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UNIVERSITY OF ALBERTA

THE EFFECT OF AGRICULTURAL PRACTICE ON A CARABID FAUNA (COLEOPTERA: CARABIDAE) IN CENTRAL ALBERTA

BY

Héctor A. Cárcamo

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND
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THE UNDERSIGNED CERTIFY THAT THEY HAVE READ, AND RECOMMEND TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH FOR ACCEPTANCE, A THESIS ENTITLED **THE EFFECT OF AGRICULTURAL PRACTICE ON A CARABID FAUNA IN CENTRAL ALBERTA** HERE SUBMITTED BY **HECTOR CARCAMO** IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN ENTOMOLOGY.

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September 8th, 1992

DEDICATION

To Rosa Lydia and Karla.

ABSTRACT

I studied the effect of agricultural practice on ground beetles using pitfall traps in experimental plots and in an uncultivated field near Edmonton, Alberta. Ground beetle abundance and species richness were higher under the organic system than in a chemical fallow, but crop type (barley, faba bean, barley-pea intercrop), and rotation had no effect on carabid abundance or species diversity. Reduced tillage was not significantly associated with increased carabid abundance or species richness but species differed in their response to tillage treatments. The carabid assemblage from an uncultivated field was conspicuously different from assemblages in the crops or in a dense fescue sward adjoining the experimental plots. Carabid abundance was highest in the meadow where the fauna was dominated by the exotic species, *Pterostichus melanarius*.

Also, the effect of conservation and conventional tillage on carabid communities was compared using pitfall trapping in two commercial barley farms during the growing season of 1991. Although, overall carabid abundance was significantly higher under conventional tillage, abundances of individual species varied in the two farms. *Agonum placidum* and two *Amara* species were more abundant in the ploughed farm while *Pterostichus adstrictus* and three *Bembidion* species were significantly more abundant in the reduced tillage farm. Slightly more carabid species were collected in this latter farm and species diversity and evenness were significantly higher.

The activity of carabid beetles and predation pressure of ground-dwelling predators was further investigated in the four crop types, using experiments to measure disappearance rate of fly pupae. Carabid captures and number of pupae lost showed similar patterns across an intercrop of peas and barley and monocultures of faba bean and barley. Both carabid activity and predation pressure were lower in plots of fescue grass than in the crops. Disappearance rate of the largest pupae was significantly lower in the fescue habitat. In choice experiments, the intercrop attracted significantly more individuals of *P. melanarius* than did the three monocultures and addition of fly pupae in the faba bean and fescue failed to alter this distribution.

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1. INTRODUCTION

1.1 BACKGROUND

1.1.1.Natural enemies in the context of sustainable agriculture.

Increased realization of problems associated with modern intensive agriculture has forced producers, extensionists, scientists and policy makers to re-evaluate their goals and search for alternative methods of production. The growing interest in organic farming throughout the world (Altieri 1992) is the direct result of concerns with current production technology (for a more detailed discussion of these ideas see Carrol et al. 1990, Gliessman 1990, Coleman 1989, Altieri 1987, Jackson 1985).

Three main problems can be recognized especially in the third world. As an economic activity, agriculture is becoming less viable. Prices of commodities have remained stable although input prices continue to increase. This trend can be expected to continue as finite resources such as fossil fuels are used up. Closely related to the economic problem is the increase in poverty that follows. This has been particularly serious in developing countries. The high inputs demanded by modern agriculture have often forced the small farmers out of production as they sell their land to the wealthier who can reap the benefits of large scale production. The result has been an increase in urban poverty as the landless migrate to the cities in search of jobs.

The environmental impact of modern agriculture is well recognized. Agrochemicals pollute water and harm wildlife. In addition, they pose a serious health risk to farm workers. Another aspect of the environmental problem is the increasing deterioration of the resource base, soil and water. In the United States alone, more than two billion tones of top soil from cultivated land find their way into water channels creating serious silting problems (Poincelot 1986). In some areas water has become a limiting factor due to pollution from agricultural chemicals and/or urban wastes. All of these factors threaten the future of food production.

Several terms have been used to describe the alternatives to the current system: organic agriculture, regenerative agriculture, sustainable agriculture, biological agriculture, alternative agriculture, ecological agriculture, low input sustainable agriculture (LISA), reduced input sustainable agriculture (RISA) and a host of others. Although there is no consensus on the exact definition of alternative agriculture, all of these terms refer to a food production system that is economically viable and ecologically and socially acceptable. I will use the term 'sustainable agriculture' as a comprehensive term embodying these three goals.

The term agroecology has been used to address the scientific aspect of sustainable agriculture (Altieri 1987). Agroecology has been described as the marriage between agriculture and ecology (Jackson and Piper 1989). Although, both sciences draw from similar bases, in the past their practitioners have walked separate roads. This has led to extreme overspecialization on the part of agronomists that has resulted in recommendation of production technologies that ignore fundamental ecological principles (Lowrance et al. 1984). For their part ecologists have generally ignored agriculture and failed to use the agroecosysem as a unit of study so that their findings are not tested in cultivated systems and cannot be used by agronomists even if they were interested (Gliessman 1990).

In the past decade there has been some progress toward establishing the scientific basis of sustainable agriculture (Carrol et al. 1990, Gliessman 1990, Altieri 1987). Interestingly, most early research has focused on tropical systems, perhaps reflecting the relative pressures from the environment and the need to find alternatives with less dependence on expensive external inputs. Traditional agricultural systems in these tropical areas are not viewed by agroecologists as primitive useless systems that should be completely replaced with modern technologies (Altieri, 1987). Instead they are studied to elucidate the ecological principles that have been incorporated as a result of thousands of years of coevolution between culture and environment.

1.1.2 The role of natural enemies, particularly carabids, in the agroecosystem.

Under industrialized agriculture, growers have typically relied on use of toxic chemicals to control arthropod pests. However, alternative means of pest control are highly desirable given the well known problems associated with the use of insecticides. One effective alternative is biological control (Huffaker and Messenger 1976), usually through the importation of specialist enemies to combat introduced pests. Natural control by the indigenous complex of natural enemies has received much less attention (Gross 1987), although under sustainable agriculture, indigenous enemies can be expected to play an important role in depressing populations of potential pests (Altieri 1992). Ecosystem modification (Speight 1983) in the form of various agricultural strategies to add heterogeneity to the agroecosystem, can substantially enhance populations of indigenous natural enemies.

Natural enemies can be divided in two general groups based on their host range. Specialist enemies such as coccinellids have a narrow host range. Other specialists, like many parasitoids, attack a single species. Much attention has been devoted to the study of relatively specialized natural enemies because of their appeal in biological control projects. Although this 'gentle' ecological approach is more desirable than chemical control, it is certainly not going to be the panacea or 'magic bullet' that will solve all of our pest problems (Gross, 1987). A more radical approach is required, one which addresses the 'problem *of* agriculture' as opposed to the 'problems *in* agriculture' (Jackson, 1985). Such an approach would rely heavily on the entire complex of natural enemies to maintain a degree of stability in agroecosystems which will minimize intervention either biological or otherwise (Gross, 1987).

Generalist enemies have a wide host range and include mostly predaceous arthropods. In agroecosystems polyphagous predators are represented by several class level taxa including Chilopoda, Araneae, Opiliones and Hexapoda. The main hexapod orders represented include, Hemiptera, Hymenoptera, Diptera, Neuroptera and Coleoptera, particularly Staphylinidae and Carabidae. This last-named family has been the focus of intensive research in both disturbed and more pristine environments particularly in temperate regions (Thiele 1977, Stork 1990, Erwin et al. 1979, Luff 1987). Some of the reasons for their popularity as stated by Stork (1990) are that these beetles are generally ubiquitous, easy to capture, taxonomically diverse yet relatively easy to identify, and perhaps most importantly, they are very attractive creatures esthetically.

In temperate agroecosystems, carabids are usually the dominant predatory arthropods (Potts & Vickerman 1974) of the ground dwelling fauna. Many researchers have been attracted to this group hoping that they can be used in specific biological control programs (Thiele 1977). As a result there are several studies of the carabid fauna of crops (e.g. Rivard 1966, Kirck 1971, Frank 1971, Doane 1981, Varis et al. 1984) and a number of studies showing that particular species can feed and have an effect on the herbivorous insects they prey upon (e.g. Hance 1987, Chiverton 1988, Edwards et al. 1979, Floate et al. 1990). In the context of agroecology, generalist natural enemies such as carabids will play an important role as a substitute for unifactorial strategies. Therefore it is necessary that we learn more about the ecology of this group in agroecosystems.

1.2 LITERATURE REVIEW: CARABIDS IN AGRICULTURAL SYSTEMS.

In the following section I provide a brief summary of faunistic studies of ground beetles in cultivated grassland and a literature review of the effect of agronomic practices on carabids, as they pertain to this study. I review in detail the effect of organic farming compared to conventional methods, crop rotations, and faunistic comparisons between cultivated and non-cultivated adjacent habitats. The literature on tillage, crop types, and vegetational diversity is reviewed in more detail in chapters 3 and 4, hence I provide only a summary in this section.

1.2.1. Carabids in cultivated grasslands.

Despite continuous disturbance in the form of cultivation, harvesting and pesticides, temperate agroecosystems can maintain one of the richest and most diverse ground beetle faunas (e.g. Niemelä and Halme 1991). Considerable effort has been invested in describing the carabid fauna in Europe and North America (Luff 1987). In Canada, however, particularly western Canada, there are few faunistic studies of carabids in agricultural fields (Doane 1981, Finlayson and Campbell 1976, Frank 1971). Considerably more work remains to be done to characterize the fauna from the various agroclimatic zones and crop habitats in the region.

Agroecosystems also provide opportunities to consider interactions among carabid species. For example, the exotic *Pterostichus melanarius* was introduced to North America from Europe, probably in ship ballast and along with nursery stock (Spence and Spence 1988). This species has dispersed into urban, highly disturbed sites in British Columbia (Spence and Spence 1988) as well as natural climax aspen-poplar forests in central Alberta (Niemelä and Spence 1991). The effects on the native fauna seemed to be negative in urban sites but in forests no effects were detected. Spence and Spence (1988) suggested that, unlike pristine grasslands, disturbed cultivated habitats were vulnerable to invasion by this species. Thus the effects of this species on native carabid assemblages is appropriately studied in agroecosystems. This is an especially fruitful approach because much is known about the ecological role of *P. melanarius* in Europe (e.g. Edwards et al. 1979).

1.2.2. Organic farming

Organic farming methods require avoidance of synthetic pesticides and fertilizers (Hill and McRae 1992). Insects, diseases and weeds, therefore, are managed through cultural and biological means. In organic farming, ecosystem manipulation (Speight 1983) to enhance natural enemies and discourage pest outbreaks is crucial to avoid severe crop losses. A few studies have compared the carabid faunas found in organic and conventional farming systems. With the only exception of Holopainen (1983), all studies have reported higher abundance of carabid numbers and species in organic or biologically managed farms (Kromp 1989, Hokkanen and Holopainen 1986, Dristschilo and Wanner 1980). In some studies the differences in abundance were quite dramatic, as number of carabids were up to twenty times higher under organic farming methods (Hokkanen and Holopainen 1986). Determining the process responsible for this pattern is a difficult task without proper experiments since farming practices varied among these organic growers or researchers. However, there appears to be consensus that organic methods result in higher heterogeneity through plant diversity or reduced tillage, more food sources and more adequate microclimatic conditions which allow higher number of carabids. Impact of this higher abundance of carabids on insect pests in organic systems and subsequent crop yields has not been studied. In Canada, equivalent faunistic studies of carabids in organic and conventional systems are not available for comparison with those in the United States and Europe.

1.2.3. Crop rotations.

Crop rotation is a common practice associated with organic farming as a strategy to deal with some insect pests, weeds and diseases (Speight 1983). Thiele (1977) cites two reports (Kirchner 1960, Kabocic-Waslic 1970) where carabids were positively affected by crop rotation. Other workers have confirmed this effect of crop rotations on carabids (Brust et al. 1986, Grégoire-Wibo 1983). However, Lövei (1984) found more carabids in continuous maize than in maize preceded by winter wheat in two farms in Hungary. The effect of crop rotations depends on the nature of the crop type (Rivard 1966) and also the timing of agronomic practices for the components of the rotation (Hance et al. 1990). Some researchers have argued that cropping system (rotation) can be more important than tillage regime in structuring carabid communities (Weiss et al. 1990).

1.2.4. Vegetational diversity.

Adding crop diversity as a component of a rotation may result in greater diversity and abundance of natural enemies (Altieri and Letourneau 1982). Root (1973) hypothesized that the lower abundance of herbivores in polycultures was caused by greater abundance and impact of natural enemies. This idea has been confirmed with carabid beetles, as higher abundance or activity has been reported in polycultures than monocultures (Brust et al. 1986, Perfecto et al. 1986, Barney et al. 1984, Uvah and Coaker 1984, Tukahirwa and Coaker 1982, Ryan et al. 1980, Speight and Lawton 1976, Dempster and Coaker 1974). Greater impact of carabids under higher plant diversity, however, could not be demonstrated against *Brassica* pests (Tukahirwa and Coaker 1982). This is the only study with carabids that manipulated predator numbers to experimentally test Root's (1973) enemies hypothesis.

1.2.5. Tillage.

Chemical fallow has been suggested as an alternative to summer fallow for prairie farmers to prevent soil erosion. This practice involves some form of conservation tillage (zero or reduced) and commonly high input of pesticides to control pests, especially herbicides for weed control (Gebhardt et al. 1985). Reduced tillage has been shown to result in increased abundance of carabid individuals (see review by Stinner and House 1990 and Chapter 3). However, in some studies the opposite pattern was reported (Barney and Pass 1986) or no differences were found between no tillage and conventional full tillage (Tyler and Ellis 1979). In most studies variation between carabid species was prevalent and even the same species responded differently to the same tillage treatments in different sites (Weiss et al. 1990). It is clear that not all carabid species respond in the same way to tillage regime (Hance et al. 1991) and that overall patterns of abundance depend on how locally dominant species are affected.

1.2.6. Uncultivated habitats.

Uncultivated adjacent habitats such as hedges, idle land, and forest wind barriers add heterogeneity to agroecosystems. These habitats can act as overwintering refuges and provide alternative food sources for natural enemies (Thomas et al. 1991), although the same applies for potential pests. In some instances these habitats have been shown to enrich the natural enemy fauna in cultivated fields (Thomas et al. 1991, Hance et al. 1991, Wallin 1985, Sotherton 1985). However, some workers have found negative edge effects as abundance of carabids was higher in the center of the field relative to the edges (Lövei 1984, Doane 1981, Hsin et al. 1979) or found similar numbers (Chapter 3). Wallin (1985,1986), using mark recapture experiments showed some movement and preferences between cultivated and adjacent habitats among some common carabid species in Sweden. More direct experiments like this are needed to show the degree of movement among these habitats by natural enemies.

1.3 OBJECTIVES OF THIS THESIS.

The study of ecological pattern and process in agroecosystems is difficult because of the variable nature of these systems. A variety of strategies and spatial and temporal scales are required to gain insight into the pattern of community structure and possible processes taking place in these habitats. It is of particular importance to supplement studies in garden test systems (experimental plots) with studies using more realistic spatial scales (commercial farms) as well as behavioural studies in the field and even under laboratory conditions. In this thesis, to some extent, I have attempted to include all of these strategies in the study of ground beetles in agroecosystems. Figure 1.1 provides an overview of the areas of investigations included in this thesis.

In Chapter 2, I ask how various agricultural practices affect the activity and community structure of a carabid fauna in Ellerslie. I used experimental plots to elucidate potential effects of specific practices such as organic farming, crop rotations, crop type and diversity, tillage and alternative sources of nitrogen. To understand the general effect of cultivation on ground beetle abundance and diversity I also studied a nearby uncultivated meadow subjected to minimum disturbance. Comparison of the assemblage in the meadow with that of the plots also allowed me to formulate some hypotheses about the potential effect of agricultural practices in mediating interactions between a dominant introduced species and the native carabid fauna.

The concerns about spatial scale are addressed in Chapter 3. I studied the ground beetle communities in two commercial farms with varying tillage regimes near Neerlandia, Alberta. This study supplements the faunistic study in Ellerslie and also provides a comparison of a ground beetle assemblage still not invaded by the exotic *P. melanarius*.

In chapter 4, I have endevoured to understand in more detail the effect of crop type on carabid beetles. I use pitfall traps to characterize activity of carabids in experimental plots with the crop types in question. I also employ artificial prey to measure overall predation pressure and laboratory observations to show that carabids can potentially eat the prey used. Furthermore, I conducted behavioural experiments using mark-release-recapture to test habitat choices in the crop types using experimental field arenas. Using this system, I also asked whether increased food availability could alter crop preference of a common carabid species.

Finally in Chapter 5, I provide a summary and a short general discussion to bring together the various studies. I end with some thoughts about future research on carabids, and natural enemies in general, in agricultural systems.

1.4 REFERENCES.

Altieri, M.A. 1992. Agroecological foundations of alternative agriculture in California. Agric. Ecosyst. & Env. 39: 23-53.

Altieri, M.A. 1987. Agroecology, the scientific basis of alternative agriculture. Westview Press, Boulder.

Altieri, M.A. & D.K. Letourneau. 1984. Vegetation diversity and insect pest outbreaks. CRC Crit. Rev. Plant Sci. 2: 131-169.

Barney, R.J. & B.C. Pass. 1986. Ground beetle (Coleoptera:Carabidae) populations in Kentucky alfalfa and influence of tillage. J. Econ. Entomol. 79: 511-517.

Barney, R.J., W.O. Lamp, E.J. Ambrust and G. Kapusta. 1984. Insect predator community and its response to weed management in spring-planted alfalfa. Prot. Ecol. 6: 23-33.

Brust, G.E., B.R. Stinner, and D.A. MacArtney. 1986. Predator activity and predation in corn agroecosystems. Environ. Entomol. 15: 1017-1021.

Carrol, C.R., J.H. Vandermeer, and P. Rosset (eds.). 1990. Agroecology. McGraw-Hill Publishing Company, New York.

Chiverton, P.A. 1988. Searching behaviour and cereal aphid consumption by *Bembidion lampros* and *Pterostichus cupreus*, in relation to temperature and prey density. Entomol. Exp. Appl. 47: 173-182.

Coleman, David C. 1989. Ecology, ecosystems, and sustainable agriculture. Ecology 70: 1590-1602

Dempster, J.P. & T.H. Coaker. 1974. Diversification of crop ecosystems as a means of controlling pests. In Biology in pests and disease control. D.P. Jones and M.E. Solomon (eds.). Willey, New York.

Doane, J.F. 1981. Seasonal captures and diversity of ground beetles (Coleoptera: Carabidae) in a wheat field and its grassy borders in central Saskatchewan. Quaest. Ent. 17: 211-233

Dritschilo, W. & D. Wanner. 1980. Ground beetle abundance in organic and conventional corn fields. Environ. Entomol. 9: 629-631.

Edwards, C.A., K.D. Sunderland, and K.S. George. 1979. Studies on polyphagous predators of cereal aphids. J. Appl. Ecol. 16: 811-823.

Erwin, T.L., Ball, G.E., and Whitehead, D.R. 1979. Carabid beetles, their evolution, natural history and classification. Proceedings of the first international symposium of carabidology. W. Junk, The Hague, Boston.

Finlayson, D.G. & Campbell, C.J. 1976. Carabid and staphylinid beetles from agricultural land in the lower Fraser valley, British Columbia. J. Entomol. Soc. B.C. 73: 10-20.

Floate, K.D., J. Doane, and C. Gillott. 1990. Carabid predators of the wheat midge (Diptera: Cecidomyiidae) in Saskatchewan. Environ. Entomol. 19: 1503-1511.

Frank, J.H. 1971. Carabidae (Coleoptera) of an arable field in central Alberta. Quaest. Ent. 7: 237-252.

Gebhardt, M.R., T.C. Daniel, E.E. Schweizer, and R.R. Allmaras. 1985. Conservation Tillage. Science 230: 625-630.

Gliessman, S.R. (ed.). 1990. Agroecology: researching the ecological basis for sustainable agriculture. Springer-Verlag, New York.

Grégoire-Wibo, C. 1983. Incidences ecologiques de traitements phytosanitaires en culture de betterabe sucriere. II. Acariens, Polydesmes, Staphylins, Cryptophagides et Carabides. Pedobiologia 25: 93-108.

Gross, H.R. Jr. 1987. Conservation and enhancement of entomophagous insects - a perspective. J. Entomol. Sci. 22: 97-105.

Hance, T. 1987. Predation impact of Carabidae at different population densities on *Aphis fabae* development in sugar beet. Pedobiologia 30: 251-262.

Hance, T., C. Grégoire-Wibo, P. Lebrun. 1990. Agriculture and ground beetle populations: The consequence of crop types and surrounding habitats on activity and species composition. Pedobiologia 34: 337-346.

Hill, S.B. & R.J. MacRae. 1992. Organic farming in Canada. Agric. Ecosyst. & Environ. 39: 71-84.

Hokkanen, H., and J.K. Holopainen. 1986. Carabid species and activity densities in biologically and conventionally managed cabbage fields. J. Appl. Ent. 102: 353-363.

Holopainen, J. 1983. Carabid beetles (Col. Carabidae) associated with cruciferous crops in organic and conventional farms in central Finland. Savonia 6: 19-27.

Hsin, C.Y., et al. 1979. Seasonal activity of carabids and the toxicity of carbofuran and terbufos to *Pterostichus chalcites*. Environ. Entomol. 8: 154-159.

Huffaker, C.B. & P.S. Messenger (eds.). 1976. Theory and practice of biological control. Academy Press, New York.

Jackson, W. 1985. New roots for agriculture. Second Edition. University of Nebraska Press, Lincoln.

Jackson, W. & Piper, J. 1989. The necessary marriage between ecology and agriculture. Ecology 70: 1591-1593.

Kabacik-Wasylik, D. 1970. Ökologische Analyse der Laufkäfer (Carabidae) einiger Agrarkulturen. Ekol. Pol. (A) 18: 137-209. *Cited by* H.U. Thiele. 1977. Carabid beetles in their environments. Springer-Verlag, Berlin, New York.

Kirchner, H. 1960. Untersuchungen zür okologïe feldbewohnender Carabiden. Dissertation, Cologne. *Cited by* H.U. Thiele. 1977. Carabid beetles in their environments. Springer-Verlag, Berlin, New York.

Kirk, V.M. 1971. Ground beetles in cropland in South Dakota. Ann. Ent. Soc. Am. 64: 238-241.

Kromp, B. 1989. Carabid beetle communities (Carabidae, Coleoptera) in biologically and conventionally farmed agroecosystems. Agric. Ecosyst. & Environ. 27: 241-251.

Lowrance, R., B.R.Stinner, and G.J.House, eds. 1984. Agricultural ecosystem: unifying concepts. John Wiley & Sons, New York.

Lövei, G.L. 1984. Ground beetles (Coleoptera: Carabidae) in two types of maize fields in Hungary. Pedobiologia 26: 57-64.

Luff, M.L. 1987. The biology of polyphagous ground beetles in agriculture. Agric. Zool. Rev. 2: 237-278.

Niemelä, J. and E. Halme. 1992. Habitat Associations of carabid beetles in fields and forests on the Åland islands, SW Finland. Ecography. 15: 3-11.

Niemelä, J. & J.R. Spence 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. Oikos 62: 351-359.

Perfecto, I., et al. 1986. Effects of plant diversity and density on the emigration rate of two ground beetles, *Harpalus pensylvanicus* and *Evarthrus sodalis* (Coleoptera: Carabidae), in a system of tomatoes and beans. Environ. Entomol. 15: 1028-31.

Poincelot, R.P. 1986. Towards a more sustainable agriculture. AVI Publishing Company Inc. Wesport, Connecticut.

Potts, G., & G.P. Vickerman. 1974. Studies on the cereal ecosystems. Adv. Ecol. Res. 8: 107-197.

Rivard, I. 1966. Ground beetles (Coleoptera: Carabidae) in relation to agricultural crops. Can. Ent. 98: 189-195.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea)*. Ecol. Monogr. 43: 95-124.

Ryan, J., F. Ryan, and F. McNaeidhe. 1980. The effects of interrow plant cover on populations of the cabbage rootfly, *Delia brassicae* (Wiedemann). J. Appl. Ecol. 17: 31-40.

Sotherton, N. 1985. The distribution and abundance of predatory Coleoptera overwintering in field boundaries. Ann. Appl. Biol. 106: 17-21.

Speight, M. R. 1983. The potential of ecosystem management for pest control. Agric. Ecosyst. & Environ. 10:183-199

Speight, M.R. and J.H. Lawton 1976. The influence of weed-cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia 23: 211-223.

Spence, J.R. & D.H. Spence. 1988. Of ground beetles and men: introduced species and the synanthropic fauna of western Canada. Mem. Ent. Soc. Can. 144: 151-168.

Stinner, B.R. & G.J. House. 1990. Arthropods and other invertebrates in conservation-tillage agriculture. Ann. Rev. Entomol. 35: 299-318.

Stork, N.E. (ed.) 1990. The role of ground beetles in ecological and environmental studies. Intercept. Andover, Hampshire.

Thiele, H.U. 1977. Carabid beetles in their environments. Springer-Verlag. Berlin, New York.

Thomas, M.B., S.D. Wratten, N.W. Sotherton. 1991. Creation of "island" habitats in farmland to manipulate populations of beneficial arthropods: predator densities and emigration. J. Appl. Ecol. 28: 906-917.

Tukahirwa, E.M., & T.H. Coaker. 1982. Effect of mixed cropping on some insect pests of brassicas: reduced *Brevicoryne brassicae* infestations and influences on epigeal predators and the disturbance of oviposition behaviour in *Delia brassicae*. Entomol. Exp. Appl. 32: 129-140.

Tyler, B.M.J. & C.R. Ellis. 1979. Ground beetles in three tillage plots in Ontario and observations on their importance as predators of the northern corn rootworm, *Diabrotica longicornis* (Coleoptera: Chrysomelidae). Entomol. Soc. Ont. Proc. 110: 65-73.

Uvah, I.I. & T.H. Coaker. 1984. Effect of mixed cropping on some insect pests of carrots and onions. Entomol. Exp. Appl. 36: 159-167.

Vandermeer, J.H. 1988. The Ecology of Intercropping. Cambridge University Press. New York.

Varis, A.L., J.K. Holopainen, and M. Koponen. 1984. Abundance and seasonal occurrence of adult Carabidae (Coleoptera) in cabbage, sugar beet and timothy fields in southern Finland. Z. Angew. Entomol. 98: 62-73.

Wallin, H. 1986. Habitat choice of some field-inhabiting carabid beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. Ecol. Entomol. 11: 457-466.

Wallin, H. 1985. Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. Pedobiologia 28: 19-34.

Weiss, M.J., E.U. Balsbaugh. Jr., E.W. French, and B.K. Hoag. 1990. Influence of tillage management and cropping system on ground beetle (Coleoptera: Carabidae) fauna in the northern great plains. Environ. Entomol. 19: 1388-1391.

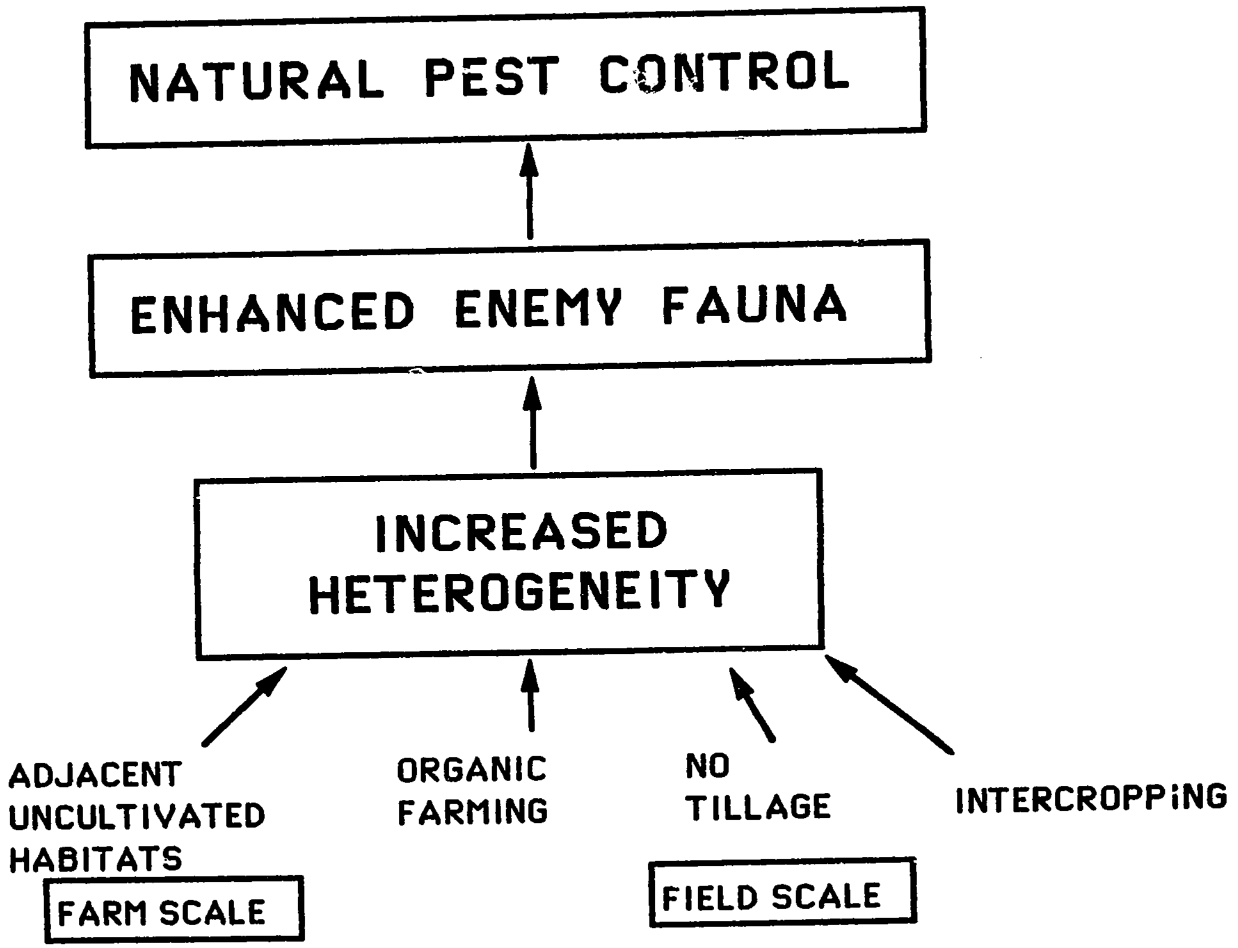
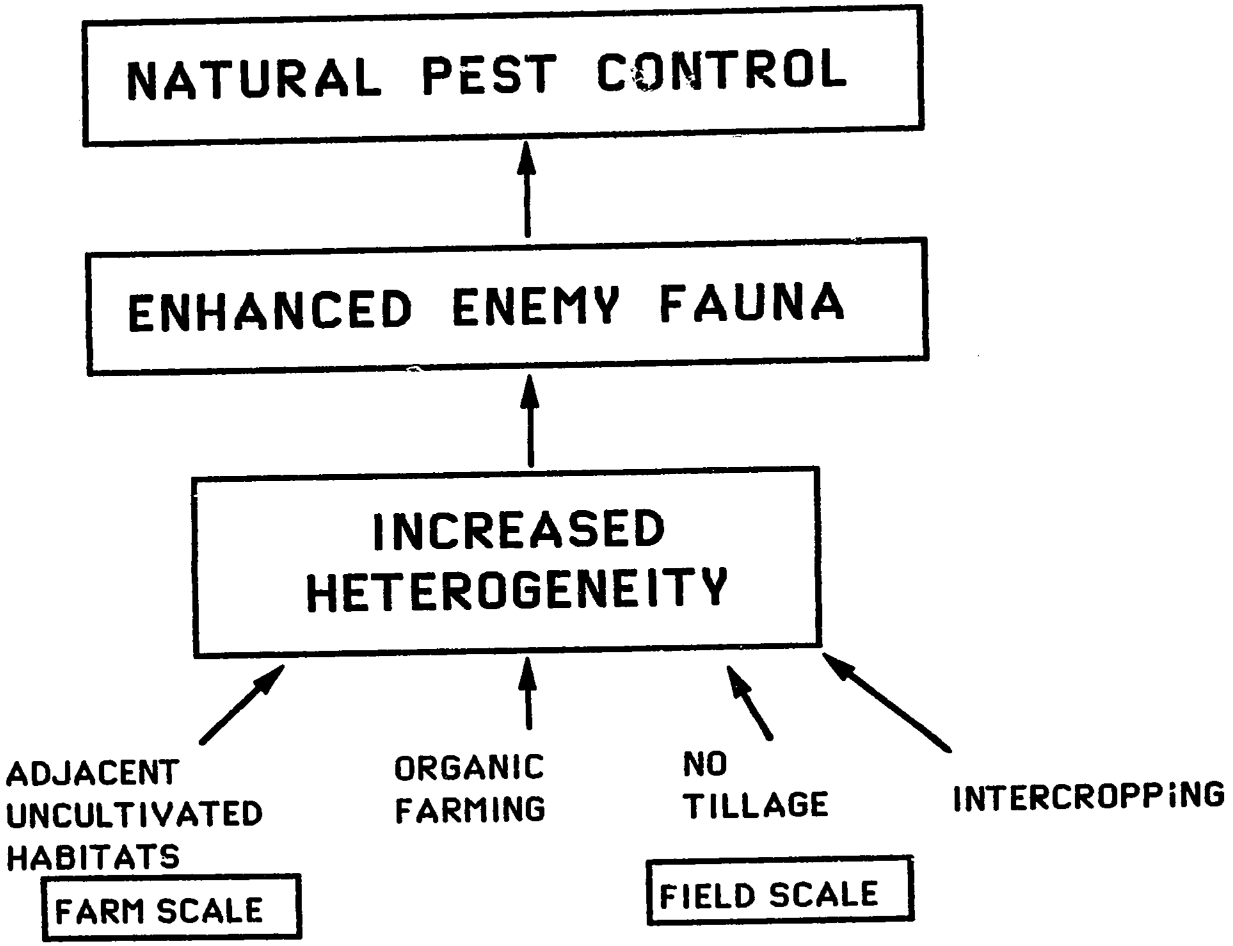


Fig. 1.1: Agricultural practices considered as potential strategies for natural pest control.



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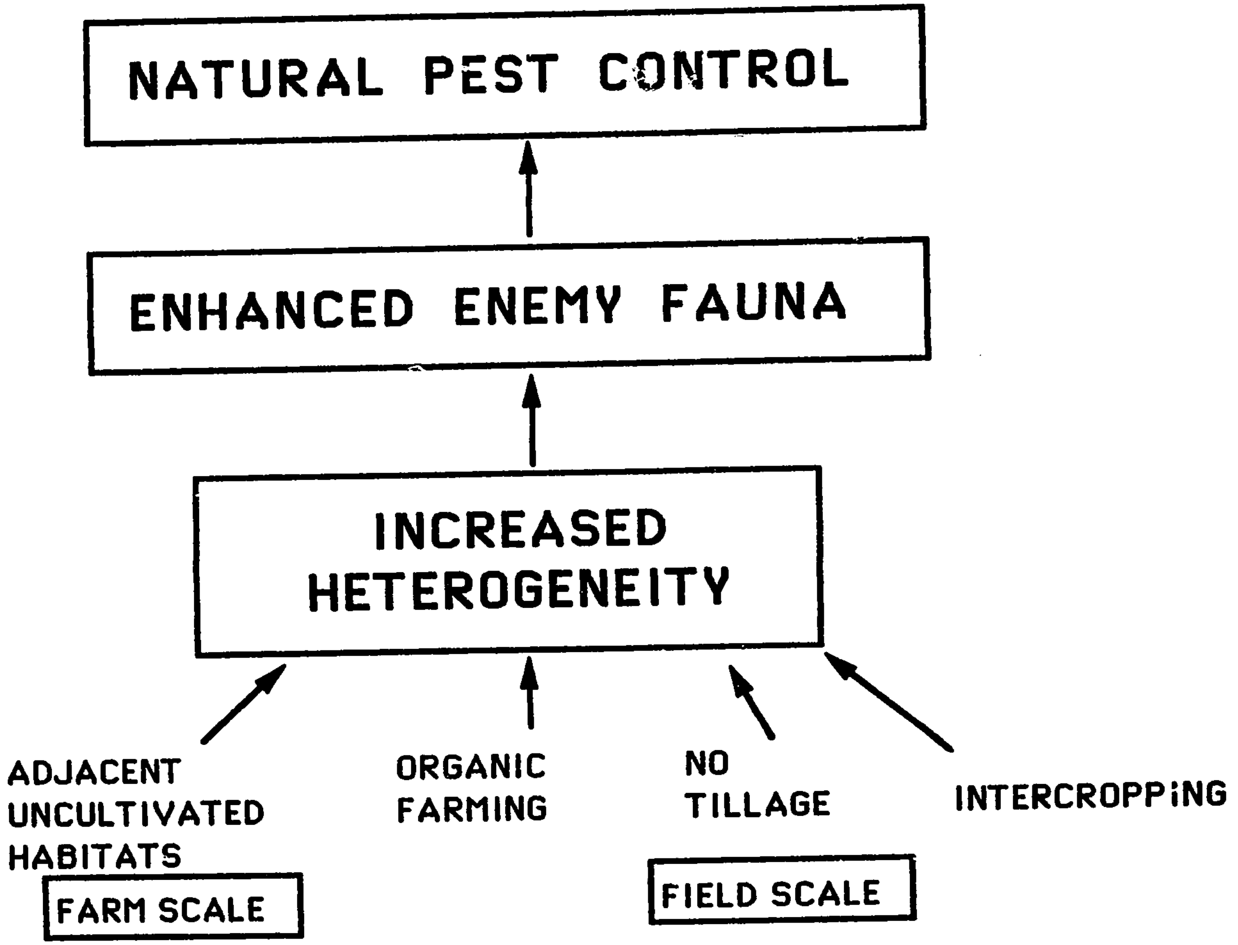


Fig. 1.1: Agricultural practices considered as potential strategies for natural pest control.

2. EFFECT OF AGRICULTURAL PRACTICE ON GROUND BEETLE ASSEMBLAGES.

2.1 INTRODUCTION

Agroecosystem modification to favour natural enemies increases natural environmental resistance against potential insect pests (Speight 1983). Strategies that increase habitat heterogeneity (see Fig.1.1) to conserve and enhance natural enemies can be divided in two categories: (1) at the field scale, heterogeneity can be added through higher plant diversity (polycultures), crop rotations, reduced tillage, use of mulches and manures common in organic farming systems, and (2) at the larger farm scale, heterogeneity can be added through the incorporation of uncultivated habitats such as idle fields, hedges, forest fragments and grassy borders near cultivated fields. Understanding how these agricultural practices affect natural enemies is fundamental for development of ecologically sound food production systems.

Carabids are mainly generalist predators that dominate the epigaeic predator fauna in temperate agroecosystems (Potts and Vickerman 1974). Although generalist predators are commonly ignored in biological control programs, there is increasing interest in their importance as natural control agents (Luff 1983). Also, it has been argued on theoretical grounds that models of biological control underestimate the potential value of generalist enemies (Murdoch 1985). The role of carabids as predators of specific insect pests has been shown repeatedly (e.g. Chiverton 1988, Hance 1987, Edwards et al. 1979, Tyler and Ellis 1979, Frank 1971a). Although they may not depress pest populations below economic tresholds on their own in some systems (Floate et al. 1990), they are an important component of a predator complex known to prevent pest outbreaks of cereal aphids in other systems (Winder 1990).

Although the literature on carabids in agroecosystems is increasing (see reviews in Thiele 1977, Allen 1979, Luff 1987), studies specifically about the effects of agricultural practice on carabid communities and populations are relatively scarce. Basedow (1991) and Kromp (1989) have found higher abundance and species diversity of carabid assemblages in organic and conventionally managed agroecosystems and Hance et al. (1990), have found significant effects of rotation and tillage on carabid activity. Stinner and House (1990) have concluded that conservation tillage enhances carabid activity.

In addition to their inherent applied value in pest control and as indicators of environmental quality (Stork 1990), studies of carabids in agroecosystems are ideal for addressing various aspects of both population and community ecology. For example the introduced species *Pterostichus melanarius* seems to affect the native fauna in urban habitats and could also potentially affect native carabid communities in cultivated habitats (Spence and Spence 1988). In agroecosystems, the possible effect of this exotic species on the native fauna may be modified by agricultural practices such as tillage regimes and study of these systems can address how disturbance can affect community structure.

In this chapter I report work toward the following objectives: (1) To compare the effects of organic farming and use of herbicides for weed control on activity and diversity of a carabid fauna; (2) To describe the effect of minimum tillage, without the confounding effect of other agronomic practices; (3) To explore the effects of crop diversity and rotation on the carabid fauna in the highly seasonal climate of central Alberta; And (4) to compare the carabid assemblages of an uncultivated field with those found in nearby agricultural plots under differing levels of cultivation.

2.2 MATERIALS AND METHODS

2.2.1 Study sites

2.2.1.1 Experimental site.

This study was conducted at the Ellerslie Research Farm of the University of Alberta located approximately 10 km southwest of Edmonton, in the parkland vegetation region. The soil type is Malmo silt loam, a Black Chernozem. I used experimental plots established in 1986 by the Department of Soil Science to study the effects of monocultures and dicultures on soil properties. Prior to this the land was under hay production from 1971 to 1984. No insecticides have been used in this site since at least 1971.

The 32 experimental plots (Fig. 1) are arranged in eight rows separated by approximately 10 m of grassy borders. The four plots (each 10 m x 25 m) are separated by 2 m of more or less bare ground but there are no physical barriers between the plots.

2.2.1.2 Uncultivated meadow.

This site is also located at the Ellerslie Research Farm, ca. 500 m from the experimental site. It consists of natural early succession vegetation, grasses, clover and various annual weedy species. It is not disturbed by agricultural practices except for being mowed occasionally in the summer. This site provided data about the carabid community in a uniform, but minimally disturbed agricultural habitat located close to the experimental plots. Comparison between the experimental plots and the uncultivated meadow allowed me to assess the general impact of cultivation on carabid abundance, diversity and dominance.

2.2.2 Trapping method and parameters studied.

Beetles were sampled using unbaited pitfall traps containing undiluted ethylene glycol as a preservative. Two traps were placed in each plot, except in the tillage study where four traps were used to compensate for the lower number of plots allocated to this aspect of the study. Beetles were collected every two weeks between April 18th and October 15th in 1991 and June 15 and October 13th in 1990, except during planting and harvesting when the traps were removed temporarily. Beetles were identified to species and sex in the laboratory using Lindroth's keys (1961-69).

The response variables studied in relation to the experimental treatments included both population and community aspects. Relative abundances of all carabid species, as indicated by their catches, was the only population parameter considered. Community structure was studied using species richness (S), the Shannon-Wiener diversity index (H'), evenness of species abundances (J'), as described by Krebs (1989). Possible interactions among dominant species were explored using Pearson correlation analysis.

2.2.3 Faunistic comparisons

The agroecosystems in Ellerslie were divided into four groups, as shown in Table 1: plots in groups A and B were subjected to various agronomic practices, while plots in C and D were not manipulated during the study. Below I use the term agroecosystems to refer to all the systems in Ellerslie, whether cultivated or not; cropping system is used in reference to the various crops under agronomic manipulations and farming method is reserved specifically for the organic or chemical crop rotations. Because this study used the plot structure of an existing study, treatments could not be allocated strictly at random to the experimental units. Specific comparisons are described below.

Abundance and diversity measures of the carabid assemblages were transformed to natural logarithms to stabilize their variances. Analysis of variance or inspection of means and standard errors based on these transformed data was used to decide whether significant differences existed. However, all figures are given using arithmetic means to facilitate comparisons.

type affect carabid assemblages : (1) Are there differences in carabid assemblages between organic and chemical treatments? (2) Does previous crop affect carabid abundance and diversity? (3) Does intercropping of peas and barley result in higher carabid abundance and diversity than the monocultures?

Eight plots were allocated to organic and eight to chemical farming methods (A, Table 1). A second factor, crop type, had the following four levels each with two replicate plots within farming method: (1) intercrop of barley and peas, (2) barley after intercrop (3) faba bean, and (4) barley after faba bean (Table 2.1).

2.2.3.2 Effect of tillage and nitrogen regimes.

The organic and chemical treatments cannot be used to assess the effect of tillage since possible effects are confounded by chemical inputs such as herbicides and fertilizer. Therefore, to assess tillage effects I used the eight plots allocated to the study of tillage and nitrogen source (Group B, Table 2.1).

2.2.3.3 Effect of general land use.

I compared the carabid fauna, in the uncultivated meadow and the fescue plots with that captured from highly managed plots to examine how general land use affects a carabid fauna. To do this I pooled catches from the four crops (among which no differences were found) in two groups representing organic and chemical methods, respectively. I also pooled the data from the nitrogen treatments in the continuous barley system according to the two tillage groups: no tillage and conventional tillage. I compared abundance in these cropping systems with that of the fescue plots and the meadow by using average trap captures per plot. This was necessary because in 1991 four traps were placed in the continuous barley plots and two in the others. I estimated species richness in these agroecosystems through rarefaction (Simberloff 1978) to compensate for low sample sizes in the fescue plots. Similarity among these agroecosystems was compared using percent similarity (Renkonen 1938, as given in Krebs 1989) and used it to carry out average cluster analysis (also in Krebs 1989).

2.2.4 Environmental parameters and carabids.

Data about weed abundances, crop biomass, grain yields, and soil moisture were collected in 1991 by staff of the Soil Science Department. These were tested for possible association with population and community parameters of the carabid assemblage through correlation analysis. I calculated estimates of weediness by averaging total weed counts per plot at the beginning and at the end of the growing season. Also I calculated mean soil moisture by averaging moisture samples for these two periods.

2.3 RESULTS.

2.3.1 Farming method and crop types.

In 1991 observed number of species was consistently higher in the organic plots (F=9.96, df=1,8, p=0.014, Table 2.2). A similar pattern was observed in 1990 but the differences were not significant (F=1.89, df=1,8, p=0.206), perhaps because the 1990 trapping period did not start until late June, thereby missing the activity peak of early spring species. Crop type had no effect on species richness in either year. Neither the Shannon-Wiener index of diversity (H') or evenness (J') differed among the treatments in either year (see Table 2.2 for 1991). This applied to both the overall assemblage and a subset comprised of only the native species. There were no differences between organic or chemical farming methods with respect to overall abundance of carabid individuals in either year (1991: F=2.07, df=1,8 p>0.05; 1990: F= 1.99 df=1,8 p>0.05).

from the analysis, there were striking differences in carabid abundance between organic and chemical farming methods (Fig. 2.2). Significantly more native beetles were caught in the organic plots than the chemical plots (1991: F=26.99, df=1,8, $p<0.001$; 1990: F=6.06, df=1,8, $p<0.05$). Crop type had no significant effect on carabid activity, nor was there significant interaction between crop type and farming method.

Abundance of dominant species (those comprising at least 1% of total capture) were compared between the two farming methods and among crop types. Except for *P. melanarius* (Fig. 2.3f), all dominant species were affected by the treatments in 1991 although the response varied across species (Fig. 2.3). In 1991, *A. cupreum* and *A. torrida* were significantly more abundant in the chemical rotation (Figs. 2.3 c & e, F=5.48 and 10.86 respectively, df=1,8 $p<0.05$). *P. adstrictus*, *P. lucublandus*, *B. quadrimaculatum* and *A. placidum*, were more abundant in plots without chemical inputs (Figs. 2.3a, b, d, g, range of F's=8.57-26.94 df=1,8 $p<0.05$). In 1990, only one species, *A. placidum* (Fig. 3h), was affected significantly by the treatments, with more individuals found in the organic plots and intercrop (Method: F=42.36 df=1,8 $p<0.01$, Crop: F=4.09 df=1,8 $p<0.05$). For the other species, the general pattern was similar to 1991, except for *A. torrida* where an opposite trend was observed.

2.3.2 Tillage and nitrogen regimes.

Tillage regime had no effect on species richness in either 1991 or 1990. In 1991, slightly more species were captured in the plots with nitrogen supplement. However the difference was not significant (Fig. 2.4a, F=3.94, df=1,4, $p>0.05$). Also, no differences in species diversity (H') or evenness (J') were observed among any of the treatments.

Although overall abundance of carabids (Fig. 2.3b) was not significantly affected by either tillage or nitrogen regime, a trend toward more carabids in the 'no tillage' plots was observed (F=3.81, df=1,4, $p>0.05$). Similar results were obtained when the dominant, highly mobile *P. melanarius* was excluded from the analysis.

Although overall effects were at best vague, some individual species were affected by tillage. For example, *B. quadrimaculatum* (Fig. 2.5a), was more abundant in the conventional tillage plots in 1990 (F=10.83, df=1,4, $p<0.05$). The pattern was similar, although of borderline significance in 1991 (F=6.16, df=1,4, $p=0.07$). Consistent trends but not statistically significant differences, were observed in both years for *A. placidum* (Fig. 2.5b) and *P. melanarius* (Fig. 2.5e), with the former more abundant in the 'conventional tillage' plots and the latter in the 'no tillage' plots. *A. torrida* (Fig. 2.5c), showed a marked trend toward higher abundance in the 'no tillage' plots in 1991 (F=4.81, df=1,4, $p=0.09$) but not in 1990 (F=0.59 df=1,4, $p>0.05$). However, this species appeared to respond positively to nitrogen supplements (1990: F=45.31, df=1,4, $p<0.01$; 1991: F=4.71, df=1,4, $p=0.09$). Of the other dominant species, *A. cupreum* was trapped significantly more frequently in the 'no tillage' plots in 1990 (Fig. 2.5d, F=32.55, df=1,4, $p<0.01$). In 1991, the same trend was observed, but probably because of high variation the results were not significant (F=2.63, df=1,4 $p>0.05$).

2.3.3 Environmental parameters and carabids.

The Pearson correlation coefficients of carabid species richness and abundance with a number of environmental variables are given in Table 3a & b. In the plots allocated to study farming method and crop rotations, carabid species richness was positively correlated with weed abundances. A similar pattern was observed for overall abundance, although the association was only marginally significant (Table 2.3a). However, for the eight plots allocated to the study of tillage and nitrogen regimes, weed abundance was negatively correlated with carabid species richness (Table 2.3b). Mean soil moisture was negatively correlated with carabid abundance, but the association with species richness was very weak. Neither of the two crop variables, biomass and grain yields were associated with carabid richness or abundance. Correlations between indices of carabid populations or community structure and other environmental variables were not significant.

2.3.4 Carabids and agricultural land use.

I assessed the impact of general agricultural activity on ground beetles by comparing the communities in the crops discussed above, with carabid assemblages from adjacent fescue plots and a nearby meadow. The twelve traps in the meadow were analyzed as six pairs, with spatial organization similar to that of the experimental plots.

I compared species richness among the six agroecosystems, (four cropping systems, fescue and meadow) by calculating an estimated number of species by rarefaction (Simberfoff 1978) using the smallest sample size, that collected in the fescue plots (305 beetles). As shown in Fig. 2.6a, estimated species richness was highest in the crops, intermediate in the fescue plots and lowest in the meadow. The same pattern in diversity was obtained by using observed species richness per plot, Shannon-Wiener diversity (H', Fig. 2.6b), or evenness per plot (J', Fig. 2.6c). This pattern was consistent in both years indicating that the meadow assemblage had the lowest species diversity.

I compared relative abundance of carabids in the Ellerslie agroecosystems, using average trap capture per plot instead of total captures per plot in order to standardize trapping effort. This was necessary because in 1991 four traps per plot were placed in the tillage and nitrogen study (8 plots) as opposed to two traps in the study of farming method and crop types (16 plots). There was a marked difference in carabid abundance between the meadow and the plots only in 1991 (Fig. 2.7, $F=17.1$ $df=1,33$ $p<0.001$). Abundance per trap in the meadow 'plots' was significantly different from all of the agroecosystems in the experimental plots (Scheffe's *a posteriori* test, $p<0.05$). The fescue plots differed significantly only from the organic and the meadow plots. No statistically significant differences were detected between the plots in continuous barley (tillage study) or those under crop rotations (farming method study). In 1990, when the trapping period was shorter, no significant differences were observed among any of the agroecosystems (Fig. 2.7) although, the same pattern of relative abundances was noticed. An interesting difference between the years is the reduced number of beetles caught from the fescue plots in 1991 compared to 1990, perhaps reflecting either a trapping effect in these plots, or a significant year to year variation in population dynamics.

Similarity of species assemblages from the six agroecosystems (Fig. 2.8) was assessed through cluster analysis using average percent similarity. In 1990, the carabid assemblages in the crops clustered according to the crop rotations. The carabid communities in the two rotation plots and those of the two tillage regimes each formed a pair of clusters, suggesting that species composition was affected by the crop rotation more than by the tillage treatment. In 1991, however, when spring species were better represented, the chemical rotation and the no tillage plots formed the first, most similar cluster. The organic rotation and conventional tillage, although, not forming a single cluster, had more similar assemblages than those of the plots with no tillage. This contradicts the findings in the previous year when tillage had no effect in structuring the community. The positions of the meadow and the fescue plots in the cluster was consistent both years with the meadow assemblage slightly more similar to the crops than was the fescue.

2.3.5 Phenology of carabids.

Seasonal activity of the more common ground beetles was described by plotting total individuals of each species against collection date (Julian day) in 1990 and 1991

(Fig. 2.9). Because trapping started late in 1990, the following results are based primarily on the trapping in 1991.

Activity of *P. melanarius* (Fig. 2.9a) overlapped little with the other common species of this genus, *P. lucublandus* and *P. adstrictus*, both early spring species. However, *P. melanarius* exhibited a partial overlap with other summer species, such as *Agonum placidum* (Fig. 2.9b) and *Amara torrida* (Fig. 9d). *A. cupreum* had a very early activity peak followed by a second lower peak early in the summer (Fig. 2.9b). This second activity peak coincides with the main activity period of its congener, *A. placidum*. The seasonal activity of common *Bembidion* species peaked early in the season (Fig. 2.9c). The larger *Bembidion bimaculatum*, not graphed in 1991 because of low numbers, showed a later activity peak in mid summer.

I tested for possible associations among species with similar phenologies in the plots and meadow using pairwise correlations of catches for all dominant species. However, no significant correlations were found for any of the species pairs and furthermore, negative correlations were very weak ($r^2<0.18$) for both the uncultivated meadow and experimental plots.

2.4 DISCUSSION

2.4.1 Agricultural practices.

In this section I discuss the effects of the various agricultural practices on carabid assemblages in the experimental plots and compare them to the published literature. I end the section with a short discussion of possible species traits and interactions that may explain the observed pattern of community structure in relation to the agricultural practices considered.

2.4.1.1 Farming method.

Whole-season catches of carabids using pitfall traps can be used to compare population densities among habitats (Baars 1979) when barriers to movement in the habitats are taken into consideration (Greenslade 1964). I collected more species and more individuals of native carabid species in the plots under organic farming method than in the chemical system. Barriers to movement seemed to be similar in both habitats with the increased weediness in the 'conventional tillage', organic plots, balanced by the higher litter residue in the 'no tillage', chemical system. Therefore, the higher number of species and native individuals from pitfall catches probably are related directly to differences in community diversity and population sizes. The lack of effect of farming method on the overall carabid abundance probably reflects the broad scale movement of the exotic species, *P. melanarius* (see Niemelä and Spence 1991). My results suggest that distances between plots were within the range of movement of *P. melanarius* (also see Baars 1979). Therefore, exclusion of this species from my analysis was necessary to detect the effect of farming method on the assemblage.

Because the two farming methods varied in chemical inputs and tillage regimes, it is not possible to determine which factor was responsible for the variation in carabid numbers. However, tillage did not appear to be very important, as shown in the next section. More likely, higher inputs of chemicals, herbicides and fertilizers, depressed carabid numbers through a toxic effect in the chemical system. Such an effect was suggested by Boiteau (1984) who showed that potato plots without herbicides harboured more carabids. In another study of predatory arthropods in commercial lawns, carabids, staphylinids and spiders were all more abundant in turf under low maintenance which received less herbicide, fertilizer and insecticide (Cockfield and Potter 1985). Laub and Luna (1992) found higher activity of *Pterostichus* and *Scarites* carabids and lycosid spiders, in plots where winter cover crop was cleared by mowing as opposed to application of the herbicide paraquat. These workers also attributed the lower populations of young armyworm larvae in this organic system to higher predation rates by generalist predators. Thus it is reasonable to attribute the higher species richness and abundance of most native species in my organic crop rotation at least in part to the lower input of herbicides.

Weed abundance is also known to affect distributions of natural enemies in agroecosystems (Altieri and Whitcomb 1979) and weed densities were significantly higher in my organic rotation. Both carabid species richness and abundance were positively correlated with weediness in the plots allocated to study farming method. This finding is in agreement with those of several other workers (Barney et al. 1984, Ryan et al. 1980, Dempster and Coaker 1974). In addition, Speight and Lawton (1976) reported greater carabid abundance and predation pressure on prey placed in wheat patches where weeds were more abundant.

One of the possible mechanisms for the effect of weeds on carabids is improved microclimatic conditions such as higher moisture (Rivard 1966). However, it is unlikely that this factor alone explained the distribution of carabids in this study since moisture levels were slightly higher in the chemical system where zero tillage resulted in greater surface residue and less water loss (Juma et al. 1992). Also, carabid abundances were negatively correlated with soil moistures, suggesting that microclimatic variables can interact with agronomic strategies such as chemical inputs.

Another likely explanation for the positive association of carabids and weeds in this study, are the direct and indirect effects of weeds on carabid nutrition. Carabids of the genera *Amara*, *Harpalus* and *Scarites* are predominantly plant feeders and some have been shown to eat weed seeds (Lund and Turpin 1977, Brust and House 1988). This hypothesis, however, was not supported in this study as the only abundant species of these genera, *Amara torrida*, was more abundant in the chemical system where weed densities were lower. In this case it is more likely that weeds harboured a greater abundance and diversity of prey (e.g. Purvis and Curry 1984) which might have attracted and supported larger populations of predatory carabids. Hokkanen and Holopainen (1986), for example, attributed greater carabid abundance in organic cabbage fields to higher number and diversity of potential prey.

2.4.1.2 Crop types, diversity and rotation.

Crop rotations, crop type and diversity did not affect carabid assemblages in this study, even though the four crop types provided fairly different vegetation structure. These results differ from most of the other studies which have reported effects of crop rotations (Thiele 1977, Brust et al. 1986, Gregoire-Wibo 1983, Lövei 1984, Weiss et al. 1990), crop types (Rivard 1966, Varis et al. 1984) and crop diversity (Brust et al. 1986b, Perfecto et al. 1986, Barney et al. 1984, Uvah and Coaker 1984, Tukahirwa and Coaker 1982) on carabid activity.

The design of my study was not particularly powerful with respect to detecting effects of crop types and rotations because the effect of farming method was highly significant. Thus crop types must be compared within farming method and the number of replicates for these comparisons was very low. Because variation in carabid captures per plot was quite high, only very strong effects would be detected. A more effective strategy to assess effects of crop type on natural enemies is to complement plot studies like mine with data from a larger scale, such as commercial fields used by Rivard (1966), Varis et al. (1986) and Cárcamo (Chapter 3) for tillage practices. Behavioural experiments to assess the relative attraction of crop types to natural enemies can also yield important information (Letourneau 1990, Chapter 4). This approach to the study of ecological processes in agroecosystems is particularly important given the spatial limitations of adjacent experimental plots as demonstrated by Bergelson and Kareiva (1987). These authors showed that establishing barriers among paired plots under monoculture and polyculture reduced the differences in arthropod abundances found without barriers.

2.4.1.3 Tillage regimes.

Tillage regime did not affect the species diversity nor overall abundance of carabids. However, *B. quadrimaculatum* and *A. cupreum*, two abundant spring species were affected. These mixed results are to some extent consistent with the published literature on the effect of tillage on carabid beetles. Higher overall abundance or activity of carabids in conservation tillage systems has been reported in some studies (Brust et al. 1986a, Ferguson and McPherson 1985, Hance et al. 1990, House and Stinner 1983, House and All 1981) but negative effects of conservation tillage (Barney and Pass 1986, Edwards 1976, Chapter 3), no effects (Mack and Buckman 1990) or variable effects (Weiss et al. 1990, House 1989, Tyler and Ellis 1979) are also common.

Tillage can depress carabid populations through direct destruction (Hance et al. 1990, Lys and Nentwig 1991). In my study, tillage took place in the spring and also in the fall, so that both spring and autumn breeders were probably affected. However, for most species no statistically significant differences were observed in either tillage regime, although a trend similar to that reported by Hance et al. (1990) was observed for *P. melanarius*. The only two species significantly affected were both spring breeders and they showed opposite responses to tillage.

2.4.1.4 Nitrogen regimes.

Synthetic nitrogen fertilizer can have both positive and negative effects on carabid beetles. High concentrations of inorganic fertilizer may be toxic to carabids and can result in lower abundances relative to unfertilized treatments (Honczarenko 1975). On the other hand, fertilizers can have an indirectly beneficial effect on both phytophagous and predatory ground beetles. Changes in plant quality caused by fertilization attracted more phytophagous carabids as well as predators that responded to increased herbivore concentrations (Lavigne 1978).

In my study, overall abundance of carabids was similar in both nitrogen treatments. However, *Amara torrida*, presumably a phytophage, was more abundant in barley supplemented with synthetic nitrogen. It is possible that this species responded to improved plant quality, as plant biomass yields in this treatment were higher than in barley without nitrogen fertilizer. One should remember, however, that in intensive conventional agriculture chemical fertilizers are commonly used in conjunction with pesticides. Cockfield and Potter (1985) reported less carabids in turf managed with high inputs of fertilizer and pesticides. As pointed out by Luff (1987), beneficial effects of fertilizers on carabids may be outweighed by adverse effects of pesticides.

2.4.1.5 General implications.

Ultimately, the pattern of carabid community structure in agroecosystems will be determined by species traits and their interaction with the biotic and abiotic environment. Predator-prey relationships are likely important biotic factors affecting distribution of carabids in agroecosystems. Hokkanen and Holopainen (1986) suggested that the lower abundance of *P. melanarius* in conventional (with chemical inputs) cabbage fields permitted the build up of the smaller *Trechus quadristriatus*, through reduction of intraguild predation by *P. melanarius*. A similar process may explain the distribution of *Bembidion quadrimaculatum* in my study. This species was more abundant in 'conventional tillage' plots where *P. melanarius* was slightly less abundant. However in another study where *P. melanarius* was absent (Chapter 3), this species was more abundant in a 'reduced tillage' farm. It may be that in the absence of predation pressure, higher prey availability in reduced tillage can determine its distribution. An alternative explanation is that species vary in their habitat preferences according to microclimatic requirements. For example, *B. quadrimaculatum* is commonly found in warmer, bare soil (Lindroth 1963) characteristic of conventional tillage systems.

Unravelling the various ecological processes that lead to the observed patterns will require an experimental approach where biological interactions are tested and resources as well as microclimatic variables manipulated and measured in more detail. It seems that specific biological traits of particular species need to be considered to explain the effects of agronomic practices.

2.4.2 Land use.

Uncultivated habitats may be important overwintering habitats and sources of natural enemies dispersing into cultivated fields (Coombes and Sotherton 1986, Wallin 1986, House and All 1981). My results agree with these reports in that the uncultivated meadow, relatively undisturbed, had the highest overall carabid abundance. It is conceivable that carabids from such habitats aid in depressing potential pests in adjacent fields. It is interesting that in the control plots under the original fescue vegetation, that received herbicides, carabid activity was lowest. This may reflect toxic effects or interactions with plant diversity. Additional experiments using mark-recapture techniques and relative seasonal activity profiles would be necessary to determine the relative contribution of uncultivated habitats to the carabid fauna in adjacent agricultural fields.

Cluster analysis of the carabid assemblages in all six agroecosystems studied in Ellerslie, revealed that species composition was affected by agricultural practice. Although crop rotations and tillage did not affect overall abundance or diversity, it was clear that species composition was affected. The different dendrograms obtained for the two years of the study may be explained by the shorter trapping period in 1990. That year crop rotation appeared to structure species composition. This probably resulted from the poor representation of the early species, *B. quadrimaculatum,* and *A. cupreum* which were affected by tillage. This dendrogram also suggested that the effects of tillage on species composition was diluted later in the season as the communities became more similar and crop rotation was the main factor distinguishing among them. In 1991, however, two early species that were affected by tillage, *B. quadrimaculatum* and *A. cupreum* were better represented and the assemblages clustered according to tillage practice. The lower similarity between the meadow, fescue and the plots in 1991, may also be attributed to better representation of the early dominant species *A. cupreum* because of earlier trapping than in 1990.

2.4.3 The carabids of Ellerslie.

Considering the large sample size (26,212 individuals) collected over two years, species richness was rather low with only about 49 species recognized (see Appendix 2). Eight species out of these 49, represented 90% of the total carabid capture in 1991, with *P. melanarius* alone accounting for 41%. Other reports of carabids in cultivated habitats in north western North America have reported a much more diverse fauna than found at Ellerslie. Frank (1971) reported 63 species from a barley farm near Calahoo, approximately 50 km NW of Ellerslie. Doane (1981), collected 87 species from a wheat field and its grassy borders in central Saskatchewan and Kirk (1971), in a comprehensive four year study of corn field and other crops in South Dakota, reported 127 species. The higher species richness of these last two studies is expected from sampling a diversity of habitats for a longer period. But the differences in species number between Ellerslie and Calahoo are somewhat puzzling.

With the exception of *P. melanarius,* all dominant species in Ellerslie were common in Calahoo. Seasonal activity patterns for these species were similar in the two sites except for the following species. For *B. quadrimaculatum* only one peak of activity was observed in late April at Ellerslie; there was no suggestion of two peaks as noted by Frank (1971) in Calahoo. On the other hand *P. lucublandus* as found by Doane (1981) and Kirk (1971), clearly had two activity peaks, one in mid June and a second one in late August. My data confirmed a suggestion by Frank (1971) about the phenology of *A. cupreum*. The peak of activity for this and *B. quadrimaculatum* occurs early in April. A second peak was quite evident in mid July, for *A. cupreum* coinciding with peak activity of *A. placidum*. Interestingly *A. cupreum*, unlike the other carabids was present in the field throughout the year at relatively high numbers, which suggests that it may have two generations a year.

The differences in species diversity between Calahoo and Ellerslie may be simply the result of differences in soil type, moisture, vegetation zones and independent changes of their carabid communities (den Boer 1981). However, the dominance of the exotic species *P. melanarius* at Ellerslie and its absence in the sites studied by Frank (1971) and Doane (1981) suggests a large potential for interspecific interactions. This idea is supported by Spence and Spence (1988) who reported a negative pairwise correlation between introduced species and native carabids, particularly between *P. melanarius* and *P. adstrictus* in urban habitats. *P. adstrictus* was very rare in the uncultivated meadow at Ellerlie where *P. melanarius* made 70% of the catch. However, at sites where *P. melanarius* was less abundant or absent *P. adstrictus* was one of the dominant species.

Although Spence and Spence (1988) concentrated on vacant urban plots, they also suggested that introduced species were established in cultivated habitats. In this study I showed that *P. melanarius* can achieve almost complete dominance of an agricultural carabid fauna, but only in relatively undisturbed fields. In experimental plots that were subjected to continuous interference from pesticides and tillage, abundance of *P. melanarius* was lower than in a less disturbed meadow. The relative stability of the nearby meadow probably allowed for high recruitment of *P. melanarius*, possibly at the expense of native carabids, such as *P. adstrictus*, *P. lucublandus* and *A. placidum*. The abundance of *A. cupreum* appeared to be enhanced in the meadow.

I hypothesize that species interactions, such as competition (Niemelä 1992) or intraguild predation (Polis 1989) are responsible for the observed pattern in community structure observed in the meadow. These effects will be more pronounced in less heterogeneic habitats. Niemelä and Spence (1991) have clearly shown that in highly heterogeneic forested habitats, *P. melanarius* does not conspicuously affect the native fauna. In the experimental plots of Ellerslie, habitat heterogeneity was much higher as the result of the various crops, and management practices. This may explain the much higher species diversity in this site compared to the more uniform uncultivated meadow.

Experimental manipulations are required to test the process-oriented explanations suggested here. Also sites with similar physical conditions, with and without *P. melanarius* and with varying levels of heterogeneity should be surveyed. These strategies should elucidate the effect of this species on native carabids in agroecosystems.

2.5 REFERENCES

Allen, R. T. 1979. The occurrence and importance of ground beetles in agricultural and surrounding habitats. *In* T.L. Erwin, G.E. Ball and D.R. Whitehead, eds. Carabid beetles: their evolution, natural history and classification. The Hague, Junk. 485-507.

Altieri, M.A. & W.H. Whitcomb 1979. The potential use of weeds in the manipulation of beneficial insects. HortScience 14: 12-18.

Baars, M.A. 1979. Catches in pitfall traps in relation to mean densities of carabid beetles. Oecologia 41: 25-46.

Barney, R.J. & B.C. Pass. 1986. Ground beetle (Coleoptera:Carabidae) populations in Kentucky alfalfa and influence of tillage. J. Econ. Entomol. 79: 511-517.

Barney, R.J., W.O. Lamp, E.J. Ambrust and G. Kapusta 1984. Insect predator community and its response to weed management in spring-planted alfalfa. Prot. Ecol. 6: 23-33.

Basedow, T. 1987. Influence of increased cultivation intensity in cereal cultivation on the ground beetle (Coleoptera, Carabidae). Kommissionsverlag. P. Parey.

Bergelson, J. & P. Kareiva. 1987. Barriers to movement and the response of herbivores to alternative cropping patterns. Oecologia 71: 457-460.

Boiteau, G. 1984. Effect of planting date, plant spacing, and weed cover on populations of insects, arachnids and entomophthoran fungi in potato fields. Environ. Entomol. 13: 751-756.

Brust, G.E. & G.J. House. 1988. Weed seed consumption in low-input soybean agroecosystems by arthropods and rodents. Am. J. Alternat. Agric. 3: 19-25.

Brust, G. E., B.R. Stinner, and D.A. MacArtney 1986a. Predator activity and predation in corn agroecosystems. Environ. Entomol. 15: 1017-1021.

______________________________ 1986b. Predation by soil inhabiting arthropods in intercropped and monoculture agroecosystems. Agric. Ecosyst. & Environ. 18: 145-154.

Chiverton, P.A. 1988. Searching behaviour and cereal aphid consumption by *Bembidion lampros* and *Pterostichus cupreus*, in relation to temperature and prey density. Entomol. Exp. Appl. 47: 173-182.

Cockfield, S.D. & D.A. Potter. 1985. Predatory arthropods in high and low maintenance turf-grass. Can. Ent. 117: 423-429.

Coombes, D.S. & N. Sotherton. 1986. The dispersal and distribution of polyphagous predatory Coleoptera in cereals. Ann. Appl. Biol. 108: 461-474.

Dempster, J.P. & T.H. Coaker. 1974. Diversification of crop ecosystems as a means of controlling pests. In Biology in pests and disease control, D.P. Jones and M.E. Solomon (eds.). Willey, New York.

den Boer, P.J. 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia 50: 39-53.

Doane, J.F. 1981. Seasonal captures and diversity of ground beetles (Coleoptera: Carabidae) in a wheat field and its grassy borders in central Saskatchewan. Quaest. Ent. 17: 211-233

Dritschilo, W., & D. Wanner. 1980. Ground beetle abundance in organic and conventional corn fields. Environ. Entomol. 9: 629-631.

Edwards, C.A. 1976. Effects of direct drilling on the soil fauna. Oulook Agric. 8: 243-244.

________, K.D. Sunderland, and K.S. George. 1979. Studies on polyphagous predators of cereal aphids. J. Appl. Ecol. 16: 811-823.

Floate, K.D., J. Doane, and C. Gillott. 1990. Carabid predators of the wheat midge (Diptera: Cecidomyiidae) in Saskatchewan. Environ. Entomol. 19: 1503-1511.

Ferguson, H.F., & R.M. McPherson. 1985. Abundance and diversity of adult carabidae in four soybean cropping systems in Virginia. J. Entomol. Sci. 20: 163-171.

Frank, J.H. 1971. Carabidae (Coleoptera) of an arable field in central Alberta. Quaest. Ent. 7: 237-252.

Frank, J.H. 1971a. Carabidae (Coleoptera) as predators of the redbacked cutworm (Lepidoptera: Noctuidae) in central Alberta. Can. Ent. 103: 1039-1044.

Gebhardt, M.R., T.C. Daniel, E.E. Schweizer, and R.R. Allmaras. 1985. Conservation Tillage. Science 230: 625-630.

Good, J.A. & R.S. Geller. 1991. The effect of cereal and grass management on staphylinidae (Coleoptera) assemblages in South Western Ireland. J. Appl. Ecol. 28: 810-826.

Greenslade, P.G.M. 1964. Pitfall trapping as a method for studying populations of carabidae (Coleoptera). J. Anim. Ecol. 33: 301-310.

Grégoire-Wibo, C. 1983. Incidences ecologiques de traitements phytosanitaires en culture de betterabe sucriere. II. Acariens, Polydesmes, Staphylins, Cryptophagides et Carabides. Pedobiologia 25: 93-108.

Hance, T., C. Grégoire-Wibo, P. Lebrun. 1990. Agriculture and ground beetle populations: The consequence of crop types and surrounding habitats on activity and species composition. Pedobiologia 34: 337-346.

Hance, T. 1987. Predation impact of Carabidae at different population densities on *Aphis fabae* development in sugar beet. Pedobiologia 30: 251-262.

Honczarenko, J. 1975. An influence of high-dose nitrogen fertilizer on the entomofauna of meadow soil. Pedobiologia 16: 58-62.

House, G.J. 1989. Soil arthropods from weed and crop roots of an agroecosystem in a wheat-soybean-corn rotation: impact of tillage and herbicides. Agric. Ecosyst. & Environ. 25: 233-244.

________, & B.R. Stinner. 1983. Arthropods in no-tillage soybean agroecosystems: community composition and ecosystem interactions. Environ. Manage. 7: 23-28.

________, & J.N. All. 1981. Carabid beetles in soybean agroecosystems. Environ. Entomol. 10: 194-196.

Hsin, C.Y., L.G. Sellers, et al. 1979. Seasonal activity of carabids and the toxicity of carbofuran and terbufos to *Pterostichus chalcites*. Environ. Entomol. 8: 154-159.

Juma, N.G., R.C. Izaurralde, M.L. Choudhary, S. Pawluk, M.J. Dudas, W.B. McGill, D.S. Chanasyk and R.F. Grant. 1992. Soil conservation strategies using conventional and alternative management systems. 29th Annual Alberta Soil Science Workshop, Lethbridge, Alberta Agriculture.

Kirchner, H. 1960. Untersuchungen zür okologïe feldbewohnender Carabiden. Dissertation, Cologne. *Cited by* H.U. Thiele. 1977. Carabid beetles in their environments. Springer-Verlag, Berlin, New York.

Kirk, V.M. 1971. Ground beetles in cropland in South Dakota. Ann. Ent. Soc. Am. 64: 238-241.

Krebs, C. J. 1989. Ecological Methodology. New York, Harper and Row.

Kromp, B. 1989. Carabid beetle communities (Carabidae, Coleoptera) in biologically and conventionally farmed agroecosystems. Agric. Ecosyst. & Environ. 27: 241-251.

Laub, C.A. & J.M. Luna. 1992. Winter cover crop suppression practices and natural enemies of armyworm (Lepidoptera: Noctuidae) in no-till corn. Environ. Entomol. 21: 41-49.

Lavigne, R. (1978). The effect of resource enrichment on the abundance of individual carabid species (Coleoptera). Cordulia 4: 101-105.

Letourneau, D.K. 1990. Mechanisms of predator accumulation in a mixed crop system. Ecol. Ent. 15: 63-69.

Lindroth, C.H. 1961-69. The ground beetles (Carabidae, exc. Cicindelinae) of Canada and Alaska. Parts 1-6. Opuscula Entomologica. xlvii + 1192 pp.

Lövei, G.L. (1984). Ground beetles (Coleoptera: Carabidae) in two types of maize fields in Hungary. Pedobiologia 26: 57-64.

Luff, M.L. 1983. The potential of predators for biological control. Agric. Ecosyst. & Environ. 10: 159-181.

Luff, M.L. 1987. The biology of polyphagous ground beetles in agriculture. Agric. Zool. Rev. 2: 237-278.

Lund, R.D. & F.T. Turpin. 1977. Carabid damage to weed seeds found in Indiana cornfields. Environ. Entomol. 6: 695-698.

Lys, J.A. & W. Nentwig. 1991. Surface activity of carabid beetles inhabiting cereal fields: Seasonal phenology and the influence of farming operations on five abundant species. Pedobiologia. 35: 129-138.

Mack, T.P. & C.B. Buckman. 1990. Effects of two planting dates and three tillage systems on the abundance of lesser cornstalk borer (Lepidoptera: Pyralidae), other selected insects, and yield in peanut fields. J. Econ. Entomol. 83: 1034-1041

Murdoch, W.W., et al. 1985. Biological control in theory and practice. Am. Nat. 125: 344-366.

Niemelä, J. 1992. Interspecific competition in ground beetle assemblages (Carabidae): What have we learned? Oikos. In press

________ & J.R. Spence 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. Oikos 62: 351-359.

Perfecto, I., B. Horwith, J. Vandermeer, B. Schultz, H. McGuinness, and A. Dos Santos 1986. Effects of plant diversity and density on the emigration rate of two ground beetles, *Harpalus pensylvanicus* and *Evarthrus sodalis* (Coleoptera: Carabidae), in a system of tomatoes and beans. Environ. Entomol. 15: 1028-31.

Polis, G.A., C.A. Myers, and R.D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev Ecol. Syst. 20: 297-330.

Potts, G., & G.P. Vickerman. 1974. Studies on the cereal ecosystems. Adv. Ecol. Res. 8: 107-197.

Purvis G. & J.P. Curry. 1984. The influence of weeds and farmyard manure on the activity of carabidae and other ground dwelling arthropods in a sugar beet crop. J.Appl. Ecol. 21: 271-283.

Rivard, I. 1966. Ground beetles (Coleoptera: Carabidae) in relation to agricultural crops. Can. Ent. 98: 189-195.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea)*. Ecol. Monogr. 43: 95-124.

Ryan, J., F. Ryan, and F. McNaeidhe. 1980. The effects of interrow plant cover on populations of the cabbage rootfly, *Delia brassicae* (Wiedemann) J. Appl. Ecol. 17: 31-40.

Sotherton, N. 1985. The distribution and abundance of predatory Coleoptera overwintering in field boundaries. Ann. Appl. Biol. 106: 17-21.

Speight, M. R. 1983. The potential of ecosystem management for pest control. Agric. Ecosyst. & Environ. 10:183-199

Speight, M.R. & J.H. Lawton. 1976. The influence of weed-cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia 23: 211-223.

Spence, J.R. & D.H. Spence. 1988. Of ground beetles and men: introduced species and the synanthropic fauna of western Canada. Mem. Ent. Soc. Can. 144: 151-168.

Stinner, B.R. & G.J. House.1990. Arthropods and other invertebrates in conservation-tillage agriculture. Ann. Rev. Entomol. 35: 299-318.

Stork, N. E. 1990. The Role of ground beetles in ecological and environmental studies. Intercept, Andover, Hampshire.

Thiele, H.U. 1977. Carabid beetles in their environments. Springer-Verlag, Berlin, New York.

Torres, J.A. 1982. Biological control and possible use of ants in biological control of insects. Science-Ciencia 9: 31-44.

Tukahirwa, E.M., & T.H. Coaker 1982. Effect of mixed cropping on some insect pests of brassicas: reduced *Brevicoryne brassicae* infestations and influences on epigeal predators and the disturbance of oviposition behaviour in *Delia brassicae*. Entomol. Exp. Appl. 32: 129-140.

Tyler, B.M.J. & C.R. Ellis 1979. Ground beetles in three tillage plots in Ontario and observations on their importance as predators of the northern corn rootworm, *Diabrotica longicornis* (Coleoptera: Chrysomelidae). Entomol. Soc. Ont. Proc. 110: 65-73.

Uvah, I.I. & T.H. Coaker 1984. Effect of mixed cropping on some insect pests of carrots and onions. Entomol. Exp. Appl. 36: 159-167.

Varis, A.L., J.K.Holopainen, and M. Koponen. 1984. Abundance and seasonal occurrence of adult Carabidae (Coleoptera) in cabbage, sugar beet and timothy fields in southern Finland. Z. Angew. Entomol. 98: 62-73.

Wallin, H. 1986. Habitat choice of some field-inhabiting carabid beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. Ecol. Entomol. 11: 457-466.

Wallin, H. 1985. Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. Pedobiologia 28: 19-34.

Weiss, M.J., E.U. Balsbaugh, Jr., E.W. French, and B.K. Hoag. 1990. Influence of tillage management and cropping system on ground beetle (Coleoptera: Carabidae) fauna in the northern great plains. Environ. Entomol. 19: 1388-1391.

Winder, L. 1990. Predation of the cereal aphid *Sitobion avenae* by polyphagous predators on the ground. Ecol. Entomol. 15: 105-110.

Fig. 1: LAY OUT OF PLOTS IN ELLERSLLIE

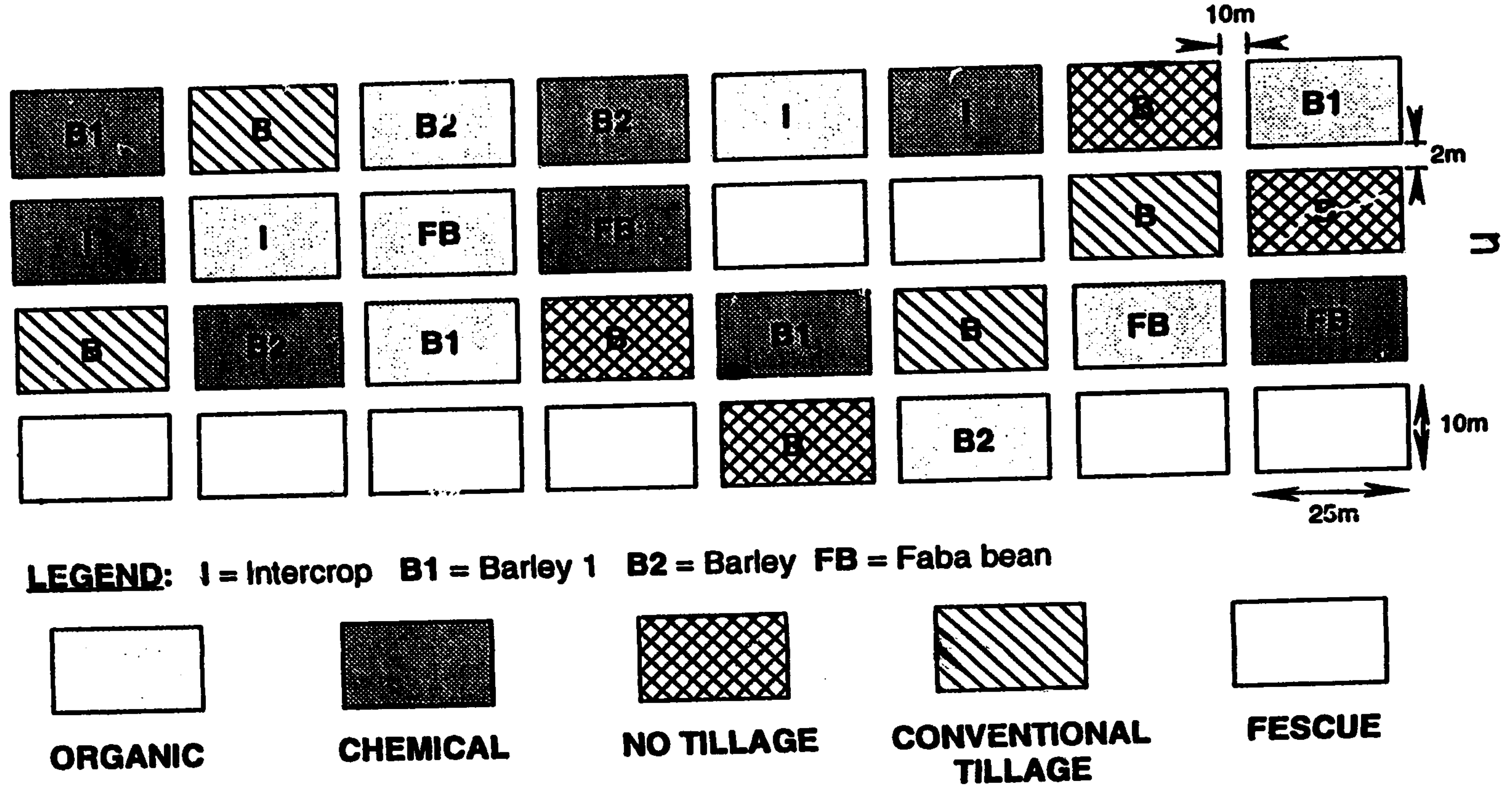
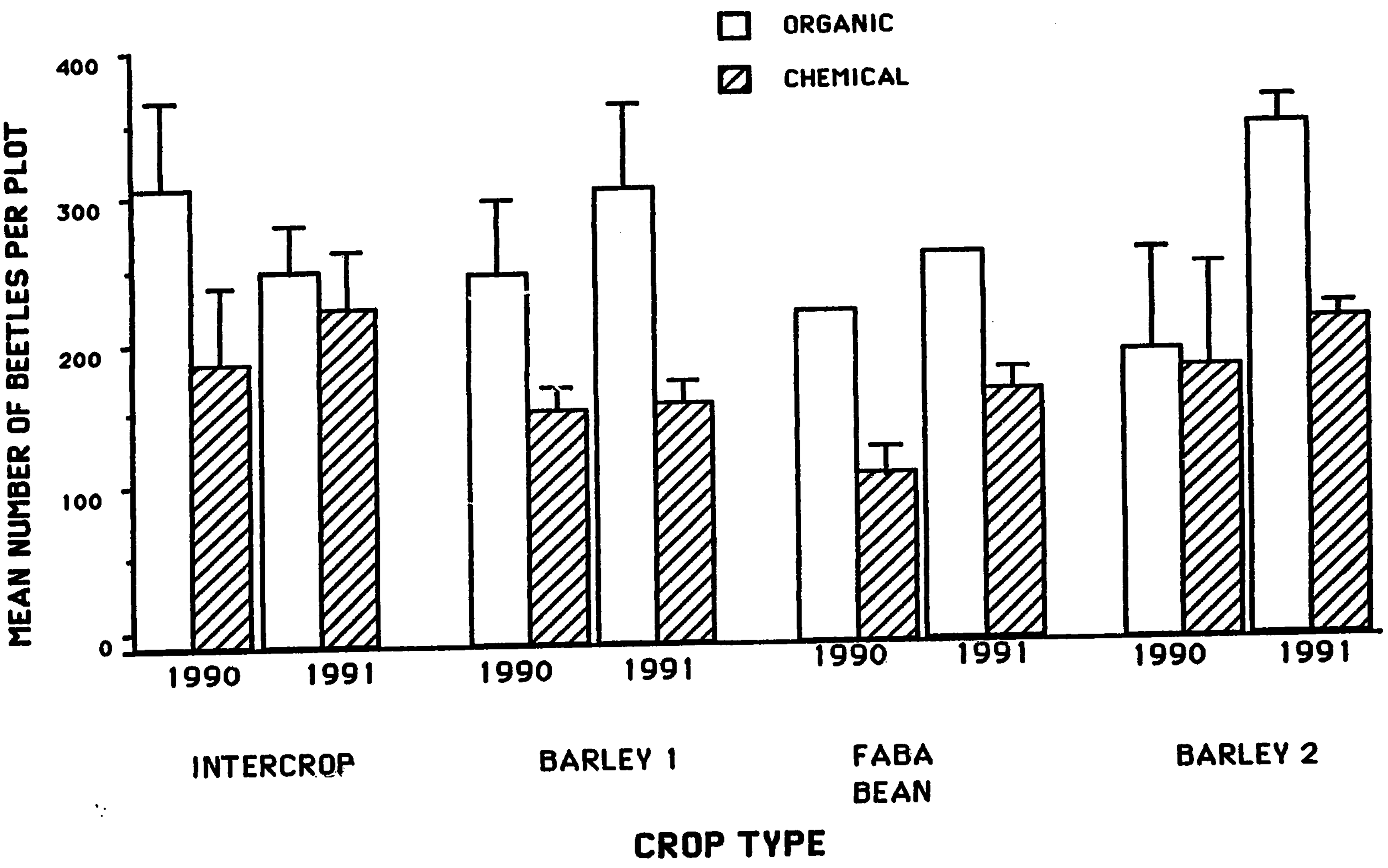


Fig. 2.2: Effect of method and crop type on abundance of native carabids



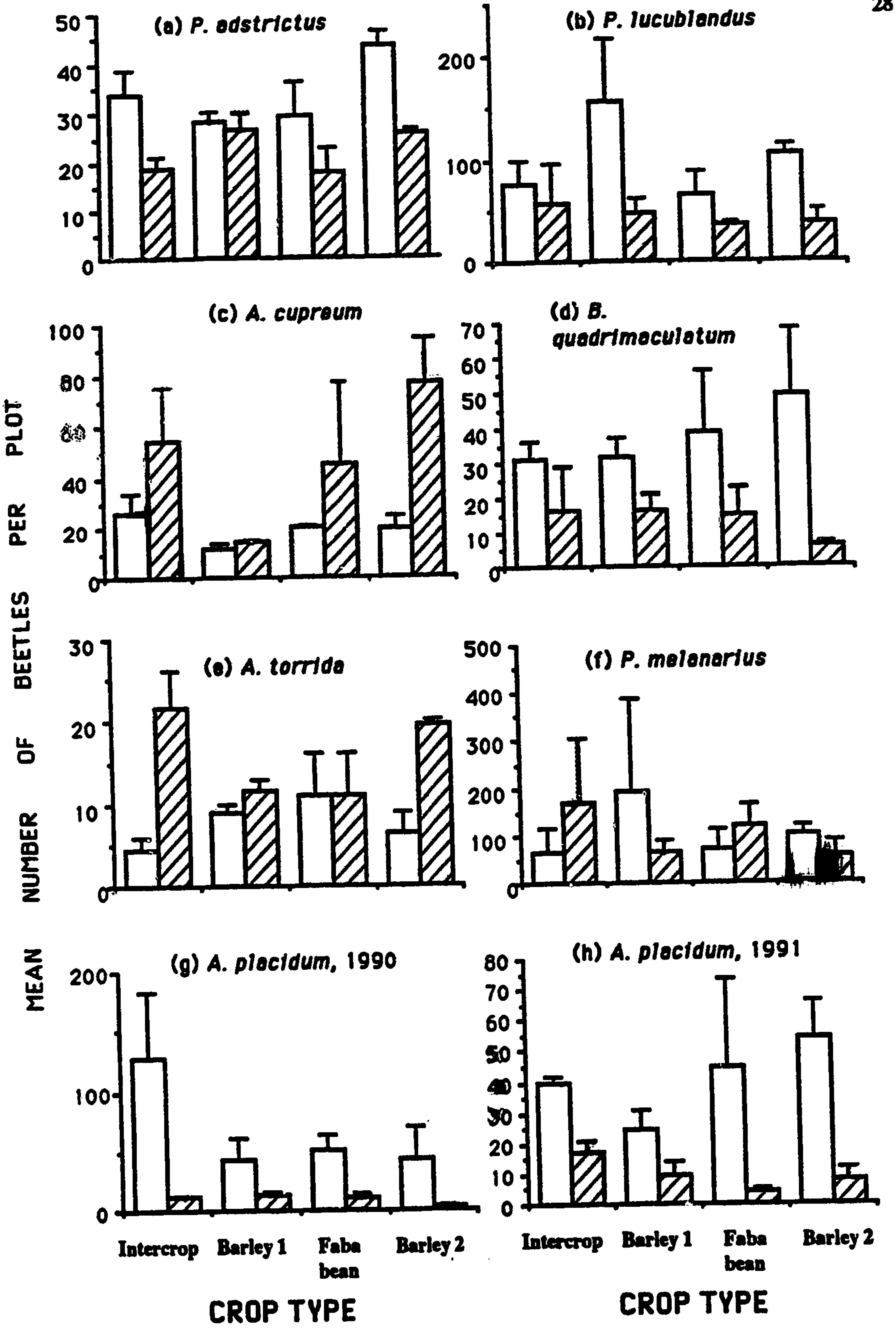


FIG. 2.3: Effect of farming method and crop type on abundance of dominant species. Entries are means±one standard error. Note different scales of y-axis.

□= organic ▨=chemical

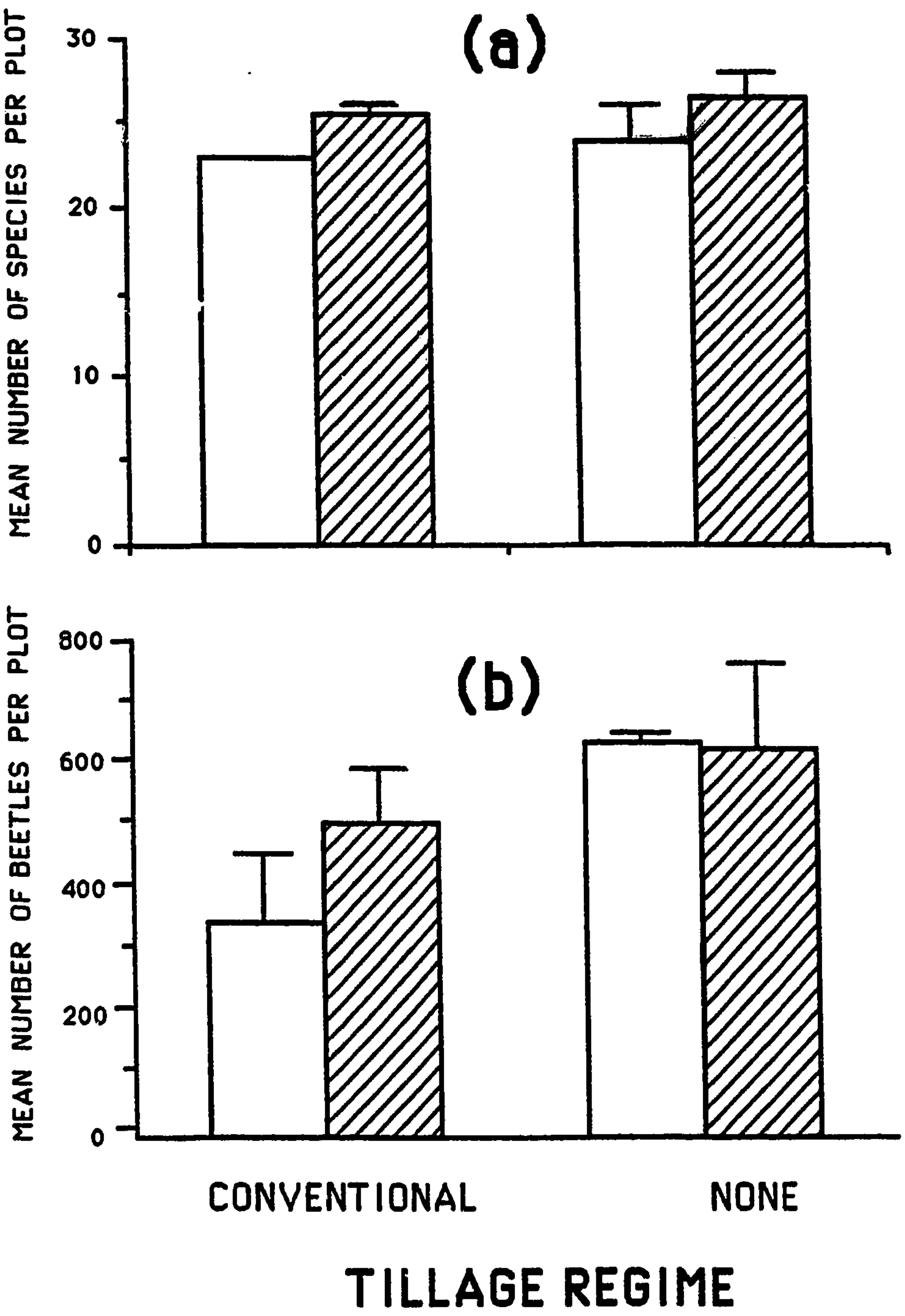


Fig. 2.4. Effect of tillage and nitrogen on (a) species richness and (b) abundance. Entries are means ± one standard error.

☐ = NO FERTILIZER ▨ = NITROGEN ADDED

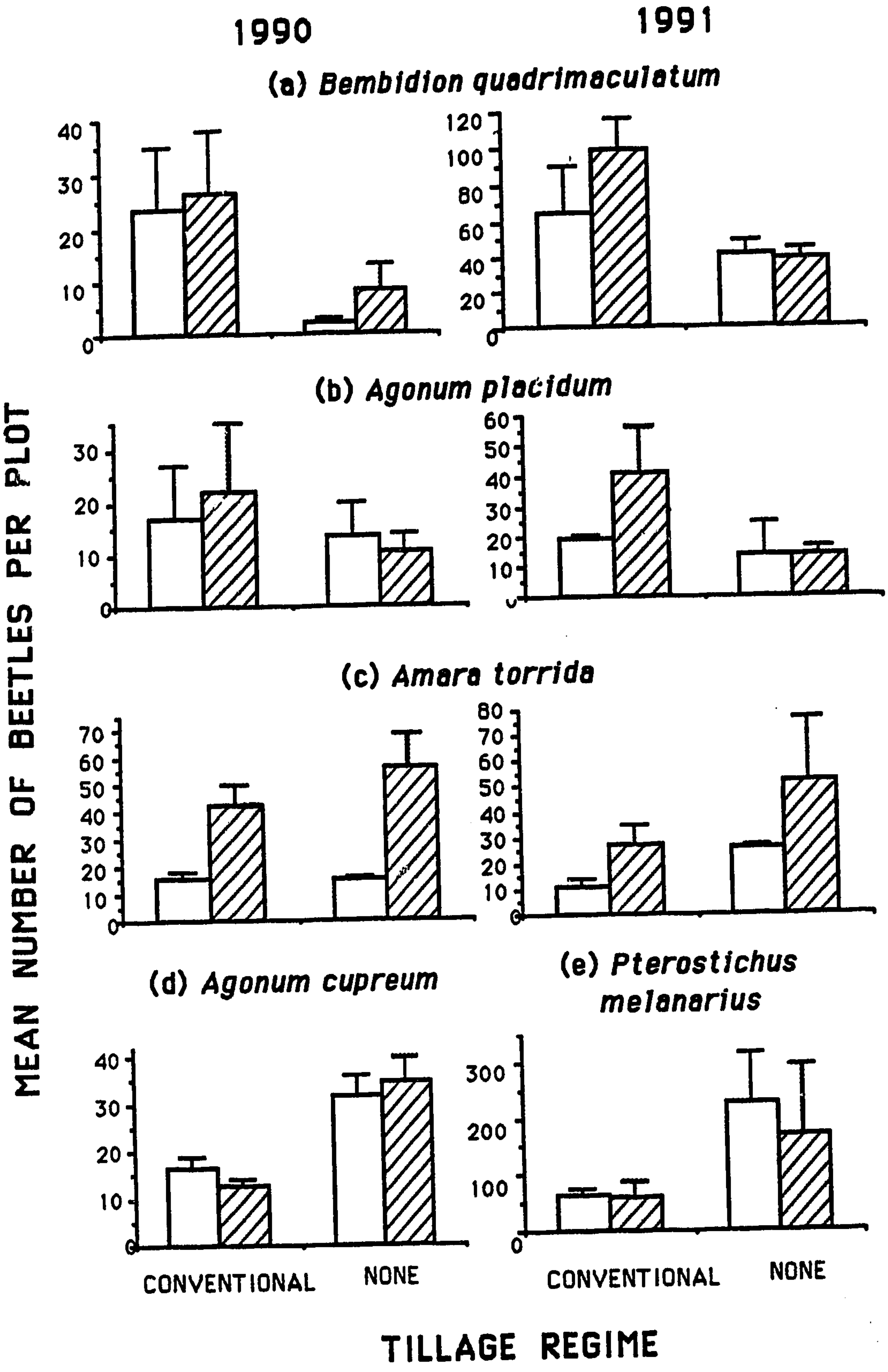


Fig. 2.5a–e. Effect of tillage and nitrogen on dominant species. Entries are means ± one standard

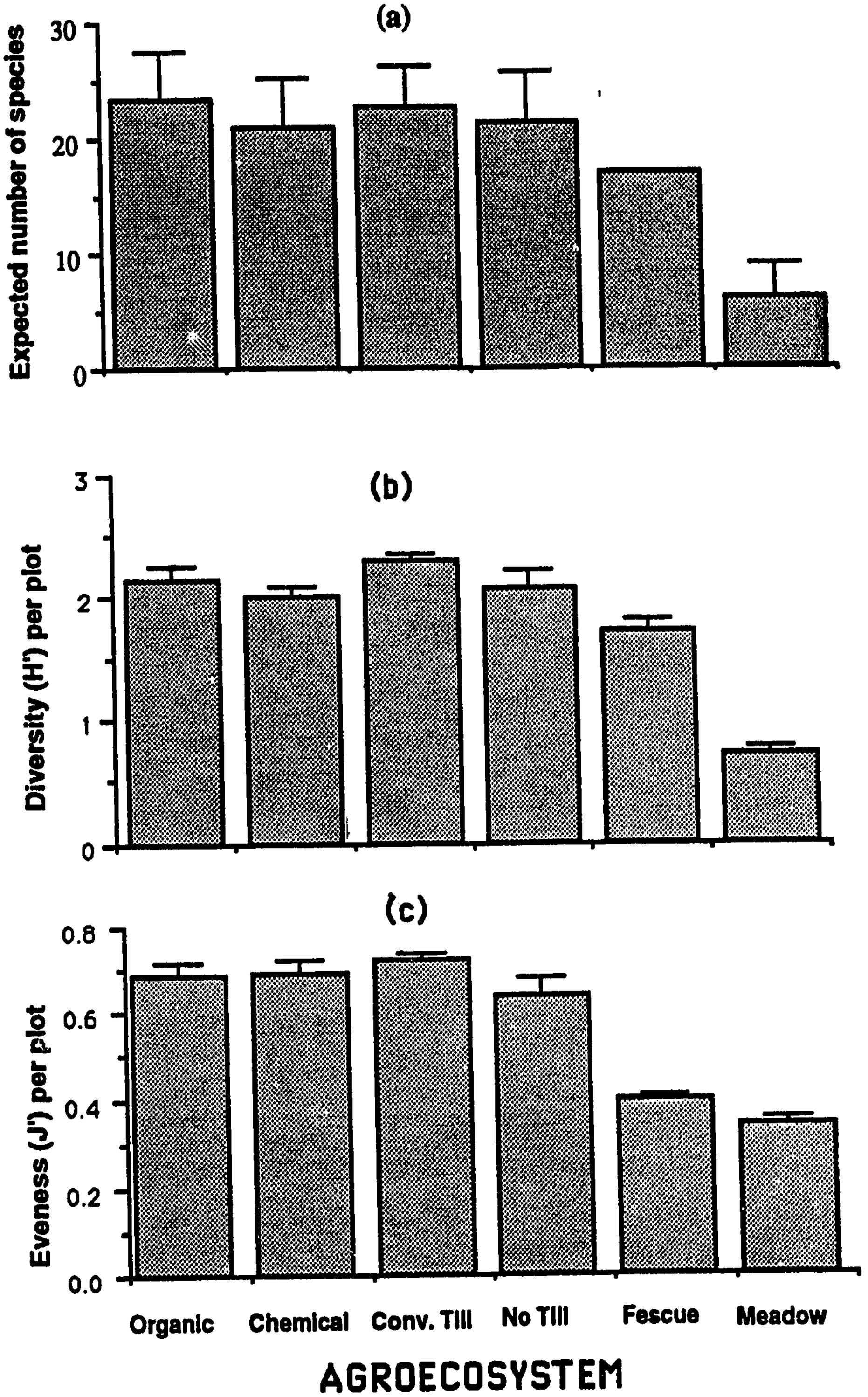
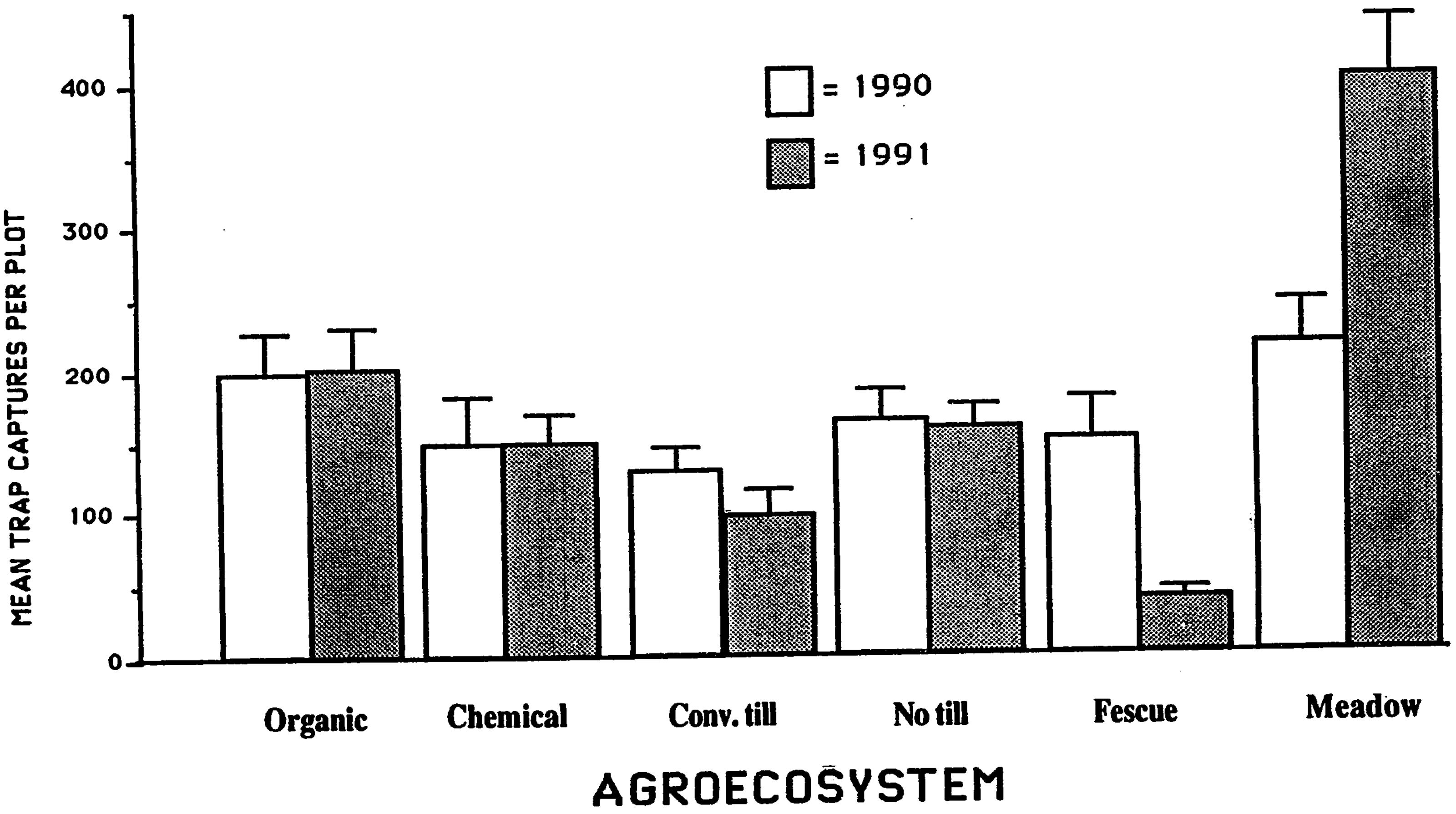


Fig. 2.6: Comparison of (a) corrected species richness, (b)Shannon-Wiener species diversity, and (c) evenness in Ellerslie agroecosystems in 1991. Entries in (a) are rarefaction estimates with 95 % confidence intervals and means with ± one standard error in (b) and (c).

Fig. 2.7. Relative abundance of carabids in Ellerslie agroecosystems.



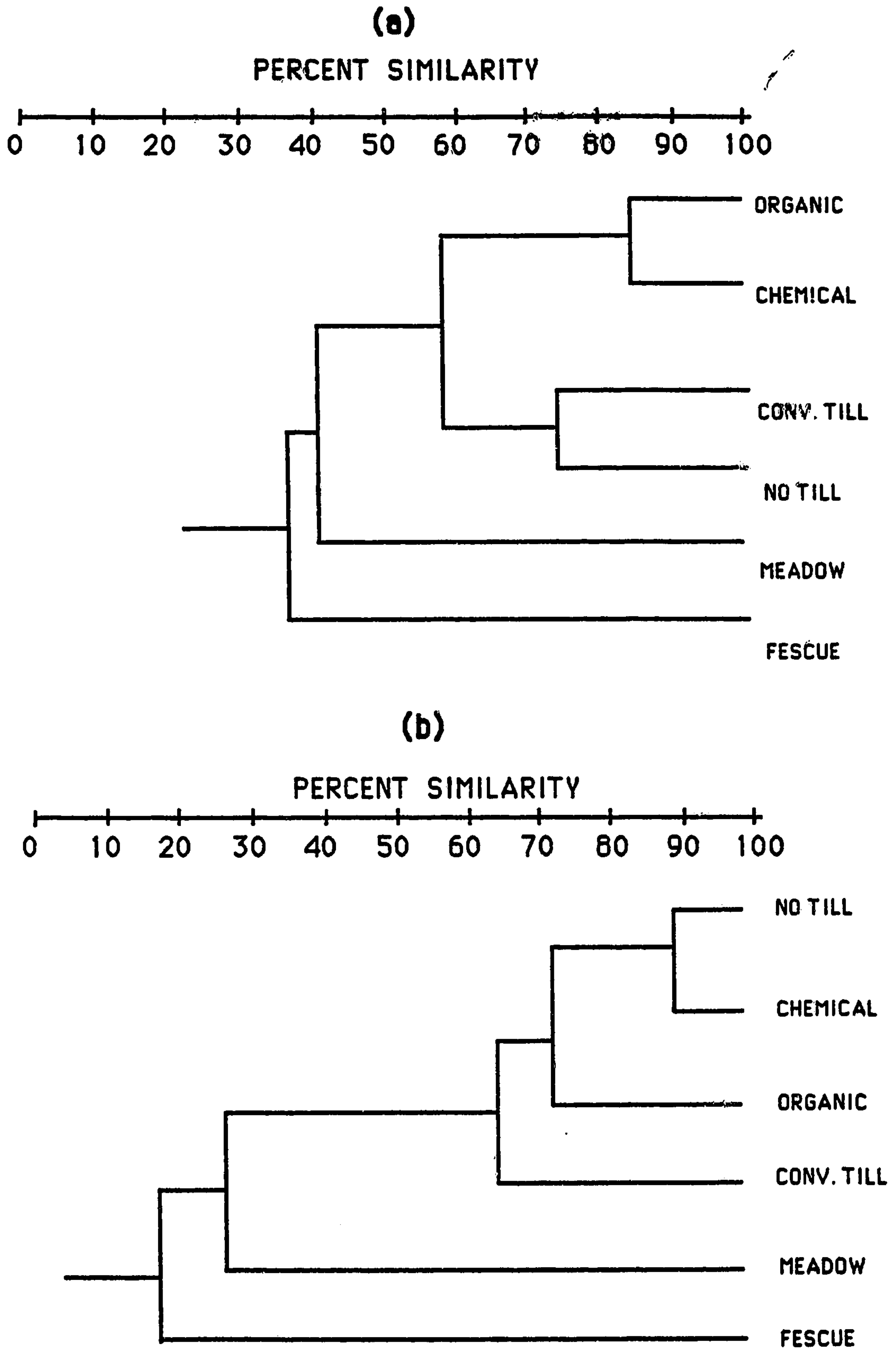


Fig. 2.8. Percent similarity of carabid assemblages in Ellerslie agroesystems in (a) 1990 and (b) 1991.

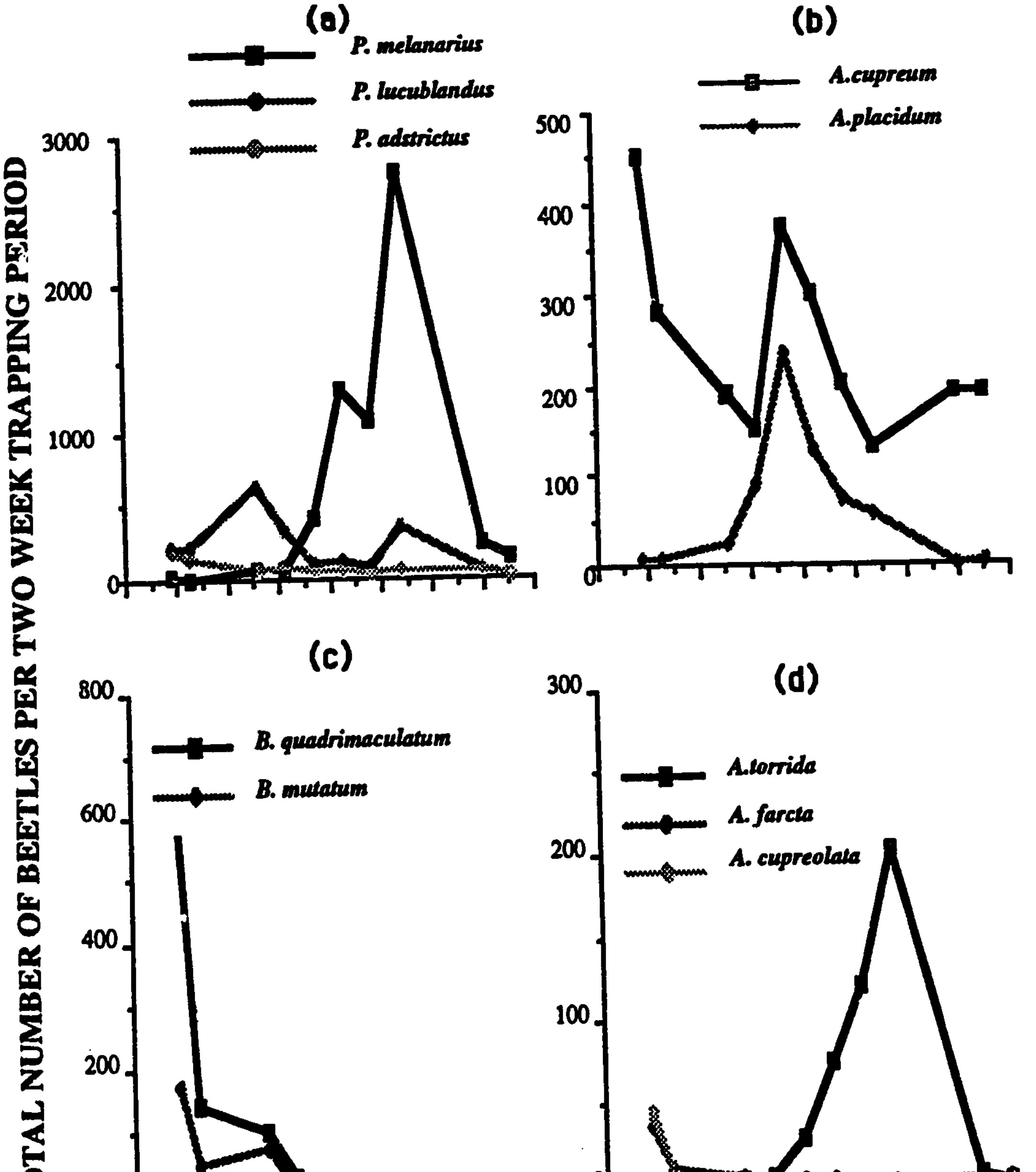


Fig. 2.9: Seasonal distribution of dominant (a) *Pterostichus*, (b) *Agonum*, (c) *Bembidion*, and (d) *Amara* species in 1991.

Table 2.1a: Crop sequence, tillage regime, method of weed control and nitrogen sources in the agroecosystems used to study carabid fauna. fb= faba bean, b= barley, i= barley-peas intercrop

CROPPING SYSTEM	Number of plots	CROP SEQUENCE	TILLAGE	WEED CONTROL	N SOURCE
(A)					
ORGANIC	8	fb-b-i-b	YES	Cultural	Soil only
CHEMICAL	8	fb-b-i-b	NO	Herbicides	Fertilizer-N
(B)					
CONV. TILL 1	2	fb-b-b-b	YES	Herbicides	Soil only
CONV. TILL 2	2	i-b-b-b	YES	Herbicides	Fertilizer-N
NO TILL 1	2	fb-b-b-b	NO	Herbicides	Soil only
NO TILL 2	2	i-b-b-b	NO	Herbicides	Fertilizer-N
(C)					
FESCUE	4	f-f-f-f	NO	Herbicides	Fertilizer-N
(D)					
MEADOW	6	Natural early succession vegetation, occasionally mowed			

Table 2.1b: Inputs in conventional and chemical plots

CROP	SEEDING (kg/ha)	HERBICIDE	RATE (L/acre)	FERTILIZER	FORMULAE	RATE (kg/ha)
BARLEY	90	Blagal	0.91	Urea	46-0-0	50
BARLEY/PEAS	60/95	Tropotox	1.10	same		
FABA BEANS	95	Basagran	0.71	same		
		Poast	0.65			
ALL CROPS		Round-up	1.61	Phosphate	0-45-0	10
FESCUE GRASS		2-4D Amine	1.22	NH4-NO3	34-0-0	50

Table 2.2: Effect of farming method and crop type on species richness, diversity and evenness (1991).

	SPECIES RICHNESS				DIVERSITY (H')				EVENNESS (J')			
TREATMENT	ORGANIC		CHEMICAL		ORGANIC		CHEMICAL		ORGANIC		CHEMICAL	
	mean	±SE	mean	±SE	mean	±SE	mean	±SE	mean	±SE	mean	±SE
INTERCROP	23.00	1.00	21.50	2.50	2.24	0.17	1.90	0.21	0.39	0.05	0.33	0.06
BARLEY 1	22.50	2.50	18.50	0.50	1.85	0.38	2.20	0.11	0.31	0.09	0.41	0.04
FABA BEAN	24.00	2.00	19.00	2.00	2.27	0.24	1.89	0.07	0.39	0.05	0.34	0.02
BARLEY 2	23.00	1.00	16.50	2.50	2.22	0.09	2.05	0.07	0.37	0.02	0.37	0.02

Table 2.3: Pearson correlation coefficients for environmental variables and carabids in Ellerslie experimental plots.

	(a) Farming method and crop type plots				(b) Tillage and nitrogen plots			
	Mean weed counts	Mean soil moisture	Crop biomass	Grain yield	Mean weed counts	Mean soil moisture	Crop biomass	Grain yield
Species richness	0.56	-0.16	-0.24	-0.25	-0.68	0.48	0.38	0.34
Significance	p<0.05	p>0.05	p>0.05	p>0.05	p<0.05	p>0.05	p>0.05	p>0.05
t 0.05 (14)=1.76								
Abundance	0.39	-0.43	-0.05	-0.01	-0.13	-0.03	0.13	0.16
Significance	0.1>p<0.05	p<0.05	p>0.05	p>0.05	p>0.05	p>0.05	p>0.05	p>0.05
t 0.05 (14)=1.76								

3. CARABID ASSEMBLAGES FROM TWO FARMS UNDER VARYING TILLAGE REGIMES IN NORTH CENTRAL ALBERTA.

3.1 INTRODUCTION

Conservation tillage is becoming a predominant feature of North American farming, particularly in the United States (Gebhardt et al. 1985). Conservation tillage, a practice ranging from reduction to absence of tillage, leaves significant proportions of plant residue on the surface (at least 30%, Andow 1992). This practice prevents soil erosion, and contributes to the accumulation of soil organic matter (Gebhardt et al. 1985). A major constraint to the adoption of conservation tillage is the management of weeds, arthropod pests and diseases under reduced tillage practices (Phillips et al. 1980). One important drawback of conservation tillage is the environmental impacts of increased pesticides that are commonly associated with this technology. Achieving a reduction of insecticide use in conservation tillage systems will require a better understanding of the impact of this practice on natural enemies.

Conservation tillage affects insects through reduced soil disturbance, increased surface residue, and changes in the weed community (Stinner and House 1990). These changes can have adverse or beneficial effects on populations of pests and their natural enemies. Soil inhabiting predators are particularly susceptible to tillage practices. In temperate agroecosystems the complex of surface dwelling predators is dominated by ground beetles (Potts and Vickerman 1974). This group of beetles is well suited to assess the impact of conservation tillage as they are taxonomically diverse (Erwin et al. 1979) and the community is sensitive to environmental perturbations (Freitag et al. 1973). In addition, carabids can aid in natural control of insect pests (e.g. Edwards et al. 1979) and seed eating species can affect weed distributions in the agroecosystem (Brust and House 1988b).

The effects of tillage on carabid assemblages have received moderate attention. Dubrovskaya (1970) found that deep cultivation with the moldboard plow had a detrimental effect on carabid abundance relative to shallow cultivation. Several studies comparing conventional tillage and minimum tillage have confirmed the findings of Dubrobskaya, in that abundance of ground beetles is greater in fields under minimum tillage (Weiss et al. 1990, Brust et al. 1986, Ferguson & McPherson 1985, House & Stinner 1983, House and All 1981, Dritschilo & Wanner 1980). However, in a few studies carabids were more abundant in conventionally tilled fields (Barney and Pass 1986, Edwards 1976), or no differences were found (Mack and Buckman 1990, Tyler and Ellis 1979). The effect of tillage can vary with the species, the crop and also between localities. No studies on the effect of conservation tillage on carabids have been conducted in the highly seasonal climate of north central Alberta.

The objective of this study was to determine the effect of tillage on carabid activity (abundances) and community structure. Also this study complements the work conducted in Ellerslie (Chapter 2) and provides a comparison at a larger scale. This study may also shed some light on the spatial distribution of carabids in a manipulated, highly uniform field. From a purely faunistic view this study describes a carabid community, not yet invaded by the exotic, *P. melanarius* (see Niemelä and Spence 1991).

3.2 MATERIALS AND METHODS

3.2.1 Sites.

The two farms are located about 4 km apart and ca. 2 km east of Neerlandia in north central Alberta. The area lies in the mixed forest region of the boreal forest-aspen parkland ecotone. The soil at both farms is Thin Black Luvisolic (Greywooded soil). The legal location for the conventional tillage farm operated by Mr. Wayne Visser is

NE34 TW61 R3 W5. Soil test results done the previous fall (1990) reported the following characteristics: pH= 7.3, salinity = 0.3 ds/ml, organic matter = 4.9 % and medium texture. The reduced tillage farm operated by Mr. Andrew Wierenga is located at NW22 TW61 R3 W5. An equivalent soil test revealed the following parameters: pH= 7.8, salinity = 0.5 ds/ml, organic matter = 6.4 %, and medium texture.

3.2.2 Agronomic practices.

3.2.2.1 Tillage

The conventional farm receives deep cultivation every fall in the form of mold board plowing. This implement penetrates the soil approximately 15 cm and effectively overturns it completely burying all residue. In addition, spring tillage included two passes with a cultivator. The same tillage was conducted for 1990 and 1988 but in 1989 a tandem disk was used instead of the plow.

In the reduced tillage farm soil is tilled using a deep tillage cultivator in the fall. This does not overturn the soil, leaving more residue on the surface. In the spring, tillage includes a pass with a vibra shank to a depth of ca. 8-10 cm and one pass with a harrow.

3.2.2.2 Crops.

Both farms were planted to barley during 1991. The varieties were Harrington for the conventional and Condor for the reduced tillage farm. In the previous 3 years barley, peas, and barley/canola were planted in the conventional farm. For the reduced tillage farm, barley, wheat and canola were planted during the same period.

Planting operations took place in the second and third week of May. An air seeder and a double press drill were used for the conventional and the reduced tillage, respectively, and seeding rates of ca. 100 kg/ha were used for both farms. Both farmers treated seeds with Vitavex, a fungicide to prevent damping off.

3.2.2.3 Fertilization and weed control.

Fertilization in the conventional farm was done in early June in the form of banding a mixture of the following: 46-0-0-0 @ 100 kg/ha, 0-0-60-0 @ 35 kg/ha and 0-0-0-90 @ 10 kg/ha. Also liquid hog manure was applied at the rate of 3000 gallons/acre before planting. This was done every year, except when peas were planted. Weeds were controlled by soil incorporation of *Avadex BW* in the previous fall. Also, *Refine* was sprayed to control broad-leaved weeds at the 3-4 leaf stage.

The reduced tillage farmer fertilized his field by applying anhydrous ammonia (50 kg/ha), injected into the soil in the form of a gas bubble. This operation is done concurrently with the vibra shank tillage operation. This allows a reduction of traffic on the field. Later, around the first week of June he applied a mixture of 8-36-10 @ 80 kg/ha. This farmer also applied manure at the same rate as at the conventional tillage farm but only every other year and none was applied in 1991. This farmer did not apply *Avadex* for wild oats; he spot sprayed with Assert the first week of June. For control of broad leaves he sprayed the whole field with Target the last week of May.

3.2.3 Pitfall trapping.

Twelve pitfall traps were set in each field on June 25, 1991. Three trapping stations were established in each field by placing 4 traps in a grid of ca. 5 m X 10 m (similar to Ellerslie plots). Trapping stations 1, and 3 were laid out ca. 100 m apart along a north-south transect with station 2 at the middle but 50 m east (see Fig. 3.1) to provide estimates of spatial variation. The first station was always set at least 100 m from the nearest edge. The nearest edges for the conventional farm were the building grounds on the north and forest wind barrier on the east. The reduced tillage field was bordered by a forest wind barrier on the north and pasture on the west side.

Pitfall traps were filled to about 3 cm with undiluted ethylene glycol used as a killing and preserving fluid. Beetles were collected from these traps at ca. two weeks until the end of August. The beetles were sorted in the lab and transferred to 95% alcohol. Identification to species level was made using Lindroth's keys to the Carabidae of Canada and Alaska (1961-9).

3.2.4 Ecological parameters studied.

I measured both population and community aspects of the ground beetles caught. Abundance was estimated from pitfall trap catches which are proportional to activity of beetles. Community measures included observed number of species, Shannon-Wiener index of diversity (H'), evenness (J'), and percent similarity (Krebs 1989, pp 361, 364 and 304 respectively). Analyses were carried out using Statview 512+ for the MacIntosh personal computer.

3.2.5 Limitations.

I only studied one farm per treatment, without true replication. Therefore, caution must be exercised about drawing conclusions on tillage effects. The three sub-sites (stations) within each farm are pseudoreplicates with respect to the general issue of tillage effects (Hulbert 1984). However, it is difficult if not impossible to find two farmers that do things identically and so, in practice this is the best way to estimate effects on a farm scale, the scale most relevant to practical application. In this case, the innovative farmer that practiced reduced tillage, also incorporated other new techniques. He planted a different variety, he injected anhydrous ammonia, he used a different fertilizer mixture and a different weed control strategy. These factors may confound the effect of tillage if they affect carabids. Thus my study is a comparison of two systems of agronomic practice centered on tillage and not a study of the single effect of tillage per se.

3.3 RESULTS.

3.3.1 Tillage regime and carabid abundance.

Total carabid captures per trap were transformed using natural logarithms to reduce heterogeneous variation. The position of the trapping station did not affect the abundance of beetles at either farm (Fig. 2a). However, there was a trend toward higher abundance at station 3 at the conventional tillage farm, and station 1 at the reduced tillage farm. Tillage was associated with an increase in overall carabid abundance, as measured by activity (Fig. 3.2a). More beetles were captured in the conventional farm than in the reduced tillage farm (F=4.81, df=1,22, p=0.04). This difference was mainly attributable to the unusually large capture of *A. placidum*, particularly at station 3 at the conventional farm.

Individual species abundances per trap were transformed (ln x +1) to stabilize heterogeneous variations and zero values. The pattern of abundance for the seven species that responded significantly to tillage regime is shown in Fig. 2b. Of the four dominant carabid genera, species belonging to *Agonum* and *Amara* were more abundant in tilled systems while *Pterostichus* and *Bembidion* species were more commonly collected under reduced tillage. However, because I trapped only during summer (June 22-August 30) after seeding, my data do not provide estimates of the actual activity of early spring species such as *Agonum cupreum* and *Bembidion quadrimaculatum*.

3.3.2 Community structure of ground beetles.

Twenty five species were found under reduced tillage compared to twenty two under conventional tillage; twenty nine species representing nine genera, were collected in total. Abundant species (>1% of catch in at least one site) per trapping station are shown in Table 1. *Agonum placidum* was by far the dominant species at both farms, comprising 43% of the catch at the reduced tillage farm and 70% of the catch at the conventional tillage farm. The abundance rank of other common species differed between the two farms. For example ***Agonum cupreum*** and ***Bembidion quadrimaculatum*** were the two other most abundant in the reduced tillage farm but in the conventional farm, *Amara torrida* and *Amara quenseli* occupied these positions. This latter species was extremely rare in the reduced tillage farm (only 5 individuals caught). The introduced *Pterostichus melanarius*, although reported from the nearby town of Barrhead (Niemelä and Spence 1991) and common in barley plots in central Alberta, (Chapter 2), probably has not yet established breeding populations in these farms as only one long wing male was captured.

There were no significant differences in species richness, diversity and evenness between trapping stations at either farm. I noted a trend toward more species at the reduced tillage farm (Fig. 3.3a) but it was only of marginal statistical significance (F=3.45, df=1,22, p=0.08). However there were highly significant differences in the Shannon-Wiener indices of diversity, H', (Fig. 3.3b, F=23.3 df=1,22, p<0.001) and evenness, J', (Fig. 3.3c, F=13.67 DF=1,22 p<0.01). These higher diversity and evenness indices for the reduced tillage farm, confirmed the pattern of relative species abundances that can be appreciated from study of Table 3.1. At the conventional tillage farm 3 species accounted for more than 85% of total captures compared to 6 species accounting for a similar proportion at the reduced tillage farm.

Differences in the carabid assemblages in the two farms were reflected in single linkage cluster analysis (shown in Fig. 3.4). Renkonen index of percent similarity was used as the measure of similarity. This index takes into account differences in species abundances (Krebs 1989) that were marked in this study. In general carabid assemblages, pooled across traps per site, clustered according to tillage regime, particularly those in the conventional tillage where percent similarity ranged from 83 to 93 %. The reduced tillage assemblages were somewhat less similar (72-81%) and only stations 3 and 1 formed a separate cluster from the conventional tillage.

3.4 DISCUSSION

Several workers have studied the distribution of carabids in agroecosystems and adjacent habitats (e.g. Niemelä and Halme 1992, Wallin 1985, Doane 1981, Frank 1971, Rivard 1966, also see Chapter 2). However, these studies did not assess natural spatial variation within uniform habitats. Agroecosystems, such as the barley farms in this fields, are particularly suited to address this question because of relatively high uniformity maintained through the agronomic practice of monocultures and the associated application of tillage and chemical technology. Understanding natural spatial variation of carabid assemblages is an important prerequisite to the interpretation of their distribution in relation to experimental treatment effects, such as tillage regimes considered in this study.

Overall carabid abundance, individual species abundances, and the three indices of community structure did not differ significantly among the three trapping stations in each of the two farms. This suggests that carabid assemblages do not have highly clumped distributions within uniform habitats that are characteristic of highly manipulated monocultures. Given the proximity and similar soil conditions of the two farms, I argue that differences in carabid assemblages among nearby farms can be attributed to the management strategies implemented by the farmers. Most conspicuous among these was the difference in degree of tillage.

In general, arthropods are expected to be more abundant in conservation tillage systems (Stinner and House 1990), although the responses can vary with species and sites (Gebhard et al. 1985). With respect to carabids, higher overall abundance in reduced tillage systems has been reported in most studies (House 1989, Brust et al. 1986, Ferguson and McPherson 1985, House and Stinner 1983). But when the studies have been extended to include more sites and cropping systems other than corn and soybeans the differences have been less clear (Weiss et al. 1990, Mack and Buckman 1990, Tyler and Ellis 1979) or carabids were least abundant and diverse in reduced tillage (Barney and Pass 1986, Edwards 1976). Assessment of tillage impact based on overall carabid abundance only, can be misleading since responses of particular species to tillage regimes commonly vary. Interesting aspects of species biology that can determine responses to tillage have been entirely ignored by simply discussing the overall abundance pattern of the assemblage. This knowledge can be important in the management of agroecosystems to enhance populations of beneficial predatory arthropods.

In this study overall carabid abundance was higher in the conventional tillage than in the reduced tillage farm but it was clear that species responses were inconsistent in the two systems. *Agonum placidum, Amara quenseli* and *Amara torrida* were more abundant in the conventional tillage farm while *Pterostichus adstrictus*, *Bembidion quadrimaculatum, B. bimaculatum* and *B. rupicola* were more abundant in the reduced tillage farm. The higher overall abundance in the conventional tillage farm resulted from the response of *A. placidum* which was by far the dominant species in the two farms. Similar effects of tillage for this species were reported by Weiss et al. (1990) and also, a similar trend was observed in the tillage study at the Ellerslie plots (Chapter 2). The specific responses of dominant species to tillage regimes has been a common factor in determining overall pattern of abundance in other studies (e.g. House 1989).

So far, to my knowledge, only Hance et al. (1990) have offered explanations for carabid species differences to tillage regimes. These authors suggested that observed species differences in various crop types were related to the time of tillage in relation to their phenology. The tillage operation that has been considered most destructive to carabids is deep ploughing with the moldboard (Dubroskaya 1970, Dritschilo and Wanner 1980). This implement was used by the conventional tillage farmer in the fall and those populations present at the time, that overwinter in the field, obviously could be substantially depressed. No studies of overwintering sites have been conducted for carabids in central Alberta, however, Wallin (1985) has suggested that spring active species are more likely to overwinter in the field than autumn breeders. Three species known to have an early activity peak (Chapter 1), *B. quadrimaculatum, B. rupicola*, and *P. adstrictus*, were less abundant in the conventional tillage farm, probably as a result of destructive fall ploughing.

Four other species, likely autumn breeders, *A. placidum, A. torrida* and *A. quenseli*, were more abundant at the conventional tillage farm. One possible explanation is that their immigration is higher at 'conventional tillage' farms. Such a pattern may result from reduced barrier to movement, microclimatic preferences, or differential distribution of prey and predators. Alternatively, higher abundance at the conventional tillage farm may result from higher recruitment as a result of reduced competition (Niemelä 1992) or intraguild predation (Polis et al. 1989) from those species that overwinter *in situ* and may be depressed through tillage. For example, it is conceivable that eggs and larvae of *A. placidum* experience reduced predation pressure from spring carabid species at the conventional farm and attain the observed high numbers.

The alternative hypothesis that carabid species overwinter in the field is supported by the fact that abundance of some carabid species did not decrease in the center of either barley field used in this study. Frank (1971) and Wallin (1985) report similar finding for other species and crops. For those species that spend their entire life cycle in the fields, behavioural traits may explain the differences in response to tillage treatments. It is possible that dominant species survive tillage disturbance below plow depth as larvae or pupae (Barney and Pass 1986) and also by having their activity peak after tillage thereby avoiding direct physical destruction such as that reported by Lys and Nentwig (1991).

Greater plant species diversity provided by perennial weeds, and increased mulching from plant residues are features attributed to conservation tillage (Stinner and House 1990). These features can provide more niches for ground beetles (House and All 1981) and also increase the number of refuges for species vulnerable to intraguild predation. More niches can ameliorate potential competition effects and more refuges may stabilize predator-prey interactions. These processes are thought to result in greater carabid species diversity in conservation tillage systems (Stinner and House 1990). My results support this prediction as slightly more species, and significantly higher species diversity and evenness were found at the 'conservation tillage' farm. Furthermore, single linkage cluster analysis suggested that distinct carabid communities inhabited the two farms.

Tillage regime may interact with other agronomic practices to affect carabid communities. Purvis and Curry (1984) reported greater carabid abundance in fields with farm yard manure. However the effect disappeared later in the season and no consistent effects were found on the late summer species *Pterostichus melanarius*. It is therefore, unlikely that differential rates of manure application caused the differences in carabid abundances found in my study. Tillage regime can also interact with cropping system. In a study of newly planted alfalfa, Barney and Pass (1986) found least diversity and abundance in the 'no tillage' treatment. Weiss et al. (1990) found that abundances of several carabid species, including *A. placidum* depended on the combinations of tillage and wheat cropping system. They concluded that cropping system was more important than tillage in structuring carabid assemblages. House (1989) reported that carabids were more abundant only in the 'no tillage' treatment with herbicide applications. However, no explanation was offered for this interaction. More studies on life history of carabid species in relation to tillage treatments will be necessary before we can fully understand their responses to soil disturbance and interactions with other agronomic practices.

I argue here that the overall pattern of carabid abundance in conservation tillage depends on how dominant species are affected by soil disturbance. In work reported in Chapter 2, the dominant species was the introduced *Pterostichus melanarius* which was slightly more abundant in the 'no tillage' plots. Only one individual of this species was found at Neerlandia, but the species is established in the nearby town of Barrhead and also relatively common in road verges just south of Barrhead (Niemelä and Spence 1991, and unpub. data). I speculate that this exotic species has the potential of affecting the structure of carabid communities in open cultivated habitats, as suggested by Spence and Spence (1988) for highly disturbed habitats associated with human settlements. In Ellerslie it dominated an uncultivated old field and some species like *A. placidum* and *P. adstrictus* were virtually absent. These two species were abundantly found in nearby experimental plots where occurrence of *P. melanarius* was significantly lower (see Chapter 2). *A. placidum* appears particularly vulnerable to competition (or predation) from *P. melanarius* because of its similarity in life style and phenology. If *P.melanarius* invades the farm habitats around Neerlandia, I predict that the pattern of overall carabid abundance could change considerably from that found in this study.

Conservation tillage systems are likely to increase given current concerns of soil erosion and agricultural sustainability. In this chapter I have shown that reduced tillage does not necessarily result in increased activity of natural enemies such as carabid beetles. These effects may be brought about by associated changes in pesticide use. Therefore, before such systems are widely recommended it is necessary to undertake more detailed studies to understand the responses of natural enemies. Investigations of processes using experimental plots should be supplemented with the more realistic scale of commercial farms.

3.5 REFERENCES

Andow, D.A. 1992. Fate of eggs of first-generation *Ostrinia nubilalis* (Lepidoptera: Pyralidae) in three conservation tillage systems. Environ. Entomol. 21: 388-393.

Barney, R.J. and B.C. Pass. 1986. Ground beetle (Coleoptera: Carabidae) populations in Kentucky alfalfa and influence of tillage. J. Econ. Entomol. 79: 511-517.

Brust, G.E. and G.J. House. 1988. Weed seed consumption in low-input soybean agroecosystems by arthropods and rodents. Am. J. Alternat. Agric. 3: 19-25.

Brust, G.E., B.R. Stinner, and D.A. MacArtney. 1986. Predator activity and predation in corn agroecosystems. Environ. Entomol. 15: 1017-1021.

Doane, J.F. 1981. Seasonal captures and diversity of ground beetles (Coleoptera: Carabidae) in a wheat field and its grassy borders in central Saskatchewan. Quaest. Ent. 17: 211-233

Dritschilo, W. & D. Wanner. 1980. Ground beetle abundance in organic and conventional corn fields. Environ. Entomol. 9: 629-631.

Dubrovskaya, N.A. 1970. Field carabid beetles (Coleoptera: Carabidae) of Byelorussia. Entomol. Rev. 49: 476-487.

Edwards, C.A. 1976. Effects of direct drilling on the soil fauna. Outlook Agric. 8: 243-244.

Edwards, C.A., K.D. Sunderland, and K.S. George, 1979. Studies on polyphagous predators of cereal aphids. J. Appl. Ecol. 16: 811-823.

Erwin, T.L., Ball, G.E., and Whitehead, D.R. 1979. Carabid beetles, their evolution, natural history and classification. Proceedings of the first international symposium of carabidology. W.Junk, The Hague, Boston & London.

Floate, K.D., J. Doane, and C. Gillott. 1990. Carabid predators of the wheat midge (Diptera: Cecidomyiidae) in Saskatchewan. Environ. Entomol. 19: 1503-1511.

Ferguson, H.F., & R.M. McPherson. 1985. Abundance and diversity of adult carabidae in four soybean cropping systems in Virginia. J. Entomol. Sci. 20: 163-171.

Frank, J.H. 1971. Carabidae (Coleoptera) of an arable field in central Alberta. Quaest. Ent. 7: 237-252.

Freitag, R., L. Hastings, W.R. Mercer and A. Smith. 1973. Ground beetle populations near a draft mill. Can. Ent. 105: 299-310..

Gebhardt, M.R., T.C. Daniel, E.E. Schweizer, R.R. Allmaras. 1985. Conservation tillage. Science 230: 625-630.

House, G.J. 1989. Soil arthropods from weed and crop roots of an agroecosystem in a wheat-soybean-corn rotation: impact of tillage and herbicides. Agric. Ecosyst. & Environ. 25: 233-244.

House, G.J. & B.R. Stinner. 1983. Arthropods in no-tillage soybean agroecosystems: community composition and ecosystem interactions. Environ. Manage. 7: 23-28.

House, G.J., & J.N. All. 1981. Carabid beetles in soybean agroecosystems. Environ. Entomol. 10: 194-196.

Krebs, C.J. 1989. Ecological methodology. Harper & Row Publishers, New York.

Lindroth, C.H. 1961-69. The ground beetles (Carabidae, exc. Cicindelinae) of Canada and Alaska. Parts 1-6. Opuscula Entomologica. xlvii + 1192 pp.

Lys, Jon-Andry & W. Nentwig. 1991. Surface activity of carabid beetles inhabiting cereal fields: Seasonal phenology and the influence of farming operations on five abundant species. Pedobiologia. 35: 129-138.

Mack, T.P. & C.B. Buckman. 1990. Effects of two planting dates and three tillage systems on the abundance of lesser cornstalk borer (Lepidoptera: Pyralidae), other selected insects, and yield in peanut fields. J. Econ. Entomol. 83: 1034-1041.

Niemelä, J. & E. Halme 1992. Habitat associations of carabid beetles in fields and forests on the Åland islands, sw Finland. Ecography 15: 3-11.

Phillips, R.F., R.L. Blevins, G.W. Thomas, W.W. Frye, and S.H. Phillips. 1980. No-tillage agriculture. Science 208: 1108-1113.

Polis, G.A., Myers, C.A. and Holt, R.D. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. Ann. Rev Ecol. Syst. 20: 297-330.

Potts, G., & Vickerman, G.P. 1974. Studies on the cereal ecosystems. Adv. Ecol. Res. 8: 107-197.

Purvis G. & Curry, J.P. 1984. The influence of weeds and farmyard manure on the activity of Carabidae and other ground dwelling arthropods in a sugar beet crop. J. Appl. Ecol. 21: 271-283.

Stinner, B.R. & G.J. House.1990. Arthropods and other invertebrates in conservation-tillage agriculture. Ann. Rev. Entomol. 35: 299-318.

Thiele, H.U. 1977. Carabid beetles in their environments. Springer-Verlag, Berlin, New York.

Wallin, H. 1985. Spatial and temporal distribution of some abundant carabid beetles (Coleoptera: Carabidae) in cereal fields and adjacent habitats. Pedobiologia 28: 19-34.

Weiss, M.J., E.U. Balsbaugh, Jr., E.W. French, and B.K. Hoag. 1990. Influence of tillage management and cropping system on ground beetle (Coleoptera: Carabidae) fauna in the northern Great Plains. Environ. Entomol. 19: 1388-1391.

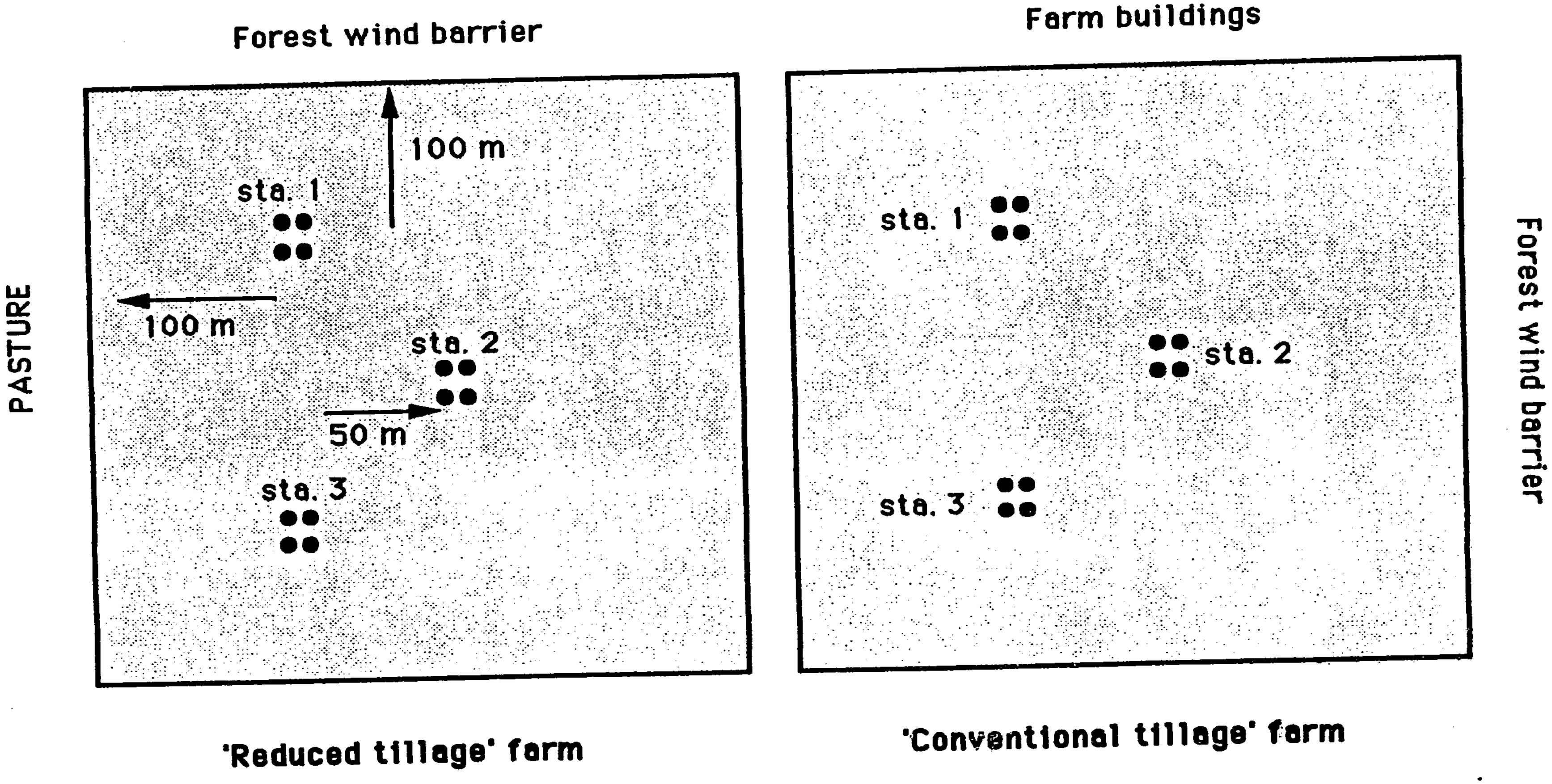


FIG. 3.1: LAY OUT OF PITFALL TRAPS IN NEERLANDIA.

Fig. 3.2a: Effect of tillage regime on carabid abundance

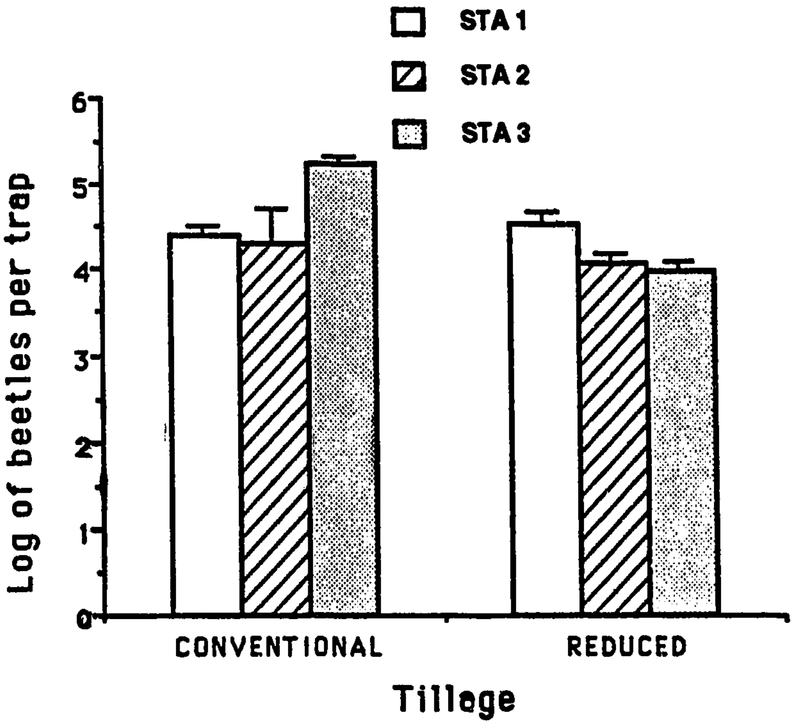
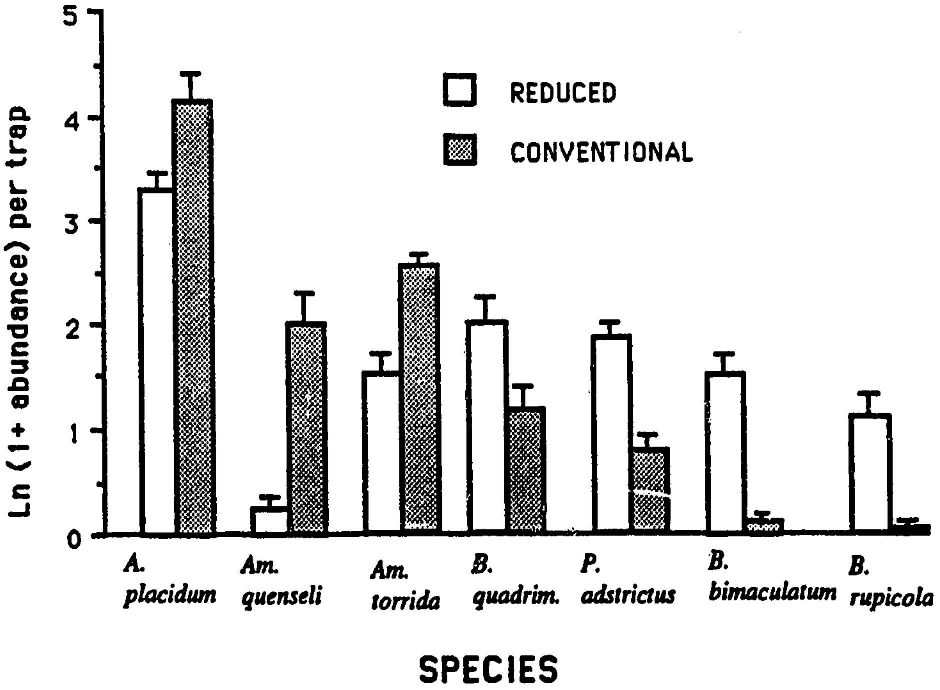


Fig. 3.2b: Effect of tillage on species abundances



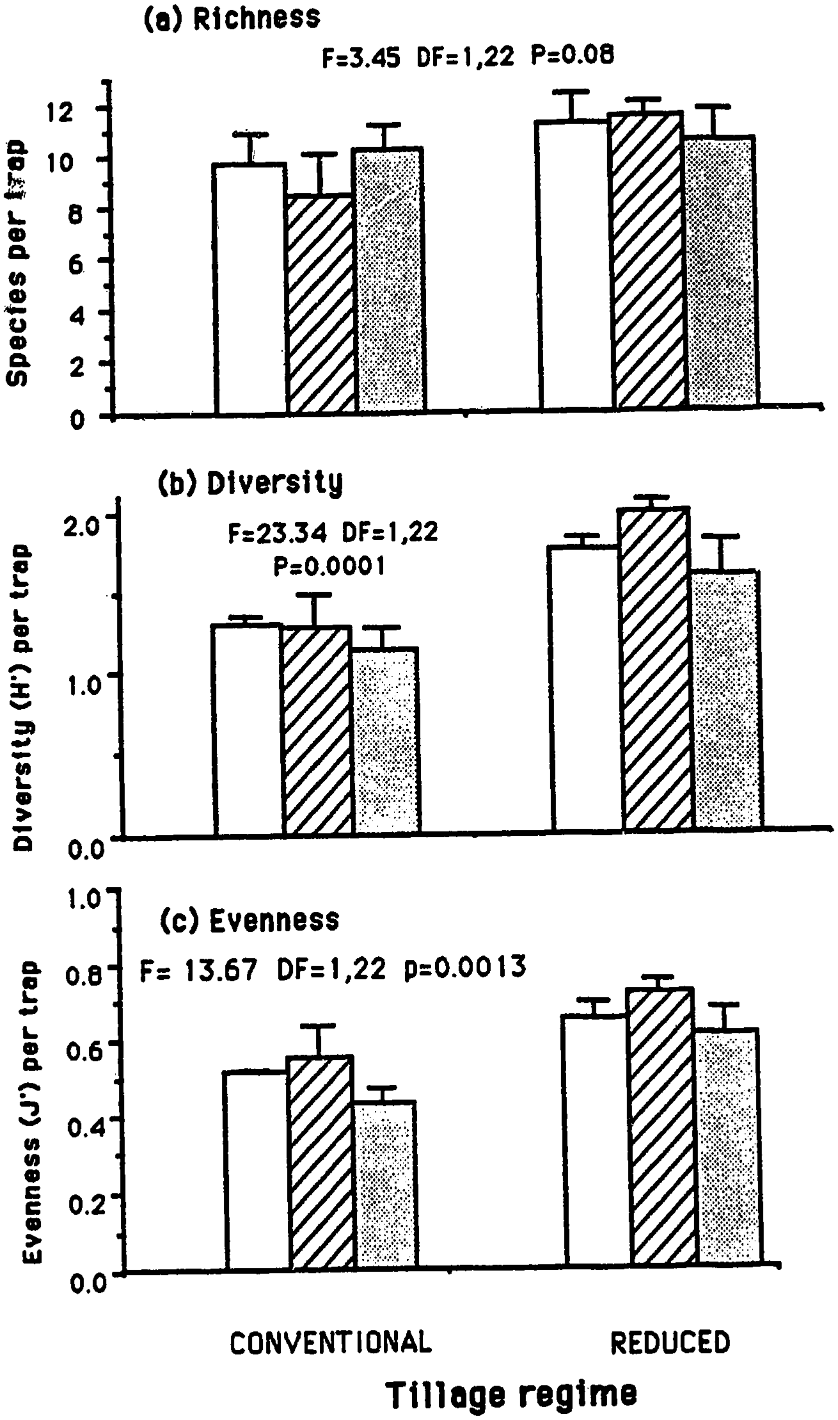


Fig.3.3: Effect of tillage regime on (a) species richness, (b) species diversity and (c) evenness.
☐ = Trapping station 1 ▨ = 2 ▒ = 3

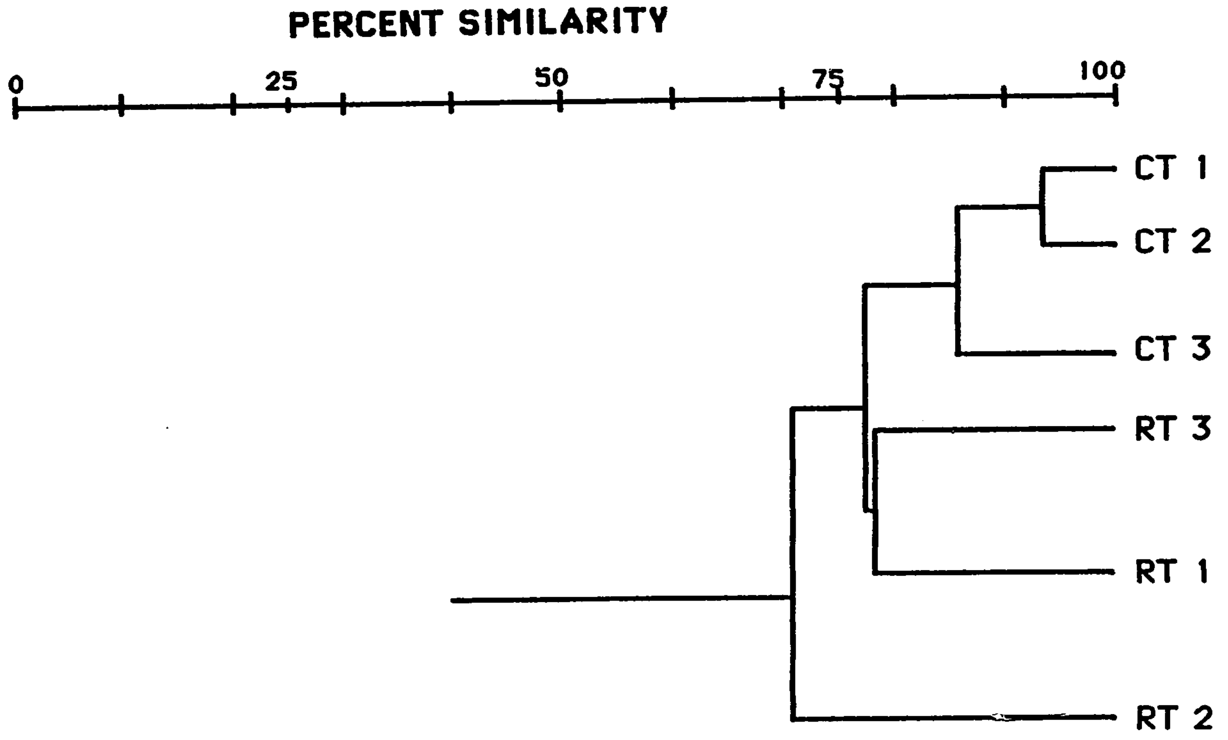


Fig. 3.4: SINGLE LINKAGE CLUSTER OF CARABID ASSEMBLAGES IN NEERLANDIA.
CT= CONVENTIONAL TILLAGE, RT= REDUCED TILLAGE

Table 3.1: Dominant carabid species from the two farms near Neerlandia.

	REDUCED TILLAGE FARM					CONVENTIONAL TILLAGE FARM				
SPECIES	STA 1	STA 2	STA 3	TOTAL	%	STA 1	STA 2	STA 3	TOTAL	%
Agonum placidum	174	74	115	363	43	208	234	529	971	66.7
Bembidion quadrimaculatum	58	35	12	105	12.4	10	5	23	38	2.61
Pterostichus adstrictus	39	18	17	74	8.77	6	7	4	17	1.17
Agonum cupreum	27	28	17	72	8.53	17	10	19	46	3.16
Bembidion bimaculatum	21	27	7	55	6.52	1	1	0	2	0.14
Amara torrida	14	20	20	54	6.4	53	54	44	151	10.4
Bembidion rupicola	21	7	6	34	4.03	1	0	0	1	0.07
Amara lacustris	12	5	10	27	3.2	11	15	22	48	3.3
Pterostichus lucublandis	7	3	5	15	1.78	1	1	0	2	0.14
Amara latior	0	9	2	11	1.3	7	6	12	25	1.72
Amara quenseli	2	1	2	5	0.59	10	20	94	124	8.52
Other*	15	12	7	34	4.03	19	28	107	154	10.6
TOTAL	388	238	218	844	101	334	361	760	1455	109

*Other species include: *Agonum anchomenoides, A. quadripunctatum, Harpalus fuliginosus, B. transversale, B. obscurellum, B. timidum, P. corvinus, P. riparius, Amara ellipsis, Calathus ingratus, Chlaenius alternatus.*

4. THE EFFECT OF CROP TYPE ON THE ACTIVITY AND DISTRIBUTION OF EPIGAEIC PREDATORS.

4.1 INTRODUCTION.

Recent interest in low-input, sustainable agriculture has focused attention on the conservation of natural enemies as an alternative to insecticides for pest control. Ground beetles (Carabidae), are the dominant group of the epigaeic predators in temperate regions (Potts and Vickerman 1974). Although there is some controversy regarding the role of carabids as predators of arthropod pests, there is increasing evidence that they can affect the population dynamics of many herbivores. For example, heavy predation by carabids in agricultural settings has been demonstrated on Lepidoptera (Best and Beegle 1977, Frank 1971, Fuller 1988), cereal aphids (Edwards et al 1979, Hance 1987, Chiverton 1988, Helenius 1989) and wheat midges (Floate et al 1990). Furthermore, the complex of predatory, ground arthropods, which carabids dominate, has been shown to regulate populations of cereal aphids (Winder 1990).

One approach to enhancing populations of endemic natural enemies, such as carabids, is to modify the habitat to favour their immigration, tenure time or recruitment (Gross 1987). Structure and diversity of ground cover in agroecosystems can influence habitat favourability and affect activity of ground predators. For instance, Rivard (1966) found that carabid activity was higher in cereals than in forage and pastures. He suggested that the effect of crop type was mediated through changes in microclimatic conditions. Varis et al. (1984) proposed a similar explanation for the higher activity of carabids in cabbage fields than in sugar beet and timothy grass. They also found that crop types affected the community composition of the carabid assemblage. The effect of crop rotations on carabids can also be attributed to the specific effect of crop types with distinct canopy structures that differentially alter microclimates. Brust et al. (1986) found that carabids were more abundant in corn fields preceded by soya beans than by corn. Also, Weiss et al. (1990) found that cropping system (rotation) was more important than tillage practices in structuring carabid communities.

The effect of crop diversity on arthropods has attracted considerable attention among agroecologists (see reviews by Andow 1991, Vandermeer 1987, Rish et al. 1983). Although far from universal, it appears that populations of insect herbivores are frequently reduced in polycultures as compared with monocultures (Rish et al. 1983). One possible explanation for this pattern, is higher abundance and impact of natural enemies in vegetationally complex systems (Root 1973). Studies that have addressed this question for carabid assemblages have generally supported this hypothesis. Higher predation pressure (Brust et al. 1986), increased carabid activity (Tukahirwa and Coaker 1982) and longer tenure times (Perfecto et al. 1986) have been reported in polycultures relative to monocultures. Weedy crops incorporate greater plant diversity than clean crops and may also behave like polycultures (Altieri and Whitcomb 1979). Higher carabid activity has been reported in weedy crops (Dempster and Coaker 1974, Speight and Lawton 1976, Ryan et al. 1980, Barney et al. 1984), although in a few studies no differences were found (Purvis and Curry 1984, Chiverton and Sotherton 1991).

Most of the studies of the effect of plant diversity on arthropods have focused on crops in tropical regions. Even the majority of the studies of intercropping that have been conducted in temperate areas, have focused on the classical polyculture of corn and beans or vegetable crops used in the tropics (e.g. McGuiness 1985, Andow 1990). In this chapter I explore the effect of crop types and diversity on the activity of ground predators and the distribution of carabids in the highly seasonal climate of central Alberta. I sought answers to the following questions: (1) Are there differences in carabid activity between crop types ? (2) Are there differences in predation pressure among crop types ? (3) Is carabid abundance correlated with predation pressure ? (4) Does the dominant introduced carabid, *Pterostichus melanarius*, exhibit preferences for crop type? (5) Can manipulation of food availability affect crop preferences of *P. melanarius* ?

4.2 MATERIALS AND METHODS.

4.2.1 Crop type and predation pressure.

Plots used in this study were part of an ongoing long term study of agronomic practice on soil properties by the Department of Soil Science of the University of Alberta (see chapter 2). The plots selected for the present study (Fig. 4.1) are part of a no tillage crop rotation with high input of agrochemicals for weed control and soil fertility. Carabid activity and impact was compared across four crops: barley, faba bean, intercrop of barley and peas and fescue grass (not part of the rotation but receiving similar chemical inputs). Only two of the four barley plots (B1, Fig. 4.1)) in the chemical rotation were used for this study. Seeding density of barley and peas in the intercropping were reduced to half that of the rate normally used in monocultures.

In the experiments to assess predation pressure, fly pupae were presented individually in the various plots for a period of 24 hours. Pupae of *Sarcophaga bullata*, *Musca domestica* and *Drosophila melanogaster* were used to represent large, medium and small size classes of prey, respectively. Except for *Drosophila*, they were placed on the ground beside a colored stirring stick used as a marker. Because of their small size pupae of *Drosophila* were glued, individually, to 4 cm squares of paper towel to facilitate their recovery and prevent dislodging by wind or rain. In the laboratory I showed that the glue used for attaching *Drosophila* pupae does not repel potential field predators and that carabids will eat fly pupae of all three sizes (Appendix 1).

For field experiments, each plot was divided into a grid 3 squares wide and 12 squares long. The 12 prey items of each size class were allocated at random to each square (ca. 3 m x 2 m). The number of pupae 'present', 'removed' or 'eaten' (broken puparium) in each size class was recorded after 24 hours. The experiment was repeated two consecutive nights in July and August. Disappearance rates were analyzed with SAS (1990) using a split-plot ANOVA, with repeated measures.

Activity of carabid beetles in each crop type was estimated from two pitfall traps placed in the middle of each plot. These traps were in operation throughout the frost free season, except during mechanized treatments to the plots, and were collected every two weeks. Overall carabid seasonal activity was reported in chapter 2. For the purpose of the present study, the beetles collected around the time of the predation pressure experiment in July and August were pooled to check for any correlations with disappearance of fly pupae.

4.2.2 Crop type and movements of *P. melanarius*.

Two field arenas, each with four adjacent plots (4 m x 4 m) were established in a square (Fig. 4.2). Stem densities of the three crop types were estimated using four 0.5 m x 0.5 m quadrat samples, positioned north of each pitfall trap. The means and standard errors for number of stems per 0.5 m^2 were as follows: intercrop, 38±4.2; barley, 39±2.1; faba bean, 7.1±2.5. Individual stem density of fescue was not estimated but a dense sward covered both plots. The two replicate arenas were laid out in a mirror image in an attempt to control for potential spatial orientation effects. Plastic lawn edging (15 cm high) was buried to a depth of ca. 5 cm around each arena to improve capture rates and minimize escape of beetles added to the plots during experiments.

One hundred *P. melanarius* were marked individually (by branding elytra with a dot code using a small soldering iron) and released simultaneously in the middle of each arena. Four empty traps, were placed in the middle of each plot and left open throughout the experiments. Carabids were collected from each trap every two days for the first week and at greater intervals for the following three weeks. Captured beetles were identified, counted and then released again in the middle of the arena. This experiment was conducted twice during August.

4.2.3 Food availability and habitat preference.

The objective of this experiment was to test the hypothesis that increased food availability influences habitat choice of *P. melanarius*. In the previous experiment less individuals were captured in fescue grass and to a lesser extent, in faba bean. Food supplements, were added by distributing 100 pupae of *Sarcophaga bullata* over a 10 x 10 grid in the fescue and faba bean plots in the west arena. Fifty male and fifty female *P. melanarius* were marked individually, as above, and released in the middle of each of the two arenas the same day. After 48 hours, beetles captured in the pitfall traps were counted in all plots and pupae present in the west arena were counted and removed. Also at this time, fresh pupae were added to the fescue and faba bean plots in the east arena, but no additional carabids were released. Beetles and fly pupae were counted again after another 48 hours. The experiment was replicated twice in early and middle September. In the second run the trapping bouts were extended to three days, before addition of new pupae, in an attempt to increase recaptures.

4.3 RESULTS.

4.3.1 Crop type and predation pressure.

Disappearance rates of the fly pupae are shown in Figure 4.3.
There were no significant differences among crop types with respect to numbers of pupae lost (F=1.67 df=3,4 $p>0.05$), but prey size, significantly affected disappearance rate (F=24.9 df=2,67 $p<0.01$), with the number of pupae taken inversely proportional to prey size. A significant interaction (F=7.88 df=6,8 $p<0.05$) was found between crop type and prey size, reflecting the fact that the number of large prey taken in the fescue plots was lower than that of the three crops. Disappearance rates did not vary between months in pooled data (Fig. 4.4b, F=3.92 df=1,67 $p>0.05$), but interestingly, the number of pupae eaten in the second day of the experiment was significantly higher in both months (Fig. 4.4a, F=13.13 df=1,67 $p<0.001$). A significant interaction between month and crop (Fig 4.4b, F=3.34 df=3,67 $p<0.05$) reflects mainly a lower disappearance rate in August in the fescue plots. Disappearance rates for the three size classes were similar in both months suggesting a lack of interaction between month and prey size (F=1.85 df=2,67 $p>0.05$).

4.3.2 Crop type and carabid activity.

Total catches of carabids on each plot were transformed to natural logarithms to stabilize large variances. Carabid activity (Fig. 4.5) did not differ significantly among the four vegetation types in either month (July: F=1.98 df=3,4 $p=0.26$; August: F=1.07 df=3,4 $p>0.05$). The distribution of the six most dominant species did not vary significantly among the types of ground covers (Table 4.1, df=3,4 range of F values=0.42-5.53 all $p>0.05$). However, the most abundant species, *P. melanarius* (Fig. 4.6) showed a trend toward higher activity in the intercrop and lower activity in the fescue plots.

Possible relationships between carabid activity and the number of pupae eaten in each plot during the two days of the experiment in July and August was studied using Pearson correlation analysis. There were no significant correlations between activity of dominant carabid species and the disappearance of pupae. The strongest correlations were for *P. adstrictus*, *A. placidum* and overall carabid activity (respective r's= 0.486, 0.311, 0.117). The correlations were weakly negative for *Amara torrida* and *Agonum cupreum*, which were the two dominant species in the fescue plots during late July to early August (see Table 4.1).

4.3.3 Crop types and movement of *P. melanarius*.

Sex of the beetles had no effect on habitat choice on either of the two dates (comparison of the number of beetles captured after one month: F=0.02 df=1,3 p=0.89; F=0.175, p>0.05 for runs 1 and 2 respectively), nor was there a significant interaction between crop and sex. Therefore, I pooled data across sexes for subsequent comparisons. Recaptures after 2, 4, 8, and 30 days were compared between dates, but the two runs of the experiment differed only after 2 days (F=8.14 df=1,8 p<0.05) when number of recaptures were very low. The interaction of crop and run for this period was not significant. For the other data about cumulative captures, there were no temporal effects or significant interactions with vegetation.

The above results allowed me to pool data across dates to analyze for possible differences in crop preferences with a one way ANOVA with four levels of vegetation. The effect of crop was highly significant in all periods (Fig. 4.7, range of F=6.21-9.32 df=3,12 p<0.01) except day 2 when the results for the significance of the differences in activity was marginal (F=3.67, df=3,12, p<0.05). *A posteriori* tests (Fisher PLSD) indicate that, after 2 days more beetles moved into the intercrop compared to the fescue plots. For the remaining periods the intercrop attracted more beetles than any of the three vegetation types (Fisher PLSD). No differences were found among these three latter vegetation types.

Data about beetles recaptured a second time were analyzed independently from those about initial recaptures because these beetles had already 'experienced' the habitat. The distribution of these 'repeats', is shown in Figure 4.8 for the entire month of trapping in the four vegetation types. Sex of beetles did not affect recaptures but date had a significant effect (F=5.82 df=1,8 p<0.05). Clearly the distribution of these 'repeat' beetles among the four vegetation types confirms the pattern observed in the initial recaptures. Far more repeat beetles moved to the intercrop than the three other vegetation types in both runs (run 1: F=16.61 df=3,4 p<0.05; run 2: F=36 df=3,4 p<0.01). The distribution of repeat beetles in the four crop followed that of initial recaptures (see Table 4.2a).

Since beetles were individually marked, I was able to consider choices made by individuals captured twice. I tested the hypothesis that individuals 'chose' the same crop a second time with chi square analysis. The observed proportion of beetles captured twice in the same plot was tested against a random distribution of recaptures (Table 4.2b). Expected values were the probability of an individual choosing the same plot twice in each block, i.e. 1/16. The observed distribution of recaptures pooled across runs departed significantly from random (X^2= 8.25 df=3 p<0.05). Further analyses with one way ANOVA suggested that more beetles were recaptured twice in the intercrop compared to the other three crop types (Fig. 4.9, run 1: F=6.39 df=3,4 p=0.052: run 2: F=29.89 df=3,4 p<0.01).

4.3.4 Food availability and habitat choice.

Presence of food supplements in faba bean and fescue plots had no effect on the distribution of *P. melanarius*, despite high rates of pupal disappearance (Faba bean-mean±S.E.: 97.3±1.11; Fescue: 53.0±12.07). Similar number of beetles were captured in these two vegetation types in the presence and absence of pupa (Figure 4.10). Also, increased food availability in these plots did not result in decreased recaptures in the adjacent intercrop and barley plots.

4.4 DISCUSSION.

4.5.1 Predation pressure and carabid activity.

Activity of ground predators can be studied directly using pitfall trap captures (Greenslade 1964) and indirectly by measuring the predation pressure (Speight and

Lawton 1976, Brust et al. 1986) exerted on a particular group of prey. Estimates of predation pressure can also be used to indicate the potential impact of natural enemies on arthropod pests in agroecoystems.

In this study I used disappearance rate of fly pupae as an estimate of predation pressure by ground predators, including carabids, and catches from pitfall traps to assess relative activity of carabids in the four crop types. My results suggest that overall predation pressure and carabid activity were not affected by the crop types, particularly among the three crops in the chemical system. There was a trend toward reduced activity in plots under fescue grass cultivation, which most likely has biological implications, as suggested by the interaction of crop type with prey size discussed below.

My results differ from findings of other workers where the nature of the crop (Rivard 1966, Varis et al. 1984) and plant diversity (Dempster and Coaker 1974, Speight and Lawton 1976, Ryan et al 1980, Tukahirwa and Coaker 1982, Barney et al. 1984, Brust et al. 1986) have affected activity of ground beetles. The main explanation offered by these workers for the effect of crop types on carabid activity is differential alteration of microclimates caused by the different crop canopies. Soil moisture is a common microclimatic indicator thought to affect carabid activity (Rivard 1966) but it has not been measured in these studies. In this study soil moisture content near the surface did not differ considerably among the four crop types. Water content ranged from 32% in the faba bean to 36 % in the intercrop. This may explain the lack of differences in predator activity in my study. Also, the three crop types, faba bean, peas-barley intercrop and two barley monocultures have been rotated in these experimental plots for the previous three years. It is possible that crop rotation has created fairly homogeneous carabid assemblages among the crop types. This hypothesis is supported by analysis of percent similarity of the carabid assemblages among the crop types in the chemical rotation and the fescue plots. The assemblages of ground beetles were quite similar in the crops (73 to 90 percent similarity) but they differed with the assemblage in the fescue plots (50 to 56 percent). This was consistent with the data on predator activity observed in these habitats.

Size of pupae was inversely related to their rates of disappearance. This pattern was not surprising since a wider range of predators can eat the small fruit fly pupae, whereas only larger predators are likely to attack the large *Sarcophaga bullata* pupae. This explanation is supported by lab observations (Appendix 1). Only the larger carabid *P. melanarius* ate *S. bullata* after 48 hours. Two other species, *P. lucublandus* and *Agonum cupreum* of intermediate size, only consumed the smallest pupa after the same period. This pattern of predation may explain the interaction between prey size and crop type, where predation of *Sarcophaga* pupae was significantly lower in the fescue than in the crops. Reduced predation pressure on the larger prey items is likely a reflection of the distribution of predator sizes in the fescue plots. *P. melanarius*, one of the largest predators (ca. 15 mm), showed decreased activity in these plots and *A. cupreum* was one of the dominant species. It appears that the thick mat developed by fescue grass poses a physical barrier preventing larger predators from effectively foraging in these habitats and as elaborated below, deterring their immigration.

Disappearance of pupae was consistently higher in the second day of the experiment in both trials across all crop types. This results suggest that more predators were attracted to the plots with pupae or that predators that found the pupae stayed longer in the area. The latter explanation is more plausible as there is evidence that movement of carabids can be affected by hunger levels (Wallin 1991). Furthermore, I showed that fly pupae availability did not affect immigration of carabids. Overall predation pressures were similar in July and August, however, predation in the fescue plots was significantly lower in August. Again, this may be related to the phenology of the smaller carabids that are usually more abundant earlier in the season.

The lack of correlation between carabid activity and predation pressure was unexpected as this group was the most abundant in my pitfall trap captures. Also, other workers have found high correlations between disappearance of *Drosophila* pupae and number of carabids in pitfall traps (Speight and Lawton 1976). One possibility is that vertebrate predators are involved in the removal of pupae. However, these predators are likely to consume the entire pupae and several remains of puparia, similar to those left in the lab by carabids, were seen in the field. Also, I observed in a few instances actual predation of the pupae by carabids, opiliones, staphylinids and anthocorids. Several workers have already argued (e.g. Floate et al. 1990) and shown experimentally (Dennis et al. 1990, Wratten 1987) that it is the entire group of ground predators that is important in the natural control of potential insect pests. Since carabids are an important component of this complex, they still merit the type of investigations illustrated in this chapter.

4.4.2 Crop types, food and habitat choice.

The second objective of this study was to test experimentally the influence of crop type and diversity on the habitat choice of ground beetles using the common introduced species, *P. melanarius*. Experimental studies of habitat choices with carabids have been undertaken with respect to forest vs. cultivated land (Wallin 1986) and in reference to farming operations (Lys & Nentwig 1991). To my knowledge, this is the first experimental investigation of the effect of crop type and diversity on the habitat choices of epigeal predators.

Similar numbers of *P. melanarius* were caught in faba bean and barley plots, suggesting that the physical nature of the crop did not affect habitat choices. Captures were lowest in the fescue plots, although not statistically different from the two crop monocultures. However, the intercrop of peas and barley attracted significantly more beetles than any of the three monocultures. These results are consistent with the distribution of *P. melanarius* in the larger rotation plots in the chemical system. However, in the rotation plots activity of *P. melanarius* in the intercrop was only slightly higher than the monocultures.

In the chemical system studied above, the effect of crop type was somewhat confounded by differences in agronomic practices. Because of the zero tillage employed in the chemical system and the crop rotation, there was considerable accumulation of residue on the surface. This layer provided shelter for ground predators and may have masked the effect of the crop canopy. In the small experimental plots there was no surface residue so that crop canopy structure could have a greater impact on the habitat choice of the beetles. The lack of difference between faba bean and barley in the small plots, confirmed that these two crop canopies did not alter the habitats sufficiently for *P. melanarius* to exhibit a preference.

The lowest activity in the fescue plots can be attributed to the thick mat which decreases immigration rates of larger predators like *P. melanarius*. Interestingly, this pattern persisted despite addition of *S. bullata* pupae to increase food availability. It seems that for this predator, vegetation structure is more important than distribution of prey. This barrier effect on ground dispersing predators, may reduce colonization and explain the pattern of lower carabid activity reported in pastures relative to cultivated habitats (e.g. Rivard 1966). It might be possible to 'enclose' large ground predators in garden plots for natural pest control purposes using fescue strips.

The higher immigration rates of *P. melanarius* in the intercrop can be considered partial evidence for Root's (1973) natural enemies hypothesis. This hypothesis states that natural enemies are more abundant and have a greater impact on herbivore pests in vegetationally complex systems (polycultures) than in simple monocultures. Increased accumulation of natural enemies in polycultures can occur as a result of higher imigration (colonization), recruitment, and reduced emigration (i.e. longer tenure times) (Sheehan 1986, Russel 1989).

The only process that has been studied using carabids is emigration rates. Perfecto et al. (1986) found that, at low plant densities, emigration rates of two carabid species were lower in a polyculture of tomatoes and beans than in a tomato monoculture. However, at higher plant densities the effect was reversed. Increased recruitment of natural enemies in polycultures has not been studied experimentally, although it is implicit in Root's (1973) hypothesis. Colonization rates, however have been shown to be higher in polycultures than in monocultures in some foliage generalist predators (Letourneau and Altieri 1987, Smith 1967). My results extend this phenomenon to ground dwelling predators.

The factors that mediate the higher colonization of polycultures by natural enemies, still remain a mystery for the most part. In an elegant experiment, Letourneau (1990) showed that diversity per se does not necessarily result in higher colonization. Rather, she suggested that plant density and architectural complexity can exert considerable influence in attracting natural enemies. Similar suggestions had been offered by Perfecto et al. (1986).

My explanation for the higher immigration of *P. melanarius* in the peas-barley intercrop is only speculative. Plant density could not account for the differences, as these were similar in the intercrop and the barley monoculture. Also, addition of *Sarcophaga* pupa to adjacent fescue and faba bean plots did not affect beetle distribution, suggesting that vegetational structure was more important than food availability. More likely the 'bushy' growth habit of peas in the intercrop, provides increased shading and more preferable microclimatic conditions in these plots. This effect was likely masked by the surface residue in the no till chemical system where only a weak trend of higher *P. melanarius* activity was found in the intercrop.

The accumulation of beetles in the intercrop could result from preferences for this habitat, implying that the beetles can recognize it. It may also result indirectly, from lower tenure times in the monocultures compared to the intercrop (Perfecto et al. 1986) or as a combination of these two processes. It seems unlikely that beetles were using visual cues to find the intercrop because the low density of pea plants might not provide a strong cue to distinguish this from the barley monoculture. It is possible that chemical cues emitted from the intercrop were detected by the beetles. Such mechanism has been reported to mediate the colonization of weedy polycultures by parasitoids (Altieri et al. 1981) but seemed not to apply for the anthocorid, *Orius tristicolor* (Letourneau 1990). More experimental tests are needed to study the factors mediating the attraction of polycultures to natural enemies.

Beetles recaptured a second time followed the same pattern of distribution in the four crop types as the initial recaptures. Analysis of beetles that were caught twice in the same plot suggests individual differences in habitat choices. The number of beetles that were taken in the same plot in two successive captures significantly departed from what would be expected from chance alone. Of particular interest is the fact that one third of the beetles initially caught in the intercrop returned to this habitat (35 out of 106). In fescue, faba bean and barley, the proportion of beetles that returned to these plots was extremely low (0/24, 2/35 and 3/44, respectively). Because of the smaller sample size of repeat recaptures in the monocultures, it is difficult to attribute this pattern to learning. However, learning has been reported for this species (Plotkin 1979) and has been observed in the field for *P. cupreus* with respect to prey searching (Chiverton 1988). Further experiments are necessary to distinguish learning in this beetle from simple individual variation in habitat selection.

4.5 REFERENCES.

Altieri, M.A , W.J. Lewis, D.A. Nordlund, R.C. Gueldner, and J.W. Todd. 1981. Chemical interactions between plants and *Trichogramma* wasps in Georgia soybeanfields. Prot. Ecol. 3: 259-263.

Altieri, M.A & W.H. Whitcomb. 1979. The potential use of weeds in the manipulation of beneficial insects. HortScience 14: 12-18.

Andow, D.A. 1991. Vegetational diversity and arthropod population response. Ann. Rev. Entomol. 36: 561-86.

Andow, D.A. 1990. Population dynamics of an insect herbivore in simple and diverse habitats. Ecology 71: 1006-1017.

Barney, R.J., W.O. Lamp, E.J. Ambrust and G. Kapusta. 1984. Insect predator community and its response to weed management in spring-planted alfalfa. Prot. Ecol. 6: 23-33.

Best, L.R. & C.C Beegle. 1977. Food preferences of five species of carabids commonly found in Iowa cornfields. Environ. Entomol. 6: 9-12.

Brust, G.E., B. R. Stinner, and D.A. MacArtney. 1986. Predation by soil inhabiting arthropods in intercropped and monoculture agroecosystems. Agric. Ecosyst. & Environ. 18: 145-154.

Chiverton, P.A. 1988. Searching behaviour and cereal aphid consumption by *Bembidion lampros* and *Pterostichus cupreus*, in relation to temperature and prey density. Entomol. Exp. Appl. 47: 173-182.

Chiverton, P.A. & N. Sotherton. 1991. The effects on beneficial arthropods on the exclusion of herbicides from cereal crop edges. J. Appl. Ecol. 28: 1027-1039.

Dempster, J.P. & T.H. Coaker. 1974. Diversification of crop ecosystems as a means of controlling pests. In Biology in Pests and Disease Control, D.P. Jones and M.E. Solomon (eds.). New York: Willey.

Edwards, C.A., K.D. Sunderland, and K.S. George. 1979. Studies on polyphagous predators of cereal aphids. J. Appl. Ecol. 16: 811-823.

Floate, K.D., J. Doane, and C. Gillott. 1990. Carabid predators of the wheat midge (Diptera: Cecidomyiidae) in Saskatchewan. Environ. Entomol. 19: 1503-1511.

Frank, J.H. 1971. Carabidae (Coleoptera) as predators of the redbacked cutworm (Lepidoptera: Noctuidae) in central Alberta. Can. Ent. 103: 1039-1044.

Fuller, B.W. 1988. Predation by *Calleida decora* (F.) (Coleoptera: Carabidae) on velvetbean caterpillar (Lepidoptera: Noctuidae) in soybean. J. Econ. Entomol. 81: 127-129.

Greenslade, P.G.M. 1964. Pitfall trapping as a method for studying populations of carabidae (Coleoptera). J. Anim. Ecol. 33: 301-310.

Gross, H.R. Jr. 1987. Conservation and enhancement of entomophagous insects - a perspective. J. Entomol. Sci. 22: 97-105.

Hance, T. 1987. Predation impact of Carabidae at different population densities on *Aphis fabae* development in sugar beet. Pedobiologia 30: 251-262.

Helenius, J. 1989. Intercropping, insect populations and pest damage: case study and conceptual model. PhD thesis. University of Helsinki. Helsinki.

Letourneau, D.K. 1990. Mechanisms of predator accumulation in a mixed crop system. Ecol. Entomol. 15:63-69.

Letourneau, D.K. & Altieri, M.A. 1983. Abundance patterns of a predator, *Orius tristicolor* (Hemiptera: Anthocoridae) and its prey, *Frankliniella occidentalis* (Thysanoptera: Thripidae): habitat attraction in polycultures versus monocultures. Environ. Entomol. 12: 1464-1469.

Lys, J.A. and W. Nentwig. 1991. Surface activity of carabid beetles inhabiting cereal fields: Seasonal phenology and the influence of farming operations on five abundant species. Pedobiologia 35: 129-138.

McGuinness, H. 1987. The influence of plant diversity and the nutritional content of the diet on the population dynamics of herbivorous pest insects. PhD thesis. University of Michigan, Ann Arbor.

Perfecto, I., et al. 1986. Effects of plant diversity and density on the emigration rate of two ground beetles, *Harpalus pensylvanicus* and *Evarthrus sodalis* (Coleoptera: Carabidae), in a system of tomatoes and beans. Environ. Entomol. 15: 1028-31.

Potts, G., and G.P. Vickerman. 1974. Studies on the cereal ecosystems. Adv. Ecol. Res. 8: 107-197.

Purvis G. and J.P. Curry. 1984. The influence of weeds and farmyard manure on the activity of carabidae and other ground dwelling arthropods in a sugar beet crop. J. Appl. Ecol. 21: 271-283.

Plotkin, H.C. 1979. Learning in a carabid beetle (*Pterostichus melanarius*). Anim. Behav. 27: 567-575.

Risch, S.J. 1980. The population dynamics of several herbivorous beetles in a tropical agroecosystem: the effect of intercropping corn, beans and squash in Costa Rica. J. Appl Ecol. 17: 593-213.

Rivard, I. 1966. Ground beetles (Coleoptera: Carabidae) in relation to agricultural crops. Can. Ent. 98: 189-195.

Russel, E.P. 1989. Enemies hypothesis: a review of the effect of vegetational diversity on predatory insects and parasitoids. Environ. Entomol. 18: 590-599.

Ryan, J., F. Ryan, and F. McNaeidhe. 1980. The effects of interrow plant cover on populations of the cabbage rootfly, Delia brassicae (Wiedemann). J. Appl. Ecol. 17: 31-40.

Sheehan, W. 1986. Response by specialist and generalist natural enemies to agroecosystem diversification: a selective review. Environ. Entomol. 15: 456-461.

Smith, J.G. 1976. Influence of crop background on natural enemies of aphids on Brussel sprouts. Ann. Appl. Biol. 83: 15-29.

Speight, M.R. and J.H. Lawton. 1976. The influence of weed-cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia 23: 211-223.

Tukahirwa, E.M., and T.H. Coaker. 1982. Effect of mixed cropping on some insect pests of brassicas: reduced *Brevicoryne brassicae* infestations and influences on epigeal predators and the disturbance of oviposition behaviour in *Delia brassicae*. Entomol. Exp. Appl. 32: 129-140.

Varis, A.L., J.K. Holopainen, and M. Koponen. 1984. Abundance and seasonal occurrence of adult Carabidae (Coleoptera) in cabbage, sugar beet and timothy fields in southern Finland. Z. Angew. Ent. 98: 62-73.

Vandermeer, J.H. 1988. The Ecology of intercropping. Cambridge University Press, New York.

Wallin, H. 1991. Movement patterns and foraging tactics of a caterpillar hunter inhabiting alfalfa fields. Functional Ecology 5: 740-749.

Wallin, H. 1986. Habitat choice of some field-inhabiting carabid beetles (Coleoptera: Carabidae) studied by recapture of marked individuals. Ecol. Entomol. 11: 457-466.

Winder, L. 1990. Predation of the cereal aphid *Sitobion avenae* by polyphagous predators on the ground. Ecol. Entomol. 15: 105-110.

Weiss, M.J., E.U. Balsbaugh, Jr., E.W. French, and B.K.Hoag. 1990. Influence of tillage management and cropping system on ground beetle (Coleoptera: Carabidae) fauna in the northern Great Plains. Environ. Entomol. 19: 1388-1391.

Wratten, S.D. 1987. The effectiveness of native natural enemies. *In* Integrated Pest Management. A.J. Burn, T. H. Coaker and P.C. Jepson, eds. pp. 89-112. AcademicPress, London.

Fig. 4.1: PLOTS SELECTED TO STUDY PREDATION PRESSURE

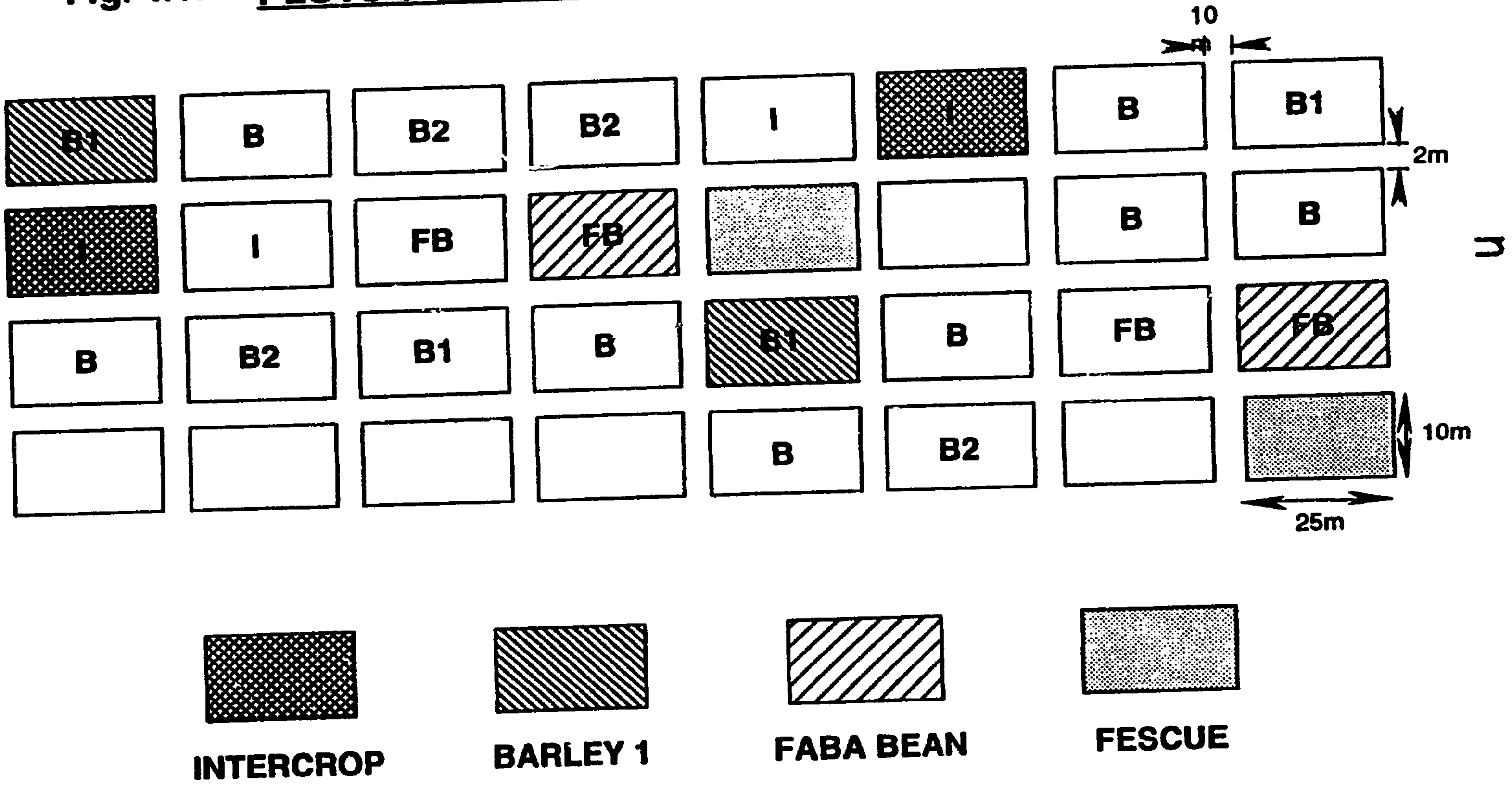
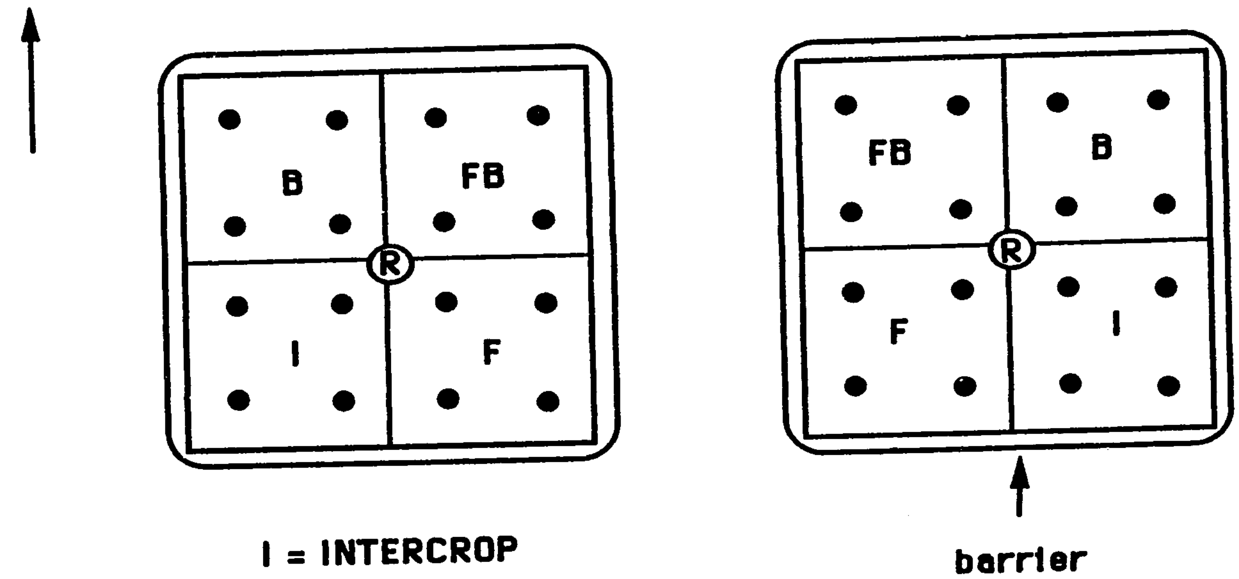


Fig. 4.2: Lay out of plots to study crop choices



I = INTERCROP
B = BARLEY
FB = FABABEAN
F = FESCUE
R= RELEASE POINT

FIG. 4.3: PUPAL DISAPPEARANCE AFTER 24 HOURS IN THE FOUR CROP TYPES

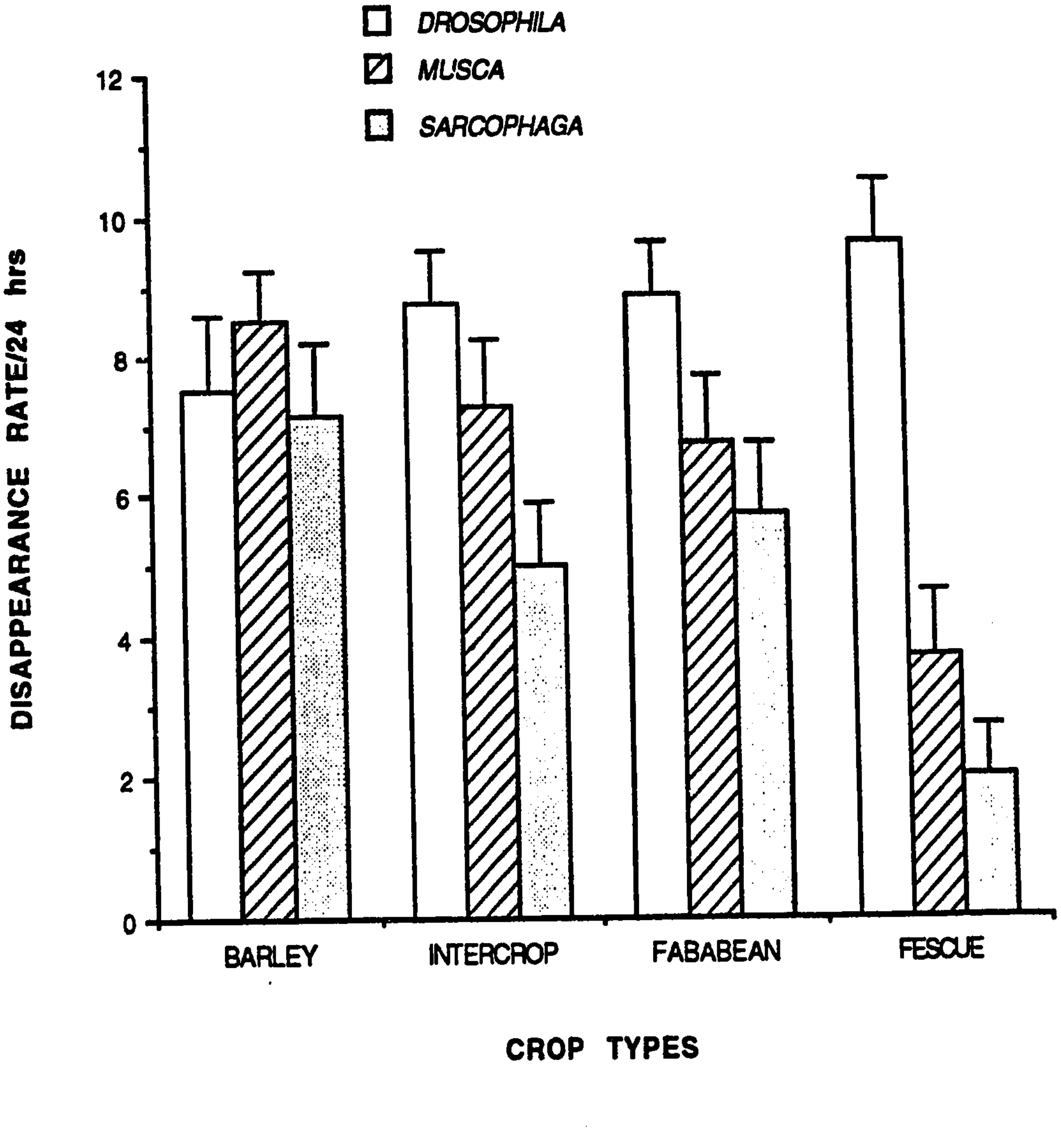


Fig. 4.4 a: Daily variation in pupal disappearance

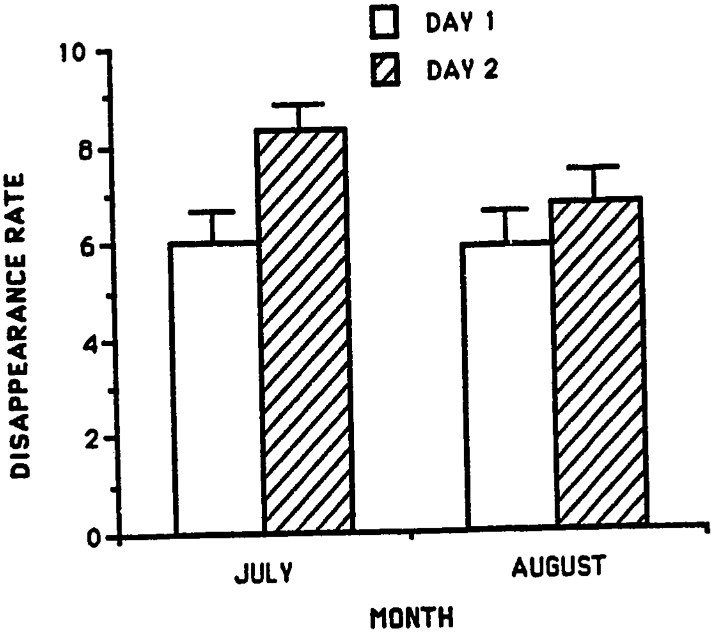


Fig. 4.4 b: Monthly variation in pupal disappearance

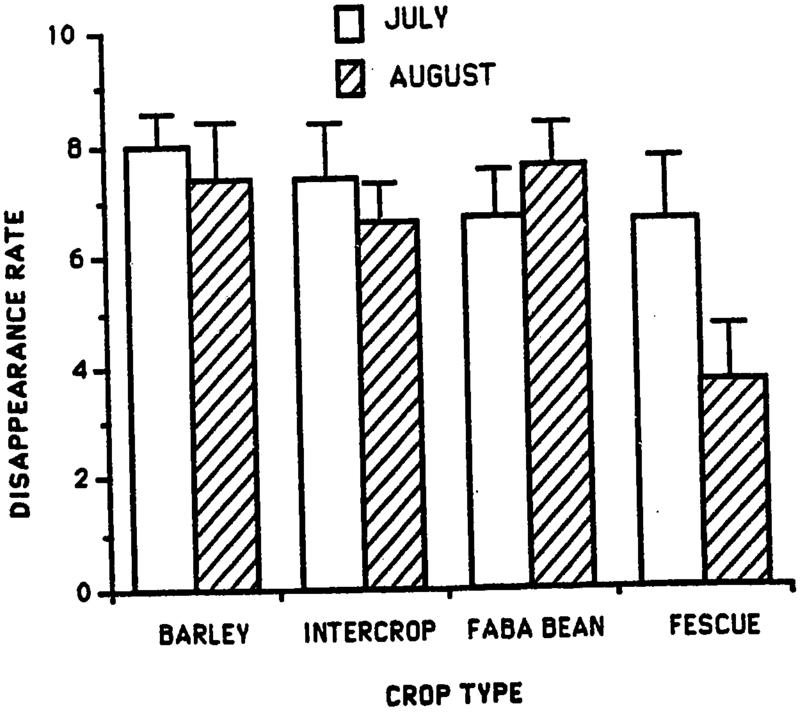


Fig. 4.5: Effect of vegetation cover on beetle activity

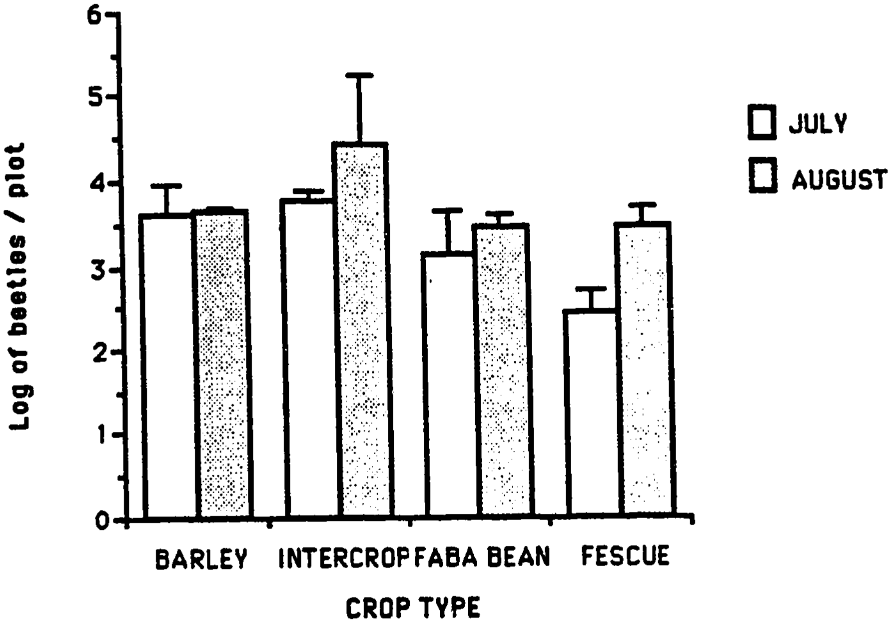


Fig. 4.6: Effect of vegetation cover on *P.melanarius* activity in August 1991.

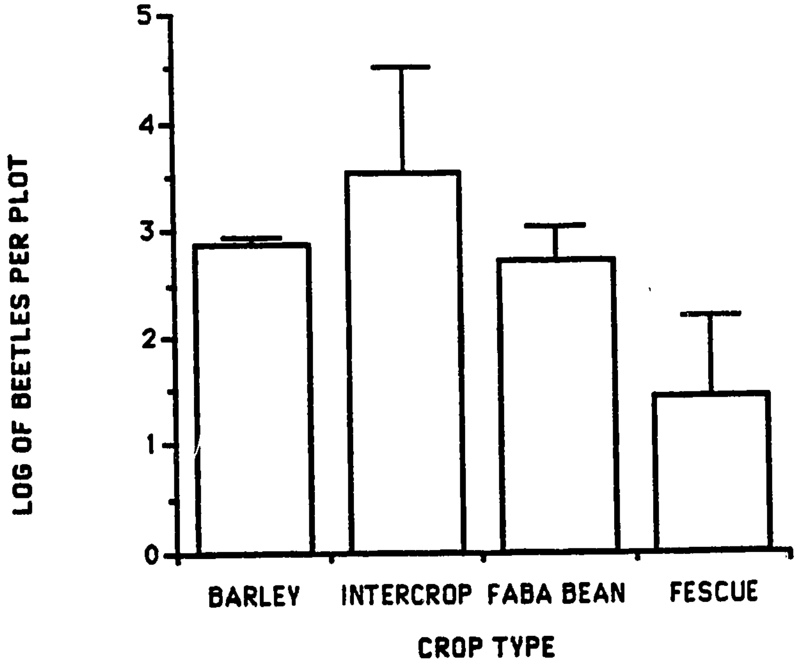


Fig. 4.7: Cumulative first time recaptures of *P. melanarius*

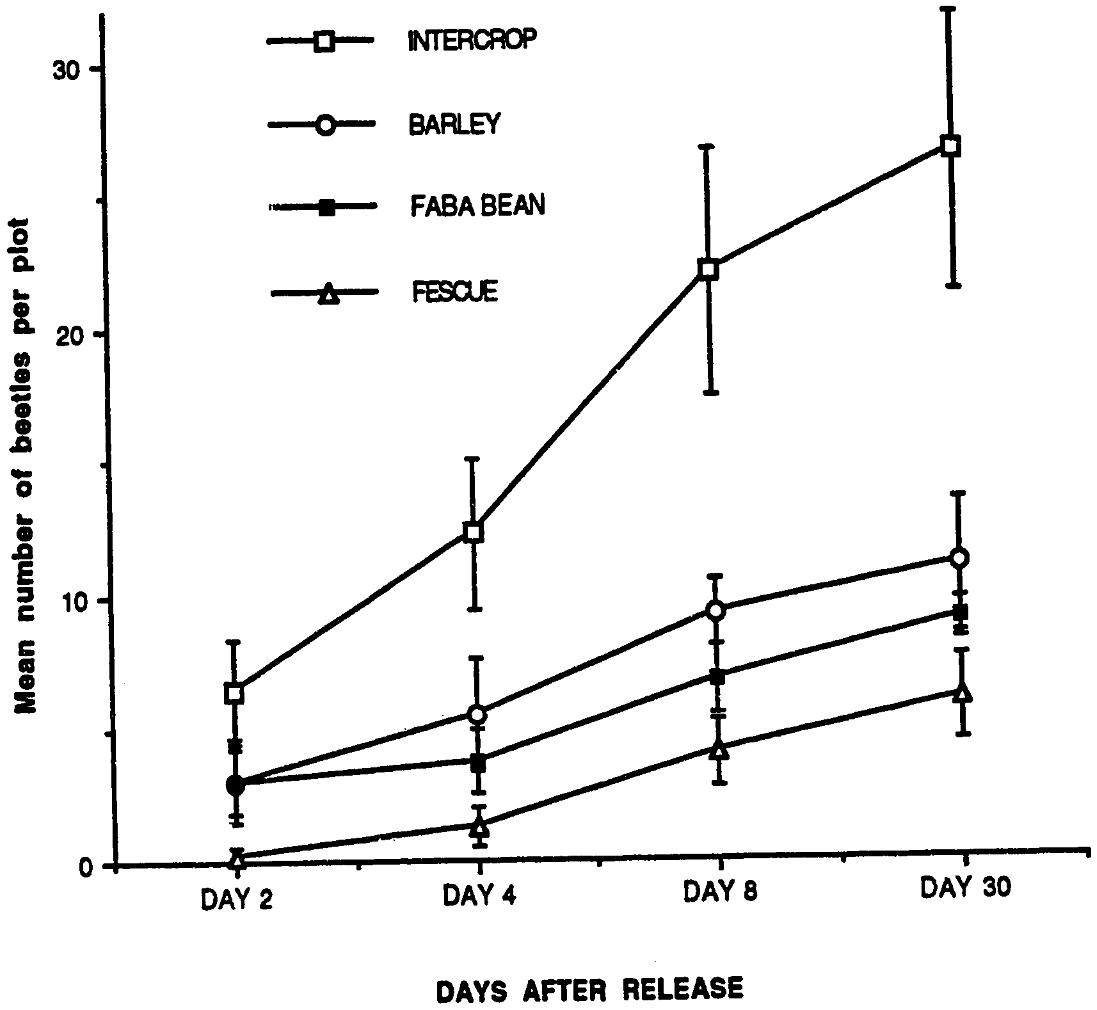


Fig. 4.8: Distribution of repeat recaptures in the four crop types.

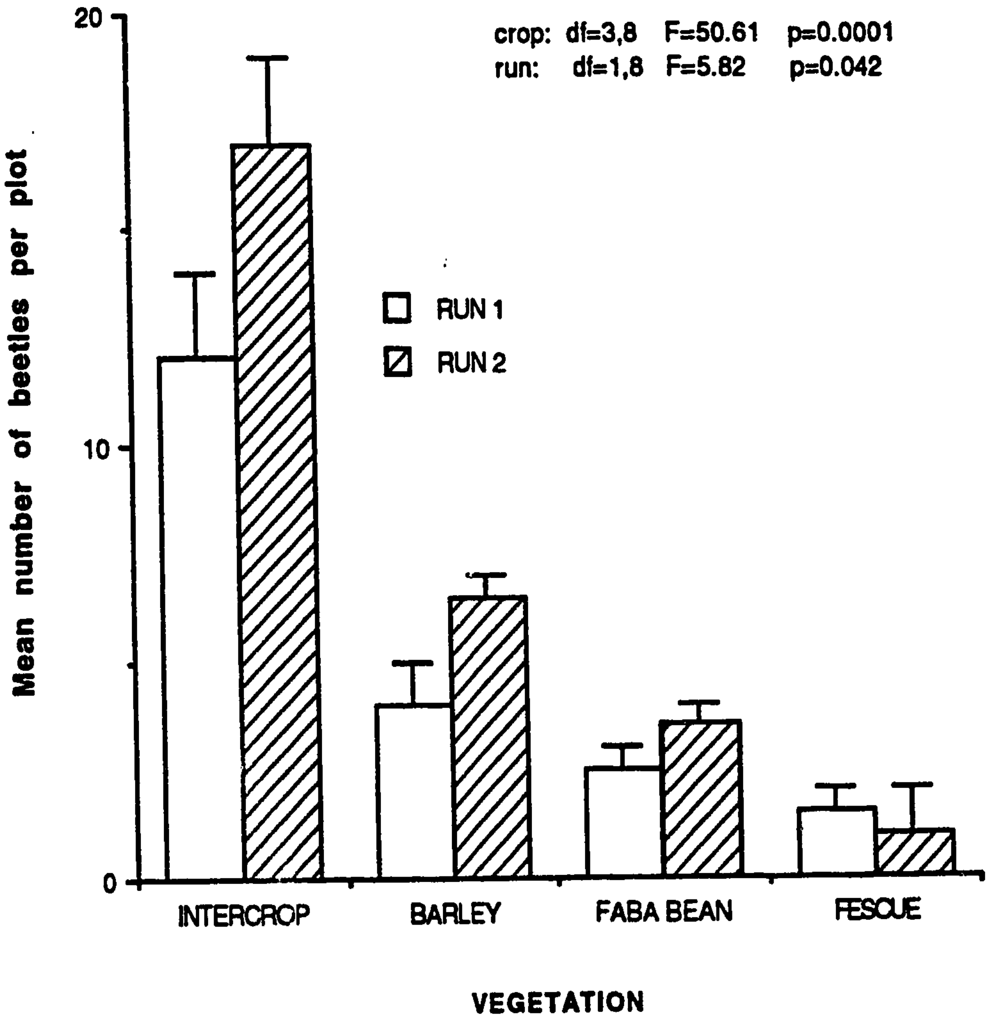


Fig. 4.9: Crop type distribution of beetles captured twice in the same plot.

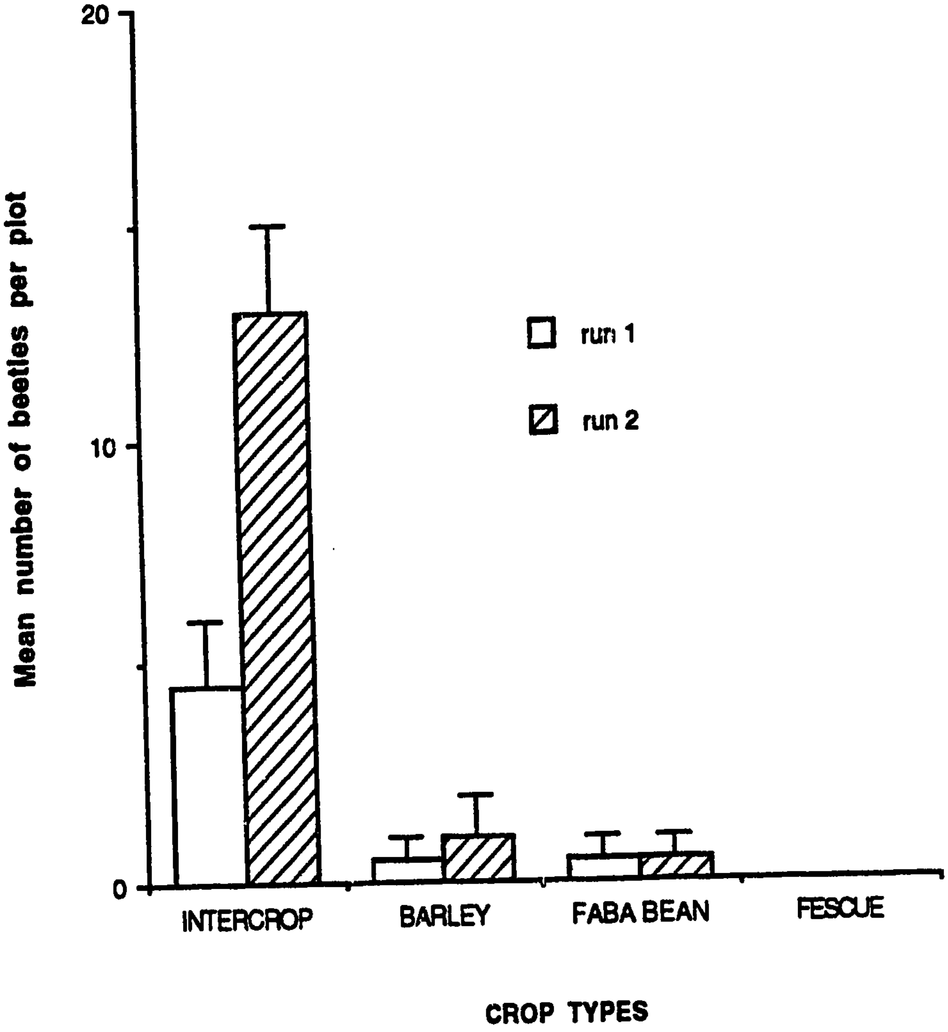


Fig. 4.10: Effect of food availability on crop choice

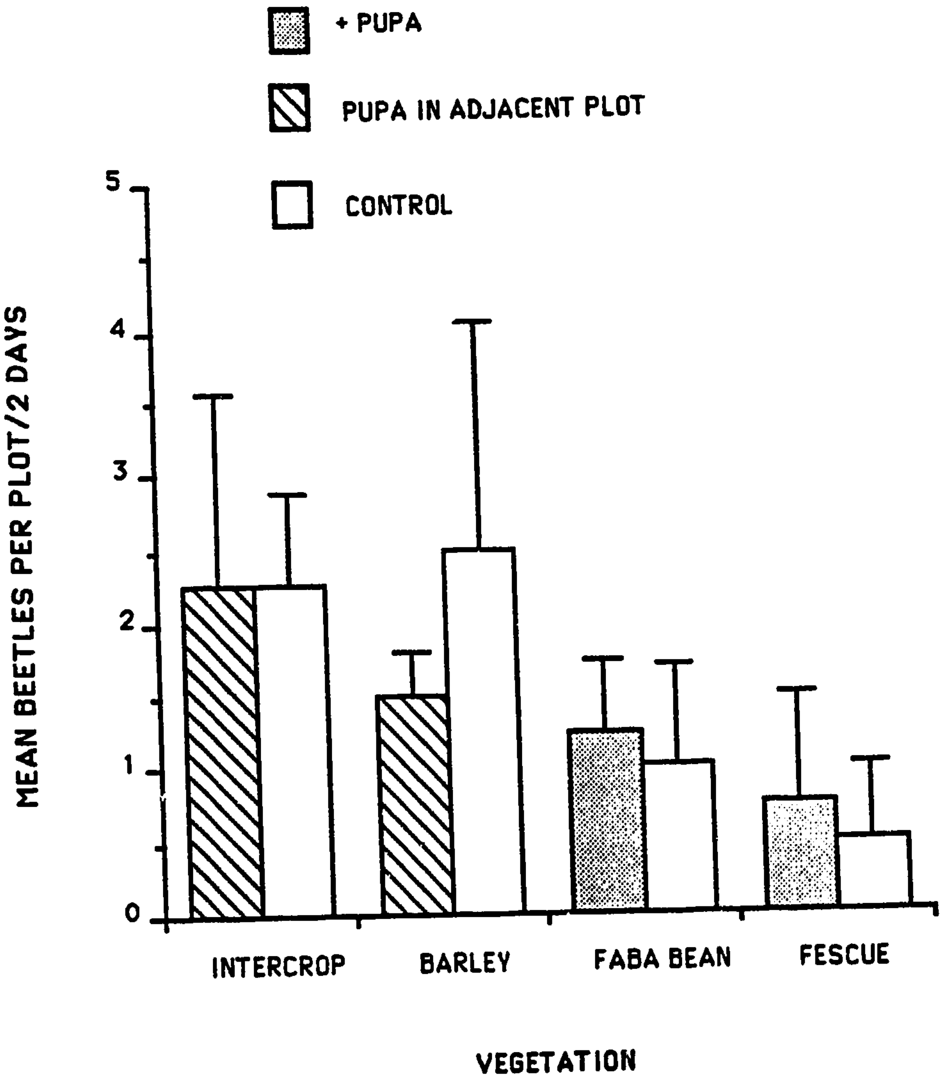


Table 4.1: Relative abundance of dominant carabids in the four crop types.

	INTERCROP				BARLEY				FABA BEAN				FESCUE				TOTAL	
SPECIES	JULY		AUGUST		JULY		AUGUST		JULY		AUGUST		JULY		AUGUST		JULY	AUG.
		%		%		%		%		%		%		%		%		
P. melanarius	6	40	105	57.07	1	6.67	36	19.6	6	40	32	17.39	2	13.33	11	5.978	15	184
P. lucublandus	13	25.49	49	70	19	37.3	9	12.9	11	21.569	11	15.71	8	15.69	1	1.82	51	70
P. adstrictus	6	24	13	44.83	16	64	12	41.4	3	12	4	13.79	0	0	0	0	25	29
Agonum cupreum	42	51.85	17	30.36	10	12.3	3	5.36	21	25.926	3	5.357	8	9.877	33	60	81	56
A. placidum	19	45.24	9	69.23	17	40.5	1	7.69	3	7.1429	2	15.38	3	7.143	1	1.82	42	13
B. bimaculatum	1	20	1	20	4	80	4	80	0	0	0	0	0	0	0	0	5	5
C. serratus	2	50	3	42.86	2	50	1	14.3	0	0	3	42.86	0	0	0	0	4	7
Amara torrida	0	0	23	51.11	3	60	8	17.8	2	40	7	15.56	0	0	7	12.7	5	45
Other*	2	12.5	6	46.15	4	25	3	23.1	7	43.75	2	15.38	3	18.75	2	3.636	16	13
Total	91	37.3	226	53.55	76	31.1	77	18.2	53	21.721	64	15.17	24	9.836	55	13.03	244	422

* See Appendix 2 for complete species list

Table 4.2a: Summary of the distribution of *Pterostichus melanarius* individuals in four crop types in the mark-recapture experiment. Entries are number of individuals with percentage of total captures in parenthesis. I/C= intercrop of peas-barley, F/B= faba bean.

	CROP TYPE				
CAPTURE	I/C	BARLEY	F/B	FESCUE	TOTAL
1sts	106 (51)	44 (21)	36 (17)	24 (11)	210
2nds	58 (59)	21 (21)	14 (14)	5 (5)	98
same crop	35 (87.5)	3 (7.5)	2 (5)	0	40

Table 4.2b: Distribution of second recaptures in relation to first crop captured. R= run or date, B= block, W= west, E= east.

Replicate	total captured	in same crop	observed proportion	Expected proportion
R1XBW	19.000	5	0.26	0.06
R1XBE	22.000	6	0.27	0.06
R2XBW	29.000	13	0.45	0.06
R2XBE	28.000	16	0.57	0.06

5. CONCLUSIONS

5.1 SUMMARY.

Agricultural practice can affect the structure and activity of ground beetles. Using faunistic studies in experimental plots (Chapter 2), I showed that organic farming methods can enhance carabid species diversity as well as activity of native species. Crop diversity and rotation, however, could not be shown to affect the carabid assemblage in either the organic or chemical farming systems. Overall carabid activity in adjacent fescue plots was lower than in the crops. Manipulation of tillage and nitrogen regimes did not affect overall carabid activity or species diversity. Two common species were affected by tillage regime, but in opposite ways and only *Amara torrida* was more abundant in plots with nitrogen addition.

Agricultural disturbance (soil tillage, crop, and chemical inputs) had a very conspicuous impact on carabid communities. The carabid assemblage from a nearby uncultivated meadow had significantly lower species richness, but much higher activity than the assemblages from the experimental plots.

The overwhelming abundance of the introduced species, *Pterostichus melanarius* at the meadow compared to the experimental plots suggests the potential for species interactions which may be affected by the intensity of agricultural practice.

Faunistic studies in adjacent experimental plots can be confounded by spatial scale effects. In Chapter three, I used a more realistic spatial scale, that of the commercial farm, to investigate effects of agricultural practice on carabid assemblages. The predominant difference between the two barley farms located near Neerlandia was tillage regime. Within each farm, number of species, diversity and activity were similar among three replicate pitfall trapping grids. This can be taken as an indication that carabid distribution in those uniform monocultures was not clumped. Overall abundance of carabids was significantly higher at the 'conventional tillage' farm (ploughed) than at the 'conservation tillage' farm. However, species varied in their responses to tillage regime and the pattern of overall abundance was caused by the dominant species *Agonum placidum*, collected more frequently at the 'conventional tillage' farm. Species richness was slightly higher at the 'conservation tillage' farm and the Shannon-Wiener indices of diversity and evenness were significantly higher at this farm than at the 'conventional farm'. Single linkage cluster analysis revealed distinct assemblages in these two farms. The variation in responses to tillage regime by individual species needs to be studied in relation to their life history strategies and possible species interactions.

Crop type and diversity could not be shown to affect carabid activity in the faunistic studies reported in Chapter 2, probably because of limitations of the experimental design. To further test effects of crop type on activity of epigaeic predators I measured disappearance rates of fly pupae in the three crop types of the chemical system and adjacent fescue plots. Predation pressure was similar in the three crop types, barley, faba bean and barley-pea intercrop, but it was higher than in the fescue plots. Furthermore, there was a significant interaction between crop type and size of pupa. This pattern of predation pressure was consistent with the pattern of carabid activity around the time of the experiments, although they were not significantly correlated. A trend of higher activity in the intercrop was noted for the dominant species *Pterostichus melanarius*. In mark-release-recapture choice experiments using field arenas, this species was recaptured more frequently in the intercrop than in any of the three other monocultures. Also, significantly more individuals returned to the intercrop plots after the first recapture while none of the beetles initially captured in the fescue returned to these plots. Addition of fly pupae to increase food availability in fescue and faba bean did not change the distribution pattern of *P. melanarius*.

5.2 GENERAL DISCUSSION

Ecosystem diversification has been called the first line of defense against potential insect pests (Speight 1983). In the previous three chapters I have studied ground beetle assemblages under some strategies that provide varying degrees of agroecosystem diversification. At the field level, I studied organic vs. chemical farming and conventional vs conservation tillage using adjacent plots and commercial farms. At the farm level, diversification can be achieved by leaving patches of uncultivated land within the matrix of cropped habitats. In Chapter 2 I investigated the carabid fauna of an uncultivated field nearby the experimental plots.

There is a very robust pattern emerging with respect to ground beetle assemblages in organic farming systems. Studies from experimental plots as illustrated in Chapter two and farm scale studies (Dristichillo and Wanner 1982, Hokkanen and Holopainen 1986, Kromp 1989) have clearly shown that organic farming systems harbour greater abundance and sometimes a greater diversity of ground beetles. It is likely that other beneficial arthropods are affected in a similar manner. Organic farming, therefore, may lead to fewer problems with insect pests as a result of enhanced activity of natural enemies.

The effect of conservation tillage on ground beetle communities is less clear than that of organic farming. I used two spatial scales, experimental plots and commercial farms, to study the effects of tillage on carabid communities. In the experimental plots, I did not find significant differences between 'no tillage' and 'conventional tillage' plots and in the farm study, overall carabid activity was higher in the 'conventional tillage' farm. I conclude that tillage disturbance does not affect all carabid species the same way, and that some species, such as *Agonum placidum* will be more abundant in conventional tillage systems. This conclusion agrees with the published work since at least a few workers have found no effect of tillage or negative effects of conservation tillage on carabid assemblages. In several studies, however, overall abundance has been higher in conservation tillage systems (see Stinner and House 1990), but even in these studies some species were negatively affected. Given current rates of soil erosion (Poincelot 1986), conservation tillage will no doubt play an important role in North American agriculture. However, its adoption should be encouraged in light of a framework of sustainability within an organic farming system. Such a strategy may enhance natural enemy communities to control potential pests.

The faunistic studies presented in Chapter two suggested no effect of crop type and diversity on carabid activity. However, crop type, in particular crop diversity has been found to strongly affect communities of arthropods (e.g. Andow 1991, Altieri and Letourneau 1984, Risch et al. 1983). In Chapter four, I conducted additional studies of predation pressure and crop choices to further investigate the potential impact of crop type on carabid beetles. Similar predation pressure across the crop types in the chemical rotation confirmed the lack of differences in overall carabid activity estimated from pitfall trap catches. The results of the crop choice experiment, on the other hand, showed a strong effect of crop diversity on the distribution of *Pterostichus melanarius*.

In the farming method study (organic vs. chemical) the lack of effect of crop diversity on carabid activity is likely the result of the experimental design. I suggest that crop rotation in my study confounded the effect of crop type by creating a fairly homogeneous carabid assemblage. Also in the chemical system (no tillage) rotation, accumulation of residue masked any differences in soil moisture that may have resulted from different crop types. The lack of physical barriers and the close proximity of several monoculture plots to the intercrop may have contributed to the lack of effect of crop complexity. It should be noted that a weak trend of more *P. melanarius* in the intercrop was noted at the beginning of its activity in July and August. In light of these considerations, and my results from the behavioural crop choice experiments, I conclude that polycultures can attract more carabid beetles than the corresponding monocultures. This conclusion agrees with previous work with carabids where greater activity (Perfecto et al. 1986, Tukahirwa and Coaker 1982) or predation pressure (Brust et al. 1986, Speight and Lawton 1976) was found in polycultures. In temperate agroecosystems, carabids may be important contributors to the associational resistance of polycultures.

5.3 FUTURE STUDIES

There are several questions that need to be answered with respect to the effects of agricultural practice on natural enemies such as carabid beetles. Many of these have to do with describing the basic pattern of species assemblages as affected by agronomic practice. With respect to testing actual processes that lead to the observed pattern there is a very long way to go as very little is known in this area. In the next section I identify some topics that I perceive deserve the attention of agroecologists.

At this point, it is still unknown what specific factors of organic farming enhance communities of carabid beetles. One of the obvious hypotheses that needs to be tested is the effect of herbicides. This, of course, needs to be separated from the effect of weed abundances that confounds impact of herbicides. To test these separate components, it will be necessary to design factorial experiments where weeds are removed by hand and compared with herbicide treatments and weedy controls.

With respect to tillage, the current pattern of carabid community responses is not very clear and more faunistic studies are required in temperate zones. One strategy that may yield important results is to undertake autoecological studies of common species to better understand their responses to tillage. The high variation observed in species responses to tillage treatments may be the result of interaction with other factors. These may include effects of tillage on prey and predator distributions and even other indirect effects mediated through potential competitors.

Research on intercropping systems in general is relatively underdeveloped in Canada. More studies of its effects on arthropods are required to confirm the patterns reported for tropical or subtropical areas. The designs of such experiments should take into account the effects of plant density and architecture that often confound the impact of plant diversity.

In addition to discovering the pattern of carabid beetles and other natural enemies under sustainable agricultural practices, it will be necessary to study their impact on potential herbivore pests. Several studies have found more carabids under organic or intercropped systems, but it is not known what the consequences are for the management of insect pests. This task will require quantifying the impact of predators on the population dynamics of herbivores through experimental manipulations.

Another area that needs attention is the unravelling of actual processes that determine the observed pattern of carabid communities in alternative agricultural systems. Practices such as organic farming, intercropping and conservation tillage are thought to result in greater heterogeneity which enhances populations of carabids. However, the specifics still need to be worked out. For example, are beetles responding to improved microclimatic conditions ? To increased prey availability ? To reduced predation or competition ? The answer, as is often the case, will be complex and will require sophisticated experimental designs that take into account the potential of various interactions among the variables.

Agroecosystems have been viewed by some workers as unsuitable units to test basic ecological theory. However, many such systems provide ideal settings to study both population and community processes that are of interest to ecologists and indispensable for the design of environmentally sound food production systems. One example is found in the problem of crop diversity and its effects on arthropod communities. Showing a pattern of higher enemy abundance in diverse systems only provides partial evidence for Root's (1973) enemies hypothesis. A complete test requires demonstrating that enemies affect the populations of herbivores. Perhaps a more effective approach is that illustrated by Andow (1990) where life tables for the herbivores are prepared in both complex and simple systems. Such an approach allows direct comparison of the enemies impact and that of herbivore movements (resource concentration).

Agroecosystems can also be used to assess effects of introduced species on the native fauna. My results suggested a strong effect of *P. melanarius* on the native species in an uncultivated meadow. This interaction is worth studying in more detail as it appears to be affected by the intensity of agricultural activity. The next step will be to conduct more faunistic studies in sites with similar conditions but without the introduced species. Also it may be of interest to survey sites that vary in intensity of agricultural activity, as it appears that less disturbed, more uniform sites may lead to stronger species interactions. Ultimately, it will be necessary to conduct competition experiments using field exclosures in open habitats, similar to those conducted by Niemelä and Spence (pers. comm.) in forested habitats.

5.4 REFERENCES

Altieri, M.A. & D.K. Letourneau. 1984. Vegetation diversity and insect pest outbreaks. CRC Crit. Rev. Plant Sci. 2: 131-169.

Andow, D.A. 1991. Vegetational diversity and arthropod population response. Ann. Rev. Entomol. 36: 561-86.

Andow, D.A. 1990. Population dynamics of an insect herbivore in simple and diverse habitats. Ecology 71: 1006-1017.

Brust, G. E., B.R. Stinner, and D.A. MacArtney 1986. Predator activity and predation in corn agroecosystems. Environ. Entomol. 15: 1017-1021.

Dritschilo, W., & D. Wanner. 1980. Ground beetle abundance in organic and conventional corn fields. Environ. Entomol. 9: 629-631.

Hokkanen, H., and J.K. Holopainen. 1986. Carabid species and activity densities in biologically and conventionally managed cabbage fields. J. Appl. Ent. 102: 353-363.

Kromp, B. 1989. Carabid beetle communities (Carabidae, Coleoptera) in biologically and conventionally farmed agroecosystems. Agric. Ecosyst. & Environ. 27: 241-251.

Perfecto, I., et al. 1986. Effects of plant diversity and density on the emigration rate of two ground beetles, *Harpalus pensylvanicus* and *Evarthrus sodalis* (Coleoptera: Carabidae), in a system of tomatoes and beans. Environ. Entomol. 15: 1028-31.

Poincelot, R.P. 1986. Towards a more sustainable agriculture. AVI Publishing Company Inc. Wesport, Connecticut.

Risch, S.J., D. Andow, and M.A. Altieri. 1983. Agroecosystem diversity and pest control: data, tentative conclusions and new research directions. Envriron. Entomol. 12: 625-629.

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*) Ecol. Monogr. 43: 95-124.

Speight, M.R. and J.H. Lawton. 1976. The influence of weed-cover on the mortality imposed on artificial prey by predatory ground beetles in cereal fields. Oecologia 23: 211-223.

Stinner, B.R. & G.J. House.1990. Arthropods and other invertebrates in conservation-tillage agriculture. Ann. Rev. Entomol. 35: 299-318.

Tukahirwa, E.M., & T.H. Coaker. 1982. Effect of mixed cropping on some insect pests of brassicas: reduced *Brevicoryne brassicae* infestations and influences on epigeal predators and the disturbance of oviposition behaviour in *Delia brassicae*. Entomol. Exp. Appl. 32: 129-140.

APPENDIX 1.

Laboratory observations of fly pupae predation by carabid beetles.

Nine out of ten *Bembidion* individuals readily fed on fruit fly pupae glued to paper towel as in the field experiments. Also, individuals of three species of common carabids were offered the three sizes of pupae over 48 hours while held in 500 ml plastic containers in the laboratory. All adults of *Pterostichus melanarius* tested (3 males and 5 females), ate all three sizes of prey after 48 hours. However, adults of *P. lucublandus* and *Agonum cupreum* (5 males and 5 females for both species) consumed only the small *Drosophila*.

APPENDIX 2.

Carabid species found in Ellerslie.

Pterostichus melanarius
P. adstrictus
P. pensylvanicus
P. lucublandus
P. corvus
Amara torrida
A. quenseli
A. farcta
A. familiaris
A. littoralis
A. obesa
A. cupreolata
A. latior
A. avida
A. apricaria
A. ellipsis
A. anthobia
Bembidion quadrimaculatum
B. mutatum
B. canadianum
B. timidum
B. nitidum
B. bimaculatum
B. rupicola
B. obscurellum
Harpalus herbivagus
H. amputatus
H. fraternum
H. carbonatus
H. egregius
Agonum placidum
A. cupreum
A. sordens
A. gratiosum
A. obsoletum
Carabus serratus
C. taedatus
Calosoma callidum
Calathus ingratus
Synuchus impunctatus
Clivina fossor
Notiophilus aquaticus
Loricera pilicornis
Cymindis crybricollis
Chlaenius purpuricollis
Dyschirius globulosus
Tachys nanus
Trichocellus cognatus