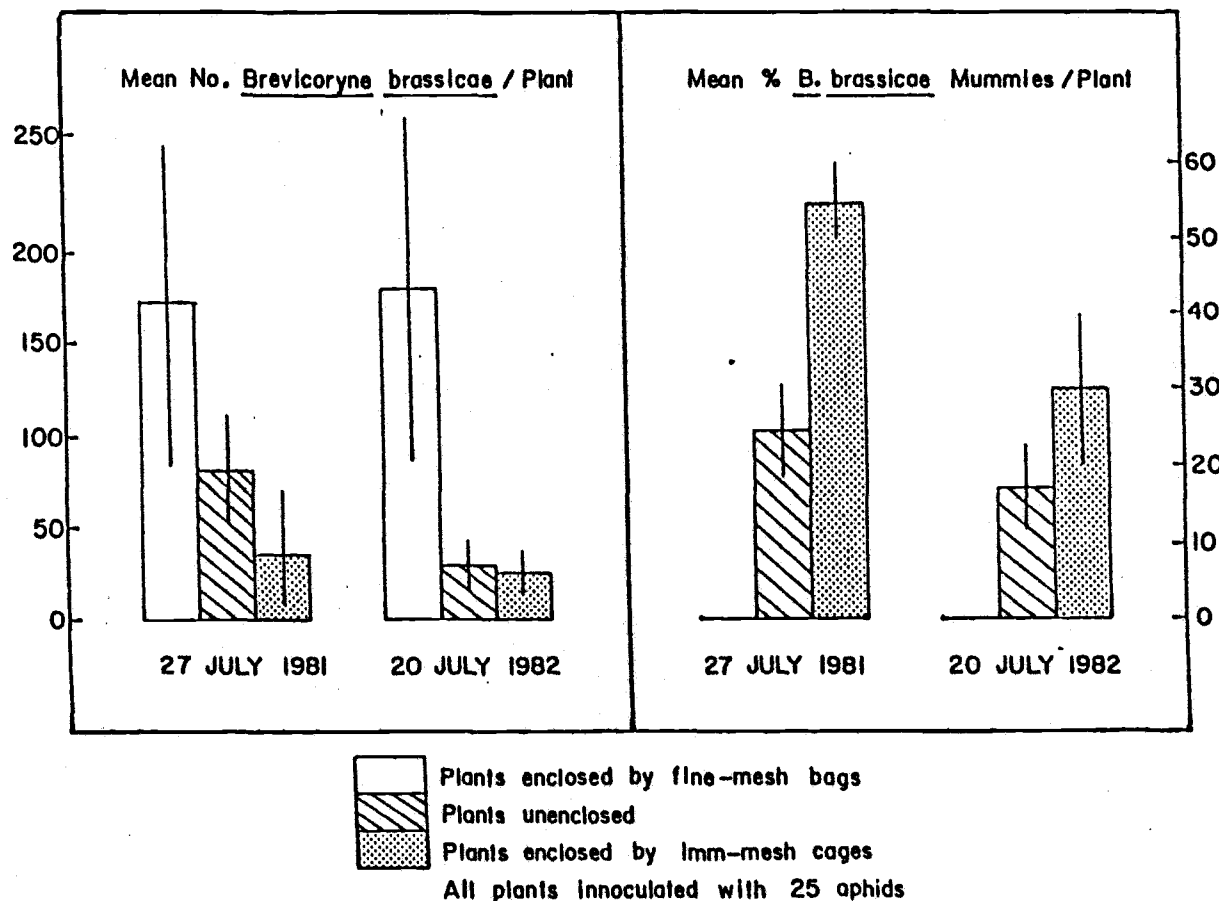
Figure II.8.   Mean ± 95% confidence limits of B. brassicae numbers and arcsine % B. brassicae mummies on 2 sample dates for plants enclosed by fine mesh bag-cages, unenclosed, and enclosed by 1 mm mesh cages; O.S.U. Entomology Farm, Corvallis, Oregon.   All plants initially inoculated with 25 B. brassicae apteri.

A total of 49 taxa were analyzed with the precipitin test for evidence of feeding relations with B. brassicae and P. rapae (Table II.12). Of these, 40 taxa were collected at least once on collard plants and 12 taxa were collected at least ten times. In terms of the frequency with which predators were collected on collard plants and the percent positive reactions, the most important predators in plot A were the syrphid S. sulphuripes, the coccinellids C. trifasciata and H. convergens and the dwarf spider E. dentosa (Table II.13). In plot B, the most important predators were S. sulphuripes, Tetragnatha laboriosa Hentz and P. opilio. However, data on the percent positive reactions and prevalence on the collard plants does not necessarily reflect the actual importance of each predator species. The importance of more active predators such as P. opilio and coccinellids will be underestimated when compared to predators like E. dentosa given the same intensity of observation, because an active predator may cause significant mortality on foliar herbivore populations without being observed.

A few aspects of the serological data are worth highlighting. First, the percent positive reactions given by S. sulphuripes larvae collected on collards planted in plots A and B did not differ from B. brassicae (97% vs. 96%), but differed markedly for P. rapae (12% in plot A and 35% in plot B) (Figure II.9). This difference may reflect the relative abundances of P. rapae and B. brassicae in the two plots; relative abundance of P. rapae was much higher than B. brassicae in plot B. Second, the expected effect of intercropping as an increase in habitat complexity is to increase the movement of natural enemies from the 'reservoir' crop (i.e., alfalfa) to the interplanted crop species (collard). This effect is exhibited clearly by T. laboriosa where abundance in the alfalfa habitat is directly related to occurrence on the collard plants (Figure II.9; Tables II.13 and II.14). The reverse is true for the six coccinellid species collected on collards (Figure II.9). Although coccinellids were common residents of the biculture (plot B) (Table II.2, II.3) and relatively uncommon in the monoculture (plot A) (Table II.3),

Table II.12 Number and percent positive precipitin reactions (in parentheses) of predators collected on collard plants (plots A and B) and off collard plants (sweep net and pitfall sampled predators combined) against _Brevicoryne brassicae_ and _Pieris rapae_ antisera; OSU Entomology Farm, Corvallis, Oregon.

| PREDATOR SPECIES | ON COLLARD | | | | OFF COLLARD | |
| | PLOT A | | PLOT B | | | |
| | Brevicoryne | Pieris | Brevicoryne | Pieris | Brevicoryne | Pieris |
| --- | --- | --- | --- | --- | --- | --- |
| Chilopoda | 0<br>0 | 0<br>0 | .2/2<br>(100) | 0/2<br>0 | 0<br>0 | 0<br>0 |
| Phalangium opilio L. | 3/11<br>(27) | 3/11<br>(27) | 20/25<br>(80) | 14/25<br>(70) | 41/130<br>(32) | 8/130<br>(6) |
| Dictyna spp. | 0<br>0 | 0<br>0 | 0/6<br>0 | 1/6<br>(16) | 0<br>0 | 0<br>0 |
| Enoplognatha ovata (Clerck) | 1/5<br>(20) | 0/5<br>0 | 0/4<br>0 | 0/4<br>0 | 0/1<br>0 | 0/1<br>0 |
| Lepthyphantes tenuis (Blackwall) | 0<br>0 | 0<br>0 | 3/4<br>(75) | 0/4<br>0 | 0<br>0 | 0<br>0 |
| Linyphiidae - Juveniles | 6/7<br>(86) | 0/7<br>0 | 1/4<br>(25) | 0/4<br>0 | 0<br>0 | 0<br>0 |
| Erigone dentosa O.P.-Cambridge | 7/17<br>(41) | 2/17<br>(12) | 13/26<br>(50) | 2/26<br>(4) | 0/6<br>0 | 0/6<br>0 |
| Micryphantidae | 1/13<br>(8) | 1/13<br>(8) | 0/12<br>0 | 0/12<br>0 | 0<br>0 | 0<br>0 |

Table II.12. (continued).

| PREDATOR SPECIES | ON COLLARD | | | | OFF COLLARD | |
| | PLOT A | | PLOT B | | | |
| | Brevicoryne | Pieris | Brevicoryne | Pieris | Brevicoryne | Pieris |
|---|---|---|---|---|---|---|
| Micrathena sp. | 0/1 0 | 0/1 0 | 0/1 0 | 0/1 0 | 0 0 | 0 0 |
| Araneidae - Juveniles | 3/7 (43) | 0/7 0 | 1/4 (25) | 0/4 0 | 0 0 | 0 0 |
| Tetragnatha laboriosa Hentz | 0/9 0 | 0/9 0 | 37/52 (71) | 4/52 (8) | 0/4 0 | 0/4 0 |
| Agelenopsis sp. | 0/2 0 | 0/2 0 | 1/3 (33) | 1/3 (33) | 0/1 0 | 0/1 0 |
| Pardosa sternalis (Thorell) | 0 0 | 0 0 | 3/6 (50) | 0/6 0 | 0/15 0 | 1/15 (6) |
| Schizocosa mccooki (Montgomery) | 0 0 | 0 0 | 0 0 | 0 0 | 0/2 0 | 0/2 0 |
| Oxyopes salticus Hentz | 0 0 | 0 0 | 2/4 (50) | 0/4 0 | 0 0 | 0 0 |
| Anyphaena sp. | 0 0 | 0 0 | 2/2 (100) | 0/2 0 | 0 0 | 0 0 |
| Misumenops celer (Hentz) | 2/5 (40) | 0/5 0 | 0/1 0 | 0/1 0 | 0/6 0 | 0/6 0 |
| Xysticus cunctator Thorell | 0 0 | 0 0 | 0/1 0 | 1/1 (100) | 0/2 0 | 0/2 0 |

Table II.12. (continued).

| PREDATOR SPECIES | ON COLLARD | | | | OFF COLLARD | |
| | PLOT A | | PLOT B | | | |
| | Brevicoryne | Pieris | Brevicoryne | Pieris | Brevicoryne | Pieris |
|---|---|---|---|---|---|---|
| Thanatus sp. | 0/1<br>0 | 0/1<br>0 | 0<br>0 | 0<br>0 | 0<br>0 | 0<br>0 |
| Philodromus sp. | 0<br>0 | 0<br>0 | 0/1<br>0 | 0/1<br>0 | 0/2<br>0 | 0/2<br>0 |
| Tibellus oblongus (Walckenaer) | 1/2<br>(50) | 0/2<br>0 | 0<br>0 | 0<br>0 | 0/2<br>0 | 0/2<br>0 |
| Eris sp. | 0/1<br>0 | 0/1<br>0 | 1/3<br>0 | 0/3<br>0 | 0/1<br>0 | 0/1<br>0 |
| Phiddipus sp. | 0<br>0 | 0<br>0 | 0/1<br>0 | 0/1<br>0 | 0<br>0 | 0<br>0 |
| Forificula auricularia L. | 0<br>0 | 0<br>0 | 1/5<br>(20) | 0/5<br>0 | 0<br>0 | 0<br>0 |
| Orius insidiosus (Say) | 0/1<br>0 | 0/1<br>0 | 3/6<br>(50) | 0/6<br>0 | 0<br>0 | 0<br>0 |
| Lygus spp. | 5/7<br>(71) | 2/7<br>(29) | 1/4<br>(25) | 0/4<br>0 | 2/11<br>(18) | 0/11<br>0 |
| Heterotoma sp. | 0<br>0 | 0<br>0 | 0/1<br>0 | 0/1<br>0 | 0<br>0 | 0<br>0 |
| Nabis spp. | 7/20<br>(35) | 2/20<br>(10) | 21/24<br>(88) | 3/24<br>(12) | 9/33<br>(27) | 0/33<br>0 |

Table II.12. (continued).

| PREDATOR SPECIES | ON COLLARD | | | | OFF COLLARD | |
| --- | --- | --- | --- | --- | --- | --- |
| | PLOT A | | PLOT B | | | |
| | Brevicoryne | Pieris | Brevicoryne | Pieris | Brevicoryne | Pieris |
| Geocoris sp. | 1/2 (50) | 0/2 0 | 6/6 (100) | 0/6 0 | 0/1 0 | 0/1 0 |
| Pentotomidae | 0 0 | 0 0 | 2/3 (67) | 0/3 0 | 0/7 0 | 0/7 0 |
| Chrysopa sp. | 1/1 (100) | 1/1 (100) | 6/7 (86) | 4/7 (57) | 2/27 (7) | 0/27 0 |
| Hemerobiidae | 2/2 (100) | 1/2 (50) | 0 0 | 0 0 | 0/1 0 | 0/1 0 |
| Staphylinidae | 0 0 | 0 0 | 1/1 (100) | 0/1 0 | 0/6 0 | 0/6 0 |
| Clivina fosser L. | 0/1 0 | 0/1 0 | 0 0 | 0 0 | 0/7 0 | 0/7 0 |
| Amara familiaria Duft. | 0 0 | 0 0 | 0 0 | 0 0 | 1/3 (33) | 0/3 0 |
| Agonum subsericeum Lec. | 0/1 0 | 0/1 0 | 0 0 | 0 0 | 0/1 0 | 0/1 0 |
| Pterostichus vulgaris L. | 0 0 | 0 0 | 0 0 | 0 0 | 1/23 (4) | 0/23 0 |
| Other Carabidae | 0/1 0 | 0/1 0 | 2/2 (100) | 0/2 0 | 0 0 | 0 0 |

Table II.12 (continued).

| PREDATOR SPECIES | ON COLLARD | | | | OFF COLLARD | |
| | PLOT A | | PLOT B | | | |
| | Brevicoryne | Pieris | Brevicoryne | Pieris | Brevicoryne | Pieris |
|---|---|---|---|---|---|---|
| Aeolus sp. | 0<br>0 | 0<br>0 | 1/1<br>(100) | 0/1<br>0 | 0/6<br>0 | 0/6<br>0 |
| Anthicus sp | 0<br>0 | 0<br>0 | 3/3<br>(100) | 0/3<br>0 | 0<br>0 | 0<br>0 |
| Coccinella trifasciata L. | 11/19<br>(58) | 2/19<br>(11) | 2/3<br>(67) | 0/3<br>0 | 1/42<br>(2) | 0/42<br>0 |
| C. undecempunctata L. | 3/6<br>(50) | 0/6<br>0 | 1/1<br>(100) | 0/1<br>0 | 0/3<br>0 | 0/3<br>0 |
| C. californica Mannerheim | 3/7<br>(43) | 0/7<br>0 | 0/2<br>0 | 0/2<br>0 | 1/1<br>0 | 0/1<br>0 |
| Hippodamia convergens<br>Guerin-Meneville | 21/23<br>(91) | 1/23<br>(4) | 0<br>0 | 0<br>0 | 0/11<br>0 | 1/11<br>(9) |
| Adalia bipunctata (L.) | 0<br>0 | 0<br>0 | 0/3<br>0 | 0/3<br>0 | 0<br>0 | 0<br>0 |
| Cycloneda polita Casey | 1/1<br>(100) | 0/1<br>0 | 0<br>0 | 0<br>0 | 0<br>0 | 0<br>0 |
| Cecidomyiidae | 2/2<br>(100) | 0/2<br>0 | 0<br>0 | 0<br>0 | 0<br>0 | 0<br>0 |

Table II.12 (continued).

| PREDATOR SPECIES | ON COLLARD | | | | OFF COLLARD | |
|---|---|---|---|---|---|---|
| | PLOT A | | PLOT B | | | |
| | Brevicoryne | Pieris | Brevicoryne | Pieris | Brevicoryne | Pieris |
| Sphaerophoria sulphuripes Thom. | 32/33 (97) | 9/33 (12) | 69/72 (96) | 25/72 (35) | 0 0 | 0 0 |
| Formicidae | 1/13 (8) | 0/13 0 | 10/14 0 | 0/14 0 | 0 0 | 0 0 |
| Number of taxa reacted | 30 | | 38 | | 27 | |
| TOTALS | 114/22 (52) | 19/221 (9) | 238/345 (69) | 56/345 (16) | 58/348 (17) | 10/348 (3) |

Table II.13. Number and percent positive reactions of the principal species of predators collected on collards grown in plots A and B during 1980, 1981 and 1982, OSU Entomology Farm, Corvallis, Oregon.

| PREDATOR SPECIES | Brevicoryne brassicae | | Pieris rapae | |
| --- | --- | --- | --- | --- |
| | PLOT A | PLOT B | PLOT A | PLOT B |
| Sphaerophoria sulphuripes Thom. | 32/33--97% | 69/72--96% | 4/33--12% | 25/72--35% |
| Coccinella trifasciata L. | 11/19--58% | 2/3---67% | 2/19--11% | 0/3--- 0% |
| Hippodamia convergens Guerin-Meneville | 21/23--91% | 0/0----0% | 1/23---4% | 0/0----0% |
| Nabis spp. | 7/20--35% | 21/24--88% | 2/20--10% | 3/24--12% |
| Erigone dentosa O.P.-Cambridge | 7/17--41% | 13/26--50% | 2/17--12% | 2/26---8% |
| Tetragnatha laboriosa Hentz | 0/9----0% | 37/52--71% | 0/9----0% | 4/52---8% |
| Phalangium opilio L. | 3/11--27% | 20/25--80% | 3/11--27% | 14/25--56% |
| TOTAL--7 PRINCIPAL SPECIES | 81/132-61% | 162/202-80% | 14/132-11% | 49/202-24% |
| Total--Other Predator Species | 34/89--38% | 76/143-53% | 6/89---7% | 6/143--4% |
| % Contribution by 7 Principal Predator Species | 70.4% | 68.0% | 70.0% | 89.0% |
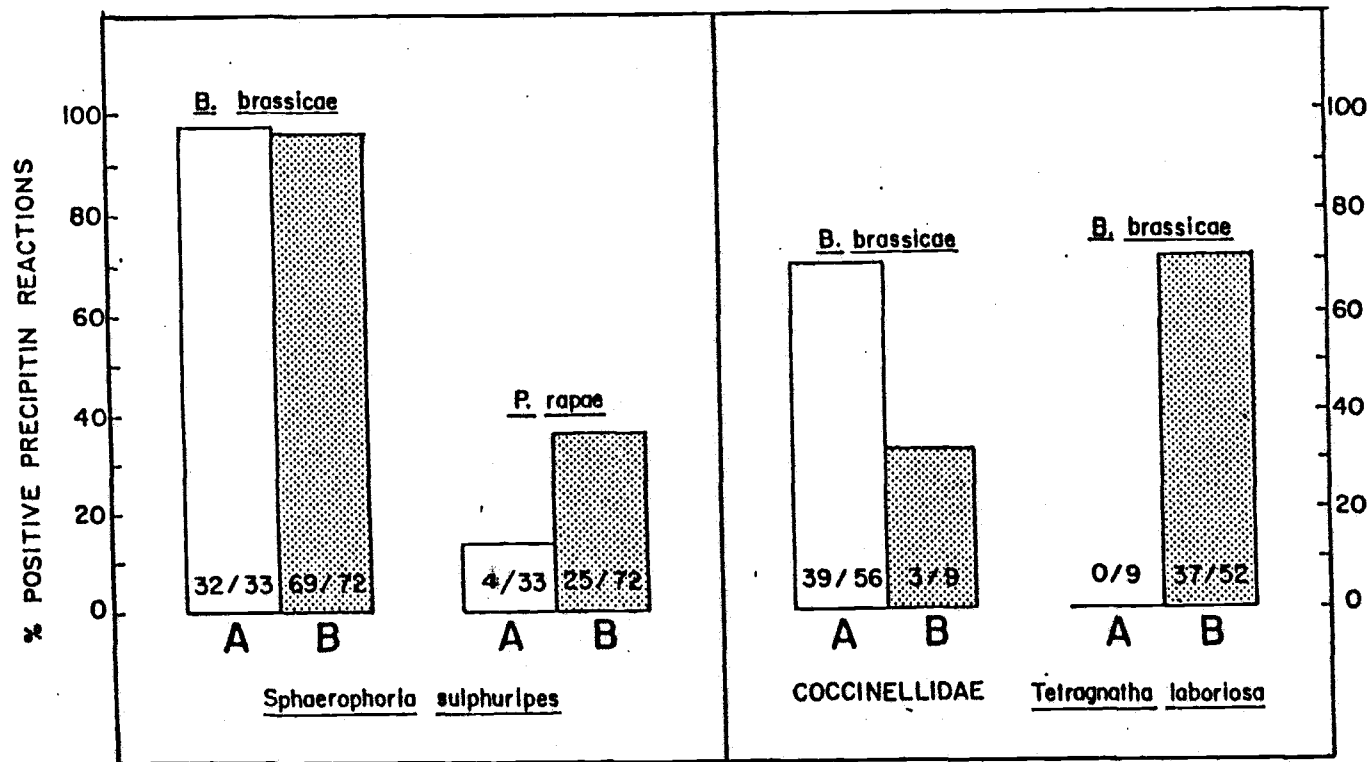
Figure II.9.  Percent positive precipitin reactions for Sphaerophoria sulphuripes collected on collards grown in plots A and B against Brevicoryne brassicae and Pieris rapae antisera and for Hippodamia convergens and Tetragnatha laboriosa against B. brassicae antiserum.

Table II.14. Number and prevalence of natural enemies observed on all collard plants during the summer of 1980 and during time periods 1, 2, 3 and 4 (1981, 1982). * Plot A=1215 visits; plot B= 1715 visits.

| NATURAL ENEMIES | PLOT A | | PLOT B | |
|---|---|---|---|---|
| | No. | No. per VISIT* | No. | No. per VISIT* |
| Phalangium opilio | 8 | .007 | 52 | .030 |
| Enoplognatha ovata | 4 | .003 | 4 | .003 |
| Other Theridiidae | 20 | .016 | 17 | .010 |
| Erigone dentosa | 59 | .049 | 90 | .052 |
| Araneidae juveniles | 42 | .035 | 52 | .030 |
| Tetragnatha laboriosa | 11 | .009 | 23 | .013 |
| Agelenopsis sp. | 2 | .003 | 4 | .003 |
| Oxyopes salticus | 0 | 0 | 2 | .001 |
| Pardosa sternalis | 0 | 0 | 9 | .005 |
| Misumenops celer | 5 | .004 | 2 | .001 |
| Xysticus cunctator | 0 | 0 | 2 | .001 |
| Tibellus oblongus | 1 | .001 | 0 | 0 |
| Phiddipus sp. | 0 | 0 | 0 | 0 |
| Other Salticidae | 2 | .002 | 3 | .002 |
| Forificula auricularia | 0 | 0 | 10 | .006 |
| Orius insidiosus | 5 | .004 | 2 | .001 |
| Lygus spp. | 3 | .003 | 3 | .002 |
| Deraocoris spp. | 3 | .003 | 4 | .003 |
| Nabis spp. | 1 | .001 | 16 | .009 |
| Pentotomidae | 0 | .004 | 4 | .003 |
| Chrysopa sp. | 2 | .002 | 4 | .003 |
| Hemerobiidae | 2 | .002 | 0 | 0 |
| Clivina fosser | 5 | .004 | 1 | .001 |
| Coccinellidae | 72 | .059 | 9 | .005 |
| Cecidomyiidae | 34 | .028 | 0 | 0 |
| Sphaerophoria sulphuripes | 169 | .139 | 73 | .045 |
| Diaeretiella rapae | 389 | .320 | 68 | .039 |
| TOTAL PREDATORS | 450 | .370 | 457 | .266 |
| TOTAL NATURAL ENEMIES | 839 | .691 | 525 | .306 |
| SPECIES RICHNESS | >21 | ---- | >24 | ---- |

more ladybird beetles were observed on collards planted in plot A than plot B (Table II.14). The presence of a natural enemy in a surrounding habitat does not necessarily guarantee its movement onto an interplanted crop. Third, the serological results for predators collected on or away from collard plants clearly indicate that the percent positive reactions for predators collected in association with collard herbivores was higher than those observed for predators not found to be associated (Figure II.10). Of 28 taxa collected both on and off of collard plants, 20 had a higher percentage of positive reactions for both herbivores when collected on the collard plants (Table II.12).

In summary, I identify 6 species of natural enemies that may have had substantial impact on B. brassicae and P. rapae populations of collard and whose influence varied with changes in plant apparency or plant habitat complexity. The aphid parasite D. rapae and the syrphid S. sulphuripes were the most important natural enemies in the collard monoculture. As members of the collard component community, these two species locate their host/prey from a distance and were influenced by the collard crop background as it related to plant apparency, not habitat complexity. The response of coccinellids to crop background modification is unusual in that although a higher number of ladybird beetles occurred in the more established alfalfa field, coccinellids showed a limited propensity to move from the alfalfa to the collard plants growing in close proximity. In terms of prevalence on collard plants, coccinellids behaved more like collard component species, but their low prevalence on collards in plot B may have been due to prey preference rather than plant apparency. The orb-web spider T. laboriosa was positively influenced by alfalfa plant height and had a greater prevalence on collards grown amongst tall alfalfa plants. Tetragnatha would be classified as an alfalfa component species and served to link the collard and alfalfa component communities through predation. The dwarf spider E. dentosa was common in both plots A and B and was also commonly observed on collard plants in both plots. The crop background did
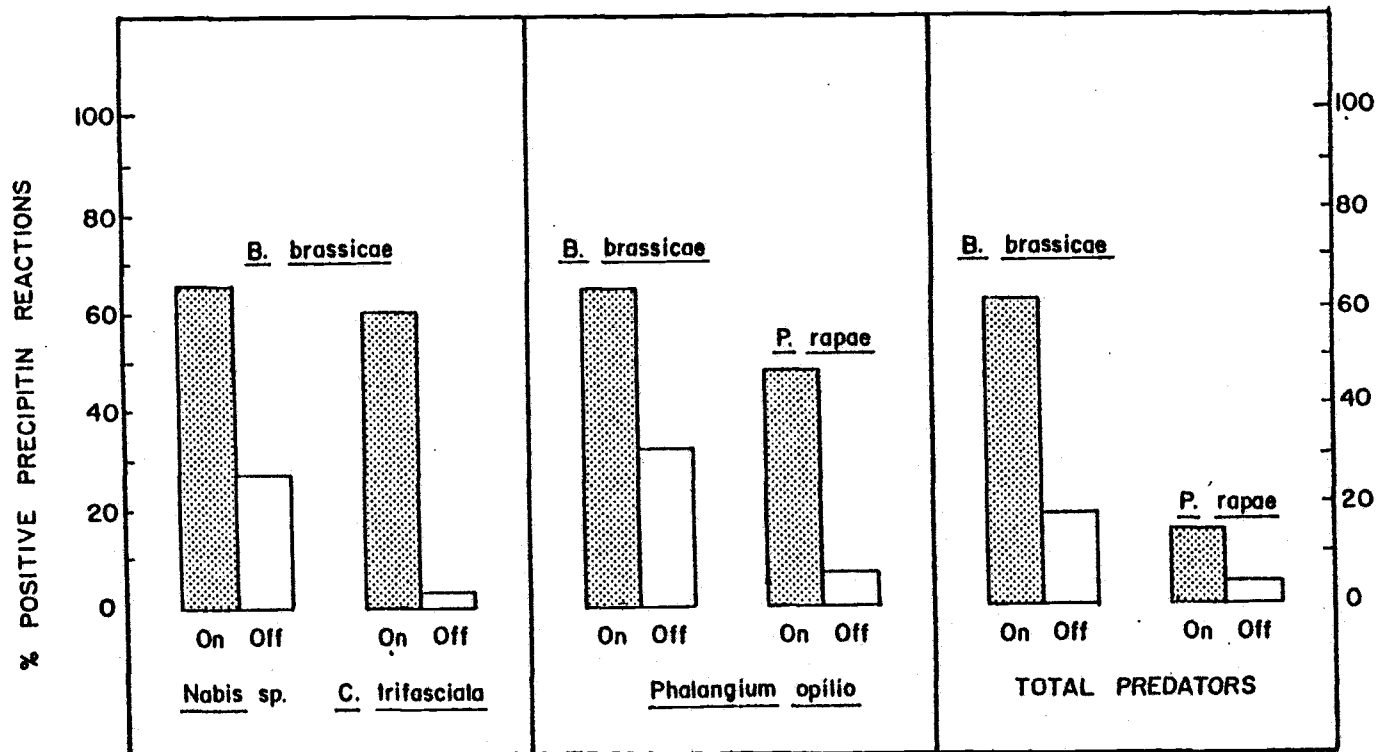
Figure II.10. Percent positive reactions for predators collected on and off of collard plants against Brevicoryne brassicae antiserum (Nabis spp. and Coccinella trifasciata) or against B. brassicae and P. rapae antisera (Phalangium opilio and TOTAL PREDATORS).

not affect dwarf spider abundance in terms of either plant apparency or habitat complexity. Erigone served as a trophic link between the ground community and the collard component community in plots A and B. The harvestman P. opilio was the most important species of natural enemy in the collard-alfalfa biculture. The harvestman served as a trophic link among the alfalfa foliage (where it was commonly collected), collard plants and the ground community in the biculture only: alfalfa thus served as an attractant to P. opilio and as a repellent to D. rapae.

## DISCUSSION

The form and strength of interaction between collard herbivores and their natural enemies was determined by the location of the collards with respect to the alfalfa plant background (Figure II.11). The alfalfa modified both microhabitat for natural enemies and plant apparency for collard specialists. To demonstrate the value of taking a three-trophic-level perspective, I will first examine how alfalfa influenced the identity of collard associates (objectives 1 and 2) and will then discuss the form and strength of the resulting interactions between herbivores and natural enemies (objective 3).

### Objective 1

Objective 1 was intended to identify the generalist natural enemies present in each of the two habitats and to document their occurrence on the interplanted collards.

The influence of the alfalfa habitat on abundance and diversity of local generalist predators was inconsistent. Foliar predators were typically more numerous and diverse in the biculture; evidently, the alfalfa foliage attracted a suite of generalized foliar predator associates such as nabids, coccinellids and chrysopids (Pimentel and Wheeler 1973). The ground predator fauna is more difficult to characterize, with some species having distinct preferences for the monoculture and others for the biculture. Since each ground predator species has its own unique set of life history characteristics, physiological tolerances and resource requirements, few generalizations can be made regarding the effect of a given crop modification (Baker and Dunning 1975). Predictions must be based on knowledge of the biology of each principal species, as well as the relevant parameters that are influenced by the crop modification, such as microclimate, refuges from predation, and the availability of suitable hunting substrates and potential prey. For example, the two most abundant ground predator species, P. opilio and P. vulgaris,

Figure II.11. A three-trophic-level model of the host plant collard, its specialist herbivores Brevicoryne brassicae and Pieris rapae and their natural enemies (Sphaerophoria sulphuripes, Diaeretiella rapae and generalist predators). A and B denote interactions occurring in the monoculture and biculture respectively due to changes in collard plant apparency and in habitat conditions for natural enemies.

had opposite distribution patterns relative to the two study plots. Harvestmen typically prefer high humidity and a well developed lower shrub layer to complete their life cycle (Clingenpeel and Edgar 1966); these conditions are not found in a region of bare soil. Pterostichus may be less dependent on diurnal hygrothermal conditions because it is nocturnal, spending the majority of the day wedged between soil particles. A recently plowed field provides an abundance of suitable refuges for P. vulgaris. The same type of comparison can be made for the other three principal taxa of generalist ground predators, P. sternalis, E. dentosa and staphylinids. The wolf spider P. sternalis and staphylinids were more abundant in the biculture, while E. dentosa was more abundant in the monoculture, demonstrating the species-specific response to changes in microhabitat conditions.

Of the nine most commonly sampled taxa of generalist predators, seven (C. trifasciata, T. laboriosa, O. insidiosus, P. opilio, P. sternalis, Nabis spp. and staphylinids) were more abundant in the biculture, while only two (P. vulgaris and E. dentosa) were more abundant in the monoculture. Only four of the nine species were commonly collected on the interplanted collards (C. trifasciata, T. laboriosa, P. opilio and P. sternalis). There was a direct relation between abundance in the habitat and occurrence on the collard plants for T. laboriosa, P. opilio and E. dentosa; C. trifasciata was more abundant on collards grown in monoculture, where it was otherwise rare. Since spatial association with collard herbivores is necessary for interaction, I would identify P. opilio and T. laboriosa as collard associates only in the biculture, C. trifasciata as an associate only in the monoculture and E. dentosa as an associate in both habitats, but more common on collards grown in monoculture.

## Objective 2

Objective 2 was designed to determine the effect of changing plant apparency on colonization of specialized collard associates.

Although host plant suitability could also have been modified by the alfalfa plant background, this research was concerned only with the short-term effects of alfalfa as estimated by the arrival of propagules on individual plants; effects of the alfalfa on movement rates and survival of herbivore species was not considered.

The colonization patterns of B. brassicae, P. rapae and D. rapae were consistent with those noted in other studies (Read et al. 1970; Cromartie 1975a; Smith 1976a,b; Theynissen and Den Ouden 1980). In each case, growing Brassica plants in association with non-related species decreased colonization rates of B. brassicae and D. rapae, but neither had an effect or increased colonization rates of P. rapae. Host locating ability of female S. sulphuripes also seemed to be affected by the crop modification, with more young larvae being observed on relatively apparent plants. Placing collards on 0.9 m stakes had the same effect as growing collards in monoculture, with the colonization patterns consistent for all four species. Evidently, the unapparency of collard plants is achieved by growing well below the boundary layer of the surrounding vegetation: most collard plants were eventually colonized when grown on 0.9 m stakes as well as within recently germinated alfalfa vegetation. Similar results were obtained by Heathcote (1969), who found that green peach aphids tended to colonize taller plants more rapidly.

Given colonization patterns of the collard associates (objective 2) and the prevalence of generalist predators on collard in each habitat (objective 1), a total of at least eleven different species interactions involving collard herbivores are possible (Figure II.12). Four additional interactions (B. brassicae vs. P. opilio, S. sulphuripes, T. laboriosa and E. dentosa) are possible given the fact that collards in the biculture were inoculated with cabbage aphids.

## Objective 3

Objective 3 was designed to identify the most important species interactions given all relationships possible as identified by objectives 1 and 2 (Figure II.12). Results from experiments under objective 3 suggest that 4 of the 15 possible species interactions were significant in terms of herbivore population dynamics. The parasite D. rapae was an important mortality factor of B. brassicae in the monoculture, the syrphid S. sulphuripes may have contributed to mortality of B. brassicae in the monoculture and the harvestman P. opilio was an important predator of both herbivore species in the biculture.

The abundance of B. brassicae was reduced by natural enemies on several occasions in both habitats. In the monoculture, the most common natural enemy removed from collards during each exclusion experiment was D. rapae. The interaction between D. rapae and B. brassicae occurred only in the monoculture, even when B. brassicae was innoculated onto plants in the biculture. Aphids on collards planted within alfalfa were rarely parasitized by D. rapae and few adult parasites were collected on the collard or in the surrounding alfalfa vegetation. Since D. rapae locates its host by using host plant cues (Read et al. 1970), changes in its sensory environment due to increased plant diversity may interfere with its searching efficiency. Any natural enemy that uses host plant cues for host location may be similarly affected by changes in plant apparency: describing the interaction between such natural enemies and their prey/host thus requires information on the location of the host plant with respect to the non-host plant community.

The presence of local non-host vegetation can also provide a spatial refuge for herbivores that can locate an unapparent host plant. For instance, cabbage aphids but not the parasite D. rapae were able to locate collards placed on 0.9 m stakes--most of the aphid populations remained unparasitized for two weeks following initial colonization of the raised plants. Host plants growing

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PLOT A

B. brassicae ────────── D. rapae
                        S. sulphuripes
                        C. trifasciata
                        E. dentosa


P. rapae ──────────────  C. trifasciata
                         E. dentosa
                         S. sulphuripes



PLOT B

*B. brassicae ────────── P. opilio
                         E. dentosa **
                         T. laboriosa
                         S. sulphuripes **


P. rapae ─────────────── P. opilio
                         E. dentosa **
                         S. sulphuripes **
                         T. laboriosa
```
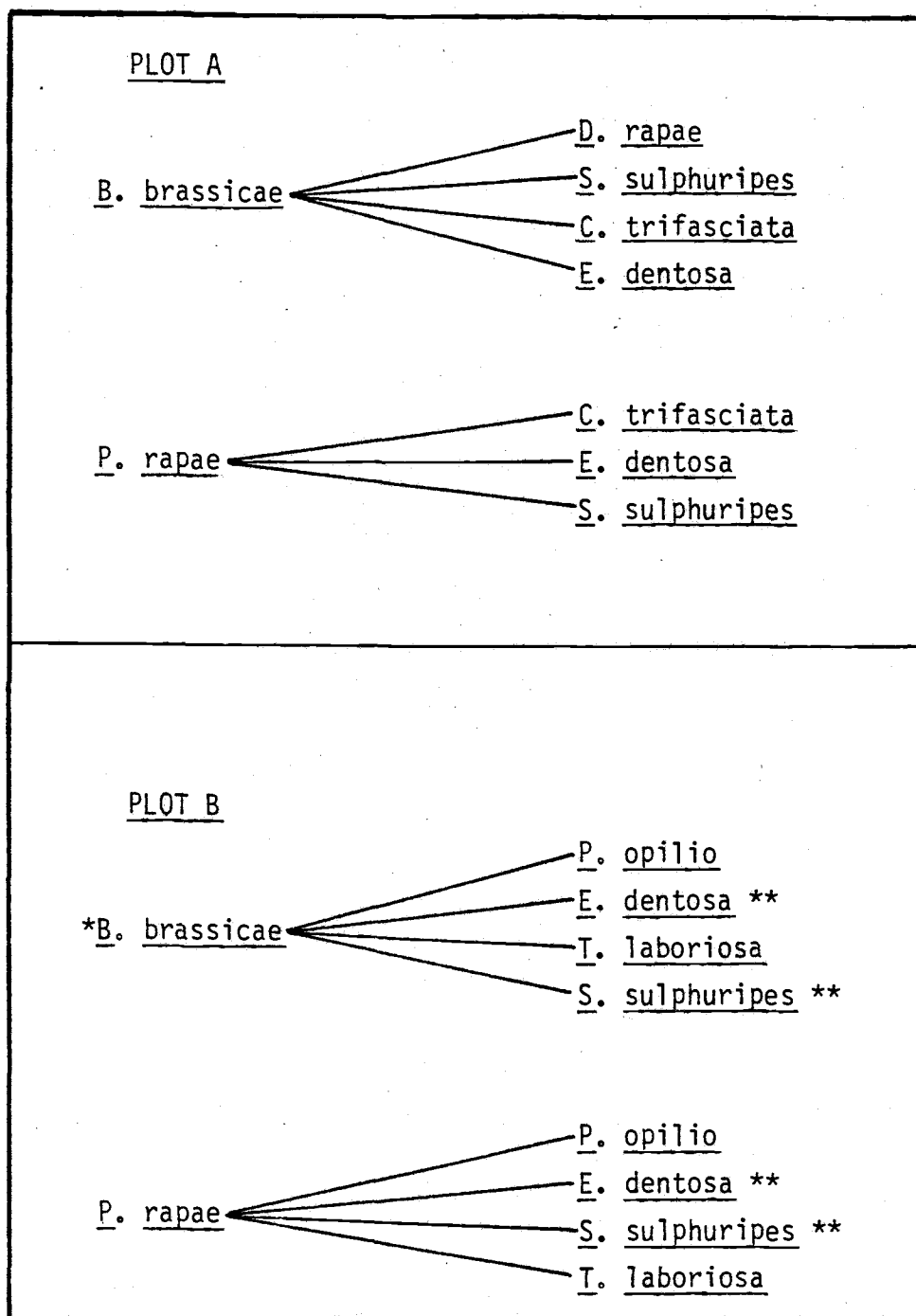
 *  Inoculated into collard-alfalfa biculture
** More common in collard monoculture

Figure II.12. The major species interactions identified by
  objectives 1 and 2 as having potential significance in
  dynamics of B. brassicae and P. rapae populations

within certain communities may provide spatial refuges for herbivores from their specialist natural enemies. Similarly, aggregation of natural enemies at high density patches may provide herbivore refuges at low density patches. Empirical data (Huffaker 1958) and a variety of theoretical models have suggested that natural enemy aggregation is a stabilizing mechanism for herbivore-natural enemy relations (Hassell and May 1973; Murdoch 1977). Properties of the plant community may stabilize herbivore-natural enemy relations by changing searching efficiency, promoting natural enemy aggregation on apparent plant patches and creating herbivore refuges on unapparent plant patches.

Because plant apparency is so closely associated with $\underline{B}$. $\underline{brassicae}$ colonization rates, any changes in plant apparency can significantly affect dynamics of local cabbage aphid populations. For instance, the experiments on controlled immigration of cabbage aphids suggest that local populations of $\underline{B}$. $\underline{brassicae}$ can be driven to low levels by natural enemies as aphid colonization rates decline. Aphid colonization rates can decline through a decrease in available alates or through changes in the surrounding plant community relative to the host plant. For example, differential growth rates of plants in a diverse assemblage can cause a mosaic of individual plant apparencies through time, with an individual plant having greater relative apparency with greater spatial dominance in the assemblage (Rausher 1981). The influence of both specialist and generalist natural enemies on herbivore populations can be significant under these conditions. As I have shown, percent mummy formation was signficiantly higher when $\underline{B}$. $\underline{brassicae}$ immigration was inhibited, while generalists such as $\underline{C}$. $\underline{trifasciata}$ and $\underline{P}$. $\underline{opilio}$ were capable of causing significant mortality on cabbage aphid populations with controlled immigration (Tables II.9, II.10, II.11). The influence of parasite specialists such as $\underline{D}$. $\underline{rapae}$ can be further increased if emerging females mate and parasitize aphids of the same isolated colony. Thus, predicting the nature of interaction between an herbivore and its suite of natural enemies requires detailed information on host plant patch dynamics. Patches may open and close

at different times for natural enemies and herbivores, depending on the availability of colonists and their respective searching abilities. The herbivore-natural enemy relation must be considered in the context of the host plant and its surrounding community.

The most common species of aphid predators on collards in the monoculture were E. dentosa, S. sulphuripes and C. trifasciata. The relative effect of these three was difficult to determine; even though all three commonly fed on B. brassicae (Tables II.12, II.13), a single syrphid probably consumes more aphids during its time on the host plant than a single dwarf spider (E. dentosa). Given that S. sulphuripes is more specialized to feed on aphids and feeding time of individual syrphids on the collard substrate was probably longer than most other predators, I would conclude that S. sulphuripes had a more substantial effect on B. brassicae populations in the collard monoculture than either E. dentosa or C. trifasciata. The effect of the alfalfa on S. sulphuripes-B. brassicae relations was similar to that observed for D. rapae: fewer syrphid larvae were found on collards grown in biculture. Although adult S. sulphuripes were commonly caught in the alfalfa foliage, alfalfa plant height was inversely related to the occurrence of syrphids on the interplanted collards (Table II.3). Thus, S. sulphuripes responded to the alfalfa background like a typical collard component species (D. rapae, B. brassicae), having a stronger interaction with B. brassicae in the collard monoculture. As with D. rapae, the location of the collard host plant determined the strength of interaction between S. sulphuripes and B. brassicae.

The serological data on S. sulphuripes suggests that syrphid prey preference was also modified by the location of the collard plants. Syrphids of the family Syrphinae are known to be primarily aphidophagous (Davidson 1922; Hamrum 1966), although other prey are sometimes consumed (Schneider 1969; Dempster 1969). Given an abundance of their preferred prey (aphids), I would predict that syrphid individuals would specialize on that prey and take a lower percentage of alternate, available species. Assuming that the

searching area of syrphid larvae initially oviposited on collard plants is limited to that plant, the predator has a choice between two relatively abundant prey (B. brassicae and P. rapae) and several other rare or incidental species. In the collard monoculture, of 33 S. sulphuripes collected, only 4 reacted with P. rapae antiserum (12%), while 35% (25/72) of those syrphids collected on collards in the biculture reacted positively with P. rapae antiserum. Due to differential colonization pattern, the abundance of P. rapae relative to B. brassicae was much greater in the biculture. These data suggest that syrphids switched from their preferred prey (aphids) to alternate prey (pierids) when the relative abundance of aphids declined (in the collard-alfalfa biculture). The diet of S. sulphuripes may therefore have been modified by the location of the host plant.

The inoculation of B. brassicae onto collard in the biculture provides an example of how a local natural enemy can influence herbivores that manage to find unapparent plants. The effects of local predators on cabbage aphids in the biculture was significant on three different occasions, with P. opilio identified as an important cause of mortality. Although I could not identify the predator species involved, aphid populations were reduced during a hand-removal experiment (f; Table II.7) and during a natural enemy inclusion experiment (h; Table II.9). I suggest that the harvestman P. opilio was the primary natural enemy involved in reduction of aphid populations in the biculture habitat for three reasons: 1) P. opilio was the most abundant predator in the biculture during all experiments and was also uncommon in the monoculture during experiment j where no effect of ground predators was observed (Table II.4); 2) P. opilio was the generalist predator most often found on collard foliage (Table II.3); and 3) Serological analysis indicated that P. opilio often fed on B. brassicae (Tables II.12, II.13). Predators like P. opilio can interact with herbivores like B. brassicae only when the herbivore's host plant is colonizable by the herbivore and grows in a suitable habitat in terms of microhabitat

conditions. Clearly, a plant community property (the alfalfa
background) determined both the form and strength of interaction
between P. opilio and B. brassicae.

Although cabbage aphid alates rarely found collards planted in
the biculture, P. rapae oviposited as many or more eggs on unapparent
plants in comparison to plants in monoculture (Table II.5). Natural
enemies were observed to have a measurable impact on P. rapae
populations during experiment j in the collard-alfalfa biculture
(aluminum cylinder experiment). Three lines of evidence suggest that
P. opilio was responsible for this effect: 1) P. opilio and E.
dentosa were the only major species of ground predators that commonly
frequented collard plants in the biculture; 2) E. dentosa was more
common in the monoculture, where no effect on P. rapae populations
was observed, while P. opilio exhibited the opposite pattern,
suggesting an association between P. opilio occurrence on collards
and P. rapae population decline; 3) Percent positive precipitin
reactions for P. opilio against P. rapae antiserum was 56%, while for
E. dentosa the figure was only 8% (Table II.13).

Mortality rates of P. rapae larvae were higher in the biculture
during experiment j (Table II.10), suggesting that the alfalfa
habitat increased the effect of P. opilio on P. rapae population
dynamics. Any specialist herbivore that preferentially oviposits on
unapparent plants may be subject to increased mortality due to
generalist predators, since unapparency may be directly related to
favorable microhabitat conditions for these natural enemies. This is
because the factors that make a plant individual unapparent (i.e.,
plant diversity) may also increase the suitability of the habitat for
natural enemies, through changes in microhabitat conditions and the
availability of alternate prey and hunting substrates. The relation
between plant apparency and habitat suitability for generalist
predators demonstrates how changes in a plant community property can
influence interactions between a generalist natural enemy and a
specialist herbivore.

Results of this study support a three-trophic-level perspective. Plant-herbivore relations cannot be decoupled from herbivore-natural enemy relations because plants have individual properties that directly affect specialized natural enemies (i.e., D. rapae) and plants are associated with communities that indirectly affect generalist natural enemies through local habitat modification (i.e., P. opilio) and changes in the relative abundance of herbivores (i.e., S. sulphuripes). Because of the variety of effects of plants on the third trophic level, the location of a plant in space and time with respect to the surrounding plant community determines the types of interactions possible between herbivores and natural enemies.

## SUMMARY

1.  The influence of natural enemies and plant apparency in
    determining the abundance of Brevicoryne brassicae L. and
    Pieris rapae L. was examined on collards grown in a collard
    monoculture and in a collard-alfalfa biculture.  This design
    was used to examine the factors affecting collard-herbivore
    abundance from a three-trophic-level perspective.

2.  The abundance and diversity of foliar arthropod predators
    was higher in the biculture.  The ground predator fauna did not
    vary as a whole, with Phalangium opilio L. and Pterostichus
    vulgaris L. the most common species in the biculture and in
    the monoculture, respectively.

3.  The occurrence of a generalist predator species on collard plants
    could not be predicted from estimates of relative abundance in
    the surrounding habitat; several locally common predators were
    rarely observed on the collard plants.

4.  Collard colonization rates of B. brassicae, the cabbage aphid
    parasite Diaeretiella rapae M'Intosh and the syrphid Sphaerophoria
    sulphuripes Thom. were higher in the monoculture, while P. rapae
    females tended to lay more eggs on collards in the biculture
    habitat.

5.  Natural enemy exclusion experiments and serological analysis
    indicated that D. rapae and S. sulphuripes were associated
    with significant mortality of B. brassicae in the monoculture
    while P. opilio was associated with significant mortality of
    both P. rapae and B. brassicae populations in the biculture.

6.  These results demonstrate that the location of the collard
    plants with respect to the surrounding plant community deter-
    mined the form and strength of interaction between collard
    herbivores and their natural enemies.

7.  An argument is made for including plant properties as parameters
    in models of herbivore-natural enemy relations:
    A. Plant apparency may influence the relation between specialist
       herbivores and their specialist natural enemies if both use

the same host plant cues for host location.

B. Changes in plant apparency over time may have substantial
effects on local population dynamics of herbivores and
natural enemies. Local patches of host plant may exhibit
either extinctions or outbreaks of herbivore populations
depending on the colonization pattern of both herbivores
and their natural enemies.

C. When herbivores respond differentially to plant apparency
(e.g. B. brassicae and P. rapae), relative abundance of
herbivores on the host plant will change; this may cause
switching of generalist predators from one herbivore to
another, depending on the location of the host plant.

D. Since plant apparency may often be inversely related to plant
species diversity, decreases in plant apparency may be
associated with increased establishment and persistence of
generalist predators that respond to plant species diversity.

7. A three trophic level approach to theories on plant defense
and predator-prey relations would add to our understanding of
patterns of herbivore abundance in nature and would offer a
theoretical framework for the design of multiple cropping systems.

CHAPTER III

Generalist Predators and Collard Herbivores:
A Test of the Natural Enemy Hypothesis

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## INTRODUCTION

Specialized insect herbivores often attain higher densities on plants grown in monoculture relative to plants grown in diversified settings (e.g., multiple cropping systems, mixed species habitats) (McAloney 1930; Pimentel 1961a; Smith 1969; Cromartie 1975b). Two major hypotheses have emerged as an explanation for this pattern. The resource concentration hypothesis (Root 1973) proposes that densities of specialist herbivores are lower in mixed species habitats due to decreased host finding capabilities or less persistence in the habitat or both. This hypothesis suggests that the perception of visual and /or olfactory cues utilized by specialist herbivores in locating host plants is in some way disrupted by the presence of non-host plants. Numerous studies have supported this hypothesis in a variety of systems (Smith 1976a; Bach 1980a; Risch 1980; Ryan et al. 1980). The natural enemy hypothesis (Pimentel 1961a) proposes that specialist herbivores are less abundant in mixed species habitats because the potential for population regulation by natural enemies (predators, parasitoids) is enhanced under these conditions. This hypothesis suggests that natural enemies are able to maintain higher densities in mixed species habitats due to a greater availability of alternate prey (hosts), supplemental food such as pollen and nectar and more favorable environmental conditions. Although increased natural enemy abundance and richness has often been observed in mixed species habitats (Smith 1969; Dempster 1969; Perrin 1975; Altieri et al. 1978; Altieri & Whitcomb 1979b, 1980), data are limited which demonstrate that natural enemies are the cause for observed decreases in herbivore densities.

The objective of this study was to determine the extent to which natural enemies influence herbivore densities on plants grown in a monoculture and in a biculture (mixed species habitat). We established four criteria suitable for examining

the natural enemy hypothesis. First, a natural enemy population must be established at the time and in the place where the herbivore's host plant exists. Second, a natural enemy must include the herbivore's host plant within its pattern of searching behavior. Third, a natural enemy must include the specified herbivore within its diet. Fourth, the rate of consumption of the herbivore by the natural enemy must cause a measurable decrease in herbivore density.

These criteria represent the sequence of events which must occur to produce herbivore suppression by natural enemies in any system. The most practical way to address these criteria is first to determine whether or not natural enemies are important in the system through enemy exclusion experiments (Criterion 4). If suppression of herbivore density is indicated, then it is necessary to determine which species of natural enemy is (are) responsible by examining the components of the predation process: distribution of predator and prey in time and space (Criterion 1), area searched (Criterion 2) and consumption of prey (Criterion 3).

We propose that a mechanistic approach of this kind is essential for understanding how mixed species habitats modify the influence of natural enemies on specialized herbivore populations.

## METHODS and MATERIALS

## Study Organisms and Habitats

The research was conducted during the summer of 1982 on a
0.69 ha plot at Oregon State University.  A collard monoculture
(Brassica oleracea acephala L.) was established on 13 August 1982
by transplanting 5 week old plants from an insect-free greenhouse
culture into the center of a 0.29 ha section of the plot.  A
total of 49 collards in a 7 X 7 array were planted at 2 m inter-
vals.  A collard-alfalfa biculture was established by  trans-
planting collards from the same greenhouse culture at the same
density in the center of a 0.4 ha, three year old alfalfa field
adjacent to the collard monoculture.  Mean alfalfa plant height
was 35.6 cm (S.E. = 2.3; n = 30) at the beginning of the ex-
periment and 62.7 cm (S.E. = 3.6; n = 30) at the conclusion of
the experiment on 1 September 1982.  Collard plants grown in a
background of alfalfa thus represented an extreme example of an
intercropping system.

Population dynamics of two Brassica specialists Brevicoryne
brassicae L. (the cabbage aphid) and Pieris rapae L. (the
imported cabbageworm) were examined on collards grown in the two
cropping systems.  It was known from the literature (Root 1973;
Smith 1976a,b; Theynissen and Den Ouden 1980) and from earlier
work in this system (McIver pers. obs.) that alates of the
cabbage aphid preferentially colonize Brassica plants grown in
monoculture and are generally unable to locate host plants when
grown in mixed species habitats (e.g., within weedy fields, in
polyculture, within alfalfa).  Furthermore, we had discovered a
significant difference in colonization rates by alates onto
collard plants grown in the monoculture habitat.  Therefore,
given the highly variable natural colonization pattern, the
number of replicates necessary to test the natural enemy
hypothesis was found to be impractical.  For these two reasons,

we inoculated all collards in both habitats with 25 apterous cabbage aphids (late instar and adults) at the beginning of the experiment. This procedure effectively reduced the influence of natural colonization on aphid abundance throughout the experiment. Inoculation of collards with P. rapae eggs or larvae was not necessary as female pierids uniformly distributed eggs among plants grown in both habitats.

Previous observations indicated that the most important natural enemies of B. brassicae and P. rapae are relatively specialized parasites [Diaeretiella rapae (M'Intosh) on B. brassicae; Apanteles glomeratus L. on P. rapae], a complex of relatively oligophagous foliar predators (syrphids, coccinellids, nabids, chrysopids) and a complex of generalist ground predators (carabids, opilionids). In this study, we focused our attention on the ground predators for two reasons. Temporal variation was low in overall abundance of species in this group relative to populations of specialized and oligophagous natural enemies. Therefore, a three week experiment involving ground predators would be least likely to produce results which had been strongly influenced by the time of the year. Also, preliminary observations supported earlier studies (Dempster 1969; Ashby & Pottinger 1974) indicating that ground predators are commonly associated with collard herbivores, and may cause significant mortality of cabbage aphids and cabbageworm eggs and larvae.

The extent to which this study represents a test of the natural enemy hypothesis for B. brassicae populations in general is questionable for two reasons: we circumvented the effect of plant apparency on B. brassicae colonization by inoculating collards in all treatments with cabbage aphid apteri and we focused our attention on a group of natural enemies that we expected would respond to our cultural modification. This methodology eliminated plant apparency and other natural enemies as factors

explaining B. brassicae abundance in our system. Our intent was
not to make a statement on the relative importance of various
factors in explaining B. brassicae abundance in general, but to
use B. brassicae as a device for examining the mechanisms of the
predation process. The study does make a more general statement
concerning P. rapae, since we did not influence its colonization
dynamics and concentrated on its primary group of natural en-
emies, the generalist predators.

## Exclusion Experiments:  Evaluation of Criterion 4

The influence of ground predators in suppressing populations
of cabbage aphids and imported cabbageworms was assessed by con-
ducting a predator exclusion experiment within each habitat.
Since many species of ground.predators are active and nocturnal,
exclusion by hand removal was inadequate. Instead, plants re-
ceiving the predator exclusion treatment were enclosed by
aluminum cylinders 30 cm high and 30 cm in diameter. At the be-
ginning of the experiment, we discovered that alate cabbage
aphids avoided colonizing plants enclosed by the cylinders.
Since alates actively colonized only those collards grown in the
monoculture, the control treatment in this habitat was achieved
by enclosing plants in cylinders raised 6 cm above the ground
surface, allowing ground dwelling predators access to the plants.
These controls were then compared to the exclusion treatment,
which consisted of collard plants enclosed by cylinders placed
flush to the ground surface. Twelve replicates for each treat-
ment were selected from the 49 available collards in the mono-
culture. In the collard-alfalfa biculture, no alates were ob-
served to colonize any of the collard plants whether or not they
were enclosed by cylinders. Therefore, in this habitat, 24
plants not enclosed by cylinders (controls) were compared with 14
plants surrounded by cylinders placed flush to the ground surface
(exclusion treatment).

Cabbage aphid populations on all collard plants in the biculture were censused on four occasions (15 August, 23 August, 27 August, 1 September); since flea beetles heavily damaged collards in the monoculture after 29 August, plants were not censused on 1 September in this habitat. Survivorship of P. rapae was estimated by dividing the total number of eggs and larvae surviving on the plants at the end of the experiment (1 September 1982) by the total number of eggs observed to be oviposited thoughout the experimental period. The hypothesis that ground dwelling predators influenced populations of B. brassicae and P. rapae in each habitat was tested with the Wilcoxon 2-sample test for B. brassicae abundance (control and treatment had heterogenous variances) and one-way ANOVA for arcsine-transformed P. rapae survivorship.

## Observations on the Components of Predation: Criteria 1, 2, 3

The distribution of ground predators in time and space was determined by estimating population densities of the most common species. A 6 X 6 grid of 36 pitfall traps spaced 3 m apart was established in each habitat to provide data for population estimates. Each trap consisted of a two-quart plastic container buried so that the lip was even with the ground surface. Traps were checked every 24 hours and individual predators were collected, preserved, identified, and their abundance determined. These data provided information on when and where various species occurred and were used to evaluate criterion 1.

To evaluate the second criterion, searching behavior, each collard plant was examined daily (mid-afternoon and dusk) for predators throughout the experiment. The relationship between ground level abundance and occurrence on collard plants was determined by comparing the number of predators found on the plants on each day to the abundance data provided by pitfall trapping.

A serological technique (precipitin test) was utilized to determine the feeding habits of the common predators. Antibodies to cabbage aphids and cabbageworm larvae were prepared by injecting extracts of the two herbivore species into separate rabbits. After about seven weeks of stimulation, rabbit blood was extracted, spun to serum and frozen. Serum containing antibodies to each herbivore species was then thawed as needed and reacted with macerated predators by double diffusion (Ouchterlony 1958). The formation of a precipitate indicated the presence of aphid and/or pierid antigen in the predator's gut. These data served as a qualitative demonstration of a trophic link between predator and prey. Because the precipitin test may also identify antigens in a predator's gut that originate from insect species closely related to the prey species studied [(e.g., B. brassicae versus Acyrthosiphon pisum (Harris) - the pea aphid found on alfalfa, or P. rapae versus Autographa californica (Speyer) - the alfalfa looper found on alfalfa)], our data on percent positive reactions must be interpreted with caution. Any active generalist predator collected on a collard plant may previously have consumed cross-reactive prey in the alfalfa habitat or elsewhere, thus giving a false positive reaction for either B. brassicae or P. rapae. However, since B. brassicae was the dominant aphid and P. rapae the dominant lepidopteran on collard plants during this study, we could assume that predators collected in association with collard would show a higher percent reactivity with B. brassicae and P. rapae antisera than the same species of predator collected away from the collard plants. We therefore used predators picked off of collard plants in addition to those collected in the alfalfa habitat (by sweep net and pitfall trap) for the serological analysis. If the percent positive reactions was significantly higher for predators collected on the collard plants, we could state that our serological data was qualitatively valid. Additionally, field observations of predator-prey interactions between the collard herbivores and ground predators were used to support the serological analysis.

RESULTS

The predator exclusion experiment yielded different results in a comparison of herbivore densities between control and exclusion treatments in the two habitats. In the monoculture habitat, no effects on either aphid abundance or pierid survivorship were conclusively demonstrated, though a trend of declining aphid abundance on controls and rising abundance on exclusion treatment plants was apparent (Figure III.1). Within the biculture habitat, there was a significantly higher density of cabbage aphids on control plants at the start of the experiment ($P < 0.05$; 15 August 1982) but a significantly lower density of aphids on the same plants at the end of the experiment ($P < 0.05$; 1 September 1982) (Figure III.2). Even though the initial establishment of aphids on the control plants was significantly higher than for exclusion plants, the density of aphids on the control plants eventually became significantly lower than on the exclusion plants. It is evident that plants enclosed by the exclusion cylinders experienced an aphid population increase, while plants in control treatments experienced a significant aphid population decrease. The treatment effect was also significant for pierids, with plants in the exclusion treatment exhibiting a higher survivorship of pierid eggs and larvae (Figure III.2).

The relative abundance of ground predators in the two habitats was compared to identify the predator(s) responsible for the significant decrease in herbivore abundance or survivorship on collards within the biculture habitat (Table III.1) (criterion 1). The five taxa in Table III.1 constituted 98.5% of the total number of ground predators collected during the experiment.

If we postulate that the influence of any predator on a prey population is related to its abundance in the system (Altieri & Whitcomb 1979b), then the most likely candidates responsible for suppression of B. brassicae and P. rapae populations in the biculture would be a harvestman, Phalangium opilio L. (Opiliones:

Figure III.1. Number of B. brassicae per plant on 3 census dates and arcsine % survivorship of P. rapae larvae for control ( ● ,n=12) and enemy-free (■ ,n=12) plants grown over bare soil at O.S.U. Entomology Farm, Corvallis, Oregon. No pair contrasts are significant different (Wilcoxon 2-sample test for B. brassicae; ANOVA for P. rapae; $p < 0.05$; error bars = S.E.)

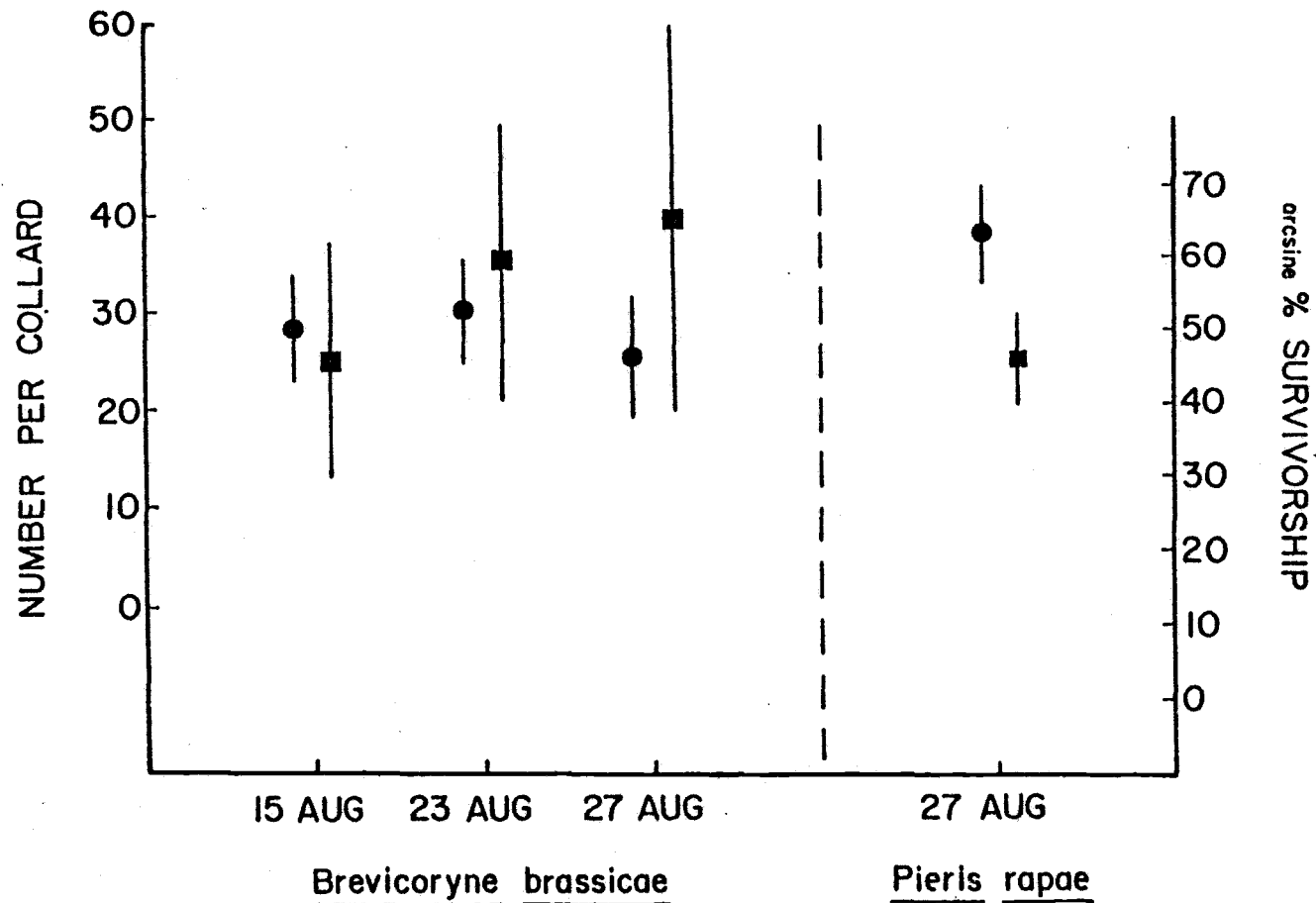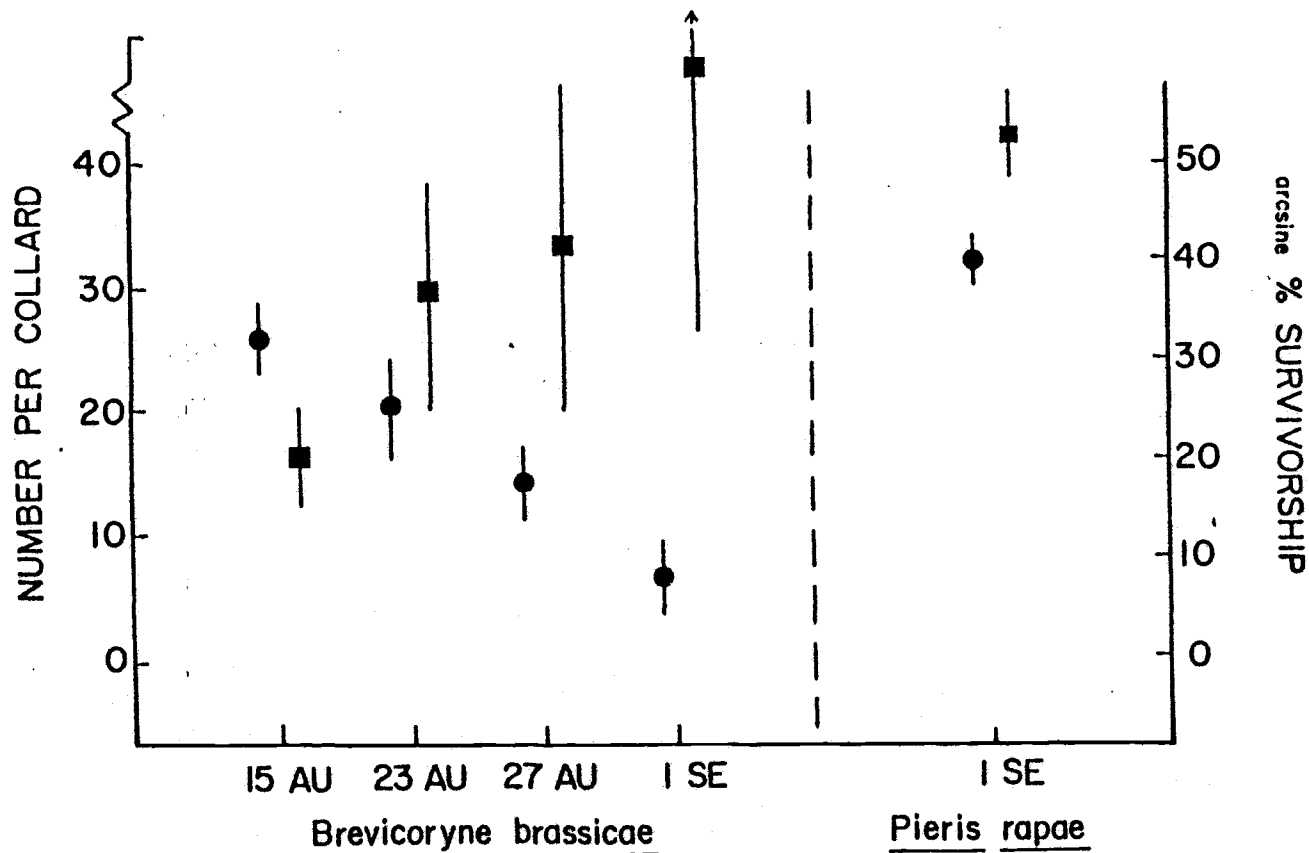Figure III.2. Mean ± S.E. of number of B. brassicae per plant on 4 census dates and arcsine % survivorship of P. rapae larvae for control (●, n=24) and enemy-free (■, n=14) plants grown in the collard-alfalfa biculture. For B. brassicae, comparisons on 15 August 1982 and 1 September 1982 are significant ($p < 0.05$; Wilcoxon 2-sample test). For P. rapae comparison is significant on 1 September 1982 ($p < 0.05$; ANOVA).

Table III.1. Mean ± 95% confidence intervals of the principal ground predators caught / day in 36 pitfall traps on 10 sample dates in the collard monoculture and in the collard-alfalfa biculture (13 August -- 1 September 1982) and the degree to which each taxa was observed on the collard plants.  * Indicates significant difference in abundance for monoculture -- biculture comparison (P<.05 ; one-way ANOVA), Corvallis, Oregon.

| PREDATOR | COLLARD MONOCULTURE | COLLARD/ALFALFA | F | PREVALENCE ON COLLARD PLANTS |
|---|---|---|---|---|
| Phalangium opilio (Adults) | 1.08 ± .72 | 11.50 ± 3.60 | 32.20* | Common |
| Phalangium opilio (Juveniles) | 35.60 ± 10.80 | 59.40 ± 11.90 | 8.84* | Common |
| Pardosa sternalis | 0 | 8.60 ± 3.20 | 29.34* | Rare |
| Staphylinidae | 5.30 ± 1.30 | 10.60 ± 5.90 | 3.05 | Rare |
| Erigone dentosa | 11.20 ± 5.40 | 2.50 ± 1.10 | 9.97* | Common |
| Pterostichus vulgaris | 19.10 ± 3.90 | 6.10 ± 2.20 | 30.08* | Rare |
| TOTAL --- All ground predators | 79.60 ± 18.0 | 102.90 ± 19.40 | 3.06 | ------ |
| ALFALFA PLANT HEIGHT (cm) | 0 | 50.10 ± 6.20 | ------ | ------ |

Phalangiidae) and a wolf spider, _Pardosa sternalis_ (Thorell)
(Araneae: Lycosidae). Although the dwarf spider, _Erigone dentosa_
O.P.-Cambridge (Araneae: Micryphantidae), a ground beetle,
_Pterostichus vulgaris_ L. (Coleoptera: Carabidae), and
staphylinids were also relatively abundant in the biculture, they
were equally or more abundant in the collard monoculture. There-
fore, the presence of _E. dentosa_, _P. vulgaris_, and staphylinids
cannot explain the observed decrease in herbivore abundance on
collards grown in the alfalfa field only. Additionally, although
slightly greater numbers of total arthropod predators were
captured in the biculture, the difference is primarily due to the
predominance of _P. opilio_. If _P. opilio_ is subtracted from each
total, more predators were captured in the collard monoculture,
namely, 42.9 predators/36 traps/day (collard monoculture) vs.
32.0 predators/36 traps/day (biculture habitat).

Determination of the most important predator species re-
sponsible for reduction of collard herbivore populations can be
narrowed further (criterion 2) by an examination of the frequency
with which _P. opilio_ and _P. sternalis_ were observed on the col-
lard plants. While _P. opilio_ was often found foraging on the up-
per and lower surfaces of collard leaves, _P. sternalis_ was never
so observed during the course of the experiment (Table III.1).
Additionally, there was a positive correlation between the re-
lative abundance of _P. opilio_ estimated by pitfall trapping and
the number actually observed on the collard plants (Figure
III.3). Although _P. opilio_ individuals were occasionally
collected on collard plants grown in the monoculture, the density
of harvestmen on collard plants (and in contact with collard
herbivores) in the monoculture was much less than in the
collard-alfalfa biculture.

The documentation of _P. opilio_ as the principal ground pre-
dator responsible for suppression of _B. brassicae_ and _P. rapae_
populations in the collard-alfalfa habitat requires iden-
tification of a trophic link between the predator and the prey
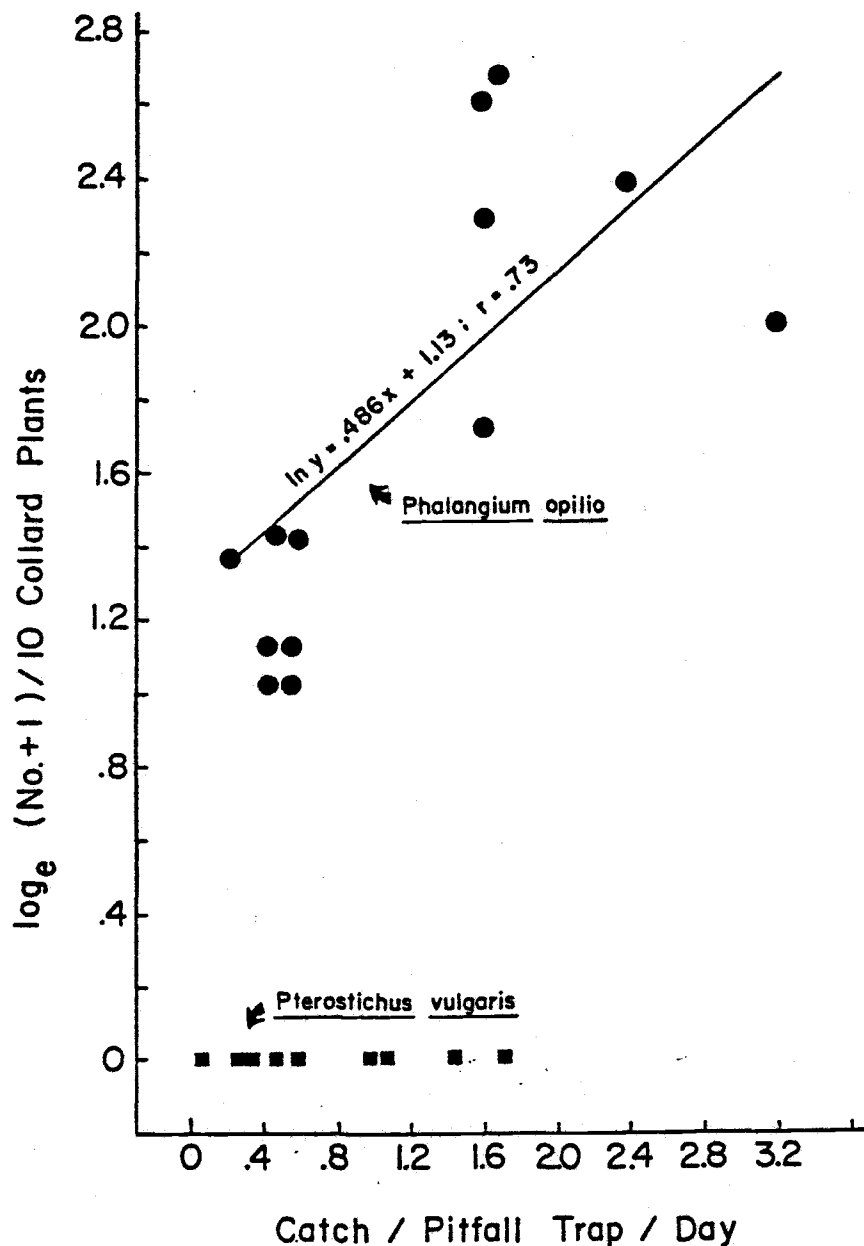
Figure III.3. Number (log$_e$) of <u>Phalangium opilio</u> individuals observed on 10 collard plants (15 August - 1 September 1982) in relation to catch per pitfall trap per day on the same day within the collard/alfalfa ( ● ) habitat and number (log$_e$) of Pterostichus vulgaris observed on 10 collard plants (15 August - 1 September 1982) in relation to catch per pitfall trap per day on the same within the monoculture habitat (■). Regression equation for <u>P. opilio</u> in the biculture: log$_e$ Y = .486 + 1.13X; r=.73; significantly different from line of slope 0 (p < 0.05;ANOVA), O.S.U. Entomology Farm, Corvallis, Oregon.

(criterion 3). Individual P. opilio collected from collard
plants yielded 64% (n = 36) positive reactions against B. bras-
sicae antiserum and 47% (n = 36) against P. rapae antiserum
(Table III.2). Percent reactivities of harvestmen collected by
pitfall trap in the alfalfa habitat were 32% (n = 130) for B.
brassicae and 6% (n = 130) for P. rapae. Reactivities against B.
brassicae and P. rapae antisera for all major ground predators
were also higher for individuals collected on the collard plants,
indicating that the serological analysis provided an adequate es-
timate of functional links between predator and prey (Table
III.2). Therefore, the existence of trophic links between P.
opilio and the two collard herbivores is established. This
contention is supported by numerous field observations of
predation by P. opilio on both B. brassicae and P. rapae on
collard plants during not only this study but earlier studies in
the system. We conclude the P. opilio was the principal species
of ground predator responsible for the suppression of both B.
brassicae and P. rapae populations on collards in the exclusion
treatment grown within the alfalfa field. The data further
suggest that the relatively low abundance of P. opilio in the
collard monoculture explains the statistically equivalent
herbivore population levels in the control and exclusion
treatments.

Table III.2. Percent positive precipitin reactions (# positive / total reacted) for the principal ground predators collected on and off collards against B. brassicae and P. rapae antisera.

| PREDATOR | Collected ON COLLARD | | Collected OFF COLLARD | |
|---|---|---|---|---|
| | B. brassicae | P. rapae | B. brassicae | P. rapae |
| Phalangium opilio | 64% (23/36) | 47% (17/36) | 32% (41/130) | 6% (8/130) |
| Pardosa sternalis | 50% (3/6) | 0 (0/6) | 0 (0/15) | 6% (1/15) |
| Erigone dentosa | 46% (20/43) | 9% (4/43) | 0 (0/0) | 0 (0/0) |
| Pterostichus vulgaris | 0 (0/0) | 0 (0/0) | 4% (1/23) | 0 (0/23) |
| Staphylinidae | 100% (1/1) | 0 (0/0) | 0 (0/6) | 0 (0/6) |
| TOTALS | 55% (47/86) | 24% (21/86) | 24% (42/174) | 5% (9/174) |

DISCUSSION

Even though natural enemies had significant effects under certain conditions in our system, we do not suggest that natural enemies are the key factors responsible for observed B. brassicae and P. rapae abundances on non-crop Brassica plants or under more realistic cropping situations. Rather, our study was designed to polarize the potential influence of certain natural enemies in two very different cropping systems, so that we could examine the mechanisms leading to herbivore suppression in the more general case. Thus, the system was chosen to provide an example of how best to study the influence of natural enemies in multiple cropping situations and not as a formal examination of the relative effects of plant apparency and natural enemies on collard herbivore populations. Several points must be considered before our findings can be extended toward understanding the general role of predators in multiple cropping systems.

The role of resource concentration in modification of cabbage aphid colonization patterns can be significant. Preliminary observations in our system support previous studies showing that cabbage aphids preferentially colonize host plants grown in monoculture (Smith 1969, 1976a,b; Theynissen & Den Outen 1980). Thus, growing collards in complex settings decreases host plant apparency to cabbage aphids and acts as an initial determinant of population size. But factors such as plant apparency and predation are not mutually exclusive as hypotheses explaining the abundance of any given herbivore species. For instance, those alates which occasionally colonize non- apparent plants may escape their specialized natural enemies in space (Smith 1976b) but still be subject to significant mortality from natural enemies whose influence is greater in complex settings (i.e., generalist predators like P. opilio). On the other hand, apparent plants may attract greater numbers of B. brassicae alates, but the more specialized natural enemies such as D. rapae

and syrphids can cause significant mortality under these conditions (Pollard 1969; McIver 1983). Therefore, explaining B. brassicae abundance involves examining a number of factors, including plant apparency as well as specialist and generalist natural enemies.

For P. rapae, decreased plant apparency (growing collards with alfalfa) had no effect or led to slightly increased oviposition rates on collards (McIver 1983). Therefore, although generalist predators may significantly influence pierid population dynamics once colonization has occurred, ovipositional behavior in relation to plant dispersion determines the initial population size of P. rapae on non-apparent plants (Harcourt 1961). Our research on P. rapae suggests that understanding exactly how multiple cropping systems alter herbivore population density requires examination of both determining factors such as plant apparency and plant dispersion as well as limiting factors such as natural enemies.

Studying the generalist ground predators of collard herbivores by using a mechanistic approach has led to several important insights. Although an abundance of a predator species may be a prerequisite for adequate herbivore suppression, presence is insufficient as evidence for cause and effect. Several studies have considered the importance of natural enemies based on species abundance within a crop or adjacent to it (Altieri & Whitcomb 1979a, 1980; Bechinski & Pedigo 1981). These studies lay the groundwork for a more critical mechanistic examination of the natural enemy hypothesis. For instance, we have shown that the abundance of P. opilio is associated with a measurable decrease in collard herbivore populations. Another generalist predator, P. vulgaris, was also very abundant in the collard monoculture throughout the experiment but was never found to be in close association with the herbivore species on the collard plants (Table III.1; Figure III.3). In this case, suppression did not follow from the determination of the high

relative abundance of a particular species of predator. Thus, many abundant species of ground predators may not include the plant foliage within their prey searching space--this will necessarily lead to a very limited impact on foliage herbivore populations.

Many species of predators may include the crop within their prey searching space and yet have no significant interaction with herbivore species found there. For example, $E.$ dentosa was frequently found on the lower leaves of collard plants, but only 9% of individual $E.$ dentosa collected in association with pierids reacted positively with $P.$ rapae antiserum (Table III.2). Studies which extend the examination of natural enemies to the determination of trophic links between predator and prey are therefore essential (Dempster 1969; Sunderland 1975; Vickerman & Sunderland 1975).

Even when a functional feeding relationship has been established, the actual suppressive influence of a predator may still be in doubt. For example, several species of predators found in the collard monoculture were shown by serological analysis to have fed on $B.$ brassicae, yet no difference in herbivore density between control and exclusion treatments was detected. Thus, the total effect of predation on $B.$ brassicae in the monoculture was insignificant relative to the experiment, even though qualitative functional links were demonstrated. While serological methods establish the existence of trophic feeding links, they cannot determine the quantity of prey consumed by a predator (McIver 1981). Serological methods, as well as trial feeding in the laboratory and direct observation are therefore useful only in suggesting a potential influence of predation on prey populations.

Finally, combining the mechanistic approach with exclusion experiments provides not only a test of the natural enemy hypothesis, but identification of the important species of predators found in each particular system. When generalist predators are involved, identification of the important species is especially

critical, because the same multiple cropping system applied to different geographical areas can involve very different complexes of generalist predators. Since the principal species of generalist predators responsible for herbivore suppression in one geographical area may be very different from those in another, recommendations on a particular cropping system design for conservation of generalist predators may have to be site specific. Also, utilizing a mechanistic approach provides information on the factors which ultimately determine the influence of generalist predators in a given system, such as habitat requirements and the existence of alternate prey. It is through this approach that we can find ways to enhance natural enemies as a component of integrated pest management.

SUMMARY

1. The influence of ground predators in determining the abundance of <u>Brevicoryne brassicae</u> L. and <u>Pieris rapae</u> L. on collards was examined in two habitats:  1) a collard monoculture and 2) a collard-alfalfa biculture.  The hypothesis that the density of collard herbivores is reduced by ground predators was examined by conducting predator exclusion experiments in both habitats.

2. Ground predators significantly reduced <u>B</u>. <u>brassicae</u> and <u>P</u>. <u>rapae</u> populations on collards in the biculture, but no significant effect was observed on collards in the monoculture.

3. The most abundant ground predator in the biculture was the harvestman, <u>Phalangium opilio</u> L..  This species was significantly less common in the monoculture habitat.

4. Serological analysis of gut contents indicated that <u>P</u>. <u>opilio</u> was associated with the decreased abundance of collard herbivores in the collard-alfalfa biculture.

5. A conceptual model is discussed providing a mechanistic approach to the study of natural enemy suppression of herbivores in multiple cropping systems.

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