

THE UNIVERSITY OF CALGARY

Effects of sulphur pollution on forest floor invertebrates

by

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Abstract

The distribution of epigeic invertebrates was studied in forests under varying regimes of exposure to sulphur compounds around two sour gas plants and at sharp acidification gradients in pine and aspen forests adjacent to a sulphur block. Invertebrates were sampled using continuous pitfall trapping at all sites and core sampling along the pine acidification gradient. Highly polluted sites had more day hunting spiders and fewer web building spiders but moderate levels of sulphur deposition did not affect most invertebrates in a negative manner. Under moderate levels of sulphur deposition, structural heterogeneity of the forest floor in terms of coarse woody debris, floristic and edaphic variables were more influential than sulphur levels or pH in structuring macroarthropod communities.

Forest edge effects partly explained the higher abundance of wolf spiders at the most polluted sites but it had no effect on other invertebrates. High sulphur contamination and subsequent acidification had a clear negative effect on earthworms, linyphiine spiders and the amaurobiid spider *Callioplus euoplus* B. & C. Ground beetles and epigeic spiders along the sharp acidification gradient at the pine forest were classified as vulnerable, resistant and favoured. It was concluded that ecological specialists carabids such as *Scaphinotus marginatus* Fischer were most vulnerable to acidification effects while ecological generalists, such as *Pterostichus adstrictus* Esch. were resistant. Although species richness of carabids and spiders was only slightly lower in the most acidified pine site, fewer species dominated the assemblages of these two groups causing a significant reduction in the evenness component of species diversity.

The observed distribution of epigeic invertebrates in forest stands acidified by elemental sulphur can be attributed to direct and indirect effects. Earthworms, snails and some Collembola can be affected negatively through direct acidity effects; however for the

majority of the remaining arthropods indirect effects are more important. These indirect effects can be partitioned into landscape level, habitat or forest type level, and microhabitat level. It is concluded that faunal structure at the acidified sites is severely affected negatively and can explain part of the loss in function (decomposition) observed in such ecosystems.

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To my wife Rosa Lydia, my daughter Karlita and my mother Margarita

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Site contamination classes and abbreviations: HS = high sulphur,

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Environmental variables: all log = number of coarse woody debris,

cor can = *Cornus canadensis*, % O. M. = % organic matter,

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Agroeca ornata, alo acu = *Alopecosa aculeata*, ama bor = *Amaurobius*

borealis, arc age = *Arctobius agelenoides*, cal euo = *Callioplus euoplus*,

clu can = *Clubiona canadensis*, clu kul = *Clubiona canadensis*,

cry exl = *Cryphoeca exlineae*, eri spp = Erigonines, gna mic =

<i>Gnaphosa microps</i> , lin spp = Linyphiines/Theridiidae, par hyp =	
<i>Pardosa hyperborea</i> , par mac = <i>Pardosa mackenziana</i> , par moe =	
<i>Pardosa moesta</i> , par uin = <i>Pardosa uintana</i> , tro ter =	
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CHAPTER 1: GENERAL INTRODUCTION AND OBJECTIVES

Sulphur pollution and epigeic invertebrates

Pollution caused by industrial activities is considered a major threat to ecosystems world-wide (McNeely 1992, Heliövaara and Väisänen 1993). Industrial pollution can be divided into acute and chronic depending on the quantity of a contaminant and the time of exposure. Chemical spills and pesticide sprays, where large amounts of toxic materials are added to a small area in one application represent examples of acute pollution. Gradual and constant release of S^0 and SO_2 from a sour gas processing plant over an area of hundreds of hectares (as studied here) is an example of chronic pollution. Effects of these two forms of pollution on organisms will vary considerably because acute pollution can have much more devastating impacts than chronic pollution.

Soil fauna, e.g. arthropods and earthworms, are important components of ecosystems that contribute significantly to their biodiversity (Lee 1991, Wilson 1987) and together with microbes perform crucial functions in organic matter decomposition (Parkinson 1988), nutrient cycling (Seastedt 1984) and soil structure formation (McGill and Spence 1985). For terrestrial ecosystems there is a general lack of information on pollution effects on invertebrates (Heliövaara and Väisänen 1993), particularly in North America. For example, data on macroinvertebrates are routinely incorporated in environmental assessments of aquatic ecosystems but soil fauna are seldom used in equivalent terrestrial environmental impact statements.

Sulphur compounds are among the pollutants contributing to acid precipitation which can negatively affect ecosystems at large regional scales in highly industrialized areas or locally near industrial facilities (Knabe 1976). Detrimental effects of sulphur pollutants on forest vegetation have been reported in the vicinity of industrial plants

(Nriagu 1978, Smith 1990). Effects of acidification on soil or litter arthropods have not received as much attention as effects on herbivorous insects (Heliövaara and Väisänen 1993).

Experimental acidification of plots (with H_2SO_4) suggests that certain microarthropod species are favoured by low pH. Bääth et al. (1980) and Hågvar (1984) found increased abundance of dominant collembolan species (e.g. *Tullbergia krausbaueri*) but reduced numbers of other species in acidified treatments. Numbers of Protura (Hågvar 1984) and mites (Bääth et al. 1980) were not affected by acidification in these studies. Abrahamsen et al. (1978) also concluded that dominant Collembola and certain mites were favoured or unaffected by artificial acidification but they noted a trend of reduced abundances for the predatory mites. Enchytraeids, however, were almost eliminated in the most acidified treatment and were reduced by application of lime which indicated a preference for slightly acidic conditions (Abrahamsen et al. 1978). These authors pointed out the importance of applying diluted acidic solutions that mimic actual inputs of acid rain to avoid “shock” responses by invertebrates.

Esher et al. (1992) conducted one of the few experimental simulations of forest floor acidification in North America and reported increased number of herbivorous mites with lower pH while predaceous mites and nematodes were unaffected. Earthworms appeared to be more susceptible to acidification in this study (Esher et al. 1992). These few experimental studies suggest that mites in general are resistant to acidification; however, as found with Collembola (e.g. Hågvar 1984), species will likely differ in their responses to acidity and the overall group response driven by tolerant dominant species can mask negative effects on sensitive species.

Studies of actual in situ effects of sulphur compounds or acidification on invertebrates are scant. These studies add greater realism to the results compared with artificial acidification; however, the variation encountered in the field is always large and

several habitat factors often mask pollutant effects on invertebrates. van Straalen et al. (1988) surveyed an area under forest decline (acidified) in Veluwe, Netherlands and concluded that relative abundance of the oribatid mite, *Platynothrus peltifer*, and the collembolan family Sminthuridae were valuable indicators of soil quality in those forests. Declining and healthy maple forests were studied by Tousignant et al. (1990) in southeast Quebec and they found, in general, lower abundances of insects, arachnids, and gastropods but higher numbers of myriapods in declining forests compared to healthy forests. From these studies it may be concluded that sulphur compounds and acidification have negative impacts on forest floor invertebrates under natural conditions that develop after prolonged exposure to industrial pollution. The small amount of work on carabids and spiders is reviewed in the introductions of Chapters 3 and 4, respectively.

Sulphur pollution near sour gas plants in Alberta

In Alberta, major sources of acidifying compounds (S° and SO_2) are the sour gas processing plants. Effects of elemental sulphur dust on ground cover and shrub vegetation in forests adjacent to sulphur blocks are well documented. In sites within 100 m downwind of sulphur blocks with a very acidic pH (<3), moss cover nearest to the source was eliminated (Kennedy et al. 1985) and understory shrub cover decreased dramatically (Maynard 1990, Legge et al. 1986). However, effects of SO_2 gas and moderate sulphur dusting at greater distances (200 m) have not been found (Maynard 1990, Maynard et al. 1994). Using controlled manipulations of elemental sulphur and liming, Visser (1991) corroborated these observations. These plant responses were attributed to acidification effects on soil chemistry. Reductions in pH can result in metal ion toxicity and deficiency of essential micro nutrients (Nyborg 1978). Decomposition of forest litter is also affected by acidification. Prescott and Parkinson (1985) reported greatest litter accumulation at a

site near a sour gas plant. They also found a corresponding decrease in rates of respiration and mass loss at this site. These patterns are probably the result of negative changes in the microbial decomposer community (Visser and Parkinson 1989, Visser 1991) coupled with potential changes in the structure of the soil fauna. In the long term, these processes can influence plant growth through changes in nutrient availability.

The invertebrates, which form the bulk of the biodiversity in most ecosystems, including forests have so far been ignored in studies of sulphur pollution around sour gas plants. One notable exception is the work of Addison (unpublished) which found reduced species richness and overall abundance of collembolans in the acidified site near the Strachan gas plant. Numbers of carabids, spiders and rove beetles were not affected in Addison's study, but these macroarthropods were not identified to species. Earthworms which may be among the most vulnerable invertebrates to acidification were not reported in Addison's study; probably because they had not invaded those sites yet. At the highly acidified site, invertebrates can be affected by direct toxic factors as well as an array of indirect factors mediated through habitat alterations at various spatial scales and predatory-prey interactions.

Thesis objectives and overview

The overall goal of this study was to investigate the effects of contamination associated with sour gas processing (elemental sulphur, sulphur dioxide and subsequent liming of sites adjacent to gas plants) on forest floor invertebrates. For the two sour gas plants considered in this study, contamination of the forest floor and potential impacts on fauna can operate at two spatial scales: (i) regional areas farther than 200 m east of the pollutant source where moderate levels of sulphur are found and with no apparent effects on pH or ground plant cover and (ii) localized areas within two hundred meters east of

the gas plants where a sharp gradient of sulphur, pH and degree of forest floor vegetational deterioration is found. Therefore, specific objectives of this study were organized following these two spatial scales and are listed below.

Objective # 1: To document the distribution and biodiversity of carabid beetles and forest floor spiders in forest sites around two sour gas plants (regional scale) under varying sulphur deposition regimes

Objective # 2: To relate environmental variables of the sites to arthropod communities and thereby gain a better understanding of the factors determining their regional distribution.

Objective # 3: To determine the distribution and diversity of forest floor invertebrates along a sharp acidification gradient in pine and aspen forests.

Objective # 4: To determine the influence of ground cover on pitfall trap estimates of invertebrate abundance and diversity.

Objective # 5: To compare invertebrate abundance and community results from pitfall traps inside enclosures with those from unfenced traps.

Objective # 6: To investigate whether forest edge confounds pollution effects on invertebrates.

Objective # 7: To rank the invertebrates studied in terms of their vulnerability to localized and regional sulphur pollution and to compare their potential as bioindicators of pollution.

The studies carried out to achieve objectives 1 and 2 are reported under Chapters 3 and 4 for carabids and spiders, respectively (Chapter 2 is a description of the general study area). These two chapters (3 and 4) are concerned with sulphur deposition at the regional spatial scale and the environmental factors that structure communities of these arthropods. These two taxa can differ markedly in their responses to microhabitat structure such as the lack of ground cover in acidified pine and aspen sites; therefore they

were presented in separate chapters. However, the results of the two taxa are integrated in the final conclusions in Chapter 6.

Objectives 3, 4, 5 and 6 are dealt with in Chapter 5. In this chapter, an effort has been made to gain a comprehensive understanding of the various factors that may explain observed pollution effects on invertebrates in the field. The various studies were designed to understand a number of indirect factors at the landscape level (forest edge from fragmentation), habitat level (aspen vs pine forests) and microhabitat level that can confound direct pollution effects. Methodological factors were also taken into account, particularly given concerns about the potential of lack of ground cover for inflating catches of surface active arthropods. This issue was addressed experimentally by manipulating ground cover, by building enclosures and using alternative sampling methods.

The final conclusions of the study are presented in Chapter 6. The chapter starts with a discussion of the effects of regional sulphur deposition on invertebrates with comments on their potential as bioindicators. It proceeds with a synthesis of the localized effects of sulphur pollution on invertebrates and a generalized model depicting the potential responses of invertebrates to chronic stress is presented. Finally some areas for further research are identified to gain more insights into how pollution affects invertebrates .

CHAPTER 2: STUDY AREA

The sites selected for this research were part of a long term study of forest health established in 1981 by Addison et al. (1984) and further described by Maynard (1990) and Maynard et al. (1994,1995). These publications have been used extensively in the following site description. Codes used in the present study and the equivalent codes used in Maynard et al. (1994) are provided in Table 2.1 to facilitate future comparisons.

The study area is located in the eastern foothills of the Rocky Mountains in south west central Alberta, ca. 200 km NW of Calgary and ca. 30 km SW of the town of Rocky Mountain House. The sites are centered around two sour gas processing plants, Strachan and Ram River (ca. 13 km apart), that began operation in the early 1970's (Addison et al. 1984). Six of the pine sites selected for this study were located in the vicinity (1-7 km) of the Ram River gas plant and had an altitude range of 1295-1433 m and were 86 to 121 years old. Eight pine and three aspen sites were in the area (0.05-12 km) of the Strachan gas plant and were all situated at approximately 1100 to 1200 m altitude; the pine sites ranged in age from 60 to 111 years old. The age of aspen stands was not available.

The climate of the area corresponds to that of the transition zone of the lower and upper boreal cordilleran (Strong and Leggat 1992) and is characterized by a short, cool and wet growing season that extends from about mid-May to mid-September. Mean summer temperatures over a thirty year period (1960-1990) were 8.5 °C (Maynard et al. 1994); however, the average day temperatures can reach around 15 °C in the month of July (see Fig. 3.2 for 1994). The bulk of precipitation falls in the growing season (70 %) with average totals of about 450 mm based on the 1960-1990 records at Base Line Mountain (Maynard et al. 1994). It is important to point out that during the intensive study of localized acidification effects during 1995 and 1996 total growing season precipitation recorded at the Base Line weather station was 593 and 342 mm, respectively.

Precipitation peaked in the month of July in 1995 but in 1996 it peaked in the month of May (Fig. 2.1). Snow formed an insignificant fraction of precipitation in the month of May of 1996.

Fourteen study sites are characterized by lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm) as the dominant tree species and with low densities of white spruce (*Picea glauca* Moench) and aspen (*Populus tremuloides* Mischx). The shrub tree layer is dominated by green alder (*Alnus crispa* Pursh), followed by white spruce (*Picea glauca*) saplings and low densities of *Salix sp.* in some sites. Varying densities of standing dead trees (snags) and logs on the ground (coarse woody debris) were found with the latter being particularly high at some sites near the Ram River gas plant (Table 3.3). The ground plant layer of the pine sites was dominated by feather mosses, mostly *Pleurozium schreberi* Mitt., ground shrubs *Vaccinium spp.*, *Rosa acicularis* Lindl. and *Linnaea borealis* L. The most common herbs were *Cornus canadensis* L. and *Maianthemum canadense* Desf.; grasses were common at most sites.

Three sites were dominated by aspen but had significant numbers of pine and/or white spruce (Table 3.3). The two aspen sites closest to the Strachan gas plant had high densities of green alder in the shrub layer. Composition of the ground layer was similar to the pine sites, except that grasses instead of feather mosses were dominant. Also, *Rosa acicularis*, *Epilobium angustifolium* L., *Cornus canadensis* and *Lathyrus ochroleucus* Hook were common components of the ground layer in aspen sites (Table 3.3).

Addison et al. (1984) and Maynard et al. (1994) conducted detailed pedon analyses of the sites and classified the soils as Brunisolic or Podzolic Grey Luvisols. Both forest types exhibited a well stratified litter-fermentation-humus (LFH) layer. The depth of the LFH layer for the pine sites ranged between 3 to 10 cm for pine sites and 6-10 cm for aspen sites. The texture of the mineral Ah or Ae horizon for most sites varied around a sandy or silty loam. Further details of edaphic and floristic parameters specific to the sites

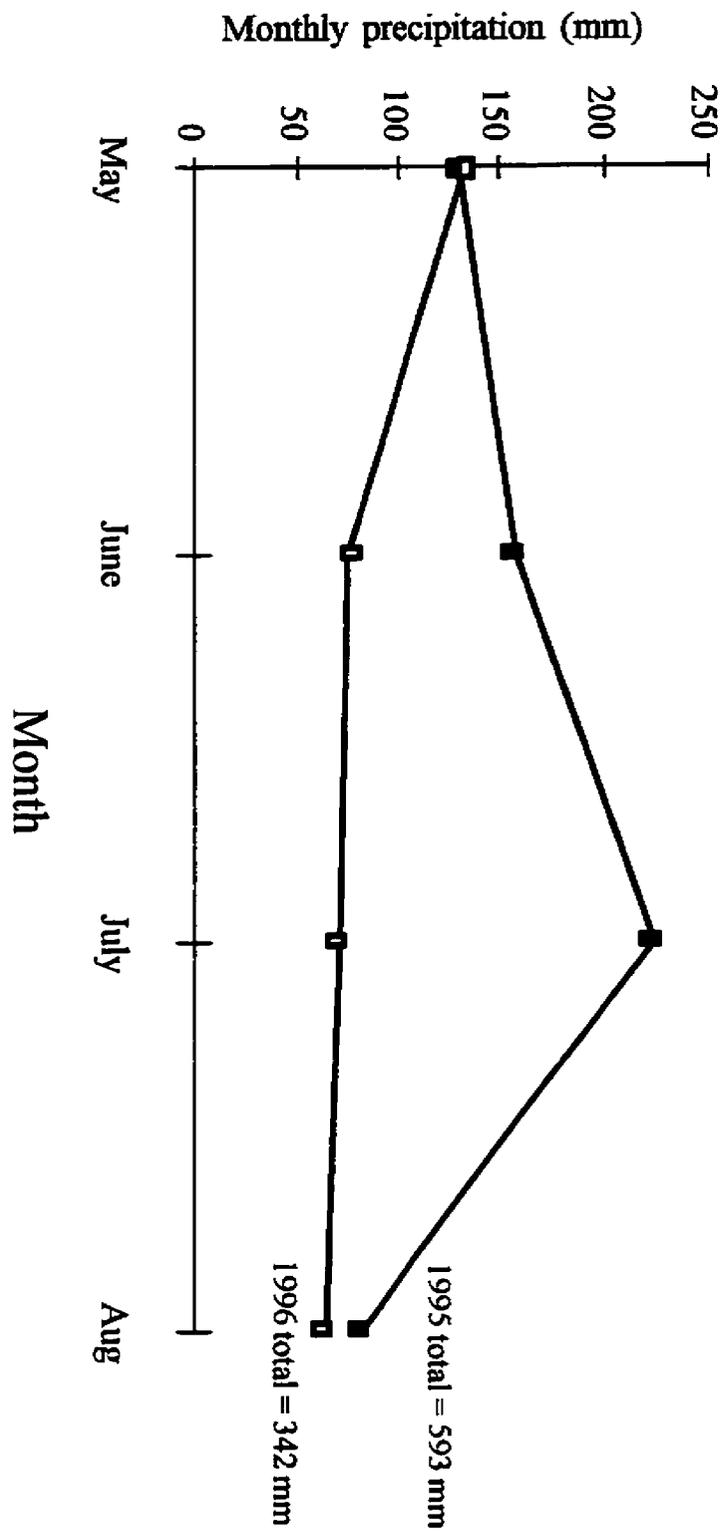
under the various sulphur contamination classes are given in Tables 3.1, 3.2 and 3.3 in Chapter 3.

Table 2.1: Codes used to designate study sites. HS = high sulphur, SD = sulphur dusted, ND = non-dusted.

Forest type	Sulphur category	Study	
		Maynard et al. (1994)	This thesis
Pine	High	1a*	HS1
	High	1b	HS2
	Dusted	2	SD1
	Dusted	34	SD2
	Dusted	5	SD3
	Dusted	12	SD4
	Dusted	30a	SD5
	Dusted	30b	SD6
	Non-dusted	13	ND1
	Non-dusted	14	ND2
	Non-dusted	23	ND3
	Non-dusted	4	ND4
	Non-dusted	6	ND5
	Non-dusted	8	ND6
Aspen	Dusted	40	SD7
	Non-dusted	41	ND7
	High	42	HS3

* Sites 1a and 1b, and 30a and b were not distinguished by Maynard et al. (1994).

Fig. 2.1: Precipitation patterns at the study area during 1995 and 1996.



CHAPTER 3: DISTRIBUTION OF CARABIDS IN SULPHUR DUSTED FORESTS

Introduction

Carabids are commonly used as bioindicators in environmental studies. In agroecosystems the detrimental effects of pesticides on non-target organisms are often inferred from the structure of carabid communities (Freitag 1979). Studies of alternative agricultural practices such as organic farming and intercropping have also used carabid assemblages as indicators of their environmental soundness (Perfecto 1986, Cárcamo et al. 1995). In forested systems, carabids have been used as indices of the environmental impact of fragmentation (e.g. Niemelä et al. 1993), fire (Holliday 1984) and herbicides (J. Addison, pers. com.).

A few studies have considered the effect of pollution on carabids. Effects of heavy metal pollution on carabids have been reported near industrial plants. Read et al. (1987) studied a carabid community in deciduous woodlands near lead-zinc smelters of southwest England. They found no effect of metal concentration in the soil on number of species and their individual abundances. However, metal concentration was significantly inversely correlated with the Shannon-Wiener index of diversity (H') as a result of common species increasing their dominance in the more polluted sites. Also, date of median capture occurred later in the most polluted sites, particularly for the species *Nebria brevicollis* Fabricius. Scarcity of prey (microarthropods) in woodlands close to smelters may have influenced carabid phenology (Read et al. 1987). Lesniak (1980) also reported changes in community structure in response to industrial pollution in pine forests of Poland and found that large carabids were replaced by small carabids in polluted sites. Also, similar to the

findings of Read et al. (1987) it was found that common carabids increased in abundance as pollution regime increased.

A number of investigations make some reference to carabids as part of the invertebrate fauna in ecotoxicological studies of heavy metals. Janssen et al. (1993) and Hunter et al. (1987) reported low accumulation of metals in carabids relative to other soil arthropods near smelters. Predatory Coleoptera larvae had greater accumulations of cadmium than adults probably as a result of the greater concentrations of this element in their more detritivorous prey (Hunter et al. 1987). In a study of metal effects on ants, Krzysztofiak (1991) reported a negative correlation between carabid abundance and heavy metal concentration. Bengtsson and Rundgren (1984) studied the effects of metal pollution on several ground living invertebrate taxa near Gusum, southeast Sweden. Species richness for spiders, harvestmen, ants, slugs and beetles (including carabids) was lower at sites contaminated with the highest levels of copper and zinc. These sites also had lower abundance of invertebrates. Two *Pterostichus* (Carabidae) species had the lowest concentrations of metals, leading Bengtsson and Rundgren (1984) to hypothesize that food levels may be more important than the toxicity of metals in determining distributions of large epigeic predators. These authors suggested that carabids are too mobile to make them good biological monitors of pollution. Occurrence of less mobile species, however, was overlooked.

Sulphur compounds are among the main pollutants contributing to acidification which can negatively affect terrestrial ecosystems (Knabe 1976). A few studies suggest that macroarthropods are susceptible to sulphur emissions. Freitag et al. (1973), have published the only comprehensive study of carabid beetles in relation to sulphur contamination. These authors used intensive pitfall trapping in mixed forests to assess the impact of exhausts (particularly Na_2SO_4) from a kraft paper mill on carabids near Thunder Bay, Ontario. Overall number of carabids increased with distance from the mill

and in general this pattern was observed for individual species. Body size of the most common species, *Agomum decentis* Say, was not affected by fallout. The authors did not report analyses of community structure. Leetham et al. (1978) reported similar results to those found by Freitag et al. (1973) on carabids exposed to experimental levels of sulphur dioxide while Bromenshenk (1978) working in the same system found the same trend for *Canthona* sp scarabs. Densities of epigeic macroarthropod fungivores were also reduced by experimental application of acidic (KHSO_4) and neutral (K_2SO_4) sulphates (Craft and Webb 1984). Compared to microarthropod responses to sulphur contaminants (e.g. Hagvår 1984), these larger invertebrates appear more consistent in their negative responses to sulphur containing pollutants; however, the variable nature of the sulphur chemicals and the low number of studies makes it difficult to draw firm conclusions.

From the above discussion it can be seen that carabids are popular organisms in environmental and ecological studies (Stork 1990). However, there is still a shortage of information on the environmental factors that structure their assemblages. Such information is essential to assess the effects of anthropogenic activities on these epigeic ground beetles, which are known to respond to edaphic variables such as moisture (Holmes et al. 1993, Niemelä and Spence 1994, Holopainen et al. 1995), organic matter content (Holopainen et al. 1995) and acidity (Paje and Mossakowski 1984, Holopainen et al. 1995). According to Thiele (1977) carabids are not associated with any particular plant species, however, there is some evidence that carabid communities within forests are associated with plant assemblages (Niemelä and Spence 1994); this however, is thought to result from covariation with abiotic factors (Niemelä and Spence 1994).

The main objective of the study reported in this chapter was to assess the effect of sulphur deposition (in combination with liming) on abundance, diversity and spatial distribution of ground beetles in forests around two sour gas processing plants. Also, an

attempt was made to relate ground beetle assemblages to variation in edaphic, floristic and structural heterogeneity of the forests.

Materials and methods

Site descriptions and contamination classes

Data given by Addison et al. (1984), Maynard (1990), and Maynard et al. (1994, 1995) were used to select 16 sites representative of the forests in the area and a range of sulphur deposition classes around the two gas plants. These 16 sites fall in the following six contamination classes (Table 3.1):

- a) Pine site (HS₁), highly impacted by very high levels of elemental sulphur and sulphur dioxide, limed, with pH of less than 3 and no plant ground cover.
- b) Highly impacted pine site (HS₂) or aspen site (HS₃) with high levels of elemental sulphur and sulphur dioxide, limed, with pH of 5-6 and partial plant ground cover.
- c) Sulphur dusted pine sites (SD₁₋₄) with detectable levels of elemental sulphur in the LFH, exposed to moderately high sulphur dioxide levels (Table 3.1), limed with pH of 4-6 and intact plant ground cover.
- d) Pine sites (SD₅₋₆); as in "c" but not limed with pH values around 4.
- e) Non dusted sites (ND₁₋₃) without elemental sulphur in LFH but exposed to SO₂ at levels higher than background, not limed, with pH of 4-5 and intact plant ground cover.
- f) Non dusted pine sites (ND₄₋₆) and one aspen site (ND₇) similar to "e" but with background levels of SO₂.

It is expected that localized processes such as habitat effects due to microclimate and direct toxic impacts of low pH are responsible for effects on organisms in the highly impacted sites near the sulphur blocks. Investigations of these processes are reported in detail elsewhere (Chapter 5). The goal of the present study was to assess whether sulphur deposition impacts carabids at sites farther than 200 m under moderate deposition levels. Therefore, on this basis, the carabid fauna in the sulphur dusted/high SO₂ sites (categories b and c) were compared with fauna in non dusted and with low or background levels of SO₂ (categories e and f).

Sampling

Pitfall traps made of 500 ml plastic cups, 10 cm diameter, with a plywood square rain cover (14 x 15 cm) held 2 cm above the trap with large nails were used; further details of this trap design were given in Spence and Niemelä (1994). Traps were placed in the ground with the rim flush with the surface and 2-3 cm of automobile radiator grade ethylene glycol were added to each trap. Five traps were deployed at each site either at 25 or 50 m intervals, depending on site area, to maintain the independence of trap catches (Digweed et al. 1995). Whenever possible traps were placed in a straight line and 50 m from the nearest forest edge. Forest study sites were separated by at least 100 m and up to ca. 25 km from each other (Fig. 3.1). Pitfall trapping occurred from May 18 to September 28, 1994 and all invertebrates were removed every 2-4 weeks.

Measurement of environmental variables

To investigate the factors that could influence the distribution of carabids, data on edaphic and floristic characteristics of the selected sites were collected. Edaphic information was gathered from a 5 cm diam. soil core of the forest floor collected within 2

m of each pitfall trap. Soil samples were maintained at 5°C until analysed for pH, organic matter content, moisture, and electrical conductivity. Because of the lack of L layer in some of the sites, most edaphic parameters were determined only for the F/H layer (Table 3.1).

Floristic composition at the sites was determined at two scales. Ground cover near each pitfall trap was assessed semi-quantitatively by placing a 1 m² grid centered around each trap and giving each plant species or type of ground cover a relative abundance score (see Table 3.2). These data were used to estimate plant species richness and relative total plant ground cover per m². Structural heterogeneity of the forest floor was further assessed by counting the number of logs (coarse woody debris) greater than ca. 10 cm diameter which were either decomposed (easily fragmented) or undecomposed (not broken by stepping on them) in a 5 m radius centered around each trap (Table 3.3). Trees, shrubs and young trees were also counted within this radius (Table 3.3). Additional data on sulphur, calcium, pH of organic soil layer (LFH), stand age, elevation, and detailed tree species composition were available from Maynard et al. (1994,1995) and used for ten of the study sites in direct ordination analyses.

Data handling

Whole-season catches in the five pitfall traps in each of the sites were pooled and standardized to a common, maximum number of 665 trap-days to take into account losses caused by wild-life interference. Ground beetle diversity was quantified using Hill's (1973) diversity numbers: species richness (N0); exponential form of the Shannon-Wiener function (N1) and the inverse of Simpson's index (N2). The first index is a basic measure of number of species in the assemblage while the other two emphasize rarity and dominance aspects, respectively. Furthermore, a separate index of evenness (*J'*) was

calculated following the procedures outlined by Magurran (1988). One way ANOVA was used to discriminate between carabid catches and community parameters between sulphur dusted and non dusted sites. All data analysed with ANOVA were tested for compliance with normality using the Wilk-Shapiro test and homogeneity of variances with Barlett's test. Where necessary, data were transformed using natural logarithms [$\ln(x + 1)$] to reduce heterogeneous variances or to ranks before testing with ANOVA. All tests were performed using the Statistix package version 3.5.

Changes in carabid species composition among study sites were assessed using Bray-Curtis percent similarity as the measure of distance and average linkage clustering (Ludwig and Reynolds 1988). Furthermore, spatial patterns in distribution and influence of environmental variables were explored using correspondence analysis (Howard and Robinson 1995) and canonical correspondence analysis (CCA; Ter Braak and Prentice 1988, Palmer 1993), respectively. For direct ordination analysis with CCA, all environmental variables were transformed using natural logarithms [$\ln(x + 1)$] as recommended by Palmer (1993). Species were considered rare and excluded when they were found in less than three sites or had less than 10 individuals represented in the total catch. This combination of indirect and direct ordination techniques is considered adequate to test the validity of the measured environmental variables in explaining the ordination axes. Furthermore, Canonical Correspondence Analysis (CCA) is a robust eigenvalue analysis used to summarize the spatial distribution of multispecies assemblages and relate them to environmental factors (Ter Braak 1986). Recent simulation studies by Palmer (1993) have demonstrated the robustness of this technique in dealing with high levels of variation (noise), peculiar distributions, and for correctly identifying relevant environmental variables. Also, unlike other ordination analysis methods, CCA does not yield an arch in the ordination diagram unless it is a true representation of the data (Palmer 1993).

Results

Ground beetle catches

Almost six thousand individuals representing thirty three species of carabid beetles were collected (Table 3.4). This carabid fauna is characteristic of the boreal-montane forest transition region (Niemelä et al. 1993, Lindroth 1961-69). Six species were dominant and accounted for 91 % of the total beetle catch; of these species, *Pterostichus adstrictus* Eschscholtz, *Platymus decentis* Say and *Calathus ingratus* Dejean were found in all sixteen sites, whereas *Calathus advena* Dejean, *Trechus chalybeus* Dejean and *Scaphinotus marginatus* Fischer were dominant overall but were absent or very rare (only one individual found) in at least one site. Only two other species, *Stereocerus haematopus* Dejean and *Pterostichus pensylvanicus* Leconte accounted for at least one percent of the carabid catch. The pattern of few dominant species for this community can be considered typical for harsh environments (Magurran 1988) such as the foothills forests of this study.

Twelve of the sites dominated by lodgepole pine and with similar vegetational ground cover (Table 3.2) were selected to assess the potential impact of sulphur deposition on ground beetle abundances as indexed by pitfall traps. For most of the common species of ground beetles, catches in the sulphur dusted sites were similar to those in undusted sites as revealed by ANOVA (Fig. 3.3). Exceptions were *S. marginatus* and *C. ingratus* which had greater average abundance in sulphur dusted sites (Fig. 3.3). Severe localized sulphur contamination effects on carabids varied considerably among the three sites (HS_{1,3}) and were investigated in more detail in the studies reported in Chapter 5.

Diversity and spatial distribution

Number of species per site ranged from 9 to 17 and the highest richness was found in site HS₁ closest to the sulphur block. The average richness for sulphur dusted and non dusted sites was twelve (Table 3.5). However, species diversity measured with the exponential form of the Shannon-Wiener index (N1, df = 1,10; F = 11.83; p < 0.01), the inverse of Simpson's diversity (N2, df = 1,10; F = 14.97; p < 0.01) and Pielou's evenness (J', df = 1,10; F = 12.65; p < 0.01) was higher in sulphur dusted sites (Table 3.5).

Patterns of diversity changes among sites (beta diversity) caused by species composition were studied using Bray-Curtis percent similarity (Ludwig and Reynolds 1988) followed by clustering analyses (Fig. 3.4). Sites ND₁ and ND₃ had the most similar species composition with 83 % similarity followed by HS₂ and SD₂ at 82 %; the aspen site with impacted ground cover (HS₃) was also very similar to the pine site (SD₁) with only moderate sulphur levels and intact vegetational ground cover (78 % similarity). Sulphur deposition category did not influence the changes in species composition since those sites with the highest level of sulphur (HS₁, HS₂ and HS₃) did not form an exclusive cluster. Similarly, sites without elemental sulphur in the LFH horizon did not fall in the same group. For example at the arbitrary level of 50 % similarity, two of the three groups formed included sites within the region of the Strachan sour gas processing plant. Group A at greater than 52 % similarity included sites adjacent to the Ram River plant except for site SD₄. Group B was formed by a triad including pine sites ND₆ and SD₄ which are more than 20 km apart and the aspen site (ND₇) which is approximately 1 km from site ND₆. Group C (>54 %) includes the sites in the vicinity of the Strachan gas plant, except for site ND₅ which is 4 km north east of the Strachan plant and highly dissimilar to any of the other sites in terms of relative ground beetle catches. These results

indicate that both forest specific variables and geographic factors are important in determining the ground beetle species composition.

Correspondence analysis of the 16 sites (Fig. 3.5) revealed similar results to the clustering classification presented above. Distances in ordination space for the most part, paralleled those found with percent similarity and clustering (Fig. 3.4); for example, pair HS₂ and SD₂ and pair ND₁ and ND₃ with a similarity of over 80 % were nearest each other in the ordination diagram (Fig. 3.5). The horizontal axis also dispersed all of the sites according to geographic location. The ten eastern sites in the Strachan region occurred toward the left or near the center of the axis (sites HS₁ and ND₆) and the six Ram River sites occurred toward the right side of the axis. Analysis of variance of the ordination scores showed highly significant differences between the eastern and western sites ($F_{1,14} = 12.14$; $p < 0.001$). The second axis (vertical) dispersed sites HS₁ and ND₂ toward the top and sites SD₃ and ND₆ at the opposite negative end (Fig. 3.5). Again, as in the clustering analysis, the results indicate that factors additional to sulphur deposition from the gas plants are primarily affecting the regional spatial distribution of the ground beetle assemblages.

Canonical Correspondence Analysis (Ter Braak 1986) was used to determine which environmental factors were most important in affecting ground beetle community distribution. Figure 3.6 shows the triplot of sites, species and environmental variables. In general the relative location in ordination space for the ten sites for which environmental information was available agrees with the results obtained with correspondence analysis (Fig 3.5); this can be taken as evidence that the variables measured explain the variation of the species data suggested by correspondence analysis (Ter Braak 1986). The first two CCA axes explained 66 % of the variance of the species data.

Environmental variables correlated with either of the two CCA axes are shown in Table 3.6 ($DF = 8$; $r = 0.63$; $p < 0.05$). For the sake of clarity, only those variables with the

highest correlations with one of the first two axes are included in the triplot diagram (Fig. 3.6). Density of coarse-woody debris (logs) per site had the highest correlation with the first CCA axis ($r = 0.93$). When logs were divided into decomposed and undecomposed, the latter had a higher correlation. Age of the stand, and density of shrubs were also significantly correlated with the first axis ($r = 0.63 - 0.74$).

A number of edaphic and floristic environmental variables were correlated with the second CCA axis (Table 3.6). Edaphic variables included percent organic matter content of the LFH, organic soil pH, and calcium content of the LFH (range of r values = 0.69-0.87, Table 3.6). Both ground cover plant variables (relative abundance of *Cornus canadensis*, grasses, plant species richness and total plant ground cover) and canopy species (lodgepole pine and white spruce) were correlated with axis 2. The length of the arrows in the triplot (Fig. 3.6) reflects the strength of the correlation with the axis to which they are associated as suggested by the angle between the arrow and the axis.

Discussion

Sulphur and carabids

The first objective of this study was to investigate the influence of sulphur contaminants resulting from sour gas processing on the ground beetle assemblages in adjacent forests. The results show that at sites farther than 200 m downwind of the sulphur block with no obvious change to ground cover or soil pH, there is no detrimental impact on carabid activity or diversity. Unlike Freitag et al. (1973) no pattern of increasing carabid abundance with distance to pollutant source or level of sulphur deposition was found. In fact, the opposite trend was observed; two species, *Scaphinotus marginatus* and *Calathus ingratus* demonstrated marginally higher activity in sites with moderate levels of

elemental sulphur in the LFH horizon. This trend was more apparent in the analysis of species diversity where the evenness component was clearly higher in sites that had moderate levels of sulphur dust compared to undusted sites and highly polluted sites (Chapter 5). These results suggest a complex non linear response of ground beetles to the sulphur deposition gradient.

The results from this study provide support to the idea that contamination effects do not result in linear population responses (Clausen 1984). At moderate levels, sulphur may act as a fertilizer. This is plausible considering that prior to establishment of the gas plants these remote forest sites may have been sulphur deficient (J. Volney, pers. comm.). At very high levels of sulphur there was a clear negative effect on abundance of a number of macroinvertebrates including the carabid *Scaphinotus marginatus*; only one specimen of this species was caught in the pine site at 50 m from the sulphur block. Localized environmental damage has been reported for this site for other components of the biota, including vegetational diversity (Maynard 1990), collembolan densities (Addison, unpub data), and microbial biomass (Visser and Parkinson 1989). The localized effects of severe sulphur contamination on the invertebrate fauna along this short gradient were investigated in more detail and are reported in Chapter 5.

The higher abundance of carabids in sulphur dusted sites may also be explained by the application of lime to these sites. According to provincial environmental regulations, sour gas plant operators are expected to lime sites near the gas plants. Four of the sulphur dusted sites (SD₁, SD₂, SD₃ and SD₄) have been limed annually at variable rates (Maynard 1990). The effect of liming on carabid beetles has not been reported in the literature, however, a preliminary study (Cárcamo, unpub. data) suggested that carabids may react positively to liming. Increased numbers of carabids in limed areas may result through predator-prey interactions. Earthworms and snails are preyed on by carabids (Judas 1989, Digweed 1993) and Huhta (1979) has shown higher earthworm colonization

and diversity on limed coniferous forests plots. The liming of the sulphur dusted plots may be considered a strong factor affecting ground beetle assemblages and is discussed further below.

Regional variation in carabid distribution

Classification and ordination analyses were undertaken to understand the spatial distribution of the ground beetle assemblages and the factors, anthropogenic or natural, that are important determinants of their distribution. Clustering of the sites using the carabid species composition suggested that site factors were more important than sulphur deposition in determining the assemblages. Sites around the Ram River and Strachan plants formed separate clusters, regardless of the amount of sulphur exposure. This result was confirmed by Correspondence Analysis; most of the eastern sites, around Strachan, were dispersed towards the left or center on CA axis one whereas all of the western sites around the Ram River gas plant were dispersed to the right end of this axis. Therefore, the most important environmental variable is related to a geographic gradient that goes east-west in this region. There is also considerable dispersion of the sites along the second axis suggesting a second environmental gradient. Direct ordination with CCA (Ter Braak 1986) uncovered coarse woody debris, site age and density of shrubs as variables most correlated with the first axis. Acidity of the organic layer, organic matter content, abundance of *Cornus canadensis*, grasses and lodgepole pine trees were the variables most correlated with the second CCA axis.

Structural heterogeneity of the forest floor in terms of coarse woody debris (logs) can influence distribution of carabid beetles. The present study is the first to demonstrate a quantitative relationship between ground beetles and the density of logs on the ground. Despite the obvious collector's knowledge that ground beetles are found underneath logs,

this variable has not been taken into account in studies of variation in ground beetle distribution in forests. Perhaps this is because most carabid studies in forests have been done in Europe where coarse woody material is not normally allowed to accumulate on the ground; for example Finnish forests have less than 2 m^3 per ha (J. K. Niemelä, pers. comm.). Previous studies in the mixed-wooded forests in north central Alberta have determined that common carabids such as *Pterostichus adstrictus* make use of logs in their larval stages (Goulet 1974). Studies with other invertebrates have found logs to be crucial habitat components; Hammond (unpub. data) has found a large number of beetle species in logs of aspen forests and Irmiler et al. (1996) have established their importance as habitat for sciarid flies and midges. Coarse woody debris is an important component of forests contributing to the diversity of the epigeic biota which includes carabids.

The number of logs was also correlated with stand age in this study; therefore, the effect of forest age in determining carabid community structure can be related to the nature of the ground cover structure of older forests. As forests age, the number of logs on the ground increases providing more suitable habitats for the epigeic fauna. In the present study, the carabid *Trechus chalybeus* was dispersed along the first (CCA) axis suggesting an association with log variability. *Trechus chalybeus* and a related species, *T. apicalis* Mtsch., are known to favour old growth forest in Alberta (Niemelä et al. 1993, Spence et al. 1996). This pattern can be explained by the abundance and quality of logs on the ground. It is possible that in addition to log density, the stage of decomposition of the logs is important. A stronger correlation was found for CCA axis one with logs that were at a later stage of decomposition ($r=0.94$) vs undecomposed logs ($r=0.76$). Because both values are very high, all logs were pooled for the presentation of results, but it is worthwhile to point out this difference as the two classes will vary in terms of moisture and abundance of microarthropod prey which carabids can exploit.

In this study, multivariate analysis revealed “western” and “eastern” ground beetle assemblages based on species relative abundances around the two sour gas plants. The eastern sites around the Strachan gas plant may be considered more boreal forest types and harbour carabid assemblages dominated by *P. adstrictus* and *P. decentis*. These two species were also dominant in the mixed-wooded forest studied by Spence et al. (1996) throughout central and northeastern Alberta but were rare in a pine forest in the Kananaskis valley at higher altitude. The more montane, western sites around the Ram River gas plant, on the other hand, were dominated by *Calathus advena* and *Trechus chalybeus*; both of these were common in a pine forest at Kananaskis (Cárcamo unpub. data) and foothills mixed-wooded forests (Niemelä et al. 1993).

The second CCA axis was correlated with a suite of variables, mostly associated with the forest floor chemistry (pH, calcium, carbon in the form of total organic matter) and vegetational structure (abundance of *Cornus canadensis*, grasses, relative plant cover and richness). Soil nutrient availability and pH are well recognized as factors structuring ground beetle communities in many habitats (Niemelä and Spence 1994, Holopainen et al. 1995, Holmes et al. 1993, Baguette 1993). Experimental studies by Paje and Mossakowski (1984) have shown pH preferences for a number of European carabids in soil microcosms which correspond with the habitat associations of the beetles. Soil pH was clearly one of the most influential variables responsible for the dispersion of the sites along the second CCA axis. The ground beetle *Amara hyperborea* Dejean was concentrated in the acidified site. *Agonum placidum* Say, a species of open habitats, followed this pattern but the trend was less marked.

The large number of variables associated with the second axis are all correlated with pH (negatively: organic matter, litter cover, tree density; positively: grasses, *Cornus canadensis*, relative plant cover, plant species richness, and calcium) and except for calcium, they may be considered of secondary importance to the ground beetle

community. For example organic matter was negatively correlated with pH and highly correlated with CCA axis 2. Higher contents of organic matter may occur from accumulation of acidic litter because of lower decomposition rates (Prescott and Parkinson 1986) which can be explained by reduced microbial activity and biomass (Visser and Parkinson 1989).

Similarly, high correlations between pH and several plant cover variables were found, especially relative abundances of *Cornus canadensis* and grasses. This can be interpreted as common responses of these plants and carabids to pH and not a direct association with carabid beetles (Thiele 1977). Previous studies reporting associations of carabids with plants have also suggested that correlations observed result from responses to a common abiotic factor such as moisture (Niemelä and Spence 1994).

Calcium was one of the environmental variables related to the second axis in the ordination analysis; it varied considerably as a result of liming of some sites and the extreme low pH of the site near the sulphur block. Calcium is an important element in the soil that affects the distribution of soil macrofauna such as snails (Hermida et al. 1995) and earthworms (Huhata 1979). These two groups are common prey of carabids (Hengeveld 1980a,b, Digweed 1993) and the distribution of malacophagous species like *Scaphinotus marginatus* may be indirectly affected by availability of calcium. In our study this species was significantly correlated with calcium ($df=8$, $r=0.66$, $p<0.05$). Also, carabid beetles may have a role in the cycling of calcium as suggested by Carter (1980); this author found that the carabid *Agonum retractum* Leconte was an important agent in the cycling of calcium in the soil. Liming appears to be an effective soil remediation strategy to maintain faunal diversity, at least for those sites that have received moderate levels of sulphur contamination.

In conclusion, regional sulphur deposition did not have a negative impact on abundances of carabid beetles measured with pitfall traps in sites that had similar and

intact ground cover; a few species were more abundant in sites that were sulphur dusted and limed. These sites also had increased species diversity as the evenness component was significantly higher. However, at very high levels, sulphur contamination can have a detrimental impact on soil fauna, but the precise mechanisms need further study.

A suite of factors affecting distribution of ground beetle assemblages were uncovered. Ordination analysis and classification suggested that geographic factors are of primary importance; the nature of the forest ground cover with respect to coarse woody debris, correlated with forest age, was the main factor structuring the carabid community. In addition calcium availability in the soil, its acidity and a host of variables related to pH were identified as important factors that further determined the distribution of carabid beetles. It was shown in this study that ground beetle diversity and distribution were affected by natural variation in forest structure firstly and only secondarily by factors of anthropogenic origin, i.e. changes in pH and calcium caused by sulphur contamination and liming. Further studies of anthropogenic effects on biological components of ecosystems should consider the simultaneous analysis of the effects of natural spatial heterogeneity relative to the anthropogenic stress of interest.

Table 3.1: Edaphic characteristics, altitude and stand age of study sites around the two sour gas plants.

CONTAMINATION CLASSES (SITE CODE)	SITE	Edaphic parameters						Other parameters	
		pH of FH (mg/kg)	Ext. S* (mg/kg)	Ca* (mg/kg)	N* (g/kg)	FH	FH	Site** altitude (m)	Stand age** (yr)
						E.C. (dS/m)	O.M. %		
a) High sulphur dust and SO₂, limed and without ground plant cover (HS)	1) HS1	2.8	6673	3500	7	1.04	63	1204	64
b) High sulphur dust and SO₂, limed with partial plant cover	2) HS2	6.3	2982	NA	NA	0.46	59	1204	64
	3) HS3@	5.6*	3860	16400	NA	0.54	35	1206	NA
c) Sulphur dusted and SO₂ exposed, limed with intact plant cover (SD)	4) SD1	5.4	322	8490	12	0.38	55	1204	88
	5) SD2	4.4	447	7700	110	0.37	62	1204	60
	6) SD3	6.7	490	18200	76	0.32	42	1204	90
	7) SD4	4.9	224	16000	138	0.21	52	1372	110
d) Sulphur dusted and SO₂ exposed, unlimed with intact plant cover	8) SD5	3.9	205	3820	165	0.20	70	1355	110
	9) SD6	4.1	188	NA	NA	0.21	59	1433	110
e) Non sulphur dusted unlimed with intact plant cover and low sulphur dioxide levels (ND)	10) ND1	5.0*	163	6180	261	NA	NA	1433	86
	11) ND2	4.3	154	4570	146	0.22	79	1295	93
	12) ND3	3.8	146	3010	170	0.23	72	1295	121
f) Non sulphur dusted, unlimed with intact plant cover and background SO₂ levels	13) ND4	5.0*	56	2810	62	NA	NA	1082	75
	14) ND5	4.4	125	4770	76	0.21	50	1113	111
	15) ND6	5.2	130	3980	149	0.18	43	1128	95
	16) ND7@	6.6	136	8220	NA	NA	NA	1115	NA

Notes: Sites in bold were used in direct ordination analysis. NA = data not available.

@ = sites with aspen forest cover; * Taken from Maynard et al. (1994 or 1995), ** taken from Addison et al. (1984).

Abbreviations: pH of FH = pH of fermentation/humus layer (FH);

Ext. S = extractable sulphur of litter-fermentation-humus layer (LFH); Ca = calcium concentration in LFH;

Total N = total nitrogen in LFH; FH O.M. = percent of organic matter in FH.

Table 3.2: Floristic composition of ground cover at study sites*.

Plant species	High sulphur (HS)					Sulphur dusted (SD)							Non-dusted (ND)						
	HS1	HS2	HS3*	SD1	SD2	SD3	SD4	SD5	SD6	SD7*	ND2	ND3	ND5	ND6	ND7**				
Mosses																			
<i>Pleurozium</i>																			
<i>scheberi</i> Mitt.	0.0	1.8	0.0	3.2	2.8	0.8	1.4	3.0	3.0	1.7	2.8	3.0	2.8	2.2	2.3				
<i>Ptilium crista-</i>																			
<i>castrensis</i> Hedw.	0.0	0.0	0.0	0.8	1.6	2.8	1.2	1.2	3.4	0.0	0.6	2.2	0.8	1.0	0.0				
Hylacomium																			
<i>splendens</i> Hedw.	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	1.6	0.4	0.0				
<i>Polytrichum sp</i>	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.0	0.4	0.0	0.0	1.0	0.6	1.0	0.0				
Shrubs																			
<i>Rosa</i>																			
<i>acicularis</i> Lindl.	0.0	0.8	0.0	0.0	0.6	0.2	0.6	0.6	0.0	1.3	0.6	0.0	1.0	1.6	1.0				
<i>Vaccinium</i>																			
<i>myrtilloides</i> Michx.	0.0	1.0	0.0	2.2	2.4	0.8	0.8	0.6	0.8	0.7	0.0	1.0	1.8	2.0	0.0				
<i>V. vitis-idaea</i> L.	0.0	0.0	0.0	0.0	0.6	0.4	1.0	2.2	2.6	0.0	3.0	0.0	2.0	1.8	1.3				
<i>V. caespitosum</i> Michx.	0.0	0.2	0.0	0.0	0.0	0.0	0.4	0.0	0.2	0.0	0.4	0.2	0.6	0.2	0.7				
<i>Ledum</i>																			
<i>groenlandicum</i> Oeder	0.0	1.0	0.0	0.0	1.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0				
<i>Viburnum</i>																			
<i>edule</i> Michx.	0.0	0.0	0.0	0.2	0.0	0.8	1.0	0.6	0.6	0.0	0.0	0.0	0.0	0.0	0.0				
Rubus																			
<i>pubescens</i> Raf.	0.0	0.0	0.0	0.0	0.0	0.6	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0				
<i>R. pedatus</i> Smith	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.4	0.0	1.6	0.0				
Herbs																			
<i>Viola renifolia</i> Gray	0.0	0.0	0.0	0.0	0.2	0.4	0.2	1.0	0.6	1.0	0.6	0.0	0.0	0.4	0.0				
<i>Lycopodium clavatum</i> L.	0.0	0.0	0.0	0.0	0.0	2.2	0.0	0.8	0.8	0.0	0.0	0.8	0.8	0.8	0.0				

Table 3.2: concluded.

Plant species	High sulphur (HS)			Sulphur dusted (SD)							Non-dusted (ND)				
	HS1	HS2	HS3*	SD1	SD2	SD3	SD4	SD5	SD6	SD7*	ND2	ND3	ND5	ND6	ND7**
<i>Petasites</i>															
<i>palmatus</i> Gray	0.0	0.0	0.0	0.0	1.0	0.0	0.6	0.0	0.0	1.0	0.0	0.0	0.0	2.0	0.0
<i>Lathyrus</i>															
<i>ochroleucus</i> Hook	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	1.3	0.0	0.0	1.2	1.6	0.7
<i>Galium boreale</i> L.	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.8	0.2	0.0
<i>Osmorrhiza</i>															
<i>depauperata</i> Philippi	0.0	0.0	0.0	0.4	0.0	1.0	0.0	0.2	1.0	0.0	0.0	0.0	0.0	0.0	0.0
<i>Fragaria</i>															
<i>virginiana</i> Duchesne	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7	0.0	0.0	0.0	0.4	2.3
<i>Arnica</i> sp	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.7	0.2	0.0	0.0	2.6	0.7
<i>Aster</i> sp	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.3
<i>Pyrola</i> sp	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.4	1.7
<i>Linnaea borealis</i> L.	0.0	0.0	0.0	1.4	1.4	1.4	1.0	2.4	1.4	1.3	2.6	1.2	1.2	0.4	0.7
<i>Epilobium</i>															
<i>angustifolium</i> L.	0.0	0.2	1.0	1.6	1.4	0.4	2.2	2.2	2.4	1.7	0.6	0.0	1.6	2.4	1.3
<i>Cornus canadensis</i> L.	0.0	1.2	0.7	3.4	1.8	2.8	2.8	2.0	2.4	1.7	0.4	2.0	2.8	2.2	2.7
<i>Maianthemum</i>															
<i>canadensis</i> Desf.	0.0	0.8	0.0	0.4	0.2	0.2	0.0	0.4	0.2	0.0	0.6	0.2	0.8	0.6	0.0
Grasses															
	0.0	1.0	2.0	2.8	1.8	2.0	2.4	0.6	1.4	4.0	1.0	0.4	1.4	3.4	3.7
Other parameters															
relative plant cover	0.0	9.8	3.7	17.4	17.6	20.6	20.4	19.4	22.0	21.3	14.6	13.8	25.0	31.6	19.3
Species richness	0.0	6.2	1.7	7.0	7.8	10.0	10.2	9.0	9.6	8.7	7.2	7.2	11.8	15.0	9.3
Litter	4.0	3.8	4.0	1.6	0.8	0.0	1.0	0.6	0.6	0.0	1.6	0.0	0.0	0.0	0.0

*Entries are averages of five (3 for aspen sites) 1 m² quadrats and represent indices of relative ground cover as follows: 0= absent,

1= <1%, 2= 1-5 %, 3= 6-20%, 4= >20%. ** Sites under aspen cover; SD7 was part of the localized study reported in chapter 5 on

Table 3.3: Densities of trees, shrubs and coarse woody debris at study sites*.

Site code*	High sulphur (HS)				Sulphur dusted (SD)						Non-dusted (ND)				
	HS1	HS2	HS3**	SD1	SD2	SD3	SD4	SD5	SD6	SD7**	ND2	ND3	ND5	ND6	ND7**
Canopy trees															
<i>Pinus contorta</i>															
Dougl.	9.80	10.40	0.00	9.00	15.00	7.20	4.20	7.40	5.40	1.33	12.80	10.80	2.80	4.60	0.33
<i>Picea glauca</i>															
Moench	0.60	0.60	0.33	0.80	0.20	1.40	1.80	0.00	0.00	0.67	0.00	0.20	3.00	0.20	4.67
<i>Populus tremuloides</i>															
Michx.	1.80	1.80	4.00	3.60	0.00	0.00	1.80	0.20	0.00	7.67	0.00	0.00	0.40	0.20	11.67
<i>Salix sp.</i>	0.20	0.20	0.00	0.00	0.00	0.00	7.60	0.00	0.00	0.33	0.00	0.00	1.00	16.60	10.00
<i>Alnus crispa</i>															
Pursh	0.20	0.40	6.67	2.00	0.00	3.40	0.40	2.20	0.80	8.67	16.00	2.80	0.20	0.00	0.00
Saplings															
<i>P. contorta</i>															
<i>P. contorta</i>	0.00	0.00	0.00	0.00	0.00	0.00	4.40	0.00	0.00	0.00	0.00	0.00	0.20	1.00	0.00
<i>P. glauca</i>															
<i>P. glauca</i>	0.80	1.20	0.00	0.60	1.40	2.60	0.00	0.00	0.00	0.00	0.40	16.80	0.00	0.00	0.00
<i>P. tremuloides</i>															
<i>P. tremuloides</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.20	0.60	0.00
Dead trees															
Coarse woody debris															
Undecomposed	2.00	4.40	5.33	3.20	1.80	3.60	3.60	7.40	8.80	5.67	2.60	6.20	1.80	1.60	1.00
Coarse woody debris															
Decomposed	1.60	1.80	1.33	1.40	1.40	2.40	3.40	11.20	9.40	1.67	3.40	6.80	2.40	4.40	3.33
<i>Snags</i>	2.40	3.40	5.00	2.60	1.80	1.80	1.80	0.80	1.80	3.33	2.00	0.80	0.40	1.20	0.00

*Entries are average number of stems or shrubs per 78.5 m² (5 m radius). ** Sites under aspen cover.

Table 3.4: Catches of ground beetles per site adjusted to a maximum of 665 trap days (rounded to the nearest integer).

Site #	High sulphur (HS)			Sulphur dusted (SD)						Non-dusted (ND)						***	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		16
Site code*	HS1	HS2	HS3**	SD1	SD2	SD3	SD4	SD5	SD6	ND1	ND2	ND3	ND4	ND5	ND6	ND7**	%
<i>Pterostichus adstrictus</i>	183	158	185	206	141	140	74	26	24	3	30	8	295	53	62	132	29
<i>Platymus decentis</i>	12	60	73	58	45	109	61	14	14	7	9	11	106	16	60	24	11
<i>Calathus ingratus</i>	81	121	67	65	105	32	36	10	11	13	19	5	27	10	15	24	11
<i>Calathus advena</i>	174	81	8	68	105	44	29	54	27	153	105	117	5	4	0	0	16
<i>Stereocerus haematopus</i>	0	20	0	24	38	5	7	7	2	2	22	0	10	1	0	0	2
<i>Pterostichus pennsylvanicus</i>	2	4	4	7	3	4	1	0	0	0	1	0	10	2	0	25	1
<i>Trechus chalybeus</i>	1	0	7	16	2	111	105	121	42	142	1	117	2	0	57	49	13
<i>Pterostichus punctatissimus</i>	0	0	0	0	0	0	5	0	0	5	12	2	0	0	4	0	0
<i>Scaphinotus marginatus</i>	1	14	61	133	92	185	23	10	17	23	12	10	6	63	1	6	11
<i>Carabus chamissonis</i>	0	3	0	2	0	0	1	0	0	0	4	0	2	1	1	1	0
<i>Patrobus foveocollis</i>	1	0	0	2	0	6	6	0	0	1	0	0	2	0	7	4	0
<i>Nebria gyllenhali</i>	0	0	0	0	3	1	0	0	0	2	0	1	21	0	0	0	0
<i>Amara hyperborea</i>	11	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Pterostichus riparius</i>	0	0	3	1	1	6	2	0	0	0	0	0	11	0	0	0	0
<i>Agonum placidum</i>	19	8	3	2	3	2	0	1	0	8	1	1	0	1	0	1	1
<i>Agonum retractum</i>	0	0	16	16	0	2	1	0	0	2	3	0	0	0	7	9	1
<i>Platymus mannerheimi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0
<i>Leistus ferruginosus</i>	0	2	1	0	0	7	1	2	0	2	0	0	0	0	0	0	0
<i>Calosoma frigidum</i>	0	1	9	1	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Carabus taedatus</i>	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
<i>Bembidion rupicola</i>	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Trechus apicalis</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
<i>Bembidion grapei</i>	4	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0

Table 3.4: Concluded

Species	High sulphur (HS)			Sulphur dusted (SD)						Non-dusted (ND)							%
	Site #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Site code*	HS1	HS2	HS3**	SD1	SD2	SD3	SD4	SD5	SD6	ND1	ND2	ND3	ND4	ND5	ND6	ND7**	
<i>Cymindis cribricollis</i>	4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Notiophilus aquaticus</i>	0	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0	0
<i>Harpalus fulvilabris</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Synuchus impunctatus</i>	1	0	3	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Amara quenseli</i>	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Agonum cupreum</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Miscodera arctica</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amara erratica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
<i>Agonum cupripenne</i>	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SUM	500	474	444	603	538	655	353	245	139	364	220	273	500	152	217	280	100

Note: * See table 1 for detailed explanation of codes; sites in bold were used in canonical correspondence analyses;

** sites under aspen forest cover. ***% = (species sum/total for all species)*100.

Table 3.5: Summary of community parameters for carabids in pine and aspen forests near sour gas plants.

Parameter	Sulphur category Site code*	Pine		Aspen		Pine			
		high	high	High	non-dusted	sulphur dusted**		non dusted**	
		HS1	HS2	HS3	ND7	SD1-6		ND1-6	
					mean	se	mean	se	
N0 (Richness)		17.00	13.00	16.00	13.00	12.00	0.95 a	11.83	0.91 a
N1 (Shannon-Wiener index)		4.68	5.58	5.82	5.55	6.10	0.44 a	4.45	0.35 b
N2 (inverse of Simpson's index)		3.54	4.48	4.10	3.70	4.98	0.48 a	3.25	0.27 b
J' (evenness)		0.54	0.67	0.64	0.68	0.73	0.04 a	0.60	0.03 b
Individuals		500.00	474.00	443.78	279.93	421.92	77.01 a	287.70	51.35 a

* see table 1 for explanation of codes; ** means of community parameters for sulphur dusted and non-dusted categories followed by different letters are significantly different ($p < 0.01$, F test)

Table 3.6: Interset correlations of environmental variables with CCA axes.

Variable	Axis 1	Axis 2
Organic soil pH	0.09	-0.85
FH % organic matter	0.00	0.88
Grasses	-0.05	-0.80
<i>Cornus canadensis</i>	0.27	-0.82
Ground plant richness	0.40	-0.66
Relative plant cover	0.35	-0.65
Undecomposed logs	0.76	0.02
Decomposed logs	0.92	0.18
all logs	0.93	0.09
Shrubs	0.65	-0.05
Stand age	0.74	-0.25
Calcium	-0.02	-0.69
<i>Picea glauca</i>	-0.14	-0.65
<i>Pinus contorta</i>	-0.35	0.80

* All correlations in bold are significant ($r > 0.63$, $df = 8$, $p < 0.05$)

Fig. 3.1: Layout of study sites around the Strachan and Ram River sour gas plants.

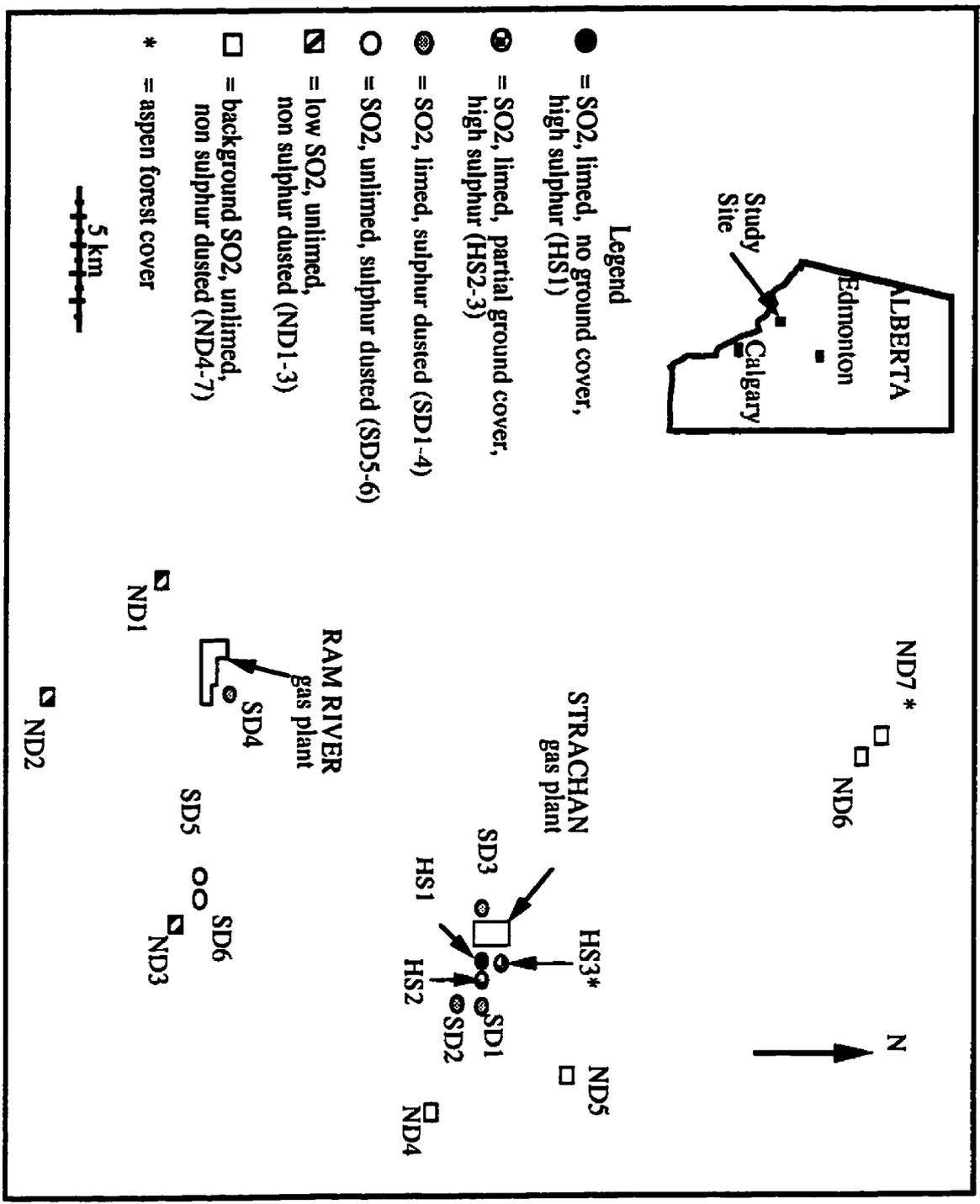


Fig. 3.2: Temperature and rainfall patterns in the study area during the growing season of 1994.

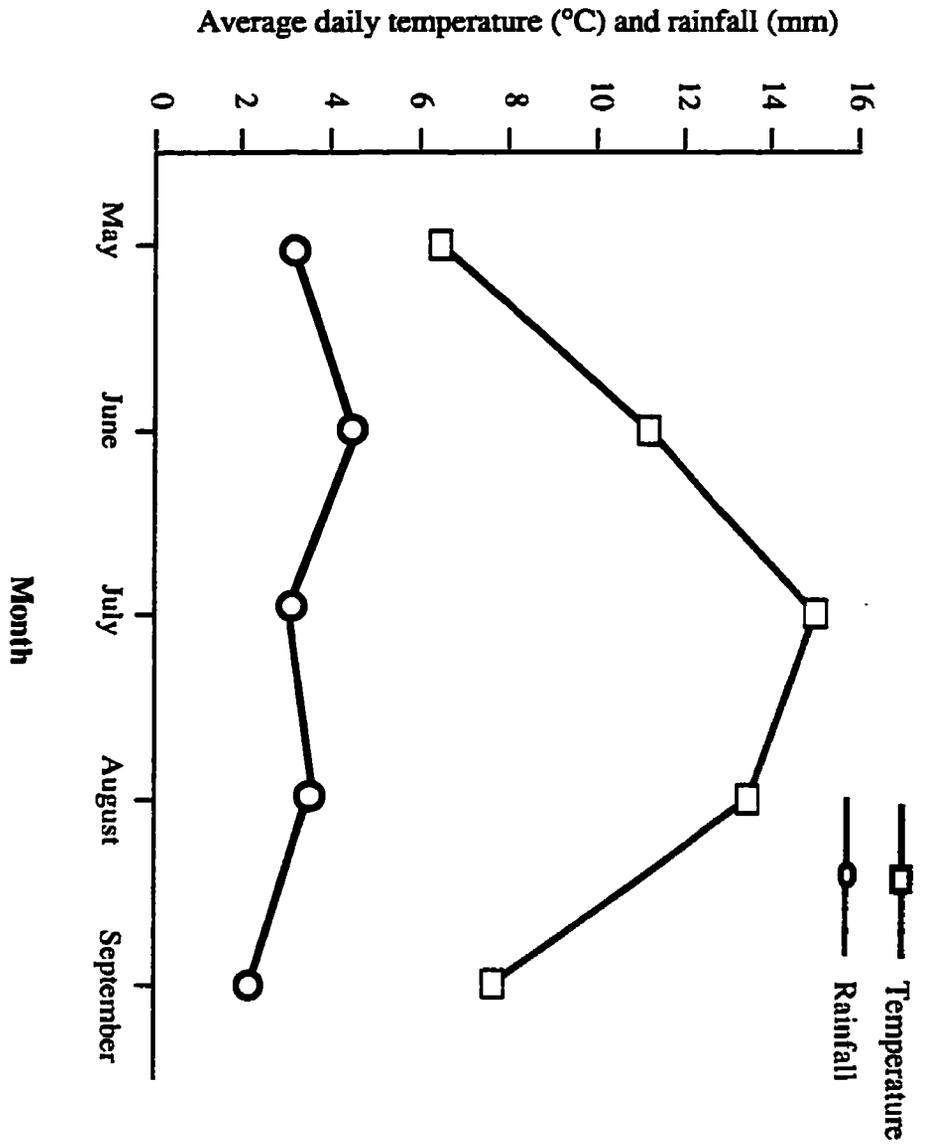


Fig. 3.3: Catches of ground beetles in sulphur dusted and non dusted pine sites.

* Marginally significant differences ($0.05 > p < 0.10$).

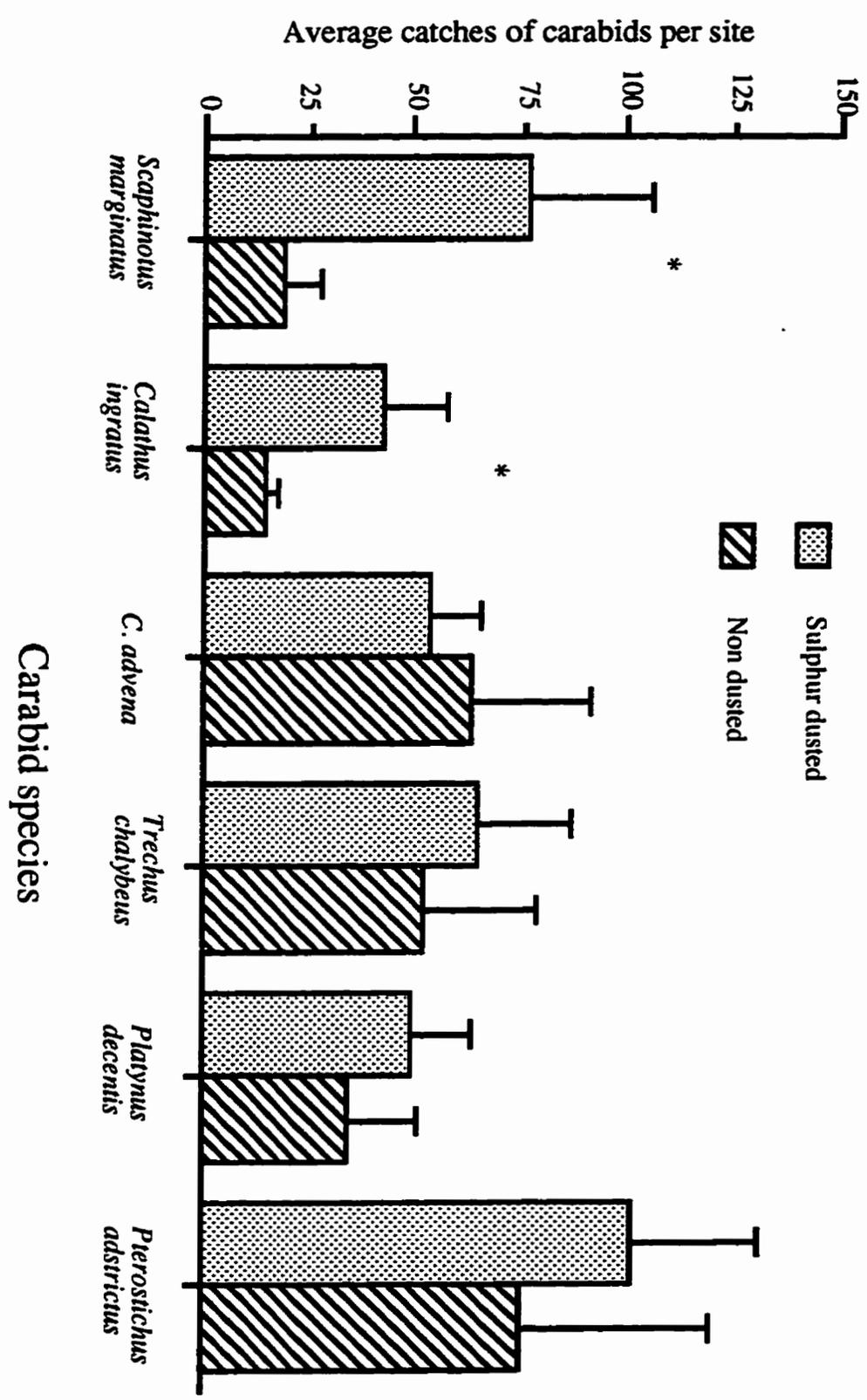


Fig. 3.4: Dendrogram of all sites using Bray-Curtis percent similarity and average linkage clustering. HS = high sulphur sites, SD = sulphur dusted, ND = non-dusted. HS₃ and ND₇ are aspen sites.

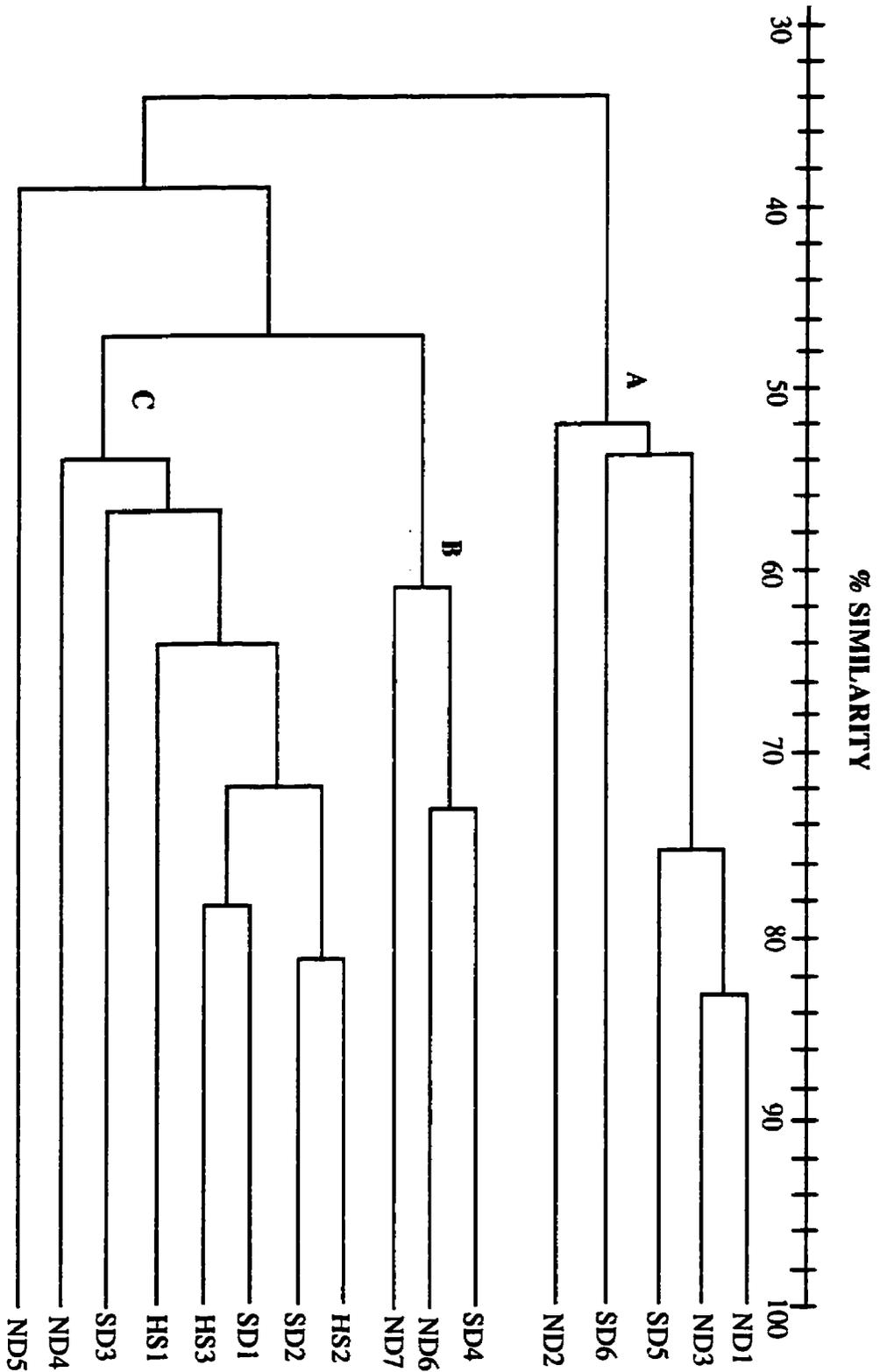
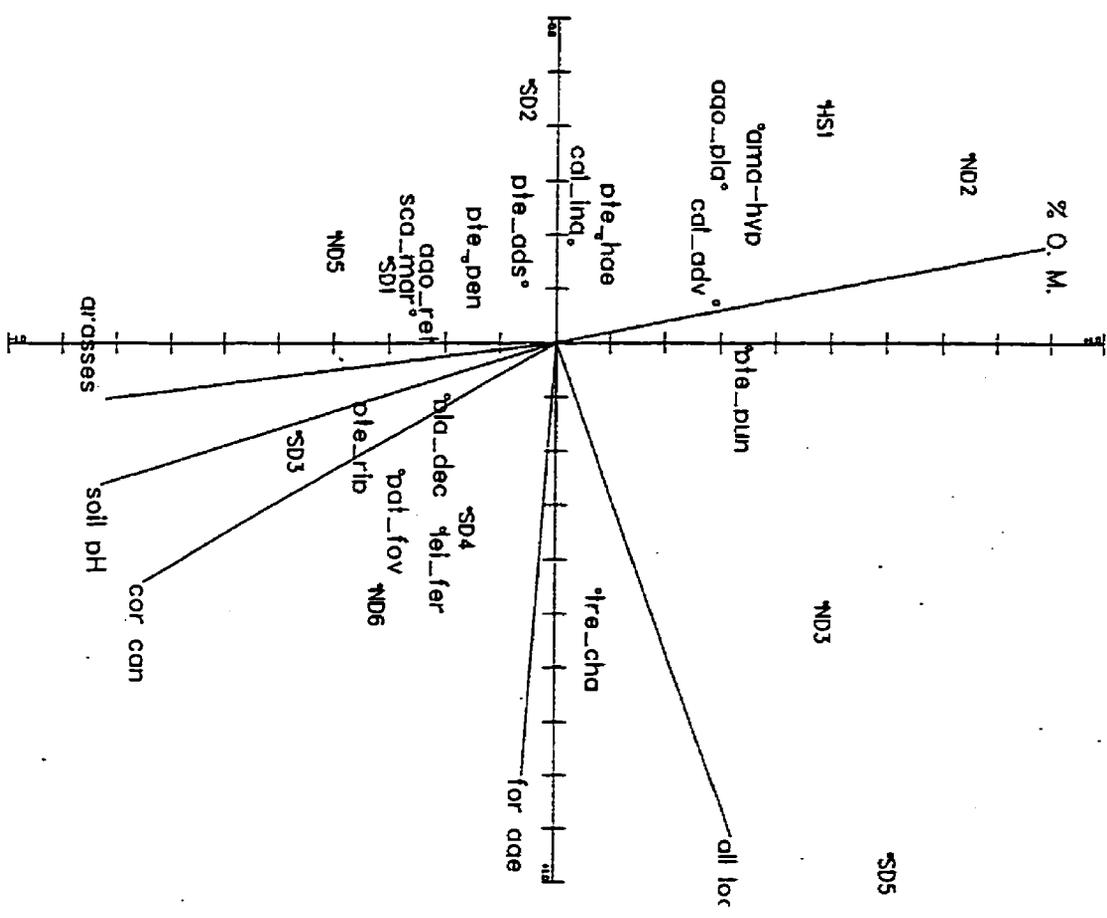


Figure 3.5: Correspondence Analysis biplot of carabid species (crosses) and sites (circles). Site abbreviations: HS = high sulphur, SD = sulphur dusted, ND = non-dusted. HS₃ and ND₇ are aspen sites. Species abbreviations: ago_ret = *Agomum retractum*, ago_pla = *A. placidum*, cal_adv = *Calathus advena*, cal_ing = *C. ingratus*, neb_gyl = *Nebria gyllenhali*, pat_fov = *Patrobis foveocollis*, pla_dec = *Platymus decentis*, pte_ads = *Pterostichus adstrictus*, pte_pen = *P. pennsylvanicus*, , pte_rip = *P. riparius*, Pte_hae = *Stereocerus haematopus*, sca_mar = *Scaphinotus marginatus*, tre_cha = *Trechus chalybeus*.

Figure 3.6: Canonical Correspondence Analysis triplot of carabid species (circles), sites (squares) and environmental variables (vectors). Site contamination classes and abbreviations: HS = high sulphur, SD = sulphur dusted, ND = non-dusted. See Figure 3.5 for species abbreviations. Environmental variables: all log = number of coarse woody debris, cor can = *Cornus canadensis*, % O. M. = % organic matter, grasses = % grass cover index, for age = stand age. See caption for Fig. 3.5 for species abbreviations.



CHAPTER 4: EFFECTS OF SULPHUR POLLUTION ON FOREST FLOOR SPIDERS

Introduction

Spiders are among the dominant epigeic predators in temperate terrestrial ecosystems (Gertsch 1979) where they affect processes such as productivity of agroecosystems by preying on insect pests (Reichert and Bishop 1990) or influence forest litter decomposition through predation on detritivore microarthropods (Clarke and Grant 1968, Kajak and Jakubczyk 1977, Kajak 1995). Spiders are attractive organisms on which to study environmental effects of anthropogenic activities because of their ecological roles, they are highly speciose and the majority of ground dwelling species can be efficiently sampled by pitfall trapping (Niemelä et al. 1986).

Furthermore, spiders can be assigned to guilds based on their foraging strategies (Post and Reichert 1977) which facilitates ecological interpretation of observed patterns and can aid in their use as indicators of habitat quality (Clausen 1986, McIver et al. 1992). Two extreme approaches with respect to the numbers of spider guilds identified can be found in the literature. For example, Post and Reichert (1977) assigned spiders to 11 guilds; a similar approach was followed by McIver et al. (1992) who assigned 11 families to 10 guilds. McIver et al. (1992) assigned Telemidae and Theridiidae to the guild that uses a scattered line to trap prey but each of the other 9 families represented a separate guild. On the other hand, Pajunen et al. (1995) opted for a more simplified system and lumped spiders into two guilds: hunting spiders and web building spiders. In the present study, an intermediate approach was used by dividing the web builders according to size and the hunters according to time of activity. Thus, forest floor spiders were divided into four broad guilds: (1) Micro-webbers: small (<3mm) spiders of the families Linyphiidae (s.

lat.) and Theridiidae; (2) Macro-webbers: larger spiders (>3 mm) of the families Amaurabiidae and Agelenidae; (3) Night-hunters (Gnaphosidae Clubionidae, Thomisidae); (4) Day hunters (Lycosidae).

Effects of elemental sulphur contamination on spider communities have not been published, although, a few studies have reported the consequences of sulphur dioxide, or other pollutants near industrial facilities on spider assemblages. Clausen (1984) and Gunnarsson (1988) found negative effects of SO₂ on tree spider community composition and attributed the effects to indirect consequences of pollution on habitat structure; these included the changed nature of the lichen community on tree trunks (Clausen 1984). Gunnarsson (1988) suggested an increased predation by birds on large spiders as a result of needle loss in spruce trees growing in a high air pollution area. Deeleman-Reinhold (1990) studied the ground spider fauna in an SO₂-polluted area over a 14 year period in Holland and found a dramatic decrease in the number of lycosid spiders but stable or higher numbers of linyphiids. Koponen and Niemelä (1993) reported the opposite pattern for ground spiders along a heavy metal pollution gradient caused by a smelter in Finland; near the smelter lycosids were dominant whereas linyphiids decreased. They suggested that the reduced plant cover benefited wandering spiders. It appears that habitat alterations wrought by pollutants such as sulphur compounds may be more important than direct toxic effects in structuring spider communities.

Ecological work on spider communities and faunistics is hindered by the lack of taxonomic work on some groups. Excellent revisions and user friendly keys for Canadian spiders are found for Thomisidae and Philodromidae (Dondale and Redner 1978), Lycosidae (Dondale and Redner 1990), Clubionidae (Dondale and Redner 1992) and Gnaphosidae (Platnick and Dondale 1992). Species identifications are also possible for the family Amaurobiidae (Leech 1972), and although no keys are available for the Agelenidae, the family is not too diverse locally and species may be morphotyped and subsequently

identified by experts (e.g. R. Bennet, British Columbia Ministry of Forestry or D. Buckle, arachnologist in Saskatoon). Species identification keys were not available for Linyphiidae (s. lat.), Theridiidae, Araneidae and Salticidae; the last two taxa were rare in the pitfall catches.

The objectives of this study were (1) to assess the effect of sulphur pollution on abundance, diversity and spatial distribution of forest floor spiders around two sour gas processing plants; and, (2) to identify those environmental factors including edaphic, floristic and structural heterogeneity of the forests that may influence spider distribution.

Materials and methods

Study sites, sampling and pollution classes.

Study sites and sampling methods were the same as those described in Chapter 3 for the study of carabid beetles; therefore, only changes applied to handling spider data are reported here. The sixteen study sites used were characterized in Tables 3.1 (edaphic characteristics), 3.2 (ground plants) and 3.3 (canopy, shrubs and coarse woody debris).

Vegetational ground cover is one of the most influential environmental factors that structures ground spider communities (Koponen and Niemelä 1993). The three sites under high sulphur pollution, although varying in forest cover (one aspen and two pine) and distance to sulphur block (50, 100, and 150 m) shared having an impacted plant ground cover which may be of paramount importance for epigeic spiders. Furthermore, multivariate analysis of spiders grouped these three sites suggesting a high degree of similarity. Therefore, for this study, these three sites were treated as replicates of the high sulphur (HS) pollution category.

To assess regional sulphur/lime pollution effects on spiders, the various sites shown in Table 3.1 were pooled into three classes: (1) Three highly impacted sites (a-b); (2) Six sulphur dusted sites (c-d); (3) Six non-sulphur dusted sites (e-f); the aspen site (ND7) was excluded for this comparison but was used in gradient analysis. Although sites within each category were far from identical, a comparison of the above categories was considered a reasonable way to test for potential effects of sulphur deposition on spider distributions.

Data handling

Whole-season catches in the five pitfall traps in each of the sites were pooled and were standardised to a common, maximum number of 665 trap-days to take into account losses caused by animals such as coyotes. For spider diversity analyses, linyphiid and theridiid spiders were excluded because of inability to achieve specific identification in these groups (see Introduction). Species diversity was quantified using Hill's (1973) diversity numbers: species richness (N0); exponential form of the Shannon-Wiener function (N1) and the inverse of Simpson's index (N2). Furthermore, a separate index of evenness (J') was calculated following the procedures outlined by Magurran (1988). All data on abundance were transformed to ranks before ANOVA because of large variations and/or presence of zeros; however, community results had smaller variances and were not transformed.

Changes in taxonomic composition of spider communities among study sites were assessed by average linkage clustering analysis with the Bray-Curtis percent similarity as the measure of distance (Ludwig and Reynolds 1988). The linyphiid spiders were included as Linyphiinae and Erigoninae. A few spiders in the family Theridiidae present in the samples were lumped with Linyphiinae because of difficulty in separating the two groups.

Spatial patterns in distribution of common taxa and influence of environmental variables were explored using correspondence analysis and canonical correspondence analysis (Ter Braak and Prentice 1988; Palmer 1993). For ordination analysis, all environmental variables and spider catches were transformed using natural logarithms [$\ln(x + 1)$] and rare taxa (those with less than 10 individuals and found in less than 3 sites) were excluded.

Results

The spider fauna

Over three thousand spider adults were caught representing 11 families. Thirty four species were recognised in seven of these families (Lycosidae, Thomisidae, Amaurobiidae, Clubionidae, Agelenidae, Gnaphosidae and Philodromidae). Of the thirty four species recognised, the lycosids were dominant and *Pardosa mackenziana* Keyserling accounted for 20 % of the entire spider catch. Other common lycosids (> 100 individuals) included *P. moesta* Banks, *P. uintana* Gertsch and *Trochosa terricola* Thorell. *Agroeca ornata* Banks (Clubionidae), *Callioplus euoplus* Bishop & Crosby (Amaurobiidae) and *Xysticus obscurus* Collett (Thomisidae) were also common. The fauna is characteristic of the boreal forest with few invasions from the Montane region; however, the paucity of spider community studies in western Canada prevents a detailed comparison.

Sulphur and spiders

The lycosid, *P. mackenziana* had significantly higher pitfall catches in sites with greatest sulphur contamination (Table 4.1; ANOVA on ranks: $df = 2,12$; $F = 5.13$; $p < 0.05$). *Trochosa terricola* had a similar pattern of abundance but the differences were only

marginally significant (Table 4.1; ANOVA on ranks: $df = 2,12$; $F = 2.97$; $p = 0.08$). *Callioplus euoplus* also had a marginally significant trend (Table 4.1; ANOVA on ranks: $df = 2,12$; $F = 3.13$; $p = 0.08$) of reduced abundance in the highly polluted sites (HS). Differences for the remaining common spiders were not statistically significant or their numbers were too low for analyses. For the micro-webbers (Linyphiidae and Theridiidae), there was a pattern of reduced activity in the most polluted (HS) sites compared to the non-sulphur dusted sites but the differences were not significant (Table 4.1; $df = 2,12$; $F = 2.19$; $p > 0.05$). These patterns were reflected in the analysis of relative guild abundances (Fig. 4.1). At the high sulphur sites, day hunters (Lycosidae) dominated the assemblage (66 %), whereas they accounted for less than 30 % in the less polluted classes (Fig. 4.1; $df = 2,12$; $F = 7.43$; $p < 0.05$). The pattern for the micro-webbers was reversed with 14% in the high sulphur sites and 41 and 43 % in the sulphur dusted and non dusted sites, respectively; these differences, however, were not statistically significant (Fig. 4.1; $df = 2,12$; $F = 1.89$; $p > 0.05$). The macro-webbers (Amaurabiidae and Agelenidae) showed a pattern of greater abundance in the intermediate (SD) pollution sites (Fig. 4.1; $df = 2,12$; $F = 5.07$; $p < 0.05$). The night hunters (Gnaphosidae, Thomisidae and Clubionidae) were evenly represented in the three sulphur classes (Fig. 4.1; 13-20 %).

Spider community structure (excluding the micro-webbers), was quantified using four commonly used diversity measures (Table 4.1). Species richness (N0), the exponential form of the Shannon-Wiener function (N1) and the inverse of Simpson's index (N2) did not differ significantly among the three pollution classes; interestingly, the number of spider species was slightly higher in the most contaminated sites. Evenness (J') was significantly lower in the highly polluted sites relative to the other two sulphur classes (Fig. 4.1; $df = 2,12$; $F = 7.45$; $p < 0.05$).

Spider regional variation

Patterns of similarity in spider composition among the sites were studied using Bray-Curtis percent similarity (Ludwig and Reynolds 1988) followed by clustering analysis (Fig. 4.2). The three sites under high levels of sulphur contamination (HS₁₋₃) formed a separate cluster at 52 % similarity; the two pine sites (HS₁₋₂) were more similar to each other (70 %) than to the aspen site (HS₃, Fig. 4.2). The remaining sites did not cluster according to sulphur presence in the LFH or location. The non-sulphur dusted aspen site (ND₇) was the least similar to any other site (22%). This difference was caused by the very large number of micro-webber spiders (588 adults) found in this site compared to any other (100 adults was the next highest catch in ND₁).

Ordination using correspondence analysis (CA) of all sixteen sites placed the three most polluted sites in the same region of the diagram (Fig. 4.3); this analysis confirmed the results found from clustering (Fig. 4.2). The four sites without elemental sulphur in the LFH and background levels of SO₂ (category “f” in Table 3.1, Chapter 3), were dispersed toward the right of axis 1 but were closer to other sites than to each other.

A complete set of environmental variables was available for 10 of the sites and these were related to spider composition using Canonical Correspondence Analysis (CCA, Fig. 4.4). In general, the relative positions of sites in the CCA triplot were similar to those observed using CA (Fig. 4.3); however, position of sites along the second axis (vertical) were reversed. Agreement between CA and CCA analyses may be considered a strong indication that the environmental variables selected explain the patterns observed in ordination space (Ter Braak 1986). Several environmental variables were highly significantly correlated (DF=8, $r > 0.77$, $p < 0.01$) with CCA axis 1 (Table 4.2). These included relative abundance of the plant species *Petasites palmatus* Gray, *Rubus pedatus* Smith, *Lathyrus ochroleucus* Hook, and *Arnica* sp. and the amount of sulphur extracted from *Cornus canadensis* leaves (taken from Maynard et al. 1995). The second (vertical)

CCA axis was highly correlated with electrical conductivity of FH, three macronutrients (N, P, K) and particularly with amount of coarse-woody debris near a pitfall trap ($r=0.83$).

Discussion

Sulphur and spiders

Contamination of sites immediately east of the sulphur block resulted predominantly from elemental sulphur. Sulphur dioxide gas also occurs at elevated levels but cannot be distinguished from the overriding high amounts of sulphur dust which destroy the plant cover (Maynard 1990, Visser 1991). Also, liming around the sour gas plants has affected the pH in some sites. Despite these confounding factors, the three highly polluted sites (HS) share a clearly impacted forest floor with reduced vegetational cover.

At the polluted sites there was a significant shift in the spider assemblage in terms of relative guild abundances. Sites with an impacted forest floor were dominated by lycosid spiders at the expense of micro-webbers, predominantly of the family Linyphiidae *s. lat.* The wolf spider, *Pardosa mackenziana*, clearly had a preference for the polluted sites closest to the sulphur block. Its dominance at these sites was reflected in the reduced species evenness of the spider assemblage. These changes in spider composition can be attributed mostly to indirect effects of contamination mediated through habitat alterations although direct toxic effects of elemental sulphur or SO₂ on micro-webbers cannot be ruled out. There was a trend of higher abundance of Erigonines in non-sulphur dusted sites compared to sulphur dusted sites; both of these site types had intact ground plant cover.

Similar studies of elemental sulphur pollution on ground spiders could not be found for comparison. However, Koponen and Niemelä (1993) found very similar results in a Finnish pine forest polluted by heavy metals produced by a smelter. The ground plant cover at their most polluted site was less than 2% and one lycosid species, *Xerolycosa nemoralis* Westring was the most abundant in their study. Linyphiid spiders typical of the old growth forest floor were not found. Koponen and Niemelä (1993) concluded that the variation in vegetation cover explained the patterns in ground spider community structure. Other studies have reported habitat modification from SO₂ pollution as the mechanism affecting spider assemblages on tree trunks (Clausen 1984) and spruce foliage (Gunnarsson 1988). Furthermore, experimental (Robinson 1981) and correlative (Greenstone 1984) studies have shown the influence of habitat structural diversity on spider distributions.

Habitat fragmentation confounds the effects of pollution in the sites used in the present study and in other similar investigations. It has been well documented that spiders respond to forest harvesting and forest edge. McIver et al. (1992) found that diurnal hunting spiders dominated clearcuts up to 19 years old, whereas old growth forests (>200 yr) were dominated by web-builders. Pajunen et al. (1995) explicitly included the effect of edge in their study of fragmentation in southern Finnish forests. They also found an increasing representation of web-builders in the interior forests relative to edges and surrounding areas and an opposite pattern with the diurnal hunters. In the present study the results in the sulphur impacted sites paralleled those patterns found in fragmented forests and suggest that forest edge influences should be considered when explaining faunal patterns in polluted sites. The higher abundance of *P. mackenziana* at the highly polluted sites in the present study may result from the proximity of these sites (50-150 m) to the forest edge. Some *Pardosa* species are known to prefer sunny habitats where they can find good spots to warm their egg sacs (Lowrie 1973).

Spider regional variation

Changes in spider species composition and relative abundances among sites were studied with clustering and ordination analysis. Sites with a highly impacted ground cover formed a separate cluster and were also in the same region of the correspondence analysis biplot. This high degree of similarity in the highly polluted sites is explained by the abundance of diurnal hunting spiders (*Lycosidae*) and the scarcity of web-builders. In sites with intact plant ground cover, presence of elemental sulphur in the soil did not result in a distinct cluster of sites suggesting that it has little effect on spiders as long as plant cover is not damaged. Also, with the exception of SD5 and SD6, sites did not cluster according to location. This can be contrasted with the clustering of sites using carabid data which formed two distinct clusters according to location (Chapter 3). The ballooning behaviour of spiders (Gertsch 1979, Ehmann 1994) gives them a higher dispersal potential than carabids and explains the similarity of the spider fauna in the region.

The aspen non dusted site (ND7) had a highly dissimilar spider fauna as shown in the cluster diagram (Fig. 4.2). Linyphiid spiders dominated this site and although species were not identified, it is known that *Allomengea pinnata* Emerton is the most common in aspen sites in the region (Buckle and Cárcamo unpub. data). This linyphiine, is known to spin webs on forest floor vegetation but later in the season it drops to the ground where it is caught in large numbers in pitfall traps (Buckle, pers. comm.). This species may be responsible for the large differences in the observed spider fauna of the aspen site and the rest of the forest sites in this study.

Direct ordination with Canonical Correspondence Analysis (CCA) suggested that forest floor stand characteristics are important in structuring ground spider communities. The correlation of the relative cover of several ground plants with the first CCA axis can

result from joint microclimatic responses or their use by spiders as substrate for building webs. For example, *Pardosa hyperborea* Thorell was abundant in pine site ND₆ and this site had a large number of gaps that allowed more light to penetrate the forest floor which may allow the development of a characteristic plant and spider community as suggested by Platen (1993). Plant community architecture can directly influence spider distribution; Greenstone (1984) showed that diversity in vegetational heights was more important than availability of prey diversity in determining the distribution of web-building spiders. It is possible that plants such as *Lathyrus ochroleucus* can provide places for web attachment for foliage dwelling linyphiines while ground cover plants like *Petasites palmatus* may do the same for dwarf erigonines. Pajunen et al (1995), reported cover of *Vaccinium vitis-idaea* L. as one of the important environmental variables explaining one of the axes in their Canonical Correspondence Analysis; in the present study this plant was correlated ($r = -0.74$, $p < 0.05$) with the second CCA axis, suggesting its importance as a determinant of spider distribution.

Sulphur content of *Cornus canadensis* foliage had a highly significant correlation with the first CCA axis. It is of interest that sulphur in the LFH was not important nor was soil pH. Also, the first axis of correspondence analysis grouped the four sites (ND₄₋₇) with lowest exposure to S^o contamination towards the most positive area of the diagram. The only group that exhibited a pattern of increasing activity in non-sulphur dusted sites were the small web-building spiders (Linyphiidae s.lat. and Theridiidae); however, sulphur in the foliage of *C. canadensis* was not significantly correlated with their activity. Additional studies under laboratory conditions are needed to understand better the direct effects of sulphur dust on the various spider groups.

Decomposed coarse-woody debris had the highest correlation with the second CCA axis. Decomposed logs can provide suitable spatial refugia for arthropods to rest in the day and also provide a source of microarthropods for spiders to feed upon. Dispersion

of spiders along the second CCA axis explained by coarse-woody debris was small, although, *Agelenopsis utahana* Chamberlin and Ivie and *Pardosa uintana* appear to have opposite distribution patterns on this axis. *Agelenopsis utahana* is a funnel web spider which may prefer litter or moss habitat to spread its flat web. *Pardosa uintana* is a hunting wolf spider which is sympatric with its close congener, *P. mackenziana* and is known to prefer moist habitats (Lowrie 1973) which may be found around decomposed logs. These results corroborate the findings of other investigators (e.g. Irmeler et al. 1996, Cárcamo and Parkinson 1997, Hammond unpub. data) showing the importance of coarse-woody debris as hot spots of invertebrate biodiversity.

In summary, negative effects of sulphur contamination on ground dwelling spiders were restricted to sites within 150 m east of the gas plant where ground plant cover was visibly reduced. The wolf spider *Pardosa mackenziana* dominated these polluted sites and significantly reduced the evenness of the spider assemblage. The guild represented by diurnal hunting spiders (Lycosidae) were dominant in these sites at the expense of small web-builders (Linyphiidae *s.lat* and Theridiidae). At the regional spatial level, moderate sulphur deposition had a positive effect on the relative abundance of “macro-webber” spiders (Agelenidae and Amaurobiidae). It is concluded that indirect effects of high sulphur contamination related to the structure of the ground habitat have caused the changes in the observed community structure of forest floor spiders. The influence of forest edge on spider communities is suspected to contribute to the observed patterns and is reported in the next chapter.

Other environmental characteristics of the forest including a number of ground plants, nutrient status and coarse-woody debris appear to be important factors determining spider distribution. These factors associated with the natural variation of forest stands seem as important in determining spider distribution as factors associated with sour gas plant contaminants. It is suggested that habitat heterogeneity be taken into account along

with anthropogenic factors when conducting similar studies on responses of biodiversity to human caused stress.

Table 4.1: Activity of forest floor spiders during the 1994 growing season in the three sulphur classes.

Entries are means and standard errors; n = 6, except for High Sulphur, n = 3. Five traps per site were pooled. *

Family	Species	High Sulphur		Sulphur Dusted		Non Dusted	
		mean	±se	mean	±se	mean	±se
Lycosidae	<i>Pardosa mackenziana</i>	117.61	41.26 a	15.06	8.20 b	26.57	10.17 b
	<i>P. moesta</i>	0.89	0.89	0.55	0.39	11.71	11.39
	<i>P. uintana</i>	1.33	1.33	10.09	5.16	12.63	9.35
	<i>P. hyperborea</i>	0.00	0.00	0.00	0.00	2.53	1.46
	<i>P. xerampelina</i>	1.44	0.29	0.00	0.00	0.33	0.33
	<i>P. tesquorum</i>	0.33	0.33	0.00	0.00	0.17	0.17
	<i>Trochosa terricola</i>	10.10	1.82	2.44	1.34	9.89	7.28
	<i>Alopecosa aculeata</i>	2.22	2.22	1.87	1.10	1.13	0.28
	<i>Pirata bryantae</i>	0.00	0.00	0.00	0.00	2.08	2.08
	<i>Arctosa alpigena</i>	0.89	0.89	0.38	0.38	0.33	0.33
<i>Arctosa rubicunda</i>	0.00	0.00	0.00	0.00	0.17	0.17	
Thomisidae	<i>Xysticus obscurus</i>	2.78	0.78	4.50	2.13	5.96	3.10
	<i>X. canadensis</i>	5.00	0.58	1.95	0.60	1.72	0.68
	<i>X. luctuosus</i>	0.44	0.44	0.00	0.00	0.00	0.00
	<i>X. emertoni</i>	0.44	0.44	0.00	0.00	0.00	0.00
	<i>Ozyptila sincera canadensis</i>	0.00	0.00	0.17	0.17	0.17	0.17
Clubionidae	<i>Agroeca ornata</i>	4.44	1.94	7.08	2.26	27.05	12.29
	<i>Clubiona canadensis</i>	2.11	0.95	2.16	0.60	2.72	0.84
	<i>Clubiona kulczynskii</i>	2.55	1.44	1.06	0.26	0.17	0.17

Table 4.1: concluded

Family	Species	High Sulphur		Sulphur Dusted		Non Dusted	
		mean	±se	mean	±se	mean	±se
Amaurobiidae							
	<i>Callioplus euoplus</i>	3.99	2.08	17.65	3.89	9.08	5.21
	<i>Amaurobius borealis</i>	0.67	0.33	1.22	0.56	0.71	0.37
	<i>Callobius nomeus</i>	0.33	0.33	0.00	0.00	0.36	0.23
	<i>Arctobius agelenoides</i>	2.11	0.95	2.82	1.48	2.22	1.77
Agelenidae							
	<i>Agelenopsis utahana</i>	6.10	3.70	0.75	0.57	0.33	0.33
	<i>Cryphoeca exlineae</i>	2.99	2.51	0.00	0.00	1.05	0.63
Gnaphosidae							
	<i>Gnaphosa microps</i>	0.00	0.00	0.77	0.57	1.37	0.62
	<i>Gnaphosa borea</i>	0.89	0.89	0.19	0.19	0.35	0.35
	<i>Haplodrassus hiemalis</i>	0.44	0.44	0.00	0.00	0.17	0.17
	<i>Orodassus canadensis</i>	0.44	0.44	0.19	0.19	0.17	0.17
	<i>G. brumalis</i>	0.44	0.44	0.00	0.00	0.00	0.00
Other	Linyphiidae (s. lat.)/Theridiidae	27.63	10.80 a	39.56	6.21 ab	68.28	13.14 ab
	Total Araneae	199.28	63.80	111.16	21.28	189.40	46.35
	Richness (N0)	16.67	2.73	11.00	1.77	12.33	2.06
	Shannon-Wiener Diversity (N1)	4.16	0.36	6.35	0.93	6.09	0.39
	Simpson's Diversity (N2)	2.23	0.25 a	5.61	0.77 b	8.77	4.25 b
	Evenness (J')	0.52	0.05 a	0.78	0.03 b	0.76	0.05 b

*Means followed by different letters are significantly different (FPLSD, $p < 0.05$).

Table 4.2: Interset correlations of environmental variables with CCA axes

Variable	Axis 1	Axis 2
FH Conductivity	-0.41	0.78
<i>Petasites palmatus</i>	0.80	-0.05
<i>Rubus pedatus</i>	0.79	-0.18
<i>Lathyrus ochroleucus</i>	0.88	-0.06
<i>Arnica sp</i>	0.79	-0.35
Decomposed logs	-0.02	-0.84
Potassium	0.25	-0.81
Phosphorus	0.01	-0.84
Nitrogen	0.17	-0.85
Sulphur in <i>Cornus canadensis</i>	-0.78	0.47

Bold correlations are significant ($r > 0.77$, $df = 8$, $p < 0.01$)

Fig. 4.1: Effect of sulphur pollution on relative abundance of spider guilds. Entries are percentages of total spider catch. * Denotes statistically significant differences ($p < 0.05$).

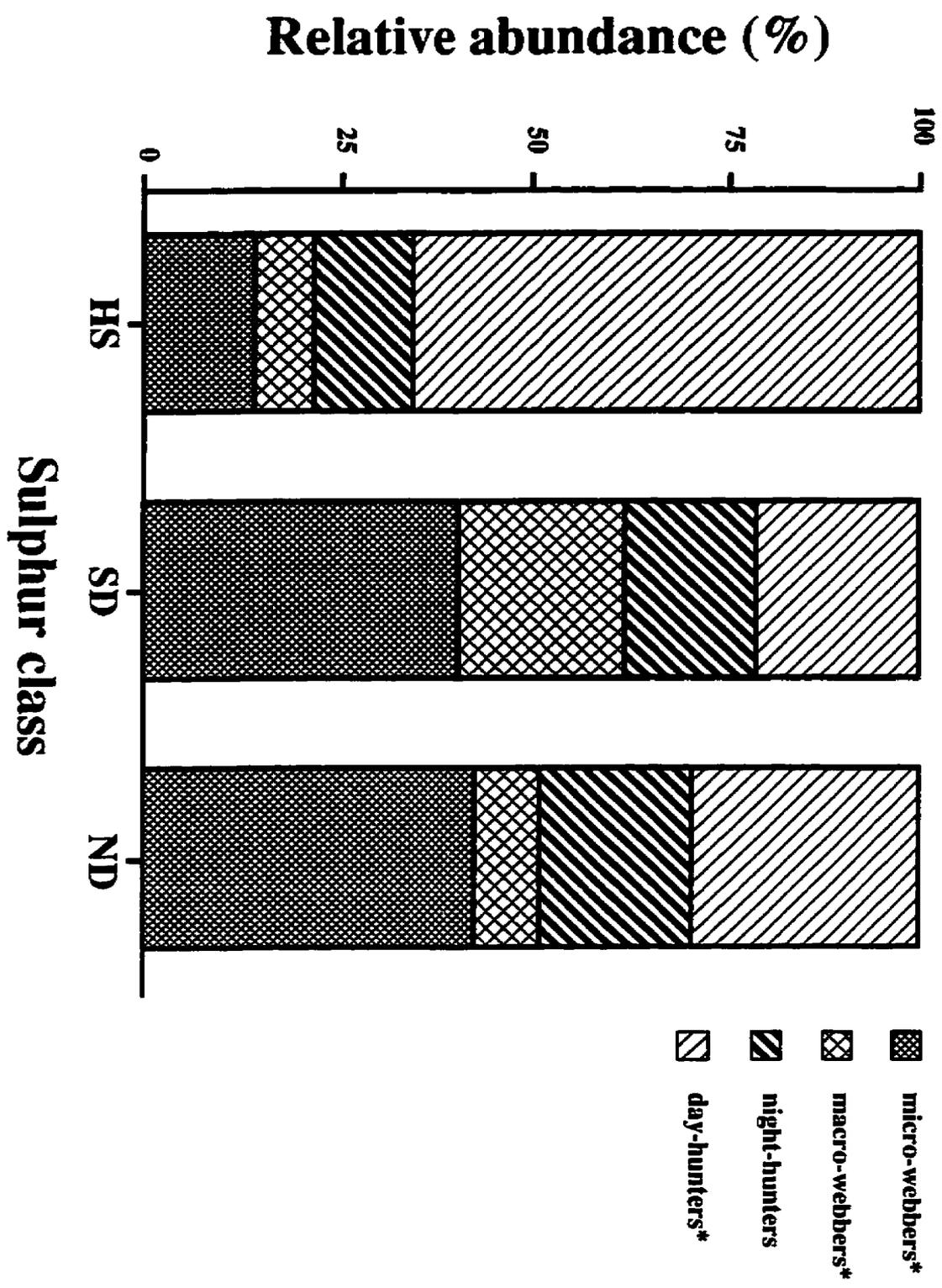


Fig. 4.2: Dendrogram of sites using Bray-Curtis percent similarity and average linkage clustering of spider assemblages. HS = high sulphur, SD = sulphur dusted, ND = non dusted.

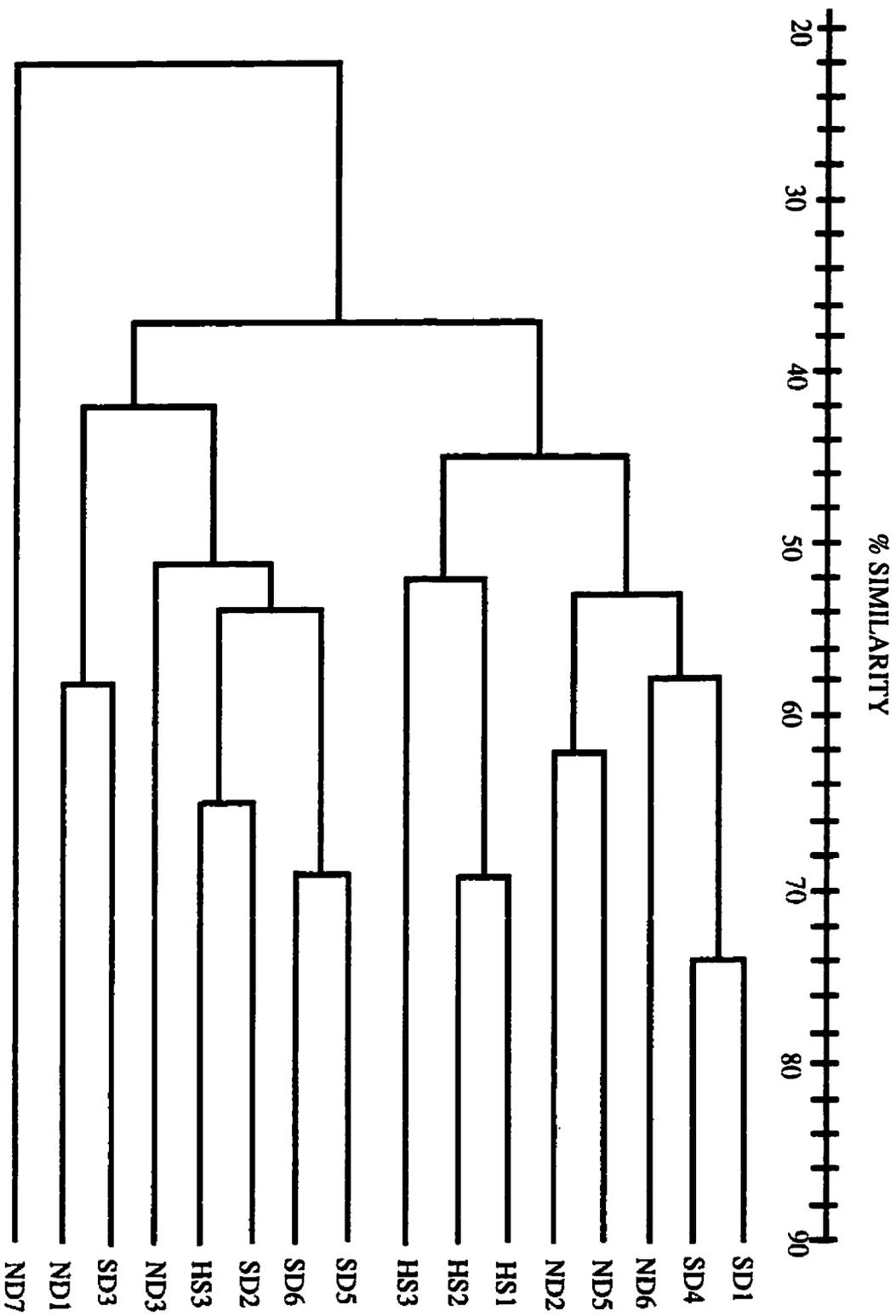
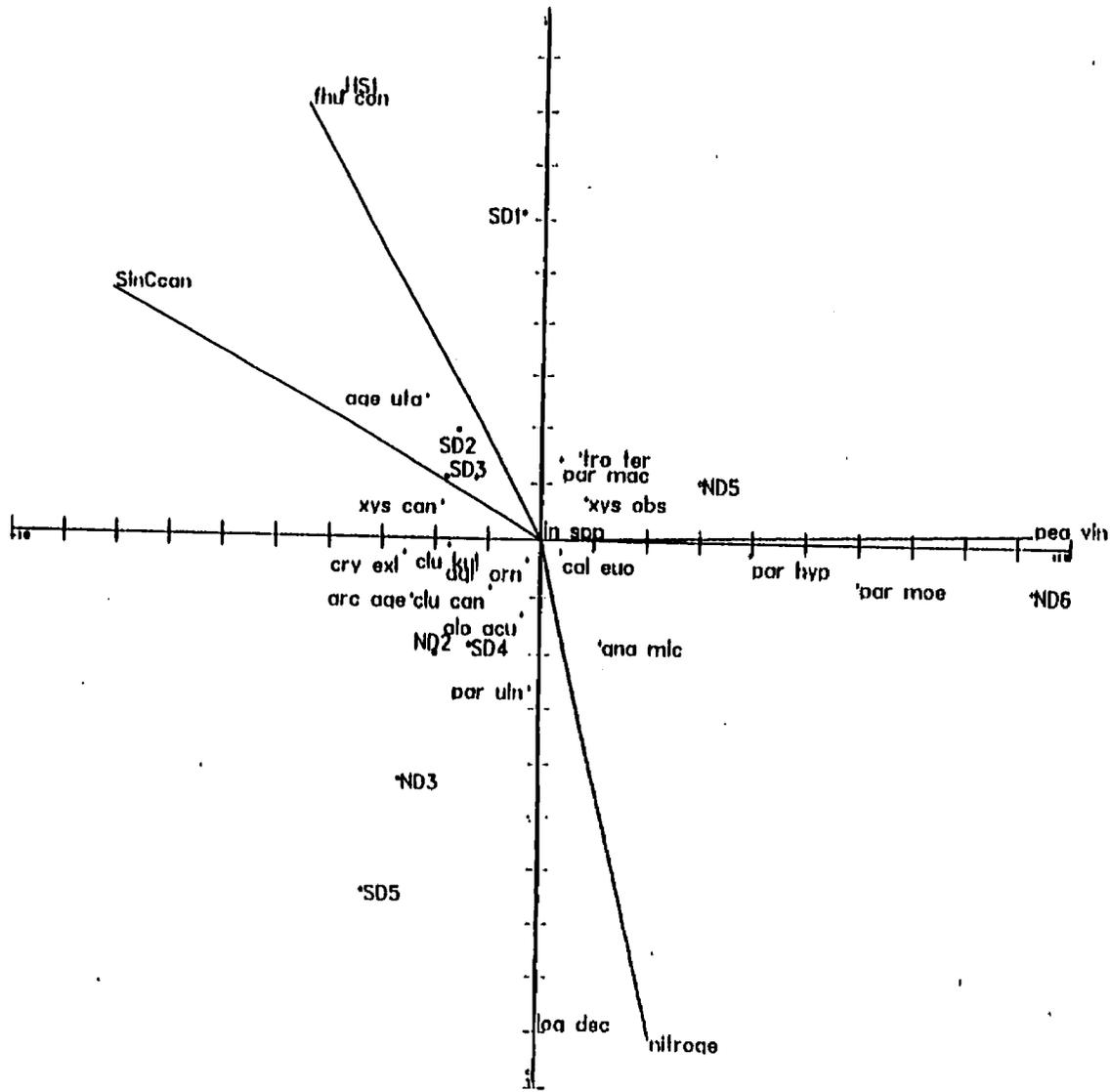


Fig. 4.3: Correspondence Analysis biplot of sites and species. **Sites:** HS = high sulphur, SD = sulphur dusted, ND = non dusted. **Species abbreviations:** age uta = *Agelenopsis utahana*, agr orn = *Agroeca ornata*, alo acu = *Alopecosa aculeata*, ama bor = *Amaurobius borealis*, arc age = *Arctobius agelenoides*, cal euo = *Callioplus euoplus*, clu can = *Clubiona canadensis*, clu kul = *Clubiona canadensis*, cry exl = *Cryphoeca exlineae*, eri spp = Erigonines, gna mic = *Gnaphosa microps*, lin spp = Linyphiines/Theridiidae, par hyp = *Pardosa hyperborea*, par mac = *Pardosa mackenziana*, par moe = *Pardosa moesta*, par uin = *Pardosa uintana*, tro ter = *Trochosa terricola*, xys can = *Xysticus canadensis*, xys obs = *Xysticus obscurus*.

Fig. 4.4: Canonical Correspondence Analysis triplot of species, sites and environmental variables. **Sites:** HS = high sulphur, SD = sulphur dusted, ND = non dusted; **Environmental variables:** fhu con = electrical conductivity of fermentation-humus layer, log dec = decomposed coarse-woody debris, nitroge= nitrogen, pea vin = *Lathyrus ochroleucus*, SinCcan = elemental sulphur in *Cornus canadensis*. **Species abbreviations:** see Fig. 4.3 caption.



CHAPTER 5: EFFECTS OF LOCALIZED SULPHUR POLLUTION ON FOREST FLOOR INVERTEBRATES.

Introduction

The regional studies reported in the previous two chapters showed that effects of sulphur contamination on most macroinvertebrates were restricted to acidified sites less than 150 m from the sulphur storage area. Therefore, a more detailed study was designed to understand better the distribution of soil fauna in these areas and the factors that cause the patterns observed. In addition to direct toxicity, indirect factors at the spatial scales of the landscape, habitat and microhabitat can affect patterns of invertebrate distribution along the acidification gradient.

At the landscape level, fragmentation leads to effects of forest edge on invertebrates. For example, Pajunen et al. (1995) found greater representation of lycosid spiders at the expense of linyphiids near forest edges relative to the inner old growth forest. From the regional sulphur study (Chapter 4) it was noted that guild composition of spiders in highly contaminated sites had a strong resemblance to spider guild composition reported in clearcuts by McIver et al. (1992). Edge effects were also reported for carabid beetles in the foothill forests of central Alberta (Spence et al. 1996). From these studies it seems that edge effects on invertebrates can explain some of the effects attributed to pollution in field studies and is a factor worth quantifying.

Interactions between habitats and pollutants can lead to differential effects on invertebrates. Forest types can vary in their ability to buffer pollutants; for example in a study of forest health at the Strachan sites, (Maynard et al. 1994), aspen forests were found more susceptible to sulphur contamination than pine forests. The regional survey of invertebrates around sour gas plants (Chapter 3 and 4; Cárcamo et al. 1997) showed that a

number of carabids with reduced populations in highly polluted pine sites had large populations in the highly polluted aspen site. To investigate this pattern further it was decided to compare the aspen fauna in the acidified site with that of a nearby non acidified aspen stand and to compare the results with those obtained in the pine acidification gradient.

Indirect microhabitat effects in the form of altered surface structural heterogeneity and microclimates resulted from the loss of vegetational cover at the sites under high sulphur pollution. Microclimatic factors such as moisture influence distribution of invertebrates (e.g. Holmes et al. 1993 for carabids) whereas vegetational plant structure can determine spider distributions (Robinson 1981). Furthermore, lack of plant ground cover reduces the impedance to arthropod mobility and may increase their catchability in pitfall traps (Greenslade 1964), the standard sampling technique for epigeic arthropods (Spence and Niemelä 1994).

The broad goal of this study was to improve our understanding of the distribution of several epigeic invertebrate taxa (at taxonomic levels of class to species) in forests severely contaminated (and acidified) with elemental sulphur. Distinguishing direct toxic pollution effects from indirect factors under field conditions is a complex task; in this study an attempt was made to elucidate a number of indirect pollution and non-pollution factors that can influence distributions of invertebrates. The following specific questions were asked:

- (1) Are epigeic invertebrate abundances or communities affected by localized sulphur pollution in pine or aspen forests?
- (2) Does ground cover influence pitfall estimates of invertebrate abundance or community parameters ?
- (3) Are results from enclosures similar to unfenced trapping ?
- (4) Does forest edge confound pollution effects ?

Methodology

Study site

Study sites selected for this study were the same ones used in the sharp gradient discussed in Chapter 3 (HS₁, HS₂, SD₁, SD₂ in Table 3.1), i.e. those near the Strachan gas plant and a pine site near a gravel pit ca. 3.5 km NE of the Strachan gas plant (site ND₅ in Table 3.1). The only exception was the aspen site under moderate sulphur deposition located ca 200 m NE of the sulphur block (Fig. 5.1); the polluted aspen site was described in Chapter 3 (site HS₃ in Table 3.1). Details about the edaphic characteristics of these pine and aspen sites were obtained from one 8 cm diam. core collected from the spot where each pitfall trap was inserted. Data gathered included fresh weights of vegetation, litter, F and H layers, moisture content of LFH material, pH, electrical conductivity and organic matter content. These edaphic data are provided in Table 5.1a, b, c, and floristic composition was outlined in Chapters 2 and 3 (see Table 3.2 and 3.3); seasonal trends in soil moisture at the acidified pine gradient are shown in Table 5.1d.

Experimental design and sampling

Distribution of invertebrates in the sharp pine acidification gradient

Two sampling methods, pitfall trapping and soil coring, were employed during 1995-6 to quantify numbers of invertebrates. Three trapping stations, each consisting of three pitfall traps spaced 3 m apart in a triangular arrangement, were established at 50 m

intervals parallel to the sulphur storage area at 50, 150 and 250 m from the block (Fig. 5.1); each of these three distances was considered a site for the purpose of this study. Traps were deployed on May 18th, 1995 and serviced every 2-4 weeks until September 23 when they were closed. One soil core was collected on June 16 at each trapping station using a 25 cm X 25 cm quadrat; on August 3 and September 23 sampling was repeated using a 21.5 cm diam. cylinder. Invertebrates were extracted from soil cores for 72 hr using Tullgren funnels. In 1996, traps were opened on May 24 and closed on September 27; samples were collected as in 1995, every 2-4 weeks. Density estimates were increased by taking two 21.5 cm diam. cores at each trapping station on June 14, August 8, and September 27. Samples were extracted for 72 hrs using a modified Kempson high gradient extractor instead of Tullgren funnels.

Effect of high sulphur pollution on aspen epigeic fauna.

Three pitfall trap stations were deployed on May 18th, 1995 and serviced as above in two aspen sites. The highly polluted aspen site was located ca. 100 m east of the S° block and had visibly affected vegetation cover (Table 3.1). Because this site was small (ca 150 m diameter) trap stations were placed at 25 m distances instead of 50m in both sites and were oriented N-S as in the pine sites. The non acidified aspen site was located about 500 m north of the acidified aspen site and had intact vegetational ground cover (see site SD₇ in Table 3.2).

Ground cover effects

To assess the impact of ground cover on pitfall catches vegetational ground cover was manipulated in the pine site at 250 m east of the sulphur block. At distances of 25 m

from the pitfall trap stations described above (Fig 5.1), three plots were chosen, each 4 m x 4 m, and all the vegetation was removed by raking the moss and clipping all the grasses and herbaceous plants. Care was taken to remove as little of the organic layer and remove mostly the live vegetation. A layer of pine needles, collected from sites under similar pollution regimes in the area, was spread on the surface to a depth of approximately 5 mm. Three pitfall traps arranged in a triangle were deployed in the middle of each plot at distances of ca. 2 m on June 1, 1995 and serviced as above. No cores were taken from these plots.

Abundance estimates using enclosures

To assess effects of high sulphur pollution on densities of macroarthropods that are difficult to sample with cores, three enclosures were built in each of two sites representative of the two extreme levels studied in the sharp gradient studied above. Because many carabid beetles are known to require coarse woody debris as shelter, it was ensured that each enclosure contained one log at a reasonably advanced stage of decomposition and that as much as possible these were uniform in all enclosures. The three enclosures in the polluted site were built approximately 60-70 m east of the sulphur block in the area highly acidified and devoid of moss cover; the 'control' enclosures were built in a site about 750 m south east of the S^o block (see Fig. 5.1). Enclosures were not built at the 250 m site because of possible cluttering with pitfall traps and devegetated plots.

Enclosures were built with coroplast (a rigid, smooth plastic) and were 2 x 2 m with approximately 15 cm buried in the ground and 30 cm above the surface. The corners of the enclosures were sealed with caulking paste to prevent animal escape and a layer of "tangle foot" was applied to the top on both sides of all walls to prevent invertebrates

from climbing over; however this did not prevent migration via aerial dispersal (e.g. ballooning spiders). Although some ground beetles have complete wings, most are considered to be non-fliers.

One pitfall trap was deployed at each corner of all enclosures on June 16, 1995 and serviced as described above. In 1996 two additional traps were dug in the middle in an attempt to exhaust arthropod populations.

Response of invertebrates to pine forest edge

Trapping stations were deployed on May 18th, 1995 as in the sulphur gradient study at approximately 50, 150 and 250 m from a gravel pit clearing in a pine forest 3.5 km NE of the Strachan plant (Fig. 5.1). This pine site had no elemental sulphur pollution and background levels of sulphur dioxide (Maynard et al. 1994). The northern edge of each line of pitfall trap stations was a highway and traps were deployed at least 50 m from this forest edge, except for the third line at 250 m from the gravel pit which had to be set about 200 m inside the forest because of excessive aspen in the area near the highway (Fig. 5.1). All traps were serviced as described above with the exception that some stations, especially those in the third line at 250 m from the gravel pit were disturbed by wild animals; a mammal repellent spray was applied to all of the pitfall traps in this site to attempt to prevent losses of invertebrates.

Data analysis

For all of the above studies, catches of invertebrates in the three pitfall traps placed at each sampling station during each year were pooled so that there were three replicate estimates of abundance per distance to the sulphur block or forest edge. Similarly, density

estimates taken three times each year at each sampling station were pooled and converted to number of invertebrates per meter square. Catches from all traps placed in each enclosure were pooled over the two trapping periods of the study (15 months total) and means and standard errors were estimated for each taxon collected based on the three enclosures in each site. Analysis of variance (ANOVA) was performed on raw values and also on ranked transformed data for samples with zero values or heterogeneous variances. To standardize the presentation of results, all statistical tests on pitfall catches (abundances) are presented on ranked data.

Community parameters calculated included overall abundance of invertebrates at the class, order or family level and four diversity indices for carabids and spiders: Hill's (1975) diversity numbers (N_0 , N_1 , N_2) and evenness (J'). These indices were chosen because they quantify the various components of community structure; N_0 is a measure of species richness while N_1 and N_2 represent the exponential form of the Shannon-Wiener index (which emphasises rarity) and the inverse of Simpson's index (which emphasises dominance), respectively. J' is a direct measure of evenness recommended by Magurran (1988) based on Shannon-Wiener diversity. Statistical testing was performed with one way ANOVA on raw community values since variances were relatively similar for these parameters.

An analysis of guild structure was also performed on spiders by modifying the scheme used by Post and Reichert (1977): (1) Micro-webbers: small (<3mm) web-building spiders of the families Linyphiidae (s. lat.) and Theridiidae; (2) Macro-webbers: larger web-building spiders (>3 mm) of the families Amaurabiidae and Agelenidae; (3) Night-hunters (Gnaphosidae, Clubionidae and Thomisidae); (4) Day hunters (Lycosidae).

Results.

Edaphic characteristics of the sites.

The pine site at 50 m east of the sulphur block had a highly acidified forest floor characterized by a thick litter layer and much reduced plant cover (Table 5.1a). The aspen site highly contaminated by elemental sulphur also exhibited these characteristics (Table 5.1c) although the pH (6.06) was much higher than the acidified pine site (2.9). Edaphic characteristics of the sites east of the gravel pit did not vary with distance to forest edge (Table 5.1b).

Differences in moisture levels of the forest floor along the pine acidification gradient were more apparent later in the growing season of 1996 (Table 5.1d). Both litter and FH layers were drier at the pine sites 50 and 150 m than at the 250 m site on September 27th. On June 14th, moisture levels were very similar at the three distances (Table 5.1d).

Pine forest acidification and ground cover

To take into account the potential impact of ground cover on invertebrate catches, results from the devegetated plots were incorporated in the statistical analysis of the pine acidification gradient.

Carabids

Five common carabids (each >1 % of total catch) had consistently and significantly lower catches at the acidified site in 1995 and 1996 (Tables 5.2 a and b). *Scaphinotus marginatus* had reduced abundance up to 150 m ($df = 3,8$; $F = 21.0$ and 22.96 , $p < 0.05$); for *Platymus decentis*, *Calathus ingratus*, *Stereocerus haematopus*, and *Pterostichus riparius* Dejean, effects were more localized as catches were reduced only at the most

acidified site at 50 m ($df = 3,8$; range of F values = 4.91 - 22.96; $p < 0.05$). *Stereocerus haematopus* was the only carabid that had higher catches in the devegetated plots relative to the nearby controls at 250 m in 1995 (FPLSD, $p < 0.05$); in 1996 the differences were not significant, although, a similar pattern was observed. Two other species, *Trechus chalybeus* and *Agonum retractum*, were moderately abundant and negatively affected at the 50 m site in 1995 ($df = 3,8$; $F = 18.57$ and 4.43 , respectively; $p < 0.05$). The same trends were observed in 1996 but the numbers were too low for meaningful testing.

Pterostichus adstrictus, the most abundant carabid, had a trend of higher catches in the devegetated site at 250 m compared to the acidified site in 1995 (FPLSD, $p < 0.05$) but in 1996 the differences were not significant ($df = 3,8$; $F = 1.42$; $p > 0.05$). *Calathus advena*, also one of the most abundant species, and *Agonum placidum*, had variable abundances along the pollution gradient and can be considered to have a neutral response. *Amara hyperborea* was the only species to have consistently higher catches in the most acidified site during both years ($df = 3,8$; $F = 12.16$ and 13.61 for 1995 and 1996, respectively; $p < 0.05$). The remaining 12 species found in 1995 and 14 in 1996, were too rare and their abundances were not analyzed.

At the community level, the responses of total catches of larvae and adult carabids were opposite along the pollution gradient (Tables 5.2 a and b). Larvae were significantly more abundant at the acidified 50 m site than in all other sites in 1995 ($df = 3,8$; $F = 15.57$; $p < 0.01$) and in 1996 the 50 m and the 150 m sites had similar abundances but greater than the 250 m sites ($df = 3,8$; $F = 9.31$; $p < 0.01$). Adults had higher abundances at the site 250 m away from the sulphur block in 1995 only ($df = 3,8$; $F = 6.58$; $p < 0.05$).

Indices of species richness and diversity along the acidified gradient and devegetated plots are shown in Table 5.2a and b. Species richness (N_0) was not significantly different in 1995 ($df = 3,8$; $F = 3.42$; $p > 0.05$) although there was a trend of more species at the 150 m site compared to the 50 m and 250 m stations with intact plant

cover (FPLSD, $p < 0.05$). Measures of species diversity and evenness were similar along the acidification gradient, including the devegetated plots ($df = 3,8$; range of F values: 0.40 - 1.37; $p > 0.05$). In 1996, there was a small but significant trend of more species at the 250 m sites compared to the 50 m acidified site. Also, species diversity measures $N1$ and $N2$ were significantly higher at 150 m compared to the 50 m site and between the devegetated plots and both of the 150 m and 50 m sites ($df = 3,8$; F values = 5.68 and 10.35, respectively, $p < 0.05$). Species evenness (J') was not significantly different in the overall ANOVA model, although pairwise comparisons (FPLSD, $p < 0.05$) revealed it to be lower in the acidified site relative to the devegetated plots at 250 m.

To summarize the carabid results, species can be divided in three categories with respect to their responses to the pollution gradient: (1) vulnerable species (five, possibly seven) with reduced abundance at the acidified site; (2) neutral or resistant species (three) had similar abundance along the acidification gradient; and (3) opportunists (one species) that increased in numbers at the most acidified site near the sulphur block. At the community levels, overall adult abundance was reduced near the sulphur block, but the number of larvae was higher at this site. The significant differences in diversity indices seen in 1996 along the gradient suggest that community structure of the ground beetle assemblage is detrimentally affected by severe acidification.

Spiders

Around 74 species of forest floor spiders were represented in the pitfall catches along the sulphur pollution gradient including the trap stations deployed in the three devegetated plots during 1995 (Table 5.3a). In 1996 the number of species recognized was 29 as linyphiids and theriidids were not identified (Table 5.3b). These two families (Linyphiidae and Theriididae) can be allocated to the guild of small spiders (mostly less

than 3 mm) that build webs on the forest floor and will be referred to as the “micro-webbers”. Most micro-webbers were represented in small numbers in the pitfall traps and although there was a trend for reduced abundances (FPLSD, $p < 0.05$) in the acidified site for three species (*Allomengea pinnata*, *Lepthyphantes alpinus* Emerton, and *Diplocentria bidentata* Emerton) the differences were not statistically significant in the one way ANOVA on ranked data ($df = 3,8$; range of F values = 1.86-3.36; $p = 0.08-0.20$). Two other micro-webbers, the linyphiine *Bathypantes pallidus* Banks and the erigonine *Sciastes truncatus* Emerton, did not differ significantly along the pollution gradient ($df = 3,8$; $F = 0.23$ and 0.86 respectively; $p > 0.05$). The other 35 species in this guild were too rare to analyze individually.

Among the larger web building and hunting spiders there were 34 species found in 1995 and 29 in 1996. The amaurobiid species *Callioplus euoplus* had significantly and consistently reduced abundance up to 150 m from the sulphur block in 1995 and 1996 ($df = 3,8$; $F = 17.55$ and 17.20 , respectively; $p < 0.01$) while the agelenid *Cryphoeca exlineae* Roth had lower abundance only at the 50 m acidified site ($df = 3,8$; $F = 4.13$ and 8.09 for 1995 and 1996, respectively; $p < 0.05$).

Agroeca ornata and *Clubiona canadensis* (Clubionidae) and *Agelenopsis utahana* (Agelenidae) had consistently similar numbers along the gradient (Tables 5.3 a and b) and can be considered neutral with respect to sulphur pollution. Three other species, *Xysticus obscurus* Collett and *X. canadensis* Gertsch (Thomisidae) and *Trochosa terricola* (Lycosidae) had inconsistent abundances between 1995 and 1996. *Xysticus obscurus* had similar numbers at all three distances and the devegetated plots in 1995; however, in 1996, abundances were significantly higher in the most acidified site at 50 m compared to the 150 m site ($df = 3,8$; $F = 4.39$; $p < 0.05$). *Xysticus canadensis* was the only spider that had significantly higher abundance in the devegetated plots than all the other trapping stations at the three distances in 1995 ($df = 3,8$; $F = 5.05$, $p < 0.05$); there were no significant

differences for 1996 among any of the pollution or ground cover categories for this species, although, the mean for the devegetated treatment was almost twice those of the other treatments ($df = 3,8$; $F = 1.73$; $p > 0.05$). *Trochosa terricola* had greater abundance in the site at 150 m than in any other site in 1995 ($df = 3,8$; $F = 7.25$; $p < 0.05$); in 1996 the numbers were very similar along the gradient and although lower at the devegetated plots, the differences were insignificant ($df = 3,8$; $F = 0.48$; $p > 0.05$). From these observations, these three species may be considered resistant to sulphur pollution stress.

Pardosa mackenziana did not differ significantly along the gradient according to the overall ANOVA both years ($df = 3,8$; $F = 1.25$ and 2.52 for 1995 and 1996 respectively; $p > 0.05$). However, the trend of higher abundances in the most polluted site was consistent in both years and pairwise comparisons in 1996 suggest that this species had greater abundance in the site at 50 m of the sulphur block than any other site (FPLSD, $p < 0.05$).

Overall numbers of spiders did not differ significantly among all sites in 1995 (Table 5.3a; $df = 3,8$; $F = 0.41$; $p > 0.05$); however, in 1996, there were fewer spiders at the 150 m site (Table 5.3b; FPLSD, $p < 0.05$). Species richness and diversity measures were calculated only for 1995 data because micro-webbers were not identified in 1996. There was a marginally significant trend for higher species richness at the 250 m site in trap stations with intact ground cover compared to the acidified trap stations at 50 m and the devegetated plots at 250 m (Table 5.3a; $df = 3,8$; $F = 3.70$; $p = 0.06$). The exponential form of the Shannon-Wiener diversity measure (Hill's N_1) and evenness (J') revealed significantly lower species diversity at the most acidified site (Table 4.3a; $df = 3,8$; $F = 5.09$ and 5.55 , respectively; $p < 0.05$). The inverse of Simpson's index (N_2) also showed the same trend and pairwise comparisons suggested lower diversity in the acidified site compared to the devegetated plots at 250 m (FPLSD, $p < 0.05$).

The guild represented by day-hunters (Lycosidae) was clearly the dominant group of spiders in the acidified site in both years (Table 5.4; ANOVA on raw percentages: $df = 3,8$; $F = 7.38$ and 5.90 for 1995 and 1996, respectively; $p < 0.05$). The night hunting spiders had similar distribution along the gradient, although in 1995 they had higher relative abundance in the devegetated plots ($df = 3,8$; $F = 5.67$; $p < 0.05$). Except for micro-webbers in 1995 when the statistical significance was marginal ($df = 3,8$; $F = 3.24$; $p = 0.08$) both groups of web building spiders had significantly higher relative abundance in the less polluted sites ($df = 3,8$; range of F values = $4.09-7.27$; $p < 0.05$).

Other invertebrates

Earthworms were not found in pitfall traps at the most acidified site during either year of the study; therefore, statistical analysis to compare their abundances to the other sites is unnecessary. The sites at 150 and 250 m had similar earthworm numbers regardless of ground cover type in both years of the study (Table 5.5a and 5.5b). Snails and staphylinids had a similar trend of reduced abundance in the most acidified site that was statistically significant in 1996 ($df = 3,8$; $F = 4.76$ and 8.09 , respectively; $p < 0.05$) but marginal in 1995 ($df = 3,8$; $F = 3.55$ and 3.69 , respectively; $p < 0.07$). Abundances of ants and Collembola were highly variable and there was no distinct pattern suggesting negative effects of acidification on either group.

Densities of invertebrates estimated from core sampling confirmed the patterns found with pitfall traps (Tables 5.6). The acidified site had significantly fewer earthworms and snails than any other site during both years ($df = 2,6$; range of F values = $7.0-13.29$; $p < 0.05$). Earthworm catches pooled from the 3 pitfall traps and density estimates per m^2 near each station from core samples were significantly correlated during both years ($DF = 7$, $r > 0.80$, $p < 0.05$). Densities of staphylinids also increased with distance from the

sulphur block but the differences were significant only in 1995 ($df = 2,6$; $F = 7.41$; $p < 0.05$). Densities of ants were similar along the gradient but collembolans were higher at 250 m than at 50 m both years ($df = 2,6$; $F = 3,58$ and 7.0 for 1995 and 1996, respectively; $p < 0.05$).

The cumulative number of snails seen underneath artificial shelters (Table 5.7) were also significantly lower at the acidified site than the two farther sites in 1995 and 1996 ($df = 2,6$; $F = 6.31$ and 27.0 , respectively; $p < 0.05$). The site at 150 m had significantly higher numbers, according to this method, than any of the other two sites in 1996 (FPLSD, $p < 0.05$). Total snails under shelters was highly significantly correlated with total pitfall catches ($r = 0.93$ and 0.81 for 1995 and 1996, respectively; $df = 7$; $p < 0.05$) but not with core estimates ($r = 0.66$ and 0.19 for 1995 and 1996, respectively). Correlations between snails in cores and pitfall traps were also low ($r = 0.54$ and 0.35 for 1995 and 1996, respectively).

Acidification in aspen forest

Carabids

Of the seven species affected negatively by acidification in the pine forest, only *Pterostichus riparius* and *Agonum retractum* were significantly lower at the acidified aspen site (Table 5.8; $df = 1,4$; $F = 15.43$ and 13.5 , respectively; $p < 0.05$). *Agonum placidum* and *Synuchus impunctatus* Say had greater abundances at the acidified site ($df = 1,4$; $F = 15.42$ and 15.43 , respectively; $p < 0.05$). The remaining six common species (each $> 1\%$ of total catch), including *S. marginatus* and *P. decentis*, had similar abundance in both aspen sites.

Overall numbers of carabid individuals and species (N_0) were similar in both forests but total larval abundance was significantly lower at the acidified site (Table 5.8; $df = 1,4$; $F = 13.5$; $p < 0.05$). There was a marginally significant trend of greater species diversity (N_1 and N_2) in the control than in the acidified aspen forest ($df = 1,4$; $F = 7.28$ and 5.07 , respectively; $p < 0.09$). Species evenness (J') was very similar in both aspen sites.

Spiders

Five of the 28 micro-webber spiders (Linyphiidae s. lat and Theriididae) were abundant enough for statistical analysis (Table 5.9). *Allomengea pinnata*, *Bathypantes pallidus* and *Diplocentria bidentata* were significantly more abundant in the control aspen site ($df = 1,4$; range of F values = 13.5 - 15.42 ; $p < 0.05$). *Robertus fuscus* had greater abundance in the acidified site ($df = 1,4$; $F = 5.82$ $p = 0.073$) while *Microneta viaria* Blackwall did not differ significantly ($df = 1,4$; $F = 3.69$ $p > 0.05$). Of the 29 species found in the other spider guilds, *Callioplus euoplus* was the only one with significantly lower abundance in the acidified aspen site ($df = 1,4$; $F = 13.5$; $p < 0.05$). *Trochosa terricola* and particularly *Pardosa mackenziana* had greater abundance in the acidified aspen site ($df = 1,4$; $F = 15.42$ and 13.5 , respectively, $p < 0.05$). Another lycosid (wolf spider) *Alopecosa aculeata* Clerck had slightly greater abundance in the acidified aspen but the differences were not significant ($df = 1,4$; $F = 2.18$; $p > 0.05$).

At the community level, overall spider abundance and species richness were similar in the two aspen sites (Table 5.9). There was a marginally significant trend of greater diversity (N_1 and N_2 : $df = 1,4$; $F = 6.70$ and 6.90 , respectively; $p < 0.062$) in the control aspen site and the evenness (J') of the spider assemblage was higher as well ($df = 1,4$; $F = 10.88$; $p < 0.05$).

Relative abundance of the spider guilds, except for night hunters, varied considerably between the two aspen sites (Table 5.10). Day hunters were much more dominant in acidified than in the control aspen stand (79 vs 31 %; $df = 1,4$; $F = 81.19$; $p < 0.01$). Both groups of web building spiders had greater representation in the control aspen site ($df = 1,4$; $F = 23.79$ and 17.72 , respectively; $p < 0.05$).

Other invertebrates

Abundance of earthworms was significantly lower in the acidified aspen site than in the control (Table 5.11; $df = 1,4$; $F = 15.43$; $p < 0.05$). Snails, staphylinids and ants had similar abundances in the two sites but Collembola were significantly higher in the acidified aspen ($df = 1,4$; $F = 13.5$; $p < 0.05$).

Abundance estimates in enclosures

Carabids

The assemblage of carabid species found inside enclosures was dominated by the same species as that found in unfenced traps (Table 5.12). Also, a similar pattern of reduced abundance in the acidified site was found for the five species considered vulnerable (*Scaphinotus marginatus*, *Platymus decentis*, *Calathus ingrathus*, *Stereocerus haematopus*, and *P. riparius*). Because of large variation among enclosures (for *C. ingrathus* and *P. haematopus*) or low numbers (for *P. riparius*) only *S. marginatus* and *P. decentis* were significantly more abundant in the enclosures at the control site 750 m away from the sulphur block ($df = 1,4$; $F = 13.5$ for both; $p < 0.05$). *Amara hyperborea* was found in the acidified enclosures only but was represented by a single individual. The

common carabids *Pterostichus adstrictus*, and *Calathus advena*, had similar average catches in enclosures at acidified and control sites which confirmed the pattern seen in the unfenced traps placed along the pine acidification gradient.

Although overall carabid abundance was higher in the control enclosures compared to those in the acidified site, the difference was not significant ($df = 1,4$; $F = 0.04$; $p > 0.05$) because one enclosure had most of the catch. The number of carabid larvae was higher in the enclosures at the acidified site, although again the differences were insignificant ($df = 1,4$; $F = 2.18$; $p > 0.05$).

Species richness per enclosure averaged nine in both sites but the structure of the assemblage was very different (Table 5.12). Hill's measures, N_1 and N_2 , revealed greater species diversity in the enclosures built in the control site than in those at the acidified site ($df = 1,4$; $F = 18.79$ and 10.31 , respectively; $p < 0.05$). Also, the measure of evenness (J') was marginally significantly higher in the control enclosures ($df = 1,4$; $F = 5.28$; $p = 0.08$).

Spiders

Only the larger web building and hunting spiders were identified to species in the second year of pitfall trapping inside enclosures (Table 5.13). The two species that were considered vulnerable at the acidified site with unfenced traps, *Callioplus euoplus* and *Cryphoeca exlineae*, also had reduced abundances in the acidified enclosures but only the former was significantly different ($df = 1,4$; $F = 13.5$; $p < 0.05$). None of the other common spiders were statistically different between the enclosure types ($df = 1,4$; range of F values = $0.04 - 3.5$). *Pardosa mackenziana*, one of the dominant species in the unfenced pitfall traps had much lower relative abundance inside the enclosures, although it was still slightly higher in the acidified enclosures. Erigonine spiders, in contrast to unfenced traps,

were not significantly lower in traps at the acidified enclosures; Linyphiines, however, were significantly higher in enclosures at the control site ($df=1,4$; $F = 15.43$; $p < 0.05$).

An estimate of diversity was available from the complete suite of all forest floor spiders identified from the enclosures in 1995. After approximately 3 months of trapping there was a similar average number of spider species per enclosure (16 ± 5.51 and 19.67 ± 4.26 , means and standard errors for acidified and control enclosures, respectively). Also, measures of species diversity did not differ between acidified and control enclosures (N1: 13.43 ± 4.39 and 15.07 ± 1.39 , respectively; N2: 19.24 ± 4.90 and 21.33 ± 3.54 , respectively) nor evenness of the spider assemblage (J' : 0.94 ± 0.01 and 0.93 ± 0.03 , respectively).

Spider guild structure inside the enclosures (Table 5.14) differed from that found with unfenced pitfall traps. Day hunting spiders were replaced in dominance by micro-webbers at the acidified enclosures and neither group differed in relative abundance between the two sites. Relative abundance of day hunters was less than 10 % in either enclosure type whereas micro-webbers were over 50-60 %. The macro-webber spider guild was the only one that differed significantly and it had greater relative abundance in the control site ($df = 1,4$; $F = 30.27$; $p < 0.01$). Night-hunters were not significantly different although they were slightly better represented in the acidified enclosures (26 % vs. 17 %).

Other invertebrates

No earthworms were found in pitfalls inside the enclosures at the acidified site although there were close to 50 per enclosure at the control site (Table 5.15). Numbers of snails and ants were also significantly higher in enclosures at the control site ($df = 1,4$; $F =$

13.5 for both; $p < 0.05$). Numbers of staphylinids and collembolans were similar at the two enclosure types ($df = 1,4$; $F = 0.38$ for both; $p > 0.05$).

Effects of forest edge

Carabids

Most of the common carabids had similar abundances at the three distances of 50, 150 and 250 m east of the forest edge (Table 5.16). *Scaphinotus marginatus* was the only common species that had significantly lower abundance at 250 m east of the forest edge ($df = 2,6$; $F = 7.0$; $p < 0.05$). *Amara hyperborea* was very rare at these study sites but the only two individuals caught were found near the forest edge.

Overall number of carabids and species richness were similar at the three distances (Table 5.16). Carabid larvae were found in numbers too low to allow analysis (total of 6). Evenness of the carabid assemblage (J') and species diversity indices ($N1$ and $N2$) had non significant differences at the three distances from the forest edge ($df = 2,6$; range of F values = 0.41-1.85; $p > 0.05$).

Spiders

A total of 75 species were found at the pine forest east of the gravel pit where edge effects were investigated (Table 5.17). One linyphiid (*Bathypantes pallidus*) and two lycosids (*Trochosa terricola* and *Pardosa mackenziana*) were the only common spiders that had significantly greater abundances near the forest edge at 50 m from the gravel pit than in the other two sites ($df = 2,6$; range of F values = 9.03-13.48; $p < 0.05$).

Callioplus euoplus had a strong, although non significant, trend towards increasing abundance away from the forest edge ($df = 2,6$; $F = 2.78$; $p > 0.05$).

Overall abundance of adult spiders was slightly higher near the forest edge but the differences were not significant (Table 5.17; $df = 2,6$; $F = 1.58$; $p > 0.05$). There was a marginally significant trend of greater species richness in trap stations closest to the edge ($df = 2,6$; $F = 3.75$; $p = 0.09$). Measures of species diversity (N1 and N2) were similar at the three distances but evenness of the spider assemblage was lower at the site 50 m from the edge ($df = 6.78$; $F = 1.58$; $p < 0.05$).

Relative abundances of the four spider guilds are shown in Table 5.18. The dominant guild in all three distances was the micro-webbers which accounted for close to 50 % at all trap stations regardless of location. Day-hunters were second in dominance and they exhibited a trend of greater relative abundance near the forest edge ($df = 2,6$; $F = 4.15$; $p = 0.074$). Night-hunters and macro-webbers ranked third and fourth, respectively, in terms of dominance; neither of these two guilds differed in relative dominance at the three distances.

Other invertebrates

None of the five other invertebrate taxa studied exhibited any consistent trend in abundance with respect to forest edge (Table 5.19). However, earthworm abundance was significantly higher at 150 m than at the two other distances ($df = 2,6$; $F = 6.31$; $p < 0.05$). Although the number of ants was much higher at 250 m than at the other two distances, the variation was also very high and the differences were not significant ($df = 2,6$; $F = 3.15$; $p > 0.05$).

Discussion

The objectives of this portion of the study were to document the distribution of epigeic invertebrates (mostly macrofauna) along the sharp acidification gradient taking into account the role of indirect factors. Assessing effects of pollutants on organisms and their communities in the field is a very complex task because of the numerous factors involved and their possible interactions.

Direct and indirect effects of pollution are difficult to separate and occur at a number of scales. For example, at the landscape level, forest fragmentation takes place whenever an industrial facility is built and this alone (without adding pollution) can be expected to impact a number of invertebrates through their responses to forest edge. At the habitat level, forest types (e.g. aspen vs pine) will differ (e.g. in forest floor structure and litter quality) and interact with pollutants to affect invertebrates differentially. Within a habitat, microhabitats are affected by pollutants so that structural heterogeneity in terms of plant and litter cover combine to affect microclimatic factors. Forest floor temperature and humidity, pH and variation in plant structural complexity are factors known to influence distribution of invertebrates. Furthermore, interactions among species may be affected in microhabitats simplified through anthropogenic activities. In the following sections an attempt is made to interpret the distribution of invertebrates in the study area in light of the direct and indirect effects of pollution at the various spatial scales identified; also, some speculations are made regarding potential biotic interactions that can explain the patterns seen.

Indirect effects at the landscape level: forest fragmentation

Field studies of pollution around industrial facilities seldom consider the potential effect of habitat edge on the spatial distribution of organisms despite its well known

influences (e.g. Pajunen et al. 1995). An effort was made in the present study to identify those species or higher taxa whose distributions are influenced by forest edge. A pine forest adjacent to a gravel pit open area was selected and pitfall trapping was carried out at 3 distances east of the forest edge (50, 150 and 250 m).

At the higher taxonomic level of family or order, forest edge did not affect distributions of spiders, carabids, staphylinids, ants, collembolans, snails or earthworms. The earthworms and one carabid species, *Scaphinotus marginatus*, had greater pitfall catches at 150 m than at either of the two other distances. These differences may result from differences in microhabitat features such as moisture which were not measured in the present study. *Scaphinotus marginatus* is known to prefer moist forest habitats (Niemelä and Spence 1995) where its favourite prey (snails), are abundant. In the present study snails were also slightly higher in pitfall traps at this distance. Because earthworms were not identified to species it is not known if the observed differences are the result of habitat partitioning between species or simply microhabitat preferences of *Dendrobaena octaedra* Savigny, the expected dominant species in coniferous forests (McLean pers. comm.).

Ground beetle species richness, diversity or evenness were similar at the three distances east of the gravel pit. Species richness of carabids is known to increase in clearcut forests because of invasion of open habitat species and remnant species from the forest (Niemela et al. 1993, Spence et al. 1996). The results for carabids found in the present study suggest that at 50 m inside the forest the assemblage is unaffected by abiotic or biotic edge factors that can alter its community structure.

Although overall numbers of spiders were similar at the three distances away from the forest edge, a number of species as well as community structure parameters differed. The spiders *Bathypantes pallidus* (Linyphiidae), *Trochosa terricola* and *Pardosa mackenziana* (Lycosidae) were more abundant near the edge. These latter two species were also collected in greater numbers at the acidified site closest to the sulphur storage

area. The opposite pattern of increasing abundance away from the edge was suggested for *Callioplus euoplus*; interestingly, this species was the only one to have consistently higher catches away from the acidified sites in both aspen and pine forests. At least for the pine site, it appears that part of this pattern is related to its natural distribution if it is a deep forest litter species. Leech (1972) described it as a species of deep deciduous litter but no reference was made to its distribution in relation to forest edge. The litter layer was thicker in the acidified sites, therefore, other factors, perhaps direct toxicity, depressed its abundance. Furthermore, in the aspen study, the control site with greater numbers of this spider was as far from the forest edge (ca. 100 m) as was the acidified site which had many fewer individuals. This can be taken as an indication that pollution effects (direct or indirect) are also involved in determining its distribution.

Furthermore, the relative abundance of the guild of day hunting spiders (Lycosidae) was also higher near the gravel pit. This paralleled the results seen in the acidification gradient in both pine and aspen forests. Other investigations have also documented greater relative abundance by day hunters in clear cut forests (McIver et al. 1992) and near forest edges (Pajunen et al. 1995). Therefore, the results of greater dominance of lycosids near the sulphur block in the pine forest can be partly explained by their response to forest edge. A similar explanation may apply to other studies of spider community structure in polluted forests (e.g. Koponen and Niemelä 1993). It can be recommended that to avoid edge effects on spider assemblages, trap stations will need to be deployed much farther than 50 m inside the forest.

Indirect effects at the habitat level: aspen vs pine

Effects of pollution on invertebrates can vary with habitat type. The sulphur polluted pine site at 150 m east of the sulphur block may be compared to the sulphur

polluted aspen site located about 100 m east of the sulphur storage area. Levels of extractable sulphur from the organic layers (LFH) for these two sites are 2982 mg/kg and 3860 mg/kg, respectively and the pH is more acidic (5.6 vs 6.3) in the aspen site. Also, from a simple visual inspection of the more deteriorated ground plant cover in the aspen site, it can be concluded that the effects of sulphur pollution are more severe there. Therefore, one would expect that invertebrates with reduced abundances at the polluted 150 m pine site compared to the 250 m unimpacted pine, would also follow the same trend in the polluted and control aspen sites.

Two species of arthropods, the carabid *Scaphinotus marginatus* and the amaurobiid spider *Callioplus euoplus* had lower abundance at the polluted pine site at 150 m than the 250 m site. Only *C. euoplus* followed the predicted pattern of reduced abundance in the acidified aspen site compared to the aspen control (pH = 7). This spider was consistently affected negatively by acidification in all three studies (pine, aspen and enclosures) and would be a good candidate for more detailed studies of direct toxicological effects under laboratory or field experiments. The abundance of *S. marginatus* was very similar in the two aspen sites. It is possible that aspen leaf litter cover maintains better moisture conditions below the surface compared to pine needle cover; *S. marginatus*, is known to prefer moist soil (Niemelä and Spence 1995). This carabid species illustrates the complexities of the factors that mask the impact of pollution on invertebrates.

The distribution of earthworms in polluted pine and aspen sites greater than 100 m away from the sulphur block showed an interesting pattern indicative of indirect effects. There were no differences in earthworm numbers in the polluted 150 m pine site (with a partly destroyed plant cover) and the pine site at 250 m. The same results were expected in the aspen sites based on the high pH values (>5). However, the polluted aspen site had many fewer earthworms than the aspen control site. This result suggests that in aspen the

worms are more vulnerable to pollution than in pine. It is unlikely that the pH of the slightly acidified aspen organic soil (5.6) is low enough to directly kill the earthworms; most earthworms, particularly *Dendrobaena octaedra*, are known to tolerate this level of acidity (Satchell 1955). A possible explanation is that the microbial community in aspen is more vulnerable to the high levels of elemental sulphur (a good fungicide) than those communities of fungi that have evolved in acidic coniferous environments. As a result the availability of microbial biomass and the reduced quality of the litter (less decomposed) as food resources for earthworms (Pearce 1978) may be reduced in acidified aspen sites causing the observed reduction of earthworm populations. This provides another example of interactions between forest type and pollution which can differentially affect populations of invertebrates.

Acidification of a pine stand: microhabitat level effects

Quantifying the effects of sulphur pollution on surface active invertebrates poses a methodological problem because of the confounding effect of reduced ground cover in highly acidified sites. Pitfall traps are recognized by most researchers as an effective technique to sample epigeic arthropods such as carabids (e.g. Spence and Niemelä 1994). However, there are a number of recognized problems with the method including the impact of ground cover impedance to beetle movement (Greenslade 1964). Furthermore, critics have pointed out that, especially for spiders, the structure of the community estimated with pitfall trapping differs from that obtained with density estimates from core sampling (Topping and Sunderland 1992). To address issues related to unfenced pitfall trap, plant cover was replaced with pine needles at the 250 m site and enclosures were built at the acidified site and a nearby control site. In the following discussion section the results of these studies are integrated with those from unfenced pitfall trapping to

understand better the invertebrate responses to acidification. To facilitate the discussion this section deals separately with the following main taxa: carabids, spiders, earthworms, snails, and other arthropods (ants, rove beetles and Collembola); comparisons among taxa are made throughout this discussion.

Carabids

Populations

Manual removal of ground cover vegetation and replacement with pine needles did not have a large lasting effect on ground beetle catches. Only one species, *Stereocerus haematopus*, had greater catches in the devegetated plots than in the adjacent controls in year 1; however, in the second year the differences had disappeared. *Pterostichus adstrictus* also had greater catches in the devegetated plots than at the acidified sites that lacked vegetation but only in the first year of the study. Three complementary explanations can be given for this pattern. First, these species can be attracted to the disturbance created by the manipulation of ground cover or the “digging in” of pitfall traps as shown by Digweed et al. (1995) with *P. adstrictus*. Second, these two species with relatively large body sizes (ca. 10 mm) can be expected to be among the most mobile beetles which can enhance their captures in the traps; therefore, depletion of populations occurred in the second year of the study as the pool of individuals inside and around the plots decreased. Finally, for the mesic carabid *P. haematopus* (Niemelä et al. 1992), the lower catches in the devegetated plots in 1996 can be the result of weather patterns. The second year of the study was much drier than the previous year when differences were seen and although surface moisture was not measured in the devegetated plots, forest floor with pine needles should be drier than those with moss cover. This difference in soil

moisture, although small, was observed in the site at 50 m without plant cover in the acidification gradient (see Table 5.1d).

Three groups of carabid species were recognized in terms of their distributions in the pine acidification gradient using unfenced pitfall trapping. Five species (*Scaphinotus marginatus*, *Platymus decentis*, *Calathus ingratus*, *Stereocerus haematopus*, and *P. riparius*) were considered vulnerable with two others being potentially vulnerable (*Trechus chalybeus* and *Agomum retractum*); three species were considered to have neutral responses to acidification (*Pterostichus adstrictus*, *Calathus advena* and *Agomum placidum*); and one species (*Amara hyperborea*) was considered an opportunist that was potentially favoured by acidification in the pine site. Data from the enclosures supported the carabid grouping given above with some exceptions. *Trechus chalybeus* was common in the acidified enclosures and would be classified as an acidification resistant species. Also *Agomum retractum* Leconte and *Amara hyperborea* were absent or very rare, respectively, inside the enclosures. The absence of *A. retractum* can be explained by the patchy nature of some less common carabids; this species is more abundant in aspen sites where it was clearly affected negatively by acidification, and therefore, can still be grouped as a vulnerable species.

Trechus chalybeus was equally abundant in the acidified and control enclosures, although it was extremely low in the unfenced traps at the acidified site. Two factors can explain this pattern. First, the area enclosed by the coroplast fences contained coarse woody debris (logs). This was done because it is generally recognized that logs are used by carabids as hiding places and inclusion of logs would maximize the estimates of carabid populations in the enclosures. *Trechus chalybeus* is one of the smallest carabids (ca 3 mm) and it is known to prefer moist soil conditions (Lindroth 1961-69); these conditions may be enhanced inside the acidified enclosures by the presence of logs and also by the reduction in wind speed over the soil surface caused by the fences around the 4 m² area.

Trechus chalybeus, was one of the carabid species whose distribution was related to logs on the ground in the ordination analysis presented in Chapter 3 of this dissertation. An alternative hypothesis explaining the lack of differences between the enclosure types is the patchy distribution of many specialist carabid beetles. Because of its small size this carabid may be considered a prey specialist; small carabids are more restricted in the size of prey they can take which consists mostly of microarthropods like springtails (Hengeveld 1980). In Chapter 3, it was shown that this carabid had a patchy distribution and it was rare in some of the sites, including the control site where the enclosures were built.

Most of the carabids vulnerable to acidification effects are to varying extents ecological specialists whereas resistant species are generalists. The best example of a specialist carabid is *Scaphinotus marginatus* which was markedly affected by sulphur contamination in the pine forest, although not in the aspen site. This species belongs to a tribe of carabids known to be mollusc prey specialists (Hengeveld 1980a,b, Digweed 1993). Furthermore, *S. marginatus* is considered a species restricted to forests (Niemelä et al. 1992) and collected more abundantly in moist, rich soils (Niemelä and Spence 1995). The lower abundance of this species in the polluted pine sites at 50 m and also at 150 m suggest that abiotic microhabitat factors are more important than snail availability. Despite the large number of snails found in the pine site at 150 m, beetle numbers were still low compared to the site at 250 m. Moisture of the organic soil was lower in the former site. Soil moisture is known to be an important factor determining the distribution of carabids in many habitats (e.g. Holmes et al. 1993, Holopainen et al. 1995) and in this study the effect of sulphur pollution and acidification on ground beetles can be attributed to differences in moisture levels that would become especially important during dry years. This was observed in the current study as the differences between the numbers of *S. marginatus* at 150 and 250 m were much greater during 1996 which was a drier year than 1995.

Species resistant to sulphur pollution belong to the assemblage of habitat generalists. *Pterostichus adstrictus* is a well known carabid with transamerican distribution and found in a wide variety of forested and open habitats, including human-disturbed urban areas (Spence and Spence 1988) and agricultural systems (Cárcamo et al. 1995). As a eurytopic species *Pterostichus adstrictus* must be able to withstand a wide array of environmental conditions which explains its large population even in the highly acidified site. Further studies in the laboratory showed that this species grows well in the acidified soil when fed on a diet of chopped earthworms and dog food (Cárcamo unpub. data). Also, a number of meristic (discrete traits, e.g. elytral punctures) and metric traits (e.g. length) showed no evidence of fluctuating assymetry for this species for a sample of individuals collected from the acidified site (McIntyre and Cárcamo unpub. data).

Agonum placidum is one of the most abundant species in agricultural areas (Cárcamo 1995) and is generally not considered a forest carabid (Lindroth 1961-69). However, in this study it was moderately abundant and ranked 5th in the polluted sites at 150 m or less in the pine site and 6th in the polluted aspen site. Also in 1994, 19 of the 29 beetles collected at the 3 distances came from the 50 m site (see Chapter 3). These results suggest that *A. placidum* is capable of invading stressed sites although it is not known if it is capable of forming permanent breeding populations.

The distribution pattern of the apparent opportunist species, *A. hyperborea* in the pine and aspen study sites is difficult to explain. According to Lindroth (1961-1969, p 679; part 5, supplementum 33): "the true habitat is sandy, rather dry soil (often moraine); during daytime the beetles are often hiding among dry leaves of *Salix* or *Alnus*". In the present study *A. hyperborea* was concentrated in the most acidified pine site at 50 m from the open sulphur storage area. It was very rare in all other sites including the acidified enclosures ca. 60 m. from the forest edge, the acidified aspen or control site (ca 100 m from edge) and was very rare in the pine site at 50 m east of the forest edge near the

gravel pit. These results suggest that this species may increase its populations in the acidified site through dispersal from the forest edge into the site where ground cover is absent which facilitates its movement. The presence of ground cover in the site near the gravel pit may prevent its incursions deeper into the forest; an alternative explanation is that this species has an extremely patchy distribution and it does not occur in the area of the gravel pit.

Carabid communities

Overall abundance of ground beetle adults increased away from the sulphur storage area, especially when the control plots without ground cover are compared with the acidified plantless site. A similar pattern was reported for carabids near a kraft mill that emitted sulphate compounds in southern Ontario (Freitag et al. 1973) In the present study this trend resulted because seven common carabid species which account for a substantial proportion of the total carabid catch were vulnerable to pollution effects. Interestingly, the abundance of carabid larvae over two years, as estimated from pitfall traps, followed the opposite pattern found with adults. Larvae were more abundant in the most acidified site in both years. This result provides evidence that some of the adult carabids were establishing breeding populations and not simply immigrating into the site. Larvae could not be identified, but a cursory examination suggested that the majority belonged to the genus *Calathus*. Because one species of this genus *C. advena* was the dominant of the two *Calathus* species found at the acidified site, it may be assumed that this was the species represented by most of the larvae. *Calathus* species in Europe are known to be ant predators (Hengeveld 1981); if *C. advena* also feeds on ants it would have no shortage of food since ants were common in the acidified site. Analysis of gut contents of this species may shed light on this question.

Differences in species richness were small but in 1996 there was a significant trend of more species away from the sulphur block. Measures of community that take into account the relative distribution of each species were more sensitive. Results using unfenced and enclosed pitfall trapping suggested reduced diversity in the acidified site. The correspondence between these two methods suggests that for carabids, unfenced pitfall trapping data is adequate to estimate species diversity indices. Diversity measures, Hill's N1 and N2, focus on rare and dominant species respectively, and they reflected the lower number of rare species at the acidified site (N1) and the fact that fewer of the species present dominated the very polluted site (N2). Similar results were found in the aspen site; therefore, it can be concluded that diversity or its various components are negatively affected by acidification.

Spiders

Enclosed vs unfenced traps.

The suite of dominant species were the same in enclosed or unfenced pitfall traps. However, there was a striking difference in the number of *Pardosa mackenziana*. This species accounted for over 60 % of the total spider catch in the unfenced trap stations at the acidified site but only 4 % inside the enclosures at the acidified site. These differences in abundance were reflected in the guild composition; day-hunters were a minor component of the spider assemblage inside enclosure in acidified and non acidified sites, whereas micro-webbers were the dominant spider group. In the unfenced traps, micro-webbers were the second dominant group after day-hunters. Investigators of spiders in agricultural fields in Europe have shown similar results and argued that pitfall traps produce inflated numbers of certain spider groups (Topping and Sunderland 1992).

Because of their wandering foraging strategy and larger body size, hunting spiders are considered more trappable than the web building, smaller micro-webbers. However, before discarding potentially valuable and arduously gathered data, some alternative considerations are necessary.

It can be argued that mobility of lycosids leads to under-representation inside enclosures. It is possible that lycosid spiders are able to escape from the area being enclosed while the enclosures were installed. This is plausible considering the size of the enclosures being only 2 m x 2 m. Linyphiid spiders are web-building for the most part and also because of their smaller size and reduced mobility they were less likely to escape from the area. It should be pointed out that males of this group have a wandering life style (mate searching) which makes them vulnerable to fall in the traps. The overall sex ratio of male to female linyphiids pitfall catches was close to 1 and around 2 for lycosids. This suggests that female linyphiids are equally trappable and the biased male catch of lycosids suggests their populations are even higher than estimated with pitfall traps.

Also, there are a number of reasons why micro-webbers can achieve greater representation inside enclosures. First, linyphiid spiders are known to disperse as juveniles and adults using the ballooning technique (Greenstone et al. 1987). All spiders are known to disperse this way as juveniles but because of their small size, linyphiids also manage to "fly" as adults. This means that enclosures are less effective in keeping out micro-webbers compared to hunting spiders. Second, micro-webbers or web-builders in general can be favoured in micro-habitats containing coarse woody debris (logs) found inside the enclosures. Logs provide microsites with high biodiversity (Irmiler et al. 1996); logs can provide the structure required for web attachment, they can produce a favourable moist microclimate and are carbon resources where arthropod detritivores may be more available for spiders to prey upon.

The pattern of greater abundance of linyphiid spiders away from the sulphur block in "bare" microhabitats (without logs) derived with unfenced pitfall traps was supported by samples collected with soil cores. In both years of the present study and in the regional survey conducted in 1994 no linyphiid spiders were found in the acidified site although their densities were 15-25 per m² in the site at 250 m.

Unfenced pitfall trapping for spiders, unlike carabids, needs to take into account the presence of coarse woody debris for the two guilds discussed above. However, for two other spider guilds, the macro-webbers and night hunters, the results were similar in unfenced and enclosed traps. In fact, for the only spider that had consistent and significant responses to acidification (*Callioplus euoplus*), the estimates of abundance (means) using both methods were very close: 1 and 22 individuals/trap station were found in the unfenced traps at the 50 and 250 m sites respectively; 1.33 and 20.0 individuals/enclosure were found inside the acid and control enclosure respectively.

From the above discussion comparing unfenced vs enclosed trapping for spiders, some conclusions can be drawn. The standard technique of using unfenced pitfall traps is adequate to sample and compare abundances of macro-webbers and night hunting spiders, especially when trapping takes place over extended periods (two years in this study); the data on *C. euoplus* provides evidence of this. For comparisons of micro-webbers and the large day-hunters, unfenced pitfall trapping seems less adequate and interpretation of the data obtained requires some caution; supplementary methods such as soil coring and direct counting are recommended. An important factor to consider is the structural heterogeneity of the microhabitat in terms of coarse woody debris. Areas with greater numbers of logs on the ground can be expected to harbour more micro-webbers relative to bare areas without logs. In the following discussion of acidification effects on spiders derived from unfenced trapping, pitfall trap stations were located in bare areas at all the gradient points.

Therefore, it is expected that the results are still valid to compare abundances along the acidification gradient, especially since core sampling supported the results for linyphiids.

Acidification and spiders

Spiders with sufficient numbers to be analyzed were divided into three groups according to their abundances in the pollution gradient: vulnerable, resistant and opportunists. Six species can be classed as vulnerable (*Callioplus euoplus*, *Cryphoea exlineae*, *Allomengea pinnata*, *Bathyphantes pallidus* Banks, *Diplocentria bidentata* Emerton and *Sciastes truncatus* Emerton). For the latter four linyphiid spiders, the effects can be related to the structural heterogeneity of the microhabitat and/or its associated microclimatic profile. Linyphiid spiders were also reported lower in clear cuts than in old growth forests (McIver et al. 1992, Pajunen et al. 1995, Buddle pers. comm.) and this suggests that the results found in the current study are associated with indirect microhabitat effects.

Data for *C. euoplus* are suggestive of direct effects or that its specialized requirements were not met in any of the acidified microhabitats studied (enclosures in pine with logs, aspen forest litter and pine forest litter). pH is unlikely to have a direct effect on any spider since they are not in close proximity with the soil; however, elemental sulphur dust or sulphur dioxide gas could be harmful for this spider or its web and worthwhile investigating further. Alternatively, its pattern may be related to predator-prey interactions that have been altered by the lack of vegetational cover.

Five species can be classed as sulphur pollution resistant (*Agroeca ornata*, *Clubiona canadensis*, *Agelenopsis utahana*, *Xysticus obscurus* and *X. canadensis*). *A. utahana* is a relatively large spider that builds an extensive funnel web on more or less flat vegetation cover such as moss (Cárcamo, personal field observation); the flat, litter-

covered ground in the acidified areas probably provides suitable substrate for this species. The other four species are night hunters and lack of ecological information on these species prevents speculation on mechanisms that make them pollution resistant.

Two lycosid species (*Pardosa mackenziana* and *Trochosa terricola*) appeared to benefit from the high sulphur pollution and acidification at the pine and aspen sites. Lycosid spiders have also been found in higher numbers in clear cut sites than in old growth stands (McIver et al. 1992) or near edges in forests as shown in a previous section of this chapter and also elsewhere by Pajunen et al. (1995). Lowrie (1973) also observed that wolf spiders prefer more open sunny spots where they can warm up their egg sacs. Therefore, lycosids found in higher numbers at the acidified site cannot be considered acidophiles. Because most field studies (e.g. the two quoted above and the present one) are based on unfenced pitfall traps it is not known if the results are a methodological artifact. However, it can be argued that in clear cuts and also in the acidified sites there is better light penetration allowing day hunters which are visual predators to find their prey more effectively. This is congruent with the fact that night hunting spiders were not favoured at the acidified sites. Furthermore, lycosid spiders' locomotive behaviour may be favoured on uniform substrates found in the acidified sites. Numerous spiders of the above species were found with egg sacs and by far the majority of the juveniles caught in pitfall traps in the acidified site belong to the wolf spider family. There were 25 times more lycosid juveniles in the acidified site than in the control site at 250 m in 1996 (Cárcamo unpub. data). This suggests that spiders were able to breed in the site and were not merely passing through.

Overall number of spiders did not vary significantly along the pine pollution gradient or the aspen sites. These results illustrate the importance of considering taxa at a lower taxonomic resolution or at least at the level of ecological guilds. The similarity in spider numbers results from the compensation effects of day hunters and linyphiids that

had opposite distribution patterns along the pollution gradient. With the carabid beetles the trend of increased abundance away from the acidified site was caused by the presence of vulnerable dominant species; in the case of spiders none of the species considered pollution vulnerable were dominant enough to affect the overall spider pattern.

Species richness was lower (about 10 fewer species) in the acidified site compared to the 250 m site with plant cover; interestingly in 1995 richness was also lower in the devegetated plots. These results point out the importance of vegetational cover for spiders. Most of the linyphiines are thought to live in the forest floor plant layer (Buckle, pers. comm), therefore, these species were removed when the moss was taken away from the plots devegetated experimentally. Interestingly, the number of species in these plots was very similar to the acidified plots that were devoid of vegetation. Also when the family Linyphiidae is broken into the two groups, Linyphiines and Erigonines, inside the enclosures, the former were significantly lower inside enclosures at the acidified site. Despite potential structures to attach their webs and moister microhabitats, these enclosures devoid of any plants had fewer linyphiines; this illustrates the importance of ground vegetation for this group.

Diversity of the spider assemblage was lower at the acidified pine and aspen site compared to sites with intact ground cover and higher pH. These results can be explained by the overwhelming dominance of the day hunting guild in acidified sites. Because of the large numbers of lycosid juveniles in acidified sites these patterns are considered of biological importance and not a methodological artifact of pitfall trapping. In part, the reduced diversity can be explained by edge effects; a similar trend of lower evenness was seen near the edge of the forest east of a gravel pit. However, the differences were much greater in the acidification gradient suggesting that other factors were important in determining the dominance of wolf spiders (e.g. increased foraging efficiency discussed above). It can be concluded that sulphur contamination affects biodiversity of the spider

assemblage at the localized spatial scale by reducing species richness and increasing the dominance of a few species favoured by disturbance and microhabitat effects induced by stress .

Earthworms in the acidification gradient

Earthworms and pitfall sampling.

This study demonstrated a very high positive correlation between season long earthworm pitfall trap catches and density estimates derived from standard core sampling and extraction techniques. This suggests that pitfalls, which are commonly used to study surface active arthropods such as carabid beetles and spiders, may also be used to study epigeic earthworms. These data suggest that *D. octaedra* has high locomotion potential along the forest floor surface to be caught in moderate numbers in pitfall traps (ca. 30 individuals per station of 3 pitfalls). In this study, many of the earthworms were poorly preserved in the pitfall traps and distinguishing them from other species in heterospecific assemblages would be difficult. Further work is needed to determine the best collection fluid and collection frequencies to obtain well preserved individuals.

Because of the lack of studies with pitfall traps it is not known if earthworm catches are affected by the type of ground substrate or trap station distances as demonstrated with carabid beetles (Spence and Niemelä 1994; Digweed et al. 1995). Peristaltic locomotion used by oligochaetes may reduce the effect of ground cover. In the present study, earthworm numbers were higher in the site that had intact vegetation cover (250 m site), suggesting that there was no impedance to their movement relative to the other non acidified site (150 m site) which had greater litter than moss cover. Soil moisture is likely more important than actual ground cover in determining movement and

catches of *D. octaedra*. Catches of earthworms were slightly lower at the site with reduced ground cover in 1996 (150 m site). The lower moisture of the litter and to a lesser extent of the FH at the 150 m site compared to 250 m, may explain the more pronounced differences in earthworm activity during 1996 relative to 1995. The second year of the study (1996) was much drier than 1995. At the highly acidified site with no plant ground cover, the potential effect of moisture was masked by the highly acidic conditions as was demonstrated in laboratory experiments discussed below.

Acidification effects.

Dendrobaena octaedra was listed by Satchell (1955) as an acid tolerant species and is frequently the only earthworm species found in acidic coniferous forests in Europe (Huhta 1979; Rundgren 1994). In Canada, this species is the dominant earthworm species in pine forests; for example during intensive sampling at a Kananaskis pine forest, only one out of several hundred individuals was identified as *Dendrodrius rubidus* Savigny while the rest were *D. octaedra* (McLean pers. comm.). All the earthworms from core samples in the present study appeared to belong to this latter species. This was expected considering that in acidic coniferous forests in Sweden (Rundgren 1994) and Finland (Huhta 1979, 1984) *D. octaedra* is the dominant earthworm species.

The two methods employed to sample earthworm populations provided consistent evidence of *in situ* detrimental acidification effects. At the site 50 m from the sulphur block, no earthworms were found in either year in pitfall traps and only one individual was retrieved from soil cores over the two years. Conditions at the highly sulphur contaminated site were too extreme for colonization and establishment of *D. octaedra*. It may be argued that if this species is transported in the hooves of cattle (grazing is frequent in the area), the lack of earthworms may simply result from cattle not entering this site

because of the absence of any plants to graze upon. However, data obtained from laboratory experiments showed that under constant moisture and temperature conditions, the majority of earthworms added to field collected acidified material failed to grow and survive as well as those incubated in non-acidified soil (Cárcamo et al. unpub. data). Therefore, the absence of earthworms in the acidified site can be attributed to harsh conditions preventing establishment and not to lack of colonization.

One of the main mechanisms preventing establishment of earthworm populations in the acidified site is direct toxic effects of high hydrogen ion concentration. Laboratory experiments have shown that under low pH, earthworms take longer to burrow into the soil (Satchell 1955) and that survivorship is significantly reduced (Satchell 1955, Cárcamo et al. unpub. data). Another factor thought to affect earthworm survivorship in acid soil is calcium deficiency (Pearce 1972); the acidified site had one of the lowest calcium concentrations in the area despite lime addition by the sour gas operators (Maynard et al. 1995). Laboratory experiments (Cárcamo et al. unpub. data) clearly showed reduced survivorship and growth of *D. octaedra* in acidified soil (pH 2.9) suggesting that H^+ concentrations were too high even for this acid resistant earthworm.

The possibility that resource quality is affecting earthworm growth cannot be ruled out from this study. In a separate, unpublished study Cárcamo and Loo showed that the survivorship period of *D. octaedra* in the most acidified soil was less than a week. This period may be long enough to starve the earthworms if the food quality is inadequate in the acid soil. Fungal biomass, which forms one of the main food resources for earthworms (Pearce 1978), is known to be lower in highly acidified soils (Visser and Parkinson 1989) and may partly explain their absence. Other potential food groups such as nematodes (Hyvonen et al. 1994) may also be less available in acid soils. Additional experiments are required to tease apart the direct hydrogen ion effect from the confounding impact of reduced food availability on earthworm fitness.

Snails in the acidification gradient

Numbers of snails were significantly lower in the acidified pine site according to the three sampling methods used (artificial shelters, cores and pitfall traps) and also in enclosed pitfall trapping at the acidified site. There was a high correlation between numbers of snails in pitfall traps and artificial shelters. According to Boag (1990) artificial shelters provide adequate estimates of snail abundances, although he noted species differences in their use of the shelters as hiding places. In 1995, a wet year, the number of snails in traps was very high compared to the other two methods.

The absence of snails in highly acidified sites ($\text{pH} < 3$) is not surprising since under low pH their calciferous shell would disintegrate. Furthermore, calcium availability is known to limit snail distribution (Hermida et al. 1995) and despite regular liming of the sites adjacent to the sulphur block, this site had the lowest calcium concentration. Pitfall catches of snails were highest in the site at 150 m with the highest pH; all sites around the gas plants have been limed but given the pH of the site at 150 m it is likely that excessive liming took place there and this can explain the trend of greater snail abundance. Snails were also very abundant in the slightly acidified aspen site (pH 5.6). This further suggests that lack of plant cover is not important, at least for certain snail species. It seems that in both the aspen and pine site (at 150 m) with high levels of elemental sulphur and reduced plant cover the snails are able to find enough food and can survive when pH is over 5.5. At the slightly acidified aspen site there were no plants on the ground for snails to feed upon, however, a large amount of aspen litter was available.

Staphylinids, ants and collembolans

Staphylinid (rove) beetles were significantly lower at the acidified pine site. Three general guilds are recognized among rove beetles: generalist predators, detritivores and fungivores (Newton 1990). Ectomycorrhizal fruit bodies (mushrooms) were probably unavailable at the acidified pine site since these fungi are absent at pH values less than 3.3 (Danielson and Visser 1989) and this may explain the lower abundance of rove beetles in the acidified site. However, numbers of rove beetles were similar under the two pollution regimes inside enclosures. Again it can be speculated that coarse woody debris found in the enclosures provide microhabitat refugia where many invertebrates encounter suitable resources; in the case of rove beetles more fungi may grow directly on the logs or in the moist soil around them. In 1996 one large mushroom was observed growing underneath the enclosure fence; it seems that the trench was capturing enough moisture for the mushroom to grow. Because rove beetles were not classified into functional groups (predators, detritivores and fungivores) it remains unknown if these groups were affected differently by sulphur pollution.

Although ants were absent from the soil cores taken at the acidified site, estimates at farther sites were highly variable resulting in non significant differences. Direct counts of ant nests and their populations are needed to obtain more precise estimates of ant abundance response to sulphur pollution. However, the results found here are in agreement with other studies of pollution effects on ants. Krzysztofiak (1991) found that ants can buffer pollution to some extent as the pH in ant hills was higher than the surrounding soil in areas polluted with heavy metals. Because most ants are generalist predators and scavengers well adapted to dry conditions (Greenslade and Greenslade 1985), it is unlikely that they were affected negatively in the acidified sites.

Pitfall catches and soil core extraction showed opposite patterns of collembolan abundance along the pine sulphur pollution gradient. There were more Collembola in the traps at the most polluted sites whereas core extraction showed greater densities in the

control sites. This difference must relate to the suite of species sampled by the different methods. Pitfall traps were capturing surface active, mobile Collembola. These Collembola were sclerotized with yellow pigmentation suggestive of adaptations to the drier litter environment and are likely litter feeder generalists without intimate contact with the soil. Therefore, they may not be affected directly by low pH or its indirect microhabitat effects. Previous studies have established the presence of acidophilic Collembola in a Swedish forest (Bååth et al. 1980). Also, Addison (unpub. data) found that a few common species survived at the acidified site at Strachan. Collembola can provide the resource base allowing macroarthropod predators to maintain viable populations at the acidified sites.

Soil cores showed reduced collembolan numbers in the acidified site. The majority of collembolans collected from soil core extractions were pale or whitish individuals which can be taken as an indication of deeper habitation of the forest floor or upper mineral soil. These individuals are in more intimate contact with the soil and are more vulnerable to direct toxic effects of low pH. Furthermore, soil dwelling collembolans are known to feed on fungi (Addison and Parkinson 1978) which were reduced at the acidified site as suggested by lower microbial biomass (Visser and Parkinson 1989). This pattern of collembolan abundance is supported by data collected by Addison (unpub. data) who found significant negative effects on several species of Collembola at the Strachan study site.

Summary

At the higher taxonomic level of family or class, earthworms and snails had consistently lower abundances at the acidified pine site using all sampling methods (unfenced or enclosed traps and soil cores). Earthworms and linyphiid spiders also had reduced pitfall catches in the acidified aspen site.

At the species level, variable responses were observed to sulphur pollution. Seven carabid species were vulnerable to sulphur pollution effects in pine forest but only two in aspen forests. Several carabid species were clearly unaffected and a few were even more abundant in the most polluted sites. Pitfall catches of only one spider (*Callioplus euoplus*) were consistently lower at all acidified sites (pine or aspen) in both unfenced and enclosed traps. A few linyphiids and one agelenid spider also had reduced catches in one of the acidified sites. Five spider species were unaffected by acidification. Two lycosid (wolf) spiders were more abundant at acidified sites but part of this pattern could be attributed to forest edge effects. It is suggested that species responses to sulphur pollution and severe acidification effects are dependent on the degree of ecological specialization of a species. Those more vulnerable to anthropogenic stress are habitat and/or prey specialists.

A small trend of increasing species richness for spiders and carabids was observed in the unfenced traps away from the acidified site. This pattern was clearer when species diversity indices were compared and was consistent between unfenced and enclosed traps for carabids. At the pine and aspen acidified sites a few species were more dominant and caused a reduction in diversity by decreasing its evenness component.

The observed distribution of epigeic invertebrates in forest stands acidified by elemental sulphur can be attributed to direct and indirect effects. Earthworms, snails and some Collembola can be affected negatively through direct acidity effects; however, for the majority of the remaining arthropods indirect effects are more important. These indirect effects can be partitioned into landscape level, habitat or forest type level, and microhabitat level. It is concluded that faunal structure at the acidified sites is severely affected negatively and may explain part of the loss in function (decomposition) observed in such ecosystems.

Table 5.1a: Soil environmental parameters at the pine acidified gradient. Entries are means of three stations.

Soil parameter	Distance from sulphur block (m) and vegetational ground cover			
	50 mean	150 mean	250 with plant cover mean	250 without plant cover mean
Mass of litter layer (g/44.2 cm ²)	52.29	24.80	16.40	8.80
Mass of vegetation (g/44.2 cm ²)	0.15	0.51	2.27	0.70
Mass of F and H layers (g/44.2 cm ²)	34.71	42.80	33.40	15.44
Moisture of LFH horizons (%)	64.20	63.40	65.10	56.88
pH	2.96	6.31	5.51	5.17
Electrical conductivity (dS/m)	1.14	0.67	0.47	0.29
Organic matter content (%)	39.70	36.70	39.00	50.00

Table 5.1b: Soil environmental parameters at the pine site east of gravel pit
Entries are means of three stations.

Soil parameter	Distance from forest edge (m)		
	50 mean	150 mean	250 mean
Mass of litter layer (g/44.2 cm ²)	1.19	1.72	1.15
Mass of vegetation (g/44.2 cm ²)	4.54	3.73	5.31
Mass of F and H layers (g/44.2 cm ²)	43.82	42.36	30.43
Moisture of LFH horizons (%)	38.52	50.38	60.32
pH	4.48	4.85	4.37
Electrical conductivity (dS/m)	0.21	0.25	0.21
Organic matter content of FH (%)	55.83	38.43	33.70

Table 5.1c: Soil environmental parameters for enclosures and aspen sites.
 Entries are means of three enclosures or trap stations.

Soil parameter	Enclosure pollution type		Aspen pollution type	
	acidified	control	acidified	control
Mass of litter layer (g/44.2 cm ²)	33.12	2.92	7.09	3.00
Mass of vegetation (g/44.2 cm ²)	0.00	7.32	0.00	1.02
Mass of F and H layers (g/44.2 cm ²)	15.60	17.09	93.60	99.78
Moisture of LFH horizons (%)	52.42	56.92	62.90	61.90
pH	3.80	5.34	6.06	7.10
Electrical conductivity (dS/m)	0.68	0.52	0.54	0.52
Organic matter content (%)	61.42	50.05	35.40	31.32

Table 5.1d: Moisture content of forest floor at the acidification gradient during 1996.

Date	Litter layer			Fermentation/humus layer		
	14.VI	08.VIII	27.IX	14.VI	08.VIII	27.IX
Distance from sulphur block (m)	percent moisture			percent moisture		
50	11.95	26.97	21.24	62.28	65.71	58.51
150	11.27	31.90	35.99	57.48	65.21	58.19
250	11.72	41.96	40.13	60.85	67.66	68.28

Table 5.2a: Carabid catches and diversity at the acidified gradient and devegetated plot.

Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost free season of 1995.*

Carabid species	Distance from sulphur block (m) and vegetational ground cover							
	50		150		250		250	
	mean	\pm se	mean	\pm se	with plant cover mean \pm se	without plant cover mean \pm se	without plant cover mean \pm se	without plant cover mean \pm se
<i>Pterostichus adstrictus</i>	38.67	11.55 a	71.67	7.88 ab	74.92	27.36 ab	101.75	8.27 b
<i>Platynus decentis</i>	5.33	2.33 a	39.00	17.00 b	31.47	10.55 b	40.48	8.27 b
<i>Calathus advena</i>	52.67	5.55 a	23.33	16.70 a	51.57	35.50 a	115.49	51.52 a
<i>C. ingratus</i>	26.00	8.62 a	49.33	6.17 ab	67.07	5.81 b	88.01	19.58 b
<i>Scaphinotus marginatus</i>	3.33	0.67 a	27.67	4.37 b	68.14	24.20 c	49.39	15.68 bc
<i>Stereocerus haematopus</i>	1.00	0.58 a	4.00	2.52 ab	7.92	3.39 b	38.25	11.87 c
<i>P. riparius</i>	0.33	0.33 a	1.67	0.33 b	4.78	0.78 b	13.00	7.43 b
<i>P. pensylvanicus</i>	0.33	0.33	1.33	0.88	1.74	1.28	1.11	0.64
<i>Trechus chalybeus</i>	0.33	0.33 a	1.00	0.00 a	9.25	2.33 b	6.68	1.70 b
<i>Amara hyperborea</i>	20.00	11.06 a	2.33	0.67 b	0.00	0.00 b	0.37	0.37 b
<i>Agonum retractum</i>	0.00	0.00 a	1.67	0.33 b	5.67	2.96 b	4.08	0.74 b
<i>A. placidum</i>	12.67	7.31 a	18.00	9.07 a	5.45	1.79 a	5.57	1.70 a
<i>A. cupripenne</i>	0.00	0.00	1.00	0.58	0.00	0.00	0.00	0.00
<i>Carabus chamissonis</i>	0.33	0.33	1.33	0.67	0.33	0.33	1.11	0.64
<i>Bembidion grapei</i>	3.00	2.08	1.33	0.88	0.00	0.00	0.00	0.00
<i>Calosoma frigidum</i>	0.67	0.33	0.33	0.33	0.67	0.33	1.11	1.11
<i>Patrobus foveocollis</i>	0.00	0.00	0.33	0.33	2.73	0.89	1.49	0.74
<i>Nebria gyllenhali</i>	0.67	0.33	0.00	0.00	0.33	0.33	0.00	0.00
<i>Cymindis cribricollis</i>	0.33	0.33	0.67	0.33	0.00	0.00	0.00	0.00
<i>Leistus ferruginosus</i>	0.00	0.00	0.67	0.67	0.00	0.00	0.37	0.37

Table 5.2a: concluded

	Distance from sulphur block (m) and vegetational ground cover							
	50		150		250 with plant cover		250 without plant cover	
	mean	± se	mean	± se	mean	± se	mean	± se
Carabid species								
<i>Miscodera arctica</i>	1.00	0.58	0.33	0.33	0.00	0.00	0.00	0.00
<i>Synuchus impunctatus</i>	0.67	0.67	0.00	0.00	0.00	0.00	1.11	0.64
<i>Amara quenseli</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.74	0.37
Community parameter								
Carabidae	167.33	40.83 a	247.33	39.35 ab	332.04	88.90 bc	470.12	50.69 c
Carabid larvae	51.333	15.07 a	8	1 b	2.3333	1.2019 c	8.6667	1.453 b
N0 (Species richness)	12.33	0.88 a	16.00	0.58 b	12.67	0.88 a	14.33	1.20 ab
N1 (Shannon-Wiener index)	5.96	0.55	6.29	0.01	6.66	0.34	6.64	0.33
N2 (Simpson's inverse)	4.66	0.64	5.22	0.31	5.29	0.33	5.17	0.48
J' (Evenness)	0.71	0.02	0.68	0.01	0.75	0.01	0.71	0.04

* Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

Table 5.2b: Carabid catches and diversity in acidified gradient and devegetated plots in 1996.

Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost free season.*

Carabid species	Distance from sulphur block (m) and vegetational ground cover											
	50			150			250 with plant cover			250 without plant cover		
	mean	\pm	se	mean	\pm	se	mean	\pm	se	mean	\pm	se
<i>Pterostichus adstrictus</i>	55.67	11.26	a	87.67	12.41	a	99.00	18.52	a	64.33	17.94	a
<i>Platynus decentis</i>	3.00	1.53	a	29.33	2.67	b	28.67	11.89	b	28.33	6.89	b
<i>Calathus advena</i>	84.33	11.26	a	22.33	15.60	b	52.67	26.62	ab	48.33	19.97	ab
<i>C. ingratus</i>	14.33	6.44	a	52.00	5.57	b	61.33	1.20	b	53.67	6.17	b
<i>Scaphinotus marginatus</i>	3.33	1.33	a	25.33	3.84	b	98.00	28.29	c	74.00	17.16	c
<i>Stereocerus haematopus</i>	0.00	0.00		5.00	3.00	ab	12.00	4.93	bc	21.67	7.88	c
<i>Pterostichus riparius</i>	0.00	0.00	a	3.00	2.52	ab	7.33	2.67	b	6.33	1.67	b
<i>P. pensylvanicus</i>	1.00	0.00		0.00	0.00		1.33	0.88		2.33	0.67	
<i>Trechus chalybeus</i>	0.33	0.33	a	0.67	0.67	a	3.33	1.67	a	7.33	4.10	a
<i>Amara hyperborea</i>	12.00	3.46	a	0.33	0.33	b	0.00	0.00	b	0.00	0.00	b
<i>Agonum retractum</i>	0.00	0.00		0.00	0.00		2.00	1.15		2.33	0.88	
<i>A. placidum</i>	5.67	3.48	a	9.33	6.84	a	4.33	1.33	a	4.00	0.58	a
<i>Platynus mannerheimi</i>	0.00	0.00		0.00	0.00		0.33	0.33		0.00	0.00	
<i>Carabus chamissonis</i>	0.00	0.00		1.33	0.33		0.33	0.33		0.00	0.00	
<i>Carabus taedatus</i>	0.00	0.00		0.00	0.00		0.33	0.33		0.00	0.00	
<i>Bembidion grapei</i>	2.33	1.86		0.67	0.67		0.00	0.00		0.00	0.00	
<i>Calosoma frigidum</i>	0.00	0.00		0.00	0.00		1.33	1.33		0.33	0.33	
<i>Patrobis foveocollis</i>	0.00	0.00		0.00	0.00		1.67	0.33		2.00	1.15	
<i>Nebria gyllenhali</i>	0.33	0.33		1.67	0.67		0.00	0.00		0.33	0.33	
<i>Cymindis cribricollis</i>	0.00	0.00		0.00	0.00		0.00	0.00		0.33	0.33	
<i>Leistus ferruginosus</i>	0.00	0.00		1.67	1.67		0.00	0.00		0.67	0.67	

Table 5.2b: concluded

Carabid species	Distance from sulphur block (m) and vegetational ground cover											
	50		150		250							
	with plant cover	without plant cover	with plant cover	without plant cover	with plant cover	without plant cover						
	mean \pm se	mean \pm se	mean \pm se	mean \pm se	mean \pm se	mean \pm se						
<i>Miscodera arctica</i>	0.33	0.33	4.67	4.67	0.00	0.00	0.00	0.00				
<i>Synuchus impunctatus</i>	0.00	0.00	0.00	0.00	0.33	0.33	0.33	0.33				
<i>Amara quenseli</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33				
<i>Loricera pilicornis</i>	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00				
Community parameter												
Carabidae	183.00	36.51	a	245.00	19.70	a	374.33	74.95	a	317.00	68.61	a
Carabid larvae	21.00	2.52	a	10.00	0.58	ab	7.00	1.53	bc	4.67	1.86	c
N0 (Species richness)	9.33	0.33	a	11.33	1.20	ab	12.67	0.67	b	13.67	0.33	b
N1 (Shannon-Wiener index)	4.09	0.40	a	5.75	0.26	b	6.14	0.53	bc	7.06	0.30	c
N2 (Simpson's inverse)	3.10	0.34	a	4.54	0.42	b	5.05	0.44	bc	5.80	0.30	c
J' (Evenness)	0.63	0.05	a	0.73	0.05	ab	0.71	0.02	ab	0.75	0.01	b

*Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

Table 5.3a: Spider catches and diversity at the acidified gradient and devegetated plots in 1995*

Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost-free season capture.*

Spider species	Distance from sulphur block (m) and vegetational ground cover							
	50		150		250 with plant cover		250 without plant cover	
	mean	\pm se	mean	\pm se	mean	\pm se	mean	\pm se
Linyphiidae (Linyphiinae)								
<i>Agyneta allosubtilis</i>	0.67	0.33	2.67	0.88	0.00	0.00	0.74	0.74
<i>Allomengea pinnata</i>	0.00	0.00 a	0.67	0.33 ab	2.02	0.56 b	1.49	1.49 ab
<i>Bathyphantes pallidus</i>	3.33	0.67 a	4.67	2.33 a	4.41	0.87 a	3.71	2.07 a
<i>Centromerus sylvatica</i>	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00
<i>Lepthyphantes alpinus</i>	0.67	0.33 a	4.33	2.33 ab	3.72	1.75 ab	7.06	2.07 b
<i>Lepthyphantes complicatus</i>	0.00	0.00	0.67	0.33	0.33	0.33	0.00	0.00
<i>Lepthyphantes duplicatus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.74	0.74
<i>Lepthyphantes intricatus</i>	0.00	0.00	1.00	0.58	2.02	0.56	1.86	0.37
<i>Lepthyphantes nr. washingtoni</i>	0.00	0.00	0.33	0.33	0.33	0.33	0.00	0.00
<i>Lepthyphantes sp. #10</i>	0.00	0.00	0.00	0.00	0.71	0.71	0.00	0.00
<i>Lepthyphantes sp., undet.</i>	0.00	0.00	0.00	0.00	0.35	0.35	0.00	0.00
<i>Microneta viaria</i>	0.33	0.33	0.67	0.33	1.33	0.67	1.49	1.49
<i>Oreonetides vaginatus</i>	0.00	0.00	0.00	0.00	1.69	0.31	2.60	2.60
<i>Oreonetides A</i>	0.00	0.00	0.33	0.33	1.74	1.28	0.00	0.00
<i>Pityohyphantes subarcticus</i>	0.00	0.00	0.00	0.00	0.33	0.33	0.00	0.00
<i>Poeciloneta A</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.37
<i>Sisicus apertus</i>	1.33	1.33	0.67	0.67	0.33	0.33	0.00	0.00

Table 5.3a: continued

Spider species	Distance from sulphur block (m) and vegetational ground cover								
	50		150		250		250		
	mean	± se	mean	± se	with plant cover	± se	without plant cover	mean	± se
<i>Walckenaeria</i>	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Zonella cultrigera</i>	0.00	0.00	0.00	0.00	2.39	1.22	2.60	1.62	
<i>Undetermined Erigoninae</i>	0.67	0.33	0.00	0.00	0.35	0.35	0.00	0.00	
<i>Theridiidae</i>									
<i>Robertus fuscus</i>	0.00	0.00	1.00	0.58	0.33	0.33	0.37	0.37	
<i>Theridion aurantium</i>	0.00	0.00	0.67	0.33	0.33	0.33	0.00	0.00	
Lycosidae									
<i>Trochosa terricola</i>	7.67	0.88 a	14.00	2.08 b	6.04	2.28 a	3.71	1.34 a	
<i>Pardosa mackenziana</i>	75.67	14.45	46.33	11.57	51.49	26.23	34.16	15.44	
<i>P. uinlana</i>	1.67	0.88	0.33	0.33	1.37	0.37	2.23	1.70	
<i>P. xerampelina</i>	4.33	1.86	0.00	0.00	0.33	0.33	0.00	0.00	
<i>P. maesta</i>	1.00	0.00	0.67	0.33	0.33	0.33	0.00	0.00	
<i>P. hyperborea</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00	
<i>P. tesquorum</i>	1.67	0.67	0.33	0.33	0.00	0.00	0.00	0.00	
<i>Alopecosa aculeata</i>	1.67	0.88	0.67	0.33	1.00	1.00	0.37	0.37	
<i>Arctosa alpigena</i>	0.00	0.00	1.67	1.20	1.00	1.00	0.00	0.00	
Agelenidae									
<i>Agelenopsis ulahana</i>	1.67	0.88	2.67	0.67	1.67	1.20	2.23	1.11	
<i>Cryphaea exilinae</i>	0.00	0.00 a	3.33	1.20 b	4.78	1.40 b	5.57	2.80 b	

Table 5.3a: continued

Spider species	Distance from sulphur block (m) and vegetational ground cover							
	50		150		250			
	with plant cover	without plant cover	with plant cover	without plant cover	with plant cover	without plant cover		
	mean \pm se	mean \pm se	mean \pm se	mean \pm se	mean \pm se	mean \pm se		
<i>Thomisidae</i>								
<i>Xysticus obscurus</i>	3.67	1.20 a	5.33	0.88 a	3.74	1.46 a	5.57	0.64 a
<i>X. canadensis</i>	3.33	0.67 a	2.67	0.88 a	2.02	0.99 a	5.57	1.11 b
<i>X. luctuosus</i>	0.33	0.33	0.33	0.33	0.33	0.33	1.11	1.11
<i>X. emertoni</i>	0.33	0.33	0.00	0.00	0.00	0.00	0.37	0.37
<i>X. elegans</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00
<i>Oziphila sincera canadensis</i>	0.33	0.33	0.00	0.00	0.33	0.33	0.00	0.00
<i>Coriarachne ulahensis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.37
<i>Philodromidae</i>								
<i>Thanatus formicinus</i>	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00
<i>Philodromus rufus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.37	0.37
<i>Amaurobiidae</i>								
<i>Callioplus euoplus</i>	0.33	0.33 a	3.00	1.15 a	20.39	0.39 b	16.71	1.70 b
<i>Amaurobius borealis</i>	0.33	0.33	0.67	0.67	2.00	1.15	0.74	0.74
<i>Arctobius agelenoides</i>	1.00	0.00	0.67	0.33	0.67	0.67	0.00	0.00
<i>Callobius nomenus</i>	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00
<i>Clubionidae</i>								
<i>Agroeca ornata</i>	1.00	1.00	1.67	0.88	2.06	0.63	4.08	1.96
<i>Clubiona canadensis</i>	2.00	0.58	1.33	0.33	1.69	0.31	1.86	0.74
<i>C. kulczyuskii</i>	0.00	0.00	1.67	1.67	0.33	0.33	0.37	0.37

Table 5.3a: concluded

Spider species	Distance from sulphur block (m) and vegetational ground cover							
	50		150		250			
	with plant cover	without plant cover	with plant cover	without plant cover	with plant cover	without plant cover		
	mean ± se	mean ± se	mean ± se	mean ± se	mean ± se	mean ± se		
<i>Gnaphosidae</i>								
<i>Micaria aenea</i>	0.00	0.00	0.00	0.00	0.33	0.33		
<i>Zelotes fratris</i>	0.00	0.00	0.00	0.00	0.00	0.00		
<i>Gnaphosa borea</i>	0.67	0.33	0.00	0.00	0.00	0.00		
<i>Gnaphosa muscorum</i>	0.33	0.33	0.00	0.00	0.00	0.00		
<i>Gnaphosa parvula</i>	0.00	0.00	0.00	0.00	0.35	0.35		
<i>Araneidae</i>								
<i>Araneus savens</i>	0.00	0.00	0.00	0.00	0.00	0.37		
<i>Araneus iviei</i>	0.00	0.00	0.00	0.00	0.33	0.33		
<i>Araniella displicata</i>	0.33	0.33	0.00	0.00	0.00	0.00		
Community parameter								
Araneae	125.00	19.08 a	125.33	5.36 a	164.18	34.71 a	127.37	21.55 a
N0 (Species richness)	23.67	1.86 a	28.00	2.00 ab	33.33	3.48 b	25.00	0.58 a
N1 (Shannon-Wiener index)	6.04	0.29 a	12.25	2.15 b	14.61	2.06 b	14.57	1.97 b
N2 (Simpson's inverse)	2.72	0.21 a	6.86	1.70 ab	8.86	2.60 ab	10.18	2.39 b
J' (Evenness)	0.57	0.03 a	0.74	0.04 b	0.77	0.07 b	0.83	0.04 b

* Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

Table 5.3b: Spider catches and diversity at the acidified pine gradient and devegetated plots in 1996*

Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost-free season capture.*

Spider species	'Distance from sulphur block (m) and vegetational ground cover							
	50		150		250		250	
	mean	se	mean	se	with plant cover mean	se	without plant cover mean \pm	se
Lycosidae								
<i>Trochosa terricola</i>	6.00	1.53 a	5.00	1.15 a	5.00	1.73 a	3.33	1.86 a
<i>Pardosa mackenziana</i>	73.00	13.32 a	25.33	10.84 b	28.33	17.68 b	25.33	11.85 b
<i>P. uintana</i>	3.33	1.45	1.00	0.58	1.00	0.58	1.33	0.33
<i>P. xerampelina</i>	1.00	0.00	0.00	0.00	0.33	0.33	0.33	0.33
<i>P. moesta</i>	0.33	0.33	0.00	0.00	0.67	0.67	0.00	0.00
<i>Alopecosa aculeata</i>	1.33	0.33	1.33	0.88	1.00	1.00	0.67	0.33
<i>Arctosa alpigena</i>	0.33	0.33	0.67	0.33	0.67	0.33	0.33	0.33
Agelenidae								
<i>Cryphoeca exlineae</i>	0.00	0.00 a	3.33	0.67 b	9.33	7.36 b	16.00	5.29 b
<i>Agelenopsis utahana</i>	5.00	2.08	4.67	0.67	3.33	1.67	2.00	1.00
Thomisidae								
<i>Xysticus obscurus</i>	5.67	2.19 a	1.00	0.58 b	2.00	0.00 ab	2.33	0.88 ab
<i>X. canadensis</i>	4.67	0.88 a	1.67	0.88 a	4.67	3.71 a	8.00	3.61 a
<i>X. emertoni</i>	0.33	0.33	0.33	0.33	0.00	0.00	0.00	0.00
<i>X. punctatus</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00
<i>X. luctuosus</i>	0.00	0.00	0.00	0.00	1.00	0.58	0.00	0.00
<i>Coriarachne utahensis</i>	0.33	0.33	0.00	0.00	0.00	0.00	0.00	0.00
Philodromidae								
<i>Philodromus pernix</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00
<i>Philodromus rufus</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.33	0.33

Table 5.3b: concluded

	'Distance from sulphur block (m) and vegetational ground cover							
	50		150		250		250	
	mean	se	mean	se	with plant cover mean	with plant cover se	without plant cover mean ±	without plant cover se
Spider species								
Amaurobiidae								
<i>Callioplus euoplus</i>	1.00	0.58 a	1.67	0.88 a	22.00	1.15 b	11.67	3.93 c
<i>C. penulti</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00
<i>Amaurobius borealis</i>	0.33	0.33	1.00	0.58	2.00	0.00	1.67	0.33
<i>Callobius nomeus</i>	0.33	0.33	0.67	0.67	1.00	0.58	1.67	1.20
<i>Arctobius agelenoides</i>	1.67	1.20	2.67	0.88	0.67	0.67	0.67	0.33
Clubionidae								
<i>Agroeca ornata</i>	3.67	0.88	4.67	1.33	6.00	5.00	3.67	1.67
<i>Clubiona canadensis</i>	5.33	0.88	2.67	1.20	2.33	1.86	3.33	1.33
<i>C. kulczynskii</i>	0.00	0.00	0.00	0.00	2.00	1.15	0.00	0.00
Gnaphosidae								
<i>Zelotes fratris</i>	0.00	0.00	0.33	0.33	0.33	0.33	1.00	0.58
<i>Micaria aenea</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.33
<i>Gnaphosa borea</i>	0.33	0.33	0.33	0.33	0.67	0.33	0.33	0.33
Araneidae								
<i>Araniella displicata</i>	0.00	0.00	0.33	0.33	0.00	0.00	0.00	0.00
Other								
Linyphiidae s. lat.**	34.33	3.48 a	32.33	2.73 a	79.33	12.81 b	64.33	4.37 b
Linyphiinae**	10.00	1.73 a	11.67	1.86 a	27.33	4.06 b	24.00	3.79 b
Erigoninae	24.33	1.76 a	20.67	4.33 a	52.00	8.89 b	40.33	2.19 b
Araneae	114.00	13.80 a	60.00	14.19 b	94.33	23.88 a	84.33	12.55 a

* Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$). ** Theridiids included.

Table 5.4: Percent guild composition of spiders at acidified pine gradient and devegetated stations
Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost-free season capture.*

		Distance from sulphur block (m) and vegetational ground cover							
		50		150		250 with plant cover		250 without plant cover	
		mean \pm	se	mean \pm	se	mean \pm	se	mean \pm	se
1995									
Micro-webbers		11.89	1.83 a	29.75	8.17 ab	39.07	7.16 b	33.12	3.61 b
Macro-webbers		2.99	0.29 a	9.24	2.56 a	20.02	3.98 b	21.69	4.59 b
Day-hunters		75.46	1.71 a	50.52	4.97 ab	33.07	11.49 b	29.59	8.89 b
Night-hunters		9.66	0.46 a	10.50	1.13 a	7.84	2.38 a	15.60	0.86 b
1996									
Micro-webbers		23.50	3.29 a	37.12	6.77 ab	46.60	7.39 b	43.86	4.53 ab
Macro-webbers		5.74	2.26 a	15.44	1.74 ab	23.71	6.37 b	23.26	3.97 b
Day-hunters		57.06	2.62 a	34.83	7.35 ab	18.74	9.23 b	20.12	8.28 b
Night-hunters		13.70	0.52 a	12.61	1.41 a	10.96	1.68 a	12.76	1.31 a

* Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

Table 5.5a: Invertebrate catches at acidified gradient and devegetated plots in 1995*

Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost-free season capture.

	Distance from sulphur block (m) and vegetational ground cover							
	50		150		250		250	
	mean \pm	se	mean \pm	se	with plant cover mean \pm	se	without plant cover mean \pm	se
Ants	62	25 a	65	32 a	178	164 a	35	21 a
Staphylinids	81	22 a	365	83 b	409	116 b	413	14 b
Earthworms	0	0 a	30	13 b	38	11 b	23	9 b
Snails	29	12 a	196	96 b	115	26 b	108	23 b
Collembola	1214	220 a	1476	363 a	577	60 b	872	142 ab

* Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

Table 5.5b: Invertebrate catches at acidified pine gradient and devegetated plots in 1996*

Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost-free season capture.

	Distance from sulphur block (m) and vegetational ground cover							
	50		150		250 with plant cover		250 without plant cover	
	mean \pm se		mean \pm se		mean \pm se		mean \pm se	
Ants	37	18 a	38	19 a	25	18 a	22	7 a
Staphylinids	31	1 a	200	50 bc	146	26 b	367	130 c
Earthworms	0	0 a	11	6 ab	31	7 b	16	7 b
Snails	3	1 a	52	14 b	37	12 b	30	2 ab
Collembola	187	9 a	654	62 b	332	91 a	343	4 a

* Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

Table 5.6: Summary of invertebrate densities along the pine acidification gradient. Entries are average densities/m² of three sampling stations (3 and 6 cores/station pooled in 1995 and 1996, respectively). *

Invertebrates	Distance from sulphur block (m)					
	50		150		250	
	mean ±	se	mean ±	se	mean ±	se
1995						
Ants	0	0 a	12	9 a	69	69 a
Staphylinids	5	2 a	35	9 b	30	15 b
Earthworms	2	2 a	126	19 b	113	50 b
Snails	0	0 a	7	0 b	5	2 b
Collembola	9734	2294 a	11194	2837 ab	17195	2614 b
1996						
Ants	0	0 a	6	6 a	9	5 a
Staphylinids	6	4 a	18	5 a	23	11 a
Earthworms	0	0 a	340	118 b	456	153 b
Snails	0	0 a	26	7 b	52	12 b
Collembola	4619	1811 a	5205	1236 a	10448	1487 b

* Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$)

Table 5.7: Snail estimates along the acidified pine gradient using three methods.

Sampling method	Distance from sulphur block (m)					
	50		150		250	
	mean	± se	mean	± se	mean	± se
1995						
shelters†	7.00	2.91 a	23.00	8.21 b	20.33	1.63 b
traps	29.33	11.92 a	195.67	96.45 b	114.67	25.85 b
cores (#/m ²)	0.00	0.00 a	7.40	0.00 b	4.93	2.47 b
1996						
shelters	5.67	3.84 a	46.67	9.13 b	21.33	1.45 c
traps	3.33	0.88 a	52.00	14.22 b	37.33	11.79 b
cores (#/m ²)	0.00	0.00 a	26.02	6.67 b	52.04	12.24 b

* means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

†Entries under shelters are averages of three stations for cumulative total number of snails seen under two (30 x 30 cm) plywood squares.

Table 5.8: Carabid catches in aspen sites. Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost-free season capture.*

Carabid species	Pollution category					
	Acidified			Control		
	mean	\pm	se	mean	\pm	se
<i>Pterostichus adstrictus</i>	85.00		16.62	81.33		28.20
<i>Platynus decentis</i>	65.00		11.02	69.00		9.02
<i>Calathus advena</i>	1.33		0.88	2.00		1.00
<i>C. ingratus</i>	37.67		4.67	32.00		5.29
<i>Scaphinotus marginatus</i>	41.00		17.04	45.00		7.00
<i>Pterostichus riparius</i>	1.67		1.20	11.67		3.67
<i>P. pensylvanicus</i>	2.00		0.58	0.67		0.33
<i>Trechus chalybeus</i>	1.67		0.67	4.67		1.67
<i>Amara hyperborea</i>	0.33		0.33	0.00		0.00
<i>Agonum retractum</i>	6.00		1.53	13.67		2.73
<i>Agonum placidum</i>	7.33		2.73	0.67		0.33
<i>Carabus chamissonis</i>	0.00		0.00	2.00		0.58
<i>Bembidion grapei</i>	0.33		0.33	0.00		0.00
<i>Calosoma frigidum</i>	11.00		2.52	17.33		9.87
<i>Patrobus foveocollis</i>	0.00		0.00	0.67		0.33
<i>Cymindis cribricollis</i>	1.67		0.33	0.33		0.33
<i>Leistus ferruginosus</i>	0.00		0.00	0.33		0.33
<i>Synuchus impunctatus</i>	5.67		1.76	0.67		0.67

Table 5.8: concluded

Community parameter	Pollution category					
	Acidified			Control		
	mean	±	se	mean	±	se
Carabidae	267.67		46.19	282.00		53.67
Carabid larvae	5.00		2.08	14.67		3.71
N0 (Species richness)	13.00		0.58	12.67		0.33
N1 (Shannon-Wiener index)	6.10		0.06	6.44		0.11
N2 (Simpson's inverse)	4.72		0.06	5.16		0.19
J' (Evenness)	0.71		0.01	0.73		0.01

* means are significantly different ($p < 0.05$); ms = $0.05 > p > 0.10$

Table 5.9: Spider catches in aspen sites. Entries are averages \pm 1 standard error for 3 trapping stations (3 traps pooled/station) for the frost-free season capture.*

Spider species	Pollution category					
	Acidified			Control		
	mean	\pm	se	mean	\pm	se
Linyphiidae (Linyphiinae)						
<i>Agyneta allosubtilis</i>	2.67		0.88	0.00		0.00
<i>Allomengea pinnata</i>	0.67		0.67	90.33		39.50
<i>Bathyphantes pallidus</i>	3.67		0.88	11.00		3.06
<i>Lepthyphantes alpinus</i>	0.00		0.00	0.33		0.33
<i>Lepthyphantes complicatus</i>	0.33		0.33	0.00		0.00
<i>Lepthyphantes intricatus</i>	1.33		0.33	1.67		0.88
<i>Lepthyphantes turbatrrix</i>	0.33		0.33	0.00		0.00
<i>Microneta viaria</i>	2.33		0.88	4.00		0.00
<i>Oreonetides vaginatus</i>	0.67		0.67	0.67		0.33
<i>Oreonetides A</i>	1.33		0.33	0.00		0.00
Linyphiidae (Erigoninae)						
<i>Ceraticelus fissiceps</i>	0.33		0.33	0.00		0.00
<i>Ceratinella brunnea</i>	0.00		0.00	0.33		0.33
<i>Diplocentria bidentata</i>	2.67		0.67	9.33		1.45
<i>Diplocentria rectangulata</i>	0.00		0.00	0.33		0.33
<i>Helophora insiginis</i>	0.00		0.00	2.67		1.45
<i>Hiliara herniosa</i>	0.33		0.33	0.00		0.00
<i>Hybauchenidium gibbosum</i>	0.33		0.33	6.00		5.00
<i>Hypsilistes florens</i>	0.00		0.00	0.33		0.33
<i>Sciastes truncatus</i>	0.33		0.33	1.67		0.33
<i>Sisicottus montanus</i>	1.00		0.58	0.33		0.33

Table 5.9: continued

	Pollution category	
	Acidified	Control
	mean \pm se	mean \pm se
Spider species		
Linyphiidae (Erigoninae)		
<i>Sisicottus nesides</i>	0.67 0.33	1.33 0.33
<i>Walckenaeria atrothibialis</i>	0.33 0.33	0.33 0.33
<i>Walckenaeria castanea</i>	0.33 0.33	1.00 0.00
<i>Walckenaeria directa</i>	1.00 0.58	0.67 0.33
<i>Walckenaeria</i>	0.33 0.33	0.00 0.00
<i>Wubana atypica</i>	0.00 0.00	0.33 0.33
<i>Zorrella cultrigera</i>	0.00 0.00	0.33 0.33
Theridiidae		
<i>Robertus fuscus</i>	11.67 3.53	2.67 1.33
Lycosidae		
<i>Trochosa terricola</i>	17.33 1.33	10.00 1.15
<i>Pardosa mackenziana</i>	195.00 37.80	* 57.33 14.19
<i>P. uintana</i>	4.33 1.45	0.00 0.00
<i>P. xerampelina</i>	4.00 3.51	0.33 0.33
<i>P. moesta</i>	1.67 0.88	4.33 2.85
<i>Alopecosa aculeata</i>	7.00 3.06	2.67 1.20
<i>Arctosa alpigena</i>	4.33 2.33	0.00 0.00
Agelenidae		
<i>Agelenopsis utahana</i>	3.67 0.88	0.33 0.33
<i>Cryphoeca exlineae</i>	0.67 0.33	0.33 0.33

Table 5.9: continued

	Pollution category					
	Acidified			Control		
	mean	±	se	mean	±	se
Spider species						
Thomisidae						
<i>Xysticus obscurus</i>	3.67		0.88	2.33		0.67
<i>X. canadensis</i>	1.00		1.00	1.33		1.33
<i>X. luctuosus</i>	3.33		0.88	1.33		0.67
<i>X. emertoni</i>	0.33		0.33	0.00		0.00
<i>Coriarachne utahensis</i>	0.33		0.33	0.00		0.00
Philodromidae						
<i>Philodromus rufus</i>	0.00		0.00	0.33		0.33
Amaurobiidae						
<i>Callioplus euoplus</i>	5.00		1.53	* 34.00		2.65
<i>Amaurobius borealis</i>	1.67		1.20	6.67		2.19
<i>Arctobius agelenoides</i>	0.33		0.33	0.00		0.00
<i>Callobius nomeus</i>	0.00		0.00	0.67		0.67
Clubionidae						
<i>Agroeca ornata</i>	0.67		0.67	0.67		0.67
<i>Clubiona canadensis</i>	1.00		1.00	1.00		0.58
<i>C. kulczynskii</i>	2.33		0.67	1.33		0.33
Gnaphosidae						
<i>Zelotes fratris</i>	0.67		0.33	0.00		0.00
<i>Gnaphosa borea</i>	0.67		0.33	0.00		0.00
<i>G. muscorum</i>	0.33		0.33	0.00		0.00
<i>Micaria aenea</i>	1.00		0.58	0.00		0.00

Table 5.9: concluded

	Pollution category					
	Acidified			Control		
	mean	±	se	mean	±	se
Spider species						
Gnaphosidae						
<i>M. pulicaria</i>	0.67		0.67	0.00		0.00
<i>Orodrassus canadensis</i>	0.33		0.33	0.00		0.00
Araneidae						
<i>Araneus savens</i>	0.00		0.00	0.33		0.33
Community parameter						
Araneae	294.00		53.52	261.00		60.10
N0 (Species richness)	30.00		0.58	26.00		2.52
N1 (Shannon-Wiener index)	5.22		0.38	8.89		1.38
N2 (Simpson's inverse)	2.28		0.12	5.64		1.27
J' (Evenness)	0.48		0.02	0.67		0.05

* means are significantly different ($p < 0.05$). $ms = 0.05 > p < 0.10$

Table 5.10: Spider guild percentages in aspen sites. Entries are averages for 3 trapping stations (3 traps/station pooled) and \pm 1 standard error for 1995 captures.

	Pollution category						
	Acidified			*	Control		
	mean	\pm	se		mean	\pm	se
Micro-webbers	11.58		1.36	*	48.80		7.51
Macro-webbers	3.78		0.96	*	17.57		3.15
Day-hunters	79.42		1.71	*	30.50		5.14
Night-hunters	5.22		0.34		3.13		1.04

* Means are significantly different ($p < 0.05$)

Table 5.11: Invertebrate catches in aspen sites. Entries are averages for 3 trapping stations (3 traps/station pooled) and ± 1 standard error for 1995 captures.

	Pollution category					
	Acidified			Control		
	mean	\pm	se	mean	\pm	se
Ants	352.33		120.14	96.00		31.79
Staphylinids	314.67		52.26	243.33		11.67
Earthworms	4.33		2.60	95.33		3.33
Collembola	3240.67		385.26	1279.67		50.40
Snails	176.33		13.37	191.33		9.33

* Means are significantly different ($p < 0.05$)

Table 5.13: concluded

	Pollution category					
	Acidified			Control		
	mean	±	se	mean	±	se
Spider species						
Gnaphosidae						
<i>Orodassus canadensis</i>	0.00		0.00	0.33		0.33
<i>Gnaphosa borea</i>	0.00		0.00	0.67		0.67
Amaurobiidae						
<i>Callioplus euoplus</i>	1.33		0.88	20.00		8.89
<i>Amaurobius borealis</i>	1.33		1.33	5.00		4.51
<i>Arctobius agelenoides</i>	1.67		1.67	2.33		1.86
Agelenidae						
<i>Agelenopsis utahana</i>	2.33		0.88	3.33		0.33
<i>Cryphoeca exlineae</i>	0.33		0.33	7.67		6.69
Other						
Salticidae	0.00		0.00	0.33		0.33
Erigoninae	35.67		10.30	59.67		35.23
Linyphiinae †	13.67		2.85	35.33		17.33
Linyphiidae s. lat. †	49.33		10.87	95.00		52.54
Araneae	87.33		30.85	178.33		99.98

* means are significantly different (FPLSD, $p < 0.05$).

† includes theridiids

Table 5.14: Spider guild percentages in enclosed pitfall traps. Entries are averages of 3 enclosures with 6 traps/enclosure pooled for 1995-6 captures.

	Pollution category					
	Acidified			Control		
	mean	±	se	mean	±	se
Micro-webbers	61.98		7.20	54.27		1.56
Macro-webbers	6.26		2.86	21.11		1.83
Day-hunters	5.84		3.55	7.90		3.44
Night-hunters	25.93		2.05	16.72		3.81

* means are significantly different (FPLSD, $p < 0.05$).

Table 5.15: Invertebrate catches in enclosed pitfall traps after two years. Entries are averages of 3 enclosures with 6 traps/enclosure pooled for 1995-6 captures.

	Pollution category					
	Acidified			Control		
	mean	±	se	mean	±	se
Ants	15.00		4.62	* 73.67		42.86
Staphylinids	126.33		59.85			23.50
Earthworms	0.00		0.00	* 47.67		7.69
Snails	24.67		9.17	* 107.67		6.17
Collembolla	1128.00		392.11			100.30

* means are significantly different ($p < 0.05$).

Table 5.16: Carabid catches and diversity at the pine site east of gravel pit.

Entries are averages and ± 1 standard error of 3 trapping stations (3 traps/station pooled) for 1995 capture.

Carabid species	Distance from gravel pit (m)					
	50		150		250	
	mean \pm	se	mean \pm	se	mean \pm	se
<i>Pterostichus adstrictus</i>	21.67	6.01	20.25	5.25	11.12	4.72
<i>Platynus decentis</i>	5.00	1.00	7.34	2.97	2.74	0.92
<i>Calathus advena</i>	21.00	18.52	10.47	8.97	6.23	6.23
<i>C. ingratus</i>	13.00	6.03	11.03	5.02	5.82	1.98
<i>Scaphinotus marginatus</i>	23.67	0.88 ab	28.98	9.03 b	9.10	2.77 b
<i>Stereocerus haematopus</i>	3.00	2.52	1.46	0.74	1.44	1.44
<i>Carabus chamissonis</i>	4.67	2.19	0.67	0.67	0.00	0.00
<i>Pterostichus pensylvanicus</i>	0.00	0.00	0.00	0.00	0.46	0.46
<i>Trechus chalybeus</i>	0.00	0.00	0.00	0.00	0.38	0.38
<i>Agonum retractum</i>	0.33	0.33	0.33	0.33	2.08	0.66
<i>Agonum placidum</i>	1.00	1.00	0.33	0.33	0.48	0.48
<i>Amara hyperborea</i>	0.67	0.33	0.00	0.00	0.00	0.00
<i>Synuchus impunctatus</i>	0.00	0.00	0.00	0.00	0.84	0.43
Community parameter						
Carabidae	94.00	26.58	80.86	15.18	40.69	9.32
N0 (Species richness)	8.00	1.00	6.67	0.67	7.33	0.33
N1 (Shannon-Wiener index)	4.79	0.36	4.29	0.31	5.07	0.16
N2 (Simpson's inverse)	3.95	0.30	3.71	0.45	4.43	0.18
J' (Evenness)	0.76	0.01	0.78	0.07	0.82	0.01

* Means not sharing letters are significantly different (FPLSD, $p < 0.05$).

Table 5.17: Spider catches and diversity at the pine site east of gravel pit. Entries are averages \pm 1 standard error of 3 trapping stations (3 traps/station pooled) for 1995 capture.

Spider species	Distance from gravel pit (m)					
	50		150		250	
	mean \pm	se	mean \pm	se	mean \pm	se
Linyphiidae (Linyphiinae)						
<i>Agyrela allosubtilis</i>	0.67	0.67	0.00	0.00	0.00	0.00
<i>Agyrela olivacea</i>	10.00	2.00	5.52	1.03	5.54	2.48
<i>Allomengea pinnata</i>	0.67	0.33	3.00	2.08	0.00	0.00
<i>Bathyphanes pallidus</i>	1.67	0.88	0.67	0.67	6.32	5.23
<i>Lepthyphantes alpinus</i>	12.00	1.53 a	3.06	1.10 b	0.48	0.48 b
<i>Lepthyphantes complicatus</i>	1.67	1.20	2.85	1.49	4.15	1.51
<i>Lepthyphantes</i> sp. #10	1.00	1.00	0.79	0.79	0.48	0.48
<i>Lepthyphantes</i> sp. #5	0.00	0.00	0.79	0.79	0.00	0.00
<i>Microneta viaria</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Oreonetides vaginatus</i>	0.33	0.33	0.33	0.33	0.00	0.00
<i>Pityohyphantes subarcticus</i>	0.00	0.00	0.33	0.33	0.00	0.00
<i>Poecilonea A</i>	0.00	0.00	0.33	0.33	0.00	0.00
<i>Sisicus apertus</i>	0.00	0.00	0.39	0.39	0.00	0.00
Linyphiidae (Erigonidae)						
<i>Ceraticelus fissiceps</i>	0.67	0.67	0.00	0.00	0.38	0.38
<i>Ceraticelus laetabilis</i>	0.00	0.00	0.00	0.00	0.46	0.46
<i>Ceraticelus brunnea</i>	0.00	0.00	0.00	0.00	0.46	0.46
<i>Diplocentria bidentata</i>	24.33	4.33	11.37	2.15	13.32	4.47
<i>Diplocentria rectangularata</i>	1.67	0.67	1.46	0.74	1.22	0.66
<i>Grammonota angusta</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Hillara herniosa</i>	0.00	0.00	0.67	0.33	1.92	1.92

Table 5.17: continued

Spider species Linyphiidae (Erigonidae)	50		150		250	
	mean \pm	se	mean \pm	se	mean \pm	se
<i>Hybauchenidium cymbalentic</i>	0.33	0.33	0.33	0.33	0.84	0.43
<i>Hybauchenidium gibbosum</i>	0.33	0.33	0.00	0.00	0.76	0.76
<i>Pocadicnemis americana</i>	1.00	0.58	2.79	1.74	3.28	1.70
<i>Sciastes truncatus</i>	1.67	0.88	2.18	0.74	5.80	2.67
<i>Scotinytus pallidus</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Sisicottus montanus</i>	3.33	1.67	0.33	0.33	0.48	0.48
<i>Sisis rotundus</i>	0.67	0.33	0.00	0.00	0.00	0.00
<i>Tapinocyba A</i>	0.00	0.00	1.00	1.00	0.00	0.00
<i>Walckenaeria atrothibialis</i>	1.00	0.58	1.12	0.69	0.00	0.00
<i>Walckenaeria arctica</i>	1.67	0.88	0.00	0.00	0.46	0.46
<i>Walckenaeria castanea</i>	0.67	0.67	2.39	0.61	4.32	0.78
<i>Walckenaeria communis</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Walckenaeria directa</i>	0.67	0.33	0.33	0.33	0.00	0.00
<i>Walckenaeria karpinski</i>	0.00	0.00	0.00	0.00	0.38	0.38
<i>Walckenaeria lepida</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Walckenaeria tricornis</i>	0.67	0.33	0.00	0.00	0.00	0.00
<i>Walckenaeria sp. C</i>	1.33	0.88	0.00	0.00	1.85	1.85
<i>Walckenaeria</i>	0.67	0.33	0.00	0.00	0.00	0.00
<i>Zorrella cultirigera</i>	1.33	0.88	2.52	0.77	2.86	2.20

Table 5.17: continued

Spider species	Distance from gravel pit (m)					
	50		150		250	
	mean \pm	se	mean \pm	se	mean \pm	se
Theridiidae						
<i>Theridion aurantium</i>	0.00	0.00	0.00	0.00	0.76	0.76
<i>T. sexpunctatum</i>	0.33	0.33	0.67	0.33	0.38	0.38
Mimetidae						
<i>Ero canionis</i>	0.33	0.33	0.00	0.00	0.00	0.00
Lycosidae						
<i>Trochosa terricola</i>	24.67	5.24 a	10.31	2.63 b	5.08	1.16 b
<i>Pardosa mackenziana</i>	26.00	3.61 a	3.73	1.27 b	8.15	3.64 b
<i>P. uittana</i>	0.67	0.33	0.00	0.00	1.61	0.99
<i>P. xerampelina</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>P. moesta</i>	0.33	0.33	0.33	0.33	6.03	6.03
<i>Pardosa hyperborea</i>	0.33	0.33	1.00	0.58	3.71	3.71
<i>Pirata bryantae</i>	0.00	0.00	0.00	0.00	2.52	1.28
<i>Alopecosa aculeata</i>	1.00	0.00	0.73	0.37	4.29	2.41
Thomisidae						
<i>Xysticus obscurus</i>	4.00	3.06	2.73	1.64	3.65	1.72
<i>X. canadensis</i>	3.33	0.67 a	2.06	0.97 ab	0.00	0.00 b
<i>X. luctuosus</i>	0.00	0.00	0.67	0.67	0.46	0.46
<i>Ozipitila sincera canadensis</i>	0.67	0.33	3.67	1.86	0.93	0.93
<i>Coriarachne utahensis</i>	0.67	0.67	0.00	0.00	0.00	0.00

Table 5.17: continued

Spider species	Distance from gravel pit (m)					
	50		150		250	
Clubionidae	mean ±	se	mean ±	se	mean ±	se
<i>Agroeca ornata</i>	6.67	0.33	13.73	2.61	7.83	5.46
<i>Clubiona canadensis</i>	1.33	0.67	0.67	0.67	0.00	0.00
<i>C. kulczynskii</i>	0.33	0.33	0.39	0.39	0.86	0.44
<i>C. oprengo</i>	0.00	0.00	0.00	0.00	0.46	0.46
Gnaphosidae						
<i>Gnaphosa borea</i>	0.33	0.33	0.67	0.67	0.93	0.93
<i>Gnaphosa muscorum</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Gnaphosa brunnalis</i>	0.00	0.00	0.00	0.00	0.38	0.38
<i>Gnaphosa microps</i>	1.67	0.67	0.00	0.00	2.54	0.58
<i>Haplodrassus hiemalis</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Orodrausus canadensis</i>	0.33	0.33	0.33	0.33	0.00	0.00
<i>Sergiolus montanus</i>	0.33	0.33	0.00	0.00	0.00	0.00
<i>Zelotes fratris</i>	1.33	0.33	0.00	0.00	0.00	0.00
Amaurobiidae						
<i>Callioplus euoplus</i>	2.33	2.33	4.12	1.94	14.37	6.39
<i>Amaurobius borealis</i>	1.67	0.33	0.33	0.33	1.78	0.51
<i>Arctobius agelenoides</i>	0.00	0.00	0.33	0.33	0.00	0.00
<i>Callobius nemeus</i>	1.00	0.00	0.00	0.00	0.00	0.00
Agelenidae						
<i>Agelenopsis utahana</i>	0.33	0.33	0.33	0.33	0.00	0.00
<i>Cryphoea exlineae</i>	0.00	0.00	0.00	0.00	0.46	0.46

Table 5.18: Spider guild percentages at pine site east of gravel pit.*
Entries are averages \pm 1 standard error of 3 trapping stations (3 traps/station pooled) for 1995 capture.

	Distance from gravel pit (m)					
	50		150		250	
	mean	\pm se	mean	\pm se	mean	\pm se
Micro-webbers	48.02	3.01	50.64	5.90	46.68	3.66
Macro-webbers	3.49	1.40	5.41	2.68	14.23	6.58
Day-hunters	34.45	3.62 a	17.12	2.73 b	22.66	6.08 ab
Night-hunters	14.04	2.39	26.83	4.26	16.43	6.71

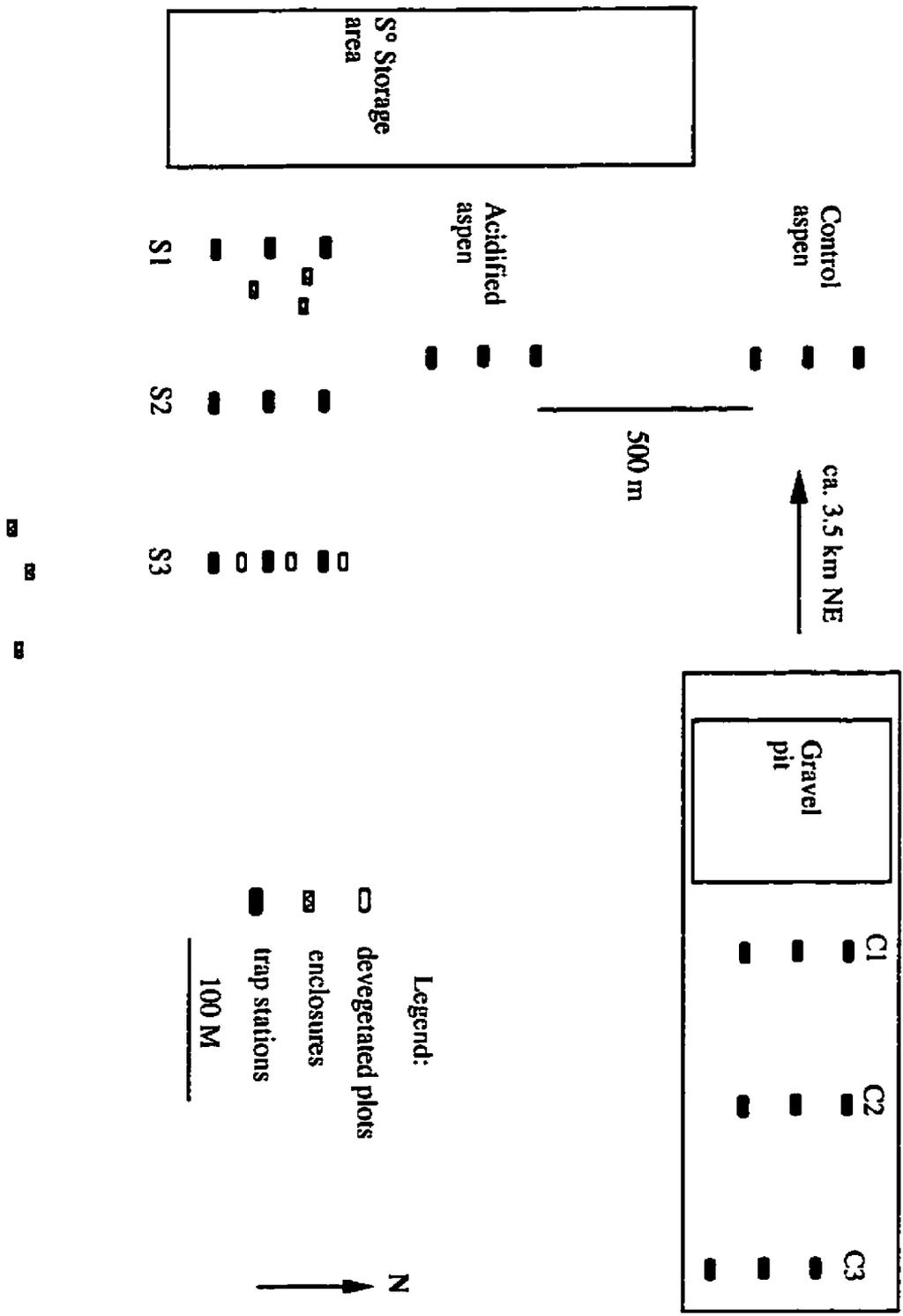
*Means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$).

Table 5.19: Invertebrate catches at pine site east of gravel pit.*
Entries are averages \pm 1 standard error of 3 trapping stations (3 traps/station pooled) for 1995 capture.

	Distance from gravel pit (m)					
	50		150		250	
	mean	\pm se	mean	\pm se	mean	\pm se
Ants	76.67	15.34	53.44	9.63	233.99	145.84
Staphylinids	263.33	68.00	246.01	68.52	256.96	44.41
Earthworms	19.67	4.98 a	67.38	17.24 b	17.07	7.66 a
Collembola	692.00	148.60	668.06	108.22	508.22	162.97
Snails	16.67	8.37	22.16	6.35	11.05	1.12

*means not sharing letters within rows are significantly different (FPLSD, $p < 0.05$)

Fig. 5.1: Layout of study sites east of the Strachan gas plant.



Control aspen

Acidified aspen

S° Storage area

S1

S2

S3

ca. 3.5 km NE

500 m

Gravel pit

C1

C2

C3

Legend:

devegetated plots

enclosures

trap stations

100 M

N

CHAPTER 6: GENERAL CONCLUSIONS

The objectives of this study were to assess sulphur pollution effects on epigeic invertebrates at regional and localized spatial scales and to elucidate some of the indirect habitat factors that confound direct toxic effects. Also, as part of the regional faunistic study of predaceous arthropods around the two sour gas plants, an effort was made to relate environmental variables (edaphic and floristic) to the distributions and community dynamics of the invertebrate groups studied. Unlike artificial acidifications of well replicated plots, which may suffer from lack of realism, field studies are difficult to replicate because of the inherently large natural variation which confounds cause-effects relationships between contaminants and organisms. Therefore, measuring as much of the natural environmental variability as possible should be considered an important component of large scale field studies of environmental pollution.

In this chapter, a number of concluding comments are made regarding the potential of the invertebrates studied as bioindicators of industrial pollution and the main aspects of habitat heterogeneity that structure macroarthropod communities. Also, a synthesis is given for the study of localized acidification effects and the results are used to construct a generalized qualitative model of pollution effects on organisms. Finally, a few areas for further research are identified.

Epigeic invertebrates as bioindicators

If invertebrate populations or their diversity declined under moderate sulphur deposition levels, this could be used as an early warning system to allow environmental managers to take mitigation steps to prevent further habitat deterioration. So far studies of moderate sulphur deposition effects on lodgepole pine forest health have not uncovered negative effects that would provide such an early warning system (Maynard et al. 1994).

Carabids and hunting spiders were not affected negatively by moderate sulphur deposition at the species or community level (Chapters 3 and 4). For example the carabid *Scaphinotus marginatus* and the spider *Callioplus euoplus* had slightly higher abundance in sites under moderate sulphur pollution, although, they were affected negatively by high levels of sulphur contamination at pine sites less than 150 m from a sulphur block (Chapter 5). These arthropod species, therefore, cannot provide an early warning system for sulphur pollution. Habitat or prey specialist species are expected to be the most sensitive to pollution stress and potential bioindicator candidates. *Scaphinotus marginatus* is one of the few carabids that can be considered an ecological specialist and its distribution in the pine study sites illustrates some of the problems with using individual species as indicators. Six of the sites that had no elemental sulphur in the LFH, had lower numbers of *S. marginatus* than the two most polluted pine sites. This pattern may be common for habitat specialists because of their limited colonization potential and specialized habitat and prey requirements. *C. euoplus* may be a specialist spider; this species was found vulnerable to localized high sulphur contamination but was absent from sites ND1 and ND2 which had no elemental sulphur in the LFH (Chapter 4). Therefore, even if specialist arthropods are vulnerable to pollution their use as bioindicators is limited by their patchy distribution at the level of the landscape.

Measures that incorporate several species populations or community structure are considered better bioindicator indices than single species abundance (Reddy 1986, Stork and Eggleton 1992). Overall abundance of the carabid and spider communities or numbers of species were not affected negatively by moderate sulphur pollution. Rare species may be the most vulnerable to stress and these species have been suggested as bioindicators (Butterfield et al. 1995). Numbers of rare carabids or their overall abundance also were similar in the two categories of sulphur contamination. Clearly, none of the commonly suggested biological measures of habitat quality applied to carabid beetles, detected

differences between the two sulphur pollution regimes considered in this study. These results can be contrasted with those of Freitag et al. (1973) where a clear increase in abundance of carabids with decreasing fallout of sulphates from a kraft mill was registered.

Linyphiid spiders had a trend of reduced abundance and significantly lower densities in sulphur dusted sites compared to non-dusted sites (Table 6.1). The majority of linyphiid spiders extracted from soil cores in the regional pollution study of 1994 (Table 6.1) were erigonines; this subfamily, however, was not affected negatively by severe acidification according to pitfall traps placed inside enclosures (Chapter 5). This suggests that erigonines are not affected directly by sulphur pollution or low pH but rather by microhabitat factors such as microclimate. The reduced abundance and density observed from unfenced pitfall traps and soil cores, respectively, may result from the lower moisture in the litter layer found in areas without coarse woody debris.

Other invertebrates were not affected by moderate sulphur deposition (see Table 6.1). Earthworms, being "ecosystem engineers" (Jones et al. 1994) are considered one of the best bioindicator taxa and they also were unaffected by moderate sulphur deposition. These results may be interpreted in two ways. First, that these invertebrates are poor indicators of habitat quality and that there should be searches for more sensitive taxa. Secondly, and most likely, the forests are not stressed by moderate levels of sulphur contamination, as already suggested by other studies of forest health (Maynard et al. 1994) and as confirmed in the present study on invertebrates.

Environmental heterogeneity

In the studies of carabid and spider regional distribution around two sour gas plants, it was clear that features of the microhabitat such as density of coarse woody

debris (logs), floristic components of the ground layer and edaphic parameters such as organic matter content of the forest floor, had an influence in structuring communities of epigeic macroarthropods. For both arthropod taxa, coarse woody debris was one of the most influential factors determining their distribution. Presence of logs inside enclosures in the localized acidification study (Chapter 5) was also thought to modify microclimate and provide resources to allow several invertebrates to maintain populations in acidified areas. It can be concluded that dead trees on the ground, particularly those at advanced decomposition stages, are crucial habitat components that contribute to maintaining high biodiversity in forests.

Localized sulphur pollution

Pollution is a well recognized threat to ecosystems and the biodiversity of organisms that contribute to their function. However, attributing cause-effect relationships between pollutants and organisms *in situ* is a task complicated by several indirect effects and biotic-abiotic interactions. In the study of localized sulphur contamination and subsequent site acidification in forests, a number of field surveys were undertaken in an attempt to tease apart some of the indirect factors that affect distribution of epigeic invertebrates along acidification gradients. The following are some of the take-home messages that can be offered.

Of the epigeic invertebrates studied, those that are intimately associated with the organic soil are the most vulnerable to toxic effects of low pH; earthworms and some collembola would be included in this group. Also vulnerable to indirect effects are those invertebrates that are in some form ecological specialists because of their microhabitat requirement (usually moisture) or restricted diet. Examples of these are mesic and snail-

feeding carabids, linyphiid spiders that need web attachment structures, and fungivorous staphylinids that exploit mushrooms.

A number of invertebrates were considered pollution resistant or even favoured by pollution. Resistant species in the family Carabidae were ecological generalist species known to occur in a variety of habitats and with a polyphagous diet. It is expected that resistant spider species will also fit this ecological profile. Species apparently favoured by pollution were thought to respond to indirect factors such as forest disturbance resulting from edge effects or structural changes to the microhabitat that facilitated their foraging strategy; examples of these groups included the wolf spiders, *Pardosa mackenziana* and *Trochosa terricola*, and the carabids *Amara hyperborea* and *Synuchus impunctatus*.

Negative pollution effects on populations were reflected in the community structure of carabid and spider assemblages. Both groups had reduced species richness in the most polluted sites and, furthermore, the assemblages were dominated by a few dominant species causing a significant reduction in species diversity.

In summary, the indirect effects of sulphur contamination on epigeic fauna could be partitioned into various spatial scales: at the level of the landscape, forest fragmentation led to edge effects; at the level of habitat type such as aspen vs pine, forest floor structure and litter type interacted with pollution; and at the microhabitat level there were effects driven by heterogeneity on the forest floor. These indirect and direct toxic effects had an overall negative consequence on the epigeic fauna; this change in faunal structure can only contribute to the severe deterioration in function of this acidified ecosystem.

Based on the responses of epigeic invertebrates to elemental sulphur contamination and severe acidification found in this study, the results may be generalized and can be summarized schematically as done in Fig. 6.1. Five categories of invertebrates can be recognized based on their vulnerability to high stress and the type of factors that cause the response. Species at the lower third can be considered vulnerable to stress whereas those

on the top are favoured directly or indirectly. The vertical middle vector can be further subdivided to allow for varying degrees of vulnerability and resistance so that those in the middle region are unaffected by stress (resistant species). Species on the left of the diagram respond to indirect habitat factors whereas those on the right are affected directly by pollution. Also, species positioned higher on the trophic web (predators) occur towards the left of the diagram.

At the lower right corner are the most vulnerable species that are likely influenced by direct effects of pollution; these would be species in direct contact with the soil and dependent on the organic soil medium such as earthworms and some collembolans. On the lower left corner are those taxa that are still vulnerable to pollution but respond to some alteration of the habitat; an example from this study is the carabid *Scaphinotus marginatus*. Species on the top left are resistant or even favoured by indirect habitat alterations at various scales; for example wolf spiders (e.g. *Pardosa mackenziana*) that prefer forest edges or may forage more effectively over litter surfaces. In this study none of the taxa included could be placed on the upper right corner of the diagram which denotes a direct positive effect on fauna. However, other studies have identified acidophilic Collembola which could fit this category.

Two other gradients can be superimposed on this diagram that were shown to apply in the present study. At least for carabid beetles, the r vs k description of life history strategies appears to be a good predictor of vulnerability to pollution. Ecological specialists on the k end of the spectrum can be considered the most severely affected by high levels of stress. Another vector included at the right hand side of the diagram denotes changes of species diversity. Under conditions of high stress, diversity (especially the evenness component) decreases towards the top of the diagram as populations of vulnerable k species are reduced and most of the community is represented by r species. This qualitative model can be helpful in predicting species responses to pollution, provided

that some autoecological information is available. Other forms of chronic pollution, for example heavy metals, will likely lead to a similar classification of invertebrate responses.

Future studies

As with most investigations, the number of questions answered in the present study does not match the number of questions raised. Following are a number of questions that could be pursued to further clarify effects of acidification (or pollution in general) on invertebrates.

In this study liming of sites adjacent to the sour gas masked potential impacts of sulphur dusting, particularly at sites farther than 100 m. Because lime can lead to increases in molluscs and lumbricids, it would be of interest to study potential effects on ground beetles that are feeding on these groups. A study is currently in progress using long term experimental plots to address how separate application of lime and elemental sulphur can influence distributions of ground beetles.

Most environmental studies of ground beetles concentrate on the imago stage and ignore the immatures. However, the latter stage may be the most vulnerable to pollution effects because of its reduced mobility and its more endogeic habits that bring them in contact with the soil. Before carabid larvae can be incorporated into environmental studies, however, there is considerable work to be done on their taxonomy. Currently there are no taxonomic keys for western North American larvae. Also, a lot of work on sampling methods is needed. In this study sampling with soil cores produced even fewer numbers than with pitfall traps. Ecological work is required to understand the microhabitat distribution to allow effective sampling. Once these barriers are overcome, incorporating carabid larvae along with the adult stages will provide a powerful tool to further assess the impact of anthropogenic activities on the environment.

A number of population studies can be suggested to understand better the mechanisms of sulphur pollution effects on invertebrates. Fluctuating asymmetry has been suggested as a bioindicator or early warning system that populations are at risk. A carabid species such as *Calathus ingratus* or *Platymus decentis* could be used for such a study. These species were affected negatively at the population level but still had enough numbers present in acidified sites to allow testing for effects on asymmetry. Another area of interest would be to investigate the feeding ecology of pollution resistant and vulnerable ground beetles that are thought to be polyphagous. It can be hypothesized that feeding habits of these species may explain differences in their pollution vulnerability.

Effects of sulphur pollution and acidification on earthworms deserves further investigation. While direct toxic effects are expected on earthworms, especially non-coniferous species, at moderately low pH such as those found in the highly polluted/limed aspen forest in this study, their mortality can be caused by resource quality. The reduced population size of earthworms in the polluted aspen was suggestive of litter quality effects. An experiment could be designed with aspen litter taken from the polluted site and food levels could be manipulated to test whether their survivorship increases with greater food availability.

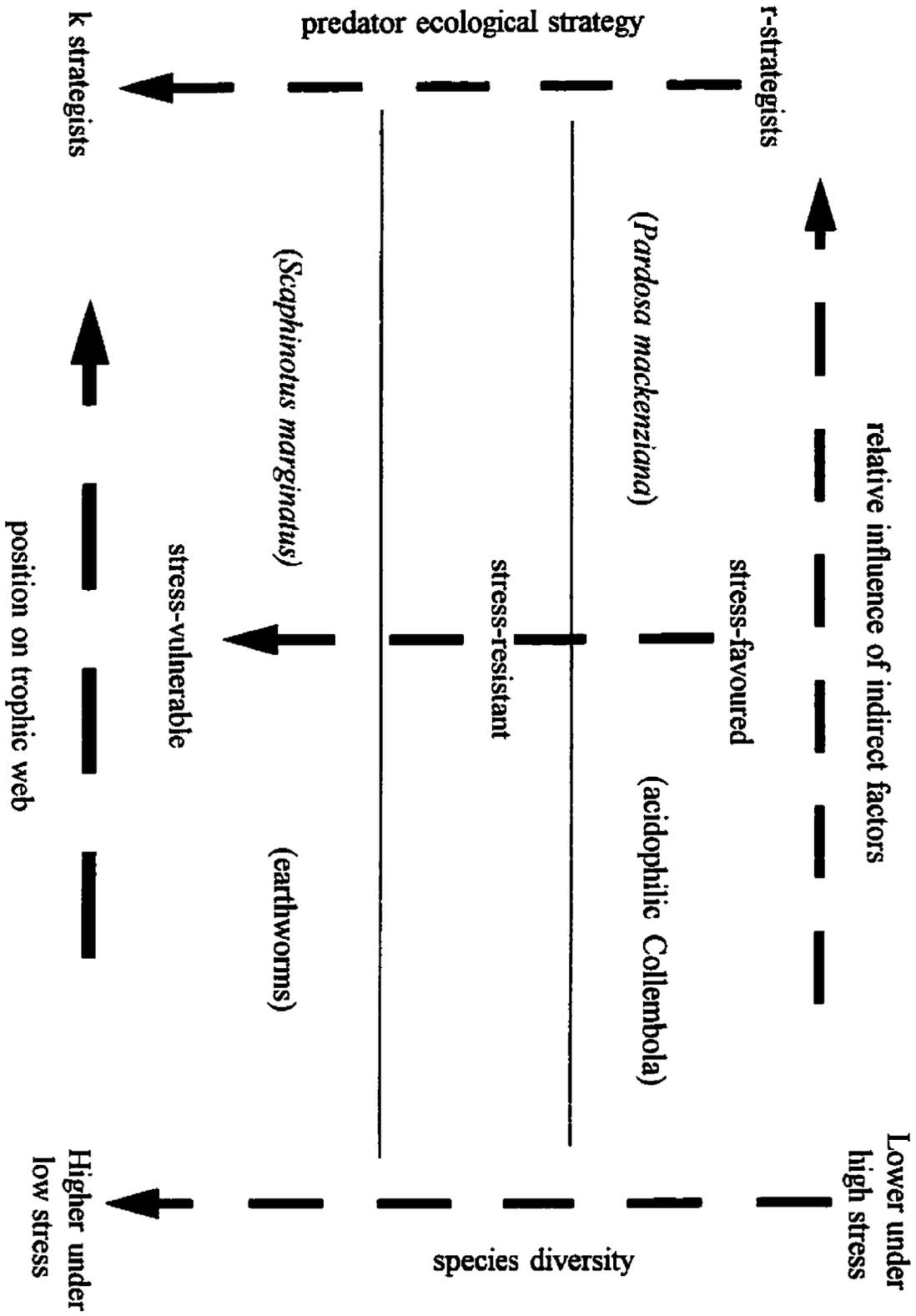
Table 6.1: Abundance and densities of selected invertebrates in sulphur dusted and non-dusted sites. Entries are means of six sites with one standard error (se).*

	Pitfall catches/site				Density/0.125 m ²			
	Dusted		Undusted		Dusted		Undusted	
	mean	se	mean	se	mean	se	mean	se
Carabidae	421.92	85.03	287.70	51.34	NA**		NA	
<i>Platymus decentis</i>	49.99	14.50	34.96	16.44	NA		NA	
<i>Scaphinotus marginatus</i>	76.66	29.42	19.28	9.24	NA		NA	
Araneae	111.01	21.03	188.91	46.50	NA		NA	
<i>Callioplus euoplus</i>	17.63	3.87	9.06	5.21	NA		NA	
Linyphiid s. lat.	39.53	6.20	67.75	12.94	0.33	0.33	3.30	1.10
Lumbricidae	89.35	26.88	68.18	26.99	11.30	3.30	10.30	6.50
Staphylinidae	715.19	171.48	676.76	104.85	4.60	2.40	7.50	1.20
Collembola	NA		NA		1432.33	650.86	1258.25	242.13

* Sampling methods and sites for these data are given in Chapter 3.

**NA = not counted or the number of individuals was too low for analysis.

Fig. 6.1: Conceptual responses of forest floor invertebrates to chronic stress



REFERENCES

- Abrahamsen, G., J. Hovland and S. Hågvar. 1978. Effects of artificial acid rain and liming on soil organisms and the decomposition of organic matter. In T. C. Hutchinson and M. Havas, eds. *Effects of acid precipitation on terrestrial ecosystems*. Plenum Press, New York. pp 341-362.
- Addison, J. and D. Parkinson. 1978. Influence of collembolan feeding activities on soil metabolism at a high arctic site. *Oikos* 30: 529-538.
- Addison, P.A., K.A. Kennedy and D.G. Maynard. 1984. Effects of sour gas processing on a forest ecosystem in west-central Alberta. *Can. For. Ser. Inf. Rep. NOR-X-265*.
- Bååth, E., B. Berg, U. Lohm, B. Lundgren, H. Lundkvist, T. Rosswall, B. Söderström, and A. Wiren. 1980. Effects of experimental acidification on soil organisms and decomposition in a Scots pine forest. *Pedobiologia* 20: 85-100.
- Baguette, M. 1993. Habitat selection of carabid beetles in deciduous woodlands of southern Belgium. *Pediobiologia* 37: 365-378.
- Bengtsson, G. and S. Rundgren. 1984. Ground-living invertebrates in metal-polluted forest soils. *Ambio* 13: 29-33.
- Bengtsson, G. and S. Rundgren. 1988. The Gusum case: a brass mill and the distribution of soil Collembola. *Can. J. Zool.* 66: 1518-1526.
- Boag, D.A. 1990. On the effectiveness of artificial shelters in the study of population attributes of small terrestrial gastropods. *Can. J. Zool.* 68: 254-262.
- Bromenshenk, J. 1978. Responses of ground-dwelling insects to sulfur dioxide. In E.M. Preston and T. L. Gullet, eds. *The bioenvironmental impact of a coal-fired power plant. Fourth Interim Report.*, U.S. Environmental Protection Agency. Colstrip, Montana. pp 673-722.

- Butterfield, J., M.L. Luff, M. Baines and M.D. Eyre. 1995. Carabid beetle communities as indicators of conservation potential in upland forests. *For. Ecol. and Manage.* 79: 63-77.
- Cárcamo, H., D. Parkinson and J. Volney. 1997. Effects of sulphur contamination on macroinvertebrates in Canadian pine forests. *Journal of Applied Soil Ecology*, *Accepted*.
- Cárcamo, H.A. 1995. Effect of tillage on ground beetles (Carabidae): a farm scale study in central Alberta. *Can. Ent.* 127: 631-639.
- Cárcamo, H.A., J.R. Spence and J.K. Niemelä. 1995. Farming and ground beetles: effects of agronomic practice on populations and community structure. *Can. Ent.* 127: 123-140.
- Carter, A. 1980. *Agomum retractum* (Coleoptera: Carabidae) in an Aspen woodland in the Canadian Rockies: population biology and chemical cycling. *Pedobiologia* 20: 101-117.
- Clarke, R. D. and P. R. Grant. 1968. An experimental study of the role of spiders as predators in a forest litter community. Part I. *Ecology* 68: 1152-1154.
- Clausen, I. H. 1984. Notes on the impact of air pollution (SO₂ & Pb) on spider (Araneae) populations in North Zealand, Denmark. *Ent. Meddr.* 52: 33-39.
- Clausen, I. H. S. 1986. The use of spiders (Araneae) as ecological indicators. *Bull. Br. Arachnol. Soc.* 7: 83-86.
- Craft, C.B. and J.W. Webb. 1984. Effects of acidic and neutral solutions on forest arthropods. *J. Environ. Qual.* 13: 436-440.
- Danielson, R.M. and S. Visser. 1989. Effects of forest soil acidification on ectomycorrhizal and vesicular-arbuscular mycorrhizal development. *New Phytologist* 112: 41-47.

- Deeleman-Reinhold, C. L. 1990. Changes in the spider fauna over 14 years in an industrially polluted area in Holland. *Acta Zool. Fennica* 190: 103-110.
- Digweed, S. 1993. Selection of terrestrial gastropod prey by Cychrine and Pterostichine ground beetles (Coleoptera: Carabidae). *Can. Ent.* 125: 463-472.
- Digweed, S., C. Currie, H. Cárcamo and J. Spence. 1995. Digging out the "digging-in" effects of pitfall traps: Influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* 39: 561-576.
- Dondale, C. D. and J. H. Redner. 1978. The insects and arachnids of Canada. Part 5. The crab spiders of Canada and Alaska (Araneae: Philodromidae and Thomisidae). Agriculture Canada, Ottawa. 255 pp
- Dondale, C. D. and J. H. Redner. 1990. The insects and arachnids of Canada. Part 17. The wolf spiders, nurseryweb spiders and lynx spiders of Canada and Alaska (Araneae: Lycosidae, Pisauridae, and Oxyopidae). Agriculture Canada, Ottawa. 383 pp
- Dondale, C. D. and J. H. Redner. 1992. The insects and arachnids of Canada. Part 9. The sac spiders of Canada and Alaska (Araneae: Clubionidae and Anyphaenidae). Agriculture Canada, Ottawa. 194 pp
- Ehmann, W. J. 1994. Organization of spider assemblages on shrubs: an assessment of the role of dispersal mode in colonization. *Am. Midl. Nat.* 131: 301-310.
- Esher, R.J., D.H. Marx, S.J. Ursic, R. L. Baker, L.R. Brown and D.C. Coleman. 1992. Effects of simulated acid rain on fine roots, ectomycorrhizae, microorganisms, and invertebrates in in pine forests of the southern United States. *Water, Air, and Soil Pollution* 61: 269-278.
- Freitag, R. 1979. Carabid beetles and pollution. In Erwin, T.L., G.E. Ball, and D.R. Whitehead. 1979. Carabid beetles, their evolution, natural history and classification. Proceedings of the first international symposium of carabidology. W.Junk, The Hague, Boston & London.

- Freitag, R., L. Hastings, W.R. Mercer and A. Smith. 1973. Ground beetle populations near a kraft mill. *Can. Ent.* 105: 299-310.
- Gertsch, W. J. 1979. *American spiders*, 2nd edition. Van Nostrand Reinhold Co., N.Y.
- Goulet, H. 1974. Biology and relationships of *Pterostichus adstrictus* Eschscholtz and *Pterostichus pensylvanicus* Lencoste (Coleoptera: Carabidae). *Quaestiones Entomologicae* 10: 3-33.
- Greenslade, P. and P. Greenslade. 1985. Ecology of soil invertebrates. *Soils: an Australian viewpoint*. CSIRO. Academic Press, London, Melbourne. pp 645-669.
- Greenslade, P.G.M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). *J. Anim. Ecol.* 33: 301-310.
- Greenstone, M. H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. *Oecologia* 62: 299-304.
- Greenstone, M.H., C.E. Morgan and A.L. Hultsch. 1987. Ballooning spiders in Missouri, USA, and New South Wales, Australia: family and mass distributions. *J. Arachnol.* 15: 163-170.
- Gunnarsson, B. 1988. Spruce-living spiders and forest decline; the importance of needle-loss. *Biol. Conserv.* 43: 309-319.
- Hågvar, S. 1984. Effects of liming and artificial acid rain on Collembola and Protura. *Pedobiologia* 27: 341-354.
- Heliövaara, K. and R. Väisänen. 1993. *Insects and Pollution*. CRC Press, Boca Raton.
- Hengeveld, R. 1980a. Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera, Carabidae). *Neth. J. Zool.* 30: 564-584.
- Hengeveld, R. 1980b. Qualitative and quantitative aspects of the food of ground beetles. *Neth. J. Zool.* 30: 555-563.
- Hengeveld, R. 1981. The evolutionary relevance of feeding habits of ground beetles (Coleoptera: Carabidae). *Ent. Scand. Suppl.* 15: 305-315.

- Hermida, J., P. Ondina, and A. Outeiro. 1995. Influence of soil characteristics on the distribution of terrestrial gastropods in northwest Spain. *Eur. J. Soil Biol.* 31: 29-38.
- Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. *Ecology* 54: 427-432.
- Holliday, N.J. 1984. Carabid beetles (Coleoptera: Carabidae) from a burned spruce forest (*Picea* spp.). *Can. Ent.* 116: 919-922.
- Holmes, P.R., D.C. Boyce and D.K. Reed. 1993. The ground beetle (Coleoptera: Carabidae) fauna of welsh peatland biotopes: factors influencing the distribution of ground beetles and conservation implications. *Biol. Conserv.* 63: 153-161.
- Holopainen, J.K., T. Bergman, E.-L. Hautala and J. Oksanen. 1995. The ground beetle fauna (Coleoptera: Carabidae) in relation to soil properties and foliar fluoride content in spring cereals. *Pedobiologia* 39: 193-206.
- Howard, P.J.A. and C.H. Robinson. 1995. The use of correspondence analysis in studies of succession of soil organisms. *Pedobiologia* 39: 518-527.
- Huhta, V. 1979. Effects of liming and deciduous litter on earthworms (Lumbricidae) populations of a spruce forest, with an inoculation experiment on *Allolobophora caliginosa*. *Pedobiologia* 19: 340-345.
- Huhta, V., R. Hyvönen, A. Koskenniemi, P. Vilkkamaa. 1984. Role of pH in the effect of fertilization on Nematoda, Oligochaeta and microarthropods. In: H. M André, Ph. Lebrun, A. De Medts, C. Gregoire-Wibo, G. Wauthy, eds. *New trends in soil biology*. Dieu-Brichart, Lovain-la-Neuve.
- Hunter, B.A., M.S. Johnson and D.J. Thompson. 1987. Ecotoxicology of copper and cadmium in a contaminated grassland ecosystem. II Invertebrates. *J. Appl. Ecology* 24: 587-599.

- Hyvönen, R., S. Andersson, M. Clarholm, and T. Persson. 1994. Effects of lumbricids and enchytraeids on nematodes in limed and unlimed coniferous mor humus. *Biol. Fertil. Soils* 17: 201-205.
- Irmeler, U., K. Heller, and J. Warning. 1996. Age and tree species as factors influencing the populations of insects living in dead wood (Coleoptera, Diptera: Sciaridae, Mycetophilidae). *Pedobiologia* 40: 134-148.
- Janssen, P.M. and R.F. Hogervorst. 1993. Metal accumulation in soil arthropods in relation to micro-nutrients. *Environmental Pollution* 79: 181-189.
- Jones, C.G., J.H. Lawton and M. Shachuk. 1994. Organisms as ecosystem engineers. *Oikos* 69: 393-386.
- Judas, M. 1989. Predator-pressure on earthworms: field experiments in a beechwood. *Pedobiologia* 33: 339-354.
- Kajak, A. 1995. The role of soil predators in decomposition processes. *Eur. J. Entomol.* 92: 573-580.
- Kajak, A. and H. Jakubczyk. 1977. Experimental studies on predation in the soil litter interface. *Ecol. Bull. (Stockholm)* 25: 493-496.
- Kennedy, K.A., P.A. Addison and D.G. Maynard. 1985. Effect of particulate elemental sulphur on moss. *Environmental Pollution* 39: 71-77.
- Knabe, W. 1976. Effects of sulfur dioxide on terrestrial vegetation. *Ambio* 5: 213-218.
- Koponen, S. and P. Niemela. 1993. Ground-living spiders in a polluted pine forest, SW Finland. *Boll. Acc. Gioenia Sci. Nat.* 26: 221-226.
- Krzysztofiak, L. 1991. The effect of habitat pollution with heavy metals on ant populations and ant-hill soil. *Ekologia Polska* 39: 181-202.
- Lee, K.E. 1985. *Earthworms: their ecology and relationship with soils and land use.* Academic Press, New York.

- Leech, R. 1972. A revision of the Nearctic Amaurobiidae (Arachnida: Araneida). Mem. Ent. Soc. Can. 84: 1-182.
- Leetham, J.W., T.J. McNary, and J.L. Dodd. 1978. Effects of controlled levels of SO₂ on invertebrate consumers. In E.M. Preston and T.L. Gullet, eds. The bioenvironmental impact of a coal-fired power plant. Fourth Interim Report., U.S. Environmental Protection Agency. Colstrip, Montana. pp 723-763.
- Lesniak, A. 1980. Changes in the structure of overground communities of Carabidae, Coleoptera as bioindicators of pollution of forest environments. In J. Spaheny, ed. Proceedings of the third International Conference Bioindicatores Deteriorationis Regionis, Praha. pp 219-21.
- Lindroth, C.L. 1961-69. The ground beetles (Carabidae, exc. Cicindelinae) of Canada and Alaska. Parts 1-6. Opuscula Entomologica. +1192 pp.
- Lowrie, D. C. 1973. The microhabitats of western wolf spiders of the genus *Pardosa*. Ent. News 84: 103-116.
- Ludwig, J.A. and J.F. Reynolds. 1988. Statistical Ecology. John Wiley & Sons, New York.
- Magurran, A. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton.
- Maynard, D. G. 1990. Biomonitoring forests near two sour gas processing plants. Can. For. Serv. Inf. Rep. NOR-X-311.
- Maynard, D. G., J. J. Stadt, K. L. Mallet and W. J. Volney. 1994. Sulphur impacts on forest health in west-central Alberta. Can. For. Serv. Inf. Rep., NOR-X-334.
- Maynard, D. G., J. J. Stadt, K. L. Mallet and W. J. Volney. 1995. Appendix to sulfur impacts on forest health in west-central Alberta. Can. For. Serv. Inf. Rep. NOR-X-334-1.

- McGill, W.B. and Spence, J.R. 1985. Soil fauna and soil structure: feedback between size and architecture. *Quaestiones Entomologicae* 21: 645-654.
- McIver, J., G. Parsons and A. Moldenke. 1992. Litter spider succession after clear-cutting in a western coniferous forest. *Can. J. For. Res.* 22: 984-992.
- McNeely, J.F. 1992. The sinking ark: pollution and the worldwide loss of biodiversity. *Biodiversity and Conservation* 1: 2-18.
- Newton, A.F., Jr. 1990. Insecta: Coleoptera, Staphylinidae adults and larvae. In D. Dindal, ed. *Soil biology guide*. John Wiley and Sons, New York. pp 1137-1174.
- Niemelä, J. K., E. Halme, T. Pajunen and Y. Haila. 1986. Sampling spiders and carabid beetles with pitfall traps: the effects of increased sampling effort. *Ann. Entomol. Fennici* 52: 109-111.
- Niemelä, J.K., J.R. Spence and D.H. Spence. 1992. Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in central Alberta. *Can. Ent.* 124: 521-540.
- Niemelä, J., D. Langor, J.R. Spence. 1993. Effects of clear-cut harvesting on boreal ground beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conservation Biology* 7: 551-561.
- Niemelä, J.K. and J.R. Spence. 1994. Distribution of forest dwelling carabids (coleoptera): spatial scale and the concept of communities. *Ecography* 17: 166-175.
- Niemelä, J., Y. Haila and P. Puntilla. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. *Ecography* 19: 352-368.
- Nriagu, J.O. 1978. *Sulfur in the environment. Part II: Ecological impacts*. John Wiley & Sons, New York

- Nyborg, M., J. Crepin, D. Hocking and J. Baker. 1977. Effects of sulphur dioxide on precipitation and on the sulphur content and acidity of soils in Alberta, Canada. *Water Air Soil Pollut.* 7: 439-448.
- Paje, F., and D. Mossakowski. 1984. pH-preferences and habitat selection in carabid beetles. *Oecologia* 64: 41-46.
- Pajunen, T., Y. Haila, E. Halme, J. Niemelä and P. Puntilla. 1995. Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. *Ecography* 18: 62-72.
- Palmer, M. W. 1993. Putting things in even better order: the advantages of canonical correspondence analysis. *Ecology* 74: 2215-2230.
- Parkinson, D. 1988. Linkages between resource availability, micro-organisms and soil invertebrates. *Agriculture, Ecosystems and Environments* 24: 21-32.
- 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.
- Pearce, T. G. 1972. Acid tolerant and ubiquitous Lumbricidae in selected habitats in north Wales. *J. Anim. Ecol.* 41: 317-410.
- Pearce, T.G. 1978. Gut contents of some lumbricid earthworms. *Pedobiologia* 18: 153-157.
- Platen, R. 1993. A method to develop an 'indicator value' system for spiders using canonical correspondence analysis (CCA). *Mem. Queen. Mus.* 33: 621-627.
- Platnick, N. I. and C. D. Dondale. 1992. The insects and arachnids of Canada. Part 19. The ground spiders of Canada and Alaska (Araneae: Gnaphosidae). *Agriculture Canada, Ottawa.* 297 pp

- Post, W. M. and S. E. Reichert. 1977. Initial investigation into the structure of spider communities. 1. Competitive effects. *J. Anim. Ecol.* 46: 729-749.
- Prescott, C.E. and D. Parkinson. 1985. Effects of sulphur pollution on rates of litter decomposition in a pine forest. *Can. J. Bot.* 63: 1436-1443.
- Read, H.J., C.P. Wheater and M.H. Martin. 1987. Aspects of the ecology of Carabidae (Coleoptera) from woodlands polluted by heavy metals. *Environmental Pollution* 48: 61-76.
- Reddy, M.V. 1986. Soil-inhabiting arthropods as indicators of environmental quality. *Acta Biologica Hungarica* 37: 79-84.
- Riechert, S. and L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology* 71: 1441-1450.
- Robinson, J. V. 1981. The effect of architectural variation in habitat on a spider community: an experimental field study. *Ecology*, 62: 73-80.
- Rundgren, S. 1994. Earthworms and soil remediation: liming of acidic coniferous soils in southern Sweden. *Pedobiologia* 38: 519-529.
- Satchell, J.E. 1955. Some aspects of earthworm ecology. In: D. K. Kevan, ed. *Soil Zoology*. Butterworths Scientific Publications, London.
- Seastedt, T.R. 1984. The role of microarthropods in decomposition and mineralization processes. *Ann. Rev. Entomol.* 29: 25-46.
- Smith, W.H. 1990. Air pollution and forests: Interactions between air contaminants and forest ecosystems. Second edition. Springer-Verlag, New York.
- Spence, J.R. and 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.
- Spence, J.R. and J.K. Niemelä. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. *Can. Entomol.* 126: 881-894.

- Spence, J.R., D.W. Langor, J. Niemelä, H.A. Cárcamo and C.R. Currie. 1996. Northern Forestry and carabids: the case for concern about old-growth species. *Ann. Zool. Fenn.* 33:173-184.
- Stork, N.G. 1990. The role of carabid beetles in ecological and environmental studies. Andover, Intercept.
- Stork, N.E. and P. Eggleton. 1992. Invertebrates as determinants and indicators of soil quality. *Am. J. Alternat. Agric.* 7: 38-47.
- Strong, W.L. and K.R. Leggat. 1992. Ecoregions of Alberta. Alberta For. Lands Wildl., Edmonton, Alberta. Publ. T/245.
- Ter Braak, C. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67: 1167-1179.
- Ter Braak, C. and I. Prentice. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18: 272-317.
- Thiele, H.U. 1977. Carabid beetles in their environments. Springer-Verlag, Berlin, New York.
- Topping, C.J. and K.D. Sunderland. 1992. Limitations to the use of pitfall traps in ecological studies exemplified by a study of spiders in a field of winter wheat. *J. Appl. Ecol.* 29: 485-491.
- Tousignant, S., J. Marteland and Y. Mauffette. 1990. Invertébrés de la litière dans des érablières saines et déperies du sud-est du Québec. *Can. J. Zool.* 68: 2445-2449.
- Uetz, G. W. 1979. The influence of variation in litter habitats on spider communities. *Oecologia* 40: 29-42.
- Van Straalen, N., M. Kraak and C. Denneman. 1988. Soil microarthropods as indicators of soil acidification and forest decline in the Veluwe area, the Netherlands. *Pedobiologia* 32: 47-55.

- Visser, S. and D. Parkinson. 1989. Microbial respiration and biomass of a lodgepole pine stand acidified with elemental sulphur. *Can. J. For. Res.* 19: 955-961.
- Visser, S. 1991. The impact of elemental sulfur dust and lime on the vegetation, soil chemistry and soil biology of a lodgepole pine stand. Progress report. Kananaskis Centre for Environmental Research. University of Calgary.
- Wilson, E.O. 1987. The little things that run the world. *Conservation Biology* 1: 344-346.
- Wise, D. H. 1993. *Spiders in ecological webs*. Cambridge University Press, Cambridge.

Appendix 1: List of carabids found in the study area

Genus	species	Authority
<i>Scaphinotus</i>	<i>marginatus</i>	Fischer
<i>Carabus</i>	<i>chamissonis</i>	Fischer
	<i>taedatus</i>	Fischer
<i>Calosoma</i>	<i>frigidum</i>	Kirby
<i>Leistus</i>	<i>ferruginosus</i>	Mannerheim
<i>Nebria</i>	<i>gyllenhali</i>	Schönherr
<i>Notiophilus</i>	<i>aquaticus</i>	Linné
<i>Loricera</i>	<i>pilicornis</i>	Fabricius
<i>Miscodera</i>	<i>arctica</i>	Paykull
<i>Patrobus</i>	<i>foveocollis</i>	Eschscholtz
<i>Trechus</i>	<i>chalybeus</i> *	Dejean
	<i>apicalis</i>	Motschulsky
<i>Bembidion</i>	<i>grapei</i>	Leconte
	<i>rupicola</i>	Kirby
<i>Pterostichus</i>	<i>adstrictus</i>	Eschscholtz
	<i>riparius</i>	Dejean
	<i>pennsylvanicus</i>	Leconte
	<i>punctatissimus</i>	Randall
<i>Stereocerus</i>	<i>haematopus</i>	Dejean
<i>Calathus</i>	<i>advena</i>	Leconte
	<i>ingratus</i>	Dejean
<i>Synuchus</i>	<i>impunctatus</i>	Say
<i>Agonum</i>	<i>retractum</i>	Leconte
	<i>placidum</i>	Say
	<i>cupreum</i>	Dejean
	<i>cupripenne</i>	Say
<i>Platynus</i>	<i>decentis</i>	Say
	<i>mannerheimi</i>	Dejean
<i>Amara</i>	<i>hyberborea</i>	Dejean
	<i>quenseli</i>	Schönherr
	<i>erratica</i>	Duftschnid
	<i>apricaria</i>	Paykull
<i>Harpalus</i>	<i>fulvilabris</i>	Mannerheim

19 genera 33 species

* This name refers to a species complex that may include *T. tenuiscapus* and/or *T. oregonensis*

Appendix 2: List of all spider species found in the study area

Family	Genus	Species	Authority		
Lycosidae	<i>Pardosa</i>	<i>mackenziana</i>	Keyserling		
		<i>uintana</i>	Gertsch		
		<i>moesta</i>	Banks		
		<i>xerampelina</i>	Keyserling		
		<i>hyperborea</i>	Thorell		
		<i>fuscula</i>	Thorell		
		<i>tesquorum</i>	Odenwall		
		<i>Trochosa terricola</i>	Thorell		
		<i>Alopecosa aculeata</i>	Clerck		
		<i>Arctosa alpigena</i>	Doleschall		
		<i>rubicunda</i>	Keyserling		
		<i>Pirata bryantae</i>	Kurata		
		Amaurobiidae	<i>Calliophus</i>	<i>euoplus</i>	Bishop & Crosby
				<i>Amaurobius borealis</i>	Emerton
<i>Arctobius agelenoides</i>	Emerton				
<i>Callobius nomeus</i>	Chamberlin				
Thomisidae	<i>Xysticus</i>	<i>obscurus</i>	Collett		
		<i>canadensis</i>	Gertsch		
		<i>luctuosus</i>	Blackwall		
		<i>emertoni</i>	Keyserling		
		<i>punctatus</i>	Keyserling		
		<i>elegans</i>	Keyserling		
		<i>Ozyptila sincera canadensis</i>	Dondale & Redner		
Clubionidae	<i>Coriarachne</i>	<i>utahensis</i>	Gertsch		
		<i>Agroeca ornata</i>	Banks		
		<i>Clubiona canadensis</i>	Emerton		
		<i>kulczynskii</i>	Lessert		
		<i>moesta</i>	Banks		
		<i>opeongo</i>	Edwards		
Agelenidae	<i>and/or</i>	<i>mutata</i>	Gertsch		
		<i>Agelenopsis utahana</i>	Chamberlin & Ivie		
		<i>Cryphoeca exlineae</i>	Roth		
Gnaphosidae	<i>Gnaphosa</i>	<i>borea</i>	Kulczynski		
		<i>brumalis</i>	Thorell		
		<i>parvula</i>	Banks		
		<i>muscorum</i>	Koch		
		<i>microps</i>	Holm		
		<i>Orodassus canadensis</i>	Platnick & Shadab		

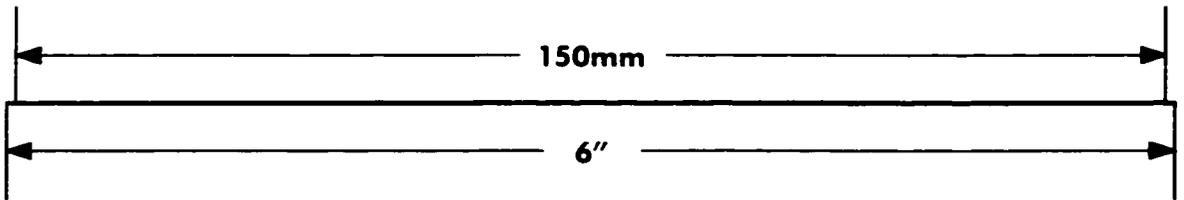
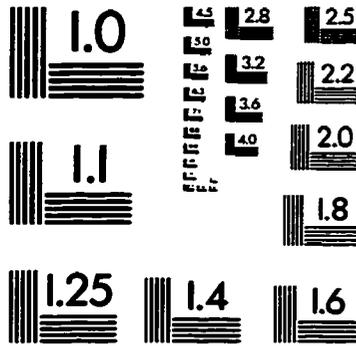
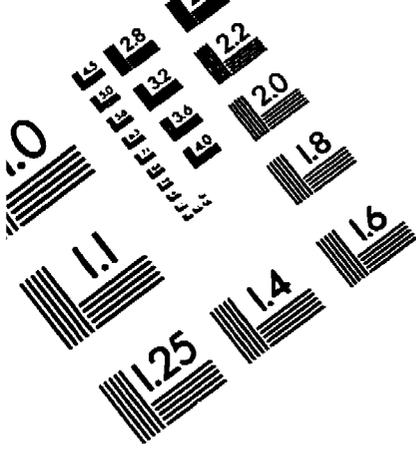
Appendix 2: continued

Family	Genus	Species	Authority
Gnaphosidae	<i>Haplodrassus</i>	<i>hiemalis</i>	Emerton
		<i>Zelotes</i> <i>fratris</i>	Chamberlin
		<i>Sergiolus</i> <i>montanus</i>	Emerton
		<i>Micaria</i> <i>aenea</i>	Thorell
		<i>pulicaria</i>	Sundevall
Philodromidae	<i>Philodromus</i>	<i>placidus</i>	Banks
		<i>pernix</i>	Blackwall
		<i>rufus</i>	Walckenaer
		<i>Thanatus</i> <i>formicinus</i>	Clerck
Araneidae	<i>Araneus</i>	<i>marmoreus</i>	Clerck
		<i>saveus</i>	Koch
		<i>iviei</i>	Archer
		<i>Araniella</i> <i>displicata</i>	Hentz
Dictynidae	<i>Dictyna</i>	<i>alaskae</i>	Chamberlin & Ivie
Salticidae	<i>Metaphidippus</i>	<i>sp.</i>	
Mimetidae	<i>Ero</i>	<i>canionis</i>	Chamberlin & Ivie
Theridiidae	<i>Enoplognatha</i>	<i>intrepida</i>	Soerensen
		<i>Robertus</i> <i>fuscus</i>	Emerton
		<i>Theridion</i> <i>aurantium</i>	Emerton
		<i>sempunctatum</i>	Emerton
Linyphiidae (Linyphiinae)	<i>Agyneta</i>	<i>allosubtilis</i>	Loksa
		<i>olivacea</i>	Emerton
		<i>Allomengea</i> <i>pinnata</i>	Emerton
		<i>Bathyphantes</i> <i>pallidus</i>	Banks
		<i>Helophora</i> <i>insignis</i>	Blackwall
		<i>Lepthyphantes</i> <i>alpinus</i>	Emerton
		<i>complicatus</i>	Emerton
		<i>duplicatus</i>	Emerton
		<i>intricatus</i>	Emerton
		<i>turbatrix</i>	OPC
		<i>nr. washingtoni</i>	
		#5	
		#10	
		<i>sp.</i>	
		<i>Microneta</i> <i>viaria</i>	Blackwall
	<i>Neriene</i> <i>radiata</i>	Walckenaer	
	<i>Oreonetides</i> <i>vaginatus</i>	Thorell	

Appendix 2: concluded

Family	Genus	Species	Authority
Linyphiidae			
(Linyphiinae)	<i>Oreonetides</i>	<i>rotundus</i>	Emerton
	<i>Pityohyphantes</i>	<i>subarcticus</i>	Chamberlin & Ivie
	<i>Poeciloneta</i>	<i>A</i>	
	<i>Sisicus</i>	<i>apertus</i>	Holm
	<i>Wubana</i>	<i>atypica</i>	Chamberlin & Ivie
Linyphiidae			
(Erigoninae)	<i>Ceraticelus</i>	<i>fissiceps</i>	O.P.C.
		<i>laetabilis</i>	Chamberlin
		<i>sp. A</i>	
	<i>Ceratinella</i>	<i>brunnea</i>	Emerton
	<i>Diplocentria</i>	<i>bidentata</i>	Emerton
		<i>rectangulata</i>	Emerton
	<i>Gonatium</i>	<i>crassipalpum</i>	Bryant
	<i>Hilaira</i>	<i>herniosa</i>	Thorell
	<i>Hybauchenidium</i>	<i>cymbadentatum</i>	C. & B.
		<i>gibbosum</i>	Sørensen
	<i>Hypsilistes</i>	<i>florens</i>	O.P.C.
	<i>Pocadicnemis</i>	<i>americana</i>	Millidge
	<i>Sciastes</i>	<i>truncatus</i>	Emerton
	<i>Scotinotylus</i>	<i>pallidus</i>	Emerton
	<i>Sisicottus</i>	<i>montanus</i>	Emerton
		<i>nesides</i>	Chamberlin
	<i>Sisis</i>	<i>rotundus</i>	Emerton
	<i>Tapinocyba</i>	<i>A</i>	
	<i>Walckenaeria</i>	<i>atrotibialis</i>	O.P.C.
		<i>arctica</i>	Millidge
		<i>castanea</i>	Emerton
		<i>communis</i>	Emerton
		<i>directa</i>	O.P.C.
		<i>exigua</i>	Millidge
		<i>karpinskii</i>	O.P.C.
		<i>lepida</i>	Kulczynski
		<i>tricornis</i>	Emerton
		<i>sp. C</i>	
	<i>Zornella</i>	<i>cultrigera</i>	Koch
	Erigoninae	2 or 3 undet. species	
13 families	58 genera	ca. 110 spp	

TEST TARGET (QA-5)



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