

# The Landscape Continuum: A Model for High-Elevation Ecosystems

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*Interactions between climate and ecosystems with complex topographic gradients generate unique source and sink habitats for water and nutrients as a result of precipitation, energy, and chemical redistribution. We examined these phenomena for a high-elevation site in the Colorado Front Range. Current changes in climate and atmospheric deposition of nitrogen to these systems are causing rapid changes in some portions of this system but not in others. Using a conceptual model that links terrestrial ecosystems to each other and to aquatic ecosystems, we report how atmospheric inputs and endogenous resources can be amplified or attenuated by transport processes. High-elevation lakes and the alpine tundra–forest ecotone are expected to receive the brunt of anthropogenic inputs obtained from (a) the redistribution of exogenous materials from the regional environment and (b) endogenous sources originating in other montane areas.*

**Keywords:** alpine, aquatic–terrestrial interactions, climate, nutrient deposition, transport processes

**T**he panoramic splendor and complexity of high-elevation ecosystems have inspired and challenged humans for centuries (figure 1). These ecosystems have been variously perceived as physical structures to be conquered, as sites of spiritual inspiration, and as some of the last untamed natural places on Earth. In our time, the perception that “mountains are forever” may provide solace to those seeking stability in a rapidly changing world. However, changes in the abundance and species composition of the native flora and fauna of mountain ecosystems are potential bellwethers of global change, because these systems have a propensity to amplify environmental changes within specific portions of this landscape. We examined the potential of high-elevation ecosystems to accumulate and redistribute exogenous materials from the atmosphere and endogenous materials from the mountains. This analysis led us to a conceptual model of the coupled relationships among high-elevation ecosystems, emphasizing the importance of transport processes.

Mountain ecosystems have traditionally been characterized as harsh and variable environments (Billings 1973). Extreme temperatures and large diurnal variation in growing-season temperatures, in conjunction with high levels of ultraviolet radiation, accompany large variations in the amount of precipitation (Bowman 2001, Bowman et al. 2002). The plants and animals that remain above the tree line survive the winter beneath the snow or by keeping living tissues under the soil surface. Vertebrates such as ptarmigan may make limited incursions above the tree line in winter, but their survival, like

that of the plants, appears to be related to their ability to avoid extreme winds. Woody vegetation growing at the highest elevations survives by sacrificing windward portions of its structure to protect leeward portions or by sheltering in snowdrifts that accumulate in and around the vegetation (Seastedt and Adams 2001). Another feature of the vascular vegetation is that the flora is composed almost entirely of perennial species; annual plants constitute less than 2% of the flora in most alpine areas (Billings 1988). Not only is longevity a requirement, but most high-elevation species have opted for very conservative growth strategies. Embryonic leaf and flowering tissues are formed up to 4 years before they emerge (Meloche and Diggle 2001). This strategy limits the ability of most plants to exploit unusually favorable growing conditions. Leaves and flowering structures can increase in size in response to a favorable environment, but their numbers are predetermined. Natural selection has not favored opportunists in this ecosystem.

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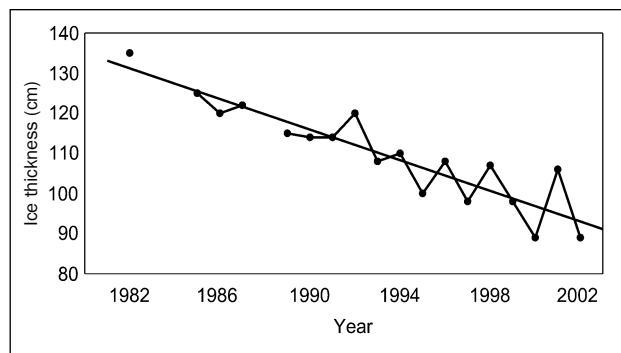
**Figure 1.** Arapaho Glacier as viewed from Niwot Ridge on the Colorado Front Range. High-elevation systems are characterized by a large percentage of surface area covered by rock and snow. Materials transported from these areas supplement atmospheric inputs of water and nutrients to alpine tundra, forest, streams, and lakes. Photograph: David Foster, Harvard University.

Compared with the terrestrial communities of the alpine regions, aquatic communities experience substantially less harsh and less variable temperature conditions. The formation of ice and an intermittent snow cover in early fall creates a barrier that protects organisms in the underlying water column from the strong winds and low temperatures experienced by the terrestrial communities. Although the cover of ice and snow limits light penetration, photosynthetic algal species adapted to low light levels continue to be abundant during winter, and their growth may be augmented by mixotrophic consumption of bacterial, particulate, and dissolved organic matter (Rodhe 1955, Spaulding et al. 1993). Furthermore, wind scour minimizes snow cover, thereby allowing photosynthesis to continue year-round. The protective role of the winter ice cover is one explanation for the high diversity of algal species in alpine lakes. Even though the summer period of ice-free conditions is short compared with the same period in lower-elevation temperate environments, it is still long compared with the life cycle of algal species, which are capable of doubling in abundance in a few days. The flux of nutrients (nitrogen, phosphorus, and silicon) during spring snowmelt can support rapidly growing phytoplankton populations dominated by diatoms in alpine lakes (McKnight et al. 1988), and large changes in the abundance of dominant algal species over the growing season are characteristic of these lakes (McKnight et al. 1988, Kolesar et al. 2002).

### Global environmental change and high-elevation systems

Human impacts on high-elevation ecosystems have been large and are occasionally dominant controls (cf. Price 1999, Beniston 2000). Two major components of global change, changes in climate and in nitrogen deposition, are affecting the biota of North American regions (Bowman et al. 2002). Directional changes in precipitation have been reported (Greenland and Kittel 2002), and an increase in precipitation of more than 10 millimeters per year for the last 50 years has occurred at our Colorado Front Range site (Greenland and Losleben 2001). This increase has affected the physical processes of alpine lakes (figure 2); ice thickness measured in late March over a 20-year interval shows a marked decline, while temperatures over this interval have remained statistically unchanged (Caine 2002). The change in ice thickness is best explained by increased winter precipitation (about 1% per year), which leads to increased flows into the lake in fall and winter. Greater volumes of water hold greater quantities of energy, and thus ice thickness in late winter is reduced.

Increases in inorganic nitrogen deposition from the atmosphere have also been detected (figure 3; Burns 2003). Annual deposition of inorganic nitrogen in wetfall (precipitation) at the Niwot Ridge National Atmospheric Deposition Program site showed an increase of 0.3 kilogram per hectare per year for the 1984–1996 interval (Williams and Tonnesen



**Figure 2.** Ice thickness (in centimeters) for an alpine lake, Green Lake Four, located in the Colorado Front Range. Although ambient temperatures have not significantly changed, ice depth and duration are on the decline. Updated from Caine (2002).

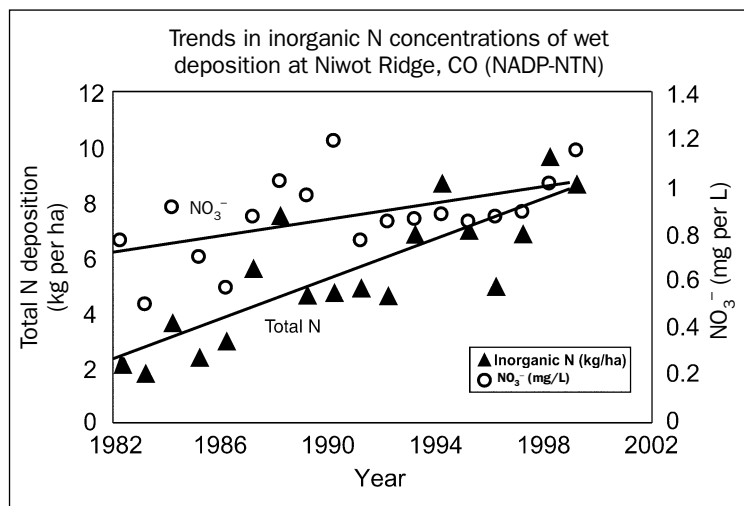
2000). The annual increase in deposition is caused by an increase in the volume-weighted concentration and by the absolute increase in precipitation that has occurred during this interval (Williams et al. 1996).

These changes in water and nitrogen inputs have not produced uniform changes in the biotic composition of alpine ecosystems. The species composition and abundance of the terrestrial flora in high mountain regions in the Southern Rockies have been stable over recent decades, compared with the levels at more anthropogenically disturbed sites at lower elevations (Korb and Ranker 2001). Alpine tundra vegetation still exhibits strong growth responses and changes in species composition when nitrogen or phosphorus (or both) is added to the vegetation (Theodose and Bowman 1997). Such experiments indicate that the vegetation is still constrained by nutrient limitations. However, certain nitrogen-loving plant species found in alpine regions, identified by their positive responses to nitrogen fertilizer treatments, are showing increases in their numbers in portions of the landscape (Katharine N. Suding, Department of Ecology and Evolutionary Biology, University of California–Irvine, personal communication, 2004). At present, these changes are subtle and difficult to detect.

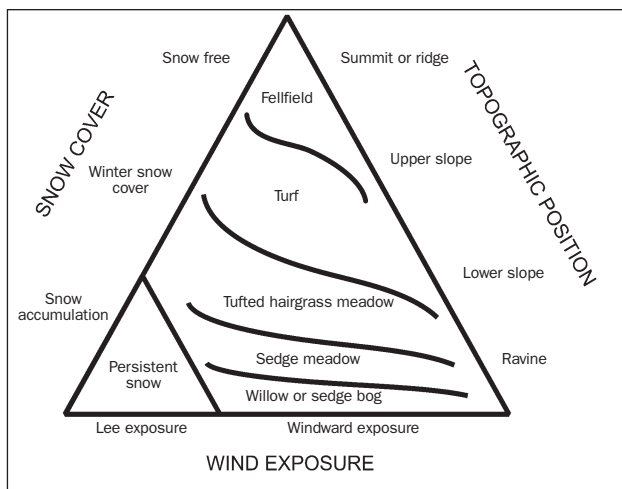
In contrast to the terrestrial ecosystems in alpine areas, which are relatively stable, lake ecosystems in the same areas are undergoing rapid change in benthic primary production and in diatom species composition (Baron et al. 2000, Wolfe et al. 2002), a response attributed to increased nitrogen deposition. The sensitivity of lake systems to nitrogen inputs could simply be related to the life history characteristics of the respective species in the two communities. However, a review of conceptual models developed for complex landscapes (Reiners and Driese 2001) and for high-elevation ecosystems suggests additional reasons for communities to show differing responses to climate and atmospheric deposition inputs.

## Conceptual models of mountains

Much of our understanding of the structure and function of alpine communities in North America developed from the contributions of Dwight Billings and his students (e.g., Billings 1973, 1988). Billings described the alpine landscape as a complex of communities distributed along moisture and energy gradients created by the interaction of wind, snow, and topography. He developed what is called the mesotopographic model of the organization of alpine communities (figure 4). About 75% of annual precipitation occurs as snow in the southern Rockies (Greenland and Losleben 2001). Wind scour removes snow from exposed areas and redeposits it downwind in protected areas. The consequences of this snow redistribution are large. First, in spite of high annual precipitation inputs that generate a surplus of water well above the evaporation potential of the area, a substantial portion of the landscape retains very little precipitation that falls as snow and shows water limitations on growth during the summer (Taylor and Seastedt 1994, Walker et al. 1994). Second, those areas that are heavily subsidized with wind-redistributed snow have a much shorter growing season because of enhanced snow cover and have a very short window of opportunity for energy capture relative to other communities within this landscape. Plant species occupying these areas have evolved growth strategies to minimize the extent to which a single resource can limit growth (Chapin et al. 1990). Thus, one might expect that snowfield plants would allocate resources to foliage to capture light energy, while plants in the dry meadow would allocate more energy to roots to obtain moisture and nutrients. The Billings model provides an excellent conceptual understanding of the heterogeneity in



**Figure 3.** Nitrate ( $\text{NO}_3^-$ ) concentrations in wet deposition, in milligrams per liter, and total inorganic nitrogen (N) deposition, in kilograms per hectare, in alpine tundra at about 3520 meters elevation. The inorganic N deposition is increasing faster than the nitrate concentrations within precipitation because the total amount of precipitation has increased over this sampling interval. Data are annual estimates provided by the National Atmospheric Deposition Program (NADP 2002).

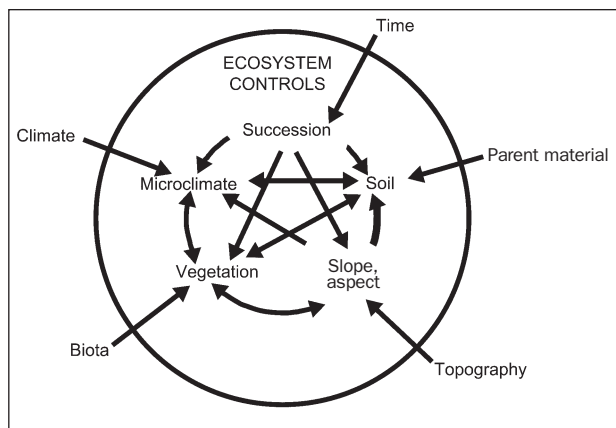


**Figure 4.** The mesotopographic model developed by Billings (1973). Alpine plant communities are formed by the spatial gradients created by snow cover, which is generated by wind exposure and topographic position.

plant species composition and the functioning of alpine communities that are generated by wind, snow, and topographic position.

Burns and Tonkin (1982) developed a broader landscape model that included more detailed topographic controls of high-elevation systems. First, they recognized that position on the landscape controls soil development and therefore the vegetation communities that can form on such soils. Mountaintops or ridgetops, valley sides, and valley bottom areas vary substantially in the quantity of water and particulates deposited or transferred by the atmosphere and in the retention capacity for these inputs. Similarly, these areas respond very differently to natural disturbances such as gopher burrowing or to anthropogenic disturbances such as trail construction and trampling from hikers. Within these top, side, or bottom areas, Burns and Tonkin (1982) divided the landscape into six “microenvironmental” sites. These sites ranged from extremely windblown areas, with more than 300 days per year free of snow, to semipermanent snowbank areas that occasionally retain a snow cover throughout the year. In addition to this snow-duration gradient, they identified the presence of wet meadows, nearly flat areas subsidized by runoff from adjacent hill slopes. Burns and Tonkin proposed that their microenvironmental sites could also be used to predict soil development. The two endpoints of their continuum, the extremely windblown areas and the near-permanent snowpack areas, both contain relatively young, undeveloped soils as a result of the absence of biotic-related weathering processes.

The state factor model of Hans Jenny (Jenny 1941, Admundson and Jenny 1997) is a powerful conceptual tool for understanding the structure and function of ecosystems such as the taiga (Van Cleve et al. 1991). In this model (figure 5), parent materials (the mineral contribution to soils), biotic composition, and the time a system has had to recover from disturbances are included with topography and climate



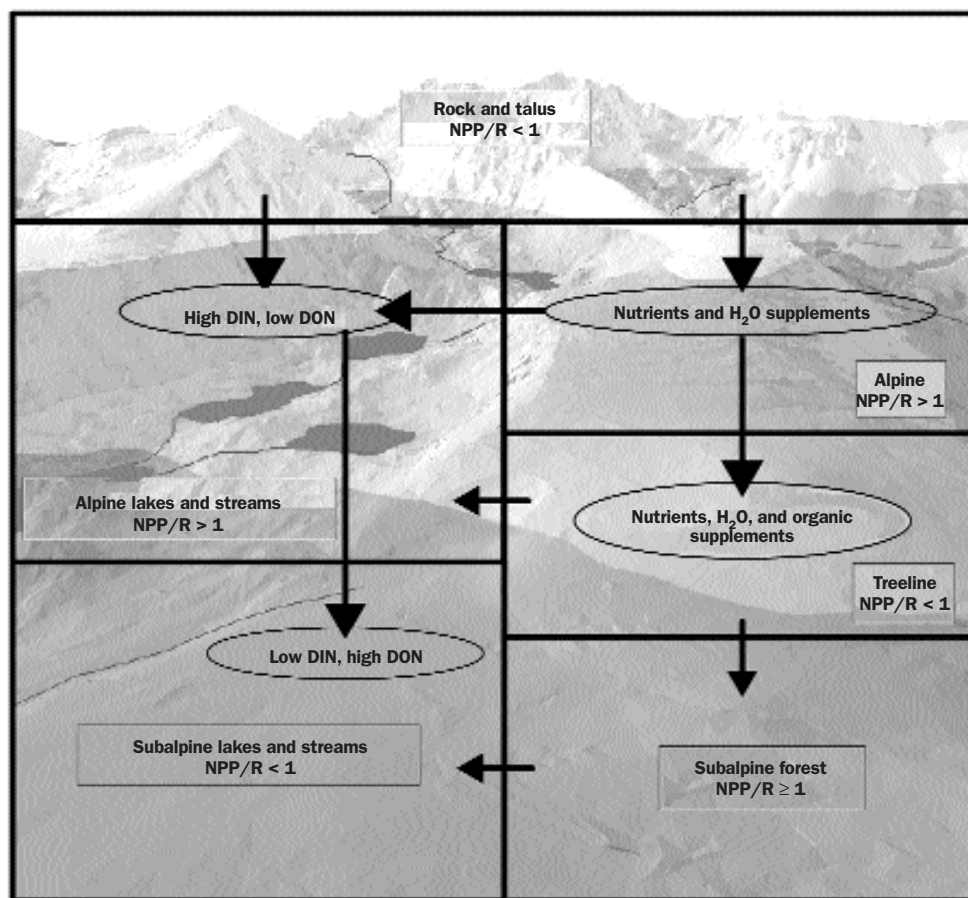
**Figure 5.** The state factor model of ecosystem organization that Jenny (1941) originally proposed for soils. The structure and function of the ecosystem are controlled by interactions among the potential biota, climate, parent material, topography, and disturbance history of an area. Interactions among these variables are responsible for ecosystem characteristics such as vegetation dominance, carbon sequestration, carbon flux, and nutrient cycling. Redrawn from Van Cleve and colleagues (1991).

as factors controlling current ecosystem structure and function. The Jenny model provides a conceptual basis for recognizing emergent properties of ecosystems (i.e., ecosystem structures such as soil or processes such as carbon flux). From a biogeochemical perspective, the explicit inclusion of all five state factors within the Jenny model is essential for understanding within-community biogeochemical processes as well as within-community change in biotic composition or function.

Reiners and Driese (2001) emphasized the significance of transport processes, a subset of propagation phenomena, as fundamental organizing agents of communities and ecosystems. Here we expand on the examples from montane systems presented in that analysis and identify the ecological consequences of these processes for high-elevation ecosystems. We attempted to accommodate both terrestrial and aquatic systems of high-elevation areas within the conceptual framework of the models described above. We included all of the factors emphasized by Jenny, as well as the explicit spatial focus provided by the models of Billings and of Burns and Tonkin. The result of this activity, the landscape continuum model (LCM; figure 6), emphasizes transport processes and their importance in high-elevation ecosystems.

Our work also builds on a prior model, developed for fluvial ecosystems, that captures the overriding significance of transport processes: the river continuum concept (RCC; Vannote et al. 1980). The RCC, as modified and expanded by many recent findings (e.g., Gomi et al. 2002), provides a conceptual framework for understanding a large-scale system in which fluvial transport processes dominate biogeochemical processes and therefore ecosystem structure and function. The





**Figure 6.** The landscape continuum model integrates terrestrial and aquatic components of high-elevation ecosystems. The three levels of shading represent block fields and talus at the highest elevations, alpine tundra in middle regions, and subalpine forest. Precipitation and dryfall containing dissolved inorganic nitrogen (DIN) with low amounts of dissolved organic nitrogen (DON) and other materials are deposited across a landscape that varies from no plant cover to 100% plant cover and from bare rock to deep organic soils. The absolute amount of atmospheric deposition of water and nutrients is greatest at the highest elevations. Redeposition by mass flow and wind scour moves materials downhill and downwind. Runoff that occurs over bare rock or frozen surfaces travels directly to aquatic systems, bypassing terrestrial biota that function as filters. Water transported through soils may contribute some DON to aquatic systems but provides very little DIN. Predictions of the ratios of net primary production (NPP) to animal and microbial respiration rates (R) vary within different communities depending on the sources of organic production (in situ or imported) relative to local respiration and export of this organic material.

ideas contained within the RCC evolved from previous geomorphologic models of river systems; one of these ideas is that the systems are structured by both the means and the extremes of the fluvial environment (e.g., floods and droughts). This provides another point of connection between the RCC and the LCM, as the composition and characteristics of the biota (or the absence thereof) of high-elevation systems have also been selected by both mean and extreme conditions. The perennial growth form and the preformation of vegetation tissues appear to be examples of the conservative strategies of plants required to survive the extremes. Similarly, growth by mixotrophic algae (algae that can also obtain energy from organic compounds; Rodhe 1955) represents an adaptation to low light conditions occurring during the winter ice and snow cover. Landslides and snow avalanches are other extreme

events that structure high-elevation ecosystems (Swanson et al. 1988) and explain patterns in both vegetation structure and biogeochemical processes.

The key similarity of the two models, however, is the significance of material transport and its consequences for community characteristics, including patterns of nutrient dynamics and carbon flux. The major difference between the RCC and the model presented here is that the RCC has just one transport agent (water), and this effect is represented primarily as a one-dimensional concept. The high-elevation system has wind, water, avalanches, and landslides as transport agents and addresses a more spatially complex system. A three-dimensional perspective is therefore required to consider the combined effect of aeolian, fluvial, and surface transport processes (Swanson et al. 1988).

### Landscape continuum characteristics

Mountains form a barrier to incoming air masses. Forced to rise, the air cools and triggers precipitation; thus, precipitation generally increases with increasing altitude (Barry 1973). Colder temperatures at higher altitudes result in lower evapotranspiration rates, so that the overall water balance in the mountains is positive and produces substantial accumulations of snow and runoff. As previously described, increasing precipitation results in increasing deposition of inorganic nitrogen (figure 3; Williams and Tonnessen 2000), other nutrients, and a host of materials of human origin. Precipitation as snow results in temporary storage of this water equivalent, and of any pollution the snow contains, for 6 to 8 months. During this period, these materials are frequently redistributed across the landscape by winds. Water and pollutants are then released during snowmelt runoff, which moves as a pulse through terrestrial and aquatic communities over a period of days to weeks. Snowmelt over frozen soils results in water moving directly to aquatic systems without being processed on or within the soil.

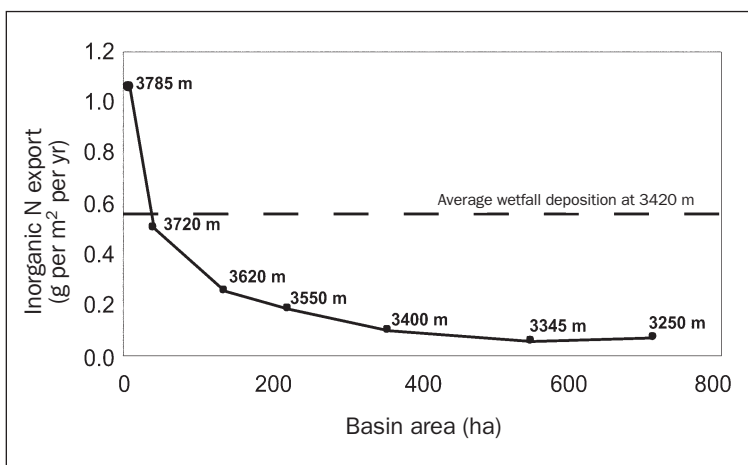
The transfer of water, nutrients, and particulates from the mountaintops downward makes this uppermost zone a source area for these materials. First, mountaintops are generally characterized by large expanses of steep, rocky terrain with limited soil development and with few if any vascular plants. Major landscape types are often talus and scree fields, exposed bedrock, and debris deposited from glacier activity. The combination of high precipitation, snowmelt runoff, limited soil and vegetation, and steep slopes results in large amounts of surface runoff and sediment transport to downslope areas. The amount of nutrients, such as inorganic nitrogen, per unit area of catchment that is exported in stream water exceeds the average wetfall inputs from the atmosphere (figure 7). The difference between wetfall inputs and stream export is accounted

for by aeolian particulate (dryfall) deposition of materials containing inorganic nitrogen and by mineralization of organic matter from aeolian inputs or from nitrogen-fixing organisms. In addition to the stream water export of inorganic nitrogen, high winds further augment the redeposition of minerals and organic materials, particularly where the dominant downwind areas are also the downhill locations (as occurs at our research site along the eastern side of the Continental Divide). In addition to the external inputs, freeze-thaw cycles and abrasion of rock surfaces also result in the downhill transport of the parent material from this zone. There is some uphill transfer of organic matter by biota (Halfpenny and Hefferman 1992), and, as in the RCC, the biota provides a mechanism for retention of materials, resisting the dominant transport mechanisms.

Aeolian deposition of particulate organic matter and minerals originating from sources outside the region is significant (Litaor 1987, Sievering 2001). Ley and colleagues (2004) estimated annual inputs of organic and inorganic particulates at talus sites to be more than 50 kilograms per hectare. They used isotopic analyses to demonstrate that particulates collected in dust collectors in the talus were primarily from external rather than local sources. Only limited amounts of deposited organic matter can be found in protected areas within the largely unvegetated uppermost zones (Ley and Schmidt 2002); the majority of the input is transported downhill. In many mountain valleys, talus fields surround the uppermost lakes; depending on their bathymetry, these lakes may retain sedimentary materials (figure 8).

In this uppermost zone, biogeochemical processes in the lakes and streams remove nitrate from upstream sources and export dissolved organic carbon (figure 9). Stream water nitrate concentrations measured in June 2000 during snowmelt runoff were about 30 microequivalents ( $\mu\text{eq}$ ) per liter (L) near the Continental Divide. Sources of this material included both snowmelt and drainage from talus slopes (Williams et al. 1996). Near the tree line, at the outflow from the second of two alpine lakes, nitrate concentrations decreased to about 3  $\mu\text{eq}$  per L, indicating that nitrate had been converted into organic forms or denitrified and returned to the atmosphere. In contrast to nitrate concentrations, dissolved organic carbon concentrations were less than 0.5 milligram carbon per L at the highest elevations and increased downslope in response to in situ carbon fixation in lakes and streams and leaching exports. While the mechanisms for the disappearance of nitrate remain a research question, the uptake of inorganic nitrogen by algae and microbes and the conversion of this material into organic forms of nitrogen are consistent with our measurements.

In the zone below the mountaintops, the wind-scoured dry meadows of the vegetated alpine regions as well as the fellfields (rocky areas containing a low cover of vascular vegetation growing in protected areas) are net sources of water, nutrients, and organic



**Figure 7.** Export of inorganic nitrogen (N) in streams, in grams per square meter per year, as a function of elevation and basin size. At the highest collection points, export exceeds atmospheric input. This is because stream measurements include inorganic N carried by all sources, and measurements of input include only the inorganic material in wetfall. Data are updated from Caine (2001).



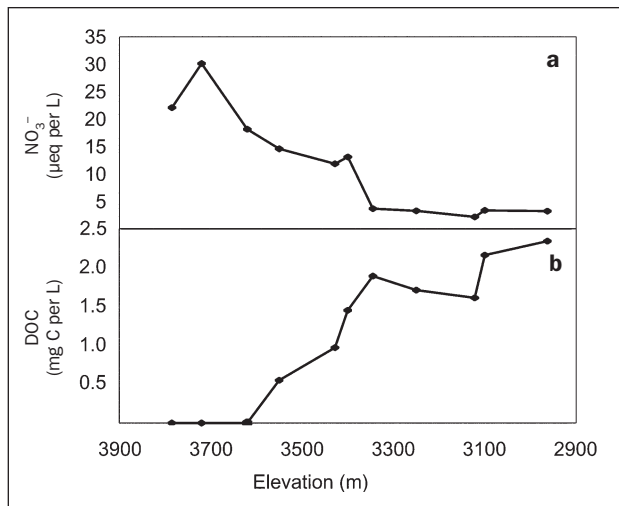
**Figure 8.** A high-elevation lake in the Colorado Front Range. The surrounding catchment area is mostly rock and talus, which, while contributing mineral components, neither retain nor greatly modify inputs from the atmosphere before the inputs are transported to wetlands and lakes. Such lakes may be particularly vulnerable to anthropogenic materials found in atmospheric deposition. Photograph: Courtesy of the University of Colorado Photography Department.

matter to lower-elevation sites. We know, for example, that decomposition of surface litter in these areas is low relative to the levels in adjacent, moist areas (O'Lear and Seastedt 1994), yet surface accumulation of this material does not occur (Burns 1980). Wind scour in the fellfield areas is so severe that soil formation is relegated to protected surface areas. The export of plant litter from these areas by wind scour implies that sites have a ratio of net primary production to heterotrophic respiration that is greater than 1; this is similar to values observed in the middle reaches of rivers (Vannote et al. 1980). The "subsidized" moist and wet meadows in alpine areas obtain water and nutrients from upland and upwind sources. The net flux of organic matter from these areas is poorly known. While portions of the alpine ecosystems undoubtedly function as a sink for materials redeposited from uphill and upwind sources, much of the Colorado alpine region is dominated by windswept fellfields and dry meadows, and these areas function as a source of inorganic and organic materials to both aquatic systems and tree-line areas.

In the uppermost alpine lakes in our study, we found that phytoplankton biomass increases steadily after ice-out and through the summer, suggesting that primary production contributes to nutrient transformations at that time. Furthermore, the increase in biomass indicates that in the water column the net ratio of phytoplankton production to heterotrophic

respiration is greater than 1. However, during winter ice cover and spring snowmelt, respiration of dissolved organic material in the lake water column and of allochthonous organic material in the lake and wetland sediments may exceed primary production. Although we hypothesize that annual production will exceed respiration (figure 6), the carbon balance of these systems remains a research question.

The redeposition of water, nutrients, and particulates is maximized in the snow deposition zones at the alpine–subalpine interface. The trees themselves provide the mechanism to scavenge these materials by functioning as wind-breaks and collectors. In the absence of a developed tree line (because of fire, avalanches, or extreme snow events), these materials are transported farther downslope. Similarly, the lakes and wetlands near the alpine–subalpine interface can store and transform particulate material and solutes from upstream. The relatively longer ice-free period for these lakes may increase the net primary production for the summer period and enhance the retention and transformation of nitrate through nutrient uptake. The alpine–subalpine interface, however, represents a transition to greater dominance of dissolved and particulate allochthonous organic matter in the carbon cycling of these lakes (McKnight et al. 1997). The surrounding landscape is more highly vegetated and has more developed soils. In these lakes and in downstream lakes



**Figure 9.** (a) Nitrate ( $\text{NO}_3^-$ ) concentrations in streams, in microequivalents per liter, as a function of elevation (in meters). (b) Dissolved organic carbon (DOC) as a function of elevation. The linear pattern of increasing concentration of organic carbon, in milligrams per liter, with decreasing elevation is affected by retention and removal within aquatic communities. Data are updated from Williams and Tonnessen (2000).

and streams, the ratio of net primary production to respiration is believed to be less than 1 on a year-round basis (figure 6).

### Effects of transport processes on soil biogeochemical processes

Landscape-scale variations in climate conditions, especially through moisture availability, drive a significant amount of the variability in both community structure and biogeochemical processes across high-elevation landscapes. However, our findings suggest that considerable biogeochemical variability can occur even within a given moisture regime in adjacent areas of the alpine landscape (Bowman et al. 2003). For example, several key biogeochemical variables, including soil carbon, total phosphorus, and plant-available phosphorus, were markedly different for dry meadow sites at three different locations in the Colorado alpine region (figure 10). These results cannot be explained either by the Billings model or by the Burns and Tonkin model, but they are consistent with a biogeochemical model that emphasizes the importance of transport processes on site characteristics.

Given that both vegetation and moisture regimes are similar among the three sites, and that topography is quite similar between the two sites that differ the most in their biochemical characteristics, the Jenny model would suggest differences in parent material composition or age as possible drivers of the observed biogeochemical variation. The rocks underlying this area are of similar origin and are extremely old (Peterman et al. 1968, Madole 1982). Variations in the rock's chemical content and weathering rates, especially in the

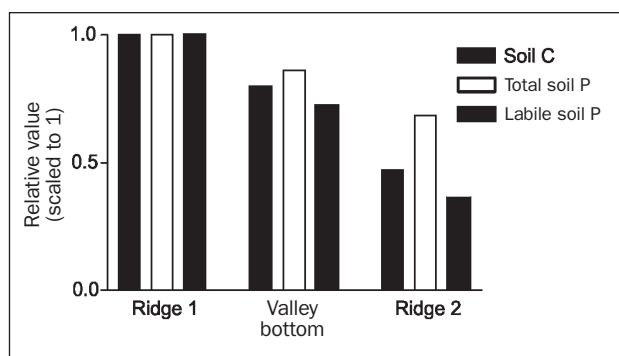
cold alpine environment, are unlikely to produce the differences seen in figure 10.

Soil age almost certainly does vary among the three sites (Burns 1980) and thus could contribute to the observed patterns. In temperate regions, glacial events are often assumed to be dominant drivers of new primary succession and soil development, and glacial chronosequences have been used to support the Jenny model (Admundson and Jenny 1997). Thus, one might expect differences in glacial history to explain some of the biogeochemical differences across the alpine landscape. The intermediate site in the valley bottom shown in figure 10 was glaciated in the most recent event (Caine 2001), and thus the soils there are unlikely to be any older than approximately 12,000 years. Because the other two sites were not glaciated (Madole 1982), it is possible that the alpine soils at these sites may be extremely old. In fact, the suggestions of phosphorus limitations to plant growth in the saddle region (Theodose and Bowman 1997) initially led us to hypothesize that relatively low phosphorus availability might be a product of very old soils, as in the pattern described by Walker and Syers (1976).

However, the phosphorus depletion described by Walker and Syers (1976) relies on losses of primary mineral forms of phosphorus caused by weathering, combined with increasing phosphorus conversion into insoluble forms (occlusion) attributable to an abundance of aluminum-rich and iron-rich secondary minerals. Such changes can occur readily in warmer, wetter regions, especially those in tropical latitudes (e.g., Crews et al. 1995), but are unlikely in the cold, dry climate of the wind-scoured alpine meadows, even over long time scales. Moreover, the highly organic alpine soils are not rich in the secondary minerals and clay that can drive phosphorus occlusion. Finally, biogeochemical conditions at one of the old sites make it generally the most fertile of the three, with respect to plant-available phosphorus. Its soils are much more like the young soils of the recently glaciated site. Thus, a simple model in which soil age and biogeochemistry are estimated from the time since glaciation does not seem to apply to this landscape.

In the absence of other possibilities, the transport-controlled alteration of soil development processes is the dominant factor explaining the differences seen in figure 10. Soil development and effective age, even on the unglaciated ridge, may be frequently altered during glacial epochs by movement of materials about the landscape. Such transport can occur by solifluction (soil flow under cold, saturated conditions) or frost creep (downslope movement caused by the physical disruption of freeze-thaw cycles; Benedict 1966). Second, we believe that atmospheric deposition of rock-derived nutrients is important to nutrient supply in the highly organic, low-mineral soils (Litaor 1987), with deposition of this material exceeding 5 grams per square meter per year in at least some areas (Ley et al. 2004). The total amount of these exogenous rock-derived nutrients probably varies considerably with both landscape position and soil age, and over longer time scales they may be distributed by solifluction and frost creep in





**Figure 10.** Soil organic carbon (C), total soil phosphorus (P), and labile, plant-available soil P in two ridge sites (with elevations of 3730 meters [m] and 3520 m) and a valley bottom site (elevation 3550 m) located across the Niwot Ridge landscape. Labile soil P is the sum of resin- and bicarbonate-extractable P from a modified Hedley sequential fractionation of total soil P (Tiessen and Moir 1994). Ridge 1 and Ridge 2 sites are thought to be unglaciated, but they experienced substantial freeze-thaw activities during the Pleistocene. The valley bottom site is below Lake 4 in the Green Lakes watershed (shown in figure 8) and was glaciated during the most recent Pinedale glacial event.

ways that enrich lower zones and impoverish higher areas. Thus, soil development in alpine regions, and its associated effects on biogeochemistry, may be driven by a complex set of transport processes causing substantial variation at small spatial scales across the landscape. In general, we propose that the downhill movement of biogeochemically important elements at both large and small scales plays a large role in the long-term development of alpine soils.

### Biotic mediation of biogeochemical fluxes

Terrestrial and aquatic plants provide mechanisms of nutrient and material retention that strongly influence biogeochemical processes (Bormann and Likens 1979). The activities of organisms at higher trophic levels can often modify these patterns of nutrient and material retention. Instead of promoting nutrient spirals or nutrient export, biotic resistance to transport processes stabilizes nutrient cycles within microenvironmental systems while concurrently altering regional energy and water balances. Some species are clearly better retention agents than others; the mobile tree islands and gophers found on Niwot Ridge represent extreme examples of biotic attenuation and amplification of transport processes, respectively. Tree islands retain snow and aeolian material within the dry meadow tundra and, by disrupting transport, make the mesotopographic model of Billings inapplicable. The outcome of this disruption mimics a portion of the Billings model on a finer spatial scale (Seastedt and Adams 2001). The trees, rather than the topography, generate the snow gradient. These trees also reduce carbon sequestration and nitrogen storage in soils,

because these substrates are deposited in surface organic mats that are eventually vulnerable to wind and water transport. In contrast, gophers are facilitators of transport processes, because their burrowing and mounding activities expose the highly organic soils of the alpine meadows to wind and rain, greatly enhancing transport of soil materials (Sherrod and Seastedt 2001).

The maximum landscape-scale impact of biota on materials occurs at the tree line, where trees function as windbreaks, collecting snow, particulates, and nutrients. Although the mechanisms responsible for the formation and location of the tree line vary (Baker and Weisberg 1995), snow depth is a major factor, particularly along the eastern side of the Continental Divide. Once trees become established, their presence results in massive drifts downwind of their locations. These drifts restrict additional tree growth and survival, often creating a series of ribbon forests and snow glades (e.g., Knight 1994). Tree-line areas receive substantial subsidies of water, nutrients, and organic material from upwind and uphill sources, and net primary productivity is most likely enhanced because of these subsidies (Monson et al. 2002). Changes in the thermal regimes of soil, in conjunction with changes in soil moisture, alter rates of decomposition, with decay rates slower than those observed on the alpine tundra surface but faster than those observed beneath completely closed canopies (Seastedt and Adams 2001). Given the organic subsidies from upwind and uphill sources, the levels of carbon dioxide released from local respiration by heterotrophs approach the levels of carbon dioxide fixed by local net primary productivity. When carbon losses due to infrequent tree-line fires are factored into this number, we calculate that more carbon dioxide exits these local areas than is fixed by plants.

### Understanding the complexity of high-elevation ecosystems

Our efforts to integrate the conceptual models of Billings (1973), Jenny (1941), and Burns and Tonkin (1982) for the biogeochemical properties of high-elevation systems produced a model system that includes processes identified by Reiners and Driese (2001) and parallels with the RCC of Vannote and colleagues (1980). Both high-elevation systems and the river continuum contain areas that receive potentially large energy and nutrient subsidies from upstream, uphill, or upwind sites. Both systems exhibit zones where the ratios of production and decomposition vary. Finally, both systems mediate anthropogenic and natural environmental changes through biotic responses that affect and are affected by transport processes.

Our studies and observations suggest a large number of testable predictions of the LCM, of which these are perhaps the most important:

- Lakes within or below block fields and talus areas will receive the largest increases of nutrients per unit area of catchment (figure 7). Net primary production is believed to exceed in situ respiration, and these lakes

will show greater changes in species composition and production than any other high-elevation ecosystems in response to increasing deposition of inorganic nitrogen.

- Alpine fellfield and dry meadow areas receive only a fraction of the precipitation and nutrients from the atmospheric deposition that falls as snow in sheltered areas. These sites also lose a fraction of the organic matter and nutrients contained in plant litter to wind scour. Therefore, these dominant communities of the alpine landscape do not experience the magnitude of nutrient enrichment caused by anthropogenic changes to other portions of the landscape. These areas will exhibit less change in plant productivity and species composition through time than more mesic areas capable of retaining atmospheric inputs.
- Tree-line areas receive among the largest subsidies of snow and particulates and are beneficiaries of the losses from fellfields and dry meadows. These systems already consist of vegetation adapted to high nutrient availability. Forest production of subalpine ecosystems will be maximized at the tree line, and these sites will be the first terrestrial areas to experience characteristics of nitrogen saturation, as described by Williams and Tonnessen (2000).

The LCM provides a conceptual framework that makes it possible to understand high-elevation systems from a biogeochemical perspective and to predict how these systems might change in response to directional change in precipitation and atmospheric chemistry. The model emphasizes landscape variation in the patterns of biogeochemical cycles, carbon fluxes, and net primary productivity, and it makes predictions about growth strategies and nutrient characteristics of plants. It easily integrates with similar concepts and principles required to understand within-community interactions, and it provides a mechanistic interpretation for how different portions of the high-elevation landscape can experience excesses and limitations of the same nutrient. Future work employing isotopic analyses should allow researchers to elucidate and test many unresolved questions. Finally, both high-elevation and high-latitude systems have been identified as being at risk from a variety of anthropogenic materials added to the atmosphere. The LCM suggests that high-elevation lakes and tree line may be the locations to experience the first negative impacts of these materials, because of the amplification effects of transport processes.

### Application of the landscape continuum model to other ecosystems

Amplification and attenuation of water and nutrient inputs to ecosystems occur in all systems that experience directional physical forces of wind and gravity. Wind-scoured, heterogeneous landscapes are found on all continents. These transport processes are significant at local scales, as represented by examples presented here, or at regional and global scales,

where materials from one continent are redeposited on another land mass (Swap et al. 1992, Chadwick et al. 1999) or in marine ecosystems (Garrison et al. 2003).

The ability of natural terrestrial landscapes adjacent to human-dominated systems to persist in their present composition and function is of growing concern. This proximity causes modifications to microclimate and atmospheric inputs and alters natural disturbance regimes. Our research indicates that what may appear to be relatively small changes in environmental drivers can be amplified within ecosystems because of the significance of transport processes in redistributing materials across the landscape.

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