THE EFFECTS OF HABITAT DISTURBANCE ON THE OCCURRENCE OF CARABID BEETLES

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THE OCCURRENCE OF CARABID BETTLES

BY

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A thesis submitted to the Faculty of Graduate Studies of the University of Manitoba in partial fulfillment of the requirements of the degree of

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ABSTRACT

Richardson, R.J. M.Sc., The University of Manitoba, October, 1982. The Effects of Habitat Disturbance on the Occurrence of Carabid Beetles. Major Professor: N. J. Holliday.

The effects of habitat disturbance on the occurrence of ground beetles were studied in agricultural and forest habitats, using pitfall traps.

During 1979 and 1980, the occurrence of carabid beetles was assessed in arable land which had been tilled, treated with herbicide or (in 1980 only) mown. Most species, such as *Amara avida*, *Pterostichus corvus* and *Anisodactylus sanctaecrucis*, were captured more frequently in the control areas than in the treatment areas. *Amara apricaria* was more commonly caught in the control areas for the first 6-8 weeks following the application of the treatments; subsequently, it was captured most frequently in the tilled areas. In 1979, *Harpalus amputatus* was caught most often in the herbicided plots from 6 weeks after the treatment application. The differences between the captures of all species were less marked in 1980 than in 1979, probably as a result of differences in the vegetation present before the treatments were applied. In 1980, the subsequent regrowth of vegetation in the different plots was more similar.

From 1978 to 1981, the indirect effects of an intense forest fire on the occurrence of carabid beetles were studied. Areas of burnt aspen and burnt spruce were compared to areas which had been similar before the fire. In the first year following the fire, *Pterostichus pensylvanicus* and *Carabus taedatus* were caught most commonly in the unburnt

sites. P. lucublandus and Dicaelus sculptilis upioides were captured most frequently in the unburnt aspen site. Harpalus laticeps was captured only in the burnt sites while P. adstrictus was captured most frequently in the burnt spruce site. Most species continued to show a similar pattern of occurrence in the following years, except H. laticeps and Calathus ingratus which were captured in the burnt aspen site in 1978 only. The occurrence of P. adstrictus changed after 1978: by 1981 there were no significant differences in the numbers of this species captured in all 4 plots. In 1981, P. lucublandus was caught for the first time in the unburnt spruce site. Agonum decentis was captured for the first time in 1981 when it was recorded in the unburnt spruce site. These last 2 species probably immigrated from adjacent more suitable habitats.

The differences observed in carabid occurrence were probably the result of the effects of habitat disturbance on the vegetation and the resulting changes in the microclimate.

FOREWORD

This thesis is written in the paper or manuscript style and includes three papers. The paper entitled "Occurence of carabid beetles (Coleoptera:Carabidae) in a boreal forest damaged by fire" has been published in the Canadian Entomologist 114:509-514 (1982). The paper "Effects of tillage and herbicide application on the occurence of ground beetles (Coleoptera:Carabidae) in an arable field" will be submitted to the Journal of Animal Ecology in a modified form with additional data. As the research project being conducted in the burnt forest habitat is a longterm one, a modified form of the paper "Changes in the occurence of ground beetles (Coleoptera:Carabidae) in a boreal forest during the first four years following a fire" will be submitted to a journal after several more years data have been collected.

I. INTRODUCTION

Carabid beetles are an important part of all temperate ecosystems (Lindroth 1957; Kulman 1974). In arable land, they have been suggested as possible agents of biological control (eg. Kulman 1974; Best and Beegle 1977; Allen 1979). Doane and Schaefer (1971) reported that *Calosoma sycophanta* L. has been used to control outbreaks of the gypsy moth (*Porthetria dispar* (L.)) and the browntail moth (*Nygmia phaeorrhoea* (Donovan)). Frank (1971) reported 21 species of carabid that fed on the eggs of the red-backed cutworm (*E. ochrogaster*). Although carabids are probably not capable of controlling outbreaks of pest insects in general, they will be an important component of any integrated pest management scheme (Thiele 1977). Carabids also play a considerable role in the ecology of forests as primary and secondary consumers (Thiele 1977).

It is therefore important to know what effects habitat disturbance has on their occurrence. The effects of different cultural practices (tilling and herbiciding) on the populations of carabid beetles occurring in an area of arable land near Glenlea, Manitoba were studied. In addition, the effects of secondary plant succession on the occurrence of carabid beetles following an intense forest fire were investigated.

II. LITERATURE REVIEW

Pitfall Trapping

The most common method used to sample populations of Carabidae is pitfall trapping, whereby small containers are placed in the ground so that they are level with the ground surface. Beetles whose paths are intercepted by the traps fall in and are unable to escape. The number of beetles captured in this manner depends not only on the population density but also on the activity of the species concerned (Mitchell 1963).

Luff (1975) discussed several factors affecting the efficiency of pitfall trapping. He found that large traps were most effective at capturing large species and small traps were most efficient for catching small species. Approximately 75% of the beetles that came into contact with the trap perimeters were captured but about 10% per day of beetles caught in metal pitfall traps were able to escape.

Under certain conditions, however, pitfall trap catches may accurately represent actual population densities and distributions. Greenslade (1964a) stated that if a species is captured in higher numbers in an area of vegetation which offers more resistance to its movement than another, then this probably represents the specie's true distribution. In addition, if two species are captured each in one type of ground cover and are never caught together, then this probably represents their true distributions as well (Greenslade 1964b).

Baars (1979a) used brandmarked carabids and known numbers of beetles released into enclosures to assess pitfall trapping as a method for estimating mean densities. He found that pitfall trap catches summed over the entire activity period of the species in question showed a satisfactory linear relationship with mean densities. This hypothesis was also tested with computer simulation studies. It was suggested that carabid beetles must "work through a fixed reproductive program each year by means of an almost constant total amount of locomotor activity which is realized step by step during spells of suitable weather". Studies using radio-actively marked beetles (Baars 1979b) demonstrated that this kind of sporadic day to day activity does occur.

Habitat Disturbance

In terrestrial habitats, most disturbances are seen as modifications of the vegetation. These disturbances can be the result of vegetation destruction by pathogens, herbivores and man (including agricultural practices)as well as by such phenomena as severe winds, fire or climatic fluctuations (Grime 1979).

Generally, soon after a single severe disturbance, species diversity decreases, that is, there are only a limited number of species which are able to survive in the new conditions brought about by the disturbance (Connell 1979). In disturbances of a less severe nature, species diversity is not as adversely affected. Connell (1978) has suggested that maximum species diversity is reached in those communities subjected to "smaller disturbances that are neither very frequent nor very infrequent". The effects of habitat disturbances are best viewed in the context of the adaptations of individual species, independent of whole communities, as it is these individual adaptations which determine responses to disturbances (Horn 1981).

Den Boer (1968) has suggested that the number of carabid beetles in populations occurring in unstable or disturbed habitats are stabilized and "spread the risk" of extinction by several different methods. Among them are phenotypic variation and the spreading of risk in space. The dimorphism exhibited by carabid beetles with respect to wing length involves both these methods.

Many species of ground beetles are dimorphic with respect to wing length and flight ability; macropterous individuals are in many cases capable of flight, while brachypterous individuals are flightless (Thiele 1977). Populations of dimorphic species generally consist of beetles of both morph types. Populations in unstable habitats often have a greater proportion of long-winged individuals, while populations in stable habitats tend to have more short-winged beetles or may even be monomorphic brachypterous (den Boer et al. 1980). It is thought that in unstable habitats, the populations are spreading their risk of extinction by investing more heavily in individuals capable of dispersing and founding new populations (den Boer 1968). In stable habitats, populations tend to become more brachypterous in nature as the macropterous beetles which leave take away the genes associated with high dispersal ability (den Boer et al. 1980).

A number of authors have reported that habitat disturbances affect the number and diversity of carabid populations. Freitag (1979) reviewed the effects of pollution on carabid populations and found ground beetles to be "highly sensitive and intolerant to a variety of polluting substances". Lavigne and Campion (1978) studied the effects of ecosystem stress (the addition of water and/or nitrogen) on populations of carabids. They found that the number of carabids increased, probably as the result of the increased plant cover and its affect on the microclimate and availability of prey items. Dritschilo and Erwin (1982) investigated the differences in abundance and diversity of carabids in cornfields subjected to different farm practices, such as the addition of pesticides. They found that both the number of individuals and the number of species were significantly lowered in disturbed plots, but that four commonly used measures of diversity showed no significant differences among the treatments. They suggested that this lack of change in diversity indeces was probably an artifact and not a true representation of the diversities in the field. It was assumed that this type of habitat stress would decrease carabid diversity. In general, most forms of habitat disturbance cause a change in the diversity of the fauna present (May 1978).

Habitat Disturbances in Arable Land

The changes in habitat that necessarily accompany agriculture can have large effects on the occurrence of epigeic arthropods inhabiting arable land. These changes can be the result of various cultural practices including tilling, herbiciding, and cutting of the vegetation in the field. The major affect of these practices is to alter the structure of the microhabitat through a modification of the plant community, from complete destruction (tilling) to the removal of just a portion of the above ground vegetation (cutting).

Altieri and Whitcomb (1979) found that by tilling fields in northern Florida at different times of the year, different populations of weeds resulted. With each type of regrowth were associated different kinds and densities of herbivorous insects as well as predatory arthropods (including several species of Carabidae). Speight and Lawton (1976) found that the number of carabids captured in pitfall traps in a winter wheat field varied directly with the abundance of the annual meadow grass Poa annua L. and not with the abundance of wheat itself. They suggested that the reason for this may be the higher humidity found under a dense carpet of vegetation such as P. annua than in more open areas such as the stands of wheat. Baker and Dunning (1975) reported that carabids of the genus Pterostichus Bon. (= Feronia Lat. in their paper) were more commonly found in areas where sugar-beets were sparse. They attributed this difference to the greater amount of shading offered by the more dense foliage. At the same time, however, they found that greater numbers of Bembidion spp. were caught on bare soil than in areas covered with vegetation. This may have been due to the lower resistance offered to their movement by the bare soil as compared to areas of vegetation. Greenslade (1964a) noted that carabids tended to be caught less frequently in areas which offered higher resistance to their movement than other areas; this would be particularly marked in small species such as Bembidion as almost any vegetation would offer considerable resistance to their movement.

Several studies have investigated the effects of herbicide application in the abundance of soil fauna in arable land. Edwards and Stafford (1979) found that the number of arthropods occurring in fields treated with different herbicides was at least initially reduced. They attributed the changes in arthropod densities to the changes in vegetation brought about by the herbicide and not to any direct effects. This is in concordance with the findings of others such as Stam et al. (1978) who found that two out of the three herbicides which they studied were relatively non-toxic to insects (coccinellids and hemipterans) and that the third, although somewhat toxic, was less toxic than insecticides tested. The effects of a single application of several herbicides in grassland soil were studied by Fox (1964) over a two year period. The numbers of earthworms (Lumbricidae), mites (Acarina) and springtails (Collembola) were not reduced by herbicide application, and the densities of other insects increased or decreased depending upon the species. These changes were attributed to the indirect effects of the herbicides on the floristic makeup of the grassland.

Using the herbicide trifluralin, Finlayson et al. (1975) found that that occurrence of carabid beetles in a minicauliflower plot was not affected. They did find, however, that there were higher numbers of carabids in untreated, unweeded plots and felt that this was probably due to the dense cover offered by the weeds found there.

A direct toxic effect of the herbicide 2,4,5-T has been shown for the forest carabid Notiophilus biguttatus Fabr., both as the result of direct spraying and of ingesting contaminated food items (collembolans) (Eijsackers 1978). In general, though, it appears that the indirect effects of the herbicides through their effects on the vegetation in the habitat are of much greater importance to the occurrence of insects in general and to ground beetles in particular.

The effects of tillage can also alter the occurrence of soil invertebrates. Loring et al. (1981) showed that immediately following tillage the numbers of collembola and pyemotid mites decreased significantly. Four months after tillage, towards the end of the sampling program, the numbers of collembola and mites increased to near pre-treatment levels. Edwards (1975) found that the number of staphylinid and carabid beetles were greater in tilled fields than in direct drilled sites (direct drilling results in less habitat disturbance than tilling). It should be noted, however, that the populations were assessed using soil core sampling taken only every two months, and that one-half of each 6.4x18.0 m plot was treated with an insecticide. The results obtained by sampling that size area only once in every two months may have been obscured by the fluctuations in population densities which normally occur over small time periods. Abbott et al. (1979), on the other hand, found that the numbers of termites, ants and beetles declined as the result of cultivation. They believed that this decline was due to the actual physical disturbance of the soil by ploughing.

Disturbance in Forest Habitats

The major disturbance occurring in many forests is fire. It is an integral part of forest ecology and many plants are adapted to survive burning. In a sequoia-mixed conifer forest in California, Kilgore and Taylor (1979) found evidence of low-intensity fires occurring as often as every 9-16 years. Rowe and Scotter (1973) reported that for most of the boreal forest in Canada, fires occur at least once every 130-140 years. Walker (1982) suggests that the spread of some species of tree into the conifer-hardwood forests in the early post-glacial period was facilitated by intense fires. Mutch (1970) hypothesised that many plant communities have developed inherent flammable properties which have led to the perpetuation of fire-dependent plants. Many forest plants are adapted to the point where they require fire. For example, white pine (*Pinus strobus* L.) and jack pine (*P. divaricata* Ait.) have serotinous cones which require the heat of a fire to open them and release their seeds (Chapman 1952; I.F. Ahlgren 1974). Other species of pine are adapted to surviving low-intensity fires at intervals of from 3 to 10 years (Chapman 1952). Stands of trembling aspen (*Populus tremuloides* Michx.) are able to produce a vigorous and dense regrowth following fires by growing from subterranean shoots and roots which are generally undamaged by the fire (Walker 1982).

The immediate effects of fire are varied and depend on (among other factors) the intensity of the fire. They range from complete destruction of all above ground vegetation in an intense burn to the killing of just the low growing under story in a low-intensity fire (Walker 1982). The immediate effects of fire on many forest insects is to reduce their numbers (Lyon *et al*. 1978). Springett (1979) found reduced numbers of arthropods (mainly collembolans and mites) in a Western Australian forest which had been burned. Not all insects are reduced in number following fire: Evans (1971) reported several beetles (including Carabidae) which are attracted to forest fires.

In a fire-damaged radiata pine (*Pinus radiata* D. Don) plantation French and Keirle (1969) reported that initially the densities of all insects (except for termites and cicadas which were insulated in the soil) were reduced. Among the first insects to recolonize the burned site were carabid beetles. Harris and Whitcomb (1974) found that most species of Carabidae were more numerous in plots from which fire had been excluded for 10 years than in annually burned plots. There were two species which were more common in the burned plots.

Factors Affecting Carabid Occurrence Following Habitat Disturbance

The reduction in the occurrence of beetles in the burnt forest habitat and in the tilled sections of the agricultural habitat occurred quickly and was probably due, to a large extent, to the physical effects of the disturbances on the carabids. After these direct effects took place, other factors, mainly the result of the subsequent vegetational changes, affected the carabid populations.

One of the major factors affecting the occurrence of carabid beetles is humidity. Rivard (1966) showed that the number of carabids caught in arable land seemed to be related to the relative humidity of the microhabitat as influenced by the type of vegetation present. As the humidity in the fields increased, the number of carabids increased. Thiele (1977) reported that, in general, ground beetles will select an area of higher humidity if offered a choice. Geiger (1966) showed that as the density of vegetation increases, so does the relative humidity due to the reduced air flow through the microhabitat. Therefore, one would expect higher numbers of Carabidae to occur in areas of high vegetation density, whether it be in arable land or forest habitats, than in areas of low plant density such as tilled areas or some more open burned forest areas.

Other factors such as the availability of food items and oviposition sites are important. Many workers have shown that the numbers of other insects and plants (potential food items) are drastically altered following many types of habitat disturbance (C.E. Ahlgren 1974; Altieri and Whitcomb 1979; Edwards and Stafford 1979; Springett 1979; Loring _et al._

1981). Goulet (1974) showed that *Pterostichus adstrictus* Eschscholtz utilizes rotten logs for oviposition sites and larval development. Any area with an increased number of dead trees, such as a boreal forest following a fire, should then tend to have a greater number of *P. adstrictus*.

OCCURRENCE OF CARABID BEETLES (COLEOPTERA: CARABIDAE) IN A BOREAL FOREST DAMAGED BY FIRE

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Abstract

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Fifteen months after an intense forest fire, the fauna of carabid beetles in burnt and unburnt sites was sampled using pitfall traps to detect the indirect effects of fire on carabids caused by habitat change. Traps were installed in burnt and unburnt sites in which the dominant tree species before the fire was either spruce or aspen. The most commonly caught species was *Pterostichus pensylvanicus* which was captured more frequently in unburnt sites, but was not affected by dominant tree species; a similar pattern of distribution of captures was found for *Carabus taedatus*. *Harpalus laticeps* was captured only in burnt sites. *P. lucublandus* and *Dicaelus sculptilis upioides* were most commonly caught in the unburnt aspen site, while *Pterostichus adstrictus* was most commonly caught in the burnt spruce site.

Résumé

Quinze mois après un feu de forêt grave, la faune carabique de parcelles brûlées ou non brûlées a été inventoriée à l'aide de trappes afin de déterminer les effets indirects du feu sur les carabes suite à la perturbation du milieu. Des trappes furent placées dans des parcelles buûlées ou intactes, oû l'espèce d'arbre dominante avant le feu était soit l'épinette, soit le tremble. L'espèce piégée le plus souvent a été *Pterostichus pensylvanicus*, laquelle fût capturée plus fréquemment dans les parcelles non brûlées, mais n'était pas influencée par l'espèce d'arbre dominante; un profil de distribution des captures similaire a été mis en évidence pour *Carabus taedatus*. *Harpalus laticeps* fût capturé seulement dans les parcelles brûlées. *P. lucublandus* et *Dicaelus sculptitis upioides* ont été capturés le plus souvent dans la parcelle de tremble intacte, alors que *Pterostichus adstrictus* a été capturé le plus souvent dans la parcelle d'épinette brûlée.

Introduction

The effects of fire upon the fauna of ecosystems have been reviewed recently (Lyon *et al.* 1978). Fire affects the arthropod fauna of an area in two ways: firstly, there are direct effects of heat and smoke upon the arthropods living at the time of the fire; secondly, there are indirect effects caused by the fire's modification of the arthropod habitat (Lyon *et al.* 1978). I. F. Ahlgren (1974) in her review of the effects of fire upon soil organisms, states that in forest fires most beetle genera are at least temporarily reduced in abundance. French and Keirle (1969) observed that fire resulted in an immediate reduction in carabid abundance in pine plantations. Some insects are attracted to forest fires and so their densities increase during and immediately following a fire. Evans (1971), in a list of insect species attracted to forest fires, includes three carabid species of the carabid genus *Agonum*.

Studies of longer term effects of forest fires on carabids are few. Harris and Whitcomb (1974), working in pine forests in Florida, compared carabid populations in annually burnt plots with those in unburnt plots. They attributed most of the observed differences to the effects of changes in vegetation and leaf litter produced by fire, rather than to direct effects of fire on carabid beetles.

The objective of the current study is to examine the indirect effects of fire upon the carabid beetle fauna of a boreal forest just north of the aspen parkland ecotone in Manitoba. To achieve this the carabid faunas of unburned and burned areas were sampled using pitfall traps, put in position 15 months after the fire. This timing was chosen to avoid confusion of the direct effects of the fire with those brought about by changes in vegetation.

Methods

In April 1977 an intense forest fire occurred in the Interlake region of Manitoba about 150 km north of Winnipeg. The burnt area was irregularly shaped with extreme dimensions of 38 km (west to east) and 29 km (north to south). Before the fire the forest consisted mainly of stands of spruce (*Picea mariana* (Mill.) B.S.P. and *P. glauca* (Moench) Voss) and of aspen (*Populus tremuloides* Michx.).

In 1978, four sites, each 50×50 m, were selected (in Township 26, Range 2 East) such that two sites were in the burnt area and two were in an unburnt area. One site in each area was in a spruce stand and one in an aspen stand. Sites were selected so that the species composition of trees in the unburnt and burnt areas before the fire (determined from aerial photographs) was similar in the two aspen stands and in the two spruce stands and so that the soil in all sites was of similar type. The soils in the sites were calcareans loams of the Fairford or Inwood series, overlying glacial till; drainage was classified as good to imperfect, and topography as level to undulating (Smith *et al.* 1975). To obtain sites with this degree of similarity in pre-burn forest composition, and soil type, it was necessary to locate burnt sites about 4.5 km from the corresponding unburnt sites.

Species composition of trees after the fire was determined using a line transect method, and the densities of living and dead trees over 2 m in height, were estimated by counting trees in belt transects. Carabids were sampled using a grid of 16 pitfall traps in each site; the distance between traps was about 12.5 m. Traps were galvanized steel tubes, 8.3 cm in diameter and 15 cm deep into which was inserted a second tube (7.8 cm diam. and 7 cm deep) of the same material. The inner tube had a lip at the top and a 65 mesh/cm screen at the bottom to retain the catch. Traps were sunk into the ground so that the lip of the inner tube was supported on the outer tube and was level with the ground surface. This arrangement enabled traps to be emptied without disturbing the ground, and the screen retained the carabids while allowing rain water to pass through. Traps were emptied after each week of trapping. In addition to pitfall trapping, 0.1 m^2 quadrat samples of soil, litter, and vegetation were taken and hand-sorted to remove carabids.

Pitfall trap catches of each of the commonly collected species were analyzed separately. Data transformed to stabilize the variance and ensure additivity before factorial analysis of variance was carried out. Orthogonal contrasts were then used to assess effects of specific sites (Snedecor and Cochran 1980).

Results

Before the fire, both aspen sites were classified as pure trembling aspen (*Populus tremuloides*) on the forest inventory maps derived from aerial photographs (Manitoba Department of Natural Resources, unpub.). The burnt spruce site was classified as pure black spruce (*Picea mariana*). The unburnt spruce site was classified as 90% black spruce, 10% trembling aspen.

Figure 1 and Table I show the characteristics of the sites after the fire. The estimates of tree density were made in winter to avoid the dense foilage of the aspen regrowth. A consequence of this timing is an underestimate of the density of dead trees since some of these had fallen and were snow-covered. This problem was particularly acute in the burnt spruce site where many dead trees had been blown down or felled. This accounts for the discrepancy between the densities shown

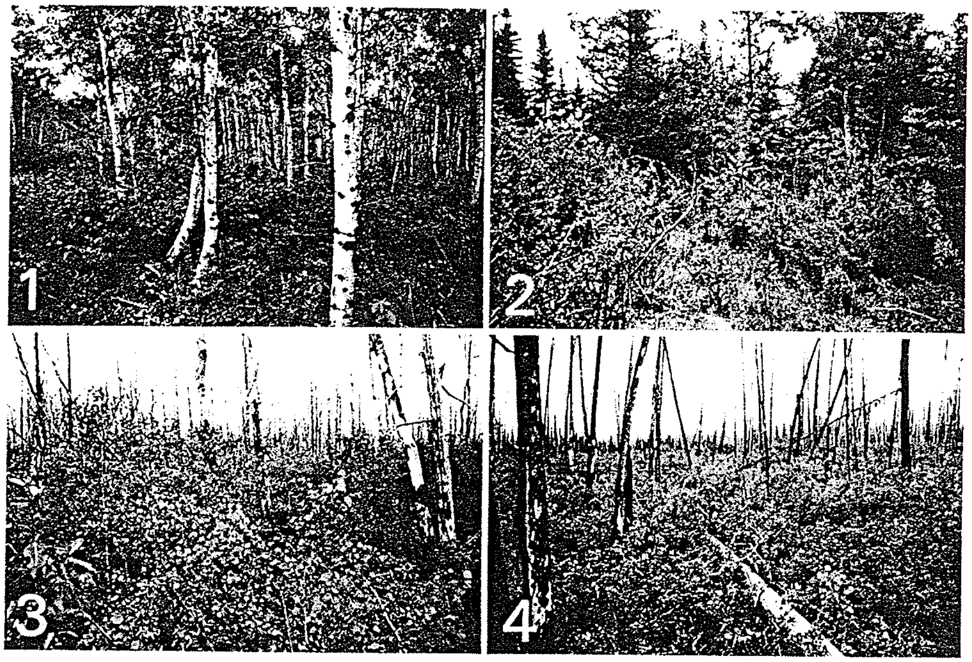

FIG. 1. Photographs of sites. 1, unburnt aspen site. 2, unburnt spruce site (area of *Cornus alba* in foreground). 3, burnt aspen site. 4, burnt spruce site.

Table I. Characteristics of study sites after the forest fire

	Unburnt aspen	Burnt aspen	Unburnt spruce	Burnt spruce
Tree density/ha				
Living	5660	17800	9084	1408
Dead	-	6200	-	1968
% species composition of living trees				
Populus tremuloides Michx.	77	97	2	73
Picea mariana (Mill.) B.S.P.	8	-	41	-
Picea glauca (Moench) Voss	8	-	20	-
Cornus alba L.	-	3	35	4
Larix laricina (Du Roi) K. Koch	-	-	2	-
Salix spp.	-	-	-	23

in Table I, and the evidence of aerial photographs that the two spruce stands were similar before the fire.

Table II shows the names and total numbers captured in pitfall traps of the most common carabid species. Trapping took place continuously for a total of 20 weeks from June to November 1978. An intensive programme of quadrat sampling of soil and litter was also carried out in each site, but no carabids were recovered.

Analysis of variance showed that there were significant differences ($P < 0.01$) in the frequency of capture of *Pterostichus pensylvanicus* between burnt and control plots: both in the first (4 July - 15 August) and second (5 September - 4 November) period of activity the frequency of capture was lower in the burnt sites. Similarly lower numbers of *Carabus taedatus* ($P < 0.001$) were caught in burnt sites than

Table II. Total number of specimens captured of the most frequently caught species of carabids

	Site			
	Aspen		Spruce	
Species	Unburnt	Burnt	Unburnt	Burnt
Pterostichus pensylvanicus Leconte	89	48	110	9
Carabus taedatus Fabricius	38	2	23	2
Harpalus laticeps Leconte	0	10	0	13
Pterostichus lucublandus Say	22	1	0	0
Pterostichus adstrictus Eschscholtz	0	3	0	13
Agonum cupripenne Say	8	2	1	5
Calathus ingratus Dejean	5	4	10	0
Dicaelus sculptilis upioides Ball	19	0	0	0
Synuchus impunctatus Say	7	0	1	1

control sites. In contrast, *Harpalus laticeps* was captured only in burnt sites ($P < 0.01$). Captures of *Pterostichus lucublandus* ($P < 0.01$), and *Dicaelus sculptilis upioides* ($P < 0.01$) were all significantly more frequent in the aspen control site than in the remaining sites. *Pterostichus adstrictus* was captured only in burnt sites and was significantly more frequent in the burnt spruce site ($P < 0.02$).

Discussion

The immediate effect of the fire was to kill the above ground vegetation. In the burnt aspen site there was then rapid dense regrowth (Table I) of the type described by C. E. Ahlgren (1974). Vegetation in the burnt spruce site was comparatively sparse after the fire, so that the habitat was quite open with many fallen trees (Fig. 1).

The catch in a pitfall trap is not necessarily indicative of the population densities of carabid species in a site. Mitchell (1963) has shown that pitfall trap catches depend upon population density and activity of beetles; the efficiency of a pitfall trap is also influenced by the vegetation immediately surrounding it (Greenslade 1964). Attempts to estimate carabid populations by soil sampling were unsuccessful, and so we have no estimate of the component of variation in pitfall trap catches which was due to factors other than differences in carabid density. However, Baars (1979) showed that a reliable relative measure of the density of a carabid species in different habitats can be obtained by continuous pitfall trapping. Hence, in the current study, comparisons of trap catches between sites for a single species probably indicate the relative density of that species in the sites. Comparisons of catches between species are more difficult to interpret, since there is no reason to believe that trap efficiency is the same for different species.

Pterostichus pensylvanicus was caught in all the sites (Table II) but captures were more frequent in unburnt sites. There were no significant differences in the frequency of capture between spruce and aspen sites ($P > 0.05$). This is in contrast to the observations of Goulet (1974), who found the species to be confined to deciduous forest litter on moist soil. Lindroth (1966) reported the species among dead leaves and moss under alder bushes on gravel soil, while Barlow (1970) and Rivard (1964) considered it a species of woodlands and their margins. Freitag (1973) reported finding a specimen of *P. pensylvanicus* in litter in a spruce forest. In the spruce unburnt site, examination of catches of individual traps did not show any association of *P. pensylvanicus* captures with the distribution of deciduous trees (mainly *Cornus alba* (Table I)). It appears then that there is a real difference in habitat preference between the *P. pensylvanicus* of Goulet's (1974) study and this study. *Carabus taedatus* was more frequently caught in control sites than in burnt sites. Lindroth (1961) reported that *C. taedatus* was a species of gravel soils with thin vegetation, or of coniferous forests, while Frank (1971) recorded the species in an arable field.

Harpalus laticeps was captured only in burnt sites, never in unburnt sites. Little is known of the ecology of *H. laticeps*; it has been reported in sandy upland woods (Blatchley 1910) and on sea shores (Lindroth 1955).

P. lucublandus was most frequently captured in the unburnt aspen site. Rivard (1964) found *P. lucublandus* on moist soils with moderate to dense ground vegetation, while the species has been reported from croplands by Kirk (1971), Lund and Turpin (1977), and Frank (1971). *Dicaelus sculptilis upioides* was captured only in the unburnt aspen site (Table II); the ecology of this insect has not previously been recorded (Lindroth 1969).

P. adstrictus was found only in burnt sites but was most common in the burnt spruce site. Goulet (1974) and Lindroth (1966) report that adults of this species are widely distributed, in woodland and open areas. The frequency of capture in the sites seems roughly in concordance with the number of fallen trees and logs there. These were most abundant in the burnt spruce, less so in the burnt aspen, and almost absent in the unburnt sites. Goulet (1974) reported that the immature stages of *P. adstrictus* occur in rotten logs.

Thiele (1977) suggested that the distributions of forest carabids are influenced by microclimate. Geiger (1966) described how dense vegetation (such as in the burnt aspen and unburnt spruce sites) reduces wind speed and allows extremes of temperature to occur. However, because of the intercorrelations of edaphic, vegetational and microclimatic factors, it is not possible to identify with certainty any one factor as being responsible for the distribution of carabid species.

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Changes in the occurrence of ground beetles (Coleoptera:Carabidae) in a boreal forest during the first four years following a fire

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ABSTRACT

The effects of plant succession following an intense forest fire on the occurrence of carabid beetles was studied using pitfall traps from 1978 to 1981. Areas of burnt aspen and burnt spruce were compared to unburnt sites which had been similar before the fire. P. pensylvanicus and C. taedatus were captured most frequently in the unburnt sites throughout the 4 years (although P. pensylvanicus did show some variation from year to year). P. lucublandus was captured most commonly in the unburnt aspen site except in 1981 when it was also recorded in the unburnt spruce plot. A. decentis was captured only in 1981 in the unburnt spruce site. Both H. laticeps and C. ingratus were recorded in the burnt aspen site in 1978 but not subsequently. In 1978 P. adstrictus was captured most frequently in the burnt spruce site. In the following years, there tended to be a much less pronounced difference in the numbers caught among the plots. Differences in microclimate produced by the effects of the fire on the vegetation are probably responsible for the observed differences in carabid occurrence. For most species, the period of 4 years following the fire is probably too short to detect any differences due to the effects of plant species replacement.

INTRODUCTION

Fire is a natural ecological process occurring in many types of plant community (Chapman 1952; Rowe and Scotter 1973; Vogl 1977) while some plants are even fire dependent (Mutch 1970; Vogl 1977). Aside from the direct effects of the fire through heat and smoke, many forest arthropods are affected indirectly through the sudden and often drastic changes in the plant community. Springett (1979) found that both the meso and microarthropod fauna of an Australian forest were reduced after a fire, while I.F. Ahlgren (1974) reported that most beetle genera are at least temporarily reduced following fires.

Rickard (1970) showed that the number of ground beetles in burned steppe vegetation was reduced. French and Keirle (1969) reported finding few carabids in fire damage radiata pine plantations, while Harris and Whitcomb (1974) reported that the numbers of most species of carabid beetles were reduced in regularly burned forest plots. The abundance of some beetles, however, increases after a fire. Evans (1971) reported several Carabidae among the beetles attracted to forest fires.

The occurrence of carabid beetles in a boreal forest following an intense crown fire in April 1977 was studied. Many of the carabids probably survived the direct effects of the fire by burrowing into the soil and under litter; in their review, Ahlgren and Ahlgren (1960) reported that during most forest fires, there is little rise in temperature 4 or 5 cm below the soil surface. The study was begun 15 months after the fire in order to study the indirect effects of plant species replacement on the populations of carabid beetles. A previous work (Richardson and Holliday 1982) reported the occurrence of ground beetles in the first year of the study. The present work reports the results of the first 4 years following the fire.

MATERIALS AND METHODS

Four sites 50 m x 50 m were selected in a boreal forest near Riverton, Manitoba (in Township 26 R2E). Two sites were in an area burnt by an intense forest fire in April 1977, while the other two sites were in unburnt areas. One site in the unburnt area was dominated by trembling aspen (*Populus tremuloides* Michx.) and the other by spruce (*Picea mariana* (Mill.) B.S.P. and *P. glauca* (Moench) Voss). Sites in the burnt area were chosen so that they were as similar as possible, before the fire, to the corresponding sites in the unburnt area. Soil types in all sites were similar. A more detailed description of the sites is given in Richardson and Holliday (1982).

Carabid populations were sampled using galvanized steel pitfall traps 7.8 cm in diameter (Richardson and Holliday 1982). In each site, traps were placed with their lips level with the ground in a 4x4 grid with 12.5 m between traps.

In 1978, traps were emptied once a week from June until November. In 1979, there were 3 trapping dates: 5 June, 17 July and 18 September. On each occasion, traps were left in place for a period of one week. Similarly, trapping occurred 4 times in 1980: 24 April, 5 June, 10 July and 4 September. In 1981 there were 5 trapping occasions: 21 April, 20 May, 24 June, 28 July and 2 September.

The data for the most commonly caught species were first transformed to ensure non-additivity and to stabilize the variance. A factorial analysis of variance was carried out and orthogonal contrasts were used to identify any differences between sites (Snedecor and Cochran 1980).

RESULTS

Table I lists the total numbers of the commoner carabids caught from 1978 to 1981. Analysis of the data showed that Pterostichus pensylvanicus was caught significantly more frequently (P<.001) in the unburnt plots than in the burnt plots in 1978 and 1981. In 1979 there were no significant differences (P>.05) while in 1980 this species was caught more frequently (P<.001) in the two aspen sites than in the spruce sites. Similarly, Carabus taedatus was caught significantly more frequently in the unburnt sites than in the burnt sites in all 4 years (1978, P<.001; 1979, P<.05; 1980,P<.001; 1981, P<.05). In addition, in 1980, it was caught most frequently in the unburnt aspen site (P<.05). In contrast P. adstrictus was captured most frequently in the burnt spruce site (P<.02) in 1978. In 1980 it was caught more frequently in the two burnt sites (P<.01), than in the unburnt areas. In 1981 there were no significant differences (P>.05), and the data from 1979 were insufficient for statistical analysis.

During the first 3 years, P. lucublandus was also caught significantly more frequently in the unburnt aspen area than in the others (1978, P<.001; 1979, P<.01; 1980, P<.01) and in 1981 was caught more frequently in unburnt sites than in the burnt areas (P<.01). Harpalus laticeps was caught only in the burnt sites (P<.01) in 1978 and only in the burnt spruce site during the following 3 years (1979, P<.05; 1980, P<.01; 1981, P<.01). Calathus ingratus was caught more frequently in the unburnt sites than in the burnt sites in 1978 (P<.05) and 1980 (P<.05) (in 1979 there were too few captures to permit statistical analysis). In 1981 this species was captured only in the unburnt spruce

Table I. Total numbers of carabids captured in each site from 1978 to 1981.

		Aspen		Spruce	
		Unburnt	Burnt	Unburnt	Burnt
P. pensylvanicus	1978	89	49	110	9
	1979	4	9	15	8
	1980	26	23	5	2
	1981	42	8	35	10
C. taedatus	1978	38	2	23	3
	1979	1	0	3	0
	1980	15	0	6	1
	1981	6	2	5	0
P. lucublandus	1978	22	1	0	0
	1979	11	0	0	1
	1980	12	0	0	1
	1981	14	0	5	1
A. decentis	1978	0	0	0	0
	1979	0	0	0	0
	1980	0	0	0	0
	1981	0	0	21	0
H. laticeps	1978	0	10	0	13
	1979	0	0	0	5
	1980	0	0	0	10
	1981	0	0	0	12
C. ingratus	1978	5	4	10	0
	1979	0	0	3	0
	1980	2	0	5	0
	1981	0	0	8	0
P. adstrictus	1978	0	3	0	13
	1979	2	1	1	2
	1980	1	3	0	4
	1981	0	3	6	4

site ($P<.05$). Agonum decentis was captured only in 1981 and then only in the unburnt spruce site ($P<.01$).

DISCUSSION

Mitchell (1963) stated that pitfall trap catches may not accurately reflect the number of carabid beetles in an area because the number caught is due to a combination of the size of the population, and to the activity of the beetles. It has been shown by Baars (1979a) however, that continuous pitfall trap catches summed over a species' whole activity period gives a satisfactory linear relationship to the mean densities of beetles occurring in the area. The data for 1978 were continuous over the trapping season and probably reflect accurately the carabid populations in the areas studied. During the following 3 years, trapping was not carried out continuously, but because trapping was carried out at the same time in each site, the effects of weather on pitfall trap catches would be similar. In addition, where pitfall traps in different types of ground cover consistently catch one species in only one habitat type, then this probably represents the species' true distribution (Greenslade 1964b).

In a previous work (Richardson and Holliday 1982) it was reported that the immediate effect of the fire was to kill the above ground vegetation. In the burnt aspen area, the regrowth of P. tremuloides was dense and rapid, probably due to this species' ability to sprout from roots and stems undamaged by the fire (Walker 1982). The burnt spruce site was initially relatively open, with only sparse regrowth, but became more dense during the course of the study period.

P. pensylvanicus was the most commonly caught species during the four trapping seasons. In 1978 and 1981 it was caught more frequently in the unburnt sites. In 1979 there were no significant differences between the sites, while in 1980 this species was captured more commonly in the two aspen sites. The reasons for these differences between the years are not known but may be related to the effects of weather on the population densities or to sampling variation. The numbers caught in 1978 and in 1981 are similar and indicate that this species' response to the indirect effects of the fire may not have changed appreciably over the 4 years of the study. Barlow (1970) reported that P. pensylvanicus avoids open areas which may account for this species being captured least frequently in the burnt spruce site which was the most open of the four plots.

C. taedatus occurred most frequently in the unburnt sites throughout the study period although the relative differences between the numbers caught in the burnt and unburnt sites seem to be diminishing.

P. lucublandus was captured most frequently in the unburnt aspen site; this is probably a reflection of this species preference for more open areas (Lindroth 1966; Frank 1971; Kirk 1971; Lund and Turpin 1977). One specimen was recorded in the burnt aspen site in 1978, but not subsequently, probably due to the dense regrowth which occurred there. The 5 individuals captured in the unburnt spruce site in 1981 were all captured in one trap at a corner of the plot on two trapping occasions. This may have been due to individuals entering the plot from more open adjacent areas: Barlow (1970) and Lévesque et al. (1976) found P. lucublandus near forest edges and clearings.

A. decentis was captured only during 1981 and then only in the unburnt spruce site. All the beetles were captured in the west half of the plot (this area of the plot was almost pure spruce). This species is common in humid forests and near water (Lindroth 1966; Lévesque *et al.* 1976) and its distribution may indicate that it moved in from an area with several small sloughs to the west of the plot. It probably spends the summer, fall and early part of the spring under the bark of fallen trees (Bousquet and Pilon 1977). As the fire occurred in the early spring, most beetles would presumably have been killed in the logs they inhabited. Those that survived the fire, probably could not have survived the more open, drier conditions which existed immediately afterwards.

In 1978, *H. laticeps* was captured in both the burnt sites. Subsequently it was captured only in the burnt spruce site. Its disappearance from the burnt aspen site may be due to the dense regrowth of *P. tremuloides* which developed there. Similarly, *C. ingratus* was captured in the burnt aspen site only in 1978 and not subsequently. Again, its disappearance could be due to the dense aspen regrowth. Lindroth (1966) reported that this species occurs among dead leaves and moss, both of which would have been destroyed by the fire, but which are common in the two control sites where *C. ingratus* was most commonly captured.

Initially, *P. adstrictus* was most commonly captured in the burnt sites, especially the burnt spruce site. In 1980 it was still captured most commonly in the burnt sites, but there was no difference between the aspen and spruce sites. In 1981, there were no significant differences between any of the plots. Goulet (1974) reported that females of this species oviposit in rotting logs and concluded that one of the main factors affecting the occurrence of this species may be the availability of suitable oviposition sites. Its greater occurrence, in 1978, in the burnt sites, with their greater number of dead and fallen trees, may be a reflection of this. In the following years, dead trees were removed from the burnt spruce site, and the relative number of *P. adstrictus* captured there decreased.

Microclimatic factors such as temperature and humidity are important factors in influencing the activity (Lévesque *et al.* 1979) and occurrence (Thiele 1977) of ground beetles. Differences in microclimate between burnt and unburnt sites, as well as between different forest types can be quite marked (Geiger 1966). Although four years is probably too short a period of time to detect the effects of plant species replacement, the effects of the fire on carabid occurrence are evident. It appears that some species, such as *H. laticeps* and *C. ingratus*, may be able to tolerate drastic habitat changes for a short while (the year immediately following the fire) before their numbers decline or disappear from an area. Most species, however, were affected immediately and their responses have remained similar throughout the study period.

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Effects of tillage and herbicide application on the occurrence of ground beetles (Coleoptera:Carabidae) in an arable field

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ABSTRACT

During 1979 and 1980, the occurrence of ground beetles was studied by pitfall trapping in plots which had either been treated with herbicide, tilled or (in 1980 only) mown. The results for the 5 most common species, *Amara avida*, *A. apricaria*, *Pterostichus corvus*, *Anisodactylus sanctaecrucis* and *Harpalus amputatus* are presented. Their responses to the treatments differed between the two years as the result of differences in the vegetation present before the treatments were applied. In general, the numbers of carabids captured in the treatment areas were lower than those captured in the control plots. *A. apricaria* showed an increase in captures in the tilled areas from 6-8 weeks after treatment in both years. *H. amputatus* was captured more commonly in the herbicided areas in 1979, 6 weeks after the application of the treatments. The effects of the treatments on the vegetation were probably responsible for the differences observed in the occurrence of the ground beetles studied.

INTRODUCTION

Because of the predacious nature of many carabid beetles, they have frequently been suggested as potential agents of biological control (Frank 1971; Kulman 1974). Thiele (1977) stated that although they probably are not capable of controlling outbreaks of pest species, carabids are certainly valuable as "natural auxiliaries in pest control". Further research might make it possible to enhance their occurrence in arable land by modifying cultural practices.

Fox (1964) found that the effects of different herbicides on the numbers of wireworms (Agriotes spp.), Collembola, Acarina, Lumbricidae and Diplopoda, varied with the herbicide used. It was concluded that the changes in population levels were due more to the indirect effects of the changes in the vegetation composition, than any direct effects of the herbicide. This same conclusion was reached by Edwards and Stafford (1979) working with similar soil organisms, although they did not consider that the herbicides tested contributed a "serious hazard to populations of soil-dwelling invertebrates". Pollard (1968) found that the numbers of almost all species of carabids present decreased in an area cleared of its soil fauna and vegetation as a result of repeated herbicide applications. Speight and Lawton (1976) captured carabids more frequently in a winter wheat field containing high densities of Poa, a lowlying, ground covering grass, than in more weed free areas. They assumed this was due to the higher humidity found under the dense vegetation.

In the current study, the effects of two cultural practices commonly used to control weed populations (herbicide application and tillage) were studied to see what effects they had on the occurrence of carabid beetles in agricultural land in south-central Manitoba.

MATERIALS AND METHODS

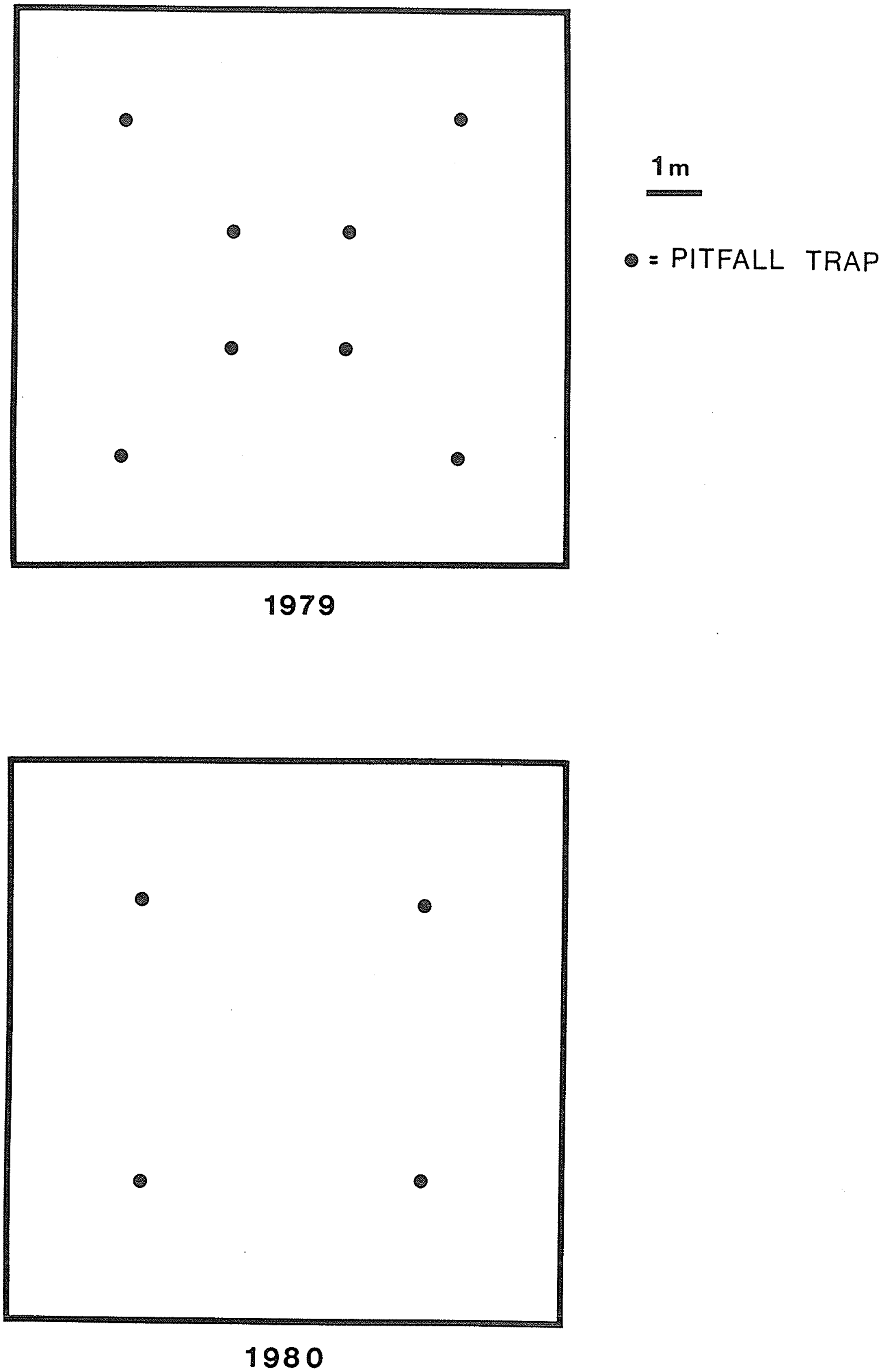
The study took place on Red River clay soil at the University of Manitoba field station (97° 18' W, 49° 39' N) near Glenlea, Manitoba. Carabid populations were sampled during 1979 and 1980 using pitfall traps. Each trap consisted of a galvanized steel tube with a 7.8 cm diameter as described in Richardson and Holliday (1982). The traps were installed level with the soil surface and were emptied twice weekly.

<u>1979</u>: A 50 m x 50 m study area was divided into a 3x3 Latin square arrangement, surrounded by a 10 m strip of tilled soil. Each treatment area was 10 m on a side and contained 8 pitfall traps as indicated in Fig. 1. On 28 May the entire area was tilled to a depth of approximately 15 cm using a tractor drawn double discer. The treatments were applied during the week of 25-27 June: the tilled areas were tilled in the same manner as they were initially and the herbicided areas were treated with Round-up ^{R} (glyphosate) herbicide at approximately 2.0 kg a.i./ha using a tractor drawn boom sprayer. A scythe was used to maintain the vegetation in the control areas at a height of about 20-30 cm. Pitfall traps were emptied twice weekly from 18 May to 25 October. In addition, soil core and sod samples were taken during June, July and August. The soil cores were 10 cm in diameter and approximately 12 cm in length. The sod samples were taken using a 0.25 m^2 quadrat, removing all soil and vegetation to a depth of about 7 cm.

The major species of the weed communities were identified 8 weeks after the treatments were applied.

<u>1980</u>: The same field was used as in 1979, but the design was changed to a 4x4 Latin square design. As in 1979, each plot was 10 m on a side,

Figure 1. Arrangement of pitfall traps within each plot in 1979 and 1980.


1m
= PITFALL TRAP
1979
1980

but contained only 4 pitfall traps as indicated in Fig. 1.

On 5 May the entire area was tilled as in 1979 and during the week of 11-14 July the treatments were applied. The vegetation in the control areas was maintained at a height of approximately 20-30 cm using a scythe. In 1979 it was possible to apply all the treatments without the tractor damaging adjacent plots (the centre plot was a control area) but in 1980 this was not possible due to the 4x4 Latin square design. Tilling was done with a self-propelled rototiller (Gem Rotovator) to a depth of about 15-20 cm. Round-up ^{R} herbicide was applied using a CP3 Knapsack sprayer (Cooper, Pegler & Co.) at approximately 1.8 kg a.i./ha. In 1980 a third treatment, cutting, was applied. This consisted of cutting the vegetation to a height of 5-8 cm using a lawn mower.

Traps were emptied twice weekly from 13 May to 14 October. In order to obviate any loss of specimens as the result of predation by birds or small mammals, all traps were covered with 10x10 cm pieces of wire mesh (1 mesh/cm) supported 5 cm above the traps. The vegetation was assessed as in 1979.

Herbicide Experiment: Two laboratory experiments were performed to determine if Round-up ^{R} had any direct effects on the survival of carabid beetles.

In the first, 12 *Amara farcta* and 12 *Pterostichus corvus* were treated with Round-up ^{R} at approximately 2.27 kg a.i./ha, while 12 of each species served as controls. There were 2 treatments. In the first, 6 individuals of each species were placed in petri dishes lined with filter paper and sprayed directly with the herbicide. In the second treatment another 6 of each species were placed in petri dishes containing soil which had been sprayed with Round-up^{R}. Six individuals of each species were untreated controls in each of the two treatments. All beetles were offered food (mixed bird seed) and water. The number surviving after 7 days were counted.

In a second experiment, the surviving individuals from the first experiment were divided into those which had previously been controls (untreated) and those which had been treated with the herbicide. Each treatment was then carried out as in the first experiment but with the beetles in each treatment being separated into 2 approximately equal halves: one-half which were previously controls, and one-half which were previously treated. Nine A. farcta and 9 P. corvus were treated with Round-up^{R} at approximately 1.88 kg a.i./ha and nine of each species were untreated controls.

Analysis: Data from pitfall trap catches were grouped in 2-week intervals; these data were transformed to stabilize the variance and reduce non-additivity. A Latin square ANOVA was carried out and in those cases where neither the row nor the column effects were significant, the data were analysed with a factorial ANOVA. A studentized range test was used to determine differences among significant treatment means (Snedecor and Cochran 1980).

RESULTS

Vegetation: In 1979, up to the point at which the treatments were applied, the major vegetation in all plots consisted of *Polygonum scabrum* Moench with some *Malva pusilla* Sm. and *Artemisia biennis* Wild. In 1980, before the treatments were applied, the vegetation in all plots consisted almost entirely of *A. biennis*, with a small amount of *P. scabrum*, *M. pusilla* and bare soil. In both years, the vegetation in the treatment plots became reestablished and at 8 weeks post-treatment (30 August in 1979, 15 September in 1980) was as outlined in Table I.

Carabids: In 1979, soil cores and sod samples were taken in all plots on 4 occasions. The numbers recovered were too few to permit statistical analysis.

Table II shows the total numbers of most commonly caught carabids during 1979 and 1980.

Amara avida was the most commonly occurring ground beetle. Fig. 2 shows the total number of individuals caught in each treatment over each two week period. In 1979, there was only one period (16 August) which showed a significant difference between treatments: *A. avida* was caught significantly more frequently in the control plots than in the two treatments ($P<.05$). Although only one date proved significantly different statistically, every date showed more beetles being caught in the control plots than in the herbicided or tilled plots. That same trend was evident during 1980 when the control plots had the highest occurrence of *A. avida* for 4 weeks in July and August (17 August, $P<.05$; Note: this statistic is based on only 1 week ending 12 August

Table I. Vegetation components in plots 8 weeks after treatment.

	Artemisia biensis Wild.	*Malva pusilla* Sm.	*Polygonum scabrum* Moench	Bare soil
1979				
Control	-	-	++	-
Herbicided	+	+	+	0
Tilled	0	-	+	+
1980				
Control	++	0	-	-
Herbicided	++*	0	-*	-
Tilled	-	-	-	++
Mown	++	0	-	-

++ Very abundant

\+ Abundant

\- Minor component

0 Not occurring

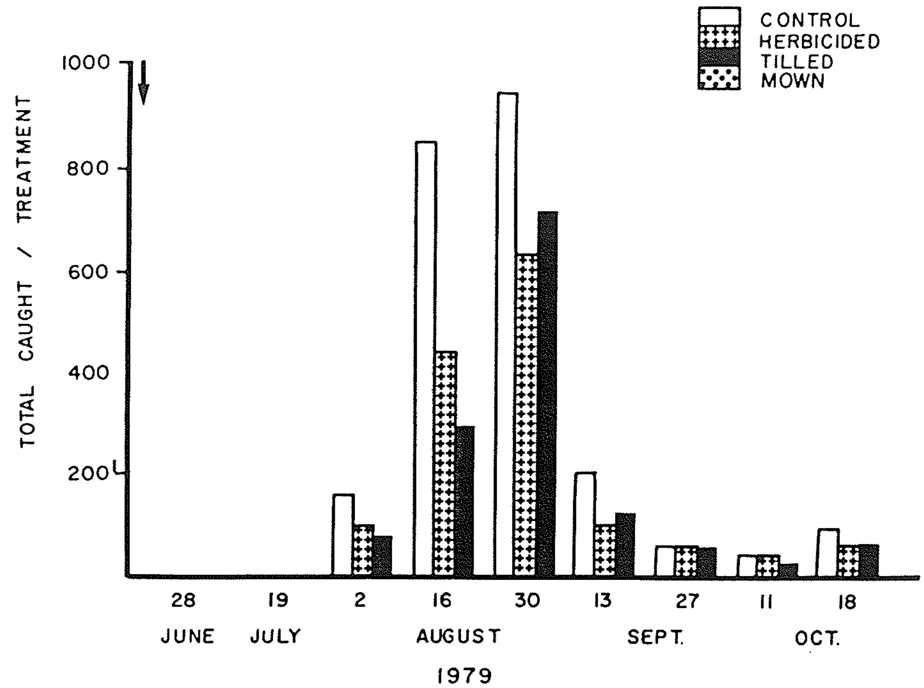
* Indicates those plants occurring were dead

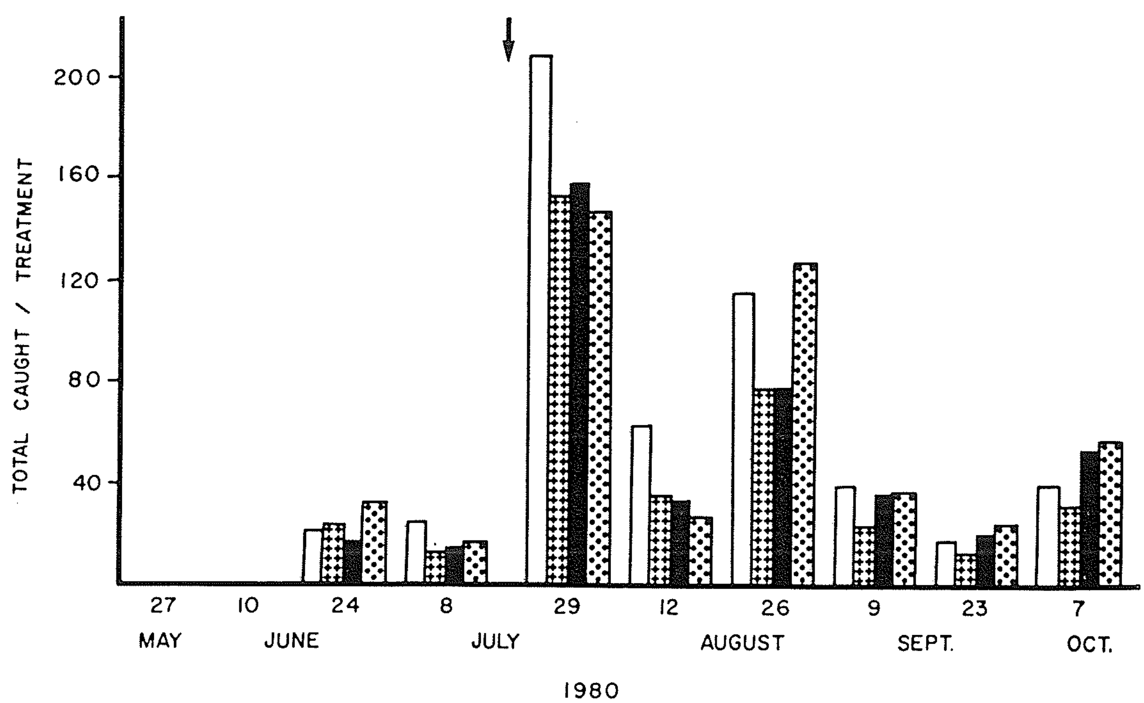
Table II. Total numbers of the species most commonly caught in pitfall traps in 1979 and 1980.

	1979	1980
Amara apricaria Paykull	5108	1632
A. avida Say	5020	1883
A. farcta Leconte	147	356
A. littoralis Mannerheim	23	31
Anisodactylus sanctaecrucis Fabricius	304	699
Bradycellus congener Leconte	258	49
Harpalus amputatus Say	533	313
H. herbivagus Say	201	58
H. pensylvanicus De Geer	198	77
Pterostichus corvus Leconte	436	824
Stenolophus comma Fabricius	356	399

Figure 2. Total number of _Amara avida_ caught in each treatment during two-week periods in 1979 and 1980.

AMARA AVIDA


CONTROL
HERBICIDED
TILLED
MOWN
TOTAL CAUGHT / TREATMENT
1000
800
600
400
200
28
19
2
16
30
13
27
11
18
JUNE
JULY
AUGUST
SEPT.
OCT.
1979


TOTAL CAUGHT / TREATMENT
200
160
120
80
40
27
10
24
8
29
12
26
9
23
7
MAY
JUNE
JULY
AUGUST
SEPT.
OCT.
1980

due to a sampling error).

A. apricaria, in 1979, was captured more frequently in the control plots than in the tilled (16 August, $P<.05$) until mid-September, and then more frequently in the tilled plots (11 October, $P<.05$) (Fig. 3). In 1980, although not significantly different, the three dates in September and October all show more captures in the tilled areas.

In 1979, *Pterostichus corvus* was captured more frequently in the control and herbicided plots than in the tilled plots on 19 July ($P<.005$), 2 August ($P<.001$) and 16 August ($P<.05$) (Fig. 4). On 27 September, the captures in the control plots were significantly higher ($P<.05$) from those in the tilled plots. In 1980, control plots had more captures than the tilled ($P<.05$) on 26 August and more than the herbicided plots ($P<.05$) on 9 September.

Anisodactylus sanctaecrucis was more frequently caught in 1979, in the control plots than in either the herbicided or tilled plots on 2 August ($P<.005$), 30 August ($P<.05$) and 13 September ($P<.01$) (Fig. 5). It was also caught more frequently in control plots than in tilled on 16 August ($P<.05$) and 18 October ($P<.05$). In 1980 however, there were no significant differences.

Harpalus amputatus, in 1979, was caught more frequently in the control and herbicided plots than in the tilled on 19 July ($P<.005$) and 2 August ($P<.01$) (Fig. 6). On 16 August all three treatments were significantly different ($P<.005$) with most beetles being captured in the herbicided plots. In 1980, there were more captures in the tilled plots than in the mown plots ($P<.01$) on 9 September. There do not, however, appear to be any evident trends, as this was the only post-treatment date

Figure 3. Total number of *Amara apricaria* caught in each treatment during two-week periods in 1979 and 1980.

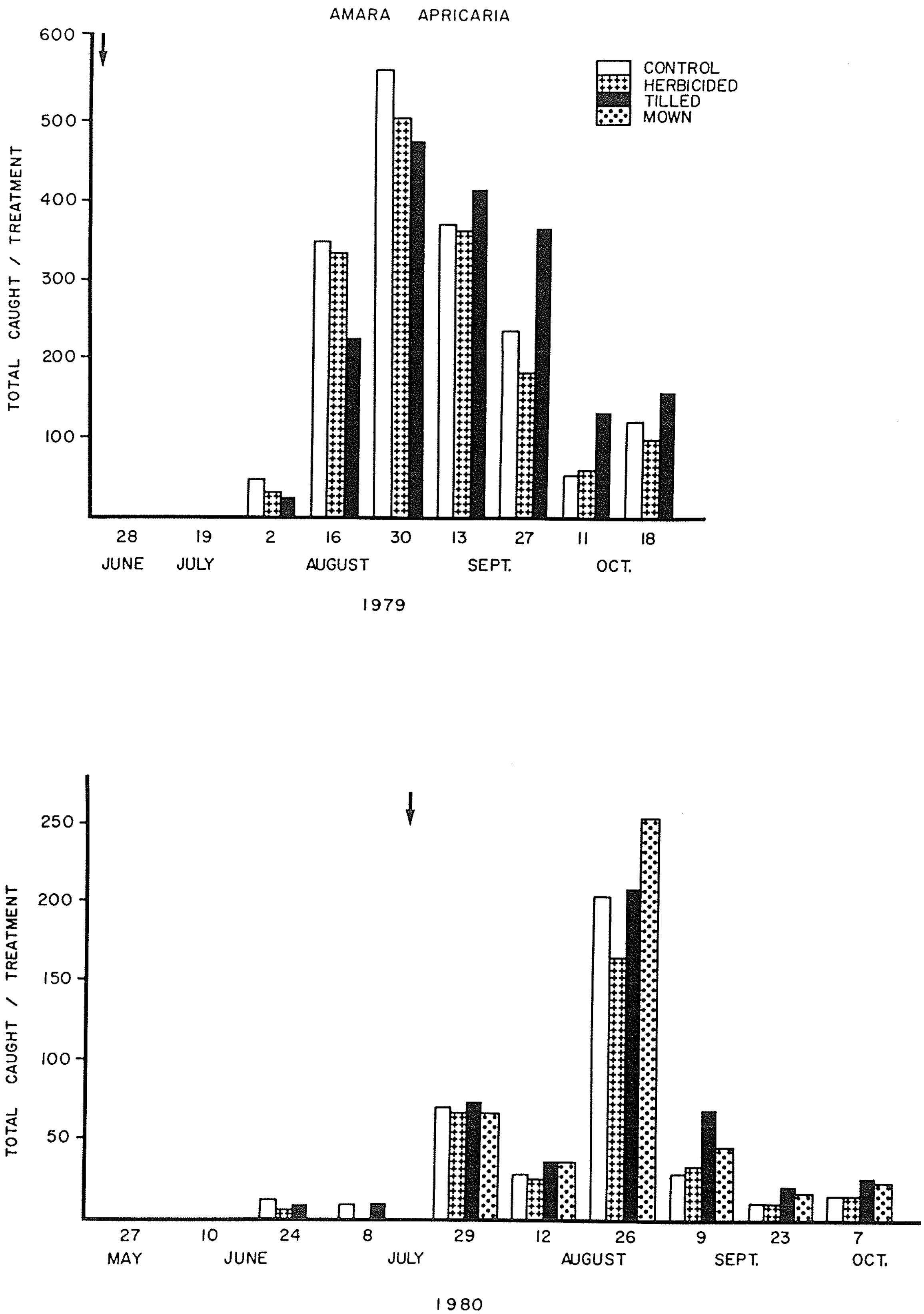
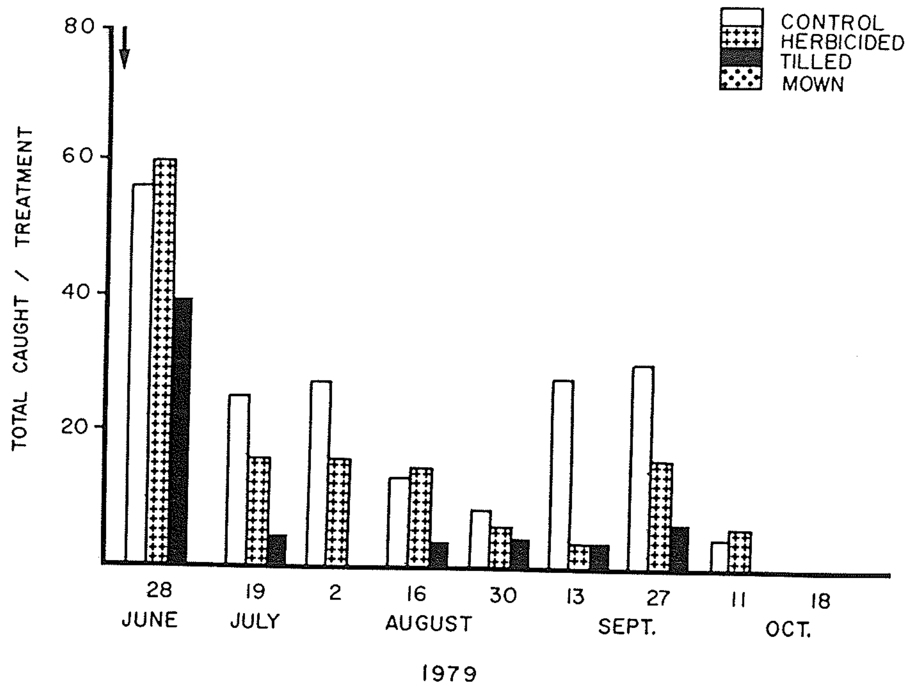

AMARA APRICARIA
CONTROL
HERBICIDED
TILLED
MOWN
TOTAL CAUGHT / TREATMENT
600
500
400
300
200
100
28
19
2
16
30
13
27
11
18
JUNE
JULY
AUGUST
SEPT.
OCT.
1979
TOTAL CAUGHT / TREATMENT
250
200
150
100
50
27
10
24
8
29
12
26
9
23
7
MAY
JUNE
JULY
AUGUST
SEPT.
OCT.
1980

Figure 4. Total number of _Pterostichus_ _corvus_ caught in each treatment during two-week periods in 1979 and 1980.

PTEROSTICHUS CORVUS



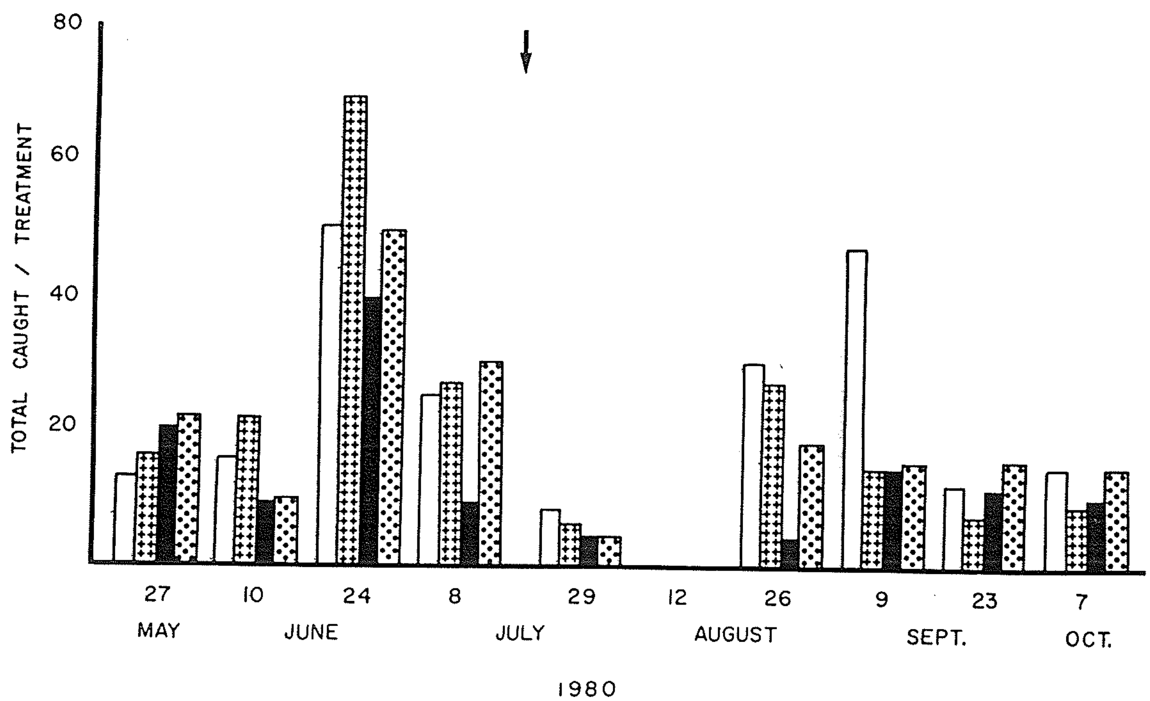


Figure 5. Total number of _Anisodactylus_ _sanctaecrucis_ caught in each treatment during two-week periods in 1979 and 1980.

ANISODACTYLUS SANCTAE CRUCIS

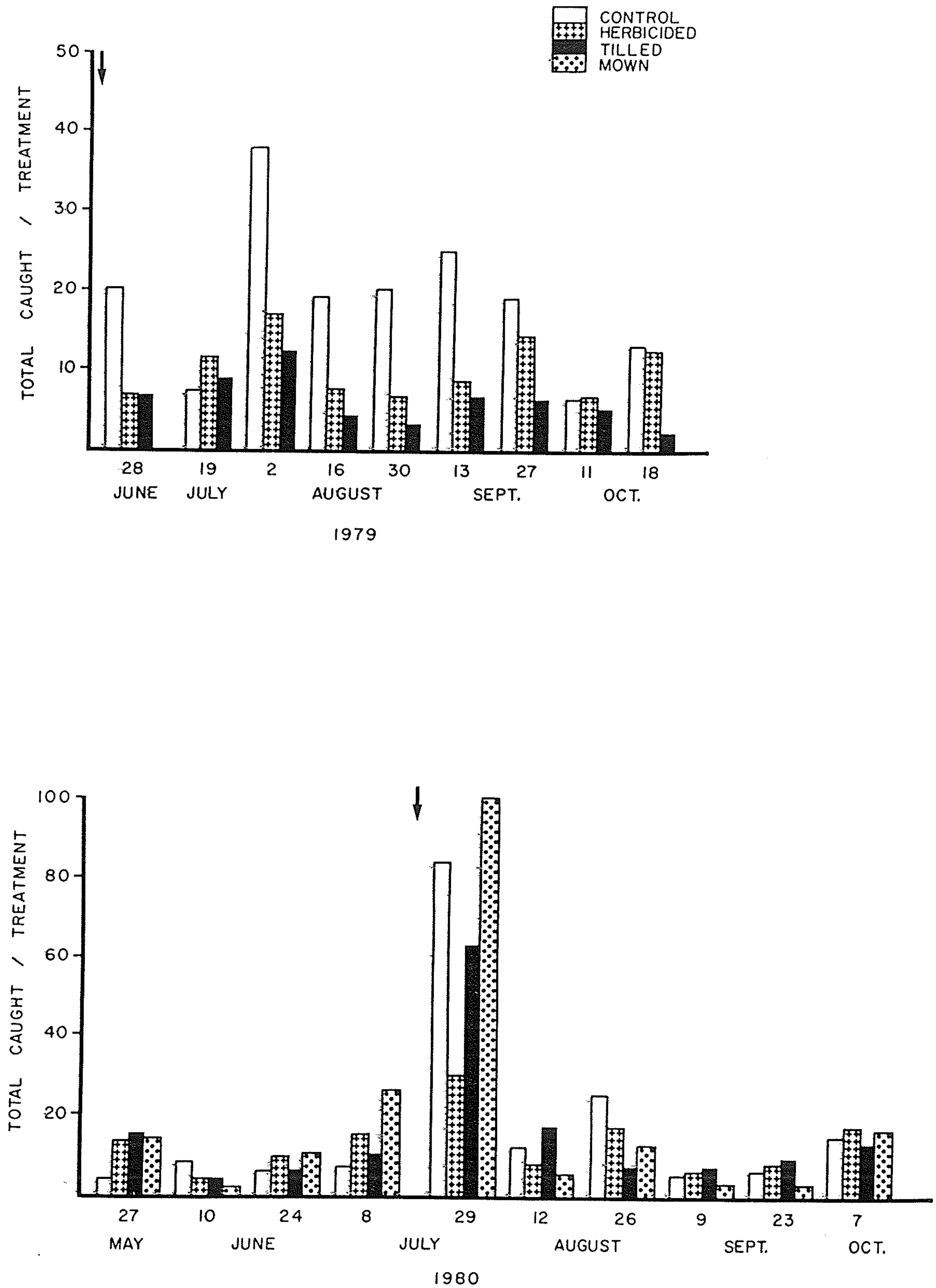
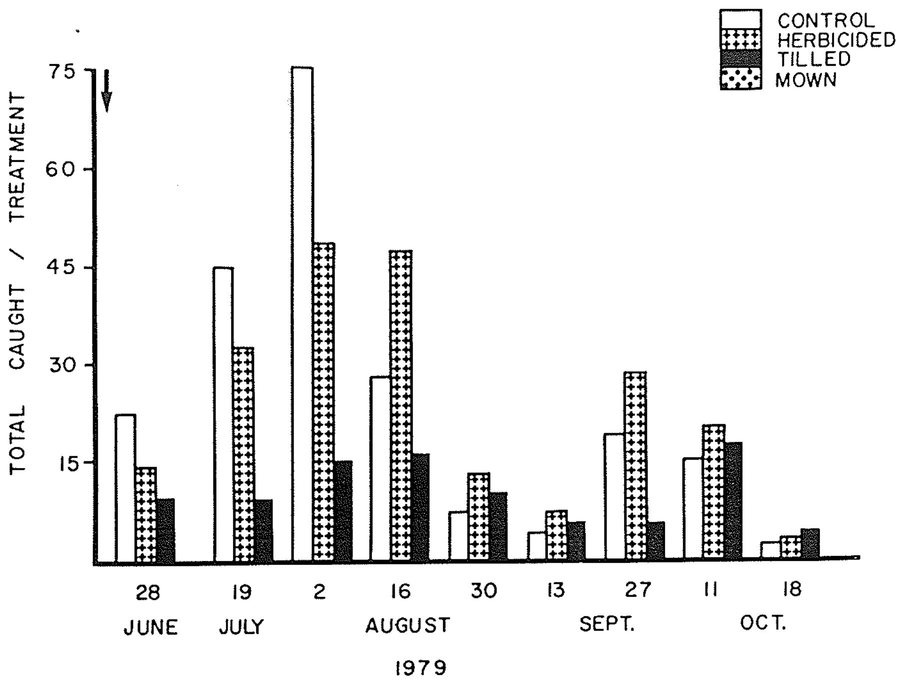
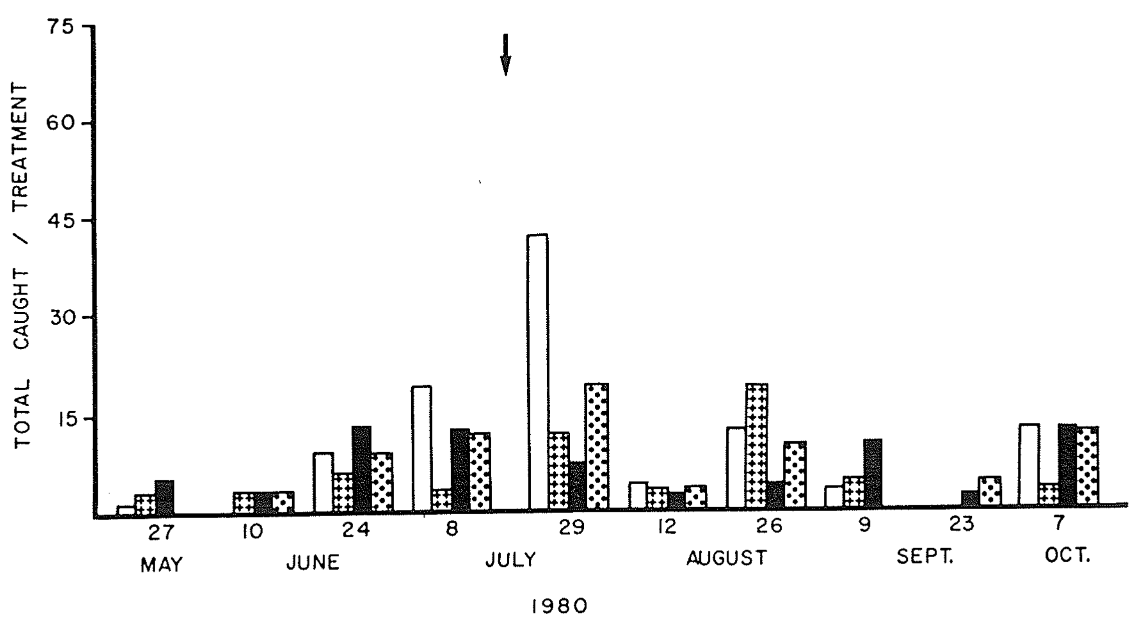


Figure 6. Total number of Harpalus amputatus caught in each treatment during two-week periods in 1979 and 1980.

HARPALUS AMPUTATUS





in which the numbers caught in the tilled plots were higher than in the others.

Laboratory Experiments: The herbicide experiments indicated that Round-up^{R} had no direct effect on the survival of the beetles tested. Table III shows the numbers of beetles surviving 7 days after the treatments were applied.

Table III. Results of herbicide experiments showing numbers surviving 7 days after treatment.

		Beetles sprayed		Soil sprayed	
		Control	Treatment	Control	Treatment
Experiment I					
Amara farcta					
	a	3/3	1/3	3/3	3/3
	b	2/3	3/3	1/3	3/3
Pterostuchus corvus					
	a	3/3	3/3	2/3	3/3
	b	2/3	2/3	2/3	2/3
Experiment II					
Amara farcta					
Controls previously		1/2	2/2	2/2	2/2
Treated previously		3/3	1/3	2/2	2/2
Pterostichus corvus					
Controls previously		1/2	2/2	3/3	2/2
Treated previously		3/3	1/2	2/2	3/3

DISCUSSION

Although the studies in each year were carried out on the same site, there were notable differences between years in the initial vegetation and the ensuing effects produced by the treatments. These were probably due in part to the land being covered for approximately one week with flood waters from the Red River in 1979 and to a very dry spring in 1980. The major component of the initial vegetation in 1979 was Polygonum scabrum, a plant belonging to a genus adapted to aquatic and marshy as well as terrestrial environments (Looman and Best 1979). The initial dominance of P. scabrum lasted throughout 1979. In 1980, A. biennis was the major component of the vegetation, while P. scabrum made up only a minor portion. The vegetation which occurred 8 weeks after the treatments were applied in the herbicided plots differed between the years as well. In 1979, most of the vegetation was alive with virtually no bare soil. In 1980, there were only a few living plants, with the bulk of the vegetation being dead, dried A. biennis. This may have been the result of i) the difference in the plants initially present and ii) the timing of the treatment applications. A. biennis is a much more substantial plant than P. scabrum, having a thicker and more substantial stem. It therefore remains erect on the fields after dying. In addition, in 1980, the vegetation was more mature when treated due to an earlier, warmer spring and because the treatments were applied two weeks later in the season.

Captures from pitfall traps represent a combination of both the size of a beetle population and its activity (Mitchell 1963). Direct population sampling using soil cores and sod samples proved unsatisfactory due to the small numbers of carabids recovered and to the destruction of the plots which necessarily occurred. Greenslade (1964) found that carabids are trapped in highest numbers in areas which offer the least resistance to their travel while Baars (1979b) showed that the highest captures of carabids occur in unfavourable habitats due to the beetles increased locomotory activity. Therefore, if captures are lower in more open areas (which offer less resistance and which are less favourable due to their lower humidity (Speight and Lawton 1976; Kirk 1974; Rivard 1966) than those which are less so, then this indicates a true difference in distribution (Greenslade 1964).

Amara avida and Pterostichus corvus were captured consistently more frequently in the control sites than in the two treatment plots. Lindroth (1969) reported A. avida was found in open, moderately dry, often culture-influenced places with a vegetation of weeds. P. corvus was also reported on rather dry, often clayish soil (Lindroth 1969). Unlike the previous species, P. corvus also was caught fairly frequently in the herbicide treated plots.

In 1979, Anisodactylus sanctaecrucis was captured more frequently in the control plots than either of the two treatment plots, but in 1980 no clear trends were visible. This is probably due to the difference in vegetation between the two years. In 1979, the control plots consisted mostly of P. scabrum, a ground covering plant, while the plots in 1980 were more open and therefore drier, due mainly to the abundance of A. biennis, a plant which grows more upright, providing a more sparse vegetation cover. Speight and Lawton (1976) found this same phenomenon with carabids of a winter wheat field, which were caught more frequently in plots containing high densities of Poa, a ground-covering weed. They attributed this difference to the more suitable environmental factors (humidity) in the plots containing Poa as well as to a greater abundance of natural prey. Kirk (1977) found that A. sanctaecrucis preferred moist areas. During 1980, the differences in humidity between treatment plots may have been less marked. This, accompanied by the possible masking effects of higher pitfall trap catches in areas of unsuitability (Baars 1979b) may account for no differences being seen between the treatment plots and the perhaps only marginally more suitable control areas in 1980.

In 1979 Amara apricaria was more commonly captured in the control sites until 8 weeks after the treatments were applied; from then until the end of the trapping season, it was more frequently captured in the tilled plots. In 1980, there was no evident effect immediately following the treatments, but 6 weeks after their application there was a trend towards more specimens being caught in the tilled areas. Lindroth (1969) reports that this species prefers "all kinds of more or less open ground with a more or less closed carpet of meadow or weed vegetation". Immediately following the treatments, the control area would most closely fit this description. After 6 to 8 weeks, the tilled areas were made up of low growing plants such as P. scabrum and M. pusilla with large areas of open ground, which provided a more suitable habitat for A. apricaria.

Following the treatments in 1979, Harpalus amputatus was initially captured most frequently in the control and herbicided areas. From 6 weeks post-treatment, it was most common in the herbicided plots, although the differences in some periods were small. Immediately following the application of the treatments in 1980, this species was found most commonly in the control areas. Subsequently, no trend was apparent in the captures. The reasons for one significant date in 1980 (9 September, which showed that captures in the tilled areas were significantly greater than those in the mown areas) are not known. H. amputatus is reported as being xerophilous, inhabiting dry, often sandy grassland (Lindroth 1969). A lack of any long-term trends in this specie's occurrence 6 weeks after the treatments had been applied in 1980 may again reflect the smaller differences observed in the nature of the vegetation that year.

The differences seen in the occurrence of ground beetles are no doubt due to the effects of the treatments on the vegetation in the plots. This is in concordance with the published literature carried out on similar ecological systems with a variety of soil organisms. The reasons for these differences are complex, involving the actual changes in the vegetation and microhabitat as well as differences in the availability of natural prey.

ACKNOWLEDGMENTS

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IV. GENERAL DISCUSSION

In the agricultural habitat, the treated plots exhibited a change in vegetation. Both the density and species composition of the vegetation was different from that in the control areas at 8 weeks post-treatment. The numbers of carabid beetles captured in the treated areas were lower than those in the control plots immediately following the application of the treatments probably due to the resulting change in the vegetation. These results were similar to those of Loring et al. (1981) who found that immediately following tillage, the numbers of collembola and pyemotid mites decreased significantly. Edwards and Stafford (1979) found a similar decrease in the number of arthropods in fields immediately following the application of herbicide.

Most carabid species continued to be caught most frequently in the control plots throughout the season. However, A. apricaria and H. amputatus became more commonly captured in the tilled and herbicided areas respectively, from 6-8 weeks following the treatments. It is not uncommon for species to react differently to the application of treatments. Fox (1964) found that the densities of various insects either increased or decreased following the application of herbicide, depending upon the species. Loring et al. (1981) found that at 4 months following tillage, the numbers of collembola and mites increased. This is similar to the changes seen in the occurrence of A. apricaria from 6-8 weeks following tillage. The differences in carabid occurrence and their changes are probably the result of the effects of the treatments on the vegetation, as suggested by Fox (1964) and Edwards and Stafford (1979).

In the burnt forest habitat, the numbers of most carabid species were initially reduced. In contrast, H. laticeps and P. adstrictus were most commonly caught in the burnt spruce site in this study. The occurrence of most species has remained similar throughout the study period, with the exception of H. laticeps, C. ingratus and P. adstrictus.

In the forest habitat, the initial disturbance occurred quickly and affected the vegetation immediately. The subsequent plant species replacement has taken place slowly. Since the first year after the fire, it has probably not changed sufficiently to have had significant effects on the occurrence of most carabid species. In the agricultural habitat, the effects of the treatments were immediate, except for the herbicide application which took 7 to 10 days to produce noticeable changes in the vegetation. The plant species replacement occurred quickly and by 8 weeks post-treatment was sufficient to have significantly affected the occurrence of the carabid beetles in the plots.

In the unburnt spruce forest, two species, P. lucublandus and A. decentis, appeared for the first time in 1981. Apparently colonization is taking place and is probably a common occurrence in carabid populations. It is probable that populations are continually exchanging individuals (den Boer 1970). This is most likely taking place in the agricultural habitat: individuals are not resident in each treatment plot, but are probably continually moving between them. They may simply be spending more time in the more suitable plots as suggested by Baars (1979b).

The use of pitfall traps alone to assess the occurrence of carabids in these different areas has its limitations. The data thus obtained must be interpreted with some discretion and cannot give all the information necessary for an in-depth population analysis, but pitfall traps can be useful tools in an initial investigation. Pitfall trapping combined with soil sampling and a mark and recapture program (where feasible) would provide more accurate information on the density and movement of carabids in the study areas. Although, as pointed out by Baars (1979b), pitfall trap catches may be well correlated with mean densities when trapping is conducted continually over the entire season.

In both the agricultural and forest habitats, the disturbances caused a change in the vegetation which in turn caused a change in the micro-climate. Areas with a higher density of vegetation also tend to have a higher level of humidity (Geiger 1966). Carabid beetles are prone to desiccation (Rivard 1966) and therefore tend to be found more commonly in habitats with high humidities. Many authors (Greenslade 1965; Rivard 1966; Kirk 1974) feel that humidity is the major factor influencing the distribution of carabids. However, because of the complex interactions of many additional factors such as prey availability and other resource needs, it is difficult to accurately assess which factor is responsible for the distribution of each species.

V. SUMMARY AND CONCLUSIONS

In general, the occurrence of ground beetles in arable land was reduced following tilling or the application of herbicide. _A. avida_, _P. corvus_ and _A. sanctaecrucis_ were captured most commonly in the control plots throughout the season. _A. apricaria_ was captured more frequently in the tilled areas from 6-8 weeks following the application of the treatments in 1979 and 1980. In 1979, _H. amputatus_ was captured most frequently in the control and herbicided plots for the first 6 weeks after the treatments were applied. Subsequently, it was most commonly found in the herbicided areas. The effects of the treatments on the vegetation in the plots were probably responsible for the observed differences in carabid occurrence rather than any direct effects. Carabids were most commonly captured in areas which had higher densities of ground covering vegetation and consequently higher humidities. The differences observed between the plots were less marked in 1980 than in 1979. This was probably due to the difference in the vegetation which was present each year before the treatments were applied, resulting in the plots being more similar (drier and more open) in 1980 than in 1979.

In the forest habitat, the occurrence of most species was reduced in those areas which had been burnt. _P. pensylvanicus_ and _C. taedatus_ were captured most frequently in the unburnt sites throughout the 4 years following the fire. Two species, _H. laticeps_ and _C. ingratus_ were recorded in the burnt aspen site only in 1978 although _H. laticeps_ continued to be caught in the burnt spruce site and _C. ingratus_ in the two unburnt sites. In 1978, _P. adstrictus_ was captured significantly more frequently in the burnt spruce site. In the following years, this difference diminished and in 1981, disappeared.

The effects of the fire on the composition and density of the vegetation which subsequently became established are probably responsible for the observed differences in the occurrence of most carabid beetles. Except for _H. laticeps_, _C. ingratus_ and _P. adstrictus_, the occurrence of most species was similar throughout the study period, suggesting that for most species, 4 years may be too short a period of time for the effects of plant succession to be detected. The differences in carabid occurrence between the burnt and unburnt areas were probably the result of microclimatic changes brought about by the changes in vegetation.

In general, drastic habitat changes which alter the density and species composition of an area's vegetation, probably alter the occurrence of carabid beetles. It is most likely that this change in carabid occurrence is due to the resulting microclimatic changes, although because of the complex interactions of edaphic, vegetational and microclimatic components, any one cause cannot be isolated.

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Appendix I. List of species captured in forest areas from 1978 to 1981

		Aspen		Spruce	
		Unburnt	Burnt	Unburnt	Burnt
Pterostichus pensylvanicus Leconte	1978	89	49	110	9
	1979	4	9	15	8
	1980	26	23	5	2
	1981	42	8	35	10
Carabus taedatus Fabricius	1978	38	2	23	3
	1979	1	0	3	0
	1980	15	0	6	1
	1981	6	2	5	0
Pterostichus lucublandus Say	1978	22	1	0	0
	1979	11	0	0	1
	1980	12	0	0	1
	1981	14	0	5	1
Harpalus laticeps Leconte	1978	0	10	0	13
	1979	0	0	0	5
	1980	0	0	0	10
	1981	0	0	0	12
Pterostichus adstrictus Eschscholtz	1978	0	3	0	13
	1979	2	1	1	2
	1980	1	3	0	4
	1981	0	3	6	4
Calathus ingratus Dejean	1978	5	4	10	0
	1979	0	0	3	0
	1980	2	0	5	0
	1981	0	0	8	0

Continued ....

Appendix I (Continued)

		Aspen		Spruce	
		Unburnt	Burnt	Unburnt	Burnt
Synuchus impunctatus Say	1978	7	0	1	1
	1979	0	0	0	0
	1980	8	0	0	0
	1981	5	4	4	1
Agonum cupripenne Say	1978	8	2	1	5
	1979	3	1	0	2
	1980	4	0	0	0
	1981	3	0	1	0
Dicaelus sculptilis upioides Ball	1978	19	0	0	0
	1979	11	0	0	0
	1980	5	0	0	0
	1981	3	0	0	0
Agonum decentis Say	1978	0	0	0	0
	1979	0	0	0	0
	1980	0	0	0	0
	1981	0	0	21	0
Sphaeroderus nitidicolis Chevrolat	1978	4	1	1	0
	1979	0	0	2	0
	1980	1	0	0	0
	1981	0	0	1	0
Carabus serratus Say	1978	1	0	1	0
	1979	1	0	2	0
	1980	1	0	1	0
	1981	0	0	0	0

Continued ....

Appendix I (Continued)

		Aspen		Spruce	
		Unburnt	Burnt	Unburnt	Burnt
Scaphinotus elevatus	1978	1	0	2	0
Fabricius	1979	0	0	2	0
	1980	0	0	0	0
	1981	0	0	0	0
Carabus maeander Fischer	1978	0	0	0	0
	1979	0	0	1	0
	1980	1	0	0	0
	1981	1	0	0	0
Notiophilus intermedius	1978	2	0	0	0
Lindroth	1979	0	0	0	0
	1980	0	0	0	0
	1981	0	0	0	0

Appendix II. List of species captured in the agricultural habitat in 1979

	Number captured
Amara apricaria Paykull	5108
Amara avida Say	5020
Harpalus amputatus Say	533
Amara carinata Leconte	477
Pterostichus corvus Leconte	436
Stenolophus comma Fabricius	356
Anisodactylus sanctaecrucis Fabricius	304
Bradycellus congener Leconte	265
Harpalus herbivagus Say	201
Harpalus pensylvanicus DeGeer	198
Amara farcta Leconte	147
Bembidion nudipenne Lindroth	45
Amara littoralis Mannerheim	23
Amara littoralis Mannerheim	18
Bembidion quadrimaculatum L.	9
Calosoma calidum Fabricius	6
Amara lacustris Leconte	3
Pterostichus femoralis Horn	3
Pterostichus melanarius Illiger	1

Appendix III. List of species captured in the agricultural habitat in 1980

	Number captured
Amara avida Say	1883
Amara apricaria Paykull	1632
Pterostichus corvus Leconte	824
Anisodactylus sanctaecrucis Fabricius	699
Stenalophus comma Fabricius	399
Amara farcta Leconte	356
Harpalus amputatus Say	313
Amara carinata Leconte	251
Bembidion nudipenne Lindroth	122
Harpalus pensylvanicus DeGeer	77
Harpalus herbivagus Say	58
Bradycellus congener Leconte	49
Amara littoralis Mannerheim	31
Pterostichus femoralis Horn	3
Calosoma calidum Fabricius	1
Pterostichus melanarius Illiger	1