# 5

# Terrestrial Ecosystems at Toolik Lake, Alaska

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## Introduction

The broad aim of terrestrial research of the Arctic LTER is to develop a predictive understanding of the distribution of tundra ecosystems in the landscape; of the controls over their structure, functioning, and biogeochemical cycles; and of their interactions with each other and with the local and regional environment. Ultimately this leads to predictions of how they will respond to anthropogenic, development-related disturbances and to global environmental change. To meet this aim the research includes a combination of (1) comparative analyses of contrasting ecosystem types, (2) long-term monitoring of key system properties and processes in relation to local weather variation and secular climate change, and (3) long-term experimental manipulations of environmental factors related to global change. The conceptual framework for this research emphasizes interactions among multiple limiting factors in regulating biodiversity and overall carbon and other element budgets, with a particular emphasis on temperature, light, and soil nutrient availability as dominant controls. Effects of varying species composition on ecosystem properties and interactions of vegetation with herbivores are also important considerations (Shaver et al. 1992, 2000).

The following sections first describe and compare the overall structure and major functions of contrasting tundras near Toolik Lake. Key physical, chemical, and biological controls over distribution and function of these ecosystems are then described and compared. This leads to a discussion of timescales and trajectories of system-level change in response to changes in the controls, followed by a discussion of how system-level changes interact with and feed back on the controls. Finally, we predict how the expected changes in global and arctic climates may alter the landscape and terrestrial ecosystems near Toolik Lake, and suggest priorities for future research.

## Biogeochemistry of Contrasting Tundras

### *A Mosaic of Ecosystems*

The landscape near Toolik Lake consists of a diverse mosaic of tundra ecosystems. The dominant plants in the vegetation of these ecosystems may be evergreen, deciduous, or graminoid, woody or herbaceous, vascular or nonvascular. There are no trees except in a few isolated groves along rivers, and annual plants are extremely rare. The distribution of these ecosystems in the landscape is predictable and largely related to topographic position and landscape age. The fundamental environmental gradients in the landscape include a topographic-moisture gradient from dry uplands to wet lowlands (Figure 5.1) and a soil pH gradient related to time since deglaciation (chapter 3). Additional differences are due to local, fine-scale drainage at any point along the topographic gradient and to snow cover or winter exposure, which is also related to topography.

All of the tundra ecosystems near Toolik Lake are underlain by continuous permafrost ~200 m thick, so there is no deep drainage of soil water; unlike the freshwater springs and larger stream and lake systems in the area, there is little or no connection with groundwater (Hinzman et al. 1991). The depth of the annually thawed “active layer” of soil varies from ~30 cm to 1–2 m depending on topographic position, soil moisture and surface water flow paths, the thickness of the overlying organic and litter layers, and the structure and density of the vegetation canopy. In some locations the annual maximum depth of thaw does not reach below the surface organic mat, and in these locations the vegetation is essentially isolated from mineral soils. Soils are all gelisols (formed over permafrost), typically cold, wet, and with high organic content. The parent material within a few kilometers of Toolik Lake is fine-grained loess and glacial deposits of age ranging from ~10,000 to >300,000 yr BP; older glacial surfaces exist farther north (Hamilton 2003).

### *Vegetation Biomass and Productivity*

The dramatic variation in species and functional-type composition of tundra vegetation (Figure 5.1 and chapter 3) is accompanied by an equally dramatic variation

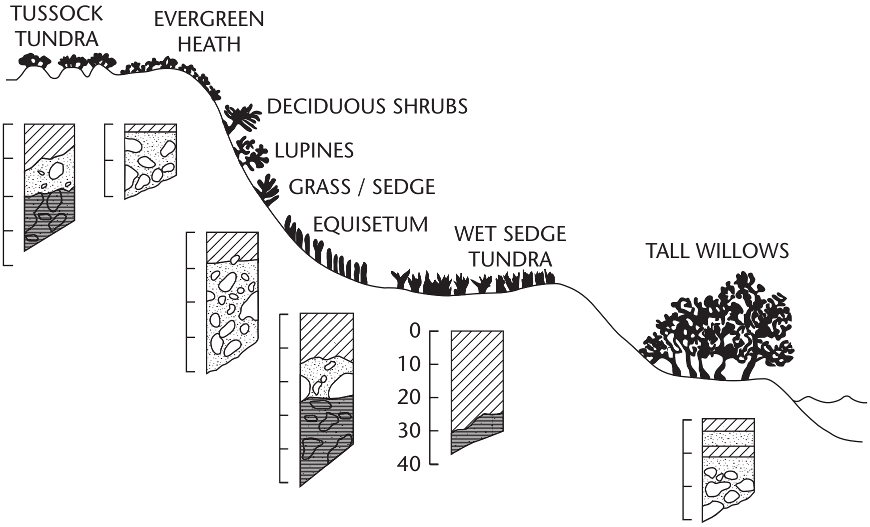

Figure 5.1 A typical toposequence of tundra vegetation and soils along a series of river terraces above the Sagavanirktok River. The horizontal distance is 50–250 m; vertical distance is 5–7 m. Soil profile depths are in centimeters. In the soil profiles, hatched areas indicate the upper organic mat with a mix of loess, till, and river gravel below. Dark shading at bottom indicates permafrost; where there is no dark shading, the profile does not extend to the bottom of the active (annually thawed) layer (from Giblin et al. 1991).

in standing biomass and its productivity. The live aboveground biomass of vegetation varies more than 15-fold among the major vegetation types in the Toolik Lake region, ranging from <90 to >1300 g $m^{-2}$ (Figure 5.2). Although the majority of the total biomass (aboveground + belowground) is always composed of vascular plants, mosses account for >40% of the aboveground biomass in several vegetation types including some shrub tundras, some tussock tundras, and relatively well-drained wet sites (no standing water). Mosses are least abundant in extremely wet tundras (under standing water most or all of the summer) and in very dry heath tundras. Lichens are the largest component of aboveground biomass in some dry heath tundras and are important components of most other vegetation types except for tall shrub tundras and very wet tundras.

The vascular plant component of aboveground biomass varies at least 11-fold from ~80 to >900 g $m^{-2}$, including wide ranges in the relative abundance of major plant forms (Figure 5.2). In general the highest vascular biomass is found in tundras dominated by erect, woody shrubs, particularly deciduous *Betula* and *Salix* species; the lowest vascular biomass is found in very dry, evergreen lichen-heaths and very wet sedge tundras. Most of the live biomass of vascular plants lies below the soil-moss surface, including belowground stems and rhizomes (Figure 5.2) as well as roots. Belowground stem and rhizome mass alone is usually greater than aboveground vascular biomass, although the ratio of aboveground (A) biomass to belowground (B) stem mass varies from 0.3 to 1.3 among vegetation types, with

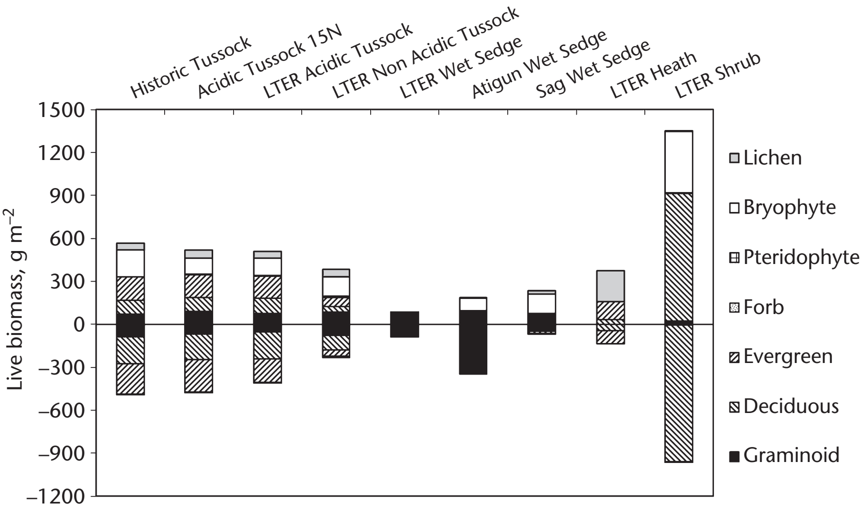

Figure 5.2 Peak-season (late July–early August) aboveground biomass and belowground stem mass in control plots of tundras near Toolik Lake. The first four sites are acidic and non-acidic tussock tundras; fifth through seventh sites are wet sedge tundras; eighth site is a dry heath; ninth site is a riparian shrub tundra. Aboveground biomass is shown as positive values on the vertical axis; belowground stem mass shown as negative values. Root biomass is not shown. Composition of the vegetation is indicated by separating biomass by plant functional type. Data are averages of harvests in 2–4 different years, except for the Atigun wet sedge and LTER shrub sites. (Original data in Shaver et al. 1998, 2001; Mack et al. 2004; Shaver and Chapin 1991; McKane et al. 1995; Gough et al. 1996, 2002; and Hobbie et al. 2005.)

belowground stems being relatively most important in wet sedge tundras. Root biomass has not been measured systematically in most of the tundras near Toolik Lake, but measurements in acidic tussock tundra range from 160 to 250 g $m^{-2}$ (Mack et al. 2004; Sullivan et al. 2007; LTER unpublished data). Combining these root data with the belowground stem and rhizome data in Figure 5.2 gives a vascular A:B biomass ratio of 0.51:1 for the LTER moist acidic tundra site; including nonvascular plants, the A:B biomass ratio is 0.77:1.

Tussock tundra is the most widespread vegetation type in Alaskan upland tundra and is well represented by sites studied near Toolik Lake (chapter 3). Within tussock tundra, the most striking differences relate to soil pH. The three acidic tussock sites at Toolik Lake are all quite similar to each other in functional-type composition and in biomass (Figure 5.2), while the nonacidic tussock site is lower in biomass and has a similar functional-type composition but very different species composition (Hobbie et al. 2005). The nonacidic tussock site also has much higher species richness, including >40 vascular species (mostly forbs), while the acidic tussock sites contain only 9–14 vascular species (Gough et al. 2000). All four of these tussock sites are on relatively young (12,000–25,000 yr BP) soils. Tussock tundras on older soils are generally lower in vascular biomass with greater moss biomass, and have lower soil pH; examples include the tussock tundras at Imnavait

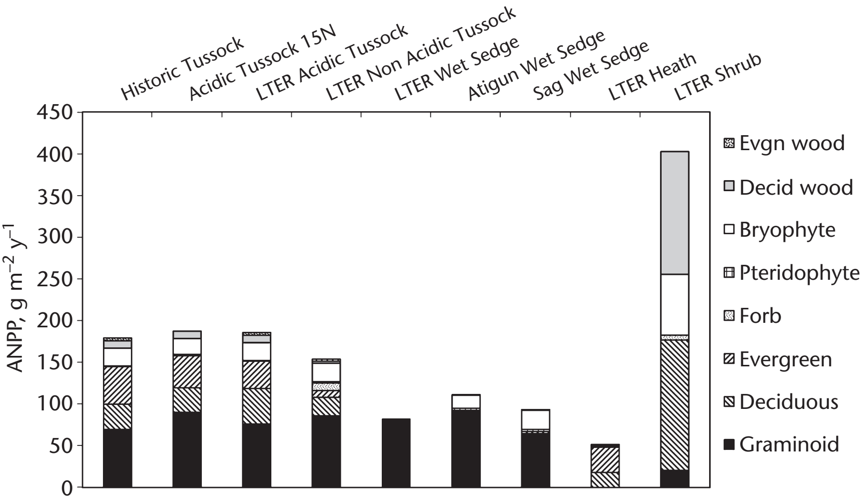

Figure 5.3. Aboveground net primary production at the same sites as Figure 5.2, determined from peak-season (late July–early August) harvests. The apical growth component of production was determined directly by separation of new leaves, twigs, and inflorescences in the harvests. Bryophyte-production and wood-production components were estimated by assuming constant percentage growth rates for bryophyte biomass and for evergreen and deciduous woody stems (Chapin et al. 1995). Lichen production was not measured or estimated at any site.

Creek and at the Sagavanirktok River, both within 50 km NE of Toolik Lake, and at Eagle Creek in central Alaska near Fairbanks (e.g., Shaver et al. 1991).

Annual aboveground net primary production of vascular plants also varies more than seven-fold, from <50 to >330 g $m^{-2}$ (Figure 5.3). Most of this production is the result of growth from apical and intercalary meristems (i.e., growth of new leaves, twigs, and inflorescences). However, in sites dominated by woody deciduous shrubs, secondary growth from cambial meristems (i.e., wood production as annual rings) accounts for 30%–45% of aboveground production (Shaver 1986; Bret-Harte et al. 2002).

Belowground stem or rhizome production also has apical and secondary growth components. The apical component is small except in graminoids (Shaver et al. 1986a; Shaver and Chapin 1991) because most belowground stems of evergreen and deciduous species actually complete their apical growth above or on the surface of the ground and are later engulfed by upward growth of mosses, which buries them. Some evergreen species like *Vaccinium vitis-idaea* also produce apical growth from belowground stems, but this is small relative to apical growth aboveground. Secondary growth of belowground stems does not occur in graminoids and cannot be measured in woody belowground stems because stem diameters do not increase with age at a measureable rate once adventitious roots begin to appear after the stems are buried by mosses.

Estimates of root production at sites near Toolik Lake are available only for wet sedge tundra and moist acidic tussock tundra (Nadelhoffer et al. 2002; Sullivan et al. 2007). These estimates (75 g $m^{-2}$ $yr^{-1}$ in wet sedge tundra and 60–160 g $m^{-2}$ $yr^{-1}$ in tussock tundra) indicate that root production is about 70%–100% of aboveground vascular production, or 35%–50% of the total vascular production.

No direct estimates of moss or lichen production are available from the Toolik Lake region. However, if it is assumed that the relative growth rate of mosses is about 17% per year (Hobbie and Chapin 1998), moss productivity ranges from near zero to >120 g $m^{-2}$ $yr^{-1}$ (Figure 5.3). Moss production may account for 40%–60% of total aboveground production in old, relatively wet tussock tundras. Lichens probably account for more than half of total production in some dry heaths (Shaver and Chapin 1991), although this has not been measured.

## Vignette 5.1. Plant Species Diversity in the Vicinity of Toolik Lake, Alaska, by Laura Gough

Plant species diversity in arctic tundra is limited overall by the low temperatures, short growing seasons, and other abiotic and biotic environmental conditions to which these species must be adapted in order to survive. There are no trees (except in a few, isolated groves) and annual plants are extremely rare. Most of the seed plants near Toolik Lake are long-lived perennials that produce new individuals clonally or vegetatively (without sexual reproduction). The graminoids, or grasslike species, survive the winter underground by storing large reserves of resources in belowground stems and roots. Dwarf shrubs, both deciduous and evergreen, maintain woody biomass aboveground through the winter and rely on snow cover during the coldest months to protect them from wind and frost damage. Perennial broad-leaved herbaceous plants, or forbs, also occur. Most arctic species produce flowers and thus are capable of reproducing sexually, although recruitment from seed is relatively rare. Mosses are a very important component of many tundra plant communities. In particular, *Sphagnum* mosses build peat and organic matter and maintain many tundra communities with highly acidic soil conditions. Lichens, consisting of a fungus and a photosynthetic organism (either a cyanobacterium or a green alga), are also important, and often serve as valuable food sources for mammals such as caribou.

Local abiotic conditions, often influenced by topographic position in the landscape, can restrict or facilitate occurrence of individual species and thus affect community diversity. Extremes of soil moisture, either very wet or quite dry, and rocky soils prevent certain species from germinating and surviving. Exposure during winter restricts some communities to very small plant species (less than 5 cm in height). There is a strong relationship between soil pH or acidity (influenced by soil age and dust inputs) and plant species diversity, so that less acidic soils support more species (Figure 5.V1). Several factors likely contribute to this relationship, including differences in element toxicity, nutrient availability, and occurrence of mosses that affect soil conditions. Soil nutrient availability has also been shown to affect plant species diversity experimentally, such that when nutrients are added, plant species diversity declines. This is likely occurring because nutrients allow one or two species to grow faster than the others, and they then competitively exclude the other species (see Vignette 5.4).

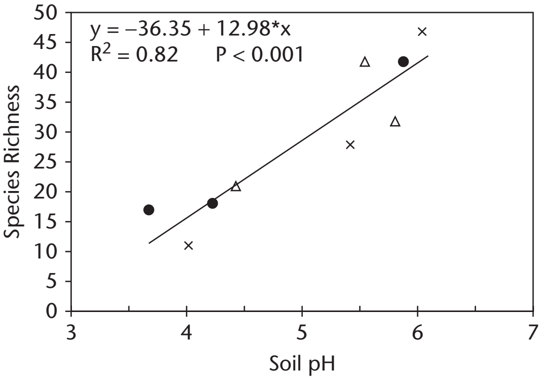

Figure 5.V1 Relationship between soil pH and vascular plant species richness for snowbed (triangle), watertrack (x), and tussock tundra (circles). From Gough et al. (2000).

Biotic factors also affect plant diversity. In the Toolik area, vascular plant species successfully partition resources such as light (by occupying different locations in the canopy) and soil nitrogen (by preferentially taking up different forms of nitrogen), suggesting niche differentiation that promotes coexistence and diversity. To date, insect herbivory has not been adequately measured, but observations suggest it is likely not very important for most plant species. Mammalian herbivory (by small mammals such as voles as well as caribou), however, may play an important role in particular tundra communities, and current research suggests it may become more important in the future with climate warming. Facilitation (positive interactions between plants) may also be important in arctic plant communities, although evidence from near Toolik is scarce to date.

Thus plant species diversity in the tundra communities around Toolik Lake is determined by the landscape position and particular characteristics of the area, such as soil moisture, nutrient availability, and exposure, as well as by interactions among plants and between plants and other organisms including mammals. As the region continues to warm, these factors are also changing, thus diversity of these communities will likely be affected as certain species benefit from these new conditions.

### *Consumers and Decomposers*

Herbivores at Toolik Lake include small and large mammals, birds, insects, and other invertebrates. These animals affect the composition and biogeochemistry of the landscape through selective consumption of live and dead plant material, through their burrowing and trampling, and through their redistribution of elements in urine and feces. Although long-term, overall consumption of vegetation by arctic herbivores is relatively small in comparison with more temperate ecosystems (usually less than 5%–10% of annual aboveground primary production; Jefferies et al. 1994), herbivory in the Arctic is strongly influenced by spatial, temporal, and species-related variation in nutritional quality. This means that intense, short-term pulses of herbivory can have considerable long-term impacts on vegetation, particularly at fine scales (1–20 m).

The area around Toolik Lake supports a number of small and large mammalian herbivores. Five species of microtine rodents occur, the most abundant being tundra voles (*Microtus oeconomus*) and singing voles (*M. miurus*). These animals appear to be food limited as tundra vole abundance increases with food subsidies (Batzli and Lesieutre 1995), although voles show strong preferences for palatable plant species and are able to consume in quantity only some of the species present, in particular sedges and some dicots. Batzli and Hentonnen (1990) suggested that vole population dynamics—cycling every 3–5 years in areas close to waterways with more preferred food, and less frequently in upland areas (G. Batzli, personal communication)—might be correlated with predator abundance, particularly of foxes and weasels, as is true for lemmings in coastal Alaska (Batzli et al. 1980). The other common and often abundant small mammal is the arctic ground squirrel (*Spermophilus parryii*), which burrows extensively in dryer, deeply thawed soils. Small mammals serve as the primary food source for a number of bird and mammal predators including jaegers, owls, several species of raptors, foxes, wolves, and weasels. Caribou serve as a food source for larger predators such as wolves and grizzly bears.

Results of >10 years of limiting herbivore access to moist acidic tundra (MAT) and dry heath tundra at Toolik Lake indicate that small mammals have small but significant effects on plant community structure, primary production, and biomass under ambient nutrient conditions and at large spatial scales (Johnson 2008). At the level of the individual plant, however, and particularly under increased soil nutrient conditions, mammals clearly affect the vegetation (Gough et al. 2007, 2008). For example, *Eriophorum vaginatum*, the abundant tussock-forming sedge in MAT, does not easily recover from intense vole damage at the level of the individual tussock, even under increased nutrient conditions. One result of this may be competitive release of other co-occurring but less palatable species, such as *Betula nana*, which has greater growth in plots exposed to animal activity. In dry heath tundra, lichens are negatively affected by herbivory and by animal disturbances, and herbivory exacerbates the fertilizer-induced dominance of the grass *Heirochloe alpina*.

Caribou (*Rangifer tarandus*) are not major foragers in the Toolik Lake region in most years, as Toolik lies within the range of the central arctic herd but is not a calving ground (Griffith et al. 2002; Cameron et al. 2002; Lenhart 2002). Caribou are present, however, every year at Toolik Lake and every 5–8 years are abundant in late summer (August); their winter activities have not been documented, but their feces are found in abundance after snowmelt in some years, particularly in vegetation such as dry heaths, which has less snow cover than surrounding areas and also has abundant lichen cover.

Interannual variability in snowmelt and vegetation phenology propagates throughout the terrestrial food web. For example, several studies have shown that interannual variability in weather and plant growth exhibits significant control over the abundance and phenology of arthropods on the tundra (MacLean and Pitelka 1971; Pitelka 1973; Myers et al. 1979). Preliminary data collected at Toolik by

J. Wingfield (personal communication) show clear correlations between interannual variability in weather and arthropod abundance. Cold spring temperatures, for example, may result in late emergence and fewer flying insects than in other years.

Higher up on the trophic ladder, and thus dependent for food and shelter on climate, vegetation, and arthropod food sources, are arctic birds. Because the arrival time of migratory songbirds is strongly photoperiod dependent, breeding success of arctic avifauna has been shown to vary as a result of interannual climate variability, most notably with the timing of spring snowmelt (Hahn et al. 1995; Skinner et al. 1998; Martin and Wiebe 2004). Wingfield et al. (unpublished data) have shown that, near Toolik Lake, interannual variability in early season breeding activity (i.e., male call, song, and flight frequencies) of Lapland longspurs are strongly correlated with spring snowmelt date. Males sing more and show greater numbers of flight displays when the tundra is snow free. Stress hormone levels of the same species are elevated during storm events. Together, these results suggest that through a complex web of multi–trophic level interactions, interannual variability in climate dictates the breeding success of the tundra's migratory songbirds from year to year.

The most abundant consumer organisms in the Toolik Lake landscape are the decomposers, including bacteria, fungi, and other microbial and invertebrate members of the soil food web (Doles 2000). These soil organisms account for the majority of the heterotrophic respiration in the ecosystem ($R_H$) and for most of the recycling of essential elements like N and P from plant litter into forms that can be used by plants (discussed below). The abundance and composition of these communities is related to the productivity and composition of the vegetation aboveground (Gough et al. 2012). They also contain in their bodies a disproportionate amount of labile forms of these essential elements; for example, Schmidt et al. (2002) found that in moist acidic tundra and wet sedge tundra at Toolik Lake and in heath tundras at Abisko, Sweden, the amount of labile N and P in microbes typically equaled or exceeded the amounts in the vegetation.

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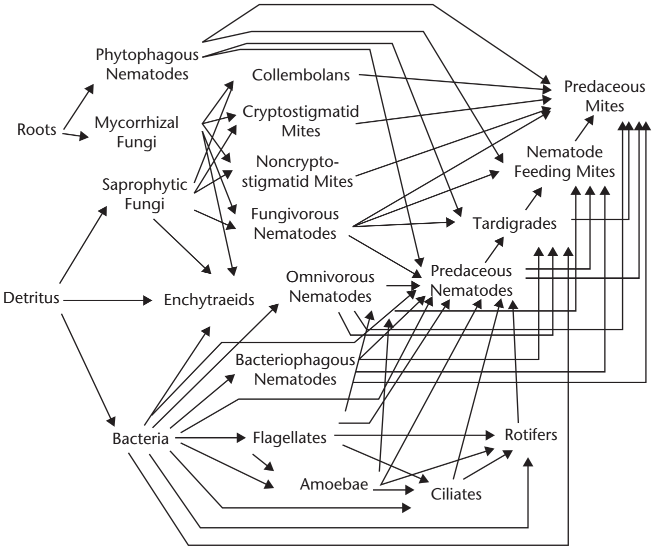
## Vignette 5.2. Belowground Food-Web Responses to Warming and Nutrient Additions, by John Moore

Soil ecological research at Toolik Lake has studied how current and anticipated changes in climate affect the dynamics of soils and soil biota in arctic tundra ecosystems. The soils of the dominant moist acidic tussock (MAT) ecosystem are characterized by a thick organic horizon overlying a poorly developed mineral layer. The microtopographic features include tussocks formed by the growth of sedges and shrubs and water-saturated inter-tussock depressions dominated by mosses. The organic layer that has formed is a result of the low pH of the plant debris (roots, stems, and leaves), soggy soils, and cold temperatures, which act to inhibit the activities of biota that decompose the materials. Over the past 30 years, the Arctic has experienced significant regional warming. A series of manipulations at Toolik Lake that included warming during the growing season with greenhouses (GH) and annual applications of nitrogen (10 g N $m^{-2}$ $yr^{-1}$ as $NH_4NO_3$) and phosphorus (and 5 g P $m^{-2}$ $yr^{-1}$ as $P_2O_5$) following snowmelt have driven shifts in plant species composition with a loss of mosses and increases in net primary production (NPP) and biomass, particularly among shrubs (Chapin et al. 1995; Gough et al. 2012). Nutrient additions dating back to 1982, have precipitated large net losses of soil organic C (40–100 g C $m^{-2}$ $yr^{-1}$) in the organic and mineral horizons (Mack et al. 2004) and changes in the size distribution and quality of soil aggregates within the mineral horizon (Simpson 2010).

Nutrient additions and warming have initiated changes in the configuration of the belowground community as well (Figure 5.V2). The soil food web experienced structural shifts in terms of the diversity of functional groups, the vertical distribution of biomass with trophic position, and horizontal distribution of biomass within energy



| Functional Groups | Upper O-Horizon (0-5 cm) | | | Lower O-Horizon (5 cm-mineral) | | | Mineral (upper 5 cm) | | |
|---|---|---|---|---|---|---|---|---|---|
| | Control | N+P | GH | Control | N+P | GH | Control | N+P | GH |
| Microbes g C m-2 | | | | | | | | | |
| Bacteria | 0.25 | 0.17 | 0.35 | 0.50ab | 0.36b | 0.97a | 0.88 | 1.11 | 1.09 |
| Fungi | 41.47 | 66.63 | 78.79 | 287.91 | 99.16 | 148.02 | 111.12 | 52.15 | 92.42 |
| Consumers mg C m-2 | | | | | | | | | |
| Herbivores | 0.41a | 0.05b | 0.08ab | 0.09 | 0.04 | 0.02 | -- | 0.02 | 0.02 |
| Bacterivores | 176.77 | 228.08 | 218.12 | 638.28a | 334.41b | 112.81b | 288.35 | 565.33 | 218.84 |
| Fungivores | 21.37 | 11.77 | 14.73 | 15.37 | 5.14 | 10.89 | 1.88 | 0.63 | 1.97 |
| Microbivores | -- | 1.35 | 1.26 | -- | 4.23 | 16.69 | -- | -- | -- |
| Predators | 45.16a | 9.55b | 53.55ab | 31.63 | 4.31 | 21.59 | 1.68 | 1.82 | 2.43 |

Figure 5.V2 The belowground food web of the moist acidic tussock (MAT) tundra with biomass estimates of functional groups for three soil horizons from control, N + P, and greenhouse (GH) treatments. Sampling occurred during the summer of 2008. N + P treatments and GH treatments were initiated in 1996 and 1989, respectively. Fungi = saprophytic fungi + mycorrhizal fungi; Herbivores = phytophagous nematodes; Fungivores = collembolans, cryptostigmatid mites, non-cryptostigmatid mites, fungivorous nematodes; Bacterivores = bacteriophaous nemaodes + flagellates + amoebae + ciliates + rotifers; Microbivores = enchytraeids; Predators = omnivorous nematodes + predaceous nematodes + tardigrades + nematode feeding mites + predaceous mites. Letters that differ indicate significant differences among treatments within soil horizon.

channels. Phytophagous nematodes declined with nutrient additions and warming, but established themselves within the mineral layers of both treatments coincident with observed increases in root densities within the mineral layers. Enchytraeids, which were absent in controls, became established in treated plots. Fungi dominate the microbial biomass in all plots, but bacteriovores are the dominant consumers, indicating great activity within the bacterial energy channel. Activity within the fungal and bacterial energy channels appears less stratified in the treated plots. Predator biomass increased at all depths with warming and declined within the organic horizons following nutrient additions. These results and others point to an ecosystem that is vulnerable to changes in temperature and nutrient availability. The results also provide insights into the types of changes we can anticipate under continued climate warming.

## *Soil Organic Matter and Element Stocks*

In tundra ecosystems, soils contain by far the largest pools of organic matter and essential elements such as C, N, and P. Near Toolik Lake the soils typically have an organic (O) horizon of varying thickness overlying a poorly developed mineral soil. The O horizon (often called the "peat layer") consists largely of poorly decomposed plant material with very little mineral content, while the lower, mostly mineral soil also contains significant organic matter and mineral elements. Because all of these soils are underlain by permafrost, the depth of the annually thawed "active layer" is a critical determinant of the volume of soil in which C and other elements actively cycle. Depending on the thickness of the O horizon and the depth of thaw, the active layer may consist entirely of organic soil, or it may include a thin (0–2 cm) O horizon above a meter or more of thawed, rocky mineral soil (Table 5.1). In most tundra soils there are also significant organic matter and element stocks below the active layer (within the top 1–2 m of permafrost), reflecting former conditions of deeper annual soil thaw and "cryoturbation" or mixing of the soil by freeze-thaw processes (Ping et al. 1997, 1998, 2008).

Both the thickness of the O horizon and the thickness of the active layer are highly variable (Table 5.1), reflecting a complex interaction among topography, soil moisture, drainage, the thermal properties of the peat and mineral soil, and the effects of surface litter and the plant canopy on heat flux into the soil. Near Toolik Lake the parent material is generally glacial till, outwash, or morainal material of various ages. The pH of the younger soils is generally close to neutral or slightly acidic (>5.5 or "nonacidic"), while the pH on older surfaces is often 3.5–4.5 or "acidic." Soil temperature and moisture also interact with the amounts and chemical composition of plant litter to determine the rate of decomposition and thus net organic matter accumulation or loss. The presence of permafrost is a key factor, because it means that soils are frozen solid in winter and thaw from the surface down only after snowmelt. Deep drainage of water does not occur through permafrost, meaning soil water must drain laterally over the permafrost surface and soils are always wet at depth. Although soil surface temperatures can exceed 30ºC in the summer, the bottom of the thawed "active layer" is always at 0ºC. The maximum thaw depth is not reached until the end of July or later, and when the soil refreezes

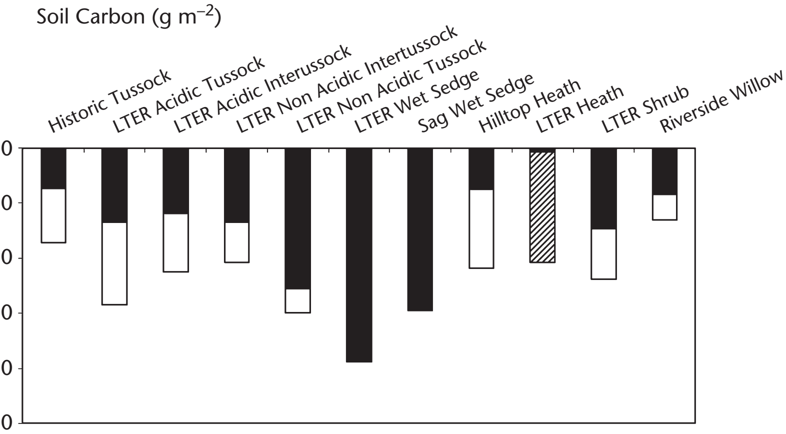
Table 5.1 Soil properties of LTER study sites near Toolik Lake.

| Community | Site | Microsite | Horizon thickness, cm | | | pH | | Bulk density, g $cm^{-2}$ | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Organic | Mineral | Active layer | Organic | Mineral | Organic | Mineral |
| Heath | hilltop heath | | 13 | 9 | 22 | 4.2 | 4.6 | 0.17 | 0.69 |
| | LTER Heath | | 3 | >1 m | >1 m | 4.5 | | 0.07 | |
| Moist acidic tundra | LTER MAT | inter-tussock | 25 | 15 | 40 | 3.7 | 4.6 | 0.07 | 0.67 |
| | LTER MAT | tussock | 17 | 17 | 34 | 3.7 | 4.3 | 0.27 | 1.01 |
| | Sagwon acidic | inter-tussock | 18 | 18 | 37 | 4.2 | 4.3 | 0.07 | 1.23 |
| | Sagwon acidic | tussock | 21 | 2 | 23 | 4.3 | | 0.05 | |
| | 1981 acidic | tussock | | | | 3.8 | 4.2 | 0.07 | 0.76 |
| Moist nonacidic tundra | LTER MNT | inter-tussock | 11 | 9 | 20 | 5.9 | 5.9 | 0.13 | 1.05 |
| | LTER MNT | tussock | 27 | 8 | 35 | | | 0.14 | 1.56 |
| | Sag tussock tundra | inter-tussock | 22 | 0 | 22 | 5.6 | 5.3 | 0.13 | |
| Shrub | LTER MAT | watertrack | 24 | 13 | 36 | 4.0 | 4.3 | 0.07 | 0.47 |
| | LTER MNT | watertrack | 21 | 0 | 21 | 6.0 | | 0.14 | |
| | LTER Shrub | | 20 | 7 | 27 | | | 0.15 | 0.83 |
| | riverside willow | | 7 | 7 | 14 | 6.8 | 6.7 | 0.27 | 0.80 |
| | Sagwon acidic | watertrack | 4 | 24 | 28 | 5.2 | 5.8 | 0.30 | 0.91 |
| Snowbed | footslope | | 14 | 0 | 14 | 6.6 | | 0.18 | |
| | hillslope | | 22 | 0 | 22 | 6.2 | | 0.27 | |
| | LTER MAT | snowbed | 3 | 6 | 9 | 5.6 | 5.5 | 0.23 | 0.48 |
| | LTER MNT | snowbed | 11 | 9 | 19 | 5.8 | 6.3 | 0.34 | 0.84 |
| | Sagwon acidic | snowbed | 8 | 20 | 28 | 4.4 | 4.3 | 0.34 | 0.95 |
| Wet sedge | LTER wet sedge | | 51 | 0 | 51 | 5.8 | | 0.12 | |
| | Sag wet sedge | | 29 | 0 | 29 | 6.1 | | 0.12 | |
| Spring sites | Echooka | poplar | 6 | 15 | 21 | 7.0 | 7.4 | 0.29 | 0.93 |
| | Echooka | source | 8 | 0 | 8 | 6.8 | | 0.12 | |

in autumn it does so both from the top down and from the bottom up. This autumn refreezing may take eight to ten weeks to complete after the mean air temperatures go below freezing in September, depending mainly on snow cover, and even then microbial activity may continue as soil temperatures descend to below –5°C to –10°C (Grogan and Chapin 1999; Schimel et al. 2006).

In the O horizon, C stocks vary 40-fold, from <500 to almost 20,000 g $m^{-2}$ (Figure 5.4; Giblin et al. 1991). Much of this variation is due simply to differences

(a) Soil Carbon (g $m^{-2}$)



(b) Soil Nitrogen (g $m^{-2}$)

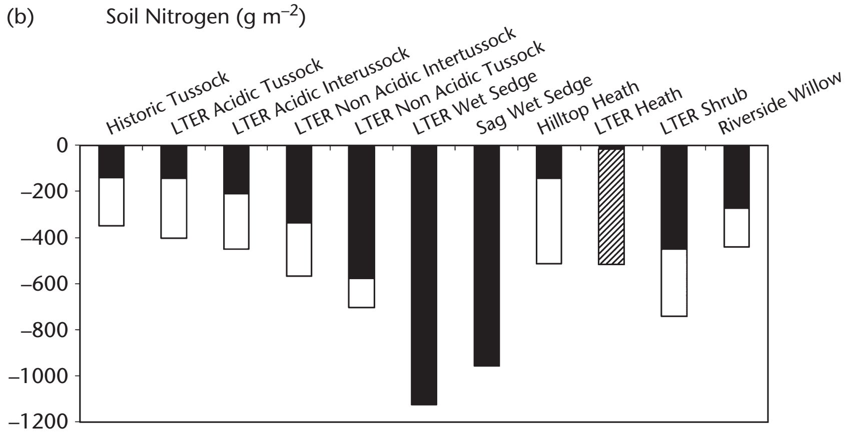


Figure 5.4. Soil C stocks (top) and N stocks (bottom) in tussock, wet sedge, heath, and shrub tundras. Shown are the total amounts of C and N within the seasonally thawed "active layer." The upper (black) segment indicates amounts within the organic horizon, and the lower (clear) segment indicates amounts within the mineral soil. Where there is no clear segment, the soil did not thaw beneath the organic mat. In the "LTER heath" site the depth of thaw is unknown so the C and N stocks in the upper 50 cm of soil are estimated (hatched segment). Inclusion of C and N stocks frozen within the upper meter of permafrost would increase the total stocks by at least 100% (Ping et al. 1997, 2008).

in the thickness of the O horizon, but variation in bulk density (usually ~0.06 g cm$^{-3}$ but varying from 0.04 to 0.14) and C concentration (usually >35% but as low as 10%–15% depending on how much mineral material is incorporated) also contribute. N stocks of the O horizon are smaller but show similar patterns of variation (from <20 to >1100 g m$^{-2}$).

In the mineral soil, C and N stocks also vary greatly but generally inversely with the O horizon, so overall C and N stocks within the active layer are less variable than in the individual organic or mineral layers (Figure 5.4). In the mineral soil, C and N concentrations are much lower but bulk density is much higher, so the mineral soil per unit area often contains more C and N than the O horizon. The mineral soil horizons, however, are also colder than the O horizons, they spend a larger portion of the year frozen, and the organic matter they contain is less readily usable by soil microbes (Weintraub and Schimel 2003, 2005; Shaver et al. 2006). For these reasons the highest rates of element turnover occur in the O horizon.

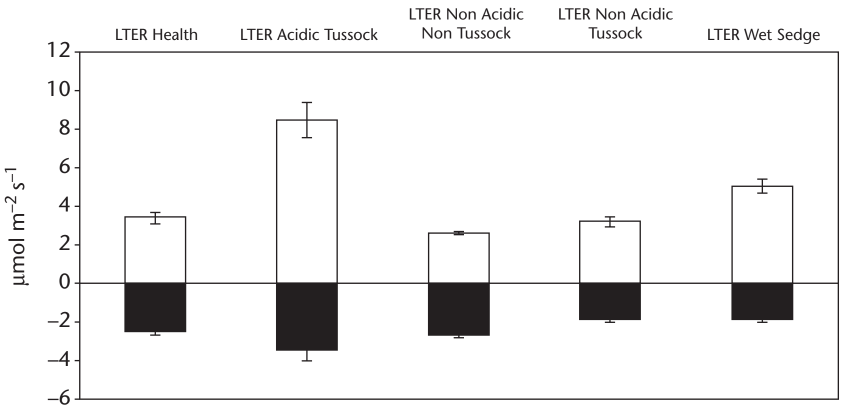
## *Inputs, Outputs, and Turnover of Carbon, Nitrogen, and Phosphorus*

### Carbon

As in virtually all terrestrial ecosystems, the main input of C to tundras is by photosynthesis (gross primary production, GPP) and the main losses of C are as respiration by plants ($R_A$, autotrophic respiration) and by heterotrophs ($R_H$), largely microorganisms; respiration of the whole ecosystem ($R_E$) is the sum of $R_A$ and $R_H$. In tundras most of the $R_H$ occurs in the soil in association with decomposition processes, and soil respiration (not including root respiration) is often considered a measure of $R_H$. Soil carbon emissions in tundras also often include a significant methane component, particularly in wet sites with anaerobic soils (Walter et al. 2006). In addition to these gaseous fluxes, C may enter and leave patches of tundra as dissolved organic and inorganic C moving in soil water across the surface of the permafrost (Kling et al. 1991; Judd and Kling 2002), and as leaf litter redistributed by wind and snow (Fahnestock et al. 2000). Lateral losses of dissolved inorganic plus organic C range from ~2–5 g C m$^{-2}$ yr$^{-1}$ (see chapter 6).

In the landscape near Toolik Lake, GPP varies with vegetation composition, topographic location, time of year, and recent and current weather conditions including radiation, rainfall, and temperature (Figure 5.5). Despite considerable variation in photosynthetic rates at the leaf level among species (Starr and Oberbauer 2003), there is a strong convergence in canopy leaf area:leaf N relationships suggesting an "optimal" canopy structure in which GPP increases similarly with both leaf area and canopy N content (Williams and Rastetter 1999). About 75% of the variation in GPP is explained by leaf area and light (photosynthetic photon flux density, PPFD) alone (Shaver et al. 2007). In the middle of the growing season and at a constant PPFD of 600 μmol photons m$^{-2}$ s$^{-1}$, GPP ranges from ~2 to 8 μmol $CO_2$ m$^{-2}$ s$^{-1}$ in wet, moist, and dry tundras at Toolik Lake and is closely correlated with canopy leaf area. Light-saturated (mid-day) GPP can be much higher (up to 15–20 μmol $CO_2$ m$^{-2}$ s$^{-1}$), but the daily average rates are in the range of 1–3 μmol $CO_2$ m$^{-2}$ s$^{-1}$ (Oberbauer et al. 2007).

(a) GPP and $R_E$



(b) NEE

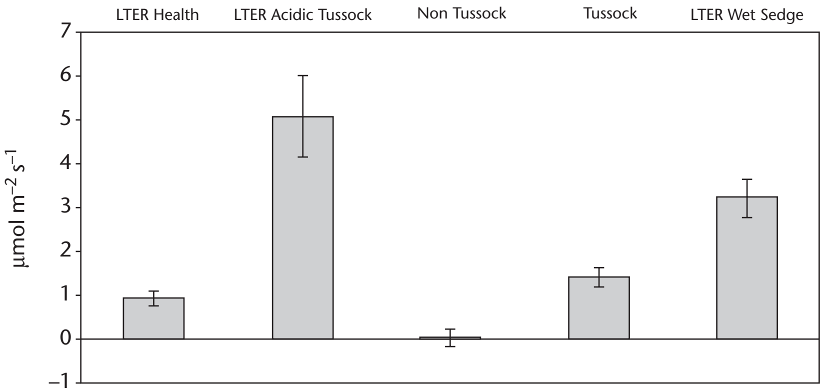


Figure 5.5 Midseason summer values for (A) GPP (open) and $R_E$ (closed) and (B) NEP (same as NEE) at core LTER sites. GPP and NEP are predicted values at 600 µmol $m^{-2}$ $s^{-1}$ PPFD (photosynthetically active photon flux density), from light response curves in Street et al. (2007).

Most studies of respiration in the Toolik Lake region have focused on whole-ecosystem respiration ($R_E$; e.g., Hobbie and Chapin 1998) or have used bulk soil respiration (without roots) as an estimate of $R_H$ (e.g., Hobbie et al. 2002; Schimel et al. 2006). Overall, $R_E$ is correlated with GPP; in the long term, GPP is the ultimate source of all C lost in respiration, so $R_E$ cannot exceed GPP indefinitely. Nonetheless, extrapolations of short-term measurements of $R_E$ to seasonal and annual estimates consistently exceed estimates of GPP in the Toolik Lake region even during midsummer (Oberbauer et al. 2007).

Winter respiration probably accounts for at least 20% of annual $R_E$ although there is great variability among estimates (3%–50%; Grogan and Chapin 1999).

One reason for the variability in “winter” respiration estimates is variation in the definition of when the “winter” starts and ends; most of the cold-season respiration actually occurs during the autumn (late September through December) and a smaller portion during the spring (May and early June; Schimel et al. 2006). Respiration rates of soil microorganisms ($R_H$) during the coldest parts of the winter are extremely low (e.g., Fahnestock et al. 1999). Such respiration is possible because even down to temperatures as low as –10ºC, liquid water films remain on soil particles and allow microbes to remain physiologically active. Although $R_A$ has not been measured through the arctic winter, there is little reason to expect that $R_A$ is significant except in the same fall and spring periods as with $R_H$; in fact it is likely that the aboveground component of $R_A$ is very low through most of the autumn as air temperatures are colder than soil temperatures in autumn, winter, and spring.

Carbon losses from methane are rarely more than 5% of the total C loss from arctic landscapes; however, because methane has a higher greenhouse warming potential than $CO_{2,}$ there may be a net greenhouse warming effect even when GPP exceeds $R_E$. Methane losses are greatest in wet, anaerobic soils and carbon-rich sediments such as the “yedoma” (loess) soils of northeast Siberia (Walter et al. 2006). Near Toolik Lake, these wet anaerobic soils include wet sedge tundras and moist tussock tundras where water is close to or above the soil surface and methane can be lost by diffusion and ebullition without passing through a surface horizon, where it may be consumed by methane oxidizers (Christensen et al. 2003). Methane losses may also be facilitated by passage through internal plant air spaces (Schimel 1995; Torn and Chapin 1993).

Net ecosystem exchange (NEE) is the balance of GPP and $R_E$. Midday, midsummer measurements of NEE near Toolik Lake range from a small net loss of C to the atmosphere (0–6 μmol $m^{-2}$ $s^{-1}$), especially in wetter sites, to net gains of ~10 μmol $m^{-2}$ $s^{-1}$ to the tundra (Figure 5.5B). Nighttime values of NEE show consistent small C losses to the atmosphere despite the lack of full darkness in summer months. The summer value of NEE is most strongly correlated with leaf area and PPFD, reflecting the strong influence of these variables on the GPP component, although there is also a significant effect of daily variation in temperature on $R_E$ (Williams et al. 2006). Integrated over a full day, midsummer NEE of tundra usually shows a net C gain of 0.5–1.5 g C $m^{-2}$ $d^{-1}$ (0.04–0.13 mol C $m^{-2}$ $d^{-1}$) and is also correlated with leaf area (McFadden et al. 2003). Over the three summer months when GPP exceeds $R_E$ on most days, cumulative NEE at Imnavait Creek near Toolik Lake varies from 50 to 95 g C $m^{-2}$ stored in the tundra (Euskirchen et al. 2012). Over longer periods, NEE may be positive or negative and is related to summer weather (especially summer rainfall) and to multiyear changes in temperature and evapotranspiration.

## Nitrogen

The main N inputs are by bacterial fixation and by deposition in rainfall and snow (Figure 5.6). The highest rates of N fixation (per g tissue) occur in the roots of

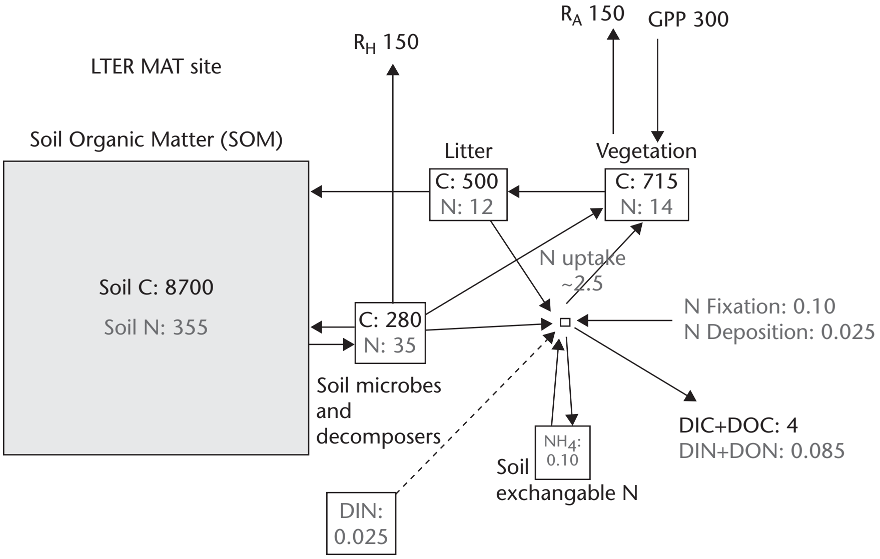


Figure 5.6 Summary of C (black) and N (grey) budgets in moist acidic tundra at Toolik Lake. Pool sizes (boxes) in g $m^{-2}$; fluxes (arrows) in g $m^{-2}$ $yr^{-1}$; the dashed box and arrow indicate the DIN pool size (very small). Values are estimates, chosen for consistency among the numerous individual studies described in this chapter.

legumes such as *Lupinus* species and actinorrhizal shrubs such as *Alnus* species, but the majority of the N fixation (per $m^2$ ground area) occurs in free-living algae or in moss-algal associations and in several lichen species. The lichen *Peltigera apthosa* in particular is widely distributed especially in moist tundra and is capable of very high rates of fixation (0.77 μmol N g $lichen^{-1}$ $h^{-1}$; Weiss et al. 2005). Although these lichens constitute important hotspots of N fixation, the algal-associated inputs are probably more important over the whole landscape (Hobara et al. 2006). At Imnavait Creek near Toolik Lake, the overall average rate of N fixation is 80–131 mg N $m^{-2}$ $yr^{-1}$. These inputs by fixation are five- to ten-fold larger than the long-term average summer (unfrozen) deposition rate of ~14 mg N $m^{-2}$ $yr^{-1}$. Winter deposition in snowfall is similar on average to the summer deposition but much more variable due to redistribution of snow, from near zero in windblown, snow-free hilltops to >50 mg N $m^{-2}$ $yr^{-1}$ in snow accumulation areas (Shaver et al. 1991).

The gross inputs of N by fixation and deposition (0.1–0.2 g $m^{-2}$ $yr^{-1}$) are considerably smaller than the annual vegetation uptake requirement for N used in NPP (0.4–4.5 g $m^{-2}$ $yr^{-1}$), indicating that most of the vegetation N supply must come from recycling of N already in the ecosystem. This recycling occurs as the mineralization of soil organic N to ammonium or nitrate, followed by plant uptake, and by short-circuits of this process including uptake via mycorrhizae (Hobbie and Hobbie 2006) and direct plant uptake of organic N (Kielland 1994; Schimel and Chapin 1996).

Table 5.2 Annual net N mineralization rates (g N $m^{-2}$ $y^{-1}$) using buried bags (Giblin et al. 1991; J. Laundre, unpublished data). In this case the year runs from early August to early August; values are means among years

| | $NH_4$ | $NO_3$ | Total N | Years |
|---|---|---|---|---|
| LTER acidic tussock | 0.40 | 0.02 | 0.42 | 1990–2006 |
| LTER nonacidic tussock | 0.03 | 0.00 | 0.03 | 1998–2006 |
| Sag river tussock | 0.15 | 0.03 | 0.18 | 1987–2005 |
| Sag river riparian shrub | 0.16 | 0.23 | 0.40 | 1985–1989 |
| Sag river wet sedge | 0.41 | 0.02 | 0.43 | 1985–1989 |
| Sag river equisetum | 0.06 | 0.01 | 0.08 | 1985–1989 |
| Sag river shrub/lupine | 0.08 | 0.04 | 0.12 | 1985–1989 |
| Sag river heath | 0.64 | 0.04 | 0.67 | 1985–1989 |

Net N mineralization rates have been estimated in several studies near Toolik Lake, under the assumption that the inorganic N supply to plants is essentially the remainder of the gross N mineralization after microbial N uptake (Table 5.2). Net N mineralization, however, is insufficient to account for total plant N uptake, usually amounting to only about one-third of the amount needed. Typically during the growing season, net N immobilization occurs, with net N mineralization occurring only during the winter. Thus, by this measure, plants appear to compete directly with microbes for uptake of N produced by gross mineralization processes, in which case net mineralization underestimates the mineral N available to plants (Schmidt et al. 2002). Alternatively, plants may use organic N in addition to mineral N (McKane et al. 2002). Both of these forms appear to be used at least for abundant, nonmycorrhizal graminoid species such as *Eriophorum vaginatum*. In the case of the majority of species that are mycorrhizal, including dominant shrubs such as *Betula nana*, N uptake via mycorrhizae probably accounts for more than half of N uptake (Hobbie and Hobbie 2006). According to these authors, the plants with low values ($^{15}$N depleted) of $^{15}$N in the leaves in Figure 5.7 are receiving large amount of N from mycorrhizal fungi.

The main losses of N from tundra ecosystems are by leaching as dissolved organic and inorganic N and by denitrification. Leaching losses, determined as the amounts of N leaving tundra watersheds in stream flow, are ~50–100 mg N $m^{-2}$ $yr^{-1}$ (Peterson et al. 1992; McNamara et al. 2008), about the same magnitude and perhaps smaller than the sum of the N inputs by fixation and deposition. Losses by denitrification are still uncertain and have not been measured directly; the only study to date (Alexander-Ozinskas 2007) indicates that under optimum conditions N loss by denitrification may be as high as 1–2 g $m^{-2}$ $yr^{-1}$ in wet and moist tundras where soils are frequently anaerobic, and near zero in drier, well-aerated heath soils. These high rates of potential denitrification are unlikely to occur under field conditions.

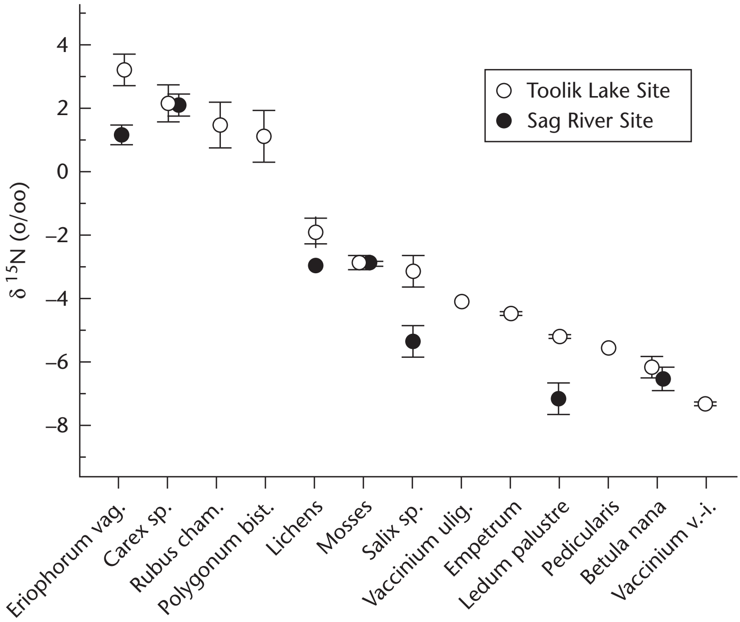


Figure 5.7. Natural abundance N isotope ratios of leaves of common species of moist acidic tundra (from Nadelhoffer et al. 1996). Leftmost species are graminoids, Rightmost species are mostly woody evergreen Ericaceae or deciduous shrubs.

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## Vignette 5.3. Mycorrhizal Fungi Provide Nitrogen to Plants: A Vital Symbiosis, by John Hobbie

Most of the plants in the Toolik region (in fact, 90% of all plants) are symbiotic with fungi; plants provide sugars to the fungi, and the fungi provide several kinds of nutrients and probably water to the plants. Threads of fungal hyphae, each 5–15 μm in diameter, attach to plant roots in several ways and extend out as far as a meter to mine the soil for carbon, nitrogen, and phosphorus. At Toolik, the ectomycorrhizal (ECM) fungi are symbiotic with birch and willow roots, while the ericoid mycorrhizae are symbiotic with ericaceous plants such as *Ledum*, blueberry, and cranberry. Exactly how much carbon and nutrients are transferred is difficult to quantify but the benefits to the plants must be large or they would not give up an estimated 20% of their net photosynthetic sugars to the fungi (Hobbie and Hobbie 2008). The functional relationship of ectomycorrhizal and ericoid mycorrhizal fungi to plants is just beginning to be understood; pure cultures show that many fungi have the enzymes to decompose proteins.

The low stature of the vegetation, the abundance of fruiting bodies of mycorrhizal fungi, and the nitrogen limitation of plant growth made the tussock tundra at Toolik an ideal location for quantification of the fungal nitrogen cycle. This is accomplished through analysis of the $^{15}$N content of soil nitrogen, of the ectomycorrhizal fruiting bodies (mushrooms) that are composed of hyphae, and of the ectomycorrhizal plant stems and foliage; it has the great advantage over other ways of studying a soil process in that the natural isotope abundance is measured and the belowground system remains undisturbed.

The process that makes the analysis possible occurs during the transfer of nitrogen from the hyphae to the plant. At Toolik (Hobbie and Hobbie 2006), the soil organic matter has a $\delta^{15}$N of +1–2‰, the plant values average ~–5‰ for ectomycorrhizal and ericoid mycorrhizal plants, and the ectomycorrhizal fungi average +7‰. Note that in Figure 5.7 this analysis applies only to the plants with negative $\delta^{15}$N values, the ectomycorrhizal and ericoid mycorrhizal plants. At the tip of the hyphae, enzymes are produced that break down soil proteins into amino acids. The hyphae take up the amino acids and transport them back to the roots. Before transfer, all the amino acids are transformed to the amino acid glutamine; this transamination process favors the light isotope, $^{14}$N, and results in glutamine with less $^{15}$N being transferred to the plant. The amino acids and chitin with more $^{15}$N remain in the hyphae. From a mass balance of the $^{15}$N, 61%–86% of the nitrogen in plants came from the fungal pathway, while 8%–17% of the net photosynthetic carbon was transferred to fungi. A slightly different analysis (Yano et al. 2010b), using the $\delta^{15}$N of hydrolysable organic nitrogen, estimated that 30%–60% of the plant nitrogen came from fungi. The warming of arctic plants, already known commonly to increase growth, also leads to a shift in their allied ECM fungal community; moreover, the new community of fungi has a distinctly different ecological function (Deslippe et al. 2011). A warming experiment took place over 18 years in acidic tussock tundra at Toolik where greenhouses raised the temperature of plants and soil ~2°C causing a dramatic increase in height of the *Betula nana*. An analysis of the internal transcribed spacer sequences of ECM fungi in 1,000 root tips from *Betula* found that the ECM fungi in control, fertilized, and fertilized-plus-warming treatments were dominated by a *Russula*-associated community, while the fungi in the warming treatment changed to a *Cortinarius*-dominated community (Deslippe et al. 2011). Based on data on fungal exploration types, the warming enhanced growth of *Betula,* which responded to an increasing nutrient limitation (likely nitrogen) by increasing organic carbon transport to roots. Growth of roots and the *Russula*-associated fungal community depleted the more labile organic and inorganic nitrogen compounds in the near vicinity of the roots. As a result, the community of ECM fungi shifted to *Cortinarius* species, which can mine nitrogen from widely dispersed and recalcitrant organic matter and transport solutes back to fruiting bodies and plants in hydrophobic rhizomorphs (a rootlike mass of hyphae associated with transport). The hyphae and rhizomorphs of *Cortinarius* species can be up to a meter long. The ECM community shifts in the experiments described here not only help in understanding how ecological function differs among mycorrhizal taxa, but may also presage changes in the diversity of ECM communities as the arctic tundra continues to become warmer and shrubbier.

## Phosphorus

Much less is known about the P cycle near Toolik Lake, although fertilizer experiments have indicated P-limitation to productivity of the vegetation in most wet sedge tundras and some moist tussock tundras (Shaver and Chapin 1986, 1995). Dissolved inorganic P in soil solution was low (0.3–0.4 μmol L$^{-1}$) and frequently below detection limits along a sequence of six tundras on a hillslope above the Sagavanirktok River, but KCl-extractable $PO_4$-P varied more than 20-fold (Giblin et al. 1991). The greatest amounts of KCl-extractable and resin-exchangeable P occurred in deeply thawed soils such as the hilltop heath, *Equisetum* tundra on a steep hillslope, and riparian shrub tundra (Figure 5.1). In younger soils most of the P occurred as primary mineral P (HCl-extractable and "residual" P), while the amounts of Fe- and Al-bound P increased in older soils.

The largest pool of actively cycling P is held in the top 30 cm of soil organic matter, about 19.5 and 22 g P $m^{-2}$, respectively, in moist tussock tundra and wet sedge tundra at Toolik Lake (Schmidt et al. 2002). Soil microbial P is the second largest organic P pool, accounting for about 3 g $m^{-2}$ in moist tundra and 1.3 g $m^{-2}$ in wet sedge. The P content of live vegetation is the smallest of these pools, less than 2 g $m^{-2}$ in moist tussock tundra and less than 1.2 g $m^{-2}$ in wet sedge (Shaver and Chapin 1991).

### *Overall Element Budgets and Stoichiometry*

An overall conceptual model of element cycling and element interactions is needed to integrate and compare the above information. We do this in the context of a generalized organic matter budget for a terrestrial ecosystem, accounting for the fact that all organic matter is composed of multiple, essential, nonsubstitutable elements and that the relative abundance of those elements changes among different kinds of organic matter. When the data on C and N cycles are combined in this way (Figure 5.6; Shaver et al. 1992), several key facts emerge:

First, the budget components include organic matter pools that differ widely in their magnitudes, turnover rates, and C:N ratios, yet they are all linked through the exchanges of these elements among pools, either as organic matter containing both C and N or as inorganic N.

Second, the "external" inputs and outputs of N (fixation, deposition, denitrification, and leaching losses) are all small relative to the "internal" exchanges of N among organic matter pools (plant uptake, litter fall, mineralization). In other words, the N cycle of this model tundra is relatively closed and depends strongly on internal recycling of N.

Third, in contrast to the situation for N, the "external" inputs and outputs of C (GPP, $R_A$, $R_H$, leaching losses) are mostly large relative to "internal" exchanges of C (litter fall, plant uptake of organic molecules, consumption by microbes, leaching losses, and [not shown in figure 5.6] herbivores); in other words, the C cycle is relatively "open" in comparison with the N cycle.

These facts indicate that controls on short- and long-term change in either the C cycle or the N cycle depend on controls over *both* elements. In particular, in the short term the C balance of such a system can be thought of as C gains (NPP = GPP–$R_A$) associated with plant N uptake balanced against C losses ($R_H$) associated with the breakdown of litter and soil organic matter into forms of N that can be taken up by plants. In the long term there are three general kinds of controls that should mediate change in overall organic matter stocks of this model ecosystem:

(1) *Controls on variability of C:N ratios in both pools and fluxes*. As the range in possible C:N ratios changes, the greater the possibilities for changes in the C budget without change in the N budget, and vice versa. The C:N ratios of pools and fluxes may change for many reasons, including changes in species composition (and thus the chemical composition of plant tissues), changes in processes like N resorption at leaf litterfall (and thus the C:N ratio of the litter), and changes in microbial growth efficiencies (and thus the amount of $CO_2$ lost per unit of microbial biomass produced).

(2) *Controls over the distribution of organic matter among plants, soils, and microbes*. For example, because soil organic matter always has a lower C:N ratio than plant biomass, the transfer of N from soil organic matter to plant biomass will result in a higher carbon storage in the ecosystem as a whole, even if there is no change in total N in the ecosystem. Microbes, in contrast, have very low C:N ratios, so consumption of soil organic matter by microbes, associated with increases in microbial biomass, results in loss of C while N is retained.

(3) *Changes in the balance of element inputs and outputs and thus total element stocks*. In the case of this model tundra, the C cycle is relatively "open" and the N cycle is relatively "closed." This means that short-term increases in C inputs (such as the expected photosynthetic response to warming) cannot be sustained without a corresponding increase in N inputs, changes in the distribution of N, or changes in C:N ratios as described above. In general it means that long-term changes in organic matter stocks and turnover in this system should be more sensitive to changes in factors controlling N balance, N turnover, and N distribution than to changes in factors controlling C balance and distribution.

By incorporating these controls and relationships between C and N, the "simple arctic model" (SAM; Shaver et al. 1992) outlined in Figure 5.6 provides an overall, integrated framework for interpretation of experimental and monitoring studies of the terrestrial Arctic LTER. This framework has proven particularly useful in developing long-term predictions (decades to centuries) of change in response to climate change and human impacts on the tundra near Toolik Lake.

## Controls on Ecosystem Structure and Function

### *Climatic and Other Environmental Controls*

The major environmental controls on tundra ecosystems near Toolik Lake include temperature, light, soil moisture, snow cover, and length of the growing season. Effects of changes in these controls have been studied in a wide range of short-term and long-term experiments, often involving factorial combinations of two or more controls. Because past research showed the productivity of these systems is consistently limited by N or by N and P availability to plants, N and P fertilization experiments were also included in all of the major terrestrial ecosystems near Toolik Lake. The major overall lessons from these experiments include:

(1) On time-scales of 1–20 years, the greatest changes in primary production, plant biomass, species composition, and soil processes are caused by N and P fertilizers, indicating strong control of the C cycle by the availability and turnover of these elements (Figure 5.8).

(2) Essentially all ecosystem processes in the tundra are temperature-limited in the sense that increases in temperature result in immediate, short-term increases in process rates. However, long-term changes in element budgets and stocks take place relatively slowly and less dramatically in response to increases in air temperature (Figure 5.8). Changes in air temperature also lead to much smaller changes in soil temperature, leading to smaller and slower changes in temperature-limited processes in the soils, including mineralization of N and P.

(3) Changes in photosynthetically active radiation have an immediate impact on photosynthesis at both leaf and canopy levels, but longer-term changes in C cycling are smaller and depend more on regulation of leaf area, which is also limited by nutrient availability and plant allocation patterns. In multiyear experiments a 50% reduction in photosynthetically active photon flux density (PPFD) during the summer results in a 25%–50% reduction in both production and aboveground biomass (Figure 5.8).

Results from tundra at Toolik Lake (Figure 5.8) are consistent with similar experiments throughout the Arctic (Shaver and Jonasson 1999; van Wijk et al. 2003; Dormann and Woodin 2002), which generally show a greater whole-system responsiveness to changes in N or P availability than to changes in temperature or light.

At present it is not possible to say which kinds of tundra (wet, moist, dry, or shrubby) are more or less responsive to these manipulations of growing conditions. Overall they all respond similarly to the changes in nutrients, temperature, and light. In experiments where N and P fertilizers have been added factorially, the response to N generally dominates especially in moist and dry tundras, although some moist tundras are P-limited and co-limitation has also been observed (Shaver et al. 1986a; Shaver and Chapin 1995). The productivity of wet sedge tundras near Toolik Lake is typically (but not always) P-limited or co-limited by P and N (Shaver et al. 1998). The greater importance of P limitation in wetter sites is probably related to the chemical immobility of P at low pH and low soil oxygen status, as well as to the common isolation of these tundras from mineral soils (as a source of P) due to their thick O horizons and shallow thaw depths (Table 5.1).

Species composition of all tundras responds strongly to changes in nutrients, temperature, light, and other manipulations such as changes in herbivory and snow cover. Here again, the greatest changes occur in response to fertilizer addition, and changes in species composition in response to other treatments often appear to be linked to secondary changes in N and P cycling. In moist acidic tundra, grasses and sedges often dominate in fertilized plots in the first 1–6 years of treatment; these graminoids may retain their dominance where *Betula* is absent (Bret-Harte et al. 2008). The long-term response (6–20 years) to nutrient addition in moist acidic

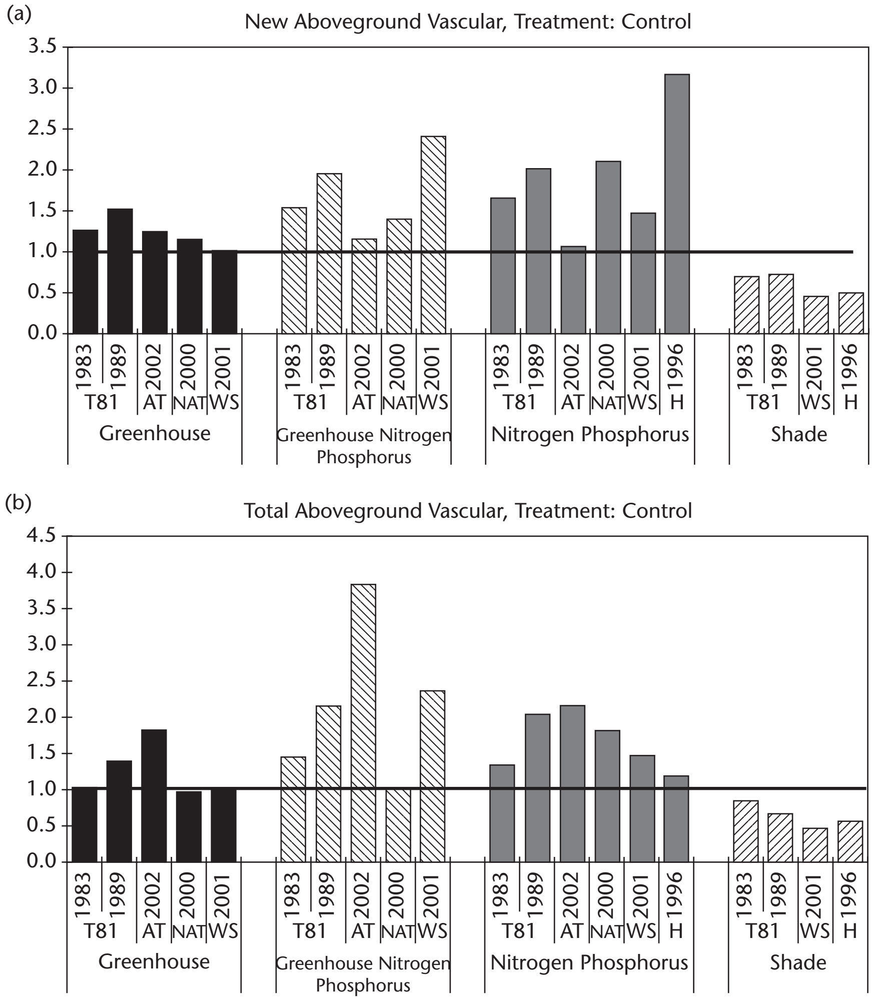

Figure 5.8 Response index (treatment value : control value) of (A) new aboveground vascular plant growth and (B) total aboveground vascular biomass in greenhouse, fertilizer, and shade treatments in acidic and nonacidic tussock, wet sedge, and heath tundras. (N.B.: Results of 1994 harvest of LTER wet sedge tundra not shown due to anomalously low production and biomass in control plots, leading to anomalously high response indices in all treatments in 1994.) The horizontal axis indicates treatment (greenhouse, greenhouse nitrogen phosphorus, nitrogen phosphorus, or shade), site (T81 = 1981 historic tussock, AT = LTER acidic tussock, NAT = LTER nonacidic tussock, WS = LTER wet sedge, H = LTER heath), and year of sampling.

tundra, however, is a dramatic increase in the rapidly growing woody shrub *Betula nana* (Shaver et al. 2001). In moist nonacidic tundra where *Betula* is rare or absent, there is a general increase in abundance of all plant functional types, resulting in an overall increase in biomass and productivity similar in magnitude to that of moist acidic tundra (Hobbie et al. 2005). In other systems, such as dry heath tundra initially dominated by evergreen shrubs and lichens, the dominant species of fertilized plots is the grass *Hierochloe alpina* (Gough et al. 2002). Warming also changes the species composition although more slowly than fertilizer addition, probably because the species changes are more limited by the temperature effect on nutrient availability than by the direct effect of warming on growth. As for the nutrient response, deciduous shrubs and forbs are typically the most responsive plant functional types to warming (Walker at al. 2006).

Mosses and lichens are also strongly affected by these treatments. Although the direct response is often similar to the vascular plants (i.e., increased growth with higher nutrients or warming), in the long term mosses and lichens generally decline or disappear in treatments where taller shrubs or other species form a closed, dense canopy (Shaver et al. 2001; Cornelissen et al. 2001). Lichen abundance is reduced by herbivores and increases in response to herbivore exclusion in dry heath and moist acidic tundras (Gough et al. 2008).

### *Effects of Species Composition on Biogeochemistry*

Variability and change in species composition are important because different species have very different responses to environmental change, and species composition has important impacts on biogeochemical cycles. A multitude of effects of species on biogeochemistry derive from differences in their growth rates, morphology, and allocation patterns. For example, because leaves of grasses and sedges grow from basal, intercalary meristems, grass and sedge species are less constrained in terms of the size and number of leaves that can be produced each year (Shaver and Laundre 1997). For this reason, grasses and sedges respond very quickly to changes in environment and dominate the initial changes in LTER fertilized plots. Other species, in particular the dominant evergreens like *Ledum palustre*, are limited in their ability to respond within the same growing season to change in the environment because the current season's growth is limited by the characteristics of the buds produced at the end of the previous season; the growth of individual shoots cannot respond fully until the following season, with growth from a new set of buds (Shaver 1981, 1983).

Vegetative demography is thus a key aspect of controls over the multiyear response to environmental change in the tundra near Toolik Lake. One of the most important differences among species in this regard is the ability to branch rapidly and to grow taller as biomass accumulates with more favorable growing conditions. Although graminoids can produce new tillers quickly (Fetcher and Shaver 1982), they cannot grow tall because they do not produce woody stems. The deciduous shrub *Betula nana*, on the other hand, is typically the dominant species in nutrient-rich moist and wet tundras because it (1) can rapidly produce new, upward-growing "long shoot" branches from the store of meristems it maintains as "short shoots" under less favorable environmental conditions and (2) can rapidly increase stem wood production by secondary growth from cambial meristems (Bret-Harte et al. 2001, 2002).

A second important effect of species composition is related to differences in their nutrient uptake, particularly N uptake in these typically N-limited systems.

Experiments using isotopically labeled N sources have shown that tundra plant species are physiologically able to acquire N in a wide range of different chemical forms, at different depths, and at different times of year (Kielland 1994; Schimel and Chapin 1996; McKane et al. 2002). The common tundra plant species are also known to differ consistently in $\delta^{15}N$, a measure of the relative abundance of N isotopes, in their tissues (Figure 5.7; Nadelhoffer et al. 1996). Because changes in $\delta^{15}N$ within plants are assumed to be negligible, the differences in $\delta^{15}N$ among species must be due to differences in sources of N taken up by those species (i.e., $NO_3^-$, $NH_4^+$, amino acids, and other forms of organic N taken up directly by roots, and N acquired via mycorrhizal symbionts). Surveys of $\delta^{15}N$ in leaves (e.g., Figure 5.7) consistently show that evergreen and deciduous shrub species have low $\delta^{15}N$ values (in the range –4 to $-8^{o}/_{oo}$), while graminoids and most forb species have much higher $\delta^{15}N$ values (in the range +4 to $0^{o}/_{oo}$). The shrub species all have ectomycorrhizae or ericoid mycorrhizae associated with their roots, and these mycorrhizae are known to transfer N to their plant hosts at low $\delta^{15}N$. Much of the N supply to evergreen and deciduous shrubs appears to be via mycorrhizae. The graminoid and forb species, on the other hand, are mostly nonmycorrhizal or endomycorrhizal and appear to meet most of their N requirement by direct uptake of a wide range of N forms (*Pedicularis*, a forb in the Scrophulariaceae, is a root hemiparasite of *B. nana* and may obtain much of its N in this way). These differences in N uptake source among species may promote diversity in the tundra vegetation and may increase the community-total N uptake in this N-limited system.

In addition to these species effects, there is also considerable within-species variation in responses to environment that must be considered in extrapolating these responses over large areas. Populations ("ecotypes") of *Eriophorum vaginatum* from south of the Brooks Range, for example, are significantly more responsive to environmental variation in reciprocal transplant experiments than are northern populations (Shaver et al. 1986b; Fetcher and Shaver 1990). A recent resurvey of these now 30-year-old reciprocal transplant experiments shows that individuals of the same species from local populations are more fit than foreign populations in common gardens (Bennington et al. 2012).

One of the best-documented effects of species composition on biogeochemistry is that of litter "quality" (relative decomposability) on decomposition and nutrient mineralization. In a comparison of decomposition rates using litter from 18 sites around the Arctic (Cornelissen et al. 2007), differences among plant functional types (deciduous, evergreen, graminoid, moss) accounted for about 30% of the explained variance in decomposition rates while "life zone" (overall differences in environment between the two experimental sites where the litter decomposed) accounted for about half of the explained variance (Figure 5.9). Among the species and ecosystems at Toolik Lake, the different kinds of litter also decompose at very different rates and immobilize and release N differently; at constant temperature the range of decomposition rates among litter types from Toolik Lake is greater than the effect of a 6ºC change in temperature (Hobbie 1996). However, when weighted-average decomposition rates are used to estimate overall community litter decomposition at different sites, the site effects (moist acidic versus

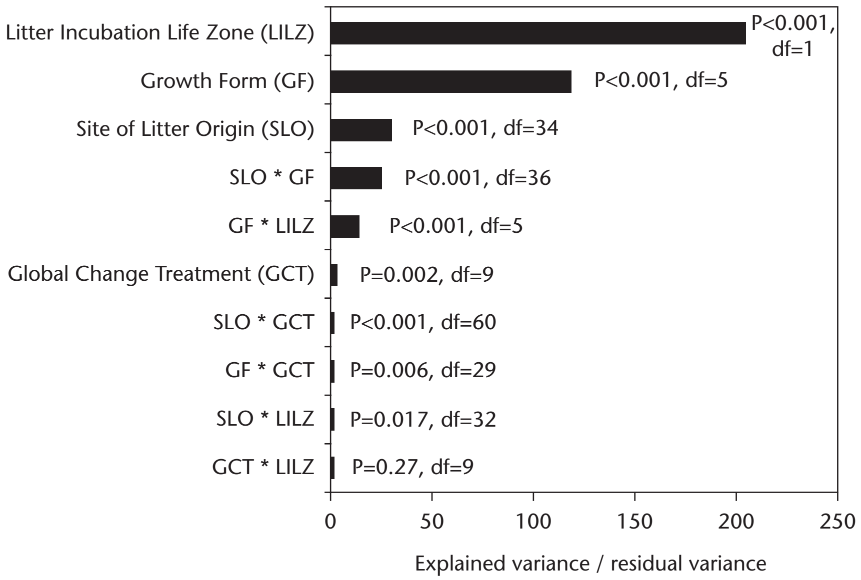

Figure 5.9 Results of a four-way analysis of variance unraveling the key biotic and abiotic effects on percentage of mass loss of leaf litters, based on the predominant plant species in 33 experiments in arctic and alpine sites in the Northern Hemisphere (see Figure 5.1). Mass loss percentage data were arcsine(square-root(100/x)) transformed prior to analysis. Total df = 1824 (from Cornellisen et al. 2007.)

nonacidic tundra) on decomposition become more important than species composition effects (Hobbie and Gough 2004). The combination of species effects on initial litter "quality" and site effects on decomposition and mineralization is ultimately related to the chemical composition and nutrient mineralization of soil organic matter (Shaver et al. 2006), and likely to the microbial community composition (Zak and Kling 2006).

Finally, differences in growth and allocation patterns among species can converge on similar overall ecosystem responses to environment despite very different component responses. For example, the concentration of N in plant tissues varies widely both among species and among tissues (leaves, stems, roots, inflorescences) as well as among sites and experimental treatments. However, when the overall N requirements of production and biomass accumulation by whole tundra vegetation are calculated, there is very little variation in overall N concentration across a ten-fold range in production and biomass in vegetation ranging from dry heath to tall shrub tundra (Shaver and Chapin 1991). In unmanipulated vegetation, this convergence in overall N use results more from changes in the mix of species and tissues with different N concentrations than from variation in N concentration within species or tissues. However, even in long-term fertilized plots where species composition has changed dramatically and N concentrations in all tissues have increased, because increases in woody stem mass (with low N concentrations) are much greater than increases in leaf mass (with high N concentrations), the overall

N concentration in the whole vegetation has not changed despite a doubling of biomass, production, and N content (Shaver et al. 2001). This convergence in N use appeared even when dominant species had been removed from the vegetation for six years, and regrowth by remaining species resulted in no change in overall N concentration (Bret-Harte et al. 2008). Together, these studies indicate strong constraints on N-allocation and N-use efficiency in these typically N-limited tundras, resulting in similar overall N use in all tundras.

The convergence among species and vegetation types in overall response to environment is particularly well illustrated by controls over canopy-level carbon exchange. In a comparison of 14 different tundras in the Kuparuk River basin (including Toolik Lake), Williams and Rastetter (1999) found a constant, linear relationship between canopy leaf area and canopy N content, irrespective of species or plant functional-type composition, and showed that this relationship was optimal for GPP at any leaf area or N content. A comparison of long-term harvest data from LTER study sites indicates that there is a very close correlation between aboveground net primary production (ANPP) and leaf area among years in control plots despite some year-to-year variation in species composition (Figure 5.10A–C) and that this relationship is continuous

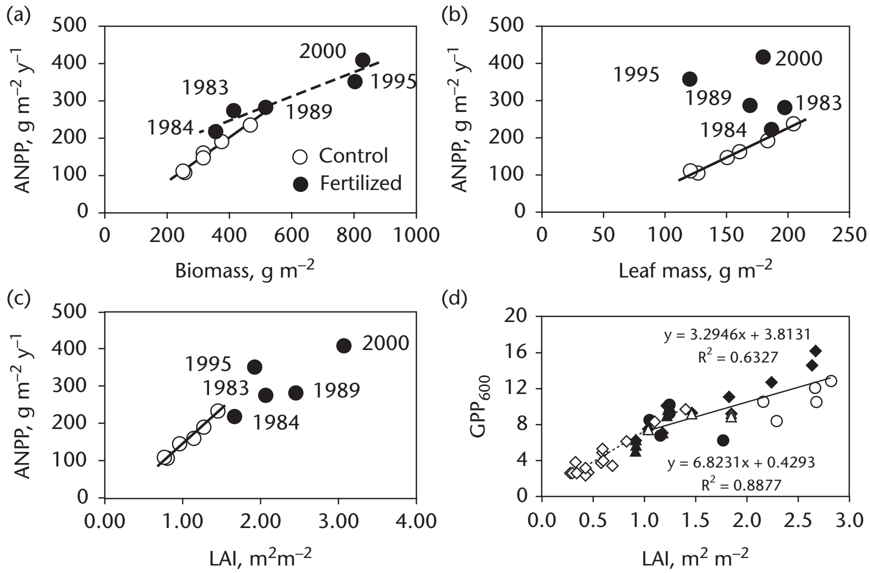

Figure 5.10 Gross primary production (GPP) and aboveground net primary production (ANPP) are closely correlated with leaf area even as species composition changes among years or with fertilizer addition. Data in panels A, B, C from control and fertilized moist tussock tundra at Toolik Lake. Data in panel D from control and fertilized plots in five different tundras at Toolik Lake. In panel D, $GPP_{600}$ is GPP at 600 μmol $m^{-2}$ $s^{-1}$ photosynthetically active photon flux. Open and filled symbols represent data from control and fertilized plots, respectively. Circles = LTER acidic tussock tundra; diamonds = nonacidic nontussock tundra; triangles = heath tundra. (Original data in Chapin et al. 1995; Shaver et al. 2001; and Mack et al 2004.)

with the relationship between ANPP and leaf area in fertilized plots despite major changes in species composition and total N mass in these plots. A similar relationship exists between canopy photosynthesis (GPP) and leaf area across contrasting tundra types both with and without fertilization (Figure 5.10D). Here again, these studies taken together indicate very strong constraints on how canopy-level $CO_2$ exchange is regulated, with ~80% of the variation in $CO_2$ exchange explained knowing only leaf area, light intensity, and temperature, irrespective of species composition (Street et al. 2007; Shaver et al. 2007). Despite a wide range of leaf morphology, leaf longevity, and leaf chemistry among the common species and tundra types, $CO_2$ exchange at the canopy level is regulated mainly by leaf area, by leaf aspect, and by leaf distribution through the canopy.

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## Vignette 5.4. Species Effects of Terrestrial Plants, by M. Syndonia Bret-Harte

It has been proposed that plant species with similar effects on ecosystem function, such as species with highly decomposable leaf litter that stimulates decomposition, can be grouped into a single "functional type." Chapin et al. (1996) identified six functional types in tussock tundra, corresponding to the recognized physiognomic growth forms (deciduous shrubs, evergreen shrubs, graminoids, forbs, mosses, and lichens). Species in a given functional type are expected to be better at replacing each other than species from other functional types, because they share similar patterns of resource acquisition and use (Symstad 2003). However, there have been few tests of this idea.

To understand how species affect ecosystem functioning and the trajectory of ecosystem response to increased nutrient availability, we variously removed (a) the dominant evergreen shrub (*Ledum palustre*), (b) the dominant deciduous shrub (*Betula nana*), (c) all mosses, and (d) the combination of mosses, *B. nana*, and *L. palustre* in the presence and absence of fertilization. We did not remove graminoids because the dominant graminoid is a tussock-forming sedge upon which many other species grow; removing it would have changed microtopography and drainage.

After six years, the remaining plants had grown enough to restore total biomass to control levels (i.e., biomass compensation had occurred) in most unfertilized removal treatments (Bret-Harte et al. 2008). Net primary productivity was not different from controls in unfertilized removal treatments. Compensation was remarkably rapid, considering how slow plant growth is in arctic ecosystems and how much biomass was removed. Contrary to prediction, the species that provided most of the compensatory growth were not from the same functional type as the removed species, but were instead the most abundant species in other functional types.

Fertilization did not increase total plant community biomass, because some growth forms and species benefited at the expense of others (Bret-Harte et al. 2008). However, under fertilization, deciduous shrub biomass increased more than any other growth form when *Betula nana* was present, but graminoid biomass increased the most when *B. nana* had been removed. *Betula nana* and many graminoid species can rapidly increase their numbers of active meristems under fertilization, which makes them good competitors under increased nutrient availability.

Changes in plant species composition might alter ecosystem N-use efficiency, because different plant species have different uptake rates and use different forms of N (McKane et al. 2002). However, N-use efficiency of plant biomass (total live plant biomass divided by total N content) was not significantly different among most unfertilized removal treatments (Figure 5.V4A), although removal changed the relative abundance of species. Only removing the combination of moss, *Betula*, and *Ledum* decreased the N-use efficiency of biomass relative to control plots; this treatment was dominated by graminoids and had not completely compensated in biomass (Bret-Harte et al. 2008). Removal did not alter N-use efficiency in net primary production, either (Figure 5.V4B). These similar N-use efficiencies probably result from the strong N limitation of plant productivity in unfertilized tundra (Shaver and Chapin 1980, 1986; Chapin and Shaver 1985; Chapin et al. 1995; Shaver et al. 2001).

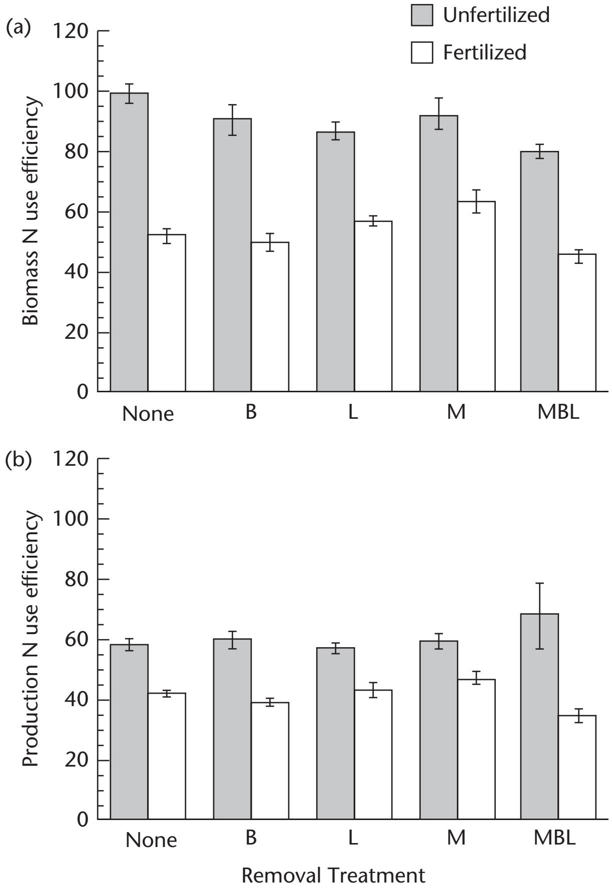

Figure 5.V4 Ecosystem N-use efficiencies of (A) total plant biomass and (B) vascular production after six years of removal and fertilization. Removal treatments were as follows: None = no removal (controls); B = removal of *Betula nana*; L = removal of *Ledum palustre*; M = removal of all mosses; MBL = combined removal of mosses, *B. nana*, and *L. palustre*.

In contrast, fertilization decreased N-use efficiency of biomass (Figure 5.V4A), increased the total N pool in live biomass, and increased N concentrations in plant tissues. Fertilization decreased the N-use efficiencies of both biomass and production most where *B. nana* biomass was the least, where plots were dominated by graminoids. Fertilized *B. nana* produces a large amount of wood of low N content, which is not produced by graminoids.

Our results suggest that plant species composition does not affect capture of N by vegetation in unfertilized tundra, but does so when nutrient limitation is released by fertilizer addition. Species composition changes the trajectory of ecosystem response to fertilizer, and can affect other aspects of ecosystem functioning. Large shrubs decrease albedo in spring, and thus alter tundra energy balance (Chapin et al. 2005). *Betula nana* is unpalatable to most mammalian herbivores, and a transition to dominance by shrubs would negatively impact caribou if it occurs over a large area. In a future shaped by climate warming and increased N deposition, shrub dominance and graminoid dominance may be alternative outcomes, depending on the local abundance of these growth forms now.

## Time-Scales and Trajectories of Change

In the absence of major disturbances like fire or permafrost thawing, change at the ecosystem level takes time because multiple, linked processes are involved and not all processes change at the same rate (Shaver et al. 2000). For this reason, annual variation in production and biomass of the tundras near Toolik Lake is poorly correlated, if it is correlated at all, with annual variation in weather variables like temperature and radiation. Productivity of moist acidic tundra, for example, varied more than two-fold between 1982 and 2000 (Figure 5.11A), but there was little indication of a long-term trend in productivity despite persistent, strong summer warming throughout the late 1980s and 1990s. Although the highest production and biomass were both measured in the final year, 2000, neither was significantly different from the long-term mean production or biomass. During this time there was also little change in species or functional-type composition of moist acidic tundra. Although the biomass of *E. vaginatum* was 30% lower in 2000 versus 1982, most of that decline took place during the early 1980s (before climate warming) and graminoid biomass was, if anything, recovering during the 1990s (Figure 5.12A). There were no clear trends in biomass of the dominant deciduous and evergreen shrubs (*Betula nana, Ledum palustre, Vaccinium vitis-idaea*), with the exception that between the final two harvests, in 1995 and 2000, *Betula* biomass doubled (Figure 5.12A).

Even the responses to strong, artificial manipulation of the environment may take many years to develop. In fertilized plots in moist acidic tundra, aboveground productivity increased 2- to 2.5-fold relative to control plots in every year they were harvested (Figure 5.11B). Aboveground biomass, on the other hand, took much longer to change because initially strong increases in production by graminoid species declined after the mid-1980s while the long-term dominant species in the fertilized plots, *Betula nana*, took about five years to emerge (Figure 5.12B). Thus the species

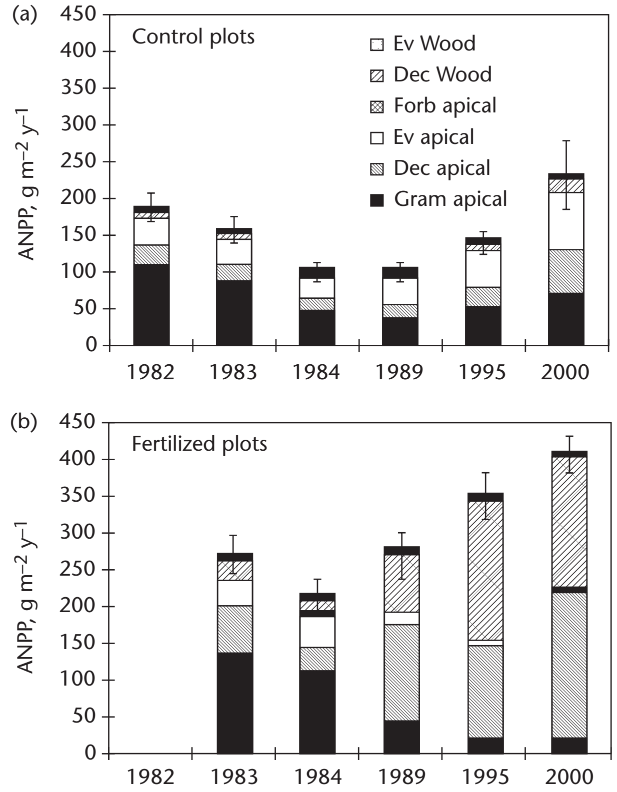

Figure 5.11 (A) Aboveground net primary production (ANPP) in unfertilized control plots of moist acidic tundra at Toolik Lake, Alaska, over six harvests between 1982 and 2000. Although the 2000 harvest occurred after 20 years of climate warming, we cannot say for sure whether the greater total ANPP and the greater productivity of deciduous shrubs in 2000 is the result of warming or is within the "normal" range of ANPP. (B) ANPP in fertilized plots at the same site, where fertilizer addition (N + P) began in 1981. The initial fertilizer response was dominated by graminoids, with a long-term dominance by deciduous shrubs and a large increase in wood production apparent only after 1989. Ev wood = wood production in evergreen shrubs; Dec wood = wood production in deciduous shrubs; Ev apical = leaf and twig production in evergreens; Dec apical = leaf and twig production in deciduous shrubs; Gram apical = leaf and culm production by grasses and sedges. Details are published in Chapin et al. (1995); Shaver et al. (2001); and Mack et al. (2004).

replacement process delayed the increase in community biomass in fertilized plots despite an immediate and sustained increase in production.

Almost all the changes in species composition that were observed in experimental plots within the first 10–15 years of treatment took place as a result of differential growth of the same individual plants that were present at the start of the experiment, with little or no establishment of new individuals by seed and thus little or no addition of new species (Shaver et al. 2001). Exceptions occurred in the dry heath

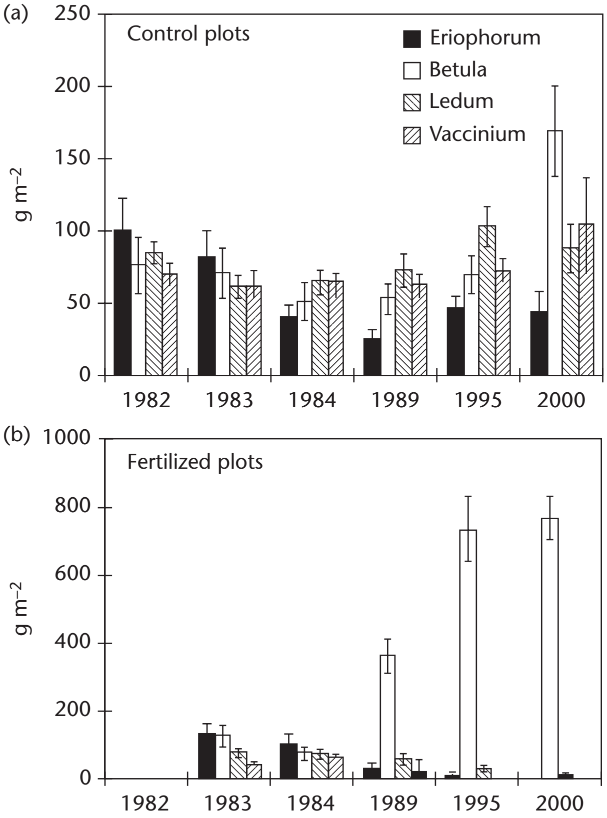

Figure 5.12 Biomass of the four most abundant species in moist acidic tundra at Toolik Lake, in (A) control and (B) fertilized plots. Here biomass includes aboveground biomass and belowground stems but not roots. Original data in Chapin et al. (1995); Shaver et al. (2001); and Mack et al. (2004).

tundra and in some tussock tundras with higher-pH soils where several grass species increased several-fold in abundance in fertilized plots, by both seed establishment and vegetative growth (Gough et al. 2002). In a few individual plots in wet sedge and heath tundras, weedy species like *Epilobium angustifolium* invaded and became very well established (Shaver et al. 1998). Nonetheless, decade-scale changes in community composition are possible by addition of new species and have been observed, for example, in the establishment of *Betula nana* in fertilized wet sedge tundra after 12 years (Boelman et al. 2003) and the invasion of fertilized, acidic tussock tundra by *Calamagrostis lapponica* and *Stellaria* species after ~15 years. These slow additions of species to experimental plots indicate potential for continued change over many decades, although their effects, if any, on overall productivity, organic matter accumulation, or biogeochemistry are both unknown and unpredictable at present.

Even processes that vary dramatically from year to year are unrelated to annual variation in weather. For example, flowering of *Eriophorum vaginatum* at Toolik

Lake varies more than 100-fold among years (Figure 5.13, top) and is correlated with the annual variation in flowering along a 300-km transect running from the Yukon River to the northern coastal plain (Figure 5.13, bottom; Shaver et al. 1986b). The most likely explanation for this observation is that flowering is a process that is controlled over several years of weather and plant response. Only after 30 years of observation is it becoming clear that years of high flowering appear to follow at least two warm summers with good growing conditions and favorable conditions for soil N mineralization and N uptake by plants (J. Laundre unpublished; LTER

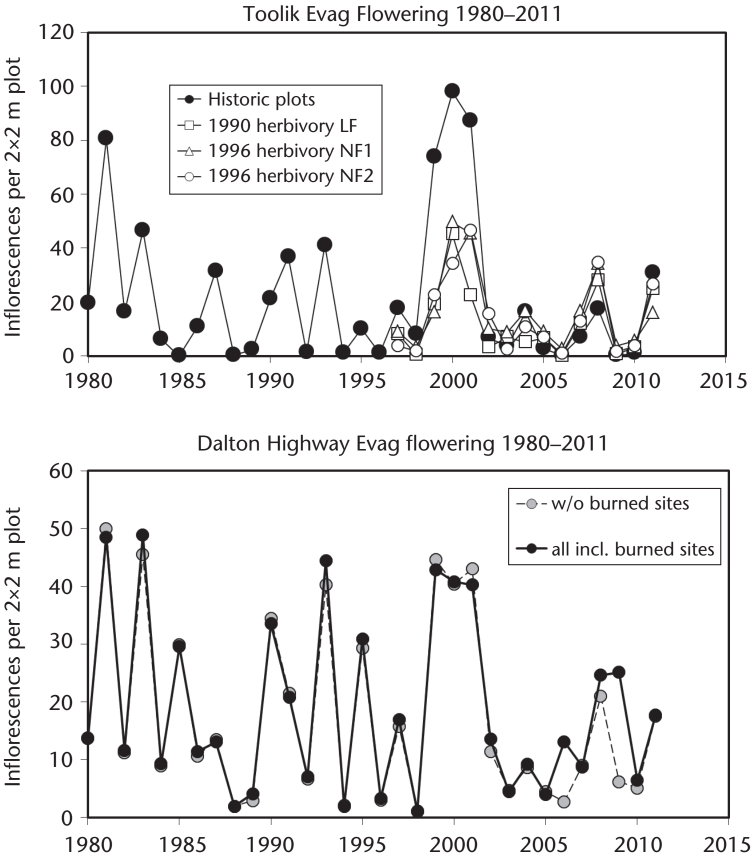

Figure 5.13 Mean number of inflorescences of *Eriophorum vaginatum* in 2 × 2 m plots at Toolik Lake (top) and in similar plots along the Dalton Highway (bottom; in most years n = 21–23 sites, 1979–2011). In the upper panel, different symbols represent different sets of unmanipulated control plots in moist acidic tundra at Toolik Lake. In this panel, "Historic plots" are the same as the "Historic tussock" plots in Figures 5.2–5.4, while "1990 herbivory" and "1996 herbivory" plots are separate, unmanipulated plots at the "LTER acidic tussock" site, also shown in Figures 5.2–5.4. In the lower panel, black symbols are means including all sites while grey symbols are means not including 3 sites that were burned in 2004-2005. Data for 1979-1982 were published in Shaver et al. (1986).

database); the same high flowering also occurs in fertilized plots in the second (but not the first) year of treatment, and secondary peaks in flowering occur in older, abandoned fertilized plots in years *following* warm years.

Overall, these long-term observations of variability and change in individual species and whole vegetation suggest that changes in production and biomass are well buffered against short-term variation in weather. The major components of this "buffering" include:

(1) *Physiological* characteristics such as the internal storage and recycling of C and nutrient resources used in growth, which make each year's production a function of resources acquired over more than one year;
(2) *Morphological* characteristics such as (for some but not all species) the need to form new buds from which each year's growth is produced, and constraints on the rate and pattern of new meristem production;
(3) *Species differences* in physiology and morphology, which means that growth of each species has a different relationship to short-term variation in weather or sustained changes in climate; and
(4) *Population dynamics* of the different species in the community, which tend to reduce overall variation in vegetation biomass because increases in some species are compensated by simultaneous decreases in others.

Soil-plant interactions also play a key role in regulating long-term change in tundra ecosystems, in particular because production and biomass accumulation are so strongly linked to soil nutrient supply. For this reason, the limited responses to greenhouse warming that were observed in tussock and wet sedge tundras (Figure 5.6) are interpreted as resulting from a relatively slow increase in soil nutrient availability in response to modest temperature increases, in contrast to the larger and more rapid responses to fertilizer addition. Similarly, in open-topped chamber warming experiments completed at more than 20 arctic and alpine sites (including Toolik Lake) as part of the International Tundra Experiment (ITEX), initial increases in individual plant growth in the first two years of treatment were frequently not sustained over longer periods, suggesting some secondary limitation, perhaps related to nutrients, that restricted the potential for sustained increases in growth (Arft et al. 1999; Walker et al. 2006; Elmendorf et al. 2011).

In addition to revealing the long-term trajectories of change in composition and processes in response to manipulation, the Arctic LTER experiments allow us to document overall changes in standing stocks of elements and organic matter. In fertilized moist tussock tundra, a total of 200 g $m^{-2}$ N and 100 g $m^{-2}$ P were added over the 20 years from 1981 through 2000 (10 g $m^{-2}$ $yr^{-1}$ N and 5 g $m^{-2}$ $yr^{-1}$ P). Increased N and P incorporation into plant biomass (Figures 5.10A–C, 5.11, 5.12) can account for only a small proportion of these amounts. This leads to the related questions: "Where did the added fertilizer nutrients go, and can we track their accumulation in some other part of the ecosystem?" When complete C and N budgets were calculated for these plots at the 2000 harvest (Mack et al. 2004), it was discovered that the total amount of N in fertilized plots was, if anything, *less than* the amount in control plots (Figure 5.14C), whereas if all of the added N had remained on the fertilized plots the total amount should have been at least 50% greater. All of the losses of N were from (a) mineral soils and (b) portions of the organic mat below 10 cm; other components of the soil-plant system gained N (Figure 5.14D). Because the N losses were from deeper soil pools, this suggests that much of the N that was lost was not from fertilizer N, but from N in older organic matter that was mineralized and either leached or denitrified. The net losses of N in fertilized plots were matched by a similar pattern of net C loss (Figure 5.14A, B), despite a doubling of productivity that should have increased total C inputs by at least 1500–2000 g m$^{-2}$ over 20 years, relative to control plots. All of the net C losses were from deeper levels of organic soil, especially from the mineral soil (Figure 5.14B), again indicating that the C lost was old-soil organic C and not recently fixed C or surface litter C.

The net long-term losses of *both* C and N in this "N-limited" moist acidic tussock tundra were not expected but still are consistent with the strong control of organic matter cycling by interactions among the C and N cycles as discussed in relation to Figure 5.6. Overall, C and N were lost or gained in similar proportions in each of the pools described in Figure 5.14, with little change in C:N ratios overall or

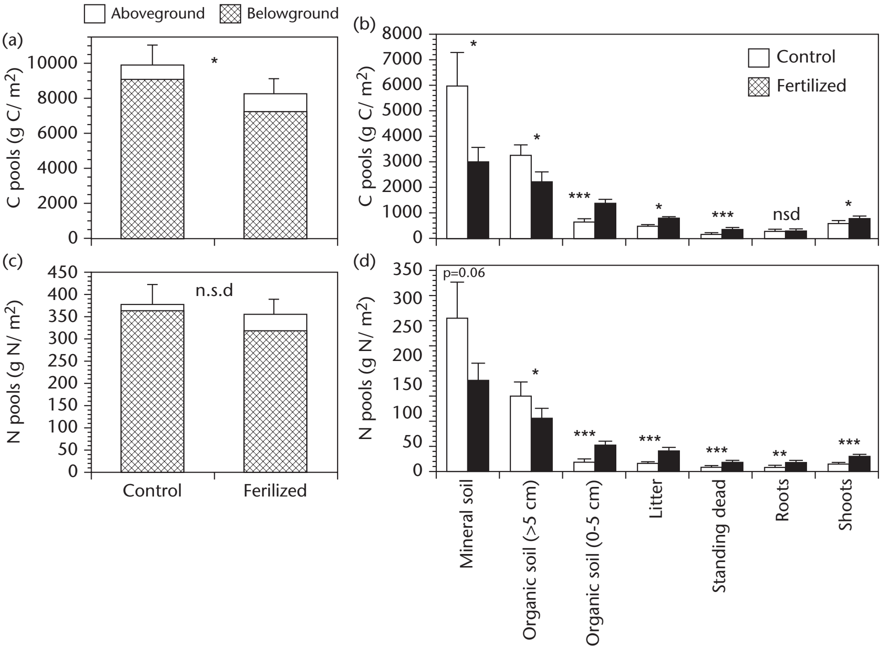

Figure 5.14 Effects of fertilizer on tundra carbon and nitrogen pools after 20 years of fertilization. Mean (±1 standard error) above- and belowground carbon (A) and nitrogen (C) pools in unmanipulated control and fertilized treatments of moist acidic tundra near Toolik Lake, Alaska. Aboveground pools include shoots, standing dead plant material, and rhizomes. Belowground pools include surface litter, roots, and organic and mineral soil. Mean (±1 standard error) carbon (B) and nitrogen (D) pools in plant and soil compartments (from Mack et al. 2004).

in individual pools. The large losses of deep, presumably older soil organic matter after 20 years of fertilization support the hypothesis that soil-decomposition processes, as well as primary production, are N-limited in these ecosystems (Schimel and Weintraub 2003). Addition of readily available N (as $NO_3^-$ and $NH_4^+$) in the fertilizer appears to have stimulated *both* C fixation by plants and also respiratory C loss by soil microbes (Nowinski et al. 2008). Much of the increased C loss must have come in association with increased denitrification and gaseous N losses (Alexander-Ozinskas 2007).

Increased downslope leaching losses of C and N are unlikely to have contributed greatly to the overall losses from fertilized plots. In the case of N, for example, the background rate of leaching loss (~0.1 g N $m^{-2}$ $yr^{-1}$, or ~2 g $m^{-2}$ over 20 years) would have had to increase ten-fold to account for only ~20 g, or ~8%, of the "missing" 240 g $m^{-2}$ of N in the fertilized plots (including 200 g N added as fertilizer plus a reduction in standing stock of ~40 g $m^{-2}$). Because the amount of water leaching from the fertilized plots should, if anything, have decreased due to higher leaf area and presumably higher evapotranspiration in fertilized plots, any large increase in downslope leaching could only have occurred as a result of large increases (ten-fold or greater) in dissolved C and N concentrations in the water moving downslope. However, the concentrations of dissolved N that were actually measured within fertilized plots were only about 3–5 times control values (e.g., Chapin et al. 1995), and any excess N in soil water is likely depleted rapidly to control levels within 1–5 m downslope (Yano et al. 2010). The maximum contribution of increased leaching to the total N loss from fertilized moist acidic tundra is thus <4%–5% of the total loss over 20 years. Using the same argument for C, increased C leaching from fertilized plots cannot account for more than about 4% of the "missing" C.

## Feedbacks and Interactions: Changes in Surface Energy Balance, C and N Balance, and Disturbance Regime

Each patch of tundra interacts with its neighbors, with the atmosphere, and with downslope aquatic ecosystems through exchanges of energy, elements, and water. These spatial interactions play an important role in regulating long-term change in tundras, and constitute an important system of feedbacks on the external drivers of change, including climate change, disturbances such as fire and thawing of permafrost, and direct human impacts. As terrestrial ecosystems respond to these drivers, changes in their surface energy balance, overall C and N balance, and leaching losses to downslope tundras and aquatic systems will create both positive and negative feedbacks.

One example of this system of feedbacks is related to the expected general increase in abundance of shrubs, especially deciduous shrubs, in response to climatic warming. An increase in shrub abundance has been predicted for over 25 years based on observed species-level responses to weather, climate, human and natural disturbance, and experimental manipulations (e.g., Chapin and Shaver 1985). The principal basis for this prediction is the higher abundance of shrubs in warmer, better-drained, and higher fertility sites, and the consistent increases in the abundance of deciduous shrubs in disturbed, warmed, and (especially) fertilized tundras throughout the Arctic (e.g., Shaver and Chapin 1986; Walker et al. 2006). Analyses of pairs of photographs taken 30–40 years apart appear to support this prediction for many alder-dominated sites in northern Alaska (Sturm et al. 2001), although isolating long-term increases in shrub abundance from annual variation and from concurrent changes in other functional types gives more equivocal results for the area around Toolik Lake (e.g., Figure 5.12A; Wahren et al. 2005).

The expected general increase in "shrubbiness" has very substantial implications for both surface energy balance and C and N cycling (Figure 5.15). Because shrub canopies absorb more energy from incoming solar radiation, particularly in spring when shrub branches emerge from the snow, they reflect less of that energy and warm up more, ultimately transferring more energy back to the air as latent and sensible heat rather than as reflected shortwave radiation. The change in the atmospheric heating is quite large, potentially as large as 8.9 W $m^{-2}$ if the tundra landscape is completely converted to shrubland (Chapin et al. 2005); this amount is *double* the global average 4.4 W $m^{-2}$ heating experienced since the last glacial maximum (or predicted due to greenhouse gas accumulations by the end of this century), suggesting that the regional feedback on climate resulting from a complete change to shrub dominance could have a greater effect on regional climate than the original driver, global warming.

Changes in shrub dominance will have major impacts on soil thermal regime and on the cycling of C and N in soils (Figures 5.15, 5.16), in addition to the direct impacts of warmer temperatures and decreases in the period of snow cover (Euskirchen et al. 2006). Because shrub vegetation accumulates deeper snow in

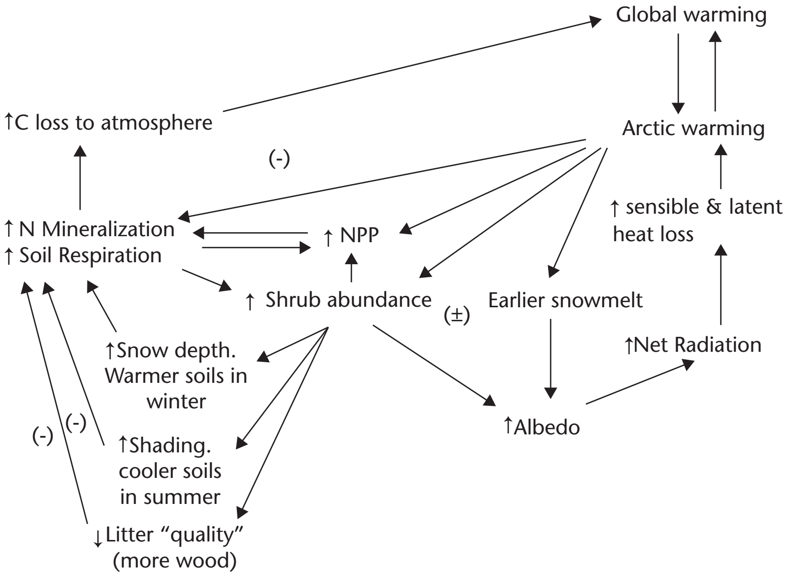

Figure 5.15 Feedbacks on drivers of change, showing the dominant connections (arrows) and whether there will be a positive or negative feedback.

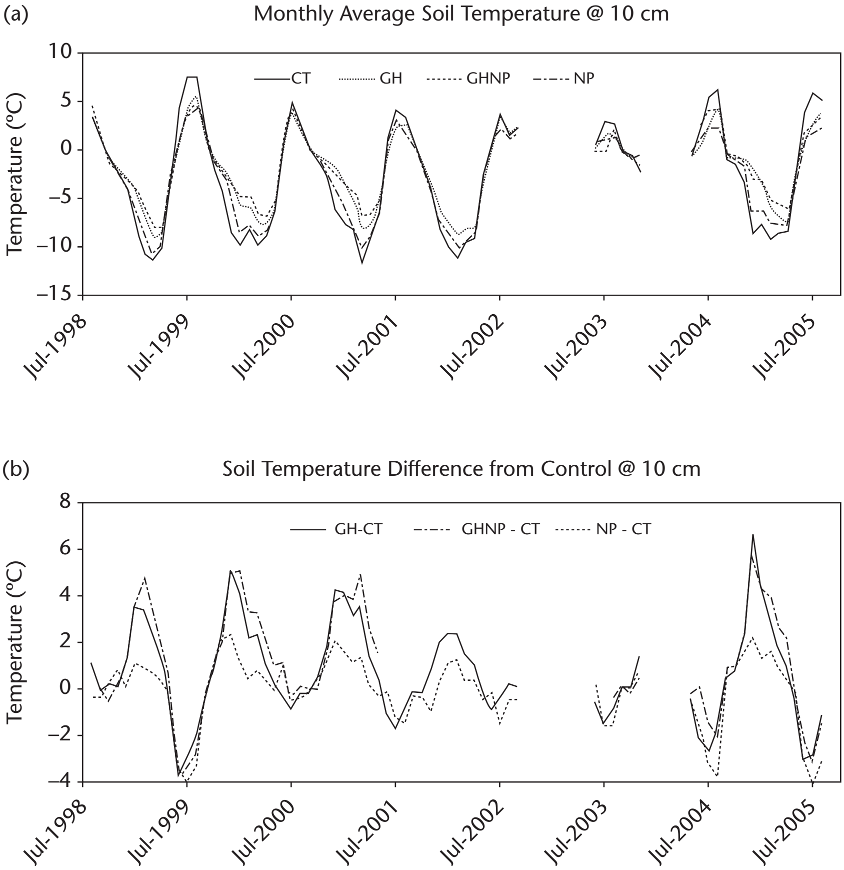

Figure 5.16 Soil temperatures beneath shrub-dominated experimental plots are warmer in winter and colder in summer than in controls. (A) Monthly average soil temperature at 10-cm depth in LTER experimental plots in moist acidic tundra (MAT) at Toolik Lake, 1993–2005. (B) Difference from control (treatment-control) in monthly average soil temperature at the same plots. CT = control plots; GH = greenhouse plots; NP = N + P fertilized plots; GHNP = greenhouse plus fertilizer plots. Source: Arctic LTER database.

winter (Sturm et al. 2001), the soils beneath shrub canopies are better insulated from very cold air temperatures, taking longer to freeze and not falling below the extremely low temperatures that would stop microbial activity (Schimel et al. 2004). Thus it is likely that mineralization of C and N and respiratory loss of C will continue for longer periods into the middle of winter and at higher rates than in tundras with less shrub cover (Borner et al. 2008). In contrast to this winter warming beneath shrub canopies, during the summer the denser shrub canopy intercepts incoming solar radiation above the soil surface and less energy reaches and warms the soil, leading to cooler soils in the summer (Figure 5.16) and shallower depth of thaw. This *negative feedback* may act to limit the magnitude of the change in community composition in the long term. However, at present it is not known which of these two opposing feedbacks will predominate in regulating the response to climate warming.

Exchange of $CO_2$ with the atmosphere will also be affected by changes in species composition, including increased shrub abundance. Here again, one of the main factors determining the net effect will be the effect of species composition on soil respiration via the effect of the canopy on soil temperatures (Figure 5.16). Another key factor is the effect of plant litter quality (decomposability) on soil and litter respiration. Shrub vegetation is not only more productive than other tundras (Figure 5.3), it also produces more wood than other tundras (Figure 5.11; Weintraub and Schimel 2005). Although higher productivity means higher litter production and thus more respiration from litter, woody litter decomposes much more slowly than most leaf litters (Hobbie 1996). Shrub tundras do have higher soil and litter respiration rates than other tundras, at least during the summer (Grogan and Chapin 1999), but they do not have above-average soil C accumulation (Figure 5.4). Thus it is still not clear whether a shift to shrub tundras should be accompanied by a net increase or a net decrease in ecosystem C stocks, although the overall rate of C turnover should be increased.

In addition to the direct effects of climate change on species composition, surface energy balance, and biogeochemical processes, changes in the regional disturbance regime have the potential to affect the entire arctic region even though the area of disturbance is relatively small. For example, in 2007 a single wildfire north of Toolik Lake released >2 Tg of carbon to the atmosphere, mostly due to combustion of the upper few centimeters of soil organic matter over an area of 1039 $km^2$, about one-half of 1% of the area of the North Slope of Alaska (Mack et al. 2011). This was the largest wildfire known to have occurred in arctic tundra, and the amount of C it released was equal to about half the annual net C sequestration of the entire arctic region (McGuire et al. 2009). In the years following this wildfire, changes in C balance in the burned tundra were also large as the burned tundra slowly regrew, initially losing C to the atmosphere as $R_E$ exceeded GPP, and then sequestering C as plant canopies recovered and GPP increased (Rocha and Shaver 2011a and unpublished data). These changes in C balance in regrowing, burned tundra were large enough to cancel any predicted increases in C sequestration due to warming climate over much larger areas, suggesting that future increases in wildfire frequency, severity, and area burned have the potential to dominate the regional changes in C balance as the climate warms. Although wildfires in northern Alaska have been rare or absent for at least 5,000 years (Hu et al. 2010), clearly the tundra plants are well adapted to at least occasional burning, as shown by the spectacular flowering of plants in 2010 and 2011 that survived the burning (M. S. Bret-Harte, A. Rocha and others, personal observation).

Disturbances such as wildfire also interact with changes in permafrost that are already occurring as the climate warms. Because wildfire reduces surface albedo and increases net radiation in burned sites, soils are warmer and depth of thaw is greater (Rocha and Shaver 2011b), leading to abundant thermokarst features on burned land. Several recent studies have found increases in thermokarst activity in northern Alaska (e.g., Bowden et al. 2008; Gooseff et al. 2009), often leading to loss of much of the organic matter in thermokarst-impacted sites. These "hot spots" of C and other element turnover have the potential to affect regional element balances because the rates of change in element stocks per unit area can be several orders of magnitude greater than slower, climate-driven rates of change over much larger areas.

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## Vignette 5.5. Decadal-Scale Changes of Vegetation from Long-Term Plots in Alaskan Tundra, by William A. Gould and Joel A. Mercado-Díaz

Climate-related changes in vegetation structure and composition may be both subtle and slow. These changes have been studied in the tundra near Toolik Lake using both experimental manipulations and long term monitoring. As part of the International Tundra Experiment (ITEX; Walker et al. 1999; Elmendorf et al. 2012), manipulations of summer temperatures have been carried out using open-topped chambers, and snow depths have been manipulated using snow fences; long-term response of plant communities to ambient climate has been monitored in two 1-km$^2$ grids located at Toolik Lake and nearby Imnavait Creek (Walker et al. 1989). Monitoring in the two grids involves resampling a set of permanent control plots at five- to seven-year intervals, beginning in 1989, using the point-frame method. In this method an aluminum frame with a paired-grid of wires is placed over vegetation plots and aligned to a set of permanent markers. By sighting downward and aligning the paired crosshairs (100 sampling points per frame), the same point can be resampled over many years. The sampling is designed to measure changes in species abundance and vegetation structure over time to understand plant community dynamics in the Alaskan tundra.

Prediction and experimental observation of tundra vegetation changes in recent decades has indicated a likely increase in the relative abundance of shrubs in response to climate warming (Sturm et al. 2001). The ITEX manipulation of summer temperature and snow depths began in 1994 and continues to show effects on vegetation. Changes in snow regimes have the largest impact. Both warming and snow effects are strongest in the moist tussock tundra relative to dry heath tundra. The most common changes associated with increased snow depths included increases in canopy height and shrub abundance and decreases in species diversity and lichen cover. Experimental warming was associated with a relative increase in shrub abundance in the moist tussock tundra. In contrast, analysis of our 20-year record of tundra vegetation structure and composition from 155 permanent monitoring plots at Toolik Lake and Imnavait Creek indicates a general increase in vascular plants. Over the last two decades the relative abundance of vascular vegetation increased by 18.6% whereas abundance of the nonvascular component of vegetation has decreased significantly: lichens by 9.3%, non-*Sphagnum* mosses by 20%, and *Sphagnum* by 28%. Graminoids, herbaceous dicots, and shrubs all increased significantly in abundance: graminoids by 25.5%, herbaceous dicots by 24%, and shrubs by 13% ($p < 0.05$) (Figure 5.V5). The canopy height, as well as the horizontal extent of the canopy, increased over time with the amount of horizontal surface having multiple strata increasing from about 60% to 80% (Mercado-Díaz 2011). The increase of canopy overstory in these plots represents a structural response to the shift in the relative abundance of vascular plants vs. bryophytes. The increase in

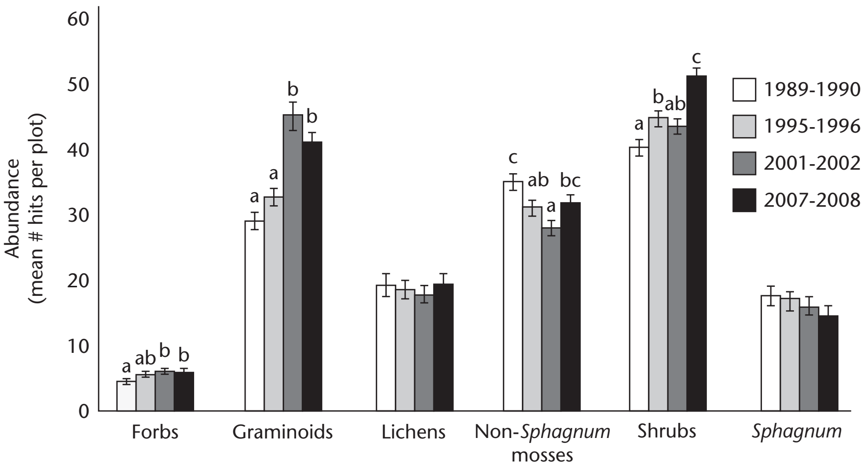

Figure 5.V5. The mean number of total hits per plot of different vegetation growth forms located at the Imnavait Creek and Toolik grids from 1989–1990 to 2007–2008 (letters above the bars indicate significant differences, error bars represent standard errors).

the abundance of vascular vegetation and in canopy height and complexity will likely affect snow redeposition and winter biological processes and will have feedbacks to nutrient allocation and cycling (Sturm et al. 2005).

## Predictions of Future State and Key Uncertainties

As global warming and other climate changes continue, tundra ecosystems will continue to respond through many decades and centuries. Over the long term (a century or more) it is reasonable to expect that tundra ecosystems will look more like the warmer ecosystems farther south, with taller, woodier vegetation including trees, higher overall species richness, higher productivity, higher organic matter accumulations in plants and soils, and higher overall rates of element cycling. Short-term changes (a decade or less) are also relatively predictable—in the short term one would again expect higher productivity and element turnover (unless there is a dramatic decline in precipitation, not currently predicted). Most of the short-term changes in species composition will result from changes in relative abundance within the existing flora and fauna, and rates of species loss will initially exceed gains so species richness may decline slightly. Most of the losses will be among subdominant species. In the vegetation, grass and sedge species will be the most responsive to change in the first 1–5 years, while it will take 5–10 years for others (like shrubs) to fully respond. The overall C balance is more likely to show a net C loss in the short term, as increases in soil respiration accompanied by increased N mineralization and plant N uptake must precede an expected increase in NPP.

Prediction of ecosystem changes between 20 and 100 years in the future is much more difficult than over shorter or longer periods. The longest-running experimental manipulation at Toolik Lake was in its 30th year in 2010 and shows no sign of reaching an endpoint in its long-term responses to fertilizer addition. Because we are generally unable to observe directly the changes in tundra ecosystems at a time scale of 20–100 years, model predictions are not well corroborated at this scale (Rastetter 1996). We can say, though, what we expect the major drivers of ecosystem change to be at this time scale, including:

- Changes in permafrost, soil drainage, and surface energy balance
- N retention and overall balance of N inputs and losses
- Changes in coupling or synchrony between processes like N mineralization and N uptake, or between plant processes and soil microbial processes
- Spatial linkages in C, nutrient, and water cycling among landscape units, especially along hillslopes (see chapter 6)
- Plant species invasions, including especially invasions of trees and shrubs
- Changes in herbivory
- Changes in disturbance regime, especially thermokarst failures and fire

Modeling studies consistently show that long-term changes are constrained by C-N interactions (Rastetter et al. 1997; McKane et al. 1997) as well as by the characteristics of competing plant species (Herbert et al. 1999). Models of the physiology of tundra canopies have also proven very successful and are well corroborated (Williams et al. 2000, 2001). However, it is clear that models lack mechanisms to explain large losses of N (and hence C) from soils in fertilized plots (Mack et al. 2004). This failure of the models is particularly surprising given how well the models predict C and N losses in litter decomposition studies (Moorhead et al. 1999). The missing mechanisms in these models might be associated with the forms of N lost from tundra ecosystems and the availability of these N forms to plants and microbes (Rastetter et al. 2005). Nevertheless, models are vital in scaling the results of plot-scale experiments to regions and the pan-Arctic (Le Dizès et al. 2003; Rastetter et al. 2003). However, as with the intermediate scale in time (20–100 yr), intermediate scales in space present particular problems for model applications and corroboration. Most prominent among these intermediate scale problems are the spatial interactions among ecosystem patches on hillslopes (Rastetter et al. 2004), the understanding of which requires the linkage of ecosystem and hydrological models (see chapter 6, Vignette 6.3).

## Conclusions

Understanding of tundra ecosystems has advanced greatly since the first studies began at Toolik Lake in the mid-1970s, including much research done at other arctic sites and not discussed in this chapter. Before the 1970s, most research on tundra was focused on specific, species-level adaptations to a cold, short growing season, on the distribution of species in relation to fine-scale environmental variation, and on broad regional patterns of distribution and abundance. Interactions among species, feedbacks on ecosystem properties in relation to species composition, soil processes in general, and nutrient limitation of plant growth received relatively little attention because the Arctic was viewed as a "cold-dominated" landscape where survival was primary and extremes of the physical environment limited the importance of both species interactions and biogeochemical limitations (e.g., Billings and Mooney 1968). There were just a few notable early studies that took an ecosystem perspective (e.g., Summerhayes and Elton 1923; Pitelka 1973), leading the way to later work on trophic interactions and whole-system biogeochemistry and feedbacks.

The focus of research on tundra ecosystems began to change rapidly in the early 1970s, in large part due to the International Biological Program's tundra biome study, which produced the first reasonably complete descriptions of tundra biogeochemical cycles (Brown et al. 1980; Bliss et al. 1981); these descriptions indicated that slow inputs and turnover of elements other than C, particularly N and P, were likely important limiting factors in tundra biogeochemistry. This knowledge was a major factor influencing the design and initial hypotheses of the long-term fertilizer, shade, greenhouse, and other experiments at Toolik Lake and other arctic sites (Shaver et al. 1992).

By the end of the 1980s it was clear that the species that live in tundra ecosystems were generally very well adapted to the cold environment and short summers. Although essentially all species and all processes within the tundra ecosystem are responsive to temperature in the short term (within a year), the primary limitation and regulator of long-term response to temperature (years to decades) is the slow input and turnover of elements like N and P, and the long time it takes for temperature change to affect this input and turnover. At the same time it was becoming clear that species interactions in tundra plant communities were much more important in determining community composition than previously believed, and that the species composition of tundra ecosystems has a major impact on biogeochemistry and on vegetation, soil, and even air temperatures. Together, these species effects and the slow change in element cycles make the tundra ecosystem much more resistant and resilient to climate warming than was expected when the research at Toolik Lake began.

Since the 1990s, the importance of physical disturbance in effecting major, long-term change has become particularly clear. Fine-scale disturbances like frost boils, ice-wedge polygon formation, and other periglacial phenomena have long been viewed as important sites of change in tundras (Walker et al. 2008); however, as the Arctic has warmed, the increasing frequency, severity, and area affected by major disturbances like thermokarst and fire has shown that these disturbances are not only where rapid change is possible, but also that extremely rapid change in a relatively small proportion of the tundra landscape can dominate the carbon or energy balance of a large region.

In sum, arctic tundras have been viewed as model systems for ecological research for decades, but the focus of that research has changed greatly since the 1970s. Before the 1970s the tundra was viewed as a useful model system because it was dominated by the physical environment, and because specific adaptations to that environment could be studied in a system where species interactions were relatively unimportant and low temperatures and short growing seasons were the primary limiting factors. After another four decades of research, at Toolik Lake and elsewhere in the Arctic, tundra is still viewed as a model system but one in which the low stature of the vegetation, low species richness, and relatively fine-grained environmental heterogeneity make tundra ecosystems particularly amenable to ecosystem-level experimentation and to studies of individual species effects on ecosystem properties. Overall, this is a major change in how ecologists think about tundra ecosystems, and it opens the way for a rich new era of whole-system experimentation, observation, and understanding.

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