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DISSERTATION

ENVIRONMENTAL CONTROLS OF THE DIVERSITY, ACTIVITY, AND FUNCTION OF SOIL NEMATODES IN THE MCMURDO DRY VALLEYS OF ANTARCTICA

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Summer 1999

COLORADO STATE UNIVERSITY

April 23, 1999

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY AMY MARIE TREONIS ENTITLED ENVIRONMENTAL CONTROLS OF THE DIVERSITY, ACTIVITY, AND FUNCTION OF SOIL NEMATODES IN THE MCMURDO DRY VALLEYS OF ANTARCTICA BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

ENVIRONMENTAL CONTROLS OF THE DIVERSITY, ACTIVITY, AND FUNCTION OF SOIL NEMATODES IN THE MCMURDO DRY VALLEYS OF ANTARCTICA

The McMurdo Dry Valleys of Antarctica are one of the most extreme terrestrial environments on Earth. The polar desert soils of the dry valleys are frozen for most of the year, poorly-weathered, ahumic, often saline and desiccated, yet they contain simple low-diversity communities of microbes and their invertebrate grazers (primarily nematodes). The objective of this research was to study ecosystem processes and invertebrate distribution in soils, incorporating studies of nematode activity as an indicator of biotic function. Nematodes are capable of employing an inactive, ametabolic, anhydrobiotic survival strategy in response to adverse environmental conditions. Understanding where and when soil nematodes in the dry valleys are anhydrobiotic and inactive is important to determining how the extreme environment influences biological processes such as decomposition across the landscape.

First, I studied nematode activity with respect to soil moisture, electrical conductivity (as a proxy for salinity), water potential, and temperature over seasonal and diurnal temporal scales. My objective was to

understand how these factors interact and influence nematode activity. For these experiments, I developed a sampling method to fix the status of nematodes in field samples so that nematode activity was not altered by transport and storage of soils. Nematodes communities in the soils studied were often found with high proportions (> 60%) in anhydrobiosis (indicated by coiled morphology). Anhydrobiosis was most strongly correlated to soil moisture content and water potential in the soils studied, with more nematodes inactive in drier soils. In the driest soils with less than 2% soil moisture content, however, coiling of nematodes was not associated with moisture content, water potential, or electrical conductivity, suggesting that unmeasured factors are influencing activity. Nematode activity did not vary greatly over seasonal (spring to fall) and diurnal temporal scales, but addition of moisture in a soil manipulation experiment and from natural snowmelt was a strong trigger for emergence from anhydrobiosis.

Second, I studied nematode anhydrobiosis in soils and sediments collected across a dry valley stream channel. I predicted that the transfer of moisture and salts in the transition zone between soils and sediments would affect the structure and activity of invertebrate communities. Diversity, but not abundance, of invertebrates was correlated to moisture in these samples. Assemblages of nematodes, rotifers, and tardigrades were found in the wettest samples, beneath flowing stream waters, where productivity was highest. In contrast, in the driest soils studied, communities consisted almost entirely of

a single nematode species, *Scottnema lindsayae*. Nematode anhydrobiosis was correlated positively to declining moisture, suggesting that this survival strategy is important for survival of *Scottnema* in the dry soil habitat.

Finally, I studied nematode activity in conjunction with field and microcosm studies of decomposition, a process regulated by soil biota. In microcosms, decomposition of cotton strips, soil microbial respiration, and nitrification were all accelerated by the addition of water over a 9-month incubation at 10°C, suggesting that soil micro- and macrobiota in dry valley soils are capable of functioning similarly to organisms in temperate soil food webs. Decomposition and soil microbial respiration were detectable at ambient soil moisture levels (< 1% gravimetric), but respiration was very low (0.0018 μmol CO_2 g^{-1} soil d^{-1}). In the field, decomposition of cotton strips was negligible after two years in soils. Soil warming and annual moisture amendment treatments did not stimulate decomposition at these sites. Many cotton strips appeared to gain strength, however, suggesting that these strips may have been in a very early stage of decomposition during which microbial colonization and activity could strengthen strips. Nematode abundance, activity, and community structure were unchanged by treatment throughout the experiment.

The results of these experiments suggest that the activity of soil biota and the functions they perform are limited in the dry valleys, particularly by low soil moisture, but also by the interactive effects of low temperatures that

limit the biological availability of water. Nematode activity, and the function of the entire soil food web as well, are probably confined to short periods of time following rare snowfall events during the austral summer. Survival strategies, such as the anhydrobiotic strategy employed by dry valley nematodes, are an important aspect of the ecology of soil biota in this extreme environment. The ability to employ an anhydrobiotic strategy allows nematodes to survive in the driest habitats, although their contribution to ecosystem function as microbial grazers may be most limited in these soils.

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ACKNOWLEDGMENTS

This dissertation represents the discoveries of several years of team study of nematodes in what I think is one of the strangest places that they live - the soils of the Antarctic Dry Valleys. I am grateful to the many people who helped make this research and my time at Colorado State University successful and rewarding. I would like to thank my advisor Dr. Diana Wall for the exceptional mentoring I received. I will always be grateful to Diana for making me think, letting me explore, and for all the wonderful opportunities I have had during the course of this work. My committee also served an important role in my professional development. Dr. Ross Virginia consistently contributed sound advice for this research, and his insights have improved my writing and interpretation skills. Dr. Debra Peters kept me on my toes during my prelims, got me to think about plants, and provided useful comments on my writing. Dr. Cathy Tate's enthusiasm about my research and the dry valleys were contagious, and I thank her for encouraging my efforts to study a dry valley stream. Dr. Ken Doxtader stimulated my thoughts about the really little things - the microbes.

This work would not have been possible without the assistance of the members of Diana's laboratory who have helped me in the lab and the field. Ericha Courtright, Mary Kratz, Bob Niles, and Laura Powers introduced me to

Scottnema and nematology in general and paved the way for my coming to CSU. On the ice as well as in the lab, Pella Brinkman, Dan Bumbarger, Ed Kuhn, Andy Parsons, and Lewis White all helped enormously. Ed Kuhn, in particular, cheerfully counted probably more nematodes than I did, and I will always be grateful for the good counting conversation. He also mopped the floor after I plastered it with sucrose - no small task. Andy Parsons helped with almost everything, but most specifically, I am grateful for him handling all the details so that I could do fun experiments. Melody Burkins shared much of her dry valley knowledge with me, and I benefited immensely from our conversations. Ana Child deserves a special note for being my colleague, fellow pistachio-lover, chocolate stasher, and friend throughout.

The scientists, graduate students, and support staff at the Natural Resource Ecology Lab provided support, encouragement, and advice on many occasions, and I consider myself lucky to have been a part of NREL. I truly enjoyed all the times Dan Reuss and I sat around and brainstormed about science, and many aspects of these experiments were improved by his innovation. I am so thankful to have shared friendship and research interests, as well as the honor of a fellowship, with Serita Frey. In other locales at CSU, many faculty and staff contributed to improving my work, including John Chandler and Greg Butters. Sally Dunphy (GDPE) and Tana Allhouse (Rangeland Ecosystem Science) both provided critical administrative assistance. Dan Binkley was a valuable source of advise on

many occasions. I also thank Tom Bongers at Wageningen Agricultural University for teaching me about all the other nematodes except *Scottnema*, and showing me a good time in The Netherlands. I owe a lot of my success to the experiences I had at the University of Illinois at Chicago, especially to Dr. John Lussenhop who taught me about soil, told me it was impolite to call it dirt, and encouraged me all along. At Dominican University, Dr. Margaret Jonah and Dr. David Craig helped to make my goal of graduate school possible.

I thank Francis and Evelyn Clark for their support through the NREL Francis E. Clark Soil Biology Fellowship. I have enjoyed meeting them and sharing my successes. This research was also supported by the McMurdo Dry Valleys National Science Foundation Long-Term Ecological Research Program (OPP 9211773, R.A. Wharton, Principal Investigator, D.H. Wall and others, Co-Principal Investigators) and by NSF OPP 9421025 (D.H. Wall, Principal Investigator).

My friends have made the past few years particularly meaningful and interesting, particularly Alex Brown, Chad Marshall, Inga Zasada, Nancy MacIntyre, Ken Schmidt, Carl Mikan, Lindsey Johnson, The Multiple Organisms (including Rich Alward, Kristy Duran, Jon Kindler, Tom Lehman, Barb Maynard, Tamera Minnick, Lee O'Brien, Cindy Reeves, and Aaron Reeves), and the NREL graduate students. Bev Dow taught me about "eye on

the prize" and PCR, too. My family, especially my brother, John Treonis, and Rachel and Betty Shattuck, were always keen to hear what I was doing. I especially thank my grandmother Johanna Bussmann, from whom I inherited my curiosity and wanderlust, for her love and support.

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"It says nothing against the ripeness of a spirit that it has a few worms."

Friedrich Nietzsche, "Human, All Too Human"

CHAPTER I:

Introduction

The ice-free dry valleys of Antarctica are one of the most extreme environments on Earth (Priscu 1998). Despite frigid temperatures and low soil moisture and organic carbon content, simple communities of microbes and invertebrate grazers (primarily nematodes) are found in the soils throughout much of the ecosystem (Freckman and Virginia 1998). Nematode densities are often comparable to those of hot desert soils, exceeding 4,000 individuals kg^{-1} (Freckman and Virginia 1998, 1991).

The objective of this dissertation was to study invertebrate distribution, diversity, and the decomposition process in dry valley soils in relation to soil properties, such as moisture, temperature, and salinity. I incorporated studies of nematode activity into this research in order to understand how changing soil properties may limit the function of soil organisms. In this extreme environment, biological activity is dependent on the presence of free water. Ecological processes should be tightly coupled to environmental variables such as precipitation, temperature, and salinity (Priscu 1998). Due to unfavorable environmental conditions, soil nematodes may be required to spend long periods of time in an inactive state known as anhydrobiosis, in which they are protected from desiccation. The distribution of nematodes across a wide range of soil habitats in the dry valleys may be related to their ability to use this ametabolic survival strategy. Long periods of inactivity by

decomposer biota may result in slow decomposition rates in the dry valley soils and explain how soil food webs are sustained on organic carbon pools (< 0.1% by weight) that are smaller than in any other terrestrial ecosystem.

My studies were designed to address three specific questions about invertebrate ecology and the importance of anhydrobiosis in dry valley soils. First, I wanted to know if dry valley soil nematodes employed an anhydrobiotic survival strategy and under what environmental conditions of soil moisture, salinity, and temperature. Second, I asked how soil properties such as moisture and salinity structure invertebrate communities across gradients in the landscape and how the activity (anhydrobiotic state) of nematodes changes across these same gradients. Finally, I wanted to know how changes in soil moisture and temperature influenced the rate of decomposition and the activity of decomposer biota.

In this introduction, I describe the environment of the McMurdo Dry Valleys of Antarctica (77°00'S, 162°52'E) focusing on the factors that characterize the soil habitat. Next, I discuss anhydrobiosis and the importance of survival strategies for soil organisms that rely on water for activity. Finally, I describe the chapters of this dissertation and their specific objectives.

THE MCMURDO DRY VALLEYS

The McMurdo Dry Valleys of Antarctica (Figure 1) are the largest area of ice-free ground on the continent and are the coldest and driest terrestrial ecosystem on Earth. Over 98% of Antarctica is covered with snow and ice, often to a depth of several kilometers. Areas of ice-free ground are found only in the coastal areas of the continent, with the exception of nunataks, the tips of mountains protruding through the polar ice. The McMurdo Dry Valleys were carved by the advances and retreats of glaciers through the Transantarctic Mountains, near the coast of the Ross Sea and McMurdo Sound. Major geomorphic features of the dry valleys include glaciers, glacier melt-fed ponds and streams, closed-basin lakes, and large expanses of barren, rocky soils (Figure 2). These valleys were first explored by members of Robert F. Scott's Antarctic expeditions in the early 1900's. (Wharton 1993)

Temperature in the dry valleys spans from -45 to 15°C (annual mean = - 20°C) (Clow et al. 1988) and precipitation, in the form of snow, is less than 10-cm water equivalent annually, most of which sublimates (Keys 1980). The extreme aridity of this unique ecosystem is caused by the desiccating foehn winds that sweep into the valleys from the higher elevations of the polar plateau. Aridity tends to be more severe in the upland valleys, while conditions may moderate nearer to the coast of the McMurdo Sound (Fountain et al. in review). The highest elevations receive the most

precipitation, but temperatures are much colder, allowing for little melt (McKay 1998). On the dry valley floors, most snowfall also sublimates, although if temperatures are warm, melting snowdrifts or snowfall may wet soils (Campbell et al. 1997a). Gradients of temperature and desiccation may be found within the dry valleys on many scales (e.g., with elevation, soil depth, or distance from lakes or streams) allowing for natural experiments investigating the impacts of these factors on biology and ecosystem function.

Microbes and invertebrates exist in many habitats in the dry valleys, although no vascular plants or vertebrates are found (Vincent 1988; Campbell and Claridge 1987; Horowitz et al. 1972). Kennedy (1993) suggested that the availability of free water for biological use is the primary factor limiting the distribution and function of organisms in the Antarctic, and therefore, diversity and abundance of organisms should be highest near sources of moisture. In the dry valleys, the majority of organisms are found in "wet" habitats such as the sediments of ephemeral glacial-melt fed streams (Chapter III, this dissertation; Alger et al. 1997; Niyogi et al. 1997; Vincent and Howard-Williams 1986) and the water column of lakes (Spaulding et al. 1994; Parker et al. 1982). However, organisms are also to be found in more unusual places, including the benthic sediments of brackish lakes (Vincent 1988; Wharton et al. 1983) as well as within the permanent ice layer covering the lakes themselves (Priscu et al. 1998). Organisms are also present in ephemeral meltpools (called cryoconite holes) on the surface of massive glaciers 50+ m

above the surface of the valley floor (Wall, unpublished observation) and on the insides of rocks as cryptoendoliths (Friedman 1982). Finally, organisms are present above the permafrost in the upper layers of the coarse, desiccated soils extending across the valleys (Freckman and Virginia 1998; Schwarz et al. 1993; Wharton and Brown 1989; Timm 1971). The breadth of habitat is astounding considering the environmental limitations as well as the general appearance of lifelessness in the dry valleys.

Some areas of the dry valleys may be truly devoid of living organisms, but researchers throughout the last 30 years have made many discoveries about the distribution, diversity, and life history strategies of many forms of life in the extreme Antarctic environments. These discoveries have contributed to the field of exobiology - the search for life on other planets (Wharton 1988) as well as the field of survival biology and cryobiology (Wharton and Ferns 1995). Research in the Antarctic Dry Valleys has also evolved into an emerging synthesis of the nature of this environment as an ecosystem - an assemblage of species interacting and modifying the environment through their role in ecosystem processes (Fountain et al. in review; Moorhead and Priscu 1998). This effort in the dry valleys has primarily been the result of research relating to the National Science Foundation's McMurdo Dry Valleys Long-Term Ecological Research Program (MCM LTER), to which this dissertation is a contribution. The LTER research is important because in this simple ecosystem, ecologists can investigate

multiple factors and large-scale processes without being overwhelmed by the biological complexity that characterizes ecosystems elsewhere. Ecological insights gained from dry valley research are applicable to more complex systems in less extreme environments.

DRY VALLEY SOILS AND SOIL BIOTA

Dry valley soils spatially dominate the landscape (Burkins et al. in review). These soils are ahumic, coarse, vegetation-free, desiccated, and often saline (Campbell et al. 1998). Across the landscape, soil features include sand dunes, boulder fields, and expanses of soil polygons created by the freezing and thawing of soils. Many researchers have studied how soil physical properties, such as moisture, salinity, and temperature vary within different regions of the dry valleys, from the coastal regions near McMurdo Sound upward and through the valleys toward the polar plateau (Virginia and Wall in press; Campbell et al. 1998; Bockheim 1997; Campbell and Claridge 1987).

Dry valley soils can be millions of years old but are poorly weathered, very coarse, and stony (Campbell et al. 1998). Soils are underlain by a shallow (25 - 70 cm) permafrost layer that may actually be dry in areas where moisture is inadequate for cementation (McKay 1998; Bockheim 1997). Because of this permafrost layer and the evaporation potential created by the low relative humidity, moisture that falls upon the soils does not percolate and solutes accumulate. Major ions in the soils are of marine origin and/or are the

products of mineral weathering, and include Na^+, Ca^+, K^+, Mg_2^+, Cl^-, SO_4^{2-}, NO_3^- (Campbell and Claridge 1987). In older soils, these accumulating ions result in high salinity (Campbell et al. 1998). Soils tend to be alkaline (pH 7-9) (Campbell et al. 1998). Despite a seemingly uniform appearance, soil properties vary patchily across the landscape as a function of topography, microclimate, and the paleohistory of the valleys (Burkins et al. in revision; Virginia and Wall in press; Campbell and Claridge 1987; Freckman and Virginia 1997).

Dry valley soils are low in organic matter content (< 1%) due, in part, to the lack of vascular plants in the dry valleys (Burkins et al. in revision; Freckman and Virginia 1997). Prior to a study by Burkins et al. (in revision), it was thought that the origin of organic material to dry valley soils was allocthonous - blown in from lake or stream systems that have higher relative productivity (Wharton 1993). Burkins et al. (in revision) showed through studies of soil organic matter C and N stable isotope signatures that organic material in many dry valley soils appears to be a legacy from a warmer epoch when a large, glacial lake covered the valley floor. When this lake receded, its benthic sediments remained to fuel the soil food webs of today. *In situ* photosynthesis by cryptic cyanobacterial colonies at soil surfaces is another potential carbon source, but it is unknown to what extent this process contributes to soil carbon accumulation (Burkins et al. in review).

Temperature and moisture are coupled soil environmental factors that affect the ecology of organisms residing in water-filled pore spaces or in water films on the surface of soil particles. Temperature regulates the phase changes of water, and water in soils can buffer the rate of temperature change. Because most dry valley soils are dark and all are non-vegetated, and because day length is 24 h during the austral summer, soil temperatures can be considerably higher than air temperature, sometimes exceeding 20°C (Campbell et al. 1997b). This warming allows for melting of snowfall or ice in the active layer, providing moisture for life. These elevated temperatures can also increase the potential for moisture losses through evaporation.

Soil temperatures vary considerably, both seasonally and diurnally, and with changes in cloud cover (Campbell et al. 1997b). This variability in time is potentially stressful to soil organisms living in an aqueous environment. These organisms must adapt quickly to changing environmental conditions. Only during the austral winter, late-February to October, are soil conditions relatively consistent, and in this case, the soil temperature is constantly below zero, and there is no free water for biological processes. No long-term datasets are compiled recording precipitation in Taylor Valley, the site for this dissertation research, although researchers working for the New Zealand Antarctic Survey have published some short-term data on snowfall in Wright Valley, reporting annual snowfall of less than 10-cm water equivalent (Keys 1980). Observations suggest that most of this snowfall sublimates rather

than melting (Campbell et al. 1997a). However, rare snowfall events combined with warm temperatures may wet soils significantly.

Despite these potential limitations, simple communities of bacteria, fungi, protozoa, nematodes, tardigrades, rotifers, and occasionally mites exist in many of these soils (Vincent 1988). Visible colonies of moss, algae, and cyanobacteria also can be found in streams and in sediments that are saturated annually by glacial melt. Invertebrate diversity is low in the dry valleys, with only one genus of tardigrade identified (*Macrobiotis*), three genera of rotifera (*Philodina*, *Habrotrocha*, and *Epiphanes*), and two genera of mites (*Stereotydeus* and *Nanorchestes*) (Schwarz et al. 1993; Greenfield 1981). Four species of nematodes are also found: *Scottnema lindsayae* (Figure 3), *Eudorylaimus antarcticus*, *Plectus antarcticus*, and *Plectus frigophilus* (Freckman and Virginia 1991; Wharton and Brown 1989; Timm 1971). Most of these nematode species are believed to be microbivorous, feeding on bacteria, yeasts, or algae (Freckman and Virginia 1997), with the exception of *Eudorylaimus*, which is classified as an omnivore/predator by morphology (Yeates et al. 1993), but has been observed with gut contents matching the color of the algae colonies from which it was extracted (Wall, unpublished results). *Scottnema* has been cultured in the laboratory on an unknown bacterium of dry valley origin (Overhoff et al. 1993). Most dry valley invertebrates are confined to stream and meltpond sediments, with the

exception of nematodes, which compose the top of the food web in most dry valley soils (Freckman and Virginia 1990, 1997).

This dissertation research builds upon the results of nearly a decade's worth of work in the dry valleys by Drs. Diana Wall (formerly Freckman) and Ross Virginia and their Nematode and Soil Ecology team members. These researchers were among the first to investigate the ecology of dry valley soils that were distant from sources of ephemeral glacial melt. They showed that nematodes in dry valley soils can be found with densities near those of nematodes in hot deserts (4000 kg^{-1} soil), although the average density is around 700 organisms kg^{-1} (Freckman and Virginia 1991). Nematodes occurred in 65% of the soils studied by Freckman and Virginia (1998) across four dry valleys, with *Scottnema lindsayae* being the predominant species found. The remaining soils do not contain nematodes.

The discovery of low-diversity nematode communities in soils far removed from significant sources of organic material or moisture spurred research into the factors controlling nematode distribution and diversity with respect to landscape features (elevation, soil polygons) and soil properties (depth, organic carbon content, inorganic and organic nitrogen content, pH, electrical conductivity, and soil moisture content) (Powers et al. 1998; Freckman and Virginia 1997, 1998; Powers et al. 1995; Courtright 1995). High salinity appears to exclude nematodes from some soils in the dry valleys

(Freckman and Virginia 1997), but relationships with other soil factors including soil moisture and carbon content appear to be interrelated and scale-dependent (Virginia and Wall in press). Manipulation experiments have been performed to investigate the effects of human disturbance (e.g., walking) (Powers et al. 1996), temperature change (Freckman and Virginia 1997), and the limits to food web structure (Wall and Virginia, ongoing long-term soil manipulation experiment, unpublished). Dry valley soil nematode communities have been shown to be very sensitive to human disturbance and changing climate (Freckman and Virginia 1997; Powers 1996).

NEMATODE SURVIVAL STRATEGIES

In hot and cold deserts across the globe, survival strategies are an important aspect of invertebrate ecology (Wall and Virginia in press, Wharton 1995; Somme 1995; Zak and Freckman 1991; Freckman and Womersley 1983). Survival strategies include the dispersal, life history, and cryptobiotic strategies used by invertebrates to avoid or tolerate environmental stresses such as desiccation and freezing (Somme 1995). Due to their small size and dependence on water for activity, soil nematodes cannot move sufficient distances to escape from harsh conditions and are especially vulnerable to changes in the soil environment (Wharton 1995; Somme 1995).

Avoidance strategies employed by nematodes, as well as rotifers and tardigrades, include inactive states. Being inactive is advantageous in variable environments because it allows organisms to avoid environmental stress in time, rather than relying on escape in space. Inactive or quiescent states include anhydrobiosis (response to desiccation), osmobiosis (response to high salinity), aerobiosis (response to declining oxygen), and cryobiosis (response to freezing temperatures) (Womersley et al. 1998). Anhydrobiosis, cryobiosis, and osmobiosis, however, are all responses to a lack of free water for biological processes (Somme 1995; Demeure and Freckman 1981), and environmental changes in soil moisture, salinity, water potential, and temperature may all contribute to induce a generalized anhydrobiotic response in soil nematodes. For example, in the natural environment, freezing of soil water is likely to have desiccating effects on nematodes due to the lowering of soil water potential by freeze-concentration of solutes as freezing occurs (Forge and MacGuidwin 1992; Pickup and Rothery 1991).

Anhydrobiosis, or "life without water" (Giard 1894), is characterized in nematodes by a loss of body water (95 - 99%), coiled morphology, and production of simple sugars that preserve molecular and membrane integrity (Higa and Womersley 1993; Womersley 1987; Madin and Crowe 1975; Bird and Buttrose 1974). Anhydrobiotic survival responses can span a continuum from quiescence or inactivity (reduced metabolism), to complete cryptobiosis (a cessation of metabolic processes), depending on the degree of

environmental stress (Womersley et al. 1998; Tsai and VanGundy 1989). Anhydrobiotic nematodes coil in response to declining body water content and to reduce the body surface area exposed to the environment (Bird and Buttrose 1974). This coiling is convenient for studies of nematode activity because anhydrobiotic nematodes can easily be distinguished from active nematodes once they are extracted from soils (Freckman et al. 1977).

Nematodes can induce anhydrobiosis repeatedly and at any stage of their life cycle in response to a fluctuating environment. Coiled nematodes have been extracted from hot desert soils, indicating that they employ an anhydrobiotic survival strategy (Freckman et al. 1987; Freckman and Mankau 1986). Hot desert soil nematodes emerge from anhydrobiosis when conditions are more favorable, such as following precipitation (Freckman et al. 1987; Whitford et al. 1981). Anhydrobiosis has been shown to confer survival to nematodes exposed to 0% relative humidity (Higa and Womersley 1993, Crowe and Madin 1975) and freezing temperatures (Forge and MacGuidwin 1991; Pickup and Rothery 1991; Tsai and Van Gundy 1989; Townshend 1984).

NEMATODE ANHYDROBIOSIS IN THE DRY VALLEY SOILS

Several studies have shown that nematode abundance in dry valley soils is not tightly coupled to moisture content (Powers et al. 1998; Freckman

and Virginia 1997) suggesting that soil moisture is not the primary factor determining habitat suitability for nematodes. Dry valley nematodes must have some adaptive strategy for surviving low soil moistures, as do nematodes in hot desert soils (Freckman and Womersley 1983). The ability to employ an anhydrobiotic survival strategy may be part of the reason that nematodes are so successful in the dry valley cold desert ecosystem, where environmental conditions and soil properties may limit the biological availability of water. An anhydrobiotic survival strategy may allow nematodes to colonize "fringe" habitats where conditions for activity may be rare and ephemeral. Long periods of inactivity by nematodes and other soil biota might also explain how soil food webs are sustained on small soil organic C pools relative to those in temperate ecosystems. Limited biotic activity should be correlated to slow rates of soil processes such as decomposition.

The purpose of this research was to contribute to the ongoing soil, ecosystem, and nematode biology research programs in the dry valleys. The overall question I addressed was: How do the extreme environmental factors that characterize the dry valleys, such as temperature, moisture, and salinity, influence nematode activity, invertebrate diversity, and ecosystem processes? (Figure 4)

The ecology of organisms in extreme environments is strongly influenced by the unique environmental conditions (Somme 1995; Freckman and Womersley 1983; Wynn-Williams 1990; Block 1984). The McMurdo Dry Valleys are an extreme environment, and soil organisms experience freezing temperatures, desiccation, and high soil salinity. It is unknown, however, how these environmental conditions interact to determine when the nematodes in the dry valley soils must utilize an anhydrobiotic survival strategy and how this determines their role in soil processes. Therefore, the central focus for this dissertation research has been to elucidate the role of anhydrobiosis in the ecology of dry valley nematodes. Anhydrobiosis, while allowing nematodes to colonize and persist in the most extreme environments, is an inactive state. Therefore, in anhydrobiosis, nematodes are uncoupled from ecosystem processes, such as trophic interactions and decomposition. Where and when nematodes are in anhydrobiosis in dry valley soils may serve as an indicator of the factors controlling biological activity, and hence ecosystem processes, such as decomposition across the landscape

Soils used for this work were collected from Taylor Valley in the McMurdo Dry Valleys from the Lake Hoare and Lake Fryxell basins (Figure 5). I concentrated on these areas because they are known to contain nematodes based on previous work by Wall and Virginia. These basins also encompass a wide range of soil properties as well as a precipitation gradient. Snowfall

tends to be heavier in the Fryxell basin than at Hoare, due to closer proximity to the McMurdo Sound (Fountain et al. in press). These basins also contain the main field camps for the MCM LTER program and therefore are well-supported logistically.

CHAPTERS

Chapter II describes the method for collection, fixation, and extraction of anhydrobiotic nematodes from dry valley soils that I developed for this dissertation research based on the method of Freckman et al. (1977). My objective was to develop a method to instantaneously fix the anhydrobiotic status of nematodes (coiled or uncoiled) at the time of collection. The dry valleys are located approximately 40 km from laboratory facilities at McMurdo Station. Therefore, usually 24 to 48 hours elapse between collection and extraction of nematodes from soils. During this time, samples are stored in insulated coolers, transported on helicopters, and stored in refrigerators. The potential changes in temperature that occur may alter the anhydrobiotic status of the nematodes from field conditions, resulting in inaccurate assessment of nematode status.

Chapter III describes field studies of nematode anhydrobiosis on temporal scales (seasonal, diurnal) as well as in relation to soil properties - temperature, moisture, salinity, and water potential. The objective of these

studies was to determine the relative importance of each property, as well as temporal changes in those properties, to the use of anhydrobiosis by nematodes in dry valley soils. I wanted to find out if dry valley nematodes employed an anhydrobiotic survival strategy, and if so, under what conditions. I also wanted to know if nematode activity changes with the predictable seasonal and diurnal variations in moisture availability and/or if nematode activity is regulated by short-term pulses of moisture resulting from stochastic events. Very few field studies have shown where and when nematodes are anhydrobiotic in their natural environment, despite their important role in soil processes.

Chapter IV describes a study of nematode communities in the soils and sediments of a stream to soil transition zone. My objective was to learn how soil properties structure invertebrate communities and influence their activity across gradients of moisture and salinity in the landscape. I chose the stream/soil transition zone for study because it incorporates a wide range of soil moisture levels and salinity that could be correlated to nematode abundance, diversity, and activity. In addition, transition zones are important landscape features for the transfer of biota and nutrients and should be important locations for shifts in biological diversity as well (Freckman et al. 1997). Stream to soil transition zones are a particularly important landscape feature in the dry valleys, because they connect glaciers with soils and lakes through the flow of moisture and the modification of

water chemistry through abiotic and biotic processes (Lyons et al. 1998). With this soil and sediment study, I predicted that I would identify specific relationships between moisture, salinity, and nematode ecology that could be applied across the dry valley landscape.

Chapter V describes the results of a decomposition study that investigated the factors that limit decomposition and soil biota in laboratory microcosms and in a similarly designed field experiment. While the work of Burkins et al. (in revision) described the potential sources of carbon to dry valley soils, little is known about the fluxes of carbon from soils via decomposition. I studied soil decomposer biota activity and abundance in conjunction with measurements of this important ecosystem process. Manipulations of soil moisture and temperature were used to investigate the limits that these environmental factors place on soil biota and decomposition in the dry valleys. I predicted that moisture would be the primary limiting factor for biological activity, and that rates of decomposition would be slow under ambient conditions in the dry valleys.

This dissertation concludes with a summary chapter (Chapter VI), highlighting the results of these studies and discussing their relevance.

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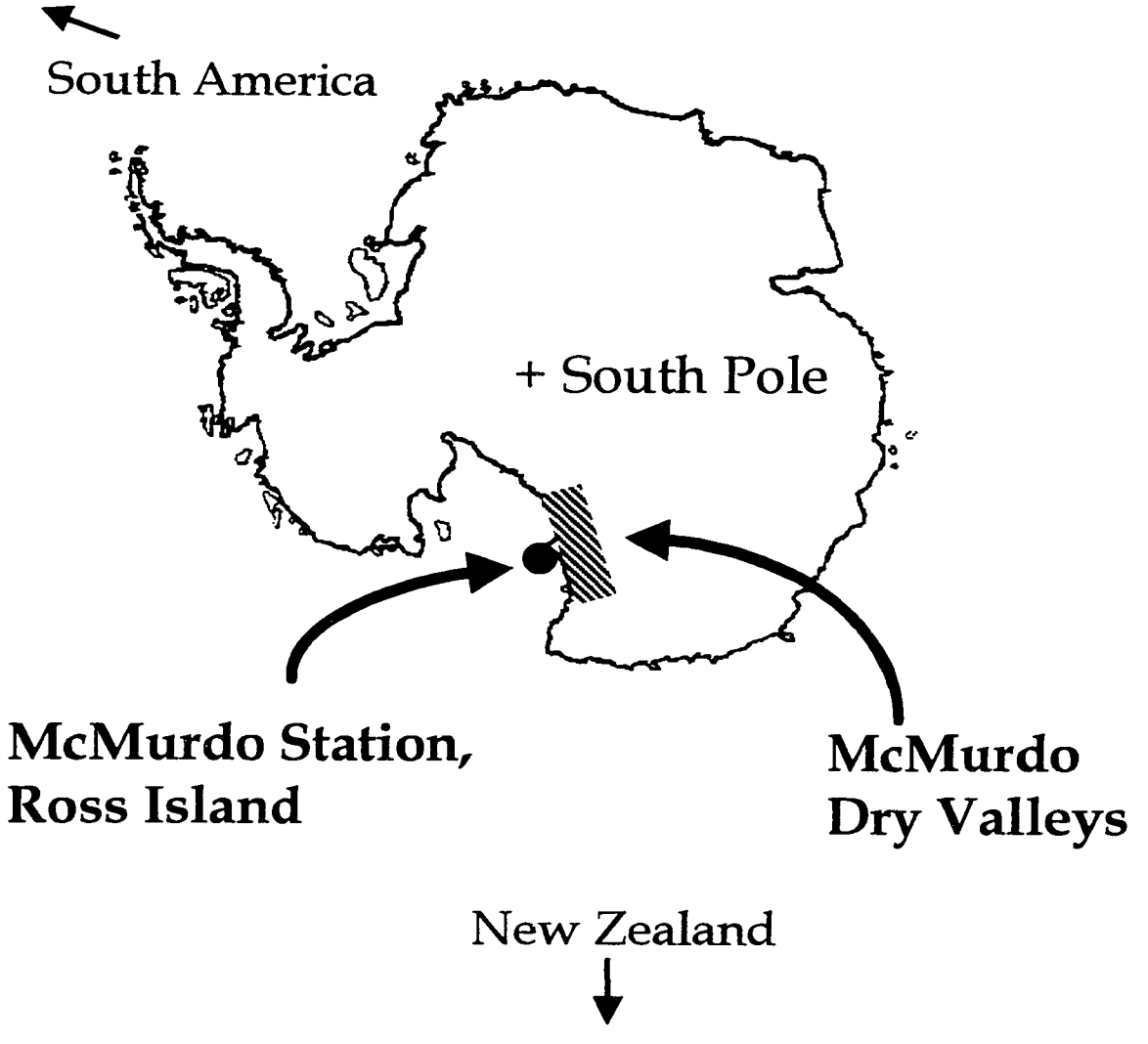


Figure 1: Location of the McMurdo Dry Valleys (77°00'S, 162°52'E), on the Antarctic continent.

Figure 2: Taylor Valley, Antarctica.

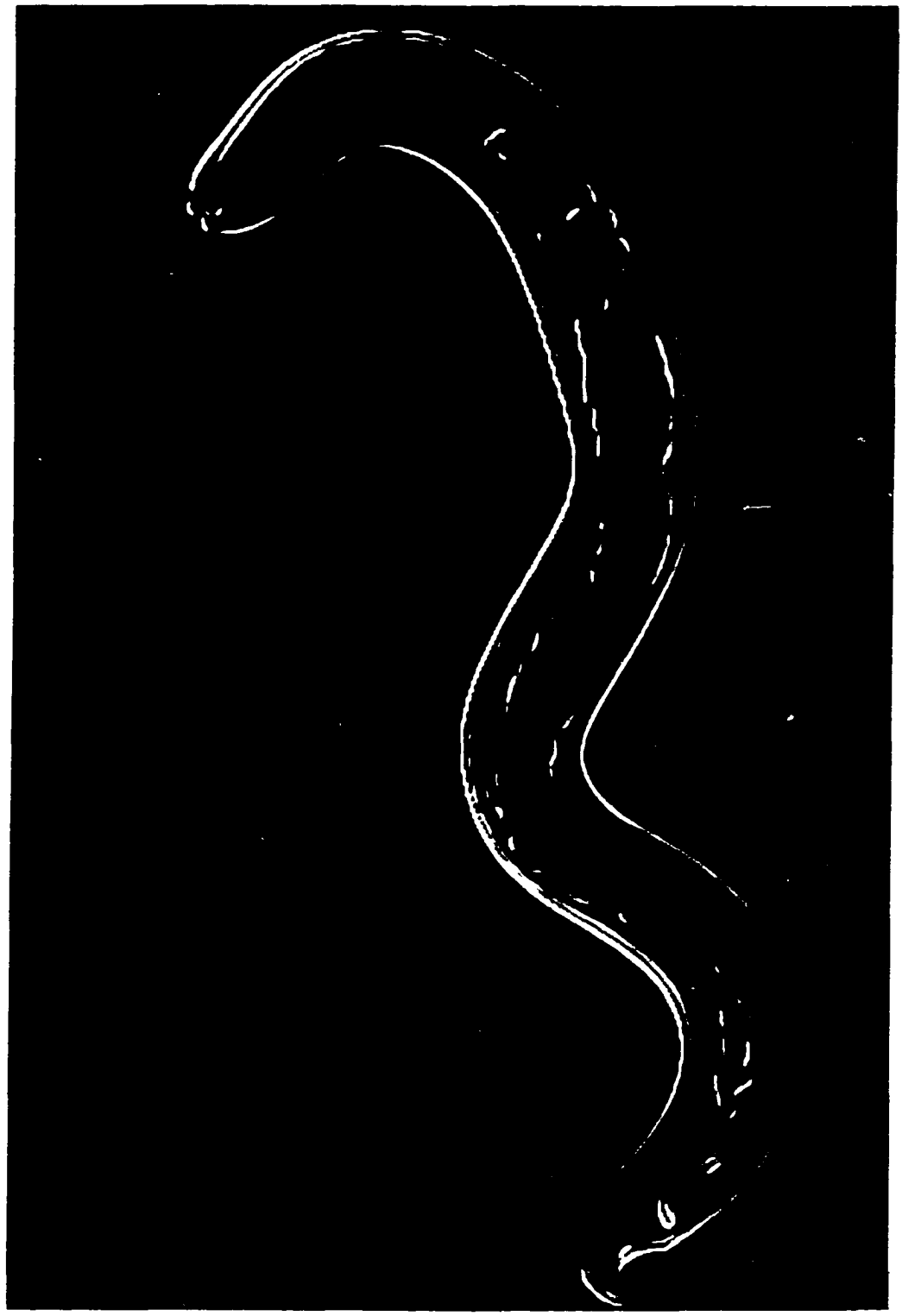
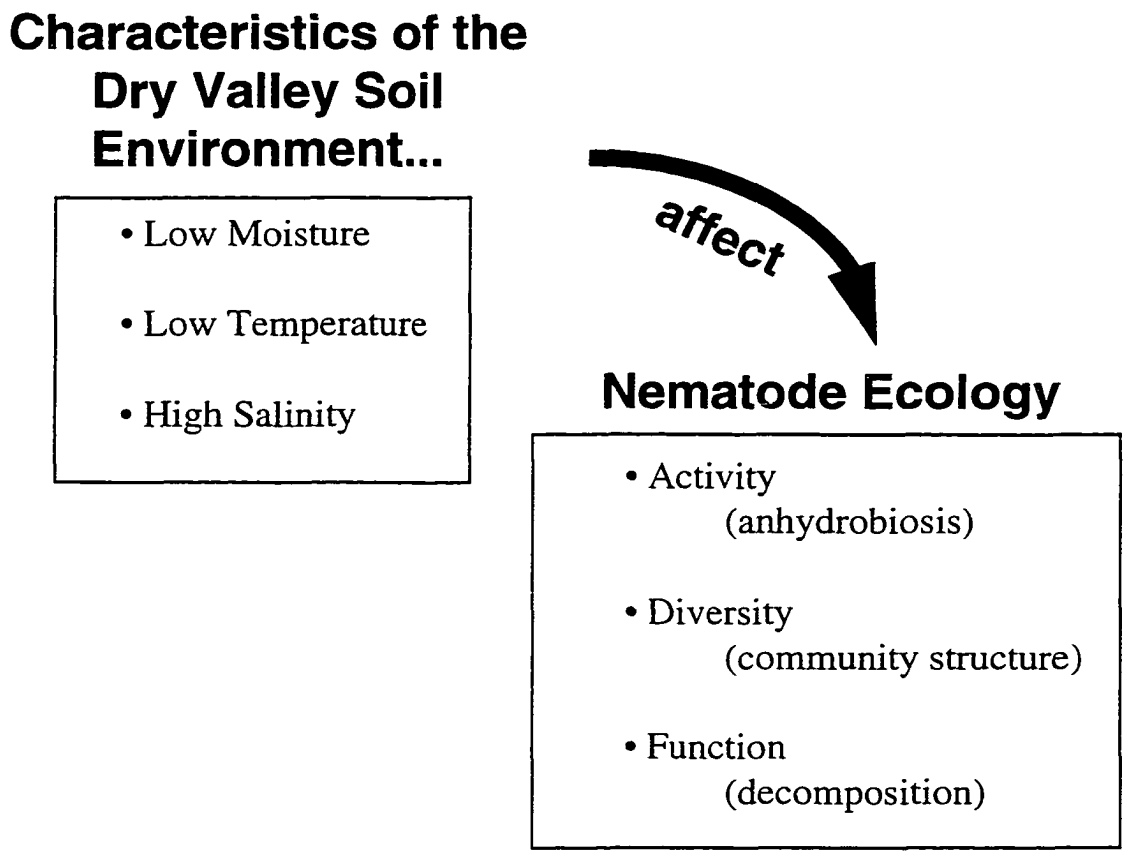


Figure 3: *Scottnema lindsayae* (Timm 1971), the endemic dry valley soil nematode. This adult male is approximately 800 μm long.



Knowledge about these interactions will help us understand:

- how nematodes persist in soils with a wide range of properties at the microhabitat and landscape scales
- the distribution and diveristy of nematode communities across the landscape
- limits to soil carbon cycling

Figure 4: Conceptual diagram of research addressed in this dissertation: How do the extreme environmental factors that characterize the dry valleys, such as temperature, moisture, and salinity, influence nematode activity, invertebrate diversity, and function?

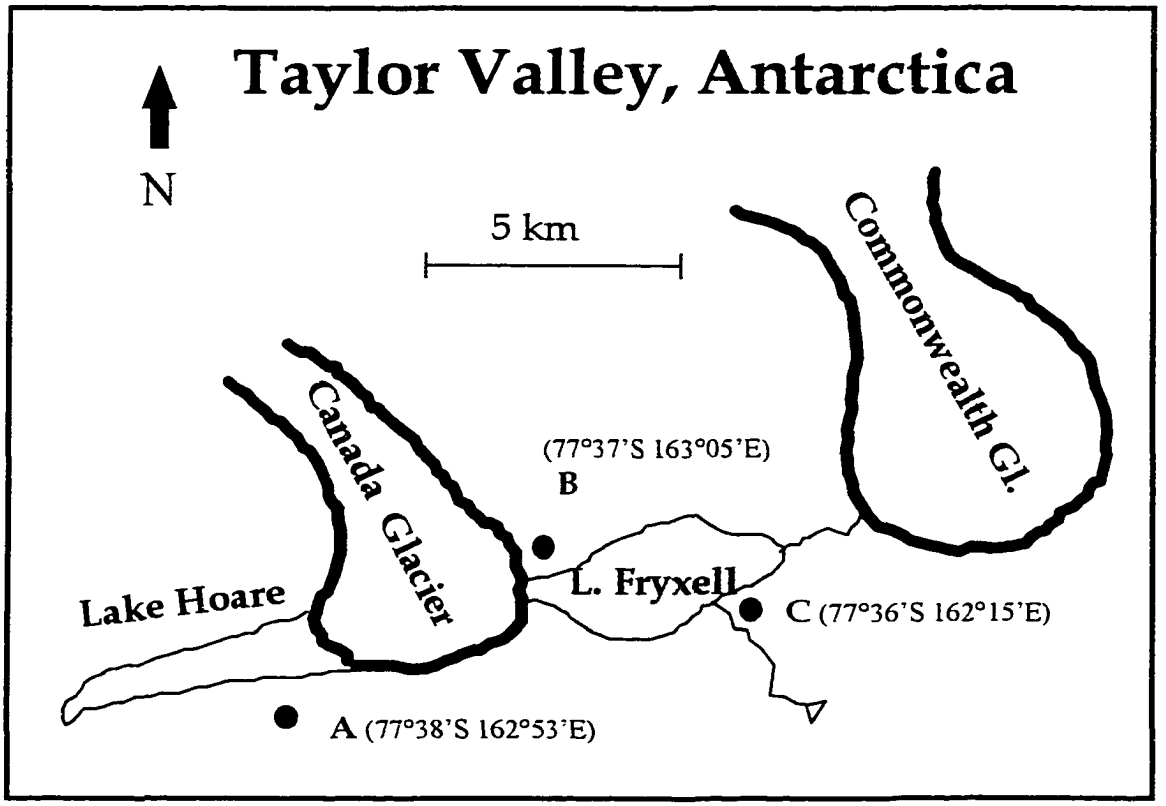


Figure 5: Location of field sampling and experimental plots for these studies in Taylor Valley, Antarctica. **A**: South side of Lake Hoare (primary site for anhydrobiosis experiments (Chapter 3), site of collections for testing fixation technique (Chapter 2), and site of a decomposition experiment plot (Chapter 5), **B**: Site of Special Scientific Interest #12, sampled for anhydrobiosis experiments (Chapter 3), **C**: South side of Lake Fryxell, site of the stream sediment to soil survey (Chapter 4) and a decomposition experiment plot (Chapter 5).

CHAPTER II:

A Fixation Method for Anhydrobiotic Nematodes in the Field

(For submission to the journal *Nematology*)

ABSTRACT

In order to study the use of anhydrobiosis by soil nematodes in the McMurdo Dry Valleys of Antarctica, a technique was developed for fixation of nematodes in soils in the field at the time of collection. The purpose of this fixation step was to prevent changes in nematode anhydrobiotic status that could be caused by temperature and moisture fluctuations in soil samples during storage and transport prior to extraction. Soils were collected at field sites in the McMurdo Dry Valleys of Antarctica and immediately poured into 0.5 L bottles containing sucrose (1.25 M). Nematodes were extracted from these soils in the laboratory with sieving and flotation/centrifugation technique using sucrose solutions instead of water (Freckman et al. 1977). High numbers of nematodes were obtained using this technique, and fixation in sucrose prevented changes in nematode anhydrobiotic status from occurring between collection and extraction. This methodology for study of a survival strategy used by soil invertebrates shows great promise for future investigations of nematode activity and anhydrobiosis in soils.

INTRODUCTION

Survival strategies are important for organisms in soils, particularly for invertebrates such as nematodes that are limited in their ability to migrate and avoid adverse conditions (Wall and Virginia in press; Somme 1995; Freckman et al. 1987; Freckman and Womersley 1983; Demeure et al. 1981). Anhydrobiosis is an inactive state that is a specific survival strategy employed by microinvertebrates in response to desiccation (Crowe 1971; Keilin 1959). Nematodes in anhydrobiosis lose 95-99% of their body water content and cease metabolic activity (Crowe 1971). These and other physiological changes (see Higa and Womersley 1993) are accompanied by morphological change - a coiling of the vermiform body that has been used to identify individuals extracted from soils as being anhydrobiotic (Womersley and Ching 1989; Freckman et al. 1987; Freckman and Mankau 1986; Townshend 1984; Freckman et al. 1977).

A handful of soil from a temperate, tropical, or agroecosystem may contain several hundred species of nematodes (Wall-Freckman and Huang 1998; Bongers and Bongers 1998; Ettema 1998; Bloemers et al. 1997; Hodda and Wanless 1994; Yeates et al. 1997). Understanding how soils support this high diversity is a major research question being addressed by ecologists and nematologists (Ettema 1998; Freckman et al. 1997). Knowledge of where and

when nematodes are anhydrobiotic and inactive in the natural environment may be useful for understanding nematode biodiversity. Different nematode species in soils may be anhydrobiotic under different environmental conditions, and this spatial and temporal partitioning of the soil habitat may allow for the coexistence of nematode species that appear to be functionally redundant (Ettema 1998; Anderson and Coleman 1982; Anderson 1975). Understanding the importance of anhydrobiosis in nematode ecology is dependent, however, on observations of the environmental conditions in the field under which nematodes are anhydrobiotic. In turn, these observations are contingent upon efficient methods for sampling and extracting nematodes from the soil matrix for microscopic identification and enumeration.

My objective was to develop a technique for sampling and extraction of nematodes from soils in order to determine the proportion of individuals that are anhydrobiotic under natural environmental conditions. The standard methods of sampling soils for nematodes involve collection of soils into polyethylyene bags, storage of samples in insulated coolers, transport to laboratory facilities, and storage for a limited amount of time prior to extraction. This process exposes soils to different temperatures and potential desiccation that could alter the anhydrobiotic status of nematodes. Therefore, I developed a method to "fix" the status of nematodes in soils in the field at the time of collection. My goals were (1) to extract nematodes in the laboratory in the state (active or anhydrobiotic, coiled or uncoiled) that

represents their condition in the field, (2) to reduce the impact on nematodes of sampling and the length of time necessary between field collection and extraction, and (3) to maximize the number of nematodes that could be extracted from the soils. First, I discuss the basic extraction technique that was used to extract nematodes from soils while retaining the coiled morphology of anhydrobiotes. Then, I will describe the comparison of fixation methods that were tested for potential use in field experiments. Finally, I will evaluate the fixation method that was used for a field experiment.

STUDY SITE

Soils used to develop and test these techniques were collected from Taylor Valley, Antarctica, which is located in the McMurdo Dry Valleys (77°S 163°E), the coldest and driest desert on the planet (Priscu 1998). The air temperature ranges from 15°C to - 45°C (mean = - 20°C) (Clow et al. 1988), and annual precipitation (snowfall) is approximately 10 cm water equivalent (Keys 1980). Gravimetric soil moisture content is often less than 1% (Virginia and Wall, in press; Campbell et al. 1997). Although barren in appearance, Freckman and Virginia (1991, 1998) showed that these polar desert soils contain nematode communities in densities comparable to that of hot deserts, although nematodes species diversity is much lower (only 1-3 species). Coiled and anhydrobiotic nematodes have been extracted from the dry valley soils,

with up to 80% of the communities being coiled, depending primarily on soil moisture and temperature (Chapter III, this dissertation).

METHODS

ANHYDROBIOTIC EXTRACTION TECHNIQUE

Anhydrobiosis is induced by desiccation and reversed when soils are wetted, and therefore standard techniques for extracting nematodes from soil that require water, such as sieving and flotation/centrifugation technique (Freckman and Virginia 1993; Byrd et al. 1966; Jenkins 1964), must be modified. In the first study of anhydrobiotic nematodes in soils, Freckman et al. (1977) extracted anhydrobiotic nematodes using a sieving and sugar flotation/centrifugation technique replacing water with solutions of potassium chloride, ethylene glycol, sucrose, or formalin. Freckman et al. (1977) found that 1.25 M sucrose was the most effective solution for use instead of water for extraction of anhydrobiotic nematodes. Further tests showed that anhydrobiotic nematodes did not rehydrate in 1.25 M sucrose solution nor did sucrose induce active or straight nematodes to coil (Freckman et al. 1977).

I slightly modified the extraction method of Freckman et al. (1977) to investigate the proportion of the total nematodes that were coiled and anhydrobiotic in dry valley soils. For this anhydrobiotic extraction technique

(AHBN), subsamples (100 g) of soils collected were brought to a volume of 250 ml with 1.25 M sucrose and stirred manually for 30 s. The solution portion of this mixture was slowly poured through two stacked sieves [#40 mesh (425 μm) over #400 mesh (38 μm)]. Nematodes and soil particles were backwashed off the bottom sieve into a beaker with a small amount of 1.25M sucrose. This solution was then slowly pipetted and layered onto 5 ml of cold (1-3°C) 2M sucrose in a 50-ml conical-bottom centrifuge tube. The nematodes, concentrated in the upper layer and at the interface of the two sucrose solutions, were centrifuged for 1 min at 1760 rpm. The supernatant, containing the nematodes, was decanted and passed through a #500 mesh (25 μm) sieve. Nematodes were backwashed off the screen with 1.25 M sucrose solution into a centrifuge tube. Samples were refrigerated for up to 72 h prior to observation.

Nematodes extracted with this AHBN technique were observed with a compound microscope (25-50 X) and classified as "coiled" or "straight". Because nematodes are immobile in the sucrose solution, straight nematodes were assumed to be active or dead at the time of extraction, and coiled nematodes to be anhydrobiotic (Freckman et al. 1977). A nematode was considered to be coiled when one end of the body curled around to touch or overlap with the inside of the body (Towson and Apt 1983). The proportion of nematodes that were coiled and anhydrobiotic (versus non-coiled) was calculated for each sample extracted.

LABORATORY COMPARISON OF FIXATION METHODS

In the laboratory, two techniques for fixation of nematodes in soils prior to AHBN extraction were compared to AHBN extraction without fixation (Table 1). I tested these techniques using four soil samples collected from Taylor Valley, Antarctica in January 1997 because these soils had low moisture contents and potentially contained anhydrobiotic nematodes. These samples were collected into polyethylene bags in the field and transported in insulated coolers to laboratories at McMurdo Station, Antarctica where 100-g subsamples of each were extracted within 48 hours using the AHBN technique (AHBNfresh, Table 1). These soils were then frozen (-20°C) and shipped to Colorado State University, where in April 1997, I performed additional tests. First, 100-g subsamples of these four soils were extracted using the AHBN technique (AHBNfrozen, Table 1).

Next, I tested two solutions for fixation of nematodes in soils that could potentially be applied to field work, using subsamples of the same four soils as above. Freckman et al. (1977), Townshend (1984, 1987), and Towson and Apt (1983) used 4-5% formalin as a fixative for anhydrobiotic nematodes in soils prior to extraction in the lab, but this chemical is hazardous to humans and considered dangerous by the U.S. Antarctic Program for frequent helicopter transportation to and from the field. If spilled, formalin could also contaminate the sensitive dry valley environment (Harris 1998). Therefore, I

compared the use of two solutions (1.25M sucrose and 95% ethanol) that could be safely used in the field for fixation of nematodes. Soil (100 g) was placed in 500-ml beakers, and 150 ml of 1.25M sucrose or 150 ml of 95% ethanol were added. Solutions were stirred to fix the soil nematodes and nematode anhydrobiotic state. The beakers were sealed with parafilm and refrigerated (5°C) for 72 h. Nematodes were then extracted using AHBN technique (AHBNethanol and AHBNsucrose, Table 1).

I evaluated these four AHBN extractions (Table 1) by comparing (1) the number of nematodes that were extracted and (2) the proportion of nematodes that were coiled. The AHBN technique does not recover as many nematodes from soils as the standard sieving and flotation/centrifugation technique using water does because the viscosity of the sucrose solutions limits the effectiveness of the sieving step. Results of the AHBN extractions are expressed, therefore, as the proportion of nematodes coiled, not as absolute numbers. Nonetheless, I wanted to maximize the number of nematodes obtained from the AHBN extractions in order to have higher confidence in estimates of the proportion of nematodes coiled in a given soil sample.

AHBNsucrose and AHBNethanol were compared with AHBNfrozen to determine if a fixation step had any impact on the number of nematodes that could be obtained or their anhydrobiotic status. AHBNfrozen was

compared to AHBNfresh to evaluate whether freezing, storage, and shipment of soils from the Antarctic to the U.S., a three to four month process, changes the anhydrobiotic state of the nematodes. From these comparisons, I determined that sucrose and ethanol were equally effective fixation methods, but due to the flammability and expense of ethanol, I used sucrose for subsequent field work.

FIELD TEST OF FIXATION METHOD

For fixation of nematodes in soils in the field, I used 500-ml wide-mouthed plastic bottles (Nalgene®) that were marked to indicate the 100-, 200-, and 300-ml levels. Bottles were pre-filled in the lab with 100-ml 1.25M sucrose. Thirty soil samples were collected from the south side of Lake Hoare, Taylor Valley, at the site of a seasonal monitoring experiment (77°38'1.15"S, 162°53'5.99"E) on three different dates (11/21/97, 12/16/97, 1/13/98) (Chapter III, this dissertation). Ten soil samples were collected on each date (10-cm depth, Powers et al. 1995) with plastic scoops for sucrose fixation + AHBN extraction (AHBNsucrose). Each sample was rapidly sieved in the field through a 2-mm sieve to remove rocks, mixed briefly in a metal pan, and using a funnel, poured to the 200-ml level into bottles containing 100-ml 1.25 M sucrose. Bottles and bags containing soils were placed in coolers for shipment to McMurdo Station, where they were stored at 4°C until they were extracted within 24 h. For anhydrobiotic extraction of fixed soils, an

additional 100 ml of 1.25 M sucrose was added to the bottles. Samples then were mixed in the bottles for 30 s, poured onto the sieves, and AHBN extraction proceeded as above. Soil moisture was determined gravimetrically (48 h at 105°C) from a 50-g soil sample that was collected into a polyethylene bag in the field (Freckman and Virginia 1993; Gardner et al. 1987).

Statistical comparisons of the number of nematodes extracted between the four AHBN techniques tested in the laboratory (Table 1) were made with ANOVA. Means were compared using using Fisher's protected least significant difference (PLSD) method. The proportion of extracted nematodes that were coiled was compared among these AHBN extraction techniques using the Kruskal-Wallis nonparametric test, since transformations failed to produce normally distributed sample means. The means of ranked data were compared using Fisher's protected least significant difference (PLSD) method. For the field experiment, linear regression analysis was used to investigate the relationship between soil moisture and anhydrobiosis, using the logarithmic transformation of soil moisture and the arcsin- transformation for percent coiled. Analyses were performed using SAS System, Release 6.12 (SAS 1989).

RESULTS

LABORATORY COMPARISON OF FIXATION METHODS

Of the four AHBN extractions compared when testing a fixation method (Table 1), more nematodes were extracted from soils that were fixed in 1.25M sucrose than from fresh soils that were not fixed (ANOVA $R^2 = 0.47$, $P = 0.047$, Figure 1). The proportion of nematodes that were coiled and anhydrobiotic showed a trend for significant differences among the four different extractions (ANOVA $R^2 = 0.44$, $P = 0.06$, Figure 2). AHBN extraction of nematodes from unfixed, fresh soils recovered the lowest proprotion of coiled nematodes, suggesting that freezing, storage, and shipment of samples might have resulted in more nematodes being anhydrobiotic (Figure 2).

FIELD TEST OF FIXATION METHOD

When the AHBN technique was used in conjunction with sucrose fixation during the 1997-98 field season, a high number of nematodes were generally extracted (mean = 152.2 ± 91.6 nematodes 100 g^{-1} soil). This result varied widely between samples from 512 to 42 nematodes 100 g^{-1} soil. The proportion of nematodes coiled in these samples (10.1 - 65.4%) was negatively correlated to the soil moisture content ($R^2 = 0.123$, $P = 0.05$, $n = 30$) (Figure 1).

DISCUSSION AND EVALUATION OF TECHNIQUES

Solutions of 1.25M sucrose were effective, inexpensive, and safe for use for fixing nematodes in soils in the field. The most nematodes were extracted using this technique, compared to AHBN ethanol, or extraction without prior fixation. I also found that shipment of soils from Antarctica to the U.S. frozen in polyethylene bags without any fixation may result in changes in the anhydrobiotic status of soil nematodes. Therefore, analysis of soils as soon as possible after collection, and by employing a fixation method, is recommended to provide the most accurate estimation of nematode status under natural conditions.

Using the sampling, fixation, and extraction technique I developed, I found that nematode anhydrobiosis in the dry valley soils investigated was correlated to soil moisture content (Figure 1). This correlation is a function of a causative relationship between declining soil moisture and increased nematode anhydrobiosis. Several studies of nematodes in soils have shown that as soils dry, the proportion of nematodes that are anhydrobiotic increases (Chapter III, this dissertation; Townshend 1984, 1987; Freckman et al. 1987; Freckman and Mankau 1986; Towson and Apt 1983; Whitford et al. 1981; Demeure et al. 1979). The important role that soil moisture plays in regulating nematode anhydrobiosis emphasizes the necessity of using

sampling and extraction techniques that ensure that nematodes are not exposed to new sources of moisture or that soils are not desiccated.

Moisture content was correlated significantly to nematode anhydrobiosis in the soils I sampled despite the narrow range encountered (0.36 - 2.46%). This suggests that very small variations in soil moisture can alter the anhydrobiotic status of nematodes. The proportion of nematodes coiled varied considerably, however, and other environmental factors, such as temperature, may also influence nematode activity in dry valley soils. In a study of nematodes over a diurnal period in the dry valleys, soil temperature varied from 2 to 14°C (5-cm depth) and significantly less nematodes were coiled (13%) at the warmest time of the day, than at any other time (27-38%) (Chapter III, this dissertation). Changes in any soil property, including temperature and moisture content, caused by collection and storage may affect the anhydrobiotic status of nematodes. Therefore, the sampling, fixation, and extraction methods I have developed for field use are valuable for minimizing changes in the activity status of soil nematodes for accurate assessment of nematode communities in dry soils.

I see great potential for use of this inexpensive and simple method for studying the inactive survival strategies of soil invertebrates in terrestrial ecosystems. Because the samples are not mixed or exposed to temperature ranges before they are extracted, the natural state of the nematode is well-

represented. This methodology would be particularly applicable to studies of nematode activity with depth, or across other spatial or temporal soil moisture/temperature gradients. Combined with measurements of soil environmental factors, analyses of the anhydrobiotic status of nematodes in soils can yield important information about nematode ecology. Studies of activity of nematodes under field conditions can serve as indicators of biological processing in soils. Knowing when and where nematodes are anhydrobiotic is fundamental for understanding their life histories and role in ecosystem processes.

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Table 1: Fixation and extraction methods compared for possible use in field experiments.

	Abbreviation
Anhydrobiotic Extraction of freshly collected soils without fixation	**AHBNfresh**
Anhydrobiotic Extraction of soils that were shipped from Antarctica to Colorado and frozen for four months without fixation	**AHBNfrozen**
Anhydrobiotic Extraction of soils that were fixed in 95% Ethanol prior to extraction	**AHBNethanol**
Anhydrobiotic Extraction of soils that were fixed in 1.25 M sucrose prior to extraction	**AHBNsucrose**

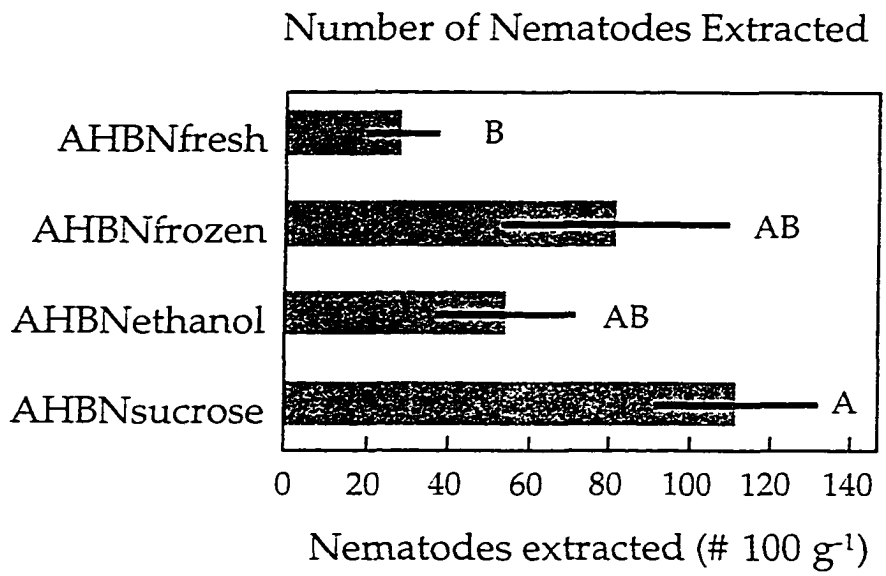

Figure 1: Total nematodes extracted with each of four Anhydrobiotic techniques (Table 1) from soils collected from Taylor Valley, Antarctica. Bars represent means with error bars (n=4). Letters indicate statistical difference.

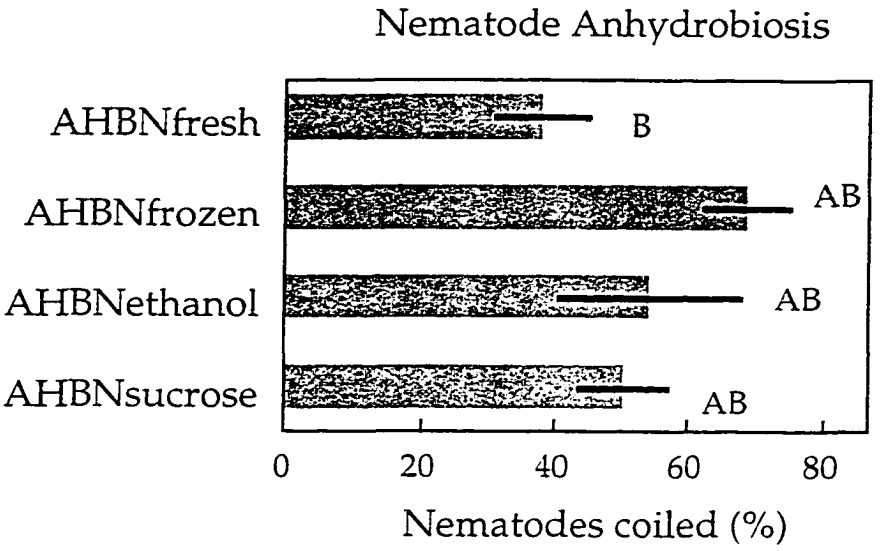

Figure 2: Comparison of the proportions of nematodes that were coiled from soils extracted with the four different extraction methods. Bars represent means with error bars (n=4). Letters indicate statistical difference.

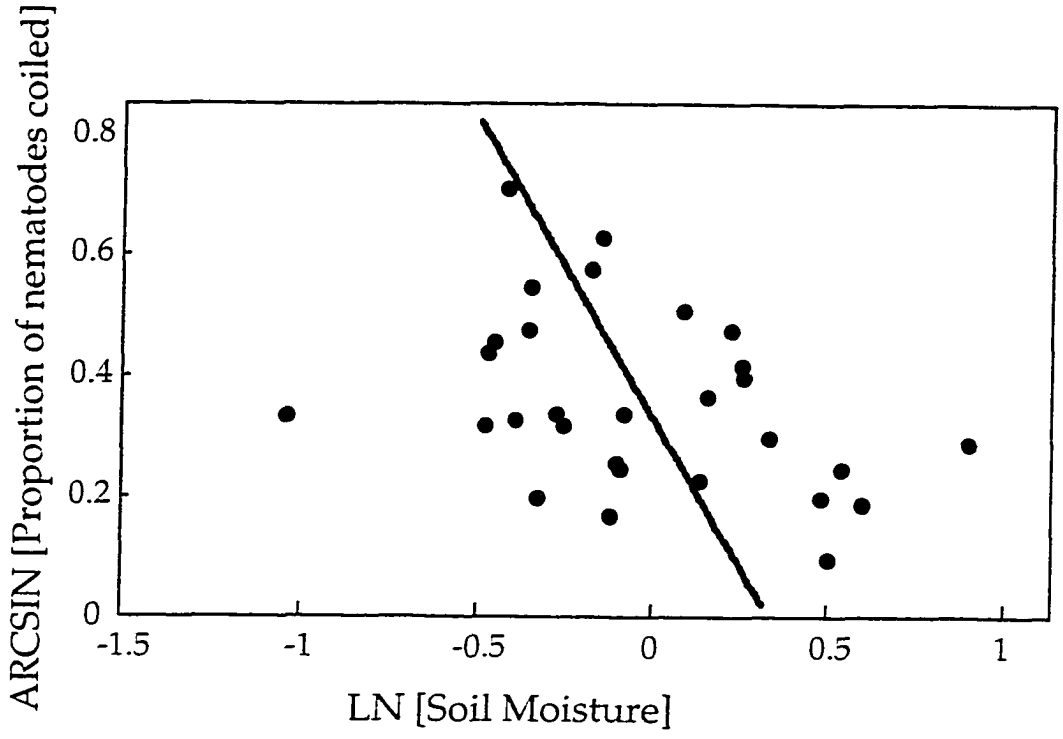

Figure 3: Relationship between soil moisture content and nematode anhydrobiosis for samples collected from Taylor Valley, Antarctica ($R^2 = 0.123$, $P = 0.05$, $n = 30$).

CHAPTER III:

The Use of Anhydrobiosis by Soil Nematodes in the Antarctic Dry Valleys

(For submission to the journal *Functional Ecology*)

ABSTRACT

Anhydrobiosis is survival strategy used by soil nematodes that is induced by desiccation. In the anhydrobiotic state, nematodes are inactive and protected from environmental stress. Few studies have been performed to learn when nematodes are anhydrobiotic in the natural environment. I studied the use of anhydrobiosis by nematodes in soils collected from the McMurdo Dry Valleys of Antarctica. Nematodes were extracted from these soils in a coiled form characteristic of the anhydrobiotic state. The proportion of nematodes coiled in the soils sampled during the austral summer ranged from 30 to 80% and was generally negatively correlated with soil moisture content. For soils with < 2% soil moisture content, however, coiling of nematodes was not correlated with soil moisture, electrical conductivity, or water potential. Wetting of soils resulted in uncoiling of nearly 100% of nematodes within 6 h and appears to be a strong trigger for emergence from anhydrobiosis. In the dry valleys, the activity of soil nematodes may be restricted to the period following stochastic snowfall events. The relevance of these results to ecology in the dry valleys is discussed.

INTRODUCTION

Survival strategies enable nematodes to persist in soils, particularly in extreme environments such as hot and cold deserts, where their activity may be limited for considerable periods of time by temperature extremes and/or desiccation (Wharton 1995; Somme 1995; Freckman and Womersley 1983). Anhydrobiosis is an inactive state that is a specific survival strategy employed by microinvertebrates in response to desiccation (Crowe and Madin 1975; Keilin 1959). Nematodes in anhydrobiosis lose 95-99% of their body water content and cease metabolic activity (Crowe and Madin 1975). These and other physiological changes (see Higa and Womersley 1993) are accompanied by morphological change - a coiling of the vermiform body that has been used to identify individuals extracted from soils as being anhydrobiotic (Freckman et al. 1977). While there have been many studies of the physiological processes involved in induction and emergence from desiccation stress and anhydrobiosis in invertebrates (Womersley et al. 1998), there are only a few published field studies of where and when these animals employ this strategy in their natural environment.

The McMurdo Dry Valleys of Antarctica (77°S 163°E) represent one of the most extreme terrestrial environments on Earth (Priscu 1998). Soils in this cold desert ecosystem are subject to freezing temperatures, desiccation,

and salt accumulation that affect the availability of moisture for biological use (Freckman and Virginia 1998; Campbell et al. 1998). Invertebrates (nematodes, rotifers, tardigrades) were present in 65% of the 415 dry valley soils sampled by Freckman and Virginia (1998) across four valleys, with 80% of these soils containing nematodes only, in low-diversity communities of up to three species. Several studies have shown that low soil moisture does not limit the distribution of nematodes in the dry valleys (Chapter IV, this dissertation; Powers et al. 1998; Freckman and Virginia 1997). These nematodes may use an anhydrobiotic survival strategy in order to persist in very dry soils.

The questions this study addressed were: Do dry valley soil nematodes use an anhydrobiotic survival strategy and if so, how do soil properties (moisture, temperature, water potential, and electrical conductivity) correlate to use of this strategy? As a measure of the use of anhydrobiosis, I determined the percentage of nematodes that were coiled in field samples. I hypothesized (1) that dry valley soil nematodes use anhydrobiosis in increasing proportions in soils where biological water availability is limited, e.g., in drier soils and with increasing salinity, and (2) that nematodes could change anhydrobiotic status in response to temporal changes in soil moisture content caused by temperature fluctuations or by wetting of soils.

STUDY SITE

The McMurdo Dry Valleys (77°S 163°E) include a large portion of the 2% of the Antarctic continent that is free of permanent ice cover. The mean annual air temperature in this ecosystem is - 20°C (Clow et al. 1988) and precipitation is less than 100 mm (Keys 1980). In addition to having low gravimetric moisture contents often less than 1%, these soils are poorly-weathered, coarsely textured (generally > 90% sand, Bockheim 1997), and can be saline due to the lack of precipitation and the accumulation of salts through weathering and atmospheric deposition (Campbell and Claridge 1998).

METHODS

Soils were collected from Taylor Valley, Antarctica in four separate experiments. First, to investigate the relationships between soil moisture, salinity, water potential, and nematode anhydrobiosis, during the 1996-97 austral summer 87 soil samples were collected from three locations, including: (1) 30 samples from the south side of Lake Hoare sampled in a 6-m^2 area (77°38'S 162°53'E), (2) 27 samples adjacent to Canada Glacier, in the Site of Special Scientific Interest #12, collected along three 100-m transects extending away from glacial meltwaters (77°37'S 163°05'E), and (3) 30 samples from the south side of Lake Fryxell sampled in a 6-m^2 area (77°36'S 162°15'E).

Second, I studied diurnal variation in soil moisture, temperature, and nematode anhydrobiosis by collecting soils every 6 h over 24-h from four adjacent 1-m^2 plots on the south side of Lake Hoare beginning at 0930 on 22 December 1997. At each sampling, additional soil samples were collected in 2-cm depth increments from the surface down to 10 cm for measuring soil moisture content to determine if moisture was moving through the soil profile with changing temperature (e.g. through evaporation or condensation). Air temperature (mercury thermometer) and soil temperature (Fluke® digital thermometer, 5- and 10-cm depth) were recorded at each sampling. Long-term soil temperature data was obtained from the McMurdo Dry Valleys Long-Term Ecological Research Program Soil Monitoring Experiment located 100-m west of the diurnal experiment site. Soil temperatures have been recorded hourly at this site at three depths (surface, 5 cm, 10 cm) since January 1995 (Model 107B Temperature Probe, Campbell Scientific, Inc., Logan, UT).

Next, in order to look for changes in soil properties and nematode communities and anhydrobiosis over a longer, "seasonal" time scale, soils were collected throughout the 1997-98 austral summer. At a site on the south side of Lake Hoare, consisting of 10 1-m^2 adjacent plots, samples were collected from each plot on 21 November 1997, 16 December 1997, and 13 January 1998.

Finally, to study the response of nematodes to soil wetting, soils were collected over 24 h after applying water. At an experimental site on the south side of Lake Hoare consisting of six adjacent 1-m^2 plots, three plots were amended with 5.6-l water (after sampling at time zero) to a 0.5-m^2 surface area of soil. Soils were collected every 6 h beginning at 1030 on 10 December 1997. Air temperature and soil temperature were recorded at each sampling.

For each of these four experiments, the soil samples (≈ 1500 g) were collected (0-10 cm depth) into sterile Whirl Pak® bags (Freckman and Virginia 1993). For the diurnal and seasonal studies, separate soil samples for extraction of anhydrobiotic nematodes were "fixed" in the field in 1.25M sucrose. This step prevented potential changes in the anhydrobiotic state of the nematodes after collection by storage and transport of samples from the field to the laboratory (Chapter II, this dissertation). Samples were transported in insulated coolers to the Crary Laboratory at McMurdo Station, Antarctica and divided into subsamples for analyses. Within 48 h of collection, nematodes were extracted from a 100-g subsample with a sieving and flotation/centrifugation technique (Freckman and Virginia 1993), and species were identified and quantified with a light microscope (25-50X). Individual nematodes were categorized by life stage (male, female, juvenile) and classified as living or dead on the basis of movement.

Sieving and flotation/centrifugation technique was also used with high molarity sucrose solutions to extract nematodes from either an additional 100-g subsample or from the soils fixed in sucrose in order to determine the proportion of the total populations that was in anhydrobiosis (Chapter II, this dissertation; Freckman and others 1977). The coiled morphology of these nematodes was used as the criteria indicating anhydrobiosis, and uncoiled nematodes were considered to have been active or dead at the time of extraction.

Moisture content was determined gravimetrically for all soils collected using 50-g soil (48 h at 105°C) (Gardner et al. 1987), and electrical conductivity (as an index of salinity) was measured on a 1:5 soil slurry using 90-g soil and a conductivity meter (YSI, Inc., Yellow Springs, OH) (US Soil Salinity Staff 1954). For each of the 87 samples collected to analyze soil properties and nematodes, soil water potential was measured on a 5-g subsample using a thermocouple psychrometer (Model SC10X, Decagon Devices, Inc., Pullman, WA).

STATISTICAL ANALYSES

The relationships between soil properties (moisture, EC, and water potential, all natural log-transformed), and nematode coiling (arcsin-transformed) were investigated by calculating Pearson correlation coefficients

between the variables. Based on preliminary evaluations of data, separate analyses were performed for soils with moisture contents from 0-2% and from 2% and higher. Seasonal, diurnal, and simulated wetting experiment results were compared using ANOVA. Data was transformed as above. Nematode anhydrobiosis data for the diurnal experiment could not be transformed to a normal distribution, and therefore I used the Kruskal-Wallis nonparametric test to compare means of ranked data (Sokal and Rohlf 1995). Analyses were performed using SAS System Release 6.12 (SAS 1989).

RESULTS

Of the nematodes extracted from each of the dry valley soils sampled for these experiments, 75-100% were identified as *Scottnema lindsayae* Timm 1971. The remaining nematodes were *Eudorylaimus antarcticus* (Steiner 1916) Yeates 1970, or more rarely, *Plectus antarcticus* de Man 1904.

Coiling of nematodes in the 87 soils sampled from Taylor Valley was correlated to soil moisture content (Figure 2A), but the pattern varied between "dry" (0 - 2%) and "moist" (> 2%) soils. The mean soil moisture content was 0.83% ± 0.09 for dry soils and 7.1% ± 0.49 for moist soils. In the moist soils, the proportion of nematodes coiled was inversely correlated to soil moisture ($r = -0.40$, Figure 2A, Table 1), although overall most nematodes (> 30%) were uncoiled. For soils with moisture contents less

than 2%, there was a high degree of variability in the proportion of nematodes coiled (from 30-80%) that was not correlated to soil properties (Figure 2A). EC ranged from 0.01 - 2.4 dS m^{-1} but was not correlated to the proportion of nematodes that were coiled in either moist or dry soils (Table 1). The two samples with the highest EC (0.5 and 2.3 dS m^{-1}), contained no nematodes, and therefore were not included in the analyses.

Soil water potential, which incorporates the effects of moisture and salinity on nematodes, explained the most variation in the proportion of nematodes coiled in moist soils ($r = 0.50$, Table 1). In these soils, water potential ranged from - 0.09 to - 2.0 MPa and was correlated to EC ($r = -0.39$) and moisture content ($r = 0.42$) (Table 1). Increasing moisture was correlated positively with water potential, and increased EC was correlated negatively with water potential (Table 1). When soil moisture was less than 2%, water potential varied widely, ranging from -0.28 to -26.9 MPa, and there was no correlation with nematode coiling (Figure 2B), soil moisture, or EC.

Soil temperature in the dry valleys varies on seasonal and diurnal time scales. Temperature data collected in Taylor Valley from January 1995 through January 1999, show that, on average, soils in the Lake Hoare basin only experienced temperatures above freezing in November, December, and January (Figure 2). In November, soil temperature was only above freezing for a few hours of the diurnal cycle, but in January and December, the soil

temperature was above zero almost continually (Figure 2). Soil temperatures generally shift daily in the austral summer through approximately a 12°C range. This is caused by changes in irradiance as the sun moves behind mountain peaks, shadowing Taylor Valley (Dana et al. 1998).

Soil moisture content increased with depth in the diurnal experiment soils from 0.46% ± 0.08 in the top 0-2 cm to 2.0% ± 0.14 at 8-10 cm (ANOVA, df = 4, $R^2 = 0.61$, $P \leq 0.0001$). Soil moisture did not change through time at any of the depths, however. Soil temperature was above 0°C throughout the experiment and increased during the first 6 h of the diurnal cycle to a maximum of 14°C, declined to hour 18 to a low of 2°C, and then rose to hour 24 (Figure 3C). The proportion of nematodes coiled (0-10 cm) changed slightly through time (ANOVA df = 4, F = 2.89, P = 0.069, Figure 3D). The fewest nematodes were coiled (13%) at hour 6 (1530) compared to other sampling times when 27-38% were coiled (Figure 3D). Uncoiling of nematodes corresponds with the time of day when the soils were warmest (Figure 6C), although soil moisture was not changed (Figure 3A,B).

On the dates soil was collected during the 1997-98 austral summer for monitoring of soil nematode communities, soil moisture averaged 1.05% ± 0.08 (n = 30), but did not vary between the three dates. The proportion of nematodes coiled also did not vary (35.4%, Figure 4). Nematode abundance was the same on all three sampling dates (mean = 2016 ± 233 nematodes kg^{-1}

dry soil), but the age structure was different (Figure 4). The proportions of living and juvenile nematodes in the communities were higher in December and January than in November (Figure 4).

Soil moisture was significantly elevated by wetting of soils (12.2%, 10 min after application), and remained higher than controls throughout the 24 h of the experiment ($P \leq 0.0001$, $df = 1$, $F = 151.3$) (Figure 5A). Soil temperature throughout the diurnal cycle was usually above freezing at the 5- and 10-cm depth, but air temperature was always below freezing (Figure 5B). A weather front moved into the valley shortly after hour 6, and increased cloudiness caused soil temperatures to drop. Water-amended soils were ice-cemented at hours 18 and 24, but only in the upper 3 cm of soil. Nematodes responded to addition of moisture, and 1 to 11% were coiled in wetted soils compared to controls (37 to 57% coiled, $P \leq 0.0001$, $df = 1$, $F = 59.9$) (Figure 5C). There were no changes in nematode abundance (average = 517.0 nematodes kg^{-1}) over time, suggesting that nematode migration did not occur, nor did water amendment (and subsequent freezing) cause nematode mortality (an average of 67.6% of nematodes were alive in all samples taken).

DISCUSSION

Nematodes are considered to be the most successful anhydrobiotic animals, and their ability to employ an anhydrobiotic survival strategy may

help to explain this phyla's almost ubiquitous distribution (Womersley 1987). Nematodes are the most abundant animal in one of the most extreme soil environments on Earth, the McMurdo Dry Valleys, despite severe temperature and moisture limitations (Freckman and Virginia 1998). In the present study, I have shown that dry valley soil nematodes employ an anhydrobiotic survival strategy, as do nematodes in hot deserts (Freckman et al. 1987; Freckman and Mankau 1986) and agroecosystems (Townshend 1984; Towson and Apt 1983). Anhydrobiosis may be a universal survival strategy employed by nematodes in soils.

Between 30-80% of nematodes were coiled in the soils studied during the austral summer. This range is similar to what has been measured in other studies of nematode anhydrobiosis (Table 3). In a broad sense, the relationship between soil moisture and coiling of nematodes appears to be similar between ecosystems and soil types. The use of anhydrobiosis may be related more to the fundamental constraints low water potentials place on nematodes than to adaptations of nematode species to their environment. All nematodes in soils may be subject to similar thresholds for tolerance of desiccation before employing an anhydrobiotic strategy becomes necessary.

Coiling of nematodes was correlated to soil moisture content and water potential in the soils I collected that had moisture contents higher than 2%. For drier soils, coiling of nematodes was not correlated to any of the soil

properties measured. This degree of variability and lack of correlations in the drier soils was unexpected, and implies that soil properties other than those studied influence the anhydrobiotic status of nematodes. These factors might include temperature or the abundance of a microbial food source in the environment. Water potential also varied in the driest soils and was not correlated to soil moisture content as expected. Measurements of nematode coiling and water potential may both vary in soils with low moisture contents as a function of microsite heterogeneity. Electrical conductivity was not correlated to nematode coiling, contrary to prediction, but it appears that at higher levels of EC (> 1 dS m^{-1}), nematodes cannot establish in the soils, precluding any effects on activity (this study; Chapter IV, this dissertation; Freckman and Virginia 1997).

These results provide some insight into the factors influencing the use of anhydrobiosis by dry valley nematodes, but do not reveal how nematodes respond to changes in their environment. Temperatures in the dry valleys fluctuate widely on temporal scales, and I was interested in how this affected soil moisture and nematode anhydrobiosis. Over a diurnal period, moisture content in the soils studied did not change, although soils were warmed and cooled considerably. Some nematodes appear to have uncoiled at the warmest time of the day, suggesting direct effects of temperature on nematodes. This result was not highly significant, however, and direct effects of temperature on nematode anhydrobiosis should be investigated further.

Whitford et al. (1981) failed to detect changes in nematode anhydrobiosis in a study of hot desert nematodes over 24 h unless rainfall wetted the soils significantly. This suggests that nematodes may not be able to respond to a changing environment on short-time scales.

Wetting of soils in the dry valleys was a very strong "trigger" for uncoiling of nematodes, as has been seen in hot desert soils (Freckman et al. 1987; Whitford et al. 1981). Most nematode activity in dry valley soils may be confined to periods following stochastic snowfall and wetting events, when changes in soil moisture content are dramatic. While some nematodes always seem to be uncoiled, possibly utilizing wet microsites, the majority of soil nematodes in dry valley soils may depend on rare precipitation events for activity. Overhoff et al. (1993) determined that the life cycle of the dry valley nematode, *Scottnema lindsayae*, was 218 days at 10°C in the laboratory. If this estimation applies to the field, these organisms may need years or even decades to complete their life cycle. The ability of organisms to interrupt growth and development by quiescent stages is, however, an important part of the life histories of Antarctic terrestrial invertebrates (Convey 1997). The results of monitoring soils throughout the austral summer in the seasonal experiment suggests that some reproductive activity and/or egg-hatching can occur within a few weeks during the austral summer, even though nematode activity may have been confined to short periods. In the field, nematodes

may be able to take advantage of ephemeral conditions for rapid feeding and reproduction.

Multiple factors influence the biology of terrestrial organisms in Antarctica (Convey 1997). In the dry valleys, spatial variability and rapid temporal changes in soil temperature and moisture status in soils already near the limits for life make these soils an extreme environment for invertebrates. Dry valley soil nematodes employ an anhydrobiotic survival strategy, and use of this strategy appears to be correlated to multiple factors, particularly soil moisture. This suggests that the processes nematodes participate in, specifically carbon cycling via grazing of decomposer microbes, may be limited by low soil moisture in this ecosystem. Further experiments in the dry valleys should explore further the impact of temperature on soil nematodes and the possibility influence the abundance of nematode food resources may have on nematode activity and survival.

Insights gained from the study of nematode anhydrobiosis in this extreme environment may be applied to other ecosystems. Knowledge of where and when soil nematodes are anhydrobiotic in soils with respect to natural environmental conditions may be important for developing management strategies for plant-parasitic nematodes and for understanding niche partitioning among the vast diversity of nematode species in soils.

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Table 1: Relationships between soil properties and nematode coiling in soils with gravimetric moisture content > 2% that were sampled from three sites in Taylor Valley. Pearson correlation coefficients (r) are given for analyses between ln-transformed soil moisture content, electrical conductivity, and water potential and arcsine-transformed proportion of nematodes coiled.

	Electrical Conductivity	Water Potential	Nematodes Coiled (%)
Soil Moisture (%)	r = + 0.29 P=0.047 n=47	r = + 0.42 P=.0037 n=47	r = -0.402 P=0.027 n=29
Conductivity ($dS\ m^{-1}$)	.	r = - 0.39 P= 0.069 n=47	r = 0.0839 P= 0.665 n=29
Water Potential (MPa)	.	.	r = -0.50 P= 0.0057 n=29

Table 2: Field studies of nematode anhydrobiosis demonstrating the relationship between soil moisture, water potential, and nematode anhydrobiosis in different ecosystems and soil types.

Soil Source	Soil Moisture (% grav.)	Water Potential (MPa)	Nematodes Coiled at or below given moisture	Soil particle size distribution	Reference
Antarctic Dry Valleys	2%	-0.6	50-79%	>95% sand	This study
Chihuahuan Desert	4.7	-0.4	60%	80% sand 13% silt 6% clay	Freckman et al. 1987
*	2 - 2.8	-0.05	80%	92% sand 4% silt 4% clay	Demeure et al. 1979
	3.4	-0.3	80%	73% sand 21% silt 6% clay	(laboratory study)
Mojave Desert	2.7	-6.2	88%	91.8% sand 4.6% clay 3.6%silt (Rundel and Gibson 1996)	Freckman and Mankau 1986
Agricultural field, Ontario	3	-1.5	58%	85% sand 10% silt 5% clay	Townshend 1984
Agricultural field, Ontario	3	- 1.5	70%	61% sand 28% silt 11% clay	Townshend 1984
Agricultural Field, Oahu, Hawaii	*	-1.5	65%	*	Towson and Apt 1983

* Not Given

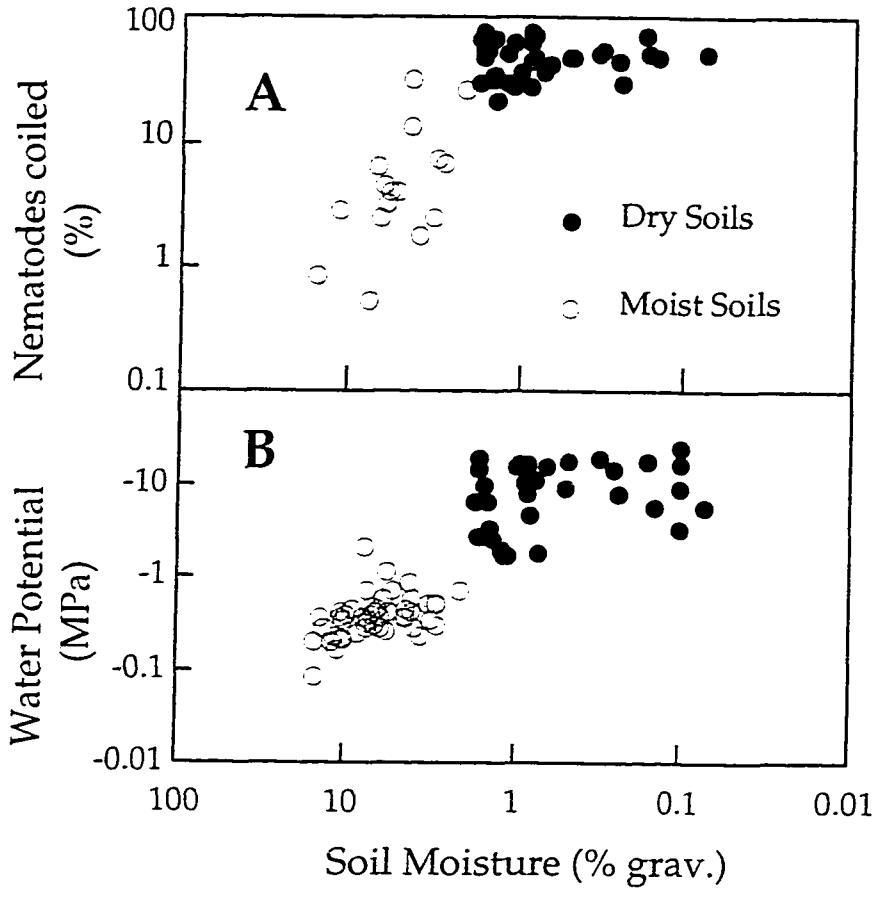

Figure 1: The relationship between soil moisture and (A) coiling of nematodes, and (B) water potential in "dry" (< 2% gravimetric soil moisture) and "moist" (>2%) soils from three sites in Taylor Valley.

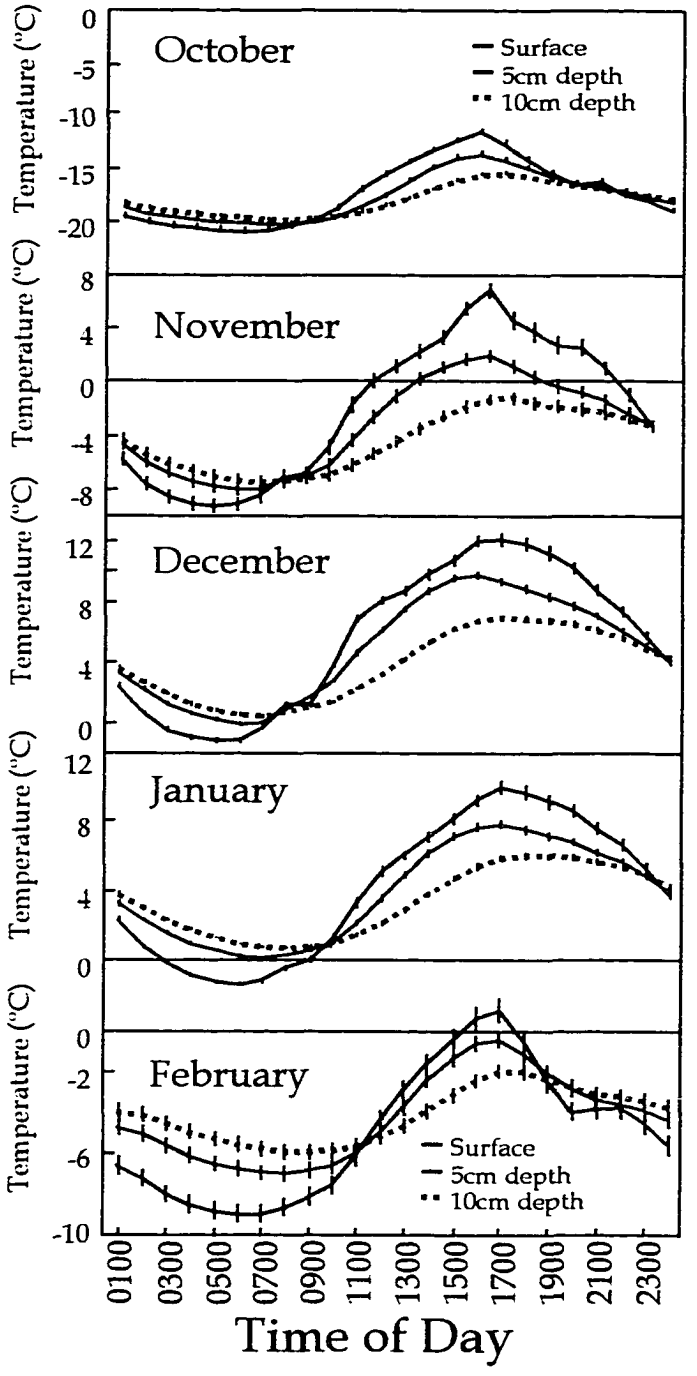

Figure 2: Diurnal air and soil temperature (5- and 10-cm depth) fluctuations during the austral summer months on the south side of Lake Hoare, Taylor Valley. Each value represents the average temperature recorded at the indicated time averaged for all the days of the month (± S.E.) over the four years for which data are available.

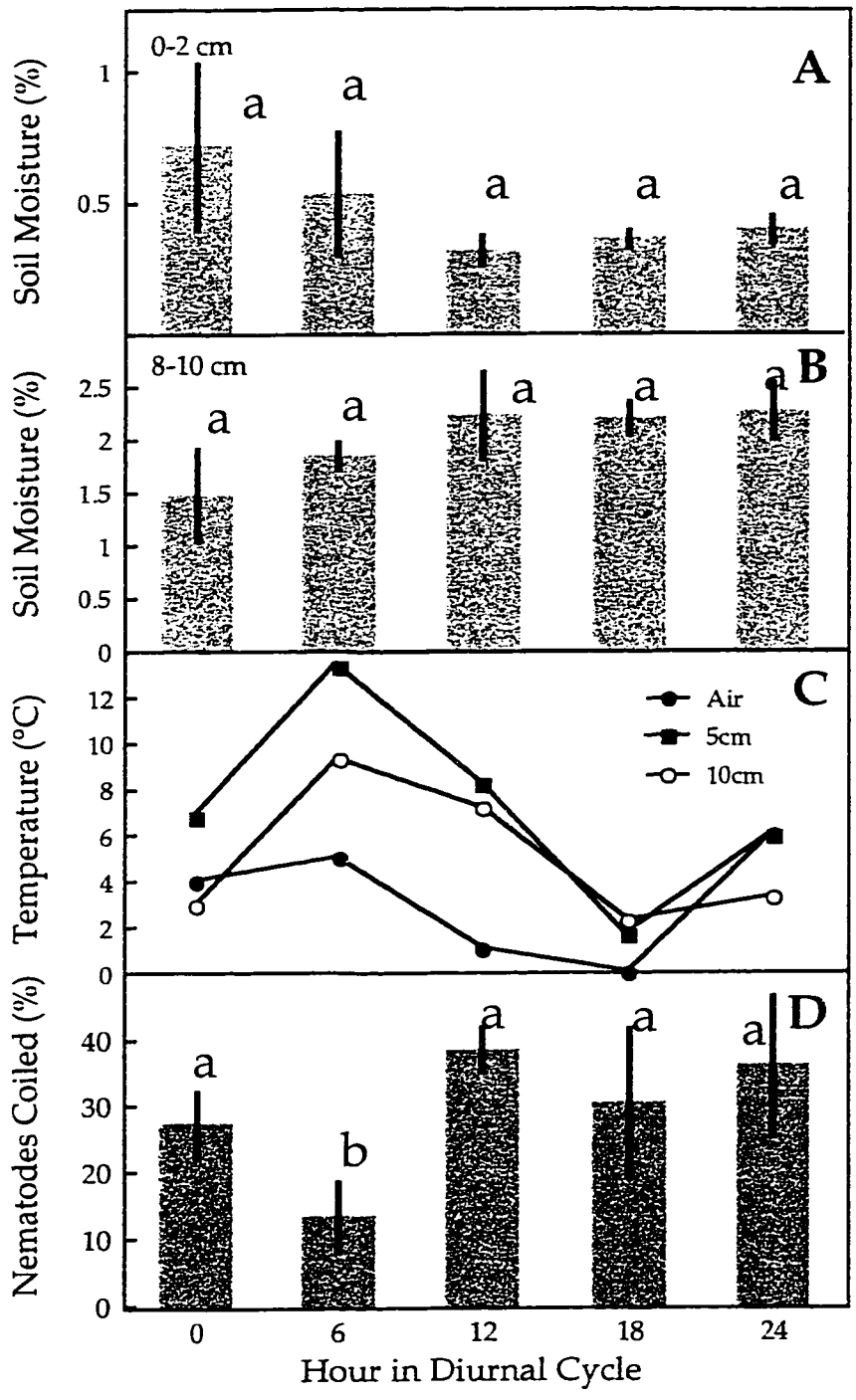

Figure 3: Diurnal patterns of: (A & B) soil moisture for two depths (0-2 cm and 8-10 cm), (C) temperature, and (D) nematode anhydrobiosis (coiling). Time 0 = 0930. Bars represent the averages for four samples (± S.E.), and bars with the same letters are not statistically different from each other (ANOVA for soil moisture, Kruskal-Wallis Nonparametric Test for nematodes coiled, P > 0.10, Student-Newman-Keuls Multiple Range Test).

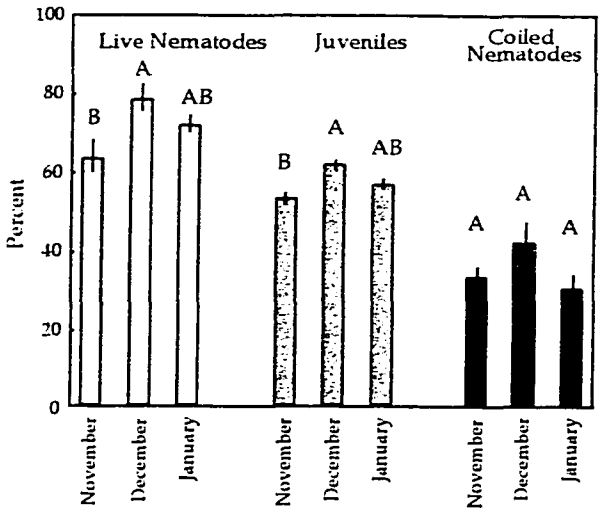

Figure 4: Nematode community structure and coiling at each of the three seasonal experiment sampling dates. Bars are the average values for 10 samples (± S.E.). Within a parameter, bars with the same letters are not statistically different from each other (ANOVA, $P > 0.05$, Student-Newman-Keuls Multiple Range Test).

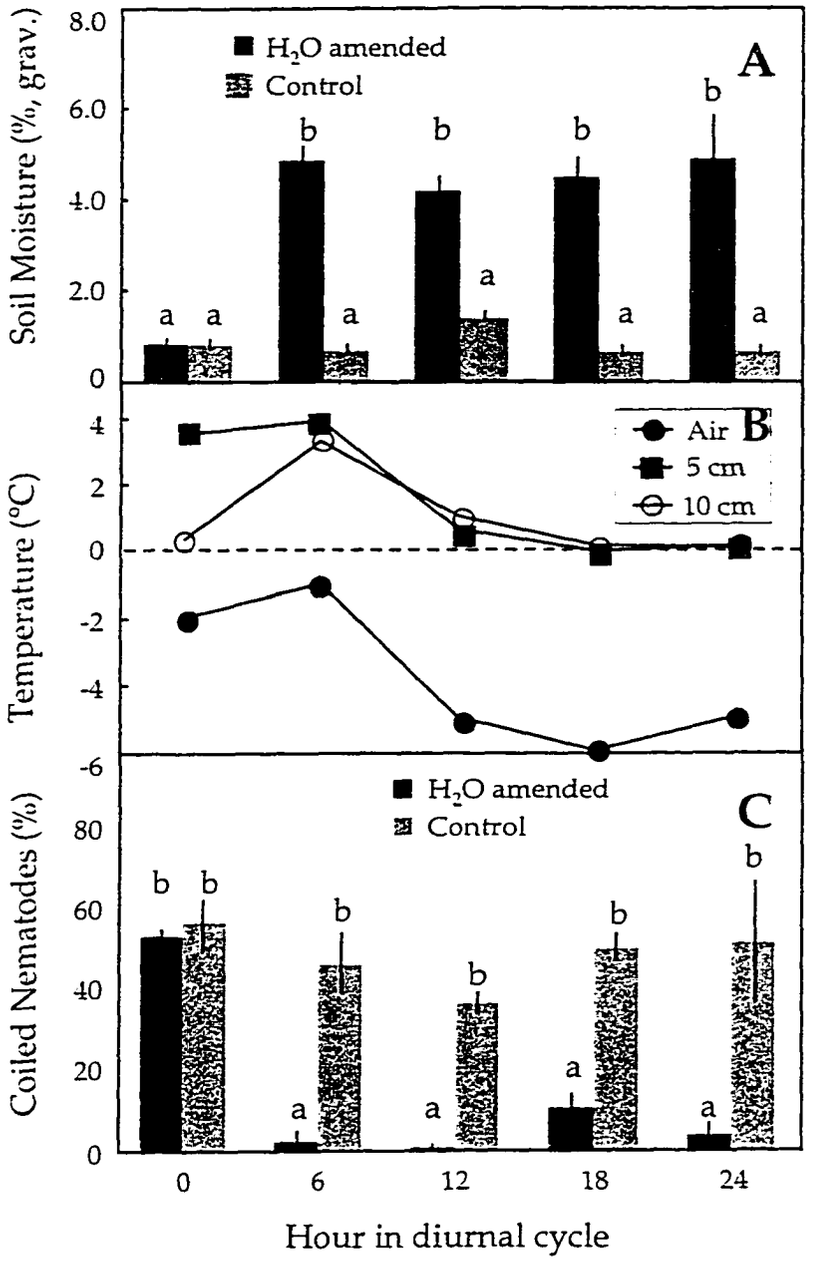

Figure 5: Soil moisture (A), temperature (B), and nematode activity (coiling) (C) throughout a diurnal cycle after wetting soils. Time 0 = 1530. Bars are the average of three samples (± S.E.), and bars with the same letters are not statistically different from each other (ANOVA, $P > 0.05$, Student-Newman-Keuls Multiple Range Test).

CHAPTER IV:

Invertebrate Biodiversity in Antarctic Dry Valley Soils and Sediments

(Accepted for publication in the journal *Ecosystems*)

ABSTRACT

I studied invertebrate communities across a transition zone between soils and stream sediments in the cold desert landscape of Taylor Valley, Antarctica. I hypothesized that hydrological and biogeochemical linkages in the functionally important transition zone between streams and surrounding soils should be important in structuring invertebrate communities. Invertebrate communities were compared along transects beginning in the saturated sediments under flowing stream water and extending laterally through the hyporheic zone to the dry soils that characterize most of the dry valley landscape. Nematodes, rotifers, and tardigrades assembled into different communities in soils and sediments, but there was no relationship between the total abundance of invertebrates and moisture. Community diversity was, however, influenced by the moisture and salinity gradients created with distance from flowing waters. The wet, low salinity sediments in the center of the stream contained the most invertebrates and had the highest taxonomic diversity. Adjacent to the stream, communities in the hyporheic zone were influenced strongly by salt deposition. Abundance of invertebrates was low in the hyporheic zone, but this area contained the most co-occurring nematode species (three species). In dry soils, communities were composed almost entirely of a single species of nematode, *Scottnema lindsayae*, an organism not found in the stream center. These results suggest spatially

partitioned niches for invertebrates in soils and sediments in the dry valley landscape based on proximity to sources of moisture and the interactive effects of salinity.

INTRODUCTION

In the hyperarid, cold desert ecosystem of the McMurdo Dry Valleys of Antarctica, soil invertebrate communities are characterized by low species and trophic diversity, making them ideal for landscape-scale biodiversity studies (Freckman and Virginia 1998). Dry valley soils and sediments contain simple communities of nematodes, rotifers, and tardigrades (Freckman and Virginia 1998). These invertebrates are primarily microbivorous (Freckman and Virginia 1997), and microbial grazers are known to be functionally important as modifiers of ecosystem processes such as carbon and nitrogen mineralization (Freckman 1988). In the extreme environment of the dry valleys, however, conditions require invertebrates to spend considerable time inactive and uncoupled from ecosystem processes - in an anhydrobiotic survival state. In anhydrobiosis, nematodes are coiled (Bird and Butrose 1974), lose > 95% of their water content (Crowe and Madin 1975), and are resistant to environmental stresses (Womersley et al. 1998; Crowe 1971).

The distribution and diversity of invertebrate communities in dry valley soils have been studied with respect to elevation, depth, and soil factors such as pH, organic carbon, salinity, and moisture (Freckman and Virginia 1998, 1997; Powers et al. 1998, 1995). Little is known, however, about

the diversity and structure of these communities in moist habitats, such as stream sediments, that are saturated for part of the year. I was interested in how invertebrate diversity, abundance, and activity change across a stream sediment to soil transition zone in the dry valleys.

Transition zones are important areas of ecosystem function because they are sites of nutrient and biota exchange (Groffman and Bohlen 1999; Freckman et al. 1997; Holland et al. 1991). For example, soils and sediments adjacent to streams (e.g., riparian areas and the hyporheic zone) are substrate for biotic and abiotic processes that modify water chemistry (Jones and Holmes 1996). In the dry valleys, where the alluvium is very coarsely structured, the bulk of water movement may occur in the sediments surrounding the stream rather than as surface flow (Conovitz et al. 1998; Runkel et al. 1998). Stream water accumulates salts and nutrients through weathering reactions and atmospheric deposition in the hyporheic zone (Lyons et al. 1998). As glacial meltwater is carried by streams from higher elevations to lakes on the valley floor, salts and nutrients accumulate and are distributed throughout the hyporheic zone (Runkel et al. 1998). Previous studies of dry valley soils (Virginia and Wall in press; Powers et al. 1998; Freckman and Virginia 1997) suggest that low soil moisture and high salinity are important factors influencing diversity of nematode communities. Therefore, the distribution of water and solutes in transition zone soils and sediments should be especially important in structuring invertebrate

communities as well as influencing whether the organisms are active or anhydrobiotic.

Diversity of soil communities is believed to be increased by moderate disturbance, microhabitat heterogeneity, niche partitioning (Wall and Moore 1999; Ettema 1998; Anderson 1975), and productivity (Moore and deRuiter in press). Temporal and spatial variation in surface and subsurface stream flow results in a great degree of habitat heterogeneity within the dry valley soil to stream transition zone (Alger et al. 1997), and I hypothesized that these transition zones are important locations for subsurface biodiversity. In addition, anhydrobiosis in nematodes is induced by desiccation, and I hypothesized that variation in moisture and salinity across the transition zone would affect nematode activity as well as diversity. I predicted that assemblages of invertebrates would be unique in soils and sediments, and invertebrate abundance and diversity would be correlated to environmental variables.

STUDY SITE

The McMurdo Dry Valleys of Antarctica (77°S 163°E) are the largest permanently ice-free area on the continent (about 2% of the land mass) and are among the most extreme terrestrial environments on Earth. Annual temperatures average -20°C (Keys 1980), and precipitation is less than 10 cm

water equivalent annually (Clow et al. 1988). Geomorphic features of the dry valleys include large expanses of dry, non-vegetated soils, glaciers, ephemeral glacier-fed streams and meltponds, and permanently ice-covered lakes. Soils represent the largest area of the dry valley landscape and are desiccated, frigid, and vegetation-free, with a shallow (approximately 0.5 m) permafrost layer (Bockheim 1997; Campbell and Claridge 1987). Soils are often saline due to the lack of precipitation and the accumulation of salts through weathering and atmospheric deposition in the absence of leaching (Campbell and Claridge 1987). Soil salinity varies with soil age, substrate, and moisture regimes (Bockheim 1997; Campbell and Claridge 1987). Invertebrates (nematodes, rotifers, and tardigrades) were present in 65% of the soils across four valleys (Taylor, Wright, Victoria, and Garwood) studied by Freckman and Virginia (1998) with 80% of these soils containing communities of nematodes only. Three species of nematodes (*Scottnema lindsayae, Eudorylaimus antarcticus, Plectus antarcticus*) have been found in dry valley soils (Freckman and Virginia 1991; Wharton and Brown 1989), as well as several rotifer species and a species of tardigrade (Schwarz et al. 1993).

HYDROLOGY

The distribution of streamflow in the dry valleys is central to the structure and function of the entire landscape. Dry valley streams originate from alpine glacial melt under the continuous daylight of the austral

summer, flow for only six to ten weeks, and empty into closed basin lakes on the valley floor (House et al. 1995). Hydrological and biogeochemical processes that occur along the stream course determine the chemistry and quantity of water inputs to lakes and thus, their productivity (Lyons et al. 1998; Green et al. 1988). The hyporheic zone is the area of subsurface flow through the sediments surrounding the surface waters of a stream (Valett et al. 1990; Schwoerbel 1961). In temperate streams, the hyporheic zone generally extends below the stream, but the hyporheic zone of dry valley streams extends relatively far laterally due to a shallow, impermeable permafrost barrier. Flow volume declines as streams move down valley because there is no runoff from soils to counter evaporative losses and precipitation is limited (Alger et al. 1997).

METHODS

During the 1997-98 austral summer, samples were collected from stream sediments and surrounding soils in the Von Guerard Stream/Harnish Creek network in Taylor Valley, Antarctica (Figure 1). This stream channel is approximately 5 km long, with an elevation change of about 500 m. The width of the stream and hyporheic zone vary considerably with topography and glacial melt volume, but the width of surface water was 0-5 m on sampling days. When visible, stream waters were shallow (< 2-cm depth). Soil and sediment samples were collected on two dates (30 November 1997

and 31 December 1997) from three transects. These transects were located in the upper (near glacial source), middle, and lower reaches of a stream (Figure 1), and were perpendicular to the stream axis, extending out 32 m from the stream center (Figure 2). Five samples (0, 8, 16, 24, and 32 m) were taken along each transect on each date, for a total of 30 samples.

For each sample, approximately 1500 g of soil or sediment (surface to 10-cm depth) were collected into WhirlPak® bags with plastic scoops (Freckman and Virginia 1993). Five g of sediment/soil also were collected from the top 1 cm for measurement of chlorophyll *a* concentration (an indicator of algal biomass) using the method of Holm-Hansen et al. (1965). Samples were mixed within the bags, placed into insulated coolers, and transported for analysis to laboratories at McMurdo Station, Antarctica. Within 24 h, nematodes, tardigrades, and rotifers were extracted from a 100-g subsample with a flotation/centrifugation technique (Freckman and Virginia 1993). Invertebrates were quantified within 48 h of extraction using a light microscope (25-50 X), and nematode species were identified visually using Timm (1971) as a reference, with the exception of *Plectus antarcticus*. This species is only distinguishable from *P. frigophilus* (also found in the Dry Valleys region) by a difference in adult body length. Adult *Plectus* were measured using image analysis (n = 25 individuals from the 6 locations where adults were found). Nematodes were classified as living or dead on the basis of movement. Soil moisture was determined gravimetrically (48 h

at 105°C), and electrical conductivity (EC), used as an indicator of salinity, was measured on a 1:5 sample slurry (U.S. Salinity Laboratory Staff 1954).

To determine the proportion of nematodes in anhydrobiosis, I extracted additional 100-g subsamples with a modified sugar flotation/centrifugation technique using a high density sucrose solution (1.25 M) instead of water (Freckman et al. 1977). I used the coiled morphology of extracted nematodes to indicate that they were anhydrobiotic, and I considered uncoiled nematodes to have been active or dead at the time of extraction.

STATISTICAL ANALYSES

Statistical analyses were performed using SAS System Release 6.11, with reference to Cody and Smith (1997) and Sokal and Rohlf (1995). Invertebrate abundance data were extrapolated to numbers kg^{-1} dry soil or sediment and were transformed using the ln(x + 1) transformation; all percentage data were transformed using the arcsin(x + 1) transformation and soil moisture and conductivity (EC) were natural log-transformed (Sokal and Rohlf 1995). I used ANOVA models to analyze the relationship between each independent variable (transect location and distance from the stream center) and abundance of invertebrates. The relationship between landscape location and moisture, EC, and chlorophyll *a* concentration also were analyzed with

ANOVA, as was the relationship between distance from the stream center and taxonomic or nematode species richness (mean number of taxa or nematode species found in samples at a given distance). Means for all ANOVAs were compared using Student-Newman-Keuls Multiple Range Test, and differences were considered significant at the 0.05 probability level. Paired sample t-tests were used to compare data from the two sampling dates. I used multiple regression to investigate the relationships between invertebrate abundance, soil moisture, and EC. The relationship between invertebrate community composition and moisture, EC, and chlorophyll *a* concentration was determined by canonical correspondence analysis (CCA) using the computer program CANOCO version 3.12 (ter Braak 1991, 1987). CCA is a direct gradient technique that relates organism distribution and abundance to measured environmental variables (Palmer 1993).

RESULTS

The gravimetric moisture content of soils and sediments was slightly higher in December (6.69%) than November (5.21%) ($n = 30$, $P = 0.06$, paired sample t-test). With the exception of higher soil moisture in December and a significant increase in the percentage of *Eudorylaimus* that were alive (see below), no differences were found between the two dates for any other variable (paired sample t-tests, $P > 0.1$ for all analyses). Therefore, the two sampling dates were combined for analysis of variance.

SOIL/SEDIMENT ENVIRONMENTAL VARIABLES

ANOVA models including transect location (upper, middle, lower) and distance along transect (0, 8, 16, 24, 32 m), explained significant proportions of the variation in moisture and EC (Table 1, moisture ANOVA $R^2 = 0.91$, EC ANOVA $R^2 = 0.87$, $P < 0.05$ for both models). The interaction term between distance and transect was significant for both moisture and EC, indicating that while moisture and conductivity differed with distance from the stream center, the patterns were different among the three transects (Table 1, Figure 3). Moisture content was similar for all three transects in the sediments beneath flowing water at 0 m (mean = 14.8%) and also at 32 m (mean = 1.9%). Moisture content declined steeply between 0 and 8 m for the middle and lower transects, and these transects were drier overall than the upper transect (Figure 3).

Soil and sediment EC was not different between sampling distances for the upper transect, but varied along the lower and middle transects (Figure 3). EC was highest at 16 m for these two transects and was significantly higher than other distances in the lower stream transect (Figure 3). Variation in chlorophyll *a* concentration was best explained by the one-way ANOVA model with distance as the independent variable (Table 1). Chlorophyll *a* concentration was significantly higher in the stream center than in the soils at 32 m (Figure 3).

Based on these results, I was able to delineate habitat types across the stream to soil transition. Stream sediments at 0 m, directly beneath flowing water, were distinct in having high moisture content and low EC at all three transects. Soils at 32 m were outside the influence of flowing waters (beyond the hyporheic zone) with low moisture contents consistent with other dry valley soils in the area. The soils and sediments adjacent to and influenced by the stream surface waters (the hyporheic zone) extended from 8-24 m, having higher moisture content than the soils. In addition, the high EC at 16 and 24 m for the middle and lower transects indicates salt deposition from stream waters.

INVERTEBRATE ABUNDANCE

Scottnema lindsayae was the most abundant invertebrate overall, with a mean abundance of 597 individuals kg^{-1} dry sample (range 0 - 5,645), followed by *Eudorylaimus* and *Plectus* with mean abundances of 295 (range = 0 - 2,577) and 183 (range = 0 - 1,591) individuals kg^{-1} dry sample, respectively. Rotifers and tardigrades averaged 202 (range 0 - 1,667) and 126 (range = 0 - 1,736) individuals kg^{-1} dry sample, respectively. More *Eudorylaimus* were alive (v. non-motile/dead) in December (82.1%) than in November (54.2%) ($n = 18$, $P = 0.02$, paired sample t-test). The averages of the differences between the two dates for all other variables (nematode species, rotifers, tardigrades, EC, chlorophyll *a* concentration, anhydrobiosis) were not significantly different from zero (paired sample t-test, $P > 0.1$ for all analyses).

INVERTEBRATE ABUNDANCE BY LOCATION

Total invertebrate abundance and the abundance of nematodes alone did not differ across the lateral transects, 0 - 32 m, although there was a trend for total invertebrates to be highest at 0 m, and lowest at 16 m (Figure 4). *Scottnema* was not observed at 0 m, and *Plectus* was absent at 32 m. *Eudorylaimus*, tardigrades, and rotifers all were more abundant at 0 m than at other distances. The percentage of living nematodes, for the taxon or by species, did not vary with distance from the stream center (data not shown). Total invertebrate abundance and the abundance of nematodes were both highest at the middle transect location (Table 2).

INVERTEBRATE-ENVIRONMENT RELATIONSHIPS

Total invertebrate abundance and the abundance of nematodes were both negatively correlated with EC, but were not related to soil moisture (Table 3). Abundance of *Eudorylaimus*, *Plectus*, and tardigrades was positively correlated with soil moisture, and negatively with EC (Table 3). *Scottnema* abundance declined with increasing moisture and EC (Table 3).

The species-environment biplot (Figure 5) shows the overall relationship between abundance of the invertebrate groups and environmental variables (CCA). The first canonical axis explained 98.2% of

the cumulative variance (eigenvalue = 0.87, F-ratio = 67.4, $P < 0.01$), and the first and second axis explained 100% of the variation. *Plectus*, *Eudorylaimus*, tardigrades, and rotifers were found in samples with relatively low EC, high chlorophyll *a*, and high moisture. In contrast, *Scottnema* was found in drier, higher EC (more saline) soils. Regression analysis showed a negative correlation between EC and *Scottnema* abundance (Table 3), but, unlike the CCA, regression analysis included samples lacking invertebrates (n=6), which were very saline compared to the rest of the samples (average = 1467 μmhos cm^{-1}, 1:5 soil slurry).

NEMATODE ANHYDROBIOSIS

Anhydrobiosis was correlated significantly with declining moisture content and increasing EC (multiple regression, $P < 0.0001$, $R^2 = 0.72$). Very few nematodes (0-3%) from the stream center were coiled and considered anhydrobiotic at the time of sampling, although coiled nematodes were found in all other locations (Figure 6). The percentage of nematodes that were coiled was not significantly different among stream locations, however (ANOVA, $P > 0.10$).

COMMUNITY RICHNESS

Nematode species and invertebrate taxonomic richness were compared across the transects by calculating the mean number of taxa or nematode

species found in the samples from each distance (Figure 7). Taxonomic richness was highest in the stream center, while nematode richness did not vary across the transects (Figure 7). Richness was lowest in the soils at 32 m, where 99% of the invertebrates found were *Scottnema*.

DISCUSSION

Biodiversity and ecosystem function in riparian and soil systems are receiving considerable attention because of the important ecosystem services these areas provide and because they are sensitive to disturbance and changing global climate (Freckman et al. 1997; Lawton 1996; Stanley and Valett 1992; Covich 1988). Biodiversity studies of transition zones, such as the stream-soil transition zone in this study, are critical because these areas are functionally important for the transfer of organisms, energy, and materials within landscapes (Wagener et al. 1998; Freckman et al. 1997). I have shown that nematodes, rotifers, and tardigrades assemble into distinct, low diversity communities in a transition from stream sediments to soils in the McMurdo Dry Valleys.

Total invertebrate abundance was not correlated with moisture in these soils and sediments, demonstrating that within the range encountered (19.6 - 0.6% gravimetric) low moisture did not limit invertebrate habitat suitability, particularly for nematodes. However, the distribution of

individual groups of invertebrates was correlated with moisture, influencing the taxonomic richness of the communities found. *Eudorylaimus*, *Plectus*, tardigrades, and rotifers were associated with high moisture habitats and may be adapted to flowing streams. *Scottnema* abundance was higher in the drier soil habitat along the transects, and soils (32 m) contained low diversity, predominantly single-species nematode communities. This suggests that *Scottnema* is an organism adapted to extremely arid conditions. *Scottnema* was not found in the stream center, and *Plectus* was not found in the soils.

The clear separation of habitats based on moisture content suggests that these dry valley invertebrates are adapted to specific niches, perhaps based on food sources and/or survival strategies. Algal communities in dry valley stream sediments were dominated by different species in sediments under flowing water and the adjacent hyporheic sediments (Alger et al. 1997) suggesting that the environment changes greatly with short distances out from the center of the stream. The abundance of *Scottnema*'s bacterial food source may be higher outside of the stream, and/or this organism's survival strategy (anhydrobiosis) may help it persist in the extreme soil environment. In addition, *Macrobiotus*, the genus of tardigrade found in the stream sediments, is known to be predaceous on nematodes in other systems (Hallas and Yeates 1972). Although *Plectus* and *Eudorylaimus* co-occur with tardigrades in stream sediments, colonization of soils by *Scottnema* may

provide escape from predation, as the majority of tardigrades were found in the stream center.

Eudorylaimus antarcticus is the only invertebrate that was found across the transition zone in the stream sediment, hyporheic zone, and soil habitats. This breadth of habitat may be linked to the nematode's feeding strategies. *Eudorylaimus* is believed to be an omnivore/predator (Yeates et al. 1993), feeding on juvenile nematodes, other invertebrates, and/or algae. *Scottnema* and *Plectus* were never found in the same sample, except in the presence of *Eudorylaimus*. The finding that they do not co-occur unless a common predator is present could be due to indirect effects of predation. Sharing a common predator can allow two species to coexist because as predators reduce the abundance of competitors, density-dependent competition for resources is lessened (Whooton 1994).

Although survival strategies are an important aspect of ecology in the Antarctic, few field studies of invertebrate communities have included analysis of whether organisms were active or anhydrobiotic. Many invertebrates have freeze-tolerant and desiccation resistant stages, such as anhydrobiotic states (Wharton and Block 1993; Pickup and Rothery 1991). In this study, anhydrobiosis of nematodes was correlated with declining moisture and increasing electrical conductivity, suggesting that anhydrobiosis is probably an important aspect of the ecology of nematodes in the dry valley

soils. Although it is not known how long these organisms must remain in anhydrobiosis, the high population density and persistence of *Scottnema* in the dry valley soils is an incredible biological feat, undoubtedly related to the extent of this organism's ability to employ anhydrobiosis.

The hyporheic zone (8-24 m) was characterized by declining moisture with distance from the stream center and areas of high salinity. Over time, salts accumulate at the perimeter of the hyporheic zone, defining the boundary to the soil environment (around 16 - 24 m for this stream). Invertebrate richness was low through the hyporheic zone compared to the stream center, although the only samples containing co-occurring *Scottnema*, *Plectus*, and *Eudorylaimus* were found here. Seasonally varying moisture and salinity in the hyporheic zone caused by variation in stream flow may increase habitat heterogeneity and facilitate the coexistence of nematode species. Small-scale disturbance and environmental heterogeneity are believed to be important mechanisms promoting nematode species diversity in soils by reducing the strength of competitive interactions among species (Wall and Moore 1999; Ettema 1998). However, invertebrate abundance was so low through the hyporheic zone that is difficult to make strong connections between environmental factors and invertebrate diversity here. Overall, the relative richness of invertebrate communities in the stream center suggests that invertebrate diversity in this stream/soil transition zone

was related to moisture-dependent productivity, which was highest in the stream center (highest chlorophyll *a* concentrations).

Salinity was an important variable affecting the distribution of dry valley invertebrates and was correlated negatively with the abundance of most invertebrate groups. Freckman and Virginia (1997) found the average salinity for 44 soils from the Dry Valleys that did not contain nematodes was 1000 μmhos cm^{-1} (1:5 slurry). These results and the results of regression analyses suggest that there may be salinity thresholds limiting habitat suitability for invertebrates in the Dry Valleys.

The comparison of the upper, middle, and lower transects sampled in this study suggest that intermediate reaches of the stream's course may be the best habitat for dry valley invertebrates. Nutrient concentrations (i.e., nitrate) usually decline and organic nitrogen increases as dry valley streams flow downstream (Howard-Williams et al. 1989) suggesting that algal productivity increases or that some algal productivity is transported downstream. In this study, invertebrate abundance was highest across the middle transect, and could be related to patterns of algae abundance and nutrient concentrations typical of this landscape position. At the lower stream transect, high salinity at many locations reduced invertebrate abundance, and along the upper transect flow volume may have been too high for communities of sediment invertebrates to establish. However, no differences in chlorophyll *a* content

were discerned between the upper, middle, and lower stream reaches in this study.

CONCLUSIONS

In the McMurdo Dry Valleys, the stream to soil transition zone has a strong influence on invertebrate biodiversity, and knowledge of biodiversity patterns in these soils and sediments is helping to develop a landscape perspective on distribution of soil biota in the dry valley ecosystem. Environmental gradients of moisture and salinity created through stream to soil transition zones influence the diversity and activity of invertebrate communities in dry valley soils and sediments. Moisture gradients and salt deposition correlate to shifts in invertebrate communities from the high diversity stream habitat to the low diversity soil habitat. Low moisture does not limit the abundance of invertebrates, however, and in soils, a single nematode species, *Scottnema lindsayae*, composes over 99% of the invertebrates present. Understanding the factors that influence diversity of biological communities is a challenge to the field of ecology. Invertebrate communities in the soils of the McMurdo Dry Valleys of Antarctica are useful for ecological study because the research is not constrained by an overwhelming degree of taxonomic complexity, as in temperate systems. Studies of biodiversity across environmental gradients, like the stream/soil

interface of this study, should help to resolve questions about the factors influencing biodiversity at landscape scales.

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Table 1: ANOVA Results for the Relationship Between Location and Soil and Sediment Properties[a]

Dependent Variable	Source	df	F	P	Model R^2
Electrical Conductivity	Distance	4	7.96	0.0012	0.91
	Transect	2	46.69	0.0001	
	Distance x Transect	8	3.28	0.0023	
Moisture Content	Distance	4	15.75	0.0001	0.87
	Transect	2	9.01	0.0027	
	Distance x Transect	8	2.96	0.034	
Chlorophyll *a*	Distance	4	3.17	0.032	0.36

[a]Distance is distance from stream center (0, 8, 16, 24, or 32 m), and Transect is transect location (upper, middle, lower).

Table 2: Invertebrate Abundance by Transect Location[a]

(#/kg)	Upper	Middle	Lower	df	F	P	R^2
Total invertebrates *	720.7 a	2074.6 b	1412.6 a	2	6.97	0.0036	0.34
Total Nematodes *	518.6 a	1532.6 b	1174.2 a	2	6.75	0.0042	0.33
Scottnema *	122.9 a	1007.1 b	661.0 a	2	4.24	0.025	0.24
Eudorylaimus	211.6 a	355.7 a	318.4 a	2	3.16	0.059	0.19
Plectus	184.1 a	169.8 a	194.9 a	2	2.96	0.069	0.18
Nematodes living (%) *	59.3 a	66.9 a	49.2 b	2	3.65	0.044	0.26

[a]Values are means; n = 10 samples/transect * denotes a significant difference among transects. Values within a row that share the same letter are not significantly different ($P > 0.05$, Student-Neuman-Keuls Multiple Range Test).

Table 3: Multiple Regression Analyses Relating Invertebrate Abundance to Environmental Factors (n = 30 samples)

Dependent Variable		P	Relationship
Total Invertebrates	Water	0.96	
	Salinity	0.0001	−
Total Nematodes	Water	0.65	
	Salinity	0.0001	−
Scottnema	Water	0.0001	−
	Salinity	0.003	−
Eudorylaimus	Water	0.0001	+
	Salinity	0.035	−
Plectus	Water	0.0001	+
	Salinity	0.027	−
Tardigrades	Water	0.0001	+
	Salinity	0.060	
Rotifers	Water	0.001	+
	Salinity	0.31	

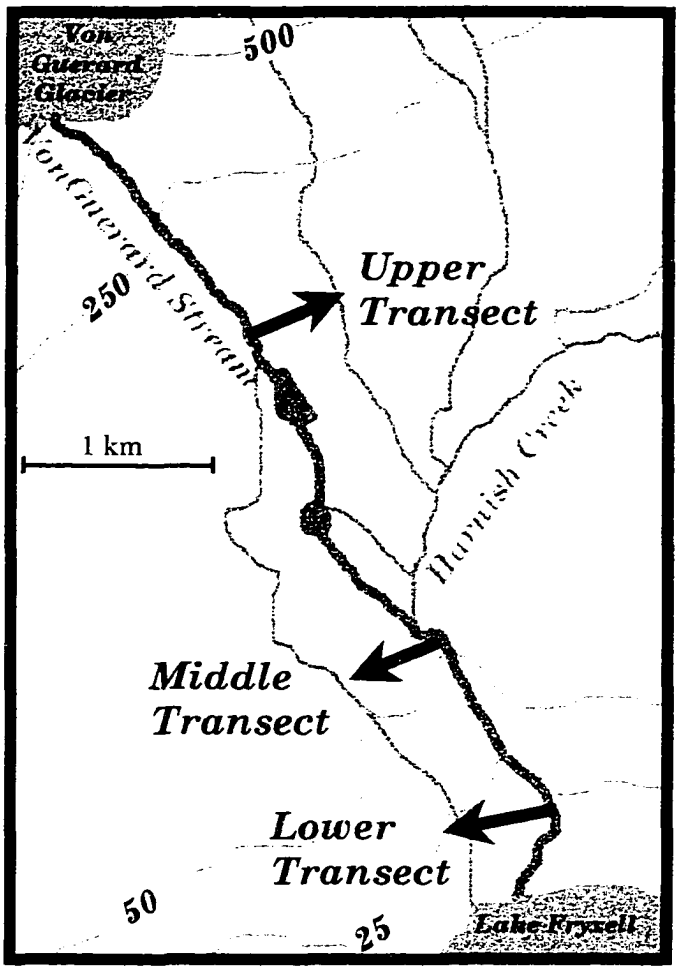

Figure 1: Map of the Von Guerard Stream/Harnish Creek network in Taylor Valley, Antarctica. Transect locations for this study and orientation are shown with arrows (➡). Elevation contours are in meters. (Upper Transect: 77°37.968'S, 163°8.178E; Middle Transect: 77°36,946'S, 163°14.975'E; Lower Transect: 77°37.328'S, 163°14.975'E)

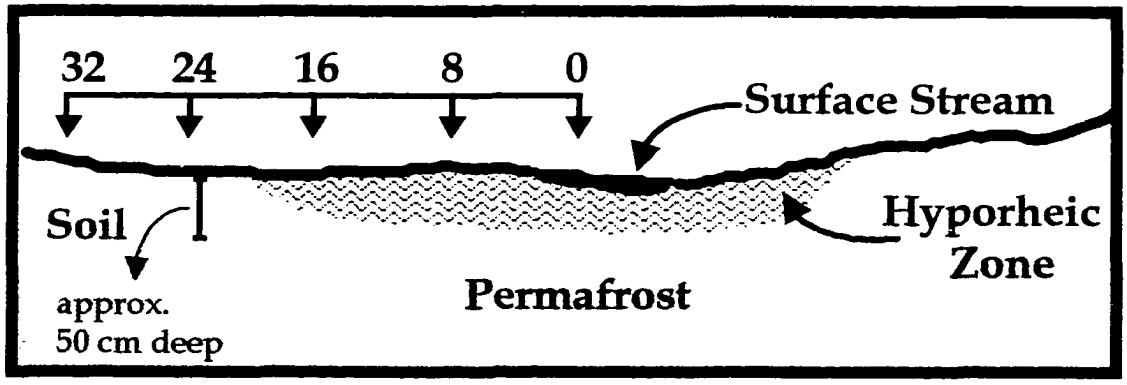

Figure 2: Cross section of a dry valley stream showing the orientation of sampling transects. Distances are in meters.

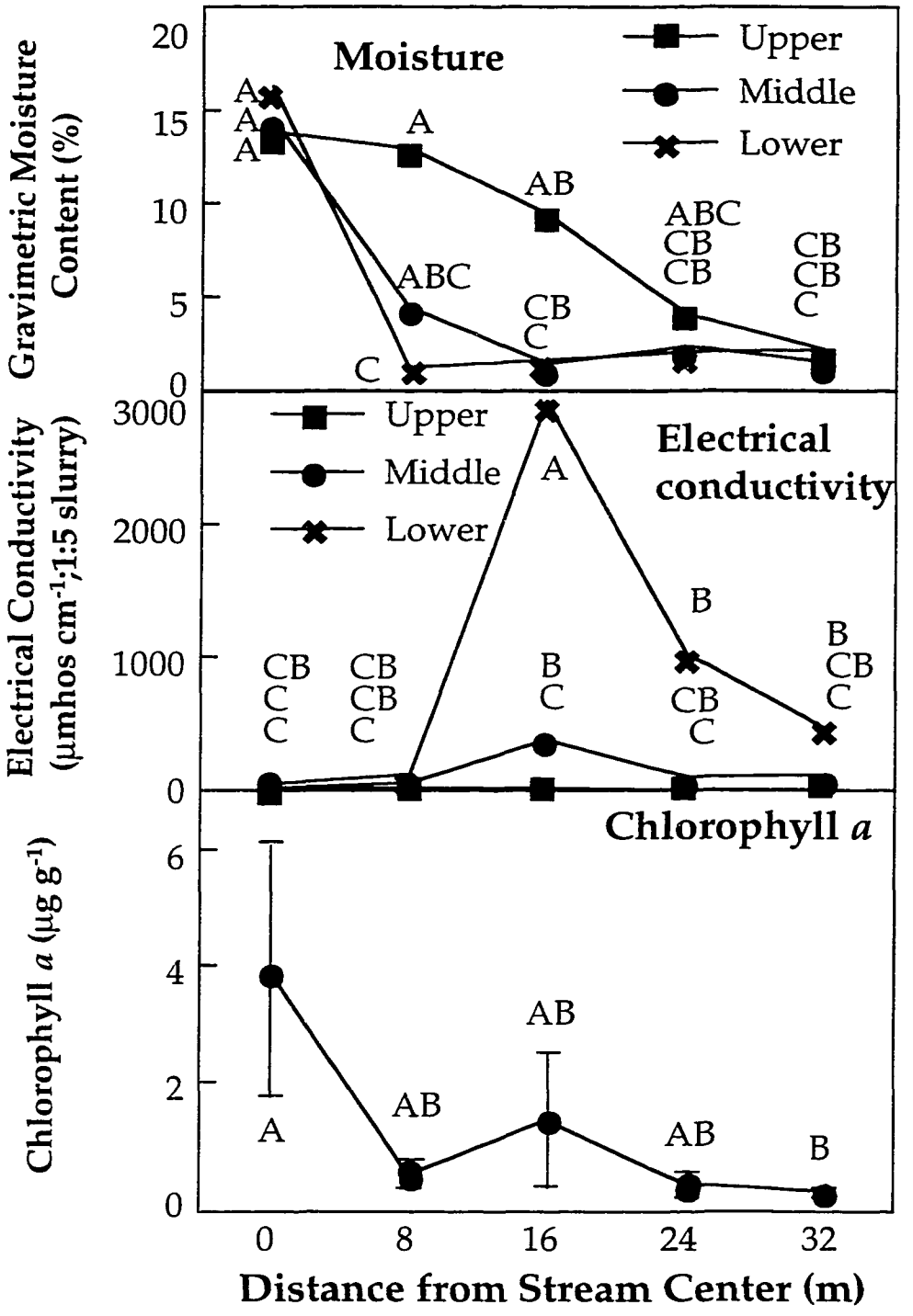

Figure 3: Soil and sediment moisture, electrical conductivity (EC), and chlorophyll *a* concentration by location. Between points within each graph, values with different letters are significantly different ($P < 0.05$, Student-Neuman-Keuls Multiple Range Test). Moisture and EC values are the means for two samples taken at each distance by transect location. Chlorophyll *a* values are the average of six samples/distance. Error bars represent ± 1 SE.

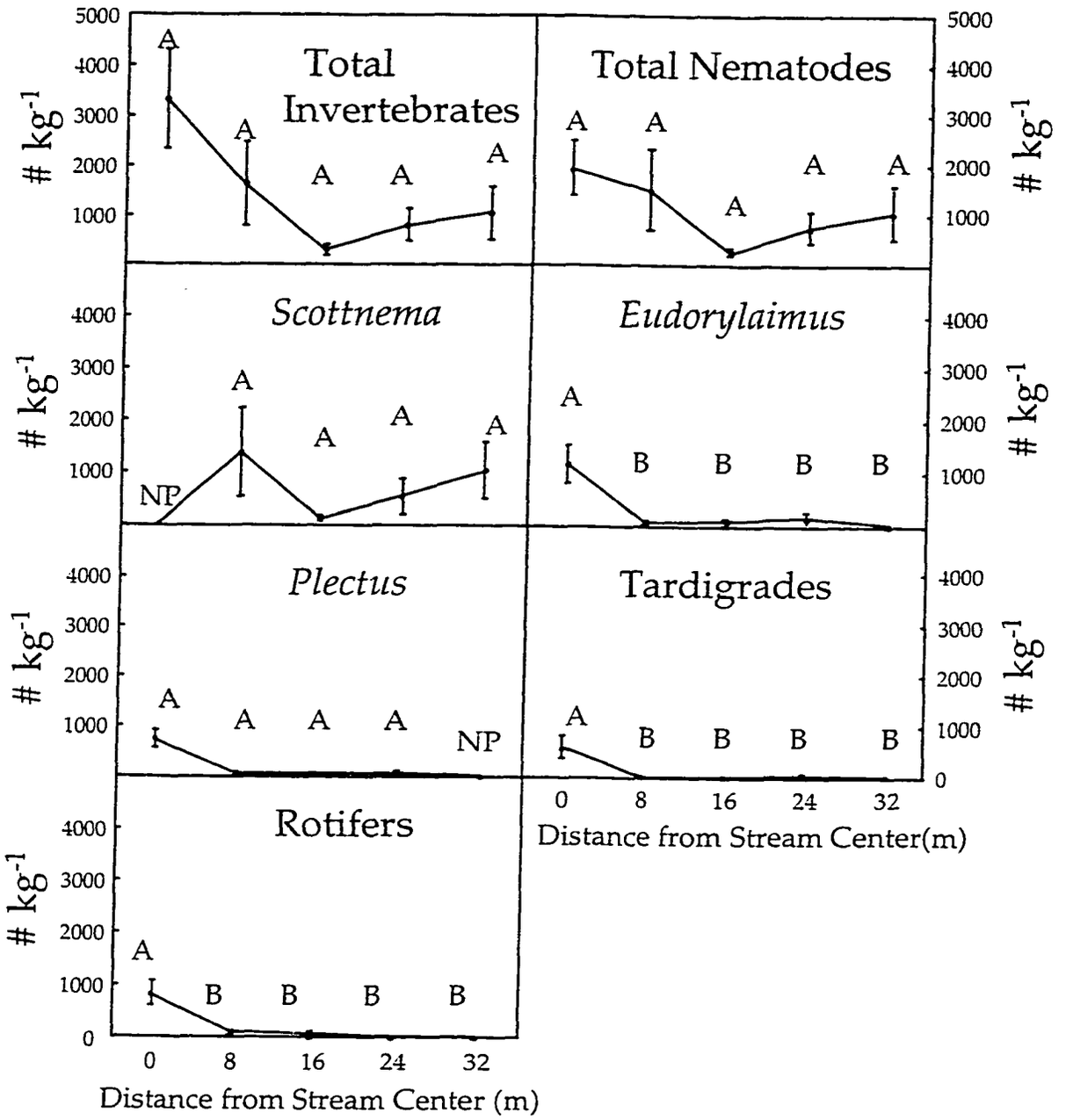

Figure 4: Invertebrate abundance by distance from the stream center (n=6 samples/distance). Within a graph, values with different letters are significantly different ($P < 0.05$, Student-Neuman-Keuls Multiple Range Test). Error bars represent ± 1 SE. NP = Not present at this location.

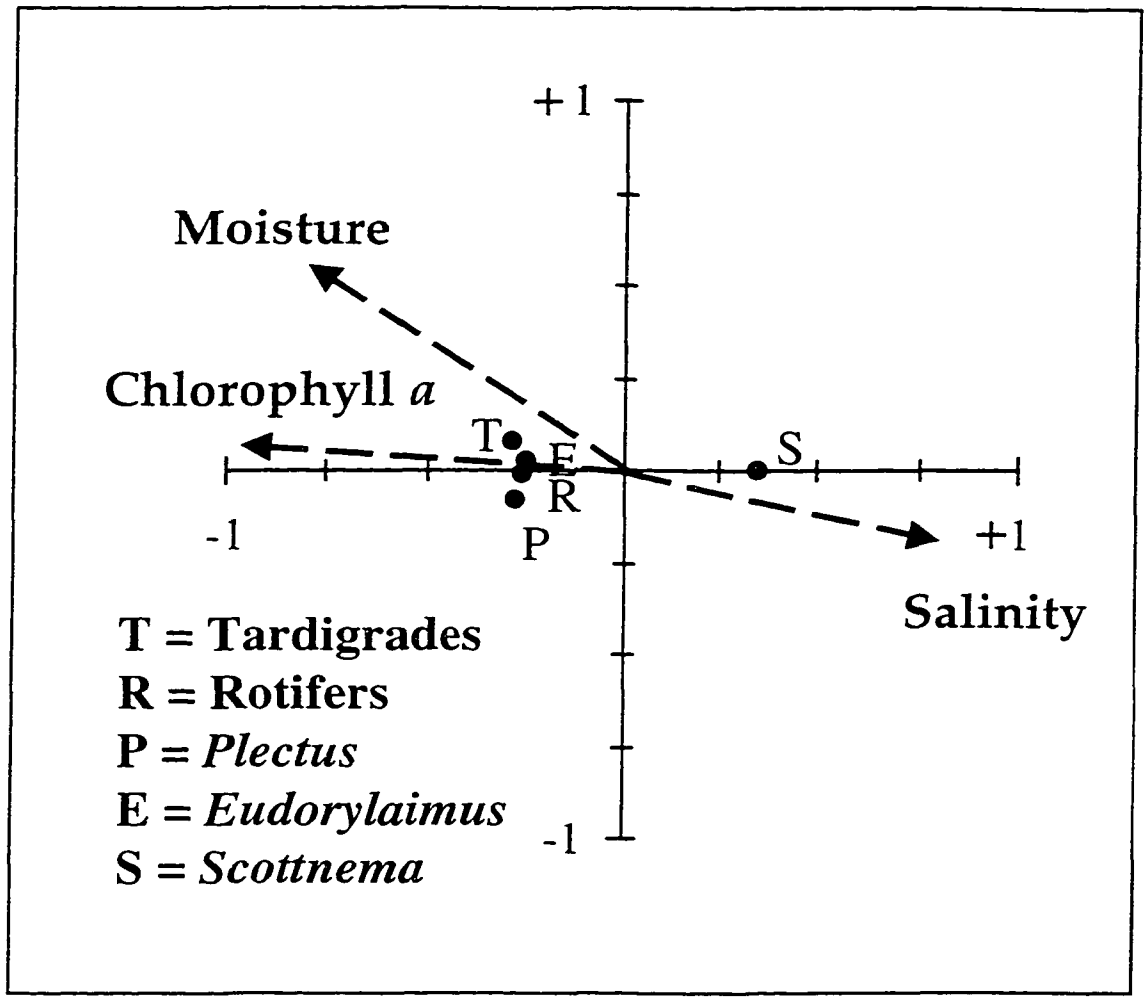

Figure 5: Species-environment biplot of invertebrate groups (•) and environmental variables (arrows). The first canonical axis is horizontal and the second is vertical. Arrows point in the direction of maximum change and their length is proportional to the rate of change. Moisture content ($r = -0.84$), salinity ($r = 0.64$), and chlorophyll *a* concentration ($r = -0.99$) were significantly correlated ($P < 0.001$) with the first canonical axis. Therefore, along the horizontal axis, the negative direction represents increasing moisture and chlorophyll *a* concentration and decreasing salinity. Moisture content was significantly correlated ($r = 0.53$, $P < 0.01$) with the second canonical axis.

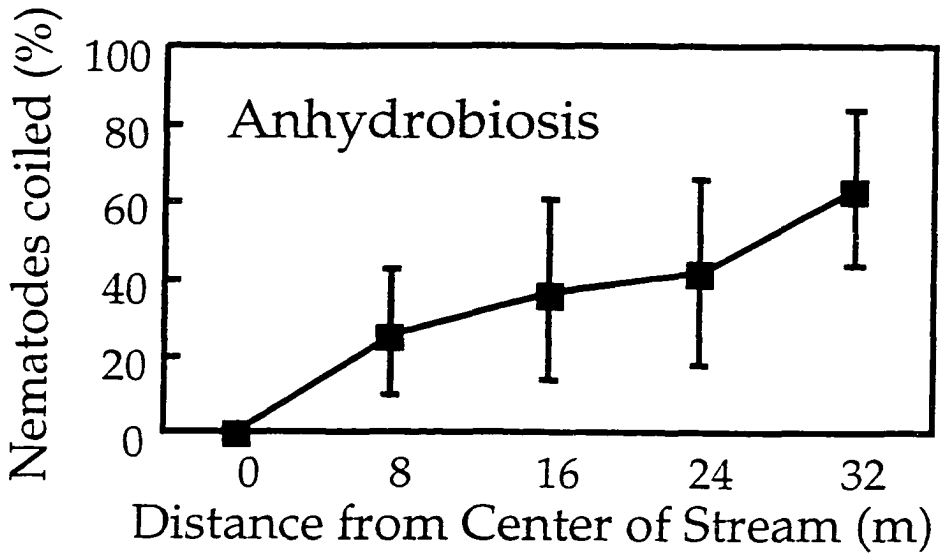

Figure 6: The proportion of nematodes coiled and anhydrobiotic by distance from the stream center. Error bars represent ± 1 SE (n = 6 samples/distance).

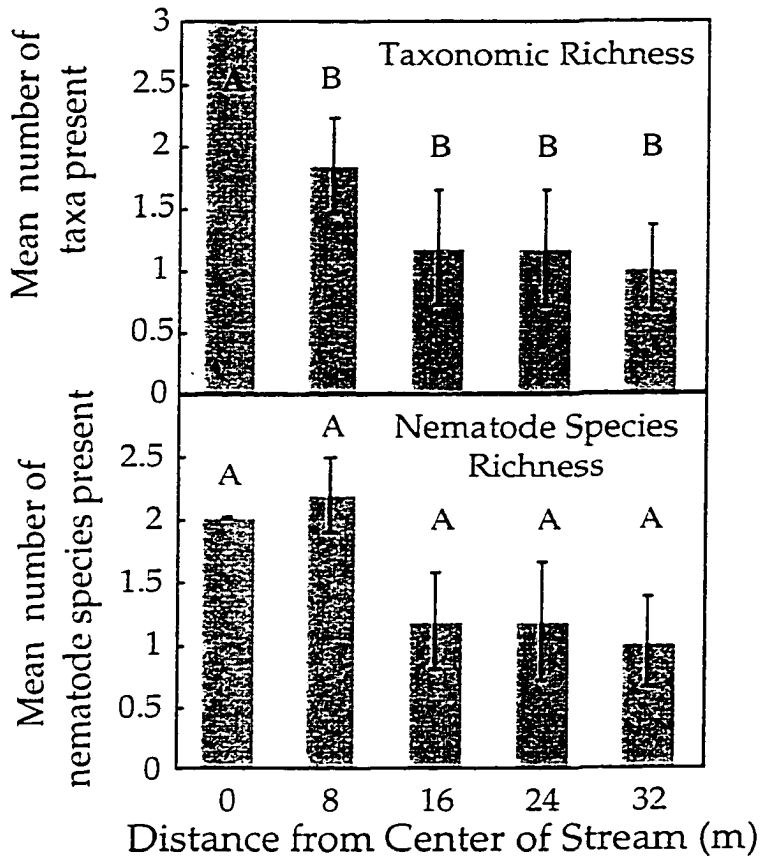

Figure 7: Richness of invertebrate communities (represented by the mean number of taxa or nematode species found) by distance from the stream center. Within a graph, values with different letters are significantly different ($P < 0.05$, Student-Neuman-Keuls Multiple Range Test). Error bars represent $\pm$ 1 SE (n = 6 samples/distance).

CHAPTER V:

Microcosm and field studies of decomposition in Antarctic cold desert soils

(To be submitted to the journal *Oikos*)

ABSTRACT

In the extreme cold desert environment of the Antarctic Dry Valleys, I studied the effects of changing moisture and temperature on rates of cotton strip decomposition and the activity and abundance of soil organisms. I hypothesized that moisture would be the primary factor limiting processes and biota in these arid soils. In microcosms incubated at 10°C for 9 months, rates of soil microbial respiration, nitrification, and cotton strip decomposition were accelerated in soils that were wetted to 10% gravimetric soil moisture content compared to soils at 0.6%. Soil bacteria, protozoa, and live nematode abundance were unchanged by the addition of water. This suggests that the potential rates of decomposition measured in moist soils in microcosms were a function of increased biotic activity, and that decomposition was not limited by the low diversity and abundance of soil biota. In the field, at two sites with different moisture regimes, nematode abundance was unchanged by soil warming, precipitation exclusion, and/or annual moisture pulses over the duration of the study. In the same plots, decomposition of cotton strips did not occur after two years in the ground, even with soil warming and addition of moisture. Rather than decomposing, many cotton strips actually gained tensile strength, particularly in water-amended plots at both sites. Abiotic (mineral impregnation) and biotic (microbial extracellular polysaccharide production) processes may be

stregthening the cotton strips under these treatments. Multiple factors control decomposition rates in terrestrial ecosystems, including climatic factors, the composition of the soil food web, and substrate quality. In the dry valleys, decomposition potential appears to be high, as indicated by microcosm results. In the field, however, environmental conditions may limit this process.

INTRODUCTION

Understanding ecosystem processes in extreme environments is an area of growing research, due to the increasing interest in these habitats and the organisms they contain. Little is known, however, about decomposition rates in the terrestrial environment of the McMurdo Dry Valleys of Antarctica - the coldest, driest, and windiest ecosystem on Earth. Knowledge of the nature of processes such as decomposition in extreme environments is key to understanding their ecosystem structure and function. Decomposition of organic material into inorganic forms (e.g. CO_2, NH_3) is a fundamental soil process that is performed by decomposer soil microbes and regulated by their invertebrate grazers (Freckman 1988). Temperature and moisture are the primary controls of decomposition rates in terrestrial ecosystems (Schlesinger 1997; Raich and Schlesinger 1992; Meentemeyer 1978) because these variables influence the activity of the soil decomposer community.

In the dry valleys, extremes of both desiccation and frigid temperatures may both limit the decomposition process by reducing biological water availability (Priscu 1998). This is not unlike extreme hot desert environments, where moisture limitations also exist that limit ecosystem processes (Somme 1995; Parker et al. 1984). In this research, I studied the potential rates of soil processes (decomposition, nitrogen mineralization, soil

microbial respiration) in microcosms containing Antarctic Dry Valley and Chihuahuan Desert soils. My objective was to determine how decomposition and soil communities differ in these two soil types. I also wanted to determine if moisture limits decomposition in dry valley soils. I tested the hypotheses that cotton strips could potentially decompose in dry valley and Chihuahuan Desert soils, and that the potential rates of decomposition, nitrogen mineralization, and soil microbial respiration would be accelerated in dry valley soils by addition of moisture. I also hypothesized that respiration rates would be higher in microcosms with cotton strips than without, providing evidence that the soil microbes are carbon-limited.

In a similarly designed field experiment in the dry valleys, I tested the hypothesis that low moisture and temperature limit the rates of decomposition of cotton strips and the activity of soil nematodes. I manipulated the soil temperature of field plots with open- and closed-top warming chambers and ammended plots with water. This hypothesis was further tested by contrasting two field sites with different moisture and temperature regimes. I predicted that decomposition of cotton strips would be highest in soils that were warmed and wetted and at the wetter field site, where nematodes would be less likely to be found in an inactive, anhydrobiotic state.

To measure decomposition rates, I used the loss of fabric tensile strength from cotton strips, which are pieces of fabric that are inserted vertically into the soil and left to degrade over time (Harrison et al. 1988). Rather than measuring the loss of strip mass through time, the strength of the strip fibers is determined by measuring the amount of energy required to rip the strips with a tensometer. This is a more sensitive indicator of decomposition that is particularly appropriate for extreme environments, where rates of decomposition are predicted to be slow. Although cotton strips are a novel substrate for dry valley decomposer organisms, the use of a standardized substrate within and between ecosystems provides a useful measurememt for comparison of deocomposition rates.

STUDY SITE

The McMurdo Dry Valleys of Antarctica, including Taylor Valley (77°S 163°E), the site of this research, compose one of the most extreme terrestrial environments on Earth. This area is part of the 2% of the continent free of permanent ice cover (Campbell and Claridge 1987). The mean annual dry valley air temperature is - 20°C (15°C to - 45°C, range) (Clow et al. 1988), and precipitation (snowfall) on the valley floors is approximately 10-cm water equivalent, most of which sublimates rather than melting (Bromley 1988). Major geomorphic features of the dry valleys include large expanses of barren, rocky soils, alpine glaciers, permanently ice-covered lakes, ephemeral

streams, and glacial meltponds. Soils spatially dominate the landscape (Burkins et al. in review) and are poorly-weathered, often saline, and have a dry or ice-cemented permafrost layer at approximately 50-cm depth (Bockheim 1997; Campbell and Claridge 1987). Dry Valley soil organic C content is low (< 1%), due in part to the lack of macrophytic vegetation (Burkins et al. in revision; Freckman and Virginia 1997). Sources of organic C are believed to include relict organic material deposited during paleolake stands, 11-23,000 ybp (a recalcitrant pool), and/or small amounts of *in situ* photosynthesis by cyanobacteria or algae (a labile pool)(Burkins et al. in revision).

Nematodes are the most abundant soil animal in the McMurdo Dry Valleys and were found by Freckman and Virginia (1998) in 65% of soils analyzed across four valleys, with rotifers and tardigrades also present in some soils (< 10%). A bacterial-feeding species of nematode dominates invertebrate communities in soils--*Scottnema lindsayae* (Chapter IV, this disseration; Virginia and Wall, in press; Powers et al. 1998; Freckman and Virginia 1998, 1997). *Eudorylaimus antarcticus* (believed to be an omnivore/predator) and two *Plectus* spp. (microbivorous) are also found (Freckman and Virginia 1998, 1997). Other microbial grazers found in dry valley soils include tardigrades and rotifers, which are primarily confined to the sediments of glacial melt-fed ponds and streams (Chapter IV, this

dissertation; Schwarz et al. 1993), and protozoa (mainly flagellates and amoebae) (Bamforth 1996).

Anhydrobiosis is an inactive state that is a specific survival strategy employed by soil nematodes and other invertebrates in response to desiccation (Crowe and Madin 1974). Anhydrobiosis allows nematodes to colonize a soils in the dry valleys with a wide range of properties (Chapter III, Chapter IV; Wall and Virginia in press). Nematodes in anhydrobiosis lose 95-99% of their body water content, cease metabolic activity, and are protected from environmental stress (Crowe and Madin 1974). These and other physiological changes (see Higa and Womersley 1993) are accompanied by morphological change - a coiling of the vermiform body that has been used to identify individuals extracted from soils as being anhydrobiotic (Freckman et al. 1977). The proportion of nematodes coiled in soils can be used as an indicator of biological activity (Chapter III, this dissertation).

METHODS

I studied decomposition of cotton strips and communites of soil nematodes in a nine-month laboratory microcosm experiment and in a two-year field experiment designed together to isolate the contributing factors controlling decomposition. My treatments involved manipulation of the

factors that are believed to limit biological activity in the dry valleys: water and temperature.

MICROCOSM EXPERIMENT

Soil was collected from multiple locations in the Bonney, Hoare, and Fryxell basins of Taylor Valley in the McMurdo Dry Valleys to a depth of 10 cm, placed in sterile Whirl Pak® bags, and kept in insulated coolers while in transport to McMurdo Station laboratory facilities in Antarctica (Freckman and Virginia 1993). These soils were shipped frozen (- 20°C) to the Natural Resource Ecology Lab at Colorado State University, Ft. Collins, CO, where they were kept frozen until used for this experiment (up to 24 mo). Soils were collected from multiple sites in Taylor Valley and then combined so that the soil used for microcosms would be representative of the dry valleys as a whole, rather than if soils had been selected from specific sites. Blending soils from multiple sites also ensures that microcosms are homogenous.

Soils was also obtained from interplant spaces in a mesquite copice dune vegetation zone (Virginia et al. 1992) at the Chihuahuan Desert Jornada Basin National Science Foundation Long-Term Ecological Research site (32°30'N, 106°30'W) to use for reference microcosms. These soils are dry and have low organic content, providing a hot desert analogue for the dry valley soils. The Jornada is located near LasCruces, NM in the northern region of

the Chihuahuan Desert. The mean annual air temperature is 14.6°C (range 4.0 to 26°C), and annual precipitation is 23 cm rainfall (Greenland 1987). To homogenize soils for allocation to microcosms, soils were bulked by pooling 100-200-g subsamples of the original dry valley or Chihuahuan Desert soils. Pooled subsamples were sieved through an autoclave sterilized 2-mm screen in a laminar flow hood to remove rocks and mixed to produce the bulked soils that were allocated randomly to microcosms. Microcosms consisted of 0.35-l (12-oz.) sterilized glass jars with threaded lids (Ball, Corp., Broomfield, CO). Sixteen microcosms contained 225-g soil (wet weight) from the dry valleys, and eight contained 175-g (wet weight) from the Chihuahuan Desert.

Cotton strips were used to assess decomposition rates using the standardized methodology of Harrison et al. (1988). Loss of fabric tensile strength relative to sterile controls is proportional to the decomposition of the fibers. The cotton strips were autoclaved before and after incubation to ensure that no biotic degradation occurred outside of the microcosms. Testing showed that autoclaving did not change the tensile strength of strips. The strips (6 x 5 cm) were cut from Shirley Soil Burial Test Fabric (Shirley Institute, UK), and a single strip was inserted vertically into the soil in each microcosm.

Treatments were factorially applied to the microcosms at the initiation of the experment, and included inserting a cotton strip into the soil or adding

water (Table 1, n=4 replicates per treatment). The water-amendment treatment consisted of pipetting 20-ml 0.2 μm filter-sterilized water into the jars. This brought the soil moisture to 9.93% ± 0.14, a value typical of Taylor Valley soils near lakes, glacial meltponds and streams (Freckman and Virginia 1997). Jars were incubated at 10°C in a dark incubator. This temperature was selected in order to assess potential decomposition rates by removing the temperature limitations imposed by the -20°C average annual dry valley temperature. At the same time, I wanted to use a temperature that occurs in the natural environment, and soil temperatures may frequently be at or above 10°C during the austral summer months (Chapter III, this dissertation). Microcosms were destructively sampled after nine months.

Soil moisture, organic C, total N, NH_4^+ and NO_3^- concentrations were measured for the 10 dry valley and four Chihuahuan Desert bulked soils that were randomly allocated to the microcosms (Table 2). Soil moisture content was measured gravimetrically for 25-g soil after 48 h at 110°C (Gardner 1987). Ten-g of soil from each bulked soil were finely ground for analyses of total soil carbon and nitrogen at Dartmouth College, NH using a Carlo Erba (Milan, Italy) elemental analyzer. For organic carbon determination, carbonate and bicarbonate were removed from the samples by treatment with HCl. Treated samples were then analyzed for the remaining organic carbon. KCl (2N)-extractable NH_4^+ and NO_3^- concentrations were determined using an

automated ion analyzer (see Virginia et al. 1992 for more detailed description of soil analytical methods).

POST-HARVEST MEASUREMENTS

Soil microbial respiration was measured immediately prior to destructive sampling. The CO_2 concentration of a 5-ml headspace gas sample withdrawn with a syringe from each of the jars through a plastic septa after a 72-h incubation period was determined using an infra-red gas analyzer (Licor Model 5262, Lincoln, NE). Prior to closing the microcosms for this incubation period, they were flushed with compressed air containing 550 ppm CO_2 to ensure that all the microcosms began with the same concentration of CO_2.

At the time of destructive sampling of microcosms, cotton strips were removed from the microcosms and rinsed with tap water to remove soil. A 2-cm width portion of each strip was cut from the center for measurement of tensile strength with a tensometer (Instron, Canton, MA) equipped with a 250-kg load cell (Harrison et al. 1988). The remaining soil in the microcosms was mixed with a flame-sterilized spatula and then weighed and subdivided for analyses.

Five-g soil samples were used to estimate bacterial cell density by direct counts after staining soil smears (1:50 dilution) with DTAF (5-(4,6-

dichlorotriazin-2-yl) aminofluorescein (Bloem et al. 1995). The number of bacterial cells and their dimensions were determined with epifluorescent microscopy using image analysis and converted to biomass (Schmidt and Paul 1982). Nematodes were extracted from 100 g of soil with a sugar flotation/ centrifugation method (Freckman and Virginia 1993) and quantified within 48 h with a light microscope (25-50 X). Nematodes were classified as living or dead on the basis of movement. Total protozoa (active and encysted) were estimated by the most-probable-number method (Ingham 1994). Five g of soil were dispersed in 50-ml sterile water on a vortex mixer for two min and diluted serially (1:10) five times into 0.9-ml sterile nutrient broth (2%) made with dry valley soil extract. One-ml aliquots of each dilution were added to 24-well cell culture plates. Plates were incubated at 10°C, and each dilution was observed with a phase contrast microscope (100 X) for the presence or absence of protozoans during the first, second and third weeks of incubation. Soil moisture, organic C, total N, NH_4^+ and NO_3^- concentrations were also measured for soil subsamples from each jar.

FIELD EXPERIMENT

During the austral summer 1996-97, a decomposition experiment was established at two sites in Taylor Valley, Antarctica. These two sites (Lake Hoare: 77°38'S 162°53'E and Lake Fryxell: 77°36'S 162°15'E) were selected because they were known to contain soil nematodes and because they had

different moisture regimes. Temperatures are slightly lower at Lake Fryxell than at Lake Hoare, but precipitation is predicted to by higher at Lake Fryxell (Fountain et al. in press). In addition, soils at lower elevations, or closer to lakes, tend to contain more soil organic matter (Burkins et al. in revision; Powers et al. 1998). The Lake Fryxell plot was located ≈ 25 m from the lake, while the plot at Lake Hoare was ≈ 100 yards away. The Lake Hoare site has low soil moisture, and is similar to the microcosm soils that were not water-amended. The Lake Fryxell sites were wetter, and analagous to the water-amended microcosms.

At each site, the experiment was composed of 30 1-m^2 plots in a 5 x 6-m rectangular array. Five soil manipulation treatments were allocated to six blocks in a randomized complete block design. The treatments were:

C = control
T = soil warming
TW = soil warming with moisture amendment
W = moisture amendment
D = soil warming and precipitation exclusion

Soil warming (Treatments T & TW) was accomplished using open-top conical chambers similar to those currently in use by the International Tundra Experiment (ITEX) (Marion et al. 1997) and an additional ongoing McMurdo LTER soil experiment (Wall and Virginia, unpublished). These chambers warm dry valley soil 2 - 5°C at the 5-cm depth (Marion et al. 1997), but also dry the soil slightly. Soil temperature was monitored at the 5-cm depth with temperature loggers (StowAway XTI, Onset Computer

Corporation, Pocasset, MA), at one plot for the T, D, and C treatments at both sites during the 1997-98 austral summer. The Lake Hoare site was established on 20 December 1996, and the Lake Fryxell site on 3 January 1997.

Soil moisture amendments (Treatments W & TW) were applied at the initiation of the experiment and again during the 1997-98 and 1998-99 austral summers by applying 5.6 L water to the surface of soils contained within the area of the base of the ITEX chamber (0.5 m^2). This application brought soils to a gravimetric soil moisture content of around 12%. Soil moisture was monitored by repeated sampling after application during the 1997-98 austral summer at the Lake Hoare site to assess how long moisture persisted in the amended plots. Soil warming and precipitation exclusion (Treatment D) were accomplished by placing closed-top polycarbonate chambers (32.4 x 53.0 x 15.0 cm) over the plot (Freckman and Virginia 1997) that excluded snowfall. I sampled soils on 11 January 1997 at the Lake Hoare site within 24 h of a snowfall event that amounted to 0.5-cm water equivalent of precipitation (A. Fountain, personal communication), to investigate the effectiveness of the precipitation exclusion treatment.

Cotton strips (12.7 x 6.0 cm) were inserted using spatulas into the soil in each plot to a depth of 10 cm. Previous studies have shown that 82 to 91% of the nematodes in the top 20 cm of soil are found at the 0 -10 cm depth (Powers et al. 1995). Soils and cotton strips were sampled annually over two years

(Time Zero, Year 1, and Year 2). The Lake Hoare plots were sampled on 20 December 1996, 21 November 1997, and 8 January 1999. The Lake Fryxell plots were sampled on 3 January 1997, 28 November 1997, and 9 January 1999. Soil samples (0 - 10 cm depth) were collected with plastic scoops into WhirlPak bags and transported in insulated coolers to laboratory facilities at McMurdo Station, Antarctica.

Within 72 h, nematodes were extracted from 100 g of soil in the same manner as for the microcosm experiment. The proportion of nematodes in that were anhydrobiotic (inactive) was also determined by extracting additional 100-g subsamples with the sugar flotation/centrifugation technique using a high density sucrose solution (1.25 M) (Chapter II, this dissertation; Freckman et al. 1977). Coiled morphology of the nematodes extracted by this method indicated that they were inactive at the time of extraction (Bird and Butrose 1974; Crowe and Madin 1974). Uncoiled nematodes were assumed to be active or dead. Soil moisture was determined gravimetrically on all samples, and soil organic C and total nitrogen were measured for six untreated samples from each site at the initiation of the experiment (Table 3).

STATISTICAL ANALYSES

Statistical analyses were performed using SAS System Release 6.12, with reference to Cody and Smith (1997) and Sokal and Rohlf (1995). For the

microcosm experiment, results were analyzed with one-way ANOVA. Means were compared between treatments using Fisher's protected least significant difference (PLSD) method, and means were considered significantly different at the $\alpha = 0.05$ level. For the field experiment, repeated measures ANOVA was used to test for significant sources of variation in dependent variables through time, by treatment, and by the interaction between time and treatment. The Lake Hoare and Lake Fryxell experiments were analyzed separately. For all repeated-measures ANOVAs in which there were significant treatment or time by treatment interaction effects, I conducted further analyses to determine at which sampling dates treatments effects were significant. For each sampling date, I performed individual ANOVAs and compared treatment means using Fisher's PLSD.

RESULTS

MICROCOSM EXPERIMENT

After nine months of incubation, treatment effects explained significant proportions of the variation between the microcosms for microbial respiration, tensile strength loss, soil moisture, organic carbon and total nitrogen content, NO_3^- concentration, protozoan density, and nematode abundance (living + dead) (ANOVA, Table 4). Cotton strip tensile strength loss (TSL) was higher in the DV H_2O microcosms (62.1%) than the DV (17.9%), but neither value was significantly different than the CH microcosms

(47.8%) (Figure 1). Therefore, while a measurable amount of decomposition occurred at ambient moisture content, this process was accelerated by the addition of moisture to the soils.

Soil microbial respiration was highest in the DV H_2O strip microcosms (0.126 μmol CO_2 g^{-1} soil d^{-1}) (Figure 1). Soils with strips (DV strip and CH strip) had significantly higher respiration rates than those without (DV and CH), and water-amended DV soils had higher respiration rates than the dry soils (DV H_2O v. DV) (Figure 1). DV microcosms had the lowest soil microbial respiration rates measured (0.0018 μmol CO_2 g^{-1} soil d^{-1}). Soil NO_3^- content was higher in DV H_2O microcosms (5.14 mg kg^{-1}) than for soils that were dry (0.623 mg kg^{-1}) (Table 5). In DV soils with cotton strips (DV H_2O strip v. DV strip), this difference is not as great (2.61 v. 0.523 mg kg^{-1}) (Table 5).

The total number of living and dead nematodes was higher in the dry DV soils than in the moist, but the number of living nematodes was not different (Table 6). Therefore, there were considerably fewer dead nematodes in the moist microcosms. The density of live nematodes in both dry valley and Chihuahuan Desert soil microcosms was 66.6 ± 14.0 nematodes kg^{-1} soil. CH microcosms contained more protozoa than DV (Table 6). Organic carbon, total nitrogen, [NH_4^+], and bacterial biomass were not different among the treatments (Tables 5,6). The number of bacterial cells averaged $1.3 \times 10^8 \pm 2.1 \times$

10^7 g^{-1}. In all microcosm treatments, nematode abundance was reduced from that of the bulked soils at the initiation of the experiment (Table 6).

FIELD EXPERIMENT

TREATMENT EFFECTS ON SOIL ENVIRONMENT

During the 1997-98 austral summer, closed-top chambers warmed the soil (5-cm depth) an average of 2.59 ± 0.12°C over controls at Lake Hoare and 4.62 ± 0.19°C at Lake Fryxell, while open-top chambers warmed the soil an average of 4.0 ± 0.21°C over controls at Lake Hoare and 6.87 ± 0.35°C at Lake Fryxell (Figure 2). The greater warming at Lake Fryxell is due to the angle of the site to the mountain peaks that compose the horizon. The valley is wider at Lake Fryxell, and this site is shaded for less of the diurnal cycle than the Lake Hoare site.

Differences in soil moisture among treatments were not detected 19 days after water was applied at the Lake Hoare site (data not shown). Therefore, the field moisture treatment served as a short-term pulse of moisture, and most likely simulates the conditions under which moisture becomes available in the field following periodic snowfall. After a 0.5-cm water equivalent snowfall, soil moisture in the closed-top chambers averaged 1.12 ± 0.3%, while moisture in the control chambers averaged 2.68 ± 0.1%, demonstrating that these chambers excluded precipitation. Treatment effects

on soil moisture were not detected at either site for any of the other sampling dates (ANOVA, df 4,20, $P > 0.05$).

TREATMENT EFFECTS ON DECOMPOSITION AND NEMATODES

At the Lake Fryxell site, neither treatment or sampling date (Year 1 or Year 2) explained significant amounts of the variability in TSL from cotton strips (Figure 3). The mean TSL for strips analyzed from this site at the end of the experiment was - 1.87% ± 0.9 (n=120). This negative TSL value indicates that strips at this site gained strength relative to control strips that were kept sterile over the one to two years that strips were in the field.

At the Lake Hoare site, significant amounts of the variability in TSL from cotton strips were explained by the interaction between treatment and sampling year (ANOVA, df 4,85, $F=3.87$, $P = 0.006$). Strips in the field for one year showed no TSL, except for Treatment W (Figure 3). Strips sampled in Year 2 had a different pattern of TSL with treatment and had either gained strength (Treatments C, TW, W) or tensile strength did not change (Treatments B &T) (Figure 3). In Year 2, the pattern of TSL was similar at Lake Hoare and Lake Fryxell (Figure 3). Treatments C, TW, and W appear to have gained tensile strength, while Treatments D & T show no change (Figure 3).

The nematodes extracted from Lake Fryxell and Lake Hoare soils, were identified as *Scottnema lindsayae*. (92.8 and 99.8% of total nematodes respectively at each site). *Eudorylaimus antarcticus* was the only other nematode species found at either site, its low abundance prevented us from analyzing the effects of treatment on this species. Nematode abundance (Table 6) was not affected by treatment at Lake Fryxell, nor did it differ through time, averaging 6780.2 ± 333.5 nematodes kg^{-1} soil. At Lake Fryxell, the proportion of nematodes that were living was not different among treatments, but more nematodes were alive across all treatments at Year 2 (88.7% ± 0.96) than at Time 0 (78.1% ± 1.2) or Year 1 (80.0% ± 1.5) (ANOVA, df 2,50, $F = 51.1$, $P \leq 0.0001$). Nematode abundance declined significantly at Lake Hoare from Time 0 to Year 2, from 1048.4 ± 76.3 nematodes kg^{-1} at Time 0, to 323.1± 38.9 kg^{-1} at Year 2 (ANOVA, df 2,50, $F = 92.6$, $P \leq 0.0001$). At Lake Hoare, the proportion of nematodes that were living (Table 3) was not different among treatments or through time.

A higher proportion (44.6%± 2.8) of nematodes were coiled and considered anhydrobiotic at the times sampled at Hoare than at Fryxell (13.5% ± 4.3), but this proportion did not change with time or treatment at either site. However, for Lake Hoare site soils sampled within 24 h of a significant snowfall, all nematodes were uncoiled in control plots (11 January 1997). Soil moisture in control plots (2.68 ± 0.1%, n=6) was elevated considerably by this

event relative to a sampling on 20 December 1996 when soil moisture averaged 0.242 ± 0.19 % for the same plots.

DISCUSSION

Soil moisture was the primary factor limiting the decomposition of cotton strips in the microcosms. Adding moisture to dry valley soils also increased soil microbial respiration rates more than just adding a strip, suggesting that the availability of water limited microbial activity to a greater extent than carbon substrate availability, despite the very low organic matter content of these soils. Soil respiration was maximized in the microcosms, however, when water and strips were both added, and secondary carbon limitations may exist in dry valley soils, as has been seen in hot deserts (Parker et al. 1984). The most important result from the microcosm experiment, however, is that the endemic dry valley soil microflora are capable of utilizing cotton strips as a substrate, even at low soil moistures.

Microbial respiration rates in microcosms ranged from 0.00178 - 0.126 $\mu molCO_2\ g^{-1}$ soil d^{-1}, with the highest rates for soils that were wetted. These values were converted to mg $CO_2\ m^{-2}\ h^{-1}$ using a bulk density of 1.85 g cm^{-3} and a depth of 10 cm (sensu Burkins et al. in review). This calculation results in a range of soil carbon flux of 42.7 - 0.605 mg $CO_2\ m^{-2}\ h^{-1}$ (Figure 4). By comparison, Parker et al. (1983) measured CO_2 flux *in situ* in the Chihuahuan

Desert for soils beneath *Larrea tridentata* canopies and reported a range of 167 - 708 mg CO_2 m^{-2} h^{-1} (Figure 4). CH microcosms respired considerably slower than this (0.936 mg CO_2 m^{-2} h^{-1}, converted using a bulk density of 1.4 g cm^{-3} and a depth of 15 cm) (Figure 4), but these soils were from interplant spaces and were incubated at 10°C, well below typical hot desert soil temperatures.

Burkins et al. (in review) measured field rates of CO_2 flux from Antarctic Dry Valley soils and obtained a mean rate (15.8 mg CO_2 m^{-2} h^{-1}) that is considerably higher than the baseline value I obtained in this study (Figure 4). This difference could be because field measurements by Burkins et al. (in review) were made during the time of the year and the diurnal cycle when temperature was optimal, and soil temperatures could have exceeded 10°C by as much as 10 degrees. In a comparison of soil respiration rates among a wide range of vegetation types by Raich and Schlesinger (1992) the desert scrub soils (e.g., Chihuahuan Desert) have one of the slowest rates, with only than the tundra and northern bogs and marshes being slower. In the dry valleys, where temperature is another limiting factor for ecosystem processes in addition to desiccation, rates of soil respiration are even lower.

In the dry valley microcosms, the significant production of NO_3^- in the water-amended microcosms was interesting, especially since changes in soil NH_4^+ concentration and total N are only marginal and weren't significant. NO_3^- in dry valley soils is believed to have an allochthonous source, arriving

via the wind from the marine environment (Campbell et al. 1998). However, these results suggest that *in situ* nitrification potentially could be substantial. In a study of nitrification potential in soils of the maritime Antarctic, Wilson et al. (1997) found that nitrifying bacteria were present but inactive in the field, and speculated that these microbes may have been transported to the Antarctic by winds from other continents. Nitrifiers in dry valley soils in the field may be similarly inactive. In the microcosms, less NO_3^- was produced in moist dry valley soils that had a cotton strip. These strips have a high carbon content (C:N ratio of 304, Leco CHN Autoanalyzer). It is likely that the nitrogen deficiency of this substrate resulted in increased nitrogen immobilization by microbes, versus soils without a cotton strip. Although the cotton strip assay is considered to be useful where slow rates of decomposition occur (Harrison et al. 1988; Heal et al. 1974) or where the use of litter bags is not feasible, a limitation to this approach is the high C:N ratio of the strips. The microcosm results suggest that microbes in dry valley soils are able to utilize latent nitrogen sources to compensate to some extent for the high C:N ratio of the cotton strips. Due to the absence of vegetation in the dry valleys, inorganic nitrogen accumulates in the soils (Campbell et al. 1998) and should be readily available to microbes in solution for uptake.

Based on the microcosm results, I predicted that I would be able to measure decomposition of cotton strips in the field, particularly at the Lake Fryxell site, where soil moisture was higher. In the field, however, significant

cotton strip decomposition was not measured for either site after two years. It is likely that the differences between the two experiments is due to differences in the total duration of biological activity. While soil temperatures during the austral summer may be >10°C on a daily basis, an average annual 5-cm-depth soil temperature of -17°C was recorded near the Lake Hoare site from 1/13/95 - 1/12/98 (MCM LTER Meteorological station data). Soil temperatures are estimated to be only above 0°C for about 55 days annually (Burkins et al. in review). Assuming that rates of decomp in microcosms apply continually when soil temperatures are above freezing, it would take about five years for decomposition of cotton strips to occur in the field to the same degree that it did in the microcosms over nine months. In the field, many cotton strips actually gained strength, possibly due to microbial activity in the initial stages of cotton strip decomposition. Microbial secretions of mucilages or networks of fungal hyphae could actually strengthen the fabric as decomposition initiates, as has been observed in other cotton strip decomposition studies (Wynn-Williams 1988; Davis 1986; French 1984). Alternatively, the impregnation of strip fibers by dissolved salts and minerals from the soil might also be able to increase the tensile strength.

Moisture regulates the activity of soil nematodes, and in this study, fewer nematodes were anhydrobiotic at the wetter Lake Fryxell site at the times samples. Nematodes were also about 10 times more abundant at this site than at Lake Hoare. I predicted that increased nematode activity would

correlate with increased cotton strip decomposition rates, but this was not the case. Again, this could be due to the "short" time scale of this experiment (two years). If cotton strips remained in the soil for several more years, differences in decomposition between the two sites may be similar to the contrast between strip decomposition in moist and dry microcosms.

I also predicted that decomposition would be accelerated during brief periods of biological activity induced by the addition of moisture pulses to field plots. The rapid response of the nematode community to a snowfall event in this study demonstrates the adaptability of these organisms to respond to moisture pulses. However, moisture pulses, as well as warming and desiccation, failed to effect changes in the soil biota or in the tensile strength of the cotton strips. Moisture pulses also did not accelerate decomposition of surface litter in a study by Whitford et al. (1986) in the Chihuahuan Desert. The authors suggested that decomposition in deserts is not dependent on large rainfall events. In the Namib Desert, however, decomposition of buried cotton strips only occurred significantly after sporadic rain, primarily due to fungal degradation and consumption by termites and beetles (Jacobson and Jacobson 1998). Jacobson and Jacobson proposed that the Namib is a more extreme desert and suggest that in the Chihuahuan Desert, soil moisture is actually available in most locations for biological activity almost year around. Therefore, the activity of decomposer biota in the Chihuahuan Desert is less coupled to large rainfall events.

Decomposition at Lake Hoare, where water was most limiting, should be most similar to the Namib at Lake Hoare. At the Lake Hoare site, nematodes were able to become active rapidly after snowfall and although not measured, probably similarly became active after I applied water amendments.

An important finding of this study is that the abundance of soil biota was also unaffected by treatments in both the microcosms and in the field. This lack of responses could possibly be due to the long life cycles and periods of inactivity characteristic of organisms in extreme environments (Convey 1997). *Scottnema lindsayae* is known to have a life cycle of 218 days at 10°C from egg to egg in the laboratory on agar plates (Overhoff et al. 1993). Under field conditions, this may translate into a long time, perhaps decades, and therefore it is reasonable that increases in the abundance of this organism were not observed over the two years of this study. The increased decomposition rates measured with water amendment in the microcosms suggest that this process is limited by activity of biota, not by their abundance or diversity. Interestingly, with water amendment in the microcosms, dead nematodes apparently became substrate for decomposition themselves as they were gone at the end of nine months. Turnover of biota in the dry valleys might be a significant source of labile carbon to sustain soil food webs.

CONCLUSIONS

Ecological processes in cold and arid environments are strongly influenced by the severe environmental conditions (Somme 1995; Gallardo and Schlesinger 1995; Wynn-Williams 1990; Vincent 1988; Block 1984). Hot and cold desert soils are both characterized by desiccation and salinity that may limit the activity of decomposer organisms that depend on biological water availability for activity (Freckman and Virginia 1998, Whitford 1989). The McMurdo Dry Valleys of Antarctica are an extreme environment with respect to climate, and this work represents the first effort to elucidate the factors controlling the rates of decomposition and the activity of decomposer biota in this ecosystem. The results of this study show that decomposition of cotton strips occurred at ambient moisture levels in microcosms, but was accelerated greatly by the addition of moisture. In the field, no decomposition was measured at two field sites with different moisture regimes, nor with soil warming and addition of moisture. Ambient rates for this process are very slow, and this result has implications for interpretation of the cycling of soil organic matter pools in this extreme environment. When conditions are favorable (moisture, temperature) and the carbon source is suitable, carbon mineralization does occur, but these conditions may occur only rarely during the austral summer, perhaps only for weeks or days (Kennedy 1993). Survival strategies, such as the anhydrobiotic survival strategy dry valley nematodes utilize, will allow communities to persist, inactive, when

conditions are not as favorable. Potential decomposition rates in the dry valleys are similar to those of hot deserts, but under field conditions, the rates of decomposition appear to be very limited.

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Table 1: Microcosm experiment treatment groups.

Microcosm Treatment Groups	Abbreviation
Dry Valley Soil	DV
Dry Valley Soil with Cotton Strip	DV strip
Dry Valley Soil - Water-Amended	DV H_2O
Dry Valley Soil with Cotton Strip - Water-Amended	DV H_2O strip
Chihuahuan Desert Soil	CH
Chihuahuan Desert Soil with Cotton Strip	CH strip

Table 2: Results of one-way ANOVAs for the microcosm experiment showing F values and levels of significance, as well as R^2 for each dependent variable measured. Treatment groups were the only source of variation investigated. (N = 4 microcosms for each of the 6 treatments, df = 5)

Dependent Variable	F	Model R^2
Microbial Respiration[§]	41.6***	0.92
Tensile Strength Loss	5.34*	0.54
Soil Moisture[§]	160.6***	0.98
Organic Carbon[§]	64.0***	0.95
Total Nitrogen[§]	10.5***	0.75
NH_4^+	0.53 ns	0.13
NO_3^-[§]	3.95*	0.52
Bacterial Biomass[§]	0.67 ns	0.07
Protozoa[§]	5.07**	0.67
Nematodes[§]	6.86***	0.66
Live Nematodes[§]	1.47 ns	0.29

[§]Natural log-transformed prior to ANOVA.
* $P<0.05$, ** $P < 0.01$, ***$P \leq 0.0001$, ns = not significant

Table 3: Soil properties and nematode abundance in bulked Dry Valley and Chihuahuan Desert soils allocated to microcosms at the initiation of the experiment.

	Dry Valley Soil	N	Chihuahuan Desert Soil	N
Soil Moisture (% grav.)	0.84	10	1.78	4
Soil Organic C (%)	0.019	10	0.129	4
Total Nitrogen (g kg^{-1})	0.020	10	0.17	4
NH_4^+ (mg kg^{-1})	0.93	6	0.79	4
NO_3^- (mg kg^{-1})	0.52	6	0.45	4
Total Nematodes (# kg^{-1})	1300.5	10	492.3	4
Living Nematodes (# kg^{-1})	845.3	10	63.5	4

Table 4: Soil properties and nematode abundance at the Lake Hoare and Lake Fryxell decomposition experiment plots in Taylor Valley, Antarctica.

	Lake Hoare	N	Lake Fryxell	N
Soil Moisture (% grav.)	0.65	30	7.0	30
Organic Carbon (%)	0.02	6	0.04	6
Total Nitrogen (g kg^{-1})	0.02	6	0.03	6
Total Nematodes (# kg^{-1})	1048.4	30	6708.2	30
Living Nematodes (# kg^{-1})	796.4	30	5346.9	30

Table 5: Soil properties in Antarctic Dry Valley and Chihuahuan Desert soil microcosms at the conclusion of a 10-month incubation at 10°C. N=4 for all variables. Treatment abbreviations are explained in Table 1.[†]

	DV	DV strip	DV H_2O	DV H_2O strip	CH	CH strip
Soil Moisture (% grav.)	0.70^{c}	0.20^{d}	10.15^{a}	9.70^{a}	1.34^{b}	1.82^{b}
Organic Carbon (%)	0.024^{b}	0.022^{b}	0.017^{b}	0.020^{b}	0.089^{a}	0.10^{a}
Total Nitrogen (g kg^{-1})	0.022^{b}	0.021^{b}	0.019^{b}	0.024^{b}	0.158^{a}	0.088^{a}
NH_4^+ (mg kg^{-1})	0.80^{a}	0.95^{a}	0.70^{a}	0.78^{a}	1.06^{a}	0.90^{a}
NO_3^- (mg kg^{-1})	0.62^{bc}	0.52^{c}	5.1^{a}	2.61^{ab}	0.37^{c}	0.55^{bc}

[†]Across each row, values marked with different superscripts differ significantly (Fisher's PLSD, $P < 0.05$).

Table 6: Soil biota in Antarctic Dry Valley and Chihuahuan Desert soil microcosms at the conclusion of a 10-month incubation at 10°C. N=4 for all variables except bacterial biomass (n=8). Treatment abbreviations are explained in Table 1.[†]

	DV	DV strip	DV H_2O	DV H_2O strip	CH	CH strip
Bacterial Biomass (μg C g^{-1} soil)	*	9.99[a]	10.61[a]	10.61[a]	*	7.24[a]
Protozoa (# g^{-1})	1.00[c]	4.10[bc]	2.70[c]	2.93[c]	22.63[a]	21.20[ab]
Total Nematodes (# kg^{-1})	738.0[ab]	1051.3[a]	87.5[d]	112.2[cd]	222.1[bc]	177.0[cd]
Live Nematodes (# kg^{-1})	60.2[a]	125.2[a]	32.8[a]	24.6[a]	70.6[a]	86.1[a]

[†]Across each row, values marked with different superscripts differ significantly (Fisher's PLSD, $P < 0.05$).
*Not determined

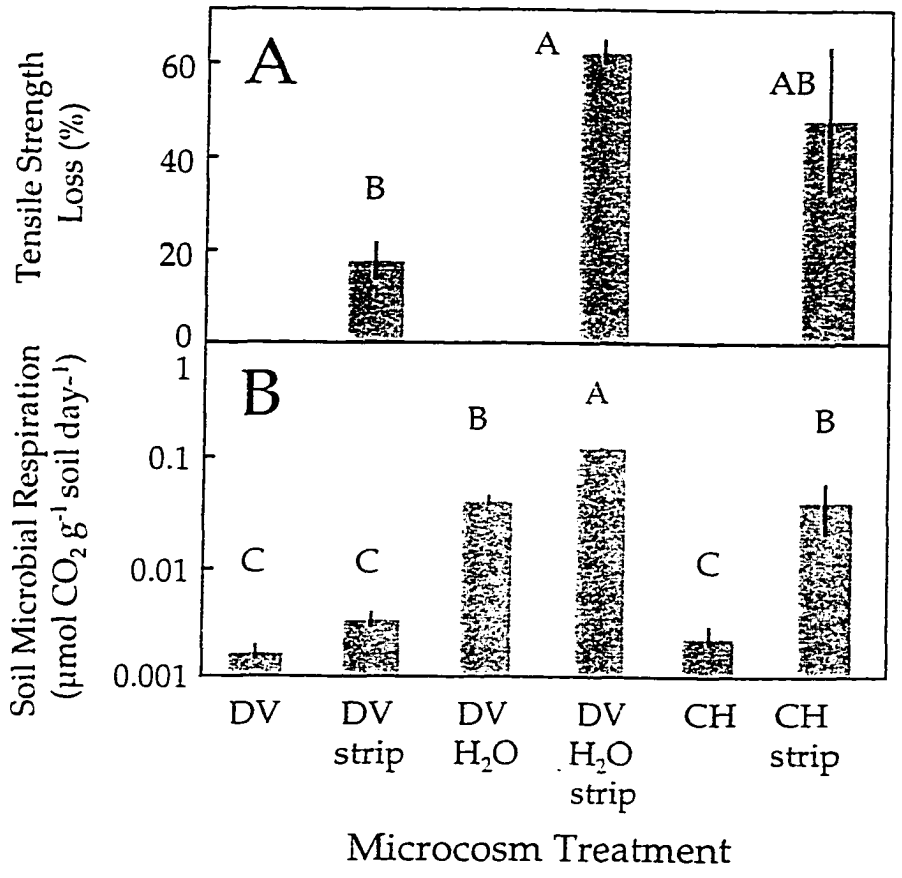


Figure 1: (A) Cotton strip tensile strength loss and (B) Soil microbial respiration in dry valley and Chihuahuan Desert soil microcosms after nine months of incubation at 10°C. Treatment abbreviations are explained in Table 1. Each bar represents the mean value for four microcosms, and error bars represent ±1 S.E. of the mean. Within a graph, bars with different letters are significantly different (Fisher's PLSD test, $P < 0.05$).

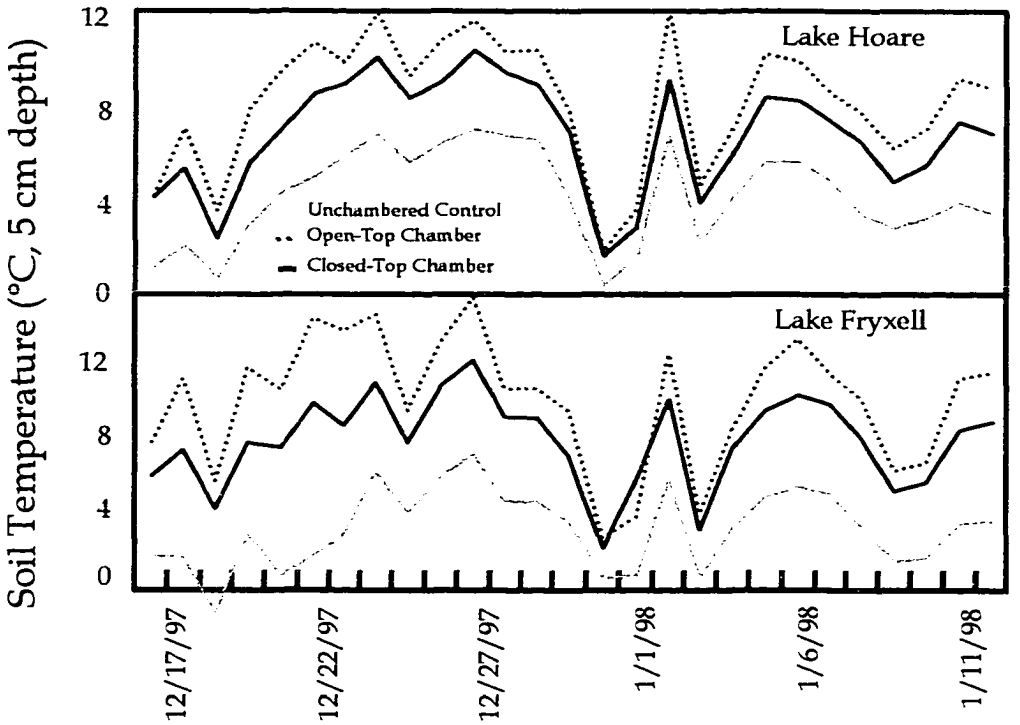
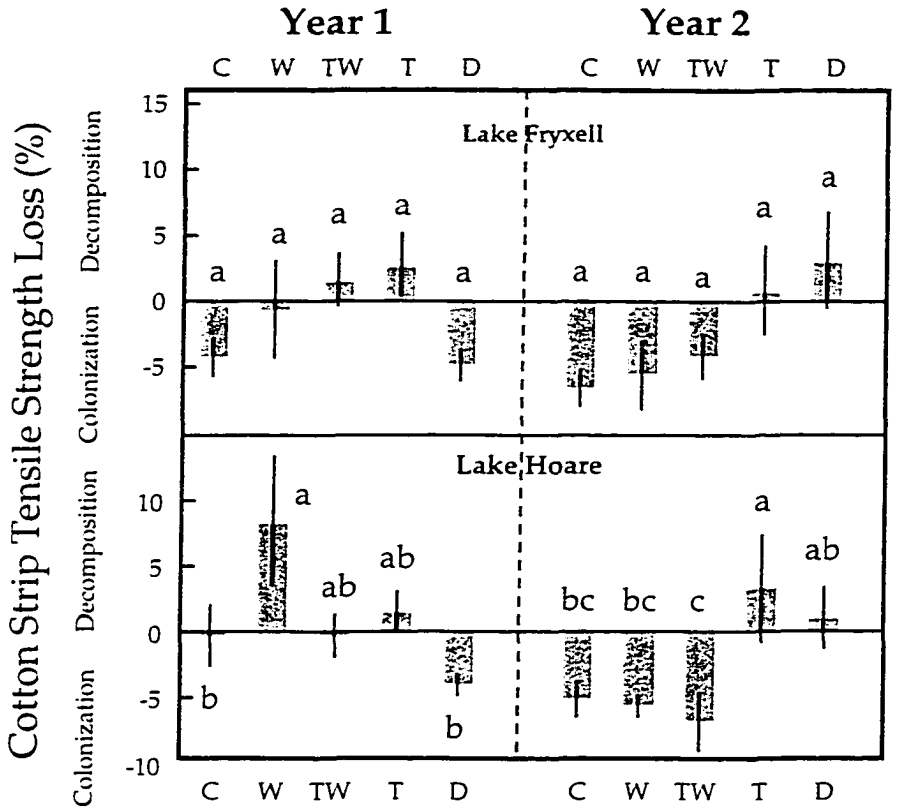


Figure 2: Soil temperature (5 cm depth) at the Lake Hoare and Lake Fryxell Decomposition Experiment sites in control plots and under closed- and open-top soil warming chambers.



D = warming + desiccation via closed-top chambers, C = control, T = warming with open-top chambers, TW = warming + annual moisture pulse, W= annual moisture pulse

Figure 3: Cotton strip tensile strength loss (TSL) after 1 and 2 years in the ground at the Lake Fryxell and Lake Hoare field experiment sites. Positive values for cotton strip TSL indicate decomposition has occurred. Negative values indicate strengthening of strips, possibly due to microbial colonization. Each bar represents the mean value for four microcosms, and error bars represent ±1 S.E. of the mean. For each site and sampling year, bars with different letters are significantly different (Fisher's PLSD test, $P < 0.05$).

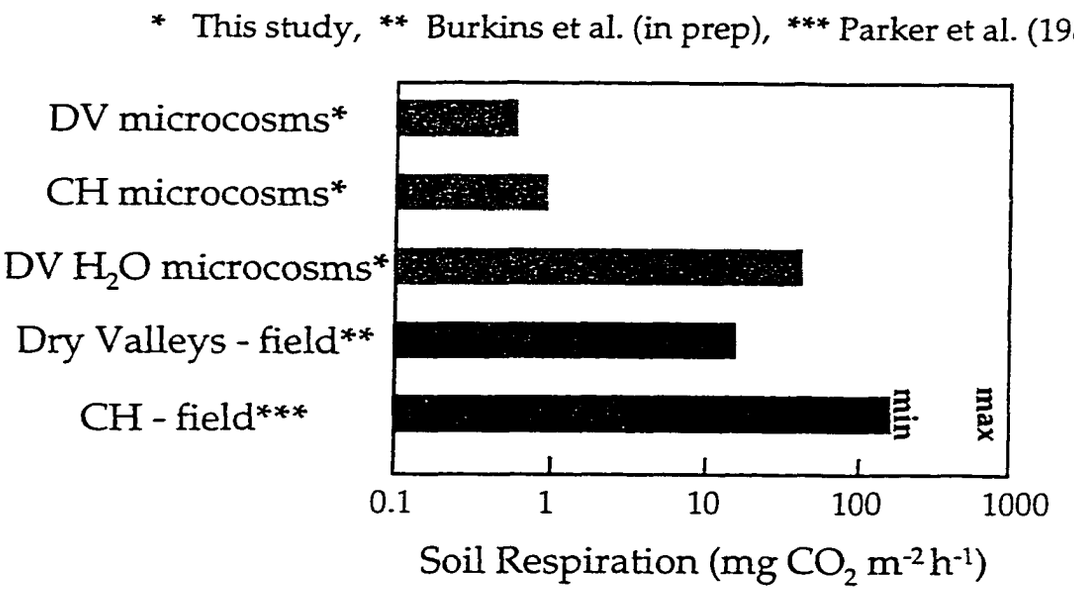


Figure 4: Field and microcosm measurements of soil CO_2 flux from Dry Valley and Chihuahuan Desert soil.

CHAPTER VI:

Summary

In cold and arid ecosystems, extreme environmental conditions strongly influence ecological processes (Wall and Virginia in press; Somme 1995; Wynn-Williams 1990; Vincent 1988; Block 1984). The McMurdo Dry Valleys of Antarctica are an extreme environment with respect to climate (Chapter 1), and this dissertation represents the first effort to elucidate limits to the activity of decomposer biota in this ecosystem.

My investigations of the use of anhydrobiosis by soil nematodes are unique and important because these were field studies. Anhydrobiosis is a survival strategy that has been rarely studied ecologically, despite much research investigating the physiological mechanisms of cryptobiosis (Womersley et al. 1998; Crowe and Madin 1975). Very few studies have made observations of where and when nematodes are anhydrobiotic under field conditions (Freckman et al. 1987; Townshend 1984; Freckman and Mankau 1986; Towson and Apt 1983; Whitford et al. 1981), and it is difficult to estimate the importance of this strategy to the ecology of invertebrates in their natural environment. The fixation method that I developed for soil samples in the field (Chapter 2) will be useful for future research because it allows for an accurate and simple assessment of nematode anhydrobiotic status that can be used for research across spatial and temporal scales.

Using the techniques I developed for sampling, fixation, and extraction of anhydrobiotic nematodes (Chapter 2), I showed that dry valley nematodes use an anhydrobiotic survival strategy in soils (Chapter 3). Anhydrobiosis should confer survival from extreme cold and desiccation, as has been shown by other researchers (Forge and MacGuidwin 1991; Pickup and Rothery 1991; Tsai and VanGundy 1989; Townshend 1984). The nematode communities in the soils I studied were often found with high proportions (> 60%) in anhydrobiosis as indicated by coiled morphology (Chapter 3). Use of anhydrobiosis was correlated most strongly to soil water potential and moisture content, with more nematodes coiled in drier soils. However, in the driest soils I studied (< 2% soil moisture content), none of the soil properties measured correlated with the proportion of nematodes coiled, suggesting that unmeasured factors may also be important in determining when nematodes are anhydrobiotic. More research needs to be done in order to fully understand the factors that limit nematode activity in dry valley soils. In particular, the nutritional status of nematodes may influence the use of a survival strategy, and relating the abundance of food (microbes) in the environment to when nematodes are anhydrobiotic is one possible area for future research.

I found that the proportion of nematodes that were anhydrobiotic in dry valley soils did not vary greatly through the austral summer or over a diurnal period (Chapter 3). Small and predictable soil environmental

changes that occur over these temporal cycles may not be sufficient to significantly alter nematode activity. Stochastic snowfall events that wet the soil may be the most important soil environmental change influencing the anhydrobiotic status of nematodes in many dry valley soils. After addition of moisture in a soil manipulation experiment, nematodes uncoiled rapidly and within six hours (Chapter 3). This change as well as the uncoiling of nematodes observed after a snowfall event (Chapter 5) were the most dramatic response of nematodes observed in these studies. However, seasonal cycles of activity probably do occur that I was unable to capture in these studies. For example, nematodes probably are not active during the austral winter when soil temperatures are too low for free water to be present. Therefore, as soils warm in November, nematodes should become more active. Sampling throughout this month would provide some new insights into the interaction between temperature, biological water availability, and nematode activity in the dry valleys.

Across the dry valley landscape, nematodes are found in soils with a broad range of properties (moisture content, salinity), from stream sediments to desiccated soils (Chapter 4; Virginia and Wall in press; Freckman and Virginia 1998; Powers et al. 1998). The density of nematodes does not appear to be limited by low soil moisture (Chapter 4, Powers et al. 1998; Freckman and Virginia 1997), and the use of an anhydrobiotic survival strategy allows dry valley nematodes to exploit habitats where moisture would otherwise be

limiting. I studied invertebrate communities and nematode anhydrobiosis in soils and sediments collected across a dry valley stream to soil transition zone (Chapter 4). Environmental gradients of moisture and salinity created through this transition zone influenced the diversity and activity of invertebrates. Diversity, but not abundance, of invertebrates was correlated to soil moisture content. In the dry soils away from stream waters, invertebrate communities had the lowest diversity and consisted almost entirely of a single nematode species, *Scottnema lindsayae*. High salinity reduced invertebrate abundance considerably in these samples, particularly at the hyporheic zone/soil boundary. Nematode anhydrobiosis was correlated positively to declining moisture, suggesting that this survival strategy is important for *Scottnema* in the dry soil habitat. Knowledge of biodiversity patterns in these soils and sediments is helping to develop a landscape perspective on distribution of soil biota in the dry valley ecosystem.

The use of anhydrobiosis by soil nematodes can indicate overall soil biotic activity, and I studied nematode activity and abundance in conjunction with measurements of decomposition in dry valley soils. (Chapter 5). Decomposition of a cotton strips occurred in dry valley soils in microcosms at ambient moisture levels, but was increased by the addition of moisture, as were the rates of nitrification and soil microbial respiration. Therefore, dry valley soil biota can potentially decompose the novel cotton strip substrate. In the field, decomposition of cotton strips did not occur at two field sites with

different moisture regimes, even after two years of incubation. Very few nematodes were anhydrobiotic at the wetter field site, indicating that biological activity was increased, but decomposition still was undetectable. This indicates that the activity of soil nematodes may not be related to the activity of heterotrophic soil microbes in the dry valley soils.

Rates of decomposition appear to be very slow in the dry valleys, and this result has implications for interpretation of the cycling of soil organic matter pools in this extreme environment. When conditions are favorable (moisture, temperature), carbon mineralization should occur, as was seen in the microcosms. Soil microbial respiration rates have been measured in the field (0.10 μmol CO_2 m^{-2} s^{-1}) (Burkins et al. in review). However, conditions allowing this degree of activity may occur only rarely during the austral summer, perhaps only for weeks or days. Survival strategies, such as the anhydrobiotic survival strategy dry valley nematodes utilize, will allow nematodes to persist, inactive, when conditions are not as favorable. Soil microbes probably employ similar cryptobiotic strategies in the absence of water. Long periods of inactivity by decomposer biota may result in slow decomposition rates in the dry valley soils and explain how soil food webs are sustained on organic carbon pools (< 0.1% by weight) that are smaller than in any other terrestrial ecosystem.

Studies of the origins of dry valley soil organic carbon suggest that organic material is a relict from when a glacial lake filled the valley floor (Burkins et al. in revision). When this lake receded (11,000 - 23,000 ybp), the benthic sediments remained behind to fuel the food webs of today (Burkins et al. in revision). Recent carbon-14 dating of soil organic material suggests that this is possible, as ages of about 6,000 years have been obtained (Wall and Treonis, unpublished results). For carbon this old to remain in the soils, the turnover time has to be very slow. In addition, sources of carbon that may replenish dry valley soil carbon pools are not obvious, although they may include *in situ* photosynthesis. Photosynthesis by cryptic cyanobacteria is currently being investigated (Burkins et al. in review). The limited activity of soil nematodes (Chapter 3) and the lack of decomposition of cotton strips after two years (Chapter 5) are both supporting evidence for slow organic turnover in dry valley soils. Burkins et al. (in review) suggest that soil organic carbon may be allocated into pools with distinct turnover times (fast and slow, possibly relict and photosynthetic, respectively), which would allow for increased biological activity than if all carbon was old. This model of soil carbon dynamics would also account for the higher turnover time that is suggested by the rates of soil microbial respiration that have been measured (Burkins et al. in review). Further research into the sources, composition, and cycling of dry valley soil organic carbon is ongoing.

CONCLUSIONS

My dissertation research on the role of anhydrobiosis in dry valley soil nematode ecology suggests that the activity of soil biota and the functions they perform are limited in the dry valleys by low soil moisture, as well as the interactive effects of low temperature. Nematode activity, and the function of the entire soil food web as well, may be confined to short periods of time (hours, days?) following rare snowfall events. Despite these limitations, nematodes are the most abundant animal in one of the most extreme environments on Earth - the McMurdo Dry Valley of Antarctica. The use of an anhydrobiotic survival strategy probably enables nematodes to be so successful in the dry valleys. As a universal nematode survival strategy, anhydrobiosis may contribute to the success of nematodes globally (Womersley 1987). In addition to the central role anhydrobiosis appears to play in the life histories of soil nematodes in the dry valleys, study of this strategy in this dissertation has also provided insights as to the limits to ecosystem and soil processes.

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