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Relay strip-cropping combines two vegetation management tactics, under-sowing and strip-management. In this study conducted from 1994 though 1997, a cover crop seed-mixture containing oats (*Avena sativa* L. var. "Monida"), common vetch (*Vicia sativa* L.), red clover (*Trifolium pratense* L.), annual ryegrass (*Lolium multiflorum* Lam.), and buckwheat (*Fagopyrum esculentum* Moench) was broadcast over established broccoli (*Brassica oleracea* L.) 32 days after planting. The broccoli was planted, under-sown, and harvested in sections alternated with strips of cover crop. The cover crop relay provided tillage and pesticide refuges for beneficial insects without taking land out of broccoli production. Relay strip-cropping increased the abundance and diversity of ground beetles (Coleoptera: Carabidae), spiders (Araneae), harvestmen (Opiliones: Phalangiidae), lady beetles (Coleoptera: Coccinellidae), and damsel bugs (Heteroptera: Nabidae) in the cropping system; however, this did not always result in increased natural enemies in the broccoli. Arthropod species varied significantly in their propensity to leave the non-crop vegetation and move into the broccoli. Movement of the lady beetle *Coccinella septempunctata* L. from the cover crop strips into the broccoli may have depressed aphid populations in 1996. The non-crop vegetation may have served as a sink rather than a source for *Nabis* species and appeared to reduce their density in the broccoli growing nearby. There was no evidence that background vegetation surrounding the broccoli reduced colonization by winged aphids. The density of the cabbage flea beetle *Phyllotreta cruciferae* Goeze was lower in the broccoli relay compared with the clean-tilled broccoli. The number of third instar imported cabbage worm *Pieris rapae* (L.) and cabbage looper *Trichoplusia ni* (Hubner) was reduced on broccoli leaves and harvested buds in the relay strip-cropping system compared with the clean-tilled system. The number of diamondback moth *Plutella xylostella* (L.) pupae was higher in the clean-tilled broccoli; percent parasitism of the pupae was similar in the two cropping systems. Although reduction in broccoli contamination associated with relay strip-cropping was significant, the residual insect contamination was unacceptable for commercial broccoli production. Relay strip-cropping may be useful for preventing soil erosion and protecting water quality. Relay strip-cropping may be a useful component of an integrated pest management program.

Conservation of Arthropod Natural Enemies in Broccoli with Relay Strip-Cropping

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Daniel M. McGrath

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Daniel M. McGrath, Author

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CONSERVATION OF ARTHROPOD NATURAL ENEMIES IN BROCCOLI WITH RELAY STRIP-CROPPING

CHAPTER 1

INTRODUCTION

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INTRODUCTION

This study evaluated the impact of relay strip-cropping on insect pests of broccoli and their natural enemies. Relay strip-cropping combines two vegetation management tactics, under-sowing and strip-management (Litsinger and Moody 1976, Vandermeer 1989). Under-sowing is the broadcast seeding of a second crop into standing vegetation after the primary crop is established (Theunissen 1994, Theunissen and Schelling 1996, Infante and Morse 1996). The timing of the under-sowing is critical. Under-sowing that follows a critical competition-free period avoids yield reduction in the primary crop (Dawson 1964, 1965, 1986). In this study, winter cover-crop seed was broadcast into established broccoli four and one half weeks after planting the broccoli (Foulds et al. 1991, Mangan et al. 1991, Infante and Morse 1996). The cover-crop germinated and became established around the developing broccoli plants. After harvest, the cover-crop and broccoli stubble were left undisturbed until the following growing season, a period of approximately 315 days.

In strip-management, fields are tilled, planted, and harvested in sections. In some strip-management schemes, cultivated areas are interspersed with permanent strips of undisturbed vegetation (Heidger and Nentwig 1989, Nentwig 1989, Lys 1994, Lys and Netwig 1994, Lys et al. 1994, Zangger et al. 1994, Wyss 1995, Hausammann 1996, Lethmayer et al. 1997). These areas of the fields or orchards are taken out of production for several years. In relay strip-cropping, strips of non-crop vegetation are tilled, planted, harvested, and reestablished each year. No land is taken out of production, thus reducing the potential cost of the conservation practice to the farmer.

In my study, alternating strips of winter cover-crop were tilled and planted to broccoli, *Brassica oleracea* L. variety italica. In other words, the early broccoli plantings developed next to residual strips of undisturbed non-crop vegetation. Later, when the first planting was established and under-sown, the remaining cover-crop strips were tilled and planted to late broccoli, a procedure called "relay" (Vandermeer 1989, Bugg et al. 1991b). The late plantings developed next to broccoli stubble (from the early planting) plus the developing cover-crop. Buckwheat (*Fagopyrum esculentum* Moench), which was a component of the cover-crop seed mix, and volunteer weeds were allowed to flower, providing nectar and pollen in the cropping system. In relay strip-cropping, tillage, planting, under-sowing, harvest, and cover-crop reestablishment proceed sequentially. The refuge from tillage and pesticide applications moves across the field during the growing season.

Concerns about soil and water conservation have prompted interest in cover-crops (Chapman et al. 1949, Chichester and Smith 1978, Palada et al. 1983, Frye et al. 1985, Hemphill 1989, Staver and Brinsfield 1990, Bruce et al. 1991, Hargrove 1991, Hemphill 1991, Lal et al. 1991, Jackson et al. 1993, Mangan et al. 1995, Knott 1996, Bottenberg et al. 1997), relay cropping (Hofstetter 1982, Edwards 1986, Bugg et al. 1991b, Foulds et al. 1991, Brown et al. 1993, Keeling et al. 1996) and strip-crop management (Chase and Duffy 1991, Rannells and Wagger 1991). Under-sowing eliminates the need for extra tillage and irrigation to establish winter cover-crops, further reducing the potential cost of the conservation practice. Under-sowing assures early establishment of cover-crops and adequate soil coverage prior to erosive rainstorms. Following harvest, cover-crops utilized remaining nutrients associated with decomposing crop residues, thus reducing the amount of nitrate nitrogen available for potential leaching into ground water (Chapman et al. 1949, Chichester and Smith 1978, Macdonald et al. 1989, Varco et al. 1989, Staver and Brinsfield 1990, Owens 1990, Libby 1990, Martinez and Guiraud 1990, Smukalski et al. 1991, Hoyt and Mikkelsen 1991, Wyland et al. 1996, Brandi-Dohrn et al. 1997). In a relay strip-cropping system, the soil is covered with growing plants during the fall, winter, and spring. The soil is bare for a period of approximately 50 days between seedbed preparation and crop canopy closure.

There are many potential benefits to soil health and water quality associated with relay strip-cropping. The primary focus of this study, however, was the impact of relay strip-cropping on the arthropod community. The following is a brief review of the literature that addresses three questions. How does the presence of non-crop vegetation affect host-plant colonization by herbivorous insects? What are the potential impacts of mixed plant culture on trophic interactions? How do tillage and pesticide refuges affect the colonization of the target crop by natural enemies?

Although my study did not evaluate the impact of host-plant defenses on the arthropod community of broccoli, host-plant defenses are very important and need to be mentioned at the beginning of this review. Host-plant defense is perhaps the most powerful force shaping the arthropod community associated with a given plant family. Broccoli, for example, is well defended. Very few insects attack it. Phytochemicals in the broccoli plants are repugnant or toxic to most herbivorous insects. When crucifer-adapted insects find a patch of broccoli, however, their populations can increase rapidly because there is little competition with other herbivores for the food resource. There is interplay between host-plant defenses and the process of finding host-plants, which I will examine more closely later (Root 1973).

The vegetation surrounding a given host-plant affects the colonization of the plants by arthropods (van Emden 1965, Cromartie 1975, Smith 1976c, Tukahirwa and Coaker 1982, Altieri and Schmidt 1987, Mangan et al. 1991, Garcia and Altieri 1992, Liburd et al. 1998). Surrounding vegetation affects interactions among host-plants, herbivores, and their natural enemies (Letourneau 1987, Vet and Dicke 1992, Marquis and Whelan 1996). Under-sowing and strip-cropping have been shown to influence the development of arthropod communities associated with several crops and cropping systems (Marcovitch 1935, Schlinger and Dietrick 1960, Nentwig 1988, Heidger and Nentwig 1989, Thomas et al. 1991, Tonhasca and Stinner 1991, Phatak et al. 1991, Grossman and Quarles 1993, Zangger et al. 1994, Masiunas et al. 1997).

Under-sowing establishes a ground cover below the primary crop, which results in changes of the color surrounding the developing plants and the contrast between the crop and the soil surface. Contrast and background color can have an impact on the colonization of crops by specialist herbivores that use visual cues to find their host-plants (Costello and Altieri 1994, Costello 1995, Liburd et al. 1998). It is more difficult for insects to find their host-plant when they are surrounded by non-host vegetation. Finding host-plants is easier when plants are growing in pure stands surrounded by bare soil (A'Brook 1973, Smith 1976c, Tukahirwa and Coaker 1982, Altieri 1984).

Under-sowing establishes a mixed culture of the broccoli, cover-crop species, and weeds. Reduction in stand purity can reduce the finding of host-plants by specialist herbivores that use olfactory cues to select their host-plants (Theunissen and den Ouden 1980, 1985, Theunissen 1994, Theunissen and Schelling 1996). Changes in stand purity also influence the tendency of specialist herbivores to remain in or to emigrate from a patch of vegetation. In a mixture of host and non-host plants, mobile herbivores are more likely to land on non-host plants. Once they have lost the scent, image, or taste of their host-plant, they have a greater tendency to leave a patch of vegetation in search of other food resources (Bach 1980a, 1980b, 1984, Kareiva 1983, 1985, 1986, Lawrence and Bach 1989).

The mixed stand of plants in the relay strip-cropping system should support a greater diversity of arthropods. The number of arthropod species in a community is closely correlated with plant species diversity (Price and Waldbauer 1994) and plant structural diversity (Andow and Prokrym 1990). Each plant family has a unique chemistry, architecture, and phenology that supports a unique assemblage of hervivores (Dethier 1954, Thorsteinson 1960, Rhoades and Cates 1976, Edwards and Wratten 1980, Kogan 1986). Plant and plant patch structural diversity gives rise to a variety of ecological niches. The insects that are attracted to the diverse assemblage of plants, in turn, serve as prey items for a diverse assemblage of generalist and oligophagous natural enemies (Altieri and Whitcomb 1979, Edwards and Wratten 1980, Risch et al. 1983, Bugg et al. 1987, Russell 1989, Andow 1991, Wratten and van Emden 1995).

Nectar and pollen sources provided by flowering plants in the relay strip-cropping system may serve as components of the diet of natural enemies. Nectar and pollen can have a positive influence on the fecundity and longevity of predators (Cowgill et al. 1993a, 1993b, Bigger and Chaney 1998) and parasitoids (Leius 1961, 1967, van Emden 1963a, Topham and Beardsley 1975, Idris and Grafius 1995, 1997, Patt et al. 1997). Increases in the diversity of plants and the presence of alternative food sources (nectar, pollen, and alternative prey items) should lead to more complex food webs (MacArthur 1955, 1958). Complex food webs, however, may or may not result in population dynamics that are desirable in agricultural systems (Pimentel 1961b, Paine 1966, Root 1973, Dempster and Coaker 1974, van Emden and Williams 1974, O'Donnell and Coaker 1975, Goodman 1975, Murdoch 1975, Risch et al. 1983, Russell 1989, Thomas and Wratten 1990, Andow 1991, Price and Waldbauer 1994, Frenzel and Brandl 1998).

The number of species that become established in a given area is correlated with the distance between the community and sources of potential colonists (Simberloff and Wilson 1969, Simberloff 1986). In this study, undisturbed strips of vegetation may serve as tillage and pesticide refuges for natural enemies. It was hypothesized that the refuges would reduce the time required for the colonization of broccoli by natural enemies following a tillage event or pesticide application.

Natural enemies that disperse from the refuge into the developing broccoli plantings should have an impact on developing insect pest populations.

Three hypotheses were tested in this project. I predicted that I) relay strip-cropping would increase the abundance and diversity of natural enemies in the broccoli. Natural enemy populations would increase by virtue of the presence of alternative prey items, nectar and pollen sources, and the presence of pesticide and tillage refuges. I predicted that II) relay strip-cropping would reduce the colonization of broccoli by the cabbage aphid, *Brevicoryne brassicae* (L.) and the cabbage flea beetle, *Phyllotreta cruciferae* Goeze. Reduced colonization would result from the vegetation background effect and the polyculture effect which will be discussed in more detail later. Finally, I predicted that III) the combined effect of reduced colonization and the increased activity of natural enemies in the relay strip-cropping system would result in a net decrease in populations of the cabbage aphid *B. brassicae*, the cabbage flea beetle *P. cruciferae*, the cabbage butterfly *Pieris rapae* (L.), the cabbage looper *Trichoplusia ni* (Hubner), and the diamondback moth *Plutella xylostella* (L.) in the broccoli. The following is a closer examination of the evidence that led to the three hypothesis.

HOST-PLANT DEFENSES AND VEGETATION MANAGEMENT

Host-plant defenses for a given plant family evolved over long periods of time within an ecological context. Host-plant defenses operate in concert with the life history and phenology of the plant species. Plant defenses operate within a spatial and temporal context, the demographics of the plant and the creatures that feed on it. When a plant is grown out of its natural context, the insects that attack it can be devastating. In a sense, vegetation management schemes may reestablish, in part, the ecological context where host-plant defenses can function effectively.

Broccoli is a member of the Cruciferae family. Host-plant defenses in the Cruciferae express themselves primarily in the form of secondary plant compounds (Dethier 1954, 1970, Fraenkel 1959, Schoonhoven and Dethier 1966, Staedler 1977, Kogan 1977, 1986, Futuyma 1983, Hansen 1983), restricted nutritional offerings (Kennedy 1958, Thorsteinson 1960), and morphological traits that restrict access and movement (Rabb and Bradley 1968, Need and Burbutis 1979). Secondary plant compounds found in the Cruciferae family including the glucosinolates and other low-molecular weight toxins are repugnant or toxic to most insects. They act primarily as qualitative defenses (operating at low concentrations) against non-adapted generalist herbivores (Feeny 1976, Rhoades and Cates 1976).

Glucosinolate concentrations vary widely in species of crucifers, both between and within populations (Siemens and Mitchell-Olds 1996). Part of this variation may be attributed to abiotic environmental factors such as light intensity, nutrients, and water availability or biotic factors such as attack by fungal pathogens and herbivores. Plant damage caused by herbivory or harsh environmental conditions stimulates the production of secondary plant compounds (Bach 1980a, Fischer et al. 1990, Siemens and Mitchell-Olds 1996) and reduces the nutritional value of the plants. A limited amount of herbivory may actually increase the chances of a crucifer surviving long enough to produce seed (Rhoades 1983).

The effects of secondary plant compounds on insects are dose dependent, even on specialist herbivores. For crucifer-specialists, the dose response starts out positive. They are attracted to the glucosinolates. Feeding is greatest when the dose is intermediate. At high levels of glucosinolate, feeding falls off in some species. In the field, for example, feeding by flea beetles on cotyledons of *Brassica* plants is influenced by glucosinolate concentration in the cotyledons. At the highest level of glucosinolates, herbivory declines slightly (Rhoades and Cates 1976, Berenbaum and Zanger 1992, Siemens and Mitchell-Olds 1996).

Phytochemicals protect the crucifers from generalist herbivores. Secondary plant compounds, however, are not an effective defense mechanism for the crucifer-specialists. Food-specialist insects have developed the capacity to neutralize or tolerate these compounds (Ehrlich and Raven 1964, Janzen 1980). The toxins themselves have become feeding and oviposition stimulants that guide the crucifer-specialists to their host-plants (Hughes et al. 1997). The larvae of *P. rapae*, *P. cruciferae* (Feeny et al. 1970, Read et al. 1970) and *P. xylostella* (Thorsteinson 1960) are attracted to mustard oil. Sinigrin, a glucoside of mustard oil, is a feeding stimulant for *B. brassicae* (Moon 1967). Defense against these specialist herbivores is by alternative mechanisms.

Cultivated crucifers are derived from early succession herbs that fit Feeny's (1976) definition of "non-apparent" plants. The ancestral mustard plants grew in small, scattered, transient patches on disturbed soil surrounded by other vegetation. In a meadow, for example, mustards often colonize gopher mounds. Small patches of mustard are difficult to find because other plant families surround them. The environment in the immediate vicinity of the mustard plants supports a diverse assemblage of herbivores and natural enemies. The vast majority of the local insects are not adapted to the mustard oils. Cruciferae-specialist insects scatter across the landscape. By the time they find small patches of their host-plants, the short-lived crucifers have already set seeds. Thus, the Cruciferae escape from damage by crucifer-specialists by virtue of their spatial distribution and the time necessary for the herbivores to find their host-plant.

Over time in natural settings, large patches of single plant species tend to become damaged by specialized feeders. In numerous successful cases of biological control of introduced weed species, the introduction of herbivorous insects reduced the density of the target weed. There was a parallel increase in vegetation diversity (Goeden and Kok 1986). In other words, mixtures of plant species replaced the target weed. Eventually, the state is reached where the feeding rate of specialist herbivores and the dispersion of their host-plants are in equilibrium. In this state, both the plant and the herbivore may be rare in the landscape. They are, however, present and still interacting. The biocontrol agent and the host-plant develop a sparse equilibrium in time and space. Large concentrations of Cruciferae do not last long in natural settings (Tahvanainen and Root 1972).

Morphological defense mechanisms also operate in an ecological context. For example, the waxy leaf coating of the *Brassica* genus that prevents water loss through the leaf cuticle also influences the colonization of the plants by insects (Eigenbrode and Espelie 1995). Wax influences leaf color. Leaf color influences colonization. Green plants are generally most reflective in the yellow-green portions of the spectrum near 550 nm (Costello 1995). Green color is attractive to many herbivorous insects (Prokopy and Owens 1983, Prokopy et al. 1983a, 1983b). A heavy wax coating increases reflectance in other wavelengths. The wax makes the plants appear white to insects. When the wax bloom is mechanically or chemically removed from green cabbage, the plants are more attractive to some crucifer-specialists. In contrast, polishing off the wax bloom from red cabbage (which enhances the red color) reduces the attractiveness of cabbage to crucifer-specialists (Eigenbrode and Espelie 1995).

Wax mediates several interactions between plants and insects including oviposition, movement, and feeding (Eigenbrode and Espelie 1995). Wax can enhance or deter these behaviors. *Brassica* plants with less wax are less susceptible to damage by insects than are normal waxy phenotypes (Stoner 1992, Eigenbrode and Espelie 1995, Verkerk and Wright 1996). The wax effect disappears, however, when *Brassica* varieties are compared in the greenhouse in the absence of natural enemies. In this case, host-plant defenses express themselves in a tri-trophic context (Letourneau 1987, Marquis and Whelan 1996). Consider the following example with cabbage.

Removal of the waxy coating from normal cabbage with mechanical polishing or detergents results in greater oviposition by *P. xylostella.* Normally, when larvae emerge from their eggs and begin feeding they form feeding-pits, which serve to protect them from natural enemies. On reduced-wax cabbage, the larvae spend more time walking around before settling. They disperse over the entire plant, and their dispersal delays the onset of feeding. On susceptible normal cabbage (more wax), the majority of the larvae remain on the originally infested leaf. They begin feeding immediately after hatching (Stoner 1992, Eigenbrode and Espelie 1995).

At the same time, larger numbers of ladybeetles and their eggs are observed on glossy cabbage plants. The tarsal setae of these predators adhered better to reduced-wax surfaces. The survival of first instar *P. xylostella* was approximately 90% lower on the reduced-wax cabbage than on normal cabbage. The less time that the young larvae spent walking around before settling, the less time they were exposed to ambient mortality factors such as desiccation, raindrop splash, and natural enemies. The dramatic impact of the behavior change on mortality only occurred in the field, however. No differences were observed in *P. xylostella* survival in the greenhouse. The plant defense mechanism in reduced-wax cabbage is not expressed where natural enemy induced mortality factors are absent (Stoner 1992, Eigenbrode and Espelie 1995).

Phytochemical and morphological aspects of host-plant defense evolve and are expressed in a natural context that includes the spatial and temporal distribution of the plants, the presence of other plant families, and the presence of a diverse assemblage of arthropods. It appears that the forms of host-plant defense expressed in *B. oleracea* are not effective when the plants are grown in large, pure stands. In this context, host-plant defense mechanisms break down. Visual and olfactory cues to the crucifer-specialists are more intense. The diversity and abundance of non-crucifer-adapted insects is limited by the availability of non-crucifer host-plants. The limited variety of prey items, in turn, limits the diversity and abundance of generalist natural enemies. In the presence of a remarkable concentration of food and in the absence of complex trophic interactions, the crucifer-specialist populations increase rapidly. Relay strip-cropping has the potential to influence the finding of host-plants and to reestablish a more complex ecological context where host-plant defenses can express themselves effectively.

VEGETATION MANAGEMENT AND COLONIZATION

In a modern cropping system, the soil and the plant community are constantly disturbed by farming operations. Insects must colonize fields over and over again. The most dramatic disturbance in annual cropping systems occurs during primary tillage and seedbed preparation. At this time, local extinction of non-mobile species may occur. The level of colonization of the crop by herbivores and their natural enemies that occurs between disturbances is determined by the net effect of immigration, emigration, natality, and mortality. All of these colonization processes are influenced by aspects of the vegetation including stand purity, host-plant density, and planting arrangement (Price 1984).

In natural situations when a significant period of time occurs between disturbances, colonization proceeds in several phases. During the immigration period, species collect in a given habitat, but they do not interact very much. High dispersal and reproductive capacities allows the early colonist insects to overcome the high mortality rates associated with dispersal and host finding. The insects that happen to find host-plants and suitable habitat rapidly exploit unoccupied resources. There is plenty to eat and there is little competition. This phase is referred to as the “non-interactive phase.” As the habitat becomes more crowded, natural enemies arrive, become established, and species begin to interact in food webs. This phase is referred to as the "interactive phase." Eventually, competition drives individuals into ecological niches where their unique characteristics are adaptive. The assemblage of plants and animals has now entered the "assortive phase." Over long periods of time during the "evolutionary phase", new relationships and new species evolve. In annual cropping systems, the arthropod community structure does not have sufficient time to reach a high level of maturity between disturbances (Simberloff and Wilson 1969, Price and Waldbauer 1994).

A typical broccoli crop is harvested ten weeks after planting. The time period between tillage, cultivation, insecticide applications that protect the seedlings, and insecticide applications that protect harvest may be as long as four weeks. The cropping system is dominated by early colonizers and may remain in the non-interactive phase for a significant portion of the cropping season. Higher level trophic interactions may not play an important role in shaping the arthropod community in annual crops. Primarily the early colonization processes, immigration and emigration shape the arthropod community. Immigration and emigration explain, in large part, the effects on arthropod community structure associated with alternative vegetation management schemes.

Early colonizers and crop-adapted species

There are three types of colonizers of agricultural fields, those present in the field at the time of planting, invaders from nearby plant communities in the vicinity of the field, and finally, the true migratory species that come from a distance (Price 1976). Herbivorous insects and the natural enemies that occur in vegetable crops must have well-developed dispersal abilities to find transient patches of their host-plants and prey items in the landscape. Examples of highly mobile early colonizers include aphids, thrips, leafhoppers, flies (Price and Waldbauer 1994), typical Lepidopteran pests (Ehler and van den Bosch 1974), damsel bugs, minute pirate bugs, big-eyed bugs, ladybeetles, and spiders (Ehler et al. 1973, Ehler 1977, Ehler and Miller 1978). In many cases, arthropods colonize vegetables in waves of progeny that disperse aerially across the landscape. Aphids (Kring 1972) and spiders (Bishop 1990) are good examples. They have large numbers of progeny that allow the species to survive the mortality associated with constant immigration and emigration from agricultural fields (Heidger and Nentwig 1989). High reproductive capacity allows the colonists that survive to take advantage of the abundant but short-lived food resources. These arthropods fit the description of "r-selected" species that tend to occupy immature ecosystems or temporary habitats (MacArthur 1955, Mac Arthur and Pianka 1966, Southwood 1977).

The early colonists must be adapted to harsh conditions associated with agricultural systems. In young plantings of vegetable row crops, the soil is exposed between the plants. The soil surface and the microclimate can be hot and dry. Colonization of row crops by herbivores and natural enemies correlates closely with plant canopy closure. Canopy closure reduces the harshness of the microclimate. Simple changes in planting arrangement or the establishment of under-story vegetation moderate the microclimate associated with crop plants and can increase the rate of colonization, especially for natural enemies (Price 1976, Mayse 1978).

In a freshly planted field, food is scarce both in terms of volume and diversity, except for insects that specialize on the crop. The first successful colonists must be herbivorous and adapted to the chemistry of the crop. Specialist herbivores function as "organizer" species for the arthropod assemblage associated with crucifers (Root 1973). As plants mature and the canopies overlap, shade develops. The environment becomes less harsh. As herbivore populations become established and grow, their natural enemies invade the field. There is no selective pressure for natural enemies to colonize vacant sites early. They would encounter a shortage of food. It is adaptive for natural enemies to lag behind (Price and Waldbauer 1994).

In natural communities, prey populations are relatively stable, cycling in abundance according to the seasons and their life histories. Stable food resources result in relatively stable and diverse assemblages of natural enemies. In agricultural systems, prey populations are highly unstable. Pest populations may explode. Prey items may be scarce following an insecticide application. Crop-adapted species of natural enemies must be able to rapidly colonize large fields following a disturbance or they must be able to tolerate extended periods of low prey availability. Spiders, for example, can spend significant periods of time motionless and without food and not suffer ill effects (Riechert and Lockley 1984).

Natural enemy populations in transient ecosystems tend to be self-limiting. When food is scarce, reproductive rates decline rapidly and in some cases, cannibalism increases (Mills 1982, Agarwala and Dixon 1992). When food is abundant, crop-adapted natural enemies invest a significant portion of their reproductive potential in areas of prey concentration and achieve rapid population increases. Coccinellidae are a good example of this phenomenon (Obrycki and Kring 1998).

Some of the common predators in vegetable cropping systems are capable of switching prey items according to the level of abundance. Prey switching is probably an adaptive behavior given the rapid changes that occur in the insect populations inhabiting transient ecosystems (Murdoch 1975). In some cases, specialist natural enemies go locally extinct in highly disrupted crop ecosystems (Ehler and Miller 1978, Miller and Ehler 1978). Generalist natural enemies are opportunistic feeders that can maintain their populations in the absence of crop pest species, switch, and rapidly exploit a food resource such as a surging pest population. Natural enemies have been shown to destroy experimentally released pest populations in a 24-hour period (Murdoch 1975, Ehler 1977).

Many important species of natural enemies overwinter on the farm. One of the successful adaptations to surviving year round in agricultural settings is habitat switching (Boivin and Hance 1994). Crop-adapted carabid species, for example, tend to move in and out of agricultural fields between plantings, moving from the middle to the field edge and back again over the course of the seasons (Wallin 1986). Grassy borders surrounding agricultural fields are suitable overwintering sites for field inhabiting carabids (Doane 1981, Desender 1982, Sotherton 1984). Some carabids use hedgerows and residual woodlands for overwintering (Ferro and McNeil 1998). Undisturbed habitat at the field edge is especially important for species that overwinter as adults (Wallin 1985). Marked carabid beetles dispersing into agricultural fields from the field edge between stand establishment and harvest can move up to 200 meters into a field from the field edges (Coombes and Sotherton 1986).

The movement of the beetles depends on the cropping cycles and the phenology of the species. If the field is plowed in the fall and planted to winter cereal, few larvae will overwinter in the field. Adult overwintering beetles may move into the field as the canopy develops and the temperatures warm up in the spring (Wallin 1985, Coombes and Sotherton 1986). Species that overwinter as larvae often mature in undisturbed field centers and disperse, as adults, out of the fields as the field dries up in preparation for mid-summer harvest (Wallin 1986). Residual local populations of carabid beetles on the farm at the end of the winter determine in large part the level of re-colonization of spring planted crops. In some cases, the concentration of natural enemies on the edges of agricultural fields can result in the depression of pest populations on the field edges in the spring (van Emden 1965, Pollard 1971, Potts and Vickerman 1974, Edwards et al. 1979, Luff 1987).

Habitat switching is also adaptive for pest populations. Herbivores also switch middle to edge. Densities of adult overwintering Colorado potato beetles tend to be higher on the field edges than in the middles regardless of post-harvest tillage regime. Apparently, the adults move toward the edges of potato fields to overwinter (Nault et al. 1997). In the spring, carrot rust fly damage is generally worse at the edge of fields (Ramert 1996, Ramert and Ekbom 1996). Crop-adapted species of herbivorous insects and their natural enemies are constantly on the move, immigrating after a disturbance, emigrating from plant patches that fail to meet their needs.

Background vegetation, stand purity, and immigration

Long-distance host-plant and prey finding by insects is mostly visual (Prokopy and Owens 1983). From as close as 40 cm away, landing by the cabbage root fly, *D. radicum*, on its host-plant was controlled entirely by visual stimuli (Prokopy et al. 1983a, 1983b). Patches of vegetation attract insects regardless of the plant assemblage in the patch. Insects land and explore the habitat. The color, textures, and contrasts of the vegetation and soil influences the propensity of an insect to land (Vinson 1976).

Plants in the Cruciferae family are adapted to unstable land surfaces and grow in disturbed soil. As crucifer-specialist insects blow across the landscape, they look for the color of plants contrasting with the brown color of disturbed soil. Landing by some species is promoted by the color of living plants against bare ground. When exploring a new habitat, insects avoid landing on bare ground regardless of the type of vegetation present. A plant surrounded by bare ground is more likely to be sampled by passing insects than a plant surrounded by vegetation (Finch 1988).

Many species of insects including several crucifer-specialists do not appear to distinguish between leaf shapes or identify host-plants prior to landing (Kostal 1993). Color and contrast alone stimulate landing. A flat green paper background, which bears no resemblance to a plant, is sufficient to cause female cabbage root flies to land. Fewer cabbage root maggot flies land on collard plants surrounded by green vegetation, green artificial plants, or a flat background of green paper than around plants surrounded by bare soil (Kostal and Finch 1994).

Fewer cabbage aphid colonies developed on cabbage surrounded by dead mulch than on cabbage surrounded by bare ground (Roberts and Cartwright 1991). Costello and Altieri (1994) found a correlation between light intensity and the number of winged cabbage aphids landing on broccoli. Broccoli surrounded by living mulch has a lower light intensity than broccoli surrounded by bare soil. Fewer aphids landed on the broccoli in the living mulch. There was a strong association between the number of winged aphids landing and the intensity of the yellow waveband.

Stand purity can influence landing by insects that use olfactory cues to discover their host-plant. Crucifers growing in mixed stands with other plant families may be more difficult to find by crucifer-specialists. Olfactory cues influence insect landing once the insect is close enough to smell its host-plant. *P. rapae* larvae, cabbage flea beetles (Feeny et al. 1970, Read et al. 1970), the diamondback moth (Thorsteinson 1960), and the cabbage aphid (Moon 1967, Read et al. 1970) are all attracted to mustard oil.

Host finding by *P. cruciferae* is guided by chemical stimuli. The presence of non-host plants appears to interfere with orientation and feeding by flea beetles. Decreased colonization in mixed stands may have been caused by repellant or masking chemical stimuli originating from the non-host plants. In sparse, randomly dispersed host-plants surrounded by non-host species, chemical stimuli may become lost in the environment (Tahvanainen and Root 1972).

However, the dilution of the olfactory signals in mixed plant stands does not explain the behavior of all of the crucifer-specialists. In large scale field experiments, Finch and Skinner (1982) found that the cabbage root maggot *Delia radicum* (L.) flies upwind or at an angle to the wind regardless of the presence of host-plant odor. Long-distance, odor-modulated behavior did not appear to be used to locate distant host crops by *D. radicum.*

Decreases in stand purity may interfere with the finding of prey and insect hosts by natural enemies. The odor of the herbivore host-plant is important for some natural enemies in locating their prey. Chemicals appear to play a major role at almost every level of the host selection process by parasitoids, including host habitat selection. The volatile chemicals – whether derived from the host's food, organisms associated with the host, the host itself, or a combination of these factors – are long-range factors responsible for directing the parasitoid to a host habitat. Long-range odors from the host's food or from a plant responding to injury by a host insect appear to be the first factors in the process of host selection. Once a parasitoid reaches the proper habitat, an egg laying female must begin a search for additional cues. Parasitoids of some phytophagous hosts have been observed to orient to the host-plant and scan or search it (Vinson 1976).

For example, the cabbage aphid parasitoid *Diaeretiella rapae* (M'Intosh) is attracted to the odor of crucifers. The wasp was attracted to clumps of 250 cabbage aphids (*B. brassicae*) removed from collards within 15 minutes of the trial. It was not attracted to a clump of 10 cabbage aphids or a clump of 250 aphids removed from collards 24 hours before the trial. The wasp was attracted to a substance from the host-plant that was still present in the aphid after 15 minutes but not after 24 hours. The parasitoid was more likely to oviposit in the green peach aphid, *Myzus* *persicae* (Sulzer), feeding on collards than on the same species of aphids feeding on sugar beets. The presence of an adjacent collard plant also increased the parasitism of *M. persicae* on sugar beet plants. The hyperparasite *Charips brassicae* L. was not attracted to collards, mustard oil or *B. brassicae*. It was attracted to the scent of female *D. rapae*, its host (Read et al. 1970).

Stand purity, patch tenure time, and emigration

Once an insect has landed in a patch of vegetation, specific chemical olfactory and gustatory cues indicate to the insect whether or not it has encountered a suitable foraging or oviposition site. Plant diversity in a patch of vegetation may interfere with the ability of an insect to smell its target. If the insect lands on a non-host-plant and tastes it, the insect is prompted to take off again. Post-alightment experience determines whether or not an insect will remain in a patch of vegetation or emigrate from the site (Kostal 1993, 1994, 1996).

Post-alightment behavior is especially important for highly mobile insects such as the cabbage flea beetle, *P. cruciferae* (Tahvanainen and Root 1972, Altieri and Schmidt 1986, Bergelson and Kareiva 1987, Garcia and Altieri 1992). The beetle is constantly landing, tasting, moving around, and taking off again. The balance between immigration and emigration is a significant determinant of flea beetle population during the brief period of time between planting and harvest of cole crops (Kareiva 1982, 1983, 1985, 1986).

Southwood (1962) defined two types of animal movement, trivial movement and migratory movement. Trivial movements occur within the habitat of the insect population and include movement from plant to plant and from plant patch to plant patch. In contrast, migratory movements carry the animal away from a given population. After completing a migratory movement and landing in a patch of vegetation, a herbivorous insect may encounter a host-plant and begin feeding. It may land on an unsuitable plant, move to another plant in the same patch of vegetation, or move to another plant patch in the immediate vicinity. The rate of host-plant encounters has a bearing on whether the insect remains in the plant patch or emigrates.

Some phytophagous insects are very active foragers that are able to leave a non-host plant after alighting on it. They move readily among patches of host-plants spending most of their time where their food is either more abundant or of higher quality. For many insects, when they land on a non-host plant, their next flights tend to be long ones (Bach 1980b, Risch 1981). Aggregation of highly mobile herbivorous insects in a given plant patch is often the result of host-plant concentration and the movement behavior of the herbivorous insect (Kareiva 1986, Bergelson and Kareiva 1987).

Trivial movements on and off plants and between plant patches explains, for some insects, the differences in pest attack between pure stands and mixed plantings (Root 1973, Trenbath 1993). Differences in pest attack are due to differences in the probability of emigration by the pest that are associated with varying levels of stand purity (Kareiva 1985). Emigration of herbivorous insects from plant patches is generally higher when the host-plants are grown in a mixture with other plant species (Risch 1981, Bach 1980b, Tukahirwa and Coaker 1982, Elmstrom et al. 1988, Andow 1990, Garcia and Altieri 1992, Kostal and Finch 1994). The accumulation of herbivores on their host-plants requires both landing and settling. Accumulation occurs due to the net effect of immigration and emigration (Kareiva 1985, 1986). Cabbage root flies and cabbage flea beetles provide specific examples of this phenomenon.

After landing on a given plant, *D. radicum* often take off again. The fly has a tendency to take off again regardless of whether it lands on a host (*B. oleracea*) or non-host plant, and regardless of whether the plant background is bare soil, non-host vegetation, or green paper. It is the nature of these flies to move about from plant to plant. The behavior of *D. radicum* when it is exploring a plant patch and exploring a host-plant includes landing (on host, non-host, soil, or other substrate), jumping on or off or back on host or non-host plants, flying away from the host patch, spiral flight around the plant canopy, movement to base of a host-plant, and exploring the soil with the ovipositor protruding (Kostal and Finch 1994). General unproductive activity, hopping about, and flying around by *D. radicum* increases when their host-plants are surrounded by clover (Tukahirwa and Coaker 1982) or grass (Kostal and Finch 1994).

When the flies left their host-plant and flew in a spiral motion above the plant canopy, 95% of the female flies landed again on their host-plants when they were surrounded by bare ground. If the flies landed on soil in the vicinity of their host-plants, they easily rediscovered their host-plant by walking or by a series of short hops. Only 51% of the flies relocated their host-plant when other vegetation (grass) surrounded the plants. The flies spiraled around and often landed on the grass. When this happened, they repeated the original landing procedure (a spiraling flight) or left the area, losing contact with their host-plant. The presence of non-host plants increased the probability that the flies would emigrate. The net effect of the non-productive movement and increased emigration was that fewer eggs were deposited around the host-plants grown in a mixed stand (Kostal and Finch 1994).

When the same comparisons were made in no-choice experiments (separate cages) the differences disappeared. In a cage, the flies were prevented from emigrating. Held by the cage in the vicinity of their host-plants, the flies had many chances to rediscover their host-plants and oviposit, regardless of stand purity (Kostal and Finch 1994).

Flea beetles (Kareiva 1985), and other Chyrsomelidae (Bach 1980a, 1984) move on and off their host-plants until they receive enough chemical stimulation to start feeding. These movements can be a major factor producing differences in beetle density between mixed or pure stands of their host-plants. Differing tenure time and emigration rates produce this effect.

P. cruciferae infestations are lower when *Brassica* are growing with other non-host plants. Flea beetles hop around and loose contact with their host-plant and the chemical stimuli that must accumulate in order for feeding to occur. Under these circumstances, the probability that the beetle will emigrate from the patch is about the same as the probability of emigrating from a patch of non-host plants (Garcia and Altieri 1992). As with the cabbage root fly, the effect of stand purity disappears when the flea beetle is prevented from emigrating from the plant patch by physical barriers in no-choice experiments (Bergelson and Kareiva 1987).

Stand purity directly affects the density and dispersion of herbivores, and indirectly affects the aggregation of their natural enemies. The manner in which herbivorous insects and their natural enemies respond to spatial variation in the density of their food resources is a fundamental attribute of ecological systems (Ives et al. 1993). Many, but not all, herbivorous insects are more likely to find and remain on their host-plants when the host-plants are concentrated and growing in large, pure stands (Tahvanainen and Root 1972, Root 1973, Cromartie 1975, 1981, Ralph 1977, Bach 1980b, 1980a, 1981, 1984, 1988, Risch 1980, 1981, Risch et al. 1983).

Host finding is influenced by olfactory and visual cues that are disrupted in mixed stands. To a generalist feeder, a diverse cropping system appears fine-grained, as if there were many small particles of food. To a specialist, a diverse cropping system appears course-grained, with a few particles of food in a matrix of non-food items. Increasing diversity of plants or prey makes very little difference to the polyphagous herbivore, predator, or parasitoid unless the more complex textured physical environment interferes with their movement. To a specialist feeder, increasing cropping system diversity makes it more difficult to locate appropriate food items or hosts (Mac Arthur and Pianka 1966).

Every time a specialist herbivore lands on a non-host plant, it must take off again. Every time it leaves a non-host plant, it is susceptible to a variety of mortality factors and it may loose track of its host-plant altogether. Insects that are moving are at greater risk of other hazards in the environment including natural enemies. Specialist herbivores spend more time moving on and off plants in a mixed stand of plants than in a pure stand of their host-plants. The net effect of this unproductive movement is that they will have lower survival and fecundity (Kareiva 1986).

In trying to understand the net impact of vegetation management on the colonization of crops by herbivorous insects, one must keep in mind that an insect may be involved in more than one activity at the same time. An adult female butterfly may be ovipositing, responding to oviposition cues, while also foraging for food and responding to a different set of behavioral cues associated with feeding. Most adult Lepidoptera, for example, feed on floral nectar. Nectar producing flowers are attractive to ovipositing adults and may result in more oviposition on plants growing nearby. In this case, the ovipositing butterfly is responding to a concentrated source of food (nectar) that my be unrelated to the concentration of its host-plant.

The impact of stand purity on oviposition of Lepidoptera is complex. Oviposition is a critical step for Lepidopteran insects because the larvae are relatively immobile and dependent on the choices made by the female moth (Renwick and Chew 1994). Oviposition involves searching, orientation, encounter, landing, surface evaluation and acceptance by the female moth. Oviposition is determined by the relative strength of opposing positive and negative cues. For most Lepidopteran insects, visual and olfactory cues are used to identify appropriate host-plants. Thus, stand purity should have an impact on oviposition.

Zhao et al. (1992) evaluated the impact of nectar producing flowers on Lepidopteran insect pests and their parasitoids in broccoli. The interactions were complex. The effect depended on the specific parasitoid and host complex. The density of the cabbage looper, *T. ni*, was not affected by the proximity of nectar producing plants even when they were inter-planted with the broccoli. Eggs and larvae of *P. rapae*, however, were much more abundant in broccoli inter-planted with nectar producing plants than in a broccoli monoculture growing 120 meters away.

During its oviposition flights, *P. rapae* tends to fly in a straight line between landings and is insensitive to stand purity and host-plant density. Flight direction, turn angles, and length of flights are unpredictable. The oviposition behavior scatters eggs on random host-plants across the landscape. The nectar feeding flights of *P. rapae* adults, however, depart significantly from Markovian (random dispersion) expectations. Nectar feeding butterflies abandon their linear flight paths upon encountering flower clusters and exhibit tight turning behavior. The probability that a butterfly will turn at a sharp angle, make a short flight, and land to sip nectar from a host-plant is not independent from previous flight behavior. *P. rapae* aggregates around host-plants near nectar sources. Foraging behavior influences oviposition behavior in the vicinity of a nectar source (Root and Kareiva 1984).

Bigger and Chaney (1998) compared arthropod density and diversity in broccoli grown in monoculture versus broccoli growing next to a flowering border of Candytuft (*Iberis umbellata* L.). The relative abundance of *P. rapae* in the two cropping systems was similar. However, the presence of the flowering border influenced the spatial distribution of *P. rapae* eggs and larvae. The mean number of *P. rapae* eggs decreased with increasing distance from the flowering patch boundary.

While herbivores are responding to the spatial distribution of their host-plants or other food resources, natural enemies are responding to changes in the spatial distribution of their prey. Pupae of the Pieris parasitoid *Cotesia rubecula* Marshall (Hymenoptera: Braconidae) were more numerous in the broccoli associated with nectar plants than in the broccoli monoculture. The aggregation of the parasitoids was due to the concentration of their Pieris host near the nectar source (Zhao et al. 1992).

The interaction of the diamondback moth, the parasitoid *Diadegma insulare* Cresson (Hymenoptera: Ichneumonidae), the broccoli, and the nectar plants was slightly different. More larvae of *P. xylostella* occurred in broccoli inter-planted with or adjacent to nectar producing plants than in the broccoli monoculture. The ovipositing moth was attracted to the nectar source. *D. insulare* parasitism was high in all plots. When broccoli plants were evenly inoculated by hand with *P. xylostella* larvae, however, there was no significant difference in percent parasitism on broccoli interplanted with nectar plants and broccoli monoculture growing 120 meter away (Zhao et al. 1992).

To assess the impact of stand purity on the density of herbivorous insects, it is necessary to keep track of forces that may be driving insect populations in different trajectories. Stand purity can affect immigration and emigration of colonizing herbivores. The net effect of immigration and emigration may result in differences in herbivore density. At the same time, natural enemies may concentrate their foraging efforts in areas of high prey concentration resulting in increased mortality rates (Hassell and May 1974, Hassell 1980). At the end of the season, the net effect of these opposing forces (prey aggregation and natural enemy induced mortality) may be neutral. Thus, there may be no useful generalities that describe how stand purity affects insect populations (Perrin 1977, Andow and Risch 1985).

T. ni orients towards volatiles from susceptible plants and is repelled by volatiles from resistant plants. Egg laying *T. ni* are more attracted to yellow substrates than other colors. *T. ni* depends on tarsal receptors for perception of oviposition deterrents on the leaf surface. *T. ni* concentrates its eggs in plant patches that contain high densities of its host-plant. Oviposition by *T. ni*, however, is deterred by frass from larvae feeding or by chemical released from damaged foliage. Volatile and non-volatile cues deter oviposition and result in evenly spaced egg distribution within a patch containing its host-plants. The diamondback moth is attracted to sinigrin, a characteristic glucosinolate present in the Cruciferae. Sinigrin stimulates oviposition in gravid moths. Females are more attracted than males; the heavier their egg load, the more intense the attraction (Renwick and Chew 1994). *P. rapae* lays most of its eggs on *Brassica* (Andrewartha 1961), but tends to avoid concentrations of its host-plants. The avoidance of host-plant concentration by *P. rapae* deserves closer examination.

The behavior of *P. rapae* females includes relatively long-distance flights that lead to the finding of host-plant patches, oviposition flights, and nectar foraging. (Kostal and Finch 1994). Root and Kareiva (1984) studied the oviposition behavior of *P. rapae* in great detail and found that the butterflies are not sensitive to host-plant density or stand purity during oviposition. Oviposition sequences were Markovian. Individual butterflies occasionally displayed directionality in short flights, but in general had no tendency to move in any particular direction as would be expected if butterflies were orienting to wind, sun position, or landmarks. The probability of any particular next move (transition from one oviposition site to the next, length of travel and angle of turns) was independent of the previous move. The distance between moves and the angle of flight between moves was not influenced by host-plant density. A short move by *P. rapae* during oviposition is not necessarily followed by a short move (aggregation). The distance between moves and the angle of flight between moves was not influenced by interplanting host-plants (collard) with potatoes, or mixtures of *Salvia officinalis* L., *Thymus* sp., or *Tagetes* sp. at constant host-plant density.

The recent past history of the butterflies had no affect on the initial behavior of female *P. rapae* entering a dense stand of collards. The frequency of oviposition was independent of previous egg-laying behavior. The turning behavior of *P. rapae* was unaffected by their proximity to the patch border regardless of the surrounding vegetation. The distance between moves and the angle of flight between moves by ovipositioning *P. rapae* was not influenced by the shape of the host-plant patch (linear vs square) or the background vegetation (scattered in a diverse meadow vs concentrated in a clean till monoculture). While the butterflies were laying their eggs, they flew over many suitable host-plants for no obvious reason. They flew out of host patches after ovipositing on only a small fraction of the available plants (Root and Kareiva 1984).

The maximum lifelong fecundity for *P. rapae* ranges from 500 to 1200 eggs per female, with as many as 150 eggs laid daily. Because these eggs are laid singly, the female must visit hundreds of plants. Females follow a linear path and pass over many suitable plants; as a consequence of this flight behavior eggs are widely scattered in space. In pure stands where collard density was manipulated, *P. rapae* oviposition was negatively correlated with host-plant density. As the number of plants per square meter increased, the eggs per plant in a given area decreased. In other words, the moth did not respond as expected to an increase in the concentration of its food resource (Root 1973, Root and Kareiva 1984).

Throughout its range, *P. rapae* utilizes hosts that are distributed in scattered and frequently disturbed patches. Most of the wild hosts are species that occupy local pockets of disturbed soil such as gopher mounds, eroded banks, and recently abandoned fields. The densities of *P. rapae* eggs and larvae are usually higher on sparse, isolated hosts than they are on dense or large stands of crucifers. There are several possible advantages of this behavior (Root and Kareiva 1984).

Egg scattering may allow *P. rapae* to escape density-dependent mortality associated with virus diseases and parasitoids. The major larval parasitoid of *P. rapae*, *Cotesia* (*Apanteles*) *glomeratus* L. is attracted to Cruciferae (Sato 1979). It may be adaptive for *P. rapae* to scatter its eggs on small, scattered patches of host-plants rather than in large concentrations of the host-plant (Maguire 1984). Egg scattering may also assist *P. rapae* to avoid density-independent mortality such as rainfall. Rainfall is one of the major causes of death for small lepidopteran larvae. Rainfall is highly variable and unpredictable from plant to plant or from field to field (Harcourt 1963).

The slow growth of insects relative to the swift changes that may occur in host-plant quality and the microclimate and the limited mobility of the juvenile life states make phytophagous insects vulnerable to losses caused by larvae being stuck in sites that deteriorate after the eggs are laid. Such problems are probably most severe for insects that commit their young to transient host-plants. In some cases, insects can override these difficulties by possessing adaptations that increase the information about the future plant quality. Ovipositing adults may sense the presence of other herbivores and conspecific eggs and larvae during oviposition. Under laboratory conditions, *P. rapae* will avoid laying eggs on plants or leaves laden with other Pieris eggs or larvae. In the field, it is not apparent that they discriminate between plants on the basis of egg load (Root and Kareiva 1984).

The oviposition behavior of *P. rapae* seems to emphasize wide-ranging movement that cause the females to sample vigorously an unpredictable environment by placing their eggs on several, scattered, and almost randomly selected host-plants. In this way the females spread the risk of mortality among their offspring and avoid a complete reproductive failure. Unpredictably variable mortality may favor an egg spreading ("bet-hedging" or "risk-spreading" oviposition strategy (den Boer 1968, 1981, 1988). *P. rapae* may conform to this model (Root and Kareiva 1984).

Stand purity and natural enemies

Stand purity influences the overall density and spatial dispersion of food resources (prey items, host insects, nectar, pollen, and Homopteran honey dew) available to natural enemies (Andow and Risch 1985). Prey items tend to be more dispersed in mixed plant stands. If the density of prey items is too low to attract the natural enemy, it will abandon the area. On the other hand, as the spatial dispersion of the non-target food resource becomes more even, the natural enemies encounter it more frequently. More frequent rewards increase the probability that the natural enemy will remain in the habitat and reproduce there.

The impact of stand purity on natural enemies is complex and usually indirect. Predacious insects (Charnov 1976, Cowie 1977), parasitoids (Hassell and May 1974), and hyper-parasitoids (Horn 1987, 1988) concentrate their foraging activities in areas of high prey density.

Stand purity influences the aggregation of their prey. It is difficult to untangle the effect of stand purity on prey aggregation, predation rates, and their net effect on prey population density.

The aggregation of predators and parasitoids in patches of high prey density explains, in part, changes in the mortality of herbivorous insects in various planting schemes. Aphids, for example, accumulate more rapidly in a monoculture surrounded by bare ground than in mixed plantings surrounded by other vegetation. As explained earlier, differential accumulation of aphids is due to the effect of surrounding vegetation on host-plant colonization. Natural enemies, then, respond to the higher density of aphids in the monoculture. Increased predation and parasitism in the monoculture depresses the growth rate of the aphid population. At the end of the growing season similar aphid densities may result in monoculture and polyculture (Smith 1976b, Altieri 1984, Thomas and Wratten 1990).

Andow and Risch (1985) evaluated ladybeetles activity in corn monoculture versus corn/bean and corn/squash polyculture. They used two prey items that had different spatial distributions. Prey included naturally occurring aphids and artificially placed egg masses of the corn stem borer, *Ostrinia nubilalis* (Walker). The aphids colonized the monoculture 5 days sooner than the polyculture. The egg masses of *O. nubilalis* were place evenly by hand. Ladybeetles invaded the plantings 35 days later.

The Coccinellidae were immediately more abundant in the corn monoculture. They were attracted to the concentration of the aphids in the monoculture. Coccinelid females committed their reproductive potential in areas of higher prey density. Coccinellid larvae were more abundant in the monoculture and the wingless coccinellid larvae were not capable of emigrating. They were forced to forage aggressively in the monoculture or face starvation.
The highly mobile adult beetles had a higher rate of emigration from the polyculture where their aphid prey were more dispersed (Andow and Risch 1985).

The coccinellid beetles responded to variation in aphid density. Further, spatial variation in prey distribution determined the relative effectiveness of the predators. The rate of predation was higher in the monoculture where aphid prey was more concentrated. Predation on evenly distributed *O. nubilalis* egg masses was higher in the monoculture. Increased predation was due to the elevated density of Coccinellidae there. By the end of the experiment, there were no significant differences in aphid densities in the various planting systems. Aphid density in the monoculture and polyculture systems had converged. However, there were fewer egg masses of the stem borers left in the monoculture compared to the polyculture (Andow and Risch 1985).

The same phenomenon occur with *B. brassicae*, that is parasitized by *D. rapae*. Parasitism rates tend to be higher where aphids aggregated regardless of stand purity or vegetative background. In small plot comparisons of monoculture and mixed culture, two aspects of colonization, differential immigration and differential mortality oppose each other, causing aphid populations in the two cropping systems to converge by the end of the growing season (Smith 1976a, 1976b). The situation is further complicated by the fourth trophic level. Hyper parasitism of *D. rapae* by *Alloxysta fuscicornis* (Hartig) tends to be greater in clean-tilled monoculture than in mixed stands. A. fuscicornis responds to aggregation of its food resource (Horn 1987, 1988). It is difficult to predict the net impact of these multi-trophic interactions. The net effect of multi-trophic interactions explains, in part, the variable results of mixed culture on insect pest populations (Risch et al. 1983).

Structural complexity and patch size

The physical structure of vegetation has a variety of effects on arthropod colonization and trophic interactions. Some arthropod species require specific three-dimensional structures in order to exist in a given habitat (Riechert and Lockley 1984). Plant and plant assemblages with complex structure offer more feeding and oviposition sites. They offer more shelter and more overwintering sites. Plant attributes including size, growth form, seasonal development, persistence and variety of above ground parts (stems, leaves, and flowers) influence the number of insect species that inhabit them. In general, trees and shrubs have richer insect faunas than herbs and grasses. The complexity of plant structures has an impact on predator/prey relationships. Vegetation structures serve as hiding places for prey and serve as the hunting arena for natural enemies (Lawton 1983).

Many insects that migrate utilize mass aerial dispersal. They accumulate at wind breaking obstacles. Ballooning spiders, for example, collect on hedgerows surrounding agricultural fields (Lewis 1969a, Lewis and Smith 1969, Lewis and Dibley 1970). Trees next to vineyards act as windbreaks, favoring fallout of migrating parasitoids present in the wind stream above the trees (Corbett and Rosenheim 1996). Even a small amount of physical relief can result in the accumulation of airborne insect. Thrips and aphids collect in greater numbers in strips of un-mowed meadow compared to mowed areas (Nentwig 1988). The same physical structures that collect and concentrate airborne insects can interfere with the over-ground dispersal of insects. Hedgerows were found to restrict the movement of ground beetles (Carabidae) across agricultural fields. The physical barriers delayed the colonization of the agricultural fields by ground beetles following insecticide applications (Mauremooto et al. 1995).

Predacious arthropod species are more diverse in undisturbed meadow than in mowed meadow. Wolf spiders (Lycosidae) occur in significant numbers only in strip-managed meadow. The primary difference in the habitats is physical structure. The wolf spiders use structural resources including hollow stems, old stalks, flowers, pioneer woody plants, and a thick layer of old vegetation and debris. These serve as overwintering sites (Nentwig 1988).

The structural complexity of a single plant or assemblage of plants has an impact on natural enemy efficiency and predation rates. Many biological control agents are limited in their ability to regulate their host population because they are not able to find their hosts at a high enough rate to meet their energy needs (Andow

1990, 1991, Andow and Prokrym 1990). The complexity and size of the plant influence how long a natural enemy takes to find prey.

There are three components to plant structure relevant to searching by natural enemies: 1) plant size or total surface area, 2) variation among parts and surfaces and, 3) the connectivity of the parts. The rate of parasitism per unit search time per individual (searching efficiency) can be significantly higher on simple surface than on the complex surface. Even when no hosts are present, female parasitoids tend to remain for longer periods of time on simple surfaces than on more complex surface (Andow and Prokrym 1990).

The behavior of coccinellid beetles was compared on collards, broccoli, cabbage and kale; foraging behavior of the ladybeetles was influenced by plant architecture. The architecture had an impact on predator mobility, falling frequency, and prey accessibility. Four species of Coccinellidae (*Hippodamia convergens* Guerin-Meneville, *H. variegata* Goetz, *Coleomegilla maculata* (Degeer), and *C. septempunctata* L.) exhibited distinct foraging strategies. Foraging strategies were measured in terms of time spent actively foraging, the rate of encountering *B. brassicae*, and the fraction of aphids encountered that the beetles actually consumed. The beetles differed in their propensity to fly away from the plants and in the frequency that they fell from the plants. The impact of plant architecture, however, was similar on all of the Coccinellidae species. The beetles were less efficient at foraging for aphids on the complex surfaces of the kale and cabbage than on the relatively simples surfaces of the collards and broccoli (Grevstad and Klepetka 1992).

Differences in plant architecture give rise to different levels of parasitism (Pimentel 1961a). A much higher percentage of the fifth-instar *P. rapae* larvae found on open-leaf cole crops (broccoli, collards, and kale) were parasitized. Parasitism on Brussels sprouts and cabbage were much less. Field observations indicated that the parasitoid *A. glomeratus* had difficulty attacking *P. rapae* larvae living in the crevices and folds of the heading cole crops.

Patch size and patch fragmentation both influence the number of arthropod species in a given habitat and the efficiency of natural enemies that forage in the habitat. In general, the number of animal and plant species in a given area tend to correlate with the size of the area available for colonization (MacArthur and Wilson 1967, Simberloff and Wilson 1969, Lawton 1983). The effect of patch size on the abundance of animal species occurs on a variety of spatial scales including landscape habitat fragments (de Vries 1994), agricultural fields (Wallin 1985), and isolated patches of vegetation (Bach 1988). Habitat sizes and shapes influence which species of insect accumulate (Rey et al. 1981, Strong 1986).

At the landscape scale, intensification of agriculture in a region often results in a relatively simplified agricultural landscape. Small undisturbed parcels disappear. Large fields covered by the same crop become the dominant features of the landscape. The size of agricultural fields can exceed the migration ability of some natural enemy species, notably, the Carabidae. Intensification of agriculture and increased field size can result in decreased abundance and species diversity of some natural enemy groups on a regional basis (Sustek 1994).

In a comparison of heath habitat fragments in the Netherlands, de Vries (1994) found that Carabidae species that were heath-specialists and had low powers of dispersal were absent in the small habitat fragments. The heath-specialists experienced heath fragments surrounded by inappropriate habitat as “islands”. As the heath habitat fragment declined below 70 hectares, the number of heath-specialist species with low powers of dispersal declined rapidly. Highly mobile carabid species and those species that were able to survive in the habitat surrounding heath fragments did not experience the fragmentation of the landscape as a barrier to colonization. Good flyers did not show a significant regression with patch size. For habitat specialist species with high powers of dispersal, a decline in their presence did not begin until the habitat fragments declined to below 8 hectares.

Wallin (1985) found that the abundance of carabid species was correlated with area at the scale of the agricultural field. The correlation was positive or negative depending on the species. For instance, *Pterostichus melanarius* Illiger was more common in large cereal fields. *Harpalus rufipes* DeGeer was more common in small fields.

The influence of patch size depends to some extent on the surrounding environment. If a patch of plants is surrounded by bare ground, mobile insects tend to move into the plant patch regardless of the type of vegetation. Landing of flea beetles on collards is often higher when collards are grown in patches surrounded by bare ground than when they are surrounded by non-host vegetation (Kareiva 1985). When an insect crosses the outside boundary of a host-plant patch, they are more likely to turn back and "rediscover" their host-plants if the patch is surrounded by bare ground (Bach 1984, 1988).

Specialist herbivorous insects tend to accumulate in large patches of host-plants surrounded by bare ground. Fewer insects collect in small patches of host-plants surrounded by non-host vegetation (Bach 1984, 1988). Flea beetles, for example, have a greater tendency to emigrate from small patches of host-plant surrounded by non-host vegetation. As the flea beetles move around in a small patch of host-plants, they are more likely to cross the boundary between host-plants and the surrounding vegetation. If they land on a non-host plant, they are more likely to fly up, loose contact with their host-plants, and emigrate from the area (Kareiva 1982, 1985, Kareiva and Shigesada 1983)

Another aspect of habitat structural complexity that can have an impact on natural enemy efficiency is fragmentation or patchiness. When golden rod (*Solidago canadensis* L.) was mowed into one long patch or a series of small patches, local explosions of aphid populations (*Uroleucon nigrotuberculatum* L.) occurred in the small patches. The fragmentation of the golden rod patches altered the aphid/coccinelid interaction primarily by altering the foraging movement of the predator *C. septempunctata.* In order to prevent the aphid population from reaching "escape density", the beetle had to efficiently aggregate in areas of high prey density. Patch fragmentation slowed the aggregation response (Kareiva 1987).

TILLAGE AND PESTICIDE REFUGES FOR NATURAL ENEMIES

The presence of patches of undisturbed non-crop habitat increases the abundance and diversity of arthropods in cropping systems (van Emden 1963a, van Emden 1963b, Luff 1966, Lewis 1969b, Pollard 1971, Greenstone 1984, Duelli et al. 1989, Thomas and Wratten 1990, Andow 1991, Kromp and Steinberger 1992, Wyss 1996). If left undisturbed for a significant period of time, non-crop vegetation becomes more genetically and structurally complex. Plant canopies become multi-layered. Shade and relative humidity increase and temperatures moderate. Soil organic matter and debris layers accumulate. Above ground and soil surface microclimates become more varied. Arthropod species diversity increases. The accumulation of diverse prey items attracts and sustains more abundant and more diverse populations of natural enemies (White and Hassall 1994).

Refuges tend to accumulate later succession species that are sensitive to disturbance and absent in annual cropping systems. For example, Nentwig (1988) compared the arthropod communities of strips of meadow vegetation that were either mowed on a regular basis or left undisturbed for 5 years. Over time, woody plant species invaded the undisturbed meadow. Organic debris collected on the soil surface. Habitat diversity increased. New species colonized the undisturbed vegetation. The ratio of phytophagous to predacious insects went down. Over five years in the strip-managed meadow, a shift occurred. The spider population shifted from early colonizer spiders in the family Linyphiidae to later succession spider species in the Lycosidae family. The changing ratio of Linyphiidae and Lycosidae may represent a shift from r-selected species to the K-end of the r-K continuum (Odum 1959).

The distance between a disturbed habitat and sources of immigrating insects affects the time required for colonization. The distance, the mobility of the species, and the time available for colonization have an impact on the diversity of the arthropod species that accumulate (Simberloff and Wilson 1969). The freshly planted agricultural field, however, is very different from an island emerging from the ocean surrounded by a barren sea. The freshly planted field is surrounded by an inhabited landscape. The landscape is rich in potential colonizing species. The distance between the edge of the landscape and the middle of the field is relatively small considering the dispersal capacity of most insects. The time available for colonization, however, is very short (Simberloff 1986).

The lack of undisturbed non-crop vegetation and the simultaneous increase in field size due to mechanization reduces the rapid spring colonization by less mobile soil-dwelling predators, especially in the center of large fields (Potts and Vickerman 1974, Edwards et al. 1979). Seasonal asynchrony can limit the success of natural enemies in depressing pest populations, especially in annual cropping systems (Ehler and Miller 1978). In order to be effective at lowering numbers of crop pests, polyphagous natural enemies must be abundant and present in crops as crop pests arrive in the system. Common generalist predators have their greatest impact on the eggs and small larvae. If natural enemies arrive late in the development of a pest population, many of the larvae have become too large to serve as prey items. The presence of undisturbed habitat may improve the synchrony of natural enemy colonization with the beginning of insect pest invasions (Luff 1987).

Ideally, natural enemies disperse from refuges into the target crop and have an impact on pest species. Coccinellidae and other beneficial insects feeding on aphids of cole crops are sometimes highest adjacent to weedy field borders (van Emden 1963b, 1965). Sorghum inter-planted in cotton was a source of *H. convergens* in the cotton. In this case, the abundance of non-crop aphids as an alternate food source early in the season attracted the Coccinellidae that later moved into the target crop (Fye and Carranza 1972).

Local refuges are especially important for natural enemies with low mobility including the ground beetles (Coleoptera: Carabidae). Many agronomically important species of ground beetles overwinter on farms. Many of the common field inhabiting carabids do not disperse by flight. Residual local populations at the end of the winter determine, in large part, the level of re-colonization of spring planted crops by these predators (Wallin and Ekbom 1988).

When a field is tilled or treated with insecticide in preparation for planting, some species of carabid beetles survive on the edges and re-colonize the field from the edge. Grassy borders surrounding agricultural fields are suitable overwintering sites for many field-inhabiting carabids. Crop-adapted carabid species gradually colonized deeper into the field from hedgerows and other non-crop vegetation on the field boundary. Their ability to switch habitats is an essential adaptation to annual cropping systems (Doane 1981, Desender 1982, Sotherton 1984).

The impact of non-crop vegetation on natural enemies in the vicinity of an agricultural crop is inconsistent, however (Russell 1989, Andow 1991). The presence of natural enemy species in the cropping system as a whole does not guarantee that they will move into the target crop, even when the non-crop vegetation is intimately mixed with the target crop. McIver (1983) found that there were significantly more foliar predators in an alfalfa-collard interplanting than in the collards alone. More predators in the interplanting did not result in more predators on the collards themselves.

Attributes of the natural enemies themselves determine, in part, whether or not they disperse from the refuge to the target crop. Life histories of the natural enemies are varied. Many native Coccinellidae are migratory; they migrate out of the agricultural valleys to higher landscape features where they overwinter. Local modifications in habitat have little impact on the overwintering success of these species (Hodek 1973, Hodek et al. 1993). There are several species of Coccinellidae that were introduced into the Pacific Northwest as biocontrol agents that spend winters on the Valley floor. Local habitat modifications may improve the survival of these exotic species. When the native Coccinellidae arrive back in the valley in the early spring before crops are planted, they aggressively explore the environment. Local refuges may provide habitat structures and alternative prey that attract and arrest them in the vicinity of the future crop. If an area is devoid of suitable prey, they may abandon the site and search other areas (Elliott et al. 1996).

Some natural enemy species are highly directed in their movements. They actively seek areas of prey concentration and make choices based on habitat preferences. Their motivation to move out of the refuge and into the target crop depends, in part, on the relative abundance of food and habitat resources. If their preferred foods are more abundant in the refuge, the refuge may become a sink rather than a source of natural enemies for the target crop (Haslett 1989, Cowgill et al. 1993b).

Several studies have found that large populations of Heteropteran predators on non-crop vegetation may fail to increase predator abundance within the fields (Bugg et al. 1987, Kemp and Barrett 1989, Bigger and Chaney 1998). In some cases, the presence of non-crop vegetation decreases the abundance of natural enemies on the target crop, in much the same way that "trap cropping" serves as a cultural control for crop pests. For example, interplanting with common knotweed did not result in higher abundance of *Geocoris* spp. (Hemiptera: Lygaeidae) or higher predation rates despite the fact that the knotweed harbored large populations of *Geocoris*. Floral resources and alternate prey on the knotweed may act to hold natural enemies and prevent them from foraging in adjacent crop vegetation. Non-crop vegetation served as a sink for these natural enemies. A reduction in plant quality, or a disturbance in the refuge such as the destruction of the flowering borders part way through the growing season may be necessary to motivate predators to move into the crop (Bugg et al. 1987, 1991a, 1991b, Bigger and Chaney 1998). Maturation of non-crop vegetation can force natural enemies to disperse (Fye and Carranza 1972).

Changing crop status affects herbivores as well as their natural enemies. Natural enemy adults may leave alfalfa strips and fly into the adjacent cotton to attack eggs and small larvae of the cabbage looper (Stern et al. 1969). If the alfalfa is not irrigated late in the season, *Lygus* adults also leave the alfalfa and migrate into adjacent cotton fields (Sevacherian and Stern 1974). Alfalfa can act as either a source or a sink for *Lygus* in cotton cropping system depending on the management of the alfalfa.

Many natural enemies have specific habitat preferences. If they are habitat-specialists and ill-adapted to the crop environment their presence in a refuge at the edge of a field may not have any impact on their numbers in the center of the field (Pollard 1968a, 1968b, Edwards et al. 1979, Wallin 1985, Thomas et al. 1992). Many of the Carabidae species present in field borders are rarely caught in the cultivated areas. The carabid species that live in these non-cultivated areas probably do not move in great numbers outside the areas and are not likely to have an impact on the pest populations present in agricultural fields (Boivin and Hance 1994).

Natural areas with stable woody structures, a variety of flowering structures, and more woody organic debris on the soil surface support spiders that are uncommon in annual cropping systems. Many of these spiders are in web building families (Araneae, Tetragnathidae) but they also include visual pursuit families (Salticidae, Lycosidae, Thomisidae). These species generally will not invade vegetable crops. Many of the spider species that occur in vegetable cropping systems are not present in adjacent natural areas (Bishop 1990, Bishop and Riechert 1990). The spiders that inhabit vegetable plantings are highly mobile in the spring. They balloon into cultivated areas in large numbers, and colonize newly planted fields from a distance. Local refuges may not be relevant sources of spiders adaptable to annual cropping systems (Riechert 1974, Riechert and Lockley 1984).

Natural enemy movement is responsible for much of the variation in the source and sink effects of non-crop vegetation (Corbett 1998). While some species direct their movements, many natural enemy species colonize the landscape by mass aerial dispersal (House and Stinner 1983) or by terrestrial processes similar to random diffusion (Kareiva and Shigesada 1983, Kareiva 1990). Spiders ballooning across the landscape, for example, have no control over their landing sites (Thomas et al. 1990, Ehmann 1994, Weyman et al. 1994). Carabid beetles appear to forage randomly (Baars 1979, Chiverton 1988, Gruttke 1994, Petit 1994). The rate of diffusion of these species is determined to a large extent by mobility. Natural enemy mobility varies a great deal; relative mobility may have a greater impact on colonization of crops than local changes in habitat structures (Corbett 1998, Freeman Long et al. 1998).

A predatory mite which has very low mobility may disperse as little as 1 sq meter per day (Corbett and Plant 1993). Parasitic wasps and hover flies (Syrphidae) are highly mobile (Freeman Long et al. 1998). A highly mobile parasitoid may have a diffusion rate on the order of 100 sq meters per day (Corbett 1998). Ladybeetles (van Emden 1965, Kareiva and Odell 1987) and ground beetles (Coombes and Sotherton 1986, Gordon and McKinlay 1986, Wallin and Ekbom 1988, Thomas et al. 1991) are probably intermediate in mobility between mites and wasps.

Given this variability, it is difficult to make any generalizations about the appropriate distances between refuges and the target crop. In general, non-crop vegetation has an impact on natural enemy density 10 to 100 meters from a source. Slowly dispersing mites, however, are only enhanced within a few meters of a refuge strip. Parasitic wasps are so highly mobile that it is difficult to detect the impact of a refuge on their distribution. Relatively small differences in mobility result in large differences in the spatial extent of the enhancement. Non-crop refuges will have their most dramatic effect as either a source or a sink for natural enemies that are not highly mobile (Freeman Long et al. 1998).

Highly mobile insects may colonize crops rapidly on spatial scales that make the presence of local refuges irrelevant (Dempster and Coaker 1974, Hoffmann et al. 1997). Coombes and Sotherton (1986) found that rove beetles (Staphylinidae) have different patterns of dispersal than the carabid beetles. The rove beetle species in his study migrated by flight. They reached peak numbers at the same time at all distances along pitfall transects. No effect of the field boundary on rove beetle dispersal was found at the spatial and temporal scales of the agricultural fields in the study.

On the other hand, blackberry patches that grow in wild areas along creeks in vine-growing regions serve as sources of parasitoids in vineyards located five kilometers away (Doutt et al. 1966, Doutt and Nakata 1973). The density of parasitic wasp species in a lettuce field was higher near strips of flowering alyssum. The effect could be detected over a distance of 11 meters in each direction or about

33 meters total. Aphid populations in the lettuce near the strips were reduced (Chaney 1998).

The spatial scale of natural enemy enhancement should influence cropping system design. Spatial scale should be considered when deciding the ratio of crop to non-crop vegetation and the extent to which they are interspersed (Corbett 1998). Fye and Carranza (1972) argued that high mobility should result in enhancement of natural enemies even with large distance between strips of interplanted non-crop vegetation. Others argue that fine grained interspersion of crop and alternate vegetation is necessary to retain highly mobile natural enemies within the system (Pollard 1971, Dempster and Coaker 1974, Perrin 1975, Sheehan 1986)

The timing of natural enemy colonization of non-crop refuges relative to the timing of the establishment of the target crop may influence the propensity of the natural enemy to invade the crop (Corbett and Plant 1993, Corbett and Rosenheim 1996, Corbett 1998). If the non-crop vegetation is established in the fall and the natural enemy overwinters there, the insect may disperse into the target crop according to its relative mobility. The refuge is more likely to serve as a source of the species in the adjacent crop. If a natural enemy does not overwinter on site, but instead, colonizes the cropping system from external sources in the spring, the non-crop vegetation may distract the natural enemy from the crop. The refuge may be more attractive than the crop. Perrin (1975) observed that perennial stinging nettle which had abundant aphids reduced the foraging of Coccinellidae on adjacent crop vegetation.

If a natural enemy overwinters in non-crop vegetation and the non-crop vegetation provides preferred habitat and food resource, enhancement of natural enemies in the target crop may occur at low levels or not at all (Corbett 1998). In some cases, non-crop vegetation can serve as a natural enemy sink regardless of when it is established. The minute pirate bug, *Orius insidiosus* (Say), was present in strips of non-crop vegetation prior to the planting of soybeans, but still failed to move into the soybean planting during the growing season. *O. insidiosus* may have preferred the non-crop habitat. It may have been attracted to prey abundant in the non-crop vegetation. In either case, the non-crop vegetation did not serve as a source of natural enemies for the target crop (Kemp and Barrett 1989).

The timing of invasion and the manner in which insect pests colonize agricultural fields has a bearing on whether resident natural enemies will have any measurable effect. Mass aerial migration can result in high densities of crop pests establishing suddenly in agricultural fields. In some cases, resident natural enemy populations are overwhelmed by the mass invasion of crop pests (Price 1984, Price and Waldbauer 1994).

Chambers et al. (1982) studied ten plantings of winter wheat focusing on the distribution of aphids in the middle versus the edge of the field. Under specific circumstances, aphid populations were depressed on the field edges. The depression in the populations was due to natural enemy pressure, which was greater on the field edges. The distribution of the aphids depended on whether the aphids (*Sitobion avenae* F.) overwintered on site or invaded the planting during the spring.

If the winter was mild, the source of the aphids in the wheat was primarily from surviving colonies that had overwintered in the crop. In this case, the aphid populations in the early spring tended to be higher in the middle of the field than on the edges of the field. The difference in the spatial distribution of the aphid population was attributed to the activity of natural enemies dispersing from non-crop vegetation on the field edges. After a hard winter, the source of the aphids in the developing wheat was from winged aphids dispersing aerially in mass during the late spring. In this case, there was no edge effect associated with predators on the field edges. There were no differences between aphid population densities in the middle and on the edges of the field (Chambers et al. 1982). In cases where there is an edge effect on prey population density associated with natural enemies, the effect is short lived. Later in the season, the natural enemies disperse across the field (Boivin and Hance 1994).

RELAY STRIP-CROPPING

Relay strip-cropping of broccoli integrates several aspects of vegetation management that should have a significant impact on the arthropods associated with broccoli. For example, the presence of under-story vegetation changes the visual contrast of the broccoli with its surroundings. Aphids are sensitive to visual contrast and background color; the understory vegetation may reduce the rate at which the winged aphids colonize the broccoli grown in the relay system (A'Brook 1973, Tukahirwa and Coaker 1982, Altieri and Schmidt 1987, Costello and Altieri 1995).

In a polyculture, a crucifer-specialist has a high probability of encountering a non-host plant. In many insects, the olfactory and gustatory cues of a non-host plant stimulate movements that result in the departure of the insects from a patch of plants even though the patch contain their host-plant. The presence of non-host vegetation growing around the broccoli should stimulate emigration by *P. cruciferea*, and reduced beetle density in the relay broccoli compared to the broccoli monoculture (Feeny et al. 1970, Tahvanainen and Root 1972, Cromartie 1975, Kareiva 1985, Altieri and Schmidt 1986, Bergelson and Kareiva 1987, Garcia and Altieri 1992).

I did not expect variation in stand purity to have an impact on the distribution of *P. rapae*. This butterfly appears to avoid concentrations of its host-plants during oviposition, scattering eggs across a landscape (Cromartie 1975, Root and Kareiva 1984, Vail et al. 1991, Frenzel and Brandl 1998). If in variation occurs in the larval density of *P. rapae* in the relay cropping system compared to the monoculture, it could be attributed to differences in mortality in the two cropping systems. One source of variable mortality would be differences in the density of natural enemies in the two systems.

The presence of a greater diversity of plants and associated insects in the relay strip-cropping system may result in a greater diversity of generalist natural enemies compared to the monoculture broccoli. Increased plant diversity may increase the abundance of generalist natural enemies by providing alternative prey, supplemental foods (nectar, pollen, aphid honeydew), and appropriate habitats. Specialist natural enemies, however, may be affected differently by vegetation diversification. The effectiveness of specialist natural enemies may be inhibited by the increased complexity of their foraging arena in the polyculture (Sheehan 1986). Futher, if broccoli pests colonize the monoculture at a faster rate than the broccoli grown in the relay, the specialist natural enemies may aggregate in the monoculture where their prey is concentrated.

Undisturbed vegetation in the vicinity of the annual planting of broccoli may conserve beneficial species that are sensitive to disturbance. These species would otherwise be absent during the early stages of colonization of the broccoli by insect pests. But non-crop vegetation can serve as either a source or a sink for natural enemies (Perrin 1975, Bugg et al. 1987, Corbett and Rosenheim 1996). The life history of the natural enemy, its relative mobility, and the timing of establishment of the non-crop vegetation influence whether the refuge will enhance the number of natural enemies on the target crop. If the natural enemy is highly mobile, one may not be able to detect the effect of non-crop vegetation on its dispersal at the spatial scale of this experiment. Futher, the size of the plots in these experiments may over-emphasize the impact of the refuge strips on natural enemies with low mobility (Corbett and Plant 1993, Corbett 1998).

Each species of herbivore and natural enemy has a unique set of attributes that sensitize the arthropod to various aspects of the cropping system. In some cases, a change in vegetation management results in more than one effect. If the multiple effects operate in opposite directions, they may cancel each other out. At the end of the season the net effect may be neutral (Read et al. 1970).

In the chapters two through five, I examined the impact of relay strip-cropping on the abundance and diversity of ground beetles (Coleoptera: Carabidae), spiders (Araneae), harvestmen (Opiliones: Phalangiidae), lady beetles (Coleoptera: Coccinellidae), and damsel bugs (Heteroptera: Nabidae). These natural enemies vary in their life cycles, mobility, and propensity to switch habitats and prey items. I expected each group to vary in their response to polyculture and the presence of a tillage and pesticide refuge.

In chapter six, I examined the impact of relay strip-cropping on insect pests of broccoli. The combination of variable herbivore colonization rates plus variable mortality associated with the density of their natural enemies should result in differences in the final population densities of these insect pests in the broccoli relay compared to the broccoli monoculture.

OBJECTIVES

The impact of polyculture on arthropod populations has been evaluated in hundreds of studies around the world for several decades. Strip-management has been advocated as a tactic for manipulating both insect pests and their natural enemies since the 1960's. This is the first study of the impact of relay strip-cropping on arthropods; the cropping system that combines polyculture and strip-management.

It has generally been found that polycultures support fewer herbivores than comparable monocultures. The mechanisms of the "polyculture effect" have been carefully studied. Polyculture interferes with the colonization of the target crop by herbivores. Polyculture generaly support higher densities of natural enemies than monoculture. Still, polyculture has not been widely adopted by commercial farmers in the United States or western Europe. Under-sowing helps to overcome some of the practical constraints on the adoption of polyculture.

Strips of undisturbed crop or non-crop vegetation serve as either a source or a sink for crop pests and their natural enemies. Strip-management also has not been widely adopted by commercial farmers. Concerns about soil and water conservation have prompted a renewed interest in cover-crops and buffer-strips. If these environmental concerns prompt farmers to overcome the practical constraints on the use of strip-management, they may also see some benefits to their pest management systems associated with the presence of tillage and pesticide refuges that conserve natural enemies in the agroecosystem.

The combination of polyculture and strip-management will influence arthropod populations in many different and sometimes opposite ways. The specific objectives of this project were:

A. To determine if broccoli grown in a relay strip-cropping system is colonized by a greater number and diversity of generalist predators compared to broccoli monoculture.

B. To determine if broccoli grown in a relay strip-cropping system is colonized by fewer herbivorous insects than a broccoli monoculture.

C. To determine if the net effects of polyculture and strip-management on herbivore colonization and natural enemy induced mortality results in reduced herbivore contamination of the harvested broccoli.

CHAPTER 2

IMPACT OF RELAY STRIP-CROPPING ON GROUND BEETLES (COLEOPTERA: CARABIDAE) IN BROCCOLI

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ABSTRACT

During the growing seasons of 1994-1996, 1,262 ground beetles (Coleoptera: Carabidae) representing 21 species were captured with pitfall trapping in a study comparing relay strip-cropping to clean-till planting of broccoli. Relay strip-cropping combines under-sowing and strip-management. A cover-crop seed mixture containing *Avena sativa* L. var. "Monida", *Vicia sativa* L., *Trifolium pratense* L., *Lolium multiflorum* Lam., and *Fagopyrum esculentum* Moench was broadcast over established broccoli 32 days after planting. The broccoli was planted, under-sown, and harvested in sections alternating with strips of undisturbed cover-crop. The abundance and diversity of ground beetles was higher in the relay strip-cropping system than in the clean-till broccoli. *Pterostichus melanarius* Illiger, *Anisodactylus binotatus* F., *Bradycellus congener* LeConte, and *Amara* species represented 87% of the total beetles captured. *Anisodactylus californicus* Dejean, *Anisodactylus rusticus* (Say), *Anisodactylus similis* LeConte, *Clivina fossor* L., *Harpalus affinis* Schrank, and *Pterostichus algidus* LeConte increased in abundance over the three-year period in the relay. *Agonum suturale* Say, *B. congener*, and the *Amara* species decreased in abundance. *B. congener* was trapped more often in the clean-till cropping system. *A. binotatus, P. algidus, A. californicus, A. similis, Loricera foveata* LeConte, *Calosoma cancellatum* Eschscholtz, and the *Amara* species were strongly associated with the cover-crop strips but were uncommon in the broccoli. *P. melanarius* readily dispersed from the cover-crop strips into the broccoli. Most of the *P. melanarius* beetles marked and released in cover-crop strips during the 1997 growing season were recaptured within 15 m of the strips.

INTRODUCTION

Ground beetles (Coleoptera: Carabidae) are an important component of the generalist predator assemblage that dwells on the soil surface. Ground beetles are not as numerous as spiders in agricultural systems but, when the relative biomass of spiders and carabids is considered, the two groups are comparable (Sunderland 1975, Nentwig 1988, Lovei and Sunderland 1996). Biomass is an important measure of the potential impact of carabids in the agroecosystem; common field-dwelling carabids can eat up to four times their body weight in a day (Thiele 1977).

Fecundity among ground beetles ranges from five to over 300 eggs per female in some species. In medium-sized carabid species including *Pterostichus melanarius* Illiger, female beetles develop 30 to 40 eggs per season (Rivard 1964).

Autumn-breeding, larval-overwintering carabids generally have one peak of activity in mid-summer. The peak corresponds with the overlap between second-year adults and the emergence and reproduction of the current generation (Kirk 1973, Wallin 1986, Basedow 1994). In a mild winter, as many as 30% of the *P. melanarius* beetles that reproduced during the summer can survive a second winter. Spring-breeding, adult-overwintering, Carabidae including *Anisodactylus binotatus* F. usually have two peaks of seasonal activity. One peak occurs in the early spring followed by a dip in the summer while the summer larvae develop. The summer dip in activity is followed by a second peak in the fall as the new generation of adults emerge and prepare to overwinter (Wallin 1985). Spring-breeding carabid species are active into the fall. They hibernate as adults, reproduce in the early spring, and must experience winter hibernation to become sexually mature. After reproduction, most of the beetles die. Very few spring-breeding beetles survive for a second egg-laying season (Thiele 1977). Thus, carabids as a group are active as adults or larvae all year round. Even in the coldest season, there are species of carabid adults and larvae foraging for prey. In the early spring, the potential of carabids as pest control agents is greatest; carabids are present when pest populations are just becoming established. Carabids are present before many of the other natural enemies have arrived or become active (Coombes and Sotherton 1986, Wratten and van Emden 1995).

Even though carabid beetles are primarily ground predators, they also have an impact on foliar insects. Many foliar insects spend significant periods of time on the soil surface where they are preyed upon by carabid beetles (Chiverton 1987b, Hagley and Allen 1990, Winder 1990, Riddick 1994, Wallin and Ekbom 1994). Exclusion experiments show that removal of ground-dwelling generalist predators often leads to increased aphid densities (Edwards et al. 1979, Sunderland 1980, Chambers et al. 1982, Coombes and Sotherton 1986, Chiverton 1986, Chiverton 1987b, Chiverton 1987a). Serological techniques have shown that *P. melanarius* feeds on the cabbage aphid, *Brevicoryne brassicae* L. (McIver 1983).

Carabid abundance and community structure is influenced to some extent by crop type (Thiele 1977, Luff 1987) and crop rotation (Lovei 1984). Crop type influences habitat structure, vegetative cover, food alternatives and availability, and specific microclimate conditions that can influence carabid density and diversity (Fadl et al. 1996). Carabid beetles are responsive to microclimate. Most Carabidae are warmth loving. Temperature preferences influence whether carabid species are associated with the forest, meadow, or open field (Thiele 1977). Carabids have relative humidity preferences. Dryness has a significant negative impact on the longevity of most carabid species. In general, carabids from moist habitats prefer higher humidity in laboratory tests. Carabids from dry habitats prefer lower humidity in laboratory tests. Forest-dwelling species seek out moist and shady habitats (Thiele 1977, Wallin 1985).

Several workers have found there can be higher carabid activity in mixed vegetation cropping systems than in simple cropping systems (Dempster and Coaker 1974, Speight and Lawton 1976, Ryan et al. 1980, Tukahirwa and Coaker 1982, Brust et al. 1986, Perfecto et al. 1986, Nentwig 1989, Thomas and Wratten 1990, Tonhasca 1993, Booij 1994). In some cases, however, changes in vegetation diversity have no observable effect on carabid activity (Purvis and Curry 1984).

The habitats available to carabid beetles in most farming landscapes include remnant wooded areas, riparian areas, hedge and fencerows of various age structures and spatial dimensions, undisturbed meadow areas, and open field grown crops. Some open-field species use the forest or hedgerow environment at certain times of the year (Sotherton 1985, Wallin 1986). Most carabid species that are associated with the moist and shady environments of the forest or riparian areas, however, do not venture into agricultural fields (Thiele 1977, Lovei and Sunderland 1996). They are habitat-specialists.

Given their general lack of prey specificity, carabid response to microclimate may be a more important influence on their distribution than their response to prey dispersion (Wishart et al. 1956, Wallin 1986). It may be habitat that draws these predators into contact with crop pests. Beetles respond to changes in microclimate associated with a given crop (Rivard 1965, 1966, Varis et al. 1984), the density of the vegetation (Perfecto et al. 1986) and stand purity (Dempster and Coaker 1974, Speight and Lawton 1976, Ryan et al. 1980, Tukahirwa and Coaker 1982, Barney and Pass 1986).

The impact of crop type on Carabidae is, in part, a reflection of tillage practices associated with the rotation. The timing of tillage in relationship to the phenology of carabid species determines, in large part, the impact of tillage on the success of the species in a given cropping system (Wallin 1985, Hance et al. 1990). Tillage operations in the temperate areas of the Northern Hemisphere tend to occur primarily in the spring. As a result, the dominant carabid species in the annual cropping systems of North America and Europe tend to overwinter as larvae, emerge as adults in the late spring, and breed in the late summer and fall. The best example of this is *P. melanarius*. It may be the most common carabid species in agricultural systems in the Northern Hemisphere (Thiele 1977, Lovei 1984).

A corn/wheat rotation will generally support fewer numbers of carabid beetles than continuous corn. Winter wheat is planted in the fall. The fall disturbance interferes with breeding activities of the autumn breeders. In the absence of weeds or other plant cover, wheat stubble provides little cover. The lack of vegetative cover reduces overwinter survival of adult beetles. Weed-free stubble is unattractive to spring-breeding species (Lovei 1984). There are usually less adult overwintering, spring-breeding carabids in root crops than in winter grains (Thiele 1977). Root crops are generally cultivated in the spring, when spring-breeding carabids are vulnerable to disturbances. Larval-overwintering carabid species are depressed by spring tillage compared to autumn tillage. The larvae, pupae, and emerging adults are sensitive to disturbance in the spring (Hance et al. 1990).

Primary tillage with a mold board plow in the fall can reduce the survival of species that overwinter in the middle of the field (Polis et al. 1989). Adult overwintering, spring-active carabid species are more negatively impacted by fall tillage than larval overwintering species. Many crop-adapted larval overwintering species emigrate from agricultural fields after harvest. They seek refuge on the field edges where they lay their eggs and thus escape the effects of the fall tillage (Wallin 1985). After fall planting there is usually a period in the spring when the field middle is somewhat empty in overwinter crops (Polis et al. 1989, Niemela 1993). The empty middles are due to the fall tillage operations. Invading beetles recruited from the field edges rapidly colonize the middle. Regardless of tillage regime, tillage refuges within the field and on the field boundary can result in increasing carabid abundance over time (Lys 1994, Lys and Netwig 1994, Lys et al. 1994).

Many types of agrochemicals have an adverse effect on carabid beetles (Jepson and Thacker 1990). Insecticides may have a greater impact on carabid populations than tillage (Thiele 1977). Insecticides can have direct toxic effects on the abundance of carabid beetles (Luff 1987). Chlorpyrifos applied in the autumn for insect control in pastures depleted carabid populations for more than one season (Asteraki et al. 1992). Insecticides can also have indirect effects. By reducing the prey available, increased beetle activity is stimulated by their search for scarce prey (Chiverton 1984). Herbicides have an indirect influence on carabids by changing the vegetation cover. Even nitrogen fertilizer caused *P. melanarius* to avoid plots with the highest concentrations and accumulated in non-fertilized control plots (Thiele 1977).

In this chapter, I examined the impact of relay strip-cropping on the abundance and diversity of ground beetles in broccoli. Relay strip-cropping combines two vegetation management tactics, under-sowing and strip-management. Under-sowing should create a more favorable habitat for Carabidae within the crop by providing soil cover between the crop rows. The polyculture should support a great number and variety of potential prey items for the foraging beetles. Strip-management assures that a tillage and pesticide refuge is present at all times in the cropping system.

In a relay strip-cropping system during the winter, undisturbed crop stubble and cover-crop provide habitat for adult-overwintering carabid species. During the early spring and fall when carabid species are searching for oviposition and overwintering sites, there is undisturbed vegetation. Availability of undisturbed ground cover should have both short and long term impacts on the carabid assemblage.

Under-sowing results in soil that is covered with vegetation prior to canopy closure. The presence of the ground cover moderates the environment and may lead to earlier colonization of the broccoli by Carabidae that are sensitive to microclimate. Under-sowing results in a mixture of plant species. The residual strips at the end of the winter are bound to be weedy. Mixed stands generally support a greater diversity of insects than monoculture. These potential prey items should attract and support a greater variety of carabid species than clean-till cropping systems (Zangger 1994).

Strip-management may conserve Carabidae that are sensitive to disturbance and that are not highly mobile. Following harvest, strips of cover-crop and broccoli stubble are left undisturbed until the following planting season. The undisturbed strips should attract fall-breeding larval-overwintering carabids that search for oviposition sites in the late summer. The undisturbed strips should be equally attractive to adult-overwintering carabid species that emerge from their puparia in the fall and seek out vegetation.

The following spring, only a portion of the winter cover-crop in the relay strip-cropping system is disturbed in preparation for the early broccoli planting. Larval overwintering carabid species will have an opportunity to complete their life cycle, pupate, and emerge as adults from the cover-crop areas. Spring tillage in clean-till cropping systems disrupts and probably kills many overwintering species before they emerge from the pupal stage. In the early spring, adult overwintering beetles are present next to developing plantings of broccoli. Their proximity should speed the colonization of the broccoli by this group as the females emerge from their winter refuge in the cover-crop and seek oviposition sites.

The residual strips should provide a steady source of prey for Carabidae over the winter, in the early spring, and between plantings. The stability of the food supply in the relay is markedly different than in monoculture where tillage, planting, pesticide applications, harvest, and stubble incorporation are constantly removing food resources from the cropping system. The constant supply of prey in the relay strips should increase the number of carabid beetles in the area over time. For a detailed review of the Carabidae literature, see Appendix A.

MATERIALS AND METHODS

Site description

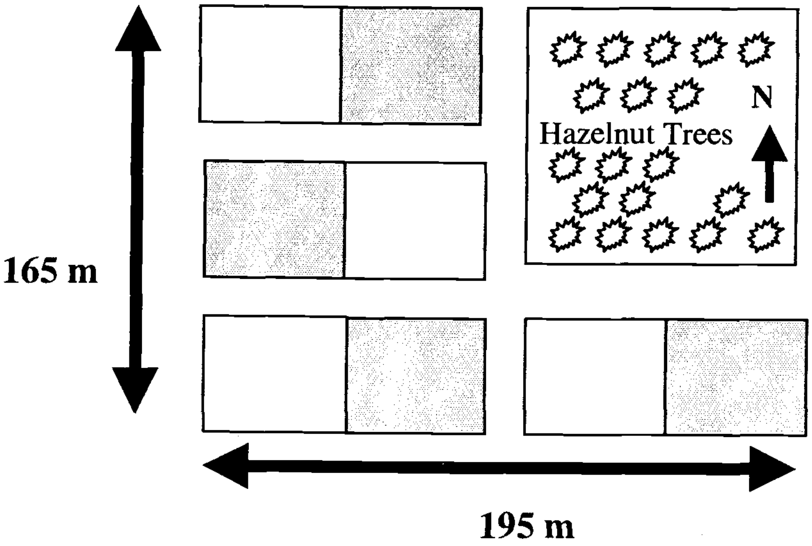
All of the experiments in this study were conducted from 1994 to 1997 at the Oregon State University Vegetable Research Farm near Corvallis, Oregon, approximately 0.4 km from the Willamette River. The soil at the experimental site is a Chehalis silty clay loam. The field had been in tall fescue (*Festuca arundinaceae* Schreb.) from 1990 to 1993. An alfalfa field bordered the experimental area to the north, hazelnut orchards bordered to the east and south, and a gravel road and building complex bordered the field to the west.

Relay Strip-Cropping Experiments 1994-1996

In the fall of 1993, 1.6 ha were sub-soiled to 45 cm, moldboard plowed to 35 cm, and roto-tilled. The area was divided into four blocks that were each 90 m long and 45 m wide, approximately 0.4 ha each. Either the west or east one half of each block was planted with cover-crop on September 24, 1993. The east and west sides of each block were maintained in separate cropping systems until the end of the 1997 growing season (Figure 2.1). The cover-crop side of each block was maintained in a continuous relay strip-cropping system, which included a winter cover-crop during each year of the experiment. The winter-fallow side of each block was maintained in a clean-till cropping system that included winter-fallow period during each year of the experiment. Hereafter, the two sides will be called broccoli relay and broccoli clean-till respectively.

In the spring, 15-m bare-ground alleys were established by disking around the perimeter of each block. Four rows of sweet corn (0.9 m between each row) were planted down the middle of the alleys between each block. Each block was then subdivided north to south with a 15-m bare-ground alley separating the clean-till and relay strip-cropping systems. The establishment of the alleys resulted in cropping system plots that were 30 m square surrounded by 15 m of bare ground and separated from the neighboring block by 4 rows of sweet corn.

Figure 2.1 Relay Strip-cropping Experiment Winter Cover-Crop vs Fallow



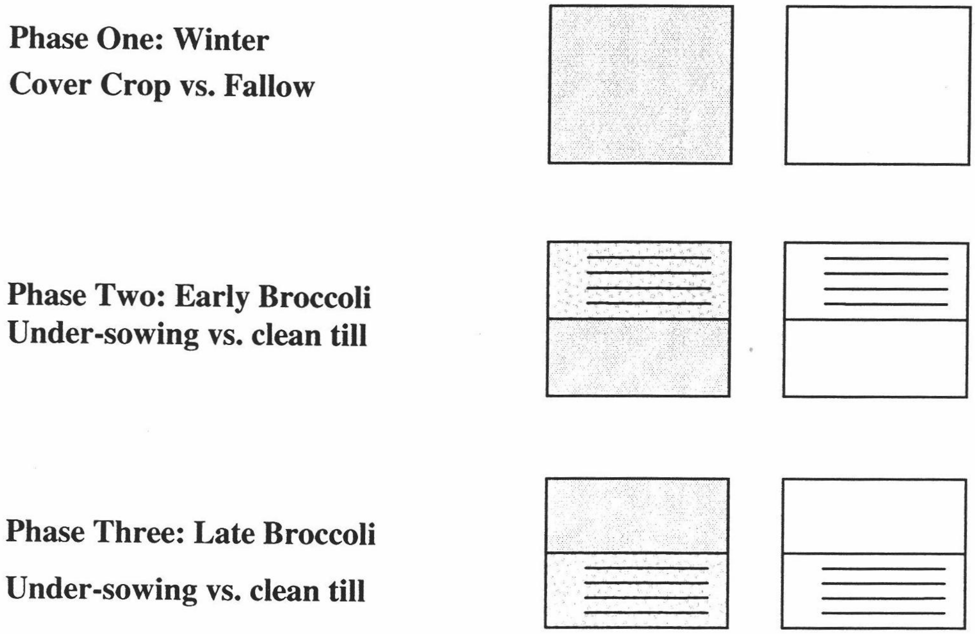
Each cropping system plot was further subdivided, into early and late broccoli plantings. Each spring, the north one-half of each block was mowed, plowed, roto-tilled, and planted from east to west across the winter-fallow and winter cover-crop sides of each blocks. The resulting plots of early broccoli plantings were 15 m wide by 30 m long growing next comparable size strips of either undisturbed cover-crop or bare ground. Four to five weeks after planting, the relay strip-cropped broccoli was under-sown with cover-crop seed while the clean-till broccoli was kept free of weeds. After harvest, the broccoli stubble in the clean-till systems was immediately incorporated into the soil with disking. Just prior to harvest of the early broccoli planting, the south one half of each block was mowed, plowed, roto-tilled and planted. The resulting plots were 15 by 30 m strips of late broccoli growing next to comparable sized strips of either cover-crop plus broccoli stubble or bare ground (Figure 2.2). Later, the broccoli relay was under-sown. After harvest, the late clean-till broccoli was disked into the soil.

At the end of the growing season, cover-crop and broccoli stubble in the broccoli relay were left undisturbed until the following growing season, and cover-crop seed was planted in the alleys. The fallow areas were kept free of weeds with fall cultivation and glyphosphate herbicide applied at a rate of 2.3 liters per hectare as needed (Roundup Ultra®, 41% glyphosphate).

On May 5, 1994 (early planting) and August 16, 1994 (late planting), the broccoli variety "Gem" was planted with a 4 row vacuum planter (Gasparto Inc.) in rows that were 0.9 m apart. Fertilizer 12-29-10 was banded at planting at a rate of 515 kg per hectare (25 kg N, 60 kg P_2O_5, 21 kg K_2O, 17 kg S per hectare). At planting or shortly there after, a 15-cm band of chlorpyrifos (0.04 kg active ingredient per 305 m of row) and DCPA (10 kg active ingredient per hectare in the band) was applied over the row. Carbaryl was applied at a rate of 1.1 kg per hectare for flea beetle control on 5/25/94 (early planting) and 8/24/94 (late planting).

Weed control in the clean-till broccoli and in the relay broccoli up to the point of under-sowing was accomplished with a combination of DCPA applied at planting, mechanical cultivation, and hand hoeing as needed. Approximately three weeks after planting, the broccoli was thinned to approximately one seedling every 30 cm. In row weeds were hoed during the same operation. Four weeks after planting, an additional 112 kg/ha nitrogen in the form of urea was broadcast over the broccoli and watered in. Four to five weeks after planting on 6/8/94 and 9/17/94 respectively, cover-crop seed was broadcast over the top of the broccoli and incorporated into the soil with mechanical cultivation. The cover-crop seed mixture contained 30 kg of oats (*Avena sativa* L. var. "Monida"), 20 kg common

Figure 2.2 Three Phases of the Relay Strip-cropping System for Broccoli



vetch (*Vicia sativa* L.), and 5 kg each of red clover (*Trifolium pratense* L.), annual ryegrass (*Lolium multiflorum* Lam.), and buckwheat (*Fagopyrum esculentum* Moench) and was planted at a rate of 65 kg/ha. The cover-crop mixture and rate were used for the all relay strip-cropping experiments.

The components of the cover-crop seed mixture were chosen for the following attributes. The Monida oat variety establishes early and provides soil cover prior to fall rains. The oat variety has a tendency to partially winterkill, limiting competition between the oat and the vetch. Common vetch grows slowly in the fall but if it is allowed to mature in the spring, it can fix significant amounts of biological nitrogen that has value in the cropping system. Common vetch has extra-floral nectar sources, small glands on the stipules located at the base of each compound leaf, that supply nectar to natural enemies of insect pests including parasitic wasps (Bugg et al. 1989) that do not have access to many floral nectar sources and Coccinellidae that need carbohydrate sources early in the spring prior to the build up of their prey populations (Ewing 1913). Clover supports a wide variety of insects that serve as prey for natural enemies. Annual ryegrass can establish in conditions where many other cover-crop species fail because of competition from the vegetable crop. Buckwheat flowers shortly after planting and provides an additional source of nectar and pollen for natural enemies (Cowgill et al. 1993, Wratten and van Emden 1995).

Plots were harvested on 7/22/94 and 11/2/94 respectively. All mature buds were cut from 3 m of row in each of four areas of around each plot (total of 12 m of row), examined for aphid contamination, trimmed to a length of 15 cm, and weighed.

In 1995 and 1996, plot dimensions and the cropping systems were identical to 1994. The broccoli variety, however, was changed to "Excelsior" and the broccoli was established by transplanting. This reflected changes in cultural practices that occurred in the Oregon's processed vegetable industry in the mid 1990s. Prior to planting, the soil was prepared, rows were marked at 0.9 m apart, and fertilizer was banded at the same rate as in 1994 using the same planter but without planting any seed. Prior to transplanting, the herbicide oxyfluorfen was applied to the soil surface at a rate of 0.56 kg/ha. Broccoli plants were transplanted into the marked rows with a single row mechanical transplanter with 40 cm between plants in the row. Early and late planting dates were 5/19/95, 7/20/95, 5/28/96, and 7/23/96 respectively. At planting or shortly thereafter, a 15-cm band of chlorpyrifos (0.04 kg active ingredient per 305 m of row) was applied over the row. Carbaryl was applied on the broccoli for flea beetle control at a rate of 1.1 kg/ha in 1995 on 5/30/95 (early planting), 8/3/95 (late planting). In 1996, chlorpyrifos applied at planting provided sufficient flea beetle control; no carbaryl was applied. Four weeks after planting, an additional 112 kg/ha of nitrogen in the form of urea was broadcast over the broccoli and watered in. Four to five weeks after planting on 6/21/95, 8/21/95, 7/1/96, and 8/26/96 cover-crop seed was broadcast over the top of the broccoli and incorporated into the soil with mechanical cultivation. Both the relay broccoli and the clean-till broccoli were cultivated at this time.

Plots were harvested on 7/31/95, 10/3/95, 8/8/96, and 10/2/96. All mature buds were cut from 3 m of row in each of four central areas of each plot (total of 12 m of row), trimmed to a length of 15 cm, and weighed. Buds were then taken to the laboratory where they were dissected and examined for contaminants. All arthropod contaminants were collected, stored in alcohol, and later sorted and counted. Carabidae species with the exception of A. *suterale* (Liebherr 1994) were identified according to the keys of Lindroth (1961-69).

Pitfall trap sampling

Pitfall trapping for each broccoli crop in the relay experiments began after the final cultivation following under-sowing four to five weeks after planting. Thirty-six sampling sites were flagged in each block with nine sites in each of the sampling areas (relay broccoli, clean-till broccoli, cover-crop, and bare ground). The nine sampling points were placed in every third row along diagonal lines from corner to corner defining an "X" centered in each sampling area. A total of one hundred and forty four pitfall samples were taken each sampling period.

Every two weeks, pitfalls were opened for 48 hours, beetles were collected and stored in alcohol for later sorting and counting, and the pitfalls were then closed. Pitfalls consisted of plastic cups that were 10 cm in diameter and 4.5 cm deep. Cups were sunk to ground level and partially filled with soapy water. Pitfalls were placed in the rows between broccoli plants.

Mark, Release, and Recapture Experiment 1997

In spring of 1997, the north half of each block was plowed, disked, and roto-tilled. On June 11, 1997 the entire field including the alleys was also planted to sweet corn except for the four 15 by 30 m strips of cover-crop in the relay strip-cropping side of each block. Fertilizer 12-29-10 was banded at planting at a rate of 515 kilograms per hectare (25 kg N, 60 kg P_2O_5, 21 kg K_2O, 17 kg S per hectare). Immediately after planting, atrazine and metolachlor herbicide (both at 2.2 kg/ha) were applied over the corn and the field was irrigated. Four weeks after planting, an additional 112 kg/ha of nitrogen in the form of urea was broadcast over the corn and watered in. The corn was kept weed free for the entire growing season with hand hoeing as needed. The experiment was confined to a single corn planting with no relay and no cover-crop under-sown in the corn.

To determine the distance that marked ground beetles dispersed from the cover-crop strips, a 3 by 3 m grid of 200 pitfalls was established which encompassed most of the experimental field. Pitfalls were placed in the rows between corn plants, sunk to ground level, and partially filled with soapy water. Three large dry pitfalls 14 cm in diameter and 19 cm deep were set up in each cover-crop strip. The dry pitfalls were partially filled with loose organic mater and covered with a square of plywood supported 3 cm above the rim of the pitfall on wooden pegs, which prevented them from collecting rain or irrigation water.

From June 9 to August 4, beetles were collected on a weekly basis from the dry pitfalls, brought to the laboratory, and marked on the elytra with a small high-speed drill and sanding attachment. Small scratch marks on various positions of the elytra allowed us to determine the source of recaptured beetles. *P. melanarius* beetles were marked and released in the cover-crop strips where they had been captured. From June 16th to August 25th the wet pitfalls making up the pitfall grid were opened on a weekly basis for 48 hours. Beetles from the grid pitfalls were collected and the pitfalls were closed. The corn was harvested on September 2, 1997. No yield data was taken.

Statistical Methods

The square root transformation consistently improved the stability of the variance of the means of the arthropod data and was applied to the data before statistical analysis. For each insect and planting period, treatments were compared on individual dates using the strip-plot ANOVA procedure (SAS version 6.12, SAS Institute Inc.). If the variance/covariance structure was appropriate, the data for each insect were also analyzed across all sampling dates within each planting period. The variance/covariance matrix for each data set was analyzed to determine if it was compound symmetric or met the Huynh-Feldt condition (Huynh and Feldt 1970). If the matrix met these conditions and the plot-by-date and lack-of-fit terms were not significant ($P>0.05$), the data were fitted to a linear model using calendar date as a continuous variable. If plot-by-date or lack-of-fit terms were significant, the data were fitted to a linear model using calendar date as a categorical variable. Then, a backward elimination technique was used to come up with the linear model that accounted for the greatest amount of variation. When cover-crop and bare ground strips were incorporated in preparation for plantings, only the two broccoli areas were available for sampling. When these data were analyzed on single calendar dates, a two-tailed, paired t-test was used to separate the means.

RESULTS

During the three-year study, 1,262 carabid beetles representing twenty-one species were trapped in pitfall traps within the relay strip-cropped and clean-tilled cropping systems. There were more individual beetles and more beetle species in the relay strip-cropping system than in the clean-till system. There were more beetles in the broccoli in the relay system than in the monoculture broccoli (Tables 2.1-2.5).

The four most abundant carabid taxa (*P. melanarius, A. binotatus, Bradycellus congener* LeConte, and the *Amara* species) represented 87.4% of the total capture over the three years. *Anisodactylus californicus, A. rusticus, A. similis, Clivina fossor* L., *Harpalus affinis* Schrank, and *Pterostichus algidus* LeConte increased in number over the three years. *Agonum suturale* Say, *B. congener*, and the *Amara* species decreased in abundance over the three years (Tables 2.1-2.5).

Fifteen taxa were trapped more often in the relay strip-cropping system than in the clean-till system. *B. congener* and *C. fossor*, however, were more common in the clean-till cropping system. *Agonum mulleri* Herbst, *A. rusticus, A. similis, Calosoma cancellatum* Eschscholtz, and *P. algidus* were trapped exclusively in the relay strip-cropping system. *A. binotatus, Loricera foveata* LeConte, *P. algidus*, and the *Amara* species were strongly associated with the cover-crop but were also captured in the broccoli. *A. californicus, A. similis,* and *C. cancellatum* only occurred in the cover-crop and were never captured in the broccoli (Table 2.4).

Table 2.1 Ground Beetles Captured in a Broccoli Relay Strip-cropping System
Corvallis, Oregon 1994

Taxa	Broccoli Relay			Broccoli Clean Till			Cover Crop			Bare Ground			Totals 1994			
													Planting		Total	
	early	late	total	early	late	total	early	late	total	early	late	total	early	late	Count	Percent
Acupalus meridianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Agonum suturale	1	1	2	4	0	4	15	0	15	0	0	0	20	1	21	3.2
Agonum mulleri	1	0	1	0	0	0	1	0	1	0	0	0	2	0	2	0.3
Amara species	6	2	8	5	0	5	67	10	77	0	0	0	78	12	90	13.8
Anisodactylus binotatus	35	5	40	6	0	6	136	9	145	6	1	7	183	15	198	30.3
Anisodactylus californicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Anisodactylus rusticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Anisodactylus similis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Bradycellus congener	1	0	1	3	1	4	13	4	17	55	5	60	72	10	82	12.6
Calosoma cancellatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Clivina fossor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Harpalus pensylvanicus	4	1	5	3	0	3	5	0	5	0	0	0	12	1	13	2.0
Harpalus affinis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Loricera foveata	0	0	0	0	0	0	2	0	2	0	0	0	2	0	2	0.3
Pterostichus melanarius	36	24	60	20	2	22	41	13	54	2	0	2	99	39	138	21.1
Pterostichus algidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Stenolophus comma	0	0	0	0	0	0	1	2	3	2	0	2	3	2	5	0.8
Annual Pitfalls 1994	180	108	288	180	108	288	180	108	288	180	108	288	720	432	1152	
Annual Pitfalls Days 1994	540	216	756	540	216	756	540	216	756	540	216	756	2160	864	3024	
Total Beetles	84	33	117	41	3	44	281	38	319	65	6	71	471	80	551	
Number of Species	7	5	7	6	2	6	9	5	9	4	2	4	9	7	9	

Table 2.2 Ground Beetles Captured in a Broccoli Relay Strip-cropping System Corvallis, Oregon 1995

Taxa	Broccoli Relay			Broccoli Clean Till			Cover Crop			Bare Ground			Totals 1995			
													Planting		Total	
	early	late	total	early	late	total	early	late	total	early	late	total	early	late	Count	Percent
Acupalus meridianus	1	0	1	0	0	0	2	0	2	1	0	1	4	0	4	1.6
Agonum suturale	1	0	1	0	0	0	0	0	0	1	0	1	2	0	2	0.8
Agonum mulleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Amara species	4	0	4	0	1	1	5	2	7	0	0	0	9	3	12	4.9
Anisodactylus binotatus	3	6	9	0	0	0	22	2	24	4	0	4	29	8	37	15.2
Anisodactylus californicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Anisodactylus rusticus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Anisodactylus similis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Bradycellus congener	3	6	9	1	2	3	0	5	5	1	0	1	5	13	18	7.4
Calosoma cancellatum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Clivina fossor	0	0	0	1	0	1	1	0	1	0	0	0	2	0	2	0.8
Harpalus pensylvanicus	1	2	3	0	1	1	0	8	8	0	1	1	1	12	13	5.3
Harpalus affinis	0	2	2	0	0	0	0	0	0	0	0	0	0	2	2	0.8
Loricera foveata	0	0	0	1	0	1	2	0	2	0	0	0	3	0	3	1.2
Pterostichus melanarius	25	73	98	7	29	36	6	8	14	0	2	2	38	112	150	61.5
Pterostichus algidus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Stenolophus comma	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0.4
Annual Pitfalls 1995	108	108	216	108	108	216	72	72	144	72	72	144	360	360	720	
Annual Pitfalls Days 1995	216	216	432	216	216	432	144	144	288	144	144	288	720	720	1440	
Total Beetles 1995	38	89	127	11	33	44	38	25	63	7	3	10	94	150	244	
Number of Species	7	5	8	5	4	7	6	5	8	4	2	6	10	6	11	

Table 2.3 Ground Beetles Captured in a Broccoli Relay Strip-cropping System Corvallis, Oregon 1996

	Broccoli Relay			Broccoli Clean Till			Cover Crop			Bare Ground			Totals 1996			
													Planting		Annual	
Taxa	early	late	total	early	late	total	early	late	total	early	late	total	early	late	Count	Percent
Acupalus meridianus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Agonum suturale	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0.2
Agonum mulleri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Amara species	3	0	3	0	1	1	36	1	37	0	0	0	39	2	41	8.8
Anisodactylus binotatus	27	3	30	3	0	3	104	3	107	1	1	2	135	7	142	30.5
Anisodactylus californicus	5	0	5	0	1	1	2	1	3	0	0	0	7	2	9	1.9
Anisodactylus rusticus	0	0	0	0	0	0	1	0	1	0	0	0	1	0	1	0.2
Anisodactylus similis	0	0	0	0	0	0	2	0	2	0	0	0	2	0	2	0.4
Bradycellus congener	7	2	9	4	4	8	5	2	7	1	4	5	17	12	29	6.2
Calosoma cancellatum	0	0	0	0	0	0	2	0	2	0	0	0	2	0	2	0.4
Clivina fossor	1	0	1	0	0	0	0	1	1	0	8	8	1	9	10	2.2
Harpalus pensylvanicus	0	2	2	0	2	2	0	6	6	0	3	3	0	13	13	2.8
Harpalus affinis	6	1	7	0	0	0	9	1	10	0	1	1	15	3	18	3.9
Loricera foveata	1	0	1	0	0	0	0	1	1	0	0	0	1	1	2	0.4
Pterostichus melanarius	53	29	82	7	10	17	45	42	87	0	2	2	105	83	188	40.4
Pterostichus algidus	3	0	3	0	0	0	0	6	6	0	0	0	3	6	9	1.9
Stenolophus comma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.0
Annual Pitfalls 1996	180	108	288	180	108	288	72	81	153	72	81	153	504	378	882	
Annual Pitfalls Days 1996	360	216	576	360	216	576	144	162	306	144	162	306	1008	756	1764	
Total Beetles 1996	106	37	143	14	18	32	207	64	271	2	19	21	329	138	467	
Taxa	9	5	10	3	5	6	10	10	14	2	6	6	12	10	13	

Table 2.4 Impact of Relay Strip-cropping on Ground Beetles - Combinded Data Corvallis, Oregon 1994-1996

Taxa	Broccoli Relay (BR)	Broccoli CleanTill (BCT)	Cover Crop (CC)	Bare Ground (BG)	Total	Percent of Total % BR	% BCT	% CC	% BG	Cropping System Relay (BR+CC)	Clean Till (BCT+BG)	Percent of Total % Relay (BR+CC)	% CleanTill (BCT+BG)
Acupalus meridianus L.	1	0	2	1	4	*25*	*0*	*50*	*25*	3	1	*75*	*25*
Agonum suturale Say	3	4	16	1	24	*13*	*17*	*67*	*4*	19	5	*79*	*21*
Agonum mulleri Herbst	1	0	1	0	2	*50*	*0*	*50*	*0*	2	0	*100*	*0*
Amara species	15	7	121	0	143	*10*	*5*	*85*	*0*	136	7	*95*	*5*
Amara conflata LeConte													
Amara californica Dejean													
Amara apricaria Paykull													
Amara littoralis Mannerheim													
Amara cupreolata Putzeys													
Anisodactylus binotatus F.	79	9	276	13	377	*21*	*2*	*73*	*3*	355	22	*94*	*6*
Anisodactylus californicus Dejean	5	1	3	0	9	*56*	*11*	*33*	*0*	8	1	*89*	*11*
Anisodactylus rusticus (Say)	0	0	1	0	1	*0*	*0*	*100*	*0*	1	0	*100*	*0*
Anisodactylus similis LeConte	0	0	2	0	2	*0*	*0*	*100*	*0*	2	0	*100*	*0*
Bradycellus congener LeConte	19	15	29	66	129	*15*	*12*	*22*	*51*	48	81	*37*	*63*
Calosoma cancellatum Eschscholtz	0	0	2	0	2	*0*	*0*	*100*	*0*	2	0	*100*	*0*
Clivina fossor L.	1	1	2	8	12	*8*	*8*	*17*	*67*	3	9	*25*	*75*
Harpalus pensylvanicus DeGeer	10	6	19	4	39	*26*	*15*	*49*	*10*	29	10	*74*	*26*
Harpalus affinis Schrank	9	0	10	1	20	*45*	*0*	*50*	*5*	19	1	*95*	*5*
Loricera foveata LeConte	1	1	5	0	7	*14*	*14*	*71*	*0*	6	1	*86*	*14*
Pterostichus melanarius Illiger	240	75	155	6	476	*50*	*16*	*33*	*1*	395	81	*83*	*17*
Pterostichus algidus LeConte	3	0	6	0	9	*33*	*0*	*67*	*0*	9	0	*100*	*0*
Stenolophus comma F.	0	1	3	2	6	*0*	*17*	*50*	*33*	3	3	*50*	*50*
1994-1996 Totals	**BR**	**BCT**	**CC**	**BG**	**Total**					**BR+CC**	**BCT+BG**		
Total Pitfalls	792	792	585	585	2754					1377	1377		
Total Pitfall Days	1764	1764	1350	1350	6228					3114	3114		
Total Beetles Trapped	387	120	653	102	1262					1040	222		
Beetle Taxa	13	10	17	9	17								

Table 2.5 Ground Beetles in a Relay Strip-cropping System (Percentages) Corvallis, Oregon 1994-1996

Taxa	1994		1995		1996		1994-1996	
	Count	Percent	Count	Percent	Count	Percent	Count	Percent
Acupalus meridianus L.	0	*0.0*	4	*1.6*	0	*0.0*	4	*0.3*
Agonum suturale Say	21	*3.8*	2	*0.8*	1	*0.2*	24	*1.9*
Agonum mulleri Herbst	2	*0.4*	0	*0.0*	0	*0.0*	2	*0.2*
Amara species	90	*16.3*	12	*4.9*	41	*8.8*	143	*11.3*
Amara conflata LeConte								
Amara californica Dejean								
Amara apricaria Paykull								
Amara littoralis Mannerheim								
Amara cupreolata Putzeys								
Anisodactylus binotatus F.	198	*35.9*	37	*15.2*	142	*30.4*	377	*29.9*
Anisodactylus californicus Dejean	0	*0.0*	0	*0.0*	9	*1.9*	9	*0.7*
Anisodactylus rusticus (Say)	0	*0.0*	0	*0.0*	1	*0.2*	1	*0.1*
Anisodactylus similis LeConte	0	*0.0*	0	*0.0*	2	*0.4*	2	*0.2*
Bradycellus congener LeConte	82	*14.9*	18	*7.4*	29	*6.2*	129	*10.2*
Calosoma cancellatum Eschscholtz	0	*0.0*	0	*0.0*	2	*0.4*	2	*0.2*
Clivina fossor L.	0	*0.0*	2	*0.8*	10	*2.1*	12	*1.0*
Harpalus pensylvanicus DeGeer	13	*2.4*	13	*5.3*	13	*2.8*	39	*3.1*
Harpalus affinis Schrank	0	*0.0*	2	*0.8*	18	*3.9*	20	*1.6*
Loricera foveata LeConte	2	*0.4*	3	*1.2*	2	*0.4*	7	*0.6*
Pterostichus melanarius Illiger	138	*25.0*	150	*61.5*	188	*40.3*	476	*37.7*
Pterostichus algidus LeConte	0	*0.0*	0	*0.0*	9	*1.9*	9	*0.7*
Stenolophus comma F.	5	*0.9*	1	*0.4*	0	*0.0*	6	*0.5*
Annual Pitfalls	1152		720		882		2754	
Annual Pitfalls Days	3024		1440		1764		6228	
Total Beetles	551		244		467		1262	
Taxa	9		11		14		17	

A. suturale, A. binotatus, L. foveata, and the *Amara* species were consistently more abundant in the early plantings than in the late plantings. *C. fossor* and *Harpalus pensylvanicus* DeGeer were consistently more abundant in the late plantings. *P. melanarius* was slightly more abundant in the later plantings, but was common in both the early and late planting periods (Tables 2.1-2.3).

Diversity and evenness of carabid species reflected by the Shannon-Weiner index (H) decreased along the continuum of cover-crop > broccoli relay > broccoli clean-till > and bare ground. H values were consistently higher in the early plantings than in the late plantings. H values for total Carabidae species captured each year were similar. H values for beetles captured pooled over the three-year period for the two cropping systems were identical (Table 2.6).

In early sampling dates, *P. melanarius* was most abundant in the cover-crop areas. After cover-crop plow down, *P. melanarius* was most abundant in the relay strip-cropped broccoli. In the late plantings, *P. melanarius* was more evenly spread across the experimental field. Pitfall trap captures declined dramatically in early October each year. *P. melanarius* density was equal or higher in the broccoli grown in the relay strip-cropping system with the clean-till broccoli on 22 out of 23 sampling dates over the three years (Table 2.7, Figures 2.3-2.8). When trap counts were analyzed on single dates, however, the difference in the beetle counts were rarely statistically significant ($P < 0.05$ paired t-test, two tailed). When the data were analyzed across sampling dates for each planting period, *P. melanarius* was significantly more abundant in the relay strip-cropped broccoli than in the clean-tilled broccoli during the early ($P = 0.0379$, $F = 5.18$, df = 1,15) and late ($P = 0.0056$, $F = 10.68$, df = 1,14) plantings of 1995 and in the early planting of 1996 ($P = 0.0001$, $F = 39.40$, df = 1,26).

Table 2.6 Impact of Relay Strip-cropping on Ground Beetle (Coleoptera: Carabidae) Species Richness and Eveness in Broccoli Corvallis, Oregon 1994-1996

Carabidae Diversity* (H_S)

	H_S		H_S
1994-1996 Combined - Relay Strip Crop Broccoli	0.4	1994 Treatments Combined	0.52
1994-1996 Combined - Clean Till Broccoli	0.2	1995 Treatments Combined	0.26
1994-1996 Combined - Cover Crop	0.6	1996 Treatments Combined	0.46
1994-1996 Combined - Bare Ground	0.1	1994-1996 Treatments Combined - Early Plantings	0.63
Relay Strip Cropping System 1994-1996	0.7	1994-1996 Treatments Combined - Late Plantings	0.34
Clean Till Cropping System 1994-1996	0.7		

* Shannon-Weiner ($H_S = -\text{ sum } p_i \log pi$) beetles per cropping system compare cover crop plus relay broccoli versus bare ground plus clean till broccoli, beetles per year and beetles in early or late plantings combine beetle counts for relay broccoli, clean till broccoli, cover crop, and bare ground.

Table 2.7 - Impact of Relay Strip-cropping on *P. melanarius* in Broccoli – Corvallis, Oregon 1994-96

	Beetles per Pitfall Trap per Day*				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0	0.06 ± 0.02 a	0.04 ± 0.02 ab	0.10 ± 0.08 a	0.15 ± 0.07 a
Broccoli Clean till	0	0.02 ± 0.02 a	0.05 ± 0.04 ab	0.03 ± 0.03 a	0.11 ± 0.02 a
Cover Crop	0.04 ± 0.01	0.12 ± 0.05 a	0.09 ± 0.04 a	0.08 ± 0.08 a	0.06 ± 0.04 a
Bare Ground	0	0.02 ± 0.01 a	0 b	0 a	0 a
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0.04 ± 0.03 a	0.17 ± 0.10 a	0.15 ± 0.02 a	0.04 ± 0.03 a	
Broccoli Clean till	0.02 ± 0.02 a	0 a	0.02 ± 0.02 bc	0 a	
Cover Crop	0.06 ± 0.03 a	0.09 ± 0.02 a	0.11 ± 0.05 ab	0.02 ± 0.02 a	
Bare Ground	0 a	0 a	0 c	0 a	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0.01 ± 0.01 a	0.02 ± 0.02 a	0.32 ± 0.09 a		
Broccoli Clean-Till	0 a	0 a	0.10 ± 0.10 a		
Cover Crop	0.03 ± 0.02 a	0.06 ± 0.03 a	na		
Bare Ground	0 a	0 a	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0.25 ± 0.08 a	0.43 ± 0.16 a	0.33 ± 0.15 a		
Broccoli Clean-Till	0.24 ± 0.17 a	0.10 ± 0.04 ab	0.07 ± 0.03 ab		
Cover Crop	na	0.08 ± 0.04 b	0.03 ± 0.03 b		
Bare Ground	na	0 b	0.03 ± 0.02 ab		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	0.07 ± 0.03 a	0.08 ± 0.03 a	0.21 ± 0.09 a	0.40 ± 0.12 a	
Broccoli Clean-Till	0.01 ± 0.01 a	0 a	0.01 ± 0.01 b	0.07 ± 0.03 b	
Cover Crop	0.28 ± 0.10 b	0.22 ± 0.13 a	na	na	
Bare Ground	0 a	0 a	na	na	
1996 Late Planting	**13-Aug**	**26-Sep**	**9-Sep**	**24-Sep**	
Broccoli Relay	0 a	0.15 ± 0.13 ab	0.28 ± 0.22 a	0.11 ± 0.07 a	
Broccoli Clean-Till	0 a	0.07 ± 0.04 ab	0.11 ± 0.06 a	0 a	
Cover Crop	na	0.33 ± 0.07 a	0.26 ± 0.11 a	0.19 ± 0.06 a	
Bare Ground	na	0.02 ± 0.02 b	0.02 ± 0.02 a	0 a	

* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5), strip plot analysis, n = 4.

Figure 2.3 Impact of Relay Strip-cropping on *Pterostichus melanarius* in Broccoli - Corvallis, Oregon 1994

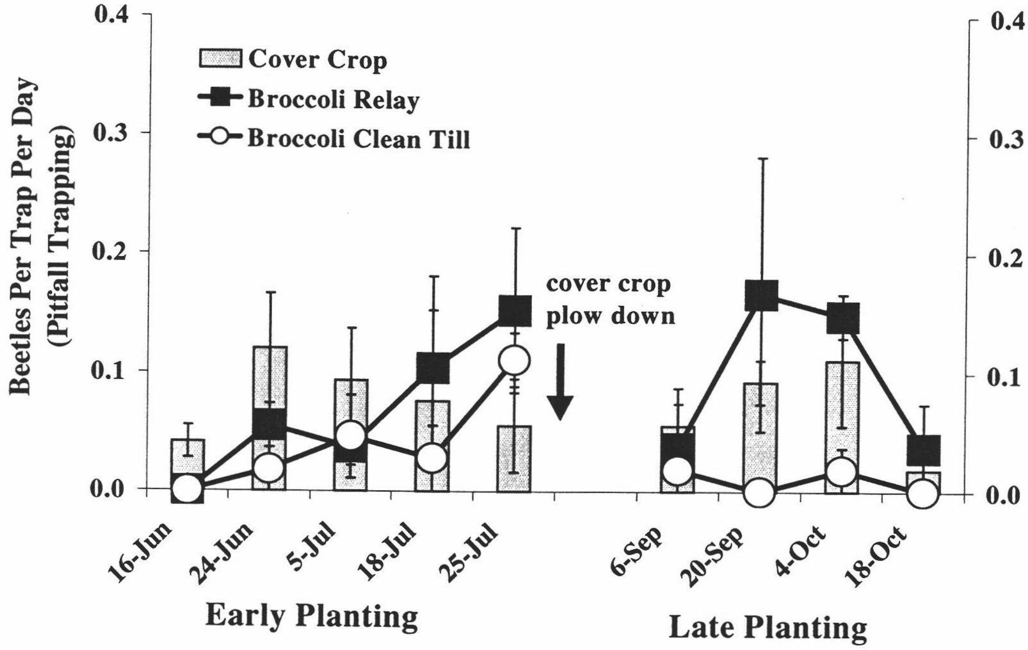


Figure 2.4 Response of *Pterostichus melanarius* to Habitat Choices in a Broccoli Relay Corvallis, Oregon 1994

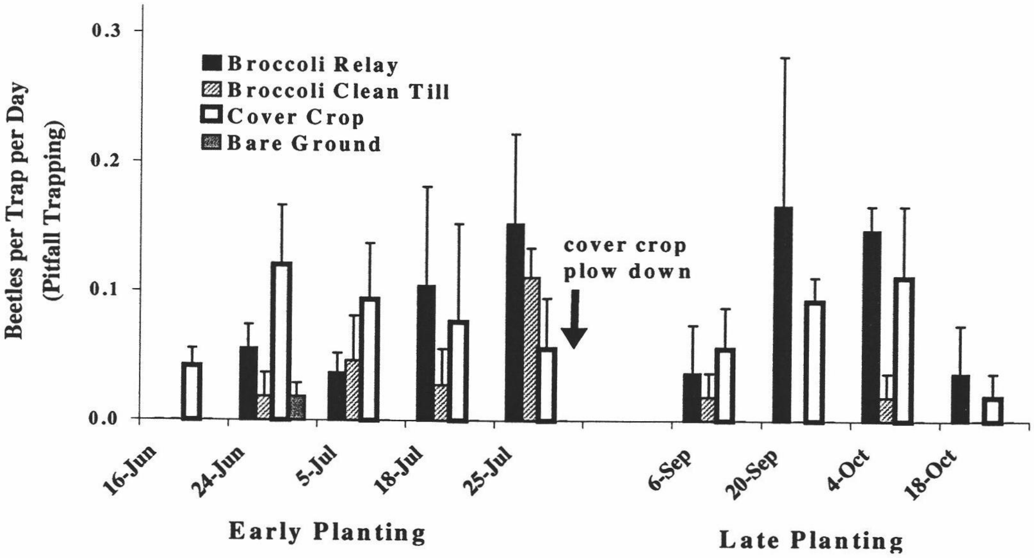


Figure 2.5 Impact of Relay Strip-cropping on *Pterostichus melanarius* in Broccoli Corvallis, Oregon 1995

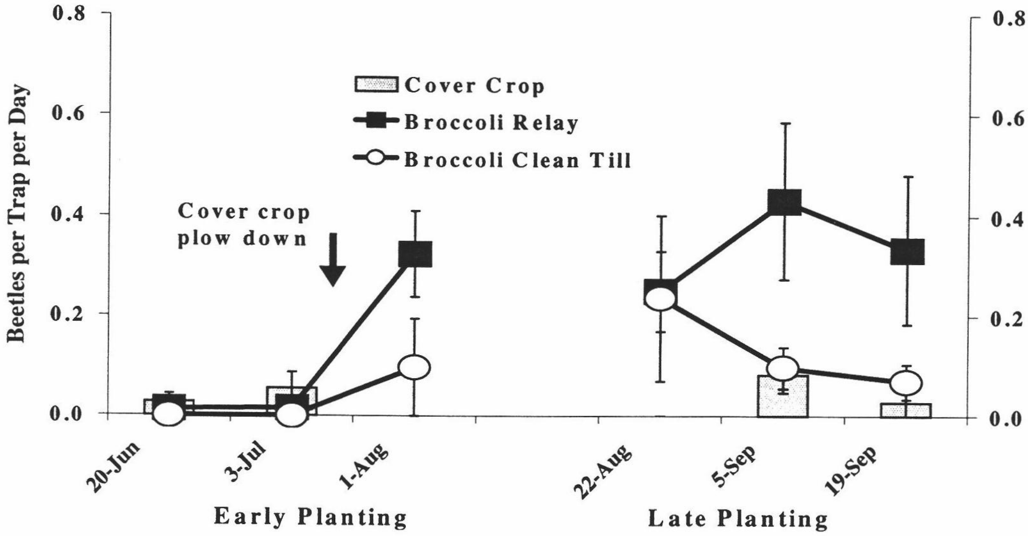


Figure 2.6 Response of *Pterostichus melanarius* to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1995

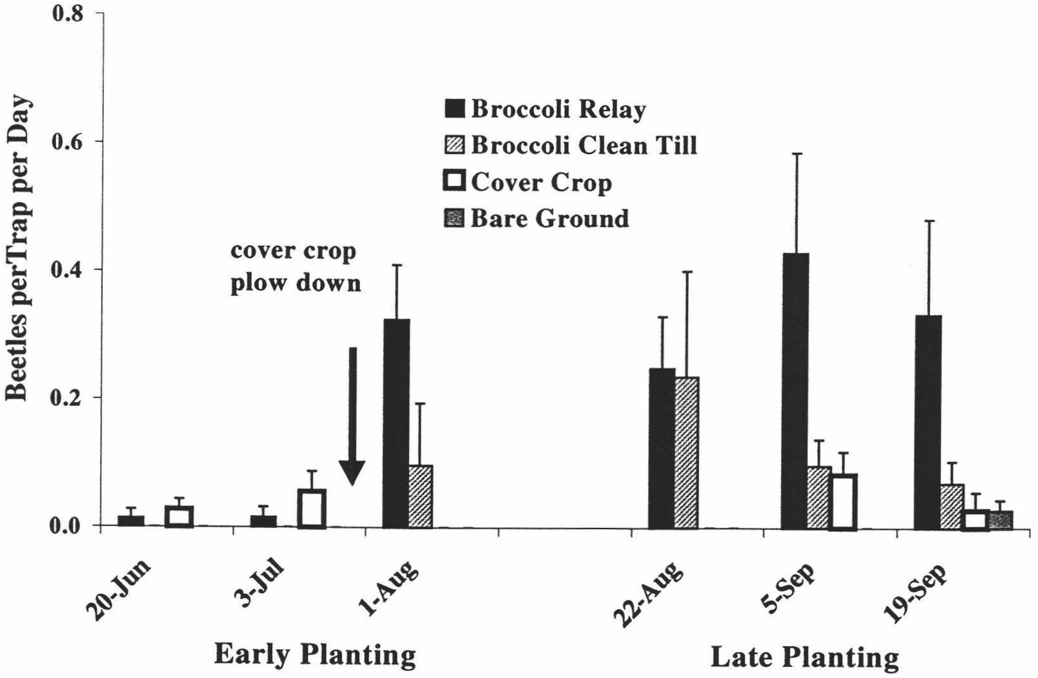


Figure 2.7 Impact of Relay Strip-cropping on *Pterostichus melanarius* in Broccoli - Corvallis, Oregon 1996

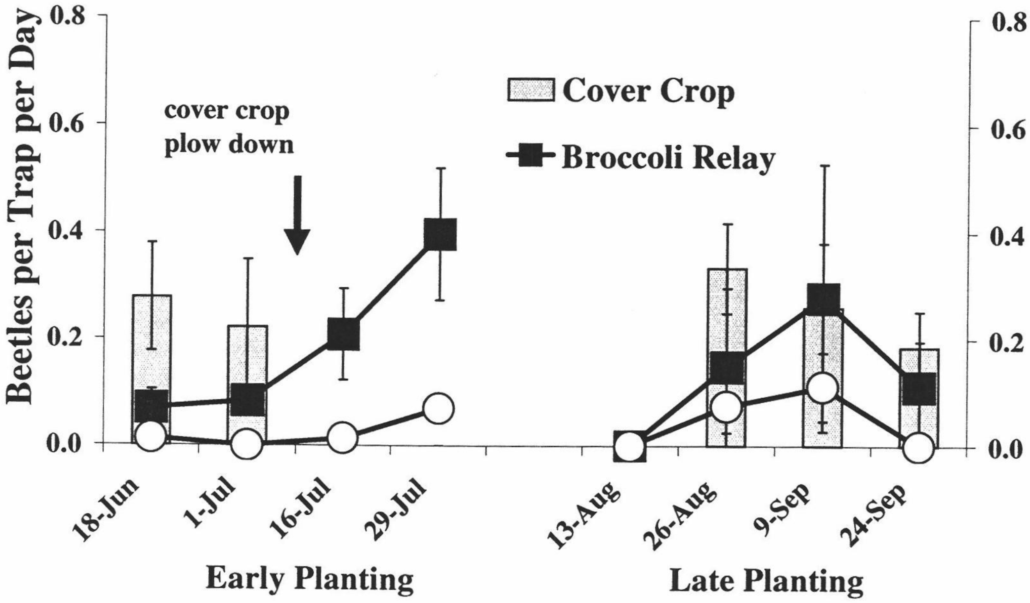
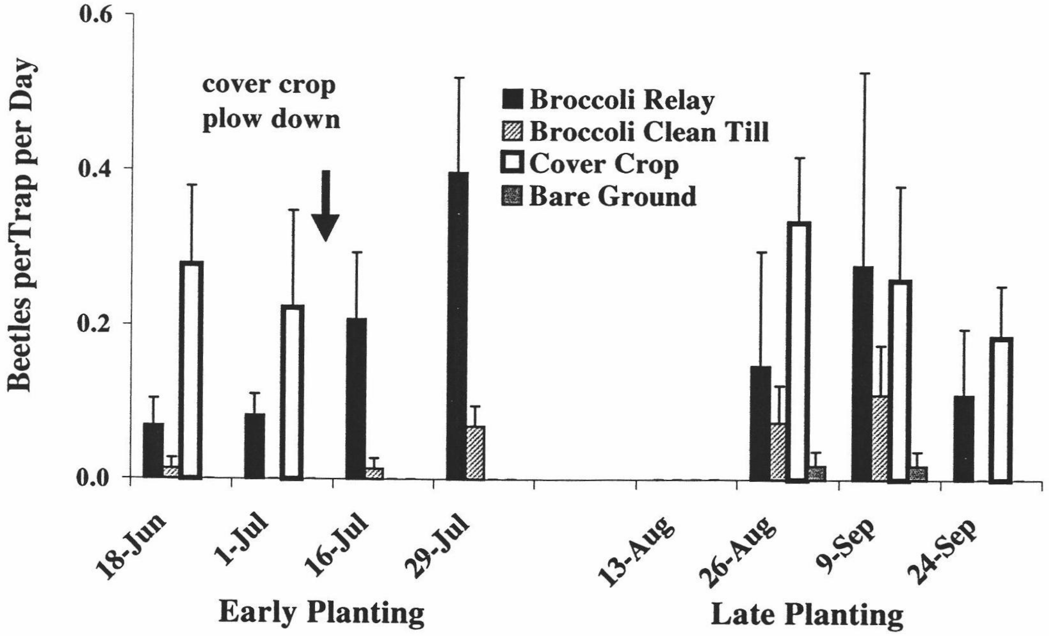


Figure 2.8 Response of *Pterostichus melanarius* to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1996



A. binotatus was most abundant in the early spring. It was absent during the middle of the summer and reappeared in low numbers at the end of the growing season (Table 2.8). Although *A. binotatus* was more abundant in the relay strip-cropping system, it was strongly associated with the cover-crop. *A. binotatus* moved into the broccoli in small numbers, however, it was never significantly more abundant in the relay strip-cropped broccoli compared with the clean-tilled broccoli (Figures 2.9-2.14).

B. congener was captured in low numbers and counts were rarely different in the relay strip-cropped versus clean-tilled broccoli. Occasionally, significantly more *B. congener* were captured in bare ground areas than in any other area (Table 2.9, Figures 2.15-2.18).

The *Amara* species were most abundant in the early spring. They were absent during the middle of the summer and reappeared in low numbers at the end of the growing season. Although the *Amara* species were more abundant in the relay strip-cropping system, they were strongly associated with the cover-crop. The abundance of *Amara* species was never significantly different in the relay strip-cropped broccoli compared with the clean-tilled broccoli (Table 2.10, Figures 2.19-2.22).

Six hundred and sixty four *P. melanarius* beetles were captured, marked, and released in sweet corn over a period of approximately two months. One hundred and fifty nine of the marked beetles and five hundred and eighty six unmarked beetles were captured in a grid of pitfall traps that encompassed approximately 1.6 ha. Ninety four percent (149/159) of the marked beetles were recaptured within 15 m of their release site in the cover-crop strips. Three percent (5/159) of the marked

Table 2.8 - Impact of Relay Strip-cropping on *A. binotatus* in Broccoli – Corvallis, Oregon 1994-96

	Beetles per Pitfall Trap per Day*				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0.03 ± 0.02 b	0.12 ± 0.04 ab	0.11 ± 0.05 a	0.03 ± 0.03 a	0.06 ± 0.03 a
Broccoli Clean till	0.01 ± 0.01 b	0.03 ± 0.01 ab	0 a	0.01 ± 0.01 a	0 a
Cover Crop	0.39 ± 0.20 a	0.51 ± 0.28 a	0.19 ± 0.10 a	0.17 ± 0.17 a	0.10 ± 0.06 a
Bare Ground	0 b	0.03 ± 0.02 b	0.03 ± 0.02 a	0 a	0 a
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0	0.06 ± 0.06 a	0.02 ± 0.02 a	0.02 ± 0.02 a	
Broccoli Clean till	0	0 a	0 a	0 a	
Cover Crop	0.02 ± 0.02	0.02 ± 0.02 a	0.04 ± 0.02 a	0.09 ± 0.05 a	
Bare Ground	0.02 ± 0.02	0 a	0 a	0 a	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0.03 ± 0.03 a	0	0.01 ± 0.01		
Broccoli Clean-Till	0 a	0	0		
Cover Crop	0.19 ± 0.14 b	0.11 ± 0.05	na		
Bare Ground	0.06 ± 0.02 ab	0	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0.06 ± 0.06	0.01 ± 0.01 a	0.01 ± 0.01 a		
Broccoli Clean-Till	0	0 a	0 a		
Cover Crop	na	0.01 ± 0.01 a	0.01 ± 0.01 a		
Bare Ground	na	0 a	0 a		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	0.22 ± 0.11 a	0.10 ± 0.08 a	0.06 ± 0.04 a	0	
Broccoli Clean-Till	0 a	0.01 ± 0.01 a	0.01 ± 0.01 a	0.01 ± 0.01	
Cover Crop	0.96 ± 0.32 b	0.49 ± 0.13 b	na	na	
Bare Ground	0 a	0.01 ± 0.01 a	na	na	
1996 Late Planting	**13-Aug**	**26-Sep**	**9-Sep**	**24-Sep**	
Broccoli Relay	0	0	0.02 ± 0.02 a	0.04 ± 0.03 a	
Broccoli Clean-Till	0	0	0 a	0	
Cover Crop	na	0	0.06 ± 0.03 a	0	
Bare Ground	na	0	0.02 ± 0.02 a	0	

* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5); n = 4.

Figure 2.9 Impact of Relay Strip-cropping on *Anisodactylus binotatus* in Broccoli - Corvallis, Oregon 1994

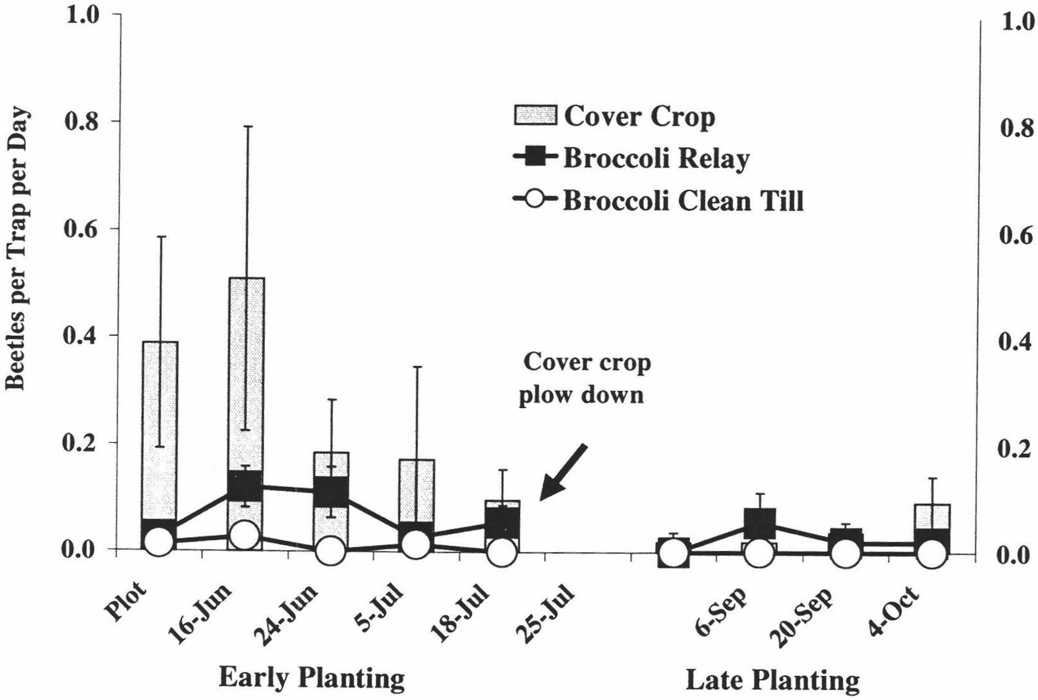


Figure 2.10 Response of *Anisodactylus binotatus* to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1994

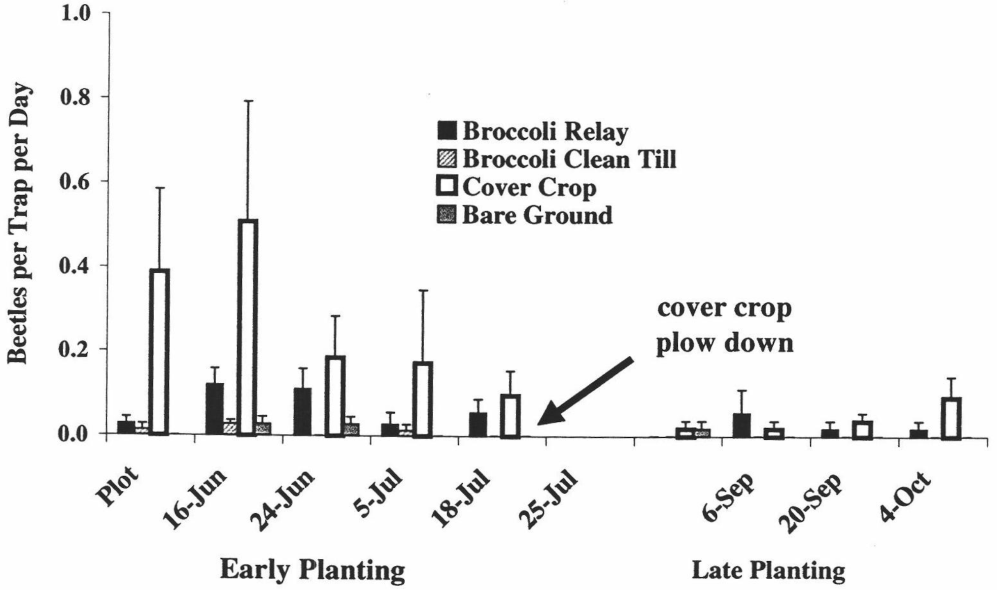


Figure 2.11 Impact of Relay Strip-cropping on *Anisodactylus binotatus* in Broccoli - Corvallis, Oregon 1995

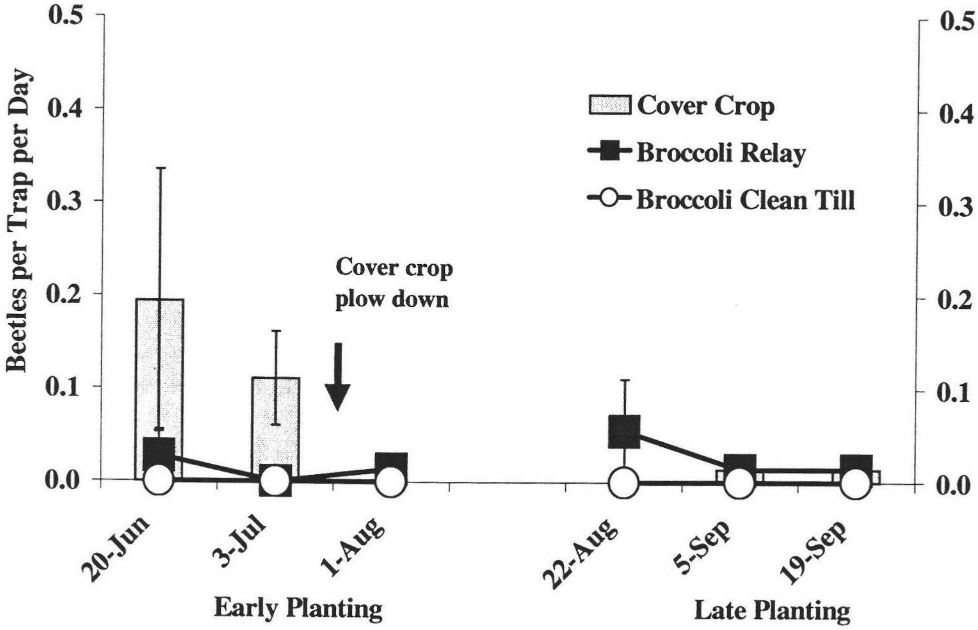


Figure 2.12 Response of *Anisodactylus binotatus* to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1995

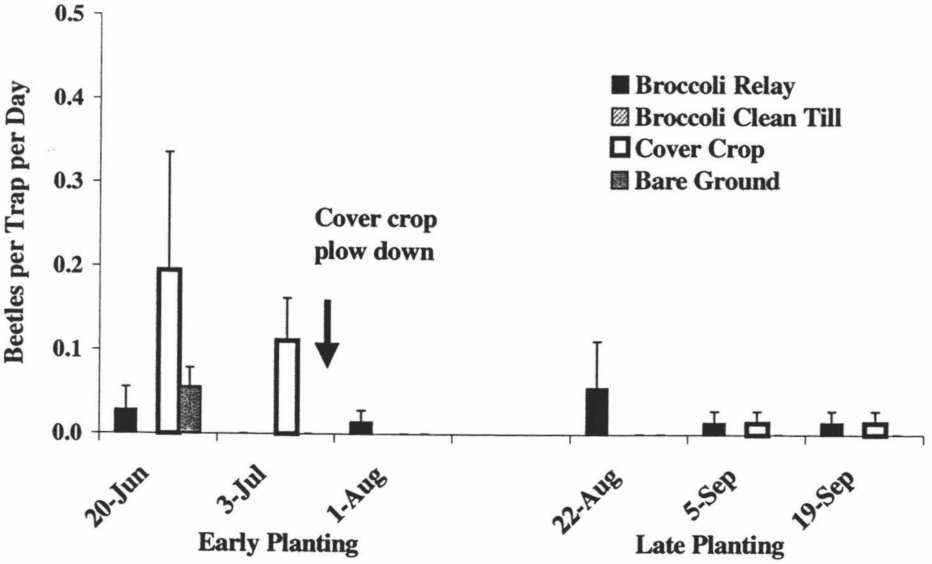


Figure 2.13 Impact of Relay Strip-cropping on *Anisodactylus binotatus* in Broccoli - Corvallis, Oregon 1996

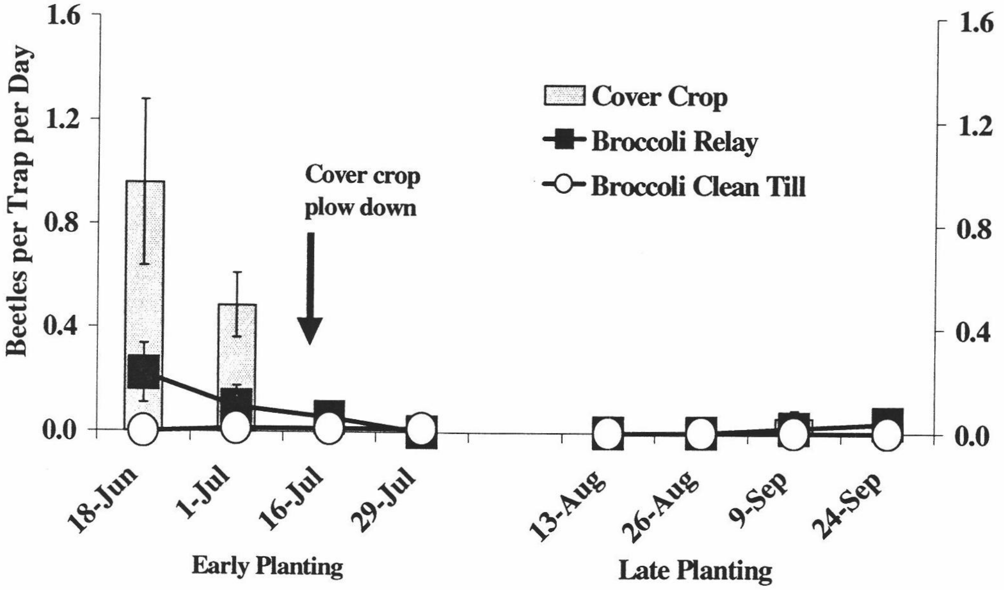


Figure 2.14 Response of *Anisodactylus binotatus* to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1996

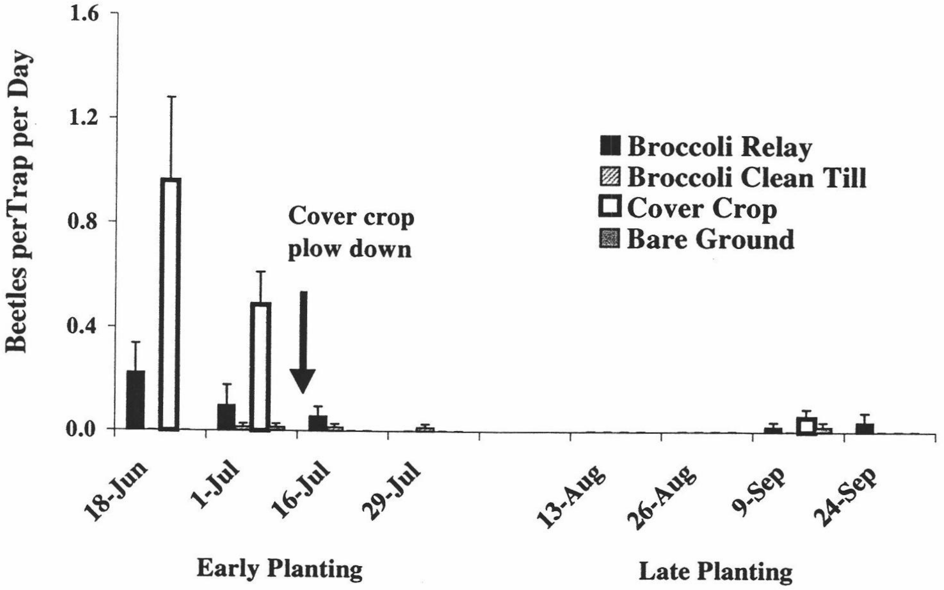


Table 2.9 Impact of Relay Strip-cropping on *Bradycellus congener* in Broccoli Pitfall Trapping - Corvallis, Oregon 1994-1996

	Beetles per Trap per Day*				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0 a	0	0.01 ± 0.01 a	0 a	0
Broccoli Clean Till	0.03 ± 0.02 a	0	0 a	0.01 ± 0.01 a	0
Cover Crop	0.07 ± 0.04 a	0.05 ± 0.02	0.02 ± 0.02 a	0.01 ± 0.01 a	0
Bare Ground	0.04 ± 0.04 a	0	0.16 ± 0.15 a	0.06 ± 0.06 a	0.36 ± 0.16
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0 a	0	0	0	
Broccoli Clean Till	0.02 ± 0.02 a	0	0	0	
Cover Crop	0 a	0	0.06 ± 0.03	0.02 ± 0.02	
Bare Ground	0.04 ± 0.02 a	0.06 ± 0.03	0	0	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0.04 ± 0.03 a	0	0		
Broccoli Clean Till	0 a	0	0.01 ± 0.01		
Cover Crop	0 a	0	na		
Bare Ground	0.01 ± 0.01 a	0	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0	0.01 ± 0.01 a	0.07 ± 0.04 a		
Broccoli Clean Till	0	0.01 ± 0.01 a	0.01 ± 0.01 a		
Cover Crop	na	0.01 ± 0.01 a	0.06 ± 0.04 a		
Bare Ground	na	0 a	0 a		

Means ± SEM, numbers followed by the same letter on the same date are not significantly different (P>0.05), strip plot analysis, n = 4.

Table 2.9 Impact of Relay Strip-cropping on *Bradycellus congener* in Broccoli (Continued)
Pitfall Trapping - Corvallis, Oregon 1994-1996

	Beeltes per Trap per Day *			
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**
Broccoli Relay	0.03 ± 0.02 a	0 a	0.01 ± 0.01 a	0.07 ± 0.01
Broccoli Clean Till	0.01 ± 0.01 a	0.03 ± 0.02 a	0.01 ± 0.01 a	0
Cover Crop	0.04 ± 0.03 a	0.03 ± 0.02 a	na	na
Bare Ground	0 a	0.01 ± 0.01 a	na	na
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**
Broccoli Relay	0	0.04 ± 0.02 a	0 a	0.33 ± 0.33
Broccoli Clean Till	0	0 a	0 a	0
Cover Crop	na	0 a	0.04 ± 0.04 a	0
Bare Ground	na	0.02 ± 0.02 a	0.06 ± 0.03 a	0

Means ± SEM, numbers followed by the same letter on the same date are not significantly different (P>0.05), strip plot analysis, n = 4.

Figure 2.15 Impact of Relay Strip-cropping on *Bradycellus congener* in Broccoli - Corvallis, Oregon 1994

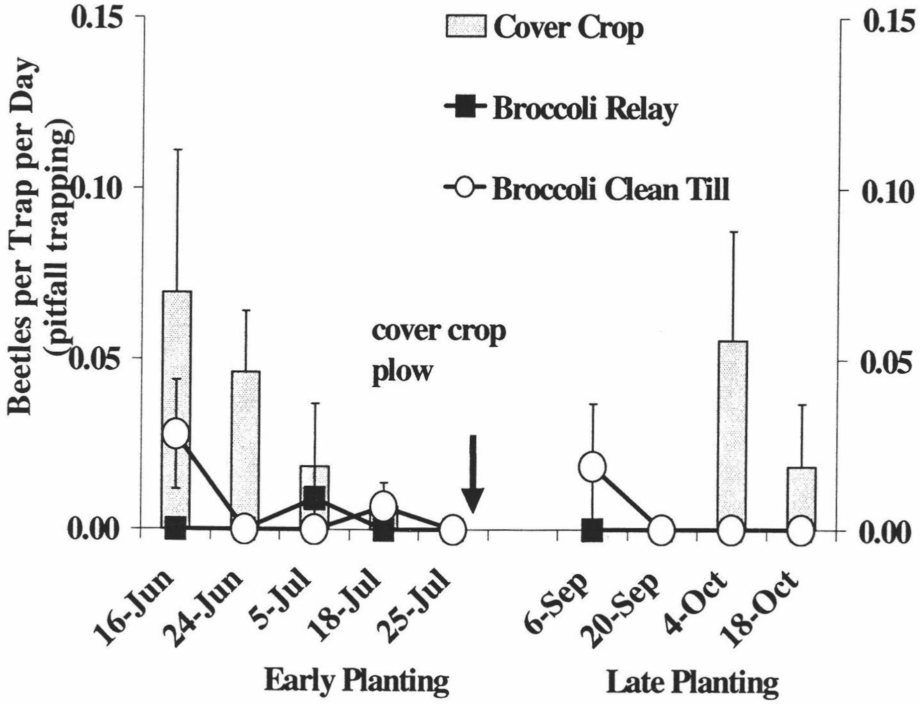


Figure 2.16 Response of *Bradycellus congener* to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1994

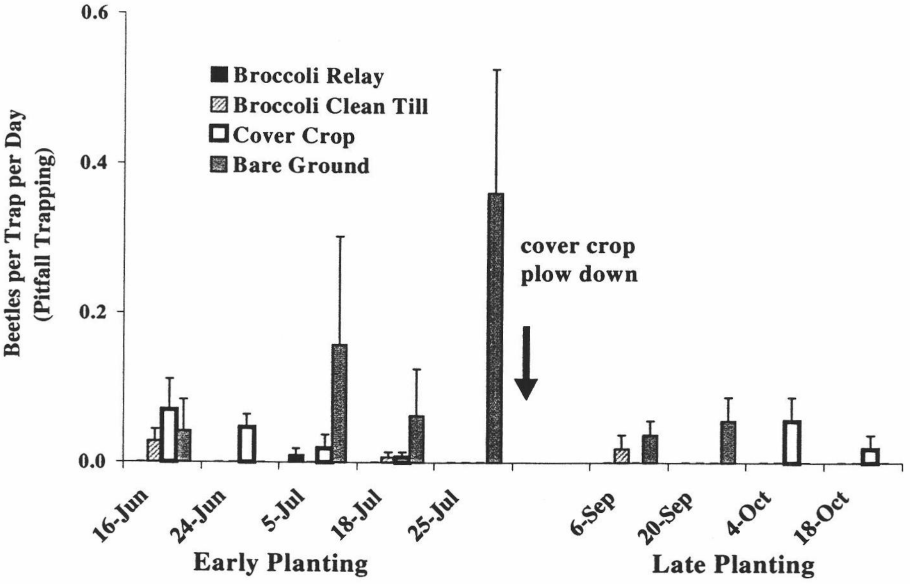


Figure 2.17 Impact of Relay Strip-cropping on *Bradycellus congener* in Broccoli - Corvallis, Oregon 1996

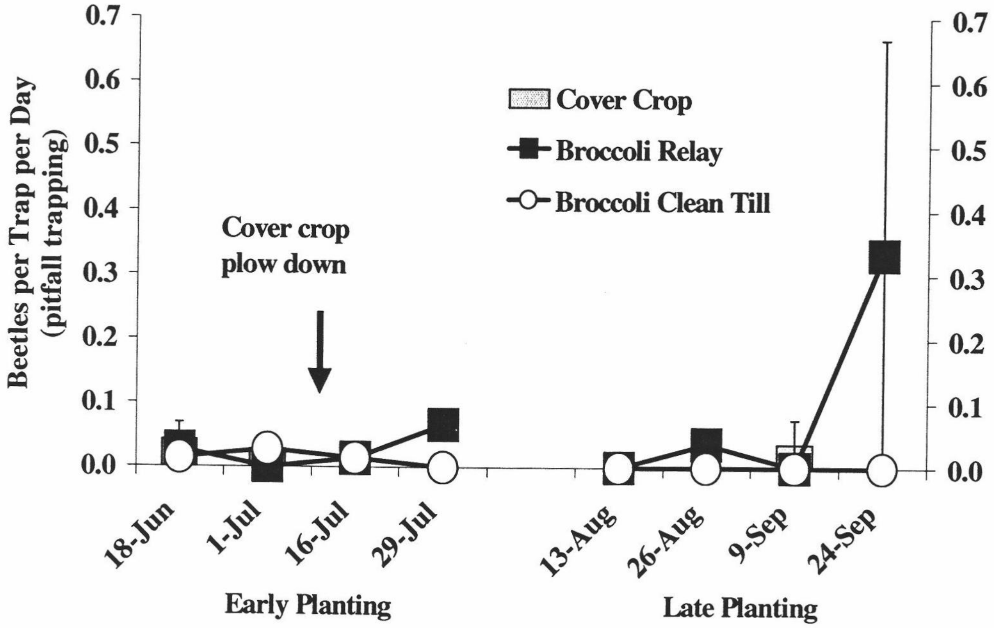


Figure 2.18 Response of *Bradycellus congener* to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1996

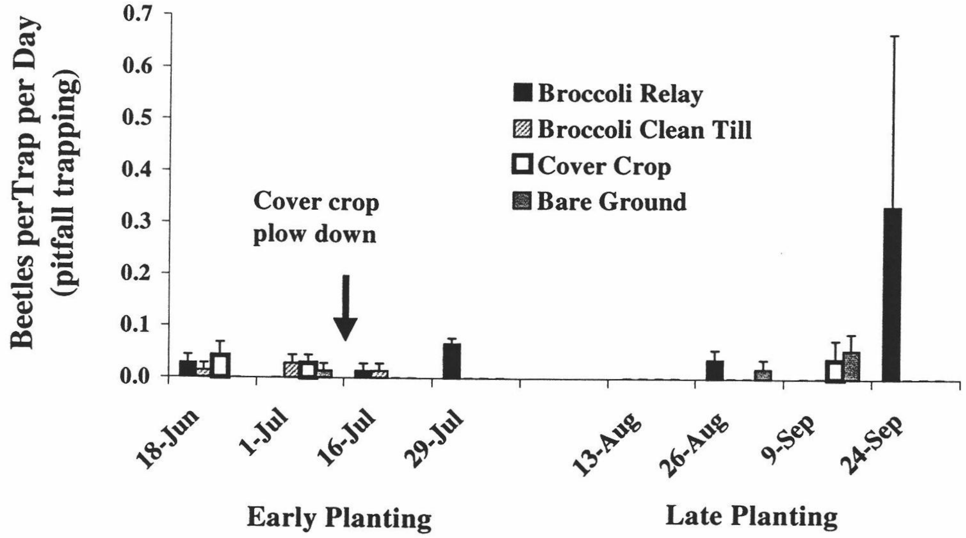


Table 2.10 Impact of Relay Strip-cropping on *Amara* species in Broccoli Pitfall Trapping - Corvallis, Oregon 1994-1996

	Beetles per Trap per Day*				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0.03 ± 0.02 a	0.02 ± 0.01 ab	0.02 ± 0.02 ab	0 a	0
Broccoli Clean Till	0.03 ± 0.03 a	0 bc	0.01 ± 0.01 b	0.01 ± 0.01 a	0
Cover Crop	0.63 ± 0.18 b	0.07 ± 0.03 a	0.07 ± 0.02 a	0.04 ± 0.02 a	0.01 ± 0.01
Bare Ground	0 a	0 c	0 b	0 a	0
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0	0	0.02 ± 0.02 a	0.02 ± 0.02 a	
Broccoli Clean Till	0	0	0 a	0 a	
Cover Crop	0	0	0.02 ± 0.02 a	0.17 ± 0.17 a	
Bare Ground	0	0	0 a	0 a	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0.03 ± 0.02 a	0	0.03 ± 0.02		
Broccoli Clean Till	0 a	0	0		
Cover Crop	0.07 ± 0.07 a	0	na		
Bare Ground	0 a	0	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0	0	0		
Broccoli Clean Till	0.01 ± 0.01	0	0		
Cover Crop	na	0.01 ± 0.01	0.01 ± 0.01		
Bare Ground	na	0	0		

* Means ± SEM, numbers followed by the same letter on the same date are not significantly different (P>0.05), strip plot analysis, n = 4.

Table 2.10 Impact of Relay Strip-cropping on *Amara* species in Broccoli (Continued) Pitfall Trapping - Corvallis, Oregon 1994-1996

	Beeltes per Trap per Day *			
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**
Broccoli Relay	0.03 ± 0.02 a	0.01 ± 0.01 a	0.01 ± 0.01	0.03 ± 0.03
Broccoli Clean Till	0 a	0 a	0	0
Cover Crop	0.44 ± 0.30 b	0.06 ± 0.04 a	na	na
Bare Ground	0 a	0 a	na	na
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean Till	0.02 ± 0.02	0	0	0
Cover Crop	na	0	0	0.02 ± 0.02
Bare Ground	na	0	0	0

* Means ± SEM, numbers followed by the same letter on the same date are not significantly different (P>0.05), strip plot analysis, n = 4.

Figure 2.19 Impact of Relay Strip-cropping on *Amara* species in Broccoli - Corvallis, Oregon 1994

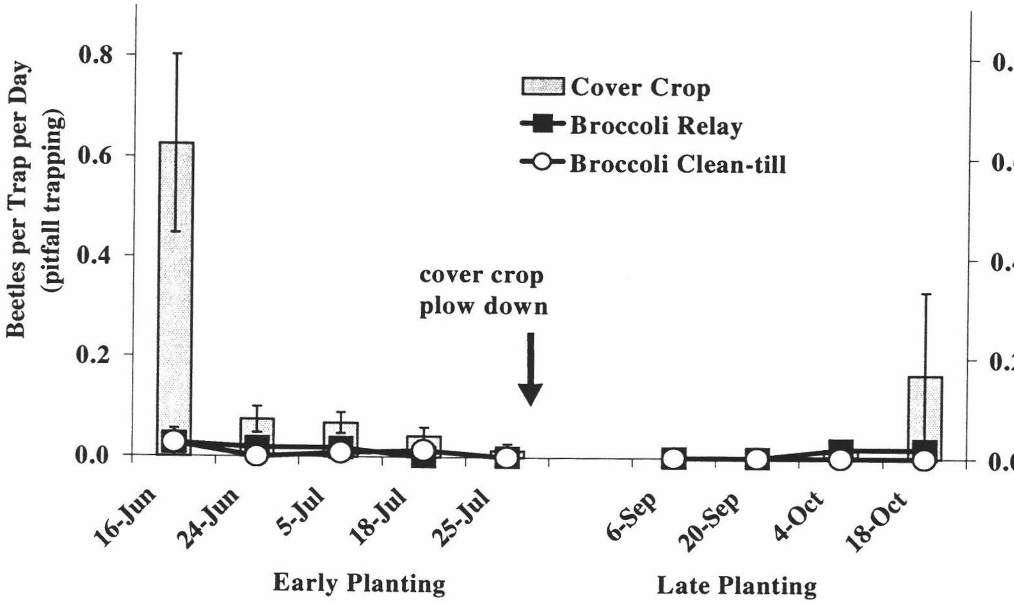


Figure 2.20 Response of *Amara* species to Habitat Choices in a Broccoli Relay - Corvallis, Oregon 1994

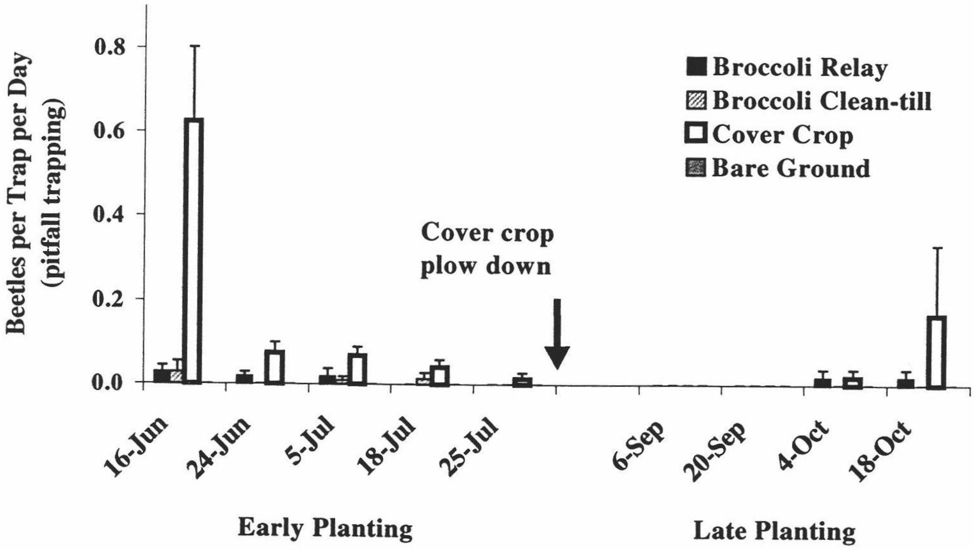


Figure 2.21 Impact of Relay Strip-cropping on *Amara* Species in Broccoli Corvallis, Oregon 1996

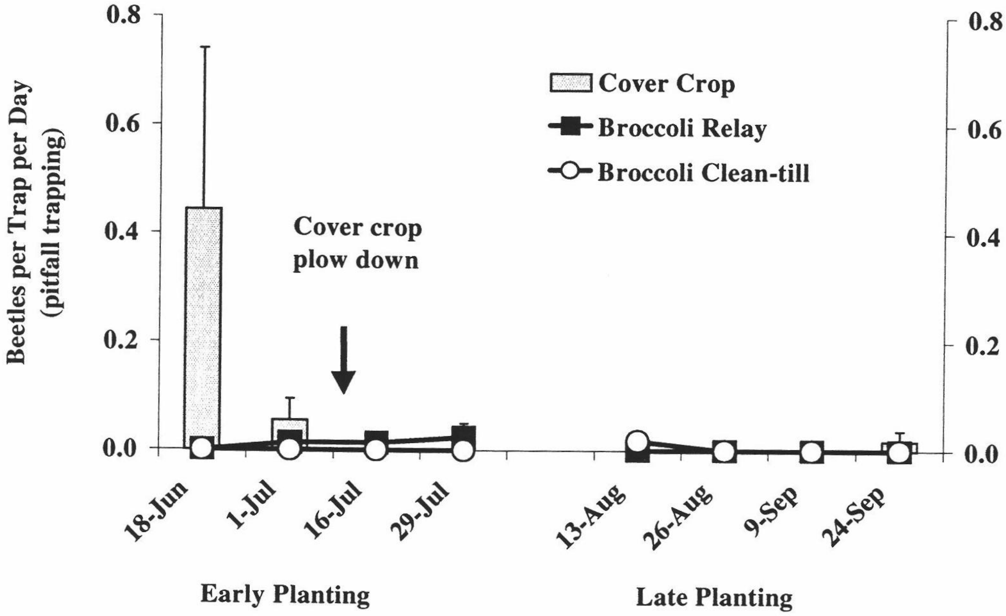
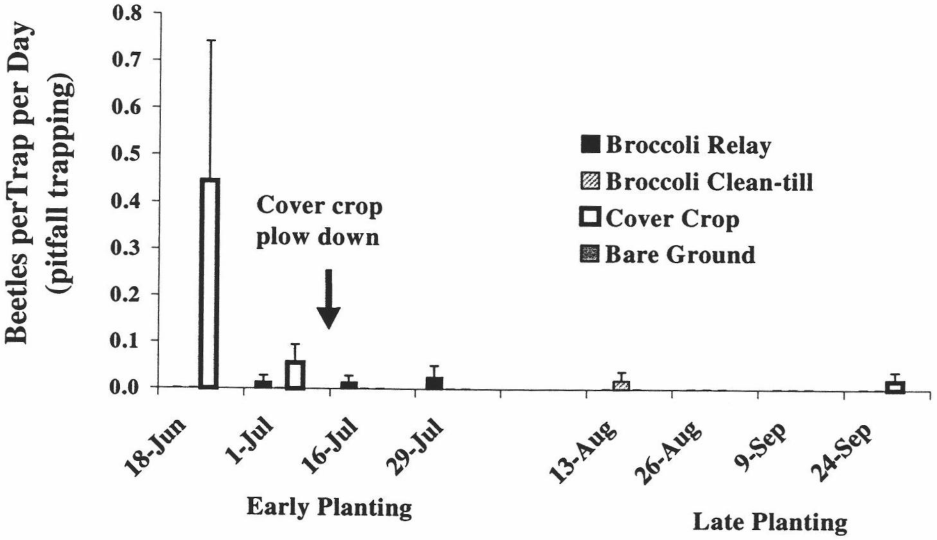


Figure 2.22 Response of *Amara* Species To Habitat Choices in a Broccoli Relay Corvallis, Oregon 1996



beetles were captured between 40 and 45 m from their release site. One marked beetle was captured 48 m from its release site approximately fourteen days after it was released (Table 2.11).

DISCUSSION

This study shows that relay strip-cropping is an effective method of conserving and perhaps enhancing Carabidae in annual cropping systems. Both the overall abundance and species diversity of Carabidae were higher in the relay strip-cropping system than in the clean-till system. The number of crop-adapted species, native carabid species, larval-overwintering species, and adult overwintering species was enhanced by the cropping system.

Under-sowing of cover-crops prior to broccoli harvest eliminated the need for irrigation and tillage for cover-crop establishment. This reduced the potential cost of the conservation practice to the farmers, and the absence of fall tillage explains, in part, the increased abundance of *P. melanarius*. *P. melanarius* breeds in the fall; it is disturbed by tillage operations at that time. Under-sowing of cover-crops prior to broccoli harvest resulted in early soil cover prior to erosive rainstorms. This enhanced the value of the cover-crops as a soil conservation practice, and created an attractive winter habitat for carabid species that overwinter as adults.

The residual cover-crop strips alternating between the strips of early planted broccoli remained undisturbed for approximately 300 days per year through the early fall, winter, and early spring. Undisturbed vegetation in the early spring explains, in part, the increased survival of carabid species that overwinter as adults

Table 2.11 *Pterostichus melanarius* Marked and Recaptured Near Cover Crop Strips in Corn Corvallis, Oregon 1997

	Date Marked and Released											
# Beetles	16-Jun	23-Jun	30-Jun	7-Jul	14-Jul	21-Jul	28-Jul	4-Aug	11-Aug	18-Aug	25-Aug	Total
Marked	20	45	60	100	130	123	134	52	none	none	none	664

Distance from Strips (m)	Date Captured (Marked Beetles)											Recapture Distance (m)	Annual Total	Annual Percent
	16-Jun	23-Jun	30-Jun	7-Jul	14-Jul	21-Jul	28-Jul	4-Aug	11-Aug	18-Aug	25-Aug			
3	na	2	2	8	3	5	13	47	na	na	34	3	114	71.7
6	na	0	0	0	0	0	1	6	na	na	6	6	13	8.2
9	na	0	0	0	0	0	0	7	na	na	4	9	11	6.9
12	na	0	0	0	0	0	1	0	na	na	4	12	5	3.1
15	na	0	0	0	0	1	0	1	na	na	4	15	6	3.8
21	na	0	0	0	0	0	1	1	na	na	0	21	2	1.3
24	na	0	0	0	0	0	0	0	na	na	1	24	1	0.6
27	na	0	0	0	0	0	0	0	na	na	1	27	1	0.6
30	na	0	0	0	0	0	0	0	na	na	0	30	0	0.0
33	na	0	0	0	0	0	0	0	na	na	0	33	0	0.0
36	na	0	0	0	0	0	1	0	na	na	0	36	1	0.6
39	na	0	0	0	0	0	0	0	na	na	0	39	0	0.0
42	na	0	0	0	0	1	0	0	na	na	1	42	2	1.3
45	na	0	0	0	0	0	1	0	na	na	1	45	2	1.3
48	na	0	1	0	0	0	0	0	na	na	0	48	1	0.6
Captured Beetles														**Total**
#Marked		na	3	8	3	7	18	62	0	na	na	390	#Marked	491
#Unmarked		na	17	19	35	34	29	52	219	na	na	181	#Unmarked	586

and breed in the early spring such as *A. binotatus*. Spring breeding carabids are not favored in many agricultural settings because there is no winter cover and generally no significant spring cover until the crop is planted and the crop canopy closes (Lovei 1984).

Delayed tillage in the cover-crop strips allowed *P. melanarius* larvae to finish their life cycle, pupate, emerge as adults, and disperse into the cropping system. The habitat preferences of *P. melanarius* change during the year according to its reproductive and foraging activities. The ability of this ground beetle to immigrate and emigrate successfully from agricultural fields and semi natural habitats assures that a portion of its population will survive tillage operations and pesticide applications. The ability to switch habitats explains, in part, why this species is dominant in many agricultural settings (Wallin 1986).

There was no evidence in this study that the introduced European species, *P. melanarius*, was depressing populations of North American native carabid species. The relay strip-cropping system enhanced the abundance of both poorly dispersing native species and highly dispersive crop-adapted species. The abundance of *P. melanarius* and the North American native species *P. algidus* were both enhanced in the relay strip-cropping system compared with the clean-till system. *P. algidus* has fused elytra and is flightless. *P. algidus* only occurred in the broccoli next to the cover-crop strips.

Some beetle species had distinct habitat preferences. Several carabid species in the genera *Anisodactylus* and *Amara* appeared to be cover-crop-specialists; they never dispersed from the cover-crop into the broccoli even though the broccoli was within 15 m. *P. melanarius*, on the other hand, had very general habitat preferences.

P. melanarius was abundant in the cover-crop during the early spring and in the broccoli during the growing season.

The second most abundant carabid species in the study, *A. binotatus*, was abundant in the early spring cover-crop, however, it was never abundant in the broccoli regardless of the cropping system. *A. binotatus* is highly mobile but it is strongly attached to meadow-like habitats (Gruttke 1994). The strength of its habitat preference suggests that *A. binotatus* may not have a direct effect on above ground pest populations in the broccoli during the growing season. *A. binotatus* is active as an adult during the winter and as a soil-dwelling predatory larva during the growing season. *A. binotatus* may be a mortality factor for insect pests that overwinter within the field. *A. binotatus* adults and larvae probably provide benefits in the cropping system even though they are not active on the soil surface during the growing season.

Not all carabid beetles were enhanced by the increase in vegetation and structural diversity associated with the relay strip-cropping systems. Both *C. fossor* and *B. congener* appeared to prefer open ground, although this may have been an artifact of pitfall sampling. Several studies have shown that plant density and other factors that impede beetle movement over the soil surface produce low "activity-density" readings from pitfall traps that do not accurately reflect differences in population density (Greenslade 1964, Spence and Niemela 1994). Small beetles such as *C. fossor* and *B. congener* may be more facile at escaping from pitfall traps that larger carabid species (Halsall and Wratten 1988, Obeng-Ofori 1993).

In general, more carabid species were caught in the early spring than in the summer. Many of the carabid species that were trapped in the broccoli (*Agonum* species, *Amara* species, *H. affinis*, *B. congener*, *A. binotatus*, *A. californicus*, and

L. foveata) were more numerous in the early planting than in the late planting. Other authors have reported increased diversity in spring pitfall samples compared to mid-summer pitfall samples (Lys and Netwig 1994, Carcamo et al. 1995).

The ability of relay strip-cropping to enhance carabid beetle activity is over emphasized by the high numbers of beetles captured in the early sampling dates. Several species, including *A. binotatus*, were abundant in the winter cover-crop early in the spring. By the middle of the growing season, *A. binotatus* was absent on the soil surface. The *Amara* species followed a similar pattern. They were enhanced in the relay strip-cropping system, but they were never abundant in the broccoli, and they were absent during the middle part of the growing season. On the other hand, some authors have argued that the potential of Carabidae as pest control agents is highest in the early spring when many pest populations are becoming established and when other natural enemies are absent (Coombes and Sotherton 1986, Wratten and van Emden 1995). I believe that the early spring and late fall activity of *A. binotatus* complements the mid-summer activity of P. *melanarius.*

H. pensylvanicus, C. fossor, and *L. foveata* were more active in the late planting of broccoli. *P. melanarius* was abundant in both the early and late plantings but did not become active in the system until late July. It increased in numbers until late summer when its activity dropped off rapidly.

The mark, release, and recapture experiment showed that the cover-crop strips (tillage and pesticide refuges) had an impact in terms of carabid density for 15 to 20 m into the field. These distances suggests that the size of the plots in the cropping system study were ideal for detecting the enhancement of carabid activity associated with the relay strip-cropping system. The results of this study must, therefore, be interpreted with caution. If the relay strip-cropping system were studied at a larger scale, the impact of the cropping system on carabid density may not have been as large.

It is important to recognize that Carabidae have an impact on pest populations in the context of their membership in the larger guild of ground-dwelling generalist predators. The feeding guild includes spiders (Araneae), harvestmen (Phalangiidae), rove beetles (Staphylinidae), ants (Hymenoptera), and other taxa. The entire assemblage of ground predators is important in the natural control of insect pests (Floate et al. 1990, Wratten et al. 1990, Wratten and van Emden 1995, Dennis and Wratten 1991, Carcamo and Spence 1994). There is general agreement among agricultural scientists that carabid beetles form an important component of the overall biological diversity found in semi-natural habitats on farmland (Thomas et al. 1998).

This study shows that relay strip-cropping is a successful technique for conserving Carabidae in annual cropping systems without taking land out of production. Evidence suggests that winter cover-crops can enhance the survival of both adult overwintering and larval overwintering carabid species if the cover-crops are not incorporated into the soil at the beginning of the growing season.

More research is needed to determine the impact that Carabidae have during the winter on the survival of resident crop pests and the impact that carabid summer larvae have on the survival of soil born crop pests during the growing season.

CHAPTER 3

IMPACT OF RELAY STRIP-CROPPING ON SPIDERS (ARAENEA) AND HARVESTMEN (OPILIONES) IN BROCCOLI

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ABSTRACT

During the growing seasons of 1994-1996, 12,114 spiders and harvestmen representing 42 spider taxa were collected in pitfall traps and vacuum samples in a study comparing relay strip-cropping to clean-till planting of broccoli. Relay strip-cropping combines under-sowing and strip-management. A mixture of cover-crop seed containing 30 kg of *Avena sativa* L. var. "Monida", 20 kg *Vicia sativa* L., and 5 kg each of *Trifolium pratense* L., *Lolium multiflorum* Lam., and *Fagopyrum esculentum* Moench was broadcast over established broccoli 32 days after planting at a rate of 65 kg/ha. The broccoli was planted, under-sown, and harvested in sections alternated with undisturbed strips of cover-crop that served as tillage and pesticide refuges. The maximum spider plus harvestmen density reached in either cropping systems was 20 individuals per square meter based on vacuum sampling during daylight hours. The majority of spiders collected in pitfall traps (59%) and vacuum samples (68%) were Linyphiidae. The two most common linyphiid species were *Erigone dentosa* O.P. Cambridge and *Lepthyphantes tenuis* (Blackwall). A single species of harvestmen, *Phalangium opilio* L. (Opiliones: Phalangiidae), represented 19% of the pitfall trap samples and 17% of the vacuum samples. The density of *E. dentosa* and *P. opilio* were significantly higher in the broccoli grown in the relay system. The overall dominance of the Linyphiidae remained the same over the three years regardless of cropping system. Lycosidae species were mostly caught in the cover-crop and were uncommon in both cropping systems.

INTRODUCTION

Spiders are ubiquitous in both natural and farm landscapes of the Northern Hemisphere (Turnbull 1973). Spiders exhibit a remarkable range of life styles and fill many ecological niches (Wise 1993). In annual cropping systems, spiders are the numerically dominant component of the predator assemblage. The diversity and densities of spiders in agriculture, however, are much lower than in natural systems. Spiders are sensitive to tillage and insecticide applications used in crop establishment and crop protection (Nyffeler and Benz 1987). There are, however, species of spiders that are uniquely adapted to habitats that are repeatedly disturbed on a large spatial scale. These species have a high capacity for aerial dispersal; they disperse freely and for long distances by "ballooning" through the air on silken threads produced by abdominal glands called spinnerets.

Ballooning allows them to migrate rapidly into large fields following tillage and insecticide applications (Turnbull 1973, Riechert 1974, Foelix 1982, Nentwig 1986, 1988, Sunderland et al. 1986, Nyffeler and Benz 1987, Nyffeler et al. 1994a, Bishop and Riechert 1990, Young and Edwards 1990, Wise 1993). Spiders are excellent survivors under the adverse conditions that typify a wide variety of agricultural habitats. Spiders have a relatively low rate of metabolism; they are capable of going for long periods without food. Their metabolism allows them to cope with the wide variations in prey abundance in agricultural crops (Nyffeler et al. 1994b).

Spiders are present and active in agricultural systems early in the growing season when many other generalist predators are absent. The early presence of spiders is particularly important when one considers the impact of spiders on aphids, which migrate in large numbers between primary and secondary host-plants (Kajak 1978). Normally, the appearance of aphidophagous predators (Syrphidae, Coccinellidae, Chrysopidae, Anthocoridae, Miridae, and Nabidae) is delayed in the early spring. Delayed arrival of these predators is necessary because they are not adaptive to arrive prior to the build up of their prey populations. Residential web-spinning spiders, however, intercept winged aphids as they colonize agricultural crops during the early part of the growing season (Wyss et al. 1995).

Spiders are also abundant during the autumn when many aphidophagous arthropod populations are declining and when winged aphids are moving from summer to winter host-plants. The reduction in colonization of winter host-plants by aphids in the autumn can have an impact on aphid populations the following growing season. Lower numbers of colonizing aphids results in fewer aphid eggs being laid, which in turn results in fewer fundatrices the following spring.

The impact of spiders in agricultural ecosystems is extended by their webs (Nyffeler et al. 1994a, Wyss et al. 1995). Estimates of their web-cover in wheat crops at the height of the season are as high as 50% of the soil surface (Sunderland et al. 1986). The web helps the spider adapt to the wide variation in abundance and size of prey items in a given habitat. The spider's web often kills more insects than the spider can consume and well in excess of their energy requirements (Nyffeler et al. 1994a). Linyphiidae, for example, typically only eat about 12% of the prey in their webs (Sunderland et al. 1987). *Erigone* species (Linyphiidae) live on the ground and spin small sheet webs horizontally over small depressions in the soil surface (Nyffeler and Benz 1987). *Erigone* diets contain up to 71% Collembola and up to 38% aphids (Clarke and Grant 1968, Nentwig 1980). In one cereal trial, an *Erigone* species caused a 58% reduction in aphid population growth (Mansour and Heimbach 1993).

Surprisingly, studies of prey items found in spider webs show that webs can be selective (Turnbull 1960, Heidger and Nentwig 1989). One finds very few natural enemies in spider webs. Many natural enemies are robust; if they encounter a spider web, they are strong enough to escape or their thick chitinous shells protect them (Nentwig 1980). Many natural enemies have good visual powers, are agile fliers, and are capable of avoiding the webs. Spider webs in the trees and shrubs are full of poor flying insects that jump and fall (leaf hoppers), or drift with the wind (aphids, thrips), and insects that are weak (Diptera) and not able to break out of the web once they become entangled. Because of this selectivity, the spider webs slow the reproduction of phytophagous insects while conserving the majority of natural enemies of insect pests in a given habitat.

Spiders are regarded as important natural enemies of agricultural pests (Nentwig 1986, 1988, Sunderland et al. 1986, Nyffeler and Benz 1987, Nyffeler et al. 1989, 1994a). Some authors argue that spiders can have a stabilizing effect on natural insect populations (Clarke and Grant 1968, Riechert and Lockley 1984). In some cases, high densities of spiders correlate with depressed densities of agricultural pests (Buschman et al. 1984, Wyss et al. 1995). There are few examples, however, of successful manipulation of spider populations that have resulted in the regulation of crop pests (Rypstra et al. 1999). Still, significant research continues to be directed at developing cropping systems that conserve and protect spider populations in agriculture (Burleigh et al. 1973, House and Stinner 1983, Ali and Reagan 1986, Heidger and Nentwig 1989, Rice and Wilde 1991, Thomas et al. 1992b, Zongo et al. 1993).

The impact of spiders on arthropod pests is a community phenomenon; it can only be achieved by the composite foraging activities of assemblages of spider species and other predators in the habitat (Riechert and Lockley 1984). The more diverse the assemblage of generalist predators, the greater the likelihood that an effective predator will encounter a pest species and dampen oscillations in the prey population. For example, the combination of spiders foraging during the crop colonization period coupled with the activity of Coccinellidae and Syrphidae later in the growing season should result in a normal level of biological control of aphids (Heidger and Nentwig 1989).

There is evidence that spiders exhibit both aggregation responses and reproductive numerical responses to increases in prey populations. Movement from patches of low prey density to higher prey density by spiders has been reported (Turnbull 1964, Riechert 1976). Spiders tend to accumulate in areas of abundant prey (Gillespie 1987). Several species of spiders exhibit increased reproductive rates in response to increases in prey consumption (Riechert and Tracy 1975, Riechert 1981, Riechert and Lockley 1984, Wise 1975, 1979).

Aggregation and reproductive responses to increases in prey density are limited by the long generation times of most spider species. Spiders are, for the most part, annual species. Generation times of many pest insects are a few weeks. Changes in spider densities are also limited by cannibalism and intra-specific competition. Spider populations show a strong self-limiting competition. Spiders compete for suitable web and hunting sites that afford adequate thermal microclimates and prey numbers. Spiders prey on each other. In an experimental release of high densities of spiders, the predatory effect was not augmented by the releases. Spiders either migrated from the area if this was permitted in the experiment or they ate each other. The spider populations tended to return to natural densities within a short time (Riechert 1981).

Field observations (Riechert and Lockley 1984) and feeding experiments in the laboratory (Nentwig 1980) show spiders to be rather unspecialized with respect to prey. Most spiders attack prey relative to their rate of encounter with them. There are, however, differences in attack rates among spiders for a given prey species. In cage studies, Reed et al. (1984) found that *Oxyopes salticus* Hentz was a particularly effective predator of early instars of *Trichoplusia ni* (Hubner). It ate approximately 7.4 larvae per day on soybean plants.

In the field, the food of most spiders consists of a rather narrow spectrum of phytophagous and detritophagous insects. Predacious and pollinating species of insects are under-represented (Nentwig 1988, 1989, Nyffeler et al. 1989, 1992, Nyffeler and Breene 1991). Overall, spiders tend to prey heavily on small plant-sucking bugs including Miridae, Cicadellidae, and Aphididae (Turnbull 1966, Kajak 1978). In the laboratory, softly chitinized insects including Diptera, Lepidoptera, some Homoptera, Miridae, and several spider families were accepted by most spiders with acceptance rates of over 50% (Nentwig 1986). Traditionally, spiders are thought to only feed on live moving prey. Recent studies reveal that they also eat eggs, dead animals, plant pollen, and artificial diets (Nyffeler et al. 1994a).

Spiders disperse by walking, climbing on silk between plants, and by ballooning (Nyffeler et al. 1994a). An adult male Lycosidae can cover a straight-line distance of up to 100 m on foot in a growing season. The normal home range of *Pardosa lugubris* (Walck.) is about 200 square meters (Turnbull 1973). Female Lycosidae move a shorter distance than males and have much smaller ranges. Walking is important for some groups of spiders, but the primary mode by which spiders colonize agricultural fields is by ballooning (Bishop 1990, Greenstone 1990, Weyman et al. 1995).

Formerly, it was believed that only the young spiders could balloon. It has been found that many of the smaller species balloon as adults as well. In the Linyphiidae, adult males and females take to the air in mass flights that occur in the autumn and early spring (Foelix 1982).

The major ballooning spider families that recolonize agricultural fields following insecticide applications and tillage operations are in the Linyphiidae, Lycosidae, and Araneidae (Riechert and Lockley 1984). Levels of ballooning activity tend to be higher in the early part of the cropping season and decline as the season progresses. Spider numbers in the fields increase as ballooning progresses, suggesting that spider ballooning early in the season into agricultural fields have a tendency to remain there if food supplies are sufficient (Nyffeler and Benz 1987).

The retention of spiders is significantly affected by availability of food supply (Weyman et al. 1994, 1995). Spider emigration is generally associated with three factors, unfavorable thermal environments (Enders 1972, Duffey 1978, Uetz and Hodge 1990, Ward and Lubin 1993), low prey availability (Waldorf 1976, Uetz and Hodge 1990), and disturbance (Nyffeler and Breene 1990, Scheidler 1990, Thomas et al. 1992b, Clark et al. 1993).

Although spiders are primarily motivated by the presence or absence of adequate numbers of prey, spiders do have preferences for various microclimates (Turnbull 1973). Spiders are sensitive, for example, to variations in moisture (Riechert and Lockley 1984). The primary adaptation by the spiders to a feast and famine existence is the non-sclerotized abdomen. The abdomen allows for consumption of large meals when they are available. The trade-off includes more water loss through the cuticle. Spider populations tend to increase in vegetable crops when plant canopies close and relative humidity increases (Buschman et al. 1984).

The loss of habitat structure has a significant impact on spider diversity in agricultural systems (Hatley and Macmahon 1980, Bishop and Riechert 1990). Experimental manipulation of vegetation in agricultural settings affects several properties of spider communities, but the most important determinant of spider species richness and the number of functional guilds in a given area remains vegetation structural complexity (Hatley and Macmahon 1980). Part of this response has to do with preferred microclimate. The main effect, however, has to do with vegetation complexity and physical structure in the habitat. Spiders respond in different ways to horizontal and vertical structures in their habitat (Robinson 1981). Habitat structures are important for both the web-building and non web-building spiders (Duffey 1962, Rushton and Eyre 1989, Rushton et al. 1989).

Vegetation structural diversity also increases the number of non web-building spiders. Vegetation, including flowers, serves as hiding spots for ambush hunters

(Thomisidae). There is evidence that ambush hunters prefer shrubs (Hatley and Macmahon 1980). Even the ground dwelling Lycosidae are attracted to areas of structural complexity (White and Hassall 1994). In part, the impact of vegetation structural complexity on the Lycosidae is linked to prey diversity and abundance. Lycosidae, however, are also attracted to shelter. Woody debris and thick layers of partially decomposed organic matter on the soil surface serve as hunting retreats and over-wintering sites that are important to Lycosidae (Nentwig 1986, 1988).

Spiders are highly sensitive to insecticides. Field studies of insecticide toxicity to spiders often produces different results than direct dermal toxicity tests conducted in the laboratory. In the field, insecticides are more toxic to spiders than would be predicted from laboratory studies. The unexpected increase in toxicity is due, in part, to the quality of spider webs and the foraging behavior of the ground dwelling spiders (Samu et al. 1992).

Generally, tillage has been found to have minimal or variable effects on foliage-inhabiting insects (Troxclair and Boethel 1984, Thorvilson et al. 1985, Hammond and Stinner 1987, Funderburk et al. 1988) and their natural enemies (McPherson et al. 1982, House and Stinner 1983, Funderburk et al. 1988, Rice and Wilde 1991). Spiders, however, are generally more abundant in reduced tillage planting systems, and the number of species is generally higher in the undisturbed old-field vegetation than in either reduced or clean-till planting systems (House and All 1981, Rice and Wilde 1991). Spiders are uniquely sensitive to tillage. Some authors argue that the effect of tillage associated with planting and stand establishment is more disruptive to spider communities than the use of pesticides. Tillage and seedbed preparation removes all of the vegetation on which spiders depend. Cultivation destroys spider egg sacks in leaf litter and crop residue on the soil surface (Riechert and Lockley 1984).

In general, cover-crops and ground covers between crop rows increase spider diversity and abundance (Daane and Costello 1998). Higher density in ground covers does not, however, guarantee elevated numbers of spiders on the target crop. If the spider species uses the ground cover as an alternative source of prey or habitat, the ground cover may be a sink rather than a source of spiders colonizing the crop. In some cases, spider abundance in the cropping system is lower when ground covers are present. The influence of ground covers varies with species (Costello and Daane 1998).

The focus of this study was to determine the impact of relay strip-cropping on natural enemies of insect pests in broccoli. Relay strip-cropping combines tactics (under-sowing and strip-management) that should have an impact on the spider assemblage in an annual vegetable cropping system. Under-sowing establishes a polyculture of vegetable crop, cover-crop species, and weeds. Although plant diversity alone is not expected to have a direct affect on the spider assemblage, the diverse assemblage of plants in the relay strip-cropping system will provide diverse habitats, structures, and prey items that should attract or retain a greater diversity of spider species than a simple monoculture. In some cases, an increase in prey diversity and abundance associated with increased plant diversity in a cropping system have resulted in significant changes in spider assemblages (Wyss et al. 1995).

In contrast to undisturbed habitats, annual crops are mostly unsuitable for the colonization by and survival of foliage-dwelling spiders. The periodic harvest of essentially all of the vegetation in an annual cropping system destroys their habitat and removes their egg sacs. Periodic colonization of the fields from surrounding habitat is necessary, and this requirement skews the spider assemblage toward those spider species that are highly mobile and capable of tolerating the harsh conditions associated with a new crop. As a result, typical monocultures are dominated by Linyphiidae. One important measure of the impact of relay strip-cropping on the spider assemblage will be its ability to reduce the dominance of the Linyphiidae in the target crop.

The ratio of Lycosidae to Linyphiidae may be an important indicator of habitat quality for spiders. In a strip-managed meadow, Nentwig (1988) found that the annual Linyphiidae biomass decreased and Lycosidae biomass increased over a five year period. The strips were rich in structures that are completely absent in annual clean-tillage cropping systems including old flower stalks, decaying hollow stems, and pioneer woody species including *Salix* species. A thick layer of old vegetation and woody debris covered the soil in the strips.

I expected to see a greater number of spiders successfully overwintering in the relay strip-cropping system than in the monoculture where the field is winter fallow. Thomas et al. (1991, 1992a) found significantly higher numbers of overwintering spiders in grass strips than in winter wheat. The type of vegetation made a significant difference in overwintering success of the spiders. Under tussock forming bunch grasses, the fluctuation in temperature extremes during the winter was diminished compared to bare soil, and this protected the overwintering predators. Lys and Nentwig (1994) evaluated the effect of strip-management on the spider fauna associated with barley and found that most of the spiders in a strip-managed barley planting overwintered in the weedy strips rather than the barley. For a more detail review of the literature related to spiders and harvestmen in agricultural settings, see Appendix B.

MATERIALS AND METHODS

The experiments described below were conducted from 1994 to 1996 at the Oregon State University Vegetable Research Farm near Corvallis, Oregon, approximately 0.4 km from the Willamette River. The details of the relay strip-cropping experiments and pitfall trapping were described in Chapter Two. Spiders and harvestmen were sampled by pitfall trapping and vacuum sampling on alternating weeks.

Vacuum sampling

Every other week, nine vacuum samples were taken in each of the four areas (broccoli relay, broccoli clean-till, cover-crop, bare ground) of each the four experimental blocks. Vacuum samples were taken directly over the broccoli rows adjacent to pitfall sampling sites. On each sampling date, vacuum samples were taken in a different cardinal direction from the pitfall sites, in the same row or in adjacent rows.

Vacuum sampling was accomplished with a gasoline powered leaf blower modified with a suction attachment, a metal cylinder, and a two person sampling team. The modified leaf blower was similar to the Allen-Vac, which has been previously described (Osborne and Allen 1999). The suction tube coming from my vacuum sampler was 12 cm in diameter and 60 cm long. A nylon screen, 30 cm from the opening, prevented insects and debris from passing further. The vacuum sampler was used in conjunction with the metal sampling cylinder that was 50 cm in diameter and 60 cm tall with two handholds cut into the top.

At each sampling site, one team member started the vacuum sampler while the other approached the sampling point with the metal cylinder taking care not to cast a shadow over the foliage. The metal cylinder was set in place with force so that it cut through the vegetation and came to rest on the soil surface. Vacuuming inside the cylinder began at once and continued for 30 seconds, then the contents of the vacuum were emptied into a zip-lock plastic bag. The other team member began immediately searching for and collecting any remaining arthropods within the cylinder using a hand held aspirator. After two minutes of searching, vegetation within the cylinder was cut, lifted out, and spread on a tarp where any remaining arthropods were collected. Arthropods from a sampling point were combined in a single zip-lock bag, stored in a cooler, and transferred to the laboratory for sorting and counting. At each sampling period, two days were required to complete 144 vacuum samples.

The efficiency of the vacuum sampling procedure was tested using marked and recaptured adult damsel bugs (*Nabis* sp.) and lady beetles (*Coccinella trifasciata* L.). Insects were collected in alfalfa with a sweep net, mixed with various colored florescent powders, and released in groups of ten per site under five gallon buckets. After five minutes, the buckets were removed, the cylinder was placed over the area, and the vacuum procedure was accomplished. Recapture of marked beetles and damsel bugs varied from 76% to 85% of those released.

Statistical methods

The square root transformation consistently improved the stability of the variance of the means of the arthropod data and was applied to the data before statistical analysis. For each insect and planting period, treatments were compared on individual dates using the strip-plot procedure (SAS version 6.12, SAS Institute Inc.). If the variance/covariance structure was appropriate, the data for each insect were also analyzed across sampling dates for each planting period as described in chapter two. During cover-crop incorporation and seedbed preparation for late broccoli plantings, spider and harvestmen samples were only taken from the early broccoli plantings. When these data sets were analyzed on single calendar dates, a two-tailed, paired t-test was used to separate the means.

RESULTS

Over three years, 12,114 spiders and harvestmen representing 42 taxa were collected in pitfall traps and vacuum samples in the two broccoli cropping systems. The maximum spider plus harvestmen density reached in either cropping systems was approximately 20 individuals per square meter based on vacuum sampling during daylight hours (Tables 3.1-3.4 and Figures 3.1-3.4). The majority of the spiders collected in pitfall traps (59%) and vacuum samples (68%) were Linyphiidae. The two most common linyphiid species were *Erigone dentosa* O.P. Cambridge and *Lepthyphantes tenuis* (Blackwall). *E. dentosa* represented 50% of all individuals collected in pitfall traps and 33% of the individuals collected in vacuum samples. *L. tenuis* represented 8% of the individuals collected in pitfall traps and 17% of the individuals collected in vacuum samples. A single species of harvestmen, *Phalangium opilio* L. (Opiliones: Phalangiidae), represented 19% of the pitfall samples and 17% of the vacuum samples during the three year study. *Tricholathys hirsutipes* Banks (Araneae: Dictynidae) represented 17% of the pitfall samples, but only 2% of the vacuum samples. *Tetragnatha laboriosa* Hentz (Araneae: Tetragnathidae) represented 8% of the vacuum samples but less than 1% of the pitfall samples. *E. dentosa, P. opilio, L. tenuis, T. hirsutipes*, and *T. laboriosa* represented 94% of the total individuals collected over the three years in pitfall traps. The five species represented 76% of the total individuals collected in vacuum samples over the three years (Tables 3.1-3.4).

When adjusted for yearly sampling effort, *T. hirsutipes* activity-density measured by pitfall captures increased from 1994 to 1996 while the activity density of *Dysdera crocata* C.L. Koch decreased. The density of *T. laboriosa* collected with vacuum sampling increased over the three years. The abundance of *E. dentosa* and overall dominance of the Linyphiidae in the two cropping systems remained about the same over the three years. Lycosidae species were mostly

Table 3.1 Spiders and Harvestmen Captured in a Broccoli Relay Strip-cropping System Pitfall Trapping - Corvallis, Oregon 1994 to 1996

	1994	1995	1996
Dictynidae			
Trichlolathys hirsutipes	508	641	959
Dictyna species	0	1	0
Cybius species	1	0	0
Amaurobidae			
Callobius species	32	12	0
Dysderidae			
Dysdera crocata	195	43	5
Theridiidae			
Theridion lawrencei	1	0	0
Theridion californicum	1	0	0
Theridion differenes	1	0	0
Dipoena nigra	0	1	0
Enoplognatha ovata	1	0	0
Linyphiidae			
Leptyphantes tenuis	621	173	150
Erigone dentosa	2800	1748	1500
Erigone species	91	38	48
Pityohyphantes brachygynus	0	2	0
Prolinyphia species	1	1	0
Ceraticelus vesperus	0	1	0
Other Linyphiidae	11	2	0
Araneidae			
Metellini curtisi	1	0	0
Nucterea species	0	1	0
Other Araneidae	1	1	0

	1994	1995	1996
Agelenidae			
Agelenidae species	6	3	1
Mimetidae			
Mimetus species	1	0	0
Lycosidae			
Pardosa vancouveri	1	0	0
Pardosa dorsuncata	1	0	0
Pardosa sternalis	1	0	3
Pardosa (juveniles)	64	12	9
Schizocosa species	5	2	1
Other Lycosidae	4	2	0
Oxyopidae			
Oxyopes salticus	5	6	1
Gnaphosidae			
Drassodes species	22	22	26
Clubionidae			
Clubiona species	1	0	9
Castianeira species	2	0	0
Anyphaenidae			
Anyphaena pacifica	1	0	0
Thomisidae			
Misumenops celer	7	3	0
Misumena vatia	1	0	0
Xysticus cunctator	8	3	0
Xysticus species	1	0	0

	1994	1995	1996
Phildromidae			
Tibellus oblongus	1	0	0
Philodromus spectabilis	1	0	0
Philodromus oneida	1	0	0
Philodromus species	1	0	0
Salticidae			
Evarcha hoyi	1	0	0
Phidippus johnsoni	1	0	0
Metaphidippus aeneolus	1	0	0
Eris species	1	0	0
Tetragnathidae			
Tetragnatha laboriosa	5	0	3
Spiders Species			
unknown	0	7	0
Phalangida-Phalangiidae			
Phalangium opilio	1508	596	160
Annual Totals			
Pitfalls	1260	720	882
Pitfall Days	3276	1440	1764
Individuals	5918	3321	2875
Taxa	42	24	14

Table 3.2 Spider and Harvestmen Families in a Broccoli Cover Crop Relay
Pitfall Percentages - Corvallis, Oregon 1994 to 1996

	Totals				Percent			
Taxa	**1994**	**1995**	**1996**	**1994-96**	**1994**	**1995**	**1996**	**1994-96**
Linyphiidae	3524	1965	1698	7187	59.55	59.29	59.06	59.36
Phylangiidae	1508	596	160	2264	25.48	17.98	5.57	18.70
Dictynidae	509	642	959	2110	8.60	19.37	33.36	17.43
Dysderidae	195	43	5	243	3.30	1.30	0.17	2.01
Lycosidae	76	16	13	105	1.28	0.48	0.45	0.87
Gnaphosidae	22	22	26	70	0.37	0.66	0.90	0.58
Amaurobidae	32	12	0	44	0.54	0.36	0.00	0.36
Thomisidae	17	6	0	23	0.29	0.18	0.00	0.19
Oxyopidae	5	6	1	12	0.08	0.18	0.03	0.10
Clubionidae	3	0	9	12	0.05	0.00	0.31	0.10
Agelenidae	6	3	1	10	0.10	0.09	0.03	0.08
Tetragnathidae	5	0	3	8	0.08	0.00	0.10	0.07
Theridiidae	4	1	0	5	0.07	0.03	0.00	0.04
Phildromidae	4	0	0	4	0.07	0.00	0.00	0.03
Salticidae	4	0	0	4	0.07	0.00	0.00	0.03
Araneidae	2	2	0	4	0.03	0.06	0.00	0.03
Mimetidae	1	0	0	1	0.02	0.00	0.00	0.01
Anyphaenidae	1	0	0	1	0.02	0.00	0.00	0.01

Table 3.3 Spiders and Harvestmen Captured in a Broccoli Relay Vacuum Sampling - Corvallis, Oregon 1994 to 1996

	1994	1995	1996
Dictynidae			
Trichlolathys hirsutipes	6	21	17
Dictyna species	0	1	2
Cybius species	0	0	0
Amaurobidae			
Callobius species	1	1	10
Dysderidae			
Dysdera crocata	2	0	2
Theridiidae			
Theridion lawrencei	0	0	0
Theridion californicum	2	7	2
Theridion differenes	0	0	0
Dipoena nigra	0	1	0
Enoplognatha ovata	6	2	3
Linyphiidae			
Leptyphantes tenuis	88	131	213
Erigone dentosa	77	352	416
Erigone species	10	104	177
Pityohyphantes brachygynus	0	0	0
Prolinyphia species	0	1	0
Ceraticelus vesperus	0	0	0
Other Linyphiidae	12	8	3
Araneidae			
Metellini curtisi	0	0	1
Nucterea species	0	1	0
Other Araneidae	0	0	1

	1994	1995	1996
Agelenidae			
Agelenidae species	0	0	0
Mimetidae			
Mimetus species	0	0	0
Lycosidae			
Pardosa vancouveri	0	3	0
Pardosa dorsuncata	0	3	0
Pardosa sternalis	0	0	0
Pardosa (juveniles)	0	4	9
Schizocosa species	0	0	0
Other Lycosidae	0	0	1
Oxyopidae			
Oxyopes salticus	0	0	0
Gnaphosidae			
Drassodes species	0	0	0
Clubionidae			
Clubiona species	0	4	0
Castianeira species	1	8	2
Anyphaenidae			
Anyphaena pacifica	0	1	0
Thomisidae			
Misumenops celer	7	4	3
Misumena vatia	0	1	0
Xysticus cunctator	8	1	1
Xysticus species	0	0	1

	1994	1995	1996
Phildromidae			
Tibellus oblongus	0	2	0
Philodromus spectabilis	0	0	0
Philodromus oneida	0	0	0
Philodromus species	0	0	0
Salticidae			
Evarcha hoyi	0	2	2
Phidippus johnsoni	0	0	0
Metaphidippus aeneolus	0	0	0
Eris species	0	0	0
Tetragnathidae			
Tetragnatha laboriosa	27	51	131
Spiders Species			
unknown	78	33	52
Phalangida-Phalangiidae			
Phalangium opilio	43	173	183
Annual Totals			
Vacuum Samples	464	698	936
Individuals Collected	368	920	1232
Taxa Collected	13	25	21

Table 3.4 Spider and Harvestmen Families in a Broccoli Cover Crop Relay Vacuum Sampling (Percentages) - Corvallis, Oregon 1994 to 1996

	Annual Totals				Annual Percentages			
Taxa	1994	1995	1996	1994-96	1994	1995	1996	1994-96
Linyphiidae	187	629	809	1625	64.48	68.37	68.56	67.99
Phylangiidae	43	173	183	399	14.83	18.80	15.51	16.69
Tetragnathidae	27	51	131	209	9.31	5.54	11.10	8.74
Dictynidae	6	22	19	47	2.07	2.39	1.61	1.97
Thomisidae	15	6	5	26	5.17	0.65	0.42	1.09
Theridiidae	8	10	5	23	2.76	1.09	0.42	0.96
Lycosidae	0	10	10	20	0.00	1.09	0.85	0.84
Clubionidae	1	12	2	15	0.34	1.30	0.17	0.63
Amaurobidae	1	1	10	12	0.34	0.11	0.85	0.50
Dysderidae	2	0	2	4	0.69	0.00	0.17	0.17
Salticidae	0	2	2	4	0.00	0.22	0.17	0.17
Araneidae	0	1	2	3	0.00	0.11	0.17	0.13
Phildromidae	0	2	0	2	0.00	0.22	0.00	0.08
Anyphaenidae	0	1	0	1	0.00	0.11	0.00	0.04
Gnaphosidae	0	0	0	0	0.00	0.00	0.00	0.00
Agelenidae	0	0	0	0	0.00	0.00	0.00	0.00
Oxyopidae	0	0	0	0	0.00	0.00	0.00	0.00
Mimetidae	0	0	0	0	0.00	0.00	0.00	0.00

Figure 3.1 Spider and Harvestmen Families in a Broccoli Cover Crop Relay - Corvallis, Oregon 1994-1996

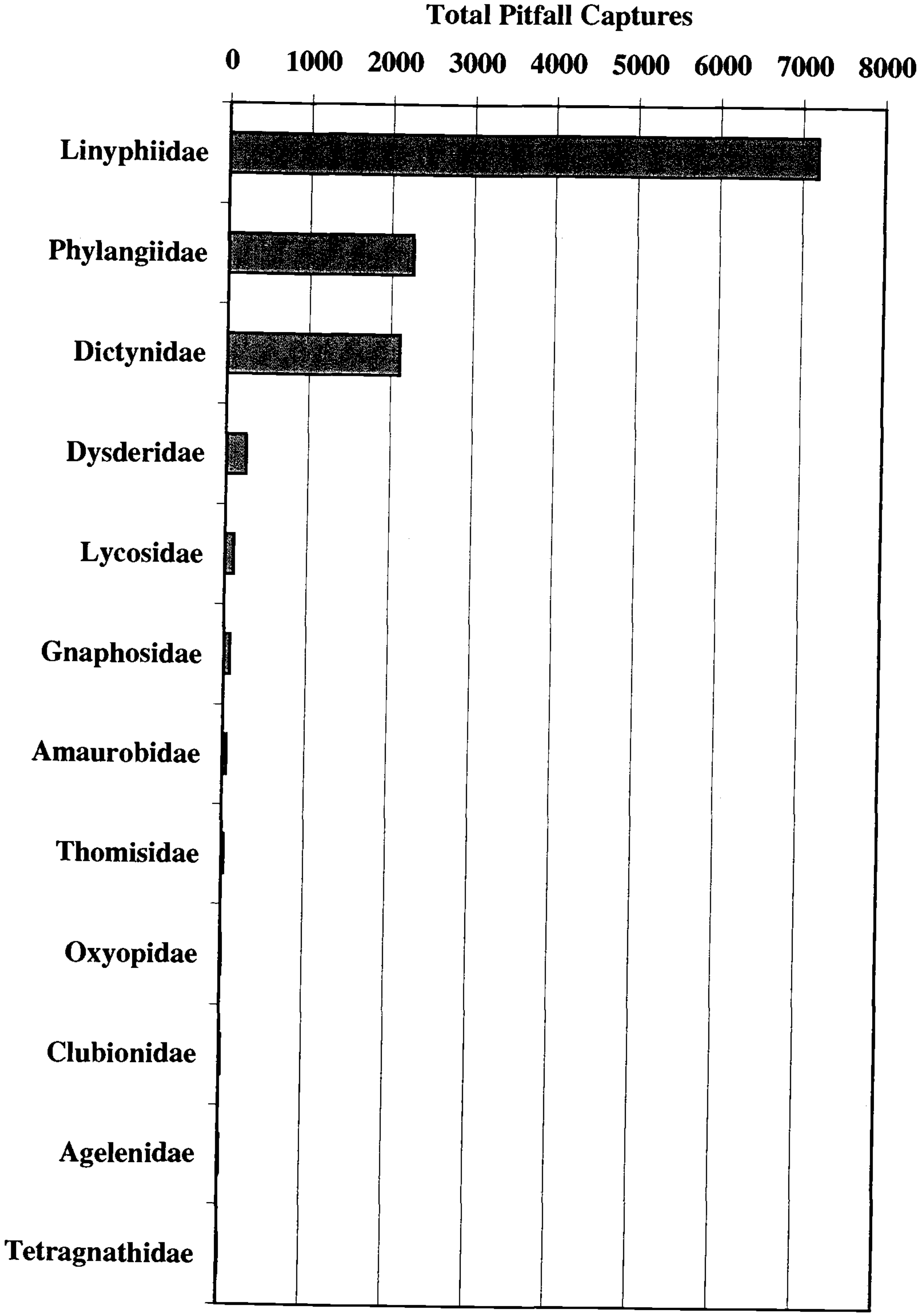


Figure 3.2 Spiders and Harvestmen in a Broccoli Cover Crop Relay - Corvallis, Oregon 1994 to 1996

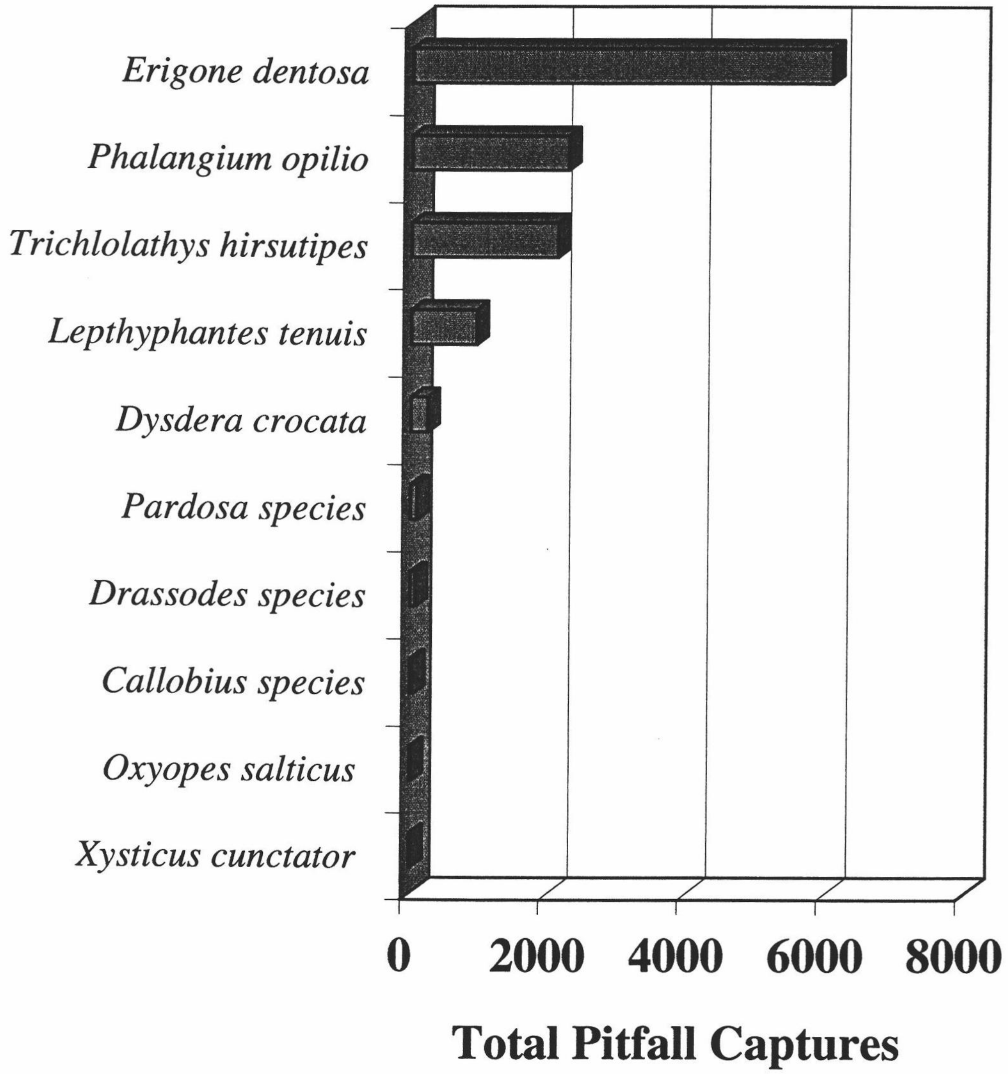


Figure 3.3 Spider and Harvestmen Families in a Broccoli Relay Strip-cropping System Corvallis, Oregon 1994-1996

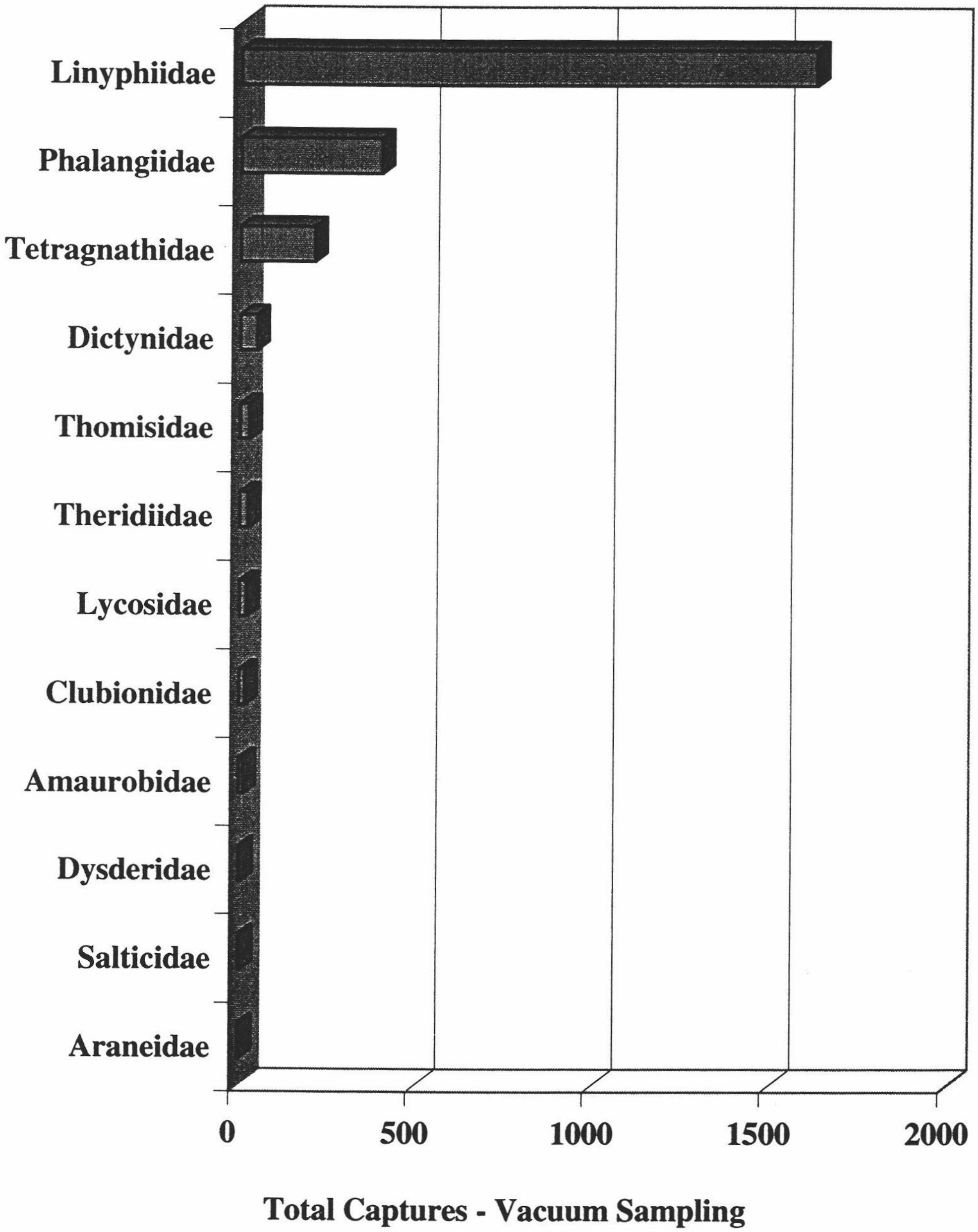
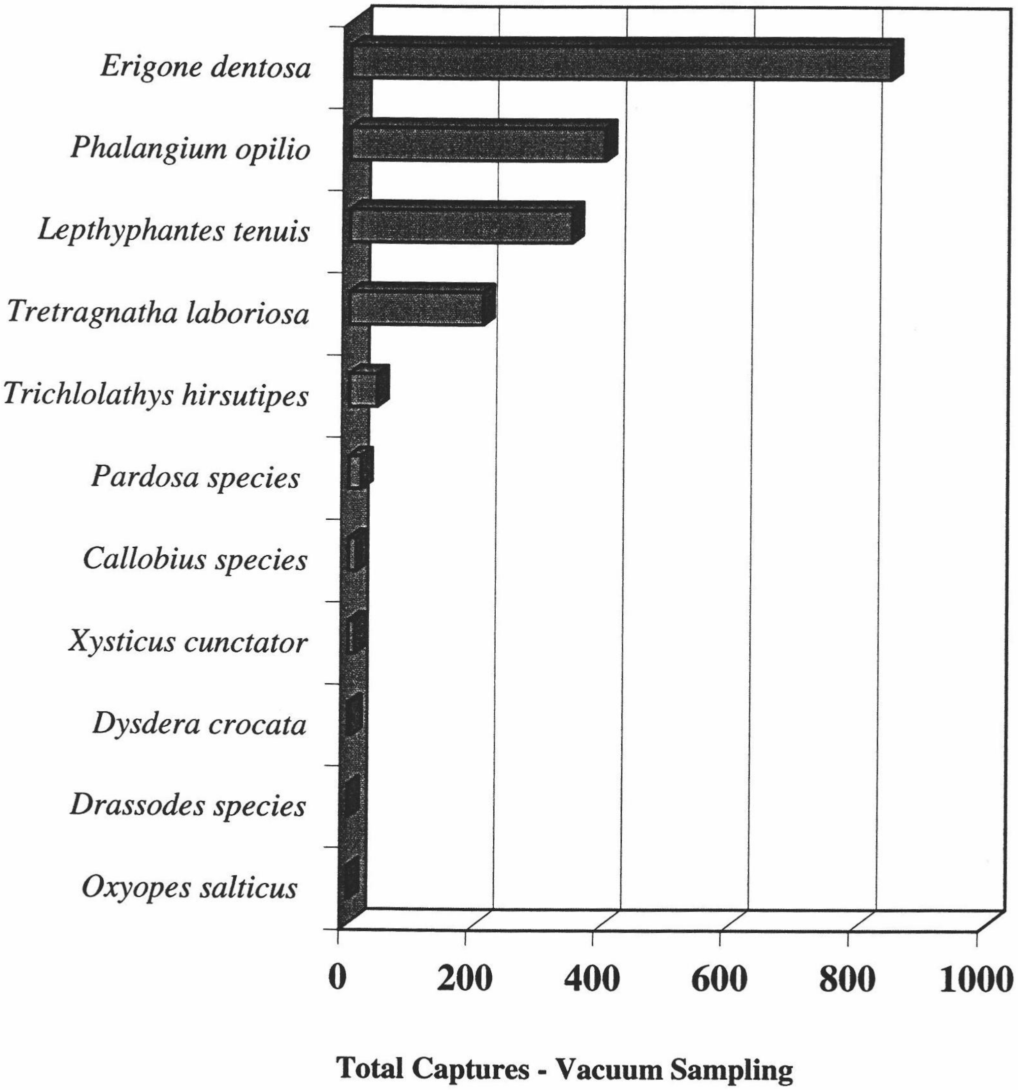


Figure 3.4 Spiders and Harvestmen in a Broccoli Relay Strip-cropping System Corvallis, Oregon 1994 to 1996



caught in the cover-crop and were uncommon in both cropping systems (Table 3.5-3.6). The majority of the lycosids caught in pitfall traps were juvenile *Pardosa* species (Araneae: Lycosidae).

E. dentosa density was high early in spring and through out the growing season. The activity-density of *E. dentosa* as measured by pitfall traps was equal or higher in the relay strip-cropped broccoli compared to clean-tilled broccoli on 16 out of 23 sampling dates over three years (Table 3.7, Figures 3.5, 3.6, and 3.7). When pitfall trap counts for *E. dentosa* were analyzed on single dates, the differences between the broccoli treatments were rarely statistically significant ($P<0.05$, strip plot analysis). When the data were analyzed across dates for each sampling period, *E. dentosa* activity-density (spiders per trap per day) as measured in pitfall traps was higher in the relay strip-cropped broccoli compared with clean-tilled broccoli during the late planting periods of 1994 ($P = 0.0346$, $F = 5.28$, $df = 1,17$) and 1996 ($P = 0.0209$, $F = 6.48$, $df = 1,17$). When vacuum sampling was used, the density of *E. dentosa* varied from 0 to 10.37 spiders per square meter in the cover-crop and was never significantly higher in the relay strip-cropped broccoli compared with the clean-tilled broccoli. From mid to late September each year, many *E. dentosa* were captured in pitfalls and vacuum samples taken on bare ground areas (Table 3.8, Figures 3.8, 3.9, and 3.10).

L. tenuis counts in pitfall traps were highest in the early spring, declined in the middle of the summer, and increased slightly in the fall. Pitfall trap counts of *L. tenuis* were consistently highest in the cover-crop strips (Table 3.9, Figures 3.11, 3.12, and 3.13). When vacuum sampling was used, the density of *L. tenuis* in the cover-crop strips varied from 0 to 10.63 spiders per square meter. Regardless of the sampling technique, the density of *L. tenuis* was never significantly different in the relay strip-cropped broccoli compared with clean-tilled broccoli. *L. tenuis* was rarely captured in pitfalls or vacuum samples in the bare ground areas (Table 3.10, Figures 3.14, 3.15, and 3.16).

Table 3.5 Impact of Relay Strip-cropping on Lycosidae in Broccoli (Pitfall) 1994-1996

	Spiders per Pitfall per Day *				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0.01 ± 0.01 a	0 a	0.01 ± 0.01 a	0.01 ± 0.01 a	0
Broccoli Clean-till	0 a	0.02 ± 0.01 a	0 a	0.01 ± 0.01 a	0
Cover Crop	0.03 ± 0.02 a	0.08 ± 0.05 a	0.11 ± 0.00 b	0.20 ± 0.08 b	0.10 ± 0.03
Bare Ground	0 a	0 a	0 a	0 a	0
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0	0	0	0.02 ± 0.02 a	
Broccoli Clean-till	0	0.04 ± 0.02	0	0.06 ± 0.03 a	
Cover Crop	0	0	0	0.02 ± 0.02 a	
Bare Ground	0	0	0.02 ± 0.02	0.04 ± 0.02 a	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0.01 ± 0.01	0 a	0.03 ± 0.03 a		
Broccoli Clean-till	0.01 ± 0.01	0.04 ± 0.03 a	0.01 ± 0.01 a		
Cover Crop	0.01 ± 0.01	0.06 ± 0.06 a	na		
Bare Ground	0	0 a	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0	0	0		
Broccoli Clean-till	0.01 ± 0.01	0	0		
Cover Crop	na	0	0		
Bare Ground	na	0	0		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	0	0	0.04 ± 0.01 a	0	
Broccoli Clean-Till	0	0.01 ± 0.01	0.01 ± 0.01 a	0	
Cover Crop	0.04 ± 0.04	0	na	na	
Bare Ground	0	0	na	na	
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**	
Broccoli Relay	0	0	0 a	0.02 ± 0.02 a	
Broccoli Clean-Till	0	0	0.03 ± 0.03 a	0.02 ± 0.02 a	
Cover Crop	na	0	0.02 ± 0.02 a	0 a	
Bare Ground	na	0	0 a	0 a	

* Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05), strip plot analysis, n=4.

Table 3.6 Impact of Relay Strip-cropping on Lycosidae in Broccoli (Vacuum) 1994-96

	Spiders per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0	0
Broccoli Clean Till	0	0	0	0
Cover Crop	0	na	0	na
Bare Ground	0	na	0	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0
Broccoli Clean Till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0	0.14 ± 0.14 a	0	0
Broccoli Clean-Till	0	0 a	0.14 ± 0.14	0
Cover Crop	0	0.56 ± 0.39 a	na	na
Bare Ground	0	0 a	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0	0.28 ± 0.16 a	
Broccoli Clean-Till	0	0.19 ± 0.19	0 a	
Cover Crop	na	0	0 a	
Bare Ground	na	0	0.14 ± 0.14 a	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0 a	0	0.28 ± 0.16
Broccoli Clean Till	0	0 a	0	0
Cover Crop	0	0.56 ± 0.23 a	0.28 ± 0.28	na
Bare Ground	0	0.14 ± 0.14 a	0	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean Till	0	0	0	0.19 ± 0.19
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0

* Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05) strip plot analysis, n=4.

Table 3.7 Impact of Relay Strip-cropping on *E. dentosa* in Broccoli (Pitfall) Corvallis, OR 1994-96

	Spiders per Pitfall per Day *				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0.49 ± 0.12 a	0.71 ± 0.21 a	0.54 ± 0.13 a	2.06 ± 0.59 a	1.32 ± 0.10 a
Broccoli Clean-till	0.36 ± 0.02 a	0.67 ± 0.08 a	1.03 ± 0.33 a	1.97 ± 0.47 a	1.11 ± 0.24 a
Cover Crop	2.35 ± 0.29 b	2.22 ± 0.28 b	1.07 ± 0.24 a	2.86 ± 0.66 a	2.00 ± 0.50 a
Bare Ground	0.25 ± 0.06 a	0.09 ± 0.03 c	0.13 ± 0.04 b	0.11 ± 0.08 b	0.08 ± 0.05 b
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0.20 ± 0.04 a	0.59 ± 0.11 ab	0.19 ± 0.08 a	0.41 ± 0.07 ac	
Broccoli Clean-till	0.19 ± 0.13 a	0.31 ± 0.07 a	0.20 ± 0.02 a	0.20 ± 0.02 a	
Cover Crop	1.56 ± 0.47 b	1.69 ± 0.34 b	1.48 ± 0.36 b	1.06 ± 0.10 b	
Bare Ground	0.30 ± 0.16 a	0.35 ± 0.16 a	0.13 ± 0.04 a	0.52 ± 0.16 c	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	1.06 ± 0.17 ab	1.24 ± 0.27 ab	2.02 ± 0.50 a		
Broccoli Clean-till	0.57 ± 0.19 a	1.92 ± 0.46 a	1.38 ± 0.20 a		
Cover Crop	1.93 ± 0.48 b	1.49 ± 0.13 a	na		
Bare Ground	0.56 ± 0.06 a	0.49 ± 0.18 b	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0.72 ± 0.11 a	0.50 ± 0.15 a	0.83 ± 0.23 a		
Broccoli Clean-till	1.04 ± 0.13 a	0.68 ± 0.18 a	0.75 ± 0.26 a		
Cover Crop	na	2.78 ± 0.25 b	2.54 ± 0.59 b		
Bare Ground	na	1.57 ± 0.10 c	1.06 ± 0.07 a		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	0.17 ± 0.05 a	0.36 ± 0.20 a	0.19 ± 0.08 a	2.44 ± 0.47 a	
Broccoli Clean-Till	0.13 ± 0.06 a	0.68 ± 0.10 a	0.26 ± 0.10 a	1.93 ± 0.31 a	
Cover Crop	0.51 ± 0.17 a	0.50 ± 0.30 a	na	na	
Bare Ground	0.15 ± 0.04 a	0.13 ± 0.03 a	na	na	
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**	
Broccoli Relay	0.41 ± 0.10 a	2.48 ± 0.42 a	1.41 ± 0.40 a	0.37 ± 0.16 a	
Broccoli Clean-Till	0.17 ± 0.07 b	1.63 ± 0.35 a	0.61 ± 0.27 a	0.24 ± 0.08 a	
Cover Crop	na	1.65 ± 0.04 a	2.54 ± 0.60 b	1.06 ± 0.40 a	
Bare Ground	na	1.17 ± 0.06 a	2.85 ± 0.26 b	1.00 ± 0.05 a	

*** Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05), strip plot analysis, n=4.**

Figure 3.5 Impact of Relay Strip-cropping on *Erigone dentosa* in Broccoli (Pitfall Trapping) Corvallis, Oregon 1994

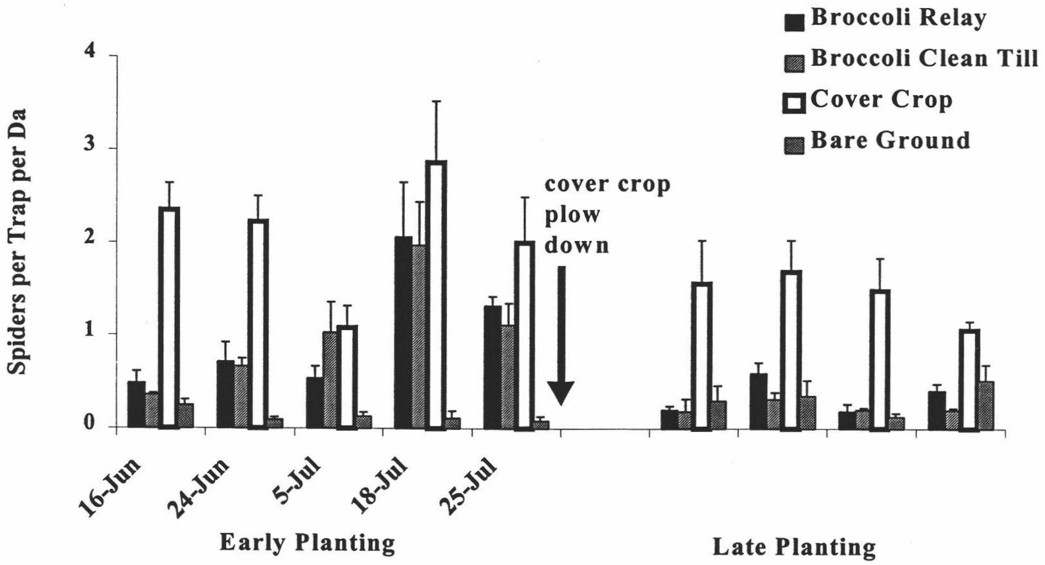


Figure 3.6 Response of *Erigone dentosa* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1995

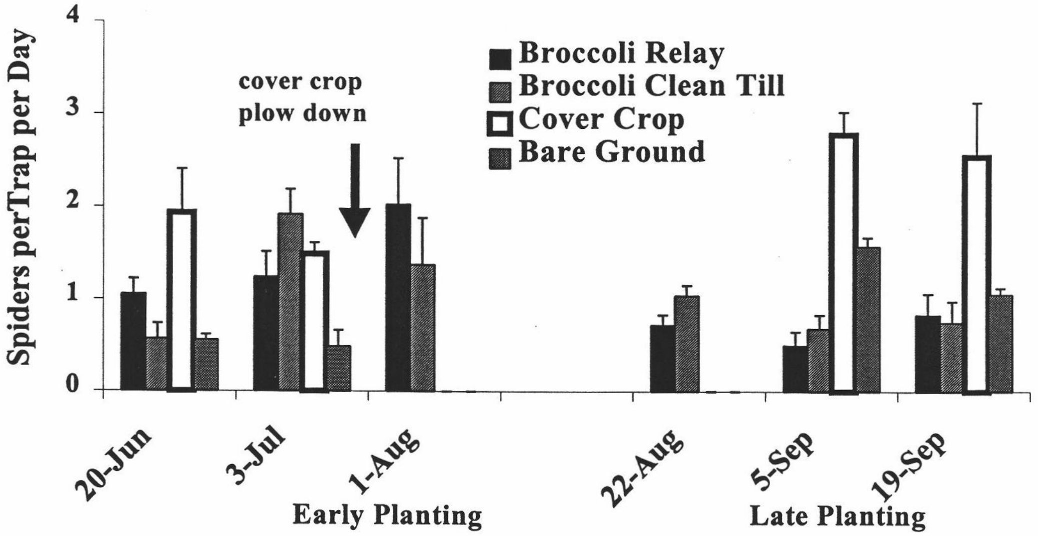


Figure 3.7 Response of *Erigone dentosa* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1996

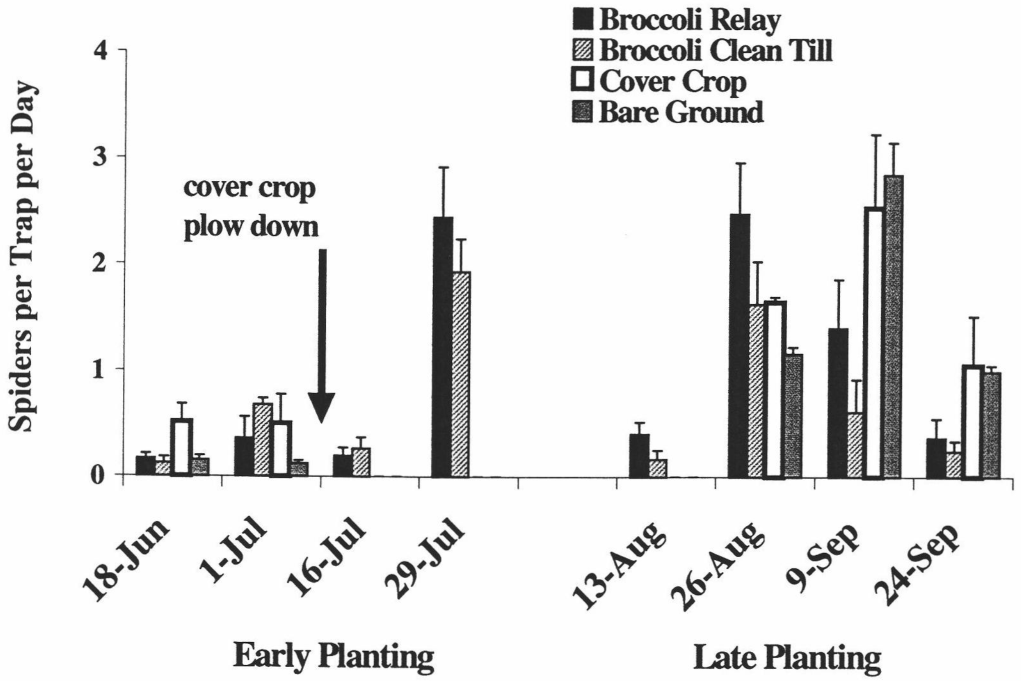


Table 3.8 Impact of Relay Strip-cropping on *E. dentosa* in Broccoli (Vacuum) Corvallis, OR 1994-96

	Spiders per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0.31 ± 0.31 a	0.56 ± 0.23 a	2.19 ± 0.60 a	0.42 ± 0.27 a
Broccoli Clean Till	0 a	0.97 ± 0.42 a	4.06 ± 0.94 a	0.83 ± 0.16 a
Cover Crop	2.50 ± 0.88 b	na	1.56 ± 0.60 a	na
Bare Ground	0.31 ± 0.31 a	na	0 b	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0.42 ± 0.36 a	0.42 ± 0.36 a	0 a	0.42 ± 0.36 a
Broccoli Clean Till	0 a	1.67 ± 0.95 a	0 a	0.42 ± 0.36 a
Cover Crop	0.42 ± 0.36 a	2.08 ± 1.30 a	2.08 ± 1.30 a	1.67 ± 0.72 a
Bare Ground	0 a	0.42 ± 0.36 a	0.42 ± 0.36 a	0.42 ± 0.36 a
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	1.53 ± 0.62 a	1.94 ± 0.53 a	4.58 ± 0.73 a	10.37 ± 0.32 a
Broccoli Clean-Till	1.94 ± 0.80 a	4.03 ± 1.00 a	6.39 ± 1.33 a	9.07 ± 1.79 a
Cover Crop	1.94 ± 0.53 a	2.08 ± 1.33 a	na	na
Bare Ground	0.56 ± 0.56 a	0.56 ± 0.39 a	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0.42 ± 0.27 a	0.56 ± 0.48 a	0.42 ± 0.42 a	
Broccoli Clean-Till	0.28 ± 0.28 a	0.19 ± 0.16 a	0.28 ± 0.28 a	
Cover Crop	na	2.22 ± 1.27 a	1.84 ± 0.94 a	
Bare Ground	na	1.85 ± 0.98 a	1.28 ± 0.73 a	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0.14 ± 0.14 a	1.81 ± 0.27 a	1.53 ± 0.62 a	3.89 ± 1.42 a
Broccoli Clean Till	0 a	3.61 ± 0.36 b	1.39 ± 0.66 a	5.97 ± 1.14 a
Cover Crop	1.39 ± 0.16 b	4.86 ± 1.05 b	2.19 ± 0.94 a	na
Bare Ground	0.14 ± 0.14 a	0.14 ± 0.14 c	0.63 ± 0.36 a	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	1.85 ± 0.58 a	1.11 ± 0.28 a	2.41 ± 0.58 a	2.04 ± 0.32 a
Broccoli Clean Till	5.37 ± 1.70 a	2.78 ± 1.00 a	3.15 ± 1.12 a	2.22 ± 0.96 a
Cover Crop	7.96 ± 0.85 a	3.52 ± 1.58 a	8.52 ± 1.53 a	9.26 ± 2.67 b
Bare Ground	1.67 ± 1.00 a	0.19 ± 0.16 a	5.19 ± 1.05 a	6.30 ± 0.58 ab

*Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05) strip plot analysis, n=4.

Figure 3.8 Response of *Erigone dentosa* to Habitat Choices in a Broccoli Cover Crop Relay (Vacuum Trapping) Corvallis, Oregon 1994

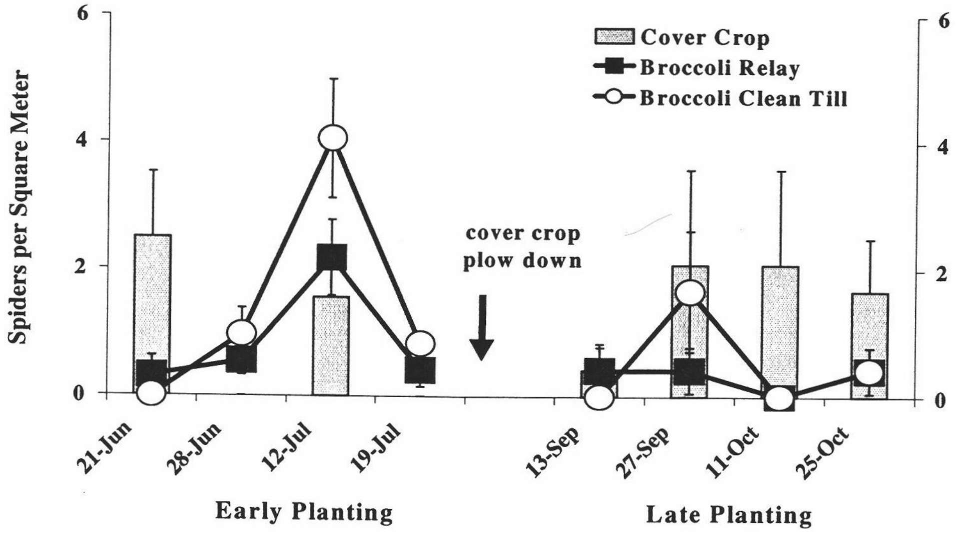


Figure 3.9 Impact of Relay Strip-cropping on *Erigone dentosa* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1995

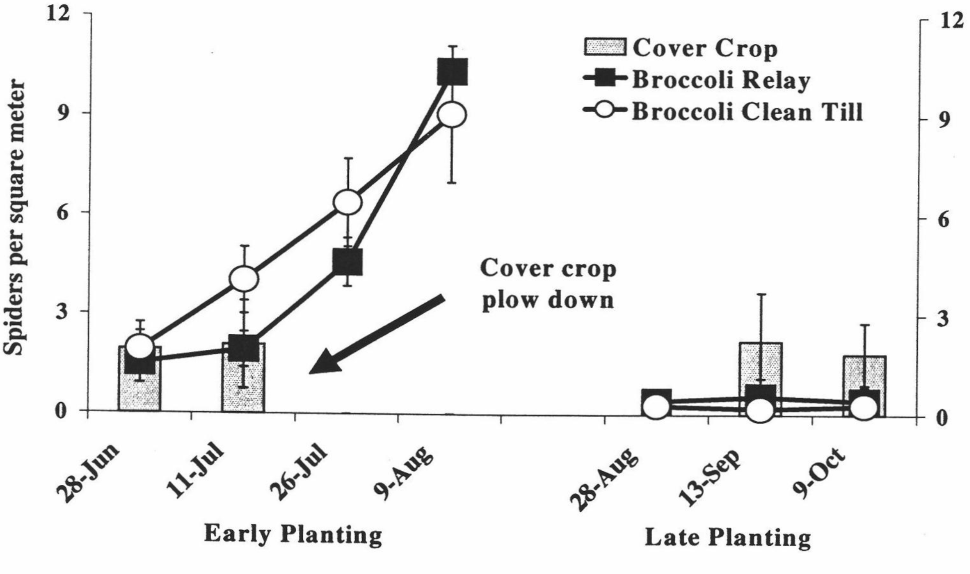


Figure 3.10 Impact of Relay Strip-cropping on *Erigone dentosa* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1996

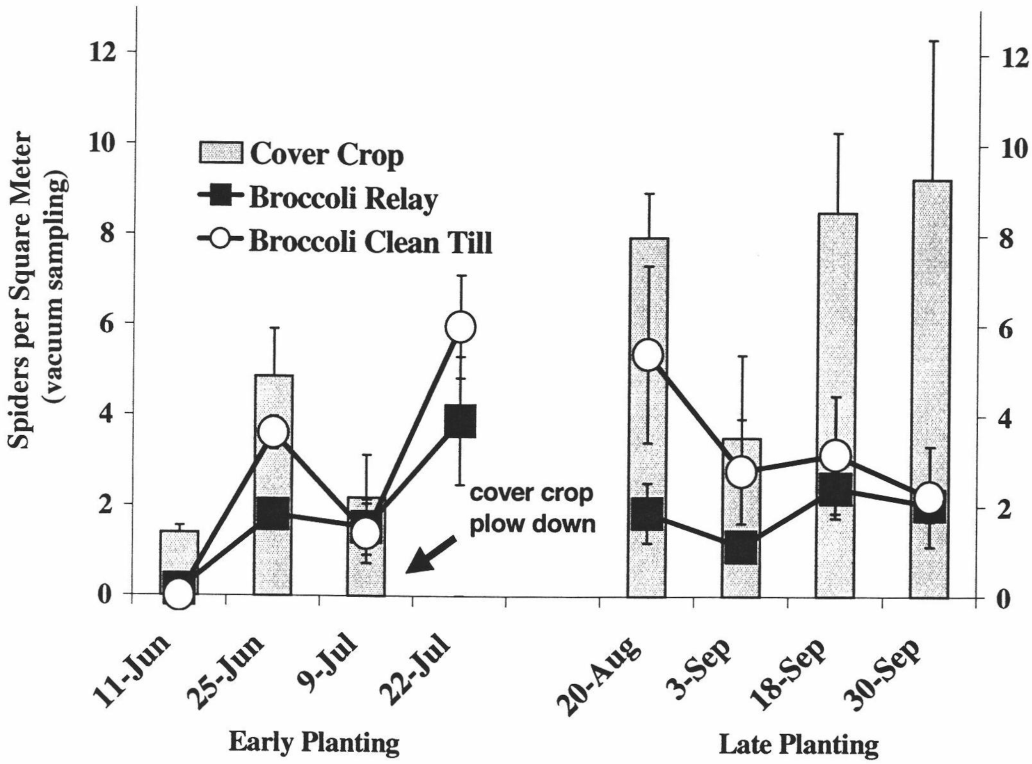


Table 3.9 Impact of Relay Strip-cropping on *L. tenuis* in Broccoli (Pitfall) Corvallis, OR 1994-96

	Spiders per Pitfall per Day *				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0.22 ± 0.06 a	0.52 ± 0.09 a	0.03 ± 0.02 a	0.13 ± 0.06 a	0.07 ± 0.05 a
Broccoli Clean-till	0.35 ± 0.08 a	0.49 ± 0.08 a	0.03 ± 0.02 a	0.06 ± 0.02 a	0.07 ± 0.03 a
Cover Crop	0.57 ± 0.18 a	0.83 ± 0.12 a	0.46 ± 0.08 b	0.51 ± 0.15 b	0.65 ± 0.09 b
Bare Ground	0 b	0.06 ± 0.03 b	0.01 ± 0.01 a	0.01 ± 0.01 a	0.01 ± 0.01 a
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0 a	0.02 ± 0.02 a	0.04 ± 0.02 a	0.04 ± 0.02 a	
Broccoli Clean-till	0 a	0.06 ± 0.03 a	0.04 ± 0.02 a	0.02 ± 0.02 a	
Cover Crop	0.06 ± 0.00 a	0.22 ± 0.06 a	0.07 ± 0.02 a	0.11 ± 0.03 a	
Bare Ground	0 a	0.00 ± 0.00 a	0.02 ± 0.02 a	0.02 ± 0.02 a	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0.03 ± 0.02 a	0.09 ± 0.03 a	0.30 ± 0.03 a	na	
Broccoli Clean-till	0.08 ± 0.02 a	0.09 ± 0.03 a	0.37 ± 0.03 a	na	
Cover Crop	0.03 ± 0.02 a	0.35 ± 0.07 b	na		
Bare Ground	0.01 ± 0.01 a	0.06 ± 0.02 a	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0.10 ± 0.03 a	0.04 ± 0.03 a	0.10 ± 0.03 a		
Broccoli Clean-till	0.13 ± 0.03 a	0.04 ± 0.01 a	0.08 ± 0.02 a		
Cover Crop	na	0.33 ± 0.10 b	0.19 ± 0.07 a		
Bare Ground	na	0 a	0.01 ± 0.01 b		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	0.07 ± 0.01 a	0 a	0.04 ± 0.03 a	0.10 ± 0.03 a	
Broccoli Clean-Till	0.07 ± 0.03 a	0.07 ± 0.03 a	0.03 ± 0.02 a	0.10 ± 0.03 a	
Cover Crop	0.49 ± 0.09 b	0.35 ± 0.08 b	na	na	
Bare Ground	0.01 ± 0.01 a	0 a	na	na	
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**	
Broccoli Relay	0.02 ± 0.02 a	0.17 ± 0.08 a	0.15 ± 0.04 a	0.04 ± 0.02 a	
Broccoli Clean-Till	0 a	0.04 ± 0.02 a	0.02 ± 0.02 a	0.06 ± 0.03 a	
Cover Crop	na	0.19 ± 0.04 a	0.19 ± 0.04 a	0.11 ± 0.03 a	
Bare Ground	na	0.07 ± 0.05 a	0.07 ± 0.05 a	0 a	

* Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05), strip plot analysis, n=4.

Figure 3.11 Response of *Lepthyphantes tenuis* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1994

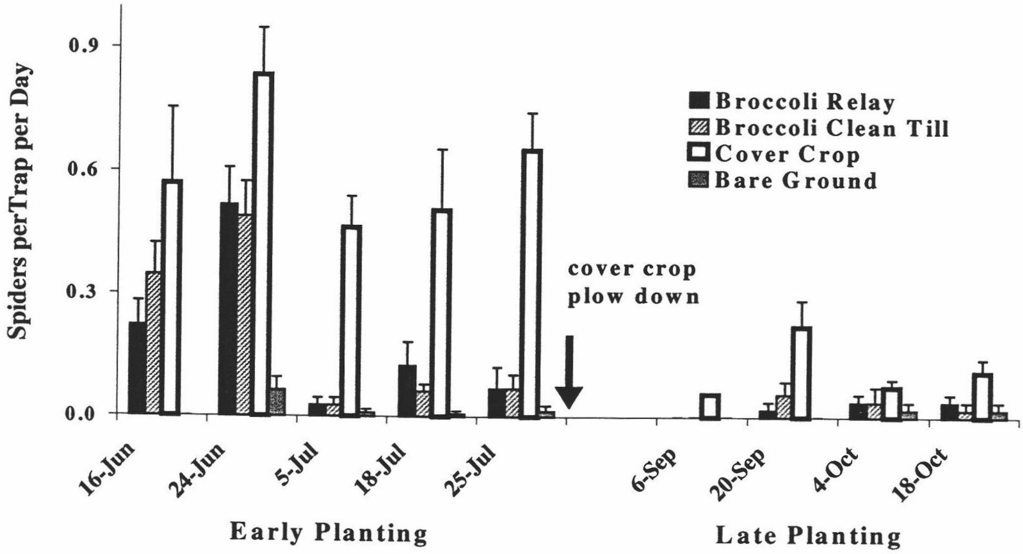


Figure 3.12 Response of *Lepthyphantes tenuis* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1995

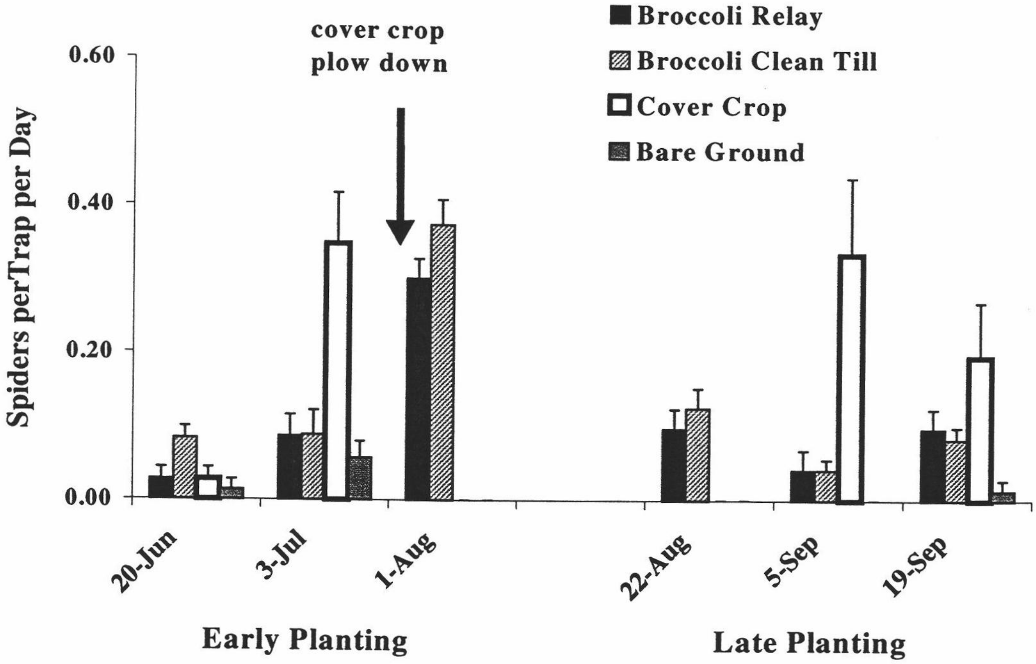


Figure 3.13 Response of *Lepthyphantes tenuis* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1996

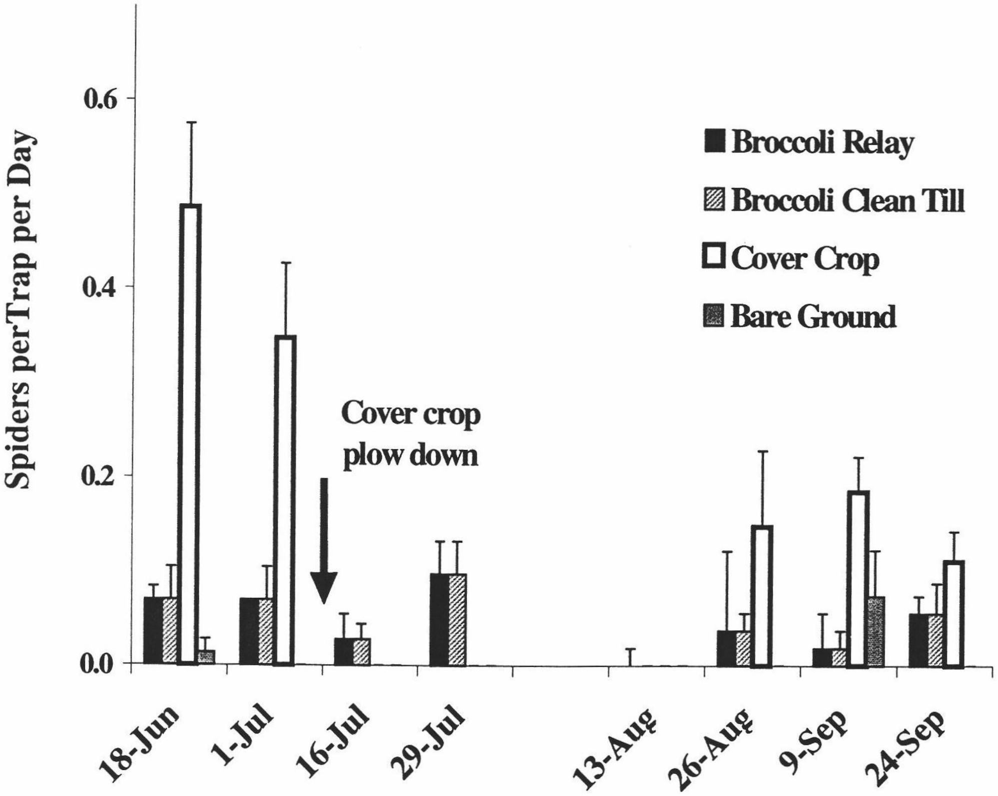


Table 3.10 Impact of Relay Strip-cropping on *L. tenuis* in Broccoli (Vacuum) 1994-96

	Spiders per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0 a	0.97 ± 0.27 a	0.31 ± 0.31 a	0 a
Broccoli Clean Till	0.63 ± 0.63 a	1.39 ± 0.58 a	0.31 ± 0.31 a	0.42 ± 0.14 b
Cover Crop	10.63 ± 1.65 b	na	1.25 ± 0.51 a	na
Bare Ground	0 a	na	0 a	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0.42 ± 0.42 a	0 a	0.42 ± 0.42 a	0.42 ± 0.42 a
Broccoli Clean Till	0.42 ± 0.42 a	0 a	0 a	0.42 ± 0.42 a
Cover Crop	0.42 ± 0.42 a	0 a	2.50 ± 0.72 b	0.42 ± 0.42 a
Bare Ground	0 a	0 a	0 a	0 a
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0 a	0.69 ± 0.27 a	0.14 ± 0.14 a	2.41 ± 0.49 a
Broccoli Clean-Till	0 a	0.69 ± 0.42 a	0.56 ± 0.23 a	1.67 ± 0.64 a
Cover Crop	0.69 ± 0.42 a	1.39 ± 0.36 a	na	na
Bare Ground	0 a	0 a	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0.69 ± 0.14 a	0.19 ± 0.19 a	0.87 ± 0.37 a	na
Broccoli Clean-Till	0.56 ± 0.39 a	0 a	0.69 ± 0.53 a	na
Cover Crop	na	0.74 ± 0.49 a	3.19 ± 0.94 b	
Bare Ground	na	0.19 ± 0.19 a	0 a	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0.14 ± 0.14 a	0.14 ± 0.14 a	0 a	0.14 ± 0.14 a
Broccoli Clean Till	0.14 ± 0.14 a	0.56 ± 0.23 a	0.28 ± 0.28 a	1.11 ± 0.45 a
Cover Crop	1.39 ± 0.66 b	7.50 ± 1.67 b	5.31 ± 1.39 b	na
Bare Ground	0 a	0.14 ± 0.14 a	0 a	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0.37 ± 0.37 a	0.37 ± 0.19 a	2.41 ± 0.81 a	1.48 ± 0.49 a
Broccoli Clean Till	0.19 ± 0.19 a	0.74 ± 0.74 a	1.11 ± 0.56 a	1.48 ± 0.19 a
Cover Crop	2.41 ± 0.37 a	0.93 ± 0.49 a	1.85 ± 0.37 a	3.33 ± 0.56 a
Bare Ground	0 a	0.19 ± 0.19 a	0 b	0 b

* Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05) strip plot analysis, n=4.

Figure 3.14 Impact of Relay Strip-cropping on *Lepthyphantes tenuis* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1994

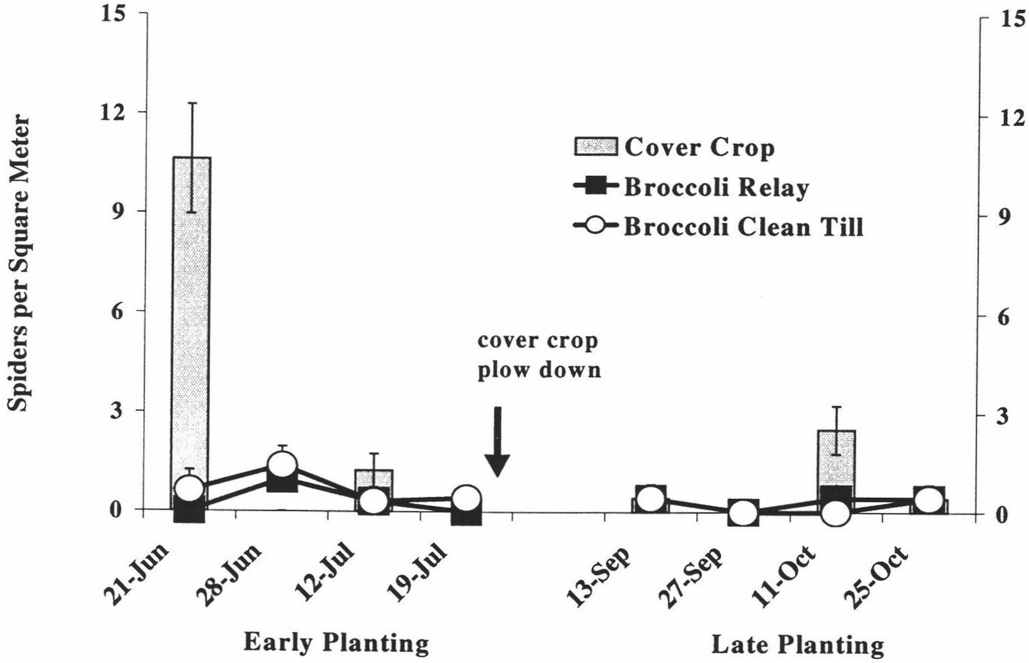


Figure 3.15 Impact of Relay Strip-cropping on *Lepthyphantes tenuis* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1995

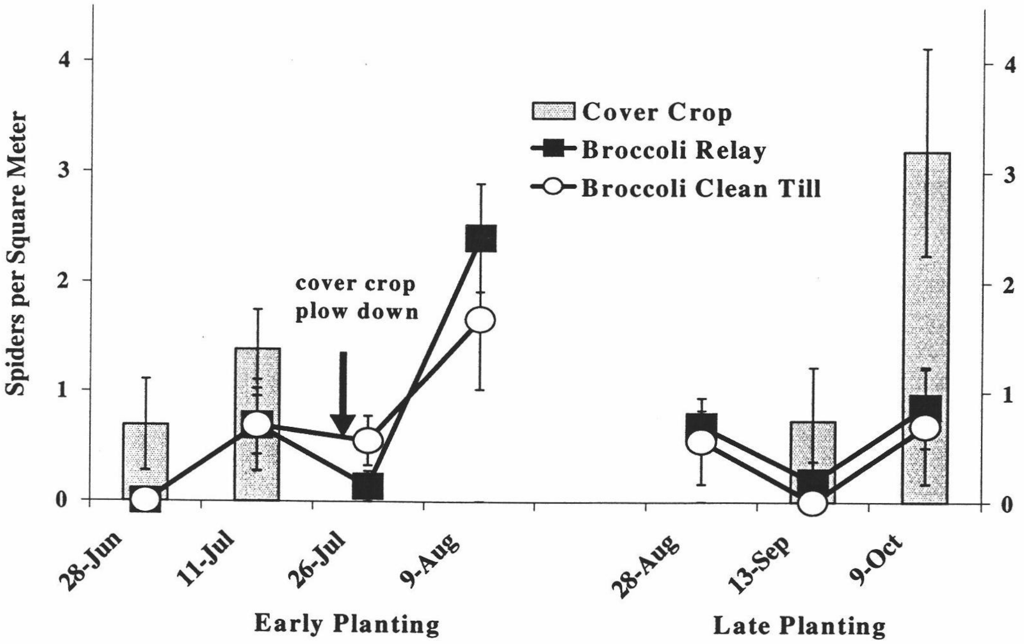
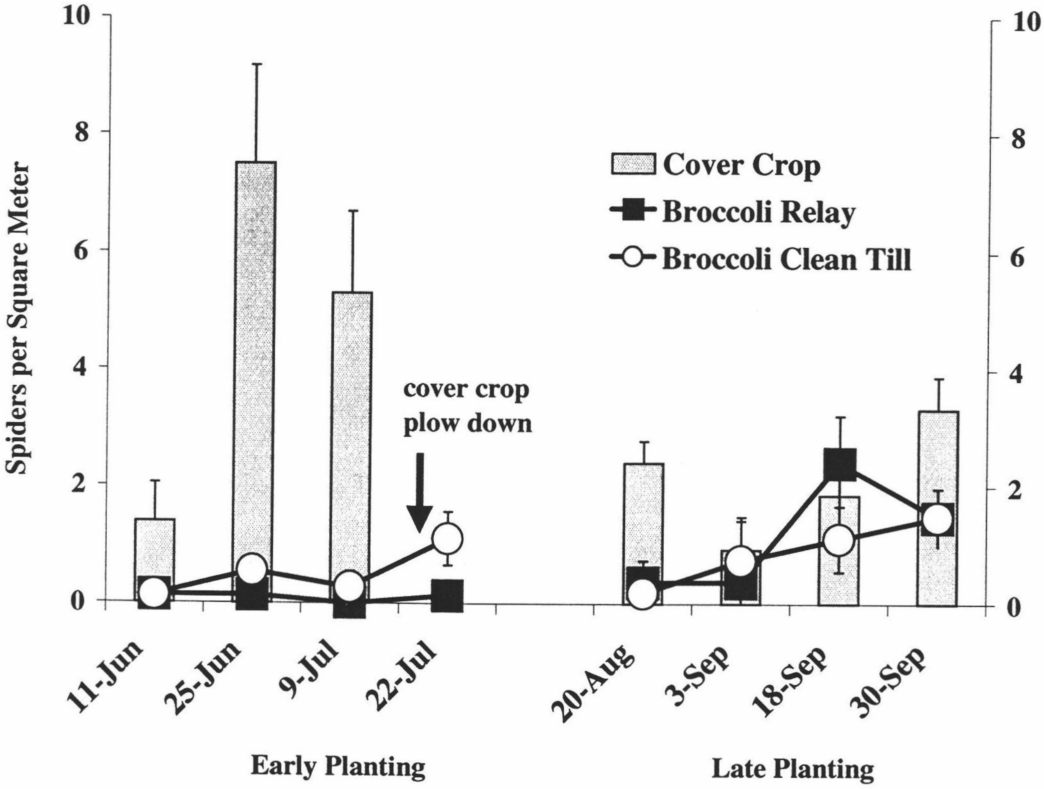


Figure 3.16 Impact of Relay Strip-cropping on *Lepthyphantes tenuis* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1996



P. opilio counts in pitfall traps were low in the early spring and increased steadily during the growing season. Pitfall trap counts of *P. opilio* were consistently highest in the cover-crop strips (Table 3.11, Figures 3.17, 3.18, and 3.19). When vacuum sampling was used, the density of *P. opilio* in the cover-crop strips varied from 0 to 5.80 harvestmen per square meter. When the data were analyzed across all dates in a given sampling period, *P. opilio* density was significantly higher in the relay strip-cropped broccoli compared with clean-till broccoli during the late planting period of 1994 as measured by pitfall trapping ($P = 0.0082$, $F = 8.81$, df = 1,18) and marginally higher in the late planting period of 1996 as measured by vacuum sampling ($P = 0.0586$, $F = 4.45$, df = 1,11). From late August through September each year, P. *opilio* was often captured in pitfalls and vacuum samples taken in bare ground areas (Table 3.12, Figures 3.20, 3.21, and 3.22).

T. laboriosa was rarely captured in pitfall traps (Table 3.13). When vacuum sampling was used, *T. laboriosa* densities varied from 0 to 3.33 spiders per square meter. *T. laboriosa* densities were generally highest in the cover-crop; their density was occasionally high in the broccoli. The density of *T. laboriosa* in the two broccoli cropping systems was similar. On one sampling date, the density of *T. laboriosa* was significantly higher ($P<0.05$, pair t-test, two tailed) in the clean-till broccoli (Table 3.14, Figures 3.23-3.25).

T. hirsutipes counts in pitfall traps were highest in the early spring, declined sharply after the end of July, and remained low in the late plantings in all three years. *T. hirsutipes* counts in pitfall traps were occasionally high in the bare ground compared with cover-crop strips and in the clean-till broccoli compared with relay strip-cropped broccoli. The differences between the broccoli treatments, however, were not statistically significant (Table 3.15, Figures 3.26-3.28). *T. hirsutipes* was rarely captured in vacuum samples. *T. hirsutipes* densities in vacuum samples varied from 0 to 0.83 spiders per square meter (Table 3.16).

Table 3.11 Impact of Relay Strip-cropping on *P. opilio* in Broccoli (Pitfall) Corvallis, OR 1994-96

	Harvestmen per Pitfall per Day *				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0.11 ± 0.06 a	0.36 ± 0.02 a	0.06 ± 0.02 a	0.07 ± 0.02 a	0.86 ± 0.17 a
Broccoli Clean-till	0.13 ± 0.03 a	0.34 ± 0.07 a	0.02 ± 0.02 a	0.16 ± 0.05 a	0.96 ± 0.27 a
Cover Crop	0.35 ± 0.08 a	0.84 ± 0.21 b	0.19 ± 0.10 a	0.87 ± 0.14 b	2.51 ± 0.84 a
Bare Ground	0.03 ± 0.03 a	0.19 ± 0.05 a	0.09 ± 0.04 a	0.21 ± 0.06 a	0.78 ± 0.23 a
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0.59 ± 0.05 a	1.00 ± 0.17 a	0.61 ± 0.27 a	0.11 ± 0.00 a	
Broccoli Clean-till	0.33 ± 0.12 a	0.65 ± 0.32 a	0.31 ± 0.14 a	0.04 ± 0.02 a	
Cover Crop	1.83 ± 0.50 b	2.06 ± 0.53 a	0.93 ± 0.59 a	0.24 ± 0.16 a	
Bare Ground	0.39 ± 0.14 a	0.74 ± 0.44 a	0.54 ± 0.16 a	0.07 ± 0.05 a	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0.01 ± 0.01 a	0.34 ± 0.13 a	0.13 ± 0.01 a		
Broccoli Clean-till	0.01 ± 0.01 a	0.46 ± 0.18 a	0.31 ± 0.22 a		
Cover Crop	0.25 ± 0.05 b	0.60 ± 0.21 a	na		
Bare Ground	0.03 ± 0.02 a	0.65 ± 0.20 a	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0.44 ± 0.21 a	0.10 ± 0.07 a	0.26 ± 0.06 ac		
Broccoli Clean-till	0.18 ± 0.04 a	0.11 ± 0.03 a	0.07 ± 0.04 a		
Cover Crop	na	1.60 ± 0.39 b	1.60 ± 0.16 b		
Bare Ground	na	0.96 ± 0.14 b	0.60 ± 0.17 c		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	0.07 ± 0.01 a	0.07 ± 0.03 a	0.01 ± 0.01 a	0.13 ± 0.13 a	
Broccoli Clean-Till	0.06 ± 0.02 a	0.07 ± 0.04 a	0.03 ± 0.02 a	0.04 ± 0.03 a	
Cover Crop	0.25 ± 0.04 b	0.22 ± 0.02 a	na	na	
Bare Ground	0.06 ± 0.02 a	0.00 ± 0.00 a	na	na	
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**	
Broccoli Relay	0.15 ± 0.02 a	0.15 ± 0.05 a	0.07 ± 0.04 a	0.11 ± 0.03 a	
Broccoli Clean-Till	0.04 ± 0.04 a	0.02 ± 0.02 a	0.05 ± 0.03 a	0.02 ± 0.02 a	
Cover Crop	na	0.04 ± 0.02 a	0.22 ± 0.06 a	0.26 ± 0.07 a	
Bare Ground	na	0.09 ± 0.05 a	0.20 ± 0.09 a	0.09 ± 0.05 a	

* Means ± SEM followed by the same letter within each sampling date are not significantly different ($P>0.05$), strip plot analysis, n=4.

Figure 3.17 Response of *Phalangium opilio* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1994

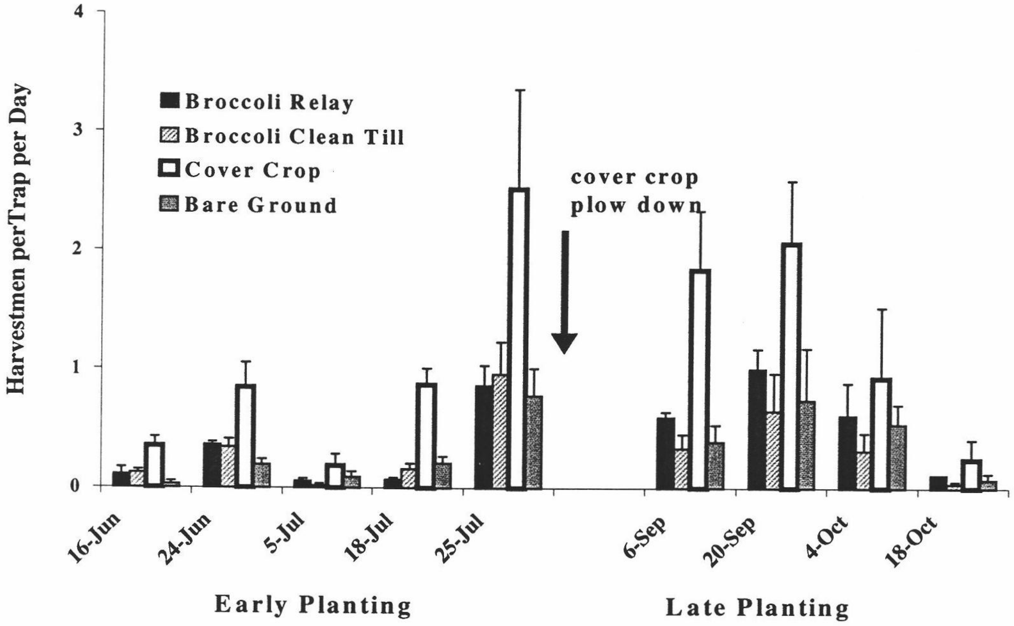


Figure 3.18 Response of *Phalangium opilio* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1995

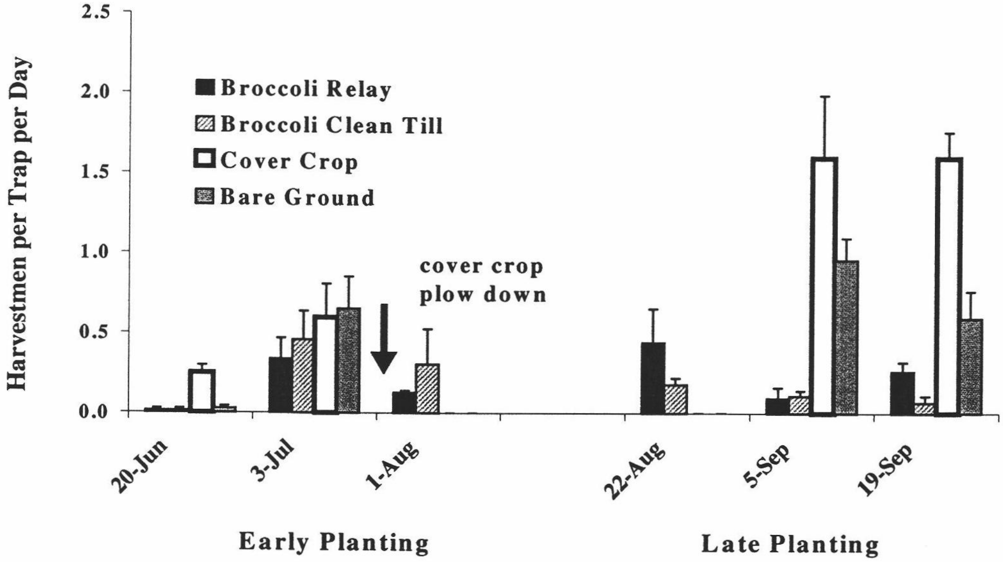


Figure 3.19 Response of *Phalangium opilio* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1996

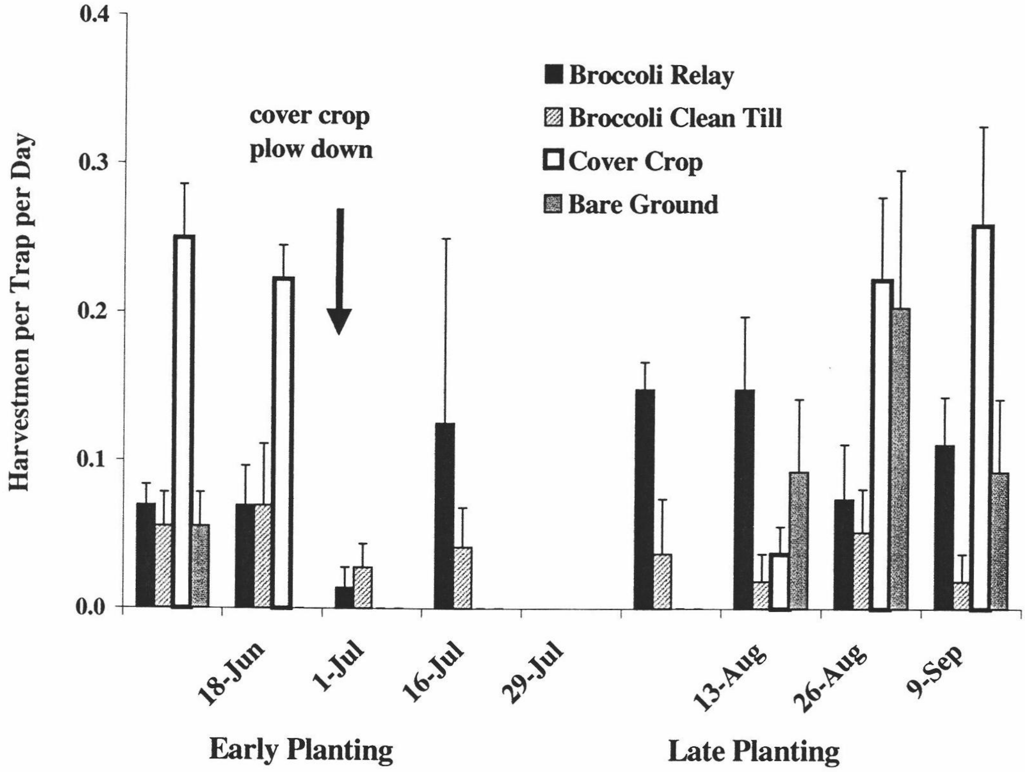


Table 3.12 Impact of Relay Strip-cropping on *P. opilio* in Broccoli (Vacuum) Corvallis, OR 1994-96

	Harvestmen per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0 a	0.14 ± 0.14 a	0 a	0.69 ± 0.14 a
Broccoli Clean Till	0.63 ± 0.36 a	0.14 ± 0.14 a	0 a	0.28 ± 0.16 a
Cover Crop	0.94 ± 0.60 a	na	0.31 ± 0.31 a	na
Bare Ground	0 a	na	0 a	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0.42 ± 0.42 a	0.42 ± 0.42 a	2.08 ± 1.10 a	1.67 ± 1.10 a
Broccoli Clean Till	0 a	0 a	0.83 ± 0.42 a	0.83 ± 0.83 a
Cover Crop	0.42 ± 0.42 a	2.50 ± 1.44 a	1.67 ± 1.67 a	0 a
Bare Ground	0.42 ± 0.42 a	0.42 ± 0.42 a	0 a	0 a
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0.97 ± 0.42 a	0.42 ± 0.42 a	0.56 ± 0.23 a	0.74 ± 0.49 a
Broccoli Clean-Till	0.42 ± 0.14 a	0 a	0.97 ± 0.42 a	2.04 ± 0.19 a
Cover Crop	4.03 ± 0.92 b	3.06 ± 1.03 b	na	na
Bare Ground	0 a	0.56 ± 0.23 a	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0.14 ± 0.14 a	0.56 ± 0.32 a	1.84 ± 0.82 a	
Broccoli Clean-Till	0.28 ± 0.16 a	0.56 ± 0.32 a	1.32 ± 0.52 a	
Cover Crop	na	5.74 ± 1.21 b	5.80 ± 1.92 b	
Bare Ground	na	0.37 ± 0.19 a	0.28 ± 0.16 a	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0.14 ± 0.14 a	0.14 ± 0.14 a	0.14 ± 0.14 a	0.56 ± 0.00 a
Broccoli Clean Till	0 a	0.14 ± 0.14 a	0.14 ± 0.14 a	0.14 ± 0.14 a
Cover Crop	0.42 ± 0.27 a	1.94 ± 0.48 b	3.13 ± 1.08 b	na
Bare Ground	0 a	0 a	0 a	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0.74 ± 0.19 a	0 a	1.30 ± 0.74 a	0.93 ± 0.49 a
Broccoli Clean Till	0.19 ± 0.19 a	0 a	0.56 ± 0.32 a	0.93 ± 0.67 a
Cover Crop	1.67 ± 0.32 a	2.04 ± 0.74 b	5.37 ± 1.13 b	3.52 ± 1.21 a
Bare Ground	0.93 ± 0.67 a	0.37 ± 0.19 a	0.56 ± 0.32 a	0 a

*Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05) strip plot analysis, n=4.

Figure 3.20 Impact of Relay Strip-cropping on *Phalangium opilio* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1994

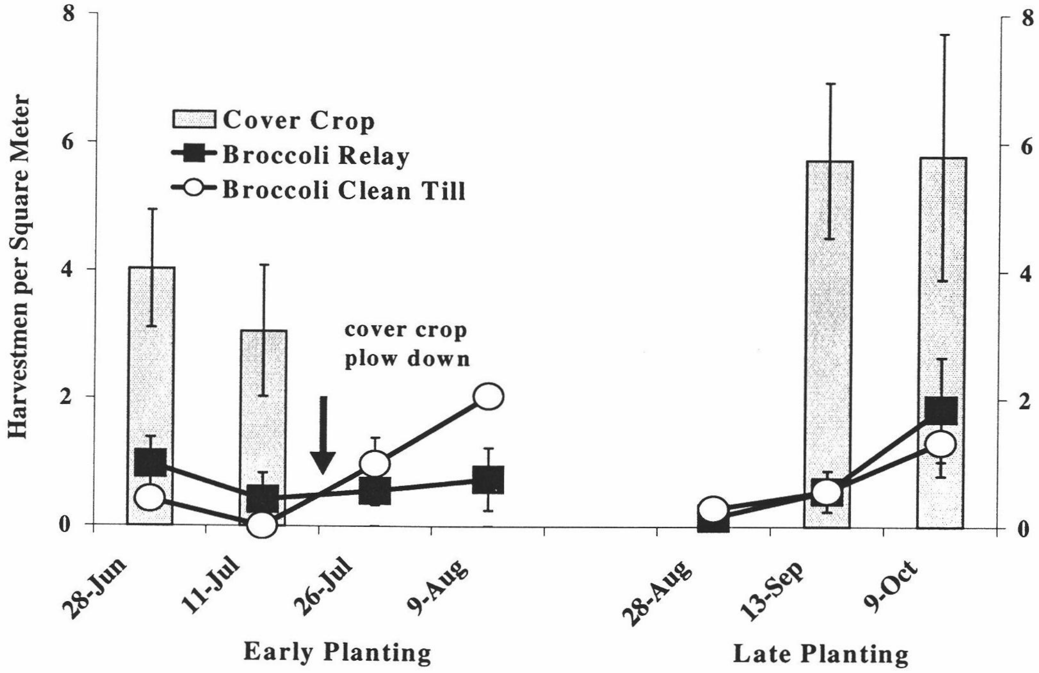


Figure 3.21 Impact of Relay Strip-cropping on *Phalangium opilio* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1995

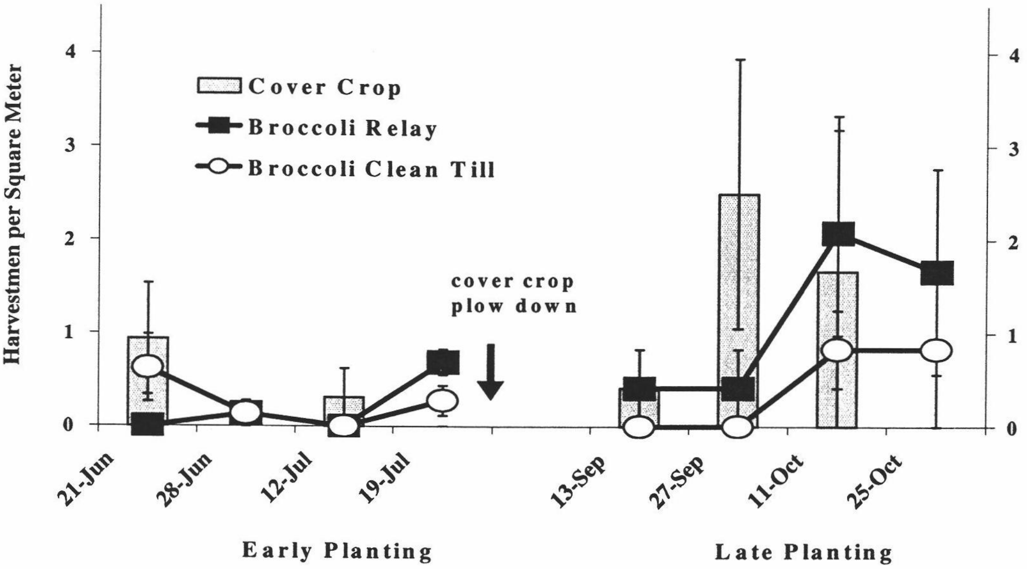


Figure 3.22 Impact of Relay Strip-cropping on *Phalangium opilio* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1996

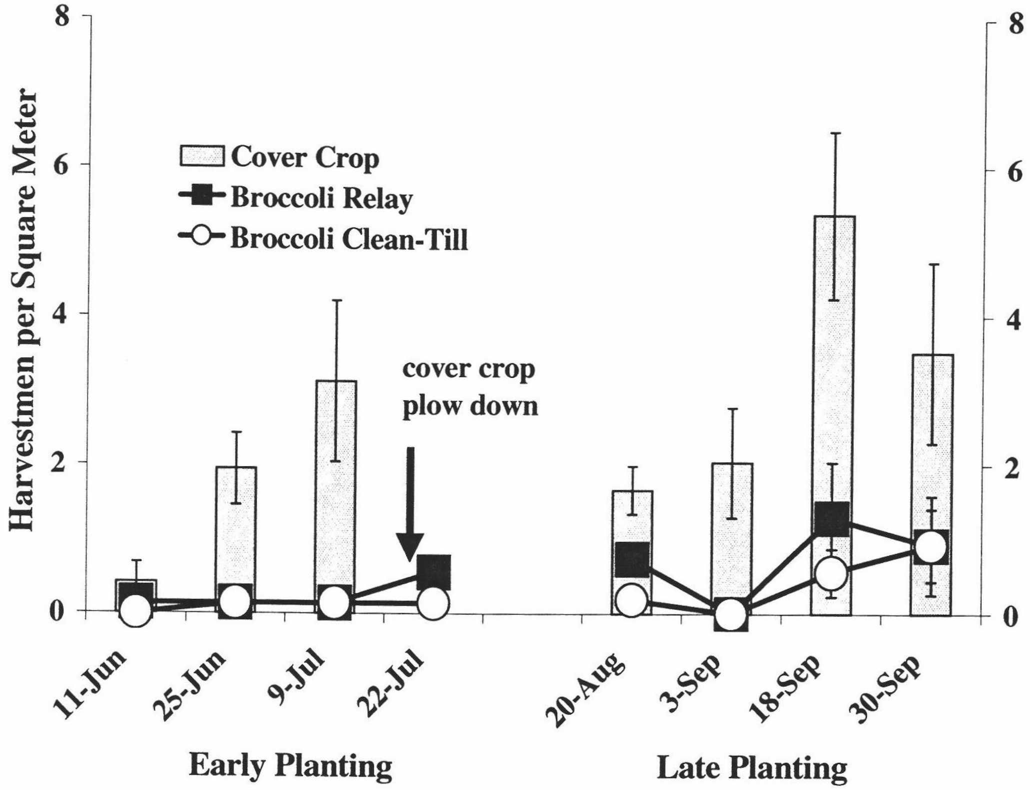


Table 3.13 Impact of Relay Strip-cropping on *T. laboriosa* in Broccoli (Pitfall) 1994-96

	Spiders per Pitfall per Day *				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0	0	0	0	0
Broccoli Clean-till	0	0	0	0	0
Cover Crop	0	0	0.33 ± 0.33	0	0.50 ± 0.29
Bare Ground	0	0	0	0	0
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0	0	0	0	
Broccoli Clean-till	0	0	0	0	
Cover Crop	0.33 ± 0.33	0	0	0	
Bare Ground	0	0	0	0	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	0	0	0		
Broccoli Clean-till	0	0	0		
Cover Crop	0	0	na		
Bare Ground	0	0	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0	0	0		
Broccoli Clean-till	0	0	0		
Cover Crop	na	0	0		
Bare Ground	na	0	0		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	0	0	0	0	
Broccoli Clean-Till	0	0	0	0.25 ± 0.25	
Cover Crop	0	0	na	na	
Bare Ground	0	0	na	na	
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**	
Broccoli Relay	0	0	0	0	
Broccoli Clean-Till	0	0	0	0	
Cover Crop	na	0	0.33 ± 0.30	0	
Bare Ground	na	0	0	0.33 ± 0.33	

* Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05), strip plot analysis, n=4.

Table 3.14 Impact of Relay Strip-cropping on *Tetragnatha laboriosa* in Broccoli (Vacuum) 1994-96

Spiders per Square Meter *

1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0	0.14 ± 0.14 a
Broccoli Clean Till	0	0	0	0.69 ± 0.14 b
Cover Crop	1.25 ± 0.51	na	1.88 ± 0.81	na
Bare Ground	0	na	0	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0.42 ± 0.42 ab	0.83 ± 0.42 a
Broccoli Clean Till	0.42 ± 0.42	0	0 a	0.00 ± 0.00 a
Cover Crop	0	0.83 ± 0.83	1.67 ± 0.42 b	0.42 ± 0.42 a
Bare Ground	0	0	0 a	0.00 ± 0.00 a
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0	0.83 ± 0.28 a	0.56 ± 0.23 a	0.19 ± 0.16 a
Broccoli Clean-Till	0	0.69 ± 0.27 a	0.83 ± 0.36 a	1.30 ± 0.16 a
Cover Crop	0.28 ± 0.28	0.97 ± 0.35 a	na	na
Bare Ground	0	0 a	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0.42 ± 0.14	0	0.28 ± 0.28 ab	
Broccoli Clean-Till	0	0	0.45 ± 0.30 ab	
Cover Crop	na	0.19 ± 0.16	1.42 ± 0.53 b	
Bare Ground	na	0	0 a	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0	0.56 ± 0.39 a	2.51 ± 1.12 a
Broccoli Clean Till	0	0	0.83 ± 0.28 a	3.33 ± 0.45 a
Cover Crop	0	0.28 ± 0.16	1.11 ± 0.79 a	na
Bare Ground	0	0	0 a	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0.19 ± 0.19 a	0.37 ± 0.19 a	1.85 ± 1.34 a	1.67 ± 0.85 a
Broccoli Clean Till	0.00 ± 0.00 a	0.37 ± 0.37 a	1.67 ± 0.64 a	2.22 ± 0.85 a
Cover Crop	0.93 ± 0.49 a	0.74 ± 0.49 a	1.67 ± 0.32 a	0.19 ± 0.19 a
Bare Ground	0 a	0 a	0.19 ± 0.19 a	0 a

*Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05) strip plot analysis, n=4.

Figure 3.23 Impact of Relay Strip-cropping on *Tetragnatha laboriosa* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1994

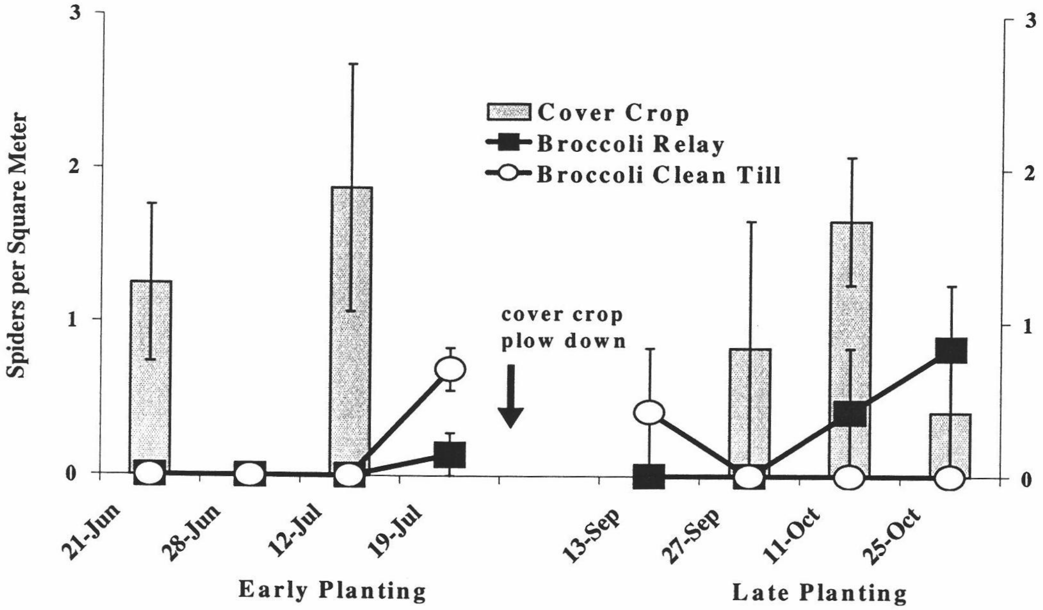


Figure 3.24 Impact of Relay Strip-cropping on *Tetragnatha laboriosa* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1995

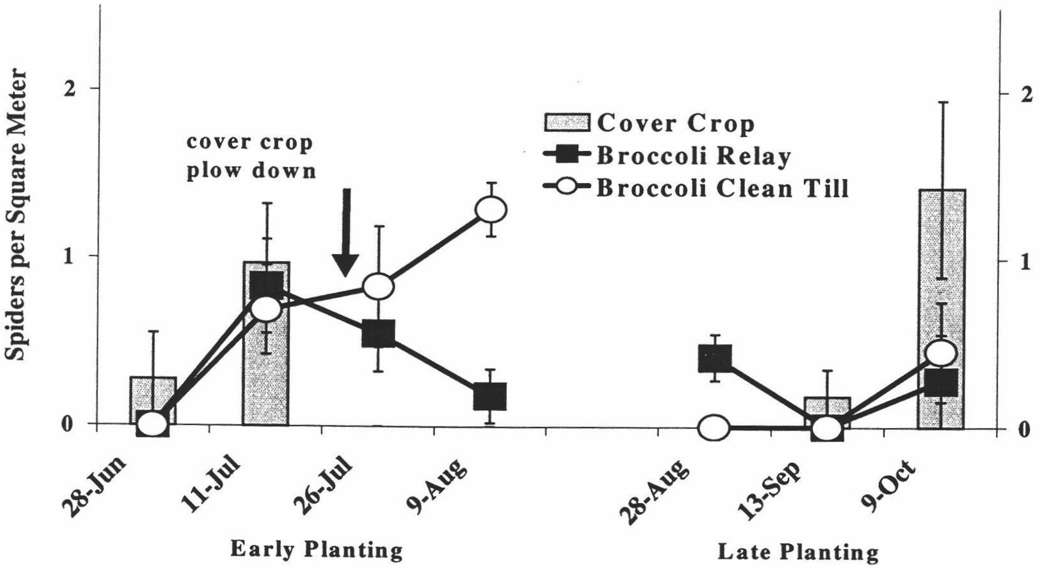


Figure 3.25 Impact of Relay Strip-cropping on *Tetragnatha laboriosa* in Broccoli (Vacuum Sampling) Corvallis, Oregon 1996

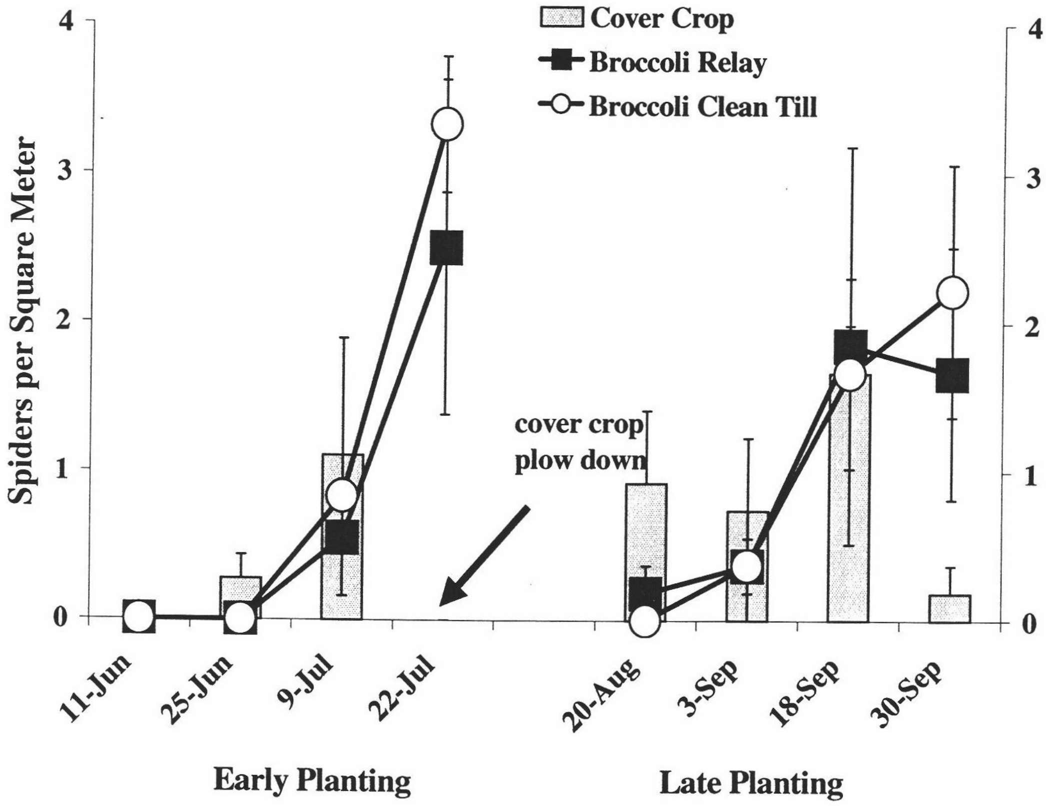


Table 3.15 Impact of Relay Strip-cropping on *T. hirsutipes* in Broccoli (Pitfall) - Corvallis, OR 1994-96

	Spiders per Pitfall per Day *				
1994 Early Planting	**16-Jun**	**24-Jun**	**5-Jul**	**18-Jul**	**25-Jul**
Broccoli Relay	0.22 ± 0.02 ab	0.31 ± 0.09 a	0.19 ± 0.11 a	0.27 ± 0.06 a	0.08 ± 0.04 a
Broccoli Clean-till	0.38 ± 0.09 a	0.51 ± 0.10 b	0.23 ± 0.08 a	0.22 ± 0.05 a	0.13 ± 0.06 a
Cover Crop	0.26 ± 0.08 ab	0.63 ± 0.04 b	0.34 ± 0.21 a	0.15 ± 0.03 ab	0.19 ± 0.04 a
Bare Ground	0.13 ± 0.04 b	0.20 ± 0.04 a	0.20 ± 0.09 a	0.09 ± 0.05 b	0.06 ± 0.02 a
1994 Late Planting	**6-Sep**	**20-Sep**	**4-Oct**	**18-Oct**	
Broccoli Relay	0	0	0	0	
Broccoli Clean-till	0	0	0	0	
Cover Crop	0.02 ± 0.02	0.02 ± 0.02	0	0.02 ± 0.02	
Bare Ground	0	0	0	0	
1995 Early Planting	**20-Jun**	**3-Jul**	**1-Aug**		
Broccoli Relay	1.10 ± 0.21 a	1.13 ± 0.35 a	0.26 ± 0.07 a		
Broccoli Clean-till	1.29 ± 0.17 a	1.39 ± 0.18 a	0.31 ± 0.10 a		
Cover Crop	0.56 ± 0.06 b	0.72 ± 0.16 a	na		
Bare Ground	1.11 ± 0.17 a	0.94 ± 0.10 a	na		
1995 Late Planting	**22-Aug**	**5-Sep**	**19-Sep**		
Broccoli Relay	0.06 ± 0.02 a	0 a	0		
Broccoli Clean-till	0.01 ± 0.01 a	0.01 ± 0.01 a	0		
Cover Crop	na	0 a	0		
Bare Ground	na	0.03 ± 0.02 a	0.03 ± 0.03		
1996 Early Planting	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	
Broccoli Relay	1.06 ± 0.09 a	1.81 ± 0.18 a	0.60 ± 0.11 a	0.30 ± 0.10 a	
Broccoli Clean-Till	0.96 ± 0.10 a	1.86 ± 0.13 a	0.40 ± 0.04 a	0.15 ± 0.03 a	
Cover Crop	1.74 ± 0.32 b	1.64 ± 0.43 a	na	na	
Bare Ground	1.03 ± 0.14 a	1.08 ± 0.20 a	na	na	
1996 Late Planting	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**	
Broccoli Relay	0.22 ± 0.03 a	0.06 ± 0.03 a	0.02 ± 0.02 a	0	
Broccoli Clean-Till	0.11 ± 0.03 b	0.02 ± 0.02 a	0.07 ± 0.07 a	0	
Cover Crop	na	0.09 ± 0.04 a	0.06 ± 0.00 a	0	
Bare Ground	na	0.06 ± 0.00 a	0.02 ± 0.02 a	0	

* Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05), strip plot analysis, n=4.

Figure 3.26 Response of *Tricholathys hirsutipes* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1994

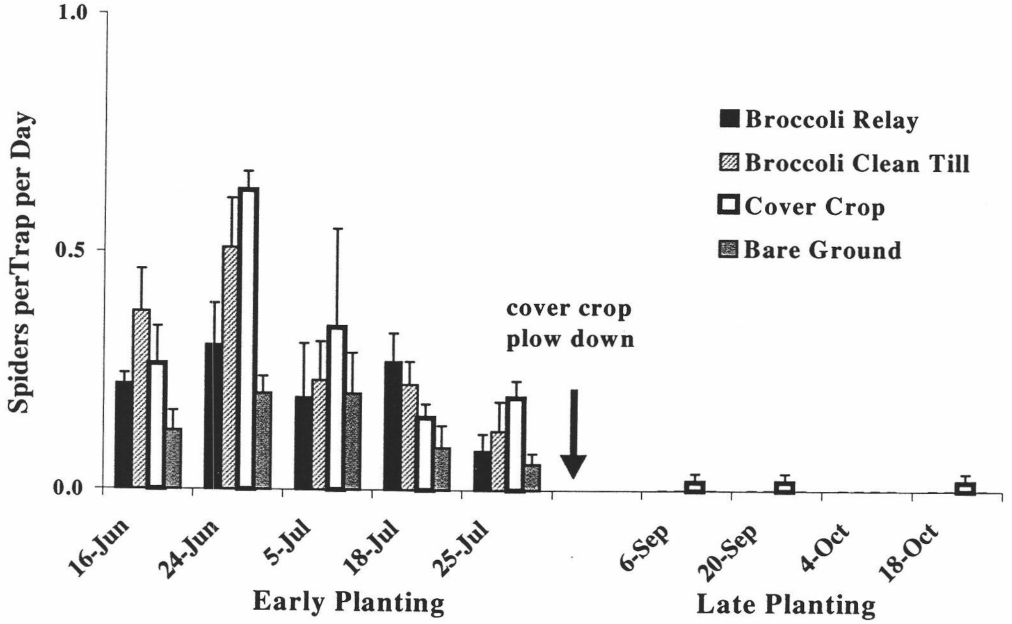


Figure 3.27 Response of *Tricholathys hirsutipes* to Habitat Choices in a Broccoli Cover Crop Relay - Pitfall Trapping Corvallis, Oregon 1995

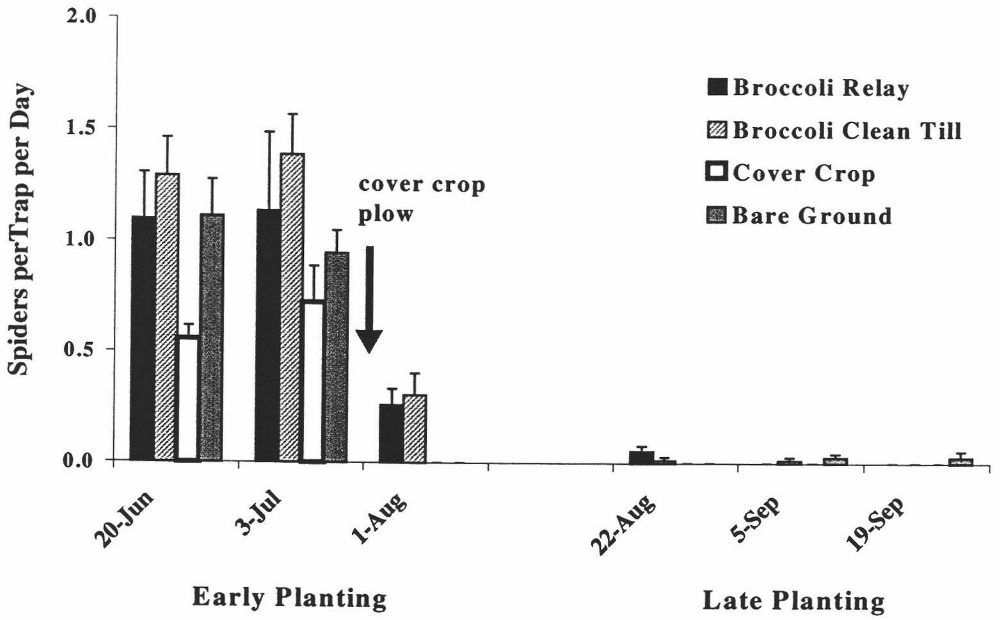


Figure 3.28 Response of *Tricholathys hirsutipes* to Habitat Choices in a Broccoli Cover Crop Relay (Pitfall Trapping) Corvallis, Oregon 1996

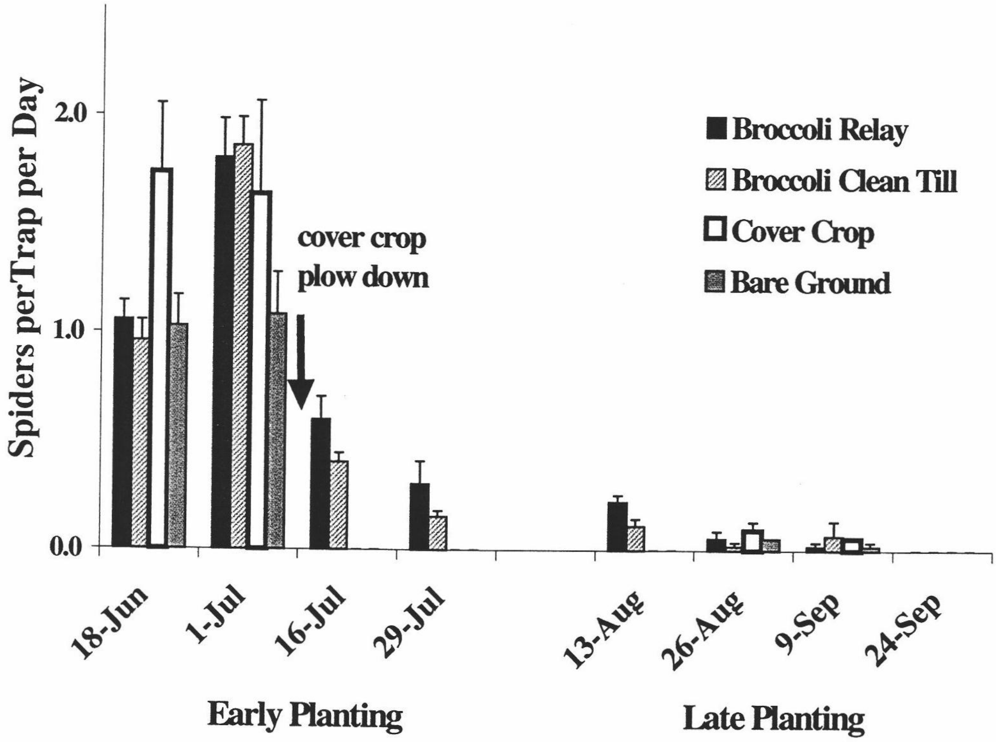


Table 3.16 Impact of Relay Strip-cropping on *T. hirsutipes* in Broccoli (Vacuum) Corvallis, OR 1994-96

Spiders per Square Meter *

1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0	0.14 ± 0.14
Broccoli Clean Till	0	0	0	0
Cover Crop	0	na	0	0
Bare Ground	0	na	0	0
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0
Broccoli Clean Till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0.28 ± 0.16 a	0.42 ± 0.27 a	0.14 ± 0.14	0
Broccoli Clean-Till	0.28 ± 0.16 a	0.83 ± 0.48 a	0.14 ± 0.14	0
Cover Crop	0.14 ± 0.14 a	0.14 ± 0.14 a	na	na
Bare Ground	0.56 ± 0.32 a	0 a	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0	0	
Broccoli Clean-Till	0	0	0	
Cover Crop	na	0	0	
Bare Ground	na	0	0	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0 a	0.28 ± 0.28 a	0.28 ± 0.28
Broccoli Clean Till	0	0.56 ± 0.23 a	0.14 ± 0.14 a	0
Cover Crop	0	0 a	0.28 ± 0.28 a	na
Bare Ground	0	0.56 ± 0.23 a	0.14 ± 0.14 a	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean Till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0

*Means ± SEM followed by the same letter within each sampling date are not significantly different (P>0.05) strip plot analysis, n=4.

The number of Lycosidae was low in all three years regardless of the cropping system. In 1994, the density of juvenile *Pardosa* species was highest in the cover-crop strips, however their density in the broccoli growing nearby remained low (Table 3.5, Figure 3.29). Vacuum sampling rarely captured Lycosidae. The density of the Lycosidae in vacuum samples varied from 0 to 0.56 spiders per square meter (Table 3.6).

In 1996, pitfall traps consistently captured more male *E. dentosa* and *L. tenuis* spiders than female spiders. Pitfall trap captures of male *L. tenuis* increased sharply in the late planting. The male to female ratio of *E. dentosa* in vacuum samples varied from 0.3 to 0.8, while the male to female ratio of *L. tenuis* varied from 0.2 to 3.0 (Table 3.17, Figures 3.30-3.31).

DISCUSSION

Spiders and harvestmen were the most abundant generalist predators observed in the broccoli cropping systems over the three-year period. Spider and harvestmen abundance and diversity in the broccoli were lower than those reported in pastures (Turnbull 1966, Turnbull 1973) and strip-managed cereals (Nentwig 1988, Nentwig 1989). The highest spider and harvestmen density in the broccoli relay was 20 individuals per square meter.

The pattern of species abundance of the spiders and harvestmen in the broccoli was logarithmic in the sense that four to five species represented over ninety percent of the individuals captured, a few species were caught in low numbers, and many rare species were captured at rates of less than 10 per year. Overall spider and harvestmen abundance and diversity was highest in the cover-crop strips. Most of the rare species were captured only in the cover-crop.

Figure 3.29 Response of Lycosidae Species to Habitat Choices in a Broccoli Cover Crop Relay - Pitfall Trapping Corvallis, Oregon 1994

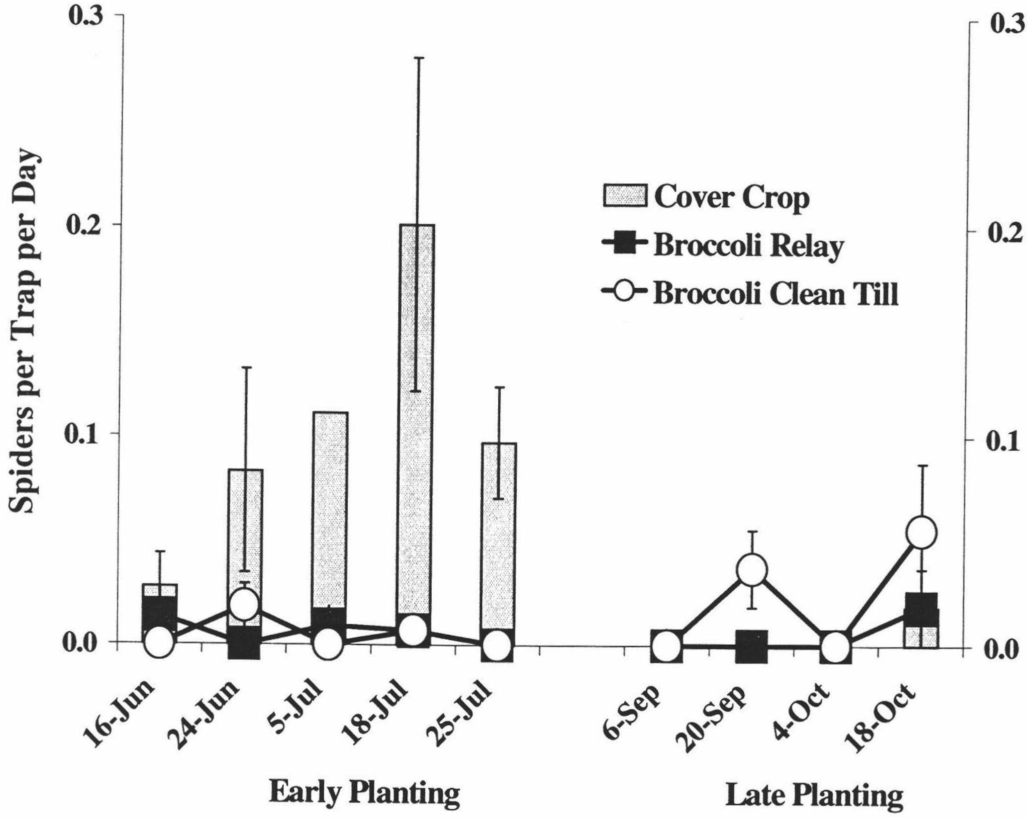


Table 3.17 Gender Bias Associated with Spider Pitfall Trapping - Corvallis, Oregon 1996

	Early Broccoli Planting				Late Broccoli Planting			
Vacuum Sampling	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Erigone dentosa - males	4	24	12	21	46	18	23	28
Erigone dentosa - females	8	51	18	50	56	26	73	67
male/female ratio	0.5	0.5	0.7	0.4	0.8	0.7	0.3	0.4
Pitfall Sampling	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	**13-Aug**	**26-Aug**	**9-Sep**	**24-Sep**
Erigone dentosa - males	55	100	25	216	17	278	328	77
Erigone dentosa - females	17	25	8	69	14	99	70	60
male/female ratio	3.2	4.0	3.1	3.1	1.2	2.8	4.7	1.3
Vacuum Sampling	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Lepthyphantes tenuis - males	5	45	12	4	9	8	17	5
Lepthyphantes tenuis - females	7	15	7	5	6	4	12	29
male/female ratio	0.7	3.0	1.7	0.8	1.5	2.0	1.4	0.2
Pitfall Sampling	**18-Jun**	**1-Jul**	**16-Jul**	**29-Jul**	**26-Aug**	**9-Sep**	**24-Sep**	
Lepthyphantes tenuis - males	33	24	3	12	18	22	10	
Lepthyphantes tenuis- females	12	7	2	2	1	1	1	
male/female ratio	2.8	3.4	1.5	6.0	18.0	22.0	10.0	

Figure 3.30 Gender Bias in Pitfall Trapping of *Erigone dentosa* Corvallis, Oregon 1996

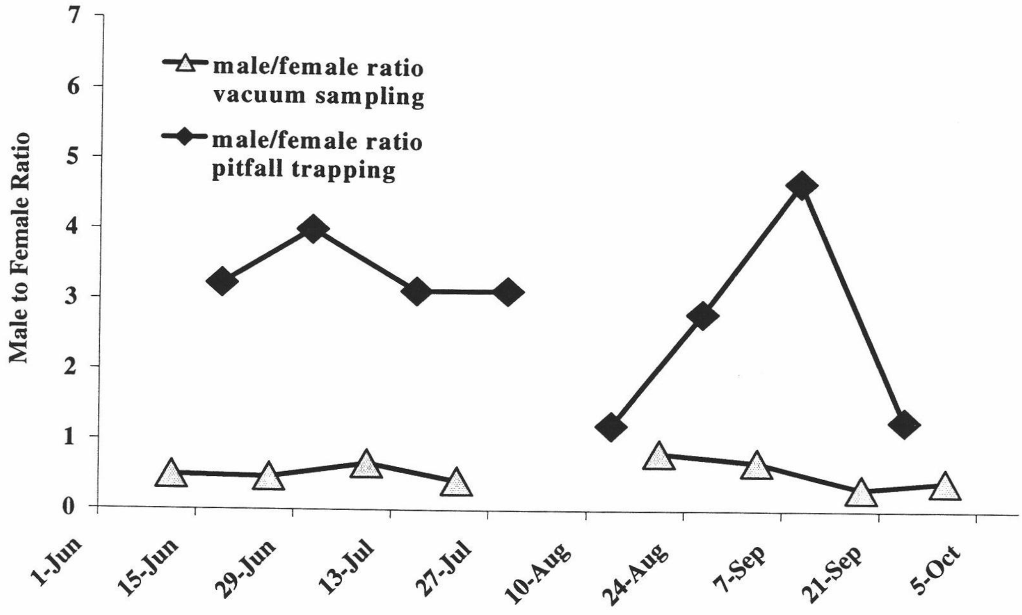
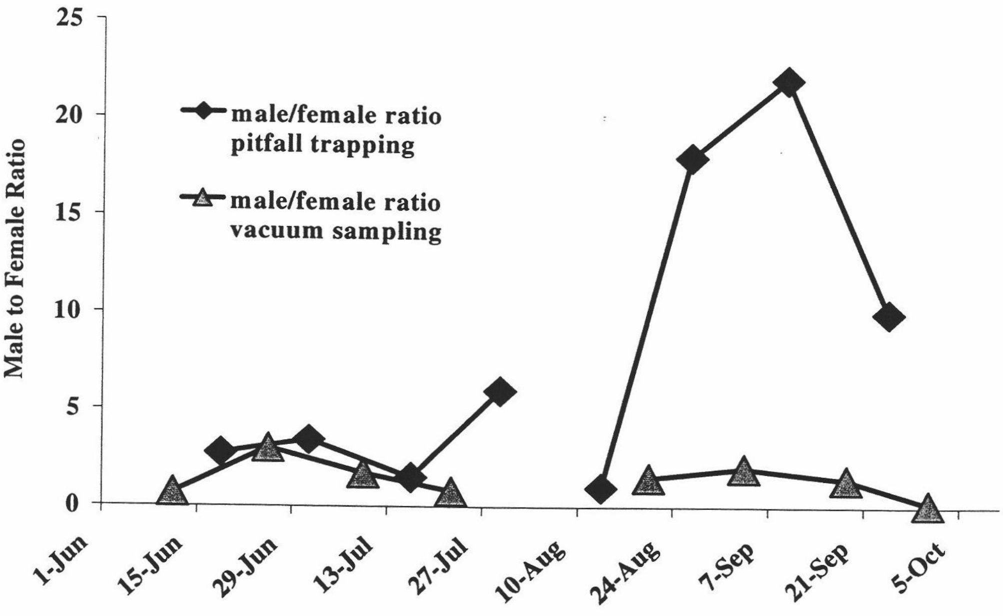


Figure 3.31 Gender Bias in Pitfall Trapping for *Lepthyphantes tenuis* Corvallis, Oregon 1996



Linyphiidae and Phalangiidae dominated the arachnid assemblages in the two cropping systems. Dominance by the Linyphiidae, especially spiders in the genera *Erigone* and *Lepthyphantes* is typical of highly disturbed horticultural crops (Nyffeler et al. 1994b). Although *P. opilio* is not as highly mobile as the Linyphiidae (*P. opilio* disperses by walking), it represented approximately 19% of the specimens collected over the three-year period.

In the relay strip-cropping system, Lycosidae never exceeded two percent of the captures. Lycosidae make up as much as forty percent of the spider assemblage in pasture systems (Turnbull 1966, Turnbull 1973). Lycosidae represented fifteen percent of the assemblage in the strip-managed cereal (Nentwig 1988), and the relative proportions of Lycosidae compared to Linyphiidae species increased over time in the strip-managed cereal. In the relay strip-cropped broccoli, Lycosidae counts remained the same or declined. My findings are similar to those of Lys and Nentwig (1994) who found that Lycosidae occurred in undisturbed strips but were absent in the strip-managed cereal.

The relative abundance of Lycosidae in the pastures and strip-managed cereals versus the broccoli systems that I studied may be the result of insecticides used in the broccoli cropping systems. Although there were insecticide refuges in my study, there were no insecticide free cropping systems. In general, fewer insecticides are used on pastures than on horticultural crops. Nentwig (1988, 1989) did not use insecticides in the strip-managed cereal system. Lycosidae are sensitive to insecticides because of the significant amount of time they spend foraging on the soil surface.

During the five-year period of the strip-managed cereal study, undisturbed weedy strips developed a layer of woody debris and were invaded by early pioneer-species of shrubs and trees. The habitat structure and woody debris may have improved the hunting success and the winter survival of the Lycosidae in the strip-managed cereals (Nentwig 1988, 1989). In the relay strip-cropping system, the cover-crop strips were disturbed once each year prior to planting. In the relay system, woody debris was limited. I did not allow trees or shrubs to establish in the broccoli fields.

As expected, pitfall trapping and vacuum sampling were biased in favor of ground or foliar dwelling spider species respectively. Ground dwelling *E. dentosa* and *T. hirsutipes*, for example, were caught in higher proportions in pitfall traps than in vacuum samples. Foliage dwelling *L. tenuis* and *T. laboriosa* were caught in higher proportions in vacuum samples. *P. opilio* was trapped in roughly equal proportions in pitfall traps and vacuum samples. The sampling results may reflect the foraging strategy of *P. opilio* that is equally divided between the ground and plant foliage. The sampling results agree with my observations of *P. opilio* behavior during the experiments; *P. opilio* was commonly observed on both the soil surface and on plant foliage.

More spider species were captured in vacuum samples than in pitfall traps. The sampling bias may simply reflect that pitfall trapping fails to capture important groups of foliar dwelling spider species (Araneidae, Thomisidae, and others). The sampling bias may also reflect the ability of some species to escape from or avoid falling into pitfall traps on the soil surface. Neither pitfall trapping nor vacuum sampling alone adequately characterized the spider assemblage in the two cropping systems.

The different male to female ratios for *E. dentosa* and *L. tenuis* captured in the pitfall traps reflects the well-known behavioral difference among male and female spiders rather than any inherent difference in sex ratios within the species. Male spiders move over greater areas of the soil surface than females during their reproductive periods. Thus, they are captured in greater numbers in pitfall traps than females. The male to female spider ratios found in vacuum samples are a more accurate reflection of true sex ratios of these species. The sharp change in male to female ratios for *L. tenuis* captured in pitfall traps during the late planting period of 1996 may correspond to a peak in their reproductive activity in the late summer.

Overall, there were clearly more spiders and harvestmen in the broccoli relay cropping system that in the clean-till broccoli. However, most of the arthropods were found in the cover-crop strips. Their presence in the strips did not necessarily result in increases in the broccoli growing nearby. Although pitfall counts for *E. dentosa* were higher in the relay broccoli compared with clean-till broccoli during two of three years, vacuum sampling did not produce similar results. The disparity in results are probably associated with the well known problems associated with pitfall trapping (Greenslade 1964, Topping and Sunderland 1992, Mommertz et al. 1996). Pitfall counts and vacuum samples for *P. opilio* were higher in the relay broccoli compared to clean-tilled broccoli in 1994 and 1996 respectively. Over ground migration from the cover-crop strips into the broccoli is a likely explanation for increase density of *P. opilio* in the relay broccoli. *P. opilio*, lacks spinnerets and migrates strictly by over ground movement. Future experiments mark, release, and recapture techniques are needed to show the importance of over ground migration of spiders and harvest men from cover-crop strips into nearby crops.

It is clear that the one acre experiment plots were inadequate in size to evaluate the impact of vegetation management on spiders that balloon. The high mobility of spiders limits the utility of small plot research strategies. Using transects from the edge of apple orchards to the middles, for example, Brown and Lightner (1997) found that spiders showed an edge effect which penetrated 33-43 m into the orchard. They found that spiders were more likely to have an edge effect than the highly mobile beetle, *Coccinella septempunctata* L. The author recommended a plot border minimum of about 30 m and plot sizes of at least 7.5 ha for sampling spiders. In a large replicated spider study in cotton, spider populations in 40 acre blocks treated or untreated with two applications of dimethoate in June converged and were statistically similar in August (Ehler et al. 1973). The authors argue that the spider numbers had completely recovered on the spatial scale of 40 acres in about 60 days. I agree.

The differences in the number of *E. dentosa* in the two cropping systems in my study is probably the result of retention of this species following ballooning rather than differences in colonization rates. The differences in the number of *P. opilio* may, however, be the result of over ground dispersal from the tillage and pesticide refuges.

Given the evidence accumulated to date, it appears that no one species of spider, even if it is abundant, can hold a prey population in check (Riechert and Lockley 1984). There is little evidence that spiders track the density of prey populations. Large changes in spider density in a given area do not always correlate with changes in prey population density (Turnbull 1973). Spider density is largely the result of movement or lack of movement by the spider assemblage. When prey populations increase, spiders remain in the area. When prey population growth slows down due to the environment, spiders get hungry, leave, and the predation pressure is diminished. The net effect of this behavior by spiders is that prey population oscillations are dampened. Biological control of pest insects by spiders may be sufficient in years of low pest population density. In other years, pest outbreaks due to abiotic factors often overwhelm naturally occurring biological control by spiders. In outbreak years, neither a higher density of spiders alone or in combination with other aphidophagous insects prevent crop damage (Wyss et al. 1995). Relay strip-cropping was effective at conserving spider populations in this broccoli production study, but this alone does not justify adoption of this conservation technique. Winter cover-crops may improve soil and water quality. Relay strip-cropping may reduce the cost of establishing winter cover-crops and may be justified in terms of soil and water conservation.

CHAPTER 4

IMPACT OF RELAY STRIP-CROPPING ON LADY BEETLES (COLEOPTERA: COCCINELLIDAE) IN BROCCOLI

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ABSTRACT

Three hundred and fourteen individuals and ten species of lady beetle (Coleoptera: Coccinellidae) were captured in vacuum samples from 1994-1996 in a study comparing relay strip-cropping to clean-tilled planting of broccoli. Relay strip-cropping combines under-sowing and strip-management. In this study, a cover-crop seed mixture containing *Avena sativa* L. var. "Monida", *Vicia sativa* L., *Trifolium pratense* L., *Lolium multiflorum* Lam., and *Fagopyrum esculentum* Moench was broadcast over established broccoli 32 days after planting. The broccoli was planted, under-sown, and harvested in sections alternating with strips of undisturbed cover-crop. The three most abundant coccinellid species were *Coccinella septempunctata* L., *Coccinella trifasciata* L., and *Harmonia axyridis* (Pallas); they represented seventy seven percent of the total beetles collected. *C. septempunctata* density varied from 0 to 6.9 beetles per square meter. *C. septempunctata* was the only coccinellid species that colonized the broccoli in significant numbers; its density was often significantly higher in the relay strip-cropped broccoli than in the clean-tilled broccoli. *C. trifasciata, Hippodamia convergens* Guerin-Meneville, *Hippodamia sinuata* Mulsant were occasionally abundant in the cover-crop strips while absent in the broccoli growing 15m away. *H. axyridis* was only collected in 1996. High coccinellid larval density sometimes occurred in cover-crop strips prior to plow down. Significant loss of reproductive potential occurred during these operations. It was difficult to manage the incorporation of cover-crop strips so that developing larval populations were protected while adult coccinellids were forced into the target crop in timely manner.

INTRODUCTION

Aphidophagous Coccinellidae occur in large numbers in agricultural systems; they are an important component of the generalist predator guild (Hagen 1962, Hodek 1967, 1973, Obrycki and Kring 1998). Coccinellidae are abundant in the early growing season when agricultural pest populations are just becoming established. For the most part, aphidophagous Coccinellidae do not specialize on individual prey species. The highly mobile adult beetles have the potential of switching from aphids on native or other non-crop vegetation to agricultural crops as aphid populations begin to expand there. The switch from non-crop vegetation to forage and egg laying in agricultural crops constitutes a rapid numerical response to changing aphid densities (Mills 1982).

The impact of aphidophagous Coccinellidae on prey populations is, to a large extent, the result of predation by coccinellid larvae (Mills 1982). The larvae are not highly mobile. Changes in aphid abundance during the growing season are dramatic. Changes in abundance pose a considerable challenge to ovipositing lady beetles. Because coccinellid larvae are much less mobile and less stress tolerant than adults, the choice of egg laying site by the female has a profound effect on the survival chances of its progeny (Lovei et al. 1991). The selection of oviposition sites by the female commits the larvae to searching for available prey in the vicinity where they hatch; they are forced to forage aggressively to avoid starvation (Rockwood 1952, Hodek 1973).

To fully appreciate the potential of the Coccinellidae as natural enemies, one must also recognize their role in the larger guild of generalist predators (Dixon 1985). Coccinellidae dislodge many more aphids than they consume; this is due to aphid escape behaviors, which include dropping from the plants when they are alarmed. Aphids dislodged to the ground are exposed to biotic and abiotic mortality factors including ground predators, spiders, high soil temperatures, and dry conditions as they search for a new host-plant (Roitberg and Myers 1978). Aphid escape behaviors can be initiated by direct contact with a predator, by plant-borne vibrations caused by foraging predators, by alarm pheromone released by disturbed conspecific aphids, or by a combination of these factors (Losey and Denno 1998). When confronted by Coccinellidae, aphids are more likely to drop off the plant, because Coccinellidae exhibit a more vigorous foraging activity. Coccinellidae dislodge more aphids than the activity of parasitoids or other predators (Brodsky and Barlow 1986).

While some species of Coccinellidae are specific in their food habits, aphid-eating members of the family are generally not restricted to any one species of aphid for their main food supply (Banks 1955, Hodek 1973, Hoffmann et al. 1997). Angalet et al. (1979) reported twenty-six species of aphids that appeared to be suitable prey for both immature and adult *Coccinella septempunctata* L. including *Brevicoryne brassicae* L. (Hagley and Allen 1990). Hodek (1973) lists several studies that assert that the *B. brassicae* is rejected by most species of Coccinellidae because of its waxy surface. *Coccinella trifasciata* L., however, had a 58-67% positive precipitin to *B. brassicae* in field tests conducted near Corvallis, Oregon. When *C. trifasciata* was gathered from collard foliage (rather than alfalfa or the ground) the intensity of the positive precipitin test significantly increased for *B. brassicae* (McIver 1983).

Coccinellidae rarely prey on Lepidoptera. In his extensive review of coccinellid prey items, Hodek (1973) does not list *Pieris* as a known prey item of any species of Coccinellidae. On the other hand, *C. trifasciata* and *H. convergens* had positive precipitin responses to *Pieris rapae* L. when they were sampled near Corvallis, Oregon (McIver 1983). Jones (1982) studied the predators of *Trichoplusia ni* (Hubner) and found that coccinellid predation was low in the presence of aphids. The aphids were more attractive prey items; the aphids completely distracted the Coccinellidae from potential Lepidopteran prey. In cage studies to determine the impact of natural enemies on *Mamestra configurata* Walker, *Coccinella transversoguttata* Faldermann alone and in combination with *Nabis* species was superior to all other treatments in reducing the number of *M. configurata* larvae (Tamaki and Weeks 1972).

Alternative foods are important for most species of Coccinellidae. Coccinellids feed extensively at floral (Angelet et al. 1979) and extra-floral (Ewing 1913) nectar, pollen (Belnavis 1989), and aphid honeydew (Elliott et al. 1996), and plant saps (Banks 1955). The larvae of several species in the genus *Psyllobora* feed on fungi (Hagen 1962). Apparently, Coccinellidae will also feed on artificially applied sugar solutions (Evans and Richards 1997).

Floral and extra floral nectar secretions from *Prunus* and *Vicia* species offer energy sources but are probably nutritionally deficient for egg or fat production in Coccinellidae (Hagen 1962). Common vetch (*Vicia sativa* L.) and alfalfa *(Medicago sativa* L.), whether infested by aphids or not, attract large numbers of coccinellid beetles that feed on the nectar expressed from glands on their leafy stipules. Winter peas lack extra floral nectar. Coccinellids do not appear on winter peas unless they are infested with aphids (Rockwood 1952).

Coccinellid species have preferences for specific crops and semi natural vegetation regardless of prey species present (Hagen 1962, Hodek 1973). Coccinellid beetles respond to vegetation on a variety of spatial scales. At the scale of a single plant, coccinellid beetles respond to plant architecture, leaf characteristics, plant color, and other aspects of vegetation regardless of the presence or absence of their prey items (Grevstad and Klepetka 1992). Some coccinellid species are more common in deciduous shrubs and trees while others are more common on low growing vegetation and field crops. Some coccinellid species prefer unmanaged vegetation; others prefer disturbed vegetation in agricultural settings. These later species are adapted to rapid colonization of disturbed sites. During their life cycle, which in some cases involves long-distance migration, most of the common species of coccinellids use both agricultural and uncultivated habitats (Mareidia et al. 1992).

Adalia bipunctata (L.) and *Harmonia axyridis* (Pallas), for example, tend to be more numerous in the trees and the shrubs than on forage and vegetable crops. *C. septempunctata* (La Mana 1995), *C. trifasciata* (McIver 1983), and *C. polita* (Rockwood 1952) tend to be more common in field crops such as alfalfa and vetch. Their presence in the alfalfa reflects preferences for prey items in a given habitat, and it also reflects habitat preferences.

In a meadow subjected to various management schemes, Nentwig (1988) observed that as the floral and faunal diversity increased over time, the density of most individual arthropod species decreased. However, populations of Coccinellidae did not decline; they increased over time in the more diverse meadows. The Coccinellidae appeared to be responding positively to the overall increase in the abundance and variety of prey items. Increases in arthropod diversity are generally associated with polyculture, and this should have an impact on distribution of Coccinellidae. In some cases, however, there are fewer Coccinellidae in mixed culture than in monoculture. In these situations, there is generally a much higher prey density in the monoculture resulting in coccinellid aggregation there.

Andow and Risch (1985) evaluated coccinellid activity in corn monoculture versus corn/bean and corn/squash polyculture. Prey items included aphids and egg masses from *Ostrinia nubilalis* Walker. The aphid infestation occurred naturally. Aphid infestation of the monoculture occurred about a week prior to the mixed cultures. The difference in colonization timing resulted in elevated aphid densities in the monoculture at the beginning of the season. The *O. nubilais* egg masses, however, were placed evenly by hand across all treatments.

The coccinellid *C. maculata* was absent from the cropping systems until 35 days after planting. When it invaded the systems, it was immediately more abundant in the corn monoculture. The coccinellid larvae followed the same pattern. They were more abundant in the monoculture than in either of the types of polyculture. Colonization by *C. maculata* of the three cropping systems involved both immigration and emigration; they accumulated in higher numbers in the monoculture where immigration exceeded emigration. The beetles had a higher rate of emigration from the polyculture where aphids were more dispersed and the coccinellids had a decreased rate of food encounter (Andow and Risch 1985).

The size and arrangement of patches of vegetation can affect the foraging efficiency of natural enemies including Coccinellidae (Hassell and May 1974, Kareiva 1987). There are examples of coccinellid aggregation resulting in significant reductions in aphid populations. Habitat or patch fragmentation can promote aphid outbreaks if it interferes with non-random searching behavior of ladybird predators and interferes with aggregation of predator in areas of high prey density (Elliott et al. 1996).

In the Willamette valley, coccinellid species are common on winter cover-crops including vetch, alfalfa, and Austrian winter peas that are infested with pea aphid (Rockwood 1952). Leguminous cover-crops in an orchard may draw Coccinellidae into the vicinity; however, their presence in the cover-crop may not result in significant changes in the number of coccinellids foraging in the target crop. Many scientists who have wrestled with this problem have speculated about techniques for manipulating vegetation (mowing) at an appropriate time to force Coccinellidae to abandon the cover-crop and move into the target crop (Bugg et al. 1991).

Banks (1955) studied the seasonal activity of *C. septempunctata* in bean fields and in non-crop vegetation in England. He found that changes in the numbers of adult beetles occurred in three phases. First, female beetles dispersed from their wintering refuges and laid eggs on stinging nettles that were infested with nettle aphids, *Microlophium evansi* L. The first cohort of eggs was deposited prior to the establishment of spring planted agricultural crops. At this point, many of the overwintered females died; some gravid female beetles, however, dispersed from the nettles to bean fields that were now supporting rapidly developing populations of the bean aphid, *Aphis fabae* Scopoli. When the first generation of coccinellids completed its development in the nettles, young beetles immigrated into the bean fields. Adult beetles that developed from eggs placed on the beans and adult beetles that developed from eggs placed on the nettles fed together in the bean fields until they ran out of prey. At this point, many beetles moved back to hibernation sites; some remained in the area feeding on pollen for a couple of weeks prior to moving back to hibernation sites.

Colonizing ladybird beetles are inept at locating prey from a distance (Hodek 1973). The coccinellid larvae and adults do not perceive their prey visually at long distances and mostly detect their prey upon contact. Adult beetles must come into contact with the aphid before it responds to it (Hagen 1962). Once they land in a plant patch, however, they are aggressive foragers. After finding prey, their search pattern changes from one of rapid movement at random to one of more intense search reflected by more frequent turning and shorter moves. The key foraging behavior that contributes to the success of *C. septempunctata*, for example, is its tendency to restrict its foraging attention to the vicinity of a recent aphid capture ("area restricted search") before continuing a wider ranging exploration (Kareiva 1986). Aphidophagous Coccinellidae continue to focus on aphids even when there are other prey items available (Tamaki and Weeks 1972). The duration and intensity of their searching behavior increases with hunger (Mills 1982).

The aggregation response of Coccinellidae has two components, the aggregation of foraging adults and the concentration of oviposition. Ovipositing beetles concentrate their egg laying in areas of high prey density or where prey populations are rapidly increasing. The oviposition behavior results in the concentration of larvae in areas of high aphid density. The impact of aphidophagous predators on prey populations is largely a result of predation by the juvenile beetle stages. Adult coccinellids generally arrive prior to the beginning of the cropping season and feed in a variety of non-crop habitats before oviposition begins in agricultural crops. The "reproductive numerical response" of the adult coccinellids to aphid density is therefore important in determining the effectiveness of these natural enemies in agricultural systems. Some species of coccinellid beetles can only respond to the lower range of aphid densities through aggregation and a reproductive numerical response. They fail to respond to higher aphid densities and their response is further reduced by density-dependent egg cannibalism (Mills 1982).

There are all degrees of movement by adult coccinellids from simple, short flights from one part of a field to another in search of food to extended migratory flights into different habitats where aggregations are usually formed. In most cases, long-distance movements are associated with reaching dormancy sites. Even though Coccinellidae are strong flyers and capable of very long migratory flights, evidence suggests that local habitat structure can produce differences in the rate at which the Coccinellidae colonizes agricultural fields (Hagen 1962). Mark, release, and recapture experiments conducted in England showed that bean plots 400 m from early season aggregation sites on stinging nettles were colonized sooner by *C. septempunctata* than plots that were 800 m away (Banks 1955). Transects of yellow sticky traps used to study the variation in *C. septempunctata* density in an apple orchards showed that there was an edge effect from non-crop vegetation on the perimeter of the orchard extending 30 m into the orchard (Brown and Lightner 1997).

Relay strip-cropping combines two vegetation management tactics, under-sowing and strip-management, that may have an impact on Coccinellidae colonizing the target crop (in this case, broccoli). Under-sowing also results in early soil cover that should improve the microclimate surrounding the target crop. Under-sowing results in a polyculture that should increase the abundance and diversity of potential prey items attractive to Coccinellidae.

Schlinger and Dietrick (1960) reported some success manipulating coccinellids with strip-managed of alfalfa. Other researchers have had poor success moving Coccinellidae out of alfalfa into the target crop (cotton) even when the alfalfa was mowed down (Hodek 1973).

Semi natural non-crop vegetation can serve as a source of colonizing coccinellid beetles if the beetles aggregate in the non-crop vegetation early in the season and then move into agricultural crops when aphid populations begin to increase there. Non crop vegetation can also serve as a sink for colonizing Coccinellidae, distracting and drawing beetles away from a target crop (Corbett 1998).

Banks (1955) argued that the coccinellids were ineffective predators of bean aphids (*A. fabae*) because the majority of the overwintered beetles were busy attacking M. *evansi* on a nearby patch of nettles while the bean aphid population was becoming established. The gravid female coccinellids committed their first cohort of predacious larvae to the nettles patch. By the time the females moved over to the bean crop, *A. fabae* infestations had already reached their maximum numbers. The coccinellid density in the beans was, however, determined by distance from nettle sites. On the one hand, the nettle aphids served as a “first food” supply for the predators recently emerged from hibernation; the nettle aphids were probably important for their survival. On the other hand, aphids on the nettles attracted incoming coccinellid beetles away from the beans.

When plants are mixed together in a polyculture, one can still detect source and sink effects at work. McIver (1983) mixed collards (the target plant) with alfalfa which is attractive to many species of Coccinellidae. More coccinellid beetles were observed in the collard-alfalfa system when the alfalfa was left tall and undisturbed than when the alfalfa was mowed. Increases in beetle numbers in the alfalfa did not, however, result in greater numbers on the collards themselves. Fewer Coccinellidae were observed on the collards surrounded by mature, unmowed alfalfa than on collards sitting in a patch of recently mowed alfalfa. Perhaps the coccinellid beetles (primarily *C. trifasciata*) found preferred prey on the alfalfa. Regardless of the mechanism, the alfalfa was a sink not a source of colonizing beetles for the interplanted collards. The challenge of relay strip-cropping as a method of manipulating coccinellids is to attract the adults into the vicinity with desireable cover-crops and to flush them into the target crop, broccoli. For a detail review of the Coccinellidae literature, see Appendix C.

MATERIALS AND METHODS

The experiments in this study were conducted from 1994 to 1996 at the Oregon State University Vegetable Research Farm near Corvallis, Oregon. The site, details concerning the relay strip-cropping experiments, and statistical methods were described in chapter two. The Coccinellid adults and larvae were captured in vacuum samples on alternating weeks beginning after the final cultivation and under-sowing and continuing until broccoli harvest. The details of the vacuum sampling proceedure were discussed in chapter three.

RESULTS

From 1994 to 1996 two thousand ninety eight vacuum samples were taken in the two broccoli cropping systems, which produced three hundred and fourteen beetles representing ten species of Coccinellidae. Three hundred and twenty nine larvae and eleven pupae were also collected in vacuum samples. The three most abundant beetle species were *C. septempunctata*, *C. trifasciata*, and *H. axyridis*; the three species represented seventy seven percent of the total beetles collected over the three years. *Cycloneda polita* Casey and *Coccinella californica* (Mannerheim) were uncommon. *Hippodamia sinuata* Mulsant, *Hippodamia convergens* Guerin-Meneville, *Psyllobora virgintimaculata* (Say), *Coccinella undecimpunctata* L., and *A. bipunctata* were rare, occurring at five or less beetles per year in the broccoli systems (Table 4.1 and Figure 4.1). All of the species collected were aphidophagous except *P. virgintimaculata,* which is a fungivore .

Coccinellidae densities were consistently highest in the early broccoli plantings and very low in the late broccoli plantings. Beetles varied in their habitat preferences. *C. undecimpunctata* and *A. bipunctata* were only collected in the cover-crop strips. *C. trifasciata, H. axyridis, C. polita, C. californica, H. sinuata,* and *H. convergens* preferred the cover-crop; seventy five percent or more of the beetles of these species were collected in the cover-crop. *C. septempunctata,* however, was widely dispersed in both the cover-crop and the broccoli. Seventy two percent of the *C. septempunctata* adults (120/167) collected over the three year period were collected in the broccoli (Table 4.1).

C. septempunctata was occasionally abundant in both the cover-crop strips and the broccoli. *C. septempunctata,* which represented fifty three percent (167/314) of all beetles collected, comprised eighty two percent (120/146) of the beetles collected in the broccoli. *C. trifasciata* which represented seventeen percent (52/314) of all beetles collected, represented only five percent (7/146) of the beetles collected in the broccoli (Figure 4.2). *H. sinuata and H. convergens* were occasionally abundant in the cover-crop strips while they were absent in the broccoli growing nearby (Figure 4.3).

Table 4.1 Coccinellidae in a Broccoli Cover Crop Relay
Corvallis, Oregon 1994-1996

Species	Total 1994	%	In Broccoli 1994	%	Total 1995	%	In Broccoli 1995	%	Total 1996	%	In Broccoli 1996	%	Total 94-96	%	In Broccoli 94-96	%
Coccinella septempunctata	**82**	*75*	**79**	*81*	**22**	*63*	**12**	*92*	**63**	*37*	**29**	*83*	**167**	*53*	**120**	*82*
Coccinella trifasciata	**9**	*8*	**6**	*6*	**2**	*6*	**0**	*0*	**41**	*24*	**1**	*3*	**52**	*17*	**7**	*5*
Harmonia axyridis	**0**	*0*	**0**	*0*	**0**	*0*	**0**	*0*	**21**	*12*	**2**	*6*	**21**	*7*	**2**	*1*
Cycloneda polita	**1**	*1*	**1**	*1*	**0**	*0*	**0**	*0*	**24**	*14*	**2**	*6*	**25**	*8*	**3**	*2*
Coccinella californica	**6**	*6*	**6**	*6*	**1**	*3*	**0**	*0*	**10**	*6*	**0**	*0*	**17**	*5*	**6**	*4*
Hippodamia sinuata	**2**	*2*	**2**	*2*	**5**	*14*	**0**	*0*	**5**	*3*	**1**	*3*	**12**	*4*	**3**	*2*
Hippodamia convergens	**5**	*5*	**2**	*2*	**4**	*11*	**1**	*8*	**5**	*3*	**0**	*0*	**14**	*4*	**3**	*2*
Psyllobora virgintimaculata	**2**	*2*	**2**	*2*	**0**	*0*	**0**	*0*	**1**	*1*	**0**	*0*	**3**	*1*	**2**	*1*
Coccinella undecimpunctata	**1**	*1*	**0**	*0*	**1**	*3*	**0**	*0*	**0**	*0*	**0**	*0*	**2**	*1*	**0**	*0*
Adalia bipunctata	**1**	*1*	**0**	*0*	**0**	*0*	**0**	*0*	**0**	*0*	**0**	*0*	**1**	*0*	**0**	*0*
Coccinellidae adults	**109**		**98**		**35**		**13**		**170**		**35**		**314**		**146**	
Coccinelidae larvae	**4**		**1**		**54**		**33**		**271**		**21**		**329**		**55**	
Coccinellidae pupae	**na**		**na**		**0**		**0**		**11**		**2**		**11**		**2**	
Vacuum Samples	**464**		**400**		**698**		**448**		**936**		**504**		**2098**		**1352**	

Figure 4.1 Coccinellidae in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

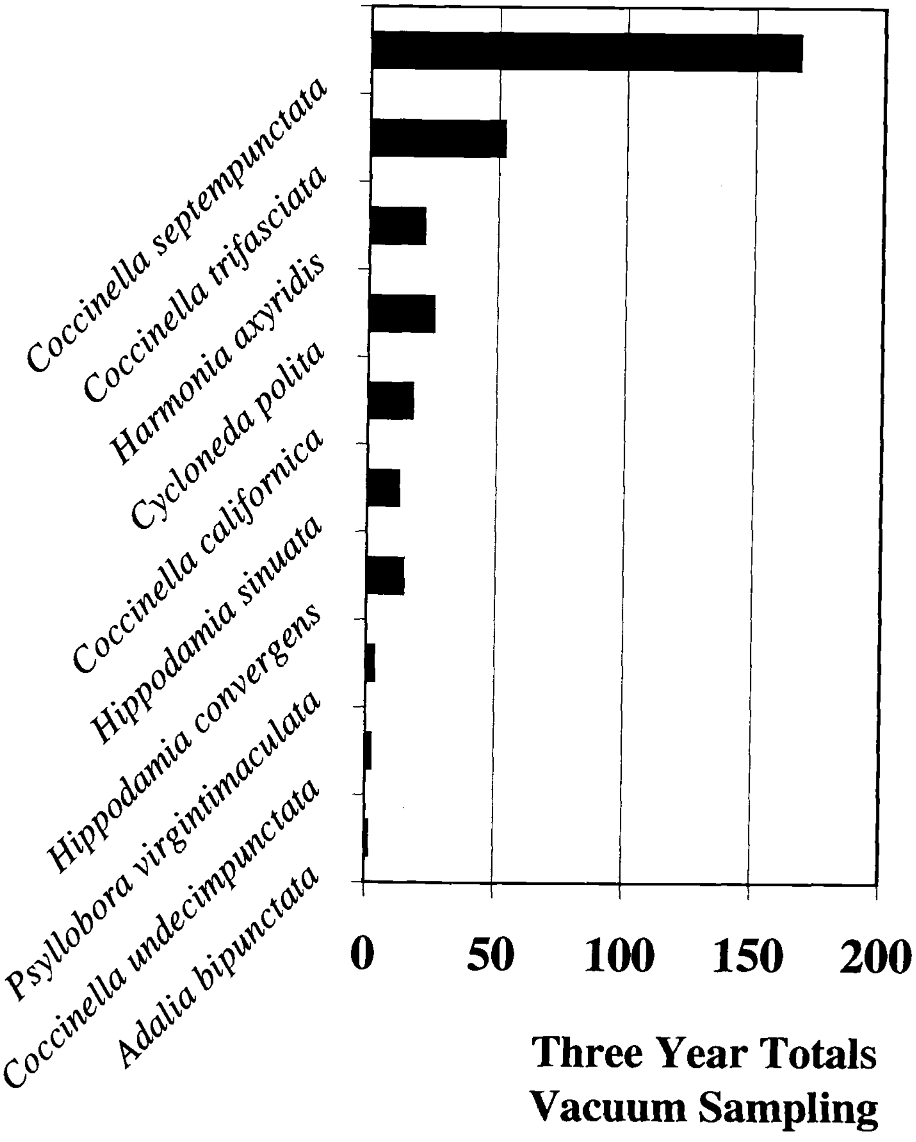


Figure 4.2 Coccinellidae in a Broccoli Cover Crop Relay
Corvallis, Oregon 1996

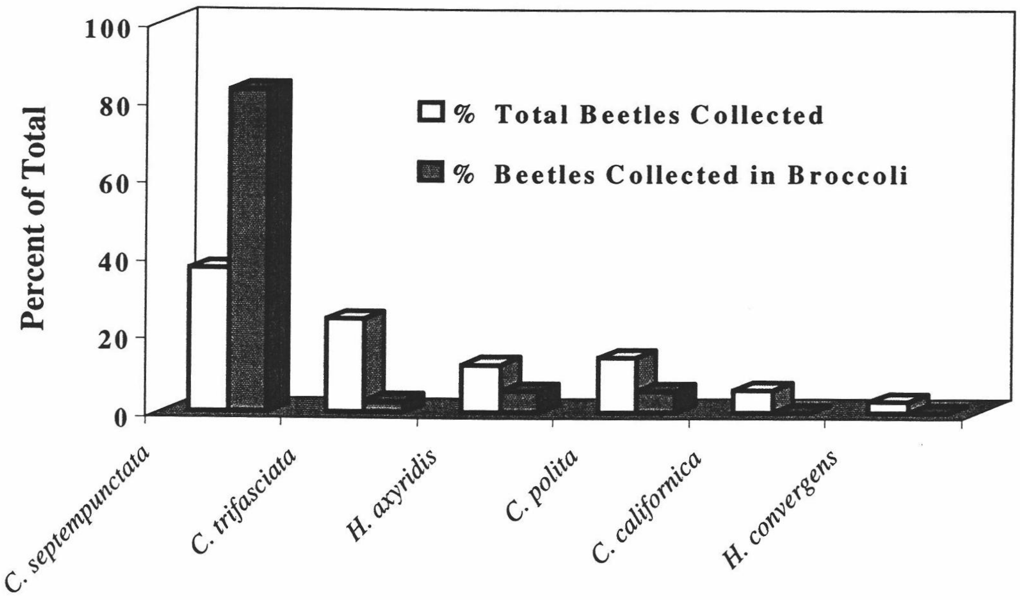
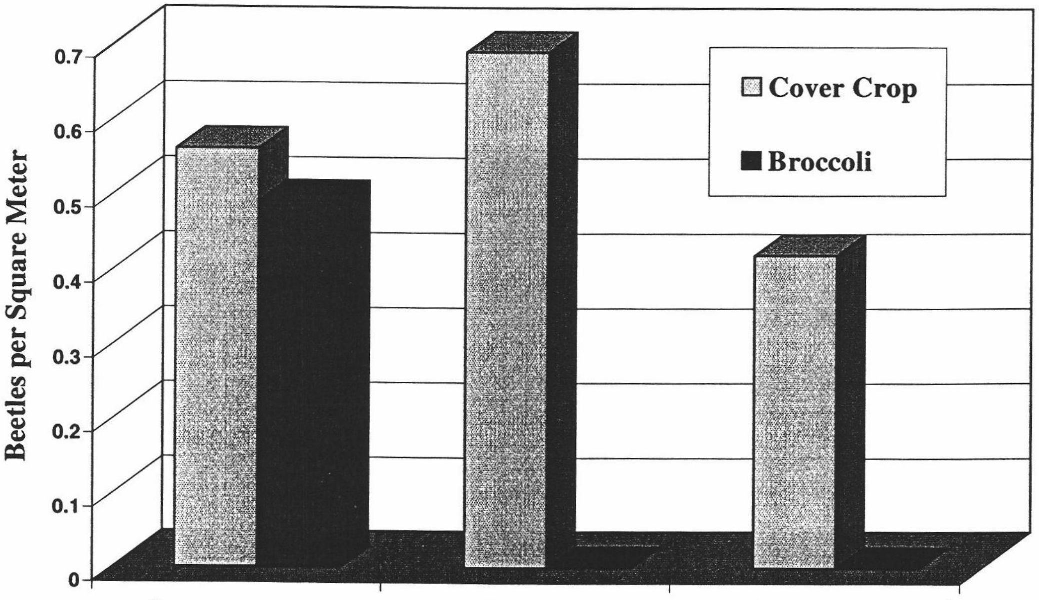


Figure 4.3 Coccinellidae in a Broccoli Cover Crop Relay
Corvallis, Oregon July 11, 1995



C. septempunctata density varied from 0 to 6.9 beetles per square meter. *C. septempunctata* density was higher in the relay strip-cropped broccoli on eight out of nine sampling dates when the species occurred in the broccoli; the difference between the broccoli treatments, however, was only statistically significant ($P<0.05$, paired t-test, two tailed) on one date (Table 4.2 and Figures 4.4-4.6). When the data were analyzed together over each sampling period, there were significantly more ($P = 0.0064$, $F = 8.96$, df = 1,24) *C. septempunctata* in the relay strip-cropped broccoli compared with clean-tilled broccoli in the early planting of 1994 (Figure 4.4). Following plow down of the cover-crop in preparation for the late broccoli planting in 1994 and 1996, adult *C. septempunctata* density increased significantly in both the relay strip-cropped and clean-tilled broccoli plots (Figures 4.4 and 4.6).

C. trifasciata density varied from 0 to 5.0 beetles per square meter, but the density of this species was never high in the broccoli, regardless of the cropping system (Table 4.3 and Figure 4.7). In 1996, high densities of *C. trifasciata* occurred in the cover-crop strips while none were found in the broccoli less than 15 m away (Figure 4.8). *H. axyridis* was only collected in 1996 when it was relatively abundant in cropping systems (Table 4.4 and Figure 4.9). *H. axyridis* density varied from 0 to 1.1 beetles per square meter. Differences in beetle density in the broccoli treatments were never statistically significant. *C. polita* was rarely caught in 1994 or 1995. In 1996, *C. polita* occurred in significant numbers in the cover-crop strips but was never abundant in the broccoli (Table 4.5).

Coccinellid larvae occurred in the cover-crop strips and in the broccoli; their densities generally corresponded with the density of the adult beetles (Table 4.6 and Figure 4.10). Larval density varied from 0 to 26.1 larvae per square meter. Approximately sixty percent of the larvae in 1996

Table 4.2 *Coccinella septempunctata* in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

	Beetle per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0.56 ± 0.39 a	1.56 ± 1.18 a	6.94 ± 1.41 a
Broccoli Clean till	0	0.14 ± 0.14 a	0 a	2.64 ± 0.50 b
Cover Crop	0.63 ± 0.36	na	0.31 ± 0.31 a	na
Bare Ground	0	na	0 a	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0
Broccoli Clean till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0.14 ± 0.14 a	0.28 ± 0.16 a	0.28 ± 0.16 a	0.19 ± 0.16
Broccoli Clean-Till	0 a	0.69 ± 0.27 a	0.14 ± 0.14 a	0
Cover Crop	0.56 ± 0.56 a	0.56 ± 0.23 a	na	na
Bare Ground	0 a	0.14 ± 0.14 a	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0	0	
Broccoli Clean-Till	0	0	0	
Cover Crop	na	0	0.31 ± 0.31	
Bare Ground	na	0	0	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0	0	2.22 ± 0.68 a
Broccoli Clean-Till	0	0	0	1.53 ± 0.57 a
Cover Crop	0.14 ± 0.14	0.28 ± 0.28	3.19 ± 0.89	na
Bare Ground	0	0	0	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0.19 ± 0.16 a
Broccoli Clean-Till	0	0	0	0.19 ± 0.16 a
Cover Crop	0.74 ± 0.42	0.19 ± 0.16	0	0.56 ± 0.28 a
Bare Ground	0	0	0	0 a

* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5), strip plot analysis, n = 4.

Figure 4.4 *Coccinella septempunctata* in a Broccoli Cover Crop Relay
Corvallis, Oregon 1994

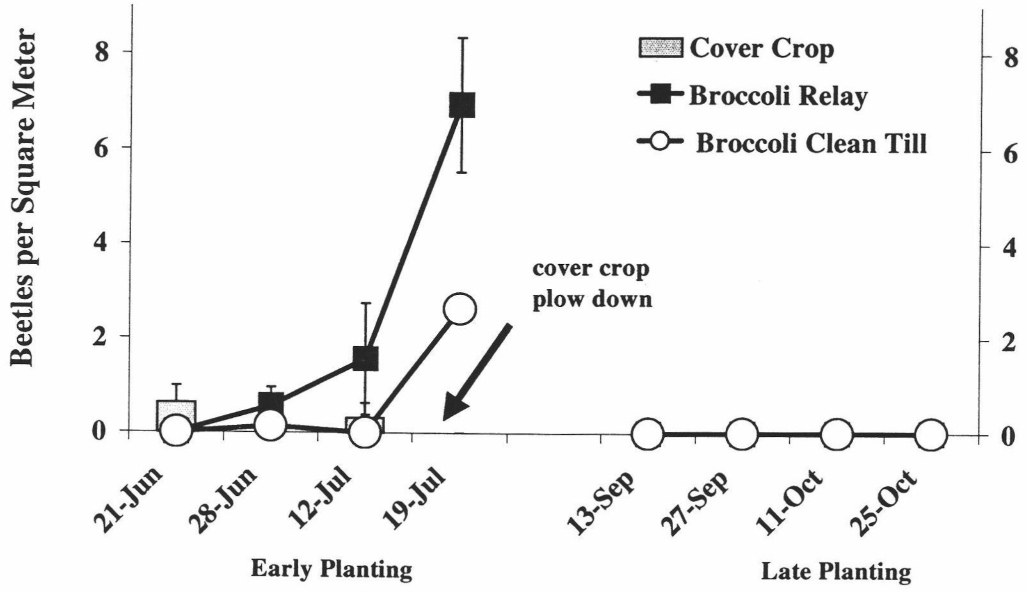


Figure 4.5 *Coccinella septempunctata* in a Broccoli Cover Crop Relay
Corvallis, Oregon 1995

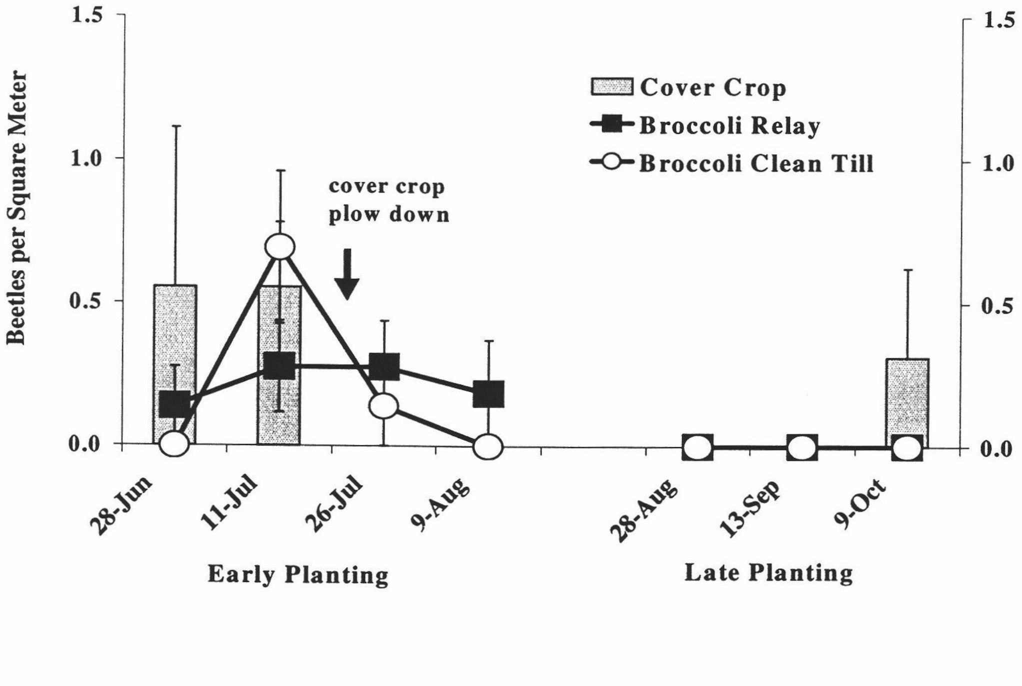


Figure 4.6 ***Coccinella septempunctata*** **in a Broccoli Cover Crop Relay Corvallis, Oregon 1996**

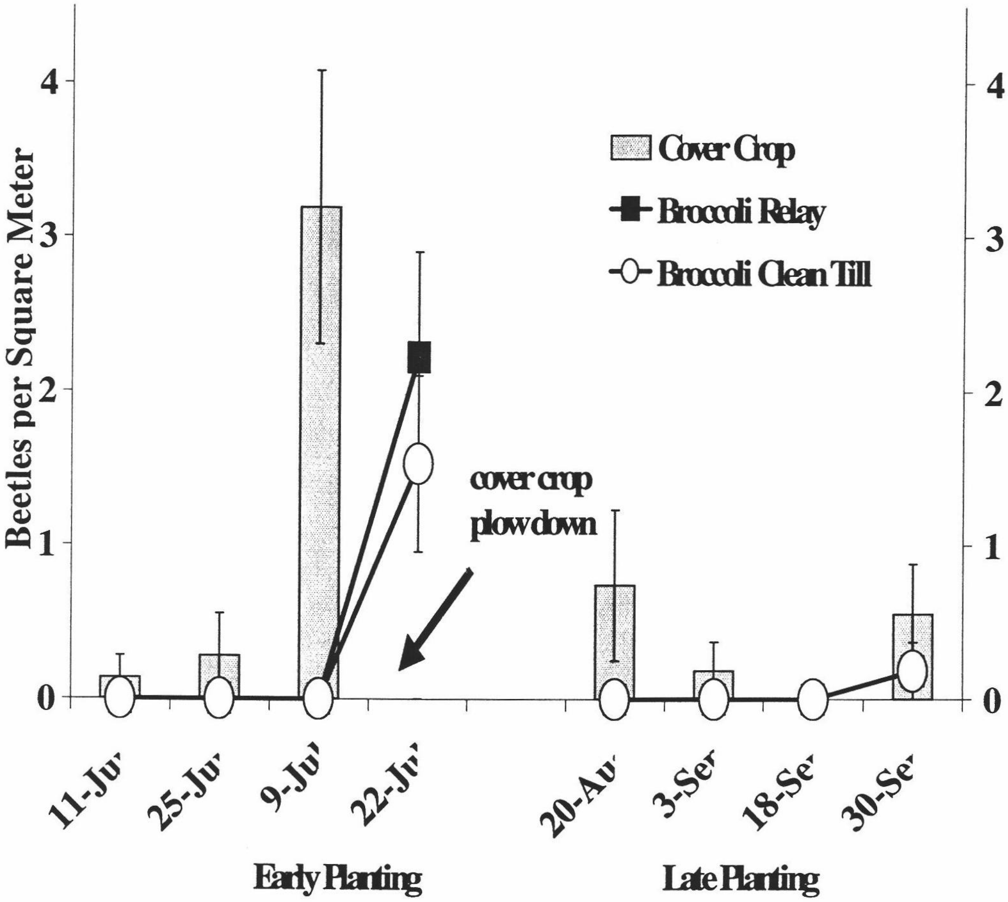


Table 4.3 *Coccinella trifasciata* in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

	Beetles per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0	0.56 ± 0.22 a
Broccoli Clean till	0	0	0	0.28 ± 0.28 a
Cover Crop	0.63 ± 0.63	na	0.31 ± 0.31	na
Bare Ground	0	na	0	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0
Broccoli Clean till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0.28 ± 0.28	0	na	na
Bare Ground	0	0	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0	0	
Broccoli Clean-Till	0	0	0	
Cover Crop	na	0	0	
Bare Ground	na	0	0	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0.14 ± 0.14	0.28 ± 0.16	5.00 ± 1.43	na
Bare Ground	0	0	0	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0	0	0	0.19 ± 0.16
Bare Ground	0	0	0	0

* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5), strip plot analysis, n=4.

Figure 4.7 *Coccinella trifasciata* in a Broccoli Cover Crop Relay
Corvallis, Oregon 1994

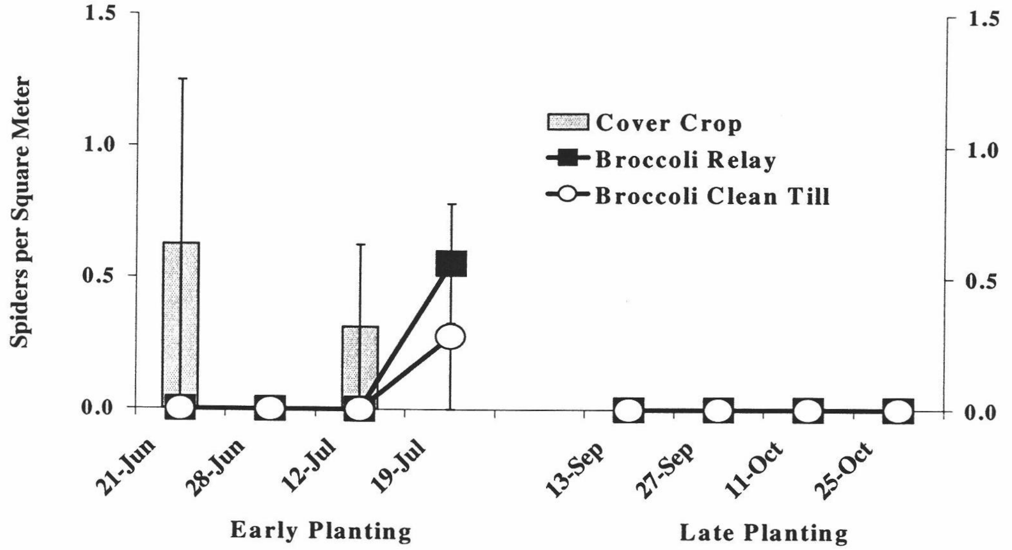


Figure 4.8 *Coccinella trifasciata* in a Broccoli Cover Crop Relay
Corvallis, Oregon 1996

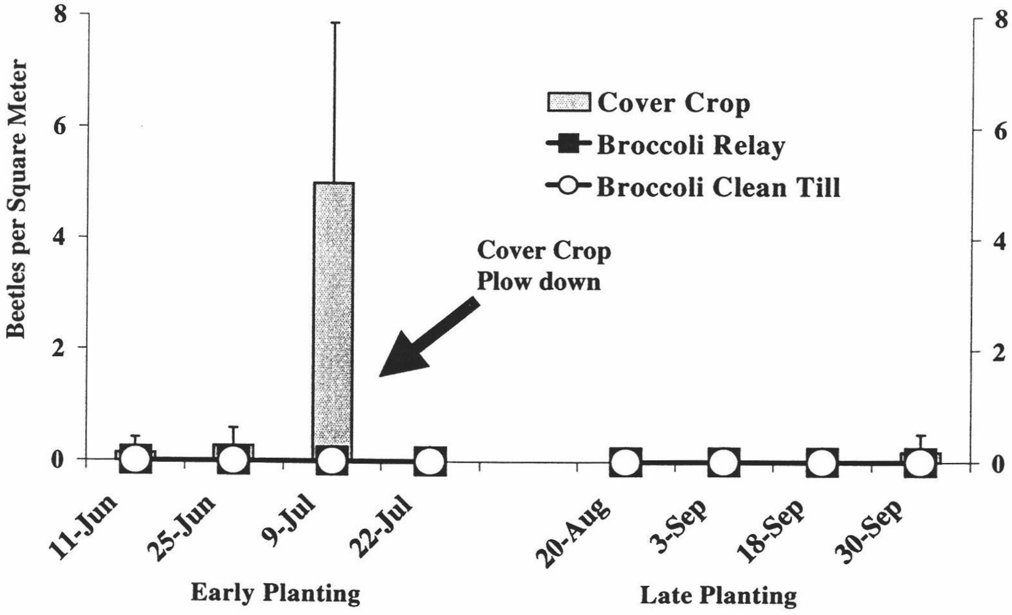


Table 4.4 *Harmonia axyridis* in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

	Beetles per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0	0
Broccoli Clean till	0	0	0	0
Cover Crop	0	na	0	na
Bare Ground	0	na	0	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0
Broccoli Clean till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0	0	na	na
Bare Ground	0	0	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0	0	
Broccoli Clean-Till	0	0	0	
Cover Crop	na	0	0	
Bare Ground	na	0	0	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0.25 ± 0.13 b	0	0.28 ± 0.14 b	0.14 ± 0.07 a
Broccoli Clean-Till	0 b	0	0.14 ± 0.07 b	0.14 ± 0.07 a
Cover Crop	0.56 ± 0.28 a	0.56 ± 0.28	1.11 ± 0.56 a	na
Bare Ground	0 b	0	0 b	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0

* Means ± SEM followed by the same letter within the same date are not significantly different ($P>0.5$), strip plot analysis, $n = 4$.

Figure 4.9 *Harmonia axyridis* in a Broccoli Cover Crop Relay
Corvallis, Oregon 1996

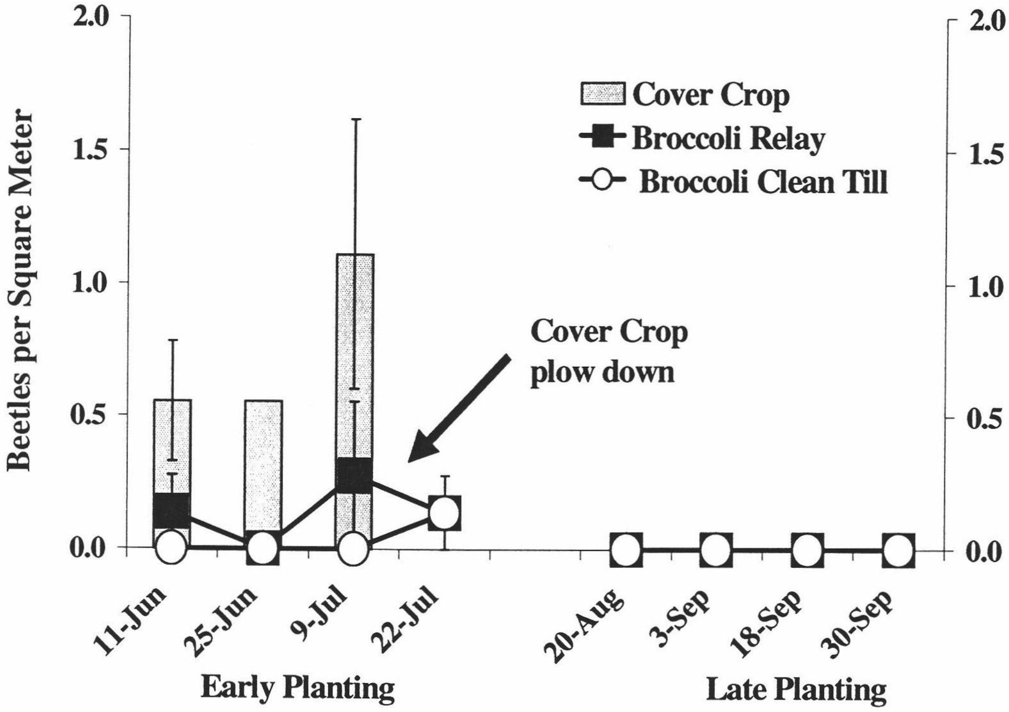


Table 4.5 *Cycloneda polita* in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

	Beetles per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0	0.25 ± 0.25
Broccoli Clean till	0	0	0	0
Cover Crop	0	na	0	na
Bare Ground	0	na	0	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0
Broccoli Clean till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0	0	na	na
Bare Ground	0	0	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0	0	
Broccoli Clean-Till	0	0	0	
Cover Crop	na	0	0	
Bare Ground	na	0	0	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0	0 b	0
Broccoli Clean-Till	0	0	0.14 ± 0.14 b	0
Cover Crop	0.28 ± 0.16	0	2.78 ± 1.04 a	na
Bare Ground	0	0	0 b	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0

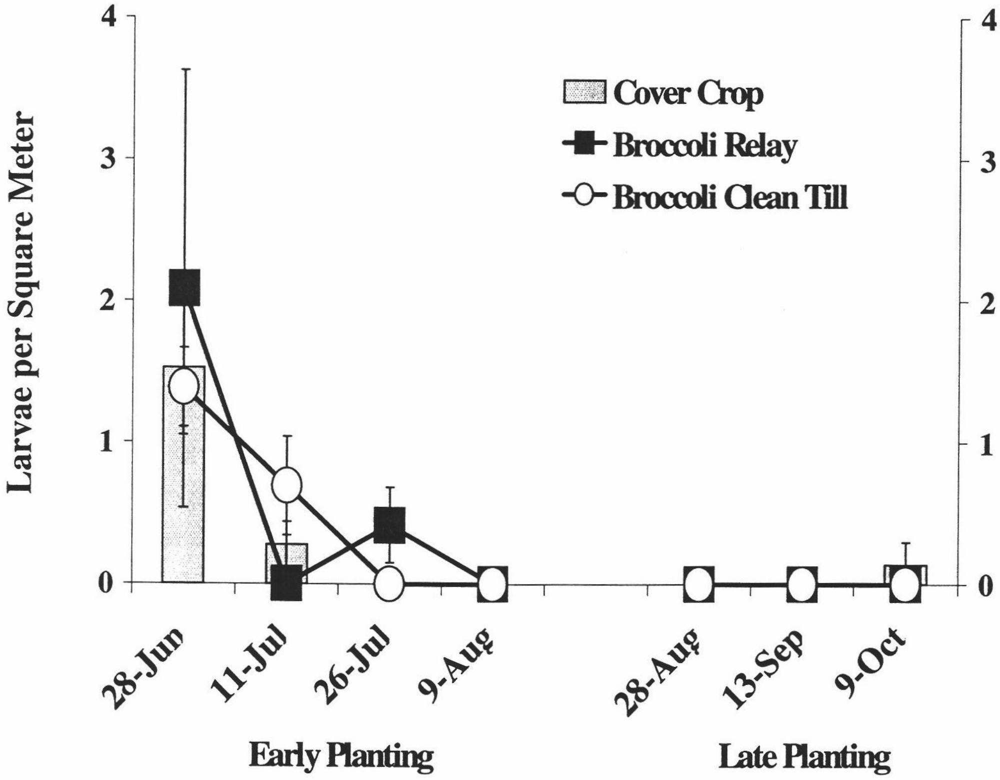
* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5), strip plot analysis, n = 4.

Table 4.6 Coccinellidae Larvae in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

	Larvae per Square Meter *			
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0	0.14 ± 0.14
Broccoli Clean till	0	0	0.94 ± 0.94	0
Cover Crop	0	na	0	na
Bare Ground	0	na	0	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0
Broccoli Clean till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	2.08 ± 1.54 a	0 b	0.42 ± 0.27	0
Broccoli Clean-Till	1.39 ± 0.28 a	0.69 ± 0.35 a	0	0
Cover Crop	1.53 ± 0.47 a	0.28 ± 0.16 ab	na	na
Bare Ground	0.97 ± 0.47 a	0 b	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0	0	
Broccoli Clean-Till	0	0	0	
Cover Crop	na	0	0	
Bare Ground	na	0	0	
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0.14 ± 0.14 b	1.25 ± 0.73 b	0.28 ± 0.16
Broccoli Clean-Till	0	0.14 ± 0.14 b	1.11 ± 0.60 b	0
Cover Crop	0.69 ± 0.53	7.92 ± 2.40 a	26.11 ± 6.01 a	na
Bare Ground	0	0 b	0 b	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0

* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5), split plot analysis, n = 4.

Figure 4.10 Larvae of Coccinellidae in a Broccoli Cover Crop Relay
Corvallis, Oregon 1995



were *H. axyridis* (Table 4.7). Total density in the broccoli never exceeded two larvae per square meter. The highest larval density of the three-year study (more than 26 larvae per square meter) was observed in 1996 in the cover-crop just prior to plow down (Figure 4.11).

DISCUSSION

The dominant species of Coccinellidae in Willamette Valley crops have changed over the past several decades. In the early 1900s, the most common coccinellid species was *H. convergens* (Ewing 1913). It was found everywhere in the lower altitudes from mid-April until mid-August. In my study, *H. convergens* was uncommon. Several native species of Coccinellidae that were listed in early surveys of Willamette Valley crops were completely absent in my collection including *Coccinella novemnotata* Herbst., *Coccinella transversoguttata* Falderman, *Hippodamia lunatomaculata* Motschulsky, *Hippodamia parenthesis* Say, *Hippodamia quinquesignata* (Kirby), *Hippodamia spuria* LeConte, *Hippodamia tibialis* (Say), *Chilocorus bivulnrus* Mulsant, *Psyllobora toedata* LeConte, and *Smilia misella* LeConte (Ewing 1913, Rockwood 1952).

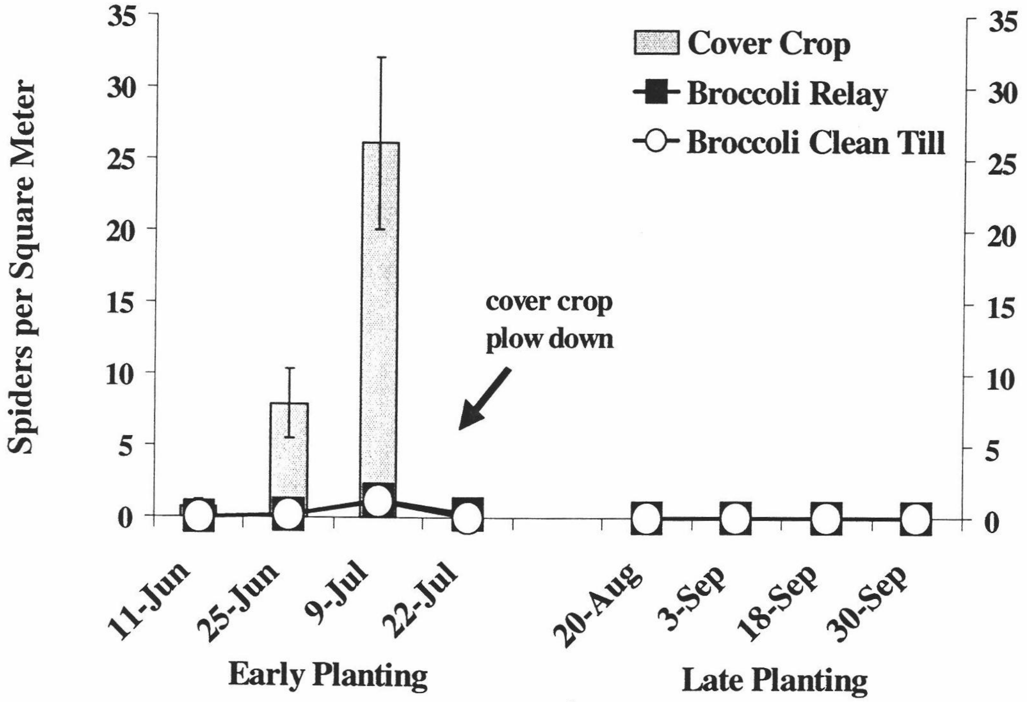
The dominant coccinellids in my study was clearly *C. septempunctata*. Native Coccinellidae were never abundant in any of the three years of the study. Apparently, *C. septempunctata* has replaced *C. trifasciata*, which was the dominant Coccinellidae in the Corvallis area during the early 1980s (McIver 1983). *C. septempunctata* and *H. axyridis* were brought to the United States from Europe and Asia for the purposes of biological control. *C. trifasciata* may be Holarctic. Similar changes in the structure and composition of the Coccinellidae community after the

Table 4.7 Larvae of *Harmonia axyridis* in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

	Larvae per Square Meter *			
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0 a	0.56 ± 0.56 a	0
Broccoli Clean-Till	0	0.28 ± 0.16 ab	0.42 ± 0.42 a	0
Cover Crop	0	1.94 ± 0.73 b	16.25 ± 3.37 b	na
Bare Ground	0	0 a	0 a	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0	0
Broccoli Clean-Till	0	0	0	0
Cover Crop	0	0	0	0
Bare Ground	0	0	0	0

* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5), split plot analysis, n = 4.

Figure 4.11 Coccinellidae larvae in a Broccoli Cover Crop Relay
Corvallis, Oregon 1996



establishment of *C. septempunctata* have been reported elsewhere (Elliott et al. 1996).

There are several factors that may explain the current dominance of *C. septempunctata*. *C. septempunctata*, survives hot temperatures better than native Coccinellidae species in Oregon and remains in the valleys longer during the summer (La Mana 1995). The species also tends to winter on the valley floor where it becomes active in the early spring. The propensity for *C. septempunctata* to disperse into the broccoli crop suggests that it is adapted to the row crop environment and not averse to foraging for *B. brassicae*. Like the other coccinellid species, however, it was consistently absent from the late broccoli planting even though the late planting of broccoli supported significant numbers of cabbage aphids.

All of the Coccinellidae that were present in the broccoli cropping systems were present in the cover-crop prior to the establishment of the broccoli. Some authors have argued that if non-crop crop vegetation is colonized by natural enemies prior to the establishment of the target crop, the non-crop crop vegetation is more likely to serve as a source for natural enemies (Corbett 1998). In my study, cover-crop strips served as source of Coccinellidae in broccoli for some species and not others, regardless of the sequence of colonization. The source versus sink effects depended, in large part, on the habitat preferences of the species.

C. trifasciata and *H. axyridis* were occasionally abundant in the relay strip-cropping system, but they were never abundant in the broccoli. Most of the native coccinellid species that occurred in significant numbers in the cover-crop strips also failed to move into the broccoli that grew less than 15 m away. There were times when *H. convergens* and *H. sinuata* were abundant in the cover-crop and completely absent in the broccoli. It appeared that the cover-crop strips were acting as a sink rather than a source of native Coccinellidae in the broccoli.

McIver (1983) observed a similar situation in his study of collards surrounded by alfalfa. The abundance of *C. trifasciata* was enhanced by the presence of the alfalfa. Elevated numbers of *C. trifasciata* in the alfalfa-collard biculture did not, however, result in elevated numbers of *C. trifasciata* on the collards themselves. The association of *C. trifasciata* with alfalfa was so strong that the species may be considered an alfalfa-specialist.

The Coccinellidae did not reproduce in the relay strip-cropping system in high numbers except during the early broccoli planting of 1996. The majority of the larvae that were collected in this planting were collected in the cover-crop strips just prior to plow down and most of them (approximately 60%) *H. axyridis*. Most of these larvae probably perished when the cover-crop was incorporated into the soil; thus, a significant proportion of the reproductive potential of the coccinellids colonizing the system was wasted.

Winter cover-crops, under-sowing, and strip-managed enhanced the number of Coccinellidae in the vicinity of broccoli. The density of *C. septempunctata* was occasionally higher in the relay strip-cropped broccoli compared with clean-tilled broccoli; the effect, however, was inconsistent. The majority of coccinellid species that were enhanced by the relay strip-cropping system remained in the cover-crop and failed to switch on to the broccoli crop. This may be the result of preferences for habitat or prey types by the Coccinellidae.

C. septempunctata occurred in higher numbers in broccoli growing next to the cover-crops compared to broccoli surrounded by bare ground; the cover-crops appeared to act as a source of *C. septempunctata*. *C. septempunctata* present in the residual cover-crop strips at crop establishment probably dispersed into the broccoli where colonies of *B. brassicae* were becoming established. In 1996, it appeared that the plow down of the cover-crop caused *C. septempunctata* adults present in the cover-crop to disperse into the broccoli. Relay strip-cropped and clean-tilled broccoli plots experienced a sudden increase in beetle counts. The beetles may have dispersed from the cover-crop strips across the entire experimental area suggesting that the scale of the experiment may have been too small to detect differences in the treatments. This will have to be resolved in future mark and recapture experiments.

The small scale of this experiment and the apparent repugnancy of *B. brassicae* to most coccinellid species limits the generalizations that one can draw from this three year experiment. I was, however, successful at attracting elevated numbers of Coccinellidae into close proximity to the broccoli. In two out of three years, maturation of the cover-crop or mechanical destruction of the cover-crop drove *C. septempunctata* out of the refuge and into the broccoli. Management of the Coccinellidae would be improved if the timing of cover-crop incorporation could be delayed to allow the maturation and escape of the coccinellid larvae developing in the cover-crop. Delay in seedbed preparation may not be practical in a commercial farming operation.

CHAPTER 5

IMPACT OF RELAY STRIP-CROPPING ON DAMSEL BUGS (HETEROPTERA: NABIDAE) IN BROCCOLI

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ABSTRACT

Two species of damsel bug (Heteroptera: Nabidae), *Nabis americoferus* Carayon and *Nabis alternatus* Parshley were captured in vacuum samples from 1994-1996 in a study comparing relay strip-cropping to clean-till planting of broccoli. Relay strip-cropping combines under-sowing and strip-management. A cover-crop seed mixture containing *Avena sativa* L. var. "Monida", *Vicia sativa* L., *Trifolium pratense* L., *Lolium multiflorum* Lam., and *Fagopyrum esculentum* Moench was broadcast over broccoli 32 days after planting. The broccoli was planted, under-sown, and harvested in sections alternating with strips of undisturbed cover-crop. *N. americoferus* and *N. alternatus* occurred in equal numbers in 1995. In 1996, seventy eight percent of the adult nabids were *N. americoferus*. Nabid density varied from 0.3 to 5.1 bugs per square meter. Nabids were present early in the growing season; density increased steadily and peaked from mid-September to mid-October. Nymphs often outnumbered adult nabids during the late growing season. On eleven out of twenty three sampling dates, nabids occurred in significant numbers in the cover-crop strips while they were completely absent in the broccoli. The density of nabids in the clean-till broccoli often exceeded the number of nabids in the relay strip-cropped broccoli; the difference between the cropping systems were never statistically significant. Cover-crop strips appeared to act as sinks rather than sources of colonizing Nabidae in the broccoli.

INTRODUCTION

Nabidae are one of the most abundant predators in agricultural systems; they can have an impact on insect pest populations (Donahoe and Pitre 1977, Taylor 1949, Grasela and Steiner 1993). Most nabid species would be considered r-strategist according to Southwood's definition (Southwood 1977). They are highly mobile, and they reproduce rapidly. Nabidae successfully colonize recently disturbed habitats. Ehler and Miller (1978) argued that r-selected natural enemies can provide control of r-selected insect pests in ephemeral agricultural crops. They cite *Nabis americoferus* Carayon as an example of such an enemy. Nabidae belong to a guild of generalist predators that operate together in complementary ways. Ehler (1977) showed, for example, that *Orius tristicolor* (White), *N. americoferus, Geocoris pallens* Stal, and *Chrysoperla carnea* (Stephens) together over the course of the growing season, maintain the density of the cabbage looper, *Trichoplusia ni* (Hubner) at non-injurious levels.

Nabid populations tend to follow the same seasonal activity patterns as *Lygus* populations (Stern et al. 1964, 1969). The peak density of *N. americoferus* in eastern Canada of three to four specimens per arc of a sweep net occurs during August (Guppy 1986). In California's San Joaquin Valley, *N. americoferus* occurs in significant numbers by mid-June, and their population increases steadily over the growing season (Eveleens et al. 1973, Ehler 1977). Nabids generally are most abundant later in the growing season as crops mature. In warm climates, definite peaks in nabid populations are observed in early July and late August (McPherson et al. 1982). Typically, nabid nymphs and adults reach total densities of less than one individual per square meter. Their numbers, however, occasionally rise as high as ten individuals per square meter. Nymphs generally outnumber adults except in the early growing season prior to the development of the first generation of the new year (Buschman et al. 1984).

Nabids feed on many different small insects (Perkins and Watson 1972a, 1972b, Lattin 1989) including aphids (Ehler 1977), thrips, whitefly nymphs, and leafhoppers (Martinez and Pienkowski 1982, Renser and Lamp 1983, Flinn et al. 1985), mirids (including *Lygus* species) (Whalon and Parker 1978, Araya and Haws 1988, 1991), spider mites (Butcher et al. 1988), leaf miners (Guppy 1986, Harcourt and Guppy 1987), and the eggs and small larvae of many species of Lepidoptera

(Ehler and van den Bosch 1974, Braman and Yeargan 1989). Prey quality influences developmental time of the nymphs. For example, *N. americoferus* nymphs develop 10 to 34% faster on leaf miners (Diptera: Agromyzidae) than on pea aphids (Guppy 1986).

Nabids prey on aphids of many different species (Cameron et al. 1983, Carrol and Hoyt 1984, Rice and Wilde 1991, Campbell and Cone 1994) and consume up to 25 aphids per day (Tamaki and Weeks 1972). This rate of consumption is significantly less than the Coccinellidae, which consume up to 200 aphids per day (Palmer 1914). Nabids foraging on plant foliage alarm and dislodge many more aphids than they consume. On the ground, the numerous ground dwelling predators prey upon these aphids (El-Agamy and Haynes 1992). In the laboratory, *Nabis alternatus* Parshley can be maintained on pea aphids (*Acyrthosiphon pisum* L.) on alfalfa (Richards and Harper 1978). *Nabis* species had a 35-88% positive precipitin tests for *Brevicoryne brassicae* L. when they were gathered from collard foliage (McIver 1983).

Nabids are common predators of the eggs and small larvae of Lepidoptera (Ehler et al. 1973, Ehler and van den Bosch 1974, Ehler 1977, Donahoe and Pitre 1977, Sloderbeck and Yeargan 1983, Elvin et al. 1983, O'Neil and Stimac 1988, Yeargan and Braman 1989, Ruberson et al. 1991). Nabids at approximately 20 per row meter in soybeans caused a 50% reduction in green clover worm larvae, *Plathypena scabra* (L.), over control plots. This density of nabids is, however, about ten times the normal level of nabids in soybeans. Nabids contribute to mortality of the green clover worm, but can not normally prevent clover worm outbreaks (Braman and Yeargan 1989).

In cage studies to determine the impact of natural enemies on the Bertha armyworm, *Mamestra configurata* Walker, *N. americoferus* alone and in combinations with *Coccinella transversoguttata* Faldermann was superior to all other natural enemies tested at reducing the armyworm population. The nabid alone was more effective at reducing armyworm numbers than the coccinellid alone. Apparently, *N. americoferus* was attracted to and could better handle the early instars of *M. configurata* better than the coccinellid predator (Tamaki and Weeks 1972).

Eveleens et al. (1973) studied the impact of insecticides on the interaction between predators including *N. americoferus* and the beet armyworm, *Spodoptera exigua* (Hubner) in cotton. Life table analysis showed that mortality of *S. exigua* in the absence of the insecticide sprays was due to predation directed at eggs and the first and second instars. *N. americoferus* feeds on small to medium size armyworm larvae. Once it finds a hatching egg cluster, *N. americoferus* tends to stay there consuming the young larvae as they emerge. Heavy outbreaks of armyworms followed treatments with the insecticide dimethoate. The insecticide dramatically depressed the density of *N. americoferus* and other predators. As the number of sprays increased, the size of the cohort of early instars of *S. exigua* increased almost linearly.

Adult nabids are capable of moving considerable distances. Edwards (1987) mentions *N. alternatus* as one of five species of insects taken on the summit of Mt. Rainier, Washington. When alfalfa is cut, adult *N. americoferus* migrate over 67 m to 122 m to half-grown alfalfa. Nabid nymphs, however, are wingless and not highly mobile. Once the female has committed her progeny to a plant patch, the young are forced to hunt for prey to avoid starvation (Rakickas and Watson 1974).

The mobility of the Nabidae allows them to rapidly colonize agricultural fields that have been sprayed with insecticide or disturbed in some other manner. Buschman et al. (1984) found that nabid populations recovered completely in about two weeks after whole field insecticide applications. In part, because of the high mobility of the Nabidae, Eveleens and van den Bosch (1973) used experimental plots placed in commercial alfalfa fields that were 1/8 by ½ mile wide. The depressing effect of the insecticide application (dimethoate) on *N. americoferus* was dramatic, but it persisted for only three weeks. The plot size (40 acres each) was too small to prevent re-colonization of the experimental plots by the nabids.

Nabidae have distinct crop preferences. Nabidae are most commonly associated with legumes, cotton, and grasses (Perkins and Watson 1972a, Stoner et al. 1975, Braman et al. 1984). In small plot studies, where the nabids could easily disperse across the treatments, the nabid densities varied significantly between crops. *N. americoferus* was strongly associated with snap beans and soybeans. Only small numbers of nabids were found in corn, tomato, or tobacco (Nordlund et al. 1984, Pfannenstiel and Yeargan 1998).

In the agricultural landscape, a significant portion of the reproductive potential of the nabid populations is lost to insecticide applications and to forage harvesting practices (Ehler and Miller 1978). Many nabid eggs and young nymphs perish during the harvest of alfalfa (Richards and Harper 1978, Godfrey and Leigh 1994). *N. alternatus* females lay most of their eggs in alfalfa stems. The timing of harvest and the harvest management scheme determine if the alfalfa crop serves as a nursery or a trap crop for the nabid populations. In the laboratory, most of the eggs that were laid in alfalfa stems died when the alfalfa was allowed to dry after oviposition. In the field, few nabid eggs survive when the alfalfa is cut for hay (Richards and Harper 1978, Godfrey and Leigh 1994). Nabid populations in hay fields depend on the migration ability of the wingless nymphs and the flying adults. Adult nabids disperse during the harvest operation, but many wingless nymphs probably perish during and after the harvest. The destruction of the nymphs may explain why nabid populations are larger and more stable when alfalfa is strip-managed. A significant amount of reproductive potential of the nabid species may be wasted in the agricultural landscape. The relative importance of this loss remains to be more fully investigated (Rakickas and Watson 1974).

Increased weed diversity can have an impact on natural enemy populations. The impact of weediness on nabids depends on the weed species. Shelton and Edwards (1983) found that differing soybean maturity dates, locations, and row spacing had little impact on predator populations. Grassy soybean fields, however, had more nabids in them than soybean fields infested with broadleaf weed or weed free soybean fields. Beans grown with maize support higher nabid densities than either crop grown in monoculture (Altieri et al. 1978)

Heteropteran predators including *Nabis* species respond to alfalfa management (Cameron et al. 1983, Thorvilson et al. 1985, Harper et al. 1989, Schaber et al. 1990). Nabids and *Lygus* both lay their eggs by inserting them into the stems of alfalfa plants. The densities of *Lygus* (Godfrey and Leigh 1994) and nabids (McIver 1983) are higher in tall unmanaged alfalfa than in the new growth alfalfa cut for hay. In block-harvested alfalfa, nabid and *Lygus* dispersal flights closely agree with alfalfa cutting dates (Braman and Yeargan 1990). The nymphs of both *Lygus* and *Nabis* are flightless; they perish during the cutting and harvest of the alfalfa managed for hay (Richards and Harper 1978). After an alfalfa harvest, nabid adults concentrate in residual patches of undisturbed vegetation even if the patches are relatively small (Grasela and Steiner 1993). Adult nabids do not move freely between strips in strip-managed alfalfa (Stern et al. 1964, 1969).

N. alternatus populations are more stable in alfalfa cropping systems when the edges of alfalfa fields are left uncut during harvest. In a study comparing conventional solid cut alfalfa versus border harvested alfalfa, 90% of the nabids concentrated in the uncut area on the border. They did not disperse. About a week later, they reinvaded the same field (Summers 1975).

Relay strip-cropping, which combines under-sowing with strip-management, should increase the density of Nabidae in the vicinity of the target crop, broccoli.

The winter cover-crop of grasses and legumes should attract and support a winter population of Nabidae. At crop establishment, the residual strips of cover-crop should concentrate Nabidae proximal to the broccoli. As the cover-crop strips mature and dry out or when the cover-crop strips are incorporated prior to the late planting of broccoli, the adult nabids may disperse into the broccoli.

Under-sowing results in an intimate mixture of broccoli, grasses, and legumes. Nabids are attracted to grasses and legumes; the polyculture should result in increases in nabids in the immediate vicinity of the broccoli. Evidence suggests that nabids prey on aphid species that attack broccoli including *Brevicoryne brassicae* (L.) (McIver 1983). Evidence suggests that nabids attack several lepidopteran pests of broccoli including *T. ni* (Ehler 1977) and *M. configurata* (Tamaki and Weeks 1972). Relay strip-cropping should, therefore, result in reduced pest populations in the broccoli. For a more detailed review of the Nabidae literature, see Appendix D.

MATERIALS AND METHODS

The experiments described below were conducted from 1994 to 1996 at the Oregon State University Vegetable Research Farm near Corvallis, Oregon, approximately 0.4 km from the Willamette River. The site characteristics and the general outline of the relay strip-cropping experiments from 1994-1996 were described in chapter two. In the relay, broccoli was under-sown with grasses (*Avena sativa* L., *Lolium multiflorum* Lam.) and legumes (*Vicia sativa* L., *Trifolium pratense* L.) that should provide attractive foraging and oviposition sites for adult nabids. Nabids should overwinter in the cover-crops and residual strips may serve as sources of colonizing nabids in the broccoli during the growing season.

Nabids were captured in vacuum samples, which was described in chapter three. Vacuum sampling began after the final cultivation following under-sowing 32 days after planting. Vacuum samples were taken every other week, nine in each of the four areas of each block. Vacuum samples were taken directly over the rows adjacent to the pitfall sites. On each sampling date, vacuum samples were taken in a different cardinal direction from the pitfall, in the same row or in the adjacent row. Vacuum samples were taken on alternating weeks until harvest.

The efficiency of the vacuum sampling procedure described above was tested using marked and recaptured adult damsel bugs (*Nabis* species). Insects were gathered in alfalfa with a sweep net, mixed with various colored florescent powders, and released in cover-crop in groups of ten per site under five gallon buckets. After five minutes, the buckets were removed, the cylinder was placed over the area, and the vacuuming procedure was accomplished. Recapture of marked damsel bugs varied from 76% to 85% of those released. In the 1995 and 1996 nabids were sorted to species, gender, and maturity according to keys by Benedict and Cothran (1975). Statistical methods have been previously described.

RESULTS

Two thousand ninety eight vacuum samples over a three-year period produced a total of two hundred and fourteen Nabidae (Tables 5.1-5.2). *N. americoferus* and *N. alternatus* occurred in equal numbers in 1995. In 1996, seventy eight percent (36/46) of the adult nabids were *N. americoferus*. The sex ratio appeared to be normal (1:1) in both species (Table 5.2, Figures 5.1 and 5.2).

Nabids were collected on twenty-two out of twenty three sampling dates over the three-year period and were mostly present in the cover-crop strips. Nabids were present early in the growing season (Figures 5.3-5.5); densities increased steadily

Table 5.1 Damsel Bugs (Nabidae) in a Broccoli Cover Crop Relay Corvallis, Oregon 1994-1996

	Damsel Bugs per Square Meter*			
1996 Early Planting	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**
Broccoli Relay	0	0	0	0.56 ± 0.32
Broccoli Clean-Till	0	0	0	0
Cover Crop	0.28 ± 0.16	0.69 ± 0.14	0.42 ± 0.27	na
Bare Ground	0	0	0	na
1996 Late Planting	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**
Broccoli Relay	0	0	0.19 ± 0.16 a	0.37 ± 0.16 a
Broccoli Clean-Till	0	0	0 a	0.19 ± 0.16 a
Cover Crop	2.22 ± 0.83	1.30 ± 0.58	5.00 ± 1.00 b	3.52 ± 0.70 b
Bare Ground	0	0	0 a	0 a
1995 Early Planting	**28-Jun**	**11-Jul**	**26-Jul**	**9-Aug**
Broccoli Relay	0	0	0.97 ± 0.14 a	2.04 ± 0.58 a
Broccoli Clean-Till	0	0	1.67 ± 0.79 a	2.78 ± 1.00 a
Cover Crop	1.25 ± 0.89	1.11 ± 0.23	na	na
Bare Ground	0	0	na	na
1995 Late Planting	**28-Aug**	**13-Sep**	**9-Oct**	
Broccoli Relay	0	0.19 ± 0.16 a	0.31 ± 0.31 a	
Broccoli Clean-Till	0	0.37 ± 0.16 a	0 a	
Cover Crop	na	1.85 ± 0.98 a	5.10 ± 2.32 b	
Bare Ground	na	0 a	0 a	
1994 Early Planting	**21-Jun**	**28-Jun**	**12-Jul**	**19-Jul**
Broccoli Relay	0	0	0.63 ± 0.36 ab	0.28 ± 0.16 a
Broccoli Clean till	0	0.14 ± 0.14	0.94 ± 0.60 ab	0.69 ± 0.42 a
Cover Crop	4.06 ± 1.18	na	2.81 ± 1.64 a	na
Bare Ground	0	na	0.00 ± 0.00 b	na
1994 Late Planting	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**
Broccoli Relay	0	0	0	0.42 ± 0.36 a
Broccoli Clean till	0	0	0	0 a
Cover Crop	2.92 ± 0.95	4.58 ± 1.57	0.83 ± 0.36	0.42 ± 0.36 a
Bare Ground	0	0	0	0 a

* Means ± SEM followed by the same letter within the same date are not significantly different (P>0.5), n = 4.

Table 5.2 *Nabis americoferus* and *Nabis alternatus* in a Broccoli Cover Crop Relay Corvallis, Oregon 1995-1996

Damsel Bugs per Sampling Date

	Early Planting 1994				**Late Planting 1994**				**Annual Totals**	
	21-Jun	**28-Jun**	**12-Jul**	**19-Jul**	**13-Sep**	**27-Sep**	**11-Oct**	**25-Oct**		
Total Nabidae	13	1	14	7	7	11	2	1	Total	56
	Early Planting 1995				**Late Planting 1995**					
Nabis americoferus	**28-Jun**	**11-Jul**	**25-Jul**		**9-Aug**	**13-Sep**	**9-Oct**			
Males	3	1	0		2	3	0		Males	9
Females	0	4	5		0	1	0		Females	10
Nabis alternatus										
Males	3	1	2		3	0	1		Males	10
Females	0	0	7		2	1	0		Females	10
Totals										
Adults	6	6	14		7	5	1		Adults	39
Juveniles	2	1	4		19	8	0		Nymphs	34
Total Nabidae	8	7	18		26	13	1		Total	73
	Early Planting 1996				**Late Planting 1996**					
Nabis americoferus	**11-Jun**	**25-Jun**	**9-Jul**	**22-Jul**	**20-Aug**	**3-Sep**	**18-Sep**	**30-Sep**		
Males	0	0	1	2	0	1	6	10	Males	20
Females	0	1	2	2	1	0	6	4	Females	16
Nabis alternatus										
Males	0	0	0	0	0	0	2	5	Males	7
Females	0	0	0	0	0	0	2	1	Females	3
Totals 1996										
Adults	0	1	3	4	1	1	16	20	Adults	46
Juveniles	2	4	0	0	10	8	11	4	Nymphs	39
Total Nabidae	2	5	3	4	11	9	27	24	Total	85

Total Nabidae 1994-96
214

Figure 5.1 *N. americoferus* and *N. alternatus* Adults in a Broccoli Cover Crop Relay Corvallis, Oregon 1995

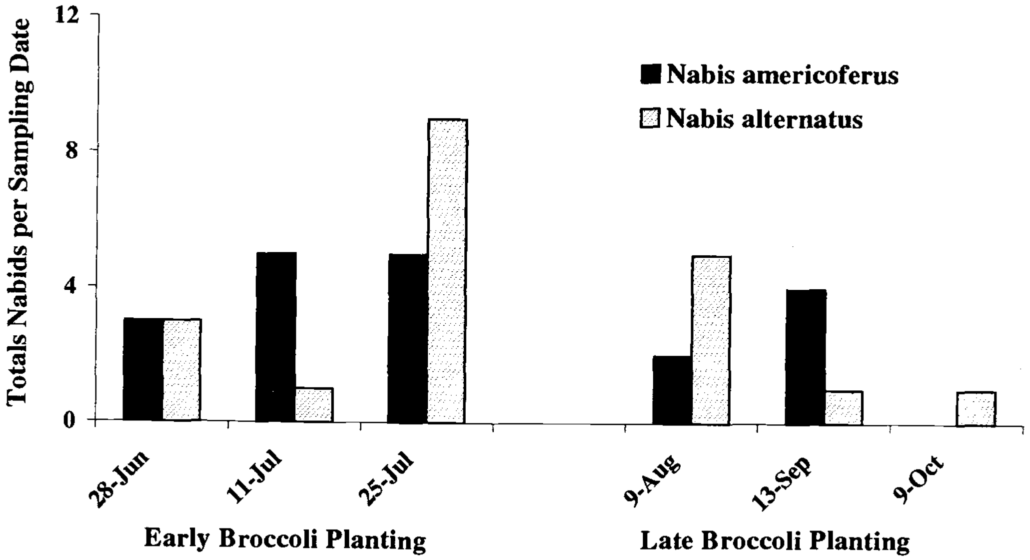


Figure 5.2 *N. americoferus* and *N. alternatus* in a Broccoli Cover Crop Relay Corvallis, Oregon 1996

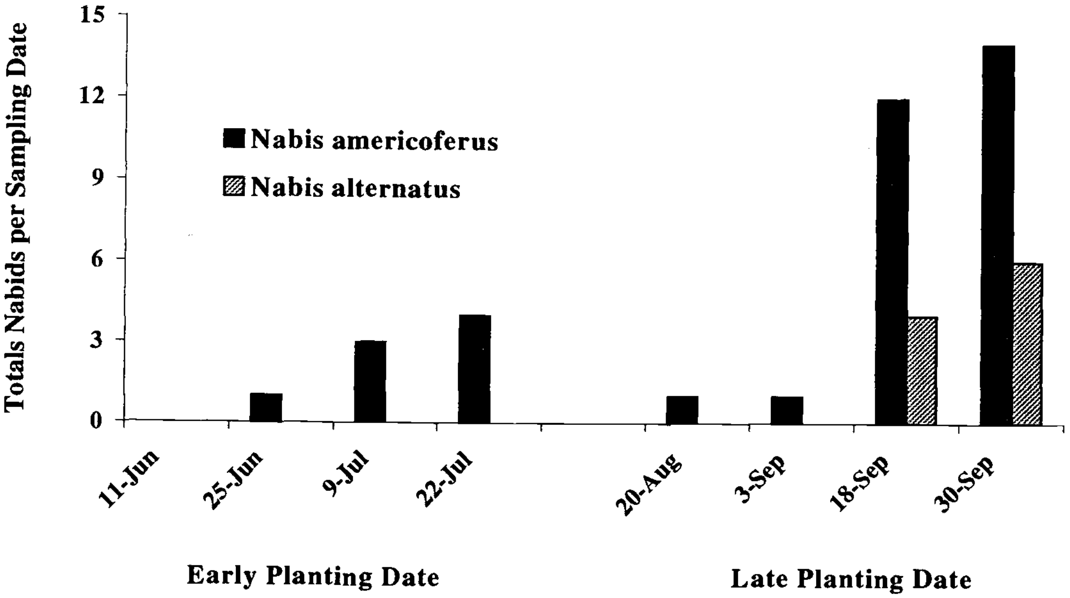


Figure 5.3 *Nabis* species in a Broccoli Cover Crop Relay
Corvallis, Oregon 1994

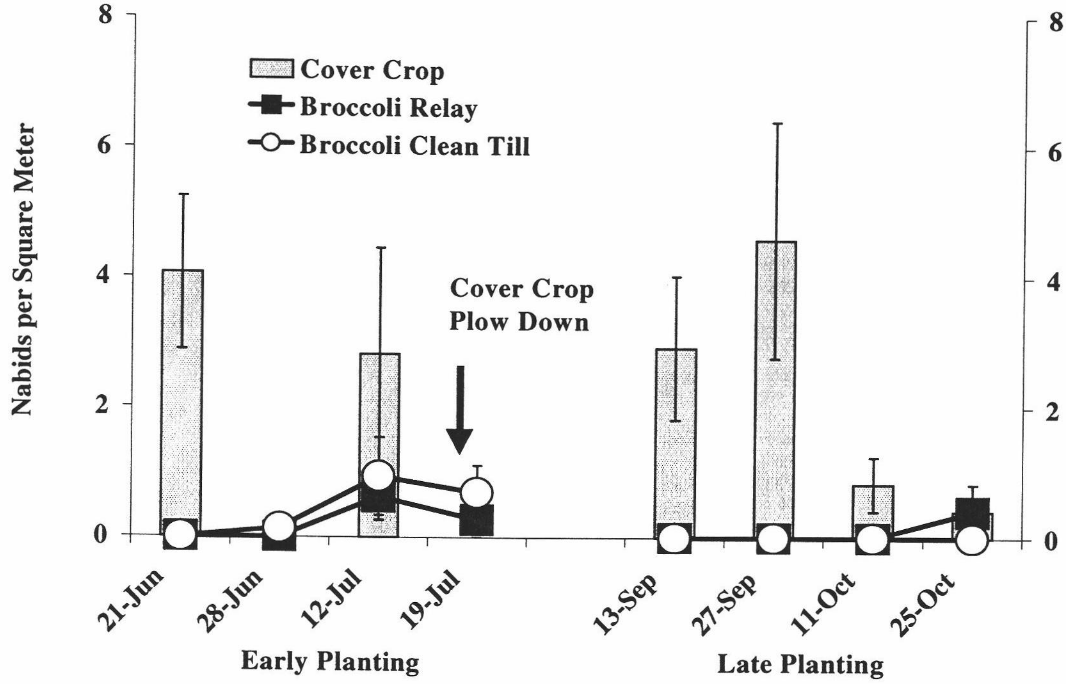


Figure 5.4 *Nabis* species in a Broccoli Cover Crop Relay
Corvallis, Oregon 1995

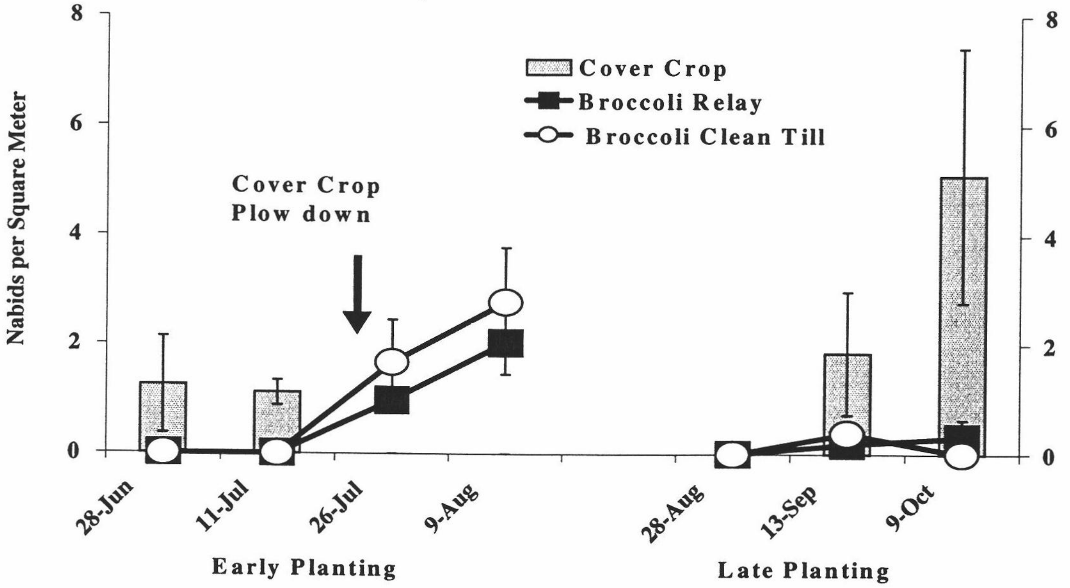
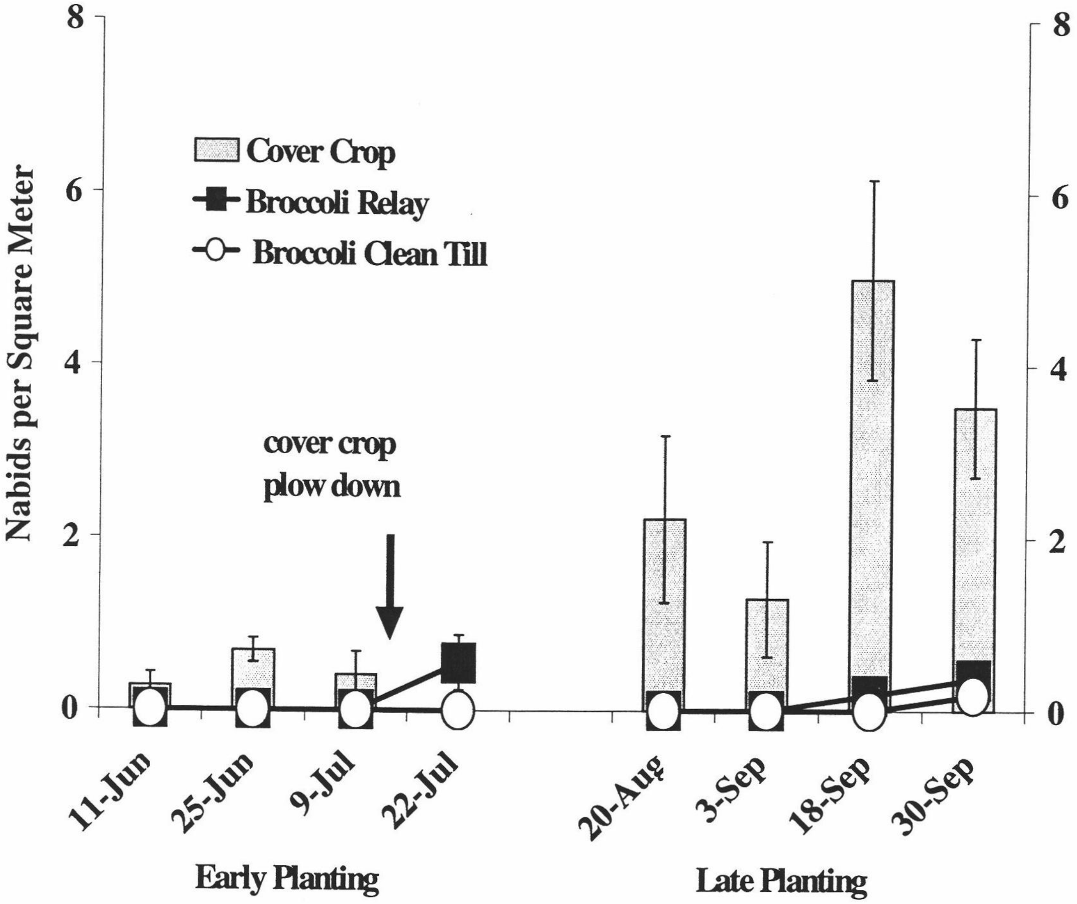


Figure 5.5 Nabis species in a Broccoli Cover Crop Relay
Corvallis, Oregon 1996



and peaked from mid-September to mid-October in all three years. Nymphs often outnumbered adult nabids during the late planting periods (Table 5.2, Figures 5.6 and 5.7). Over the two year period, forty six percent (73/158) of the individuals collected were nymphs.

Nabid densities varied from 0.3 to 5.1 bugs per square meter in the cover-crop strips (Table 5.1, Figures 5.3-5.5). Nabid densities in the two broccoli cropping systems varied from 0 to 2.8 bugs per square meter. On eleven out of twenty three sampling dates, nabids occurred in significant numbers in the cover-crop strips while they were completely absent in the broccoli regardless of the cropping system. Nabid density in the clean-till broccoli often exceeded nabid density in the relay strip-cropped broccoli, but the differences between the two cropping systems were never statistically significant ($P>0.05$).

DISCUSSION

Winter cover-crops of grasses and legumes were attractive to and supported significant numbers of nabids in all three years of this study. Nabid densities in the residual cover-crop strips during the growing season were high (up to five bugs per square meter) and similar to densities reported in other studies (Buschman et al. 1984). Adult nabids may have concentrated in the residual cover-crop strips following the incorporation of the other half of the cover-crop plots. Similar behavior has been reported in studies of strip cut alfalfa where adult nabids concentrate in patches of undisturbed vegetation following alfalfa harvest even if the patches are relatively small (Grasela and Steiner 1993). High densities of nabids in the residual cover-crop strips did not, however, enhance nabid density in the broccoli. Nabids failed to move into the broccoli even though it was growing within 15 m of the cover-crop strips and supported significant numbers of potential prey items.There was no evidence of limiting factors such as prey availability, cannibalism, inbreeding depression, competition, or mortality associated with insecticide applications that could explain the absence of significant numbers of

Figure 5.6 Nabidae Adults and Nymphs in a Broccoli Cover Crop Relay Corvallis, Oregon 1995

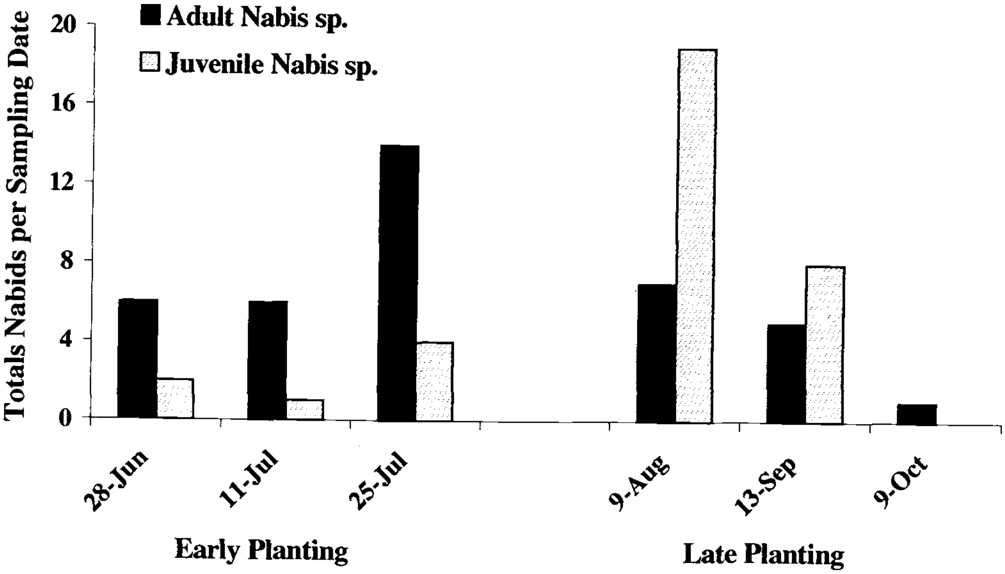
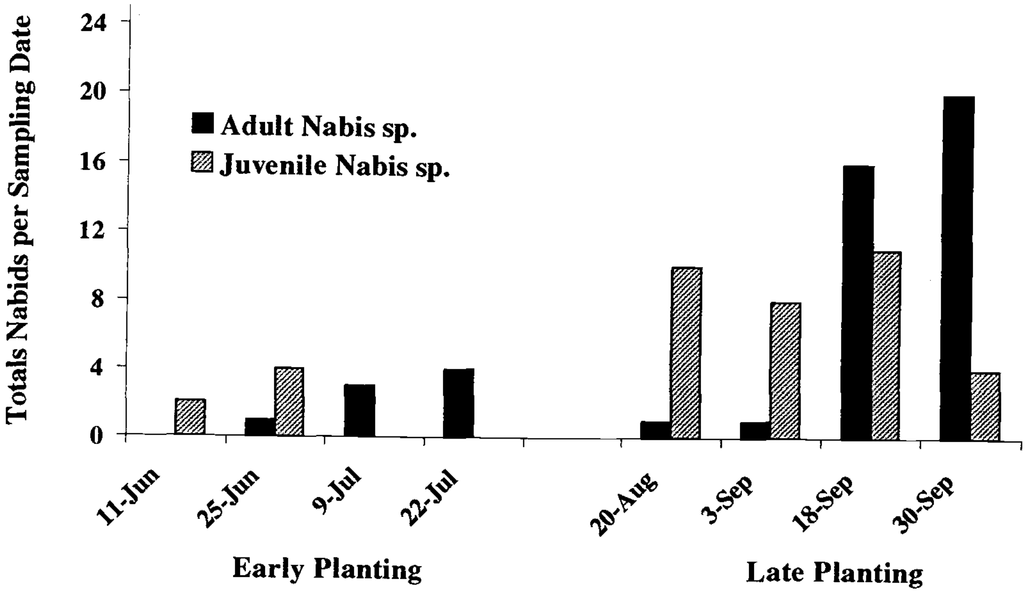


Figure 5.7 Nabidae Adults and Nymphs in a Broccoli Cover Crop Relay Corvallis, Oregon 1996



nabids in the broccoli during periods when high numbers occurred in the cover-crop strips. Nabids have strong preferences for certain plants (Perkins and Watson 1972a, Stoner et al. 1975, Braman et al. 1984). Apparently, they are not attracted to crucifer plants. The under-sown cover-crop developing around the broccoli plants was not attractive enough to draw the nabid out of the established cover-crop strips.

Prior to harvest of the early broccoli planting, cover-crop strips were incorporated into the soil in preparation for the late planting. From this point forward, broccoli stubble plus the developing cover-crop from the first planting supported high densities of adult and juvenile nabids. The presence of high densities of nabids in the cover-crop plus broccoli stubble did not, however, enhance nabid density in the late planting of broccoli.

Nabid densities in the early plantings of 1994 and 1995 were consistently depressed in the relay broccoli compared with clean-tilled broccoli. The cover-crop strips may have been acting as a sink rather than a source for nabids in the developing broccoli. The differences, however, were never statistically significant.

Eventually, high densities of nymphs developed in the cover-crop and broccoli stubble strips after harvest of the first broccoli planting. Regardless of the source of colonizing nabids, adult nabids gave rise to another generation of nabids late in the growing season in the strips of cover-crops and broccoli stubble. Although the relay strip-cropping system did not result in increased nabid density in the target crop, it may have contributed to the overall success of the nabid population in the vicinity of the crop.

Predator response to vegetation diversity and mixed cropping systems is variable (Risch et al. 1983, Andow 1991). Crop preference by predators regardless of prey densities explains part of this variation. My findings are similar to the findings of other small plot studies where the nabids could easily disperse across the treatments but remain strongly associated with their preferred crop. *N. americoferus* strongly associates with legumes. Only small numbers of these nabids are found in corn, tomato, or tobacco when snap beans or alfalfa are in the vicinity (Nordlund et al. 1984, Pfannenstiel and Yeargan 1998).

Cover-crop strips and cover-crop seedlings intimately mixed with the target crop (via under-sowing) attracted *Nabis* species into the vicinity of the broccoli. The preference of the nabids for the grasses and legumes was so strong, however, that the interplanting and the strip-management had no impact on the nabid density on the broccoli plants themselves. These results are similar to those reported elsewhere (Stern et al. 1964, McIver 1983, Harper et al. 1989, Schaber et al. 1990, Godfrey and Leigh 1994). Vegetation that is attractive to Heteroptera often serves as a trap crop; the vegetation usually does not serve as a source of Heteroptera in target crops that are less attractive to the bugs. This appears to be the case for broccoli.

Nabid nymphs occurred at significant densities in the cover-crop strips just prior to plow down. It is likely that many of the flightless nymphs perished during this operation. This situation is similar to that of alfalfa cut for hay. Significant reproductive potential of the nabid population may be lost during the incorporation of the cover. Future studies of conservation tactics for Nabidae should be directed at manipulation of non-crop vegetation outside the cropping system. This will allow for greater flexibility in the timing of harvesting, mowing, or incorporating the non-crop vegetation during times when the nabid population is less vulnerable.

CHAPTER 6

SUMMARY: THE IMPACT OF RELAY STRIP-CROPPING ON INSECT PESTS OF BROCCOLI

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ABSTRACT

Relay strip-cropping combines under-sowing with strip-management. In this study, cover-crop seed was broadcast into established broccoli four and one half weeks after planting. The broccoli was planted, under-sown, and harvested in sections alternated with strips of cover-crop, which provided a tillage and pesticide refuge for beneficial insects. Under-sowing four weeks after planting had no impact on colonization of the broccoli by winged aphids. The density of *Phyllotreta cruciferae* Goeze was generally lower in the relay than in the broccoli monoculture. The number of third instar *Pieris rapae* (L.) and *Trichoplusia ni* (Hubner) was significantly reduced on the leaves and in the harvested buds in the relay broccoli compared with clean-tilled broccoli. The number of *Plutella xylostella* (L.) pupae was higher in the clean-tilled broccoli; percent parasitism of the pupae was similar between the two treatments. Relay strip-cropping increased the abundance and diversity of ground beetles (Coleoptera: Carabidae), spiders (Araneae), harvestmen (Opiliones: Phalangiidae), lady beetles (Coleoptera: Coccinellidae), and damsel bugs (Heteroptera: Nabidae) in the cropping system; however, this did not always result in increased natural enemies in the broccoli. Arthropod species varied significantly in their propensity to leave the cover-crop strips and move into the broccoli. Natural enemy induced mortality may explain, in part, the differences in survival of the lepidopteran larvae. Although reductions in bud-contamination associated with relay strip-cropping were statistically significant, the residual contamination of the broccoli by insects was unacceptable for commercial production and marketing.

INTRODUCTION

In this chapter, I examine the impact of relay strip-cropping on insect pests of broccoli. Root (1973) divided the above ground crucifer-specialists into three feeding guilds, "sap-feeders" including the cabbage aphid (*Brevicoryne brassicae* L.), "pit-feeders" including the cabbage flea beetle (*Phyllotreta cruciferae* Goeze), and "strip-feeders" including the diamondback moth (*Plutella xylostella* (L.)), the cabbage looper (*Trichoplusia ni* (Hubner)), and the cabbage butterfly (*Pieris rapae* L.). These insects are the focus of this chapter. Each insect has a unique set of attributes that can be used as analytical probes in evaluating the impact of relay strip-cropping on the arthropod community.

It has long been noted that large pure stands of cole crops accumulate heavier loads of herbivorous insects than mixed stands of cole crops and other plant families. The differential loading varies according to insect species. *P. cruciferae* Goeze, for example, is sensitive to stand purity. *P. cruciferae* densities are generally lower in mixed plant stands than in pure stands of their host-plant (van Emden 1965, Tahvanainen and Root 1972, Root 1973, Smith 1976a, Tukahirwa and Coaker 1982, Kareiva 1985, Altieri and Schmidt 1987, Stoner 1992, Costello 1995). *P. rapae* avoids concentrations of its host plants during oviposition and is unaffected by stand purity (Maguire 1984, Root and Kareiva 1984).

The insects that colonize cole crops have a capacity to assimilate a class of phytochemicals known as glucosinolates or mustard oil glucocides. Glucosinolates are repulsive or toxic to the majority of insects. They constitute one of the primary defense mechanisms of the Cruciferae family. To the crucifer-specialists, however, the toxins are feeding and oviposition stimulants that guide the insects to their host-plants and arrest them there.

Plant defense against crucifer-specialists is accomplished by alternative mechanisms (Ehrlich and Raven 1964, Feeny et al. 1970, Hughes et al. 1997).

In nature, large pure stands of cruciferous plants are rare. Over time, crucifer-specialists reduce the density of mustard patches. There is a parallel increase in vegetation diversity. Mixtures of plant species replace the pure stand. Eventually, the state is reached where the feeding rate of the crucifer-specialists and the dispersion of their host-plants are in equilibrium. In this state, both the mustard plants and the crucifer-specialists may be rare in the landscape. They are present, however, and still interacting. The crucifer-specialists and the mustard plants develop a sparse equilibrium in time and space (Tahvanainen and Root 1972).

Once equilibrium is achieved, the mustard plants occur in relatively small patches on disturbed soil surrounded by other vegetation. A mustard plant might germinate on a fresh gopher mound in a meadow surrounded by a forest. Secondary plant compounds protect the mustards from non-adapted generalist herbivores in the local area. In the meantime, the crucifer-specialists disperse across the landscape. Most of them perish. A few encounter their host plant and reproduce rapidly, taking advantage of a rich, unclaimed, but short-lived food source. By the time the crucifer-specialists discover isolated patches of mustards, many of the plants have set seeds. The plants escape from damage by virtue of their spatial and temporal dispersion and their surroundings that interfere with their discovery. The mustard plants are protected, in part, by the interplay between host plant resistance and the ecological context in which host plant selection by crucifer-specialists occurs (Feeny 1976).

Relay strip-cropping should have an impact on the colonization and survival of broccoli by crucifer-specialists. *B. brassicae*, for example, is sensitive to the color and contrast of the background vegetation or soil surrounding its host plant during the host plant finding process (Cromartie 1975, Costello 1995). The highly mobile *P. cruciferae* has a difficult time settling and feeding in a mixed stand (Kareiva 1985, Bergelson and Kareiva 1987, Garcia and Altieri 1992). *P. xylostella* and *T. ni* tend to lay more eggs in pure stands of crucifer plants than in mixed stands (Grez and Gonzalez 1995, Justus and Mitchell 1996, Riggin-Bucci and Gould 1997, Bigger and Chaney 1998). Their natural enemies tend to accumulate there as well, aggregating in areas of high prey densities. *P. rapae* does not respond to changes in host plant density (Cromartie 1975, Root and Kareiva 1984, Maguire 1984); instead, it scatters its eggs across the landscape, increasing the probability that some of its progeny will escape mortality factors that are unevenly distributed in the environment (Hassell and May 1973, 1974, Waage 1979). The moths and the butterflies are involved in two activities at the same time, oviposition and nectar feeding. They tend to aggregate around nectar sources, and the aggregation changes the pattern of their oviposition (Zhao et al. 1992, Bigger and Chaney 1998).

Relay strip-cropping may successfully reduce insect loads on broccoli if the cropping system reestablishes elements of the ecological context in which host plant resistance can express itself efficiently. By manipulating stand purity and planting arrangement, one can interfere with the process of host plant finding. By reducing stand purity, the probability that crucifer insects will encounter non-host plants, become confused, and emigrate from the area can be increased. Mixed stands of plants support a greater diversity of insects and their natural enemies. By reducing stand purity, the pressure on the crucifer-specialists by generalist natural enemies can be increased. Relay strip-cropping provides a refuge from tillage operations and pesticide applications, which may conserve natural enemies that are sensitive to disturbance and that are not highly mobile. Relay strip-cropping, which combines under-sowing and strip-management, is bound to have multiple and in some cases contradictory impacts on the insect pests of broccoli and their natural enemies. The net effect of relay strip-cropping, may vary according to the insect pest species.

Brevicoryne brassicae (L.)

There are several aspects of vegetation that influence aphid colonization and population growth in cole crops. Interplanting non-host vegetation among crucifers or changing the color of the background surrounding developing crucifer plants often reduces *B. brassicae* numbers. The reduction in aphid colonization occurs whether the interplant is a weed (Smith 1976a, 1976b, 1976c, Horn 1988), a living mulch or cover-crop (Dempster and Coaker 1974, Andow et al. 1986, Roberts and Cartwright 1991, Costello and Altieri 1994, 1995, Costello 1995), a second vegetable crop (O'Donnell and Coaker 1975), or an artificially colored mulch (Schalk et al. 1979, Summers et al. 1995, Liburd et al. 1998). Evidence suggests that the differences are due to factors that affect the host plant selection process.

The impact of interplanting on aphids varies according to the type, size, color, texture, and relative proportion of interplanted vegetation (Andow et al. 1986), the height of the interplanted vegetation relative to the target crop (McIver 1983), the timing of interplant establishment relative to the target crop, and the percent of the soil surface covered by the interplanted vegetation (Costello 1995) or colored mulch (Liburd et al. 1998). *B. brassica* population densities were higher on cabbage grown in a living mulch of grass than cabbage grown in a living mulch of clover (Andow et al. 1986). Both of the living mulches reduced aphid colonization compared with bare ground. Significantly higher numbers of alate *B. brassicae* were observed on the collards grown in the short alfalfa compared with tall alfalfa. When the collards were grown in pots that were suspended on stakes at the height of the tall alfalfa canopy, the difference between the two treatments was significantly reduced (McIver 1983).

B. brassicae numbers per plant were significantly higher in *Brassicae* plots with a yellow soil cover than bare ground (Liburd et al. 1998). Reflective mulches are known to reduced aphid colonization (Summers et al. 1995). Differences in alate aphid colonization are correlated with different levels of light reflectance. Lower intensity light reflected by broccoli grown in living mulch was less attractive to incoming aphids than the higher intensity light reflected from clean-cultivated broccoli. The number of alates in the broccoli was highly correlated with the intensity of the yellow waveband (Costello and Altieri 1994).

Winged *B. brassicae* use a combination of visual and olfactory cues to locate their host-plants (Prokopy and Owens 1983). Yellow is believed to influence *B. brassicae* alighting on plants of the appropriate physiological state (Kennedy 1958). Saturated blue colors have low reflectance energy in the green region and are apparently less attractive to *B. brassicae*. Early in the growing season, vegetables growing in a monoculture are surrounded by bare ground. Living mulch or other materials covering the soil provide a very different visual background effect. Crucifer host-plants surrounded by other vegetation are more difficult for the incoming crucifer specialist to see (Liburd et al. 1998).

It is not clear whether *B. brassicae* can distinguish between suitable and unsuitable host-plants without sampling them (Kennedy and Stroyan 1959). Early studies suggested that chemical (olfactory) cues were not as important as visual cues during the colonization of plants by the aphids. Olfactory cues are detected only after visually mediated random landings on plants. The lack of sensitivity to olfactory cues by the aphids is now being questioned, and experimental evidence to support an olfactory role is accumulating. Olfactometer and electrophysiological studies have demonstrated that alate *B. brassicae* are attracted to volatiles from *B. oleracea.* Sinigrin, one of the primary glucosinolates of mustard oil, stimulates feeding by *B. brassicae* (Moon 1967, Read et al. 1970). The presence of sinigrin enhances the number of alate *B. brassicae* landing in clear, uncolored, water pan traps. The scent of crucifer plants growing in a mixed stand of other plant families is probably more difficult for the incoming crucifer-specialists to detect (Pickett et al. 1992).

Natural enemies can also respond to the smell of the host plant of their preferred prey item. *Diaeretiella rapae* (M'Intosh) was attracted to the odor of crucifers or a dilute solution of mustard oil (allyl isothiocyanate). *D. rapae* was attracted to clumps of *B. brassicae* removed from collards. The effect only lasted for fifteen minutes, and there was a rate response. Two hundred aphids removed from collards twenty-four hours earlier were unattractive. Two hundred aphids removed fifteen minutes earlier were attractive. A clump of ten *B. brassicae* recently removed from collards was not attractive. The parasitoid oviposited more often in *M. persicae* feeding on collards than in *M. persicae* growing on sugar beets. The presence of an adjacent collard plant increased the parasitism of *M. persicae* on sugar beet plants. The hyperparasitoid *Charips brassicae* L. was not attracted to collards, mustard oil or *B. brassicae.* It was attracted to the scent of its host, *D. rapae* (Read et al. 1970).

It is important to note that the difference in aphid numbers accumulating in mixed and pure stands of crucifers is usually most dramatic at the beginning of the season (Dempster and Coaker 1974, Costello and Altieri 1995) or immediately following an insecticide spray (Andow et al. 1986). The difference between mixed and unmixed cropping systems sometimes disappears by the end of the season. After immigration when aphid colonies are established, natality and mortality factors including the relative abundance and activity of natural enemies may cause aphid population densities to converge in different cropping systems. Aphid population growth is sometimes slower in monoculture than in polyculture. Generalist predators tend to be more abundant in polyculture. The specialist parasitoid, *D. rapae*, is often more prevalent in monoculture. The affects of interplanting on host plant colonization and the affect of interplanting on natural enemy induced mortality of *B. brassicae* may operate in opposite directions. The opposing factors would result in the two aphid populations, which started out very different, converging by the end of the season (Costello and Altieri 1994, 1995, Costello 1995).

Dempster and Coaker (1974) sowed clover then transplanted Brussels sprouts and cauliflower into the clover two weeks later. During the early growing season, aphid density was consistently higher on the cole crops surrounded by bare ground than on cole crops surrounded by clover. Later, the difference between the monoculture and the polyculture disappeared. In several studies that followed, researchers noted that significantly higher numbers of alate (winged) *B. brassicae* arrive on *Brassica* monoculture than in *Brassica* polyculture (O'Donnell and Coaker 1975, Theunissen and den Ouden 1980, Costello and Altieri 1994, Costello and Altieri 1995). Andow et al. (1986) reported that peak aphid densities on cabbage occurred eight days after insecticides were applied. Very few natural enemies were present at that time. Costello and Altieri (1995) noted that the polyculture effect was short-lived. Early in the growing season the numbers of alate aphids were significantly lower on the broccoli growing in living mulch of clover. The number of alate aphids per sample on the first sampling date was eight times greater on the broccoli in clean culture than in the living mulch. By the last sampling date, no differences remained.

Mixed planting has both direct and indirect effects on the natural enemies. Mixed planting directly affects natural enemies by providing alternative food and microclimates within the habitat. Levels of vegetation structural complexity result in different search arenas for the natural enemy. Plants or plant patches that are complex take longer to explore. In some cases, vegetation provides a barrier, which interferes with the searching ability of specialist natural enemies. By affecting the density, dispersion, and behavior of their prey items, mixed planting has an indirect effect on natural enemies. Natural enemies have a greater tendency to aggregate in areas of high prey concentration regardless of the vegetation type (Sheehan 1986, Andow and Risch 1987).

The impact of interplanting on natural enemies of *B. brassicae* has been variable. Generalist predators are sometimes more abundant in mixed plant stands. Under-sowing of clover in Brussels sprouts increased the number of Carabidae (*Pterostichus melanarius* Illiger, *Harpalus rufipes* DeGeer), Phalangiidae (*P. opilio*), and Staphylinidae (unspecified) compared with clean hoed plots (Dempster 1969). McIver and Belnavis (1986) found that the generalist predator *Coccinella trifasciata* L.was more common in a tall alfalfa/collard cropping system. Increased numbers of predators in the alfalfa did not, however, result in higher numbers on the collard themselves. Specialist parasitoids are sometimes more abundant in pure plant stands than in mixed stands (Smith 1976c, Dempster and Coaker

1974, Andow et al. 1986, Costello and Altieri 1994, Costello and Altieri 1995).

Smith (1976a) was one of the earliest researchers to demonstrate that interplanting non-crop vegetation around cole crops has a significant impact on aphids. The numbers of *B. brassicae* early in the season were higher on Brussels sprouts in hand-hoed plots than in weedy plots. Parasitism of *B. brassicae* on Brussels sprouts, however, was reduced when weeds surrounded the plants. Higher rates of parasitism occurred in monoculture compared with weedy culture, even when aphid densities in the two planting systems were equivalent (Smith 1976c). The aphid parasitoid *D. rapae* was more common in a short alfalfa/collard system than in the tall alfalfa/collard system (McIver and Belnavis 1986).

The effect of interplanting on parasitism is not consistent. No changes in parasitism *of B. brassicae* were found when the cole crop interplant was mustard (Kloen and Altieri 1990). No changes in parasitism of *B. brassicae* was found when the interplant was hairy vetch (*Vicia sativa* L.) or fava bean (*Vicia fava* L.)(Altieri 1984). In some cases, parasitism is higher in polyculture (Letourneau 1987, Horn 1988). An intercrop such as *V. fava* that provides food resources other than hosts may attract parasitoids. Floral and extra floral nectar can increase the longevity and fecundity of parasitoids (Leius 1960, 1961a, 1961b, 1963, 1967, Shahjahan 1974, Idris and Grafius 1995, 1997). Wasps (including parasitoids) were more common on the broccoli growing next to flowering *Iberis* than broccoli growing in isolation. Aphid parasitism was slightly higher near the nectar source. The interplay between nectar sources and prey distribution may explain the variable aggregation of natural enemy in interplanted cole crops (Bigger and Chaney 1998).

Attributes of the host plant influence natural enemy induced mortality of *B. brassicae*. Plant architecture in the cole crops varies significantly between curly leafy kale, flat leafed collards, and tightly wrapped cabbage. The foraging behavior of Coccinellidae including *Hippodamia convergens* Guerin-Meneville and *Coccinella septempunctata* L. was significantly influenced by these differences (Grevstad and Klepetka 1992). The various leaf types had an impact on predator mobility, falling frequency, prey accessibility, and the propensity of the predator to fly away. Aphid predation rates were highest on the flat-leafed collards. *B. brassicae* numbers were reduced over 95% on broccoli varieties that have less wax coating on their leaves (Stoner 1992). Wax tends to gum up the tarsi of the foraging beetles. The beetles spent more unproductive time cleaning and grooming on waxy plants. Reduced wax allowed more efficient predation (Eigenbrode et al. 1995).

The presence of non-host vegetation changes the texture and complexity of the habitat that a natural enemy must search to discover its prey. Habitat complexity can promote aphid outbreaks if it interferes with non-random searching behavior of predators or interferes with the aggregation of predators in areas of high prey density. Populations of the aphid *Uroleucon nigrotuberculatum* L. increased rapidly when patches of golden rod (*Solidago canadensis* L.) were divided into small patches (Kareiva 1987, 1990, Kareiva and Odell 1987). Aphid colonization rates were the same in the patchy and continuous goldenrod. However, twenty-six aphid outbreaks occurred in the patchy golden rod habitat while only nine aphid outbreaks occurred in the continuous goldenrod habitat.

The difference in aphid population stability appeared to be related to the foraging efficiency of the coccinellid predator, *C. septempunctata*, in the two habitats. When foraging beetles were removed by hand from the golden rod, aphid populations consistently increased relative to the control. When beetles were marked and released, it took longer for the beetles to aggregate in patches of high aphid concentration when the vegetation was divided into small patches (Kareiva 1987).

Phyllotreta cruciferae Goeze

Phyllotreta forages non-randomly (Kareiva 1982, 1985). It may emit an aggregation pheromone (Peng and Weiss 1992). When foraging for their host plant, *P. cruciferae* is attracted to mustard oil and its components. Mustard oil influences the ability of the beetles to discover their host plant. It also influences their propensity to settle and to begin eating (Feeny et al. 1970, Read et al. 1970). The amount of damage that *P. cruciferae* does to *Brassica* species varies as a function of glucosinolate concentrations in the cotyledons. At very high level of glucosinolates, herbivore activity declines slightly (Siemens and Mitchell-Olds 1996).

B. oleraceae varieties that have less wax coating on their leaves are more susceptible to damage by *P. cruciferae* than normal, waxy broccoli plants (Stoner 1992). Mechanical removal of the wax-crystals from normal *Brassica* varieties increases feeding damage by *P. cruciferae*. *P. cruciferae* has tarsal adhesive setae that have better traction on reduced-wax leaves. On reduced-wax varieties, *P. cruciferae* tends to feed over the entire surface of the leaf. On normal waxy *B. oleraceae*, *P. cruciferae* is more restricted in its feeding (Eigenbrode and Espelie 1995).

Interplanting generally reduces the number of *P. cruciferae* on cole crops compared with pure stands (Tahvanainen and Root 1972, Cromartie 1975). The presence of non-host plants depresses *P. cruciferae* numbers in two ways. Non-host plants seem to interfere with host plant finding, and their presence tends to increase the rate at which *P. cruciferae* emigrates from a plant patch (Kareiva 1985, Bergelson and Kareiva 1987, Elmstrom et al. 1988, Garcia and Altieri 1992).

P. cruciferae is relatively inept at finding their host-plants (Kareiva 1985). When marked beetles were released eight meters from collard plants, about 19% were recovered when the collards were surrounded by bare ground. When the collards were surrounded by goldenrod, only 6% of the beetles were recovered. Broccoli surrounded by black weed control cloth (no weeds) had six times as many *P. cruciferae* as weedy control plots (Liburd et al. 1998).

Collards interplanted with tomato or tobacco accumulated fewer *P. cruciferae* than pure stands of collards. The number of *P. cruciferae* per collard plant was higher in the monoculture on all thirty-eight sampling dates. The monoculture was colonized more rapidly and experienced greater feeding damage. Predators and parasitoids appeared to have a negligible influence on the beetles in both habitats. The presence of non-host plants probably interfered with both the visual and olfactory cues used by *P. cruciferae* to orient to their host-plants. In mixed stands, other odors may have masked the chemical stimuli originating from the host-plants (Tahvanainen and Root 1972).

The foraging behavior of *P. cruciferae* is very different from other *Brassica* specialists. Consider the difference between *P. rapae* and *P. brassicae*. The oviposition decision of the *Pieris* butterflies commits her progeny to a given location (Root 1973, Root and Kareiva 1984, Trenbath 1993). The *Pieris* larvae are not highly mobile. *P. cruciferae*, on the other hand, are very capable of taking off after they land. *P. cruciferae* is constantly moving from plant to plant and from plant patch to patch. When they land on a non-host plant, their next flight tends to be long (Bach 1980b, Risch 1981). They move among patches of host-plants spending most of their time where their food is abundant and of higher quality. *P. cruciferae* tends to concentrate in pure stands of their host plant (Root 1973, Cromartie 1975, Bergelson and Kareiva 1987).

Analyses of the movement behavior of *P. cruciferae* and other highly mobile insects in mixed versus pure plant stands has shown that emigration rates are greater in mixed stands (Bach 1980b, Risch 1981, Kareiva 1982, 1983, 1985, 1986, Bergelson and Kareiva 1987, Elmstrom et al. 1988, Andow 1990, Garcia and Altieri 1992). The mixed systems attracted fewer marked beetles and lost more of the marked beetles that were placed in them. The time spent in the plant patches by beetles released in monoculture broccoli was longer than in the mixed culture. In the mixed stand, the beetles hopped around and seemed to loose contact with their host plant and the chemical stimuli that must accumulate for feeding to begin. The probability that the beetles would emigrate from the mixed stand was about the same as the probability of their emigration from a patch of non-host plants (Garcia and Altieri 1992).

There are several factors that influence the strength of the effect of interplanting on *P. cruciferae* numbers. Flea beetle species vary in their sensitivity to the presence of non-host vegetation. The effect may vary according to the type of non-host vegetation (Kareiva 1985). The height of non-host plants relative to the *Brassica* plants is important. In those cases where emigration rates were unaffected by interplanting, the height of the non-host plants was much lower than the height of the *Brassica* plants (Andow et al. 1986, Weiss et al. 1994). Sensitivity of *P. cruciferae* to non-host vegetation depends, in part, on host plant density. Bergelson and

Kareiva (1987) grew collards at two densities, alone and in combination with potatoes. *P. cruciferae* was significantly more abundant in the higher density collard plantings regardless of the interplanting.

P. cruciferae tends to be more abundant on collards in large patches. There was more emigration from small patches of collards (four plants) surrounded by grass than in larger patches (sixteen plants) surrounded by grass (Bergelson and Kareiva 1987). Kareiva (1985) argued that the impact of patch size has more to do with patterns of emigration than immigration. Small host plant patches surrounded by alternative vegetation are hard to find and easy to lose. Even when collard patches were loaded with large numbers of *P. cruciferae* at the beginning of an experiment, the inoculations rapidly decayed in the small host plant patches as beetles left the patch. Single host-plants surrounded by grass, weeds, or bare ground never maintained high *P. cruciferae* populations.

Pieris rapae (L.)

The impact of various vegetation management schemes on herbivorous insects is complex. One must take into account that the insects may be engaged in more than one activity at the same time. The visual and olfactory cues that shape the behavior of an insect during oviposition may be very different and operating in the opposite direction from the cues that shape its behavior while foraging for nectar.

Some insects are responsive to changes in the background color of their host-plants regardless of whether the color is from vegetation, colored cloth, or soil. The height of the non-host plant vegetation changes its impact on the herbivore. Low growing vegetation may simply change the background color. Tall vegetation may interfere visually with host plant selection. Fragrant non-host plants may interfere with the olfactory cues used by the herbivore to orient toward its host plant.

P. rapae is capable of identifying crucifer plants (Root and Kareiva 1984). Adults and larvae of *P. rapae* are attracted to mustard oil (Read et al. 1970). Host plant oviposition stimulants have been identified and extracted from *Brassica* plants (Hughes et al. 1997). Glucosinolates are important in host recognition by *P. rapae*. There are oviposition deterrents associated with certain plants and with the eggs of *P. rapae*. Oviposition by *P. rapae* is determined by the relative strength of opposing positive and negative cues. Some crucifers including *Iberis* species are rejected by egg laying *P. rapae*. They produce oviposition deterrents that are stronger than the attraction of the glucosinolates present in the plant (Renwick and Chew 1994).

Physical characteristics of the host plant have an impact on the success of *P. rapae* (Eigenbrode et al. 1995). *P. rapae* were 80% fewer in natural infestations on glossy lines of broccoli (low wax) than on normal-wax standard varieties. Artificial infestation experiments showed that glossy resistance acts on both the egg and the larval stages. The resistance of glossy type Brassica lines to *P. rapae* expresses itself in the field but not in controlled environments or in the greenhouse. Again, there is an interaction between the waxy leaf coating, the behavior of the *Pieris* larvae, natural enemies, and other mortality factors (Stoner 1992).

During oviposition, the butterfly is not sensitive to host plant density or stand purity; it moves randomly (Root and Kareiva 1984). Most specialist herbivores are more likely to find and remain on host-plants that are concentrated in pure, dense stands (Tahvanainen and Root 1972, Cromartie 1975, 1981, Ralph 1977a, 1977b, Bach 1980a, 1980b, 1981, Risch 1980, 1981). Root (1973) referred to this behavior as a response to "resource concentration". *P. rapae* does not respond positively to resource concentration.

The densities of *P. rapae* eggs and larvae are usually higher on sparse or isolated host-plants than they are on plants in dense or large stands. The time it takes for a female *P. rapae* to approach and find a suitable host was no greater in an area where a few scattered collards grew among weeds than it was in a patch containing hundreds of collard plants surrounded by bare soil. Ovipositing *P. rapae* females flew over and failed to oviposit on 30 to 50% of the suitable host-plants in a plant patch for no obvious reason. They readily flew out of a patch of host-plants after laying only a few eggs. The flight pattern was not influenced by the shape of the host plant patch (Root and Kareiva 1984).

P. rapae is unaffected by the color of the background surrounding its host-plants. Broccoli surrounded by black, yellow, green, or blue cloth had the same number of eggs and larvae as broccoli surrounded by weeds or bare ground. Low growing vegetation usually has no impact on *P. rapae* oviposition (Liburd et al. 1998). *P. rapae* was not responsive to the presence or absence of the weed spurry (*Spergula arvensis* L.) surrounding Brussels sprouts (Theunissen and den Ouden 1980). Egg counts on Brussels sprouts surrounded by *Matricaria inodora* L. were spotty and similar when the weeds were mowed low and prevented from flowering (Dempster 1969). The flight pattern of ovipositing *P. rapae* was not influenced by background vegetation in a grassy meadow (Root and Kareiva 1984). Reduced tillage systems where crops were planted into mowed residues of hairy vetch, perennial ryegrass, or rye grain had no affect on *P. rapae* numbers (Masiunas et al. 1997). However, *P. rapae* egg densities on cabbage were lower when the cabbage was grown in a living mulch of clover. There may be a chemical oviposition deterrent in clover. Cabbage surrounded by low growing grasses had the same number of *P. rapae* larvae as bare ground (Andow et al. 1986).

When vegetation is allowed to grow tall, host-plants may be hidden visually. The effect is inconsistent. The inconsistency may be the result of differences in visual and olfactory cues used by *P. rapae* to orient to its host plant. *P. rapae* laid equivalent numbers of eggs on collards in short-mowed and tall unmowed alfalfa (McIver 1983). When *M. inodora* weeds surrounding Brussels sprouts were allowed to flower and grow tall, *P. rapae* egg numbers on Brussels sprouts were reduced (Dempster 1969). Egg laying by *P. rapae* on collards was not influenced by interplanting the host-plants with potatoes, or mixtures of *Salvia officinalis* L., *Thymus* sp., or *Tagetes* sp. when host plant density was held constant (Root and Kareiva 1984).

P. rapae responds differently to stand purity than *P. cruciferae or P. xylostella*. *P. crucifereae* accumulates in lower number on cabbage surrounded by tomatoes (Tahvanainen and Root 1972). Ovipositing *P. xylostella* are inhibited by the odor of tomatoes (Gupta and Thorsteinson 1960a, 1960b). *P. rapae* deposited more eggs on collards surrounded by tomato than collards surrounded by other collards. Tomatoes surrounding the collard plants were flowering. The ovipositing *P. rapae* may have been responding to the nectar source (Maguire 1984).

P. rapae is attracted to and will aggregate around nectar sources. Aggregation near flowering plants indirectly affects oviposition. Eggs tend to be clumped around nectar sources (Root and Kareiva 1984). Eggs and larvae of *P. rapae* were much more abundant on broccoli interplanted with

Anise hyssop, *Agastache foeniculum* (Pursh), than on broccoli growing in a monoculture growing 120 m away (Latheef and Irwin 1979, Latheef and Irwin 1980). The effect may depend on the type of non-crop vegetation. The relative abundance of *P. rapae* eggs and larvae on broccoli was not significantly influenced by the presence of a flowering border of *Iberis* (Bigger and Chaney 1998). In fact, the number of eggs increased with increasing distance from the flowering border are rejected by egg laying *P. rapae* because they produce oviposition deterrents. The oviposition deterrents may confound the impact of the nectar source (Renwick and Chew 1994).

In weedy plots dominated by *M. inodora* , *Senecia vulgaris* L., *Sinapis arvensis* L., *Sonchus arvensis* L. and in plots under-sown with clover (*Trifolium pratense* L.), *P. rapae* laid similar numbers of eggs on Brussels sprouts as in clean-tilled plots. There was a significant reduction in the larval survival in the weedy and clover plots, and the majority of the mortality occurred between egg hatch and the third instar. Oviposition by *P. rapae* was unaffected by the presence of the background vegetation, while mortality of the small instars (1-3) of *P. rapae* was increased by fifty percent (Dempster 1969).

Increases in *P. rapae* mortality in mixed plantings may be due to the activity of natural enemies. The presence of the clover increased the numbers of *P. melanarius*, *H. rufipes*, *P. opilio*, and rove beetles (unspecified Staphylinidae) around the Brussels sprouts compared with clean-hoed plots (Dempster 1969). Oviposition by *P. rapae* on the collards was unaffected by the height of surrounding alfalfa. Mortality of *P. rapae* larvae, however, was higher on collards that were growing in tall, unmowed alfalfa. *P. opilio* was more common in the tall alfalfa, and when ground dwelling predators were excluded with raised cylinders, *P. rapae* survival increased slightly (McIver 1983).

When broccoli interplanted with nectar producing *A. foeniculum* was compared with broccoli growing in monoculture, interactions between *P. rapae* and its parasitoids were variable and complex. The effect depended on the specific parasitoid and host complex. *Cotesia rubecula* Marshall (Braconidae) were more numerous on broccoli associated with nectar plants than on broccoli grown in monoculture. The parasitoid was probably responding to the aggregation of its host, *P. rapae*, rather than the presence of the nectar source (Zhao et al. 1992).

Plutella xylostella (L.)

P. xylostella discriminates between plants when laying its eggs. It lays significantly fewer eggs on Shepherd's purse (*Capsella bursa-pastoris* (L.)) than on *Brassica* species (Bigger and Fox 1997). It lays more eggs on Candytuff (*Iberis umbellata*) than on collards (*B. oleracea*) even though the larvae perform poorly on *I. umbellata*. Many crucifer weeds sustain the feeding and reproduction of *P. xylostella* (Talekar and Shelton 1993). Harcourt identifies *Barbarea vulgaris* as a preferred weed host of *P. xylostella* and suggests that the rapid spread *of B. vulgaris* in eastern Ontario may be linked with the establishment of *P. xylostella* in Canada (Harcourt 1957). Non-host plants may contain glucosinolates but they also contain oviposition inhibitors. *P. xylostella* is inhibited by the odor of tomato (Gupta and Thorsteinson 1960a, 1960b). Extracts of white clover sprayed on Brussels sprouts reduces oviposition by *P. xylostella* but the effect was variable and weak (Dover 1986).

The relative amount of wax on the leaves of *Brassica* species and varieties has a significant impact on the mortality of *P. xylostella.* Cultivated *B. oleracea* (cabbage, broccoli, cauliflower, Brussels sprouts, etc.) have a dense coating of crystalline surface lipids that produce a characteristic 'wax bloom'. Several *Brassica* mutations eliminate this waxy bloom and produce plants, which are "glossy" in appearance. Many of these glossy mutations confer resistance to insect pests including *P. xylostella* (Eigenbrode et al. 1995).

Mortality increases on glossy plants. Increased mortality is partly the result of the behavior of the *P. xylostella* larvae. The first instar larvae take longer to "settle" on glossy *Brassica* leaves. The larvae move more rapidly, spend more time walking, are more dispersed, and establish fewer leaf mines on glossy plants than on normal-waxy plants. This behavior exposes the small larvae to external mortality factors including weather and natural enemies (Eigenbrode et al. 1995).

The potential of natural enemies to influence the ecology and evolution of insect-herbivore-plant interactions is well recognized (Price et al. 1980). Glossy *Brassica* resistance to *P. xylostella* is a classic example of the complex interactions that occur between plants, herbivores, and the natural enemies. Glossy resistance to *P. xylostella* only occurs in the field where natural enemies are active. The resistance is not expressed in controlled environments in the absence of natural enemies (Eigenbrode et al. 1995).

The waxy covering on normal plants reduces the searching efficiency of natural enemies. In small enclosure studies, adult minute pirate bugs (*O. insidiosus*) and larval *C. carnea* spent less time walking and more time grooming or scrambling in an ineffective forward motion on waxy cabbage than on glossy cabbage. Electron micrographs showed that waxy debris collected on the tarsi of these natural enemies on the normal cabbage. On glossy (wax-free plants) the predators found and attacked first instar *P. xylostella* more quickly (Eigenbrode et al. 1996).

H. convergens, *O. insidiosus*, and *C. carnea* are relatively ineffective predators of *P. xylostella* on normal waxy *Brassica* plants. They have difficulty moving around and foraging on the waxy plants. In greenhouse cage experiments, *H. convergens*, *O. insidiosus*, and *C. carnea* caused significant reductions in *P. xylostella* on glossy type cabbage plants. All three predators failed to reduce *P. xylostella* on normal waxy cabbage (Eigenbrode et al. 1995).

The combination of increased "settling time" for the first instars and the increased searching efficiency by the natural enemies on glossy *Brassica* plants explains, in part, the increase in mortality of *P. xylostella* on glossy *Brassica*. In the greenhouse, where external mortality factors are eliminated, glossiness does not depress *P. xylostella* populations. Glossy resistance to *P. xylostella*, however, does not appear to depend entirely on predation. Abiotic factors present in the field interact with the glossy trait to produce resistance. Increased exposure of larvae to drowning, desiccation, and other stresses contributes to their mortality (Eigenbrode et al. 1995).

While ample evidence exists for the physical mechanisms believed to cause resistance in glossy-leaf *B. oleracea* breeding lines, the relative importance and the mechanisms of chemical resistance of these lines is not well understood (Verkerk and Wright 1996a). When the polar fractions of ethanol extracts of partially resistant glossy breeding lines of cabbage were incorporated into artificial diets, their impact on the survival of *P. xylostella* varied. Extracts from the leaves of some resistant glossy lines when incorporated into media reduced *P. xylostella* survival by up to 19%. Resistance in the glossy line is partly chemical (Eigenbrode et al. 1990).

Glossy host plant resistance is not seen as a viable method of control because on its own it does not appear to offer adequate control. All *Brassica* species (even those from glossy leaf lines) are susceptible to *P. xylostella* until at least six weeks after germination. Intrinsic resistance of a given host plant tends to increase with age. Resistance of *B. oleracea* is greatly affected by the environment, growing conditions, and incident light. Most of the horticultural varieties preferred by farmers and consumers are the waxy varieties that are more susceptible to *P. xylostella* (Verkerk and Wright 1996b).

Background color surrounding *Brassica* plants does not consistently affect oviposition by *P. xylostella. P. xylostella* laid the same number of eggs on Brussels sprouts (*B. oleracea gemmifera* L.) surrounded by green versus transparent plastic sheets (Dover 1986). Weed free broccoli surrounded by black, yellow, green, or blue colored cloth and broccoli surrounded by weeds had the same number of *P. xylostella*, *P. rapae*, and *T. ni* as control plants surrounded by bare ground (Liburd et al. 1998).

Interplanting can have an impact on *P. xylostella* populations. Characteristics of the interplanted vegetation determine the interactions between herbivore, host plant, and natural enemies. The impact of mixed planting depends on the type of plant material used, the timing of the development of the interplanted vegetation, the height of the interplant, and the presence or absence of flowers. The interactions are often complex and pulling in opposite directions.

In some cases, *P. xylostella* density is reduced in polyculture compared with *Brassica* monoculture. The effect is weak and inconsistent (Talekar et al. 1986). *P. xylostella* oviposition was reduced on Brussels sprouts grown among sage (*Salvia officinallis* L.) or thyme (*Thymus vulgaris* L.) or clover (*Trifolium repens* L.). Oviposition was also reduced when plastic plant models or green plants were placed among the Brussels sprouts. The effect of interplanting may be, in part, simply a visual hiding effect (Dover 1986).

In some cases, interplanting can result in undesirable effects (Latheef and Irwin 1980). Most adult Lepidoptera feed on floral nectar. The presence of flowering plants generally produces a localized effect influencing the spatial distribution of eggs (Bigger and Chaney 1998). More *P. xylostella* larvae occurred in broccoli interplanted with *A. foeniculum* than on a broccoli monoculture. Nectar producing flowers apparently attracted *P. xylostella* adults. This attraction resulted in more oviposition on the cole crops growing nearby (Zhao et al. 1992).

In some cases, the presence of non-host plant material mixed with *Brassica* plants increases parasitism of *P. xylostella.* Parasitism of *P. xylostella* was significantly higher in cabbage plots surrounded by tomato plants. Removal or addition of tomato plants reversed the effects. When tomatoes were removed, parasitism was reduced (Bach and Tabasnik 1990). In situations where *P. xylostella* concentrates its oviposition in a *Brassica* monoculture, parasitoids may respond to the concentration of their host insects regardless of the purity of the stand. In some cases, parasitism is higher in monoculture (Horn 1987).

The presence of flowering interplanted vegetation can have a direct impact on parasitoid populations. Flowers increase the longevity and fecundity of some parasitoids (Leius 1960, 1961a, 1961b, 1963, 1967, Idris and Grafius 1995, 1997, Shahjahan 1974, Syme 1977). The longevity of *D. insulare* was significantly higher when it fed on nectar from the *B. vulgaris*. And, the presence of flowering weeds increased the parasitism of *P. xylostella* by *D. insulare* (Idris and Grafius 1993, 1995).

Generalist predators may also have an impact on the survival of *P. xylostella* on cole crops interplanted with other vegetation. When tomatoes were mixed with cabbage, fewer first and second instar *P. xylostella* survived. Plots with no tomatoes had four times as many small larvae surviving. The increased numbers could not be explained by differences in parasitism. The primary parasitoid in the experiment attacked late instar *P. xylostella*. Laboratory oviposition experiments showed that *P. xylostella* did not discriminate between cabbage grown alone and cabbage grown surrounded by tomatoes. Weather, predators or other factors were involved in the changes in mortality (Bach and Tabasnik 1990).

Trichoplusia ni (Hubner)

Background color and background vegetation surrounding cole crops may not influence the rate of oviposition of *T. ni*. Liburd et al. (1998) found that broccoli surrounded by weeds, and broccoli surrounded by either black, yellow, green, or blue cloth (no weeds) supported similar populations of *T. ni* as broccoli surrounded by bare ground. *T. ni* oviposition on cabbage was unaffected by the presence of a tall, dead mulch of hairy vetch or rye grain compared with cabbage grown in bare ground. *T. ni* mortality, however, was higher in the living mulch. Cabbage grown in a dead mulch of rye grain required seven sprays with Bt while the bare ground plots required eight sprays with Bt based on the number of *T. ni* larvae. There may have been increased natural enemy activity in the living mulch (Roberts and Cartwright 1991).

The presence of a variety of fragrant herbs and flowers does not reduce oviposition by *T. ni* on cabbage (Latheef and Irwin 1979, 1980). The density of *T. ni* in broccoli was not affected by the presence of nectar producing *A. foeniculum* whether they were planted near by or interplanted with broccoli (Zhao et al. 1992).

The relative abundance of *T. ni* was not significantly influenced by the presence of flowering Candytuff (*I. umbellata*) surrounding cabbage or broccoli plantings. The presence of the flowering borders did, however, influence the spatial distribution of *T. ni* and *P. rapae* eggs. The pattern of this effect was opposite for the two insects. The mean number of *P. rapae* eggs significantly decreased with increasing distance from the patch boundary of the monocrop surrounded by bare ground. In other words, *P. rapae* oviposition was heavier near the edge between the cole crops and the bare ground. When the crops were surrounded by flowering plants, the distribution of *P. rapae* eggs in the cole crops was even. The *T. ni* eggs in the monoculture surrounded by bare ground were distributed evenly. In the cabbage or broccoli surrounded by flowering *Iberis*, the number of *T. ni* eggs increased with increasing distance from the flowering border (Bigger and Chaney 1998).

Relay Strip-Cropping

Relay strip-cropping changes several aspects of the broccoli environment that should have impacts on the herbivores described above and their natural enemies. The relay establishes an understory of non-host vegetation surrounding the broccoli plants. Changes in background color and the presence of non-host plants may reduce the clarity and strength of visual and olfactory signals that guide the herbivores to their host-plants. Several studies have shown that incoming *B. brassicae* are sensitive to background color during the colonization process. The density of alate *B. brassicae*, may be a useful indicator of the impact of relay strip-cropping on insects that are sensitive to background vegetation during the host plant selection process.

For the highly mobile herbivores that are capable of emigrating from a patch of vegetation, the presence of non-host plants may lead to confusion and loss of contact with olfactory and gustatory cues that arrest the herbivore in the plant patch. Several studies indicate that *P. cruciferae* is sensitive to stand purity. It tends to leave mixed stands and accumulate in areas where its host-plants are growing in monoculture. *P. cruciferae* density, therefore, will be a useful indicator of the impact of relay strip-cropping on emigration rates of crucifer-specialists that are sensitive to stand purity.

P. rapae may be a useful indicator of relative natural enemy activity in the relay strip-cropping and clean-till cropping systems. *P. rapae* does not respond to host plant density or stand purity during its oviposition flights. It should scatter its eggs evenly across the broccoli plantings. Difference in the relative survival of the early instars would, therefore, result from differing mortality factors in the two cropping systems.

T. ni and *P. xylostella* tend to concentrate their egg laying in areas of high host plant density. They may provide an indication of the impact of stand purity in the two cropping systems. *T. ni* tends to have discrete egg laying periods in the Pacific Northwest. Once oviposition begins, *P.*

xylostella pressure tends to increase steadily during the growing season due to multiple overlapping generations of larvae and moths. Because of this variation, the two insects should give us a variety of indications of the impact of relay strip-management on colonization and natural enemy activity compared with the clean-till cropping system.

Relay strip-cropping should enhance the numbers of natural enemies associated with the broccoli. Under-sowing results in soil that is covered with vegetation. The presence of the ground cover changes the microclimate near the soil surface and may lead to earlier colonization by natural enemies that are sensitive to microclimate. Under-sowing results in a mixture of plant species. Mixed stands generally support a greater diversity of insects than monoculture. The presence of a diverse assemblage of alternative prey should support a greater number of generalist natural enemies. Strip-management provides a refuge in the cropping system that may conserve natural enemies that are sensitive to disturbance and that are not highly mobile. Differences in natural enemy density in the two systems should be reflected in the density of aphids and Lepidopteran pests (especially the eggs and small larvae) on the broccoli.

Nectar and pollen sources in the cropping system may enhance the longevity and fecundity of natural enemies including Syrphidae and parasitic Hymenoptera. Specifically, the parasitism of *P. xylostella* by larval/pupal parasitoid *D. insulare* should be a useful indicator of the impact of nectar and pollen in the relay strip-crop. *D. insulare* is common, easy to recognize, and may respond to the presence of nectar and pollen.

Relay strip-cropping, in many regards, is a radical departure from clean-tilled broccoli. Relay strip-cropping integrates vegetation management tactics that have been shown to interfere with host plant finding, emigration rates, and natural enemy induced mortality of broccoli pests. Based on the biological interactions of the pests and their natural enemies it was reasonable to expect differences in pest densities in the clean-till and relay strip-cropping systems.

There are several aspects of the relay strip-cropping system, however, which could have a negative impact on natural enemies. The mixed planting presents natural enemies with a search arena that is more complex than a pure stand of broccoli. The complexity of the habitat may reduce the efficiency of specialist natural enemies in searching for their prey or host insects. Natural enemies that accumulate in the tillage and pesticide refuges may or may not move into the target crop. It is possible that the alternative food and habitat resources in the refuge and in the crop may draw natural enemies away from the broccoli or arrest them in the refuge. Natural enemies that are habitat specialists may not be motivated to move from the refuge into the vegetable crop.

The presence of nectar and pollen sources in the relay strip-cropping may increase the activity of some natural enemies in the cropping system. Nectar can also influence the spatial distribution of some of the Lepidoptera in ways that are not favorable to the crop. The outcome of the interactions between nectar foraging, egg distribution, prey density, and the aggregation of natural enemies is difficult to predict. The assemblage of insect pests associated with broccoli has been extensively studied. The reactions of these well-characterized insect pests should provide us with many insights concerning the value of relay strip-cropping as a pest management tactic. For a more detail review of the literature pertaining to these insect pests of broccoli, see Appendix E.

MATERIALS AND METHODS

The experiments described below were conducted from 1994 to 1996 at the Oregon State University Vegetable Research Farm near Corvallis, Oregon, approximately 0.4 km from the Willamette River. The site characteristics, the relay strip-cropping experiments, and the statistical methods were described in chapters two and three. The same cover-crop mixture and rate were used for both the relay strip-cropping experiments and the under-sowing timing experiments described below.

Under-sowing Timing Experiments 1994 and 1996

Under-sowing experiments were conducted in 1994 and 1996 to determine when under-sowing could be accomplished without depressing broccoli yield. In 1994, the broccoli variety “Gem” was direct seeded and later under-sown with cover-crop seed. In 1996, the broccoli variety “Excelsior” was transplanted and later under-sown. In both cases, the experiments were laid out as randomized complete block designs with four replications. Individual plots were three meters wide and six meters long.

On August 16, 1994, broccoli was direct seeded in rows that were 0.9 m apart using a four-row vacuum planter (Gasparto Inc.). Fertilizer 12-29-10 was banded at planting at a rate of 515 kg per ha (25 kg N, 60 kg P2O5, 21 kg K2O, 17 kg S per ha). At planting, a 15-cm band of Chlorpyrifos was applied over the seed rows at a rate of 0.04 kg active ingredient per 305 m of row. Two weeks after seeding, the broccoli was thinned to approximately one plant every 30 cm and an additional 112 kg of nitrogen per ha in the form of urea was broadcast over the broccoli and watered in. Plots were kept weed free by hand hoeing until they were either under-sown or harvested.

In 1996, a seedbed was prepared and rows were marked 0.9 m apart with the same planter that was used in 1994. Fertilizer was banded at the 1994 rate but seeds were not planted. On July 24, 1996, broccoli was transplanted by hand into the marked fertilizer rows with 40 centimeter between plants in the rows. Plot dimensions, insecticide and fertilizer applications, the cover-crop seed mixture and rate, and other cultural practices were the same as in 1994.

The treatments in 1994 consisted of cover-crop seed broadcast over the top of the broccoli at 0, 2, 4, 6, 8, and 10 weeks after planting. In 1996, the treatments were cover-crop broadcast over the top of the broccoli at 0, 2, 4, 6, and 8 weeks after planting. The cover-crop used in both 1994 and 1996 contained 30 kg Oats variety "Monida" (*Avena sativa*), 20 kg common vetch (*Vicia sativa*), and 5 kg each of red clover (*Trifolium pratense*), annual ryegrass (*Lolium multiflorum* Lam.), and buckwheat (*Fagopyrum esculentum)* planted at a rate of 65 kg per ha. Appropriate innoculant was applied to the legume seed prior to planting and the seed was raked into the soil by hand. Plots were irrigated as needed with over head sprinklers. On November 2, 1994 and on October 4, 1996 all harvestable buds were cut from 3 m of row in the center of each plot, trimmed to a length of 15 cm, and weighed. The above ground plants were harvested and weighed.

On October 2, 1996, arthropod vacuum samples were taken from each 0.2 square meter areas in the center of each plot as (described below). The arthropods were transferred to alcohol, and later sorted and counted. The Shannon-Weiner information measure (Wilson and Bossert 1971) was calculated for each treatment based on the single arthropod sample.

Leaf sampling

In 1995 and 1996 relay strip-crop experiments, aphid and lepidopteran insect pest populations on broccoli were determined on a weekly basis by leaf sampling. One hundred leaves were randomly selected from each of the two broccoli areas in each of the four blocks. Leaves were examined in the laboratory. Aphids were sorted and counted as alate, apterous, and parasitized forms. Total aphids and leaves were air-dried and weighed. Lepidopteran insects were sorted to egg, larval stage, and pupae. Head capsule widths were measured and used to determine larval instars.

Statistical Methods

The under-sowing-timing experiments were analyzed as randomized complete block designs with four replications. Multiple comparisons of mean bud and whole plant yields were made using the Tukey's Studentized Range (HSD) Test. Cole crop specialist insects and broccoli yield data were only collected from the broccoli plots. When these data sets were analyzed on single calendar dates, a two-tailed, paired t-test was used to separate the means.

RESULTS

Under-sowing of cover-crop seed at the time of broccoli planting and up to two weeks after planting significantly depressed final broccoli yield of whole plant biomass and harvested buds (Table 6.1). The depression in yield occurred in both direct seeded (1994) and transplanted broccoli (1996). If under-sowing was delayed four weeks after planting, yield was

Table 6.1 - Impact of Undersowing on Broccoli Yield *
Corvallis, Oregon 1994 and 1996

Harvest Date:	November 2, 1994		October 10, 1996	
Weeks after planting prior to interseeding	Broccoli Buds (gms dry wt.)	Broccoli Whole Plants (gms dry wt.)	Broccoli Buds (gms dry wt.)	Broccoli Whole Plants (gms dry wt.)
0 Weeks	434.3 ± 25.7 a	1035.4 ± 26.7 a	199.8 ± 19.2 a	803.5 ± 81.5 a
2 Weeks	449.7 ± 10.3 ab	1114.0 ± 26.8 ab	235.3 ± 40.2 ab	1013.2 ± 68.8 a
4 Weeks	499.0 ± 48.5 bc	1344.9 ± 81.3 bc	307.3 ± 13.6 b	1328.3 ± 70.5 b
6 Weeks	524.8 ± 37.8 c	1390.2 ± 55.0 c	316.3 ± 28.8 b	1338.7 ± 60.4 b
8 Weeks	543.0 ± 18.0 c	1384.9 ± 40.0 c	332.7 ± 14.1 b	1390.1 ± 30.0 b
10 Weeks	550.0 ± 41.4 c	1419.6 ± 54.1 c	na	na

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* Means ± SEM buds and whole plants harvested from 3 meters of row per plot. Numbers followed by the same letter are not significantly different (P>0.05) Tukey's Studentized Range (HSD) Test.

not significantly depressed in either planting system (Table 6.1, Figures 6.1-6.2). Although under-sowing four and one half weeks after planting did not depress yield, the relay strip-cropping system depressed broccoli yield when broccoli was planted following plow down and incorporation of cover-crop strips (Table 6.2, Figure 6.3). Broccoli yield-depression in the relay strip-cropping system was statistically significant ($P < 0.05$, paired t-test, two tailed) in one planting over the three years.

A greater number of arthropods and arthropod species accumulated in the broccoli by harvest time when cover-crop seed was undersown shortly after planting. There was an inverse relationship between the timing of under-sowing and insect biodiversity measured by the Shannon-Weiner Diversity Index H (Table 6.3, Figure 6.4).

The percentage of broccoli leaves that were infested with *B. brassicae* varied from 1% to 90% (Table 6.4). In 1994, aphid leaf infestation declined at the end of the late planting. In 1995 and 1996, aphid pressure declined at the end of the early broccoli planting prior to harvest, but continued to increase until harvest of the late broccoli plantings. When aphid leaf infestation was analyzed for each separate date, leaf infestation was significantly greater ($P < 0.05$, paired t-test, two tailed) in the relay strip-cropped broccoli than the clean-tilled broccoli on four sampling dates over the three year period. When apterous (wingless) aphid density on leaves was analyzed across sampling dates for each planting period, aphid density was significantly greater ($P = .0066$, $F = 8.00$, $df = 1,52$) in the relay strip-croppped broccoli compared with clean-tilled broccoli in the early planting of 1996. Alate aphid leaf counts were not significantly different in the two cropping systems on any sampling date (Tables 6.5-6.8, Figures 6.5-6.6).

Figure 6.1 Impact of Undersowing on Broccoli Yield
Corvallis, Oregon 1994

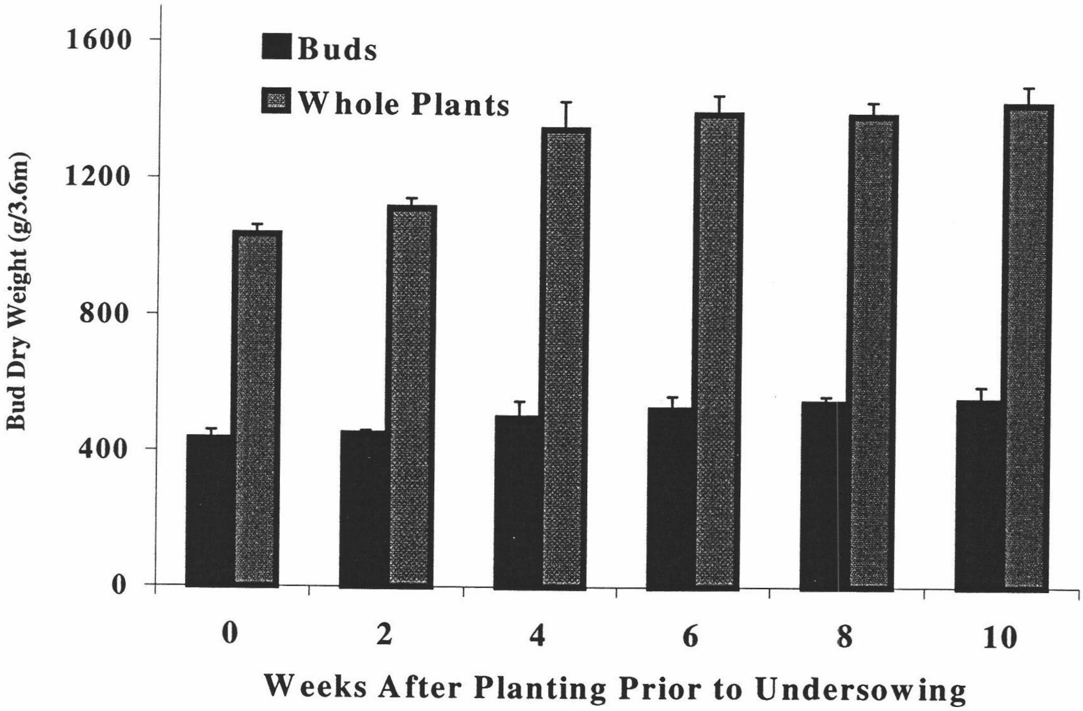


Figure 6.2 Impact of Undersowing on Broccoli Yield
Corvallis, Oregon 1996

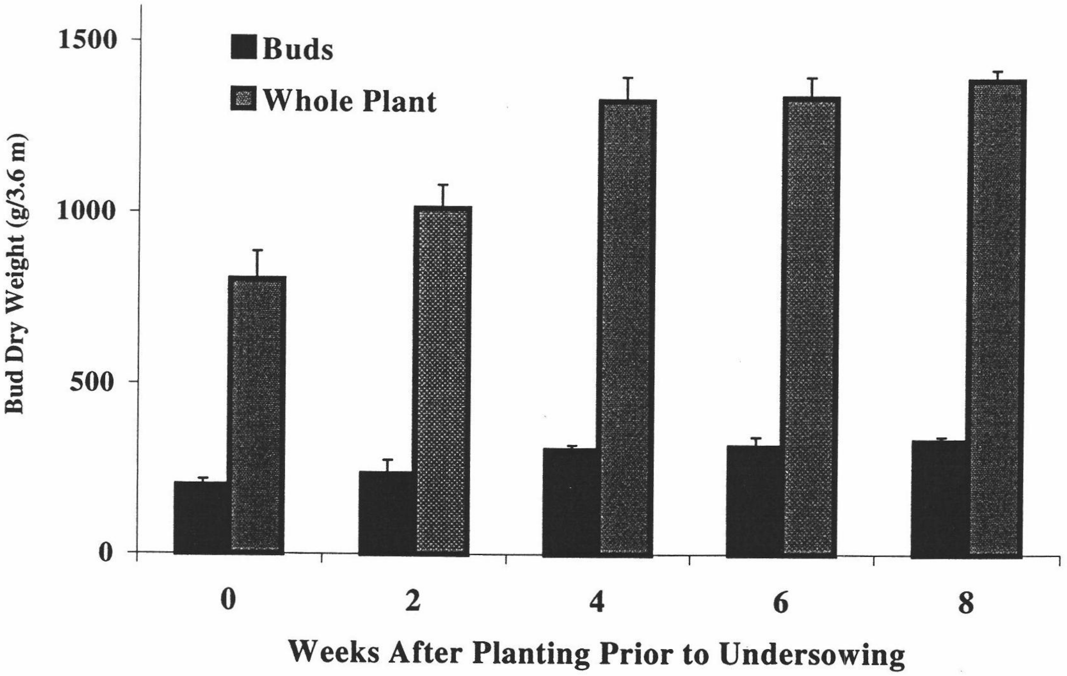


Table 6.2 Impact of Relay Strip-cropping on Broccoli Yield Corvallis, Oregon 1994-1996

	Early Planting		Late Planting	
Cropping System	**Bud Yield* (gms)**	**Bud Diameter (cm)**	**Bud Yield* (gms)**	**Bud Diameter (cm)**
	22-Jul-94	22-Jul-94	2-Nov-94	2-Nov-94
Broccoli Relay	2283.3 ± 102.1 a	16.6 ± 0.5 a	2261.7 ± 77.7 a	15.8 ± 0.4 a
Broccoli Clean Till	2369.8 ± 80.9 a	16.9 ± 0.2 a	2526.6 ± 387.6 a	16.7 ± 0.4 b
	31-Jul-95	31-Jul-95	3-Oct-95	3-Oct-95
Broccoli Relay	2434.0 ± 275.0 a	15.5 ± 0.5 a	4817.0 ± 456.0 a	19.9 ± 1.0 a
Broccoli Clean Till	2508.0 ± 456.0 a	16.0 ± 0.3 a	5833.0 ± 395.0 b	21.1 ± 0.4 a
	8-Aug-96	8-Aug-96	2-Oct-96	2-Oct-96
Broccoli Relay	5630.0 ± 812.4 a	19.2 ± 1.6 a	3217.7 ± 397.1 a	17 ± 1.3 a
Broccoli Clean Till	6709.2 ± 251.3 a	21.3 ± 0.8 a	3990.3 ± 671.5 a	19 ± 1.8 a

* Mean ± SEM grams per 3.6 meters followed by the same letter are not significantly different ($P > 0.05$), paired t-test, two tailed, $n = 4$.

Figure 6.3 Impact of Relay Strip-cropping on Broccoli Yield
Corvallis, Oregon 1994-1996

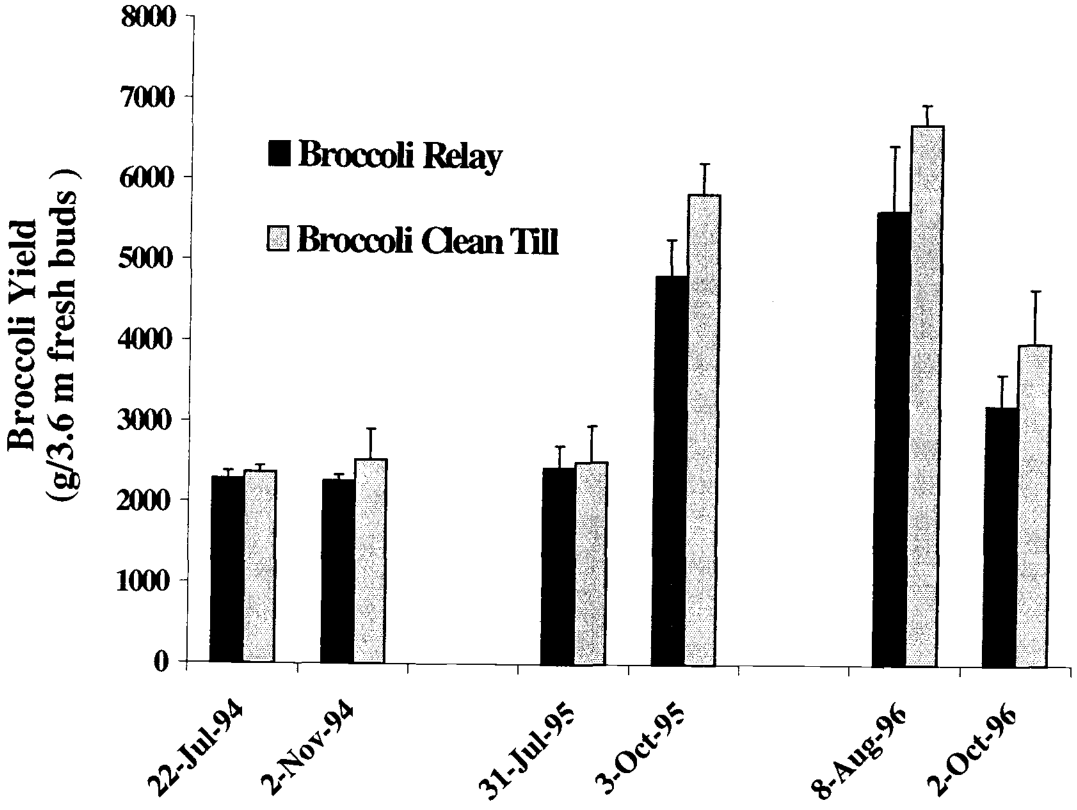


Table 6.3 Impact of Under-sowing on Arthropods in Broccoli - Corvallis, Oregon 1996

Taxa		Weeks after planting prior to undersowing broccoli with cover crop seed				
		0 Weeks	2 Weeks	4 Week	6 Weeks	8 Weeks
Heteroptera**		Arthropods per 0.2 Square Meters *				
Miridae	Lygus	0.6 ± 0.4	0.4 ± 0.2	0	0	0
Reduviidae		0.2 ± 0.2	0	0	0.2 ± 0.2	0
Anthocoridae	Orius triticolor	0.2 ± 0.2	0	0	0	0
Lygaeidae	Geocoris sp.	0	0	0	0.2 ± 0.2	0
Cicadellidae		0.6 ± 0.4	0.2 ± 0.2	0	0.2 ± 0.2	0
		0	0	0	0	0
Coleoptera**		Arthropods per 0.2 Square Meters *				
Carabidae	Bradycellus congener	0	0.2 ± 0.2	0	0	0
Staphylinidae	Bisnius sp.	0.2 ± 0.2	0.4 ± 0.2	0	0	0
Staphylinidae	Creophilus maxillosus (L.)	0	0.2 ± 0.2	0	0	0
Staphylinidae	Platystethus americanus Erichson	0	0	0.2 ± 0.2	0	0
Staphylinidae	Aleochara bimaculata Gravenhorst	0.2 ± 0.2	0	0	0	0.2 ± 0.2
Staphylinidae	unknown Staphylinidae	0.6 ± 0.2	0	0	0	0
Scarabaeidae		0	0	0	0.4 ± 0.4	0
Chrysomelidae	Phyllotreta	0.2 ± 0.2	0	0.2 ± 0.2	0.2 ± 0.2	0
Chrysomelidae	Diabrotica	0.6 ± 0.4	0.6 ± 0.4	0.2 ± 0.2	0	0

* Mean ± SEM, vacuum sampling at harvest October 10, 1996. ** Several genera and species may be involved.

Table 6.3 Impact of Under-sowing on Arthropods in Broccoli - Corvallis, Oregon 1996 (Continued)

Taxa		Weeks after planting prior to undersowing broccoli with cover crop seed				
		0 Weeks	2 Weeks	4 Week	6 Weeks	8 Weeks
Diptera**		Arthropods per 0.2 Square Meters *				
Tipulidae		0.6 ± 0.6	0.2 ± 0.2	0	0.2 ± 0.2	0
Mycetophilidae		0.8 ± 0.4	0.4 ± 0.2	0.2 ± 0.2	0.6 ± 0.4	0
Sciaridae		3.4 ± 0.6	5.0 ± 1.8	2.0 ± 0.8	0.8 ± 0.6	1.6 ± 0.4
Chironomidae		0.4 ± 0.4	0	0	0.2 ± 0.2	0
Longchopteridae		0.2 ± 0.2	0.2 ± 0.2	0	0	0
Phoridae		0	0.2 ± 0.2	0	0	0
Sphaeroceridae		27.4 ± 2.7	25.0 ± 9.9	16.6 ± 5.3	3.2 ± 2.7	1.2 ± 0.7
Drosophilidae		1.6 ± 0.7	1.0 ± 0.4	0.4 ± 0.2	0.2 ± 0.2	0.2 ± 0.2
Ephydridae		0.2 ± 0.2	0	0	0	0
unknown Diptera		0.6 ± 0.4	0.2 ± 0.2	0.4 ± 0.2	0	0
Hymenoptera**		Arthropods per 0.2 Square Meters *				
Eulopidae		0	0.2 ± 0.2	0.2 ± 0.2	0	0
Braconidae		2.2 ± 1.0	1.2 ± 0.6	1.6 ± 0.2	0.6 ± 0.2	1.0 ± 0.5
Ichneumonidae		0.8 ± 0.5	0	0	0	0
Ichneumonidae		0.2 ± 0.2	0	0	0	0
Mymaridae		0.2 ± 0.2	0	0	0	0
Proctotrupidae		0.2 ± 0.2	0	0	0	0
Formicidae		0	0.6 ± 0.4	0.2 ± 0.2	0.6 ± 0.4	0
Formicidae	Myrmidicae (SBF)	0.4 ± 0.4	0	0	0	0

* Mean ± SEM, vacuum sampling at harvest October 10, 1996. ** Several genera and species may be involved.

Table 6.3 Impact of Under-sowing on Arthropods in Broccoli - Corvallis, Oregon 1996 (Continued)

Taxa		Weeks after planting prior to undersowing broccoli with cover crop seed				
		0 Weeks	2 Weeks	4 Week	6 Weeks	8 Weeks
Areaneae**		Arthropods per 0.2 Square Meters *				
Linyphiidae	Lepthyphantes tenuis	1.2 ± 0.6	0	0.6 ± 0.2	0.2 ± 0.2	0
Linyphiidae	Erigone dentosa	1.6 ± 0.9	1.4 ± 0.6	0	0.4 ± 0.2	0.6 ± 0.2
Tetragnatha	Tetragnatha laboriosa	0.2 ± 0.2	0.4 ± 0.2	0.6 ± 0.4	0	0.2 ± 0.2
unknown spiders		0	0.6 ± 0.2	0	0	0
Phalangiidae	Phalangium opilio	0.6 ± 0.2	0	0	0	0
Lepidoptera**		0.4 ± 0.2	0.4 ± 0.2	0.2 ± 0.2	0	0.2 ± 0.2
Neuroptera	Chrysopa carnea	0.2 ± 0.2	0.2 ± 0.2	0	0	0
Psocoptera**		2.8 ± 1.1	1.6 ± 0.5	4.8 ± 1.5	2.8 ± 0.7	3.0 ± 0.9
	Number of Taxa	31	23	15	16	9
	Shannon-Weiner (H)	0.87	0.56	0.52	0.33	0.26

* Mean ± SEM, vacuum sampling at harvest October 10, 1996. ** Several genera and species may be involved.

Figure 6.4 Impact of Undersowing on Arthropod Diversity and Broccoli Yield
Corvallis, Oregon 1996

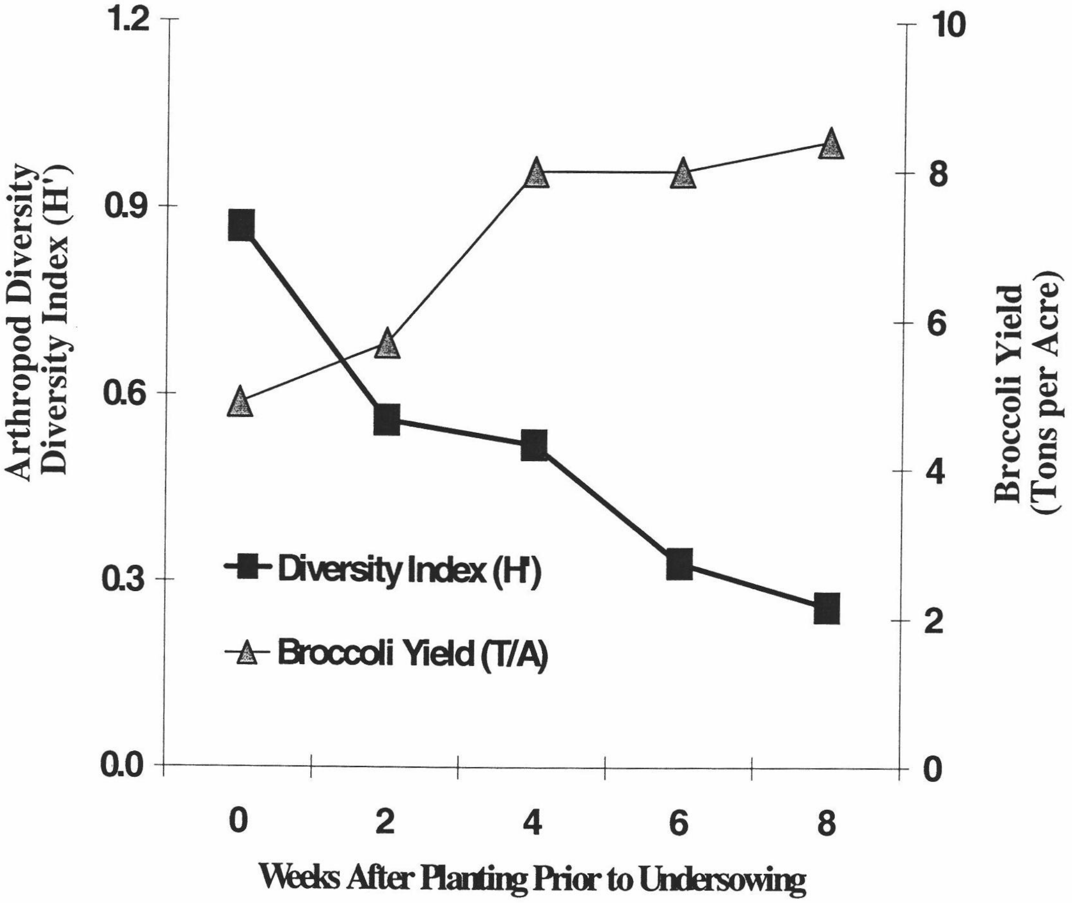


Table 6.4 Impact of Relay Strip-cropping on *Brevicoryne brassicae* in Broccoli, % Infested Leaves
Corvallis, Oregon 1994-1996

Late Planting '94	**01-Sep-94**	**06-Sep-94**	**12-Sep-94**	**19-Sep-94**	**26-Sep-94**	**04-Oct-94**	**10-Oct-94**	**16-Oct-94**
Broccoli Relay	15.00 ± 4.36 a	64.00 ± 5.04 a	83.00 ± 9.86 a	67.67 ± 5.37 a	24.33 ± 2.85 a	22.33 ± 6.13 a	28.00 ± 2.31 a	13.67 ± 1.20 a
Broc. Clean Till	24.00 ± 5.69 a	72.00 ± 6.44 a	90.00 ± 1.53 a	74.00 ± 6.03 a	17.33 ± 2.34 a	16.33 ± 2.03 a	25.67 ± 4.18 a	7.33 ± 2.03 b

Early Planting '95	**21-Jun-95**	**25-Jun-95**	**03-Jul-95**	**10-Jul-95**	**17-Jul-95**	**24-Jul-95**	**01-Aug-95**
Broccoli Relay	40.00 ± 0.89 a	60.50 ± 2.47 a	67.00 ± 3.27 a	59.00 ± 2.68 a	38.00 ± 3.81 a	21.75 ± 3.64 a	10.50 ± 1.66 a
Broc. Clean Till	45.00 ± 7.05 a	64.25 ± 3.25 a	64.75 ± 3.33 a	51.00 ± 5.05 a	38.25 ± 2.02 a	23.00 ± 2.27 a	9.25 ± 2.14 a

Late Planting '95	**21-Aug-95**	**28-Aug-95**	**05-Sep-95**	**18-Sep-95**	**02-Oct-95**
Broccoli Relay	10.00 ± 1.58 a	10.50 ± 1.19 a	11.50 ± 2.22 a	32.00 ± 3.03 a	62.00 ± 2.35 a
Broc. Clean Till	7.75 ± 1.93 b	7.00 ± 1.00 a	7.75 ± 1.55 b	28.50 ± 2.22 a	66.75 ± 4.48 a

Early Planting '96	**10-Jun-96**	**17-Jun-96**	**24-Jun-96**	**01-Jul-96**	**08-Jul-96**	**17-Jul-96**	**23-Jul-96**	**29-Jul-96**
Broccoli Relay	6.67 ± 3.14 a	5.56 ± 1.43 a	na	53.89 ± 3.99 a	62.22 ± 1.28 a	66.67 ± 2.40 a	58.33 ± 3.67 a	66.11 ± 2.29 a
Broc. Clean Till	10.56 ± 1.40 a	2.22 ± 0.91 a	na	49.44 ± 4.39 a	50.00 ± 4.49 b	37.78 ± 28.06 a	62.22 ± 3.14 a	65.56 ± 4.11 a

Late Planting '96	**05-Aug-96**	**13-Aug-96**	**19-Aug-96**	**26-Aug-96**	**05-Sep-96**
Broccoli Relay	1.48 ± 1.48 a	2.22 ± 0.00 a	0.74 ± 0.74 a	5.93 ± 0.74 a	3.70 ± 0.74 a
Broc. Clean Till	3.70 ± 1.96 a	2.22 ± 1.28 a	2.22 ± 2.22 a	4.44 ± 0.00 a	4.44 ± 0.00 a

	09-Sep-96	**16-Sep-96**	**23-Sep-96**	**30-Sep-96**
Broccoli Relay	7.41 ± 1.48 a	19.26 ± 3.23 a	37.04 ± 1.96 a	23.67 ± 4.84 a
Broc. Clean Till	9.63 ± 4.12 a	26.67 ± 5.59 a	50.37 ± 1.96 b	31.00 ± 2.00 a

* Mean + SEM, numbers followed by the same letter within each date and insect stage are not significantly different (P >0.05),

Table 6.5 Impact of Relay Strip-cropping on *Brevicoryne brassicae* in Broccoli Early Planting - Corvallis, OR 1995

Aphids per 100 Leaves*	21-Jun		25-Jun		3-Jul		10-Jul		17-Jul		24-Jul		1-Aug	
Alates														
Broccoli Relay	3.25 ± 0.95	a	8.75 ± 2.93	a	9.25 ± 1.49	a	26.75 ± 5.98	a	14.50 ± 3.12	a	2.50 ± 1.26	a	0.75 ± 0.48	a
Broccoli Clean Till	2.75 ± 0.48	a	13.75 ± 1.44	a	7.25 ± 1.03	a	19.25 ± 3.17	a	12.25 ± 2.95	a	2.50 ± 1.32	a	0.00 ± 0.00	a
Apterae														
Broccoli Relay	43.25 ± 14.39	a	130.75 ± 31.72	a	139.50 ± 28.19	a	198.00 ± 37.42	a	21.25 ± 7.77	a	13.75 ± 5.68	a	2.50 ± 0.65	a
Broccoli Clean Till	55.00 ± 8.10	a	175.00 ± 51.67	a	149.25 ± 47.90	a	153.50 ± 20.42	a	20.00 ± 3.76	a	10.50 ± 5.17	a	7.00 ± 3.56	a
Parasitized														
Broccoli Relay	3.50 ± 1.26	a	13.50 ± 4.44	a	21.50 ± 5.78	a	14.25 ± 2.46	a	7.50 ± 3.57	a	1.50 ± 0.65	a	2.50 ± 1.19	a
Broccoli Clean Till	3.50 ± 0.87	a	9.75 ± 2.29	a	13.25 ± 3.73	a	6.50 ± 0.50	b	12.75 ± 5.56	a	2.50 ± 1.85	a	4.25 ± 1.89	a
% Parasitized														
Broccoli Relay	11.20 ± 4.94	a	10.07 ± 2.26	a	15.03 ± 4.43	a	7.73 ± 2.06	a	26.64 ± 9.71	a	18.52 ± 11.03	a	45.83 ± 11.02	a
Broccoli Clean Till	5.87 ± 0.79	a	5.88 ± 1.50	a	18.98 ± 12.79	a	4.26 ± 0.59	a	36.40 ± 13.41	a	27.18 ± 11.99	a	37.82 ± 15.38	a
ug aphid/100 gm leaf														
Broccoli Relay	3.12 ± 0.35	a	1.53 ± 0.83	a	3.71 ± 0.72	a	3.49 ± 0.54	a	1.35 ± 0.27	a	0.19 ± 0.08	a	0.13 ± 0.09	a
Broccoli Clean Till	3.65 ± 0.36	a	5.77 ± 0.87	a	4.11 ± 0.93	a	2.60 ± 0.39	a	1.49 ± 0.31	a	0.18 ± 0.04	a	0.14 ± 0.08	a

* Mean ± SEM alate, apterous, and parasitized aphids per 100 leaves, numbers followed by the same letter within each date and insect stage are not significantly different (P >0.05), paired t-test, two tailed, n = 4.

Table 6.6 Impact of Relay Strip-cropping on *Brevicoryne brassicae* in Broccoli, Late Planting - Corvallis, Oregon 1995

Aphids per 100 Leaves*	21-Aug	28-Aug	5-Sep	18-Sep	2-Oct
Alates					
Broccoli Relay	4.25 ± 0.85 a	3.25 ± 1.38 a	2.75 ± 0.25 a	15.25 ± 3.17 a	32.75 ± 7.04 a
Broccoli Clean Till	5.25 ± 1.49 a	3.00 ± 0.41 a	2.25 ± 0.48 a	9.25 ± 1.55 a	25.00 ± 5.21 a
Apterae					
Broccoli Relay	13.00 ± 5.05 a	23.25 ± 9.28 a	10.00 ± 3.34 a	159.00 ± 28.18 a	614.00 ± 70.67 a
Broccoli Clean Till	27.50 ± 1.55 a	8.25 ± 1.60 a	5.25 ± 2.46 a	93.75 ± 19.47 a	532.75 ± 87.96 a
Parasitized					
Broccoli Relay	0.25 ± 0.25 a	0.25 ± 0.25 a	0.50 ± 0.50 a	2.00 ± 0.58 a	9.00 ± 6.39 a
Broccoli Clean Till	0.25 ± 0.25 a	0.00 ± 0.00 a	0.00 ± 0.00 a	5.00 ± 3.79 a	10.75 ± 5.76 a
% Parasitized					
Broccoli Relay	2.27 ± 2.27 a	0.48 ± 0.48 a	2.78 ± 2.78 a	1.44 ± 0.61 a	1.24 ± 0.74 a
Broccoli Clean Till	0.93 ± 0.93 a	0.00 ± 0.00 a	0.00 ± 0.00 a	4.47 ± 3.02 a	2.01 ± 0.96 a
ug Aphid/100 gm leaf					
Broccoli Relay	0.09 ± 0.04 a	0.18 ± 0.09 a	0.11 ± 0.04 a	1.24 ± 0.34 a	7.72 ± 1.00 a
Broccoli Clean Till	0.23 ± 0.03 a	0.02 ± 0.01 a	0.08 ± 0.03 a	0.97 ± 0.22 a	9.45 ± 1.25 a

* Mean ± SEM, alate, apterous, and parasitized aphids per 100 leaves, numbers followed by the same letter within each date and insect stage are not significantly different (P >0.05), paired t-test, two tailed, n = 4.

Table 6.7 Impact of Relay Strip-cropping on *Brevicoryne brassicae* in Broccoli Early Planting - Corvallis, Oregon 1996

Aphids per 100 Leaves*	10-Jun	17-Jun	24-Jun	1-Jul	8-Jul	17-Jul	23-Jul
Alates							
Broccoli Relay	0.56 ± 0.60	0.56 ± 0.56	3.89 ± 1.90 a	18.33 ± 3.67 a	26.67 ± 4.80 a	51.67 ± 11.34 a	20.56 ± 9.74 a
Broc. Clean Till	0	0	2.22 ± 0.91 a	11.11 ± 1.57 a	35.00 ± 9.62 a	48.89 ± 12.41 a	26.11 ± 8.95 a
Apterae							
Broccoli Relay	6.11 ± 2.78 a	21.67 ± 5.76 a	63.33 ± 19.30 a	426.11 ± 22.34 a	501.67 ± 71.53 a	1458.89 ± 287.54 a	1177.22 ± 771.58 a
Broc. Clean Till	9.44 ± 3.44 a	7.22 ± 4.19 a	27.22 ± 13.89 a	325.56 ± 35.93 b	468.33 ± 76.60 a	567.22 ± 88.06 a	547.22 ± 183.36 a
Parasitized							
Broccoli Relay	0	0.56 ± 0.56	1.67 ± 0.56 a	6.67 ± 3.01 a	31.11 ± 7.31 a	56.11 ± 13.53 a	86.11 ± 44.82 a
Broc. Clean Till	0	0	0.56 ± 0.56 a	5.56 ± 2.94 a	19.44 ± 2.10 a	26.11 ± 8.33 a	44.44 ± 16.15 a
% Parasitized							
Broccoli Relay	0	0.01 ± 0.01	0.04 ± 0.02 a	0.02 ± 0.01 a	0.06 ± 0.02 a	0.04 ± 0.00 a	0.09 ± 0.02 a
Broc. Clean Till	0	0	0.01 ± 0.01 a	0.02 ± 0.01 a	0.04 ± 0.00 a	0.04 ± 0.01 a	0.12 ± 0.06 a
ug aph/100g lf							
Broccoli Relay	0.60 ± 0.05 a	1.28 ± 0.29 a	1.54 ± 0.35 a	5.32 ± 0.91 a	5.29 ± 0.50 a	15.78 ± 3.25 a	16.48 ± 14.77 a
Broc. Clean Till	4.44 ± 0.44 a	0.77 ± 0.53 a	2.42 ± 1.30 a	3.99 ± 0.66 b	3.87 ± 0.79 a	4.63 ± 1.24 a	8.04 ± 3.31 a

* Mean ± SEM, alate, apterous, and parasitized aphids per 100 leaves, numbers followed by the same letter within each date and insect stage are not significantly different (P >0.05), pair t-test, two tailed, n = 4.

Table 6.8 Impact of Relay Strip-cropping on *Brevicoryne brassicae* in Broccoli
Late Planting - Corvallis, Oregon 1996

Aphids per 100 Leaves*	13-Aug	19-Aug	26-Aug	5-Sep	9-Sep	16-Sep	23-Sep
Alates							
Broc. Relay	2.22 ± 0.00 **a**	2.22 ± 2.22 **a**	1.48 ± 1.48 **a**	0.74 ± 0.74 **a**	3.70 ± 0.74 **a**	8.15 ± 2.67 **a**	19.26 ± 4.12 **a**
Broc. Cl.Till	0.74 ± 0.74 **a**	1.48 ± 0.74 **a**	1.48 ± 0.74 **a**	2.96 ± 0.74 **a**	6.67 ± 1.28 **a**	8.89 ± 1.28 **a**	22.22 ± 2.22 **a**
Apterae							
Broc. Relay	8.15 ± 8.15 **a**	5.93 ± 5.93 **a**	25.93 ± 8.54 **a**	25.19 ± 15.47 **a**	118.52 ± 53.06 **a**	528.89 ± 269.30 **a**	362.96 ± 74.51 **a**
Broc. Cl.Till	3.70 ± 3.70 **a**	37.78 ± 31.11 **a**	23.70 ± 12.66 **a**	64.44 ± 28.89 **a**	82.96 ± 29.55 **a**	262.22 ± 48.30 **a**	751.85 ± 187.69 **a**
Parasitized							
Broc. Relay	0.74 ± 0.74	0	0	0.74 ± 0.74	0.74 ± 0.74	22.96 ± 20.78 **a**	2.96 ± 0.74 **a**
Broc. Cl.Till	0	1.48 ± 0.74	0.74 ± 0.74	0	0	2.96 ± 0.74 **a**	15.56 ± 7.14 **a**
% Parasitized							
Broc. Relay	0.03 ± 0.03	0	0	0.01 ± 0.01	0	0.02 ± 0.02 **a**	0.01 ± 0.01 **a**
Broc. Cl.Till	0	0.12 ± 0.11	0.02 ± 0.02	0	0	0.01 ± 0.00 **a**	0.02 ± 0.01 **a**
ug Aph/100g lf							
Broc. Relay	0.55 ± 0.30	0.39 ± 0.42 **a**	0.30 ± 0.26 **a**	0.56 ± 0.11 **a**	1.10 ± 0.17 **a**	7.43 ± 4.61 **a**	2.38 ± 0.32 **a**
Broc. Cl.Till	0	0.54 ± 0.51 **a**	0.46 ± 0.28 **a**	0.88 ± 0.26 **a**	0.84 ± 0.42 **a**	2.24 ± 0.25 **a**	7.00 ± 4.12 **b**

* Mean + SEM alate, apterous, and parasitized aphids per 100 leaves, numbers followed by the same letter within each date and insect stage are not significantly different (P >0.05), pair t-test, two tailed, n = 4.

Figure 6.5 Impact of Relay Strip-cropping on Alate *Brevicoryne brassicae*
Corvallis, Oregon 1995

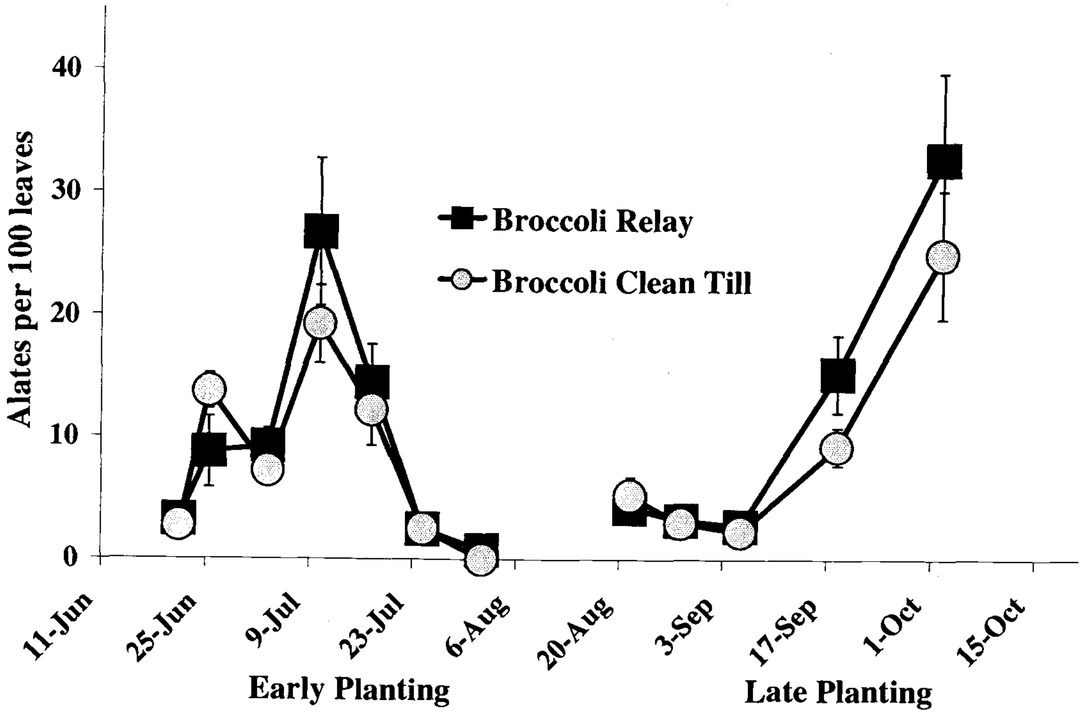
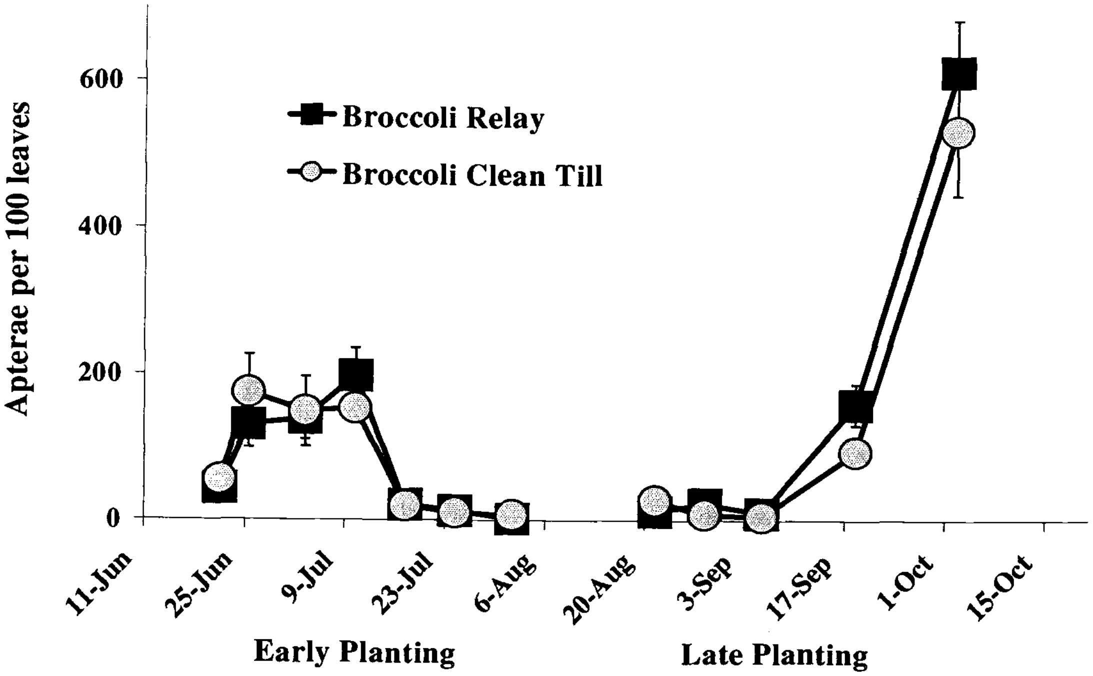


Figure 6.6 Impact of Relay Strip-cropping on Apterous *Brevicoryne brassicae*
Corvallis, Oregon 1995



Total dry aphid versus leaf biomass was unaffected by cropping system (Figure 6.7).

The number of parasitized aphids and the percent parasitism of aphids on the leaves tended to be higher during the early broccoli plantings (Tables 6.5-6.8, Figures 6.8-6.9). When analyzed across sampling dates for each planting, the number of parasitized aphids was significantly greater ($P = .0145$, $F= 6.35$, $df = 1,58$) in the relay strip-cropped broccoli than in the clean-tilled broccoli in the early planting of 1996. Percent parasitization, however, was similar in the two planting systems ($P = 0.2920$, $F= 1.13$, $df = 1,58$).

Infestation of broccoli buds by *B. brassicae* varied from 6% to 75% (Table 6.9, Figure 6.10). Bud-contamination was consistently higher in the late plantings. Aphid bud infestation at harvest was never significantly different in the broccoli relay compared with clean-tilled broccoli ($P > 0.05$, paired t-test, two tailed).

P. cruciferae densities varied from 0 to 226 beetles per square meter in the six plantings over three years . *P. cruciferae* was completely absent in the late planting in 1994. Beetle density was highest during the late planting period then drop off rapidly at the end of the growing season in 1995 and 1996. Most of the beetles were captured in the broccoli. Relatively few beetles were captured in the cover-crop or bare ground, even when the cover-crop was intermingled with broccoli stubble following harvest of the early plantings (Table 6.10, Figures 6.11-6.13). When beetle counts were analyzed on each separate date, beetle density in the clean-tilled broccoli was equal to or higher than in the relay strip-cropped broccoli on nineteen out of twenty three sampling dates over the three year period. When beetle density was analyzed across sampling dates for each broccoli

Figure 6.7 Impact of Relay Strip-cropping on Aphid biomass (*B. brassicae*) Corvallis, Oregon 1995

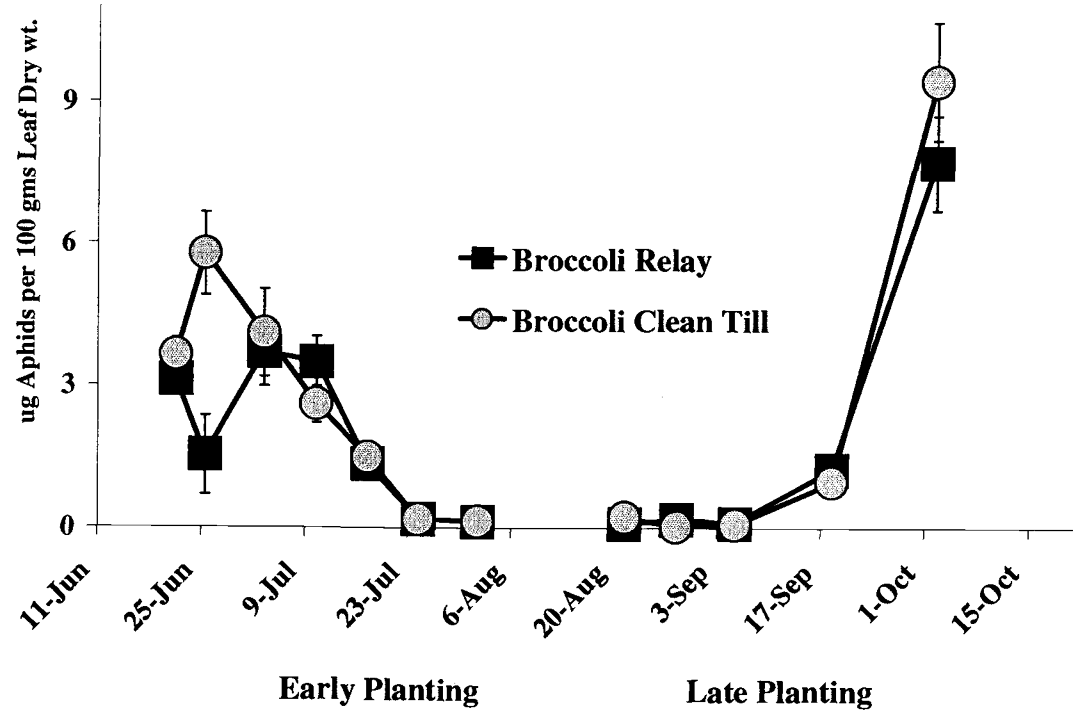


Figure 6.8 Impact of Relay Strip-cropping on Parasitized *Brevicoryne brassicae* Corvallis, Oregon 1995

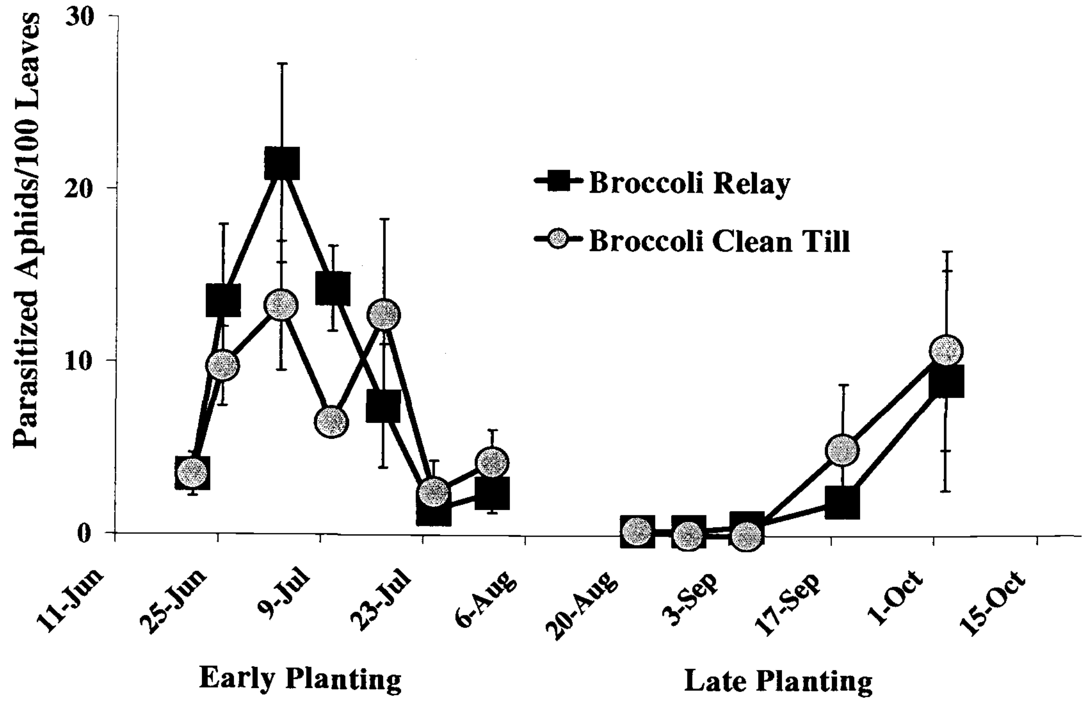


Figure 6.9 Impact of Relay Strip-cropping on % Parasitized *Brevicoryne brassicae*
Corvallis, Oregon 1995

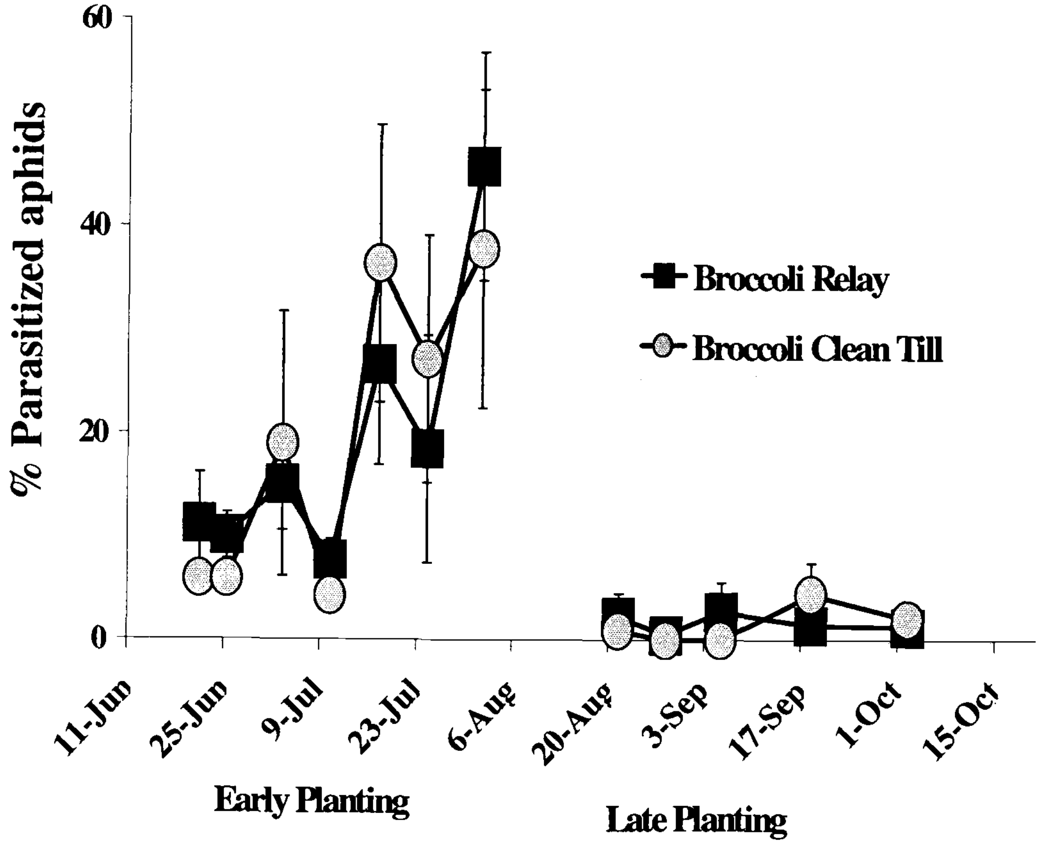


Table 6.9 Contamination of Broccoli Buds by *Brevicoryne brassicae* Corvallis, Oregon 1994-1996

%Infested Buds

	Early Planting	**Late Planting**
Cropping System	22-Jul-94	2-Nov-94
Broccoli Relay	11.9 ± 2.1 a	75.3 ± 16.4 a
Broccoli Clean Till	10.6 ± 2.1 a	62.0 ± 12.1 a
	31-Jul-95	3-Oct-95
Broccoli Relay	6.5 ± 1.8 a	29.75 ± 5.8 a
Broccoli Clean Till	9.0 ± 3.5 a	21.75 ± 4.5 a
	8-Aug-96	2-Oct-96
Broccoli Relay	14.3 ± 4.7 a	55.3 ± 18.9 a
Broccoli Clean Till	12.0 ± 5.3 a	53.3 ± 23.7 a

* Mean ± SEM, numbers followed by the same letter within each date are not significantly different ($P > 0.05$), pair t-test, two tailed, $n = 4$.

Figure 6.10 Contamination of Broccoli Buds by *Brevicoryne brassicae* Corvallis, Oregon 1994-1996

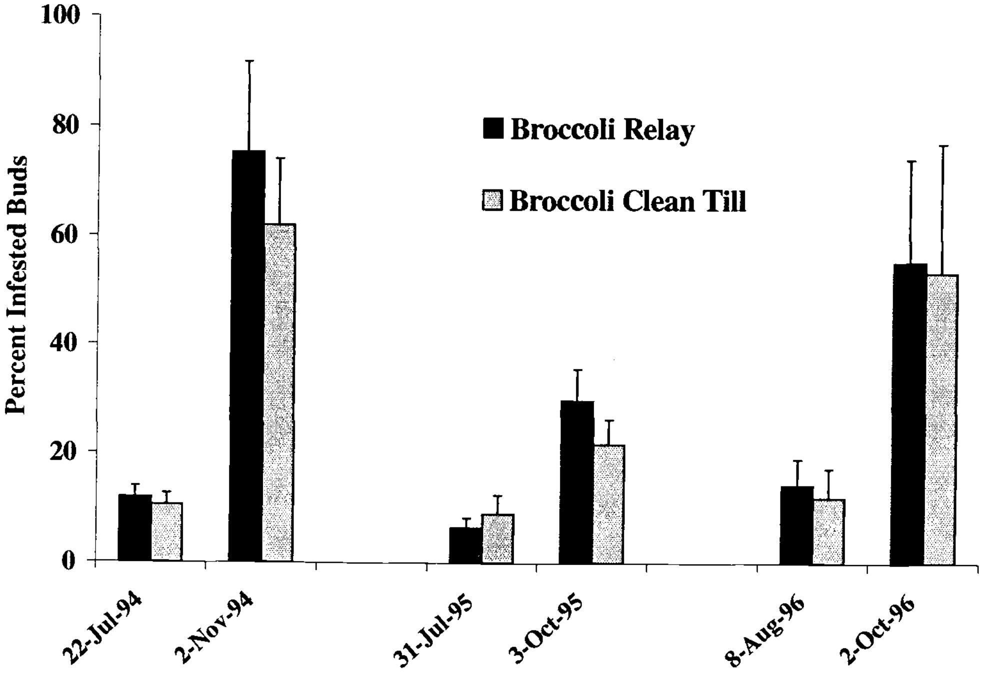


Table 6.10 Impact of Relay Strip Cropping on *Phyllotreta cruciferae* in Broccoli, Corvallis, Oregon 1994-1996

	Beetles per Square Meter*							
1996 Early Planting	**11-Jun-96**		**25-Jun-96**		**09-Jul-96**		**22-Jul-96**	
Broccoli Relay	0.14 ± 0.14	a	8.89 ± 2.09	a	10.56 ± 4.19	a	17.08 ± 2.14	a
Broccoli Clean-Till	2.08 ± 1.05	b	10.42 ± 0.80	a	8.33 ± 0.82	a	39.17 ± 14.78	a
Cover Crop	0		0		0		na	
Bare Ground	0		0		0		na	
1996 Late Planting	**20-Aug-96**		**03-Sep-96**		**18-Sep-96**		**30-Sep-96**	
Broccoli Relay	7.59 ± 4.43	a	60.19 ± 39.62	a	77.96 ± 33.34	ab	3.33 ± 1.82	a
Broccoli Clean-Till	63.70 ± 33.78	b	226.30 ± 98.08	b	115.00 ± 20.14	b	5.56 ± 2.17	a
Cover Crop	20.00 ± 3.06	ab	33.33 ± 6.48	a	9.07 ± 1.03	a	7.04 ± 1.96	a
Bare Ground	14.44 ± 3.94	ab	6.48 ± 3.92	a	1.11 ± 0.56	a	0.56 ± 0.32	a
1995 Early Planting	**28-Jun-95**		**11-Jul-95**		**26-Jul-95**		**09-Aug-95**	
Broccoli Relay	17.64 ± 7.16	a	26.67 ± 7.09	a	28.06 ± 7.40	a	52.78 ± 19.43	a
Broccoli Clean-Till	22.78 ± 5.45	a	35.69 ± 6.24	b	33.47 ± 3.00	a	103.33 ± 6.35	a
Cover Crop	0.28 ± 0.16	b	0	c	na		na	
Bare Ground	0.14 ± 0.14	b	0	c	na		na	
1995 Late Planting	**28-Aug-95**		**13-Sep-95**		**09-Oct-95**			
Broccoli Relay	112.78 ± 55.17	a	102.59 ± 13.39	a	2.85 ± 0.35	a		
Broccoli Clean-Till	110.42 ± 37.03	a	35.93 ± 9.05	b	2.92 ± 1.61	a		
Cover Crop	na		5.00 ± 0.73	c	1.01 ± 0.36	a		
Bare Ground	na		0.37 ± 0.16	d	0.31 ± 0.31	a		
1994 Early Planting	**21-Jun-94**		**28-Jun-94**		**12-Jul-94**		**19-Jul-94**	
Broccoli Relay	85.31 ± 15.52	a	126.67 ± 19.51	a	2.81 ± 1.29	a	0	
Broccoli Clean till	97.50 ± 22.33	a	129.58 ± 13.82	a	1.25 ± 1.25	a	0.00 ± 0.27	
Cover Crop	0.63 ± 0.63	b	na		1.25 ± 0.72	a	na	
Bare Ground	0		na		0.31 ± 0.31	a	na	
1994 Late Planting	**13-Sep-94**		**27-Sep-94**		**11-Oct-94**		**25-Oct-94**	
Broccoli Relay	0	a	0		0		0	
Broccoli Clean till	0	a	0		0		0	
Cover Crop	0.42 ± 0.42	a	0		1.25 ± 0.72		0.42 ± 0.42	

Figure 6.11 Impact of Relay Strip-cropping on *Phyllotreta cruciferae* in Broccoli Corvallis, Oregon 1994

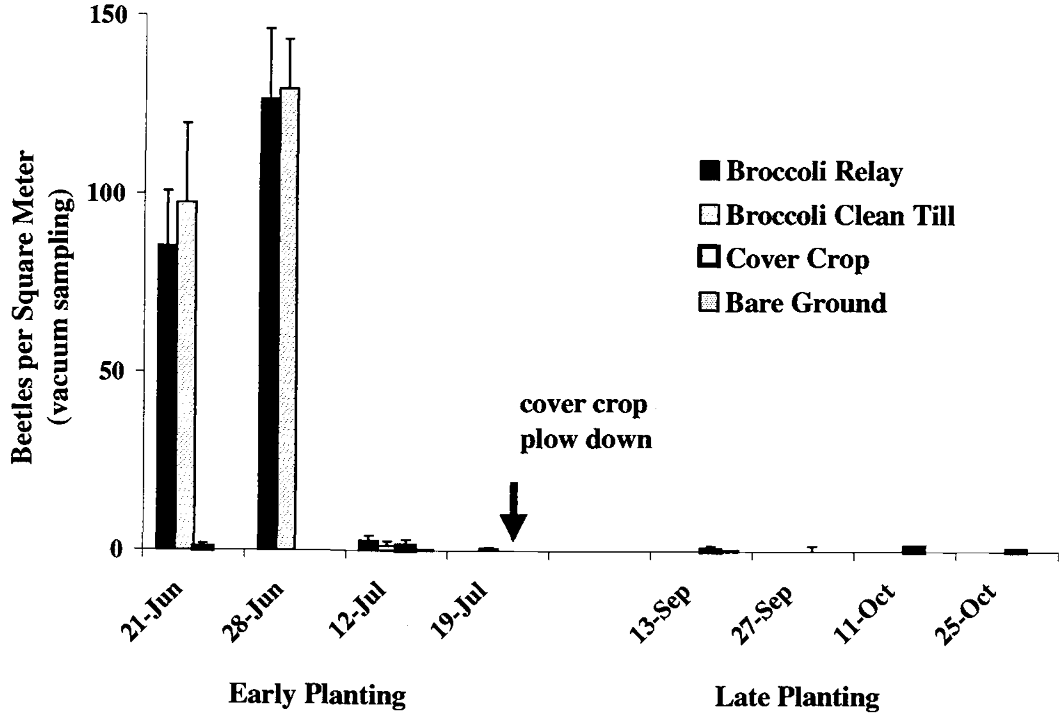


Figure 6.12 Impact of Relay Strip-cropping on *Phyllotreta cruciferae* in Broccoli Corvallis, Oregon 1995

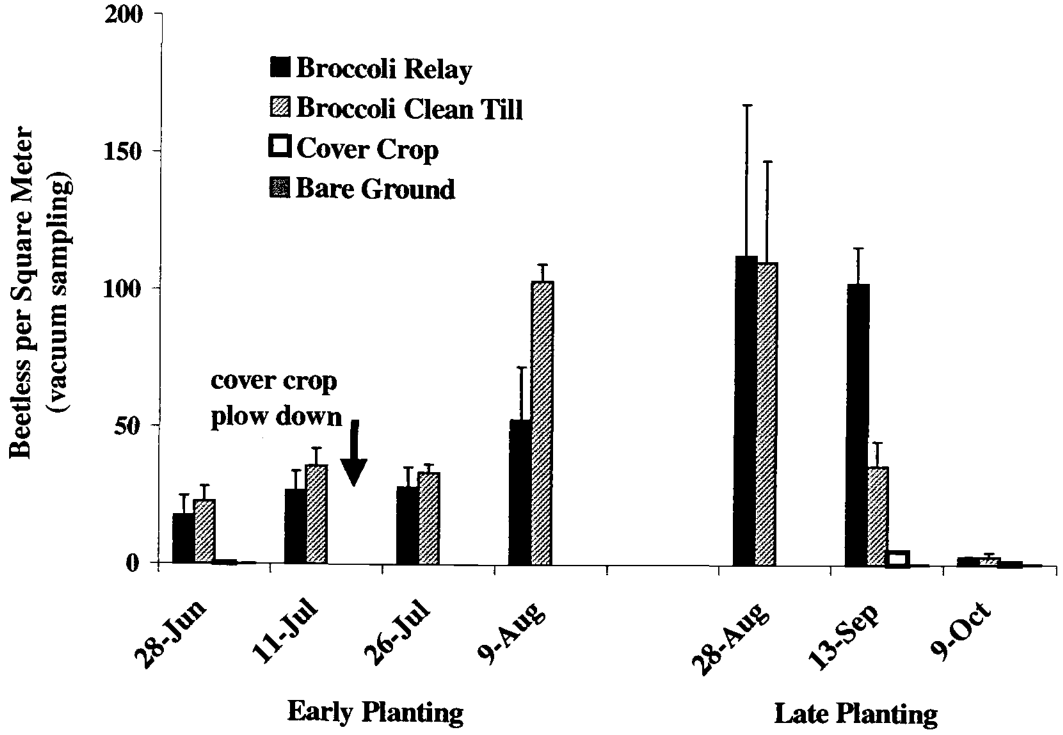
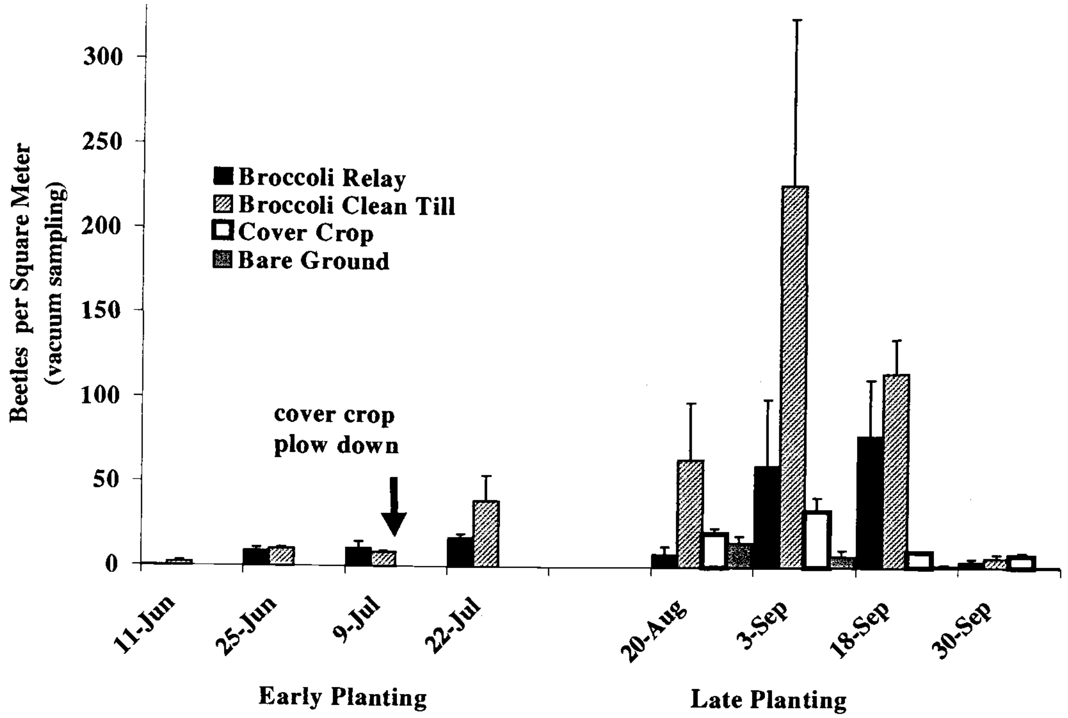


Figure 6.13 Impact of Relay Strip-cropping on *Phyllotreta cruciferae* in Broccoli Corvallis, Oregon 1996



planting, the number of beetles per square meter was significantly greater in the clean-tilled broccoli than in the relay strip-cropped broccoli in the early planting of 1995 (P = 0.0146, F = 7.02, df = 1,22) and in both the early (P = 0.0494, F = 4.29, df = 1,24) and late (P = 0.0028, F = 12.22, df = 1,17) broccoli plantings of 1996.

The density of *P. rapae* eggs and larvae sampled from broccoli leaves varied from 0 to 13 insects per 100 leaves in 1995 and 1996. When *Pieris* leaf counts were analyzed on single dates or analyzed across all dates for each planting period, the number of eggs, first through fifth instar, and pupae on the leaves was not significantly different in the two cropping systems (Tables 6.11-6.14, Figures 6.14-6.17). Infestation of broccoli buds by larvae and pupae of *P. rapae,* varied from 0.11 to 1.29 total contaminants per bud in 1995 and 1996 (Table 6.15, Figures 6.18-6.19). There were significantly more third instar larvae per bud at harvest (P < 0.05, paired t-test, two tailed) in clean-tilled compared with relay strip-cropped broccoli in early 1995. There were significantly more fifth instar larvae per bud at harvest (P < 0.05, paired t-test, two tailed) in clean-till compared with relay strip-cropped broccoli in early 1996.

P. xylostella larvae and pupae on broccoli leaves varied from 0.8 to 195 total contaminants per 100 leaves in 1995 (Table 6.16) and from 0 to 31.9 total insects per 100 leaves in 1996 (Table 6.17). In 1995, *P. xylostella* counts were higher in the early planting period. In 1996, *P. xylostella* leaf counts were low during the early planting period and increased during the late planting period.

When weekly *P. xylostella* leaf counts were analyzed across sampling dates for each broccoli planting, counts of second through fourth instar larvae per 100 leaves were not significantly different in the relay strip-crop

Table 6.11 Impact of Relay Strip-cropping on *Pieris rapae* in Broccoli Early Planting - Corvallis, Oregon 1995

		Eggs, Instars or Pupa per 100 Leaves*						
		21-Jun	25-Jun	3-Jul	10-Jul	17-Jul	24-Jul	1-Aug
Broccoli Relay	**Egg**	1.50 ± 1.50 **a**	0	1.75 ± 1.75 **a**	5.00 ± 5.00 **a**	0.75 ± 0.75	0	0.50 ± 0.29
Broccoli Clean till		0.25 ± 0.48 **a**	0.75 ± 0.58	0.50 ± 0.29 **a**	2.75 ± 1.70 **a**	0	1.00 ± 1.00	0
Broccoli Relay	**1st Instar**	0	0	0.25 ± 0.25	0.25 ± 0.25	1.75 ± 0.63 **a**	0	0.75 ± 0.75 **a**
Broccoli Clean till		0	0	0	0	1.75 ± 1.18 **a**	1.50 ± 0.65	0.50 ± 0.50 **a**
Broccoli Relay	**2nd Instar**	0	0.25 ± 0.25	0.25 ± 0.25 **a**	0.50 ± 0.29 **a**	2.50 ± 1.19 **a**	2.50 ± 1.89 **a**	2.25 ± 1.60 **a**
Broccoli Clean till		0	0	0.25 ± 0.25 **a**	0.67 ± 0.58 **a**	3.50 ± 1.50 **a**	2.75 ± 1.55 **a**	1.25 ± 0.48 **a**
Broccoli Relay	**3rd Instar**	0	0	0	0	0	0.50 ± 0.50	0.25 ± 0.25 **a**
Broccoli Clean till		0	0	0	0	0.25 ± 0.25	0	0.25 ± 0.25 **a**
Broccoli Relay	**4th Instar**	0	0	0	0	0.25 ± 0.25 **a**	0.75 ± 0.75 **a**	0.50 ± 0.29
Broccoli Clean till		0	0	0	0	0.75 ± 0.48 **a**	0.25 ± 0.25 **a**	0
Broccoli Relay	**5th Instar**	0	0	0	0.25 ± 0.25	0	1.00 ± 1.00	0
Broccoli Clean till		0	0	0	0	0	0	0
Broccoli Relay	**Pupa**	0	0	0	0	0.25 ± 0.25	0	0.75 ± 0.75
Broccoli Clean till		0	0	0	0	0	0.50 ± 0.50	0

* Means ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different ($P > 0.05$), pair t-test, two tailed, n = 4.

Table 6.12 Impact of Relay Strip-cropping on *Pieris rapae* in Broccoli
Late Planting - Corvallis, Oregon 1995

	Eggs, Instars and Pupa per 100 Leaves				
	21-Aug	28-Aug	5-Sep	18-Sep	2-Oct
Broccoli Relay **Egg**	0.50 ± 0.50 a	1.25 ± 0.95 a	2.25 ± 1.93 a	1.75 ± 1.75 a	2.75 ± 0.00
Broccoli Clean till	1.25 ± 0.95 a	2.00 ± 1.35 a	1.00 ± 1.00 a	0.75 ± 0.75 a	0
Broccoli Relay **1st Instar**	1.25 ± 0.63 a	1.25 ± 0.75 a	0.75 ± 0.48 a	0.25 ± 0.25 a	0
Broccoli Clean till	0.50 ± 0.29 a	0.50 ± 0.29 a	0.50 ± 0.29 a	0.75 ± 0.75 a	0
Broccoli Relay **2nd Instar**	3.25 ± 1.60 a	1.75 ± 0.63 a	0.50 ± 0.29 a	1.50 ± 0.65 a	0.75 ± 0.75 a
Broccoli Clean till	2.75 ± 0.48 a	3.75 ± 1.31 a	0.50 ± 0.50 a	0.75 ± 0.48 a	0.75 ± 0.75 a
Broccoli Relay **3rd Instar**	0	2.00 ± 1.08 a	0.75 ± 0.25 a	0.25 ± 0.25 a	0.25 ± 0.25
Broccoli Clean till	0.75 ± 0.48	0.25 ± 0.25 a	0.25 ± 0.25 a	0.25 ± 0.25 a	0
Broccoli Relay **4th Instar**	0	0	0.25 ± 0.25 a	0.25 ± 0.25 a	0
Broccoli Clean till	0	0	0.50 ± 0.29 a	0.75 ± 0.48 a	0.25 ± 0.25
Broccoli Relay **5th Instar**	0	0	0.75 ± 0.75 a	0.25 ± 0.25 a	0
Broccoli Clean till	0	0.25 ± 0.25	0.50 ± 0.29 a	0.25 ± 0.25 a	0.25 ± 0.25
Broccoli Relay **Pupa**	0	0.50 ± 0.29 a	0	0	0
Broccoli Clean till	0	0.25 ± 0.25 a	0	0	0

* Means ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different (p>0.05), pair t-test, two tailed, n = 4.

Table 6.13 Impact of Relay Strip-cropping on *Pieris rapae* in Broccoli
Early Planting - Corvallis, Oregon 1996

		Eggs, Larvae, and Pupa per 100 Leaves*							
		10-Jun	17-Jun	24-Jun	1-Jul	8-Jul	17-Jul	23-Jul	29-Jul
Broccoli Relay	**Egg**	0.56 ± 0.56	0	0	1.67 ± 0.56 a	0.56 ± 0.56 a	0.56 ± 0.56 a	1.67 ± 1.06 a	0
Broccoli Clean till		0	0.56 ± 0.56	0.56 ± 0.56	1.67 ± 1.06 a	0.56 ± 0.56 a	2.78 ± 1.67 a	1.67 ± 1.06 a	1.67 ± 1.06
Broccoli Relay	**1st**	0	0	0	4.44 ± 3.14	0.56 ± 0.56 a	2.22 ± 1.57	0.56 ± 0.56	0
Broccoli Clean till	**Instar**	0	0	0	0	0.56 ± 0.56 a	0	0	0
Broccoli Relay	**2nd**	0	0	0	0.56 ± 0.56	0	1.11 ± 1.11	0.56 ± 0.56	0.56 ± 0.56 a
Broccoli Clean till	**Instar**	0	0.56 ± 0.56	0.56 ± 0.56	0	0	0	0	1.10 ± 0.64 a
Broccoli Relay	**3rd**	0	0	0.56 ± 0.56 a	0.56 ± 0.56	1.67 ± 1.06	1.11 ± 0.64 a	0.56 ± 0.56 a	0
Broccoli Clean till	**Instar**	0	0	0.56 ± 0.56 a	0	0	0.56 ± 0.56 a	1.11 ± 1.11 a	1.11 ± 0.64
Broccoli Relay	**4th**	0	0	0	0	0	0	1.11 ± 1.11 a	0
Broccoli Clean till	**Instar**	0	0	0	0	0	0.56 ± 0.56	2.22 ± 0.91 a	0
Broccoli Relay	**5th**	0	0	0	0	0	0	0	0
Broccoli Clean till	**Instar**	0	0	0	0.56 ± 0.56	0	2.22 ± 1.57	0.56 ± 0.56	0
Broccoli Relay	**Pupa**	0	0	0	0	0	0	0.56 ± 0.56 a	0
Broccoli Clean till		0	0	0	0	0	0	0.56 ± 0.56 a	1.11 ± 0.64

* Larvae or pupa per 100 leaves, means ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different (p>0.05), pair t-test, two tailed, n = 4.

Table 6.14 Impact of Relay Strip-cropping on *Pieris rapae* in Broccoli Late Planting - Corvallis, Oregon 1996

		Eggs, Instars, and Pupa per 100 Leaves*							
		5-Aug	13-Aug	19-Aug	26-Aug	5-Sep	9-Sep	16-Sep	23-Sep
Broc. Relay	**Egg**	11.11 ± 4.44 a	20.74 ± 6.46 a	5.19 ± 4.12 a	5.19 ± 4.12 a	1.48 ± 1.48 a	3.70 ± 2.67 a	4.44 ± 2.22 a	3.70 ± 2.67 a
Broc. Cl. Till		7.41 ± 2.67 a	18.52 ± 4.12 a	9.63 ± 1.96 a	2.96 ± 1.96 a	1.48 ± 0.74 a	2.96 ± 2.96 a	8.15 ± 2.92 a	3.70 ± 2.67 a
Broc. Relay	**1st**	0	2.22 ± 2.22 a	2.96 ± 1.96 a	10.37 ± 4.86 a	5.19 ± 1.48 a	4.44 ± 2.57 a	7.41 ± 4.13 a	4.44 ± 0.00 a
Broc. Cl. Till	**Instar**	0.74 ± 0.74	1.48 ± 0.74 a	1.48 ± 1.48 a	5.93 ± 3.23 a	2.22 ± 1.28 a	8.15 ± 3.23 a	4.44 ± 4.45 a	6.67 ± 4.63 a
Broc. Relay	**2nd**	0	0.74 ± 0.74 a	0	10.37 ± 5.93 a	5.19 ± 2.67 a	2.22 ± 2.22 a	2.96 ± 0.74 a	8.15 ± 1.96 a
Broc. Cl. Till	**Instar**	0	0.74 ± 0.74 a	1.48 ± 1.48	13.33 ± 3.39 a	8.15 ± 0.74 a	3.70 ± 2.67 a	12.59 ± 7.73 a	9.63 ± 6.58 a
Broc. Relay	**3rd**	0	0	0	2.22 ± 2.22 a	2.22 ± 1.28 a	1.48 ± 0.74 a	2.22 ± 0.00 a	4.44 ± 3.39 a
Broc. Cl. Till	**Instar**	0	0	0	6.67 ± 3.85 a	6.67 ± 2.57 b	2.22 ± 1.28 a	2.96 ± 0.74 a	6.67 ± 4.63 a
Broc. Relay	**4th**	0	0	0.74 ± 0.74 a	1.48 ± 0.74 a	0	2.96 ± 0.74 a	0	0
Broc. Cl. Till	**Instar**	0	0	0.00 ± 0.00 a	3.70 ± 1.48 a	4.44 ± 2.22	0.74 ± 0.74 a	0.74 ± 0.74	0.74 ± 0.74
Broc. Relay	**5th**	0	0	0.74 ± 0.74 a	1.48 ± 0.74	0.74 ± 0.74 a	1.48 ± 1.48 a	0	1.48 ± 1.48 a
Broc. Cl. Till	**Instar**	0	0	0.74 ± 0.74 a	0	2.22 ± 1.28 a	3.70 ± 1.96 a	2.22 ± 1.28	0.74 ± 0.74 a
Broc. Relay	**Pupa**	0	0	0	1.48 ± 0.74	0.74 ± 0.74	0.74 ± 0.74	0	0
Broc. Cl. Till		0	0	0	0	0	0	0.74 ± 0.74	0

* Means ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different (p>0.05), pair t-test, two tailed, n = 4.

Figure 6.14 *Pieris rapae* eggs in Broccoli
Corvallis, Oregon 1995

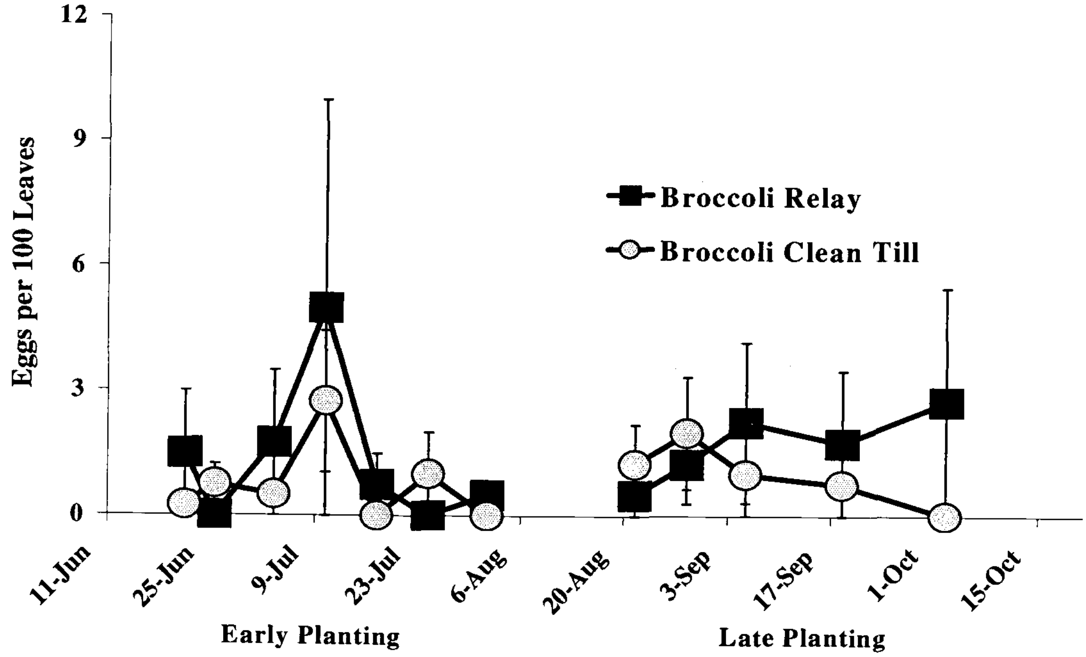


Figure 6.15 *Pieris rapae* 4th Instars in Broccoli
Corvallis, Oregon 1995

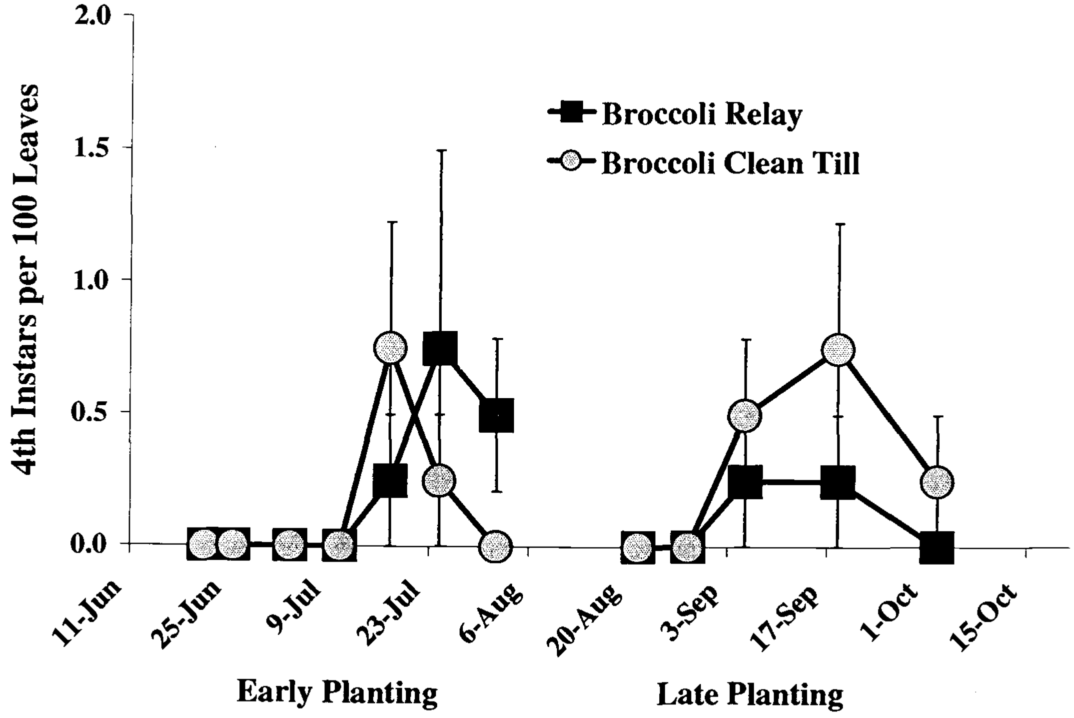


Figure 6.16 *Pieris rapae* Eggs in Broccoli
Corvallis, Oregon 1996

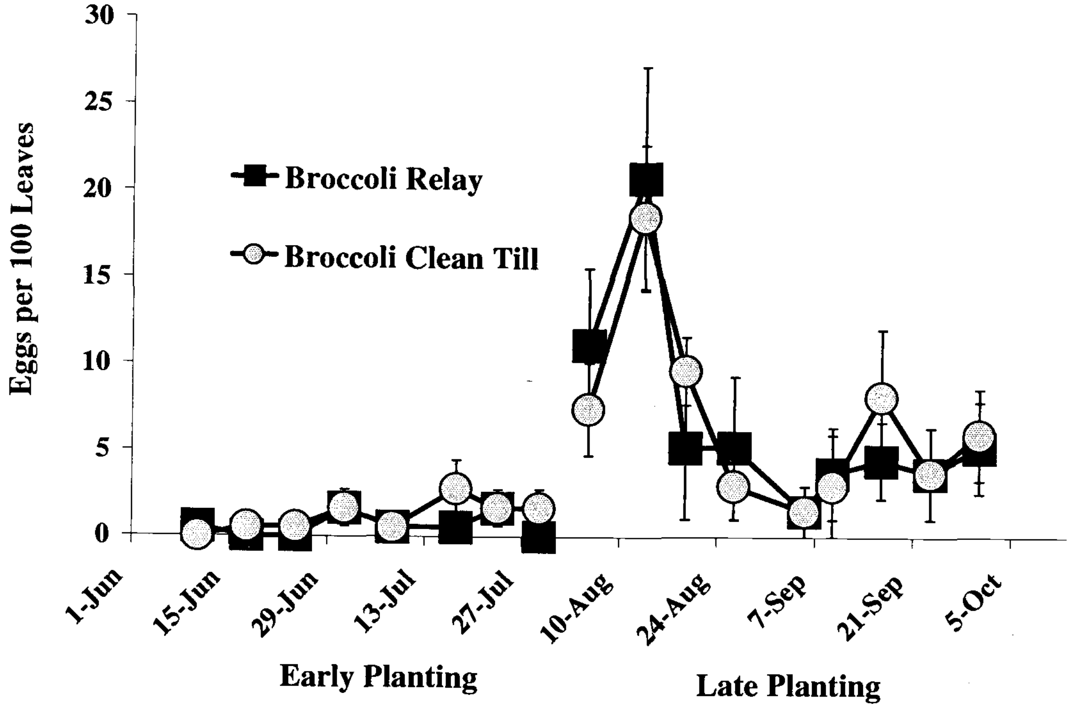


Figure 6.17 *Pieris rapae* 3rd Instars in Broccoli
Corvallis, Oregon 1996

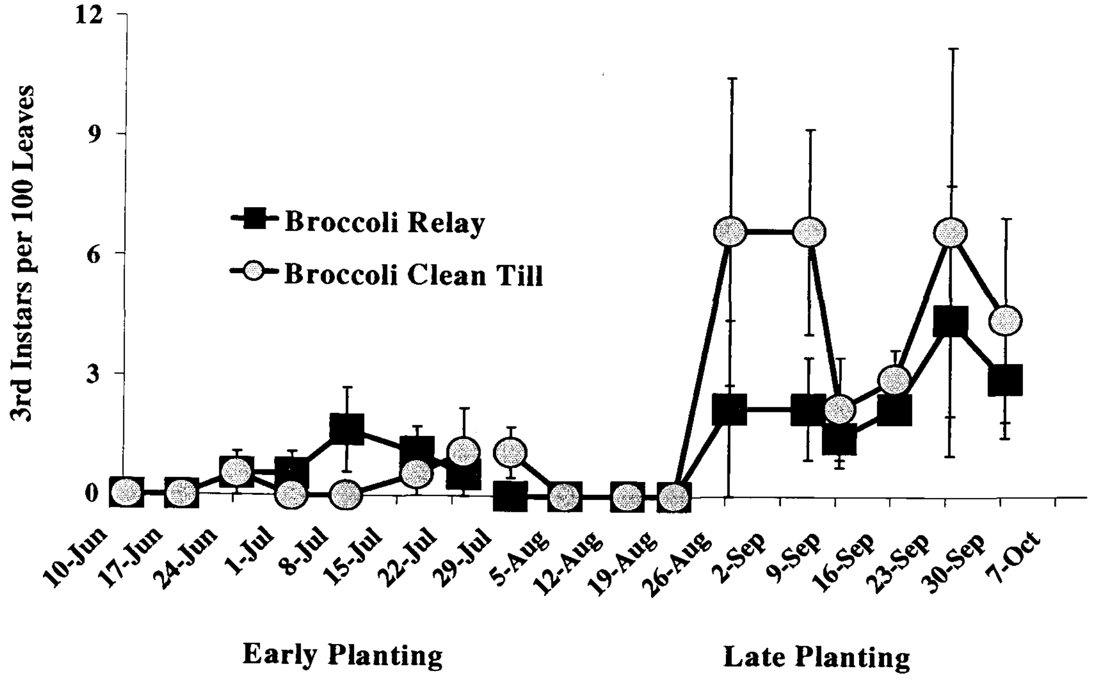


Table 6.15 Contamination of Broccoli Buds by *Pieris rapae,* Corvallis, Oregon 1994-1996

	Contaminants per Bud *						
Harvest Date	**eggs**	**1st Instar**	**2nd Instar**	**3rd Instar**	**4th Instar**	**5th Instar**	**Pupa**
22-Jul-94							
Broccoli Relay	0	0	0	0.01 ± 0.01 **a**	0	0.11 ± 0.05 **a**	0
Broc. Clean Till	0	0	0.01 ± 0.01	0.01 ± 0.01 **a**	0.01 ± 0.01	0.08 ± 0.04 **a**	0
31-Jul-95							
Broccoli Relay	0	0	0.03 ± 0.02 **a**	0.03 ± 0.02 **a**	0.21 ± 0.01 **a**	0.31 ± 0.15 **a**	0.05 ± 0.03 **a**
Broc. Clean Till	0	0	0.02 ± 0.02 **a**	0.09 ± 0.04 **b**	0.15 ± 0.08 **a**	0.24 ± 0.06 **a**	0.06 ± 0.04 **a**
3-Oct-95							
Broccoli Relay	0.02 ± 0.01	0	0	0.01 ± 0.01	0.06 ± 0.01 **a**	0.22 ± 0.11 **a**	0
Broc. Clean Till	0	0	0	0	0.07 ± 0.02 **a**	0.17 ± 0.03 **a**	0.01 ± 0.01
8-Aug-96							
Broccoli Relay	0	0.02 ± 0.02	0.02 ± 0.01 **a**	0.04 ± 0.02 **a**	0.51 ± 0.15 **a**	0.26 ± 0.08 **a**	0
Broc. Clean Till	0	0	0.08 ± 0.05 **a**	0.11 ± 0.02 **a**	0.53 ± 0.19 **a**	0.14 ± 0.01 **a**	0
2-Oct-96							
Broccoli Relay	0	0	0	0.02 ± 0.02 **a**	0.07 ± 0.03 **a**	0.77 ± 0.09 **a**	0.07 ± 0.04 **a**
Broc. Clean Till	0	0	0	0.05 ± 0.02 **a**	0.06 ± 0.02 **a**	1.09 ± 0.12 **b**	0.09 ± 0.03 **a**

* Mean + SEM , numbers followed by the same letter within each date and insect stage are not significantly different (P>0.05), paired t-test, two tailed, n = 4.

Figure 6.18 *Pieris rapae* Contamination of Broccoli Buds
Early Planting - Corvallis, Oregon 1995

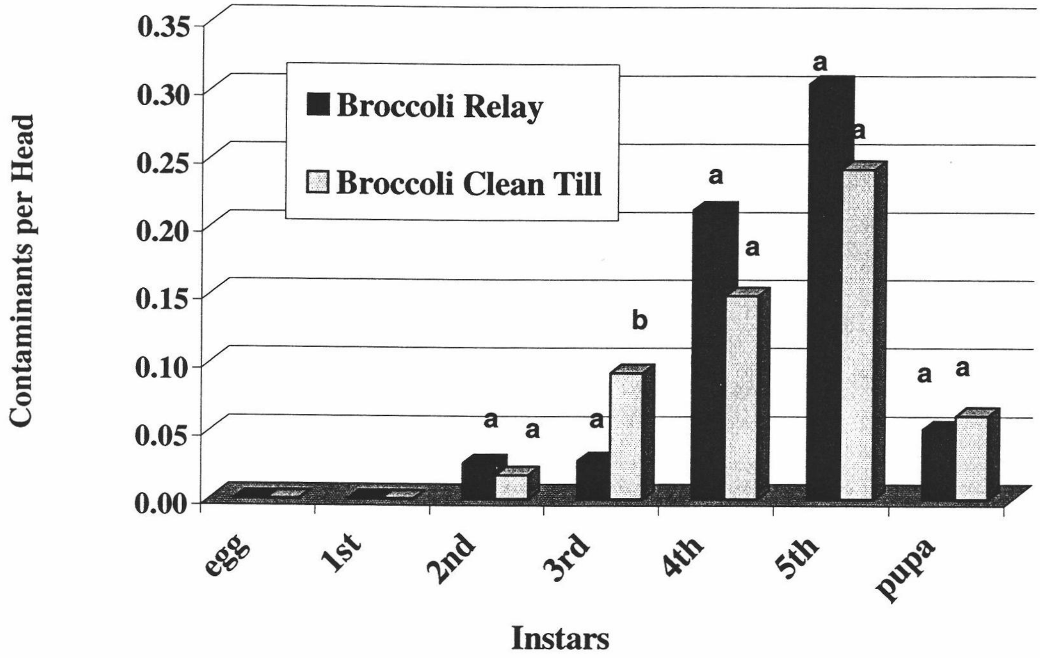


Figure 6.19 *Pieris rapae* Contamination of Broccoli Buds
Late Planting - Corvallis, Oregon 1996

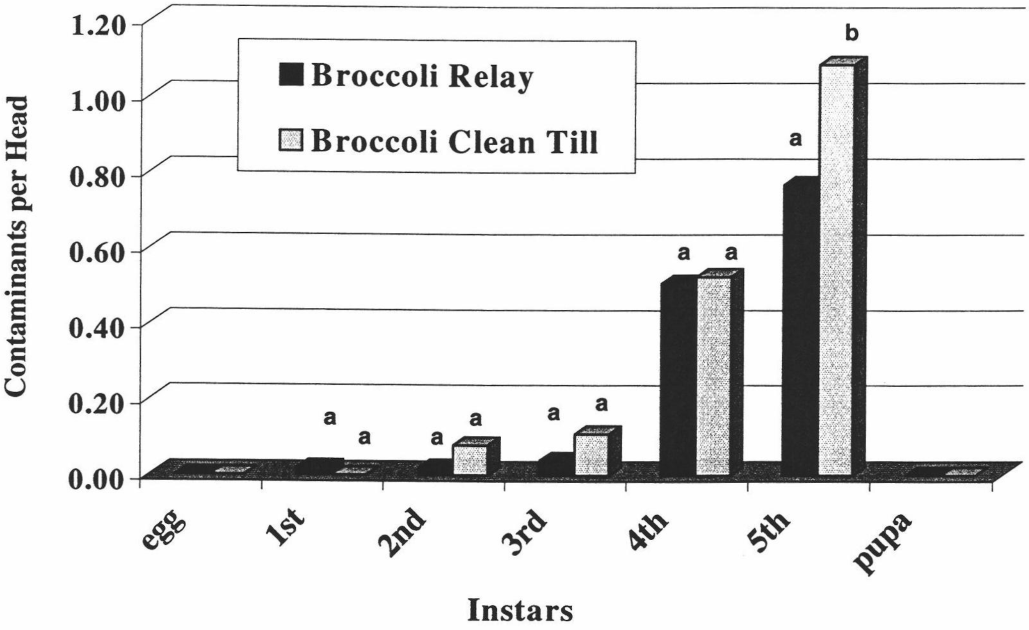


Table 6.16 Impact of Relay Strip-cropping on *Plutella xylostella* in Broccoli Corvallis, Oregon 1995

		Larvae and Pupa per 100 Leaves *						
Early Planting		**21-Jun**	**25-Jun**	**3-Jul**	**10-Jul**	**17-Jul**	**24-Jul**	**1-Aug**
Relay	**2nd Instar**	0.3 ± 0.3 a	1.3 ± 0.5 a	1.0 ± 0.4 a	7.3 ± 3.4 a	59.3 ± 15.2 a	8.0 ± 4.2 a	2.8 ± 1.8 a
Clean till		0.3 ± 0.3 a	1.3 ± 0.6 a	1.3 ± 1.3 a	9.3 ± 1.8 a	43.5 ± 7.1 a	8.5 ± 2.1 a	4.0 ± 1.5 a
Relay	**3rd Instar**	0.5 ± 0.3 a	0.5 ± 0.5 a	0.3 ± 0.3 a	0.8 ± 0.5 a	95.0 ± 35.6 a	30.5 ± 11.2 a	7.3 ± 2.6 a
Clean till		0.5 ± 0.3 a	0.8 ± 0.5 a	0.5 ± 0.3 a	1.0 ± 0.7 a	73.0 ± 17.6 a	35.0 ± 2.7 a	7.5 ± 3.7 a
Relay	**4th Instar**	0	0.5 ± 0.3 a	2.0 ± 1.0 a	1.3 ± 0.6 a	36.3 ± 8.3 a	90.3 ± 12.3 a	24.8 ± 7.5 a
Clean till		0	0.3 ± 0.3 a	1.5 ± 1.2 a	1.0 ± 1.0 a	26.5 ± 6.0 a	94.3 ± 10.4 a	17.8 ± 2.3 a
Relay	**Pupa**	0	0	1.5 ± 0.5 a	1.8 ± 0.6 a	4.5 ± 2.1 a	50.5 ± 5.7 a	31.3 ± 3.3 a
Clean till		0	0.8 ± 0.5	2.5 ± 0.3 a	3.3 ± 1.0 a	3.3 ± 2.3 a	52.3 ± 9.9 a	20.3 ± 3.7 a
Relay	**%Parasitized**	0	0	0	0	20.8 ± 9.5 a	9.0 ± 3.3 a	17.5 ± 7.6 a
Clean till	**Pupa**	0	0	0	0	10.0 ± 10.0 a	10.3 ± 1.0 a	6.5 ± 2.6 a
Late Planting		**21-Aug**	**28-Aug**	**5-Sep**	**18-Sep**	**2-Oct**		
Relay	**2nd Instar**	10.3 ± 2.8 a	11.5 ± 4.3 a	1.5 ± 0.6 a	0.5 ± 0.5 a	1.0 ± 0.6 a		
Clean till		13.0 ± 4.2 a	14.5 ± 6.3 a	2.5 ± 1.3 a	1.0 ± 0.6 a	1.8 ± 0.5 a		
Relay	**3rd Instar**	22.5 ± 7.9 a	21.8 ± 9.5 a	7.3 ± 1.9 a	3.0 ± 1.1 a	1.3 ± 0.5 a		
Clean till		28.8 ± 5.5 a	19.3 ± 1.7 a	6.5 ± 1.0 a	2.8 ± 0.9 a	2.5 ± 0.5 a		
Relay	**4th Instar**	39.0 ± 3.3 a	39.5 ± 9.4 a	38.8 ± 9.2 a	7.8 ± 1.4 a	1.8 ± 0.9 a		
Clean till		38.0 ± 13.3 a	40.0 ± 8.4 a	20.8 ± 5.2 b	5.5 ± 1.3 a	2.5 ± 0.3 a		
Relay	**Pupa**	3.0 ± 0.9 a	11.5 ± 3.5 a	26.0 ± 5.2 a	19.5 ± 4.8 a	6.8 ± 0.5 a		
Clean till		4.3 ± 1.7 a	20.5 ± 2.6 a	29.8 ± 6.2 a	31.5 ± 1.9 a	10.8 ± 2.8 a		
Relay	**%Parasitized**	15.0 ± 15.0 a	57.9 ± 7.9 a	43.8 ± 5.9 a	59.1 ± 9.0 a	72.5 ± 8.9 a		
Clean till	**Pupa**	27.8 ± 24.2 a	42.2 ± 7.6 a	42.5 ± 5.1 a	56.6 ± 3.8 a	61.2 ± 2.3 a		

* Means ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different (p>0.05), paired t-test, two tailed, n = 4.

Table 6.17 Impact of Relay Strip-cropping on *Plutella xylostella* in Broccoli, Corvallis, Oregon 1996

		Larva or Pupa per 100 Leaves								
Early Planting		**10-Jun**	**17-Jun**	**24-Jun**	**1-Jul**	**8-Jul**	**17-Jul**	**23-Jul**	**29-Jul**	
Relay	**2nd Instar**	0.6 ± 0.6	0	0	0.6 ± 0.6	1.1 ± 0.6	0	0	0	
Clean till		0	0	0	0	0	0	0	0	
Relay	**3rd Instar**	0	0	0	0	1.7 ± 1.7 a	0	0	0	
Clean till		0	0	0.6 ± 0.6	0.6 ± 0.6	1.7 ± 1.1 a	0	0	0	
Relay	**4th Instar**	0	0	0	0	0	0	0	0	
Clean till		0	0	0	0	0	0	1.1 ± 0.6	0	
Relay	**Pupa**	0	0	0	0	1.1 ± 1.1 a	0	0.6 ± 0.6	0	
Clean till		0	0	0	0	1.1 ± 0.6 a	1.1 ± 1.1	0	0.6 ± 0.6	
Relay	**% Para. Pupa**	0	0	0	0	0	0	0	0	
Clean till		0	0	0	0	0	0	0	25.0 ± 25.0	
Late Planting		**5-Aug**	**13-Aug**	**19-Aug**	**26-Aug**	**5-Sep**	**9-Sep**	**16-Sep**	**23-Sep**	**30-Sep**
Relay	**2nd Instar**	0	0	0	0.7 ± 0.6	0.7 ± 0.6	2.2 ± 1.3 a	0.7 ± 0.7 a	0.7 ± 0.7 a	3.0 ± 2.0 a
Clean till		1.5 ± 0.5	0	0	0	0	0.7 ± 0.7 a	3.0 ± 1.5 a	2.2 ± 1.3 a	1.5 ± 1.5 a
Relay	**3rd Instar**	0	0	0	0.7 ± 0.7 a	2.2 ± 1.3 a	6.7 ± 3.9 a	0.7 ± 0.7 a	0.7 ± 0.7 a	4.4 ± 1.3 a
Clean till		0	0	0	1.5 ± 1.5 a	0.7 ± 0.7 a	2.2 ± 1.3 a	2.2 ± 0.0 a	2.2 ± 2.2 a	3.0 ± 2.0 a
Relay	**4th Instar**	0	0	0	0.7 ± 0.7	3.7 ± 1.5 a	8.1 ± 4.1 a	5.2 ± 2.0 a	2.2 ± 1.3 a	5.2 ± 0.7 a
Clean till		0	0	0	0	5.2 ± 5.2 a	2.2 ± 1.3 a	3.0 ± 0.7 a	4.4 ± 2.2 a	5.2 ± 1.5 a
Relay	**Pupa**	0	0	0	0	8.1 ± 1.5 a	11.1 ± 1.3 a	11.1 ± 4.6 a	8.1 ± 3.2 a	19.3 ± 3.7 a
Clean till		0	0	0	0	5.2 ± 3.2 a	8.9 ± 1.3 a	5.9 ± 1.5 a	8.9 ± 4.4 a	11.9 ± 1.5 a
Relay	**% Para. Pupa**	0.7 ± 0.7	0.7 ± 0.7	0.7 ± 0.7	0.7 ± 0.7	11.1 ± 11.1 a	16.7 ± 16.7 a	12.0 ± 7.2 a	16.7 ± 16.7 a	4.8 ± 4.8 a
Clean till		0	0	0	0	6.7 ± 6.7 a	6.7 ± 6.7 a	100.0 ± 0.0 b	4.2 ± 4.2 a	11.1 ± 11.1 a

* Means ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different ($p>0.05$), pair t-test, two tailed, $n = 4$.

versus clean-till cropping systems in either 1995 or 1996 (Tables 6.16-6.17, Figure 6.20). Pupa counts analyzed across sampling dates were significantly higher on broccoli leaves gathered in the clean-tilled broccoli compared with relay strip-croppedped broccoli in the late planting of 1995 ($P = 0.0009$, $F = 13.71$, $df = 1,30$). Percent parasitism was not significantly different between the treatments (Tables 6.16-6.17, Figures 6.21-6.22).

Bud-contamination by larvae and pupae of *P. xylostella* varied from 0.4 to 11.43 total contaminants per bud in 1995 (Table 6.18, Figure 6.23-6.24). Bud infestation was very low in 1996. Buds were primarily contaminated by the fourth instars and pupae. Bud infestation tended to be higher in the clean-till system but the differences were never statistically significant ($P > 0.05$, paired t-test, two tailed).

T. ni eggs, larvae, and pupae on broccoli leaves varied from 0 to 31 insects per 100 leaves in 1995 (Table 6.19-6.20) and from 0 to 2.8 insects per 100 leaves in 1996 (Table 6.21-6.22). In 1995, *T. ni* leaf counts were highest in the early planting period (Figures 6.25). In 1996, *T. ni* leaf counts were low during the entire growing season. When *T. ni* counts were analyzed on separate dates, there were significantly more second instar larvae ($P < 0.05$, paired t-test, two tailed) gathered from broccoli leaves on one only out of seven plantings dates in the early planting period of 1995. No other differences between the cropping systems were significant (Tables 6.19-6.22). When weekly *T. ni* leaf counts were analyzed across sampling dates in each planting, counts of eggs, first through fifth instar larvae, and pupae were not significantly different in the relay strip and clean-till cropping systems in either 1995 or 1996.

Bud-contamination by *T. ni* varied from 0.19 to 1.1 total contaminants per bud in 1995 (Table 6.23). Bud infestation was very low in 1996.

Figure 6.20 Third Instar *Plutella xylostella* in Broccoli
Corvallis, Oregon 1995

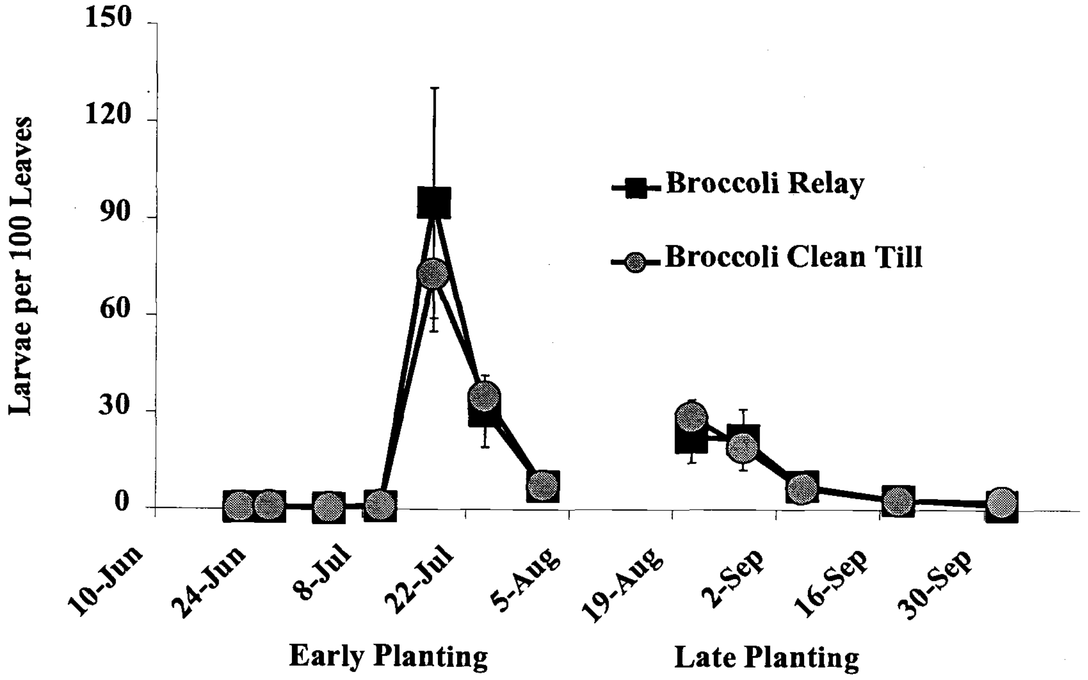


Figure 6.21 Parasitized Pupae of *Plutella xylostella* in Broccoli
Corvallis, Oregon 1995

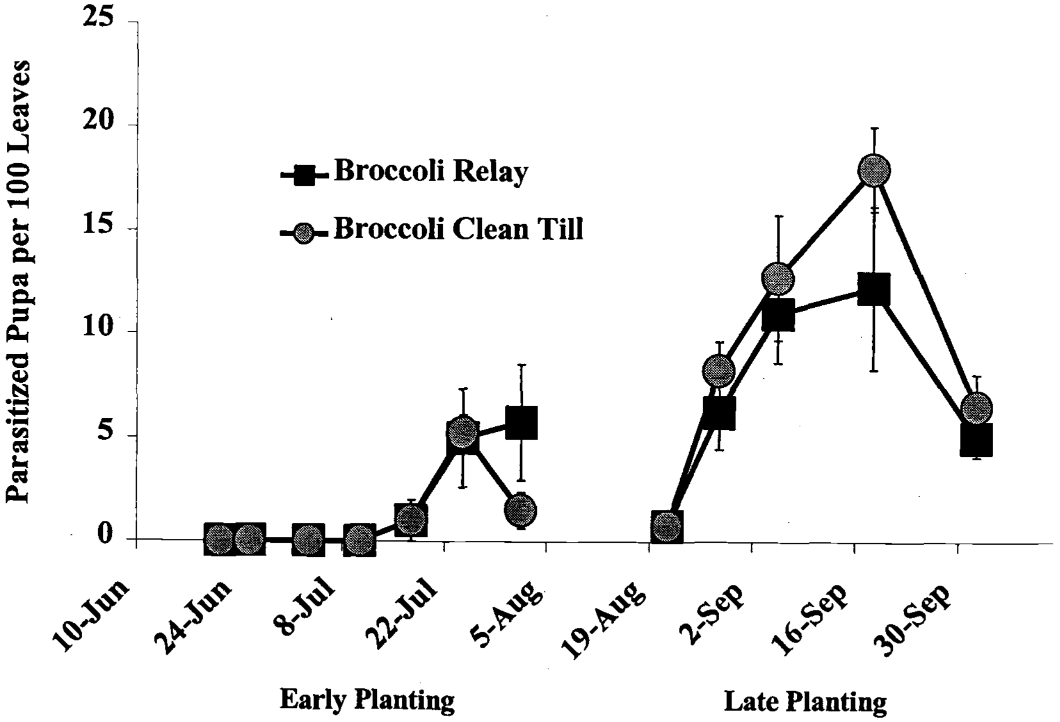


Figure 6.22 Percent Parasitized *Plutella xylostella* Pupae in Broccoli
Corvallis, Oregon 1995

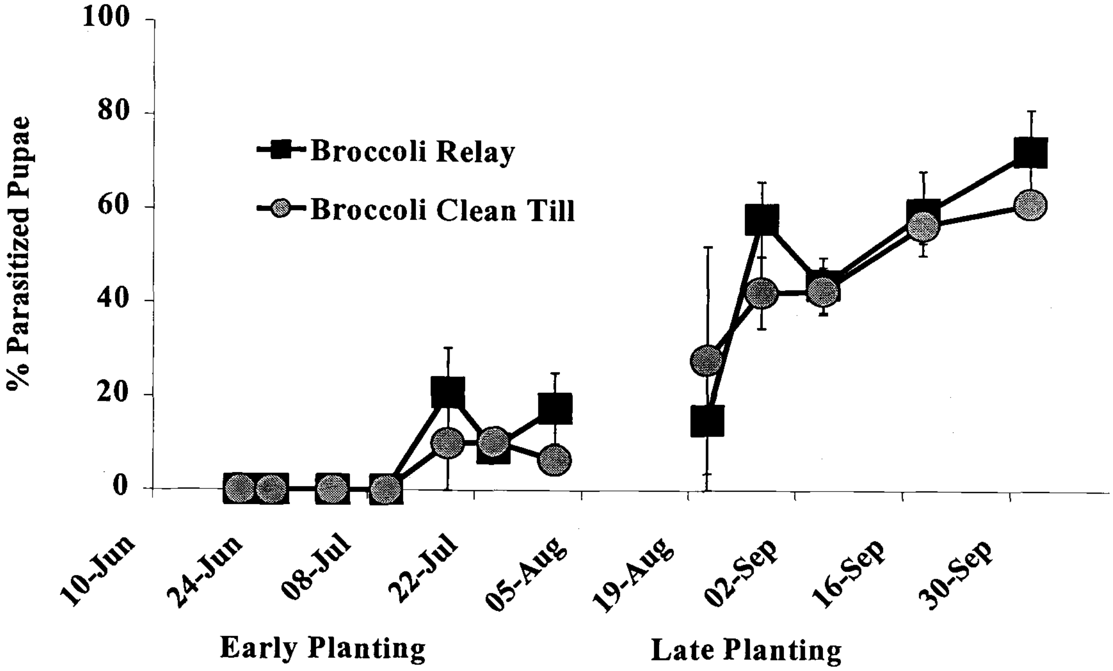
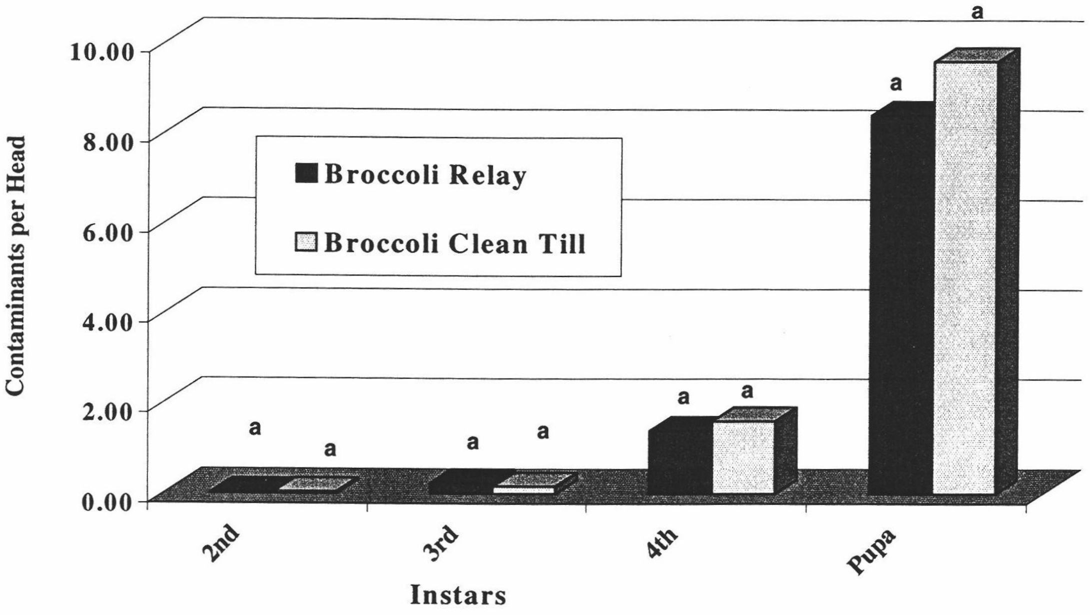


Table 6.18 Contamination of Broccoli buds by *Plutella xylostella*
Corvallis, Oregon 1995

		Contaminants per Bud *			
Harvest Date	**Treatment**	**2nd Instar**	**3rd Instar**	**4th Instar**	**Pupa**
31-Jul-95	Broccoli Relay	0.02 ± 0.02 a	0.22 ± 0.08 a	1.39 ± 0.48 a	8.43 ± 2.61 a
	Broccoli Clean Till	0.04 ± 0.03 a	0.16 ± 0.05 a	1.60 ± 0.32 a	9.63 ± 2.12 a
3-Oct-95	Broccoli Relay	0.02 ± 0.02 a	0.07 ± 0.03 a	0.14 ± 0.07 a	0.17 ± 0.09 a
	Broccoli Clean Till	0.01 ± 0.01 a	0.10 ± 0.02 a	0.22 ± 0.07 a	0.36 ± 0.09 a

* Mean ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different ($p>0.05$), pair t-test, two tailed, n = 4.

Figure 6.23 Contamination of Broccoli Buds by *Plutella xylostella* Early Planting - Corvallis, Oregon 1995



Fiigure 6.24 Contamination of Broccoli Buds by *Plutella xylostella* Late Planting - Corvallis, Oregon 1995

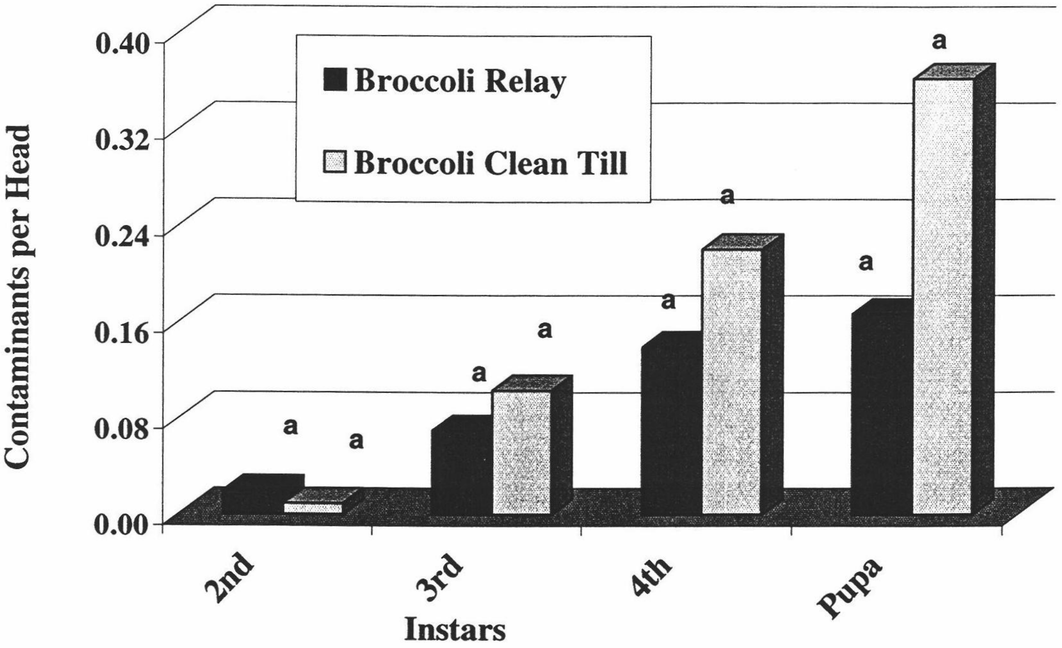


Table 6.19 Impact of Relay Strip-cropping on *Trichoplusia ni* in Broccoli
Early Planting - Corvallis, Oregon 1995

		Eggs, Instar, and Pupa per 100 Leaves*						
		21-Jun	25-Jun	3-Jul	10-Jul	17-Jul	24-Jul	1-Aug
Relay	**Egg**	0	0	3.00 ± 3.00 a	0	0	1.75 ± 1.75 a	0
Clean till		0	0	0.50 ± 0.50 a	2.50 ± 2.50	2.75 ± 2.75	1.25 ± 1.25 a	0.25 ± 0.25
Relay	**1st Instar**	0	0	3.75 ± 3.42	5.00 ± 1.41 a	1.00 ± 0.41 a	0	1.00 ± 1.00 a
Clean till		0	0	0	2.25 ± 1.65 a	4.50 ± 1.66 a	0.50 ± 0.29	0.25 ± 0.25 a
Relay	**2nd Instar**	0	0	0	4.50 ± 2.60 a	3.50 ± 1.26 a	0.25 ± 0.25 a	8.00 ± 2.61 a
Clean till		0	0.50 ± 0.50	0.25 ± 0.25	1.00 ± 0.41 a	10.25 ± 6.42 a	2.50 ± 0.29 b	4.50 ± 1.55 a
Relay	**3rd Instar**	0	1.00 ± 0.71 a	0	2.25 ± 0.85 a	15.50 ± 2.66 a	4.25 ± 1.38 a	4.50 ± 0.65 a
Clean till		0	0.75 ± 0.48 a	0	1.25 ± 0.48 a	12.00 ± 2.55 a	3.25 ± 1.25 a	5.00 ± 2.12 a
Relay	**4th Instar**	0	0	0.75 ± 0.48 a	1.00 ± 0.41 a	8.75 ± 2.10 a	2.25 ± 0.85 a	2.25 ± 1.11 a
Clean till		0.25 ± 0.25	0.75 ± 0.75	0.25 ± 0.25 a	0.25 ± 0.25 a	8.00 ± 1.08 a	4.75 ± 1.93 a	1.00 ± 0.41 a
Relay	**5th Instar**	0.50 ± 0.50	0.50 ± 0.29 a	0.25 ± 0.25 a	0	2.00 ± 0.82 a	1.25 ± 1.25 a	0.50 ± 0.29
Clean till		0	0.50 ± 0.50 a	0.25 ± 0.25 a	0.50 ± 0.29	1.75 ± 0.75 a	1.75 ± 1.11 a	0
Relay	**Pupa**	0	0	0	0	0.25 ± 0.25 a	0	0
Clean till		0	0	0	0	1.00 ± 0.71 a	0	0.25 ± 0.25

* Means ± SEM, numbers followed by the same letter within each date and insect stage are not significantly different

Table 6.20 Impact of Relay Strip-cropping on *Trichoplusia ni* in Broccoli
Late Planting - Corvallis, Oregon 1995

		Eggs, Instars, and Pupa per 100 leaves*				
		21-Aug	28-Aug	5-Sep	18-Sep	2-Oct
Relay	**Egg**	1.00 ± 0.58 a	0	0	0.75 ± 0.48	0
Clean till		0.50 ± 0.50 a	0	0.50 ± 0.50	0	0
Relay	**1st Instar**	0.50 ± 0.50 a	0.25 ± 0.25 a	0	0.25 ± 0.25	0
Clean till		0.25 ± 0.25 a	0.25 ± 0.25 a	0	0	0
Relay	**2nd Instar**	0.50 ± 0.29 a	0.75 ± 0.48 a	0	0	0
Clean till		1.50 ± 0.87 a	0.25 ± 0.25 a	0	0.25 ± 0.25	0
Relay	**3rd Instar**	0.75 ± 0.25 a	2.25 ± 1.11 a	0.50 ± 0.29 a	1.25 ± 1.25 a	0.75 ± 0.48
Clean till		0.50 ± 0.50 a	2.75 ± 0.63 a	1.50 ± 0.29 a	1.00 ± 0.71 a	0
Relay	**4th Instar**	0.50 ± 0.50 a	0.75 ± 0.48 a	2.50 ± 1.04 a	0.50 ± 0.50 a	0.50 ± 0.50 a
Clean till		0.75 ± 0.48 a	0.50 ± 0.29 a	1.50 ± 0.65 a	1.00 ± 0.71 a	0.25 ± 0.25 a
Relay	**5th Instar**	0	0	1.00 ± 0.41 a	0.50 ± 0.50 a	0
Clean till		0.50 ± 0.50	0.25 ± 0.25	0.50 ± 0.50 a	0.75 ± 0.48 a	0
Relay	**Pupa**	0	0	0	0.50 ± 0.29 a	1.00 ± 0.41 a
Clean till		0	0	0	0.75 ± 0.25 a	0.75 ± 0.48 a

* Means + SEM, numbers followed by the same letter within each date and insect stage are not significantly different (P>0.05), pair t-test, two tailed, square root transformed data.

Table 6.21 Impact of Relay Strip-cropping on *Trichoplusia ni* in Broccoli
Early Planting - Corvallis, Oregon 1996

Eggs, Larva, and Pupa per 100 Leaves *

		10-Jun	17-Jun	24-Jun	1-Jul	8-Jul	17-Jul	23-Jul	29-Jul
Relay	**Egg**	1.11 ± 1.11	0	2.22 ± 1.28 a	0	0.56 ± 0.56 a	1.11 ± 0.64 a	1.11 ± 1.11	0.56 ± 0.56 a
Clean till		0	0.56 ± 0.56	0.56 ± 0.56 a	0	2.22 ± 0.91 a	1.11 ± 1.11 a	0	0.56 ± 0.56 a
Relay	**1st**	0	0	0	0	0	1.11 ± 0.64	0.56 ± 0.56	0.56 ± 0.56
Clean till	**Instar**	0	0	0	0	0.56 ± 0.56	0	0	0
Relay	**2nd**	0	0	0	0	0	0	0	0
Clean till	**Instar**	0	0	1.11 ± 1.11	0	0	0	0	1.11 ± 0.64
Relay	**3rd**	0	0	0	0	0	0	0	0
Clean till	**Instar**	0	0	1.11 ± 1.11	0	0	0	0	0
Relay	**4th**	0	0	0.56 ± 0.56	0	0	0	0	0
Clean till	**Instar**	0	0	0	0	0	0	0	0
Relay	**5th**	0	0	0	0	0	0.56 ± 0.56	0	0.56 ± 0.56
Clean till	**Instar**	0	0.56 ± 0.56	0	0	0	0	0	0
Relay	**Pupae**	0	0	0	0	0	0	0	0
Clean till		0	0	0	0	0	0	0	0

* Means + SEM, numbers followed by the same letter within each date and insect stage are not significantly different (P>0.05), pair t-test, two tailed, n = 4.

Table 6.22 Impact of Relay Strip-cropping on *Trichoplusia ni* in Broccoli Late Planting - Corvallis, Oregon 1996

		Eggs, Larva, and Pupa per 100 Leaves *								
		5-Aug	13-Aug	19-Aug	26-Aug	5-Sep	9-Sep	16-Sep	23-Sep	30-Sep
Relay	**Egg**	0	0	0	0	0	0	0	0	0
Clean till		0.74 ± 0.74	0	0	0	0	0	0	### ± 2.96	0
Relay	**1st**	0	0	0	0	0	0	0	0	0
Clean till	**Instar**	0	0	0	0	0	0	0	0	0
Relay	**2nd**	0	0	0	0	1.48 ± 0.74	0	0	0	0
Clean till	**Instar**	0	0	0	0	0	0	0	### ± 0.74	0
Relay	**3rd**	0	0	0	0	0	0	0	0	0
Clean till	**Instar**	0	0	0	0	0.74 ± 0.74	0.74 ± 0.74	0	### ± 0.74	0
Relay	**4th**	0	0	0	0	0.74 ± 0.74	0	0	0	0
Clean till	**Instar**	0	0	0	0	0	0	0	0	0
Relay	**5th**	0	0	0	0	0.74 ± 0.74	0	0	0	0
Clean till	**Instar**	0	0	0	0	0	0	0	0	0
Relay	**Pupa**	0	0	0	0	0	0	0	0	0
Clean till		0	0	0	0	0	0	0	0	0

* Means + SEM, numbers followed by the same letter within each date and insect stage are not significantly different (P>0.05), pair t-test, two tailed, n = 4.

Figure 6.25 Third Instar *Trichoplusia ni* in Broccoli
Corvallis, Oregon 1995

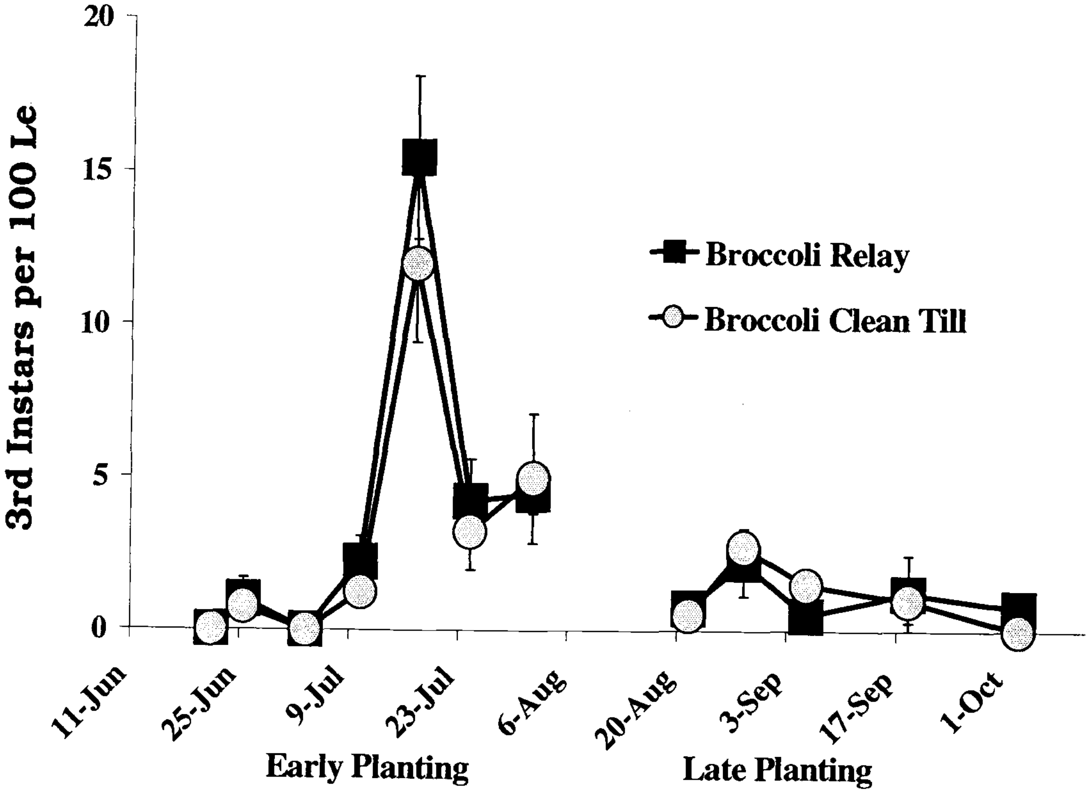


Table 6.23 Contamination of Broccoli Buds by *Trichoplusia ni*
Corvallis, Oregon 1995

Harvest Date	egg	1st Instar	2nd Instar	3rd Instar	4th Instar	5th Instar	Pupa
31-Jul-95							
Broccoli Relay	0	0	0.04 ± 0.03 **a**	0.08 ± 0.03 **a**	0.41 ± 0.07 **a**	0.40 ± 0.09 **a**	0.18 ± 0.06 **a**
roccoli Clean Till	0	0.01 ± 0.01	0.03 ± 0.03 **a**	0.15 ± 0.04 **b**	0.32 ± 0.05 **a**	0.45 ± 0.14 **a**	0.09 ± 0.06 **a**
3-Oct-95							
Broccoli Relay	0	0	0	0	0.04 ± 0.02 **a**	0.15 ± 0.05 **a**	0.00 ± 0.00 **a**
roccoli Clean Till	0	0	0	0	0.06 ± 0.05 **a**	0.17 ± 0.03 **a**	0.03 ± 0.03 **a**

* Mean + SEM alate, numbers followed by the same letter within each date and insect stage are not significantly different (p>0.05), pair t-test, two tailed, n = 4.

Buds were primarily contaminated by the fourth and fifth instars and pupae of *T. ni* (Figures 6.26-6.27). Bud infestation in general tended to be higher in the clean-till cropping system. Bud infestation of third instar larvae was significantly higher in the clean-tilled broccoli than in the relay strip-cropped broccoli the early planting of 1995 ($P < 0.05$, paired t-test, two tailed).

DISCUSSION

There was no evidence in these experiments that colonization of the broccoli by alate *B. brassicae* was reduced by relay strip-cropping compared with clean-till monoculture. The failure of the under-sowing to reduce aphid colonization was probably due to the late timing of under-sowing relative to the planting and development of the broccoli. The understory vegetation in the relay strip-crop was established too late to influence the colonization of broccoli by the winged aphids.

The impact of surrounding vegetation on aphid immigration tends to be most dramatic during the early growing season when aphids fly from their winter hosts into the agricultural fields. Later in the season, the effect of background vegetation often disappears. In most cases where background vegetation or background color reduced colonization of a target crop by alate aphids, the back ground was established prior to planting the target crop (Dempster 1969, Smith 1976a, Cromartie 1975, Costello and Altieri 1994). Other researchers have noted the importance of the timing in the establishment of non-crop vegetation and the relative impact of surrounding vegetation on colonizing insects. The type of vegetation serving as the interplant, the timing of establishment of the intercrop, the percent soil cover, and the percent vertical height compared with the target

Figure 6.26 Contamination of Broccoli Buds by *Trichoplusia ni*
Early Planting - Corvallis, Oregon 1995

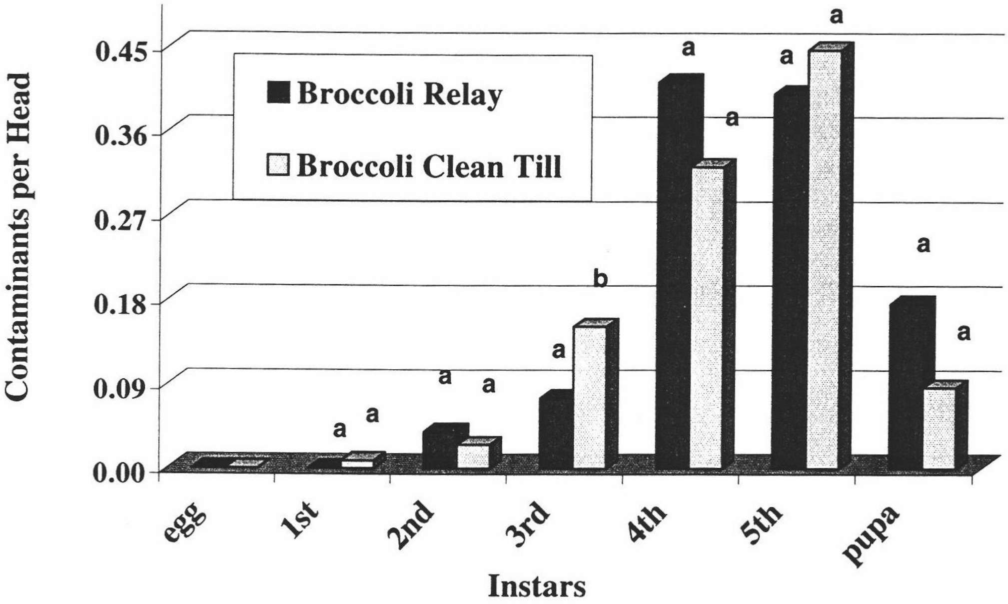
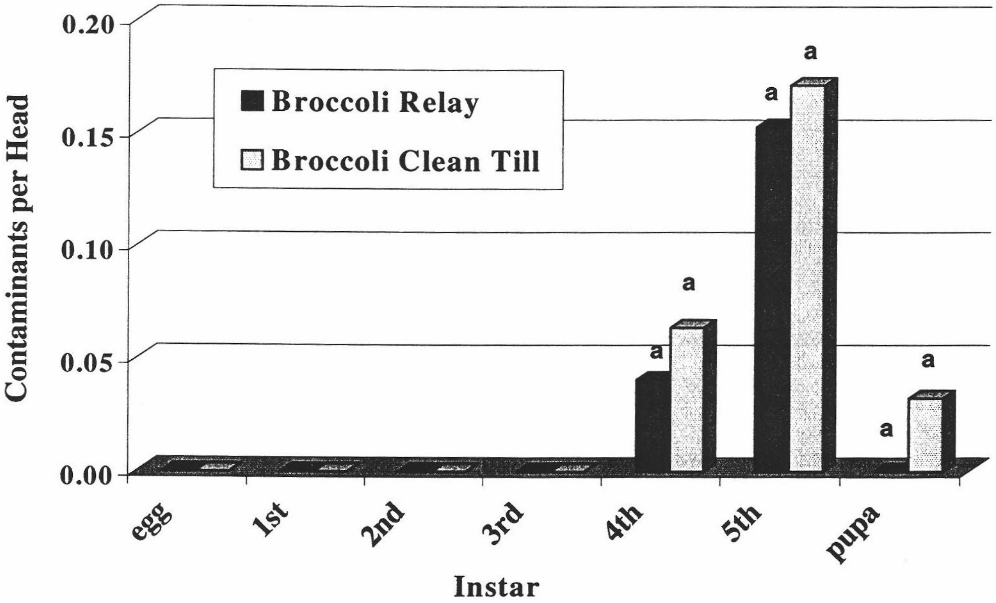


Figure 6.27 Contamination of Broccoli Buds by *Trichoplusia ni*
Late Planting - Corvallis, Oregon 1995



crop determines the impact of non crop vegetation on the visual and olfactory cues that influence host plant selection by aphids and other insects (Theunissen and den Ouden 1980, 1985, Theunissen 1994, Costello 1995, Costello and Altieri 1995).

The need for early establishment of background vegetation around the broccoli presents us with a dilemma. If the understory vegetation is established earlier, the broccoli yield will be depressed. The power of under-sowing as a tactic for reducing aphid colonization may not be justified given the high quality standards in a commercial broccoli production system. The economic trade off associated with yield loss may limit the practical application of under-sowing as a pest management strategy.

P. cruciferae density was significantly lower in the relay strip-cropped broccoli than in the clean-tilled broccoli. Since *P. cruciferae* has very few natural enemies, these differences can best be explained by differences in beetle emigration rates in the two cropping systems. The tendency of *P. cruciferae* to leave mixed plantings at a greater rate than it leaves cole crop monocultures has been demonstrated in mark, release, and recapture experiments (Kareiva 1985, Bergelson and Kareiva 1987, Garcia and Altieri 1992). The impact of relay strip-cropping on flea beetles occurs during the colonization phase and is related to emigration. Broccoli is most susceptible to stand reduction by *P. cruciferae* in the seedling stage. The relay strip-cropping system did not provide any benefits during the establishment period because under-sowing was delayed for four and one half weeks. Although beetle densities were consistently lower in the relay strip-cropping system than in the clean-till system, no benefits to the system in terms of increased yield or other benefits were detected. Reduced pressure from *P. cruciferae* alone would not justify adoption of the relay strip-cropping system.

There were significantly fewer early instars of *P. rapae* in the relay strip-cropped broccoli compared with clean-tilled broccoli. Reduced survival of the small larvae resulted in significantly fewer larval contaminants of the harvested broccoli buds. There were also significantly fewer third instar larvae of *T. ni* in harvested broccoli buds in the relay strip-cropped broccoli compared with clean-tilled broccoli. These results can not be explained by variation in colonization of the two broccoli systems; the density of lepidopteran eggs deposited in the two systems was the same. Differences in survival of small lepidopteran larvae in the relay strip-cropped broccoli is probably the result of difference in mortality factors in the two cropping systems, and most likely the result of natural enemy induced mortality.

Relay strip-cropping increased the abundance and diversity of several groups of natural enemies of the broccoli herbivores, with the possible exception of the Nabidae. The increased density of natural enemies in the relay broccoli could explain the reduction in the survival of the small instars compared with clean-tilled broccoli. Reduction in the number of early instars of lepidopteran pests associated with the activity of generalist predators has been demonstrated previously for *P. rapae* (Dempster 1969) and *T. ni* (Ehler and van den Bosch 1974, Ehler 1977). The depression in the number of small instars of *P. rapae* and *T. ni* in the relay strip-cropped broccoli and bud-contamination was statistically significant. The lowest levels of contamination of the broccoli buds, however, would be unacceptable in a commercial production system.

There were significantly fewer pupae of *P. xylostella* on the broccoli leaves in the relay strip-cropping system. This difference may have been the result of increased parasitism in the relay strip-cropped broccoli compared with clean-tilled broccoli; percent parasitism of *P. xylostella* was significantly higher in the relay cropping system. The potential of parasitoids to significantly reduce the density of *P. xylostella* in cole crops has been previously demonstrated with innoculative releases of biological control agents (Biever et al. 1994). Bud infestation with fourth instar and pupae of *P. xylostella* was consistently lower in the relay strip-cropped broccoli, but the differences were never statistically significant in the two planting systems. The lowest levels of contamination of the broccoli buds by *P. xylostella* in this study would be unacceptable in a commercial production system.

Relay strip-cropping had a significant impact on *P. cruciferae, P. rapae, T. ni, and P. xylostella.* In the case of *P. cruciferae*, there was no evidence of natural enemy induced mortality. It is likely that *P. cruciferae* was responding to stand purity as reported elsewhere (Kareiva 1985, Garcia and Altieri 1992). For the lepidopteran insects, it is likely that the differences in the two systems was due to impact of natural enemy induced mortality. Relay strip-cropping increased the abundance and diversity of ground beetles (Coleoptera: Carabidae), spiders (Araneae), harvestmen (Opiliones: Phalangiidae), lady beetles (Coleoptera: Coccinellidae), and damsel bugs (Heteroptera: Nabidae). It is likely that the relay strip-cropping system enhanced the number and diversity of other groups of natural enemies, which were not documented in this study.

The clearest difference observed in the natural enemy assemblages in the two systems was among the Carabidae. There were clearly more beetles and more beetle species active in the relay strip-cropping system than in the clean-till system. Even though carabid beetles are primarily ground predators, they also have an impact on foliar insects. Many foliar insects spend significant periods of time on the soil surface where they are preyed upon by carabid beetles (Chiverton 1987, Hagley and Allen 1990, Winder 1990, Riddick 1994, Wallin and Ekbom 1994). The impact of relay strip-cropping on ground beetle abundance in this study, however, should be interpreted with caution. Ground beetles have intermediate levels of mobility, dispersing between 15 and 100 m during a typical growing season (Wallin and Ekbom 1988). The spatial and temporal scale of the relay strip-cropping experiments was similar to these measures and would, therefore, tend to over emphasize the potential impact of relay strip-cropping on the carabid assemblage (Corbett and Plant 1993). Relay strip-cropping needs to be tested on a full-scale commercial basis of twenty to forty acres per plot before it can be recommended as a method for conserving ground beetles in agricultural systems.

The number of the various larval instars was similar in the two systems. The number of total pupae in the relay strip-cropped broccoli was reduced compared with the clean-tilled broccoli. I was not able to detect increased activity of parasitoids of *P. xylostella* in the relay strip-cropped broccoli. The most common parasitoid in our study was probably a *Diadegma* species (Harcourt 1986, Sastrosiswojo and Sastrodiharjo 1986, Mustata 1992, Ooi 1992, Idris and Grafius 1995). The larval/pupal parasitoid *D. insulare* regulates *P. xylostella* populations and is common in the U.S. and Canada (Muckenfuss et al. 1992, Idris and Grafius 1993, Riggin-Bucci and Gould 1997). It can be recognized by the broad white stripe around the pupa (McCalley et al. 1992). Parasitoids often aggregate in areas of increased host density (Smith 1976a, Horn 1987). Although there were more pupae and more parasitized pupa in the clean-tilled broccoli compared with the relay strip-cropped broccoli, I did not observe a difference in the percentage of parasitized pupae in the two cropping systems.

Parasitism of *P. xylostella* was generally higher in the late plantings when nectar sources (flowering buckwheat and flowering weeds) were abundant in the relay strip-cropping system. This result has to be interpreted with caution because the parasitoid has high mobility. It seems, therefore, unlikely that I could detect differences in parasitoid activity associated with the flowering buckwheat in the two cropping systems at the spatial scale of this experiment. Future studies of the impact of relay strip-cropping on parasitism need to be conducted using mark, release, and recapture techniques (Freeman Long et al. 1998).

Relay strip-cropping had multiple impacts on the insect pests of broccoli in this study. The vegetation management system had impacts on colonization of the broccoli by insect pests and their natural enemies. Relay strip-cropping conserved natural enemies in the vicinity of the broccoli even when aggressive tillage and pesticide programs were used during the broccoli establishment period. The net effect was a detectable reduction of insect pest numbers on the harvested broccoli. The impact, however, was subtle. The impact of relay strip-cropping on insect pests and their natural enemies alone does not justify the adoption of this conservation practice. Relay strip-cropping may improve soil and water quality. Relay strip-cropping may reduce the cost of establishing winter cover-crops and may be justified in terms of soil conservation.

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APPENDICES

APPENDIX A: CARABIDAE LITERATURE REVIEW

INTRODUCTION

Ground beetles (Coleoptera: Carabidae) are one of the dominant groups of soil surface dwelling) predators in northern temperate regions (Sunderland 1975, Lovei and Sunderland 1996). Carabidae are not as numerous as spiders but, when the relative biomass of spiders and Carabidae are considered, the two groups are comparable (Nentwig 1988). Biomass is an important measure of their potential impact in the agroecosystem. Common field-dwelling carabids can eat up to four times their body weight in a day (Thiele 1977).

Carabids as a group are active as adults or larvae all year round. Even in the coldest season, there are species of carabid adults and larvae foraging for prey. In the early spring, the potential of carabids as pest control agents is greatest. Carabids are present when pest populations are just becoming established. Carabids are present before many of the other natural enemies have arrived or become active (Coombes and Sotherton 1986, Wratten and van Emden 1995).

Exclusion experiments show that removal of polyphagous predators often leads to increased aphid densities (Edwards et al. 1979, Sunderland 1980, Chambers et al. 1982, Coombes and Sotherton 1986, Chiverton 1986, Chiverton 1987b, Chiverton 1987a). Serological techniques show that the common crop inhabiting carabid *Pterostichus melanarius* F. feeds on the green peach aphid, *Myzus persicae* (Sulzer) (Hance 1987, Hance et al. 1990) and the cabbage aphid, *Brevicoryne brassicae* L.(McIver 1983).

Even though carabid beetles are primarily ground predators, they also have an impact on foliar insects. Many foliar insects spend significant periods of time on the soil surface where they are preyed upon by carabid beetles (Chiverton 1987b, Hagley and Allen 1990, Winder 1990, Riddick 1994, Wallin and Ekbom 1994).

Despite the general recognition that carabids are important carnivores, debate about their role as biological control agents persists (Coaker 1965, McIver 1983). Carcamo and Spence (1994) added 100 *P. melanarius* beetles to 8 by 8-meter arenas containing various crops. Fly pupae were artificially placed in the plots and disappeared in all crop types. There were differences in beetle activity, but there was no correlation between carabid activity and predation pressure. Predation by opiliones, staphylinids, and anthocorids was more important. McIver (1983) observed higher rates of mortality for *Pieris rapae* L. larvae on collards growing in tall alfalfa but found no evidence that the increased morality was the result of *P. melanarius* activity. *Phalangium opilio* L. was often found foraging on the upper and lower surfaces of collard leaves. He attributed the enhanced mortality to *P. opilio.*

Still, Carabidae provide subtle and indirect benefits to agricultural systems (Vasconcelos et al. 1996, Evans and England 1996, Evans and Richards 1997). It is important to recognize that Carabidae have an impact on pest populations in the context of their membership in the larger guild of ground dwelling generalist predators. The feeding guild also includes spiders (Araneae), harvestmen (Phalangiidae), rove beetles (Staphylinidae), ants (Hymenoptera), and other taxa. The entire assemblage of ground predators is important in the natural control of insect pests (Floate et al. 1990, Wratten et al. 1990, Wratten and van Emden 1995, Dennis and Wratten 1991, Carcamo and Spence 1994). There is general agreement among agricultural scientists that carabid beetles form an important component of the overall biological diversity found in semi-natural habitats on farmland (Thomas et al. 1998).

BIODIVERSITY

Carabidae (Coleoptera) is the largest family within Coleoptera, with an estimated 40,000 or more species worldwide (Thiele 1977). There are approximately 2500 species Carabidae in North America above Mexico (Allen 1979).

The basic body structure of the many Carabidae varies little from species to species (Lindroth 1961-69, Thiele 1977). Ground-dwelling forest and open-field species exhibit scarcely any morphological differentiation. In Carabidae (Adephaga) the coxae of the hind legs are fused with the first sternite. The key character that separates the Adephaga from the modern beetles is that the coxae of the hind legs divide the first abdominal segment. The antennae are filiform and invariably 11-jointed. The legs always have five tarsal segments. Without exception, the legs are slender and evolved for running. The German name for ground beetle is "Laufkafer" or "running beetle". Most male carabid beetles have dilated protarsi, which are used when mounting the female beetle during copulation. They can be used to separate males and females in selected genera including *Pterostichus* and *Anisodactylus* (Holliday and Hagley 1978, Riddick 1994)

Relatively few carabid species are caught in agricultural fields compared to natural settings (Lovei 1984). Rivard (1964a) collected 159 species of Carabidae in fields and surrounding areas of Ontario, Canada. Thirty of these species were restricted to wooded areas. About 48% of the species were collected in dry, open ground. About 38% were collected on moist soils. Only 12 of the 159 species were numerous in the centers of agricultural fields. Common crop-adapted species included *P. melanarius*, *Harpalus pensylvanicus* (DeGeer), and *Stenolophus comma* F. Carabid species were considered rare if 10 or fewer individuals were collected over a three-year period. A species was considered abundant if over 200 were collected in three years. Forty-nine carabid species were captured over an eight-year period in insecticide free cropping systems and in surrounding meadows in British Canada. The majority of species trapped were encountered in less than one percent of the catches. Eighty two percent (40/49) of the species represented less than one percent of the total capture. *P. melanarius* was by far the most abundant species representing 41% of all captures (Carcamo 1995, Carcamo et al. 1995).

In Canada and the United States, many of the dominant carabid species have been introduced from Europe (Rivard 1964a, 1965a, Frank 1971b, Kirk 1971, Finlayson and Campbell 1976) primarily from the British Isles. They came to North America in the rock and soil that served as ballast for the wooden merchant sailing ships that traveled between the two continents. These European beetles have dispersed and become dominant species in a variety of agricultural systems through out North America and Canada (Lindroth 1957).

Concerns have been raised about the risk these alien species may pose to native carabid assemblages (Carcamo et al. 1995). Niemela and Spence (1994), however, found no evidence that introduced carabid species were depressing species richness in native Carabidae. The general trend in carabid assemblages in the agricultural landscapes of both western Europe and North America is that a few common species have become relatively more dominant at the expense of a larger number of rare species. The dominance of a few species is mostly interpreted as a result of the loss of natural and semi-natural habitats as agriculture has become more intensive (Desender et al. 1994).

In our study conducted near Corvallis, Oregon we saw the same pattern. The two species that dominated the assemblage were the European Carabidae, *P. melanarius* and *Anisodactylus binotatus* F. Several other European carabid species were captured in our study including *Acupalus meridianus* L., *Clivina fossor* L., *Harpalus affinis* Schrank, *Agonum mulleri* Herbst, *Amara apricaria* (Paykull), and *S. comma.*

P. melanarius may be the most common Carabidae in annual cropping systems around the world (Thiele 1977, Lys et al. 1994, Lovei and Sunderland 1996). It was first recorded in Oregon in 1957 (Lindroth 1957). *P. melanarius* is synonymous with *Feronia melanarius* (Sunderland 1975) and *Pterostichus vulgaris* (Lindroth 1957, Thiele 1977). It thrives in disturbed habitats and arable fields. The chances of this carabid species being transported by humans are good because of its association with highly disturbed, anthropogenic habitats (Asteraki 1994).

A. binotatus is native to the British Isles, Europe, and Western Siberia; it was found in Oregon by 1957. It is a ground dwelling carabid with intermediate moisture preference. It breeds in the spring and has summer larvae. The larvae pupate, emerge in the late summer, and overwinter as adults. *A. binotatus* is also found on waste ground and disturbed soils. It eats a mixture of animal and plant food. It is macropterous and a good flyer. It is often taken in Pacific Northwest green houses. It was probably introduced with nursery stock or potting media (Lindroth 1957).

The most common North American native species in our study was *Bradycellus congener* LeConte. It is a small and highly mobile beetle. It is a strong flyer. It is mostly found near woods or in the woods. It readily moves into agricultural fields after tillage and following a pesticide application. Other native carabid species captured in our study included *H. pensylvanicus*, *Amara conflata* LeConte, *Amara californica* Bajean, *Anisodactylus californicus* Say, *Anisodactylus rusticus* Say, *Anisodactylus similis* LeConte, and *Pterostichus algidus* LeConte (Rivard 1965a).

BIOLOGY AND DEVELOPMENT

Eggs, Oviposition, Fecundity

The eggs of ground beetles are usually pale, ovoid, and often with microscopic textures (Luff 1987). Egg weight depends strongly on temperature, with heavier eggs being produced at lower temperatures (Ernsting and Issaks 1994). Hatchling weight and size are positively related to egg weight. Among carabid species, egg size increases with the body size of the species. The biomass of eggs produced per individual can be as high as 50% of the biomass of the female beetle. Carabid females lay their eggs singly or in groups in the soil or in mud cells (Thiele 1977).

Fecundity among ground beetles ranges from five to over 300 eggs per female in some species. *S. comma* produced about five eggs per female. In medium-sized carabid species including *P. melanarius*, *H. pensylvanicus*, and *Amara* spp., the range per female is 30 to 40 eggs per female per season (Rivard 1964b). *P. chalcites* can lay up to 702 eggs per female. Fecundity is affected by the climate, diet, and habitat (Wallin et al. 1992). Zangger (1994) studied the number of eggs and the length of the egg-laying period for carabids in a strip-managed cereal compared to a cereal monoculture. Female carabids were more numerous and their stomachs were more likely to be full in the strip-managed cereal. The numbers of eggs in their ovaries were higher and the egg-laying period was extended in the strip-managed cereal compared to the cereal monoculture.

Depending on the species, eggs may be laid all at once or over a long period of time. Eggs usually hatch in 3-10 days depending on the temperature and species. Most carabid species have three larval stages. Relatively little is known of the larval biology of carabids, especially of the predatory species. In species that overwinter as larvae, there may be a developmental diapause, usually in the third instar (Luff 1987). The larvae of most species are omnivorous and many of the predatory species are cannibalistic (Barney and Pass 1986). Carabid larvae are primarily sub surface dwelling, but the third instar of *P. melanarius* is often caught on the soil surface in pitfall traps (Thiele 1977).

Adult carabids are both physically and physiologically tough. The carabid head has large, prognathous mandibles. Mouthpart adaptations reflect both the type of food and the feeding methods employed by carabids. Most carabid beetles "root" for prey items on and below the leafy duff and soil surface. Both the eyes and antennae of most carabids are placed laterally, a position best suited for crevice penetration. The filiform shape of antenna forms an elongate probe, which is essential to a fast moving beetle with only moderately efficient vision. Leg specialization in the Carabidae consists of the various combinations of running and horizontal wedge pushing adaptations (Evans 1994).

Development and Seasonal activity

In Northern temperate climates, nearly all Carabidae are univoltine; one generation reproduces each year (Thiele 1977). In some species, a significant percentage of adult beetles survive the winter and have a second period of reproduction. Each species shows a characteristic annual activity cycle, which depends on their life span and the time of year that they reproduce (Luff 1987).

In the older literature, Carabidae are divided into spring and autumn breeding groups. These designations may be unreliable because there are several more complex annual patterns of reproduction and activity. Breeding can vary according to geography. We may need to consider periods of reproduction and activity separately (Thiele 1977). Two characterizations fit most species of Carabidae that are encountered in the agricultural settings: the autumn-breeding, larval-overwintering species (hibernate, at least in part, as larvae), and the spring-breeding, adult-overwintering species (hibernate exclusively as adults) (Wallin 1986).

Temperature and day-length play an important role in determining the rhythm of reproduction and activity in carabid beetles. Some species of spring-breeding carabids need long daylength for sexual maturation. Dormancy of some carabid species is controlled by temperature. In most carabid species, dormancy occurs at some point during the cycle of development and involves either quiescence or an obligatory physiological dormancy. Some species of the autumn-breeding carabids have a summer dormancy or aestivation, which prevents sexual maturity until the fall (Thiele 1977).

P. melanarius is an autumn breeder that overwinters as a larvae. A small portion of its population overwinters as second year adults (Wallin 1986). The larvae are active in the soil during the winter and go through three instars. An obligatory dormancy occurs in the third instar (Luff 1987). The dormancy is a genetically fixed stage of development and is independent of external factors. Cold is obligatory for completion of their life cycle. At continued temperatures of 15C and above, the animal reaches the third larval stage and never achieves metamorphosis. After they emerge from their puparium in the spring, adults of both sexes achieve sexual maturity in about three weeks at approximately 20C regardless of photoperiod. No dormancy occurs in the course of adult development. Under normal circumstances, the development of *P. melanarius* requires about 9.5 months to complete (Thiele 1977).

Carabids that overwinter as larvae must eat during the winter. The starvation capacity of several species of larval Carabidae ranged from three to twenty eight days (Luff 1994). Larval overwintering seems to be an adaptation to mild winters, ensuring activity and accumulation of energy over the winter leading to breeding and egg production in the summer and fall. Even in the coldest season, overwintering carabid larvae can be very active. Adult carabid beetles, however, are generally inactive during the winter (Thiele 1977).

Typically in northern temperate climates, the first carabid activity cycle begins in late April or early May, peaks in June or early July, then falls off rapidly in August and September (Thiele 1977). The apparent drop in activity during late summer reflects the lack of activity on the soil surface during the summer by the spring breeding carabids whose larvae are developing underground. The second cycle, if it occurs, may begin in late August or early September, peak in late September or October, and then decline rapidly in November. Pitfall trap counts generally show that the greatest carabid activity-density occurs in mid- spring and late summer. Seasonal peaks occur during breeding group activity periods and when generations of overwintering beetles overlap with the new generation (House and All 1981, Lys 1994, Carcamo 1995, Carcamo et al. 1995).

Autumn-breeding, larval-overwintering carabids generally have one peak of activity in mid summer. The peak corresponds to the overlap between second year adults and the emergence and reproduction of the current generation (Kirk 1973, Wallin 1986, Basedow 1994). In a mild winter, as many as 30% of the *P. melanarius* reproductive in the summer can survive a second winter. Spring-breeding, adult-overwintering, Carabidae including *A. binotatus* usually have two peaks of seasonal activity. One peak occurs in the early spring followed by a dip in the summer while the summer larvae develop. The summer dip in activity is followed by a second peak in the fall as the new generation of adults emerge and prepare to overwinter (Wallin 1985). Spring-breeding carabid species are active into the fall. They hibernate as adults, reproduce in the early spring, and must experience winter hibernation to become sexually mature. After reproduction, most of the beetles die off. Very few spring-breeding beetles survive for a second egg-laying season (Thiele 1977).

To resolve the variable effect of tillage and other farming operations on carabid populations, Fadl et al. (1996) studied ovary and egg development along with the seasonal activity of *P. melanarius*. A small number of adult female beetles with mature ovaries were caught in March and April. These beetles laid eggs during the previous autumn and then successfully overwintered. From May until mid July most of the captured female beetles had immature ovaries. Beetle activity-density peaked in late July. From mid July to September the new generation of females reached maturity and the majority of the new eggs were laid. The phenology of *P. melanarius* could be considered three fold: 1) an early period with few females of high egg production, 2) a middle period with high beetle frequency and low egg numbers, and 3) a late period with high numbers of beetles and egg laying (Basedow 1994).

Microclimate and habitat preferences

Carabid beetles are responsive to microclimate and habitat variability (Thiele 1977). Given their general lack of prey specificity, carabid response to microclimate may be a more important influence on their distribution than their response to prey dispersion (Wishart et al. 1956, Wallin 1986). It may be habitat that draws these predators into contact with crop pests. Beetles respond to changes in microclimate associated with a given crop (Rivard 1965b, 1966, Varis et al. 1984), the density of the vegetation (Perfecto et al. 1986) and stand purity (Dempster and Coaker 1974, Speight and Lawton 1976, Ryan et al. 1980, Tukahirwa and Coaker 1982, Barney and Pass 1986).

Most Carabidae are warmth loving. Temperature preferences influence whether carabid species are associated with the forest, meadow, or open field. The development of carabid larvae in the soil is accelerated by rising temperature. Overwintering larvae of some species may require cold to overcome larval dormancy (Thiele 1977).

Thomas et al. (1992a) investigated temperature along with vegetation, prey density, and predator gut fullness in raised banks covered with either tussock forming or mat forming grasses. The tussock grasses were preferred overwintering habitat for many carabid species. Although there was no significant difference in the mean temperature at the base of the various grasses, there were differences in temperature fluctuation. Tussock forming grasses including *Dactylis glomerata* and *Holcus lanatus* provide less variable temperature environments than the mat forming grasses *Agrotis stolonifera* and *Lolium perenne* or cereals (Thomas et al. 1991).

Carabids have relative humidity preferences. Dryness has a significant negative impact on the longevity of most carabid species. In general, carabids from moist habitats prefer higher humidity in laboratory tests. Carabids from dry habitats prefer lower humidity in laboratory tests (Thiele 1977). Forest dwelling species seek out moist and shady habitats (Wallin 1985).

More beetles and more beetle species are trapped in clay soils than sandy soils. There are many factors associated with soil types that influence beetles including particle size, the tendency of the soil to form cracks, moisture retention, and a tendency for plants growing in a given soil to rapidly form a closed canopy. Soil fertility stimulates rapid canopy closure, which in turn causes the relative humidity to rise (Thiele 1977).

Mean soil moisture sometimes correlates with overall carabid abundance (Carcamo 1995, Carcamo et al. 1995). Carabid larvae can survive flooded soil conditions longer than adult beetles. Carabids are, however, unable to survive sustained periods of high water. Nearly all of the carabid species that are trapped on floodplain soils have summer rather than winter larval development (Thiele 1977). Species with winter larvae (including *P. melanarius*) do not build up stable populations in floodplains. Winter flooding skews carabid fauna toward spring breeding species that colonize riparian areas and lay their eggs after winter floods have subsided. Carabid species including *Amara* and *Agonum* species that inhabit riverbanks are generally capable of relatively long distant flight. The adults fly away in the autumn and fly back to their stream bank positions in the spring (Zulka 1994).

The habitats available to carabid beetles in most farming landscapes include remnant wooded areas, riparian areas, hedge and fencerows of various age structures and spatial dimensions, undisturbed meadow areas, and crops growing in open fields. Very few of the carabid species that are associated with the moist and shady environments of the forest or riparian areas venture into agricultural fields (Thiele 1977, Lovei and Sunderland 1996). They are habitat specialists. The value of woodland-strip hedges and fencerows in contributing to carabid abundance in agricultural fields, therefore, has been evaluated in several studies. It is generally agreed that hedges and fencerows are used by important open-field species as overwintering and in some cases, oviposition sites. Remnant beetle populations disperse across the farm landscape from hedgerows and fencerows on the field boundaries after tillage and pesticide applications (Pollard 1968a, 1968b, Sotherton et al. 1981, Sotherton 1985, Desender 1982, Asteraki et al. 1992a, 1995, Petit 1994, Gruttke 1994).

The fauna of cultivated areas may have little in common with that of the forests. The distinctions between forest and cropland carabid species, however, are not clear-cut. Some open-field species use the forest or hedgerow environment at certain times of the year (Sotherton 1985, Wallin 1986).

P. melanarius is nocturnal and relatively abundant in remnant-wooded areas and forests. It is eurythermic (adapted to a variety of temperature regimes). It is skotophilic (prefers low light conditions) and hygrophilic (moisture loving). When marked and released during the fall on the boundary between the forest and the field, it consistently chooses the forest habitat. And yet, during the summer it is one of the most common carabid species in agricultural fields. The habitat preferences of *P. melanarius* change during the year according to its reproductive and foraging activities. The ability of this ground beetle to immigrate and emigrate successfully from agricultural fields and semi natural habitats assures that a portion of its population will survive tillage operations and pesticide applications. The ability to switch habitats explains, in part, why this species is dominant in many agricultural settings (Wallin 1986).

Beetle phenology and agricultural practices influence the distribution of beetles in various habitats (Wallin 1986). After harvest, open-field carabid species may be forced to leave the area due to lack of vegetative cover, and lack of prey. It is advantageous to carabid beetles to have the ability to move back and forth between shelter on the field edges and into the fields depending on the season and prey abundance (Wallin and Ekbom 1988).

Adult-overwintering carabids are not favored in many clean tillage agricultural settings because there is no winter cover and little cover in the early spring (Lovei 1984). Day-active carabid species seek out dry, sun-exposed warmer parts of agricultural fields (Wallin 1985). Moisture loving *P. melanarius* withdraws into hedges in the hottest months of the year (Thiele 1977). In a study of managed versus unmanaged meadow, more beetles and more species were captured in mown meadow during the early spring. Later in the summer, the situation reversed itself. In July and August, most beetles were captured in the unmown meadow. The beetles appeared to move into drier areas during the wet spring. They moved into moist areas during the hottest part of the summer (Nentwig 1988).

The hedgerow and the fencerow are colonized by different species of Carabidae. *C. fossor* spends the dry late summer in the hedgerow, but overwinters in agricultural fields (Asteraki et al. 1995). Its larvae occur in greater numbers in agricultural fields than in undisturbed strips on the field boundaries (Lys and Netwig 1994). *H. affinis* was trapped in weedy fencerows surrounding pasture, but not trapped at all in hedgerows of hawthorn surrounding the same pasture (Asteraki et al. 1992b). *P. melanarius* was more common in weedy fence lines than in hawthorne hedgerows. *A. binotatus* was abundant in meadow habitats; it was uncommon in the hedgerows and older woodlots (Gruttke 1994). *H. pensylvanicus* preferred the forest over the cultivated field, but preferred the undisturbed meadow over the forest (House and All 1981).

There are carabid species that prefer the environments associated with agricultural production (Lys and Nentwig 1991). These species are referred to as "open field" or "crop-adapted" species (Thiele 1977). Several carabid species regularly occur in cereal fields in relatively large numbers. Just as in Europe, crop-adapted species of the genera *Amara, Harpalus, Pterostichus*, and *Agonum* are prominent in farmlands of North America. When crop-adapted species are placed at the edge of the forest, they move away from the forest and into the open field (Wallin 1986).

Crop-adapted carabid species are tolerant of dry conditions and habitat structure of the open fields (Speight and Lawton 1976) or they are capable of rapidly colonizing agricultural systems after disturbances. During dry conditions, irrigated vegetable crops are attractive. High mobility and preference for moist conditions during the summer suggest that crop-adapted species may have originated from species that evolved in riparian areas and salt marshes (Thiele 1977).

Carabid beetles respond to vegetation types. Carabid diversity tends to decrease while overall abundance increases along the series: perennial grasses – winter cereals – annual spring sown crops. Crop type and cropping system determine the variation in crop canopy, which in turn determines the temperature and relative humidity on the soil surface. Crops with an early and persistent ground cover tend to be richer in carabid species. Late sown and more open-canopy crops support fewer carabid species (Luff 1987). More carabid beetles, for example, are caught in winter wheat, peas, and sugar beets than in potatoes, onions, or carrots (Booij 1994).

Although no species of carabid is confined to a particular crop, it is generally found that carabid assemblages in winter cereals differ from the assemblages in root crops. There tends to be a greater proportion of autumn-breeding species in the root crops. Beetle activity is often higher in cereal crops than in pastures (Thiele 1977). These differences may be due to moisture differences (Rivard 1964a, 1964b).

Carabid activity was greater in cabbage than in sugar beets or Timothy grass. The different levels of beetle activity may be due to differences in cultivation regimes associated with the various crops rather than the crops themselves (Varis et al. 1984).

Several workers have found that there can be higher carabid activity in mixed cropping systems compared to monoculture (Dempster and Coaker 1974, Speight and Lawton 1976, Ryan et al. 1980, Tukahirwa and Coaker 1982, Brust et al. 1986a, Perfecto et al. 1986, Nentwig 1989, Thomas and Wratten 1990, Tonhasca 1993, Booij 1994). However in some cases, changes in vegetation diversity has no observable effect on carabid activity (Purvis and Curry 1984).

When one hundred *P. melanarius* were marked and released in the center of enclosures with four crop choices, more beetles were trapped in a mixed planting of barley and pea than in pure stands of barley, pea, fava bean, or fescue grass. *P. melanarius* tended to stay in the mixed planting even though suitable prey items were placed in the plots with single plant species. There was no correlation between crop biomass and beetle abundance. Beetle gender had no effect on crop choice. The physical nature of the crop seemed to determine crop choice. The shadier environment in the mixed planting may have been more attractive to the beetles than the open environment of the monoculture (Carcamo and Spence 1994).

It is important to control for changes in plant density when increasing plant diversity and comparing its effects on natural enemies. Emigration of carabids was reduced in polyculture plots compared to tomato monoculture. However, when the overall plant density in the polyculture was controlled and kept the same as the monoculture, the beetles were more abundant in the monoculture. In general, carabid activity in dense plant stands is lower than in low plant density stands regardless of the stand purity (Perfecto et al. 1986).

Carabid abundance and community structure are very different in agricultural fields under different crop management schemes (Lovei 1984) crop types (Thiele 1977, Luff 1987) and crop rotations (Brust et al. 1986b, 1986a, Weiss et al. 1990). Brust et al. (1986b) observed more carabids in cornfields preceded by soybeans than in corn monoculture. In other cases, vegetable crop monoculture is more favorable to carabids than crops grown in rotation. Lovei (1984) trapped 5386 beetles and 26 species in a corn-corn rotation. He caught 1825 beetles and 34 species in a corn-bean rotation. Each crop rotation has a unique sequence of tillage operations. It is difficult to separate the effects of crop rotation from the effects of tillage timing on the Carabidae.

To some extent, the abundance of carabid species in a given habitat depends on the area of the habitat. The abundance of *P. melanarius* in cereal fields, for example, is positively correlated with field size. The larger the field, the more *P. melanarius*. Other species are more common in small fields. The effect of habitat fragment size depends to a large extent on the mobility of the carabid species (Wallin 1985).

In a comparison of heath fragments in the Netherlands, carabid species that have low powers of dispersal were often absent in the smaller habitat fragments. The critical size was 70 hectares. As the heath habitat fragment declined below 70 hectares, the number of heath-habitat specialist carabid species with low powers of dispersal started to decline. However, for habitat specialist species with high powers of dispersal, a decline in the presence of the species did not begin until the areas declined to below 8 to 25 hectares (de Vries 1994).

Clean tillage planting systems and removal of natural and semi natural habitat from the farming landscape appear to reduce the number of carabid species present.

The reduction in overall carabid abundance may, in turn, reduce interspecific competition. The result may be a greater abundance of the remaining crop-adapted species (Niemela 1993, Niemela and Spence 1994).

Foraging behaviors

The mouth parts of ground beetles vary structurally in adapting to the diversity of the feeding mechanisms that they use to capture and eat prey (Forsythe 1982, 1983). The body structure of carabids is related to their burrowing habits. The body form is wedge like and facilitates "wedge-pushing". Wedge-pushing is defined as vertical oscillations combined with horizontal pushing with both the dorsal and ventral body surfaces in contact with the substrate. Wedge-pushing allows Carabidae to penetrate and forage in organic duff and leaf litter associated with their natural habitats (Wallin and Ekbom 1988, Evans 1994).

Most carabid species forage on the ground (Luff 1987). Carabid beetles will occupy cracks in the soil if they are available. Many carabid species burrow in the soil. *C. fossor* is equipped with burrowing feet (Thiele 1977). Male and female *P. melanarius* actively burrow into the soil in open fields (Wallin 1986, Wallin and Ekbom 1988).

A few carabid species forage plants, but most of these carabids are seed feeders (Vickerman and Sunderland 1975). *C. fossor* was occasionally found on collard plants (McIver 1983). There seems to be no knowledge that *P. melanarius* has ever been found on plant foliage.

Several species of Carabidae forage for weed seeds and store them in their burrows (Kirk 1972, Luff 1980). *P. melanarius, Amara* spp., *Anisodactylus* spp., *Agonum* spp., and *Harpalus* spp. eat grass seeds in significant quantities, even if animal matter is offered at the same time. Many species of *Amara* are found climbing on plants and are reported to feed heavily on ripe grass seeds. The occurrence of Cruciferae seeds favors the presence of *Amara.* The seeds of *Poa annua* and *Polygonum aviculare* are favorite foods of *Amara cupreolata* Putzeys (Johnson and Cameron 1969). The larvae of *Amara*, however, are all carnivorous (Thiele 1977).

Consumption of plant materials varies among carabid species. *Harpalus rufipes* consumes about 50% animal matter (mostly aphids and ants), where as *Harpalus aeneus* is almost 100% phytophagous (Vasconcelos et al. 1996). *P. melanarius* eats a wide variety of foods and generally contains about 10% plant materials in their guts (Sunderland 1975). Plant consumption varies according to the season. In the spring, *Pterostichus cupreus* may have as much as 67% plant material in its gut, however by summer, only 20% plant material (Thiele 1977).

H. pensylvanicus feeding behavior is characterized as facultatively phytophagous. The species is known to feed on plant material, but it is entomophagous when prey is available (House and All 1981). *H. pensylvanicus* will feed on freshly crushed corn ears and stalks after harvest. The larvae construct vertical underground burrows where they cache a supply of grass seeds for their winter food supply (Kirk 1973). *H. rufipes* is attracted to and eats umbelliferous seeds (Speight and Lawton 1976).

Though some species are phytophagous, the occasional injury that carabid beetles cause to agronomic crops is seldom of economic importance (Rivard 1964a, Sunderland 1975). Some carabids eat seedling cereals. *C. fossor* has been observed eating germinating corn seeds (Johnson and Cameron 1969). The seedcorn beetle, *S. comma* may cause economic damage to cereals (Kirk 1975). *Harpalus* and *Pterostichus* species occasionally damage strawberry fruit, especially when they are thirsty (Luff 1974). *P. melanarius* can damage Douglas fir plantings and sugar beet roots (Sunderland 1975).

The adults of most carabid beetles and nearly all of their larvae are predaceous on other species (Rivard 1964a, Sunderland 1975, Lovei and Sunderland 1996). Carabinae and Harpalinae can be kept for months reared on beef (Thiele 1977). *P. melanarius* and *H. pensylvanicus* are commonly reared on wax moth larvae (Rivard 1965b). The natural diet of *P. melanarius* contains nine-tenths animal matter. It prefers caterpillars, spiders and ants. It does poorly, however, when raised on a diet of aphids (Thiele 1977).

In agricultural settings, Carabidae are faced with situations involving extremely high or low prey densities. Carabids species vary in their response to prey density (Sunderland 1975, Chiverton 1987b). *P. melanarius* has been shown to switch between prey items reflecting seasonal abundance of prey taxa. After harvest, the availability of prey in agricultural fields crashes. The loss of available food probably forces the beetles to leave the area (Wallin and Ekbom 1988).

Studies on searching behavior in Carabidae have shown that hungry individuals move differently than satiated individuals. Behaviors such as turning often or reducing speed restrict an insect to areas with high prey density. In areas of low aphid density, hungry *P. melanarius* exhibit a combination of directed movements and high speed. This behavior leads to a greater area searched and increased chances of finding prey during periods of low prey density (Wallin and Ekbom 1994). Hunger level has a significant and species-specific effect on the behavior patterns and speed of movement of Carabidae in low and high aphid densities. In general, hungry carabids forage more actively than satiated carabids (Baars 1979a, 1979b, Lys and Nentwig 1991, Wallin and Ekbom 1994).

Carabidae are voracious predators. *P. melanarius* has one of the highest rates of food consumption among beetles tested, eating more than three times its own weight per day (Vasconcelos et al. 1996). The mean weight of *P. melanarius* females is 0.16 +/- 0.02 g. In the laboratory fed with earthworms, lepidopteran caterpillars, field snails, and potato beetle larvae, etc. *P. melanarius* ate 0.507 g of meat per day on average (Wallin and Ekbom 1994). As predatory organisms, the energy turnover of carabids in the ecosystem is comparable to that of chilopods and spiders (Thiele 1977).

Carabid beetles display both specialist and generalist foraging behavior (Hengeveld 1980, Wallin and Ekbom 1994). They are considered inefficient predators. Carabidae generally do not show a highly positive search pattern. In arena trials with lepidopteran prey, *P. melanarius* wandered around aimlessly even though they were in close proximity to their prey (Vasconcelos et al. 1996). Carabidae usually find their prey by chance (Coaker and Williams 1963).

Carabid species of the same size show similar preferences with respect to prey in a given habitat (Thiele 1977). Carcamo and Spence (1994) found that the rate of disappearance of fly pupa placed in beetle arenas was inversely related to the size of the pupa. Only the larger predators attacked the larger fly pupa. Where *P. melanarius* was the dominant beetle species, more of the larger pupa disappeared. Where *P. melanarius* numbers were lower and the smaller *A. cupreum* was active, there was reduced predation of the larger pupa.

The pursuit of prey by carabid beetles is induced by visual cues, particularly prey movement. The beetles also respond to olfactory cues. Foraging beetles sense the previous presence of prey on a substrate. They respond by slowing down and reducing their movement. In the majority of carabid species that are nocturnal, olfactory and tactile cues are particularly important in prey location (Luff 1987).

Prey Items

The composition of the diets of Carabidae in the North America and in Europe has been extensively reviewed (Sunderland 1975, Chiverton 1984). Most carabids are not exclusively predators but consume carrion and some plant materials at least at certain times of the year (Kirk 1972, 1973, Sunderland 1975, Lovei 1984). Polyphagous carabids feed on a wide range of insects and plant products (Johnson and Cameron 1969, Luff 1974, Sunderland 1975, Edwards et al. 1979, Chiverton 1987b, Sunderland et al. 1987, Hagley and Allen 1990, Baines et al. 1990, Floate et al. 1990, Clark 1993, Clark et al. 1994). A high degree of food specialization in adults occurs in only a few genera. Most genera and species of Carabidae are opportunistic feeders (Thiele 1977).

Food items reported for *P. melanarius* include wireworms, earthworms, slugs, Lepidopteran larvae and adults, carabid larvae, smaller carabid adults including *Bembidion* and *Trechus* species (Sunderland 1975). The predominant prey items found in the gut of *P. melanarius* foraging in spring barley in Great Britain were spiders, rove beetles, and Diptera. About 4% of the contents were spider fragments (cephalothorax and chelicerae) including fragments of *Erigone atra* males (Linyphiidae). About 15% of the contents were earthworm fragments (chaetae and skin). About 40% of the contents were made up of fragments of other beetles (legs and head parts) and beetle larvae (tarsus, sclerotized abdominal cuticle) including fragments of *Philonthus* spp. (Staphylinidae). About 7% of the contents were made up of Diptera fragments (heads, tarsal claws, and rarely wing fragments) including Scatophagidae and Dolichopodidae. About 4% of the contents were unidentified eggs. About 4% of the contents were unidentified plant materials. Further gut content analysis has shown that *P. melanarius* eats significant quantities of aphids, Heteropterans, coccinellid larvae, and syrphid larvae (Chiverton 1984).

Harpalus species eat *P. rapae* larvae, cabbage root maggot fly eggs and larvae, earthworms, slugs, aphids, jassid and delphacid nymphs, carabid larvae, fungal spores and pollen, strawberry seeds and the seeds of twenty other plant species. The gut contents of *H. rufipes* from spring barley and winter wheat fields contained beetles (22%) including Carabidae and Staphylinidae, beetle larvae (22%), Diptera (5%), aphids (17%) and plant material (17%). The gut contents of *Loricera pilicornis* gathered in spring barley contained about 88% Collembola fragments. None of the gut contents of *P. melanarius* contained Collembola fragments (Sunderland 1975).

Carabidae eat the eggs and pupae of the cabbage root fly, *Delia radicum* L. and can reduce crop damage. Beetles with positive precipitin tests for D. brassicae included *P. melanarius* (11%), *C. fossor* (12%), *H. rufipes* (14%), *Amara familiaris* (22%), and *Agonum dorsale* (4%). When carabids were excluded with barriers and with insecticide treatment, there was an inverse relationship between the number of beetles, cabbage root maggot densities, and damage in cauliflower and cabbage. Carabids were responsible for 47% to 79% reductions in maggot eggs (Wishart et al. 1956, Coaker and Williams 1963, Coaker 1965, 1966, Ryan et al. 1980).

Ground beetles are useful predators on aphids (Edwards et al. 1979, Tukahirwa and Coaker 1982, Hance 1987, Hamon et al. 1990). Several studies have shown a negative correlation between ground beetle activity-density and aphid density in cereals (Sunderland 1975, 1980, Vickerman and Sunderland 1975, Edwards et al. 1979, Chiverton 1986, Chiverton 1987a, 1987b, Chiverton 1988, Winder 1990, Wratten et al. 1990, Lys 1994, Wallin and Ekbom 1994). Serological techniques show that *P. melanarius* feeds on *M. persicae* (Hance 1987, Hance et al. 1990) and *B. brassicae* (McIver 1983). The gut content of *P. melanarius* beetles gathered in spring barley contained about 15% aphid fragments (siphunculi and tarsal claws) (Sunderland 1975).

Ground predators come into contact with aphids when they drop from plants. Foliar predators and changes in plant quality stimulate aphid drop. The bird cherry-oat aphid *Rhopalosiphum padi* L., for example, migrates to the oat crop at the beginning of June. The environment in the crop is relatively dry at the beginning of the season, and the aphids tend to live at the base of the oat plants or under the soil surface, where they are exposed to predators (Chiverton 1987b, Winder 1990). As the oats mature, aphids leave the plants and move about on the soil surface. Here, they are preyed upon by carabid beetles (Wallin and Ekbom 1994).

There is some debate as to what extent predators, which forage for aphids on the ground, are contributing extra mortality to the aphid population. Many aphids die from exposure to harsh conditions on the soil surface. Exclusion experiments, however, show that removal of polyphagous predators often does lead to increased aphid densities (Edwards et al. 1979, Sunderland 1980, Chambers et al. 1982, Coombes and Sotherton 1986, Chiverton 1986 , 1987a, 1987b).

Carabid beetles prey on lepidopteran larvae (Frank 1971a, Hagley and Allen 1988, O'Neil and Stimac 1988, Laub and Luna 1992, Clark et al. 1994, Weseloh et al. 1995). Ground predators come in contact with foliar dwelling lepidopteran larvae when they drop to the ground to escape predation or when they are looking for pupation sites (Riddick 1994, Riddick and Mills 1995). *P. melanarius* had positive precipitin tests for the winter moth, *Operophthera brumata* (Frank 1967). *P. melanarius* feeds on all larval stages of *Mamestra brassicae* (Vasconcelos et al. 1996). Predator exclusion experiments show that ground dwelling Carabidae can contribute to the reduction in lepidopteran pest populations (Brown and Goyer 1982, Brust et al. 1985).

A number of carabid beetles eat *P. rapae* larvae (Allen 1979). Substantial loss of young Pieris larvae has been attributed to carabid beetle predation (Dempster and Coaker 1974, McIver 1983). Dempster (1969) reported catching significant numbers of *H. rufipes* and *P. melanarius* that appeared to have an impact on the survival of *P. rapae*. Beetles were more common in weedy vegetable plots than in clean culture plots. *P. rapae* mortality was higher in the weedy plots. Mortality was focused on the small larvae.

Diabrotica eggs, larvae, and adults are eaten by *H. pensylvanicus* (Kirk 1973, House and del Rosario Alzugaray 1989). Earthworms and slugs are a significant source of food for *Carabus* species. Slugs including *Agriolimax agretis* are attacked and ingested by *Carabus auratus, C. cancellatus, and C. granulatus*. These carabids have been observed climbing plants to attack slugs (Thiele 1977).

Movement and Redistribution

Ground beetles disperse by running, flying, or by passive transportation in soil and other agricultural materials (Lindroth 1957, Rivard 1965b, Gordon and McKinlay 1986, Matalin 1994). Many Carabidae are capable of flight, but the propensity to fly varies significantly among species (Luff 1987). Dispersal from hedgerows into arable fields by common crop-inhabiting species is by running (Coombes and Sotherton 1986, Wallin and Ekbom 1988, Gruttke 1994). The larvae of the Carabidae are not highly mobile (Thiele 1977).

Field inhabiting carabid beetles are characterized by high rates of movement (Wallin and Ekbom 1988). The potential for activity implies that carabids have the capacity to respond immediately to prey heterogeneity, changes in plant cover, changes in ground structure, temperature and humidity (Speight and Lawton 1976, Thiele 1977, Wallin 1985). Distribution of carabid beetles within any given field is seldom random or even. Their distribution may be the result of local changes in behavior rather that an underlying aggregated distribution. Within-field distribution may, for example, be the result of prey aggregation (Ericson 1977, 1978).

Windowpane trap catches of flying carabid beetles are generally low in comparison with pitfall catches (Wallin 1985). Agricultural land recently reclaimed from the sea in the Netherlands yielded 31 species of carabids caught in windowpane traps. During the same period, 67 species of carabids were captured in pitfall traps on the soil surface. The number of species caught flying into established agricultural settings tends to be much lower (Thiele 1977).

Readily flying carabid beetles including *Amara, Agonum,* and *Bradycellus* species are small or medium-sized beetles. They inhabit ephemeral habitats including riparian areas that flood each winter. Each year, they must recolonize these areas. *Agonum* and *Amara* species are known to use flight for dispersal more than most carabid species (Wallin 1985). Very few flight records exist for large carabid beetle species such as *P. melanarius* (Luff 1987).

Over 112 carabid species have been collected on the ocean shores of Finland, indicating that large numbers of flying carabids are carried out to sea by air currents and fall onto the water surface. *C. fossor, Acupalus dorsalis, A. familiaris,* and several *Agonum* sp. were among the most commonly encountered species washing up on the Finish shoreline (Thiele 1977).

Wing dimorphism occurs in some species. In other species, autolysis of the flight muscles occurs after egg ripening. The proportion of winged versus non-winged individuals of a colonizing carabid species tends to diminish after several years. The decrease in winged individuals results in effective geographical isolation of the population. Dispersal followed by isolation results in the evolution of new species. The unique pattern of carabid colonization explains, in part, the remarkable species richness in the family Carabidae (Thiele 1977, Niemela and Spence 1994).

In the Netherlands, the re-colonization of sea polders (reclaimed salt flats) by Carabidae has been studied for many decades. There is a tendency for wing dimorphism in carabid populations to change as fresh polders mature. In young sites, *P. melanarius* have about 25% macropterous (normal winged) individuals and 75% brachypterous (nonfunctioning wings). *P. melanarius* populations in old sites have about 2% macropterous individuals and 98% brachypterous (Thiele 1977).

In Europe, following dramatic, large-scale disturbances such as strip-mining operations, Bembidion, *Harpalus*, and *Amara* species are among the earliest colonizers. As replanted forest canopies become dense after 10 to 25 years, the proportion of winged carabid species diminished from 80% to 20%. The proportion of flightless forest species increases (Thiele 1977).

P. melanarius is a relatively recent immigrant to North America. It is abundant near Edmonton, Canada. The proportion of macropterous individuals increases from 20% near the city to 65% in the most distant and probably most recently founded populations (Niemela and Spence 1994).

Breeding experiments suggest that in Carabidae, the macropterous trait is recessive. The requirement for a double recessive expression of the winged state may explain why founder populations (with a narrow genetic base) have a higher percentage of macropterous individuals (Thiele 1977).

Walking is recognized as the normal means of locomotion of carabids within their territory (Rivard 1965b). Barriers on the soil surface and ingress trenches reduce carabid beetles in experimental plots. The same barriers fail to reduce numbers of rove beetles (Staphylinidae). Rove beetles readily fly over the barriers (Coaker 1965, Ramert and Ekbom 1996).

Carabid beetles disperse by walking small distances each day in random directions. This pattern of carabid movement with small displacements, moderate velocity, and random choice of direction has been described as "random walk" (Baars 1979b, Petit 1994). Periods of random walk alternate with periods of directed movement when large distances are covered per day in a more of less consistent direction. The largest rates of directed movement occur in the least favorable habitats. When beetles are hungry, they emigrate from an area (Baars 1979b).

P. melanarius tends to move in the direction parallel to crop rows. Following the threshing of wheat and again following the harrowing of wheat fields, the distance per day traveled by marked *P. melanarius* beetles increases. After harvest, *P. melanarius* switches movement from random dispersion to directed movement (Lys and Nentwig 1991). *P. melanarius* can move over long distances. Their ability to cross long distances explains, in part, why it is trapped in such a wide variety of habitats. It moves frequently from field to field and from field to adjacent uncultivated habitats. *P. melanarius* changes its pattern of movement when it enters a wooded habitat. It changes from directed movement to random movement. The change may reflect its preference for the woodland habitat (Wallin and Ekbom 1988).

Rates of dispersal on the soil surface have been assessed by release and recapture of marked carabid beetles (Greenslade 1964a, Rivard 1965b, Gordon and

McKinlay 1986) and by tracking individual beetles with harmonic radar (Wallin 1985, Wallin and Ekbom 1988). Dispersal of carabid beetles over large areas is possible even without flight. Mean estimates of movement range from 5 to 20 meters per day for the medium to large species. For some species, there may be differences between the rates of movement of the beetle genders. In general, males tend to be more mobile than females. Mobility of the genders, however, varies with their reproductive cycles (Ericson 1977).

P. melanarius is highly mobile compared to other species of Carabidae. *P. melanarius* can reach running speeds of up to 0.6 meters per minute (33.6 mph) (Wallin and Ekbom 1994). The range of movement by *P. melanarius* has been estimated at 3 to 30 m per night (Wishart et al. 1956, Wallin 1986, Lys and Nentwig 1991). *P. melanarius* beetles marked and released in oats were recaptured 6 meters (about 20 ft) away the following day. Marked beetles were trapped 12 meters (about 40 ft) away after four days. Slightly higher proportions of males of *P. melanarius* were captured at a greater distance than females. Three male *P. melanarius* were found 18 meters (about 60 ft) away after one day. After one month, marked *P. melanarius* have been caught 60m from release sites. The maximum amount covered in one month by a marked *P. melanarius* beetle was 250 m (Rivard 1965b, Thiele 1977).

The nature of the soil surface has an impact on the speed of travel and the area searched by hunting carabids. *C. auratus* covered about seven meters per minute at 22C on a smooth, bare, firm substrate (a dirt path). It hunts for prey in a serpentine pattern creating a trail about three cm wide. Thus, it covers an area of about 0.2 square meters per minute. In a harrowed field, *C. auratus* covered only 2.5 meters per minute. In rye grain, it covered about 1.8 meters per minute. In an old meadow, it covered only 0.5 meters per minute. Environmental resistance to movement in grass and meadow may explain why *P. melanarius* prefers a field with open rows when it is foraging for food (Thiele 1977).

Carabid activity tends to be lower as plant density increases (Greenslade 1964b, Rivard 1965b, 1966, Perfecto et al. 1986). Crop type may or may not effect carabid mobility. It is difficult to separate the effects associated with plant architecture from those associated with the cropping system. *P. melanarius* dispersed more slowly in oats than in cultivated corn (Rivard 1965b). Similar numbers of *P. melanarius* were caught, however, in barley and in fava bean. The physical nature of the crop did not seem to effect habitat choice. The effect of crop type on mobility may depend more on planting arrangement, plant density, and soil surface residue rather than on crop type alone (Carcamo and Spence 1994).

Landscape features can interfere with carabid movement. Gruttke (1994) analyzed hedges interconnected by meadow strips and old semi-natural habitat. *A. binotatus* was abundant in meadow habitats. Even though it has good powers of dispersion, it was uncommon in the hedgerows and in the older woodlots nearby. The hedgerows appeared to be a barrier rather than a corridor for dispersion of the *A. binotatus*. The hedges slowed the redistribution of the beetles following an insecticide application.

The rate of beetle movement and the distance between the crop and the source of beetles determines how quickly a carabid population recovers in a field after a pesticide application. The rate of recovery (slope of the regression line for time/distance) varies according to species. It took about 14 days for *Pterostichus cupreus* numbers to recover following an insecticide spray when the source of beetles was 20 meters away. *Trechus quadristriatus* took 7 days to recover at the same distance. It took about 30 days for carabid numbers as a whole to recover following a pesticide application when the source of beetles was 40 meters away (Berraondo et al. 1998).

Because of the relatively low rate of recovery by Carabidae following pesticide applications, some have advocated the use of pesticide and tillage refuge strips within agricultural fields (Nentwig 1988, 1989, Thomas et al. 1991, Zangger 1994). There was a significant negative correlation between the distance separating weedy strips (12, 24, 36, and 78 meters) and the number of Carabidae in the cereal crop growing between the strips. Carabid beetle activity/density was 12 times higher in barley when strips occurred every 24 meters compared to 78 meters (Lys 1994, Lys et al. 1994).

Many crop-adapted Carabidae survive agricultural operations by migrating between two habitats, the field center and the undisturbed boundary vegetation (Boivin and Hance 1994). The movement of the beetles depends on the cropping cycles and the phenology of the beetles. When fields are left fallow during the winter, adult-overwintering beetles do not disperse from hibernation sites at the field edges until crops are planted in the spring (Pollard 1968a, 1968b, Wallin 1985, Coombes and Sotherton 1986). If a field is plowed in the fall and planted to winter wheat, adult-overwintering beetles may move into the field as the canopy develops and the temperature warms up in the spring (Wallin 1986). The opposite is also true. Carabid species that overwinter as larvae in the middle of cereal fields migrate to the edges as adults when the fields dry up in preparation for summer harvest (Wallin and Ekbom 1988).

Field edges often support higher numbers of carabid beetles and a greater number of carabid species than the middle of fields (Pollard 1968b). Higher species diversity on the edges may be the result of plant diversity associated with weeds on the field margins, greater habitat stability on the edges, or movements of beetle populations. In the middle of agricultural fields, crop-adapted beetle species dominate. Species diversity in the middle of fields tends to be lower while carabid abundance may be higher (Speight and Lawton 1976, Lovei 1984). Species diversity may be higher on the field edges where dominant crop-adapted species are less numerous (Hsin et al. 1979). Both diversity and abundance of Carabidae were higher on field edges during the early part of the growing season before crop-adapted species moved out into the spring planted crop. If the field centers in the winter and early spring are devoid of prey items, hungry beetles may be more "active" there. Greater activity would result in greater pitfall captures without a significant difference in abundance (Desender 1982).

Many field carabid populations appear to be fairly stable even though they are subject to continual disturbances associated with agricultural practices. Population persistence results from a sufficient ability for dispersal and redistribution from residual populations. Spatial heterogeneity and migration from one patch to another stabilizes larger populations. Local disruptions result in beetle populations of different ages. The different aged beetles are susceptible to different environmental perturbations. Thus, increasing the number of age groups in a population tends to increase stability. The combination of a large number of factors on a multitude of sub-populations, phenotypes, and age groups can result in more uniform fluctuations in carabid population density (Luff 1987).

Intensification of agriculture in a region often results in a relatively simplified agricultural landscape. Small undisturbed parcels disappear. Large fields covered by the same crop become the dominant features of the landscape. The size of the fields can exceed the migration ability of some carabid species. The chance that a non-mobile species will find a refuge with sufficient food for reproduction is diminished. Isolation of non-mobile species in a fragmented landscape can result in decreased beetle abundance and species diversity in Carabidae in agricultural landscapes as a whole (Sustek 1994).

Life span and Mortality Factors

Adult carabids normally live one to three years. Most live about a year. When one considers the duration of the whole generation, the life span of adult overwintering, spring breeding carabids is generally shorter than that of larval overwintering, autumn breeders (Thiele 1977, Allen 1979).

Predators of carabid beetles include mice, bats, insectivorous birds, sparrow hawks, owls, frogs and toads, and other predatory arthropods including spiders and other carabid beetles (Thiele 1977). Moles are important predators of carabid beetles and their larvae. Adult *H. pensylvanicus* are preyed on by skunks (Kirk 1974).

Like most insects, carabid beetles host a variety of parasites and pathogens including parasitic wasps, tachinid flies, fungi, entomophagous nematodes, mites, and other disease organisms (Lovei and Sunderland 1996). Mites (Acari) are among the more important parasites of Carabidae. The mites most commonly found on Carabidae are in the family Podapolipidae in the genera *Eutarsopolipus* and *Dorsipes*. *Eutarsopolipus pteroshichi* lives beneath the elytra of *P. melanarius*. Wasps in the family Proctotrupidae in the genera *Phaenoserphus* and *Prototrupes* parasitize carabid larvae. Adult Carabidae seldom contain many Hymenoptera. The role of parasites and diseases in carabid dynamics is little known and thought to be small. However, the mortality of woodland *Pterostichus* species can be high during the larval stage and during reproduction (Luff 1987).

The larvae of many predacious carabid species are cannibalistic. Carabid larvae are aggressive toward members of their own species (Thiele 1977). Cannibalism is so prevalent among the carabids that it makes it difficult to maintain laboratory cultures of the beetles. Cannibalism may play a role in limiting the density of carabid beetles in natural settings (Barney and Pass 1986).

Biotic factors such as competition, predation, parasitism, and the availability of food supplies probably influence the frequency of carabid species. Since most carabids live for one year, competition among species may only be revealed as a delayed density dependent effect over several years. Biotic factors, however, tend to have less influence on carabid population dynamics than abiotic factors. Biotic factors do not, as a rule, limit the occurrence of a species to a particular habitat in temperate climates (Thiele 1977).

IMPACT OF AGRICULTURAL PRACTICES

The densities of carabids are very different in agricultural fields under various management systems (Lovei 1984). Tillage, pesticide applications, and other management activities are known to be deleterious to ground beetle populations (Luff and Rushton 1989). In some cases the overall abundance of carabid beetles is reduced by tillage (House and del Rosario Alzugaray 1989, Weiss et al. 1990, Lys and Nentwig 1991, Carcamo and Spence 1994). In other cases, the overall abundance of carabid beetles increases with tillage while species diversity is reduced compared to undisturbed vegetation in the surrounding area (Asteraki et al. 1995, Carcamo 1995).

Changes in tillage practices produce variable effects on carabid beetle species (House 1989, House and del Rosario Alzugaray 1989, Mack and Backman 1990, Weiss et al. 1990, Tonhasca and Stinner 1991, Tonhasca 1993). In general, predaceous arthropods and carabid beetle densities increase when conservation tillage practices are adopted (Dritschilo and Wanner 1980, House and All 1981, House and Stinner 1983, House and del Rosario Alzugaray 1989, Troxclair and Boethel 1984, Weiss et al. 1990). The increase in arthropod density is due, in part, to the presence of plant residues and to reduced habitat disturbance (Brust et al. 1985).

Sometimes tillage has no observable impact on carabid density (Mack and Backman 1990). The overall pattern of carabid abundance in conservation tillage systems depends on how the dominant carabid species are affected by soil disturbance. Under certain circumstances, beetle densities are higher in conventional tillage systems (Barney and Pass 1986, Carcamo et al. 1995). The tillage effect depends on the carabid species (Carcamo 1995), the timing of the tillage event (Wallin 1985, Polis et al. 1989, Hance et al. 1990, Niemela 1993), and other factors.

There are several possible explanations for the variable effect of tillage on carabid species. Tillage regimes may change the distribution of prey items and the predators may follow. Some carabid species prefer the open microclimate of clean-tillage planting systems (Tonhasca and Stinner 1991, Tonhasca 1993). Clean-till cropping systems present less physical barriers to foraging carabid species. Clean-tillage allows them to move in and out of fields, avoiding or rapidly recovering from the destructive effects of tillage, pesticide applications, or harvest operations. Adult overwintering carabid beetles can escape the effects of fall tillage by migrating to the edges of the fields where they lay their eggs (Carcamo 1995, Carcamo et al. 1995). Some carabid species survive tillage by moving below the plow layer (Barney and Pass 1986).

The density of all taxonomic groups of soil arthropods tends to be higher in weedy cropping systems than in conventional tillage systems where herbicides are used. Various combinations of tillage with or without herbicides cause changes in weed pressure and weed composition. Carabid species respond to these changes (Tonhasca 1993). Carabid beetles including *H. pensylvanicus* and *Amara* spp. consume weed seeds. They may be attracted to cropping systems that are rich in a specific weed resource. Seed gathering carabids may, themselves, have an impact on weed population shifts (House 1989).

Carabid abundance and community structure is influenced to some extent by crop type (Thiele 1977, Luff 1987) and crop rotation (Lovei 1984). Crop type influences habitat structure, vegetative cover, food alternatives and availability, and specific microclimate conditions that can influence carabid density and diversity (Fadl et al. 1996). The impact of crop rotation on Carabidae is, in part, a reflection of tillage practices associated with the rotation. A corn/wheat rotation will generally support fewer numbers of carabid beetles than continuous corn. Winter wheat is planted in the fall. The fall disturbance interferes with breeding activities of the autumn breeders. In the absence of weeds or other plant cover, wheat stubble provides little cover. The lack of vegetative cover reduces overwinter survival of adult beetles. Weed-free stubble is unattractive to spring breeding species (Lovei 1984).

There are usually less adult overwintering, spring breeding carabids in root crops than in winter grains (Thiele 1977). Root crops are generally cultivated in the spring, when spring breeding carabids are vulnerable to disturbances. Larval-overwintering carabid species are depressed by spring tillage compared to autumn tillage. The larvae, pupae, and emerging adults are sensitive to disturbance in the spring (Hance et al. 1990).

The timing of primary tillage in relationship to the phenology of carabid species determines, in large part, the impact of tillage on the success of the species in a given cropping system (Wallin 1985, Hance et al. 1990). Tillage operations in the temperate areas of the Northern Hemisphere tend to occur primarily in the spring. As a result, the dominant carabid species in the annual cropping systems of North America and Europe tend to overwinter as larvae, emerge as adults in the late spring, and breed in the late summer and fall. The best example of this is the *P. melanarius*. It may be the most common carabid species in agricultural systems in the Northern Hemisphere (Thiele 1977, Lovei 1984).

Primary tillage with a mold board plow in the fall can reduce the survival of species that overwinter in the middle of the field (Polis et al. 1989). Adult overwintering, spring-active carabid species are more negatively impacted by fall tillage than larval overwintering species. Many crop-adapted larval overwintering species emigrate from agricultural fields after harvest. They seek refuge on the field edges where they lay their eggs and thus escape the effects of the fall tillage (Wallin 1985).

After fall planting there is usually a period in the spring when the field middle is somewhat empty in overwinter crops (Polis et al. 1989, Niemela 1993). The empty middles are due to the fall tillage operations. Invading beetles recruited from the field edges rapidly colonize the middle. Regardless of tillage regime, tillage refuges within the field and on the field boundary can result in increasing carabid abundance over time (Lys 1994, Lys and Netwig 1994, Lys et al. 1994).

House and All (1981) evaluated the relative abundance of Carabidae including *H. pensylvanicus* in clean-till and no-till soybeans, an old unmanaged field, a nearby woods, and fescue grass field. Carabid fauna was more abundant and species rich in reduced tillage soybeans than in clean till soybeans. *H.*

pensylvanicus was five times more abundant in the reduced tillage system than in the clean till system. It was ten times more abundant in the old unmanaged field than in the clean till soybeans. It was more abundant in the forest than in the cultivated soybeans but much less abundant in the forest than in the old field vegetation.

Brust et al. (1985) evaluated no-till versus clean-till corn and the impact of ground dwelling predators on black cutworm (*Agrotis ipsilon*) damage. Most of the predators in his system were Carabidae. Other predators included Lycosidae, Phalangiidae, and Staphylinidae. There were significantly more carabids in the no till planting system. When enclosures, trapping, or insecticide sprays removed carabids, cutworm damage increased. It appeared that endemic soil predators were a major contributing factor in reducing black cutworm damage potential in corn (Brust et al. 1986a, 1986b).

High and low intensity tillage regimes were studied in Alberta, Canada. Tillage, herbicides, and fertilizers were used but no insecticides were applied. In this case, reduced tillage did not increase the activity-density of beetles. There were more beetles in crop grown with an aggressive tillage regime. Reduced tillage did, however, increased diversity and evenness of carabid species. The tillage effect varied according to species (Carcamo 1995, Carcamo et al. 1995).

A. placidum can be a dominant carabid species where aggressive fall tillage regimes are used (Weiss et al. 1990). Twenty-five species of Carabidae were captured in spring planted barley. The larval overwintering, autumn breeders including *Agonum placidum* Say and two *Amara* species were more abundant in a conventional cropping system where fields were mold-board plowed, roto tilled, and harrowed in the fall. *Agonum* and *Amara* carabid species are highly mobile and may have invaded the fields following the tillage operations. *P. melanarius*, which is a larval overwintering, autumn breeder was adversely affected by the fall tillage. In the conventional tillage cropping system, carabid diversity was lower than in the reduced tillage system. The assemblage in the conventional system was dominated by three abundant species, which accounted for more than 85% of the total captures (Carcamo 1995, Carcamo et al. 1995).

Total seasonal catches of carabid beetles were not strongly influenced by soil cultivation history. During the main emergence phase of the new generation, however, very low numbers of *P. melanarius* were trapped in spring cultivated fields compared to autumn cultivated fields. Very high numbers were captured after the middle of July. There was a qualitative difference between the beetles caught in the early spring crops compared to uncultivated or autumn cultivated. Virtually no newly emerged females with immature ovaries were trapped throughout the entire season on fields that were cultivated in April or May. The females captured in the early spring cultivated crops had mature ovaries (Fadl et al. 1996).

Further experimental studies showed that newly emerging beetles were destroyed by early spring tillage. Spring cultivation reduced the numbers of *P. melanarius* emerging from pupation by as much as 80% compared with cultivation for winter sown crops. Mature females emigrated from fall planted winter cereal, grass fields, and other tillage refuges outside the field boundaries of the early-cultivated crops. They migrated into and redistributed themselves across the spring cultivated fields (Fadl et al. 1996). The destruction of the emerging cohort and the redistribution of maturing beetles from tillage refuges may explain the delay of approximately one month in the peak density of *P. melanarius* in spring cultivated sugar beet fields compared with fall planted or late spring planted cereal (Hance et al. 1990). The redistribution of beetles across the landscape may explain why the impact of tillage systems is most pronounced early in the season. The effect of tillage dissipates toward the end of the season as the beetle populations disperse (House 1989).

Many types of agrochemicals have an adverse effect on carabid beetles (Jepson and Thacker 1990). Insecticides may have a greater impact on carabid populations than tillage (Thiele 1977). Insecticides can have direct toxic effects on the abundance of carabid beetles (Luff 1987). Chlorpyrifos applied in the autumn for insect control in pastures depleted carabid populations for more than one season (Asteraki et al. 1992b). Insecticides can also have indirect effects. By reducing the prey available, increased beetle activity is stimulated by their search for scarce prey (Chiverton 1984). Herbicides have an indirect influence on carabids by changing the vegetation cover. Even nitrogen fertilizer caused *P. melanarius* to avoid plots with the highest concentrations and accumulated in non-fertilized control plots (Thiele 1977).

There were more native species of carabid beetles in a conventional tillage system when herbicides (MCPA, Diclofop methyl, bentazon, 2,4-D, Cyanazine) and fertilizers (urea, ammonium nitrate, and phosphate 0-45-0) were not used compared to a conventional tillage system that used the chemical inputs. There were several interactions, however, that make the effects difficult to explain. Fertilizers and herbicides depressed *A. placidum* and *Bembidion quadrimaculatum* numbers. *P. melanarius* was depressed by tillage but not by the chemicals. *A. cupreum* and *Amara torrida* were more abundant in tilled plots where fertilizers and herbicides were used. There were no significant differences in overall carabid abundance associated with the herbicides and fertilizers regardless of tillage or crop types unless *P. melanarius* (the dominant species) was pulled out of the data set. Perhaps the native species were more abundant in plots where *P. melanarius* was depressed by the tillage and less dominant (Carcamo 1995, Carcamo et al. 1995).

Insecticide applications can lower carabid beetle numbers caught in pitfall traps for up to six weeks following sprays (Berraondo et al. 1998). Carabid beetle abundance and species richness can be significantly higher in biologically managed cabbage fields compared to conventionally managed cole crops. The carabid abundance may result, in part, from the abundance of prey in biologically managed systems (Hokkanen and Holopainen 1986).

Treatment of pastures with Chlorpyrifos depressed numbers of *Loricera pilicornis*. It was not active at the time the chemical was applied. Several days after the insecticide application, there was abundant prey in the treated field for polyphagous beetles including *P. melanarius*. *P. melanarius* was not significantly effected by the insecticide. The effect of Chlorpyrifos on *L. pilicornis* appeared to be indirect. Chlorpyrifos killed the Collembola. The density of *L. pilicornis* (a Collembola specialist), was depressed by lack of Collembola prey (Asteraki et al. 1992b).

Basedow (1994) found that soil surface dwelling Collembola (Isotomidae) and predators per square meter were identical in the low chemical input and organic wheat fields. Surprisingly, there were more Collembola in high chemical input wheat. The robust plant canopy in the well-fertilized wheat may have created a more favorable microclimate for the Collembola. The sparsely planted wheat in the organic system may have been dryer and less hospitable to the Collembola. Despite the increased number of prey items, there were more Carabidae, Staphylinidae, and Araneae in the reduced chemical cropping systems.

Insecticides can have variable effects on different insect species (Coaker 1966). Aldrin and dieldrin residues reduced numbers of *Aleochara* sp. (Staphylinidae), but increased the numbers of *Bembidion lampros* (Carabidae). *Harpalus* spp. and *P. melanarius* were unaffected by insecticide concentrations that were toxic to the cabbage root fly and its eggs. Small carabids of the size of *B. lampros* succumbed 12 times more rapidly to insecticides than *P. melanarius* (Thiele 1977). Univoltine carabid species, which complete their life cycle within the fields and their immediate boundaries, might be at greater risk from continued exposure to insecticides due to their limited potential for dispersal (Jepson and Thacker 1990).

Carabid beetles are found in their preferred habitats, which vary according to the species and the available choices. Within an agricultural setting, carabid beetles choose between cultivated fields and semi-natural patches of vegetation within and beyond the field boundaries. A single species may occupy different types of vegetation according to their reproductive cycle (Thiele 1977).

Within the field boundary, plant diversity may result in higher colonization by natural enemies. It is difficult to evaluate plant diversity without also considering changes in plant density and the complexity of the vegetation. Plant density and patch architectural complexity can have a positive or negative effect on the attraction and retention of natural enemies to a plant stand (Perfecto et al. 1986, Letourneau 1987, 1990). Several workers have found there can be higher carabid activity in complex vegetation cropping systems than in simple cropping systems (Dempster and Coaker 1974, Speight and Lawton 1976, Ryan et al. 1980, Tukahirwa and Coaker 1982, Brust et al. 1986a, Perfecto et al. 1986, Nentwig 1989, Thomas and Wratten 1990, Tonhasca 1993, Booij 1994). In some cases, changes in vegetation diversity have no observable effect on carabid activity (Purvis and Curry 1984).

P. melanarius was more abundant in immature alfalfa that was mowed on a regular basis compared to the tall, undisturbed alfalfa. *P. melanarius* pitfall captures were over ten fold more common in a short alfalfa collard versus tall alfalfa collard planting. The opposite results were observed with the harvestman, *P. opilio*. When ground predators were excluded from collard plants with raised cylinders, the survival of *B. brassicae* and *P. rapae* increased in the tall alfalfa collard system. Exclusion of ground predators in the short alfalfa collard system had no impact on the survival of *B. brassicae* and *P. rapae*. *P. opilio* is the most likely explanation for decreased survival of *B. brassicae* in the unprotected collards (McIver 1983).

P. melanarius is primarily a woodland species in Scandinavia and central Europe (Thiele 1977). It is a larval overwintering species, which prefers to spend the winter in the woods rather than cereal fields (Wallin 1986). Its high powers of dispersal enables it to exploit meadows and cultivated fields. During the growing season, *P. melanarius* is usually more abundant in cultivated oats or cultivated corn than in grass pasture (Rivard 1965b). It may prefer the more open habitat found in the cultivated cereal crops for foraging. *P. melanarius* prefers to move along the bare ground between plant rows rather than across crop rows (Gordon and McKinlay 1986, Wallin and Ekbom 1994).

In a study of hedgerows and fencerows surrounding pasture, *P. melanarius* was more common in weedy fence lines than in hawthorne hedgerows. Carabid species catches did not correlate with plant species diversity, vegetation structural characteristics, or soil moisture. Some species of ground beetle were more abundant in the hedgerow early in the season and more abundant in the fencerows at the end of the season (Asteraki et al. 1995).

The abundance of *P. melanarius* in cereal fields was positively correlated with field size. *P. melanarius* was more common in larger fields. *H. rufipes*, however, was more common in small fields (Wallin 1985).

CONSERVATION TACTICS

Seminatural vegetation on the field boundaries

The role of field boundaries as habitat for carabid beetles has been widely studied. Field boundary habitats vary in terms of plant diversity, structural diversity, spatial arrangement, and spatial scale. The quality of the field boundary determines which carabid species will be present at the edge of the arable field (Luff 1966, Pollard 1968a, 1968b, Sotherton et al. 1981, Desender 1982, Sotherton 1984, 1985, 1991, Coombes and Sotherton 1986, Thomas et al. 1991, 1992b, Asteraki et al. 1992a, 1995, Asteraki 1994, Gruttke 1994, Petit 1994).

Wide hedgerows referred to as a "woodlot-strip hedgerows" or a node where narrow hedgerows meet to form an island of forest habitat contain a different carabid fauna than narrow linear features. Carabid species use these different habitats or they disperse to adjacent habitats depending on preferences, the season of the year, and their dispersal behavior during reproduction (Gruttke 1994).

Carabids have been divided into various functional groups including true forest species (Thiele 1977), corridor forest species (Petit 1994), meadow species (Asteraki et al. 1995), and open field species (Gruttke 1994). Many of the forest species are unable to fly. They have low powers of dispersal. Carabid species living in a hedgerow node are often unrelated to field species. Carabid species living in hedgerow linear features occur at low density and show a high intensity of movement compared to the woodland species. The "corridor forest species" can be found in hedgerows at significant distances from the nearest forest. Carabid species that are adapted to open meadow habitats are uncommon in hedgerows and woodlots even though they have good powers of dispersion (Gruttke 1994).

Some field dwelling species move in and out of agricultural fields from the field boundaries. They use hedges, undisturbed weedy strips along fencerows, and raised grass banks as overwintering sites. Carabid species may retreat to moisture conserved on the field boundary when the center of the fields dry out in mid summer (Desender 1982, Sotherton 1984, Coombes and Sotherton 1986).

In an agricultural setting, an unsprayed weedy area on the field boundary will contain a greater abundance and variety of prey items than the agricultural fields that receive regular applications of herbicide and insecticide. After an insecticide application, the surviving beetles find prey on the field boundary. Undisturbed areas surrounding arable fields can act as a reservoir from which ground beetles, spiders, and other beneficial invertebrates can re-invade the field after primary tillage and pesticide applications create localized extinction of some species (Sotherton 1984, 1985).

Thiele (1977) studied the fauna of the wide woodland-strip hedgerows (10-20 m) and adjacent fields in Germany. About 95% of the carabid fauna in the woodland-strip hedgerow were forest species. They contained an "impoverished" woodland fauna. On adjacent grain fields, only 2.5% of the forest carabids were found within 10m of the hedge. As few as 1% of the hedge species were found in an adjacent potato field. Mark and recapture trials showed that the forest species, *Pterostichus cristatus*, was strongly attached to the hedgerow habitat. It did not move into the field. *P. melanarius*, on the other hand, preferred the grain and potato fields over the hedge. The difference between the carabid fauna of the woodland-strip hedges and the potato field was greater than the difference between the hedge and the nearby pasture. The wide woodland-strip hedges were of more use in conserving woodland carabid species than in aiding pest control in the agricultural fields.

Narrow hedgerows, however, contain important field species, which overwinter in the hedges and move into agricultural fields during the growing season (Pollard 1968a, 1968b, Coombes and Sotherton 1986). The important field species *P. melanarius*, for example, occurs in significant numbers within hedgerows at certain times of the year (Luff 1987). In another European study, the carabid fauna of narrow hedgerows of hazel and hawthorne were compared to weedy fencerows surrounding a managed pasture. The soils on the edge of the hedgerows tended to be drier than the soil along the edge of the fencerows. The hedgerows were more structurally complex and had a deeper layer of decomposing organic matter. There was a greater abundance and diversity of flora and fauna in the hedgerows. Still, the carabid species catches did not correlate very well with field margin flora, vegetation structural characteristics, soil moisture, sward management intensity, or sward physical characteristic. The number of carabid species was higher in the hedgerow. However, many of the species (29%) occurred solely in the hedgerow. These carabid assemblages may be relicts of woodland assemblages. They were not active colonizers of agricultural fields (Asteraki et al. 1992a, 1992b, 1995, Asteraki 1994).

Some of the species appeared to be hedgerow habitat specialists. *Trechus obtusus*, for example, was only found in the hedgerows. The appearance of habitat specialization may, however, have been the result of its poor dispersal capabilities. *T. obtusus* is wingless. It cannot rapidly recolonize agricultural field after a disturbance. *Trechus quadristriatus* and *C. fossor* were present in both the fencerows and the hedgerows. *T. quadristriatus* and *C. fossor* are strong flyers and can colonize disturbed habitats effectively (Asteraki et al. 1995).

Nebria brevicollis was abundant in the hedge margins in the early summer. It was more abundant in the fencerows in the fall. N. brevicollis experiences a summer diapause. The hedge margin was undisturbed and rich in prey items. The habitat and abundant prey in the hedge margin made it a suitable feeding site for the beetle prior to the summer diapause. *N. brevicollis* breeds in the fall. It may have dispersed from the hedgerow into the open field and fencerows to breed. The open field species *H. aeneus* and *H. rufipes* were trapped in weedy fencerows surrounding a pasture. They were not trapped at all in hedgerows of hawthorn surrounding the same pasture. It is hard to make generalizations about the importance of field boundary habitat to the fauna of the agricultural field. The faunal contribution of the hedgerow and fencerow habitats to the carabid fauna of agricultural fields is related to the dispersal capacity, reproductive behavior, and habitat preferences (Asteraki et al. 1992b, 1995).

Gruttke (1994) studied hedgerows to determine if they serve as corridors that allow forest carabid species to disperse between fragments of woodland habitat. Carabid species were characterized by groups including “widespread species”, which were present in the hedgerows immediately after planting, “rare species” caught only once or twice in the hedgerows, and “ non dispersing species” found only in their original habitats. Only two highly eurytopic carabid species out of 85 species recorded in the study used the habitat strip as a corridor or stepping-stone. Seven woodland carabid species and another 18 species associated with open field sites showed no tendency to disperse into or along young hedges. There was little evidence to support the notion that reconnection of isolated habitat fragments with new hedgerows is an effective means of effecting dispersal of carabid populations between woodland patches. Open country carabid species failed to use the hedgerow for dispersal. The hedgerows may have been too young or too short or not close enough. It appeared that the hedgerows acted as a physical barrier that interfered with the dispersal of *A. binotatus*, a common field dwelling carabid species.

A weedy fencerow may contain many of the carabid species, which are trapped in nearby hedgerows (Desender 1982). Weedy fencerows may be adequate to contain significant densities of Carabidae that are relevant in agricultural situations. But there is a third habitat, the raised bank that is often associated with old hedgerows. Clipped hedgerows with raised grassy banks may be better overwintering sites than flat grassy strips along fencerows (Kromp and Steinberger 1992). Raised banks with rough grass tussocks support high densities of Carabidae, Staphylinidae, Dermoptera, and Araneae (Luff 1966, Thomas et al. 1991, 1992b).

There may be significant differences in the carabid fauna of woodlot-strip hedgerows, raised grassy banks associated with the hedgerows, and flat grassy strips associated with field margins and fencerows. The presence of banks up to four meter high increased the numbers of overwintering predators. Higher numbers of certain species of Carabidae and Staphylinidae were found on raised grass banks compared to flat grass strips. Their abundance may have been due to drainage on the banks (Sotherton 1985). It may have been the result of the temperatures associated with grass mats, tussock grasses, and leaf (Luff 1966, Desender 1982, Thomas et al. 1991).

Carabidae, Staphylinidae, and Araneae were more abundant on the ridges than in the winter grain. Raised banks of the tussock forming grass *D. glomerata* supported significantly higher numbers of total Carabidae than the field of winter wheat or the mat forming grass *L. perenne*. In year one, there was not a great deal of difference between the ridges and cereal. In year two, the abundance of the predators in the ridge was higher than the cereal. There were more Staphylinidae and Araneae in the tussock grass (*D. glomerata*) than the mat forming grass (*A. stolonifera*). The Carabidae were less selective (Thomas et al. 1991).

The dominant carabid beetle, *Demetrias atricapillus*, accounted for 78% of the predatory carabids caught on the ridge. There were no significant differences between the mean temperatures recorded over two winters. However, the variation in temperatures was different. Within the soil where digging beetles overwinter and within the tussock grass mounds, daily variation in temperature was less than on the soil surface, in the winter wheat, or in mat forming grasses including *L. perenne*. Predators that cannot dig in the soil (spiders) may choose the tussock grass as overwintering sites. Carabidae may be less sensitive to grass types because they dig in the soil and can seek refuge there (Thomas et al. 1991, 1992b).

Weeds, cover crops, under-sowing, and strip-management

Lack of cover during the winter and early spring reduces the survival of carabid species, which overwinter as adults. Grain stubble in the absence of weeds or other plant cover supports fewer numbers of Carabidae than weedy crop stubble or cover crops (Lovei 1984). Winter grains and cover crops provide shelter and support early aphid populations that support resident natural enemies. These sites are attractive to overwintering adults (Chiverton 1987b, Winder 1990, Wallin and Ekbom 1994).

During the growing season, mixed plant stands tend to support a greater number of carabid species (Uvah and Coaker 1984, Perfecto et al. 1986). In general, a diverse stand of plants supports a more diverse assemblage of arthropod species that can serve as prey items for Carabidae. Plant density and plant structural diversity influence microclimate and the ease with which carabid beetles move during foraging activities. In some cases, predation by Carabidae is higher in weedy crops (Speight and Lawton 1976). The net effect of mixed planting on the predatory activity of Carabidae may be positive or negative. The effect depends, in part, on the carabid species.

Carabid species richness is positively correlated with weed abundance (Carcamo 1995). Removal of the weedy ground flora at the foot of hedgerows reduces the number of carabid species in the hedgerows (Pollard 1968b). Carabid beetles were more numerous in weedy potatoes compared to herbicide treated potatoes (Boiteau 1984). Carabid densities were higher in weedy cereals compared to clean herbicide-treated cereals (Potts and Vickerman 1974, Speight and Lawton 1976). Reduction in beetle numbers or beetle activity in weed-free fields may be the result herbicide toxicity, lack of prey, or the absence of shelter or suitable microclimate (Luff 1987).

In some cases, the presence or absence of weeds has no impact on the carabid assemblages. In other cases, the effect of weeds depends on the carabid species. Activity/density of *Amara* species were higher in weedy winter wheat while the activity/density of *Pterostichus* species was greater in weed-free wheat. *Amara* species are weed seedeaters. They may have been attracted to the food resource in the weedy cereal. Plant density in the weedy wheat may have interfered with the movement of the *Pterostichus* species. Different pitfall captures in the two cropping systems may have reflected differences in activity rather than density (Purvis and Curry 1984).

Sowing cover crops into standing crops has a variable effect on carabid species. Under-sowing of red clover into Brussels sprouts and cauliflower reduced the apparent number of Bembidion species (Carabidae) compared to bare ground (Dempster and Coaker 1974). More of these small beetles were trapped in pitfalls placed in the bare ground. The under-sowing increased the number of *P. melanarius*. More *P. melanarius* were caught in plots where Brussels sprouts were growing in white clover living mulch or white clover under-sowing than on bare ground (O'Donnell and Coaker 1975).

Sowing of clover into standing Brussels sprouts increased the number of *P. melanarius, H. rufipes*, *P. opilio*, and Staphylinidae compared to clean-hoed plots. Oviposition by *P. rapae* on sprouts was unaffected. Survival of *P. rapae* to the 3rd instar, however, was reduced by nearly 50% by the under-sowing. Oviposition by the cabbage root fly was reduced in Brussels sprouts that were under-sown with clover. Damage to the sprouts by root maggots was higher in the bare ground compared to the under-sown sprouts. Mean fresh plant weight was higher in the under-sown sprouts. The difference in plant weight was probably due to the differential impact of the root maggot. Significantly more alate *B. brassicae* were trapped in water pans in the bare ground compared to under-sown sprouts. Significantly more *B. brassicae* aphids were observed on the plants in the bare ground (Dempster and Coaker 1974).

When the insecticide chlorfenvinphos was applied to control root maggot, the clover under-sowing still enhanced natural enemies and reduced pests on the Brussels sprouts. Cabbage root maggot damage was greater on Brussels sprouts in bare ground plots compared to under-sown plots regardless of the insecticide application. In fact, the root maggot damage was significantly worse on the bare ground plus insecticide compared to the clover under-sowing plus insecticide. These effects may have been associated with colonization of the Brussels sprouts by aphids and root maggots rather than variation in predation pressure by natural enemies (Dempster and Coaker 1974).

The diversity of carabid species tends to be higher in strip-managed cropping systems than in monoculture. Nentwig (1988) studied a meadow that was either left undisturbed or was mowed on a regular basis. Thirty-seven species of carabids were trapped but only five species constituted 80-90% of the captures: *A. mulleri*, *Poecilus versicolor* Sturm, *Pterostichus vernalis*, *Bembidion lunulatum*, and *C.*

fossor. These common species were more numerous and dominant in the mowed blocks than in the strip-mown block. The diversity of carabid species, however, was higher in the strip-managed area.

The presence of weedy strips in agricultural fields tends to increase the abundance and the number of species of carabid beetles in the fields. Carabid pitfall captures tended to be higher in weedy strip-managed barley than in monoculture. From 1989 to 1991, 40 species of Carabidae were captured in conventional cereal and 54 species were captured in the strip-managed cereal. *A. binotatus* was more common in weedy strip-managed cereal than in monoculture. The most numerically important species were *P. melanarius* and *P. cupreus.* Over 70 percent of the *P. melanarius* that were marked and released in monoculture barley migrated into an area of cereal that was strip-managed. The distance between the strips was significant. When the distance between the strips was increased from 12 meters to 78 meters, no effect was detected (Lys et al. 1994).

The movement of the beetles into the strip-managed system may be evidence that the living conditions were better there. A combination of better environmental conditions on the soil surface in the weedy strips and a greater abundance of prey items may have attracted the beetles. Their movement may have been the result of overwintering behavior. Most of the common carabid beetles in a strip-managed barley field overwintered in the weedy strips rather than in the barley. Carabid beetle abundance increased over a three-year period with the strip-management (Lys and Netwig 1994). Dissection of carabid beetle in strip-managed cereal in Switzerland showed that the beetles were better fed in a strip-managed cereal than in a monoculture. Female beetles carried more eggs and their reproductive period lasted longer in the strip-managed area cereal compared to monoculture. The increased reproductive activity may have led to higher densities of the beetle in the next generation (Zangger 1994, Zangger et al. 1994). The impact of strip-management varied according to species. *C. fossor* overwintered in greater numbers in the barley than in nearby weedy strips. *L. pilicornis* and *Agonum muelleri* Herbst were caught at about equal rates in the strip versus the monoculture cereal (Lys et al. 1994).

IMPACT OF RELAY STRIP CROPPING ON CARABIDAE

In a series of relay strip cropping experiments, we combined two vegetation management tactics (under-sowing and strip-management) that should create a more favorable habitat for Carabidae within the crop and provide a safe refuge within the field from tillage operations and pesticide applications. A tillage and pesticide refuge is present at all times in a relay strip cropping system. During the winter, there is vegetative cover to protect adult overwintering carabid species. During the early spring and fall when carabid species are searching for oviposition and overwintering sites, there is undisturbed vegetation. Availability of undisturbed ground cover should have both short and long term impacts on the carabid assemblage.

Under-sowing results in soil that is covered with vegetation prior to canopy closure. The presence of the ground cover moderates the environment and may lead to earlier colonization of the broccoli by Carabidae that are sensitive to microclimate. Under-sowing results in a mixture of plant species. The residual strips at the end of the winter are bound to be weedy. Mixed stands generally support a greater diversity of insects than monoculture. These potential prey items should attract and support a greater variety of carabid species than clean till cropping systems.

Strip-management may conserve Carabidae that are sensitive to disturbance and that are not highly mobile. Following harvest, strips of cover crop and broccoli stubble are left undisturbed until the following planting season. The undisturbed strips should attract fall breeding larval-overwintering carabids that search for oviposition sites in the late summer. The undisturbed strips should be equally attractive to adult-overwintering carabid species that emerge from their puparia in the fall and seek out vegetation.

The following spring, only a portion of the winter cover crop in the relay strip cropping system is disturbed in preparation for the early broccoli planting. Larval overwintering carabid species will have an opportunity to complete their life cycle, pupate, and emerge as adults from the cover crop areas. Spring tillage in clean till cropping systems disrupts and probably kills many overwintering species before they emerge from their pupae. In the early spring, adult overwintering beetles are present next to developing plantings of broccoli. Their proximity should speed the colonization of the broccoli by this group as the females emerge from their winter refuge in the cover crop and seek oviposition sites.

The residual strips should provide a steady source of prey for Carabidae over the winter, in the early spring, and between plantings. The stability of the food supply in the relay is markedly different than in monoculture where tillage, planting, pesticide applications, harvest, and stubble incorporation are constantly removing food resources from the cropping system. The constant supply of prey in the relay strips should increase the number of carabid beetles in the area over time.

If the abundance and diversity of carabid beetles is enhanced, we may see an impact of the carabid beetles on relevant insect pest populations in the broccoli grown in the relay strip cropping system compared to the monoculture. Carabid beetles are known to prey upon aphids and lepidopteran insects, especially the eggs and small larvae of the Lepidoptera.

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APPENDIX B: SPIDER AND HARVESTMEN, LITERATURE REVIEW

INTRODUCTION

Spiders are ubiquitous in both natural and farm landscapes of the Northern Hemisphere (Turnbull 1973). Spiders exhibit a remarkable range of life styles and fill many ecological niches (Wise 1993). In annual cropping systems, spiders are the numerically dominant component of the predator assemblage. The diversity and densities of spiders in agriculture, however, are much lower than in natural systems. Spiders are sensitive to tillage and insecticide applications used in crop establishment and crop protection (Nyffeler and Benz 1987). There are, however, species of spiders that are uniquely adapted to habitats that are repeatedly disturbed on a large spatial scale. These species have a high capacity for aerial dispersal; they disperse freely and for long distances by "ballooning" through the air on silken threads produced by abdominal glands called spinnerets. Ballooning allows them to migrate rapidly into large fields following tillage and insecticide applications (Turnbull 1973, Riechert 1974, Foelix 1982, Nentwig 1986, 1988, Sunderland et al. 1986, Nyffeler and Benz 1987, Nyffeler et al. 1994a, Bishop and Riechert 1990, Young and Edwards 1990, Wise 1993). Spiders are excellent survivors under the adverse conditions that typify a wide variety of agricultural habitats. Spiders have a relatively low rate of metabolism; they are capable of going for long periods without food. Their metabolism allows them to cope with the wide variations in prey abundance in agricultural crops (Nyffeler et al. 1994b).

Spiders are present and active in agricultural systems early in the growing season when many other generalist predators are mainly absent. The early presence of spiders is particularly important when we consider the impact of spiders on insect pests such as aphids, which migrate in large numbers between primary and secondary host plants (Kajak 1978). Normally, the appearance of aphidophagous predators (Syrphidae, Coccinellidae, Chrysopidae, Anthocoridae, Miridae, and Nabidae) is slightly delayed. Delayed arrival of these predators is necessary because it is not adaptive for aphid predators to arrive prior to the build up of their prey populations. Residential web-spinning spiders, however, intercept winged aphids as they colonize agricultural crops during the early part of the growing season (Wyss et al. 1995).

Spiders are also abundant during the autumn when many aphidophagous arthropod populations are declining and when winged aphids are moving from summer to winter host plants. The reduction in colonization of winter host plants by aphids in the autumn can have an impact on aphid populations the following growing season. Lower numbers of colonizing aphids results in fewer aphid eggs being laid, which in turn results in fewer fundatrices the following spring.

The impact of spiders in agricultural ecosystems is extended by their webs (Nyffeler et al. 1994a, Wyss et al. 1995). Estimates of their web-cover in wheat crops at the height of the season are as high as 50% of the soil surface in agricultural fields (Sunderland et al. 1986). The web helps the spider to adapt to the wide variation in abundance and size of prey items in a given habitat. The spider's web often kills more insects than the spider can consume and well in excess of their energy requirements (Nyffeler et al. 1994a). Linyphiidae, for example, typically only eat about 12% of the prey in their webs (Sunderland et al. 1987).

Surprisingly, studies of prey items found in spider webs show that spider webs can be selective (Turnbull 1960, Heidger and Nentwig 1989). One finds very few natural enemies in spider webs. Many natural enemies are robust. If they encounter a spider web, they are strong enough to escape or their thick chitinous shells protect them (Nentwig 1980). Many natural enemies have good visual powers, are agile fliers, and are capable of avoiding the webs. Spider webs in the trees and shrubs are full of poor flying insects that jump and fall (leaf hoppers), or drift with the wind (Aphids, thrips), and insects that are weak (diptera) and not able to break out of the web once they become entangled. Because of this selectivity, the spider webs slow the reproduction of phytophagous insects while conserving the majority of natural enemies of insect pests in a given habitat.

Spiders are regarded as important natural enemies of agricultural pests (Nentwig 1986, 1988, Sunderland et al. 1986, Nyffeler and Benz 1987, Nyffeler et al. 1989, 1994a). Some authors argue that spiders can have a stabilizing effect on natural insect populations (Clarke and Grant 1968, Riechert and Lockley 1984). In some cases, high densities of spiders correlate with depressed densities of agricultural pests (Buschman et al. 1984, Wyss et al. 1995). There are few examples, however, of successful manipulation of spider populations that have resulted in the regulation of crop pests (Rypstra et al. 1999). Still, significant research continues to be directed at developing cropping systems that conserve and protect spider populations in agriculture (Burleigh et al. 1973, House and Stinner 1983, Ali and Reagan 1986, Heidger and Nentwig 1989, Rice and Wilde 1991, Thomas et al. 1992b, Zongo et al. 1993).

The impact that spiders have on arthropod pests is a community phenomenon; it can only be achieved by the composite foraging activities of assemblages of spider species and other predators in the habitat (Riechert and Lockley 1984). The more diverse the assemblage of generalist predators, the greater the likelihood that an effective predator will encounter a pest species and dampen oscillations in the prey population. For example, the combination of spiders foraging during the crop colonization period coupled with the activity of Coccinellidae and Syrphidae later in the growing season may provide a normal level of biological control of aphids (Heidger and Nentwig 1989).

A number of schemes have been proposed to describe the predatory strategies of spider assemblage (Uetz et al. 1999). For example, spiders can be divided into forms distributed on the ground and on plant foliage, spiders that use webs to capture prey and those that either pursue or ambush their prey, those that hunt during the day, and those that hunt at night. Turnbull (1973) listed web builders, wandering jumpers (visual pursuit), and sit and pounce (ambush) hunters. Hatley and MacMahon (1980) identified nocturnal hunters including Gnaphosidae and Clubionidae, web builders including Theridiidae and Linyphiidae, agile hunters including Lycosidae and ambush hunters such as the Thomisidae. The Lycosidae represent the "sit and wait" functional group. The Salticidae represent the "active forager" functional group (Nentwig 1986).

Approximately half of the known spider families do not build webs to catch their prey. Many of these spiders are ground dwelling predators. To a large extent, the predatory Carabidae and Staphylinidae share the habitat of the ground dwelling spiders (including the Lycosidae and many Linyphiidae) and the harvestmen (Phalangiidae). In some cases, the peak seasonal activity of the Lycosidae and Carabidae complement each other. The Lycosidae are active in the early spring while many Carabidae are active in the summer. Together with Carabidae and Staphylinidae, *Erigone* species (Linyphiidae) are the most abundant ground-dwelling predators of insects in agricultural fields (Nyffeler and Benz 1987). Although the many species of spiders, ground beetles, rove beetles, and ants share the same ecological niche, there is little evidence of competition between these groups in Northern Temperate climates (Thiele 1977). Although there are cases where two species of spider appear to compete and inhibit each other (Spiller 1986), in most cases spiders occur stratified horizontally, temporally, and vertically. The stratification significantly limits interspecific competition between spiders (Turnbull 1973).

Given the evidence accumulated today, it appears that no one species of spider, even if it is abundant, can hold a prey population in check (Riechert and Lockley 1984). There is little evidence that spiders track the density of prey populations. Large changes in spider density in a given area do not always correlate with changes in prey population density (Turnbull 1973). Spider density is largely the result of movement or lack of movement by the spider assemblage. When prey populations increase, spiders remain in the area. When prey population growth slows down due to the environment, spiders get hungry, leave, and the predation pressure is diminished. The net effect of this behavior by spiders is that prey population oscillations are dampened. Biological control of pest insects by spiders may be sufficient in years of low pest population density. In other years, pest outbreaks due to abiotic factors often overwhelm naturally occurring biological control. In outbreak years, neither a higher density of spiders alone or in combination with other aphidophagous insects prevent crop damage (Wyss et al. 1995).

BIODIVERSITY

The order Araneae is made up of over 30,000 species (Coddington and Levi 1991). Turnbull (1966, 1973) surveyed 37 published studies of spiders in a wide variety of environments in Northern Europe. He found an overall mean density of 130 spiders per square meter across the habitats. Densities ranged from 0.6 spiders per square meter on mowed grassy meadow in Poland to 842 per square meter on a good pasture in England. Over the summer in an English pasture, 1791 spiders were taken, representing 43 species from 13 families. The most common species were four Lycosidae (789/1791) and 13 species of Linyphiidae (712/1791). Together the two families made up 84% of the spiders collected. The two most common species of Lycosidae made up 41% of the total. One species of Thomisidae made up 4%, one species of Clubionidae made up 2%, one species of

Tetragnathidae made up 2% , and one Dictynidae represented 1%. The logarithmic frequency distribution with a couple of dominant species, a few species in low percentages, and many rare species is typical of most agricultural settings around the world.

Linyphiidae and Lycosidae are usually the dominant families of spiders in agricultural settings. In a mown meadow in Germany over a 5 year period, Nentwig (1988) collected 90 species of spiders. Fifty percent of the species (61% of the individuals) were Linyphiidae and fifteen percent were Lycosidae (30% of the individuals). The remaining taxa included 9 Gnaphosidae, 6 Salticidae, and 9 other families together contributed less than 9% of the remaining individuals. In New Zealand, 23 species of spiders were collected in native tussock habitat, pasture, and arable habitats. The three habitats were subjected to various levels of disturbance, and spider species richness varied with the intensity of disturbance. At the highest level of disturbance, two spider species were dominant in an abandoned pasture. At the lowest level of disturbance, 16 species of spiders were common. Spider densities varied between 1.8 and 130 individuals (Topping and Lovei 1997).

Young and Edwards (1990) analyzed 29 faunal surveys of spiders in the United States and found that about 600 species of spiders occur in US field crops. Rich spider faunas were found in cotton (>300 species), soybeans (>250 species), and alfalfa (>200 species). Nyffeler et al. (1994b) reported a significantly lower average number in horticultural crops. Depressed spider counts may be due to the higher level of pesticides and tillage in horticultural crops compared to field crops.

The European Linyphiidae dominated by *Erigone* and *Leptyphantes* species are common in agricultural settings around the world (Riechert and Lockley 1984, Sunderland et al. 1986, Nyffeler and Benz 1987, Wise 1993, Topping and Lovei 1997). The three most abundant spiders in cultivated fields in the United Kingdom agriculture are *Erigone dentipalpis* Wider, *Bathyphantes gracilis* Blackwall and

Lepthyphantes tenuis (Blackwall) (Turnbull 1966). *L. tenuis* and *Erigone dentosa* were common on the soil surface in alfalfa near Corvallis, Oregon (McIver 1983).

In the past, *Erigone* species were referred to as Micryphantidae. Now, Linyphiidae-Linyphiinae and Linyphiidae-Erigoninae (<3mm in length) are considered sub families (Nyffeler et al. 1994a, Nyffeler et al. 1994b). They are aeronautic invasive species that readily overcome physical barriers to colonize agricultural fields (Ramert and Ekbom 1996). *Erigone* species are less dominant in hedgerows than in agricultural fields (White and Hassall 1994). Although Linyphiidae are present in orchard systems, they are not dominant there (Wyss et al. 1995).

Although they are small, the Linyphiidae are important polyphagous predators (Topping 1993). In winter wheat, Linyphiidae density can reach densities of up to 150 individuals per square meter and represent 70% to 97% of the total spiders assemblage (Sunderland et al. 1987). In one cereal trial, *E. atra* caused a 58% reduction in aphid population growth (Mansour and Heimbach 1993). *Erigone* species live on the ground (Nyffeler and Benz 1987) and spin small sheet webs horizontally over small depressions in the soil surface. *Erigone* diets contain up to 71% Collembola and up to 38% aphids (Clarke and Grant 1968, Nentwig 1980).

Tetragnatha laboriosa is another abundant spider species in field crops in the United States (Wise 1993). Unlike the *Erigone* species, *T. laboriosa* requires three-dimensional structure on which to form its web. *T. laboriosa* invades semi perennial vegetation including alfalfa and may be an alfalfa associate. McIver (1983) found that *T. laboriosa* was more common in the tall undisturbed alfalfa than in the mowed alfalfa, and was more common on collards surrounded by the tall, undisturbed alfalfa than on collards surrounded by mowed alfalfa.

BIOLOGY AND DEVELOPMENT

Spiders reproduce sexually. With a few exceptions, the female spiders are larger than the males (Foelix 1982). Female spiders generally live longer than males. They must live long enough to lay eggs and build cocoons. Sexual differentiation in spiders only becomes apparent in the last one or two instars when the male pedipalps become swollen. Females show few external signs until after the final molt. The external indication of sex in female spiders is the epigynal plate under the forepart of the abdomen, usually between the openings of the book lungs. The book lung is basically a flat plate with a pair of openings. Evidence suggests that female spiders emit a sex pheromone (Turnbull 1973).

Males spiders are very agile, and in some species male spiders balloon just as the young spiders do. Because of their small body size, males need fewer molts to reach maturity than do females. Males mature earlier. After their last molt, the males have conspicuously thickened palpal tarsi. The male palps function as copulatory organs. In contrast to females, most male spiders change their habitats after their last molt. They leave their retreats or webs and become vagabonds. In many cases, they do not catch prey anymore. As soon as they have charged their palps with sperm, they start to wander and search for females (Foelix 1982).

Within a few weeks of copulation the female spider is ready to begin laying her eggs. Female spiders lay eggs in batches. The eggs are never directly exposed to the environment but are inserted directly into an egg case or cocoon. A typical cocoon consists of a basal plate and a cover plate which enclose and protect the egg mass. In the simplest case, only a few silk threads are wrapped around the eggs. Several egg sacs may be produced per female. The total mass of eggs that a female spider produces can be large compared to the body weight of the female. Some species produce as many as 2000 eggs per cocoon and as many as 4 to 5 cocoons each made at an interval of about 45 days. Each cocoon contains successively fewer eggs. One of the main advantages of the egg case is the favorable humidity level that is maintained around the eggs. In many species, the egg cases are constructed inside the spider's retreat. About one week after hatching, the spiderlings crawl from the egg chamber and mature within the retreat (Foelix 1982).

The female spider usually does not survive long after the eggs are laid. There are exceptions. Thomisidae, Salticidae, Gnaphosidae, Clubionidae guard their eggs. Female Lycosidae trail their eggs sacs behind them. The emerging spiderlings ride on her back for about two weeks. The newly emerged spiderlings climb immediately onto their mother's back, where they hold fast to her abdominal hairs. In all, a female wolf spider might carry over 100 spiderlings on her back. During the seven to eight days spent on the mother's back the spiderlings live exclusively from their yolk supply. They enjoy some protection from predators and adverse microclimate conditions. On leaving, they carry a substantial volume of egg yolk in their abdomen and do not eat immediately. The brood disperses. If they are prevented from dispersing, cannibalism occurs. The energy reserves of newly independent juveniles is limited. The first prey must be captured quickly. Failure at this point probably accounts for the bulk of juvenile mortality (Turnbull 1973).

Spiders pass through a number of instars, each followed by a molt of the integument. Metamorphosis is gradual; early nymphal stages of spiders molt every few days. Later instars need several weeks to prepare for the next molt. Small spiders need fewer molts (about five) to mature whereas large spiders pass through about ten molts to reach the adult stage. The final molt complete sexual organs and secondary sexual characteristics. Molting is preceded by a period of fasting (Foelix 1982).

Turnbull (1962) studied the food requirements of *Linyphia triangularis* Clerck (Araneae:Linyphiidae) in an oak forest in England. Egg sacs were collected in the autumn, and spiderlings were fed fruit flies (*Drosophila melanogaster*). All spiders receiving six or more fruit flies per day matured. Spiders receiving insufficient food died in molting or died of disease. None of the well-fed spiders died of disease. *L. trinagularis* was able to metabolize about 27% of its food. Regardless of food consumption, all spiders that matured did so in five stages. Males were fully developed following the fourth molt and did not require food in the adult stage. Females fed heavily in the adult stage, but virtually all of the food was utilized in the production of eggs.

No relationship could be found between food consumption and egg numbers. But the more food consumed by the female, the heavier the eggs. Variation in egg weight was due to variation in yolk size. Yolk size had a bearing on the successful emergence of the spiderlings from the eggs. The size of yolk influenced how long a spiderling could go before its first meal. A straight-line relationship between the quantity of food consumed per day and the daily growth of *L. triangularis* was found, but development proceeded at a low rate even when no food was supplied (Turnbull 1962).

FORAGING

Spiders exhibit a wide range of foraging behavior (Turnbull 1973, Riechert and Bishop 1990, Wise 1993, Nyffeler et al. 1994a). All spiders are carnivores. Most spiders are polyphagous and insectivorous. Predation rates for spiders (number of prey killed per spider per day) are variable depending on factors such as spider size, age, sex, physiological events in the spider's life, weather conditions, and prey availability. Aspects of spider physiology help them adapt to unstable prey abundance in agricultural cropping systems. They are generalist feeders.

They have relatively low metabolic rates. They conserve energy with sit-and-wait foraging behaviors. They are territorial and in some cases, cannibalistic. Territoriality and cannibalism allows their populations to be self limiting (Riechert 1974, 1981, Riechert and Lockley 1984, Wise 1975, 1993, Greenstone 1978, Olive 1982, Nyffeler and Benz 1987).

Feeding by spiders is erratic, with short intervals of intense feeding interspersed with periods of fasting. Spiders have evolved under conditions of food limitation (Wise 1975, 1979). They have the ability to reduce their metabolic rates during periods of starvation. A well developed digestive system, a dispensable abdomen, and the capacity to store fat allows spiders to feed in excess under conditions of food abundance and to go without food for long periods of time. Despite the capacity cope with starvation, the retention of spiders in a given habitat is still significantly affected by availability of food supply (Weyman et al. 1994, 1995).

One can divide spiders into two foraging groups: the wandering spiders and the more sedentary web building spiders. Both the wandering and the sedentary spiders produce webs, but only web weavers spin and use webs to catch prey. Approximately half of the known spider families catch their prey without webs. The wandering spiders either “sit and wait” or “actively forage” for prey (Foelix 1982).

Webs form aerial filters that intercept potential prey that would otherwise pass beyond the reach of the spider’s perception. Web-building spiders do not, therefore, seek out prey in the conventional manner of a predator. The prey of the web builders moves through the stratum that is occupied by the web. Webs amplify the spider’s effective size and command of the space about them (Turnbull 1973).

Suitable sites for aerial webs occur in clearly definable parts of the plant community and are most common in the shrubby vegetation below the tree canopy. The absence of web-supporting structures in the form of shrubs and trees is responsible for the dearth of aerial web builders in pastures and in many other agricultural settings. Suitable sites for web construction must also have microclimate characteristics that suit the physiological needs of the spider. Temperature, humidity, sunlight, air currents, and wind influence web site choice. The site must yield appropriate quantities and forms of prey to meet the energy requirements of the spider (Turnbull 1973).

Linyphiidae make horizontal sheet webs on the soil surface and maze webs in plant foliage. The linyphiid spiders hang upside down below their webs. This position below the web provides them with protection from predators. When prey land, the spiders grab the prey from below and pull them through the web. *Erigone* species build webs on the ground surface. Small irregularities of the soil surface are all that is needed to support them (Wise 1993).

Without a web, a spider cannot detect prey. Therefore, if the structural requirements for web building are present, a web building spider randomly builds a web to determine if the site will yield adequate prey. Turnbull (1964) studied the web site chosen by *Achaearanea tepidariorum* (Araneae; Theridiidae) in a laboratory setting. Fruit flies were released in various settings and spiders were placed in cages in various microclimates around the laboratory. Fruits flies were added to some cages and not others. The use of cages and artificial prey allowed the author to test for microclimate preferences with and without food resources present. No spiders remained in a cage devoid of fruit flies after the third day no matter where the cage was placed among several microclimates in the room. On the other hand, no spider left a cage that contained a fruit fly culture no matter where the cage was placed in the room. The spiders built webs in many structurally and climatically suitable sites only to abandon them due to lack of prey. They never abandoned sites where ample prey was provided.

The spiders located sources of prey through a series of random moves. Air movement played an important role in site selection. Air currents carried their silk bridges from spinneret to a distant object. Therefore, air currents influenced where webs are placed. If adequate prey were forthcoming at a site, random movements cease and the space was systematically "searched" in the sense that the area is filled with web. If prey were not forthcoming within a short period of time, the web was abandoned and random movements resumed. Two factors caused spiders and fruit flies to end up in the same place in the laboratory by different mechanisms. Firstly, the fruit flies fell into a light trap associated with the laboratory window. Secondly, the lab air vent sucked silk bridges toward the same place. Spiders stayed there because there was adequate food (Turnbull 1964).

Heidger and Nentwig (1989) studied the habit of *Dictyna arundinacea* (L.) (Dictynidae) during web site selection. After landing, *D. arundinacea* explored its new environment. It explored the plant that it landed on. It crawled or ballooned short distances (10 cm or several meters) to other plants in the same patch. It appeared to be gathering information about the structure of its habitat. Juveniles spent less time exploring their environment before building their web than adult females that were more circumspect.

There is evidence in the literature that spiders exhibit both aggregation and reproductive numerical responses to increases in prey populations. Movement from patches of low prey density to higher prey density by spiders has been reported (Turnbull 1964, Riechert 1976). Spiders tend to accumulate in areas of abundant prey (Gillespie 1987). Several species of spiders exhibit increased reproductive rates in response to increases in prey consumption (Riechert and Tracy 1975, Riechert 1981, Riechert and Lockley 1984, Wise 1975, 1979).

In laboratory studies, the more prey supplied to spiders per day, the more prey were captured. However, the increase in the rate of capture did not keep pace with the increased rate of supply. The spiders consumed virtually the same quantity of food at the completion of each developmental stage regardless of the rate at which prey were supplied (Turnbull 1962, Provencher and Coderre 1987).

In general, spider populations are relatively stable and not highly responsive to changes in prey density within a given cropping season (Riechert and Lockley 1984). Aggregation and reproductive responses to increases in prey density are limited by the long generation times of most spider species. Spiders are, for the most part, annual species. Generation times in many pest insects are a few weeks. Changes in spider densities are also limited by cannibalism and intra-specific competition. Spider populations show a strong self-limiting competition. Spiders compete for suitable web and hunting sites that afford adequate thermal microclimates and prey numbers. Spiders prey on each other. In an experimental release of high densities of spiders, the predatory effect was not augmented by the releases. Spiders either migrated from the area if this was permitted in the experiment or they ate eachother. The spider populations tended to return to natural densities within a short time (Riechert 1981).

PREY ITEMS

Field observations (Riechert and Lockley 1984) and feeding experiments in the laboratory (Nentwig 1980) show spiders to be rather unspecialized with respect to prey. Most spiders attack prey relative to their rate of encounter with them. There are, however, differences in attack rates among spiders for a given prey species. In cage studies, Reed et al. (1984) found that *Oxyopes salticus* Hentz was a particularly effective predator of early instars of *Trichoplusia ni*. It ate approximately 7.4 larvae per day on soybean plants.

In order to assess prey selectivity among spider species, one must account for the behavior of the spiders (both web building and non web building species) and the selectivity of the webs themselves. The spider species composition of United States field crops is estimated to be 44% web-weavers that spin a catching web and 56% visual pursuit or sit and wait hunters (Young and Edwards 1990). Small web weavers such as *Tetragnatha* have a relatively narrow feeding niche. The active hunting spiders have a broader feeding niche (Nyffeler et al. 1994b).

Prey movements beyond the control of the spider determine if the prey enter the web. Turnbull (1960) evaluated the factors that determine which insects approach the web, enter the web, and are eaten by the spider. Some insects crawl, some hop or jump, some drift on air currents. Of the 581 insects removed from the webs of *L. triangularis*, 532 were winged adult insects, 42 were jumpers, and 7 were walkers.

Spider webs are selective. For example, spider's webs do not often capture Lepidoptera (Young and Edwards 1990, Nyffeler et al. 1994b). Apparently, the wing scales of the moths and butterflies which flake off render the adhesives of spider webs ineffective and allow these insects to escape. Web selectivity is based on the physical nature of the web and the characteristics of the web site (Nentwig 1980).

Webs sieve certain prey out of the air stream. Nentwig (1980) collected prey species from the webs of Linyphiidae and from various insect traps placed in the vicinity of the webs. Water pan and sticky traps were place at three heights (0.8, 1.2, and 1.6 meters) and pitfall traps were place in three positions in the same area. The yellow pan traps captured 60% aphids, 13.5% Chironomidae, and 13%

Brachycera. Pit fall traps contained 26% Collembola, 18% Brachycera, and 14% Chironomidae. Actual prey in the webs were mostly Aphidae and Chironomidae which together made up 70%.

Body size and abundance are criteria for selection of prey from the catch in the web by Linyphiidae (Nentwig 1980). The more abundant and the larger the prey, the more often it is consumed. Most spiders feed on prey that are small relative to their own body size (Wise 1993, Nyffeler et al. 1994a). From newly hatched spiderlings to mature adults, spiders increase many fold in body size. Their webs increased in size, and so did their prey size. The length and the weight of the spider correlates with the prey chosen out of the catch (Turnbull 1960).

In the field, the food of most spiders consists of a rather narrow spectrum of phytophagous and detritophagous insects. Predacious and pollinating species of insects are under-represented (Nentwig 1988, 1989, Nyffeler et al. 1989, 1992, Nyffeler and Breene 1991). Overall, spiders tend to prey heavily on small plant-sucking bugs including Miridae, Cicadellidae, and Aphididae (Turnbull 1966, Kajak 1978). In the laboratory, softly chitinized insects including Diptera, Lepidoptera, some Homoptera, Miridae, and several spider families were accepted by most spiders with acceptance rates of over 50% (Nentwig 1986). Traditionally, spiders are thought to only predate on live moving prey. Recent studies reveal that they also eat eggs, dead animals, plant pollen, and artificial diets (Nyffeler et al. 1994a).

Some Heteroptera, Staphylinidae, Carabidae, Opiliones, Cedicomyidae, Acari, and parasitic Hymenoptera used poison, odor, and defensive glands to fight off spider attacks (Nentwig 1980). Mites are often caught and die in spider webs. They are seldom eaten. Thickly chitinized insects (Coleoptera) and arthropods that are aggressive or employ chemical defenses were mainly refused by spiders (Formicoidea, many Heteroptera, Myriapoda). Beetles are also rejected. Beetles may also be unattractive to spiders because they are non social and occur at relatively low densities. Spiders that specialize tend to focus on social arthropods (Nentwig 1986). Spiders prey on honey bees, bumble bees and other beneficial insects. Beneficial insects may constitute a significant proportion of the diet of some spiders in certain circumstances (Nyffeler et al. 1989, Nyffeler and Breene 1991).

Turnbull (1973) observed that certain insects that were ensnared in spider webs are carefully cut out and discarded by the spider. In some cases, the spider failed to respond or even retreated from the prey item. Spiders can be inconsistent in choosing or rejecting prey items. It is dangerous to make generalizations. A hungry spider may attack a distasteful prey. A satiated spider may reject a desirable prey. Imminence of molt, alarm, time of day, intensity of light, moisture, temperature, or wind may influence the state of the spider and its predisposition to a prey item. A single rejection or even a number of rejections in a row merely demonstrate that at the time of presentation, the prey were not desired. Familiarity influences acceptance. If this is true, a strange prey item thrust upon a spider may be rejected even though it may be acceptable later (Turnbull 1960).

An idealized prey of the web building spiders would be a slender, elongate insect with big wings, long appendages, and abundant hairs, spines, or other appendages (antennas, legs, etc) (Turnbull 1960). It would be highly mobile, but it would not be a strong, adroit flyer. It would not be primarily visually oriented. It would drift in the wind or jump frequently, or tend to drop from upper to lower vegetation layers. It would not be very big (ideally 1-3 mm for spiders of 1-5 mm body length). It might be attracted to the shrubby vegetation supporting a spider's web by microclimate or some product of the plants and animals that occupy the site (Nentwig 1980).

The food of web building spiders is unlikely to be tied to any particular taxonomic group (Turnbull 1960). The prey taxa commonly found in spider webs (Chironomidae, Linoniidae, Tipulidae, Cecidomyidae, Cantharidae, Aphidae, Homoptera, and Thysanoptera) are poor flyers and frequently drift in the wind. Some of these groups have poor eyesight (Nentwig 1980). The prey composition derived from the webs of *Dictyna arundinacea* (L.) included dipterans, aphids, and thysanopterans. As a whole, there were more weak flying insects and very few strong flying insects (Heidger and Nentwig 1989).

Syrphidae, Dolichopodiae, other Brachycera, Staphylinidae, parasitic Hymenoptera, and perhaps Mycetophilidae have good flying ability and good eyesight. They are rarely captured in spider webs (Nentwig 1980). Coccinellidae and Syrphidae are rarely found in spider webs. Few parasitic wasps are caught in spider webs (Heidger and Nentwig 1989).

Carabidae seldom enter spider webs because they are mostly on the ground. Many Coleoptera and caterpillar-like larvae of insects are strong enough to free themselves of spider webs. Tipulidae and Opiliones have the ability to shed legs and thus escape from spider webs. Most Brachycera including Sciaridae (excluding Syrphidae and Dolichopodiadae) avoid the vegetation layer where the webs of spiders are mostly found. Tipulidae and Aphidae are abundant in the lower vegetation layers where the webs of Linyphiidae are placed. Aphids are often caught (Nentwig 1980).

Pollinating insects are under-represented in the webs of the Linyphiidae. Parasites and predators are under-represented (Opiliones, parasitic Hymenoptera, Carabidae, Dolichopodidae, predatory Heteroptera). Detritophages are seldom caught (Staphylinidae, Mycetophilidae, Sciaridae, Psychodidae, and perhaps Collembola). Phytophages are often caught and consumed (Thysanoptera, Aphidae, Homoptera, Cecidomyidae, Acari). At the same time predators and parasites are proportionally caught less, with the result that the destruction of phytophages is even greater (Nentwig 1980).

Spiders are known to be important predators of cereal aphids (Sunderland et al. 1986). Linyphiidae have been shown in European wheat to trap up to 40% of diet cereal aphids. They may play a role in regulating the size and frequency of cereal aphid outbreaks (Potts and Vickerman 1974, Edwards et al. 1979, Chambers et al. 1982). Linyphiidae feed on *Rhopalosiphum padi* (L.) (Chiverton 1987, Sunderland et al. 1986, 1987, Nyffeler and Benz 1988). Mansour and Heimbach (1993) found that *Erigone atra* had the highest ability to feed on aphids and caused a 58% reduction in aphid population development. *Erigone* hunts on the plants and traps with its web. *L. tenuis* showed a lower ability to reduce aphid populations. In experimental cages with wheat, *E.atra* build small webs a few mm above the ground surrounding the wheat plant. It was also observed searching for food on the wheat plants themselves. *L. tenuis* build larger webs a few cm from the ground covering all the base area of the cage. Aphids were captured mainly in the webs while they were moving down to the ground from the plants.

Very few species of non web building spiders specialized on any one prey type. For those spiders that do specialize, the most common prey taxa are other spiders, social insects which occur locally in great abundance including ants, or termites, and to a lesser extent, bees and wasps (Thomisidae). Although complete specialization is uncommon, the rate of acceptance prey items varies widely. *Misumena* 9% (Thomisidae) only accepted 9% of the prey items offered in a laboratory study. *Cupiennius* (Ctenidae) accepted 77% of the prey species offered. Some *Dysdera* species are reported to prey on Isopoda with a high degree of selectivity. Foliage-dwelling Oxyopidae hunt mainly for pollinating insects on vegetation. Ground dwelling Oxyopidae hunt ants (Nentwig 1986).

Prey specialization is common in Salticidae and Thomisidae. Thomisidae specialize in both habitat and prey. Ground dwelling Thomisidae tend to specialize on ants. Flower dwelling species tend to specialize on Brachycera, bees, wasps, and Lepidoptera, what one would expect to find attending flowers (Nentwig 1986).

Pardosa (Lycosidae) species are intermediate in prey selectivity. Their favorite prey are Collembola, Diptera, Cicadina, Aphidoidea, and Araneae (Nentwig 1986). They rarely eat Coleoptera, parasitic Hymenoptera, Lepidoptera, or Formicoidae. Still, Lycosidae are not very specialized, and the degree of specialization may vary according to habitat type. *Pardosa* species are common in a wide variety of habitat types. *Pardosa agrestis* juveniles move around on wheat plants and on the ground. Adults are only found on the ground and accepts a wide variety of prey types (Mansour and Heimbach 1993).

MOVEMENT AND DISPERSAL

Spiders disperse by walking, climbing on silk between plants, and by ballooning (Nyffeler et al. 1994a). An adult male Lycosidae can cover a straight-line distance of up to 100 meters on foot in a growing season. The normal home range of *Pardosa lugubris* is about 200 square meters (Turnbull 1973). Female Lycosidae move a shorter distance than males and have much smaller ranges. Walking is important for some groups of spiders, but the primary mode by which spiders colonize agricultural fields is by ballooning (Bishop 1990, Greenstone 1990, Weyman et al. 1995).

Formerly, it was believed that only the young spiders could balloon. It has been found that many of the smaller species balloon as adults as well. In the Linyphiidae, adult males and females take to the air in mass flights that occur in the autumn and early spring (Foelix 1982).

Spiders balloon for relatively long distances during migratory periods (Foelix 1982). Spiders have been caught from airplanes flying at several thousand meters altitude. Darwin noted in 1882 that many small spiders had been blown into the rigging of the Beagle 100 kilometers off the coast of South America. Spiders in the family Linyphiidae were among the first to colonize the newly emerged islands near the volcano Krakatoa. Spiders also balloon short distances, as little as a few meters, while they are exploring a habitat (Heidger and Nentwig 1989).

The major ballooning spider families that recolonize agricultural fields following insecticide applications and tillage operations are in the Linyphiidae, Lycosidae, and Araneidae (Riechert and Lockley 1984). Levels of ballooning activity tend to be higher in the early part of the cropping season and decline as the season progresses. Spider numbers in the fields increase as ballooning progresses, suggesting that spider ballooning early in the season into agricultural fields have a tendency to remain there if food supplies are sufficient (Nyffeler and Benz 1987).

The retention of spiders is significantly affected by availability of food supply (Weyman et al. 1994, 1995). Spider emigration is generally associated with three factors, unfavorable thermal environments (Enders 1972, Duffey 1978, Uetz and Hodge 1990, Ward and Lubin 1993), low prey availability (Waldorf 1976, Uetz and Hodge 1990), and disturbance (Nyffeler and Breene 1990, Scheidler 1990, Thomas et al. 1992b, Clark et al. 1993).

The high mobility of spiders limits the utility of small plot research strategies. Using transects from the edge of apple orchards to the middles, for example, Brown and Lightner (1997) found that spiders showed an edge effect which penetrated 33-43 meters into the orchard. He found that spiders were more likely to have an edge effect than the highly mobile beetle, *Coccinella septempunctata*. The author recommended a plot border minimum of about 30 meters and plot sizes of at least 7.5 hectares for sampling spiders.

SEASONAL ACTIVITY AND WINTER SURVIVAL

Most temperate region spiders live for one year; some live for two. Spiders have a variety of strategies for reproduction, migration, and winter survival. In many species, the reproductive period lasts from late summer until late fall. If the egg sacs are constructed during late fall, hatched spiderlings remain inside the cocoon until spring (Foelix 1982).

For other species, the main reproductive period is in the spring. Young females over-winter in reproductive diapause. In many cases, only females are found in the spring. They lay their eggs in April or May. The new cohort of spiderlings hatch in mid summer, and for a period of time the assemblage consists of two generations of females (one young and one old) plus a single new generation of males (Foelix 1982).

The majority of spiders migrate as juveniles during the crop establishment period in the early spring. Ballooning declines as the season progresses. Spider numbers in agricultural fields reflect ballooning activity and tend to increase as ballooning progresses. Spiders that balloon into agricultural fields have a tendency to remain there if food supplies are sufficient (Nyffeler and Benz 1987).

Following the growing season, about eighty five percent of the spider fauna in typical agricultural settings over-winter on the soil, mainly in leaf litter. Leaf litter is a good insulator which protects spiders against cold and desiccation, and mortality during the winter is surprisingly low. Spiders overcome winter conditions by carefully selecting appropriate microhabitats and by reducing their metabolic rate which increases their resistance to cold. Some spiders including many species of Linyphiidae are active as adults during the winter (Foelix 1982).

HABITAT PREFERENCES

Although spiders are primarily motivated by the presence or absence of adequate numbers of prey, spiders do have preferences for various microclimates (Turnbull 1973). Spiders are sensitive, for example, to variations in moisture (Riechert and Lockley 1984). The primary adaptation by the spiders to a feast and famine existence is the non-sclerotized abdomen. The abdomen allows for consumption of large meals when they are available. The trade-off includes more water loss through the cuticle. Spider populations tend to increase in vegetable crops when plant canopies close and relative humidity increases (Buschman et al. 1984).

The loss of habitat structure has a significant impact on spider diversity in agricultural systems (Hatley and Macmahon 1980, Bishop and Riechert 1990). Experimental manipulation of vegetation in agricultural settings affects several properties of spider communities, but the most important determinant of spider species richness and the number of functional guilds in a given area remains vegetation structural complexity (Hatley and Macmahon 1980). Part of this response has to do with preferred microclimate. The main effect, however, has to do with vegetation complexity and physical structure in the habitat. Spiders respond in different ways to horizontal and vertical structures in their habitat (Robinson 1981). Habitat structures are important for both the web-building and non web-building spiders (Duffey 1962, Rushton and Eyre 1989, Rushton et al. 1989).

Increases in vegetation structural complexity results in increased numbers of web-building spider species (Hatley and Macmahon 1980, Bishop and Riechert 1990). Web-building spiders species require three dimensional structures in order to form their webs, so it is primarily the loss of woody habitat that has an impact on these species. Spider diversity tends to be highest in perennial cropping systems such as orchards where physical habitat structure, microclimate, and potential prey populations are more stable (Riechert and Lockley 1984).

Vegetation structural diversity also increases the number of non web-building spiders. Vegetation, including flowers, serves as hiding spots for ambush hunters (Thomisidae). There is evidence that ambush hunters prefer shrubs (Hatley and Macmahon 1980). Even the ground dwelling Lycosidae are attracted to areas of structural complexity (White and Hassall 1994). In part, the impact of vegetation structural complexity on the Lycosidae is linked to prey diversity and abundance. Lycosidae, however, are also attracted to shelter. Woody debris and thick layers of partially decomposed organic matter on the soil surface serve as hunting retreats and over-wintering sites that are important to Lycosidae (Nentwig 1986, 1988).

IMPACT OF AGRICULTURAL PRACTICES

In natural habitats, spiders can occur at densities of up to 800 individuals per square meter (Turnbull 1973). Spider densities in vegetable crops, however, are severely limited by the disruptive effects of insecticide applications (Brown et al. 1983, Thomas and Wratten 1990, Jagers-op-Akkerhuis 1993), cultivation (House and Stinner 1983, Rice and Wilde 1991, Clark et al. 1993), harvest of above-ground vegetation (Turnbull 1973), and other agricultural practices. Insecticides and tillage suppress both the density and diversity of the spider assemblages.

Spiders are highly sensitive to insecticides. Field studies of insecticide toxicity to spiders often produces different results than direct dermal toxicity tests conducted in the laboratory. In the field, insecticides are more toxic to spiders than would be predicted from laboratory studies. The unexpected increase in toxicity is due, in part, to the quality of spider webs and the foraging behavior of the ground dwelling spiders (Samu et al. 1992).

Spider webs catch spray droplets with greater overall efficiency than paper or leaf surfaces. Web takes up 20 times more the insecticide spray per unit area than do paper strips. Solid surfaces deflect moving air. Deflection prevents a portion of incoming spray droplets, especially the small droplets, from landing on solid surfaces. Air moves through spider webs. A greater proportion of the smaller droplets collects on the web. Further, many species of spiders recycle their webs, and this further increases their exposure to insecticides (Samu et al. 1992).

Some groups of spiders spend a significant proportion of their lives on the soil surface where they come into contact with pesticide residues. Thiodan (pyrethroid), Endosulfan (Chlorinated hydrocarbon), and Ayrozophos (Organo phosphate) were more toxic to the ground dwelling Lycosidae, for example, than to the foliage dwelling Linyphiidae when the spiders were exposed to the insecticides sprayed on filter paper or on moist sand. Direct dermal toxicity tests did not produce the same results. Lycosidae spend more time in contact with the soil surface pesticide residues. The species of Linyphiidae tested spend less time in direct contact with the soil surface. The time they spend foraging on the soil surface explains, in part, why Lycosidae occur in low numbers in many conventional vegetable production systems (Mansour et al. 1992).

Generally, tillage has been found to have minimal or variable effects on foliage-inhabiting insects (Troxclair and Boethel 1984, Thorvilson et al. 1985, Hammond and Stinner 1987, Funderburk et al. 1988) and their natural enemies

(McPherson et al. 1982, House and Stinner 1983, Funderburk et al. 1988, Rice and Wilde 1991). Spiders, however, are generally more abundant in reduced tillage planting systems, and the number of species is generally higher in the undisturbed old-field vegetation than in either reduced or clean till planting systems (House and All 1981, Rice and Wilde 1991). Spiders are uniquely sensitive to tillage. Some authors argue that the effect of tillage associated with planting and stand establishment is more disruptive to spider communities than the use of pesticides. Tillage and seedbed preparation removes all of the vegetation on which spiders depend. Cultivation destroys spider eggs sacks in leaf litter and crop residue on the soil surface (Riechert and Lockley 1984).

House and All (1981) evaluated the relative abundance of arthropods in three cropping systems and two semi-natural habitats: clean till and no till soybeans, a fescue grass field, undisturbed old field vegetation, and a woodland fragment. All groups of arthropods including spiders were higher in the no till than the conventional till soybeans. Spiders were higher in undisturbed old field vegetation than in either soybean system. The old field vegetation was spatially heterogeneous and stratified, and this may have promoted higher species diversity among spiders. Increased weediness associated with reduced tillage systems may be responsible for a significant proportion of the increase in spider diversity in reduced tillage cropping systems (Buntin et al. 1995).

RESPONSE TO VEGETATION MANAGEMENT

Spider families vary in their sensitivity to changes in vegetation management. White and Hassall (1994) observed that the number of nocturnal hunters (Clubionidae and Gnaphosidae), agile hunters (Lycosidae), and ambush hunters (Thomisidae) were positively related to vegetation structural complexity. Catches of web building Linyphiidae, however, were not related to vegetation structural complexity.

Population densities and biomass of foliage-dwelling spiders in annual crops are generally low (Nyffeler and Benz 1987). Low population density is due, in part, to the total removal of vegetation at harvest. Annual cropping systems are dominated by highly mobile ground dwelling spiders including the Lycosidae and the Linyphiidae. The net effect of the disturbances in annual cropping systems is that the fresh weight of prey items consumed by foliage-dwelling spiders is low (Kajak 1978).

In comparing the spider fauna in various crops, we need to keep in mind the intensity and the patterns of disturbance associated with the crop. In pasture land, for example, the species richness of spiders tends to increase as the intensity of grazing decreases (Rushton and Eyre 1989, Topping and Lovei 1997). In heavily grazed pastures, the spider assemblage is dominated by *Erigone* and *Lepthyphantes* species (Linyphiidae). Rushton et al. (1989) found that Clubionidae and Lycosidae increased as pasture management and grazing intensity decreased while *Erigone* species decreased with reduced disturbance. Populations of *Erigone* spiders were very small in the abandoned pastures. Spider diversity was enhanced by the cessation of grazing, but the overall abundance of spiders (all species combined) was lower in the abandoned pasture compared with a moderately grazed pasture.

Lycosidae are sensitive to disturbance and attracted to perennial structures. McIver (1983) collected *Pardosa sternalis* Thorell (Lycosidae) in alfalfa, and found that it was significantly more common in tall undisturbed alfalfa than in alfalfa that was mowed regularly. Its enhanced presence in the tall alfalfa was unexpected because P. sternalis is strictly a ground predator; it was absent from the foliage of either alfalfa. Lys and Nentwig (1994) studied a strip management production system for cereals and found that Lycosidae were abundant in the undisturbed weedy strip where they occurred at densities up to 54 spiders per square meter. None were trapped, however, in the cereal itself.

Cover crops

In general, cover crops and ground covers between crop rows increase spider diversity and abundance (Daane and Costello 1998). Higher density in ground covers does not, however, guarantee elevated numbers of spiders on the target crop. If the spider species uses the ground cover as an alternative source of prey or habitat, the ground cover may be a sink rather than a source of spiders colonizing the crop. In some cases, spider abundance in the cropping system is lower when ground covers are present. The influence of ground covers varies with species (Costello and Daane 1998).

The enhancement of spiders on the target crop by the presence of ground cover implies that spiders move between the cover crop and the target crop. Movement by spiders from ground cover to crop may be motivated by increased numbers of prey in the crop or movement of prey species between the ground cover and the target crop. The circumstances that prompt a spider species to move between the cover crop and the target crop are not well understood (Wyss et al. 1995, Costello and Daane 1998).

In California vineyards, for example, Costello and Daane (1998) found that the maintenance of ground cover in grape vineyards in California increased spider species diversity in vineyards as a whole. There were, however, no major differences in spider species richness or total abundance on the vines themselves with different ground cover management systems. With selected spider species, ground cover increased abundance, but the ground cover did not affect the species richness or evenness in the cropping systems. Six species of spiders comprised over 90% of the collected spiders on the vines, regardless of the cover crop treatment. Total spider abundance (species combined) on the vines tended to be higher early in the season when no cover crop was present, because the abundance of some spider species was depressed by the presence of the ground cover.

Distinctly different spiders within a given crop are associated with plant foliage versus the soil surface. Therefore, we should expect very different responses to ground covers that may or may not be relevant to the spider fauna on the crop itself. Spider families associated with soybean foliage, for example, are dominated by Oxyopidae, Thomisidae, and Salticidae. Lycosidae and Linyphiidae dominate spider assemblages on the ground in soybeans (Ferguson et al. 1984).

Costello and Daane (1998) found that the spider assemblages in the ground cover surrounding grape vines were quite different from that in the grapevines and that this difference explained, in part, why the ground covers had little impact on the spider assemblage on the vines. There was little movement of spiders between ground cover and the vines. The most common spider taxa collected on the grape vines were in the families Corinnidae, Clubionidae, and Salticidae. The most common spider taxa on the ground cover below the vines, were Linyphiidae and Lycosidae. These spiders generally do not forage on the plant foliage. Only one group of spiders in the family Oxyopidae were common on both the vines and the ground cover. The most common Linyphiidae on the soil surface, *E. dentosa*, was more abundant in the cropping system when ground covers were absent.

Crop diversity alone does not have a direct effect on spider diversity. Sorghum and corn associated with cotton, for example, did not significantly affect the abundance of spiders (Burleigh et al. 1973). Spiders were not affected by corn and soybean inter-cropping versus monoculture (Tonhasca and Stinner 1991). More spiders were observed around Brussels sprout grown in bare ground than on sprouts grown in weedy ground (Dempster 1969). Increases in orb weaving

Araniella species (Araneidea) in orchards were associated with weedy strips, but the increase could not be explained by the presence of diverse species of weeds. The weeds did not serve as habitat for these tree inhabiting spiders. Instead, the spider numbers probably increased because the weeds enriched the environment with prey items (Wyss et al. 1995).

Web location depends on structural features necessary for web construction, the thermal properties of the site, and prey availability (Riechert and Tracy 1975, Riechert 1976). It is difficult to separate the effects of vegetation structural diversity and prey availability. Diverse vegetation provides diverse prey as well as structural diversity. Plants with attractive structures such as flowers are likely to support greater densities of potential prey for spiders, and the retention of spiders is significantly affected by availability of food supply (Weyman et al. 1994, 1995).

Conservation headlands

Farmers in England are encouraged by the government to manage field margins for wildlife and beneficial insects by reducing herbicide applications within 6 meters of the field boundary. Reduced herbicide applications, for example, results in weedy borders that provide seed, insects, and refuge for ground dwelling birds including pheasant and quail. The weedy borders also provide early season pollen, nectar, aphid honeydew, and alternative prey for pollinators and natural enemies of crop pests. Collectively, these semi-managed borders are called "conservation headlands" (Chiverton 1989).

Conservation headlands have been shown to be beneficial to carabid beetles (Sotherton 1985, Cardwell et al. 1994), heteropteran predators (Hassall et al. 1992), hoverflies (Cowgill et al. 1993a, Cowgill et al. 1993b), and butterflies (Dover et al. 1990). They do not, however, seem to benefit spiders. Perhaps spiders are sensitive to limited disturbance and the selective use of pesticides on conservation headlands (White and Hassall 1994).

White and Hassall (1994) found that the only type of conservation headland that produced a significant change in spider species richness was the completely unmanaged headland that had tall, uncut weeds, and some young pioneer shrubs and trees. The unmanaged headlands developed significantly higher populations of Lycosidae than the weedy headlands, the clean-sprayed headlands, the cereal crops, or the bare ground. The change was very gradual, however. The spider community in the unmanaged headlands took four to ten years to begin to diverge significantly from the clean-sprayed and the selectively-sprayed headlands. *Erigone* species (Linyphiidae) persisted and continued to dominate the spider assemblage after ten years of selective pesticide applications and reduced tillage on the semi-managed conservation headlands. The *Erigone* species were better adapted than the Lycosidae species to occasional pesticide applications and moderate levels of soil disturbance (Gibson et al. 1992).

Hedges

Permanent structures on the field boundary can have an impact on the abundance and the species richness of spiders. When carried by the wind, ballooning spiders accumulate at wind-braking obstacles such as hedgerows and strips of vegetation. The accumulation and establishment of species takes several years and varies according to the habitat preferences of the spider species (Lewis 1969a, Lewis 1969b, Lewis 1970, Nentwig 1988).

White and Hassall (1994) studied the spider fauna in barley and wheat fields surrounded by several types of field boundaries including clean sprayed, selectively sprayed (broad leaf weeds allowed), unsprayed, and hawthorn hedge. The spiders present in the cropping system, the borders, and the hedgerow tended to be highly aeronautic invasive species including *E. atra* (Linyphiidae). There were no differences in the abundance of Linyphiidae in the various habitats. The barley, the clean-sprayed borders, and the weedy borders, however, supported fewer spider species overall than the unmanaged borders or the hawthorn hedges. There were significantly more Lycosidae in the hedgerows. Low numbers of Thomisidae were capture in the hedgerows, but none were captured in the barley.

Relay Strip Cropping

The focus of this study is to determine the impact of relay strip cropping on natural enemies of insect pests in broccoli. Relay strip cropping combines two vegetation management tactics (undersowing and strip management) that should have an impact on the spider assemblage in an annual vegetable cropping system. The undersowing establishes a polyculture of vegetable crop, cover crop species, and weeds. Although plant diversity alone is not expected to have a direct affect on the spider assemblage, the diverse assemblage of plants in the relay strip cropping system will provide diverse habitats, structures, and prey items that should attract a greater diversity of spider species than a simple monoculture. In some cases, an increase in prey diversity and abundance associated with increased plant diversity in a cropping system have resulted in significant changes in spider assemblages (Wyss et al. 1995).

In contrast to undisturbed habitats, annual crops are mostly unsuitable for the colonization by and survival of foliage-dwelling spiders. The periodic harvest of essentially all of the vegetation in an annual cropping system destroys their habitat and removes their eggs sacs. Periodic colonization of the fields from surrounding habitat is necessary, and this requirement skews the spider assemblage toward those spider species that are highly mobile and capable of tolerating the harsh conditions associated with a new crop. As a result, typical monocultures are dominated by Linyphiidae. One important measure of the impact of relay strip cropping on the spider assemblage will be its ability to reduce the dominance of the Linyphiidae in the target crop.

The ratio of Lycosidae to Linyphiidae may be an important indicator of habitat quality for spiders. In a strip managed meadow, Nentwig (1988) found that the annual Linyphiidae biomass decreased and Lycosidae biomass increased over a five year period. The strips were rich in structures that are completely absent in annual clean tillage cropping systems including old flower stalks, decaying hollow stems, and pioneer woody species including *Salix* species. A thick layer of old vegetation and woody debris covered the soil in the strips.

We expect to see a greater number of spiders successfully overwintering in the relay strip cropping system than in the monoculture where the field is winter fallowed. Thomas et al. (1991, 1992a) found significantly higher numbers of overwintering spiders in grass strips than in winter wheat. The type of vegetation made a significant difference in overwintering success of the spiders. Under tussock forming bunch grasses, the fluctuation in temperature extremes during the winter was diminished compared to bare soil, and this protected the overwintering predators. Lys and Nentwig (1994) evaluated the effect of strip management on the spider fauna associated with barley and found that most of the spiders in a strip managed barley planting overwintered in the weedy strips rather than the barley.

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APPENDIX C: COCCINELLIDAE LITERATURE REVIEW

INTRODUCTION

Aphidophagous Coccinellidae occur in large numbers in agricultural systems; they are an important component of the generalist predator guild (Hagen 1962, Hodek 1967, 1973, Obrycki and Kring 1998). Coccinellidae are abundant in the early growing season when agricultural pest populations are just becoming established. For the most part, aphidophagous Coccinellidae do not specialize on individual prey species. The highly mobile adult beetles have the potential of switching from aphids on native or other non-crop vegetation to agricultural crops as aphid populations begin to expand there. The switch from non-crop vegetation to forage and egg laying in agricultural crops constitutes a rapid numerical response to changing aphid densities (Mills 1982).

The impact of aphidophagous Coccinellidae on prey populations is, to a large extent, the result of predation by coccinellid larvae (Mills 1982). The larvae are not highly mobile. The selection of oviposition sites by the female commits the larvae to searching for available prey in the vicinity where they hatch; they are forced to forage aggressively to avoid starvation (Rockwood 1952, Hodek 1973).

To fully appreciate the potential of the Coccinellidae as natural enemies, one must also recognize their role in the larger guild of generalist predators (Dixon 1985). Coccinellidae dislodge many more aphids than they consume; this is due to aphid escape behaviors, which include dropping from the plants when they are alarmed. Aphids dislodged to the ground are exposed to biotic and abiotic mortality factors including ground predators, spiders, high soil temperatures, and dry conditions as they search for a new host plant (Roitberg and Myers 1978).

Aphid escape behaviors can be initiated by direct contact with a predator, by plant-borne vibrations caused by foraging predators, by alarm pheromone released by disturbed conspecific aphids, or by a combination of these factors (Losey and Denno 1998). When confronted by Coccinellidae, aphids are more likely to drop off the plant, because Coccinellidae exhibit a more vigorous foraging activity. Coccinellidae dislodge more aphids than the activity of parasitoids or other predators (Brodsky and Barlow 1986).

In North America about 180 species of Coccinellidae have been imported for use in the biological control of homopteran insects, especially scales, since the 1880's (Gordon 1985). About 27 species of exotic Coccinellidae are now established in North America (La Mana 1995). Most of the successful biological control programs utilizing Coccinellidae have been against sedentary prey in the scale superfamily (Homoptera: Coccoidea) (Hodek 1973, Mills 1982). Scale insects are sessile; their life histories and those of their coccinellid predators tend to be highly synchronized. One of the most highly acclaimed successes in the history of classical biological was the introduction of *Rodolia cardinalis* Mulsant into California in the mid 1880's (Hagen 1962). This coccinellid beetle successfully controlled the cottony cushion scale, *Icerya purchasi* Maskall and saved the citrus industry in California. There are few examples of biological control by aphidophagous coccinellids (Chambers et al. 1982, Mills 1982, Kring et al. 1985, Rice and Wilde 1991, Flint et al. 1995, Neil et al. 1997, Dixon et al. 1997, Obrycki and Kring 1998).

BIODIVERSITY

More than 4000 species of Coccinellidae are known worldwide, including 475 species in 57 genera in America north of Mexico (Gordon 1985). Ewing (1913) listed several native species of Coccinellidae which were common near

Corvallis, Oregon in the early 1900s: *Hippodamia spuria* LeConte, *Hippodamia parenthesis* Say, *Coccinella novemnotata* Herbst., *Coccinella transversoguttata* Faldermann, *Chilocorus bivulnrus* Mulsant, *Psyllobora toedata* LeConte, and *Smilia misella* LeConte. Other native Coccinellidae collected in alfalfa, clover and vetch in the mid 1950's included *Hippodamia tredecimpunctata tibialis* (Say), *Hippodamia lunatomaculata* Motschulsky, *Hippodamia quinquesignata* (Kirby) (Rockwood 1952). None of these species have been reported in recent surveys (McIver 1983, Belnavis 1989, La Mana 1995).

McIver (1983) reported that the exotic species *Coccinella trifasciata* L. was the dominant coccinellid species in an alfalfa and collard cropping system near Corvallis, Oregon. The native species H. convergens and *Coccinella californica* Mannerheim were also common in the 1980's. *C. trifasciata* remains one of the most common coccinellid species in vegetable crops across North America (Hagley and Allen 1990, Mareidia et al. 1992, Hoffmann et al. 1997).

In the mid 1990's, La Mana (1995) sampled trees, shrubs, and agricultural fields with a sweep net and a beating sheet in western Oregon. He encountered 13 species of Coccinellidae and reported the growing dominance of the European species *Coccinella septempunctata* L. and the emergence of the newly introduced species, *Harmonia axyridis* Pallas. The abundant species, which constituted 92% of the adult beetles collected, were *C. septempunctata*, *H. axyridis*, *Cycloneda polita* Casey, and *Adalia bipunctata* L. *C. septempunctata* has become the most common species of Coccinellidae in vegetable crops across the North America (Hagley and Allen 1990, Mareidia et al. 1992, Hoffmann et al. 1997).

Coccinella septempunctata L.

C. septempunctata is a eurytopic species that is found on a wide variety of plants and cropping systems throughout Europe (Hodek 1973). *C. septempunctata* was imported and released several times into the United States beginning in 1956. One of the first residential population of the beetle was discovered in 1973 (Angelet et al. 1979). The advent of the Russian wheat aphid caused an increase in rearing and distribution efforts in the western states that have resulted in establishment of *C. septempunctata* throughout the west (Gordon and Vandenberg 1991). *C. septempunctata* is now widely establish throughout North America (Obrycki et al. 1987, Schaefer et al. 1987, Humble 1991).

When coccinellids are released intentionally, there are often long delays between the releases and time of establishment. There was a long delay for *C. septempunctata*, which was released several times before it became established on this continent about 17 years later. Once it becomes established in an area, however, *C. septempunctata* has often become the dominant species. *C. septempunctata* has outnumbered native coccinellids in New Jersey every year since 1974 (Angelet et al. 1979). *C. septempunctata* has become the most common coccinellid in surveys of alfalfa, corn, soybean, triticale, and native habitat in southwestern Michigan (Mareidia et al. 1992). *C. septempunctata* has displaced *C. trifasciata* as the dominant species in Oregon field crops (La Mana 1995).

Coccinella trifasciata L.

C. trifasciata is native to Europe and Asia. It was first observed in Oregon in 1957 (Lindroth 1957). *C. trifasciata* was the most abundant Coccinellidae collected in the alfalfa and collards (McIver 1983) and in mint, filberts, and weeds near Corvallis, Oregon in the 1980's. *C. trifasciata* was common throughout the season in field crops, orchards, and in both the arboreal and meadow habitats of the McDonald Forest near Corvallis. Counts for *C. trifasciata* increased steadily from April through August. In August, *C. trifasciata* was concentrated in clover and alfalfa (Belnavis 1989).

Harmonia axyridis Pallas

H. axyridis is a color-polymorphic, semi-arboreal predator of Homoptera and Psocoptera. The number of spots and the color of the elytra cannot be used to distinguish this species with confidence; adult coloration is variable, and there is an interaction between genetics and temperature (Hagen 1962). The degree of adult dark melanization increases with decreasing temperature experienced by the larvae. The dark coloration may assist ladybird beetles to warm themselves in the sun. The structure of the male genitalia varies little intraspecifically and must be used distinguish this polymorphic coccinellid from other species. There are three main adult elytral color forms for H. axyridis in western Oregon. Most of the adults encountered are of the orange-elytra/black spot morph (f. succinea), a black morph with two red elytral spots (f. conspicua), and a black morph with four red spots (f. spectabilis) (La Mana 1995).

H. axyridis was introduced from Asia to the United States by USDA-APHIS for biological control of pear psylla, pecan aphid, and other arboreal Homoptera. Releases of *H. axyridis* date back as far as 1916 in California. Mass releases of *H. axyridis* in Washington State took place in the early 1980's in the Yakima area. On July 18, 1991, an adult was collected in King County in western Washington. The first recorded occurrence of the species in Oregon was in also in October of 1991. Four years later, the beetle became the dominant semi arboreal coccinellid beetle in Western Oregon representing as much as 70% of the coccinellid beetle collected on shrubs and trees. Although considered a semi arboreal species, *H. axyridis* has been recorded from field crops such as alfalfa and mint. *H. axyridis* is one of the few Coccinellidae species whose larvae are common in trees and shrubs during the fall in western Oregon; *H. axyridis* often completes two generations per year in the Willamette Valley (La Mana 1995).

Adalia bipunctata L.

A. bipunctata is a widespread polymorphic species generally found in tree habitats in the British Isles, Europe, Asia, and Northern China (Hagen 1962, Hodek 1973). It was reported in Washington state in the early 1950's (Lindroth 1957). *A. bipunctata* is observed in a variety of deciduous habitats with relatively low numbers on alfalfa. It is common in apple orchards (Hagley and Allen 1990). Both adults and larvae are found in significant numbers in young tree plantations (Mareidia et al. 1992).

A. bipunctata has a live cycle about one week shorter than *C. septempunctata* (Banks 1955). The first coccinellid collected in the spring is often *A. bipunctata*; it's population tends to peak in the early part of the growing season (Belnavis 1989). *A. bipunctata* is active when the hazelnut aphid (*Myzocallis coryli* Goetze) begins to increase in April; it is collected in hazelnut trees most of the growing season. *A. bipunctata*, however, is very rare in alfalfa and in clover (Belnavis 1989) even though it is a predator of the pea aphid, *Acyrthosiphon pisum* Harris (Hoffmann et al. 1997). In Europe, *A. bipunctata* can be more abundant than *C. septempunctata* in beans (Banks 1955). *A. bipunctata* is found on aphid infested peas and vetch, in some years and not in other years. In general, *A. bipunctata* is rare in forage and vegetable crops (Rockwood 1952).

Coccinella undecimpunctata L.

C. undecimpunctata was introduced from Europe and released in Washington State in 1965 (Frazer and McGregor 1992). By 1970, it had become widespread in British Columbia. It is adapted to cool climates. Its populations in the Willamette valley are limited by high levels of parasitism (Belnavis 1989). McIver (1983) reported that *C. undecimpunctata* was present but uncommon in his alfalfa-collards cropping system.

Native species

Hippodamia convergens Guerin-Meneville is one of the most common native coccinellid species in North America (Buschman et al. 1984, Gordon 1985). It mainly feeds on aphids and is strongly associated with alfalfa and other leguminous crops (Mareidia et al. 1992). *H. convergens* was once the most common coccinellid species in Oregon field crops. *H. convergens* was found everywhere in the lower altitudes from about mid April until mid August when it migrated to wintering sites (Ewing 1913, Rockwood 1952).

Hippodamia sinuata Mulsant is another native species collected in small numbers in Willamette Valley field crops. *H. sinuata* is mostly found on clover, alfalfa, and on corn in the late summer; it experiences a high level of parasitism (Belnavis 1989).

C. californica is one of the larger bodied native coccinellids in Western Oregon (Hagen 1962); it is not common. The native *C. polita* is common on vetch and alfalfa in western Oregon (Rockwood 1952). *Cycloneda* species feed on *A. pisum, R. maidis, and Sitobion avenae* F. (Hoffmann et al. 1997).

LIFE HISTORY AND BIOLOGY

Oviposition

Coccinellids are oviparous. Eggs are usually laid in clusters attached to vertical surfaces or on the undersides of leaves (Agarwala and Dixon 1992, 1993). Hidden oviposition sites are important given the significant amount of cannibalism and interspecific egg predation that occurs in the Coccinellidae. *C. septempunctata* are orange and larger than the eggs of many other species (Banks 1955). They are laid in batches of about 25, although as many as 65 eggs have been observed in some batches. Coccinellids oviposit when they arrive at feeding sites in the spring, and lay eggs in the vicinity of prey (Hagen 1962, Hodek 1973).

The egg-laying period of the aphidophagous Coccinellidae is critical to their survival: oviposition timing varies according to species and often correlates with peak abundance of preferred aphid species. Some species including *A. bipunctata* lay their eggs well before aphid populations peak in abundance (Hemptinne et al. 1992). Cannibalism and starvation can cause significant mortality of the early *Adalia* cohorts. The oviposition period for *C. septempunctata* generally starts before *H. axyridis* and lasts for a shorter period. Because of their late start, *H. axyridis* fourth instars sometimes have to complete their development when aphids are becoming scarce (Hironori and Katsuhiro 1997).

Changes in aphid abundance during the growing season are dramatic. Changes in abundance pose a considerable challenge to ovipositing ladybirds. Because coccinellid larvae are much less mobile and less stress tolerant than adults, the choice of egg laying site by the female has a profound effect on the survival chances of its progeny (Lovei et al. 1991). Synchronization of coccinellid reproduction with early development of aphid populations maximizes predator fitness (Hemptinne et al. 1992).

Several lines of evidence suggest that egg laying females make assessments and decisions about where and how many eggs to lay in a given situation. Egg laying females also make choices regarding the quality of the food source. The choices are important because larvae will indiscriminately eat toxic prey items. Female ladybirds lay eggs in response to the overall density of aphids within the activity radius of the larvae (Lovei et al. 1991). *Hippodamia* species, for example, require about 1 mg of aphids per alfalfa stem to keep adults in the field and to stimulate reproduction (Hodek 1973).

Semiochemicals influence the choice of oviposition site by Coccinellidae (Doumbia et al. 1988). Gravid females are deterred from ovipositing when kept in a petri dish that has previously contained conspecific larvae. Chloroform extracts of the larval tracks also deter oviposition. The substance left behind in larval tracks is thought to be a contact oviposition-deterring pheromone. Gravid *A. bipunctata* lay fewer eggs in the presence of larvae of their own species but not of other species (Hemptinne et al. 1992). In the presence of conspecific larvae, the adult beetles become agitated; they have a greater tendency to leave the area. Species specific oviposition deterring pheromones are thought to promote spreading of offspring more equally among patches of aphids and plants (Doumbia et al. 1988).

Egg hatch and cannibalism

First instar Coccinellidae rupture the chorion using an egg-bursting appendage on the thorax. Upon hatching, the larvae remain huddled on the egg cluster consuming unhatched eggs. If alternative prey items are scarce, there can be significant cannibalism (Agarwala and Dixon 1992, 1993). Depending on the species, the temperature, and the availability of alternative food in the vicinity of the egg cluster, first instar larvae leave the egg mass in 12 to 48 hours to search for other foods (La Mana 1995).

The Coccinellini, Hippodamini, and some Psylloborini deposit their eggs in batches; this placement is conducive to cannibalism. Cannibalism is controlled by semiochemical on egg surfaces. Water extracts of coccinellid eggs promotes cannibalism (intraspecific) but deters egg predation (interspecific) by other species of Coccinellidae (Doumbia et al. 1988). Differential hatching among the egg batches may provide food for the young larvae hatching early. Cannibalism may be adaptive, helping the Coccinellidae to adjust to available food. The first cannibalistic feeding can be beneficial in low prey density areas. In low prey density situations, cannibalism nearly doubles the life of the surviving larvae and increases their searching capacity (Hagen 1962).

Fecundity and reproductive numerical response

Coccinellid eggs are mostly fertile. Food stress does not change egg size; however, food stress experienced during larval and adult life can result in variation in the number of eggs and the size of egg clusters (Dixon and Guo 1993). Minimum egg size is constrained by the minimum size at which first instar larvae can survive, capture active prey, and complete their development before aphids become scarce. When supplied with excess food, larger *C. septempunctata* females produce larger clusters of eggs than smaller female beetles. The size of the egg clusters is associated with greater numbers of ovarioles in the gonads of larger beetles. The significant variation in the size of coccinellid population from year to year is, in part, the result of cycles in the availability of food for the previous generation (Banks 1955).

Mills (1982) argues that the fecundity of some species of Coccinellidae can be related to aphid density, and that coccinellids can mount a reproductive numerical response to aphid populations. *Hippodamia* species required a minimum of 0.5 aphids per 100 square centimeters of leaf surface to begin reproduction. The maximum rate of reproduction of 31.5 eggs per adult occurred when the aphid density was above nine aphids per 100 square centimeters. At this point, prey were sufficiently abundant to satiate the adult coccinellids allowing them to spend a significant portion of the their day inactive, digesting, and producing a maximum number of eggs. The maximum aggregation response of gravid female beetles was 0.02 beetles per 100 square centimeters; at this beetle density, 0.4 eggs were laid per 100 square centimeters of leaf surface.

Development

In Northern temperate regions, Coccinellidae generally progress from egg to large larvae in 23-35 days (Banks 1955, Hagen 1962). In nearly all Coccinellidae, there are four larval instars (Hodek 1973). The developmental time of the immature beetles varies with temperature. Larval development is more rapid and larvae consume more aphids as temperature increases. The developmental threshold for *C. septempunctata* was 11.7 C; it required 275 degree days to complete its life cycle (Michels and Behle 1991). *C. trifasciata* requires about 227 degree days above a developmental threshold of 12.7 C (Miller and LaMana 1995). *H. axyridis* requires about 270 degree days above the lower threshold of 11.2 C to complete its life cycle (La Mana 1995). The native *H. convergens* has a lower minimum threshold (6.7 C) than *C. septempunctata*; however, it requires 351 degree days to complete its life cycle (Michels and Behle 1991). Most species of Coccinellidae in the Willamette Valley have one to two generations per year (Belnavis 1989).

Seasonal activity

Banks (1955) studied the seasonal activity of *C. septempunctata* in bean fields and in non-crop vegetation in England. He found that changes in the numbers of adult beetles occurred in three phases. First, female beetles dispersed from their wintering refuges and laid eggs on stinging nettles that were infested with nettle aphids, *Microlophium evansi*. The first cohort of eggs was deposited prior to the establishment of spring planted agricultural crops. At this point, many of the overwintered females died; some gravid female beetles, however, dispersed from the nettles to bean fields that were now supporting rapidly developing populations of the bean aphid, *Aphis fabae* Scopoli. When the first generation of coccinellids completed its development in the nettles, young beetles immigrated into the bean fields. Adult beetles that developed from eggs placed on the beans and adult beetles that developed from eggs placed on the nettles fed together in the bean fields until they ran out of prey. At this point, many beetles moved back to hibernation sites; some remained in the area feeding on pollen for a couple of weeks prior to moving back to hibernation sites.

The coccinellid population peaks that occurred during the growing season reflected overlapping generations of overwintered beetles plus newly emerged adult beetles. There were two population maxima in the study. The first maximum represented the accumulation of overwintered beetles on the nettle plants that supported high numbers of aphids in the early spring. The second maximum was associated with the emergence of the new generation of adult beetles and the overlap of the two populations of adult beetles. Rapid declines in beetle counts in the nettles were associated with dispersal following the emergence of the new generation of adult beetles. Rapid declines in beetle counts in late August were associated with movement of beetles back to their hibernation sits (Banks 1955).

In Oregon, late in July or early in August coccinellids run short of aphid food. For a brief period of time, they may feed in significant numbers on flower pollen of various plants, but most of the migratory Coccinellidae begin to leave the valley when aphid populations decline in order to finish building their fat reserves in the mountains. By the middle of August, a definite migration begins. When migrating to dormancy sites, females usually have immature ovaries. They quit the valleys and move upward, often flying without stopping until they reach the highest visible point for several miles around. They are attracted to prominent landmarks at the close of their migration (Ewing 1913).

Diapause and dormancy

Coccinellidae exhibit many combinations of voltinism and diapause (Hodek 1967). Coccinellidae vary in the intensity of diapause that they experience (La Mana 1995). *C. trifasciata*, for example, exhibits an intense diapause; it enters into diapause at the beginning of the dry period and does not oviposit again until the following spring. *C. septempunctata* is more flexible; it exhibits several types of voltinism depending on the latitude and climate (Hagen 1962). In Greece, for example, *C. septempuntata* can develop as many as five generations per year (Katsoyannos et al. 1997). In cool northern latitudes of Western Europe and of the United States, *C. septempunctata* is almost entirely univoltine. Occasionally *C. septempunctata* will produce a second generation in the late summer but these progeny usually fail to survive the winter (Angelet et al. 1979).

Aphidophagous coccinellids in northern temperate climates spend the late summer and all of the winter in a state of reproductive diapause. Diapause is characterized by increases in the fat body and atrophy or non-development of the ovaries in females. Adult diapause allows the beetles to endure long periods of starvation during the seasons of aphid scarcity. The development of the ovaries progresses very little from the end of summer to the following spring. The fat body gradually is expended through the winter. Diapausing beetles live for nine to ten months without producing eggs; they pass the winter without food. For long periods of time, they remain perfectly still (Hagen 1962).

The cues that stimulate the onset of diapause and the duration of diapause are variable even within a given population (Hodek 1967). In many species of aphidophagous Coccinellidae, diapause is induced by photoperiod (Hagen 1962). When the critical photoperiod occurs, beetles that have found sufficient food for fat synthesis show directional flight toward aggregation sites (Hodek et al. 1993). *C. septempunctata* is sensitive to day length. In northern temperate climates, long days result in winter diapause of *C. septempunctata* (Hodek and Okuda 1997). On the east coast of the United States, *C. septempunctata* begins to migrate to hibernation sites from about mid July to through August. However, adult beetles feeding on pollen and nectar may not enter hibernation until the flowering plants die back (Angelet et al. 1979).

If migratory coccinellids are experimentally held at lower altitudes during the winter, mortality is high unless they are refrigerated (Ewing 1913). When *C. septempunctata* is gathered from the field in November, brought into the laboratory, warmed up, and put on a 20 L: 4 D daylight cycle, 24% of the females still remain in diapause. This response constitutes an obligatory diapause occurring in a proportion of the population (Hodek and Okuda 1993). However, by culturing *C. septempunctata* under optimal conditions (ample food, long photoperiod, moderately warm temperatures) one can break the dormancy of the beetle over a period of several generations in the laboratory (Hagen 1962).

Habitat preferences

Coccinellids prefer moderately warm temperatures. At 15 C, *H. convergens* does not develop to the adult stage. As temperatures increases, *H. convergens* takes fewer days to develop and consumes more aphids (Michels and Behle 1991). If temperatures are very high, however, the native coccinellids migrate out of the agricultural valleys up into the cool mountains (Hagen 1962). *C. septempunctata,* however, survives hot temperatures better than native coccinellid species and remains in the valleys longer during the summer (La Mana 1995).

Temperature influences the vertical distribution of Coccinellidae in vegetation over the growing season. Coccinellid adults and larvae are thermophillic. In wheat in the early growing season, for example, larval and adult

C. septempunctata remain close to the ground on the lower part of wheat tillers. By June, most adults and larvae are found in the upper parts of the tillers, an area also preferred by their aphid prey (Ferran et al. 1991).

Coccinellid species have preferences for specific crops and semi natural vegetation (Hagen 1962, Hodek 1973). *A. bipunctata* and *H. axyridis*, for example, tend to be more numerous in the trees and the shrubs than on forage and vegetable crops. *C. septempunctata* (La Mana 1995), *C. trifasciata* (McIver 1983), and *C. polita* (Rockwood 1952) tend to be more common in field crops such as alfalfa and vetch. Their presence in the alfalfa reflects preferences for prey items in a given habitat, and it also reflects habitat preferences.

Coccinellid beetles respond to vegetation on a variety of spatial scales. At the scale of a single plant, coccinellid beetles respond to plant architecture, leaf characteristics, plant color, and other aspects of vegetation regardless of the presence or absence of their prey items (Grevstad and Klepetka 1992). Some coccinellid species are more common in deciduous shrubs and trees while others are more common on low growing vegetation and field crops. Some coccinellid species prefer unmanaged vegetation; others prefer disturbed vegetation in agricultural settings. These later species are adapted to rapid colonization of disturbed sites. During their life cycle, which in some cases involves long distance migration, most of the common species of coccinellids use both agricultural and uncultivated habitats (Mareidia et al. 1992).

Grevstad and Klepetka (1992) used four crucifers species that varied markedly in structure and leaf surface to test the impact of plant architecture on predation effectiveness of several Coccinellidae. The architecture varied significantly between curly-leaf kale, smooth-leaf collards, wrap-leaf cabbage, and broccoli with leaves and florets. Plant morphology had an impact on predator mobility, falling frequency, and prey accessibility. The four species of

Coccinellidae evaluated (*Hippodamia varigata, H. convergens, Coccinella apunctata*, and *C. septempunctata*) exhibited distinct foraging strategies as measured by the time they spent actively foraging, the rate of encountering aphids (*Brevicoryne brassicae* L.), and the fraction of aphids encountered that they consumed. The coccinellids differed in their propensity to fly away from the plant and in the frequency that they fell from the plant. The impact of plant architecture was similar on all species of coccinellid; the more complex plant surfaces slowed down the predation rate.

Crucifers vary in the amount of waxyness on their leaves. Waxyness can accumulate in the tarsi of insects including Coccinellidae and interfere with movement. The mobility of H. convergens, for example, was impeded by wax crystals on the surface of normal waxy cabbage compared to glossy type cabbage. The accumulation of wax in their tarsi caused the beetles to spend less time foraging for prey and more time grooming and scrambling in an ineffective forward motion (Eigenbrode et al. 1996).

Foraging and egg laying coccinellid beetles respond to plant color; they are attracted to plants that appear to be under stress. Color reflects a variety of plant stresses including the presence of aphid colonies, nutrient stress, moisture stress, or plant disease. On aphid free plants, coccinellids were significantly more abundant on yellow nutrient stress maize (*Zea mays* L.) than on non-stressed green corn plants (Lorenzetti et al. 1997).

Coccinellids have obvious preferences for various crops in the agricultural landscape. Eight sites were evaluated near Corvallis, Oregon, and the greatest number of coccinellids was collected in clover, alfalfa, and filberts. The least number of beetles were collected in MacDonald Forest (Belnavis 1989).

H. convergens, C. californica, C. undecimpunctata, and *C. trifasciata* are widely distributed among various habitats and are generally found in field crops including mint, alfalfa, weeds and herbaceous plants such as vetch. *C. polita* and *A. bipunctata* were somewhat restricted to hazelnut but are sometimes found in significant numbers on field crops. *H. sinuata* was found almost exclusively in clover (Belnavis 1989). *C. septempunctata* is cosmopolitan but it seems to prefer agricultural field crops and managed orchards to deciduous or unmanaged habitats. *C. septempunctata* is abundant in alfalfa, corn, beans, wheat and triticale. *A. bipunctata* is more common in deciduous and bushy habitats than in field crops. They seem to prefer managed deciduous habitats including apple orchards over wild areas. *C. munda*, which is most abundant in deciduous and bushy habitats, seems to prefer unmanaged deciduous bushy habitats over managed apple orchards (Mareidia et al. 1992).

In the Willamette valley, coccinellid species are common on winter cover crops including vetch, alfalfa, and Austrian winter peas that are infested with pea aphid (Rockwood 1952). For the reasons mentioned earlier, however, cover crops loaded with Coccinellidae may or may not be a source of Coccinellidae colonizing agricultural crops. Leguminous winter cover crops in an orchard may draw Coccinellidae into the vicinity; however, their presence in the cover crop may not result in significant changes in the number of coccinellids foraging in the tree canopy. Many scientists who have wrestled with this problem have speculated about techniques for manipulating vegetation (mowing) at an appropriate time to force Coccinellidae to abandon the cover crop and move into the target crop (Bugg et al. 1991).

Winter aggregations

In some years, Coccinellidae migrate to wintering sites as early as mid July. There appears to be a relationship between the abundance of aphids in the

Willamette Valley and the tenure time of the coccinellid populations on the valley floor, which varies from year to year. A sudden failure of the food supply might lead some of the beetles to migrate earlier than usual. They may have a better chance of survival without food and with a minimum of activity in the mountains than in fields in warmer situations.

By mid-September in the Willamette Valley, most coccinellid species have migrated to wintering sites. Aggregating Coccinellidae have three characteristics in common. They are species that are associated with ephemeral prey, mostly aphids, and not with the more sessile Homoptera. They exhibit long periods of dormancy or diapause. Mating generally occurs at the aggregation site shortly before the beetles disperse at the termination of dormancy. Additional mating is observed at feeding grounds following dispersal. Some authors believe that aggregations are formed basically for bringing the sexes together. Most authors agree that aggregations are not formed for feeding since no suitable food is usually present at the aggregation sites. Some beetles aggregate on or near mountain peaks among wind-swept rocks. Aggregations are not necessarily associated with any plant species (Hagen 1962).

Native Coccinellidae including *H. convergens* migrate to wintering sites in late summer (Rockwood 1952), and there is a tendency for the coccinellids to return to the same wintering sites each year. Cashes of coccinellids have been observed scattered in various sites in the west Cascade Mountains. Each species tends to bunch up with its own kind. *H. sinuata* caches have been found on Bald Peak south of Forest Grove and Peterson's Butte near Lebanon. They often occur well down in the crowns of bunch grass, fescue, around wild rose bushes, blackberry vines, and poison oak on southwest facing slopes. The beetles usually come to Bald hill in September and October. *H. convergens* aggregations are also observed in the MacDonald Forest (Belnavis 1989).

H. convergens usually aggregate near water, on stumps, bracken, small bushes, and small trees. Caches have been discovered in Clear Creek Canyon near Forest Grove, on wetlands rushes near Forest Grove reservoir, in the foothills near Rickreall, and on the summit of Mary's Peak west of Corvallis, Oregon (Rockwood 1952). H. convergens overwinters in McDonald forest, a mixed oak (*Quercus garryana*), Douglas fir (*Pseudotsuga menziesii*) forest adjacent to meadow and riparian areas along Oak creek about five miles northwest of Corvallis (Belnavis 1989).

Unlike *H. convergens, C. septempunctata* does not make long distance migrations to hibernation sites. It aggregates within the breeding area (Hagen 1962, Hodek 1973). *C. septempunctata* sometimes hibernates on dry hills or at the base of prominent objects in vast flat areas or large valleys. Angelet et al. (1979) observed several common hibernating sites for *C. septempunctata* including the tussock grass, *Agrostis gigantea* Roth, common mullein, *Verascum thapsus* L., and the branches of the Scotch pine, *Pinus sylvestris* L. and red pine, *Pinus resinosa* Aiton. In pine trees, clusters from 5 to 250 beetles have been observed. There may be several small aggregations in one tree. In grass, there may be less than 10 beetles in a clump. In large grass tussocks, aggregations of as many as 400 have been observed. In part, the lack of migratory flight has been credited with the relatively slow colonization of the United States by *C. septempunctata* during the 1970's.

Upon termination of dormancy in the spring, the disbanding of aggregations can be one of simple dispersal or a migration flight driven by wind patterns. For *H. convergens*, the flight behavior leaving the aggregation sites begins during periods of no wind and warming temperatures with a directly vertical takeoff. The beetles fly upwards as long as the temperature permits; upper level winds determine the direction of the flight. The wind blows them into the valleys in the early spring, and into the mountains in the summer (Hagen 1962). At the end of dormancy, many of the species of coccinellid beetles mate before dispersal (Hodek et al. 1993). During this dispersal flight, ovaries are partly mature. In the spring, they arrive back in the Willamette Valley by mid April (Ewing 1913).

H. axyridis disperses from winter aggregations to feeding sites in March. It is the most common beetle sampled in trees and shrubs in early April. Oviposition can occur as early as April and sometimes continues until October. The larvae of *H. axyridis* are abundant in May and June, low in August, and often high again in September and October (La Mana 1995).

H. convergens appears to leave its wintering site earlier than *H. sinuata*. The beetles leave on days when temperatures are sufficiently high to permit normal activity. The beetles usually leave their wintering sites in April, but they have been observed in the Willamette Valley as early as February or March. By mid April when the coccinellids arrive, aphid colonies are growing rapidly. By the first of June, thousands of coccinellids are found on common vetch. When prey items run short in the early summer, aggregations of coccinellids are seen feeding on pollen (Ewing 1913).

Mortality factors

Coccinellidae have few natural enemies. Occasionally, *C. septempunctata* larvae and adults are fed upon by the predaceous pentatomid *Podisus maculiventris* Say (Hagen 1962). Several unidentified species of centipedes and spiders feed on the beetles. Birds including sparrows (*Passer domesticus*) and robins eat coccinellid larvae and pupae (Banks 1955).

The bright reddish color displayed by most of the large coccinellid adults is apparently aposematic, acting as a warning to potential predators. Otherwise, the large aggregations of beetles during dormancy would provide an attractive food source for mammals, birds, and other predators. The response of a Japanese quail (*Coturnix japonicus*) was more deterred by color pattern than by smell or taste. The birds could detect the smell of the insects, but rarely used it as a cue to toxicity (Marples et al. 1994). Coccinellid larvae and adults when disturbed eject drops of a glandular secretion "reflex blood". The yellowish fluid is bitter and repugnant to most predators (Hagen 1962).

Cannibalism

While field observations suggest that there is very little predation of Coccinellidae by other predators, their survival is dependent to a large extent on the level of cannibalism by adult coccinellids and their older larvae. Larvae of coccinellid beetles attack their own eggs, the eggs of other coccinellid species, and small coccinellid larvae. Cannibalized eggs are identifiable by the yellow-stained egg remnants in contrast to the white egg base of successfully hatched eggs (Mills 1982). Cannibalism can destroy over 50% of the coccinellid eggs and young coccinellid larvae present in an egg batch (Banks 1955).

Most cannibalism results from late instar larvae that have dispersed from other egg batches that consume egg clusters in their vicinity. Larvae dispersing from eggshells after hatching probably encountered other coccinellid egg batches on the lower leaves more readily than the aphid colonies at the top of the leaves. Cannibalism varies over the growing season and can become more intense at the end of the oviposition period (Agarwala and Dixon 1992).

Several factors influence the level of cannibalism in a colony of Coccinellidae (Agarwala and Dixon 1992). Cannibalism increases as egg density rises. In the absence of adequate numbers of aphid prey, cannibalism increases.

Starved first instar coccinellid larvae are more vulnerable to cannibalism than well-fed larvae. When female coccinellids arrive in large numbers and lay eggs where aphid densities are low, the resulting coccinellid larvae attack unhatched coccinellid eggs as readily as they attack the aphids that are present. The occurrence of cannibalism is not strictly determined by the relative abundance of aphids; cannibalism is also observed where aphids are abundant (Banks 1955).

Cannibalism not only depends on food scarcity; the age and gender structure of a coccinellid colony also influences the intensity of cannibalism. Eggs and young coccinellid larvae are more vulnerable to cannibalism than older larvae. Late instar larvae tend to cannibalize younger larvae rather than larvae of their own age class. Late instars eat more conspecific eggs than early instars. Adult male Coccinellidae eat more conspecific eggs than female beetles (Agarwala and Dixon 1992).

Egg cannibalism and egg predation by other species of Coccinellidae are controlled by semiochemicals (Agarwala and Dixon 1992). Chemical cues inhibit interspecific consumption of eggs by coccinellid adults and larvae. The larvae and adults of *C. septempunctata*, for example, are reluctant to eat conspecific eggs if the eggs are painted with a water extract from the eggs of other coccinellid species. Chemical cues in eggs that inhibit interspecific egg predation increase in strength as cluster size grows (Agarwala and Dixon 1993). The coccinellid adults are, in adversity, more likely to cannibalize their own eggs than to prey on the eggs of other species. If larvae from one species are forced to eat eggs from another coccinellid species, their survivorship is reduced (Hironori and Katsuhiro 1997).

Cannibalism is thought to be adaptive in Coccinellidae if it promotes the chances of survival of the remaining larvae; it appears to do so. Ladybird beetles forage in ephemeral habitats where aphid colonies show a patchy distribution in space and time. The foraging beetles encounter unstable food supplies and interspecific competition from other coccinellid species sharing the same habitat, and in many cases, the same food resource. In an uncertain environment, cannibalism serves to synchronize the reproduction and development of the coccinellid community with the phenology of the prey population (Agarwala and Dixon 1992).

Cannibalism is an adaptation by aphidophagous coccinellids to the life cycle of their prey. The host-alternation and aestivation by which aphids overcome periods of food shortages result in sudden declines in their abundance soon after the coccinellid egg laying period begins (Dixon 1971). Under these conditions the ability to cannibalize eggs enhances the likelihood of at least some of the coccinellid larvae surviving to maturity (Mills 1982). Coccinellid eggs are better food, in terms of early larval growth and survival, than are aphids (Agarwala and Dixon 1992).

The impact of aphidophagous Coccinellidae on agricultural pests is restricted by cannibalism. The utility of inundative releases of Coccinellidae is restricted by cannibalism; in the absence of sufficient prey, or in the presence of large numbers of beetles, coccinellid eggs plus small larvae are consumed by the coccinellids themselves. The coccidophagous coccinellids, which have been successfully used in biological control, tend to belong to coccinellid families that lay their eggs singly, often concealed beneath their prey. Concealing eggs allows these coccinellid species to escape the levels of egg cannibalism that limits the numerical response of the aphidophagous species (Mills 1982).

Parasitism

Parasitism is an important regulator of some species of Coccinellidae. In temperate regions, coccinellids are generally parasitized in the autumn before they migrate to their wintering sites. The parasitoids winter as first instar larvae in the abdomen of the hibernating, adult beetles (Kadono-Okuda et al. 1995).

The parasitoid *Dinocampus coccinellae* (Shrank) (Hymenoptera: Braconidae) is common and attacks several species of Coccinellidae in Oregon (Belnavis 1989). *D. coccinellae* parasitized approximately 27% of the beetles collected from April to August near Corvallis, Oregon. Parasitism was highest in July and August. Coccinellids collected in mint and clover had significantly higher levels of parasitism than beetles collected in other sites. Of the species collected, *H. sinuata* had the highest level of parasitism (56%), while *C. californica* had the lowest level of parasitism (4%). *A. bipunctata* was never found parasitized. *D. coccinellae* does attack the recently introduced species *H. axyridis*, though at relatively low rates (La Mana 1995).

Other mortality factors

Coccinellid populations are affected by aphid abundance in the previous year and by wintering success (Smith 1965, Wright and Laing 1982). Both cultivated and uncultivated habitats play an important role in supporting winter populations of *C. septempunctata* (Mareidia et al. 1992). In poorly drained wintering sites, as many as 25% of the beetle aggregations are killed by the fungus *Beauveria bassiana* Balsamo (Angelet et al. 1979).

Starvation limits coccinellid populations under certain circumstances. Many newly emerged coccinellid larvae die of starvation. Young coccinellid larvae have difficulty finding aphid colonies when infestation levels are low. When aphid populations are very high, honeydew on heavily infested plants hinders the feeding and development of the young larvae (Banks 1955).

PREY ITEMS, ALTERNATIVE FOODS, AND FORAGING

Lady beetles are important predators of homopteran pests, particularly aphids and scales. The majority of coccinellid prey are Homopterans (Aphidoidea and Coccoidea), Acarina, and Thysanopterans (Hodek 1973).

While some species of Coccinellidae are specific in their food habits, aphid-eating members of the family are generally not restricted to any one species of aphid for their main food supply (Banks 1955, Hodek 1973, Hoffmann et al. 1997). Angalet et al. (1979) reported twenty-six species of aphids that appeared to be suitable prey for both immature and adult *C. septempunctata* including *Myzus persicae* Sulzer and *B. brassicae*. C. *septempunctata* forages for aphids on both herbaceous plants as well as perennial tree crops, where it consumes the arboreal apple aphid, *Aphis pomi* DeGeer (Hagley and Allen 1990).

Although coccinellids will eat a variety of prey, they do have preferences (Hodek 1973). Among the most sought after species of aphids in the Willamette Valley are the black cherry aphid (*Myzus cerasi* F.), the Snow-ball plant aphid (*Aphis viburni* Scopoli), the Rosy Apple aphid (*Aphis sorbi* Kalt.), and the European Grain aphid (*Aphis avenae* F.) (Ewing 1913).

There are some species of aphids that are not suitable for Coccinellidae (Hagen 1962). For example, the elder berry aphid *Aphis sambuci* is not suitable for *C. septempunctata*. If one forces the larvae of *C. septempunctata* to eat this aphid species, 100% of the larvae die. The glycoside sambunigrin, which is present in the host plant, is transferred to the body of the aphid. When the beetle eats it, enzymes split it into cyanic acid and other compounds that are toxic. *A. fabae* is rejected by many species of aphidophagous coccinellid; some coccinellid species fail to complete their development if they are forced to feed on *A. fabae* (Ewing 1913).

Interestingly, the semi arboreal *H. axyridis* eats *A. fabae* and appears to do well on it (La Mana and Miller 1996).

Coccinellids are remarkably absent and not very active in *B. brassicae* colonies (George 1957). Hodek (1973) lists several studies that assert that the *B. brassica* is rejected by most species of Coccinellidae because of its waxy surface. *C. trifasciata*, however, had a 58-67% positive precipitin to *B. brassicae* in field tests conducted near Corvallis, Oregon. When *C. trifasciata* was gathered from collard foliage (rather than alfalfa or the ground) the intensity of the positive precipitin test significantly increased for *B. brassicae* (McIver 1983).

Equally important for the coccinellid populations are the aphid species available for pre-diapause feeding in late summer. Angelet et al. (1979) observed that the mealy plum aphid *Hyalopterus pruni*, for example, plays an important role in the late summer feeding of *C. septempunctata*. During this period, the beetles store body fat that insures their survival during the winter. Improperly fed *C. septempunctata* entering into hibernation do not survive cold winter temperatures (Hodek 1973).

Coccinellidae rarely prey on Lepidoptera. In his extensive review of coccinellid prey items, Hodek (1973) does not list *Pieris* as a known prey item of any species of Coccinellidae. On the other hand, *C. trifasciata* and *H. convergens* had positive precipitin responses to *Pieris rapae* when they were sampled near Corvallis, Oregon (McIver 1983). Jones (1982) studied the predators of *Trichoplusia ni* (Hubner) and found that coccinellid predation was low in the presence of aphids. The aphids were more attractive prey items; the aphids completely distracted the Coccinellidae from potential Lepidopteran prey. In cage studies to determine the impact of natural enemies on *Mamestra configurata* Walker, *C. transversoguttata* alone and in combination with *Nabis* species was superior to all other treatments in reducing the number of *M. configurata* larvae (Tamaki and Weeks 1972).

Alternative foods are important for most species of Coccinellidae. Coccinellids feed extensively at floral (Angelet et al. 1979) and extra-floral (Ewing 1913) nectar, pollen (Belnavis 1989), and aphid honeydew (Elliott et al. 1996), and plant saps (Banks 1955). The larvae of several species in the genus *Psyllobora* feed on fungi (Hagen 1962). Apparently, Coccinellidae will also feed on artificially applied sugar solutions (Evans and Richards 1997).

When *C. septempunctata* runs out of aphid prey in the late summer, it has been observed feeding on the pollen and nectar from several species of flowering plants (Angelet et al. 1979). *H. convergens* numbers may increase at Kiger island (near Corvallis, Oregon) in July even though numbers declined in the agricultural areas. The increase may be the result of mid summer aggregation. Most coccinellids observed at Kiger Island in July appeared to be feeding on pollen from *Tansy vulgare* (Belnavis 1989).

Floral and extra floral nectar secretions from *Prunus* and *Vicia* species offer energy sources but are probably nutritionally deficient for egg or fat production in Coccinellidae (Hagen 1962). Faba bean (*Vicia faba* L.), common vetch (*Vicia sativa* L.), and alfalfa *(Medicago sativa* L.) whether infested by aphids or not, attract large numbers of coccinellid beetles that feed on the nectar expressed from glands on their leafy stipules. Winter peas lack extra floral nectar. Coccinellids do not appear on winter peas unless they are infested with aphids (Rockwood 1952).

Aphid honeydew is fed upon by a variety of aphidophagous Coccinellidae (Hagen 1962, Elliott et al. 1996). Aphid honeydew is more nutritionally complex than floral nectar; honeydew contains free amino acids and may be nutritionally sufficient for fat synthesis by Coccinellidae.

Foraging behavior

Colonizing ladybird beetles are inept at locating prey from a distance (Hodek 1973). The coccinellid larvae and adults do not perceive their prey visually at long distances and mostly detect their prey upon contact. Adult beetles must come into contact with the aphid before it responds to it (Hagen 1962). Once they land in a plant patch, however, they are aggressive foragers. After finding prey, their search pattern changes from one of rapid movement at random to one of more intense search reflected by more frequent turning and shorter moves. The key foraging behavior that contributes to the success of *C. septempunctata*, for example, is its tendency to restrict its foraging attention to the vicinity of a recent aphid capture ("area restricted search") before continuing a wider ranging exploration (Kareiva 1986). Aphidophagous Coccinellidae continue to focus on aphids even when there are other prey items available (Tamaki and Weeks 1972). The duration and intensity of their searching behavior increases with hunger (Mills 1982).

Adult coccinellid beetles are highly dispersive during their foraging and oviposition season. Coccinellid beetles are strong flyers and very capable of flying across trial grounds at the spatial scale that most agricultural research is conducted. When evaluated at the appropriate scale, the number and size of aphid colonies in a plant patch can often explain most of the variation in beetle density and tenure time. The average number of *C. septempunctata* found on fireweed stems (*Epilobium angustifolium*), for example, was 10 to 20 times greater on plants containing large aphid colonies than when the stem contained no aphids. There is a strong population-level aggregation of lady beetles in areas of high aphid density (Ives et al. 1993).

During a local search, adult and larval coccinellids are positively phototactic and negatively geotactic. Attraction to light and movement in the opposite direction of gravity results in a general movement by beetles and larvae toward the actively growing extremities of the plants where many aphid species also feed. On plants, the edges and prominent veins of leaves determine the pattern of search (Hagen 1962).

The vertical distribution of adult and larval *C. septempunctata* on plants changes with the season in response to changes in the distribution of aphid populations (Ferran et al. 1991). Adult Coccinellidae tend to spend less time foraging on the upper surface of leaves and petioles than on the under surfaces of leaves and petioles. Some species of aphids use this to their advantage. The Sycamore aphid (*Monaphis antennata*), for example, occupies the upper surfaces of the leaves and petioles of their host plant. Occupation of the upper leaf surfaces is unusual and is thought to be a specific adaptation to predation pressure by Coccinellidae. These aphids are encountered later and less often by coccinellids than aphids experimentally moved to the lower leaf surface (Hopkins and Dixon 1997).

Adult male Coccinellidae are less active and consume fewer aphids than females. At high prey densities, females spend more time in area restricted search than when prey were scarce. The males, however, do not show this functional response to increased aphid abundance. Males do, however, respond to contact with a chloroform soluble substance in the elytra of conspecific females (perhaps a sex pheromone) with area restricted search behavior (Hemptinne et al. 1996).

Coccinellid beetles of various sizes have unique foraging niches. For example, the tiny coccinellid beetle *Scymnus frontalis* is better adapted to hunt for Russian wheat aphid, *Diuraphis noxia*, than the large-bodied *C. septempunctata*. Wheat leaves infested with aphids tend to remain furled. The leaf coiling limits access to the aphids by the large-bodied coccinellid species and their late larval instars (Kauffman and Laroche 1994).

In general, searching animals usually spend more time where the object of their search is plentiful (Hassell and May 1974, Hassell 1980). Predators aggregate in response to the aggregation of prey or other food resources. The Coccinellidae-aphid interaction is an excellent example of the aggregation response. For example, the presence and concentration of the pea aphid (*Aphis pisum*) or aphid honeydew attracts *C. septempunctata* and causes it to aggregate in alfalfa (Elliott et al. 1996). The ability of Coccinellidae to control aphids in large part depends on their rapid aggregation (Kareiva 1987).

The parameters of the Coccinellidae-aphid interaction include the number of predators per unit area versus the prey per unit area and the time spent by the predator versus the density of the prey. When these parameters are plotted for *C. septempunctata*, they form a sigmoidal curve with a low plateau, a high plateau, and a transition zone. In the transition zone, *C. septempunctata* is highly responsive to changes in prey density. Where prey density is low, *C. septempunctata* spends a constant minimum time searching plant patches. Where prey density is high, *C. septempunctata* spends a constant maximum time searching plant patches. When the prey density falls between these limits there is a marked increase in time spent per unit area by the predator as prey density increases (Kareiva 1987).

The aggregation response of Coccinellidae has two components, the aggregation of foraging adults and the concentration of oviposition. Ovipositing beetles concentrate their egg laying in areas of high prey density or where prey populations are rapidly increasing. The oviposition behavior results in the concentration of larvae in areas of high aphid density. The impact of aphidophagous predators on prey populations is largely a result of predation by the juvenile beetle stages. Adult coccinellids generally arrive prior to the beginning of the cropping season and feed in a variety of non-crop habitats before oviposition begins in agricultural crops. The “reproductive numerical response” of the adult coccinellids to aphid density is therefore important in determining the effectiveness of these natural enemies in agricultural systems. Some species of coccinellid beetles can only respond to the lower range of aphid densities through aggregation and a reproductive numerical response. They fail to respond to higher aphid densities and their response is further reduced by density-dependent egg cannibalism (Mills 1982).

The potential of Coccinellidae as aphid biological control agents in agricultural systems is limited by their synchrony with developing prey populations. The coccinellids that attack the more sedentary prey, such as the scale insects and mealy-bugs, usually display close synchrony with their prey. They reproduce as the prey is increasing and become quiescent or hibernate when their prey is dormant (Hagen 1962). The establishment and development of aphidophagous coccinellid populations is often poorly synchronized with prey populations developing on agricultural crops (Banks 1955). *C. septempunctata* has been successful in part, because adult densities are highly correlated with the density of pea aphid, *A. pisum* (Hironori and Katsuhiro 1997).

In the warmer temperate climates, there is only partial synchrony among the native Coccinellidae and their prey. During the spring, the coccinellids exhibit their greatest activity and usually respond reproductively to aphid abundance, but during the summer many coccinellid species seem to disappear even though some aphids are still abundant. The beetles may reappear in the fall and reproduce; the emerging adults usually enter hibernation. Prior to the introduction of irrigated vegetable crops and a variety of introduced aphid species, this life history was adaptive. The valleys probably supported very few aphids during the summer on the native vegetation that dried down in mid summer. The period of aestivation and hibernation of the native Coccinellidae coincided with periods of aphid scarcity in natural systems (Hagen 1962).

Intraguild interference and competition

Release of generalist predators is, by definition, bound to have non-target effects. There is also the possibility of competitive exclusion of other natural enemies (Rosenheim et al. 1993, Rosenheim and Wilhoit 1993, Rosenheim et al. 1995). The collection and release of natural enemies in classical biological control programs has been criticized because of the potential non-target effects on the indigenous fauna including natural enemies (Ehler and Miller 1978, Ehler and Hall 1982, Ehler 1984, 1990).

Ferguson and Stiling (1996) compared four different combinations of predators and parasitoids and their impact on aphids caged on marsh elder in Florida. The impact of the predators and the parasitoids on aphid densities were not additive. Parasitoids reduced aphid populations more than parasitoids in combination with Coccinellidae, because the Coccinellidae ate parasitized aphids. The addition of coccinellids to cages containing parasitoids reduced the ability of the parasitoids to reduce aphid densities. Cage studies that pair natural enemies and test for interference and competition can produce misleading results, however. Natural enemies that might compete or interfere with each other in a cage may forage in different hunting niches in nature (Lorenzetti et al. 1997).

There is growing evidence that the establishment of exotic Coccinellidae for biological control purposes can have an impact on native Coccinellidae. For example, seven species of native Coccinellidae inhabited alfalfa, corn, and small grains in eastern South Dakota prior to the invasion by *C. septempunctata.* The structure of the native coccinellid community changed after *C. septempunctata* became established, in part, because of the reduced abundance of *A. bipunctata* and *C. transversoguttata.* The annual abundance of *A. bipunctata* averaged 20 times lower in corn after the invasion. The addition of *C. septempunctata* to the community did not significantly change the total abundance of coccinellids in the crops. Total abundance may have been limited by total aphid availability. The introduction of a new species may have resulted in the reductions in native species while not having any net effect on the biological control of the aphid pests (Elliott et al. 1996).

Intraguild synergism

The impact of Coccinellidae on aphid populations is amplified by the foraging activity of soil dwelling generalist predators. Coccinellid beetles stimulates dislodgment of aphids from their host plants. Dropping immediately reduces the risk to aphids from foliar predators, but dropping increases their risk of predation from ground-foraging predators (Losey and Denno 1998).

Aphid presence and activity on the ground is documented by the abundance of aphids caught in pitfall traps (Losey and Denno 1998). A significant proportion of aphid dispersal occurs due to dislodgment from a plant onto the soil following by overland movement to another host plant (Montgomery and Nault 1977). Eventually, aphids on the ground find their way back to their host plants. While they are on the ground, however, their survival is dramatically reduced by environmental conditions on the soil surface and by exposure to the ground dwelling predators including spiders, rove beetles, ground beetles, harvestmen, and others (Hagley and Allen 1990, Losey and Denno 1998).

For example in a Maryland orchard study, Coccinellidae (C. septempunctata and A. bipunctata) Carabidae (*Amara aenea, Harpalus aeneus, Anisodactylus sanctaecrucis, Pterostichus melanarius* Illiger and *Harpalus pensylvanicus* DeGeer) and Staphylinidae (primarily *Philonthus* spp.) tested positive to serological test for the arboreal aphid, *A. pomi.* Coccinellidae foraging high in the foliage of the apple trees drove aphids to the ground where they were preyed upon by the soil dwelling predators (Hagley and Allen 1990).

McConnell and Kring (1990) observed similar interactions between the sorghum aphid, *Schizaphis graminum*, and *C. septempunctata*. The beetle consumed 0.5 to 0.9 aphids per minute at low and high aphid densities respectively. The beetle dislodged approximately 1.7 aphids per minute at low densities and up to 3.5 aphids per minute at high aphid densities. In other words, *C. septempunctata* dislodged four to five times as many aphids as it consumed.

Herbivorous insects have many behaviors and morphological features used in defense against attacks by predators and parasitoids. The defenses result in some benefits, but they also have costs associated with them. Typically, the costs associated with morphological adaptations to defense have a negative impact on reproduction and result in lower fecundity (Losey and Denno 1998). Other costs associated with defense may include lost opportunities for feeding or mating, or increased risk of mortality from natural enemies or other sources. The interruption of feeding and the disruption of aphid reproduction by dislodgment from their host plants reduce the growth rate of aphid populations (Roitberg and Myers 1979, Roitberg et al. 1979).

Historically, aphids were thought to possess few defenses and were thus highly vulnerable to attack from predators and parasitoids (Losey and Denno 1998). In fact, aphids respond to tactile or visual cues when approached or attacked by a predator or parasite. The most prevalent behavioral responses of aphids to attack by predators or parasitoids (Ruth et al. 1975) are behavioral. Escape behaviors include synchronized twitching, kicking, attack with the frontal horns, walking away, and dropping from the plant (Roitberg and Myers 1978). Escape behaviors can be initiated by either direct contact with a predator, by sensing plant-borne vibrations caused by a foraging predator, by detecting alarm pheromone released by a disturbed conspecific aphid, or by a combination of these factors (Losey and Denno 1998). Of the suite of possible escape behaviors, dropping, leaping or falling from the host plant in response to enemy attack is the most common response among aphid species (Dixon 1985).

Many factors influence the propensity of aphids to drop from plants. Aphid life stage may be important. Adult aphids show a slightly higher propensity to drop from their host plants than juvenile apterous and immature aphids in the presence of a predator. The reluctance of immature aphids to drop compared to adults may be associated with their inability to relocate plants and their susceptibility to desiccation on the ground. During hot weather, aphids are not as responsive to alarm pheromone as they are during cool weather. Low humidity tends to deter dropping behavior by aphids perhaps because they are more subject to desiccation when the humidity is low (Roitberg and Myers 1978).

Generally, as aphid density increases, so does their propensity to drop from their host plant (Dixon 1985). However, at low to moderate aphid densities, the influence of aphid density on the propensity of aphids to abandon their host plants is not strong (Losey and Denno 1998). At high densities, aphids can lower the nutritional quality of their host plants. Declines in food quality may influence their willingness to abandon the resource. The potential for sensing alarm pheromone might explain the affect of aphid density on their propensity to drop. Single aphids on plants (colonizing stage) face a higher risk of predation by coccinellids because they do not share the benefit associated with alarm pheromones (McConnell and Kring 1990). In the absence of foliar-foraging predators, *A. pisum* has a very low propensity to drop from its host plant, even when aphid densities are high (Losey and Denno 1998).

Of the many factors influencing the propensity of aphids to drop from plants, predator species may have the greatest effect on the escape response. The mechanisms underlying this positive association may be predator size, the intensity of substrate vibration, the aggressiveness of the predator foraging, or perhaps increases in the volume of alarm pheromone associated with different predators. Coccinellids appear to stimulate significantly more aphids dropping than other predators (Losey and Denno 1998).

When confronted by a coccinellid, pea aphids are more likely to drop off the plant rather than walk away. When approached by a syrphid larvae, however, they are more likely to walk away (Brodsky and Barlow 1986). The proportion of pea aphid (*A. pisum*) dropping from alfalfa when heteropteran predators were present (*Nabis americoferus* Carayon, *Geocoris punctipes*, and *Orius insidiosus* (Say) ranged from 11% to 16% and was significantly higher than those dropping in the absence of predators. The proportion of *A. pisum* dropped when *C. septempunctata* was present reached over 50% and was significantly higher than the dropping stimulated by heteropteran predators (Losey and Denno 1998).

When compared with other predators and parasites, coccinellids exhibit a more vigorous foraging activity and induce more dislodgment of aphids (Brodsky and Barlow 1986). The aggressive foraging movements of adult and larval coccinellid beetles stimulates the release of the aphid alarm pheromone trans-B-farnesene which causes many more aphids to dislodge from their host plants and fall to the ground where many perish (Bowers et al. 1972, McConnell and Kring 1990). The more alarm pheromone produced, the more likely adjacent aphids will escape (Clegg and Barlow 1982).

MOVEMENT AND CRITICAL DISTANCES

There are all degrees of movement by adult coccinellids from simple, short flights from one part of a field to another in search of food to extended migratory flights into different habitats where aggregations are usually formed. In most cases, long-distance movements are associated with reaching dormancy sites. Even though Coccinellidae are strong flyers and capable of very long migratory flights, evidence suggests that local habitat structure can produce differences in the rate at which the Coccinellidae colonizes agricultural fields (Hagen 1962).

Mark, release, and recapture experiments conducted in England showed that bean plots 400 meters from early season aggregation sites on stinging nettles were colonized sooner by *C. septempunctata* than plots that were 800 meters away (Banks 1955).

Transects of yellow sticky traps used to study the variation in *C. septempunctata* density in an apple orchards showed that there was an edge effect from non crop vegetation on the perimeter of the orchard extending 30 meters into the orchard (Brown and Lightner 1997).

Evans and Richards (1997) manipulated the distribution of *C. septempunctata* with sugar water and demonstrated that significant differences in beetle distribution could be detected on the scale of a typical agricultural field. Sucrose dissolved in water was sprayed on small plots in the center of an alfalfa field. Coccinellid density increased as much as thirteen times in the plots within 48 hours. *C. transversoguttata* was more responsive than *C. septempunctata.* Coccinellid densities in the surrounding alfalfa were reduced two-thirds from their former density out to 40-150 meters from the sugar sprayed plots.

Chambers et al. (1982) observed an effect on *C. septempunctata* colonization of an individual agricultural field that was associated with vegetation on the edge of the field. Under mild winter conditions in an early fall planting of wheat, a population of *S. avenae* began to rise rapidly. On average, the aphid populations peaked in the middle of the fields four days before the edges. The edge effect was strongly associated with vegetation on the edge of the wheat field. However, when the pattern of *C. maculata* was assessed at incremental distances into a cornfield, there was no indication that colonization of the field began from the field edge (Hoffmann et al. 1997).

IMPACT OF AGRICULTURAL PRACTICES

Tillage

Generally, tillage has been found to have minimal effect on most foliage-inhabiting insects including foliage inhabiting natural enemies. In some cases, there can be great numbers of foliage inhabiting predators in clean till systems (Troxclair and Boethel 1984, Thorvilson et al. 1985, Hammond and Stinner 1987, Funderburk et al. 1988, Buntin et al. 1995).

For example, Buntin et al. (1995) found that the primary predacious taxa in a soybean crop were damsel bugs (*Nabis* species), coccinellids (*C. septempunctata, Coleomegilla maculata* DeGeer, and *H. convergens*) spiders (Araneae), and a bigeyed bug (*Geocoris* species). No till planting systems had fewer damsel bugs or had no effect on their populations compared to chisel plow or moldboard plow planting systems. No till planting systems had fewer bigeyed bugs or had no effect on their populations compared to chisel plow or moldboard plow. The reduced tillage systems were weed free. The no till soybean-planting systems had no consistent effect on spider or coccinellid populations compared to chisel plow or moldboard plow.

Rice and Wilde (1991) evaluated above ground predator densities in conventional, reduced, and no till corn Nabidae, Coccinellidae, and Chrysopidae were unaffected or significantly higher in the clean tillage corn. Spiders were either unaffected or more abundant in the no tillage corn. Tonhasca and Stinner

(1991) also found that Coccinellidae were higher in the clean till corn compared to corn/bean inter cropping.

Pesticides

Insecticides influence coccinellid assemblages directly by toxic effects and indirectly by changing prey abundance. Larval instars vary in their susceptibility to pesticides; thus, the timing of insecticide applications is important. If the insecticide interferes with egg laying by the Coccinellidae, the results are amplified during the growing season (Whitford and Showers 1988, Banken and Stark 1997).

The relative toxicity of various insecticides to Coccinellidae is influenced by their specific behaviors. Jepson et al. (1995) evaluated the toxicity of dimethoate to *C. septempunctata* and *Tachyporus hypnorum* (Coleoptera: Staphylinidae) in the laboratory and the field. Standard direct toxicity tests in the laboratory suggested *that C. septempunctata* was more susceptible to dimethoate than *T. hypnorum.* Field tests produced the opposite results. Dimethoate is rapidly lost from foliage under field conditions. T. hypnorum spends more time on the ground than *C. septempunctata.* The actual toxicity of the insecticide in the field was the result of differences in foraging behavior between the insects and the differential fate of the chemical under field conditions.

In orchard systems, species and densities in all developmental stages of *C. septempunctata* were higher in an insecticide free apple orchard in Hungary during a three-year study. The number of larvae that were observed in the insecticide free apple orchard was about twice that in the treated orchard (Lovei et al. 1991).

Herbicides generally have little direct effect on Coccinellidae. Reduction in herbicide use in reduced till planting systems does, however, result in significant increases in weediness. The presence of weeds and aphid prey sometimes influences the distribution of Coccinellidae (Buntin et al. 1995).

RESPONSE TO HABITAT MANAGEMENT

Polyculture

In a meadow subjected to various management schemes, Nentwig (1988) observed that as the floral and faunal diversity increased over time, the density of most individual arthropod species decreased. However, populations of Coccinellidae did not decline; they increased over time in the more diverse meadows. The Coccinellidae appeared to be responding positively to the overall increase in the abundance and variety of prey items. Increases in arthropod diversity are generally associated with polyculture, and this should have an impact on distribution of Coccinellidae. In some cases, however, there are fewer Coccinellidae in mixed culture than in monoculture. In these situations, there is generally a much higher prey density in the monoculture resulting in coccinellid aggregation there.

Andow and Risch (1985) evaluated coccinellid activity in corn monoculture versus corn/bean and corn/squash polyculture. Prey items included aphids and egg masses from *Ostrinia nubilalis* Walker. The aphid infestation occurred naturally. Aphid infestation of the monoculture occurred about a week prior to the mixed cultures. The difference in colonization timing resulted in elevated aphid densities in the monoculture at the beginning of the season. The *O. nubilais* egg masses, however, were placed evenly by hand across all treatments.

The coccinellid *C. maculata* was absent from the cropping systems until 35 days after planting. When it invaded the systems, it was immediately more abundant in the corn monoculture. The coccinellid larvae followed the same pattern. They were more abundant in the monoculture than in either of the types of polyculture (Andow and Risch 1985).

Colonization by *C. maculata* of the three cropping systems involved both immigration and emigration; they accumulated in higher numbers in the monoculture where immigration exceeded emigration. The beetles had a higher rate of emigration from the polyculture where aphids were more dispersed and the coccinellids had a decreased rate of food encounter (Andow and Risch 1985).

At the end of the growing season, there were no significant differences in the number of aphids per plant in the polyculture and monoculture. The concentration of coccinellids in the monoculture (where aphids colonized the corn at the highest density) slowed aphid population growth relative to the polyculture. The aphid populations in the mixed cultures and monoculture converged. Predation on *O. nubilalis* eggs masses, however, was higher in the monoculture where coccinellid densities were also highest (Andow and Risch 1985).

Planting arrangement

Row spacing is a critical feature of vegetable cropping systems, because row spacing determines the time period between crop establishment, canopy closure, and the rise in relative humidity associated with row closure. Many insect and natural enemy species invade vegetable plantings at the time of canopy closure when temperatures and relative humidity at the soil surface moderate (Buschman et al. 1984).

The size and arrangement of patches of vegetation can affect the foraging efficiency of natural enemies including Coccinellidae (Hassell and May 1974, Kareiva 1987). There are examples of coccinellid aggregation resulting in significant reductions in aphid populations. Habitat or patch fragmentation can promote aphid outbreaks if it interferes with nonrandom searching behavior of ladybird predators and interferes with aggregation of predator in areas of high prey density (Elliott et al. 1996).

Kareiva (1987) studied the impact of "patchiness" of golden rod (*Solidago canadensis*) on *C. septempunctata* foraging on the aphid *Uroleucon nigrotuberculatum.* The golden rod was mowed into patches surrounded by grass or it was left intact. The coccinellid beetles were marked and released.

Aerial aphid colonization rates were the same in the patchy and continuous patches of goldenrod. Removal of *C. septempunctata* from an experimental plot consistently caused the aphid populations to increase in density relative to control populations. Increased patchiness led to local explosions of aphid populations. Aphid colonies were eliminated twice as frequently in the continuous as in the patchy goldenrod habitats. Over 4 years, 26 aphid outbreaks occurred in patchy golden rod habitat while only 9 aphid outbreaks occurred in continuous goldenrod habitat (Kareiva 1987).

Kareiva (1987) argues that patch fragmentation affected the aphid/Coccinellidae interaction primarily by altering the foraging movement of the coccinellid. Patch fragmentation reduced hunting efficiency. Goldenrod patchiness slowed the rate at which the lady beetles aggregated at patches of high aphid density. By the time the beetles aggregated, the aphid population growth rates were so high that they swamped any impact by the coccinellids.

Relay strip-cropping

Relay strip-cropping combines two vegetation management tactics, under-sowing and strip management, that may have an impact on Coccinellidae colonizing the target crop (in this case, broccoli). Under-sowing also results in early soil cover that should improve the microclimate surrounding the target crop. Under-sowing results in a polyculture that should increase the abundance and diversity of potential prey items attractive to Coccinellidae.

Schlinger and Dietrick (1960) reported some success manipulating coccinellids with strip management of alfalfa. Other researchers have had poor success moving Coccinellidae out of alfalfa into the target crop (cotton) even when the alfalfa was mowed down (Hodek 1973).

Semi natural non-crop vegetation can serve as a source of colonizing coccinellid beetles if the beetles aggregate in the non-crop vegetation early in the season and then move into agricultural crops when aphid populations begin to increase there. Non crop vegetation can also serve as a sink for colonizing Coccinellidae, distracting and drawing beetles away from a target crop (Corbett 1998).

Banks (1955) argued that the coccinellids were ineffective predators of bean aphids (*A. fabae*) because the majority of the overwintered beetles were busy attacking M. *evansi* on a nearby patch of nettles while the bean aphid population was becoming established. The gravid female coccinellids committed their first cohort of predacious larvae to the nettles patch. By the time the females moved over to the bean crop, *A. fabae* infestations had already reached their maximum numbers. The coccinellid density in the beans was, however, determined by distance from nettle sites. On the one hand, the nettle aphids served as a "first food" supply for the predators recently emerged from hibernation; the nettle aphids were probably important for their survival. On the other hand, aphids on the nettles attracted incoming coccinellid beetles away from the beans.

When plants are mixed together in a polyculture, we can still detect source and sink effects at work. McIver (1983) mixed collards (the target plant) with alfalfa which is attractive to many species of Coccinellidae. More coccinellid beetles were observed in the collard-alfalfa system when the alfalfa was left tall and undisturbed than when the alfalfa was mowed. Increases in beetle numbers in the alfalfa did not, however, result in greater numbers on the collards themselves. Fewer Coccinellidae were observed on the collards surrounded by mature, unmowed alfalfa than on collards sitting in a patch of recently mowed alfalfa. Perhaps the coccinellid beetles (primarily *C. trifasciata*) may have found preferred prey on the alfalfa. Regardless of the mechanism, the alfalfa mixed was a sink not a source of colonizing for the interplanted collards. The presence of a natural enemy in a surrounding habitat does not necessarily guarantee its movement into the target crop.

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APPENDIX D: NABIDAE LITERATURE REVIEW

INTRODUCTION

Nabidae are one of the most abundant predators in agricultural systems; they can have an impact on insect pest populations (Donahoe and Pitre 1977, Taylor 1949, Grasela and Steiner 1993). Most nabid species would be considered r-strategist according to Southwood's definition (Southwood 1977). They are highly mobile, and they reproduce rapidly. Nabidae successfully colonize recently disturbed habitats. Ehler and Miller (1978) argue that r-selected natural enemies can provide control of r-selected insect pests in ephemeral agricultural crops. They cited *Nabis americoferus* Carayon as an example of such an enemy. Nabidae belong to a guild of generalist predators that operate together in complementary ways. Ehler (1977) showed, for example, that *Orius tristicolor* (White), *N. americoferus*, *Geocoris pallens* Stal, and Chrysoperla carnea (Stephens) together over the course of the growing season maintain the density of the cabbage looper, *Trichoplusia ni* (Hubner) at non-injurious levels.

BIODIVERSITY

Nabidae is a small family of the true bugs (Hemiptera: Heteroptera) containing 31 genera and about 380 species (Lattin 1989). The two most common species in Oregon vegetable and field crops are *N. americoferus* Carayon, and *Nabis alternatus* Parshley (McIver 1983). Before 1960, *N. americoferus* was thought to be synonymous with *Nabis ferus* L. a widespread species introduced into North America from Europe. The North American species is a distinct form from *N. ferus* and was named *N. americoferus* by Carayon in the early 1960's. *N. americoferus* and *N. alternatus* are polyphagous predators commonly associated with grasses, cotton, alfalfa, and other legumes (Stoner et al. 1975, Braman et al.

1984, Braman and Yeargan 1988). Although *N. alternatus* occurs in Oregon along side of *N. americoferus* (McIver 1983), it is more abundant in the southern desert valleys of California (Ehler 1977).

BIOLOGY AND LIFE HISTORY

N. americoferus spends the winter in alfalfa fields and in other field crops, or in crop residue on the ground. Nabid females winter as adults in reproductive diapause in the vicinity of agricultural fields. In Kentucky, wintering nabids begin producing the first generation of the year in early March (Braman and Yeargan 1988). To the north in eastern Canada, activity resumes in late March or early April and oviposition begins in mid-April. Thus, nabids are present and active in the agricultural landscape early in the growing season (Guppy 1986).

In the spring, nabid females mature, experience a short pre-oviposition period, and then begin laying eggs. In laboratory studies at 23 C, *N. americoferus* had a pre-oviposition period that lasted for 7-10 days and an oviposition period that lasted for 9-32 days (Braman and Yeargan 1988). *N. americoferus* lays an average of 8 eggs per day and a total of about 150 eggs per female (Guppy 1986). *N. alternatus* lays about 280 eggs during their lifetime that last 70-80 days. Thus, nabids have a high reproductive potential (Perkins and Watson 1972a).

Nabidae insert their eggs into plant stems (Richards and Harper 1978, Lattin 1989). *Nabis* species concentrate their egg laying in leguminous plants; they have distinct host plant preferences. In the laboratory, green beans can be used as oviposition sites for *N. alternatus* (Perkins and Watson 1972a). If it is caged and forced to do so, *N. americoferus* will oviposit in soybeans (Braman and Yeargan 1990, Pfannenstiel and Yeargan 1998); in the field, however, *N. americoferus* rarely places its eggs in soybean stems even though adults can be present in high numbers in soybean crops. Alfalfa is clearly a preferred host plant of *Nabis* species; females have distinct preferences for alfalfa stems at a specific size and maturity. In the laboratory, nabid females place their eggs in alfalfa stems that are 1.5 – 1.7 mm or smaller in diameter (Richards and Harper 1978, Guppy 1986).

Nabid eggs hatch in about a week at 28 C. Nabids are active shortly after hatching and begin feeding immediately (Lattin 1989). *Nabis* species have five larval instars; the nymphs are wingless (Perkins and Watson 1972a). *Nabis* species vary in their developmental rates. *N. americoferus*, for example, develops faster from egg to adult than *Nabis roseipennis* Reuter at a variety of constant temperatures (Braman et al. 1984, Braman and Yeargan 1990).

In laboratory studies, *N. americoferus* was responsive to temperature. As the temperature increased from constant 18 C to constant 31 C, the duration of the nymph stages decreased. At 18 C, *N. americoferus* required 70 days to complete its life cycle. At 30 C *N. americoferus* required only 23 days. The developmental thresholds for *N. americoferus* were 11 C for eggs and 10.6 C for the nymph stages; the mean developmental time from eggs to adults was between 474 to 494 degree days (Braman et al. 1984, Guppy 1986).

In Canada, nymphs of the first generation of *N. americoferus* are present from mid-April to late July (Guppy 1986). Generally, from early April to late October approximately 1085 degree days accumulate suggesting that in northern climates, only two generations of *N. americoferus* complete their life cycle each year. In Kentucky, the wintering generation of *N. americoferus* begins laying eggs in alfalfa in March (Braman et al. 1984). In a typical growing season, the accumulation of approximately 2,100 degree days allows the development of three generations per year. In Arizona, *N. alternatus* and *N. americoferus* have as many as five generations per year. Based on these degree day assumptions, *Nabis* species have the potential to complete two to three generations per year in the Willamette Valley depending on the climate each year (Stoner et al. 1975).

At 24 C the second or third generation of female *N. americoferus* respond to a critical photoperiod of about 14 hours of light per day by entering into reproductive diapause. The nymph stage is most sensitive to daylength. Once the critical daylength occurs, individual nymphs continue to develop but do not finish maturing sexually until the spring (Braman and Yeargan 1988).

Adult nabids winter in alfalfa fields and within a week of completing their post-diapause development begin to oviposit in the same fields. These individuals constitute the last generation of the previous year. Since they are already established in alfalfa, their oviposition is synchronized with new plant growth. Dispersal flights most closely agree with alfalfa cutting dates and not with spring flights associated with redistribution and colonization of new oviposition sites (Braman and Yeargan 1990).

Under laboratory conditions of 28 C with 15 hours of daylight, *N. alternatus* lives about 38 days (Perkins and Watson 1972a). In nature, nabid populations are prey limited. *N. alternatus* live about four days without food. Nabid populations are also limited by inbreeding depression and by cannibalism (Braman et al. 1984, Guppy 1986, Grasela and Steiner 1993).

A variety of organisms prey upon the eggs, nymphs, and adults of Nabidae including wasps (Sphecidae), other predatory bugs (Pentatomidae, Reduviidae), and spiders (Lattin 1989). Parasitism can be high in Nabid populations. Stoner et al. (1975) recorded parasitism of up to 48% in Arizona of *N. alternatus* and *N. americoferus* by tachinid parasites.

Inbreeding depression is a significant limitation on nabid population growth. Female nabids lay many eggs; successful egg hatch can exceed 90% at temperatures from 18 to 31C. In laboratory cultures, however, survival from nymph to adult is low. Regardless of environmental conditions, only 10-25% of *N. americoferus* nymphs survived to sexual maturity. Most of the deaths occur during the fourth and fifth instars. Cage size, relative humidity, temperature, and prey quality did not influence survival (Braman et al. 1984, Guppy 1986).

Grasela and Steiner (1993) studied the genetics of *N. americoferus* and *N. alternatus* populations and found that both populations had low levels of heterozygosity. In agricultural landscapes, nabid populations are highly inbred due to a combination of their life histories and agricultural practices. Nabid populations winter inside or close to the fields that they invade during the spring. Nabids do not disperse very far even when a field is harvested. Overlapping generations and close proximity allow for a significant amount of mating between closely related individuals of the preceding generation. Frequent disruption of nabid populations in agroecosystems upsets the demographic and genetic structure of residential populations. Local patches of nabids perish when alfalfa is harvested, survivors colonize the field after crop reestablishment, and there is a constant narrowing of the genetic base of the nabid colony.

Cannibalism can be significant among nabid nymphs (Guppy 1986). In laboratory cultures, nabids often attack other individuals who are immobilized during the molting process. In the field, female nabids lay their eggs in clusters. Proximity promotes cannibalism when other prey items are scarce. Cannibalism may be adaptive and serve as a self-limiting factor governing population density of nabid species in unstable ecosystems (Perkins and Watson 1972a, 1972b).

Nabid populations tend to follow the same seasonal activity patterns as *Lygus* populations (Stern et al. 1964, 1969). The peak density of *N. americoferus* in eastern Canada of three to four specimens per arc of a sweep net occurs during August (Guppy 1986). In California's San Joaquin Valley, *N. americoferus* occurs in significant numbers by mid June, and their population increases steadily over the growing season (Eveleens et al. 1973, Ehler 1977). Nabids generally are most abundant later in the growing season as crops mature. In warm climates, definite peaks in nabid populations are observed in early July and late August (McPherson et al. 1982). Typically, nabid nymphs and adults combined reach total densities of less than one individual per square meter. Their numbers, however, occasionally rise as high as ten individuals per square meter. Nymphs generally outnumber adults except in the early growing season prior to the development of the first generation of the new year (Buschman et al. 1984).

PREY ITEMS AND FORAGING BEHAVIOR

Some plant feeding by nabids occurs, but no development follows in the absence of insect prey (Ridgway and Jones 1968). When available moisture is in short supply, the longevity of *N. americoferus* increases when they are allowed to feed on cotton plants. It is likely that moisture is the chief objective of plant feeding by nabids (Stoner 1972).

Nabids feed on many different small insects (Perkins and Watson 1972a, 1972b, Lattin 1989) including aphids (Ehler 1977), thrips, whitefly nymphs, and leafhoppers (Martinez and Pienkowski 1982, Renser and Lamp 1983, Flinn et al. 1985), mirids (including *Lygus* species) (Whalon and Parker 1978, Araya and Haws 1988, 1991), spider mites (Butcher et al. 1988), leaf miners (Guppy 1986, Harcourt and Guppy 1987), and the eggs and small larvae of many species of Lepidoptera (Ehler and van den Bosch 1974, Braman and Yeargan 1989). Prey quality influences developmental time of the nymphs. For example, *N. americoferus* nymphs develop 10 to 34% faster on leaf miners (Diptera: Agromyzidae) than on pea aphids (Guppy 1986).

Nabids prey on aphids of many different species (Cameron et al. 1983, Carrol and Hoyt 1984, Rice and Wilde 1991, Campbell and Cone 1994) and consume up to 25 aphids per day (Tamaki and Weeks 1972). This rate of consumption is significantly less than the Coccinellidae, which consume up to 200 aphids per day (Palmer 1914). In the laboratory, *N. alternatus* can be maintained on pea aphids (*Acyrthosiphon pisum*) on alfalfa (Richards and Harper 1978). *Nabis* species had a 35-88% positive precipitin tests for *Brevicoryne brassicae* L. when they were gathered from collard foliage (McIver 1983).

In cage studies to determine the impact of natural enemies on the green peach aphid, *Myzus persicae* (Sulzer), *N. americoferus* was effective in reducing aphid populations. The effect, however, was short lived. In control cages, aphids per plant increased steadily. In cages where nabids were introduced (8 per cage), aphid numbers declined for the first week; then, the aphid population increased at the same rate as the control population. The final aphid count was reduced by the nabids compared to the control; it did not appear, however, that the nabids had the capacity to regulate the aphid population (Tamaki and Weeks 1972).

Flea beetles (*Phyllotreta* spp.) have very few natural enemies (Burgess 1980). Coleoptera, in general, are protected by their tough elytra. Nabidae are relatively large bodied and have long piercing mouthparts (Cohen 1990) that are not deterred by the tough shell. *N. alternatus*, was observed attacking the cabbage flea beetle *Phyllotreta cruciferea*e Goeze in sweep net samples taken from rape seed. It was a rare event, however, and may have been associated with close proximity in the sweep net (Burgess 1982, Culliney 1986).

Nabids are common predators of the eggs and small larvae of Lepidoptera (Ehler et al. 1973, Ehler and van den Bosch 1974, Ehler 1977, Donahoe and Pitre 1977, Sloderbeck and Yeargan 1983, Elvin et al. 1983, O'Neil and Stimac 1988, Yeargan and Braman 1989, Ruberson et al. 1991). Nabids at approximately 20 per row meter in soybeans caused a 50% reduction in green clover worm larvae, *Plathypena scabra* (L.), over control plots. This density of nabids is, however, about ten times the normal level of nabids in soybeans. Nabids contribute to mortality of the green clover worm, but can not normally prevent clover worm outbreaks (Braman and Yeargan 1989).

In cage studies to determine the impact of natural enemies on the Bertha armyworm, *Mamestra configurata* Walker, *N. americoferus* alone and in combinations with *Coccinella transversoguttata* Faldermann was superior to all other natural enemies tested at reducing the armyworm population. The nabid alone was more effective at reducing armyworm numbers than the coccinellid alone. Apparently, *N. americoferus* was attracted to and could better handle the early instars of *M. configurata* better than the coccinellid predator (Tamaki and Weeks 1972).

Eveleens et al. (1973) studied the impact of insecticides on the interaction between predators including *N. americoferus* and the beet armyworm, *Spodoptera exigua* (Hubner) in cotton. Life table analysis showed that mortality of *S. exigua* in the absence of the insecticide sprays was due to predation directed at eggs and the first and second instars. Heavy outbreaks of armyworms followed treatments with the insecticide dimethoate. The insecticide dramatically depressed the density of *N. americoferus* and the other predators. As the number of sprays increased, the size of the cohort of early instars of *S. exigua* increased almost linearly.

N. roseipennis significantly reduces the number of surviving first and second instars of *T. ni* in soybeans (Reed et al. 1984). In field cage studies, the nabid ate about 6.2 *T. ni* larvae per day. *N. americoferus* adults and nymphs also preyed on *T. ni* larvae of all sizes. Life table analysis of *T. ni* in insecticide and control plots show that the egg to small larvae ratio goes up in the absence of natural enemies. In the untreated plots, 3.5 eggs in the untreated plots resulted in 1.9 larvae. In the insecticide treated plots, 1.9 eggs resulted in 1 larvae. Virtually all of the *T. ni* eggs and small larvae in the insecticide treated plots survived to later instars. In the control plots, only 50% survived (Ehler et al. 1973, Ehler and van den Bosch 1974, Ehler 1977, Ehler and Miller 1978).

Adult *N. americoferus* are mostly found on leaves high in the plant canopy. There foraging activity is greatest from mid morning to early afternoon (Braman and Yeargan 1989). Adult and nymph aggregation patterns differ. Nymphs tend to be more aggregated. Adult distribution is less aggregated and in some cases random (Braman and Yeargan 1990).

N. americoferus prefers small to medium size larvae (Eveleens et al. 1973). Once it finds a hatching egg cluster, *N. americoferus* tends to stay there consuming the young larvae as they emerge. Nabids foraging on plant foliage alarm and dislodge many more aphids than they consume. On the ground, the numerous ground dwelling predators prey upon these aphids (El-Agamy and Haynes 1992).

MOBILITY

Adult Nabids are capable of moving considerable distances. Edwards (1987) mentions *N. alternatus* as one of five species of insects taken on the summit of Mt. Rainier, Washington. When alfalfa is cut, adult *N. americoferus* migrate over 67 to 122 meters to half-grown alfalfa. Nabid nymphs, however, are wingless and not highly mobile. Once the female has committed her progeny to a plant patch, the young are forced to hunt for prey to avoid starvation (Rakickas and Watson 1974).

The mobility of the Nabidae allows them to rapidly colonize agricultural fields that have been sprayed with insecticide or disturbed in some other manner. Buschman et al. (1984) found that nabid populations recovered completely in about two weeks after whole field insecticide applications. In part, because of the high mobility of the Nabidae, Eveleens and van den Bosch (1973) used experimental plots placed in commercial alfalfa fields that were 1/8 by ½ mile wide. The depressing effect of the insecticide application (dimethoate) on *N. americoferus* was dramatic, but it persisted for only three weeks. The plot size (40 acres each) was too small to prevent re-colonization of the experimental plots by the nabids.

HABITAT PREFERENCES

Nabids do well under warm conditions (Perkins and Watson 1972a) but they require adequate moisture to survive. For example, *N. alternatus* was more abundant in cotton that was irrigated every week than in cotton that was irrigated every two weeks (Flint et al. 1994).

N. americoferus prefers open habitats, particularly for oviposition. The adults emigrate from the soybeans as the canopy closes (Pfannenstiel and Yeargan 1998). On cotton, adult nabids were found higher on the plant than the nymphs. On an individual alfalfa plant, adult *N. americoferous* adults concentrated their oviposition in the upper region of the plant (Guppy 1986) while the nymphs remain lower on the plant (Braman and Yeargan 1989). Adult *N. alternatus* followed a similar pattern (Richards and Harper 1978). In alfalfa, only a small number of first and second instars of *N. americoferus* were captured in sweep-net samples because they prefer the lower parts of the plants. The later instars and the adults forage high in the alfalfa canopy (Guppy 1986). *Nabis* are significantly more common on tall mature alfalfa than on young recently mowed alfalfa (Stern et al. 1964, 1969, McIver 1983).

Nabidae have distinct crop preferences. Nabidae are most commonly associated with legumes, cotton, and grasses (Perkins and Watson 1972a, Stoner et al. 1975, Braman et al. 1984). In small plot studies where the nabids could easily disperse across the treatments, the nabid densities varied significantly between crops. *N. americoferus* was strongly associated with snap beans and soybeans. Only small numbers of nabids were found in corn, tomato, or tobacco (Nordlund et al. 1984, Pfannenstiel and Yeargan 1998).

N. americoferus and *N. alternatus* are often the most numerous insect predators in alfalfa (Perkins and Watson 1972a, Richards and Harper 1978). In cotton, nabids do not become numerous until mid summer. The delay in nabid population establishment may be the result of insecticide applications during cotton establishment or changing microclimate as the cotton canopy closes. Nabids migrate into cotton fields when the plants become large enough and mature enough to support sizeable populations of herbivorous prey. The timing of the invasion of the cotton crop, however, often corresponds with the cutting and drying of local alfalfa fields for harvest. Nabids may only move into cotton when their preferred host plants are unavailable. Given the preference of *N. americoferus* and *N. alternatus* for legumes regardless of the prey availability on alternative crops, the concept of generalist may be an inappropriate term for these predators, at least in terms of habitat preferences (Pfannenstiel and Yeargan 1998).

COMPETITION AND INTERFERENCE

Nabids compete with and sometimes prey on other generalist predators. For example, Nabidae can be significant predators of lacewings (*C. carnea*) and reduce the ability of lacewings to regulate the cotton aphid (Rosenheim et al. 1993). When high densities of lacewing eggs were experimentally released in cotton, they produced only a modest and transient suppression of the cotton aphids. It was found that native *Nabis* species were eating many of the experimentally distributed lacewing eggs. Follow-up cage experiments showed that the nabids could generate sufficient lacewing mortality to release aphid populations from regulation (Rosenheim and Wilhoit 1993, Rosenheim et al. 1993).

Nabis species also interfere with foraging Coccinellidae. When *N. americoferus* was added to a cage containing aphids and coccinellids, the nabid interfered with the regulation of *M. persicae* by *C. transversogullata* (Tamaki and Weeks 1972).

Prey items of *N. americoferus* include *Orius* adults and nymphs of both *Orius* and *Nabis* species (Braman and Yeargan 1989). However, predation of predators on other predators in nature is often limited by other factors. Under experimental conditions, *N. roseipennis* interfered with and sometimes preyed on *Orius insidiosus* (Say). In the field, *N. roseipennis* and *O. insidiosus* had different population peaks. When they occurred at the same time, *Orius* tended to be higher in the plant and associated with flowers and pods; N. *roseipennis* tended to occur mostly on the leaves. In natural situations, the populations tend to be separated spatially and temporally (Clements and Yeargan 1997).

IMPACT OF AGRICULTURAL PRACTICES

In the agricultural landscape, a significant portion of the reproductive potential of the Nabid populations is lost to insecticide applications and to forage harvesting practices (Ehler and Miller 1978). Many nabid eggs and young nymphs perish during the harvest of alfalfa (Richards and Harper 1978, Godfrey and Leigh 1994).

Nabids are susceptible to many of the commonly used insecticides in agriculture. Nabid numbers, however, recover within a period of a few weeks even when insecticides are applied over large areas of cropland (Ehler et al. 1973, Eveleens et al. 1973).

N. alternatus females lay most of their eggs in alfalfa stems. The timing of harvest and the harvest management scheme determine if the alfalfa crop serves as a nursery or a trap crop for the Nabid populations. In the laboratory, most of the eggs that were laid in alfalfa stems died when the alfalfa was allowed to dry after oviposition. In the field, few Nabid eggs survive when the alfalfa is cut for hay (Richards and Harper 1978, Godfrey and Leigh 1994). Nabid populations in hay fields depend on the migration ability of the wingless nymphs and the flying adults. Adult Nabids disperse during the harvest operation, but many wingless nymphs must perish during and after the harvest. The destruction of the nymphs may explain why nabid populations are larger and more stable when alfalfa is strip-managed. A significant amount of reproductive potential of the Nabid species may be wasted in the agricultural landscape. The relative importance of this loss remains to be more fully investigated (Rakickas and Watson 1974).

Generally, tillage has minimal effects on foliage-inhabiting insects (Troxclair and Boethel 1984, Thorvilson et al. 1985a, Hammond and Stinner 1987). The abundance of some heteropteran predators including *Nabis* species may actually be lower in no-till compared to conventional planting systems (McPherson et al. 1982, Funderburk et al. 1988). Weed-free no-till soybean plantings had fewer *Nabis*, *Geocoris*, and spider species or had no effect on their populations compared to chisel plow or moldboard plow planting systems. The planting systems had little consistent effect on soybean defoliation or pod damage by herbivorous insects (Buntin et al. 1995).

Rice and Wilde (1991) evaluated above ground predator densities in conventional, reduced and no till corn. Populations of some, but not all, predator groups were affected by the treatments. Nabidae were unaffected. *H. convergens* were either unaffected by the treatments or significantly higher in the clean till corn. Spiders were more abundant in the no till corn.

Tillage, the previous crop, and pesticide programs can have both separate and interactive influences on foliage insect communities (Hammond and Stinner 1987). In soybean conservation tillage systems, nabids and Lygus species were most numerous in no-till fields previously planted with soybeans where no insecticides had been used. They were more abundant in both early and late summer when soybean was the previous crop versus corn. There was an interaction between tillage and the previous crop. *Lygus* numbers were higher in no-till than conventional tillage plantings when soybean was the previous crop. *Nabis* was not sensitive to tillage. However, *Nabis* density was higher when soybean was the previous crop (Hammond and Stinner 1987).

Nabids are highly susceptible to most insecticides (Eveleens et al. 1973, Lentz et al. 1983, Martinez and Pienkowski 1983). However, as stated earlier, nabids are highly mobile. If they are present in pesticide refuges outside the fields, their populations can recover rapidly (Buschman et al. 1984)

Nabids are sensitive to moisture and irrigation scheduling. Nabid species are more abundant in cotton and in alfalfa when the crops are irrigated on a short cycle. In fact, irrigation scheduling has been one of the factors limiting adoption of strip-cropping for management of *Lygus* bugs and nabids in cotton and alfalfa cropping systems (Stern et al. 1964, 1969, Flint et al. 1994).

RESPONSE TO VEGETATION MANAGEMENT

Between-row spacing may have an impact on nabid densities; the effect, however, is inconsistent. Mayse (1978) reported that narrow row spacing and high-density plantings of soybean were favorable for the population growth of nabids. He argued that the more rapid canopy closure in the narrow rows resulted in a more rapid development of a favorable microclimate for immigrating arthropods. Buschman et al. (1984) found that Geocoridae and spiders were slightly higher in the narrow rows, but there was no clear response to row spacing by Nabidae or Coccinellidae. Lam and Pedigo (1998) found no significant differences in nabid densities between narrow row and wide row reduced till soybean.

Increased weed diversity can have an impact on natural enemy populations. The impact of weediness on nabids depends on the weed species. Shelton and Edwards (1983) found that differing soybean maturity dates, locations, and row spacing had little impact on predator populations. Grassy soybean fields, however, had more nabids in them than soybean fields infested with broadleaf weed or weed free soybean fields. Beans grown with maize support higher nabid densities than either crop grown in monoculture (Altieri et al. 1978)

Strip-management of alfalfa and cotton has long been recommended as a strategy for manipulating Heteropteran pests including *Lygus* bugs. By harvesting alfalfa in strips rather than in large blocks, the movement of *Lygus* from alfalfa into adjacent cotton fields and damage to the cotton bolls is reduced. For the technique to work, the alfalfa must be managed with multiple cuts and irrigation to keep it green and attractive to the *Lygus* (Stern et al. 1964, 1969).

Heteropteran predators including *Nabis* species respond in an identical manner to alfalfa management (Cameron et al. 1983, Thorvilson et al. 1985b, Harper et al. 1989, Schaber et al. 1990). Nabids and *Lygus* both lay their eggs by inserting them into the stems of alfalfa plants. The densities of *Lygus* (Godfrey and Leigh 1994) and nabids (McIver 1983) are higher in tall unmanaged alfalfa than in the new growth alfalfa cut for hay. In block-harvested alfalfa, nabid and *Lygus* dispersal flights closely agree with alfalfa cutting dates (Braman and Yeargan 1990). The nymphs of both *Lygus* and *Nabis* are flightless; they perish during the cutting and harvest of the alfalfa managed for hay (Richards and Harper 1978). After an alfalfa harvest, nabid adults concentrate in residual patches of undisturbed vegetation even if the patches are relatively small (Grasela and Steiner 1993). Adult nabids do not move freely between strips in strip-managed alfalfa (Stern et al. 1964, 1969).

N. alternatus populations are more stable in alfalfa cropping systems when the edges of alfalfa fields are left uncut during harvest. In a study comparing conventional solid cut alfalfa versus border harvested alfalfa, 90% of the nabids concentrated in the uncut area on the border. They did not disperse. About a week later, they reinvaded the same field (Summers 1975).

RELAY STRIP CROPPING

Relay strip-cropping, which combines under-sowing with strip-management, should increase the density of Nabidae in the vicinity of the target crop, broccoli. The winter cover crop of grasses and legumes should attract and support a robust winter population of Nabidae. At crop establishment, the residual strips of cover crop should concentrate Nabidae proximal to the broccoli. As the cover crop strips mature and dry out or when the cover crop strips are incorporated prior to the late planting of broccoli, the adult nabids should disperse into the broccoli.

In this study, under-sowing resulted in an intimate mixture of broccoli, grasses, and legumes. Nabids are attracted to grasses and legumes; the polyculture should result in increases in nabids in the vicinity of the broccoli. Evidence suggests that nabids prey on aphid species that attack broccoli including *M. persicae* and *B. brassicae*. Evidence suggests that nabids attack several lepidopteran pests of broccoli including *T. ni* and *M. configurata*. Pest populations should be reduced in the broccoli.

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APPENDIX E: BROCCOLI INSECT LITERATURE REVIEW

INTRODUCTION

In this chapter, we examine the impact of relay strip cropping on insect pests of broccoli. Root (1973) divided the above ground Crucifer specialists into three feeding guilds, "sap feeders" including the cabbage aphid (*Brevicoryne brassicae* L.), "pit feeders" including the cabbage flea beetle (*Phyllotreta cruciferae* Goeze), and "strip feeders" including the diamondback moth (*Plutella xylostella* (L.)), the cabbage looper (*Trichoplusia ni* (Hubner)), and the cabbage butterfly (*Pieris rapae* L.). They are the focus of this study. Each insect has a unique set of attributes that we can use as analytical probes in evaluating the impact of relay strip cropping on the arthropod community.

It has long been noted that large pure stands of cole crops accumulate more heavy loads of herbivorous insects than mixed stands of cole crops and other plant families. The differential loading varies according to insect species. *P. rapae* avoids concentrations of its host plants and is unaffected by stand purity. *P. cruciferae* is sensitive to stand purity. *P. cruciferae* densities are generally lower in mixed stands (van Emden 1965, Tahvanainen and Root 1972, Root 1973, Smith 1976a, Tukahirwa and Coaker 1982, Kareiva 1985, Altieri and Schmidt 1987, Stoner 1992, Costello 1995).

The insects that colonize cole crops have developed the capacity to assimilate a class of phytochemicals known as glucosinolates or mustard oil glucocides. Glucosinolates are repulsive or toxic to the majority of insects. They constitute one of the primary defense mechanisms of the Cruciferae family. To the crucifer specialists, however, the toxins are feeding and oviposition stimulants that guide the insects to their host plants and arrest them there. Plant defense against crucifer specialists is accomplished by alternative mechanisms (Ehrlich and Raven 1964, Feeny et al. 1970, Hughes et al. 1997).

In nature, large pure stands of mustard family plants are rare. Over time, crucifer specialists reduce the density of mustard patches. There is a parallel increase in vegetation diversity. Mixtures of plant species replace the pure stand. Eventually, the state is reached where the feeding rate of the crucifer specialists and the dispersion of their host plants are in equilibrium. In this state, both the mustard plants and the crucifer specialists may be rare in the landscape. They are present, however, and still interacting. The crucifer specialists and the mustard plants develop a sparse equilibrium in time and space (Tahvanainen and Root 1972).

Once equilibrium is achieved, the mustard plants occur in relatively small patches on disturbed soil surrounded by other vegetation. A mustard plant might germinate on a fresh gopher mound in a meadow surrounded by a forest. Secondary plant compounds protect the mustards from non-adapted generalist herbivores in the local area. In the meantime, the crucifer specialists disperse across the landscape. Most of them perish. A few encounter their host plant and reproduce rapidly, taking advantage of a rich, unclaimed, but short-lived food source. By the time the crucifer specialists discover isolated patches of mustards, many of the plants have set seeds. The plants escape from damage by virtue of their spatial and temporal dispersion and their surroundings that interfere with their discovery. The mustard plants are protected, in part, by the interplay between host plant resistance and the ecological context in which host plant selection by crucifer specialists occurs (Feeny 1976).

Relay strip cropping should have an impact on the colonization and survival of broccoli by crucifer specialists. *B. brassicae*, for example, is sensitive to the color and contrast of the background vegetation or soil surrounding its host plant during the host plant finding process (Cromartie 1975, Costello 1995). The highly mobile *P. cruciferae* is sensitive to stand purity. It has a difficult time settling and feeding in a mixed stand (Kareiva 1985, Bergelson and Kareiva 1987, Garcia and Altieri 1992). *P. xylostella* and *T. ni* tend to lay more eggs in pure stands of crucifer plants than in mixed stands (Grez and Gonzalez 1995, Justus and Mitchell 1996, Riggin-Bucci and Gould 1997, Bigger and Chaney 1998). Further, their natural enemies tend to accumulate there as well, aggregating in areas of high prey densities. *P. rapae* does not respond to changes in host plant density (Cromartie 1975, Root and Kareiva 1984, Maguire 1984). Instead, it scatters its eggs across the landscape, increasing the probability that some of its progeny will escape mortality factors that are unevenly distributed in the environment (Hassell and May 1973, 1974, Waage 1979). The moths and the butterflies are involved in two activities at the same time, oviposition and nectar feeding. They tend to aggregate around nectar sources, and the aggregation changes the pattern of their oviposition (Zhao et al. 1992, Bigger and Chaney 1998).

Relay strip cropping may be successful at reducing insect loads on broccoli if the cropping system reestablishes elements of the ecological context in which host plant resistance can express itself efficiently. By manipulating stand purity and planting arrangement, we can interfere with the process of host plant selection. By reducing stand purity, we can increase the probability that crucifer insects will encounter non-host plants, become confused, and emigrate from the area. Mixed stands of plants support a greater diversity of insects and their natural enemies. By reducing stand purity, we can increase the pressure on the crucifer specialists by generalist natural enemies. Relay strip cropping provides a refuge from tillage operations and pesticide applications, which may conserve natural enemies that are sensitive to disturbance and that are not highly mobile.

The working hypotheses tested in this study are: a) relay strip cropping will reduce colonization of broccoli by *B. brassicae* and *P. cruciferae,* and b) survival of aphids and Lepidopteran pest of broccoli will be reduced in the relay strip cropping system due to enhanced activity of natural enemies in the relay compared to the broccoli monoculture. A summary of the life histories of the crucifer specialists provides the necessary background to interpret results. We pay special attention to the ways that these insects respond to changes in vegetation management.

BREVICORYNE BRASSICAE (L.)

B. brassicae is a green aphid with a waxy bloom. It is a crucifer specialist and a major pest of Brassica crops. *B. brassicae* and most of its host plants are native to northern Europe (Hughes 1963). The green peach aphid (*Myzus persicae* (Sulzer)) is also common on cole crop seedlings (Flint 1992). *M. persicae* is a generalist that feeds on a wide range of plants. It is generally not of economic importance in broccoli production because it does not contaminate the bud (Sheehan and Shelton 1989). Thus, we focused on *B. brassicae.*

B. brassicae prefers to feed on the younger plant tissues. It forms dense colonies around the plant's youngest leaves and flowering parts (George 1957, Hughes 1963), a feeding habit of particular economic importance because the aphids tends to move into the floral buds of the developing broccoli head. Aphids in the broccoli heads are difficult to control with insecticides. Contaminated broccoli buds are unmarketable either as fresh market or processing broccoli (Sheehan and Shelton 1989). Insecticides are applied frequently against *B. brassicae*. When the densities of aphids are high, growers may spray several times to prevent populations from reaching economically significant levels (Costello and Altieri 1994).

Monitoring *B. brassicae* population trends in a field and understanding the factors influencing the population is difficult. The aphid generations overlap. *B. brassicae* lives on host plants that have a very short life cycle. Apterous (wingless) colonies of aphids on newly colonized host plants have short generation times resulting in remarkable population increases. The explosive population growth allows *B. brassicae* to effectively exploit short-lived plant resources, such as broccoli (Hughes 1963).

For the species to survive, individuals must repeatedly migrate from exhausted host plants to fresh host plants, mostly during the summer months. The alate (winged) aphids are poor flyers. They are borne by the wind and reach new food sources largely by chance. Only a very small proportion of the population succeeds in colonizing new host plants (Kennedy and Stroyan 1959).

Winged individuals can be formed as soon as the first apterous (wingless) colonies start reproducing. When high aphid densities are reached, alate offspring become more numerous. The delayed build up of alate aphids allows steady emigration of individual aphids while at the same time permitting the population on a given plant to build up to high levels (Hughes 1963).

Life cycle and seasonal activity

The life cycle of *B. brassicae* is complex and includes polymorphism. It has two phases. During the spring and summer while host plants are actively growing, the predominant aphid form is the degenerate, apterous, parthenogenetic (asexual reproduction), viviparous (gives birth to live young) female. Each cohort of females proceeds through four instars and matures into successive generations of apterous, parthenogenetic, viviparous females. Rapid embryonic and nymph development results in the overlapping of generations, a key factor in speeding the numerical increase of the aphid colonies (Hughes 1963).

During the early spring, wild crucifer host plants begin to flower. Flower heads appear to be the only favorable feeding sites at this time, and they are sometimes choked with *B. brassicae*. Physiological changes occur within the plants and the aphids, which stimulate the production of alate parthenogenetic females. Physiological changes in the aphids occur when host plants mature and become less succulent or when aphid colonies become crowded. Winged parthenogenic females migrate to other crucifer hosts to establish new colonies. The result is a constant cycle of short, low intensity aphid flights during the spring and summer (Bonnemaison 1965, Raworth et al. 1984).

In the fall, the proportion of alate females increases dramatically and major aphid migratory flights occur. They are carried in mass by the wind and most perish. The aphids that survive, however, are widely dispersed across the landscape. As cold weather approaches, winged males and oviparous wingless females are born. They mate and produce eggs that survive the winter on the aerial parts of wild host plants (Hughes 1963).

Depending on the area and the intensity of the winter, the first generation of wingless parthenogenetic females in the spring is initiated either by eggs (deposited in the fall) or by winged migrants. Aphid eggs hatch into the last forms, the fundatrix or stem mothers. The stem mothers produce the first generation of alate, parthenogenetic females, and the annual cycle starts again (Hughes 1963).

Different climates produce variations in the life cycle of *B. brassicae*. In cold climates the sexual forms of the aphid are produced at the approach of winter as described above. In warmer climates, viviparous females may survive the winter. In southern California and in warmer areas of the Pacific Northwest, parthenogenetic females continue to give birth to live offspring throughout the year. As many as 16 generations are produced during a growing season and up to 21 generations are produced during the entire year (Berry 1998, Flint 1992).

Adult longevity is inversely related to temperatures; longevity is longer under cooler conditions than under warm conditions, but the same number of progeny is produced. Each female generates from 80 to 100 nymphs during her lifetime of about one month (Hughes 1963, Berry 1998).

The density of *B. brassicae* can reach up to 30,000 aphids per plant in the field and 120,000 aphids per plant in a laboratory culture (Raworth et al. 1984). High aphid population density may have a negative impact on aphid fecundity (Hughes 1963). However, Raworth et al. (1984) did not find a strong relationship between aphid density, fecundity, or developmental time. Density did affect the weight of the progeny. Under crowded conditions, the nymphs were smaller.

Some studies suggest that nitrogen levels in the host plant have a significant impact on the fecundity of aphids including *B. brassicae* (van Emden 1966, van Emden and Bashford 1969, Culliney and Pimentel 1986, Jansson and Smilowitz 1986). Growth rates decreased and the number of alate aphids produced increased on nutrient-stressed (unfertilized) plants in some studies. Other studies failed to show a significant impact of nitrogen fertilizer on aphid population growth, even when the differences in leaf nitrate-nitrogen was dramatic (Costello and Altieri 1994, 1995). Water stress has not been consistently shown to have a significant effect on aphids fecundity (Raworth et al. 1984).

Hughes (1963) reported a developmental threshold temperature of 41 F (5 C) with no upper threshold for *B. brassicae*. Raworth et al. (1984) reports a developmental threshold of 44.1 F (6.7 C) with no upper threshold. Numbers of aphids tend to decline in warm temperatures. Generation time (birth to birth) for apterous females is between 255 DD (laboratory) to 300 DD (field) (Flint 1992, Raworth et al. 1984).

Dispersal and host plant selection is essential to the survival of *B. brassicae* populations. Their host plants are not perennial. Only by migration of the winged individuals can the species reach the few host plants, which are in a suitable state for feeding during the summer and winter. As they are weak flyers, *B. brassicae* can make no progress against winds of more than 2 ft/sec (60 cm/sec). In the spring, they fly up into the air stream and beat their wings just hard enough to keep themselves suspended. They are carried passively on the wind for long distances. When they run out of energy or find a suitable patch of plants, the aphids stop flying and tumble out of the air stream. Their crucifer host plants tend to occur on disturbed soils. The falling *B. brassicae*, thus, are attracted to plants growing on disturbed sites surrounded by bare soil (Hughes 1963). Although *B. brassicae* will respond to olfactory cues from its host plant, there is no specific attraction of the *B. brassicae* to host plants over distances of more than a few meters (Kennedy 1958).

B. brassicae land indiscriminately on host plants and non-host plant alike. Most of the incoming *B. brassicae* land, then take off again from both host and non-host plants. An almost undetectably lower probability of take-off from host plants may account for the gradual accumulation of *B. brassicae* on crucifer plants (Kennedy and Stroyan 1959, Thorsteinson 1960). This behavior results in an intensively dispersive pattern of host encounters. Most (99%) of migrating aphids die in the process of colonization, including many of those individuals that find and then abandon host plants. They would have survived if they had stayed (Kennedy and Stroyan 1959).

In general, aphid migrations occur in the spring and fall (Chambers et al. 1982). Flight activity often correlates well with the occurrence of *B. brassicae* infestations in the field. In some years, the dominant aphid infestations begin with immigrating alates. The first flights are aphids emigrating from the flower heads of host plants on which they over-wintered. Immigration flights are slight or intense depending on the winter (Hughes 1963).

Mortality factors

The timing, intensity, source, and synchrony of aphid infestations and their natural enemies vary from year to year. By the end of July, aphid populations often crash even when no insecticides are applied, probably due to senescence of host plants (Chambers et al. 1982).

Several factors contribute to the decline in aphid populations including deterioration of host plant quality, emigration from host plants, adverse weather conditions, pathogens, parasitoids, and predators. *B. brassicae* infestations on new host plants tend to increase until the food supply becomes inadequate. When the quality of the food supply declines, aphids react by lowering their reproductive rate and by increasing their rate of emigration. When the aphid population growth is slowed due to changes in the host plant, other factors including fungal disease and natural enemies begin to reduce aphid numbers even further (Hughes 1963, Chambers et al. 1982).

Fungal diseases become a major determinant of aphid density after dense infestations have developed (Hughes 1963). Dense colonies of *B. brassicae* are attractive to predators and parasitoids. These natural enemies can have a significant impact on aphid population growth. When predators and parasitoids are removed by hand or are excluded by fine mesh cages, *B. brassicae* counts go up (McIver 1983).

The parasitoid, *Diaeretiella rapae* M'Intosh (Hymenoptera: Braconidae) tends to specialize on crucifer-feeding aphids, but it will attack a range of other aphid species including the green peach aphid, M. persicae (Sheehan and Shelton 1989). Parasitism of *B. brassicae* varies but is generally low, probably as a result of high rates of hyperparasitism of *D. rapae* (George 1957).

Aphidophagous coccinellids are effective aphid predators (Tamaki and Weeks 1972). In cage studies *Coccinella transversogullata* ate up to 200 aphids per day. *C. transversogullata* reduced the rate of growth and eventually caused the aphid population to crash. Most Coccinellidae, however, are not very active in *B. brassicae* colonies (George 1957, Hughes 1963), perhaps as a result of the flavor and smells of the aphids growing on their mustard family host plants. However, *Coccinella septempunctata* is reported to thrive on *B. brassicae* prey in laboratory cultures (El Hag and Zaitoon 1996).

Other predators of the *B. brassicae* include hover flies (Syrphidae) (Hughes 1963), Cecidomyiidae (George 1957), and damsel bugs (Nabidae). *Nabis* species gathered from collard foliage had positive precipitin tests (35-88% positive) for *B. brassicae* (McIver 1983). *Nabis americoferus* and *Geocoris bullatus* were effective in reducing aphid populations in green house studies. The effect was short lived, however. Nabids consumed 4-23 aphids per day, and aphid numbers declined during the first week. After that, the aphid populations increased at the same rate as control populations. *Nabid* or *Geocoris* densities of one predator per plant were not enough to regulate the aphid populations. *Nabid* or *Geocoris* lacked prey specificity. When an alternative prey species was added to the mix, the Nabids and the Geocorids ceased to have any impact on the aphid population (Tamaki and Weeks 1972).

McIver (1983) reported that several species of spiders and harvestmen were positive for *B. brassicae* in precipitin tests: *Dictyna* species, *Enoplognatha ovata* Clerck, *Lepthyphantes tenuis* Blackwall, Linyphiidae juveniles, *Erigone dentosa*, *Tetragnatha laboriosa*, *Pardosa sternalis* Thorell, *Oxyopes salticus* Hentz , *Misumenops celer* Hentz, *Xysticus cunctator* Thorell, and *Phalangium opilio*. When ground dwelling predators including *P. melanarius* (Coleoptera: Carabidae) were excluded from collards with raised cylinders, *B. brassicae* populations increased on some sampling dates.

The impact of a single predator species on the population trends of *B. brassicae* is arguably small. However, the natural enemy community as a whole has a significant impact on aphid populations. Foliar and ground dwelling predator guilds interact. Foliar predators including Coccinellidae dislodge many more aphids than they eat. Soil dwelling predators encounter and attack aphids on the soil surface (El-Agamy and Haynes 1992).

In general, the levels of aphid abundance at which natural enemy attack begins and the relative powers of increase of the aphids are such that *B. brassicae* numbers are primarily limited by the food supply not natural enemies (Hughes 1963). In general, natural enemies depress *B. brassicae* numbers after emigration and density induced decline of reproductive rate have reduced the potential increase of the colonies. Natural enemies alone seldom keep aphid density below damaging numbers (Berry 1998).

Potential responses to vegetation management

There are several aspects of vegetation that influence aphid colonization and population growth in cole crops. We know that interplanting non-host vegetation amidst crucifers or changing the color of the background surrounding developing crucifer plants often reduces *B. brassicae* numbers. The reduction in aphid colonization occurs whether the interplant is a weed (Smith 1976a, 1976b, 1976c, Horn 1988), a living mulch or cover crop (Dempster and Coaker 1974, Andow et al. 1986, Roberts and Cartwright 1991, Costello and Altieri 1994, 1995, Costello 1995), a second vegetable crop (O'Donnell and Coaker 1975), or an artificially colored mulch (Schalk et al. 1979, Summers et al. 1995, Liburd et al. 1998). Evidence suggests that the differences are due to factors that affect the host plant selection process.

The impact of interplanting on aphids varies according to the type, size, color, texture, and relative proportion of interplanted vegetation (Andow et al. 1986), the height of the interplanted vegetation relative to the target crop (McIver 1983), the timing of interplant establishment relative to the target crop, and the percent of the soil surface covered by the interplanted vegetation (Costello 1995) or colored mulch (Liburd et al. 1998). *B. brassica* population densities were higher on cabbage grown in a living mulch of grass than cabbage grown in a living mulch of clover (Andow et al. 1986). Both of the living mulches reduced aphid colonization compared to bare ground. Significantly higher numbers of alate *B. brassicae* were observed on the collards grown in the short alfalfa compared to the tall alfalfa. When the collards were grown in pots that were suspended on stakes at the height of the tall alfalfa canopy, the difference between the two treatments was significantly reduced (McIver 1983).

B. brassicae numbers per plant were significantly higher in *Brassicae* plots with a yellow soil cover than bare ground (Liburd et al. 1998). Reflective mulches are known to reduced aphid colonization (Summers et al. 1995). Differences in alate aphid colonization are correlated with different levels of light reflectance. Lower intensity light reflected by broccoli grown in living mulch was less attractive to incoming aphids than the higher intensity light reflected from clean cultivated broccoli. The numbers of alates in the broccoli was highly correlated with the intensity of the yellow waveband (Costello and Altieri 1994).

Winged *B. brassicae* use a combination of visual and olfactory cues to locate their host plants (Prokopy and Owens 1983). Yellow is believed to influence *B. brassicae* alighting on plants of the appropriate physiological state (Kennedy 1958). Saturated blue colors have low reflectance energy in the green region and are apparently less attractive to *B. brassicae*. Early in the growing season, vegetables growing in a monoculture are surrounded by bare ground. Living mulch or other materials covering the soil provide a very different visual background effect. Crucifer host plants surrounded by other vegetation are more difficult for the incoming crucifer specialist to see (Liburd et al. 1998).

It is not clear whether *B. brassicae* can distinguish between suitable and unsuitable host plants without sampling them (Kennedy and Stroyan 1959). Early studies suggested that chemical (olfactory) cues were not as important as visual cues during the colonization of plants by the aphids. Olfactory cues are detected only after visually mediated random landings on plants. The lack of sensitivity to olfactory cues by the aphids is now being questioned, and experimental evidence to support an olfactory role is accumulating. Olfactometer and electrophysiological studies have demonstrated that alate *B. brassicae* are attracted to volatiles from *B. oleracea*. Sinigrin, one of the primary glucosinolates of mustard oil, stimulates feeding by *B. brassicae* (Moon 1967, Read et al. 1970). The presence of sinigrin enhances the number of alate *B. brassicae* landing in clear, uncolored, water pan traps. The scent of crucifer plants growing in a mixed stand of other plant families is probably more difficult for the incoming crucifer specialists to detect (Pickett et al. 1992).

Natural enemies can also respond to the smell of the host plant of their preferred prey item. *D. rapae* was attracted to the odor of crucifers or a dilute solution of mustard oil (allyl isothiocyanate). *D. rapae* was attracted to clumps of *B. brassicae* removed from collards. The effect only lasted for fifteen minutes, and there was a rate response. Two hundred aphids removed from collards twenty-four hours earlier were unattractive. Two hundred aphids removed fifteen minutes earlier were attractive. A clump of ten *B. brassicae* recently removed from collards was not attractive. The parasitoid oviposited more often in *M. persicae* feeding on collards than in *M. persicae* growing on sugar beets. The presence of an adjacent collard plant increased the parasitism of *M. persicae* on sugar beet plants. The hyperparasitoid *Charips brassicae* was not attracted to collards, mustard oil or *B. brassicae*. It was attracted to the scent of its host, *D. rapae* (Read et al. 1970).

It is important to note that the difference in aphid numbers accumulating in mixed and pure stands of crucifers is usually most dramatic at the beginning of the season (Dempster and Coaker 1974, Costello and Altieri 1995) or immediately following an insecticide spray (Andow et al. 1986). The difference between mixed and unmixed cropping systems sometimes disappears by the end of the season. After immigration when aphid colonies are established, natality and mortality factors including the relative abundance and activity of natural enemies may cause aphid population densities to converge in different cropping systems. Aphid population growth is sometimes slower in monoculture than in polyculture. Generalist predators tend to be more abundant in polyculture. The specialist parasitoid, *D. rapae*, is often more prevalent in monoculture. The affects of interplanting on host plant colonization and the affect of interplanting on natural enemy induced mortality of *B. brassicae* may operate in opposite directions. The opposing factors would result in the two aphid populations, which started out very different, converging by the end of the season (Costello and Altieri 1994, 1995, Costello 1995).

Dempster and Coaker (1974) sowed clover then transplanted Brussels sprouts and cauliflower into the clover two weeks later. During the early growing season, aphid density was consistently higher on the cole crops surrounded by bare ground than on cole crops surrounded by clover. Later, the difference between the monoculture and the polyculture disappeared. In several studies that followed, researchers noted that significantly higher numbers of alate (winged) *B. brassicae* arrive on *Brassica* monoculture than in *Brassica* polyculture (O'Donnell and Coaker 1975, Theunissen and den Ouden 1980, Costello and Altieri 1994, Costello and Altieri 1995). Andow et al. (1986) reported that peak aphid densities on cabbage occurred eight days after insecticides were applied. Very few natural enemies were present at that time. Costello and Altieri (1995) noted that the polyculture effect was short-lived. Early in the growing season the numbers of alate aphids were significantly lower on the broccoli growing in living mulch of clover. The number of alate aphids per sample on the first sampling date was eight times greater on the broccoli in clean culture than in the living mulch. By the last sampling date, no differences remained.

Mixed planting has both direct and indirect effects on the natural enemies. Mixed planting directly affects natural enemies by providing alternative food and microclimates within the habitat. Levels of vegetation structural complexity result in different search arenas for the natural enemy. Plants or plant patches that are complex take longer to explore. In some cases, vegetation provides a barrier, which interferes with the searching ability of specialist natural enemies. By affecting the density, dispersion, and behavior of their prey items, mixed planting has an indirect effect on natural enemies. Natural enemies have a greater tendency to aggregate in areas of high prey concentration regardless of the vegetation type (Sheehan 1986, Andow and Risch 1987).

The impact of interplanting on natural enemies of *B. brassicae* has been variable. Generalist predators are sometimes more abundant in mixed plant stands. Under-sowing of clover in Brussels sprouts increased the number of Carabidae (*P. melanarius, Harpalus rufipes*), Phalangiidae (*P. opilio*), and Staphylinidae (unspecified) compared to clean hoed plots (Dempster 1969). McIver and Belnavis (1986) found that the generalist predator *Coccinella trifasciata* was more common in a tall alfalfa/collard cropping system. Increased numbers of predators in the alfalfa did not, however, result in higher numbers on the collard themselves. Specialist parasitoids are sometimes more abundant in pure plant stands than in mixed stands (Smith 1976c, Dempster and Coaker 1974, Andow et al. 1986, Costello and Altieri 1994, Costello and Altieri 1995).

Smith (1976a) was one of the earliest researchers to demonstrate that interplanting non-crop vegetation around cole crops has a significant impact on aphids. The numbers of *B. brassicae* early in the season were higher on Brussels sprouts in hand-hoed plots than in weedy plots. Parasitism of *B. brassicae* on Brussels sprouts, however, was reduced when weeds surrounded the plants. Higher rates of parasitism occurred in monoculture compared to weedy culture, even when aphid densities in the two planting systems were equivalent (Smith 1976c). The aphid parasitoid *D. rapae* was more common in a short alfalfa/collard system than in the tall alfalfa/collard system (McIver and Belnavis 1986).

The effect of interplanting on parasitism is not consistent. No changes in parasitism *of B. brassicae* were found when the cole crop interplant was mustard (*Brassica hirta*) (Kloen and Altieri 1990). No changes in parasitism of *B. brassicae* was found when the interplant was hairy vetch (*Vicia sativa* L.) or fava bean (*Vicia fava* L.)(Altieri 1984). In some cases, parasitism is higher in polyculture (Letourneau 1987, Horn 1988). An intercrop such as *V. fava* that provides food resources other than hosts may attract parasitoids. Floral and extra floral nectar can increase the longevity and fecundity of parasitoids (Leius 1960, 1961a, 1961b, 1963, 1967, Shahjahan 1974, Idris and Grafius 1995, 1997). Wasps (including parasitoids) were more common on the broccoli growing next to flowering *Iberis* than broccoli growing in isolation. Aphid parasitism was slightly higher near the nectar source. The interplay between nectar sources and prey distribution may explain the variable aggregation of natural enemy in interplanted cole crops (Bigger and Chaney 1998).

Attributes of the host plant influence natural enemy induced mortality of *B. brassicae*. Plant architecture in the cole crops varies significantly between curly leafy kale, flat leafed collards, and tightly wrapped cabbage. The foraging behavior of Coccinellidae including *Hippodamia convergens* and *Coccinella septempunctata* was significantly influenced by these differences (Grevstad and Klepetka 1992). The various leaf types had an impact on predator mobility, falling frequency, prey accessibility, and the propensity of the predator to fly away. Aphid predation rates were highest on the flat-leafed collards. *B. brassicae* numbers were reduced over 95% on broccoli varieties that have less wax coating on their leaves (Stoner 1992). Wax tends to gum up the tarsi of the foraging beetles. The beetles spent more unproductive time cleaning and grooming on waxy plants. Reduced wax allowed more efficient predation (Eigenbrode et al. 1995).

The presence of non-host vegetation changes the texture and complexity of the habitat that a natural enemy must search in order to discover its prey. Habitat complexity can promote aphid outbreaks if it interferes with non-random searching behavior of predators or interferes with the aggregation of predators in areas of high prey density. Populations of the aphid *Uroleucon nigrotuberculatum* increased rapidly when patches of golden rod (*Solidago canadensis*) were divided up into small patches (Kareiva 1987, 1990, Kareiva and Odell 1987). Aphid colonization rates were the same in the patchy and continuous goldenrod. However, twenty-six aphid outbreaks occurred in the patchy golden rod habitat while only nine aphid outbreaks occurred in the continuous goldenrod habitat.

The difference in aphid population stability appeared to be related to the foraging efficiency of the coccinellid predator, *C. septempunctata*, in the two habitats. When foraging beetles were removed by hand from the golden rod, aphid populations consistently increased relative to the control. When beetles were marked and released, it took longer for the beetles to aggregate in patches of high aphid concentration when the vegetation was divided into small patches (Kareiva 1987).

PHYLLOTRETA CRUCIFERAE GOEZE

P. cruciferae is a small, shiny, steel-blue jumping beetle (Coleoptera: Chrysomelidae). Several species of flea beetle attack vegetable crops including the striped flea beetle, *P. striolata*, the western striped flea beetle, *P. ramosa*, and the western black flea beetle, *P. pusilla* (Flint 1992). The principle species attacking cole crops in Oregon is *P. cruciferae* (Berry 1998, Fisher et al. 1998). *P. cruciferea e* was introduced from Europe to the Pacific Northwest during the early 1920's (Milliron 1953).

P. cruciferae feeding on spring planted crucifer seedlings cause significant losses (Meister 1969, Weiss et al. 1994). Adults of *P. cruciferae* feed primarily on cotyledons and 1st true leaves. Infested plants may lose 100% of their leaf area (Siemens and Mitchell-Olds 1996). Newly emerged seedlings are susceptible to *P. cruciferae* damage for several weeks. Relatively low populations can cause economic damage. An average of one or two adults per 7.6 m of row on plants in the cotyledon through the two leaf stages can delay maturity and reduce stands (Berry 1998). *P. cruciferae* also causes severe losses just after transplanting or thinning. Once plants are well established and have five or more leaves, they can tolerate several beetles per plant without significant economic damage (Flint 1992, McCalley et al. 1992).

Life cycle and seasonal activity

During the winter on a warm sunny day, one can find a few adult *P. cruciferae* on wild crucifer plants. The majority of the beetles, however, remain motionless in reproductive diapause with reduced metabolic and behavioral functions (Bonnemaison 1965). In the early spring, *P. cruciferae* begins feeding on wild crucifer hosts. *P. cruciferae* prefers cultivated crucifers to wild crucifers and young seedlings over mature plants. When early cole crop plantings are emerging, *P. cruciferae* adults move in. They feed on the underside of leaves causing numerous small, round pits (Meister 1969).

Female beetles lay golden brown eggs about 0.5 mm long in clusters in the soil near the base of host plants. Each female lays about thirty-seven eggs per mating. Eggs hatch in two to three weeks and larvae feed on roots of the host plant for about a month. The newly hatched larvae are about one millimeter in length, almost transparent, with the head and anal plates appearing large in proportion to the remaining body parts. The damage to the plants by larval root feeding is minimal. The larvae pass through three instars then pupate in tiny cells, which they construct out of soil. The pupa stage lasts about two weeks (Meister 1969).

The new generation of adult beetles begins to emerge during late July and continues emerging for about a month. The overwintering generation and the new generation of adult beetles overlap from about the middle of July until the middle of August. They feed for six to eight weeks (Meister 1969). Peak abundance of *P. cruciferae* usually occurs at the end of August or the beginning of September, and coincides with the peak emergence of the new generation. Towards the end of August and early September, the beetles seek wintering sites. Their migration to overwintering sites results in an abrupt drop in field populations (Tahvanainen and Root 1972).

P. cruciferae spends the winter on weeds, leaf litter, crop debris, in grassy field borders, and in hedgerows along field margins. Grass sod appears to be a favored wintering site. The beetles emerge in large numbers in the early spring. Mating and oviposition begins again in early June. The ratio of males to females in the population as a whole is one to one (Meister 1969). Some researchers report higher percentage of females in early season samples. The skewed sex ratio in the early samples may be related to aggregation of the females searching for oviposition sites (Weiss et al. 1994). Females emerge from wintering sites before the males. *P. cruciferae* is bivoltine, with two life cycles per year in New York (Kareiva 1985). In the Willamette Valley, there is usually one generation of *P. cruciferae* per year (Berry 1998).

Mortality factors

Natural enemies do not effectively control *P. cruciferae* (Flint 1992, McCalley et al. 1992). Predation of *P. cruciferae* by *Geocoris bullatus* (Burgess 1977), *Chrysopa carnea* (Stephens) (Burgess 1980), and *Nabis alternatus* (Burgess 1982, Culliney 1986) has been observed. Carabid beetles captured in pit fall traps will have parts of *P. cruciferae* in their intestines. The presence of the beetle parts in the Carabid stomachs is probably an artifact of their being trapped in the same arena as *P. cruciferae*. Natural encounter between *P. cruciferae* and Carabidae are probably infrequent. *P. cruciferae* tends to remain on the upper, vertical leaves of their host plants at night. Most species of Carabidae are nocturnal hunters, and they are mostly poor climbers (Tahvanainen and Root 1972).

Adult *P. cruciferae* are occasionally caught in spider webs, but they are rarely eaten by spiders (Tahvanainen and Root 1972). Like most Coleoptera, *P. cruciferae* is well protected by its hard shield-like elytra (Olmstead and Denno 1993). *P. cruciferae* is sometimes observed escaping from the horizontal webs of the linyphiid spiders on the soil surface (Andow et al. 1986).

The larvae of a braconid wasp, *Microtonus vittatae*, parasitize adults of *P. cruciferae*. The parasitoid is a North American species, which has extended its host range from native flea beetles to the introduced *P. crucifera* (Smith and Peterson 1950). Parasitism of *P. cruciferae* by *M. vittate* tends to be somewhat higher in the monoculture than in mixed plantings (Tahvanainen and Root 1972). Another parasite *of P. cruciferae*, *Perilitus epitricis*, has been observed in the Pacific Northwest but it occurs infrequently (Berry 1998).

Response to vegetation management

Phyllotreta forages non-randomly (Kareiva 1982, 1985). It may emit an aggregation pheromone (Peng and Weiss 1992). When foraging for their host plant, *P. cruciferae* is attracted to mustard oil and its components.

Mustard oil influences the ability of the beetles to discover their host plant. It also influences their propensity to settle and to begin eating (Feeny et al. 1970, Read et al. 1970). The amount of damage that *P. cruciferae* does to *Brassica* species varies as a function of glucosinolate concentrations in the cotyledons. At very high level of glucosinolates, herbivore activity declines slightly (Siemens and Mitchell-Olds 1996).

B. oleraceae varieties that have less wax coating on their leaves are more susceptible to damage by *P. cruciferae* than normal waxy broccoli plants (Stoner 1992). Mechanical removal of the wax crystals from normal *Brassica* varieties increases feeding damage by *P. cruciferae*. *P. cruciferae* has tarsal adhesive setae that have better traction on reduced wax leaves. On reduced wax varieties, *P. cruciferae* tends to feed over the entire surface of the leaf. On normal waxy *B. oleraceae*, *P. cruciferae* is more restricted in its feeding (Eigenbrode and Espelie 1995).

Interplanting generally reduces the number of *P. cruciferae* on cole crops compared to pure stands (Tahvanainen and Root 1972, Cromartie 1975). The presence of non-host plants depresses *P. cruciferae* numbers in two ways. Non-host plants seem to interfere with host plant finding, and their presence tends to increase the rate at which *P. cruciferae* emigrates from a plant patch (Kareiva 1985, Bergelson and Kareiva 1987, Elmstrom et al. 1988, Garcia and Altieri 1992).

P. cruciferae is relatively inept at finding their host plants (Kareiva 1985). When marked beetles were released eight meters from collard plants, about 19% were recovered when the collards were surrounded by bare ground. When the collards were surrounded by goldenrod, only 6% of the beetles were recovered. Broccoli surrounded by black weed control cloth (no weeds) had 6 times as many *P. cruciferae* as weedy control plots (Liburd et al. 1998).

Collards interplanted with tomato or tobacco accumulated fewer *P. cruciferae* than pure stands of collards. The number of *P. cruciferae* per collard plant was higher in the monoculture on all thirty-eight sampling dates. The monoculture was colonized more rapidly and experienced greater feeding damage. Predators and parasitoids appeared to have a negligible influence on the beetles in both habitats. The presence of non-host plants probably interfered with both the visual and olfactory cues used by *P. cruciferae* to orient to their host plants. In mixed stands, other odors may have masked the chemical stimuli originating from the host plants (Tahvanainen and Root 1972).

The foraging behavior of *P. cruciferae* is very different from other *Brassica* specialists. Consider the difference between *P. rapae* and *P. brassicae*. The oviposition decision of the *Pieris* butterflies commits her progeny to a given location (Root 1973, Root and Kareiva 1984, Trenbath 1993). The *Pieris* larvae are not highly mobile. *P. cruciferae*, on the other hand, are very capable of taking off after they land. *P. cruciferae* is constantly moving from plant to plant and from plant patch to patch. When they land on a non-host plant, their next flight tends to be long (Bach 1980b, Risch 1981). They move among patches of host plants spending most of their time where their food is abundant and of higher quality. *P. cruciferae* tends to concentrate in pure stands of their host plant (Root 1973, Cromartie 1975, Bergelson and Kareiva 1987).

Analyses of the movement behavior of *P. cruciferae* and other highly mobile insects in mixed versus pure plant stands has shown that emigration rates are greater and tenure times are shorter in mixed stands (Bach 1980b, Risch 1981, Kareiva 1982, 1983, 1985, 1986, Bergelson and Kareiva 1987, Elmstrom et al. 1988, Andow 1990, Garcia and Altieri 1992). Marked and released *P. cruciferae* in a broccoli monoculture and broccoli mixed with either fava bean or hairy vetch. The mixed systems attracted fewer marked beetles and lost more of the marked beetles that were placed in them. The tenure time of the beetles released in the monoculture broccoli was longer than in the mixed culture. In the mixed stand, the beetles hopped around and seemed to loose contact with their host plant and the chemical stimuli that must accumulate in order for feeding to begin. The probability that the beetles would emigrate from the mixed stand was about the same as the probability of their emigration from a patch of non-host plants (Garcia and Altieri 1992).

There are several factors that influence the strength of the effect of interplanting on *P. cruciferae* numbers. Flea beetle species vary in their sensitivity to the presence of non-host vegetation. The effect may vary according to the type of non-host vegetation (Kareiva 1985). The height of non-host plants relative to the *Brassica* plants is important. In those cases where emigration rates were unaffected by interplanting, the height of the non-host plants was much lower than the height of the *Brassica* plants (Andow et al. 1986, Weiss et al. 1994). Sensitivity of *P. cruciferae* to non-host vegetation depends, in part, on host plant density. Bergelson and Kareiva (1987) grew collards at two densities, alone and in combination with potatoes. *P. cruciferae* was significantly more abundant in the higher density collard plantings regardless of the interplanting.

P. cruciferae tends to be more abundant on collards in large patches. There was more emigration from small patches of collards (four plants) surrounded by grass than in larger patches (sixteen plants) surrounded by grass (Bergelson and Kareiva 1987). Kareiva (1985) argues that the impact of patch size has more to do with patterns of emigration than immigration. Small host plant patches surrounded by alternative vegetation are hard to find and easy to lose. Even when collard patches were loaded with large numbers of *P. cruciferae* at the beginning of an experiment, the inoculations rapidly decayed in the small host plant patches as beetles left the patch. Single host plants surrounded by grass, weeds, or bare ground never maintained high *P. cruciferae* populations.

PIERIS RAPAE (L.)

P. rapae is a widespread and perennial pest of cole crops. It was introduced into North America from Europe in the 1860s (Root 1973, Root and Kareiva 1984). It is now distributed across the United States and Canada. *P. rapae* populations in Oregon and Washington vary markedly from one location to the next and between years (Biever et al. 1992).

The adults are white with numerous black marks on the wings. The larvae are velvety-green with a faint yellow dorsal stripe and a row of yellow spots running laterally along the body. Eggs are oblong, white to cream colored, and usually laid on the undersides of the leaves (Berry 1998).

Pieris larvae make round holes in the leaves of their host plant. During the pre budding periods, broccoli can tolerate a significant amount of damage by *P. rapae* larvae without suffering a depression in yield. Larvae and excrement, however, are significant contaminants in processed broccoli (Vail and Lentner 1989, Maltais et al. 1994).

Life cycle and seasonal activity

P. rapae spends the winters primarily on wild Cruciferae as a diapausing pupa from which the butterfly emerges to mate and lay eggs beginning in early April to mid May. Estimates of *P. rapae*'s maximum lifelong fecundity range from 500 to 1200 eggs per female, with as many as 150 eggs deposited per day (Root and Kareiva 1984). Eggs are laid singularly. In the Pacific Northwest, eggs of *P. rapae* are observed through out the growing season with a peak in late August (Biever et al. 1992, Maltais et al. 1994). The first brood is usually laid on wild host plants in April prior to the first cole crop plantings. Larvae develop through five instars with a total development time from egg to egg laying adult of 24 to 30 days at 22C (Richards 1940). There are from three to five generations per year depending on the climate. As the summer progresses, an increasing percentage of pupae become dormant in preparation for winter. (Berry 1998).

Oviposition is a critical step for *P. rapae* because the larvae are relatively immobile and dependent on the choices made by the female moth (Renwick and Chew 1994). *P. rapae* lays most of its eggs on Brassica plants. *P. rapae* only flies in moderate weather, restricting feeding and oviposition to sunny, warm (18-24C) periods, and concentrating most egg laying in the late morning and afternoon (Andrewartha 1961). Following extended periods of cool weather, females heavily loaded with eggs tend to increase their rate of oviposition (Root and Kareiva 1984).

In the laboratory, there is some evidence that *P. rapae* will avoid laying eggs on *Brassica* leaves that are laden with conspecific eggs and larvae. The oviposition deterrent is associated with *Pieris* eggs and accessory glands on the larvae. It is received by the antennae and chemoreceptors on the tarsi of the ovipositing female (Renwick and Chew 1994). In the field, however, it is not apparent that females discriminate between plants on the basis of the presence of eggs and larvae. Root and Kareiva (1984) found that egg laying *P. rapae* did not avoid collard plants that harbored high densities of *Pieris* eggs even when artificial cohorts of up to 100 eggs per plant were created.

The flight behavior of *P. rapae* during oviposition and adult feeding has been studied in detail. The flight behavior includes relatively long distance flights when the butterfly is searching for a patch of plants that contains its host plant. Long flights are followed by short, hopping, oviposition flights (Root and Kareiva 1984). Oviposition flights are interrupted by flights associated with adult feeding on nectar from flowers. *P. rapae* are strong flyers and able to discriminate their host plant from diverse and variable non-host backgrounds (Kostal and Finch 1994).

In a given field, individual butterflies may display directionality in short flights, but in general have no tendency to move in any particular direction as would be expected if butterflies were orienting to wind, sun position, or landmarks. The probability of any particular next move (transition from one landing site to the next, length of flight, or angle of turn) is independent of the previous move. The history of a female *P. rapae* (previous habitat and oviposition behavior) has no apparent effect on the initial behavior of a moth entering a patch of host plants (Root and Kareiva 1984).

Since the *Pieris* females usually lay their eggs singly on plants, the ovipositing females visit hundreds of plants during oviposition flights. During this process, ovipositing females pass over many apparently suitable plants. The oviposition behavior results in eggs being widely scattered over large areas. During the course of her life, a typical female may lay her eggs on plants that grow several kilometers apart (Root and Kareiva 1984).

The *Pieris* butterflies invest a significant amount of energy in flight per egg and time per egg. There are several potential explanations for this behavior. First, cultivated crucifers are derived from early succession herbs that fit Feeny's (1976) definition of non-apparent plants. In natural settings, Cruciferae occur at low densities in small, short-lived patches. *P. rapae* may be adapted to oviposit on isolated, widely scattered host plants. The presence of large concentrated areas of host plants in agricultural settings may not influence this instinctual behavior. The *Pieris* moths continue to scatter eggs even in the presence of large concentrations of their host plant.

The *Pieris* oviposition strategy may be a response to natural enemies and other mortality factors that are distributed unevenly in the natural environment. A major larval parasitoid of *P. rapae*, *Cotesia glomeratus*, is attracted to crucifer host plants. The natural enemy aggregates in areas where there are high densities of crucifers. Thus, it may be adaptive for *P. rapae* to scatter its eggs on small, isolated host plant patches rather than in large concentrations of host plant (Sato 1979). Studies have failed to show, however, significant evidence supporting density-dependent mortality among eggs and larvae of *P. rapae.* Instead, mortality is highly variable and unpredictable from plant to plant or from field to field. The spatial variation in *Pieris* mortality raises a third possible explanation for the oviposition behavior (Root and Kareiva 1984).

The oviposition behavior of *P. rapae* causes the female to vigorously sample an unpredictable environment by placing eggs on several scattered and seemingly random host plants. The behavior allows the insect to spread risk. By spreading its eggs across a large territory with highly variable microclimates and natural enemy densities, the female minimizes the likelihood of total reproductive failure. Some of its progeny will survive and reproduce the next generation (den Boer 1968, 1981).

Although oviposition sequences are random, the nectar feeding flights of *P. rapae* adults are not random. The probability that a butterfly will turn at a sharp angle, make a short flight, and land to sip nectar from a host plant is dependent on previous flight behavior. *P. rapae* aggregates around host plants that provide nectar. Aggregation around nectar sources influences the spatial distribution of *P. rapae* eggs (Root and Kareiva 1984).

Mortality factors

Rainfall and irrigation cause a significant proportion of the mortality experienced by small P. rapae larvae. In older larvae, viral diseases become a primary cause of death (Berry 1998). In laboratory culture virus related mortality can reach 24-44% of the larvae (Dempster 1967).

The most important predators of *P. rapae* are Coccinellidae, Nabidae, Chrysopidae, and ground dwelling predators including the Carabidae. McIver (1983) analyzed forty-nine taxa with the precipitin test for reaction to *P. rapae*. The most consistent positive precipitin tests from predators gathered on collards were from *Sphaerophoria sulphuripes* (Syrphidae), the Coccinellidae *C. trifasciata* and *H. convergens*, the spiders *Erigone dentosa* (Linyphiidae) and *Tetragnatha laboriosa* (Tetragnathidae) and the harvestman *Phalangium opilio*.

When ground dwelling predators were excluded with raised cylinders, *P. rapae* survival increased in one out of seven sampling dates. The increased survival may have been due to the exclusion of *P. opilio*. *P. opilio* precipitin test for *P. rapae* was 27-56% positive. When *P. opilio* was gathered from the foliage of the collards (rather than the ground) the intensity of the positive precipitin test increased for *P. rapae* (McIver 1983). *H. rufipes* is an important predator of *P. rapae* (O'Donnell and Coaker 1975). *P. melanarius* feeds on *P. rapae* but it may not be an important mortality factor (Dempster 1967, 1969, Dempster and Coaker 1974).

Several parasitoids attack *P. rapae*. The solitary endoparasite *Cotesia* (= *Apanteles*) *rubecula* Marshall (Hymenoptera: Braconidae) is one of the most common parasitoids of *P. rapae* in British Columbia and Washington State. It was accidentally introduced into British Columbia in 1963. It was first reported in Washington State in 1984. It was recovered in northern Oregon but was absent in Corvallis, Oregon in 1988. It is fairly specific to *P. rapae* and generally kills the larvae by the third or fourth instar and forms a white cocoon. Parasitism of *P. rapae* by *C. rubicula* is highly variable and ranges from 0 to 100%. *C. rubicula* failed to extend its range farther south into the Willamette Valley. The geographical limits of *C. rubicula* may be the result of its diapause characteristics. Diapause in this species is stimulated by photoperiod. In the vicinity of Corvallis, *C. rubecula* may enter diapause prematurely while ambient temperatures are still warm. Warm temperatures limit the ability of the parasitoid to survive the obligatory diapause period (Biever et al. 1992).

A related species, *C. glomeratus*, also attacks *P. rapae* but it is mostly a parasite of the harmless native species, *Pieris brassicae*. *C. glomerata* is a gregarious braconid parasite, which was introduced from England in the late 1800's. It is established throughout North America (Zhao et al. 1992). *C. glomeratus* is attracted to crucifer host plants (Sato 1979). It does not kill *P. rapae* larvae until they are mature, after significant feeding and foliar damage has occurred. *C. glomerata* was displaced by *C. rubecula* north of Corvallis. *C. glomerata* is recovered from *P. rapae* south of Corvallis, Oregon (Biever 1992). *Itoplectis conquisitor* Say is a native parasitoid of many Lepidoptera pupae in North America including *P. rapae* and *T. ni.* It attacks the larvae. *I. conquisitor* has been observed feeding on body fluids of *P. rapae* (Leius 1961a).

Response to vegetation management

The impact of various vegetation management schemes on herbivorous insects is complex. One must take into account that the insects may be engaged in more than one activity at the same time. The visual and olfactory cues that shape the behavior of an insect during oviposition may be very different and operating in the opposite direction from the cues that shape its behavior while foraging for nectar.

Some insects are responsive to changes in the background color of their host plants regardless of whether the color is from vegetation, colored cloth, or soil. The height of the non-host plant vegetation changes its impact on the herbivore. Low growing vegetation may simply change the background color. Tall vegetation may interfere visually with host plant selection. Fragrant non-host plants may interfere with the olfactory cues used by the herbivore to orient toward its host plant.

P. rapae is capable of identifying crucifer plants (Root and Kareiva 1984). Adults and larvae of *P. rapae* are attracted to mustard oil (Read et al. 1970). Host plant oviposition stimulants have been identified and extracted from *Brassica* plants (Hughes et al. 1997). Glucosinolates are important in host recognition by *P. rapae*. There are oviposition deterrents associated with certain plants and with the eggs of *P. rapae*. Oviposition by *P. rapae* is determined by the relative strength of opposing positive and negative cues. Some crucifers including *I. amara* are rejected by egg laying *P. rapae*. They produce oviposition deterrents that are stronger than the attraction of the glucosinolates present in the plant (Renwick and Chew 1994).

Physical characteristics of the host plant have an impact on the success of *P. rapae* (Eigenbrode et al. 1995). *P. rapae* were 80% fewer in natural infestations on glossy lines of broccoli (low wax) than on normal-wax standard varieties. Artificial infestation experiments showed that glossy resistance acts on both the egg and the larval stages. The resistance of glossy type Brassica lines to *P. rapae* expresses itself in the field but not in controlled environments or in the greenhouse. Again, there is an interaction between the wax leaf coating, the behavior of the *Pieris* larvae, natural enemies, and other mortality factors (Stoner 1992).

During oviposition, the butterfly is not sensitive to host plant density or stand purity; it moves randomly (Root and Kareiva 1984). Most specialist herbivores are more likely to find and remain on host plants that are concentrated in pure, dense stands (Tahvanainen and Root 1972, Cromartie 1975, 1981, Ralph 1977a, 1977b, Bach 1980a, 1980b, 1981, Risch 1980, 1981). Root (1973) referred to this behavior as a response to “resource concentration”. *P. rapae* does not respond positively to resource concentration.

The densities of *P. rapae* eggs and larvae are usually higher on sparse or isolated host plants than they are on plants in dense or large stands. The time it takes for a female *P. rapae* to approach and find a suitable host was no greater in an area where a few scattered collards grew among weeds than it was in a patch containing hundreds of collard plants surrounded by bare soil. Ovipositing *P. rapae* females flew over and failed to oviposit on 30 to 50% of the suitable host plants in a plant patch for no obvious reason. They readily flew out of a patch of host plants after laying only a few eggs. The flight pattern was not influenced by the shape of the host plant patch (Root and Kareiva 1984).

P. rapae is unaffected by the color of the background surrounding its host plants. Broccoli surrounded by black, yellow, green, or blue cloth had the same number of eggs and larvae as broccoli surrounded by weeds or bare ground. Low growing vegetation usually has no impact on *P. rapae* oviposition (Liburd et al. 1998). *P. rapae* was not responsive to the presence or absence of the weed spurry (*Spergula arvensis*) surrounding Brussels sprouts (Theunissen and den Ouden 1980). Egg counts on Brussels sprouts surrounded by *Matricaria inodora* L. were spotty and similar when the weeds were mowed low and prevented from flowering (Dempster 1969). The flight pattern of ovipositing *P. rapae* was not influenced by background vegetation in a grassy meadow (Root and Kareiva 1984). Reduced tillage systems where crops were planted into mowed residues of hairy vetch, perennial ryegrass, or rye grain had no affect on *P. rapae* numbers (Masiunas et al. 1997). However, *P. rapae* egg densities on cabbage were lower when the cabbage was grown in a living mulch of clover. There may be a chemical oviposition deterrent in clover. Cabbage surrounded by low growing grasses had the same number of *P. rapae* larvae as bare ground (Andow et al. 1986).

When vegetation is allowed to grow tall, host plants may be hidden visually. The effect is inconsistent. The inconsistency may be the result of differences in visual and olfactory cues used by *P. rapae* to orient to its host plant. *P. rapae* laid equivalent numbers of eggs on collards in short-mowed and tall unmowed alfalfa (McIver 1983). When *M. inodora* weeds surrounding Brussels sprouts were allowed to flower and grow tall, *P. rapae* egg numbers on Brussels sprouts were reduced (Dempster 1969). Egg laying by *P. rapae* on collards was not influenced by interplanting the host plants with potatoes, or mixtures of *Salvia officinalis*, *Thymus* sp., or *Tagetes* sp. when host plant density was held constant (Root and Kareiva 1984).

P. rapae responds differently to stand purity than *P. cruciferae or P. xylostella. P. crucifereae* accumulates in lower number on cabbage surrounded by tomatoes (Tahvanainen and Root 1972). Ovipositing *P. xylostella* are inhibited by the odor of tomatoes (Gupta and Thorsteinson 1960a, 1960b). *P. rapae* deposited more eggs on collards surrounded by tomato than collards surrounded by other collards. Tomatoes surrounding the collard plants were flowering. The ovipositing *P. rapae* may have been responding to the nectar source (Maguire 1984).

P. rapae is attracted to and will aggregate around nectar sources. Aggregation near flowering plants indirectly affects oviposition. Eggs tend to be clumped around nectar sources (Root and Kareiva 1984). Eggs and larvae of *P. rapae* were much more abundant on broccoli interplanted with Anise hyssop, *Agastache foeniculum,* than on broccoli growing in a monoculture growing 120 meters away (Latheef and Irwin 1979, Latheef and Irwin 1980). The effect may depend on the type of non-crop vegetation. The relative abundance of *P. rapae* eggs and larvae on broccoli was not significantly influenced by the presence of a flowering border of *I. amara* (Bigger and Chaney 1998). In fact, the number of eggs increased with increasing distance from the flowering border. *I. amara* are rejected by egg laying *P. rapae* because they produce oviposition deterrents. The oviposition deterrents may confound the impact of the nectar source (Renwick and Chew 1994).

In weedy plots dominated by *M. inodora* , *Senecia vulgaris* L., *Sinapis arvensis* L., *Sonchus arvensis* L. and in plots under-sown with clover (*Trifolium pratense* L.), *P. rapae* laid similar numbers of eggs on Brussels sprouts as in clean till plots. There was a significant reduction in the larval survival in the weedy and clover plots, and the majority of the mortality occurred between egg hatch and the third instar. Oviposition by *P. rapae* was unaffected by the presence of the background vegetation, while mortality of the small instars (1-3) of *P. rapae* was increased by fifty percent (Dempster 1969).

Increases in *P. rapae* mortality in mixed plantings may be due to the activity of natural enemies. The presence of the clover increased the numbers of *P. melanarius*, *H. rufipes*, *P. opilio*, and rove beetles (unspecified Staphylinidae) around the Brussels sprouts compared to clean-hoed plots (Dempster 1969). Oviposition by *P. rapae* on the collards was unaffected by the height of surrounding alfalfa. Mortality of *P. rapae* larvae, however, was higher on collards that were growing in tall, unmowed alfalfa. *P. opilio* was more common in the tall alfalfa, and when ground dwelling predators were excluded with raised cylinders, *P. rapae* survival increased slightly (McIver 1983).

When broccoli interplanted with nectar producing *A. foeniculum* was compared to broccoli growing in monoculture, interactions between *P. rapae* and its parasitoids were variable and complex. The effect depended on the specific parasitoid and host complex. *Cotesia rubecula* Marshall (Braconidae) were more numerous on broccoli associated with nectar plants than on broccoli grown in monoculture. The parasitoid was probably responding to the aggregation of its host, *P. rapae*, rather than the presence of the nectar source (Zhao et al. 1992).

PLUTELLA XYLOSTELLA (L.)

The diamondback moth, *Plutella xylostella* (L.), is believed to have originated in the Mediterranean area (Harcourt et al. 1955, Harcourt 1957). It is now almost universally distributed wherever cole crops are grown. Diamondback moth occurs throughout the western United States and British Columbia (Berry 1998). Worldwide it is one of the most serious pests of crucifers. These vegetables have high cosmetic standards (Talekar 1992, Talekar and Shelton 1993). In Malaysia, major outbreaks of *P. xylostella* cause as much as 90% crop loss. About $1 billion dollars is spent annually worldwide on its control (Verkerk and Wright 1996b).

P. xylostella is often controlled by insecticides applied for other pests. It is sometimes controlled by natural enemies (McCalley et al. 1992). In the Pacific Northwest it occasionally becomes numerous and destructive (Berry 1998). In some cases, *P. xylostella* densities take off and remain high all season (Maltais et al. 1994). Yield of broccoli is generally not affected by the larvae during the prebud stage even with populations of up to 12 larvae per plant (Vail and Lentner 1989). However, *P. xylostella* is a serious contaminant in both fresh market and processing broccoli. The late instars tend to move up into elongating broccoli buds where they form netted cocoons on narrowly spaced vertical surfaces (Maltais et al. 1994).

Prior to the introduction of pesticides in the late 1940s, diamondback moth was not considered a major pest of cole crops. *P. xylostella* has a long history of becoming resistant to pesticides; this has contributed to its pest status. It was one of the first insects to develop resistance to DDT (Perez et al. 1995, 1997, Perez 1997). In many countries, it has become resistant to every pesticide available including *Bacillus thuringiensis* (Talekar and Shelton 1993, Riggin-Bucci and Gould 1997).

The capacity of *P. xylostella* to develop insecticide resistance is due, in part, to its short generation time and the nature of its host plant. In tropical regions, the insect completes its lifecycle in about three weeks and passes through as many as twenty generations in a year. The short generation time provides many opportunities for the population to respond to selective pressure by pesticides (Talekar and Shelton 1993).

P. xylostella feeds exclusively on cole crops and wild Cruciferae. The same biochemical pathways that allow the *P. xylostella* to overcome the toxicity of the glucosinolates also stimulates insecticide resistance (Shelton et al. 1991). During the growing season, adult moths tend to stay in the area where they hatch. Their tendency to remain in a given area makes it possible for rapid inbreeding. Once resistance is acquired, it is persistent. In a study conducted in Thailand, a population of *P. xylostella* that had developed resistance to a variety of pesticides retained that resistance for 40 generations without further exposure to the pesticides (Talekar and Shelton 1993).

P. xylostella is oligophagous, the larvae feeding on several cultivated and wild members of the Cruciferae family (Berry 1998, Riggin-Bucci and Gould 1997). *P. xylostella* is attracted to glucosinolates (mustard oil). Herbivory mainly increases with glucosinolate concentrations in the plant tissues of various *Brassica* species. Herbivory does not vary significantly between mechanically damaged and undamaged brassica plants (Siemens and Mitchell-Olds 1996).

The glucosinolate sinigrin is a specific oviposition stimulant with a dose response by *P. xylostella* (Thorsteinson 1960, Spencer 1996, Verkerk and Wright 1996b). Sinigrin is perceived via contact chemosensilla on the antennae, tarsi, and ovipositor of *P. xylostella* (Justus and Mitchell 1996). Females are more attracted than males to sinigrin and the heavier their egg load, the more intense the attraction (Renwick and Chew 1994). Less polar volatile compounds have also been found to be highly effective in stimulating oviposition by *P. xylostella.* These compounds do not appear to be related to glucosinolates (Hughes et al. 1997).

A variety of strategies have been used to manage insecticide resistant populations of *P. xylostella.* They include release of parasitoids and natural enemy conservation (Verkerk and Wright 1996b), glossy host-plant resistance, mass trapping with pheromones, trapping with yellow sticky traps and mustard trap crops (Bigger and Fox 1997), pheromone disruption (McLaughlin et al. 1994), crop residue destruction, crop rotation, diatomaceous earth, intercropping, irrigation management (Harcourt 1957), botanical repellants, physical barrier (row covers), and sterile male release (Bahari 1994). The diamondback moth remains one of the most serious pests of cole crops worldwide.

Biever (1992) monitored *P. xylostella*, *T. ni*, and *P. rapae* from 1986-1987 in Oregon and Washington. The insects varied markedly from one location to the next and between years. *P. rapae* was the most abundant. *P. xylostella* was next in abundance, and *T. ni* was uncommon during the survey. Seven species of parasitoids were recovered from *P. xylostella.* Rates of parasitism varied significantly over time and among locations. Parasitism of *P. xylostella* ranged from 0 to 100%. The most common parasitoid was *Diadegma insulare* (Cresson) (Hymenoptera: Ichneumonidae).

Life cycle and seasonal activity

Females of *P. xylostella* live on average 16 days (from 7 to 47 days). Females fed on honey or sugar water live longer and lay more eggs than starved females. Most (95%) females begin ovipositing on the day of emergence. Egg laying lasts about 10 days. Fecundity at 25C is about 241 eggs per female. The number of eggs varies from 18 to 356 eggs per female (Harcourt 1957, Wakisaka et al. 1992).

Oviposition begins shortly after dusk and reaches its peak about two hours later. Few eggs are laid after midnight. Eggs are typically laid in depressions on the leaf, along the midrib, and on larger veins or on the concave surfaces of the smaller veins (Harcourt 1957). Eggs are minute, scale-like, disc-shaped, pale green or yellow. As many as 164 eggs per plant have been observed. Incubation takes about six days (Berry 1998, McCalley et al. 1992).

Larvae are pale green and small, about 8-10 mm long, with a slender body that is pointed at both ends when mature. The prolegs on the last segment are spread apart and form a distinctive "V" at the caterpillar's rear end. *P. xylostella* passes through four larval instars (Harcourt 1957). Larvae feed for 10 to 30 days depending on temperature. When disturbed, the larva wriggles backwards very rapidly and often drop from the leaf, suspended on a fine silken thread. Afterwards, the larvae ascend the thread and regain the leaf surface when the disturbance as passed (Berry 1998, McCalley et al. 1992).

First instar larvae bore through the epidermis and mine the spongy mesophyll tissue of the leaf. Mines show up as white markings on the leaves. About 70% of the larvae feed on the lower leaf epidermis. The second instar becomes a surface feeder. The larvae chew irregular patches in the leaves. All of the leaf tissues are consumed except the veins and the upper epidermis. The feeding pattern causes a "windowing" effect that is distinctive of the species (Harcourt 1957). Late in the 4th stadium, the larvae stop feeding and construct an open-network cocoon on the leaf surface. Construction of the cocoon is followed by one or two days of quiescence, which is referred to as the prepupal stage (Talekar and Shelton 1993). Adults emerge from the pupa in 10 to 14 days and immediately begin laying eggs for another generation (Berry 1998).

Moths are gray or brown. The male moths have yellow marks on the inner margins of each front wing. These form three yellow diamond-shaped spots in the middle when their wings are folded. The wingspan is short, 18 to 20 mm (Berry 1998). Moths are inactive during the day. They usually rest motionless on the lower surfaces of the plants. When disturbed, they fly, spiraling up in narrow circles above the plant. They become active just before dusk, and move to the blossoms of nearby weeds to feed (Harcourt 1957). Moths may migrate from field to field after crop residue of an early crop is incorporated (McCalley et al. 1992).

The diamondback moth has a relatively short generation time and will complete several generations per year if adequate host plants are available and the climate is suitable (Berry 1998, McCalley et al. 1992, Riggin-Bucci and Gould 1997). *P. xylostella* has between 4 and 17 generations per year in temperate and tropical regions respectively (Idris and Grafius 1996a), and the generations overlap. The developmental period from egg to emergence of new adults can be as short as 15-19 days (Wakisaka et al. 1992). One generation of *P. xylostella* requires about 283 degree days at 7.3C In the field, degree-days per generation vary from 280-293 (Butts 1981).

If conditions are favorable, *P. xylostella* enters diapause and spends the winter as an adult in crop residues around agricultural fields (Wakisaka et al. 1992). If conditions remain favorable, it can develop slowly over the winter. In warm climates, *P. xylostella* breeds continuously during the winter. It occurs year-round throughout vegetable growing areas along the south coast of California and the San Joaquin Valley (McCalley et al. 1992). In the north, the eggs, larvae, and moths perish during the winter. The transition zone begins at about the 36th parallel latitude. The moth apparently does not survive the winter in latitudes above 45 degrees (Harcourt 1957).

Although *P. xylostella* is a weak flyer, it is carried by the wind and is capable of migrating long distances in this manner. Annual migrations of over 3000 km have been reported (Talekar and Shelton 1993). In eastern Canada, annual populations of *P. xylostella* originate by adult migrations from the United States, carried north by wind currents and arriving on contaminated seedlings (Butts 1981).

In Ontario, *P. xylostella* moths are active from mid-May to early October. *P. xylostella* is abundant in the spring and early summer before the cabbage loopers and the imported cabbage worms become active. In southern California, *P. xylostella* abundance is high in March and April and again in June through August (McCalley et al. 1992). Even though *P. xylostella* generations tend to overlap, distinct moth count peaks are sometimes observed (Butts 1981).

In a typical year in the Pacific Northwest, adult *P. xylostella* emerge or become active in May or early June and begin laying eggs (Berry 1998). The first generation often develops on Cruciferae weeds. The first eggs of *P. xylostella* are often laid in the yellow rocket weed (Barbarea vulgaris)

(Harcourt 1957, Idris and Grafius 1996b). Subsequent generations breed on cultivated crucifers (Siemens and Mitchell-Olds 1996). Once *P. xylostella* densities rise, they tend to remain high all season in broccoli (Maltais et al. 1994). In the Pacific Northwest, population levels of *P. xylostella* usually peak in mid August (Biever et al. 1992).

Mortality factors

Diamondback adults and larvae are small, delicate, and susceptible to weather conditions. Cool cloudy weather reduces the activity of the adult female moths and can shorten their productive lives (Berry 1998). Most life table studies report that the majority of *P. xylostella* are killed in the immature stages (Harcourt and Guppy 1987, Wakisaka et al. 1992). Heavy rains from June to September can limit the population of *P. xylostella* (Talekar et al. 1986). Rainfall was found to be a major mortality factor affecting diamondback moth larvae from egg hatch through the middle of the last instar (Harcourt 1957, 1963). Low survival rates in the summer is sometimes attributed to high temperatures and a decline in plant quality during hot weather (Wakisaka et al. 1992).

Irrigation has been used to depress *P. xylostella* populations (McHugh and Foster 1995). Irrigation dislodges small larvae, reduces mating flight activity, and probably increases disease incidence. Sprinkler irrigation for short periods at dusk over several weeks reduces *P. xylostella* infestations and can increase yields of cabbage compared to drip tape irrigation (Talekar et al. 1986). In a study of sprinkler and drip irrigation systems conducted in Illinois, the use of evening intermittent irrigation (8pm to 11:30pm for 30 minutes on/off) maintained diamondback moth populations below one larva or pupa per plant through an entire growing period. Reductions of up to

86% were achieved compared to drip irrigation. In a related study, intermittent overhead irrigation caused a 7-fold reduction in diamondback moth oviposition on watercress in greenhouse tests conducted in Hawaii (Tabashunk and Mau 1986).

Generalist predators help regulate *P. xylostella* larvae, but their effect is usually not sufficient to reduce their numbers below damaging levels (Berry 1998). From the egg to the middle of the fourth instar, natural enemies are thought to be less important than abiotic mortality factors (Harcourt and Guppy 1987, Wakisaka et al. 1992). Coccinellidae, *Geocoris*, *Orius*, and *Nabis* species, and Chrysopidae are often listed as predators of *P. xylostella* but quantitative assessments of their impact are rare (Muckenfuss et al. 1992). The most abundant predators on collards in North Carolina were lady bird beetles including *C. septempunctata* and *H. convergens*, *Nabis* species, and harvestmen (Phalangiidae) (Wakisaka et al. 1992, Riggin-Bucci and Gould 1997). In cage experiments, *H. convergens* (Coccinellidae), *Orius insidiosus* (Anthocoridae), and *C. carnea* caused significant reductions in *P. xylostella* (Eigenbrode et al. 1995). The larvae of some species of hover flies (Syrphidae) prey on *P. xylostella* and account for a large proportions of arthropod predation on the early-instars (Wratten et al. 1995). A ground beetle, *Amara obscuripes*, was observed eating pupae of *P. xylostella* in Japan (Wakisaka et al. 1992).

Linyphiid spiders were observed feeding on *P. xylostella* larvae and adults (Wakisaka et al. 1992). Decline in populations of *Pardosa* species due to pyrethroid insecticides has been associated with a resurgence in *P. xylostella* populations (Muckenfuss et al. 1992).

A wide range of egg, larval and pupal parasitoids of *P. xylostella* have been recorded in the literature (Lim 1986, Talekar and Shelton 1993). Areas of the world that are most highly plagued by *P. xylostella* lack effective larval parasitoids. Temporary absence of parasitoids can give rise to local surges in *P. xylostella* populations (Talekar and Shelton 1993). Parasitism rates of 70-100% have been reported in the United States (Biever et al. 1992, Idris and Grafius 1993) and Canada (Harcourt 1986).

Diadegma species can be a major mortality factor of *P. xylostella* (Harcourt 1986, Sastrosiswojo and Sastrodiharjo 1986, Mustata 1992, Ooi 1992, Idris and Grafius 1995). The larval/pupal parasitoid *D. insulare* regulates *P. xylostella* populations and is common in the U.S. and Canada (Muckenfuss et al. 1992, Idris and Grafius 1993, Riggin-Bucci and Gould 1997). D. insulare pupates within the *P. xylostella* cocoon. It can be recognized by the broad white stripe around the pupa (McCalley et al. 1992). D. insulare is an effective forager. Percent parasitism of *P. xylostella* was similar on curly leaf kale and flat-leafed broccoli (Idris and Grafius 1996a). Parasitism by D. insulare tends to increase as the season progresses (Biever et al. 1992).

The parasitoids *Diadegma semiclausum* and *Cortesia plutellae* have been successful in controlling diamondback moth populations in different climates. *D. semiclausum* has been more successful in cooler climates. *C. plutellae* has been more successful in warm climates (Talekar and Shelton 1993). Low doses of neem extract applied to susceptible brassica cultivars were found to give enhanced parasitism by *D. semiclausum* in the laboratory and reduced damage by *P. xylostella* in a field experiment (Verkerk and Wright 1996b).

Response to vegetation management

P. xylostella discriminates between plants when laying its eggs. It lays significantly fewer eggs on Shepherd's purse (*Capsella bursa-pastoris*) than on *Brassica* species (Bigger and Fox 1997). It lays more eggs on Candytuff (*Iberis umbellata*) than on collards (*B. oleracea*) even though the larvae perform poorly on *I. umbellata*. Crucifer weeds that sustain feeding and reproduction of *P. xylostella* include *Barbarea vulgaris, Beta vulgaris, Brassica kaber, C. bursa-pastoris,* and *Raphanus raphanistrum* (Talekar and Shelton 1993). Harcourt identifies *B. vulgaris* as a preferred weed host of *P. xylostella* and suggests that the rapid spread *of B. vulgaris* in eastern Ontario may be linked with the establishment of *P. xylostella* in Canada (Harcourt 1957). Non-host plants may contain glucosinolates but they also contain oviposition inhibitors. *P. xylostella* is inhibited by the odor of tomato (Gupta and Thorsteinson 1960a, 1960b). Extracts of white clover sprayed on Brussels sprouts reduces oviposition by *P. xylostella* but the effect was variable and weak (Dover 1986).

The relative amount of wax on the leaves of *Brassica* species and varieties has a significant impact on the mortality of *P. xylostella*. Cultivated *B. oleracea* (cabbage, broccoli, cauliflower, Brussels sprouts, etc.) have a dense coating of crystalline surface lipids that produce a characteristic 'wax bloom'. Several *Brassica* mutations eliminate this waxy bloom and produce plants, which are "glossy" in appearance. Many of these glossy mutations confer resistance to insect pests including *P. xylostella* (Eigenbrode et al. 1995).

Mortality increases on glossy plants. Increased mortality is partly the result of the behavior of the *P. xylostella* larvae. The first instar larvae take longer to "settle" on glossy *Brassica* leaves. The larvae move more rapidly, spend more time walking, are more dispersed, and establish fewer leaf mines on glossy plants than on normal-waxy plants. This behavior exposes the small larvae to external mortality factors including weather and natural enemies (Eigenbrode et al. 1995).

The potential of natural enemies to influence the ecology and evolution of insect-herbivore-plant interactions is well recognized (Price et al. 1980). Glossy *Brassica* resistance to *P. xylostella* is a classic example of the complex interactions that occur between plants, herbivores, and the natural enemies. Glossy resistance to *P. xylostella* only occurs in the field where natural enemies are active. The resistance is not expressed in controlled environments in the absence of natural enemies (Eigenbrode et al. 1995).

The waxy covering on normal plants reduces the searching efficiency of natural enemies. In small enclosure studies, adult minute pirate bugs (*O. insidiosus*) and larval *C. carnea* spent less time walking and more time grooming or scrambling in an ineffective forward motion on waxy cabbage than on glossy cabbage. Electron micrographs showed that waxy debris collected on the tarsi of these natural enemies on the normal cabbage. On glossy (wax free plants) the predators found and attacked first instar *P. xylostella* more quickly (Eigenbrode et al. 1996).

H. convergens, *O. insidiosus*, and *C. carnea* are relatively ineffective predators of *P. xylostella* on normal waxy *Brassica* plants. They have difficulty moving around and foraging on the waxy plants. In greenhouse cage experiments, *H. convergens*, *O. insidiosus*, and *C. carnea* caused significant reductions in *P. xylostella* on glossy type cabbage plants. All three predators failed to reduce *P. xylostella* on normal waxy cabbage (Eigenbrode et al. 1995).

The combination of increased "settling time" for the first instars and the increased searching efficiency by the natural enemies on glossy *Brassica* plants explains, in part, the increase in mortality of *P. xylostella* on glossy *Brassica*. In the greenhouse, where external mortality factors are eliminated, glossiness does not depress *P. xylostella* populations. Glossy resistance to *P. xylostella*, however, does not appear to depend entirely on predation. Abiotic factors present in the field interact with the glossy trait to produce resistance. Increased exposure of larvae to drowning, desiccation, and other stresses contributes to their mortality (Eigenbrode et al. 1995).

While ample evidence exists for the physical mechanisms believed to cause resistance in glossy-leaf *B. oleracea* breeding lines, the relative importance and the mechanisms of chemical resistance of these lines is not well understood (Verkerk and Wright 1996a). When the polar fractions of ethanol extracts of partially resistant glossy breeding lines of cabbage were incorporated into artificial diets, their impact on the survival of *P. xylostella* varied. Extracts from the leaves of some resistant glossy lines when incorporated into media reduced *P. xylostella* survival by up to 19%. Resistance in the glossy line is partly chemical (Eigenbrode et al. 1990).

Glossy host plant resistance is not seen as a viable method of control because on its own it does not appear to offer adequate control. All *Brassica* species (even those from glossy leaf lines) are susceptible to *P. xylostella* until at least six weeks after germination. Intrinsic resistance of a given host plant tends to increase with age. Resistance of *B. oleracea* is greatly affected by the environment, growing conditions, and incident light. Most of the horticultural varieties preferred by farmers and consumers are the waxy varieties that are more susceptible to *P. xylostella* (Verkerk and Wright 1996b).

Background color surrounding *Brassica* plants does not consistently affect oviposition by *P. xylostella*. *P. xylostella* laid the same number of eggs on Brussels sprouts (*B. oleracea gemmifera* L.) surrounded by green versus transparent plastic sheets (Dover 1986). Weed free broccoli surrounded by black, yellow, green, or blue colored cloth and broccoli surrounded by weeds had the same number of *P. xylostella*, *P. rapae*, and *T. ni* as control plants surrounded by bare ground (Liburd et al. 1998).

Interplanting can have an impact on *P. xylostella* populations. Characteristics of the interplanted vegetation determine the interactions between herbivore, host plant, and natural enemies. The impact of mixed planting depends on the type of plant material used, the timing of the development of the interplanted vegetation, the height of the interplant, and the presence or absence of flowers. The interactions are often complex and pulling in opposite directions.

In some cases, *P. xylostella* density is reduced in polyculture compared to *Brassica* monoculture. The effect is weak and inconsistent (Talekar et al. 1986). *P. xylostella* oviposition was reduced on Brussels sprouts grown among sage (*Salvia officinallis* L.) or thyme (*Thymus vulgaris* L.) or clover (*Trifolium repens* L.). Oviposition was also reduced when plastic plant models or green plants were placed among the Brussels sprouts. The effect of interplanting may be, in part, simply a visual hiding effect (Dover 1986).

In some cases, interplanting can result in undesirable effects (Latheef and Irwin 1980). Most adult Lepidoptera feed on floral nectar. The presence of flowering plants generally produces a localized effect influencing the spatial distribution of eggs (Bigger and Chaney 1998). More *P. xylostella* larvae occurred in broccoli interplanted with *A.*

foeniculum than on a broccoli monoculture. Nectar producing flowers apparently attracted *P. xylostella* adults. This attraction resulted in more oviposition on the cole crops growing nearby (Zhao et al. 1992).

In some cases, the presence of non-host plant material mixed with *Brassica* plants increases parasitism of *P. xylostella.* Parasitism of *P. xylostella* was significantly higher in cabbage plots surrounded by tomato plants. Removal or addition of tomato plants reversed the effects. When tomatoes were removed, parasitism was reduced (Bach and Tabasnik 1990). In situations where *P. xylostella* concentrates its oviposition in a *Brassica* monoculture, parasitoids may respond to the concentration of their host insects regardless of the purity of the stand. In some cases, parasitism is higher in monoculture (Horn 1987).

The presence of flowering interplanted vegetation can have a direct impact on parasitoid populations. Flowers increase the longevity and fecundity of some parasitoids (Leius 1960, 1961a, 1961b, 1963, 1967, Idris and Grafius 1995, 1997, Shahjahan 1974, Syme 1977). The longevity of *D. insulare* was significantly higher when it fed on nectar from the *Barbaris vulgaris*. And, the presence of flowering weeds increased the parasitism of *P. xylostella* by *D. insulare* (Idris and Grafius 1993, 1995).

Generalist predators may also have an impact on the survival of *P. xylostella* on cole crops interplanted with other vegetation. When tomatoes were mixed with cabbage, fewer first and second instar *P. xylostella* survived. Plots with no tomatoes had four times as many small larvae surviving. The increased numbers could not be explained by differences in parasitism. The primary parasitoid in the experiment attacked late instar *P. xylostella.* Laboratory oviposition experiments showed that *P. xylostella* did not discriminate between cabbage grown alone and cabbage grown surrounded by tomatoes. Weather, predators or other factors were involved in the changes in mortality (Bach and Tabasnik 1990).

TRICHOPLUSIA NI (HUBNER)

T. ni is a polyphagous, North American native Lepidoptera (Ehler 1977). *T. ni* is widespread and found throughout the western United States and parts of Canada. In California, the larvae feed on cole crops, lettuce, cotton plants, sugar beets, celery, alfalfa, and tomatoes. Other hosts include beans, potatoes, melons, cucumbers, squash, and citrus (Shorey et al. 1962). The insect can be successfully reared on lima bean plants. *T. ni* feeds on peas, sugarbeets, lettuce, celery, cole crops, and various weeds in the Pacific Northwest (Berry 1998). It is often listed as one of the leading agricultural pests in the United States (Shorey et al. 1962, Ehler and van den Bosch 1974, East et al. 1994). It occurs in significant numbers sporadically in Oregon (Berry 1998). The larvae generally do not affect cole crop yields. The larvae are, however, a serious contaminant of processed broccoli and cauliflower (Maltais et al. 1994).

Life cycle and seasonal activity

Oviposition by *T.* ni involves searching, orientation, encounter, landing, surface evaluation, and acceptance of the host plant by the female moth. The moths depend on tarsal receptors for perception of oviposition attractants and deterrents on leaf surfaces. *T.* ni orients towards volatile substances emitted by potential host plants. Volatile and tactile cues deter or enhance oviposition. Egg laying *T. ni* are more attracted to yellow substrates than other colors. Oviposition is deterred by frass from larval feeding or by chemicals released from damaged foliage. As a result, *T. ni* eggs tend to be distributed evenly in a patch of host plants (Renwick and Chew 1994).

T. ni can lay 300-600 eggs per female in a lifetime (Ehler et al. 1973). Although eggs are not deposited in masses, the females will lay large numbers of eggs in a short period of time and may place several eggs on a single plant. Normally, one egg is found per leaf. Shorey et al. (1962) followed one female moth for nine minutes. It laid at least one egg on 112 cabbage plants before it flew out of the field.

Eggs are generally cemented to a vertical or lower surface of vegetation. Most of the eggs are placed in the upper half of the plant, seldom at the terminals. Eggs are deposited on the underside of mature leaves where the larvae hatch and begin feeding. Cabbage looper eggs hatch in three to ten days depending on the temperature. At temperatures at or below 14C, egg-hatching time is lengthened considerably (Ehler 1977).

The cabbage looper is considered a warm weather insect. The total developmental time (egg to egg laying adult) of *T. ni* ranges from about 24 days at 32 C to 95 days at 14 C. Newly emerged larvae eat the remains of the egg before they begin eating plant leaves. The number of instars of *T. ni* depends on growing conditions. The number of instars at various temperatures and media varies from five to seven (Shorey et al. 1962). In most cases, *T. ni* has five instars (Ehler and van den Bosch 1974).

At the end of the larval period, the larvae generally move to a vertical surface of a leaf or other substrate. On heading cabbage, for example, the area between adjoining leaves is often selected. On broccoli, larvae move up into the elongating flower bud and establish their cocoon among the florets (Shorey et al. 1962). In the field, *T. ni* occasionally forms pupa on clods of dirt or other debris on the soil surface. There is a brief prepupal period while the larvae spins a loose web. The webbing partially folds the edges of leaves in and around the larva. After harvest, pupae of *T. ni* are often found in the plant debris at the soil surface (Ehler et al. 1973, Ehler 1977).

The moths emerge from the pupa during daylight hours (Shorey et al. 1962). In the field, adult moths are semi-nocturnal, usually feeding and ovipositing at dusk. If the weather is cloudy and cool, the moths can be active during the day. Adult *T. ni* are active fliers and are well represented in black light collections (Ehler 1977).

Adult moths feed on the blossoms and extra floral nectar sources of crops and wildflowers. In cage tests, feeding on nectar significantly increased the fecundity of *T. ni* females compared to those caged with plants that lacked floral or extra-floral nectar sources (Shorey et al. 1962).

In the Pacific Northwest, *T. ni* spends the winter as a pupa in the soil, on crop residue, or in trash near the base of host plants (Berry 1998). In California, *T. ni* larvae are found during the winter on cole crops. Hibernal diapause has not been demonstrated for *T. ni* (Ehler and van den Bosch 1974).

Cabbage looper population densities build up gradually in the spring and decrease markedly in the late fall (Shorey et al. 1962). Cabbage loopers have two generations per year in the Pacific Northwest (Biever et al. 1992). Adult *T. ni* emerge in May and deposit eggs from late May to June. Eggs hatch in about a week and larvae feed for about 3-4 weeks, then form cocoons. Adults from the second-generation lay eggs and larvae develop in

August. It is this second generation that causes the most damage in Oregon cole crops (Berry 1998).

In southern California, where the growing season is long and warm, *T. ni* has at least three generations per year (Ehler and van den Bosch 1974, Ehler 1977). Generation time can be as short as 26 days. The generations are usually discrete, and each cohort is bigger than the next. In Eastern Canada, *T. ni* is often not a problem in broccoli because egg laying and seasonal activity are not in sync with broccoli planting and harvesting dates (Maltais et al. 1994).

Mortality Factors

Cool weather has a significant negative effect on the development of *T. ni* populations. If any stage of *T. ni* is maintained for extended periods of time below 23C, the fecundity of the resulting adults is significantly reduced (Shorey et al. 1962). Jones (Jones 1982) found that abiotic mortality factors were not as important as parasitization and predation of *T. ni* in southern California. Mortality of *T. ni* is inflicted by predators, several parasitoids, and a nuclear polyhedrosis virus (Ehler et al. 1973, Ehler and van den Bosch 1974, Ehler 1977).

Disease often regulates large *T. ni* larvae late in the growing season. Polyhedral viruses may kill 90 to 95% of the larvae (Berry 1998). Nuclear Polyhedral Viruses occur naturally and are highly virulent pathogens. They have potential as bio-insecticides against pest Lepidoptera including *T. ni* (Milks 1997). In the field, the relative importance of naturally occurring virus is variable and depends on the instar and the time of year. Since cole crops are planted in succession (unlike cotton), there is more temporal continuity for polyhedral virus epidemics to build up (Ehler 1977).

T. ni is preyed upon by a predominantly native fauna of natural enemies. Natural enemies of *T. ni* tend to be more numerous and more effective in the early season than in the late season (Jones 1982). In California, a complex of generalist predators maintains *T. ni* populations at innocuous levels. *C. carnea* larvae, *Orius tristicolor* (White) adults and nymphs, *Geocoris pallens* (Stal) adults and nymphs prey on eggs and small larvae of *T. ni*. *Nabis americoferus* (Carayon) adults and nymphs prey on *T. ni* larvae of all sizes (Ehler et al. 1973, Ehler and van den Bosch 1974, Ehler 1977).

When *T. ni* form pupae on clods of dirt or other debris on the soil, they are susceptible to ground beetles, spiders, and other ground dwelling predators (Shorey et al. 1962). Spiders feed on *T. ni* (Ehler and van den Bosch 1974) but ground beetles and spiders are not considered important mortality factors. Predation on *T. ni* by Coccinellidae tends to be low in the presence of aphids. The aphids are a more attractive prey to Coccinellidae. Earwigs prey on *T. ni* larvae (Jones 1982).

Ehler (Ehler and van den Bosch 1974) lists seven Hymenopteran parasitoids and one Tachinidae that attack eggs, larvae, and pupa of *T. ni* in California. It is difficult to separate the relative importance of predators and parasitoids in the regulation of *T. ni*. Jones (1982) found that in California over 50% of the eggs of *T. ni* on celery were parasitized by *Trichogramma* species. While predators consumed many of these parasitized eggs, it would not be accurate to assign their mortality to the predators. They would have died anyway. Parasitism of *T. ni* in the Pacific Northwest varies from year to year and can be very low in *T. ni* outbreak years (Biever et al. 1992).

Early season treatment of cotton for control of *Lygus* bugs eliminates most of the natural enemies of *T. ni.* In the absence of natural enemies, *T. ni* can become a significant pest and require treatment in cotton later in the season (Stern et al. 1969). *T. ni* populations often reestablish at levels that are significantly higher than the levels prior to the treatment. Resurgence of cabbage looper populations following insecticide applications provides evidence that natural enemies have a significant impact on the regulation *T. ni* populations (Ehler et al. 1973).

Life table analysis of the *T. ni* in treated and untreated cotton showed that in the untreated plots, 3.5 eggs resulted in 1.9 larvae. In the insecticide treated plots, 1.9 eggs resulted in 1 larvae. Most of the eggs and small larvae in the treated plots survived to later instars. In the control plots, only 50 % survived. In subsequent experiments, selective insecticides were used to suppress natural enemy populations. The *T. ni* egg to small larvae ratio went up. The loss of eggs and small larvae was consistently the major intra-generation mortality factor. Most of the mortality was attributable to predation (Ehler et al. 1973, Ehler and van den Bosch 1974, Ehler 1977).

Responses to vegetation management

Background color and background vegetation surrounding cole crops may not influence the rate of oviposition of *T. ni.* Liburd et al. (1998) found that broccoli surrounded by weeds, and broccoli surrounded by either black, yellow, green, or blue cloth (no weeds) supported similar populations of *T. ni* as broccoli surrounded by bare ground. *T. ni* oviposition on cabbage was unaffected by the presence of a tall, dead mulch of hairy vetch or rye grain compared to cabbage grown in bare ground. *T. ni* mortality, however, was higher in the living mulch. Cabbage grown in a dead mulch of rye grain required seven sprays with Bt while the bare ground plots required eight sprays with Bt based on the number of *T. ni* larvae. There may have been increased natural enemy activity in the living mulch (Roberts and Cartwright 1991).

The presence of a variety of fragrant herbs and flowers does not reduce oviposition by *T. ni* on cabbage (Latheef and Irwin 1979, 1980). The density of *T. ni* in broccoli was not affected by the presence of nectar producing *A. foeniculum* whether they were planted near by or interplanted with broccoli (Zhao et al. 1992).

The relative abundance of *T. ni* was not significantly influenced by the presence of flowering Candytuff (*I. umbellata*) surrounding cabbage or broccoli plantings. The presence of the flowering borders did, however, influence the spatial distribution of *T. ni* and *P. rapae* eggs. The pattern of this effect was opposite for the two insects. The mean number of *P. rapae* eggs significantly decreased with increasing distance from the patch boundary of the monocrop surrounded by bare ground. In other words, *P. rapae* oviposition was heavier near the edge between the cole crops and the bare ground. When the crops were surrounded by flowering plants, the distribution of *P. rapae* eggs in the cole crops was even. The *T. ni* eggs in the monoculture surrounded by bare ground were distributed evenly. In the cabbage or broccoli surrounded by flowering *Iberis*, the number of *T. ni* eggs increased with increasing distance from the flowering border (Bigger and Chaney 1998).

IMPACT OF RELAY STRIP CROPPING ON BROCCOLI PESTS

Relay strip cropping changes several aspects of the broccoli environment that should have impacts on the herbivores described above and their natural enemies. The relay establishes an understory of non-host vegetation surrounding the broccoli plants. Changes in background color and the presence of non-host plants may reduce the clarity and strength of visual and olfactory signals that guide the herbivores to their host plants. Several studies have shown that incoming *B. brassicae* are sensitive to background color during the colonization process. The density of alate *B. brassicae*, therefore, will be a useful indicator of the impact of relay strip cropping on insects that are sensitive to background vegetation during the host plant selection process.

For the highly mobile herbivores that are capable of emigrating from a patch of vegetation, the presence of non-host plants may lead to confusion and loss of contact with olfactory and gustatory cues that arrest the herbivore in the plant patch. Several studies indicate that *P. cruciferae* is sensitive to stand purity. It tends to leave mixed stands and accumulate in areas where its host plants are growing in monoculture. *P. cruciferae* density, therefore, will be a useful indicator of the impact of relay strip cropping on tenure time of crucifer specialists that are sensitive to stand purity.

P. rapae may be a useful indicator of relative natural enemy activity in the relay strip and clean till cropping systems. *P. rapae* does not respond to host plant density or stand purity during its oviposition flights. It should scatter its eggs evenly across the broccoli plantings. Difference in the relative survival of the early instars would, therefore, result from differing mortality factors in the two cropping systems.

T. ni and *P. xylostella* tend to concentrate their egg laying in areas of high host plant density. They may provide an indication of the impact of stand purity in the two cropping systems. *T. ni* tends to have discrete egg laying periods in the Pacific Northwest. Once oviposition begins, *P. xylostella* pressure tends to increase steadily during the growing season due to multiple overlapping generations of larvae and moths. Because of this variation, the two insects should give us a variety of indications of the impact of relay strip management on colonization and natural enemy activity compared to the clean till cropping system.

Relay strip cropping should enhance the numbers of natural enemies associated with the broccoli. Under-sowing results in soil that is covered with vegetation. The presence of the ground cover changes the microclimate near the soil surface and may lead to earlier colonization by natural enemies that are sensitive to microclimate. Under-sowing results in a mixture of plant species. Mixed stands generally support a greater diversity of insects than monoculture. The presence of a diverse assemblage of alternative prey should support a greater number of generalist natural enemies. Strip management provides a refuge in the cropping system that may conserve natural enemies that are sensitive to disturbance and that are not highly mobile. Differences in natural enemy density in the two systems should be reflected in the density of aphids and Lepidopteran pests (especially the eggs and small larvae) on the broccoli.

Nectar and pollen sources in the cropping system may enhance the longevity and fecundity of natural enemies including Syrphidae and parasitic Hymenoptera. Specifically, the parasitism of *P. xylostella* by larval/pupal parasitoid *D. insulare* should be a useful indicator of the impact of nectar and pollen in the relay strip crop. *D. insulare* is common, easy to recognize, and may respond to the presence of nectar and pollen.

Relay strip cropping, in many regards, is a radical departure from clean till monoculture of broccoli. Relay strip cropping integrates vegetation management tactics that have been shown to interfere with host plant finding, patch tenure time, and natural enemy induced mortality of broccoli pests. Based on the biological interactions of the pests and their natural enemies it was reasonable to expect differences in pest densities in the clean till and relay strip-cropping systems.

There are several aspects of the relay strip cropping system, however, which could have a negative impact on natural enemies. The mixed planting presents natural enemies with a search arena that is more complex than a pure stand of broccoli. The complexity of the habitat may reduce the efficiency of specialist natural enemies in searching for their prey or host insects. Natural enemies that accumulate in the tillage and pesticide refuges may or may not move into the target crop. It is possible that the alternative food and habitat resources in the refuge and in the crop itself may draw natural enemies away from the broccoli or arrest them in the refuge. Natural enemies that are habitat specialists may not be motivated to move from the refuge into the vegetable crop.

The presence of nectar and pollen sources in the relay strip cropping may increase the activity of some natural enemies in the cropping system. Nectar can also influence the spatial distribution of some of the Lepidoptera in ways that are not favorable to the crop. The outcome of the interactions between nectar foraging, egg distribution, prey density, and the aggregation of natural enemies is difficult to predict. The assemblage of insect pests associated with broccoli has been extensively studied. The reactions of these well-characterized insect pests should provide us with many insights concerning the value of relay strip cropping as a pest management tactic.

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