

THE MCMURDO DRY VALLEY ECOSYSTEM: ORGANIZATION, CONTROLS, AND LINKAGES

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The McMurdo Dry Valleys comprise one of the coldest and driest ecosystems on our planet. Despite these extremes, a variety of life exists in their soils, streams, lakes, glacial and lake ice meltwater pools, and rocks. The biota generally are dominated by prokaryotes, with eukaryotes restricted to the less stressful sites. Higher life forms include bryophytes, rotifers, tardigrades, and nematodes; vascular plants, insects, and vertebrates are lacking. Key conditions limiting life are liquid water and energy. In the presence of liquid water, radiant energy drives photoautotrophic production that provides heterotrophic communities with a carbon and energy supply. Spatio-temporal linkages between landscape components augment productivity of some communities and permit others to exist in places and at times that otherwise would be impossible. For example, organic matter supporting some soil food webs originates in lakes and streams. This organic matter is then transported to the soils by wind (spatial link among present ecosystem components) or made available by wind erosion of ancient lake and stream beds (temporal link to past ecosystems). Owing to tight spatio-temporal linkages, which we believe are necessary for the existence of life in extreme environments, ecological research in the McMurdo Dry Valleys must extend beyond isolated communities and focus on integrating system components. Herein we summarize existing knowledge of the McMurdo Dry Valley ecosystem emphasizing results from other papers in this volume. We focus on linkages among ecosystem components that augment or enable community existence.

INTRODUCTION

From the time of its formal definition, the term "ecosystem" has explicitly emphasized dynamic interactions among biotic and abiotic components of the environment [Tansley, 1987]. Indeed Stephen Forbes provided such a context in his earlier presentation to the Illinois Natural History Society in 1887 [Forbes, 1887]. Since then, studies have yielded insights to ecosystem structure and energy flow [Odum, 1957; Teal, 1962; Odum, 1969], element transfers [Schulze and Zwölfer, 1987], responses to disturbance [Pickett and White, 1985; Reynolds and Tenhunen, 1996] and functional linkages among landscape elements [Turner

and Gardner, 1991].

Because of the complexity of ecosystems, their study requires a multidisciplinary approach. Owing to their scalar dimensions in time and space, ecosystem studies must focus on relatively large areas over long periods. One of the broadest sets of ecosystem studies ever designed is the Long-Term Ecological Research (LTER) program, currently funded by the US National Science Foundation. At present, there exist 18 LTER sites ranging from the tropical rain forest of Puerto Rico through the northern Chihuahuan Desert of New Mexico, USA, and including prairie, forest, and tundra biomes [Van Cleve and Martin, 1991]. The McMurdo Dry Valleys LTER site presents an end-member

ecosystem of this group in that the Antarctic dry valleys are among the driest and coldest deserts on this planet. Even so, biological communities exist in the soils, lakes, and streams of the dry valleys.

The biological communities of the McMurdo Dry Valleys are relatively simple, being dominated by microbiota, lacking higher plants and animals, and consisting of relatively short food chains. However the basic ecological processes of primary and secondary production, decomposition, nutrient cycling and energy flux within these ecosystems demonstrate complex interactions among biological entities, as well as between biota and abiotic factors of the environment. Thus the McMurdo Dry Valleys offer a natural laboratory for study of basic ecological processes without the complications introduced by a plethora of higher organisms.

The presence of liquid water defines the primary limiting condition for life in this extreme environment. Liquid water is present in streams and soils only during the austral summer and even then freeze-thaw cycles are frequent. Prokaryotes dominate many of these ecosystems with eukaryotes occurring in the less stressful habitats. The extreme environment, coupled with a paucity of higher trophic groups, implies strong "bottom-up" controls on ecosystem structure with minimal influence of "top-down" controls exerted by herbivory or predation common to other environments [e.g., *Carpenter*, 1988]. In addition, the transport of water, nutrients, and organic carbon between glaciers, streams, lakes, and soils defines functional linkages that enhance biological activities in the dry valleys. While such linkages among landscape elements have been shown to exert considerable influence on ecosystem structure and function [*Turner and Gardner*, 1991], their impacts are particularly evident in extreme environments, such as deserts [*Schlesinger et al.*, 1990] and tundra [*Shaver et al.*, 1991; *Reynolds and Tenhunen*, 1996].

The purpose of this manuscript is to present a conceptual model of the major components of the dry valley ecosystems, with particular reference to the studies presented by other chapters within this volume. Owing to space constraints and the current status of our knowledge of certain system components, we cannot address all aspects of the dry valley system. Hence we focus on processes affecting primary production and linkages defining the transfer of organic carbon among system components. As in all ecosystems, and of particular importance in desert systems, the production of organic carbon initiates a cascade of biotic and

abiotic transformations. This chapter, in conjunction with the other chapters in this book, provides a framework for future research initiatives within the McMurdo Dry Valleys of Antarctica. Insights to ecosystem processes gained from these studies will broaden our understanding of origins and persistence of life in extreme environments.

CONCEPTUAL MODEL OF THE DRY VALLEY SYSTEM

The climate of the McMurdo Dry Valleys is extremely arid, with most of the total annual precipitation (< 10 cm) falling as snow during the winter [*Clow et al.*, 1988]. Ambient air temperatures hover near freezing during the austral summer, so that most of the heat required for warming substrates and melting ice is provided by radiant energy [Figure 1; *Fountain et al.*, this volume]. Life exists in the soils, rocks (endoliths), streams, and lakes of the McMurdo Dry Valleys, but is faced with a paradox: sufficient heat is required to provide liquid water and adequate solar energy is needed to drive photosynthesis; however exposure to radiant energy in this low humidity environment also means exposure to desiccation and rapid freeze-thaw cycles. With air temperatures rarely exceeding 0°C, large differences in the energy balance of microsites result from modest differences in orientation to the sun [*Dana et al.*, this volume; *Prentice et al.*, this volume]. Thus topographic features play a significant role in determining the spatial and temporal distribution of radiant energy in the dry valleys (Figure 1). Similarly, the orientation of glacial faces providing most of the water entering dry valley streams and lakes strongly affects the amount and timing of ice melt [*Fountain et al.*, this volume] and flow patterns of streams [*Conovitz et al.*, this volume].

The spatial and temporal distributions of liquid water and photosynthetically active radiation (PAR) do not always overlap, nor do they necessarily correspond to the availability of adequate nutrients to support primary production, or organic carbon to support heterotrophs. However the glaciers, streams, lakes, and soils of the dry valleys are linked by aeolian and hydrological transfers of materials that compensate for some site-specific limitations (Figure 1). For example glaciers and streambed soils are sources of many solutes that increase in concentration as water flows from glaciers to streams to lakes, with important mechanisms of concentration being the evaporation of water [*Lyons et al.*, this volume; *Green et al.*, this

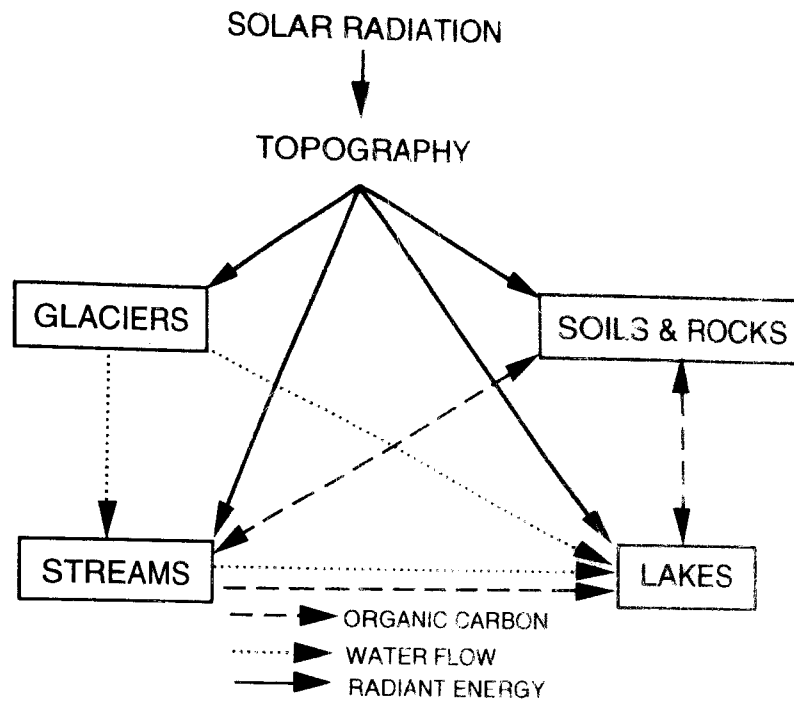


Fig. 1. Conceptual model of topographic effects on the distribution of incident radiation and the principle flow of organic carbon and water among habitats of the McMurdo Dry Valleys.

volume], and freeze-concentration [Howard-Williams *et al.*, 1989]. In addition to solutes, hydrologic processes move sediment and organic matter within streams and from streams to lakes [McKnight *et al.*, this volume]. Aeolian connections also are important linkages between dry valley components, e.g., winds deposit sediments and organic matter on glaciers and lake ice surfaces and exchange organic matter between lakes, streams and soils throughout the dry valleys [Adams *et al.*, this volume; Lyons *et al.*, this volume].

In summary, biological activity within the dry valley ecosystem is controlled by the spatial-temporal distribution of radiant energy and liquid water, with additional constraints imposed by the availability of inorganic nutrients and organic carbon. Moreover linkages between components of the dry valley landscape may ameliorate certain limitations to biota on some sites. Within this conceptual framework, similarities and differences in the controls on the ecological communities of the dry valleys can be elucidated with reference to a generic model of biomass dynamics.

GENERIC BIOMASS MODEL

Biological activity generally occurs where conditions permit liquid water to exist [Kennedy, 1993] and

supplies of both nutrients and energy are adequate (Figure 2; see also Vincen *et al.*, [1993a]). Organic matter may accumulate through on-site photosynthesis or allochthonous inputs, and be lost through on-site respiration, release of dissolved organic carbon or mechanical erosion via wind and water. However ecosystems within the dry valleys differ with respect to the importance of various environmental controls. Herein we compare and contrast the primary controls on biological activities in the major ecosystems of the dry valleys: the microbial mats found in stream and lake beds, lake phytoplankton communities, cyanobacterial communities growing within permanent lake ice, and soil communities. Terrestrial bryophyte and endolithic communities also exist in the dry valleys but are discussed elsewhere [e.g., Friedmann 1982].

Microbial Mats

Filamentous cyanobacteria (e.g., *Phormidium* spp., *Nostoc* spp.; McKnight *et al.*, this volume; Hawes *et al.*, this volume) usually dominate the algal component of benthic microbial mats found in dry valley streams and lakes. Herbivory appears to be low or absent in both environments and many of the same cyanobacterial species comprise a significant fraction of the

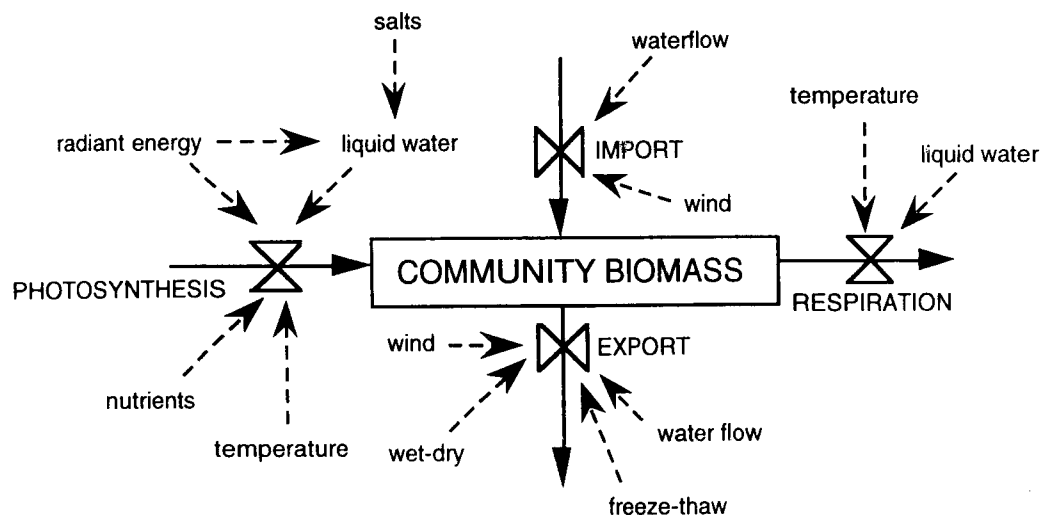


Fig. 2. General model of biomass dynamics in the McMurdo Dry Valley ecosystem, including inputs, outputs, and major factors controlling losses and gains of biomass.

communities in both environments. However the primary controls on biomass accumulation differ between streams and lakes.

In stream ecosystems liquid water is available only in summer and is provided by glacial melt, with timing, amount, and duration of flow controlled by the orientation of glacier faces to the sun, geometry of the stream, and extent of the hyporheic zone [Fountain *et al.*, this volume; Conovitz *et al.*, this volume]. The composition, distribution, and abundance of mats largely correlate to the stability of the streambed, with mats being most abundant in reaches with moderate gradients and stable stone pavements [Howard-Williams *et al.*, 1986; Alger *et al.*, 1996; McKnight *et al.*, this volume]. Mats dominated by *Nostoc* spp. occupy moist areas of stream margins and in slow-moving current, while *Phormidium* spp. are more common in channels with faster current [Alger *et al.*, 1996]. Sedimentation and abrasion appear to cause the major losses of mat in streams, and frequent freeze-thaw, wetting-drying, and flooding events probably compromise the structural integrity of mats [Howard-Williams *et al.*, 1986]. Wind erosion of exposed, freeze-dried mats also may occur during winter. Thus frequent dramatic changes in water flow and temperature regimes may physically disrupt the microbial mats and enhance material export.

Losses and gains of organic matter by microbial mats may occur through transport of organic material, photosynthesis, and respiration. Vincent *et al.* [1993b] speculated that movements of dissolved and particulate

organic matter constituted major sources and sinks for mat biomass in Antarctic streams, which is consistent with reported patterns of mat distributions. However few observations of organic matter export have been reported; Howard-Williams *et al.* [1989] found substantial losses of dissolved and particulate organic N and P from streams in Taylor Valley, and Vincent and Howard-Williams [1986] noted significant downstream movement and accumulation of mat materials. In contrast, metabolic activities of mats have received much attention. Photosynthesis of stream mats generally saturates at low light intensities ($< 200 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$), and thus rarely is limited by the radiant energy regime when liquid water is present and the mats are active [Howard-Williams and Vincent, 1989; Hawes *et al.*, this volume]. Although micro-environmental measurements imply that light intensity becomes limiting just beneath the surface of these mats due to heavy pigmentation [Vincent *et al.*, 1993a, 1993b], intact mats show little negative response to light intensities exceeding saturation. For this reason Hawes *et al.* [this volume] argue that water temperature is the major control on net primary production of mat communities through its effects on light-saturated photosynthesis and respiration [Vincent and Howard-Williams, 1989; Hawes, 1993].

Nutrient availability could limit stream mat production, but concentrations of nitrogen and phosphorus are relatively high in stream waters [Howard-Williams *et al.*, 1989; Alger *et al.*, 1996]. Studies have shown significant reductions in nitrate and urea

concentrations along the lengths of dry valley streams [Howard-Williams *et al.*, 1989; Hawes and Brazier, 1991], suggesting significant nutrient uptake by mat communities [Moorhead *et al.*, this volume]. However in situ nutrient enrichment experiments demonstrated no limitation of nitrogen or phosphorus availability on photosynthesis or pigment content of stream mats [Howard-Williams and Vincent, 1989].

Benthic mats within the dry valley lakes, in contrast to streams, are not subject to freeze-thaw or wet-dry cycles. The only exceptions are mats in shallow water at the lake margins where the water freezes to the bottom of the water column during winter and thaws during summer. Otherwise the permanent ice covers (3–5 m thick) on the lakes provide a physical barrier that, in combination with salt gradients, leads to stable stratification of the underlying water column [Spigel and Priscu, this volume]. Water input arrives from glacial melt, either directly or via inputs from meltwater streams. Thus benthic mats are permanently hydrated and ambient temperature varies little over time.

Also in contrast to stream cyanobacterial communities, light intensity probably restricts photosynthesis of mats throughout much of the lake. This is because only a small fraction of the ambient radiation is transmitted through lake ice and further attenuation occurs within the water column [Howard-Williams *et al.*, this volume]. Considerable variation in light transmission to the underlying liquid water column exists among lakes, being controlled by physical characteristics of the ice [McKay *et al.*, 1994]. However transmission seldom exceeds 5% of incident intensities for lakes at the McMurdo Dry Valley LTER site [Howard-Williams *et al.*, this volume]. In addition, long wavelengths of light (> 600 nm) are more severely attenuated than short wavelengths [Lizotte and Priscu, 1992]. Thus the light environment rather than temperature within dry valley lakes is presumably the major factor limiting primary production of benthic mats [Moorhead *et al.*, in press].

Nutrient concentrations clearly affect phytoplankton productivity in Antarctic lakes [Vincent, 1981; Priscu *et al.*, 1989; Priscu, 1995], but relatively little is known of nutrient controls on benthic mats. Studies have shown that concentrations of nutrients (e.g., soluble reactive phosphorus and ammonium) within microbial mats are much greater than in the overlying water column, suggesting a rapid, internal cycling of nutrients [Vincent *et al.*, 1993b]. Moreover Hawes *et al.* [1993] proposed that benthic mats in seasonal

ponds on the McMurdo Ice Shelf may serve as nutrient sinks, accumulating biomass and nutrients over time due to the absence of grazing losses or mass export. A similar paradigm presumably exists in the benthic mats of the dry valley lakes.

Benthic mats in lakes probably experience little disturbance, except for those in the shallow moat regions (previously mentioned). In deeper water mat liftoff due to the accumulation of entrained gas bubbles and occasional burial by sedimentation may represent the major disturbances experienced by these communities [Wharton, 1994]. However liftoff is limited to the shallower portions of the lake where light intensity is high (relative to deeper zones), and sedimentation occurs when a crack in the overlying ice permits sediments on the ice surface or entrained within the ice to pass into the water column [Adams *et al.*, this volume]. Thus burial of benthic mats in this manner appears to be localized and infrequent.

Losses of mat materials from the lake may occur via a process described by Parker *et al.* [1982]. In brief, mats in shallow water receive sufficient radiant energy to produce bubbles of oxygen within the mats. This provides sufficient buoyancy to float portions of mats to the bottom of the overlying ice cover and into open moat water, where they freeze into the ice during winter. Annual ablation of ice from the top of the ice layer and freezing of water to the bottom results in the upward movement of entrained mat materials until they are exposed on the ice surface. This mechanism is responsible for accumulations of mat materials along the shores of the seasonally melted margins of the lakes where the exposed material is readily distributed by wind.

Lake Phytoplankton

Phytoplankton communities of dry valley lakes exist in an environment characterized by low light intensity and stable stratification of the water column, both attributes resulting from the permanent ice covers on these lakes (previously discussed). While light intensity shows daily and seasonal variations, many other physical and chemical factors vary little over time. However vertical variations in environmental parameters may be large, with large gradients of salinity, temperature, and ionic concentrations occurring over depth [Angino *et al.*, 1964; Hawes, 1985; Spigel and Priscu, 1996; Spigel and Priscu, this volume]. The lack of wind-induced vertical mixing allows these gradients to persist over long periods,

possibly since the evolution of the lakes [Spigel and Priscu, 1996; Priscu, 1995; Priscu, in press].

Light intensity and spectral composition also vary with depth in dry valley lakes [Lizotte and Priscu, 1992; Howard-Williams *et al.*, this volume; Lizotte and Priscu, this volume], and phytoplankton occur in relatively distinct, stratified layers [Vincent, 1981; Lizotte and Priscu, 1992; Lizotte and Priscu, this volume]. Phytoplankton show a considerable degree of shade adaptation, and response to temperature, with differences in photosynthetic capacity and efficiency between depths [Lizotte and Priscu, 1992; Neale and Priscu, 1995; Neale and Priscu, this volume]. Little evidence of photosaturation exists, so primary production is limited virtually always by light availability. In addition to light limitation, Priscu [1995] demonstrated that the addition of phosphorus, or nitrogen plus phosphorus, stimulated photosynthesis of phytoplankton in most lakes of Taylor Valley, particularly in the upper water column. Internal nutrient regeneration has a major role in regulating phytoplankton production in the upper water column during the austral summer [Priscu *et al.*, 1989]. Vertical nutrient profiles suggest that deep primary production maxima often are driven by diffusion of nutrients from underlying, nutrient-rich layers of water. A similar situation exists in Lake Vanda, located in the adjacent Wright Valley, wherein a deep layer of maximum chlorophyll concentration exists just above a hypersaline, nutrient-rich zone [Vincent, 1981; Vincent and Vincent, 1982; Priscu, 1995]. Light intensity also has been shown to regulate inorganic nitrogen uptake in these lakes [Priscu *et al.*, 1987; Priscu *et al.*, 1988; Priscu, 1989; Priscu and Woolston, in press]. Thus concentrations of phytoplankton and maximum rates of production are determined by the juxtaposition of favorable light, nutrient, and salinity regimes in these stratified lakes [Priscu, 1995]. Changes in nutrient availability, temperature, and light regime may be responsible for seasonal changes in the location, density, succession, and productivity of phytoplankton communities.

The inflow of water from melting glaciers and streams provides inputs of nutrients and organic matter to the dry valley lakes [Green *et al.*, 1988; Howard-Williams *et al.*, 1989; Lyons *et al.*, this volume]. Much of this input water appears to disperse across the lake just beneath the ice cover. This supposition is supported by observations of relatively high nutrient concentrations just beneath the ice cover, the lack of appreciable mixing between layers of water, and movements of ions released in tracer experiments

[Lizotte and Priscu, 1992; McKnight *et al.*, 1993; Spaulding *et al.*, 1994; Spigel and Priscu, this volume]. Aeolian deposits of sediments and organic matter from microbial mats are present on the surfaces of lake ice and originate from surrounding land surfaces and seasonally dry stream beds. Some of these materials enter the water column via the formation of cracks or conduits through the ice cover. Surface deposits of dark colored materials also may absorb sufficient radiant energy to melt a significant portion of the ice [Adams *et al.*, this volume; Fritsen and Priscu, this volume; see below], allowing direct entry to the underlying water column.

The overall biomass of phytoplankton communities in these lakes should decline with cellular respiration and potential grazing [Laybourn-Parry *et al.*, 1997; James *et al.*, this volume] during the continuously dark winter months. However photoadaptation has been demonstrated for phytoplankton in this [Lizotte and Priscu, 1992; Neale and Priscu, 1995; Neale and Priscu, this volume] and other systems [e.g., Geider *et al.*, 1996], and may include reductions in respiration rates with declining light intensity [Prezelin and Sweeney, 1978]. Degradation rates of phytoplankton are slow, especially over winter [Priscu, 1992; Lizotte and Priscu, this volume], and preliminary sediment trap collections suggest significant settling of cells from the water column during winter (Priscu, unpublished data). An unknown portion of the organic nitrogen associated with sinking organic matter is regenerated as ammonium within the water column [Priscu *et al.*, 1989] which then can be oxidized to nitrous oxide, nitrite or nitrate by nitrifying bacteria [e.g., Voytek *et al.*, this volume; Priscu *et al.*, 1996; Priscu, in press]. Under anaerobic conditions, present in the bottom waters of some of the lakes, the oxidized nitrogen can be reduced to nitrogen gas through denitrification [Ward and Priscu, in press; Priscu, in press].

Grazing by microzooplankton and protozooplankton may affect phytoplankton communities [James *et al.*, this volume], although these systems lack many of the phytoplankton grazers found in other aquatic communities. Mixotrophic phytoplankton species recently have been identified and phagotrophy observed [Laybourn-Parry *et al.*, 1997; James *et al.*, this volume; Laybourn-Parry, pers. communication]. These processes would allow the phytoplankton to utilize heterotrophic metabolism during low light conditions (i.e., in deep water or during winter). Fish are completely absent from the lakes eliminating predation on the lower trophic levels.

Ice Communities

A recent discovery is that biological activity is associated with sediments entrained within the ice covers on lakes in the Taylor Valley [Wing and Priscu, 1993; Adams *et al.*, this volume; Fritsen and Priscu, this volume]. Owing to the mineral nature of ice, these organisms can be referred to as cryptoendolithic in the same manner as those found in dry valley sandstone [Friedmann, 1982]. Although the mechanisms of establishment and perpetuation of these novel communities are just being determined, it appears that sediments, with associated cyanobacterial and bacterial cells, are deposited on the surface of lake ice by aeolian transport. These materials absorb sufficient radiant energy during the summer to allow sinking into the ice cover through meltwater channels, eventually attaining a depth at which the absorption of radiant energy is insufficient to drive further melting (usually mid-depth in the ice-covers of most lakes). These channels freeze during autumn, sealing each microcosm within solid ice. Ablation occurs primarily from the upper surface of the ice covers on lakes, with accumulation resulting from freezing of water to the undersides. This moves the entrained microcosms upward during the winter, with subsequent summer melting moving the microcosms downward through meltwater channels, the result being constant vertical positioning within the ice cover. Biotic and abiotic losses and gains have shown that biomass accumulates primarily through biological growth [Fritsen and Priscu, *in press*]. Photosynthetic studies have shown that the cyanobacterial communities saturate at relatively low light levels [$<50 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$; Fritsen and Priscu, *in press*] and show temperature optima near 18°C (Priscu and Fritsen, unpublished). These results together with 16S ribosomal DNA signatures imply that the microbial assemblages are of terrestrial origin [Gordon *et al.*, *in press*] and are comprised of complex cyanobacterial/bacterial consortia.

Soil Communities

Although soils of the dry valleys once were considered to be nearly devoid of life, recent studies have demonstrated a wide distribution of microbiota [Powers *et al.*, 1995; Freckman and Virginia, this volume]. Soil communities in the McMurdo Dry Valleys tend to be simple, have few trophic groups, exist in films of water on soil particles, and often are dominated by nematodes, which fill key trophic positions often

including that of top predator [Overhoff *et al.*, 1993; Freckman and Virginia, 1997; Freckman and Virginia, this volume]. Studies of nematodes in other Antarctic systems have revealed considerable cold-hardiness and freezing tolerance in the group [e.g., Pickup, 1990a, 1990b, 1990c; Wharton and Block, 1993], as well as the ability to enter an anhydrobiotic state upon desiccation [Pickup, 1988]. Soil nematodes of warm desert ecosystems also can enter anhydrobiotic states upon desiccation [Freckman, 1986; Freckman and Mankau, 1986; Freckman *et al.*, 1987], suggesting a common response to water-limiting conditions under hot or cold conditions. In fact mechanisms underlying freeze-tolerance and desiccation-resistance are similar [Crowe and Madin, 1975], and at least some species of nematode demonstrate greater freeze-tolerance when they are in an anhydrobiotic state [Pickup and Rothery, 1991]. Thus the frequent dominance of nematodes in soil trophic webs may result from their ability to survive the cold, dry conditions that characterize dry valley soils.

Factors controlling the spatial distribution of biota in the McMurdo Dry Valleys are uncertain. Although Kennedy [1993] concluded that the abundances and distributions of organisms in Antarctica were closely correlated to moisture availability, Freckman and Virginia [1997] reported no correlation between nematodes and soil moisture in the McMurdo Dry Valleys. Furthermore neither soil carbon nor nitrogen content were correlated to nematode distributions in this region [Freckman and Virginia, 1997]. However field studies demonstrated that increasing soil water, carbon, and temperature tended to increase abundances of microbivorous species while decreasing abundance of omnivore-predator species [Freckman and Virginia, 1997]. Powers *et al.* [1994] noted that nematode distributions in Taylor Valley appeared to be influenced by soil pH and salinity, but relationships between distributions, diversity, and abundance of nematodes and environmental factors remain equivocal.

The origins of the organic matter driving soil communities are largely unknown [Burkins *et al.*, *in press*]. Cyanobacteria are present in soils, but moisture conditions at the soil surface are seldom favorable for photosynthesis or growth. Nematode densities are highest at 2.5–10 cm depth, where moisture conditions are more favorable [Powers *et al.*, 1995], but light intensities are insufficient to drive photosynthesis. Allochthonous inputs of organic matter from lakes, streams and the distant ocean may provide the base of these detrital food chains, and buried sediments from

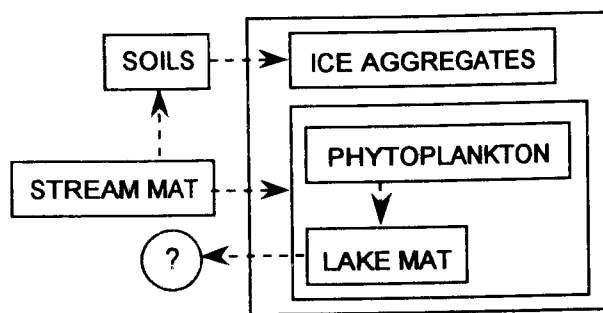


Fig. 3. Flow diagram illustrating major transfers of organic carbon between biological communities in the McMurdo Dry Valleys.

ancient lake beds also may supply soil communities [Burkins *et al.*, in press; Freckman and Virginia, this volume].

In summary, the existence and complexity of soil communities in the McMurdo Dry Valleys are strongly limited by a variety of environmental factors, such as low temperature and moisture availability, high pH and salinity, and low organic carbon content. Soil biota demonstrate a very patchy distribution throughout the McMurdo Dry Valleys, probably reflecting a patchwork of microenvironmental conditions. Soils are cold, dry and saline [Campbell *et al.*, this volume], and the simple food webs appear to be based largely on allochthonous inputs of organic matter from other times or places. Freeze-thaw cycles are frequent in surface soils and deeper soils remain frozen; more agreeable conditions probably exist at intermediate depths [Freckman and Virginia, this volume].

LINKAGES

Linkages for the transport of organisms and materials between components of the dry valley landscape enable the existence and augment production of various biological communities (Figure 1). Two major transport mechanisms, fluvial and aeolian, move three major currencies throughout the dry valleys: water, nutrients, and organic matter (including organisms). Inorganic sediments also are moved by wind and water, but travel in much the same manner as organic matter (Figure 3).

Water flows from glaciers through streams to lakes, hydrating the stream beds and benthic mats, carrying solutes and organic matter from the glaciers into the streams, and from the streams into the lakes [Lyons *et al.*, this volume]. Mat communities in streams are metabolically active within minutes of hydration

[Vincent and Howard-Williams, 1986], utilize inorganic nutrients and urea from the water column [Howard-Williams *et al.*, 1989], and fix molecular nitrogen from the atmosphere [Howard-Williams *et al.*, 1989]. Concentrations of other ions and both dissolved and particulate organic compounds increase along the length of streams, providing inputs of these materials to recipient lakes [Howard-Williams *et al.*, 1989; Lyons *et al.*, this volume]. These nutrient inputs may stimulate production of phytoplankton communities, especially near the ice-water interface [Lizotte and Priscu, 1992; Spaulding *et al.*, 1994; Priscu, 1995].

Dryfall and wetfall (via snow) add nutrients to land and ice surfaces in the dry valleys [Lyons *et al.*, this volume]. Fluvial movements carry these nutrients into streams and lakes, as previously mentioned. However, aeolian transport is responsible for distributing sediments and organic materials around the dry valleys and probably is responsible for placing most of these materials found on surfaces of glaciers and lake ice. Perhaps the redistribution of organic matter by wind also is an important determinant of soil community development and wind erosion may expose buried sediments from ancient lake beds. Despite this uncertainty, the establishment of lake ice communities described by Adams *et al.* [this volume] and Fritsen *et al.* [this volume], and the structure of soil trophic webs [Freckman and Virginia, this volume], depend upon the availability of organic matter that probably originates elsewhere.

CONCLUSIONS

The availability of liquid water provides a necessary condition for life, but the spatial-temporal distribution of liquid water is discontinuous in the McMurdo Dry Valleys. The lakes in Taylor Valley are permanently hydrated, but of limited spatial extent. The streams are hydrated only during the brief, austral summer, and experience frequent freeze-thaw and wet-dry cycles even during this period. Much of the soil in the dry valleys rarely or never has adequate moisture to support metabolically active organisms, but the margins of streams, lakes, and melting glaciers, in variety of favorable microenvironments for soil communities.

Within this spatial-temporal mosaic of suitable moisture conditions, life is affected by other conditions and resources. Gradients of light, temperature, nutrient concentration, and salinity control the abundance and distribution of phytoplankton and benthic mats in the

dry valley lakes. Data support the over-riding importance of streambed characteristics in the establishment and persistence of mat communities in streams. Distributions of soil organisms and development of food webs are related to moisture, pH, salinity, and temperature regimes in soils, as well as the availability of organic carbon.

Linkages between system components are responsible for the establishment of some biological communities in the dry valleys, and augment the productivities of others. For example, aeolian inputs of organic matter appear to represent the source of cells establishing communities entrained within lake ice, serve as a source of organic carbon important to the development of soil food webs, and add to the accumulation of mat materials on lake bottoms. Nutrients accompanying movements of water, sediments, and organic matter are utilized by microbial mats and plankton communities in streams and lakes. Finally the movement of water from glaciers to lakes defines the presence of both lakes and streams.

A common characteristic of the biological communities in the dry valleys is the dominance of prokaryotes as the principle autotrophs and decomposers. Cyanobacteria often dominate photoautotrophic production under extremely stressful conditions, such as in alkaline or saline waters, and geothermal streams. In the dry valleys cyanobacteria are an important component of microbial mats in streams and lakes, phytoplankton communities in certain lakes, lichen symbioses, endolithic communities, and soils. Heterotrophic bacteria are the primary decomposers in all of these systems. The close association between cyanobacteria and bacteria in many of the dry valley communities may represent a consortial arrangement promoting survival under stressful conditions.

FUTURE RESEARCH DIRECTIONS

Perhaps the most important aspects of the McMurdo Dry Valley system are the transport mechanisms that move critical materials between sites. Although fluvial processes have been studied in some detail [e.g., *Prentice et al.*, this volume; *Lyons et al.*, this volume; *Conovitz et al.*, this volume], the transport of organic matter, sediments, and solutes requires further investigation. This is particularly important with regard to nutrient dynamics along streams and the impacts of stream chemistry on recipient lakes [e.g., *Green et al.*, this volume]. Aeolian transport mechanisms have been identified as being important in a

qualitative manner, but have yet to be quantified with respect to the timing, amounts, sources and sinks of materials being moved.

Of the major habitats of the dry valleys, the soil ecosystems are perhaps least understood. Only recently have detailed investigations begun to identify the types and amounts of life distributed in soils throughout the dry valleys. Correlations between distributions of key groups of soil invertebrates and physical-chemical characteristics of soils are revealing likely controls on the structure of soil communities. However little information on the metabolic characteristics, population dynamics, or material cycling within soil trophic webs has been obtained.

Microbial mat communities are common throughout the streams and lakes of the dry valleys and considerable effort has been directed toward evaluating their composition and metabolic features. However internal structure, carbon dynamics, and nutrient cycling processes in these mats are not well-known. Moreover their contributions of organic matter to other dry valley ecosystems appear to be substantial, although the type, amount, and origin of mat materials found in various habitats has not been determined, nor have the losses of mat types from various habitats been quantified. Preliminary colonization studies have begun, but mechanisms of accumulation and factors controlling structure of these communities are not well-known.

Lake systems pose a number of questions for study. The influence of the permanent ice covers as potential barriers to the flux of metabolic and abiotic gases is only beginning to be understood [e.g., *Prisco et al.*, 1996; *Prisco*, 1997]. The role of lake sediments in oxygen dynamics, nutrient cycling, and organic matter accumulation have not been examined. Vertical movements of ions in these stratified lakes appears to be by molecular diffusion of soluble compounds and settling of particulate materials. The role that microorganisms have in metal geochemistry in the saline bottom waters of certain lakes is still uncertain, though it is currently under study [e.g., *Green et al.*, this volume]. Organic carbon dynamics in lakes, particularly the vertical flux of particulate organic carbon, is just beginning to be quantified. Grazing of phytoplankton is low and dominated by microzooplankton and protozooplankton, many exhibiting a wide range of feeding strategies suggesting bottom-up controls on community structure. Phagocytotic phytoplankton species have recently been identified, although their role in the microbial loop, particularly with respect to the regula-

tion of bacterial plankton numbers, has yet to be quantified. The role of bacterioplankton as sources or sinks of organic carbon and the relationship between net primary productivity and bacterial respiration still remains to be determined. Finally no estimates of energy or nutrient flux through these communities have been made, nor have the population dynamics of planktonic species been characterized.

In a larger context, the primary sources, sinks, and transformations of major elements, such as carbon, nitrogen, and phosphorus, have not been elucidated completely either within particular communities or between communities. Although considerable evidence suggests that transport of these materials between locations may be an important factor contributing to the overall structure and function of the McMurdo Dry Valley system, few data are available to quantify these flows or their consequences to recipient systems. Broad-scale studies of material fluxes within and between components of the dry valley system are sorely needed. Most of what is currently known about ecosystem processes within the McMurdo Dry Valleys has resulted from data collections and experimental manipulations made during the austral summer. Logistics have not yet advanced to the level that would support winter research either through on-site data collection or remote sensing. It is imperative that future research address winter processes. For example, lake phytoplankton and bacterioplankton biomass is low at the end of winter and generally increases through the summer [Lizotte *et al.*, 1996; Priscu, unpublished data]. However little is known about growth and loss rates during autumn and winter. Many ecosystem processes may never be delineated completely without annual data collection and experimental manipulation.

The compendium of chapters published within this book volume represents a first attempt at bringing together much of what is known about processes and linkages within the McMurdo Dry Valleys. These studies clearly show that the presence of liquid water produces a cascade of ecosystem events which are tightly coupled. We believe that tight temporal and spatial coupling among ecosystem components is the key to metabolic activity and ultimate survival of organisms within the McMurdo Dry Valleys.

In closing it is important to note that although the McMurdo Dry Valleys are among the most isolated locations on earth, they are experiencing increasing levels of anthropogenic stress and disturbance [Harris, this volume]. Aside from the obvious contributions of human industries to the reduction in stratospheric ozone

concentrations over Antarctica, increasing levels of sulfur, nitrogen, and other compounds in the atmosphere, and global warming, humans are also visiting Antarctica in ever-increasing numbers. Conditions supporting scientific research have improved dramatically, increasing both the number and duration of scientific visits. In addition recent entrepreneurial ventures are promoting tourism and providing access to the dry valleys via helicopter. The impacts of human activities, including scientists and tourists, only now are being explored.

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