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Review

Controls on the distribution of productivity and organic resources in Antarctic Dry Valley soils

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The Antarctic Dry Valleys are regarded as one of the harshest terrestrial habitats on Earth because of the extremely cold and dry conditions. Despite the extreme environment and scarcity of conspicuous primary producers, the soils contain organic carbon and heterotrophic micro-organisms and invertebrates. Potential sources of organic compounds to sustain soil organisms include *in situ* primary production by micro-organisms and mosses, spatial subsidies from lacustrine and marine-derived detritus, and temporal subsidies ('legacies') from ancient lake deposits. The contributions from these sources at different sites are likely to be influenced by local environmental conditions, especially soil moisture content, position in the landscape in relation to lake level oscillations and legacies from previous geomorphic processes. Here we review the abiotic factors that influence biological activity in Dry Valley soils and present a conceptual model that summarizes mechanisms leading to organic resources therein.

Keywords: Antarctica; carbon; decomposition; Dry Valleys; respiration; soil

1. INTRODUCTION

Antarctica is the Earth's fifth largest continent and covers 14×10^6 km^2, making it approximately 50% larger than the USA. Most of the continent is south of the Antarctic circle (66°S), the majority capped by a permanent icesheet. However, about 0.35% is ice-free for some or all of the year (British Antarctic Survey 2004). The Dry Valleys on the east side of the Transantarctic Mountains in the Ross Dependency (Victoria Land), between longitudes 170°W and 170°E and adjacent to the Ross Sea and Ice Shelf, comprise the largest such area. The Dry Valleys occupy approximately 15 000 km^2 and are substantially ice-free due to their isolation from the ice plateau by the barrier created by the Transantarctic Mountains. The remaining ice-free land in Antarctica is along parts of the coast line, in volcanically heated regions, on isolated nunataks, on the peaks of high mountains (some over 4000 m) and on sub-Antarctic islands close to sea level.

The ice plateau covering most of the continent defines the climatic conditions of Antarctica and its Dry Valleys. The prevailing katabatic winds radiate from the South Pole and, descending from the polar plateau, channel dry air at high speeds through the valleys of the Transantarctic Mountains, leading to ablation of snow and ice from the valleys. The drying influence of the wind and the low precipitation (typically only a few centimetres of water equivalent per annum) makes the Dry Valleys arguably the driest desert on Earth. Temperatures are well below 0 °C for much of the year: only during the short summer do the air and ground temperatures rise above 0 °C. Generalized relations of ice and liquid water distribution, fluxes, prevailing winds and organisms with geomorphology in continental Antarctica are summarized in figure 1.

The Dry Valleys include large areas that were not overrun by ice at Pleistocene glacial maximum and have been at least partially ice-free since the Mid–Late Miocene. Terrestrial habitats have, therefore, existed in this region for possibly up to 12–13 Myr (Denton *et al.* 1993). The major geomorphic features of Antarctica were predominantly formed by ancient water-based glaciers and have emerged comparatively recently with the partial recession of the ice-sheet (Campbell & Claridge 1987, 2000; Taylor 1922). Landforms produced by more recent fluvial and glacial processes include moraines, patterned ground, alluvial fans, outwash plains and deltas, gravel and dunes, screes and solifluction deposits (Campbell & Claridge 1987). Soils that have formed in these features are skeletal and typically characterized by absence of structure and cohesion, low moisture and organic matter contents (Beyer *et al.* 1999), and often high salt concentrations

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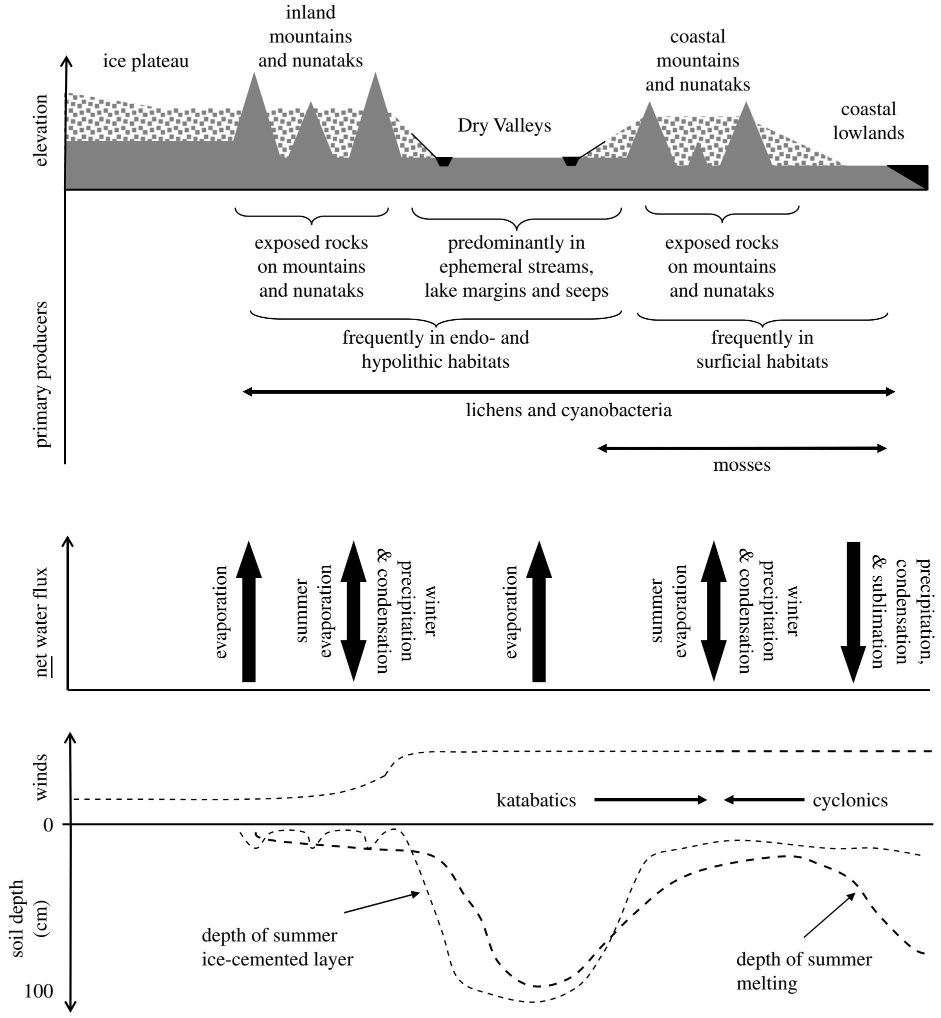


Figure 1. Generalized relations of ice and liquid water distribution, net water fluxes, prevailing winds and primary producers with geomorphology in continental Antarctica. The diagram has been adapted from Janetschek (1970). It should be noted that the water fluxes are indicative net fluxes, and it is not intended to imply that precipitation only occurs during the winter and that evaporation only occurs during the summer in the Dry Valleys.

due to limited leaching (Bockheim 1997; Campbell & Claridge 2000). Organisms have had a relatively minor role in soil formation because biological communities in the soils are sparse, with low biomass (Bargagli *et al.* 1999; Treonis *et al.* 1999; Stevens & Hogg 2002; Moorhead *et al.* 2003) and their distribution is strongly influenced by water availability (Kennedy 1993).

As with hot deserts (Noy-Meir 1973; Ludwig & Whitford 1981), availability of water in Antarctic Dry Valley soils varies in time and space. However, unlike hot deserts in which the liquid–vapour phase transition determines biologically available water, the liquid–ice interface is critical to soil biota in the Dry Valleys. Liquid water is available in summer through melting of near-surface permafrost and light snowfalls, in streams and rivers through glacial melting, and on lake margins through thawing of ice caps and the development of moats. When temperatures hover around 0 °C, lake-edge moats undergo diurnal freeze–thaw cycles. Furthermore, lakes with outgoing drainage experience a diurnal ‘tide’ as inputs of glacial meltwater temporarily exceed drainage when glacier surfaces are warmed by the sun and then subsequently decline when feeder glaciers are in shade as the sun moves around the horizon (or sets). Both processes provide water inputs to the soils at the lake margins. The ephemerality of available water is driven by the interaction of position in the landscape and weather conditions (figure 2). At generally wet, downslope sites, along shallow streambeds and at lake margins, warm sunny conditions maximize inflows of meltwater and wet surface soils favour biota, while cool cloudy conditions reduce inflows and freeze surface soil. By contrast, in dry, upslope habitats, soils are severely dehydrated by sunny conditions rapidly evaporating almost all permafrost meltwater, but their surfaces can be diurnally moist over the permafrost during cooler, cloudy conditions. Evaporative losses from hillslopes are ameliorated by desert pavements of pebbles that mulch the soil surface, as has been observed in hot deserts (Cooke *et al.* 1993). Where these pavements consist of translucent quartzitic fragments, hypolithic communities of cyanobacteria and eukaryotic algae can be active, even under very sunny conditions (Schlesinger *et al.* 2003). During unusually warm summers, extensive melting of snowfields and permafrost generate subsurface flows of water down hillslopes, leading to seeps and springs (Lyons *et al.* 2005), and thereby create sudden yet ephemeral streams to which biota respond rapidly (McKnight *et al.* 1999; Gooseff *et al.* 2003).

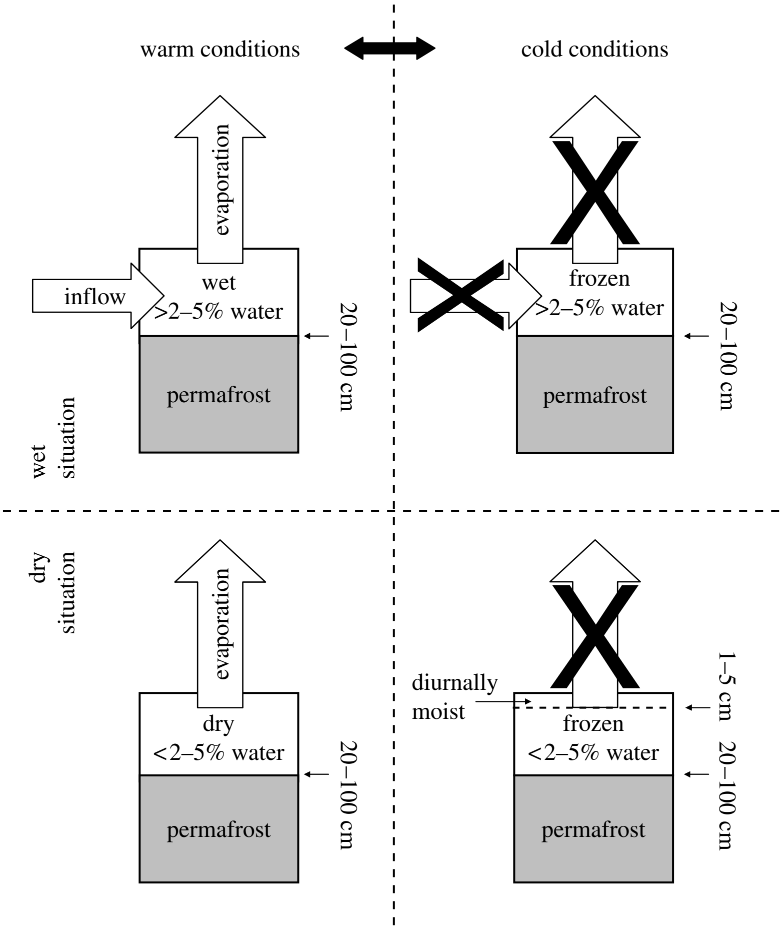


Figure 2. Summary of soil moisture and water fluxes for soils under different environmental conditions in the Dry Valleys. For justification of the 2–5% cut-off in water content see Treonis *et al.* (1999), Elberling (2003), Barrett *et al.* (2004) and Elberling *et al.* (in press).

2. HETEROTROPHIC ORGANISMS IN THE DRY VALLEYS

There have been few comprehensive surveys of the diversity of organisms in the Dry Valleys, but Adams *et al.* (in press) recently summarized the limited information with a view to establishing a baseline to facilitate future biodiversity and functional ecological investigations. Nevertheless, the Dry Valleys are highly significant sites in ongoing studies of ecosystem processes, because of their presumed relative biological simplicity, and for monitoring the effects of environmental changes, because their biota operates at environmental extremes.

Despite the limited information on organisms in Dry Valley soils, there is clear evidence that these soils support biologically mediated processes and communities of heterotrophic organisms. Respiration, nitrogen (N) mineralization and a variety of substrate-induced responses have been measured under laboratory conditions (Barrett *et al.* 2002, 2005, in press; Hopkins *et al.* in press). Small but consistent net emissions of CO_2 from Dry Valley soil surfaces are reported *in situ* (Burkins *et al.* 2002; Parsons *et al.* 2004; Elberling *et al.* in press) indicating heterotrophic activity, but responses to exotic substrates (cotton strips) are not consistently observed (Treonis *et al.* 2002).

Dry Valley soils contain a diverse range of heterotrophs (reviewed by Adams *et al.* in press), including bacteria and fungi, protozoa, tardigrades, rotifers, collembola, acari and notably microbivorous and detritivorous nematodes. The last group are the most widely studied (Freckman & Virginia 1997; Treonis *et al.* 1999; Virginia & Wall 1999; Coutright *et al.* 2001; Doran *et al.* 2002). All these consumers form the highest trophic layer in the terrestrial community (‘McMurdo’s equivalent of elephants and tigers’; Wilson 2002; Wall 2005), and their presence indicates a reliable supply of organic substrates.

Estimates of organic carbon (C) turnover in the Dry Valleys are in the range 20–130 years (Burkins *et al.* 2002; Elberling *et al.* in press), and Barrett *et al.* (2005) reported that large proportions of the organic C and N in Dry Valley soils are potentially mineralizable within a relatively short period (90 days) under optimal conditions. The estimates of C mineralization in the Dry Valleys are fast by comparison with soils in temperate regions, which are typically in the range of centuries to millennia (Kirschbaum 2000; Hopkins & Gregorich 2005).

Spatial differences of a hundredfold or more in soil organic C concentration (Elberling *et al.* in press), respiration flux (Elberling *et al.* in press; Hopkins *et al.* in press) and microbial biomass concentration (Barrett *et al.* in press) show the biological heterogeneity of the Dry Valley landscapes. This heterogeneity ranges from microenvironments within a soil profile (Gregorich *et al.* in press) to macroenvironments within a mosaic of landscape elements (Elberling *et al.* in press), and relates to both horizontal and vertical spatial patterns in availability of liquid water and soil temperature (figure 2). In addition, there is evidence for an assemblage of anaerobic micro-

Figure 3. Examples of sources of organic resources for heterotrophic organisms in the Dry Valleys: (*a*) surficial lichen; (*b*) hypolithic algal/cyanobacterial community (the stone was buried to the depth indicated by the arrow); (*c*) endolithic community in sandstone (the arrow indicates organisms (black coloration) exposed by exfoliation of the sandstone); (*d*) hypolithic moss; (*e*) surficial moss in ephemeral stream bed; (*f*) remains of Adélie penguin; (*g*) mummified crab-eater seal; (*h*) area of lake shore from which cyanobacterial mat has been removed (presumably by wind); (*i*) wind-blown foam (presumed to be derived from decomposing lacustrine detritus) accumulation at lake shore; (*j*) lacustrine detritus stranded close to lake shore following a recent fall in lake level; (*k*) cyanobacterial mat from ancient lake shore exposed following erosion of the overlying soil/sediment.

organisms (Hopkins *et al.* in press), especially in the wetter sites where methanogenesis and denitrification have been detected (Gooseff *et al.* 2004; Gregorich *et al.* in press). However, unlike less extreme terrestrial ecosystems, in which primary producers are usually abundant and macroscopic, and their spatial patterning across the landscape conspicuous, the provenance of organic resources to support the heterotrophic organisms in the Dry Valleys is more complex (Barrett *et al.* 2004).

3. *IN SITU* TERRESTRIAL PRIMARY PRODUCTION

The occurrence of significant net primary production depends on environmental conditions and the distribution of organisms. Figure 1 summarizes relationships between some soil and climatic factors and primary producers along a transect from the polar plateau through the Transantarctic Mountains towards the coast. Within the Dry Valleys, primary producers adopt different habits, including development of epilithic, hypolithic and endolithic communities—respectively on, under and inside rock and soil surfaces—on hillslopes and desert pavements in dry habitats and microbial mat and filamentous communities in wetter habitats, such as lake margins and in stream beds (figure 3). Cyanobacteria often dominate the primary producer biomass, with, for example, *Nostoc commune* forming conspicuous films and mats in ephemeral streams and at lake margins during summer (Vincent 1988), as well as growing epiphytically on mosses (Alfinito *et al.* 1998) and with *Gloeocapsa* sp. adapted to extremely dry conditions by growing endolithically (Friedmann & Ocampo 1976; Friedmann 1982; Friedmann *et al.* 1993). Eukaryotic algae are widely reported in Antarctica from most ice-free areas, including in ephemeral streams and at lake margins, on wetter soils, as epiphytes on mosses, in cyanobacterial mats and predominantly in lakes (Cathey *et al.* 1981; Hawes & Schwarz 1999; Pocock *et al.* 2004). Mosses in the Dry Valleys form conspicuous communities at wet seeps and springs, and less obviously beneath a thin layer of translucent soil particles and on the soil surface fringing stones sheltered from the wind.

There are estimates of net primary production for selected organisms and for the biomass of some groups of primary producers at selected sites (Green *et al.* 1992, 1998; Schwarz *et al.* 1992; Kappen *et al.* 1998; Pannewitz *et al.* 2005, 2006). However, these data are sparse on an areal basis and over a range of environmental conditions; thus, estimating net primary production for Dry Valley soils is difficult. Friedmann *et al.* (1993) estimated the net primary production at between 11 and 17 kg C ha^{-1} yr^{-1} from the endolithic microbial community, of which 50–85 g C ha^{-1} yr^{-1} enters microbial biomass and the remaining metabolites percolate into soils and rocks and are potentially available to heterotrophs. However, they stress that this production may be restricted to as little as 20% of the surface area in the Dry Valleys. It is generally assumed that the growth rate of primary producers in the Dry Valleys is slow (Johnston & Vestal 1991) and Bonani *et al.* (1988) made a preliminary report that crypotendolithic organisms from the Dry Valleys may be thousands of years old. However, more recent evidence suggests a mean age for such material of less than a century (B. Büdel *et al.* 2005, unpublished work). At sites of ephemeral water flow, which may represent only a few per cent of the land surface (Elberling *et al.* in press), are significant hotspots of productivity capable of rapid responses to incoming water (McKnight *et al.* 1999; Conovitz *et al.* 2006). For comparison, Noy-Meir (1973) estimated above- and below-ground productivity in excess of 1 t C ha^{-1} yr^{-1} for a range of hot desert ecosystems worldwide and up to ten times as much for semi-desert ecosystems.

Nitrification has been detected in Dry Valleys soils, but the potential rates are very small and it is presumed that chemoautotrophic sources of organic C are negligible (Hopkins *et al.* in press), except perhaps at localized sites of large NH_4^+ concentrations such as at lake margins (Gregorich *et al.* in press).

4. TEMPORAL SUBSIDIES (LEGACIES)

Considerable reference has been made to the role of ancient lake sediments as sources of soil organic matter in the Dry Valleys, which has been redistributed by geomorphic processes (the so-called 'legacy C'; Burkins *et al.* 2000). The principal evidence for its presence comes from the Taylor Valley, which contained palaeolake Washburn between about 10 000 and 23 000 years ago (Péwé 1960). The evidence comprises C and N stable isotope signatures, which distinguish ancient C from contemporary sources, and indirect geomorphic evidence (Burkins *et al.* 2000; Higgins *et al.* 2000). Large lakes with levels far higher than present may also have occurred in both the Wright and Victoria Valleys (Hall *et al.* 2001, 2002; Hall & Denton 2002, 2005), the sediments from which may also contribute to contemporary C cycling. Indeed, there are conspicuous deposits of algal detritus on lake terraces above Lake Vanda, the current lake in the Wright Valley (Hall *et al.* 2001), but their quantitative contribution to contemporary C cycling has not been investigated and there are apparently no radiocarbon dates for soil organic matter.

Estimates of the turnover of contemporary organic C in other Dry Valleys soils are astonishingly fast, ranging between 20 and 120 years (Burkins *et al.* 2002; Elberling *et al.* in press), supported by rapid mineralization of soil C and N in laboratory studies (Barrett *et al.* 2002, 2005; Hopkins *et al.* in press). The implications of these fast turnover times are either that legacy C deposits may be about to be exhausted, or that the legacy C is either so stable or protected that it contributes little to contemporary C cycling. If the latter is true, contemporary C cycling in Dry Valleys soils must be sustained largely, if not exclusively, by modern sources of organic matter.

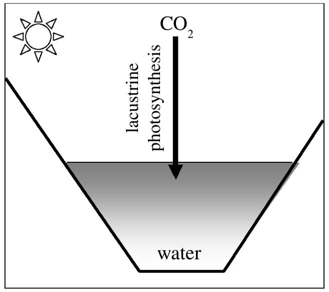
5. SPATIAL SUBSIDIES

(a) *Imports of resources*

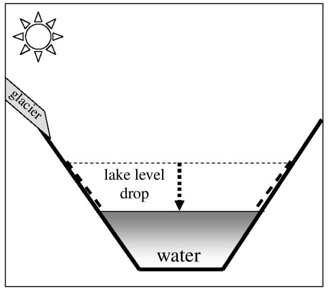
The Dry Valleys benefit potentially from imports of organic resources in the form of bird guano and feathers (Greenfield 1992; Marshall 1998; Legrand *et al.* 1998), wind-blown marine detritus and the arrival of inopportune seals and penguins that wander into the Dry Valleys and die, presumably from starvation or exhaustion (figure 3). Mummified seal carcasses are relatively frequent occurrences in the Dry Valleys and have persisted because of the cold and drying conditions (Péwé *et al.* 1959; Claridge 1961; Webb & Leckie 1977). Although apparent radiocarbon ages up to millennia have been reported for mummified seals and penguins in the Dry Valleys, the large ^{14}C depletion of the Antarctic marine reservoir makes these substantial over-estimates, and ages in the range of a few decades to two to three centuries are more realistic (Dort 1971, 1981; Mabin 1986). At the sites of deposition these subsidies could make a major contribution to biological processes in soils, at least when and where there is liquid water, and Lewis-Smith (1997) hypothesized that nutrient enrichment adjacent to mummified soils encourages colonization of the soil surface by lichens.

(b) *Redistribution of resources within valleys*

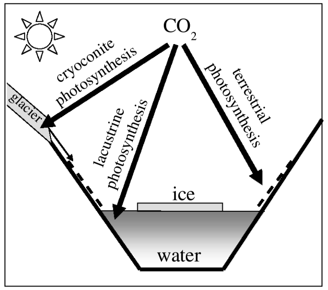
The Dry Valleys contain hotspots of productivity, which can act as point sources of resources. The relatively large standing biomass in lakes, most notably as cyanobacteria mats, and imbalances between primary production and consumption in the absence of macro-consumers, make lakes obvious sources of organic resources (Elberling *et al.* in press). Productivity in lakes in Dry Valleys is in the range 10–100 g C m^{-2} yr^{-1} (Vincent 1988). Transfer of only a modest fraction of this to the land surface could be sufficient to sustain the measured rates of soil respiration (Moorhead *et al.* 2003; Elberling *et al.* in press). Rapid turnover of organic matter in Dry Valley soils is also consistent with regular inputs of relatively labile organic residues (Hopkins *et al.* 2005, in press; Elberling *et al.* in press). Aeolian transport of lacustrine microbial mats, endolithic communities and organisms (Wilson 1965; Parker *et al.* 1982; Nienow & Friedmann 1993; Greenfield 1998; Moorhead *et al.* 2003; Nkem *et al.* 2006) supports the hypothesis that particulate (modern) matter is transported from productive sites (lakes) to low-productivity



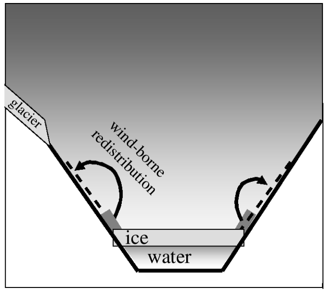
1. Photosynthesis in palaeolake.



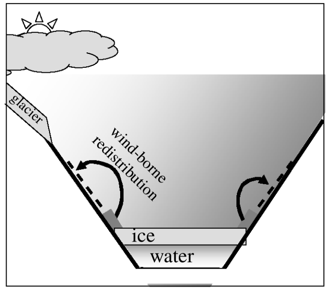
2. Lake level decline leaving organic deposits on palaeo-lake shores.



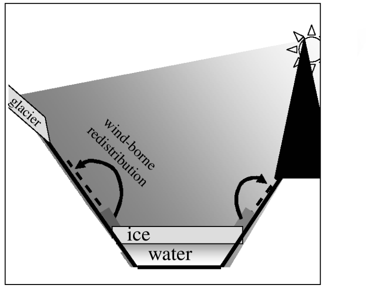
3. Modern photosynthesis in glacial, terrestrial and lacustrine habitats.



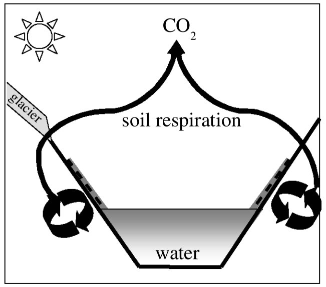
4a. Water freezes during winter and lake level decline as ephemeral stream flow ceases. Cyanobacterial bacterial biomass left stranded is redistributed by the wind.



4b. Water freezes during cold summer periods and lake level decline as ephemeral stream flow ceases. Cyanobacterial bacterial biomass left stranded is redistributed by the wind.



4c. Water freezes diurnally as glaciers are shaded by mountains and lake level declines as ephemeral stream flow ceases. Cyanobacterial bacterial biomass left stranded is redistributed by the wind.



5. Modern heterotrophic activity in soils fuelled by organic C from modern terrestrial photosynthesis and both by spatial subsidies from lacustrine and glacial sources, and temporal subsidies from ancient sources (legacy organic matter).

Figure 4. Conceptual summary of the sources and transfers of organic resources in the Antarctic Dry Valleys.

sites (soils). Increases in soil respiration along transects towards a lake and the decreasing organic C concentration with soil depth (Elberling *et al*. in press) provide indirect evidence of redistribution of lacustrine detritus from wet sites at lake edges to surrounding drier soils (Elberling *et al*. in press; Hopkins *et al*. in press). The mechanism proposed by Elberling *et al*. (in press) relies on lacustrine organic detritus washing up at the lake edge, where it is dried and dispersed by the wind (figure 3). Seasonal, diurnal and/or weather-dependent fluctuations in lake level resulting from periods when feeder streams stop flowing and glacier surfaces freeze may all contribute to wash-up and stranding of lacustrine detritus.

6. CONCLUSIONS

Information about C-transformation processes and rates in Antarctic soils and the contributions they make to C cycling in Dry Valley ecosystems is relatively limited. Furthermore, there are insufficient data to assess comprehensively the controls on productivity and the contributions they may make to heterotrophic activity in soils of the Dry Valleys. However, all processes discussed above are in operation in at least some Dry Valleys and their relative magnitudes vary between valleys. We propose the scheme summarized in figure 4 as a conceptual model, bringing together current observations on temporal and spatial subsidies, *in situ* productivity and redistribution of lacustrine detritus. This scheme attempts to unify different aspects of C cycling in the Dry Valleys, namely legacy versus contemporary organic C sources and terrestrial versus lacustrine organic C sources, in a manner that illustrates that they are not mutually exclusive. The challenge for understanding the landscape ecology, productivity and biodiversity of Antarctic Dry Valleys is to quantify the relative magnitude of each process, the causes of variation in magnitude of processes between valleys, and their sensitivity to environmental change.

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