Chapter 12 Biological Phosphorus Cycling in Arctic and Alpine Soils

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12.1 Introduction

Climate change is having disproportionately large effects on arctic and alpine ecosystems (McGuire 1995; McGuire and Hobbie 1997; Melillo et al. 1995). Furthermore, soils from arctic environments play important roles in the global carbon (C) cycle because they contain a disproportionately large reservoir of soil C (Post et al. 1982). Because both primary production and decomposition have the potential to be limited by phosphorus (P) availability in arctic and alpine environments, understanding the biological controls on P cycling and availability is necessary to understand the impacts of environmental changes in these regions. The objective of this review is to draw together current knowledge on biological P cycling in arctic and alpine soils. The main topics considered are: the unique aspects of these environments and how they might influence biological P cycling; the dominant controls on P availability in these systems; interactions between seasonal dynamics and P cycling; studies on natural P availability; and responses of plants and soil microorganisms to P fertilization experiments.

The relative lack of literature on P dynamics, particularly biological P cycling, in arctic and alpine ecosystems is notable, especially for the high arctic. A disproportionate number of the studies that are available have been conducted in northern Alaska, USA (especially near Toolik Field Station), in the area near Abisko, Sweden, and in the Rocky Mountains of Colorado, USA. Thus, information from large areas of the arctic in North America and Europe is lacking, and the same is true for many alpine areas around the world.

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12.2 Characteristics of Arctic and Alpine Soils

There are many similarities between the cold climates of arctic and alpine regions, as evidenced by the similarities between their plant communities. For example, 37% of the alpine plant species in the mountains of Colorado, USA, also occur in the arctic (Bliss 1956). Environmental conditions in both regions may vary markedly, with precipitation, angle of insolation, photoperiod, fluctuations in daily temperature, atmospheric thickness, partial pressure of atmospheric gases, and the duration of the plant growing season all depending upon altitude, latitude, and geographical position (Richardson et al. 2003). Even though there is greater seasonal variability in air temperatures in arctic than in alpine regions, the presence of permafrost in arctic soils tends to buffer soil temperatures from fluctuations, and results in smaller seasonal fluctuations in soil temperatures in arctic regions than in mid-latitude alpine regions (Richardson et al. 2003). There are gradients of environmental severity in both arctic and alpine environments, with conditions becoming increasingly harsh with latitude and elevation, respectively (Bliss 1956).

To a limited extent, it is possible to generalize about large, highly variable regions; for example, water is more often limiting in alpine soils than in low arctic soils (Bliss 1956; Richardson et al. 2003), although both environments encompass a wide range of soil moistures. This is because relative humidity tends to decrease with increasing elevation, which can exacerbate moisture stress in alpine environments (Richardson et al. 2003). In arctic soils, permafrost often isolates the active layer, preventing the deep drainage of water (Bliss 1956). However, drier polar desert and semidesert become predominant in the high arctic. Alpine soils less frequently have continuous permafrost to trap soil moisture, and therefore lack the ability to retain water that arctic soils possess (Richardson et al. 2003). Alpine regions tend to be characterized by topographic gradients in moisture availability that are caused by the high topographic relief (Billings 1973). Steep slopes serve to enhance runoff (Richardson et al. 2003), and ridge tops or plateaus often experience strong winds that blow snow onto leeward slopes, leading to differences in snow-pack depth and high spatial variation.

In alpine environments, topographic gradients in moisture availability result in steep gradients in plant community composition and primary productivity (Billings 1973). Although alpine floras may differ among regions, there are often similar patterns of vegetation across the topographic gradients: cushion and rosette plants on ridges and between rocks; herbaceous plants and graminoids along the slopes; dwarf shrubs with herbaceous dicots and graminoids below the melting snowdrifts; and sedges, grasses, low shrubs, and mosses in poorly drained areas (Billings 1973). Higher moisture availability and primary productivity in areas of snow accumulation result in increased soil organic matter content and biological activity. For example, of the alpine plant communities on Niwot Ridge in the Rocky Mountains of Colorado, USA, wet meadows growing in relatively flat, low lying areas have the highest soil moisture, plant productivity, soil organic matter, microbial biomass, and microbial activity (Costello and Schmidt 2006; Fisk and Schmidt 1995; Fisk

et al. 1998). In locations where the snow accumulation is so high that it inhibits plant growth, however, organic matter accumulation may be inhibited, as has been found to be the case on some leeward slopes at Niwot Ridge (Litaor et al. 2005).

In many arctic soils, the wet, cold conditions tend to inhibit decomposition, and as a result, organic matter often accumulates, especially in flat, poorly drained areas (Schimel et al. 1996). In the alpine tundra, the bog and wet meadow soils have comparable moisture availability to arctic soils, whereas other alpine soils tend to be well drained after snow melt (Bliss 1956). Thus, although organic soils can predominate in poorly drained alpine areas, these are the only alpine soils that tend to be similar to their arctic counterparts (Bliss 1956). Otherwise, alpine soils are often drier and tend to have less accumulated organic matter than arctic soils.

In soils where the lack of moisture inhibits soil development, the total P pool may be relatively higher than in wetter soils of similar age and parent material, but a greater proportion of the total P pool is likely to be bound in primary minerals (Cross and Schlesinger 1995; Walker and Syers 1976). As soil organic matter content decreases, soil P availability to plants and soil microorganisms becomes increasingly controlled by geochemical, rather than biochemical, reactions (Cross and Schlesinger 1995).

12.3 P Availability and Uptake in Arctic and Alpine Soils

The widely acknowledged controls on soil P availability include soil organic matter content, age, parent material, pH, and concentrations of soluble aluminum, iron, and calcium cations (Brady and Weil 2008). Tundra soils often contain significant amounts of soil organic matter, especially where they are not well drained. Soils rich in organic matter are often low in plant-available P due to the occlusion of P in organic matter (Walker and Syers 1976). In order for soil microorganisms and plant roots to acquire P from organic sources, they must first mineralize the organic P with phosphatase enzymes, which mineralize phosphate by hydrolyzing it from organic P compounds such as nucleic acids (for more detail on phosphatases see Nannipieri et al. 2011). Even if the organic matter contains enough total P to meet plant and microbial demand, energy and resources are required for organisms to produce the phosphatase enzymes that are necessary to liberate P from soil organic matter, limiting the rate of P mineralization (Allison et al. 2011; Sinsabaugh and Moorhead 1994). Thus, sites high in organic matter may exhibit P limitation on plant growth.

12.3.1 P Forms and Distribution in Arctic Soils

Giblin et al. (1991) conducted a study of nutrient dynamics across a toposequence of Alaskan arctic tundra plant communities in northern Alaska, USA (Table 12.1),

Vegetation types	Location	Description	
Arctic shrub	Northern Alaska, USA	A moist tundra community that generally occurs on moderately hilly topography with silty to gravelly soils. Dominated by relatively high-stature (>1-2 m) <i>Betula nana</i> and <i>Salix pulchra</i> shrubs with several other shrub species as lesser components (e.g., <i>Vaccinium vitis-idaea</i>)	
Arctic tussock	Northern Alaska, USA	Found on well-drained, often gravelly soils in some upland sites and along water tracks. Dominated by the sedge <i>Eriophorum vaginatum</i> . Also includes <i>Carex</i> <i>bigelowii</i> , feather mosses (e.g., <i>Hylocomium</i> <i>splendens</i> , <i>Dicranum elongatum</i>), <i>Sphagnum</i> <i>rubellum</i> , and a mix of dwarf deciduous and evergreen shrubs (e.g., <i>Salix</i> spp., <i>Betula nana</i> , <i>Vaccinium</i> <i>vitis-idaea</i> , <i>Empetrum nigrum</i>)	
Arctic wet sedge meadow	Northern Alaska, USA	Occurs in low-lying areas and is dominated by low-stature (<20–30 cm) rhizomatous sedges such as <i>Carex</i> aquatilis and <i>Eriophorum angustifolium</i> , with some <i>Eriophorum scheuchzeri</i>	
Arctic heath	Northern Sweden	Dominated by ericaceous dwarf shrubs such as Vaccinium uliginosum, Empetrum hermaphroditum, Rhododendron lapponicure, Dryas octopetata, and prostrate Betula nana. Contains a scattered mix of forbs and graminoids, with abundant mosses covering most of the ground	
Arctic fellfield	Northern Sweden	Has a thin, discontinuous organic horizon, and uneven vegetation cover dominated by <i>Empetrum</i> <i>hermaphroditum</i> , <i>Cassiope tetragona</i> , and <i>Vaccinium</i> <i>vitis-idaea</i> , with scattered forbs and a discontinuous moss cover	
Alpine dry meadow	Rocky Mountains, Colorado, USA	This community occurs where relatively little snowpack accumulates, and the soils are dry throughout the growing season relative to adjacent plant communities. Dominated by <i>Kobresia myosuroides</i> (50–70% of total cover), with <i>Acomastylis rossii</i> , <i>Polygonum viviparum</i> , and one or more species of <i>Trifolium</i>	
Alpine wet meadow	Rocky Mountains, Colorado, USA	Occurs in low-lying areas that melt out relatively late (mid-June to mid-July). Comprised mostly of the sedge <i>Carex scopulorum</i>	

Table 12.1 Descriptions of the arctic and alpine vegetation types most frequently discussed in this review (Fisk et al. 1998; Jonasson et al. 1996; Seastedt and Vaccaro 2001; Weintraub and Schimel 2003)

and concluded that most of these arctic plant communities occur on highly weathered soils with low concentrations of primary mineral P and relatively high proportions of the mineral P bound to Al and Fe (samples were sequentially extracted with 1 M NH₄Cl to remove P loosely bound to carbonates; then with citrate–dithionate–bicarbonate followed by 1 M NaOH to remove strongly adsorbed P plus P bound in Fe or Al oxides; then with 0.5 M HCl to remove P from apatite minerals). This

distribution of P results in low P inputs from weathering, with decomposition responsible for replenishing most or all of the soil solution P (Chapin et al. 1978; Giblin et al. 1991). Chapin et al. (1978) found that 64% of the P in the upper 20 cm of a wet sedge meadow soil in Barrow, Alaska, USA, is organic (dissolved inorganic and organic P were measured on soil solution collected with a pressure membrane apparatus; labile P was extracted from soil with an anion exchange resin, and exchangeable P was determined by ³²P exchange with soil; organic P was calculated by subtracting inorganic P before and after ashing). Furthermore, they found that 84% of the inorganic P is non-exchangeable, and that most of the small pool of exchangeable P is tightly complexed by iron. They estimated that annual plant P demand in the wet sedge meadow on the arctic coastal plain in Alaska, USA, is 150 times larger than the pool of dissolved inorganic P and 6.5 times the labile P pool. Given the distribution of soil P they observed, the authors concluded that the replenishment of the dissolved P pool and P demand must be met by decomposition in this environment, and that biologically mediated P mineralization is the primary driver of P cycling in these organic-matter-rich soils.

Giblin et al. (1991) found dissolved P concentrations in soil water and in soil potassium chloride and calcium chloride extractions to be variable, but consistently low (frequently below detection) during the growing season (June to August), with substantially higher, but still low, concentrations in organic horizons relative to the mineral soil. These results are consistent with other observations of low concentrations of dissolved and labile P in arctic soils (Chapin et al. 1978; Chapin and Shaver 1981; Jonasson et al. 1993). Furthermore, Giblin et al. (1991) observed greater seasonal and interannual variability in extractable P than in extractable inorganic N.

Several studies have concluded that one of the largest reservoirs of potentially available soil P in arctic soils is the microbial biomass. Giblin et al. (1991) hypothesized that low arctic soil P availability in the summer could be at least partly due to microbial P immobilization during the growing season because they observed 1–2 orders of magnitude more P in microbial biomass (estimated by comparing P extracted from soils treated with a biocide, such as chloroform, or hexanol in this case, with P extracted from untreated soils) than in the extractable P pool across the toposequence they sampled in the arctic tundra of Alaska, USA. In a study of arctic heath and fellfield soils in northern Sweden, Jonasson et al. (1996) found that microbial biomass accounted for ~35% of total P, compared to ~3.5% of total N. Inorganic extractable P content was less than 1% of the total soil pool in the same soils.

12.3.2 P Forms and Distribution in Alpine Soils

As discussed above, alpine soils may be similar to tundra soils, but can be drier and contain less organic matter, depending on topographic position. Where organic matter contents are low, soil P availability may be more dependent on geochemical, rather than biochemical, reactions.

In a study of alpine Spodosols and Inceptisols collected at 2,000–2,400 m in the eastern Pyrenees of France, Cassagne et al. (2000) found that despite significant differences in P distribution among horizons between the two soil types, both soils from their higher altitude sites, at or above treeline, contained up to 10% of total P as soluble, exchangeable inorganic P [anion exchange resin P as measured by the Hedley et al. (1982) P sequential fractionation scheme]. The proportion of resin P in these soils is high compared to soils from other ecosystems (Cassagne et al. 2000), and suggests that P may be relatively available in the higher altitude soils of this alpine ecosystem. It is important to note, however, that this labile P pool is subject to significant temporal variability in response to plant and microbial uptake, and the date of collection was not reported in this study. NaOH-extractable organic P comprised over 45% of total P in all depths of the Inceptisols. NaOH-extractable organic P was generally lower in the Spodosols, particularly in the eluvial horizons, but tended to increase with depth. Overall, these soils were found to have relatively high total and organic P contents. The authors suggest that low mineralization rates associated with low temperatures are probably responsible for the accumulation of organic matter.

Makarov et al. (1997) found that organic P amounted to 92–99% of NaOHextractable P (P adsorbed to Fe and Al oxides and carbonates or associated with humic acids; Cross and Schlesinger 1995) across a toposequence of alpine soils in the northern Caucasus. Cassagne et al. (2000) also found that NaOH-extractable organic P was a major component of the alpine Spodosols and Inceptisols in their study. Moreover, they observed little difference in NaOH-extractable organic P between depths in the Inceptisols. The authors interpreted this finding as an arrest of biological P transformation or translocation, possibly due to low temperatures. However, microbial activity and phosphatase production may continue even at low temperatures (Brooks et al. 1998; Lipson et al. 1999, 2002; Schmidt et al. 2004; see discussion below). An alternative explanation is that an accumulation of readily mineralized organic P is the result of relatively low plant and microbial P demand.

Turner et al. (2004) characterized soil P chemistry across a latitudinal alpine (and arctic) gradient consisting of three tundra heath/birch forest sites on Spodosols in the Fennoscandian mountains: Dovrefjell (Sør-Tröndelag, Norway; subarctic), Abisko (Norrbotten, Sweden; arctic) and Joatka (Finnmark, Norway; arctic). They used NaOH–EDTA extraction and solution ³¹P nuclear magnetic resonance spectroscopy to determine the distribution of P compounds in these subarctic–arctic alpine soils. They observed a diverse mixture of inorganic and organic P compounds, with similar composition to peat. High concentrations of inorganic polyphosphate and orthophosphate diesters were present, which the authors suggest are at least partly derived from microbial biomass and probably reflect high microbial biomass P (e.g., Jonasson et al. 1996). At the same time, these compounds are relatively labile, indicating that these soils contain a large pool of potentially bioavailable soil organic P. The authors concluded that the high concentrations of easily degraded P compounds reflect the accumulation of organic matter resulting from slow decomposition in these cold, acidic soils (Turner et al. 2004).

In a study of P availability across a topographic and snow-depth gradient in the Rocky Mountains of Colorado, USA, Litaor et al. (2005) found a larger percentage of organic P (36–79% of total P) than inorganic P (10–45% of total P), based on the Hedley et al. (1982) P fractionation scheme. They also found that the relatively low-lying level sites, where runoff from snowmelt accumulated, contained more organic P than the windward or leeward slopes, and had the highest concentrations of soluble P. This provides additional evidence that organic P accumulates in areas with relatively high moisture availability, and that this results in higher P availability. Furthermore, the authors observed significant correlations between P availability (soil solution P and resin and sodium bicarbonate-extractable P) and aboveground biomass of graminoids, the dominant plant group. However, they did not observe significant correlations with aboveground plant biomass as a whole, or with herbaceous or forb plant groupings. These results suggest that some alpine species may be P-limited even though primary productivity as a whole may not appear to be.

12.3.3 P Mineralization Dynamics in Arctic and Alpine Soils

Differences in plant litter quality may cause relatively large differences in net P mineralization between soils and litter from contrasting plant communities, even in soils in close proximity to one another (Giblin et al. 1991; Jonasson et al. 1993; Schmidt et al. 1999). However, although few studies have been conducted, net P mineralization (measured as dissolved inorganic P accumulation over time on anion exchange resins) in arctic soils has generally been found to be low, or even negative, during the growing season (Giblin et al. 1991; Jonasson et al. 1993; Nadelhoffer et al. 1991).

Although data are limited for arctic and alpine environments, studies in other environments have observed an accumulation of labile soil P at the onset of winter. For example, Fabre et al. (1996) observed significantly increased concentrations of sodium bicarbonate-extractable inorganic and organic P (representative of labile P adsorbed on soil particles) and NaOH-extractable inorganic P beginning in November and continuing through March in a temperate floodplain forest soil in southern France. They hypothesize that this increase in extractable P was caused by P leaching from fresh litter inputs in the fall, a limitation of P mineralization resulting from low temperatures, and low plant and microbial uptake. Chen et al. (2003) also observed substantial winter increases in bicarbonate-extractable organic P concentrations in forest and grassland soils on the south island of New Zealand. They hypothesized that reduced microbial P mineralization resulting from low temperatures, as well as the leaching of dissolved organic P from fresh litter fall in the forest soil, leads to the accumulation of labile soil organic P.

Thus, it has been hypothesized that low temperatures prohibit microbial activity, and therefore P mineralization, during the winter (Cassagne et al. 2000; Chen et al. 2003; Fabre et al. 1996). Recent studies, however, demonstrate that microbial

biomass and enzyme activities are relatively high in snow-covered soils (Brooks et al. 1998; Lipson et al. 1999, 2002; Schmidt et al. 2004), and that a significant proportion of yearly decomposition can occur beneath the snowpack (Schmidt and Lipson 2004). A deep snowpack can create a thermal buffer and sustain soil temperatures at or around 0°C, maintaining the presence of liquid water and protecting the microbial community from harsh winter conditions.

Additionally, a laboratory incubation of soils from several arctic plant communities in northern Alaska, USA, found that dissolved inorganic P release from tussock tundra and wet sedge meadow organic soils was 5–10 times greater at 3°C than at either 9°C or 15°C (Nadelhoffer et al. 1991). This could be because P immobilization increases more rapidly with temperature than gross P mineralization in these soils, or because of an inhibition of cold-adapted phosphatases with increasing temperature.

The results described above indicate that winter is actually an extremely active time for tundra microbial communities. For example, the highest levels of microbial biomass in an alpine soil were observed under the snowpack (Lipson et al. 1999). Although microbial activity may continue beneath the snow, snowmelt and its effects on microorganisms (such as lysis resulting from freeze-thaw effects and changes in osmolarity with snowmelt) can have significant effects on P cycling. Lipson et al. (1999) observed a crash in the microbial biomass and a pulse of nutrients in response to spring snowmelt, which they hypothesized to be derived from lysed microbial cells. These nutrients may be flushed from the system with snowmelt or taken up by plants as the growing season begins. In tundra soils, P is also rapidly released after the soil thaws in the spring (Chapin et al. 1978; Schimel et al. 1996). Chapin et al. (1978) estimate that the spring pulse of dissolved inorganic P from a crash in microbial biomass at snowmelt represents as much as 30% of annual plant P uptake in a wet sedge meadow on the arctic coastal plain of Alaska, USA. This P may be taken up immediately, or may enter the exchangeable P pool, which can serve as a buffer for large pulses of phosphate. This pulse of nutrients represents a large proportion of the annual flux (i.e., up to 50% of the microbial biomass), and is derived from nutrient mineralization in the soil, rather than nutrient release from the melting snowpack (Schimel et al. 1996).

Thus, it has been hypothesized that high winter P mineralization could be the result of microbial turnover in the winter (Giblin et al. 1991). In a test of this hypothesis in two arctic soils collected from a tree-line heath and a high-altitude fellfield near Abisko Scientific Research Station in northern Sweden, Schmidt et al. (1999) found that this pattern held only for the fellfield soil. Thus, while the pattern of high levels of P release in winter has been observed in both arctic and alpine soils, it does not appear to be a universal feature of cold soils. It is currently unclear, however, why this occurs in some soils but not others. Some studies have found that some cold-adapted microbial communities may be relatively resistant to freeze–thaw cycles (Lipson and Monson 1998; Lipson et al. 2000; Grogan et al. 2004). Soil temperature, moisture content at the time of freezing, variability in the timing of snowfall and the depth of the snowpack, and the rate of soil thaw are additional factors that have the potential to influence microbial P release at snowmelt. There is

also the possibility for relatively high rates of P loss when large pulses of P are released at snowmelt (Larsen et al. 2007).

12.3.4 Seasonal Dynamics of Arctic and Alpine Plant P Uptake

Arctic and alpine systems have relatively short, snow-free growing seasons, when plants are active and taking up nutrients from the soil (Lipson and Monson 1998; Weintraub and Schimel 2005). In order to understand the biological controls on soil P cycling in arctic and alpine ecosystems, it is necessary to consider the seasonal dynamics of nutrient uptake and the predominant role of winter.

Differences in soil moisture availability between arctic and alpine tundra environments often result in alpine plants having deeper penetrating roots than their arctic counterparts (Bliss 1956), which may cause differences in the distribution and timing of root C inputs to, and nutrient uptake from, the soil. Root C inputs to the soil are one of the principal sources of labile C to mycorrhizae and microbial decomposers during the growing season (Bertin et al. 2003; Kuzyakov 2002). Differences in the distribution and timing of root growth and exudation among plant species and across plant communities have the potential to result in significant differences in soil microbial P cycling across both time and space by influencing microbial C uptake, nitrogen (N) and P acquisition (including phosphatase activity) and P immobilization (e.g., Weintraub and Schimel 2005; Weintraub et al. 2007). This influence has the potential to vary between arctic and alpine regions, and among plant communities within these regions, based on the timing and depth of root growth.

Previous research indicates that arctic and alpine plant growth early in the growing season often does not depend on nutrient uptake from the soil, but instead depends on nutrients stored in plant tissues (Chapin et al. 1980, 1986; Mullen and Schmidt 1993; Shaver and Kummerow 1992). This adaptation is necessary for growth in cold climates with a short growing season because these soils may remain frozen for several weeks after air temperatures are above freezing, at the time of year when solar radiation is highest. The most intensive period of root growth in deciduous tundra plants generally does not start until after leaf expansion is well underway (Shaver and Kummerow 1992). On the other hand, high rates of spring N uptake in alpine plants have also been observed (Bilbrough et al. 2000; Jaeger et al. 1999; Mullen et al. 1998). This may be because winter and spring arctic air and soil surface temperatures are often much lower than those in alpine regions, possibly extending dormancy (Bilbrough et al. 2000), and because moisture availability often becomes limiting after snowmelt in alpine soils. However, the limited evidence available also suggests that P uptake in arctic and alpine plants occurs after N uptake. For example, the Rocky Mountain alpine herb Ranunculus adoneus takes up N during snowmelt (Mullen et al. 1998), but takes up P much later in the growing season (Mullen and Schmidt 1993). This evidence, along with data on the timing of plant N and P accumulation in response to fertilization of arctic tussock and wet sedge meadow tundra (Shaver and Chapin 1995), and the seasonal dynamics of soil N and P availability in these two communities and shrub tundra (Weintraub and Schimel 2005), indicate that deciduous plant N uptake generally occurs earlier in the growing season than P acquisition in the tundra communities for which data are available.

12.3.5 The Role of Phosphatases in P Acquisition

A study of arctic and temperate strains of mycorrhizal fungi in the genus Hebeloma found that phosphatase activity (measured by using an artificial substrate that releases a colored or fluorescent reaction product when acted upon by the enzyme) in the arctic strains was highest at 2°C relative to 6°C, 12°C, or 22°C, and was only significantly higher than the temperate strains at 2°C (Tibbett et al. 1998). On average, the arctic strains also grew more slowly at all temperatures than the temperate strains. This suggests that organisms in cold soils can respond to the kinetic constraints imposed on enzyme activity by low temperatures, either by increasing enzyme production or by producing isozymes that are more active at low temperatures. Furthermore, phosphatase activity and microbial metabolism have been detected at soil temperatures as low as -20°C (Bremner and Zantua 1975; Christner 2002; Mikan et al. 2002), providing additional evidence for soil microbial activity and nutrient cycling in cold soils. Löffler et al. (2008) also observed significant phosphatase activity in soils collected frozen in March from an alpine altitudinal gradient in the Norwegian arctic. Because their samples were analyzed within an hour of thawing, they concluded that the enzyme activity they observed was not the result of in vitro production, but rather reflected the extant pool of soil enzymes. Bremner and Zantua (1975) attribute the occurrence of enzyme activity in soils at subzero temperatures to enzyme-substrate interactions in unfrozen water at the surfaces of soil particles (enzyme activities were measured at subzero temperatures by combining soils and enzyme assay substrates prior to freezing, incubating at subzero temperatures, and subsequent analysis of the reacted substrate). A similar conclusion was reached by Mikan et al. (2002) in a study of soil respiration at subzero temperatures.

In a study of seasonal dynamics of soil nutrient availability in arctic tundra (tussock, shrub, and wet sedge meadow plant communities), Weintraub and Schimel (2005) observed rapid increases in potassium sulfate-extractable phosphate in tussock and wet sedge meadow soils (Fig. 12.1). Extractable phosphate concentrations in shrub increased gradually in late July, and continued to increase until the end of August. By the end of the growing season, shrub had the highest extractable phosphate concentrations of any soil in this study. Nadelhoffer et al. (1991) concluded that wet sedge meadow soils may be P-limited, but Weintraub and Schimel (2005) determined that P availability was strongly seasonal, and was actually relatively high in wet sedge meadow soils in late July. Weintraub and Schimel (2005) attributed the elevation in arctic tundra soil phosphate availability they observed late in the



Fig. 12.1 Seasonal dynamics of 0.5 M potassium sulfate-extractable soil phosphate from three different plant communities (intertussock samples were collected between *Eriophorum vaginatum* tussocks in the tussock tundra community) at Toolik Field Station in northern Alaska in the summer of 2000. Reprinted with permission from Weintraub and Schimel (2005)

growing season to increases in root and microbial phosphatase activity. This conclusion was based on previous research demonstrating significant phosphatase activity on, and organic P utilization by, the roots of *Eriophorum vaginatum*, the predominant plant in the tussock tundra community (Kroehler and Linkins 1988, 1991; Moorhead et al. 1993). Moorhead et al. (1993) estimated that, on an annual basis, *E. vaginatum* root surface phosphatases mineralize almost twice as much P as is required for plant growth. Thus, the authors concluded that *E. vaginatum* may meet much of its P demand from the activities of root phosphatases, and estimated that approximately 28% of total annual tussock phosphatase activity (plants and soil combined) occurs during a brief late season pulse in soil P availability (Moorhead et al. 1993). As a result, they suggested that the majority of P uptake in *E. vaginatum* occurs late in the growing season, after the period of growth, and that this P is then stored in the rhizomes for use during the following growing season.

Because organisms generally only produce phosphatase in response to P demand, there is often an inverse relationship between phosphatase activity and inorganic P availability (Sinsabaugh and Moorhead 1994; Tibbett et al. 1998). However, the findings of Weintraub and Schimel (2005) indicate that P availability and phosphatase activity can also be positively correlated when phosphatase activity ity mineralizes phosphate in excess of organisms' demand.

Further, Moorhead and Linkins (1997) found that after a 3-year exposure of tussock tundra to elevated CO_2 (680 µmol mol⁻¹), phosphatase activity was higher on *E. vaginatum* root surfaces, ectomycorrhizal rhizomorphs and mantles associated with *Betula nana* roots, and in the organic soil horizons associated with plant

roots. Their results indicate that tussock tundra plants respond to elevated CO_2 by increasing their investment in P acquisition. Increased phosphatase activity in tussock organic horizon soils could be an indication of increased labile C availability resulting from increased rhizodeposition in the elevated CO_2 treatment, because root exudates may stimulate microbial phosphatase production (Weintraub et al. 2007).

Chapin et al. (1988) observed elevated microbial phosphatase activity in water tracks (channels with water drainage) in tussock tundra in northern Alaska (USA). These water tracks are associated with increased water and nutrient flux to roots and to higher plant productivity. Although the cause of increased soil phosphatase was not explicitly determined, it probably resulted from increased microbial P demand in response to the elevated C and N availability that the authors observed in the water tracks.

In a subalpine conifer forest at 3,050 m in the Rocky Mountains of Colorado, USA, Weintraub et al. (2007) observed relatively high levels of microbial biomass and phosphatase activity in O horizon soils (soils with a high percentage of organic matter) beneath the ~1 m snowpack in April. Phosphatase activities in this soil were higher beneath the snow in April 2005 than they were at any time until August 2005 (when the dataset ends), due to increasingly dry conditions as the growing season progressed. Weintraub et al. (2007) also observed a trend toward increased organic horizon microbial phosphatase activity in response to increases in rhizodeposition associated with the spring initiation of photosynthesis by the trees in this forest. These results exemplify how the seasonal dynamics of soil moisture availability and root growth and exudation can influence microbial P acquisition from the soil.

12.4 P Limitation in Arctic and Alpine Soils

P is often limiting to plant growth in arctic and alpine soils (Billings and Mooney 1968). Nutrient addition studies conducted in the arctic tundra at Toolik Field Station in northern Alaska, Abisko Research Station in northern Sweden, and in the alpine tundra at Niwot Ridge LTER in the Rocky Mountains of Colorado, indicate that plant growth in both arctic and alpine environments is typically N-limited, but P may be co- or solely limiting at times (Jonasson et al. 1999; Shaver and Chapin 1986; Theodose and Bowman 1997).

12.4.1 Case Studies from Arctic P Addition Experiments

Chapin et al. (1975) found that the addition of N, P, and potassium (NPK fertilizer) consistently increased production of the wet sedge meadow tundra in Barrow, Alaska, USA (Table 12.2). This increase was particularly evident when a high-P fertilizer was applied, and a high-P fertilizer stimulated production more than a

Study	Location	Vegetation type(s)	Treatment
Chapin et al. (1975)	Northern Alaska, USA	Wet sedge meadow	NPK commercial fertilizer addition 45 g m ^{-2} , 8–32–16 in one plot and 20–10–10 in the other
Chapin and Shaver (1985)	Northern Alaska, USA	Tussock, wet sedge meadow	NPK commercial fertilizer addition: 25 g m ⁻² N, 25 g m ⁻² P, and 31 g m ⁻² K applied in July 1978. Sampling occurred during the 1979–1981 growing seasons
Kielland and Chapin (1994)	Northern Alaska, USA	Tussock, shrub, wet sedge meadow. drv heath	10 g m ^{-2} P as triple superphysication Sampling occurred 2 years of the formula of the superphysication
Shaver and Chapin (1995)	Northern Alaska, USA	Tussock, wet sedge meadow	N (25 g m ⁻²), P (25 g m ⁻²), and K (31.6 g m ⁻²) added singly and in all possible combinations. Different plots were set up in 1976, 1977, and 1978, with fertilizer applied only in the year the experiment was set up. Sampling occurred during 1076-1020 errowing searons
Jonasson et al. (1996)	Northern Sweden	Arctic heath and fellfield	NEX FILILIZER (5.1.25:3.75 gm ⁻²) followed by a second addition IPRE firtuitizer (5.1.25:3.75 gm ⁻²) followed by a second addition
Jonasson et al. (1999)	Northern Sweden	Arctic heath and fellfield	NPK fertilization: 4.9 g m ⁻² N, 1.3 g m ⁻² P, 6.0 g m ⁻² K, and 0.8 g m ⁻² Mg in 1989. From 1990 to 1992, additions were $10.0, 2.6, 9.0, \text{ and } 0.8 \text{ g m}^{-2}$, respectively. No fertilization in 1993, when sampling occurred
Nadelhoffer et al. (2002)	Northern Alaska, USA	Tussock, wet sedge meadow	N and P additions once per year starting in 1988 and continuing through sampling in 1994 and 1995. Annual additions were 10 g m ⁻² N, and 5 g m ⁻² P, except in 1988 when 10 g m ⁻² P was added
Madan et al. (2007)	Svalbard	High arctic polar semidesert	Factorial combination of N (0.5 g m ⁻² year ⁻¹ in low N plots, and 5 g m ⁻² year ⁻¹ in high N plots) and P (1 g m ⁻² year ⁻¹) added five times during 2000–2002 the growing seasons
Fertilizer was applied once :	at the beginning of the gr	owing season in the year of sampl	ing unless noted

high-N fertilizer. Nadelhoffer et al. (2002) measured changes in fine root N and P concentrations in response to fertilization in tussock and wet sedge meadow tundra at Toolik Field Station in northern Alaska, USA. They found that root N and P increased in both communities, but that P concentrations increased more than N concentrations in wet sedge tundra, whereas relative increases in N and P concentrations in roots from tussock tundra plant were similar. These results suggest that wet sedge meadow tundra is P-limited, consistent with the findings of Chapin et al. (1975), whereas tussock tundra is likely co-limited by N and P.

A factorial N and P addition study in high arctic mixed heath in Svalbard by Gordon et al. (2001) found that this tundra community is also co-limited by N and P. Bryophytes, in particular, were found to respond strongly to P addition with increased biomass. This result is contrary to the findings of other studies at lower latitude tundra sites, where increased shrub and graminoid growth in response to fertilization resulted in most bryophytes being shaded out (Gordon et al. 2001).

A study of P uptake in Alaskan (USA) arctic tundra plants by Kielland and Chapin (1994) found that P uptake significantly increased in response to fertilization for plants from tussock, deciduous shrub, and dry heath tundra communities, but not wet sedge meadow. They also observed a significant correlation between plant P accumulation and 0.1 N sulfuric acid-extractable soil P (a measure of exchangeable P). Furthermore, P uptake capacity was correlated with soil P availability across all growth-forms. These results indicate that plant P uptake is typically dependent upon its availability in this environment, and suggest an unmet plant P demand. Thus, Kielland and Chapin (1994) conclude that the soil processes that govern P availability largely control the P absorption of the tundra species in their study.

A long-term (3–10 years) large scale fertilization experiment across multiple tussock and wet sedge meadow sites in northern Alaska, USA, by Shaver and Chapin (1995) found that the same plant communities were limited by different nutrients in different locations, and that it is not possible to conclude that a particular tundra community is always N- or P-limited. An examination of leaf N: P ratios suggested that N limitation was approximately three times more frequent than P limitation in tussock tundra, whereas P limitation was at least four times as common as N limitation in wet sedge meadow (Shaver and Chapin 1995). In accordance with the finding that tundra communities do not always consistently respond to increases in nutrient availability, Chapin and Shaver (1985) found that plant species in tussock and wet sedge meadow tundra in northern Alaska (USA) respond individualistically to nutrient additions, and that species that are more typical of nutrient-rich sites tended to respond more strongly to fertilization than species associated with nutrient-poor sites.

Jonasson et al. (1996) measured the changes in microbial biomass C, N, and P pools in response to NPK fertilization in heath and fellfield tundra soils in northern Sweden. They found that microbial biomass did not increase in response to fertilization, but they observed significant increases in microbial N and P. They also observed increased microbial respiration, suggesting increased microbial activity. Jonasson et al. (1999) found that the addition of fertilizer to Swedish arctic heath

and fellfield soils led to greater increases in microbial P than N. The high proportion of soil P in microbial biomass (Jonasson et al. 1996) suggests that there may be intense competition between plants and microbes for P, and that P release from microbial biomass has the potential to be a significant P source to plants (Schimel et al. 1996). However, Jonasson et al. (1999) found that microbial biomass P increased only when soil inorganic P availability increased, suggesting that microorganisms acquired additional P only in cases of declining P-sink strength in plants. This in turn suggests that, at least in some tundra communities, plants can successfully compete against soil microorganisms for P.

Madan et al. (2007) conducted a factorial N and P addition study at a high arctic semidesert in Svalbard. They observed relatively few effects on the plant community using an N deposition rate of 0.5 g N m⁻² year⁻¹ (five times ambient deposition). However, they observed less bare soils, and a trend toward increased plant species richness and diversity when they also added 1.0 g P m⁻² year⁻¹. Although the N deposition rate of 0.5 g N m⁻² year⁻¹ is somewhat realistic for the future at five times ambient deposition, their P application rate of 1.0 g P m⁻² year⁻¹ was three orders of magnitude higher than ambient deposition levels, and is therefore unrealistic for the foreseeable future. On the basis of these results, the authors concluded that low P availability is likely to limit the response of this polar semidesert vegetation to N deposition.

12.4.2 Case Studies from Alpine P Addition Experiments

A study of aboveground production responses to N and P additions in wet and dry meadow alpine tundra communities at Niwot Ridge in the Rocky Mountains of Colorado, USA (Table 12.3) found dry meadow to be N-limited and wet meadow to be co-limited by N and P (Bowman et al. 1993). Wet meadow forbs increased tissue P concentrations after P fertilization nearly three times more than wet meadow graminoids, and two times more than dry meadow forbs and graminoids (Bowman 1994; Bowman et al. 1993). Following up on this research, a 4-year nutrient addition study in dry and moist alpine tundra communities at Niwot Ridge concluded that there was clear evidence of P limitation affecting the overall production of both of these alpine tundra communities (Seastedt and Vaccaro 2001). This disparity with earlier findings may be because the study plots used by Seastedt and Vaccaro (2001) contained a higher proportion of species sensitive to P limitations, had higher N availability, or both. The Seastedt and Vaccaro (2001) study occurred on old, organic-matter-rich soils that were not affected by the most recent glaciation, and the combination of high organic matter content and soil age may have exacerbated P limitation.

Another study at Niwot Ridge found that within both wet and dry meadow community types, different plant functional groups responded individualistically to N and P fertilization, based on assessment of growth form and mycorrhizal

Study	Location	Vegetation type(s)	Treatment
Bowman et al. (1993)	Rocky Mountains, Colorado, USA	Alpine wet and dry meadows	N and P factorial fertilization, with N applied as 25 g m ⁻² urea osmocote pellets, and P applied as 25 g m ⁻² P_2O_5 osmocote pellets in mid-June 1990 and early July 1991, with sampling in 1991
Bowman (1994)	Rocky Mountains, Colorado, USA	Alpine wet and dry meadows	Same plots as Bowman et al. (1993), sampled in 1991
Theodose and Bowman (1997)	Rocky Mountains, Colorado, USA	Alpine wet and dry meadows	Same plots as Bowman et al. (1993), sampled from 1990 to 1994. Fertilizer application continued through 1994, with the exception of 1992, when no fertilizer was applied
Seastedt and Vaccaro (2001)	Rocky Mountains, Colorado, USA	Alpine wet and dry meadows	N and P factorial fertilization. In September 1993 and August 1994, 20 g m ⁻² N and 2 g m ⁻² P were added. No fertilizer was added to any plots in 1995, and in 1996 and 1997 10 g m ⁻² N as (NH ₄) ₂ SO ₄ and 1 g m ⁻² P as P ₂ O ₅ was applied in July of each vear. Sampling occurred in 1997
Soudzilovskaia and Onipchenko (2005)	Northwestern Caucasus, Russia	Alpine heath	N and P factorial fertilization. N was added as urea (9 g N m ⁻² year ⁻¹); P was added as double superphosphate (CaH ₄ (PO ₄) ₂) (2.5 g P m ⁻² year ⁻¹). Fertilizer was applied at the beginning of every growing season from 1999 to 2002, the period when the study was conducted

Table 12.3 Alpine nutrient addition studies

Fertilizer was applied once in the year of sampling unless noted

associations (Theodose and Bowman 1997). In particular, N_2 fixing and nonmycorrhizal forbs in the dry meadow community were found to be P-limited. Sedges, the dominant functional group in the dry meadow community, were unaffected by fertilization, however. A long-term increase in grasses was also observed in both the wet and dry meadow alpine tundra communities in response to P fertilization.

Taken together, these studies from Niwot Ridge Colorado, USA, indicate that the areas with the deepest snowpack (wet meadow) are likely to have relatively high N availability, and are more likely to be P-limited. This is because accumulated N deposition in snow is redistributed along with the snowpack and its meltwater (Bowman 1994; Bowman et al. 1993; Theodose and Bowman 1997; Walker et al. 1993). These results exemplify how the landscape heterogeneity, climate, and snow distribution interact to influence the relative degree of P limitation across the landscape. Alpine communities on Niwot Ridge with high inputs of water and N from snow are co-limited by N and P availability, whereas communities with low snow cover and drier soils are limited by N and/or water availability (Bowman et al. 1993; Theodose and Bowman 1997).

Additionally, a factorial nutrient addition study conducted by Soudzilovskaia and Onipchenko (2005) in an alpine heath community in northwestern Caucasus, Russia, concluded that community plant density and flowering was co-limited by N and P. However, they also found that different plant species had different responses to the nutrient addition treatments. In response to P addition, they observed increases in *Festuca ovina* and decreases in *Carex* spp., suggesting that an increase in P availability altered the competitive dynamics between these plants, which were the most abundant at their site, with *Carex* spp. being more N-limited and Festuca ovina more P-limited. These results add to the growing body of evidence that P availability may constrain vegetation responses to increased N availability in alpine communities, and that changes in the relative availabilities of soil N and P are likely to alter plant competitive dynamics and, ultimately, community composition. This conclusion is supported by the findings of Arnesen et al. (2007), who analyzed the relationships between plant community composition and bedrock-derived soil nutrients and pH in rocky alpine habitats in northern Norway. They found that after soil pH (correlated with carbonate content at their sites), P availability was the soil factor that best explained the floristic variation among their sites. They also noted that in exposed alpine habitats plant litter is likely to be transported off site, increasing the dependence on bedrock-derived nutrients.

12.5 Conclusions

Organic P has generally been found to predominate in the arctic soils studied, which are mostly from the low arctic, where there is a lower proportion of polar desert than in the high arctic, which has not been well studied. The combination of relatively high moisture availability, often from snow accumulation and redistribution, along with low temperatures, can result in the accumulation of soil organic matter, including organic P. Poorly drained alpine soils where snowmelt water accumulates may be similar to these arctic soils in that both tend to have relatively high organic matter content, with P cycles dominated by biological P cycling. Alpine soils are often drier than low arctic soils, however, with less accumulated organic material. As soil organic matter content decreases, soil P availability to plants and soil microorganisms may become increasingly controlled by geochemical, rather than biochemical, reactions. As has been found to be the case in the wet meadow tundra at Niwot Ridge in the Rocky Mountains of Colorado, USA, redistribution of the snowpack can result in the redistribution of deposited N along with snow, alleviating N limitation and potentially exacerbating P limitation where snowmelt water accumulates (Theodose and Bowman 1997). Given the increasing intensity of N deposition, the potential for elevated N availability to exacerbate P limitation warrants additional investigation.

It has been hypothesized that low temperatures and frozen soil prohibit microbial activity, and therefore P mineralization, especially during the winter, and that this is the ultimate cause of organic P accumulation in arctic and alpine soils. However, phosphatase activity and microbial metabolism have been detected at soil temperatures as low as -20° C, and winter has actually been found to be an extremely active time for alpine tundra microbial communities. Further study will be required to resolve this apparent contradiction.

Although microbial activity may continue beneath the snow, snowmelt and its effects on microorganisms can have significant effects on P cycling, resulting in a rapid release of P when the soil thaws in the spring. The microbial biomass is one of the largest reservoirs of potentially available soil P in arctic and alpine soils, and a release of microbial P in the spring can represent a large proportion of the annual flux. The release of P from microbial biomass at snowmelt has not been found to occur consistently, however, and the controls on this process and the extent to which it may be responsible for soil P losses are not well understood.

Net P mineralization and available P in arctic and alpine soils have typically been found to be low during the growing season. However, elevated soil phosphate availability late in the growing season has been observed in low arctic tundra communities, and has been attributed to late summer increases in root and microbial phosphatase activity, and may be associated with late growing season plant nutrient accumulation to support growth the following spring (Weintraub and Schimel 2005). There is little data available on the activity of arctic and alpine root phosphatases, however, and further investigation into their dynamics, their interaction with plant phenology, and their influence on soil P availability and the possibility of organic P uptake is warranted.

The results of P fertilization studies in arctic and alpine ecosystems have been mixed, with some plant communities, such as alpine wet meadow, showing signs of P limitation to primary productivity, whereas other communities are either N-limited or co-limited by N and P. A cross-site comparison of fertilization experiments in the Alaskan (USA) arctic concluded that the same plant communities may be limited by different nutrients in different locations, presumably as a result of site-specific differences in edaphic factors such as parent material and soil age.

Because both primary production and decomposition have the potential to be limited by P availability in arctic and alpine environments, which may change if decomposition rates, plant phenology and community composition are altered by climate change, understanding the biological controls on P cycling and availability is necessary to understand the impacts of environmental changes in these regions. Our current understanding of P limitation in arctic and alpine ecosystems comes largely from a few intensively studied areas, however, and often lacks mechanistic detail. In order to predict how P limitation may affect primary productivity and decomposition as the climate changes, more mechanistic studies across a more representative range of arctic and alpine environments will be required.

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