

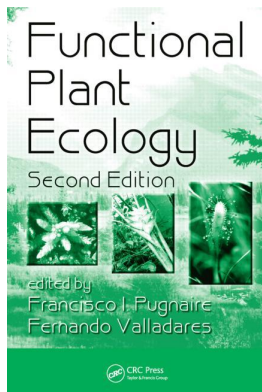
This article was downloaded by: 10.3.97.143

On: 05 Dec 2023

Access details: *subscription number*

Publisher: *CRC Press*

Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: 5 Howick Place, London SW1P 1WG, UK



## **Functiona Plant Ecology**

Francisco I. Pugnaire, Fernando Valladares

## **Arctic Ecology**

Publication details

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch12>

Sarah E. Hobbie

**Published online on: 20 Jun 2007**

**How to cite :-** Sarah E. Hobbie. 20 Jun 2007, *Arctic Ecology from: Functiona Plant Ecology* CRC Press

Accessed on: 05 Dec 2023

<https://www.routledgehandbooks.com/doi/10.1201/9781420007626.ch12>

**PLEASE SCROLL DOWN FOR DOCUMENT**

Full terms and conditions of use: <https://www.routledgehandbooks.com/legal-notices/terms>

This Document PDF may be used for research, teaching and private study purposes. Any substantial or systematic reproductions, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The publisher shall not be liable for an loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

# 12 Arctic Ecology

*Sarah E. Hobbie*

## CONTENTS

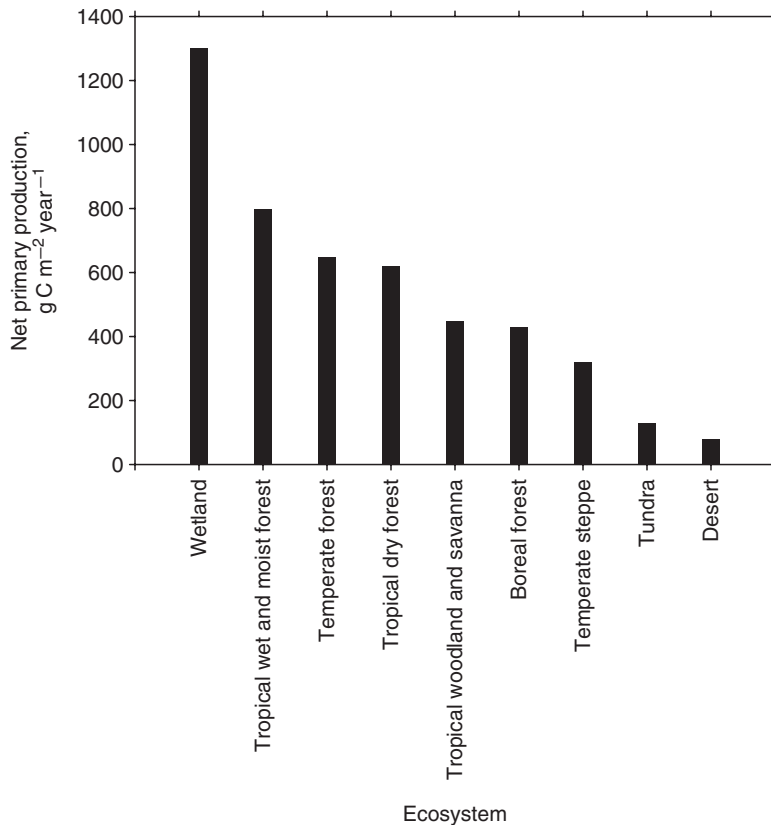
Introduction .....	369
Characteristics of Arctic Plant Populations .....	370
Plant Species Interactions in Arctic Ecosystems .....	371
Ecophysiology of Arctic Plants .....	373
Carbon.....	373
Nutrients.....	373
Growth .....	374
Individual Plant Responses to Environmental Factors.....	375
Ecosystem Responses to Environmental Factors.....	377
Acknowledgments .....	380
References .....	380

## INTRODUCTION

The Arctic encompasses the region of the globe that lies north of the latitudinal tree line. Its environment is extreme in myriad ways, with low mean annual temperatures and precipitation, short growing seasons, and cold soils that are often underlain by permafrost, thawing only incompletely during the growing season. Consistent with the extreme environment, productivity is lower in the Arctic than in most other regions of the world (Figure 12.1).

The Arctic comprises a variety of vegetation types at both small and large scales (Bliss and Matveyeva 1992). The High Arctic, consisting primarily of the islands of the Canadian Arctic Archipelago, is characterized by polar desert and semidesert—large patches of bare, unvegetated ground are interspersed with vegetation dominated by cushion plants, forbs, and dwarf shrubs. In contrast, the Low Arctic has near-continuous cover of tundra vegetation with varying proportions of dwarf shrubs, sedges, mosses, lichens, and forbs. Within both the High Arctic and the Low Arctic, large variation in both species composition and plant productivity occurs at relatively small spatial scales (meters to kilometers) because of variation in topography and parent material, and consequently in drainage, nutrient availability, and snow cover (Walker et al. 1994).

Because of its severe environment, the Arctic has long been of interest to plant physiological ecologists (Billings and Mooney 1968). The Arctic has received much less attention from other areas of plant ecology, particularly population and community ecology, for both practical and theoretical reasons. The long-lived nature of most tundra species and their low rates of sexual reproduction (see later) make study of plant populations and manipulation of plant densities *in situ* difficult. Furthermore, some plant ecologists (Savile 1960, Grime 1977, Callaway et al. 2002) have suggested that competitive interactions are unimportant relative to



**FIGURE 12.1** Net primary production (NPP) in various ecosystems of the world. (Data from Houghton, R.A. and Skole, D.L., *The Earth as Transformed by Human Action*, B.L. Turner, W.C. Clark, R.W. Kates, J.F. Richards, J.T. Matthews, and W.B. Meyer, eds, Cambridge University Press, Cambridge, UK, 1990. With permission.)

abiotic factors in structuring communities in high-stress environments, such as the Arctic, perhaps steering population and community ecologists away from working at high latitudes.

In this chapter, I take a broad view of arctic plant ecology. I touch on the unique characteristics of arctic plant populations and discuss the accumulating evidence regarding the importance of interspecific interactions in structuring arctic ecosystems. I briefly review the physiological ecology of arctic plants, but I refer the reader to numerous previous reviews and books on this topic (Billings and Mooney 1968, Bliss et al. 1981, Chapin and Shaver 1985a, Körner and Larcher 1988, Chapin et al. 1992). The major emphasis of this chapter is on the synthesis of a large amount of recent experimental work in tundra to evaluate the hypotheses that were formulated during these earlier ecophysiological studies.

## CHARACTERISTICS OF ARCTIC PLANT POPULATIONS

Relatively little is known about arctic plant populations, perhaps because of the long-lived nature and the infrequent sexual reproduction of arctic plant species. In the closed communities of the Low Arctic, reproduction from seed is relatively rare (Callaghan and Emanuelsson 1985, McGraw and Fetcher 1992, Gough 2006), and few annual plant species occur (Hultén 1968). Low rates of sexual reproduction may result from low allocation to total reproductive

effort, although allocation to viable seed is not necessarily lower in arctic species than in temperate ones (Chester and Shaver 1982). Low rates of recruitment from seed may also result from the paucity of suitable germination sites in these closed communities and from high mortality of young seedlings (McGraw and Shaver 1982, Callaghan and Emanuelsson 1985, Gough 2006). Recruitment from seed increases after natural and human-caused disturbance, particularly for graminoid species, often from seed stored in the seed bank (Chapin and Chapin 1980, McGraw 1980, Freedman et al. 1982, Gartner et al. 1983, 1986, Grulke and Bliss 1988, Ebersole 1989, McGraw and Vavrek 1989). In the more open vegetation of the High Arctic, recruitment from seed is more common (Callaghan and Emanuelsson 1985) and increases with fertilization (Robinson et al. 1998).

In contrast with sexual reproduction, asexual reproduction is nearly ubiquitous in the Arctic. Many arctic plant species possess rhizomes (belowground stems) or stolons, or produce adventitious roots from aboveground stems that are overgrown by mosses and subsequently become belowground stems. Ramets can ultimately become independent of one another, making the recognition of individual genets in intact tundra difficult. Although demographic analysis at the level of individual genets is therefore problematic, understanding the demography of plant parts within ramets can enlighten studies of the response of arctic plants to environmental perturbations (McGraw and Fetcher 1992). For example, demographic analysis of shoots or tillers can indicate whether changes in production or biomass at the ecosystem level result from changes in branching, shoot growth, or shoot mortality (McGraw 1985a, Chapin and Shaver 1985c, Bret-Harte et al. 2001); alternatively, demographic analyses may indicate when turnover of plant parts has changed with no change in total biomass (Fetcher and Shaver 1983).

## PLANT SPECIES INTERACTIONS IN ARCTIC ECOSYSTEMS

Species interactions have been studied much less in arctic ecosystems than in temperate ecosystems, presumably because of the difficulty of manipulating densities of long-lived, slow-growing, often woody, perennial species that occur only rarely as seedlings (Gough 2006). Despite the lack of experimental evidence, many have hypothesized that direct limitation by stressful abiotic factors (e.g., low temperature) is much more important than are species interactions in structuring plant communities in the Arctic (Savile 1960, Warren Wilson 1966, Billings and Mooney 1968, Grime 1977). Others have suggested that competitive interactions are important because of low nutrient availability and help explain community responses to environmental manipulations (Chapin and Shaver 1985b, Chapin et al. 1995).

Most studies of competitive interactions in the Arctic have found little evidence for strong negative interactions in tundra with a few exceptions (Fetcher 1985, McGraw 1985a, Jonasson 1992, Shevtsova et al. 1995, Hobbie et al. 1999, Bret-Harte et al. 2004, Gough 2006). For example, in subarctic Scandinavia, only one of the three dwarf shrubs (*Vaccinium vitis-idaea*) responded positively to removal of other dwarf shrubs (Shevtsova et al. 1995), and a separate study found no positive effects of dwarf shrub removal on any of a number of species in several different tundra types (Jonasson 1992). In Alaskan tussock tundra, where seven species were removed individually in separate treatments and numerous species responses measured, only two pairs of species exhibited negative interactions (Hobbie et al. 1999). In a separate study, various combinations of shrub and moss removals had little effect on abundance of remaining species or growth forms (Bret-Harte et al. 2004). Similarly, *Dryas octopetala* showed no response to removal of all neighbors after 3 years in Alaskan tundra (McGraw 1985a).

A few studies have demonstrated negative interactions among species in the Arctic. *Eriophorum vaginatum* responded to dwarf shrub removal with increased tillering (Fetcher 1985).

Another study that manipulated ramets by outplanting, rather than removal, demonstrated competitive interactions between two species of *Eriophorum* in Alaska (McGraw and Chapin 1989). In the High Arctic, moss removal increased growth of forbs (Sohlberg and Bliss 1986), and shoot biomass of two species, *Luzula confusa* and *Salix polaris*, was reduced in the presence of heterospecific neighbors (Dormann et al. 2004). None of the studies demonstrating negative interactions between tundra species distinguished competitive interactions from other kinds of negative interactions such as allelopathy or effects of species on abiotic conditions such as soil temperature.

Species removal studies have found as much evidence for positive interactions among plant species in arctic ecosystems as for negative interactions. Several dwarf shrub species responded negatively to removal of other dwarf shrubs in Sweden and Finland (Jonasson 1992, Shevtsova et al. 1995). Mosses in tussock tundra and in boreal Canada also responded negatively to shrub removal, which was attributed to photoinhibition of photosynthesis under high light intensities (Murray et al. 1993) and increased evaporative stress (Busby et al. 1978) when the shrub canopies were removed. Thus, facilitation may be important in determining performance of some species in the Arctic, particularly at high elevations where temperatures are coldest and abiotic stresses like wind scouring most severe (Callaway et al. 2002), and could explain the clustering of plant species in some tundra environments (Callaghan and Emanuelsson 1985, Carlsson and Callaghan 1991).

The lack of evidence for strong competitive or other kinds of negative interactions in tundra supports Grime's (1977) contention that in high-stress environments plants are directly limited by abiotic factors, and that competitive interactions are relatively unimportant. However, several other explanations exist for the general failure to demonstrate strong competitive interactions in the Arctic. Arctic species respond individualistically to manipulations of various environmental factors (Chapin and Shaver 1985b), suggesting that growth of co-occurring species may be limited by different factors (see later). In addition, arctic plants may minimize competition for nitrogen (N) by partitioning their use of the N pool (e.g., into inorganic and organic N, see later) (McKane et al. 2002). Arctic plant species may also partition their uptake of nutrients in time and space. The timing of root initiation in the spring differs among species and among growth forms (Shaver and Billings 1977, Kummerow et al. 1983). In particular, evergreens begin root growth earlier in the spring than do deciduous species that initiate roots only after leaf expansion has begun. Such interspecific differences in the timing of root growth could have important consequences for nutrient acquisition in arctic ecosystems that are often characterized by a pulse of nutrient mineralization in the spring (Kielland 1990, Nadelhoffer et al. 1992). Different species also show characteristic rooting depths (Shaver and Billings 1975), perhaps partitioning their use of nutrients in space. Consistent with these observations, a study in Alaskan tussock tundra that added labeled forms of N to the soil at different depths and in different seasons found that most species showed greater N uptake earlier than later in the growing season, and some species showed greater uptake from shallow than from deep soil depths (McKane et al. 2002).

Even if it does occur, competition may be difficult to demonstrate in arctic tundra where annual uptake of nutrients is a relatively small proportion of the annual nutrient requirement of a species and plants grow relatively slowly. Removing a single species may have only a minor effect on nutrient availability for the remaining species over the timescale of most experiments. Indeed, in one study that measured inorganic nutrient availability in removal treatments, removal demonstrably increased soil N availability only in treatments in which several codominant species were removed simultaneously (Bret-Harte et al. 2004). Studying competitive interactions by increasing plant densities (e.g., by outplanting or seed-sowing) may be a more effective way of demonstrating the importance of competitive interactions than removals; however, such manipulations are problematic with arctic species, since they

are generally slow growing, perennial, and ramets may suffer high mortality from transplant shock (Gough 2006). The true reason for the lack of strong competitive interactions in tundra deserves more exploration.

## ECOPHYSIOLOGY OF ARCTIC PLANTS

Ecophysiological research on arctic plants generally indicates that resource acquisition is not directly limited by cold temperatures. This observation has led to the hypothesis that growth and productivity in arctic ecosystems are limited more by the indirect effects of cold temperatures (i.e., short growing season length and low nutrient availability) than by their direct effects (Chapin 1983). After reviewing the observations that led to these generalizations, I evaluate how well recent experimental evidence supports these generalizations.

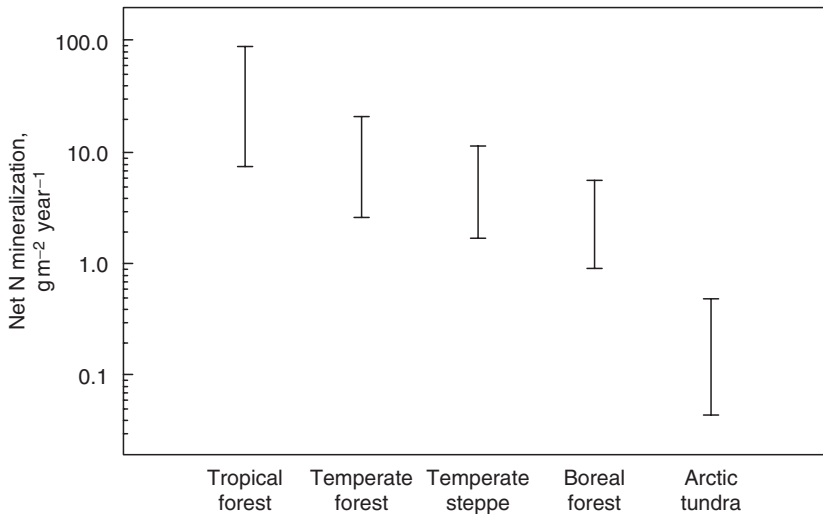
### CARBON

In terms of carbon gain, arctic plants may be limited more by the length of the growing season than by low irradiance or low photosynthetic rates due to cold temperatures per se. Although average irradiance during daytime hours is less in the Arctic than those at lower latitudes, the average daily irradiance is comparable, because of the 24 h photoperiod of the northern summer (Chapin and Shaver 1985a). However, many of the long days occur early in the growing season when the ground is still snow-covered or the soil is still frozen. Thus growing season length, rather than light intensity per se, may limit plant growth. Evergreen vascular and nonvascular plants effectively extend the growing season by photosynthesizing under the spring snow pack when days are long, taking advantage of elevated CO<sub>2</sub> concentrations, sufficient light, and near-freezing air temperatures under snow (Kappen 1993, Starr and Oberbauer 2003).

The photosynthetic temperature optima and carbohydrate status of tundra plants provide additional indirect evidence that arctic species are not carbon-limited during the growing season. Although photosynthetic temperature optima are often above ambient air temperatures (Tieszen 1973, Oechel 1976), many tundra species have relatively broad photosynthetic temperature optima, allowing them to achieve near-maximum rates at fairly low temperatures (Tieszen 1973, Johnson and Tieszen 1976, Limbach et al. 1982, Semikhatova et al. 1992). Relatively large pools of total nonstructural carbohydrate in arctic plants also suggest that they are able to acquire carbon in excess of their growth requirements (Chapin and Shaver 1985a). Interestingly, photosynthesis in arctic plants may be more sensitive to soil than to air temperature. For two arctic sedges, photosynthesis and stomatal conductance increased greatly with soil warming between 0°C and 10°C (Starr et al. 2004), suggesting that carbon gain could be sensitive to future soil warming, particularly warming associated with loss of permafrost.

### NUTRIENTS

Nutrient uptake in tundra plants is also relatively insensitive to the direct effects of low temperature. Rather, cold temperatures limit nutrient uptake indirectly, by causing low rates of nutrient supply. For example, cold temperatures reduce nutrient inputs from N<sub>2</sub> fixation (Chapin and Bledsoe 1992) and weathering and recycling of nutrients during decomposition (Figure 12.2) (Nadelhoffer et al. 1992). Although temperatures in arctic soils are colder than optimum temperatures for nutrient uptake (Chapin and Bloom 1976), tundra species have a higher potential for nutrient uptake at low temperatures than do warm-adapted species (Chapin 1974).



**FIGURE 12.2** Net nitrogen mineralization rates measured in various ecosystems of the world. (Reprinted from Nadelhoffer, K.J., Giblin, A.E., Shaver, G.R., and Linkins, A.E., *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*, F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds, Academic Press, San Diego, CA, 1992. With permission.)

Tundra species use acquired nutrients efficiently, relying heavily on stored nutrients to support growth and retranslocating much of the nutrients from senescing tissues. Stored nutrients supply the majority of the nutrients to current growth (Berendse and Jonasson 1992) and may allow arctic plants to grow during times when soil nutrients are frozen and unavailable (Shaver and Kummerow 1992). Many arctic plant species retranslocate a relatively high percentage of nutrients from senescing tissues, although their retranslocation efficiencies are not consistently higher than those of temperate species (Chapin and Shaver 1989, Jonasson 1989, Berendse and Jonasson 1992).

One potential way that arctic plants effectively increase the pool of nutrients available for uptake is by using organic N directly, rather than by relying on soil microbes to mineralize N from organic compounds. As in other ecosystems, there is growing evidence that arctic plants may short-circuit the N cycle in this way (Lipson and Nasholm 2001). Such use of organic N would help explain the large discrepancy between annual N uptake and annual net N mineralization rates in the Arctic (Giblin et al. 1991, Kielland 1994). Concentrations and turnover of free amino acids are relatively high in tundra soils (Kielland 1995, Weintraub and Schimel 2005). Both mycorrhizal and nonmycorrhizal species from tussock tundra take up and grow on amino acids in solution culture (Chapin et al. 1993, Kielland 1994) and in situ (Schimel and Chapin 1996, McKane et al. 2002, Nordin et al. 2004). Furthermore, both ericoid and ectomycorrhizal species have proteolytic capabilities and can transfer organic N from soil to the host plant (Read 1991) and many of the common arctic species have these types of mycorrhizal associations. Estimates of N acquisition via ericoid and ectomycorrhizal species range between 61% and 86% of plant N, much of which is likely accessed in organic form (Hobbie and Hobbie 2006).

## GROWTH

Whether cold temperatures directly limit growth of arctic plants is unclear. The relative growth rates of arctic plants are similar to those of temperate species, suggesting that length of the growing season, rather than cold temperatures during the growing season itself, limits

biomass accumulation in the Arctic (Chapin and Shaver 1985b, Semikhatova et al. 1992). On the other hand, ambient temperatures are often suboptimal for growth (Kummerow and Ellis 1984, Körner and Larcher 1988) and manipulations of temperature in situ sometimes increase plant growth (see later). Thus, growth of some species may be directly limited by cold temperature.

## INDIVIDUAL PLANT RESPONSES TO ENVIRONMENTAL FACTORS

During the past decade, numerous studies in various arctic habitats have examined the response of plant growth, biomass, reproduction, phenology, and production to manipulations of environmental factors. These experiments allow us to evaluate the generalizations and hypotheses proposed earlier. Three general patterns emerge from studies that examined individual plant responses (primarily growth) to environmental manipulations. First, of the various factors manipulated (including nutrients, temperature, water, light, and CO<sub>2</sub>), plant growth most often responds to increased nutrient availability. Second, in almost all studies demonstrating a positive response of species growth to nutrient addition, there are exceptions—species that either do not respond or respond negatively to nutrient addition. Third, manipulation of environmental factors besides nutrients has less predictable results. Later, I explore each of these points in detail. For simplicity, I have subsumed a number of different kinds of measurements (e.g., current year's shoot length, branching, tillering) under the word *growth*. I have also included changes in total biomass in growth although many studies did not determine whether change in biomass resulted from changes in individual shoot growth or from changes in shoot demography (branching or mortality).

Fertilization studies in both the Low Arctic and the High Arctic in North America and in Europe have demonstrated generally positive biomass responses of deciduous shrubs and graminoids (grasses and sedges) and negative responses of lichens and mosses (Dormann and Woodin 2002, van Wijk et al. 2003a). In subarctic Sweden, addition of N, phosphorus (P), and potassium (K) increased the growth or biomass of numerous species in heath tundra (Havström et al. 1993, Parsons et al. 1994, 1995, Michelsen et al. 1996, Press et al. 1998), in a fellfield (a relatively open, rocky community, Michelsen et al. 1996), and in graminoid and shrub tundra (Jonasson 1992). Fertilization increased growth and biomass of many species in upland tussock tundra, wet meadow (sedge-dominated) tundra, and heath tundra in Alaska (McKendrick et al. 1978, 1980, Shaver and Chapin 1980, 1986, 1995, Chapin and Shaver 1985b, 1996, Shaver et al. 1986, 1996, 1998, Gough et al. 2002, Hobbie et al. 2005). Although most studies added N, P, and K simultaneously, when nutrients were added separately, this response was usually to N rather than P in upland tundra (Shaver and Chapin 1980, Gebauer et al. 1995, but see McKendrick et al. 1980). Some studies showed little response to N or P alone, but large responses to their combined addition (Gough et al. 2002, Gough and Hobbie 2003). Wet meadow tundra, on the other hand, is more often P-limited (Shaver and Chapin 1995, Shaver et al. 1998). In the High Arctic, fertilization also increased growth, biomass, reproduction, and seedling establishment of some species (Henry et al. 1986, Wookey et al. 1994, 1995, Robinson et al. 1998).

Despite numerous examples of positive growth or biomass responses to nutrient addition in a variety of tundra ecosystems, many studies demonstrated exceptions—species that did not respond or responded negatively to nutrient addition (Shaver and Chapin 1980, 1986, Chapin and Shaver 1985b, 1996, Havström et al. 1993, Shaver et al. 1996, 1998, Press et al. 1998, Robinson et al. 1998, Cornelissen et al. 2001, Graglia et al. 2001). The unresponsive species often differed among studies, and intercomparison is further complicated because fertilization experiments varied in duration, in amount or types of fertilizer applied, in the timing of fertilization relative to plant phenology of nutrient uptake, and in the species whose responses were measured. Several possible reasons for these lack of responses to



fertilization exist. Some species in tundra may be limited by factors other than low nutrient availability (see later) (Chapin and Shaver 1985b). Species may not be able to respond to additional nutrients in the presence of superior competitors, and understory species may be vulnerable to increased shading by overstory species whose biomass increases with nutrient addition (Chapin and Shaver 1985b, 1996, McGraw 1985b). Indeed, in a study that combined species removals and fertilization, some species responded more to nutrient addition when neighbors were removed (Bret-Harte et al. 2004). Thus, while many species may respond positively to fertilization in the short term, long-term fertilization often reduces species richness and leads to dominance by one or a few species, such as *Betula nana* in Alaskan tussock tundra (Shaver et al. 2001).

Nonvascular species (bryophytes and lichens) often showed negative responses to fertilization, particularly in Low Arctic studies (Cornelissen et al. 2001, van Wijk et al. 2003a, see Robinson et al. 1998 for contrasting results in the High Arctic). These species may be moisture-rather than nutrient-limited (Murray et al. 1989a,b, Tenhunen et al. 1992), perhaps explaining their lack of (or negative) response to nutrient addition (Jonasson 1992, Chapin et al. 1995). They may also be negatively affected by greater shading and litter accumulation in fertilized plots (Cornelissen et al. 2001, van Wijk et al. 2003a).

After nutrients, increased temperature is the environmental factor that most often increases growth or biomass in the Arctic. Warming increased growth of about half of the dominant species in tussock tundra (Chapin and Shaver 1985b, 1996, Shaver et al. 1986). Warming also increased growth of some species in Swedish subarctic tundra (Havström et al. 1993, Parsons et al. 1994, 1995, Michelsen et al. 1996) and resulted in greater growth and reproduction and earlier phenology in the High Arctic (Havström et al. 1993, Welker et al. 1993, Wookey et al. 1995). Meta-analyses of warming experiments throughout the Arctic suggest that shrubs and graminoids in particular grow more and exhibit earlier phenology with experimental warming (Arft et al. 1999, Dormann and Woodin 2002, Walker et al. 2006). In Alaska, increased shrub biomass in response to experimental warming is consistent with greater shrub biomass during past warming events in the Holocene (Brubaker et al. 1995, Hu et al. 2002) and in the past century as inferred from repeat aerial photography (Sturm et al. 2001, Hinzman et al. 2005). Changes in shrub biomass with warming have regional-scale implications for climate, as decreased albedo associated with greater shrub biomass could significantly amplify future high-latitude warming (Chapin et al. 2005).

Besides their sensitivity to growing season temperature, arctic plant species also respond to increased growing season length. For example, species exhibit earlier growth and earlier senescence, and leaf area index is higher throughout the growing season when the snow-free period begins earlier and ends later in the season (Oberbauer et al. 1998, Starr et al. 2000).

Far fewer manipulations of light, water, and CO<sub>2</sub> have been done in the Arctic than those of nutrients or temperature. Shade decreased growth and biomass particularly of overstory species in both the Low Arctic (Chapin and Shaver 1985b, 1996) and the High Arctic (Havström et al. 1993). Water is rarely limiting in tundra (Oberbauer and Dawson 1992, Gold and Bliss 1995) and water addition had few effects on growth or biomass in subarctic Sweden (Parsons et al. 1994) or in the High Arctic (Henry et al. 1986, Wookey et al. 1994, 1995, Dormann and Woodin 2002). Addition of flowing water to a tussock tundra slope increased the growth of some species (Murray et al. 1989b, Oberbauer et al. 1989), but this might have been a result of greater flow of nutrients, rather than a direct water effect (Chapin et al. 1988). In studies in arctic and subarctic tundra, respectively, elevated CO<sub>2</sub> did not alter photosynthetic rate or growth of individual tillers of *E. vaginatum* in Alaskan tussock tundra (Tissue and Oechel 1987) and had little or negative effects on dwarf shrub growth in subarctic Sweden (Gwynn-Jones et al. 1997).

The response of biomass or production at the shoot or whole-plant level to environmental manipulations is not readily predicted from the physiological response of leaves or roots. For example, photosynthetic responses to treatments generally do not translate directly into growth responses (Bigger and Oechel 1982, Wookey et al. 1994, Gebauer et al. 1995, Chapin and Shaver 1996). Similarly, the response of phenology and nutrient uptake provides little indication of how species respond at the community level (Chapin and Shaver 1996).

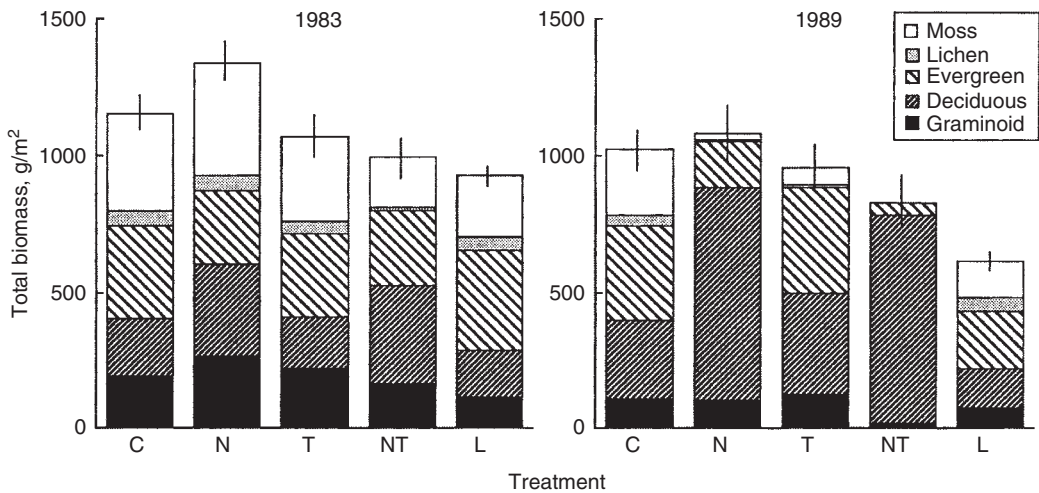
In summary, at the individual level, arctic plants are most often nutrient-limited; however, some species in some regions may be limited by other environmental factors such as low temperature. Some studies have suggested that the indirect effects of temperature (i.e., low nutrient availability) are more likely to limit growth at the southern extent of species' ranges in the Arctic, whereas cold temperatures directly limit growth at the northern extent of species' ranges (Havström et al. 1993). Although this idea is compelling, too few species have been studied experimentally over a range of latitudes to determine whether this pattern is general.

## ECOSYSTEM RESPONSES TO ENVIRONMENTAL FACTORS

Although individual plants respond to both nutrients and temperature, net primary production (NPP) and total plant biomass respond more consistently to nutrient addition alone than to manipulation of other environmental factors. However, fewer studies have measured total production and biomass than individual plant growth or biomass, and even measurements of total production have mostly excluded root production. Vascular aboveground net primary production (ANPP) and total biomass increased with nutrient addition in Low Arctic moist tundra (Chapin and Shaver 1985b, Shaver and Chapin 1986, Chapin et al. 1995, Hobbie et al. 2005), wet tundra (Shaver et al. 1998), and heath tundra (ANPP only) (Gough et al. 2002), subarctic heath, graminoid, and shrub tundra (Jonasson 1992, Press et al. 1998), and High Arctic sites on Ellesmere Island and Svalbard (Henry et al. 1986, Robinson et al. 1998). Fine root production also increased, although not significantly, in wet and moist arctic tundra (Nadelhoffer et al. 2002) and root biomass increased in a moist nonacidic tundra (van Wijk et al. 2003b) with fertilization. However, where mosses are a significant component of the community, decreased moss biomass largely offset increased vascular plant biomass, resulting in little change in total plant biomass after long-term fertilization (Chapin et al. 1995, Press et al. 1998, Hobbie et al. 2005).

Although vascular plant biomass generally increases with long-term fertilization, one study demonstrated a decline in total ecosystem carbon storage because nutrient addition increased losses from soil carbon pools (Mack et al. 2004). The exact mechanism responsible for depleted soil carbon pools is unknown. However, greater soil organic matter or litter decomposition with added nutrients and a shifts in species composition to more shallow-rooted species—whose roots decompose more quickly than deeply rooted species because of warmer soil temperatures near the soil surface—could have contributed to this. In contrast with nutrients, elevated CO<sub>2</sub> has little effect on net ecosystem production in tundra because of downregulation (Grulke et al. 1990, Oechel et al. 1994).

Experimental warming led to a significant but much smaller increase in ANPP than did nutrients in Alaskan tussock tundra, although this increase was attributed to the indirect effects of temperature on ANPP acting through increased soil nutrient availability (Figure 12.3) (Chapin et al. 1995). By contrast, increased temperature had little effect on total plant biomass and production in Alaskan wet sedge (Shaver et al. 1998) and moist nonacidic (Gough and Hobbie 2003) tundras, and no effect on total biomass in a subarctic heath tundra in Sweden (Press et al. 1998). Most studies that increase air temperature also increase soil temperature as well, making it difficult to attribute changes in ANPP to the direct or indirect effects of warmer temperatures. However, one study in Alaskan tussock



**FIGURE 12.3** Total aboveground net primary production (NPP) by growth form of tussock tundra in response to environmental manipulations near Toolik Lake, Alaska, measured 3 (1983) and 9 (1989) years after initiation of treatments. Treatments are control (C), nutrient addition (N), warming (T), nutrient addition-warming (NT), and light attenuation (L). (From Chapin III, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., and Laundre, J.A., *Ecology*, 76, 694, 1995. With permission.)

tundra that manipulated air temperature alone found no response of ANPP (Hobbie and Chapin 1998).

One potential indirect consequence of warming, extended growing season, also seems to increase NPP. Experimental extension of the growing season via snow removal and exclusion increased leaf area index throughout the growing season (Oberbauer et al. 1998). Consistent with this, earlier snowmelt and longer growing season length at high latitudes correspond with greater plant growth at high latitudes, as inferred from satellite data (Myneni et al. 1997, Zhou et al. 2001).

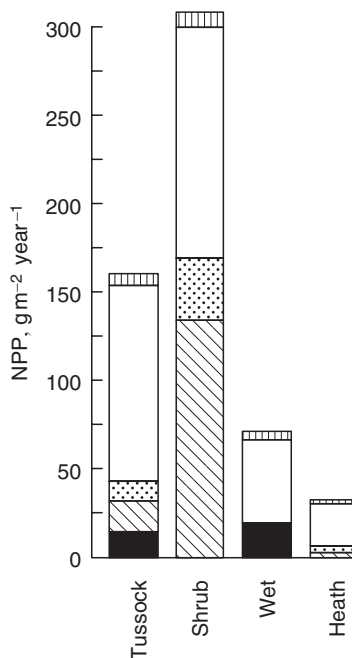
Some evidence suggests that responses to warming are greatest where soil resources are not limiting. Meta-analyses of warming responses across a number of sites suggest that tundra responds more to warming in the Low Arctic than the High Arctic where nutrient availability is presumably higher. Tundra also responds more to warming where soil moisture is optimum (i.e., in mesic sites more than in dry or very wet sites) (Walker et al. 2006). Interestingly, however, experimental studies have not shown significant positive interactions between warming and nutrient addition for NPP (Chapin et al. 1995, Gough and Hobbie 2003), although artifacts associated with plastic greenhouses (shading, greater herbivory) may explain this lack of positive interaction (McKane et al. 1997, Gough and Hobbie 2003).

A significant issue that has motivated much of the earlier research in recent decades is whether high-latitude ecosystems respond to warming in ways that exacerbate (positive feedback) or ameliorate (negative feedback) rising atmospheric CO<sub>2</sub> and warming. Because of the large stocks of carbon stored in tundra and boreal ecosystems, these ecosystems have received a great deal of attention as potential sources of CO<sub>2</sub> to the atmosphere as climate warms and decomposition rates increase (Post 1990). However, empirical and modeling studies suggest that climate warming could ultimately increase carbon sequestration. Recent climate warming in Alaska stimulated greater carbon efflux from tundra initially, but the stimulation diminished over time (Oechel et al. 1993, 2000). Biogeochemical models of tundra suggest that long-term warming combined with elevated CO<sub>2</sub> increases NPP and soil organic matter decomposition, but that increased carbon uptake more than offsets greater

carbon losses from decomposition, resulting in greater net ecosystem production and carbon sequestration, primarily because warming stimulates decomposition of soil organic matter and increases N availability, leading to a net transfer of N from soils to vegetation, with their higher C:N ratio (McKane et al. 1997, Rastetter et al. 1997, Le Dizes et al. 2003). In addition, in some tundra ecosystems, greater nutrient availability leads to increased woody production as shrubs become more abundant (Shaver et al. 2001) and wood has a relatively high C:N ratio. That, combined with elevated CO<sub>2</sub>, results in higher vegetation C:N ratios overall, also contributing to greater ecosystem carbon sequestration.

In summary, experimental evidence supports the contention that NPP in the Arctic is limited primarily by the indirect effects of low temperature, namely low soil nutrient availability resulting from slow decomposition in cold soils and short growing season length. In contrast, tundra shows little capacity to respond to changes in aboveground conditions or resources (i.e., warmer air temperature or elevated CO<sub>2</sub>) without an accompanying increase in nutrient availability. Although NPP is decreased by light attenuation, it is unknown, but unlikely, that increased light availability would stimulate NPP.

These conclusions based on experimental evidence are generally consistent with patterns of NPP across Arctic landscapes. Primary production can vary up to 10-fold among different vegetation types within relatively small distances in the Arctic (Figure 12.4) (Shaver and Chapin 1991). Gently sloping mesic areas of tussock tundra have intermediate levels of production (Shaver and Chapin 1991, Shaver et al. 1996), although even within mesic tundra, NPP can vary significantly (Hobbie et al. 2005). In contrast, the lowest productivity is found on well-drained ridge-tops supporting heath tundra and poorly drained low areas



**FIGURE 12.4** Total net primary production (NPP, excluding roots) of the vascular plants in each of four tundra vegetation types near Toolik Lake, Alaska. Total NPP is indicated by the height of the bar. Within each bar, inflorescence production is indicated by vertical stripes, leaf production by open, apical stem growth (current year's twigs) by dots, secondary stem growth by diagonal stripes, and belowground rhizome growth by solid. (From Shaver, G.R. and Chapin III, F.S., *Ecol. Monogr.*, 61, 1, 1991. With permission.)

supporting wet meadow tundra (Shaver and Chapin 1991). The highest productivity is found in areas of flowing water (riparian areas and water tracks) that support more productive graminoid or shrub tundra (Chapin et al. 1988, Hastings et al. 1989, Shaver and Chapin 1991).

The variation in productivity across arctic landscapes is proximately related to variation in nutrient availability. For example, the highest production is found on deeply thawed soils that offer protection from wind, in sites dominated by N fixers (Shaver et al. 1996), in sites influenced by animals that disturb the soil and import nutrients, increasing nutrient availability (McKendrick et al. 1980), and in sites influenced by flowing water, which increases bulk flow of nutrients and stimulates net N mineralization (Chapin et al. 1988). Additionally, edaphic factors, such as parent material, can influence nutrient availability and NPP. For example, Alaskan moist acidic tundra has 10-fold greater net N mineralization rates and is twice as productive as moist nonacidic tundra (Hobbie and Gough 2002, Hobbie et al. 2005). In general, vegetation types with the greatest productivity are associated with soils that have relatively high rates of net N mineralization (Chapin et al. 1988, Kielland 1990, Giblin et al. 1991, Hobbie and Gough 2002).

## ACKNOWLEDGMENTS

Sydonia Bret-Harte, Laura Gough, and Dave Hooper provided helpful comments on an earlier version of this chapter.

## REFERENCES

- Arft, A.M., M.D. Walker, J. Gurevitch, J.M. Alatalo, M.S. Bret-Harte, M. Dale, M. Diemer, F. Gugerli, G.H.R. Henry, M.H. Jones, R.D. Hollister, I.S. Jonsdottir, K. Laine, E. Levesque, G.M. Marion, U. Molau, P. Molgaard, U. Nordenhall, V. Raszhivin, C.H. Robinson, G. Starr, A. Stenstrom, M. Stenstrom, O. Totland, P.L. Turner, L.J. Walker, P.J. Webber, J.M. Welker, and P.A. Wookey, 1999. Responses of tundra plants to experimental warming: Meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69: 491–511.
- Berendse, F. and S. Jonasson, 1992. Nutrient use and nutrient cycling in northern ecosystems. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate*. Academic Press, San Diego, CA, pp. 337–356.
- Bigger, C.M. and W.C. Oechel, 1982. Nutrient effect on maximum photosynthesis in arctic plants. *Holarctic Ecology* 5: 158–163.
- Billings, W.D. and H.A. Mooney, 1968. The ecology of arctic and alpine plants. *Biological Review* 43: 481–529.
- Bliss, L.C. and N.V. Matveyeva, 1992. Circumpolar arctic vegetation. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 59–89.
- Bliss, L.C., O.W. Heal, and J.J. Moore, ed, 1981. *Tundra Ecosystems: A Comparative Analysis*. Cambridge University Press, Cambridge, UK.
- Bret-Harte, M.S., G.R. Shaver, J.P. Zoerner, J.F. Johnstone, J.L. Wagner, A.S. Chavez, R.F. Gunkelman IV, S.C. Lippert, and J.A. Laundre, 2001. Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* 82: 18–32.
- Bret-Harte, M.S., E.A. Garcia, V.M. Sacre, J.R. Whorley, J.L. Wagner, S.C. Lippert, and F.S. Chapin III, 2004. Plant and soil responses to neighbor removal and fertilisation in Alaskan tussock tundra. *Journal of Ecology* 92: 635–647.
- Brubaker, L.B., P.M. Anderson, and F.S. Hu, 1995. Arctic tundra biodiversity: A temporal perspective from late Quaternary pollen records. In: F.S. Chapin III and C. Körner, eds. *Arctic and Alpine Biodiversity: Patterns, Causes and Ecosystem Consequences*. Springer-Verlag, Berlin, pp. 111–125.

- Busby, J.R., L.C. Bliss, and C.D. Hamilton, 1978. Microclimate control of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. Ecological Monographs 48: 95–110.
- Callaghan, T.V. and U. Emanuelsson, 1985. Population structure and processes of tundra plants and vegetation. In: J. White, ed. The Population Structure of Vegetation. Junk, Dordrecht, pp. 399–439.
- Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J. Lortie, R. Michalet, L. Paolini, F.I. Pugnaire, B.J. Cook, E.T. Aschehong, C.Y. Armas, and B. Newingham, 2002. Positive interactions among alpine plants increase with stress: a global experiment. Nature 417: 844–848.
- Carlsson, B.A. and T.V. Callaghan, 1991. Positive plant interactions in tundra vegetation and the importance of shelter. Journal of Ecology 79: 973–983.
- Chapin, F.S., III, 1974. Morphological and physiological mechanisms of temperature compensation in phosphate absorption along a latitudinal gradient. Ecology 55: 1180–1198.
- Chapin, F.S., III, 1983. Direct and indirect effects of temperature on arctic plants. Polar Biology 2: 47–52.
- Chapin, F.S., III and A. Bloom, 1976. Phosphate absorption: adaptation of tundra graminoids to low temperature, low-phosphorus environment. Oikos 26: 111–121.
- Chapin, D.M. and C.S. Bledsoe, 1992. Nitrogen fixation in arctic plant communities. In F.S. Chapin, III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. Academic Press, San Diego, CA, pp. 301–320.
- Chapin, F.S., III and M.C. Chapin, 1980. Revegetation of an arctic disturbed site by native tundra species. Journal of Applied Ecology 17: 449–456.
- Chapin, F.S., III and G.R. Shaver, 1985a. Arctic. In: B.F. Chabot and H.A. Mooney, eds. Physiological Ecology of North America. Chapman and Hall, New York, pp. 16–40.
- Chapin, F.S., III and G.R. Shaver, 1985b. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66: 564–576.
- Chapin, F.S., III and G.R. Shaver, 1985c. Individualistic growth response of tundra plants to environmental manipulations in the field. Ecology 66: 564–576.
- Chapin, F.S., III and G.R. Shaver, 1989. Differences in growth and nutrient use among arctic plant growth forms. Functional Ecology 3: 73–80.
- Chapin, F.S., III and G.R. Shaver, 1996. Physiological and growth responses of arctic plants to a field experiment simulating climatic change. Ecology 77: 822–840.
- Chapin, F.S., III, N. Fetcher, K. Kielland, K.R. Everett, and A.E. Linkins, 1988. Productivity and nutrient cycling of Alaskan tundra: Enhancement by flowing soil water. Ecology 69: 693–702.
- Chapin, F.S., III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds, 1992. Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective. Academic Press, San Diego, CA.
- Chapin, F.S., III, L. Moilanen, and K. Kielland, 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. Nature 361: 150–153.
- Chapin, F.S., III, G.R. Shaver, A.E. Giblin, K.J. Nadelhoffer, and J.A. Laundre, 1995. Responses of arctic tundra to experimental and observed changes in climate. Ecology 76: 694–711.
- Chapin, F.S., III, M. Sturm, M.C. Serreze, J.P. McFadden, J.R. Key, A.H. Lloyd, A.D. McGuire, T.S. Rupp, A.H. Lynch, D.S. Schimel, J. Beringer, W.L. Chapman, H.E. Epstein, E.S. Euskirchen, L.D. Hinzman, G.J. Jia, C.-L. Ping, K.D. Tape, C.D.C. Thompson, D.A. Walker, and J.M. Welker, 2005. Role of land-surface changes in arctic summer warming. Science 310: 657–660.
- Chester, A.L. and G.R. Shaver, 1982. Reproductive effort in cottongrass tussock tundra. Holarctic Ecology 5: 200–206.
- Cornelissen, J.H.C., T.V. Callaghan, J.M. Alatalo, A. Michelsen, E. Graglia, A.E. Hartley, D.S. Hik, S.E. Hobbie, M.C. Press, C.H. Robinson, G.H.R. Henry, G.R. Shaver, G.K. Phoenix, D. Gwynn Jones, S. Jonasson, F.S. Chapin III, U. Molau, C. Neill, J.A. Lee, J.M. Melillo, B. Sveinbjornsson, and R. Aerts, 2001. Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? Journal of Ecology 89: 984–994.

- Dormann, C.F. and S.J. Woodin, 2002. Climate change in the arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* 16: 4–17.
- Dormann, C.F., R. Van Der Wal, and S.J. Woodin, 2004. Neighbor identity modifies effects of elevated temperature on plant performance in the High Arctic. *Global Change Biology* 10: 1587–1598.
- Ebersole, J.J., 1989. Role of seed bank in providing colonizers on a tundra disturbance in Alaska. *Canadian Journal of Botany* 67: 466–471.
- Fetcher, N., 1985. Effects of removal of neighboring species on growth, nutrients, and microclimate of *Eriophorum vaginatum*. *Arctic and Alpine Research* 17: 7–17.
- Fetcher, N. and G.R. Shaver, 1983. Life histories of tillers of *Eriophorum vaginatum* in relation to tundra disturbance. *Journal of Ecology* 71: 131–147.
- Freedman, B., N. Hill, J. Svoboda, and G. Henry, 1982. Seed banks and seedling occurrence in a high arctic oasis at Alexandra Fjord, Ellesmere Island, Canada. *Canadian Journal of Botany* 60: 2112–2118.
- Gartner, B.L., F.S. Chapin III, and G.R. Shaver, 1983. Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. *Journal of Applied Ecology* 20: 965–980.
- Gartner, B.L., F.S. Chapin III, and G.R. Shaver, 1986. Reproduction of *Eriophorum vaginatum* by seed in Alaskan tussock tundra. *Journal of Ecology* 74: 1–18.
- Gebauer, R.L.E., J.F. Reynolds, and J.D. Tenhunen, 1995. Growth and allocation of the arctic sedges *Eriophorum angustifolium* and *E. vaginatum*: effects of variable soil oxygen and nutrient availability. *Oecologia* 104: 330–339.
- Giblin, A.E., K.J. Nadelhoffer, G.R. Shaver, J.A. Laundre, and A.J. McKerrow, 1991. Biogeochemical diversity along a riverside toposequence in arctic Alaska. *Ecological Monographs* 61: 415–435.
- Gold, W.G. and L.C. Bliss, 1995. Water limitations and plant community development in a polar desert. *Ecology* 76: 1558–1568.
- Gough, L., 2006. Neighbor effects on germination, survival, and growth in two arctic tundra plant communities. *Ecography* 29: 44–56.
- Gough, L. and S.E. Hobbie, 2003. Responses of moist non-acidic arctic tundra to altered environment: Productivity, biomass and species richness. *Oikos* 103: 204–216.
- Gough, L., P.A. Wookey, and G.R. Shaver, 2002. Dry heath arctic tundra responses to long-term nutrient and light manipulations. *Arctic, Antarctic and Alpine Research* 34: 211–218.
- Graglia, E., S. Jonasson, A. Michelsen, I.K. Schmidt, M. Havström, and L. Gustavsson, 2001. Effects of environmental perturbations on abundance of subarctic plants after three, seven and ten years of treatments. *Ecography* 24: 5–12.
- Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- Grulke, N.E. and L.C. Bliss, 1988. Comparative life-history characteristics of two high arctic grasses, Northwest Territories. *Ecology* 69: 484–496.
- Grulke, N.E., G.H. Reichers, W.C. Oechel, U. Hjelm, and C. Jaeger, 1990. Carbon balance in tussock tundra under ambient and elevated CO<sub>2</sub>. *Oecologia* 83: 485–494.
- Gwynn-Jones, D., J.A. Lee, and T.V. Callaghan, 1997. Effects of enhanced UV-B radiation and elevated carbon dioxide concentrations on a sub-arctic forest heath ecosystem. *Plant Ecology* 128: 243–249.
- Hastings, S.J., S.A. Luchessa, W.C. Oechel, and J.D. Tenhunen, 1989. Standing biomass and production in water drainages of the foothills of the Philip Smith Mountains, Alaska, USA. *Holarctic Ecology* 12: 304–311.
- Havström, M., T.V. Callaghan, and S. Jonasson, 1993. Differential growth responses of *Cassiope tetragona*, an arctic dwarf-shrub, to environmental perturbations among three contrasting high- and sub-arctic sites. *Oikos* 66: 389–402.
- Henry, G.H.R., R. Freedman, and J. Svoboda, 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. *Canadian Journal of Botany* 64: 2502–2507.
- Hinzman, L.D., N.D. Bettez, W.R. Bolton, F.S. Chapin III, M.B. Dyurgerov, C.L. Fastie, B. Griffith, R.D. Hollister, A. Hope, H.P. Huntington, A.M. Jensen, G.J. Jia, T. Jorgenson, D.L. Kane, D.R. Klein, G. Kofinas, A.H. Lynch, A.H. Lloyd, A.D. McGuire, F.E. Nelson, W.C. Oechel, T.E. Osterkamp, C.H. Racine, V.E. Romanovsky, R.S. Stone, D.A. Stow, M. Sturm, C.E. Tweedie, G.L. Vourlitis,

- M.D. Walker, D.A. Walker, P.J. Webber, J.M. Welker, K.S. Winker, and K. Yoshikawa, 2005. Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change* 72: 251–298.
- Hobbie, S.E. and F.S. Chapin III, 1998. The response of tundra plant biomass, aboveground production, nitrogen, and CO<sub>2</sub> flux to temperature manipulation. *Ecology* 79: 1526–1544.
- Hobbie, S.E. and L. Gough, 2002. Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. *Oecologia* 131: 453–463.
- Hobbie, J.E. and E.A. Hobbie, 2006. <sup>15</sup>N in symbiotic fungi and plants estimates nitrogen and carbon flux rates in arctic tundra. *Ecology* 87: 816–822.
- Hobbie, S.E., A. Shevtsova, and F.S. Chapin III, 1999. Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos* 84: 417–434.
- Hobbie, S.E., L. Gough, and G.R. Shaver, 2005. Species compositional differences on different-aged glacial landscapes drive contrasting responses of tundra to nutrient addition. *Journal of Ecology* 93: 770–782.
- Houghton, R.A. and D.L. Skole, 1990. Carbon. In: B.L. Turner, W.C. Clark, R.W. Kates, J.F. Richards, J.T. Matthews, and W.B. Meyer, eds. *The Earth as Transformed by Human Action*. Cambridge University Press, Cambridge, UK, pp. 393–408.
- Hu, F.S., B.Y. Lee, D.S. Kaufman, S. Yoneji, D.M. Nelson, and P.D. Henne, 2002. Response of tundra ecosystem in southwestern Alaska to Younger-Dryas climatic oscillation. *Global Change Biology* 8: 1156–1163.
- Hultén, E., 1968. *Flora of Alaska and Neighboring Territories*. Stanford University Press, Stanford, CA.
- Johnson, D.A. and L.L. Tieszen, 1976. Aboveground biomass allocation, leaf growth, and photosynthesis patterns in tundra plant forms in arctic Alaska. *Oecologia* 24: 159–173.
- Jonasson, S., 1989. Implications of leaf longevity, leaf nutrient reabsorption, and translocation for the resource economy of five evergreen species. *Oikos* 56: 121–131.
- Jonasson, S., 1992. Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos* 63: 420–429.
- Kappen, L., 1993. Plant activity under snow and ice, with particular reference to lichens. *Arctic* 46: 297–302.
- Kielland, K., 1990. *Processes Controlling Nitrogen Release and Turnover in Arctic Tundra*. Ph.D. thesis. University of Alaska, Fairbanks.
- Kielland, K., 1994. Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology* 75: 2373–2383.
- Kielland, K., 1995. Landscape patterns of free amino acids in arctic tundra soils. *Biogeochemistry* 31: 85–98.
- Körner, C. and W. Larcher, 1988. Plant life in cold climates. *Symposium of the Society of Experimental Biology* 42: 25–57.
- Kummerow, J. and B. Ellis, 1984. Temperature effect on biomass production and root/shoot biomass ratios in two arctic sedges under controlled environmental conditions. *Canadian Journal of Botany* 62: 2150–2153.
- Kummerow, J., B.A. Ellis, S. Kummerow, and F.S. Chapin III, 1983. Spring growth of shoots and roots in shrubs of an Alaskan muskeg. *American Journal of Botany* 70: 1509–1515.
- Le Dizes, S., B.L. Kwiatkowski, E.B. Rastetter, A. Hope, J.E. Hobbie, D.A. Stow, and S. Daeschner, 2003. Modeling biogeochemical responses of tundra ecosystems to temporal and spatial variations in climate in the Kuparuk River Basin (Alaska). *Journal of Geophysical Research D—Atmospheres* 108: 8165. doi: 10.1029/2001JD000960.
- Limbach, W.E., W.C. Oechel, and W. Lowell, 1982. Photosynthetic and respiratory responses to temperature and light of three Alaskan tundra growth forms. *Holarctic Ecology* 5: 150–157.
- Lipson, D. and T. Nasholm, 2001. The unexpected versatility of plants: organic nitrogen use and availability in terrestrial ecosystems. *Oecologia* 128: 305–316.
- Mack, M.C., E.A.G. Schuur, M.S. Bret-Harte, G.R. Shaver, and F.S. Chapin III, 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431: 440–443.
- McGraw, J.B., 1980. Seed bank size and distribution of seeds in cottongrass tussock tundra. *Canadian Journal of Botany* 58: 1607–1611.
- McGraw, J.B., 1985a. Experimental ecology of *Dryas octopetala* ecotypes. III. Environmental factors and plant growth. *Arctic and Alpine Research* 17: 229–239.



- McGraw, J.B., 1985b. Experimental ecology of *Dryas octopetala* ecotypes: Relative response to competitors. *New Phytologist* 100: 233–241.
- McGraw, J.B. and F.S. Chapin III, 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology* 70: 736–749.
- McGraw, J.B. and N. Fetcher, 1992. Response of tundra plant populations to climatic change. In F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 359–376.
- McGraw, J.B. and G.R. Shaver, 1982. Seedling density and seedling survival in Alaskan cotton grass tussock tundra. *Holarctic Ecology* 5: 212–217.
- McGraw, J.B. and M.C. Vavrek, 1989. The role of buried viable seeds in arctic and alpine plant communities. In: M.A. Leck, V.T. Parker, and R.L. Simpson, eds. *Ecology of Soil Seed Banks*. Academic Press, San Diego, CA, pp. 91–106.
- McKane, R.B., E.B. Rastetter, G.R. Shaver, K.J. Nadelhoffer, A.E. Giblin, J.A. Laundre, and F.S. Chapin III, 1997. Climatic effects on tundra carbon storage inferred from experimental data and a model. *Ecology* 78: 1170–1187.
- McKane, R.B., L.C. Johnson, G.R. Shaver, K.J. Nadelhoffer, E.B. Rastetter, B. Fry, A.E. Giblin, K.J. Kielland, B.L. Kwiatkowski, J.A. Laundre, and G. Murray, 2002. Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature* 415: 68–71.
- McKendrick, J.D., V.J. Ott, and G.A. Mitchell, 1978. Effects of nitrogen and phosphorus fertilization on carbohydrate and nutrient levels in *Dupontia fisheri* and *Arctagrostis latifolia*. In: L.L. Tieszen, ed. *Vegetation and Production Ecology of an Alaskan Arctic Tundra*. Springer-Verlag, New York, pp. 565–578.
- McKendrick, J.D., G.O. Batzli, K.R. Everett, and J.C. Swanson, 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arctic and Alpine Research* 12: 565–578.
- Michelsen, A., S. Jonasson, D. Sleep, M. Havström, and T.V. Callaghan, 1996. Shoot biomass,  $\delta^{13}\text{C}$ , nitrogen, and chlorophyll responses of two arctic dwarf shrubs to in situ shading, nutrient application and warming simulating climatic change. *Oecologia* 105: 1–12.
- Murray, K.J., P.C. Harley, J. Beyers, H. Walz, and J.D. Tenhunen, 1989a. Water content effects on photosynthetic response of *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia* 79: 244–250.
- Murray, K.J., J.D. Tenhunen, and J. Kummerow, 1989b. Limitations on moss growth and net primary production in tussock tundra areas of the foothills of the Philip Smith Mountains, Alaska. *Oecologia* 80: 256–262.
- Murray, K.J., J.D. Tenhunen, and R.S. Nowak, 1993. Photoinhibition as a control on photosynthesis and production of *Sphagnum* mosses. *Oecologia* 96: 200–207.
- Myneni, R., C.D. Keeling, C.J. Tucker, G. Asrar, and R.R. Nemani, 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698–702.
- Nadelhoffer, K.J., A.E. Giblin, G.R. Shaver, and A.E. Linkins, 1992. Microbial processes and plant nutrient availability in arctic soils. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 281–300.
- Nadelhoffer, K.J., L. Johnson, J. Laundre, A.E. Giblin, and G.R. Shaver, 2002. Fine root production and nutrient use in wet and moist arctic tundras as influenced by chronic fertilization. *Plant and Soil* 242: 107–113.
- Nordin, A., I.K. Schmidt, and G.R. Shaver, 2004. Nitrogen uptake by arctic soil microbes and plants in relation to soil nitrogen supply. *Ecology* 85: 955–962.
- Oberbauer, S.F. and T.E. Dawson, 1992. Water relations of arctic vascular plants. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 259–279.
- Oberbauer, S.F., S.J. Hastings, J.L. Beyers, and W.C. Oechel, 1989. Comparative effects of downslope water and nutrient movement on plant nutrition, photosynthesis, and growth in Alaskan tundra. *Holarctic Ecology* 12: 324–334.

- Oberbauer, S.F., G. Starr, and E.W. Pop, 1998. Effects of extended growing season and soil warming on carbon dioxide and methane exchange of tussock tundra. *Journal of Geophysical Research* 103: 29075–29082.
- Oechel, W.C., 1976. Seasonal patterns of temperature response of CO<sub>2</sub> flux and acclimation in arctic mosses growing in situ. *Photosynthetica* 10: 447–456.
- Oechel, W.C., S.J. Hastings, G. Vourlitis, M. Jenkins, G. Riechers, and N. Grulke, 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* 361: 520–523.
- Oechel, W.C., S. Cowles, N. Grulke, S.J. Hastings, W. Lawrence, T. Prudhomme, G. Riechers, B. Strain, D. Tissue, and G. Vourlitis, 1994. Transient nature of CO<sub>2</sub> fertilization in arctic tundra. *Nature* 371: 500–503.
- Oechel, W.C., G.L. Vourlitis, S.J. Hastings, R.C. Zulueta, L. Hinzman, and D.L. Kane, 2000. Acclimation of ecosystem CO<sub>2</sub> exchange in the Alaskan Arctic in response to decadal climate warming. *Nature* 406: 978–981.
- Parsons, A.N., J.M. Welker, P.A. Wookey, M.C. Press, T.V. Callaghan, and J.A. Lee, 1994. Growth responses of four sub-arctic dwarf shrubs to simulated environmental change. *Journal of Ecology* 82: 307–318.
- Parsons, A.N., P.A. Wookey, J.M. Welker, M.C. Press, T.V. Callaghan, and J.A. Lee, 1995. Growth and reproductive output of *Calamagrostis lapponica* in response to simulated environmental change in the subarctic. *Oikos* 72: 61–66.
- Post, W.M., 1990. Report of a workshop on climate feedbacks and the role of peatlands, tundra, and boreal ecosystems in the global carbon cycle. 3289, Oak Ridge National Laboratory, Oak Ridge, TN.
- Press, M.C., J.A. Potter, M.J. Burke, T.V. Callaghan, and J.A. Lee, 1998. Responses of a subarctic dwarf shrub heath community to simulated environmental change. *Journal of Ecology* 86: 315–327.
- Rastetter, E.B., R.B. McKane, G.R. Shaver, K.J. Nadelhoffer, and A.E. Giblin, 1997. Analysis of CO<sub>2</sub>, temperature, and moisture effects on carbon storage in Alaskan arctic tundra using a general ecosystem model. In: W.C. Oechel, T. Callaghan, T. Gilmanov, J.I. Holten, B. Maxwell, U. Molau, and B. Sveinbjörnsson, eds. *Global Change and Arctic Terrestrial Ecosystems*. Springer, New York, pp. 437–451.
- Read, D.J., 1991. Mycorrhizas in ecosystems. *Experientia* 47: 376–391.
- Robinson, C.H., P.A. Wookey, J.A. Lee, T.V. Callaghan, and M.C. Press, 1998. Plant community responses to simulated environmental change at a High Arctic polar semi-desert. *Ecology* 79: 856–866.
- Savile, D.B.O., 1960. Limitations of the competitive exclusion principle. *Science* 132: 1761.
- Schimel, J.P. and F.S. Chapin III, 1996. Tundra plant uptake of amino acid and NH<sub>4</sub><sup>+</sup> nitrogen in situ: plants compete well for amino acid N. *Ecology* 77: 2142–2147.
- Semikhatova, O.A., T.V. Gerasimenko, and T.I. Ivanova, 1992. Photosynthesis, respiration, and growth of plants in the Soviet Arctic. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 169–190.
- Shaver, G.R. and W.D. Billings, 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. *Ecology* 56: 401–410.
- Shaver, G.R. and D.W. Billings, 1977. Effects of daylength and temperature on root elongation in tundra graminoids. *Oecologia* 28: 57–65.
- Shaver, G.R. and F.S. Chapin III, 1980. Response to fertilization by various plant growth forms in an Alaskan tundra: nutrient accumulation and growth. *Ecology* 61: 662–675.
- Shaver, G.R. and F.S. Chapin III, 1986. Effect of fertilizer on production and biomass of tussock tundra, Alaska, U.S.A. *Arctic and Alpine Research* 18: 261–268.
- Shaver, G.R. and F.S. Chapin III, 1991. Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs* 61: 1–31.
- Shaver, G.R. and F.S. Chapin III, 1995. Long-term responses to factorial NPK fertilizer treatment by Alaskan wet and moist tundra sedge species. *Ecography* 18: 259–275.

- Shaver, G.R. and J. Kummerow, 1992. Phenology, resource allocation, and growth of arctic vascular plants. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 193–211.
- Shaver, G.R., F.S. Chapin III, and B.L. Gartner, 1986. Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. *Journal of Ecology* 74: 257–278.
- Shaver, G.R., J.A. Laundre, A.E. Giblin, and K.J. Nadelhoffer, 1996. Changes in live plant biomass, primary production, and species composition along a riverside toposequence in Arctic Alaska, U.S.A. *Arctic and Alpine Research* 28: 363–379.
- Shaver, G.R., L.C. Johnson, D.H. Cades, G. Murray, J.A. Laundre, E.B. Rastetter, K.J. Nadelhoffer, and A.E. Giblin, 1998. Biomass accumulation and CO<sub>2</sub> flux in wet sedge tundras: responses to nutrients, temperature, and light. *Ecological Monographs* 68: 75–97.
- Shaver, G.R., M.S. Bret-Harte, M.H. Jones, J. Johnstone, L. Gough, J. Laundre, and F.S. Chapin III, 2001. Species composition interacts with fertilizer to control long-term change in tundra productivity. *Ecology* 82: 3162–3181.
- Shevtsova, A., A. Ojala, S. Neuvonen, M. Vieno, and E. Haukioja, 1995. Growth and reproduction of dwarf shrubs in subarctic plant community: annual variation and above-ground interactions with neighbors. *Journal of Ecology* 83: 263–275.
- Sohlberg, E.H. and L.C. Bliss, 1986. Responses of *Ranunculus sabinei* and *Papaver radicum* to removal of the moss layer in a high-arctic meadow. *Canadian Journal of Botany* 65: 1224–1228.
- Starr, G. and S.F. Oberbauer, 2003. Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. *Ecology* 84: 1415–1420.
- Starr, G., S.F. Oberbauer, and E.W. Pop, 2000. Effects of lengthened growing season and soil warming on the phenology and physiology of *Polygonum bistorta*. *Global Change Biology* 6: 357–369.
- Starr, G., D.S. Neuman, and S.F. Oberbauer, 2004. Ecophysiological analysis of two arctic sedges under reduced root temperatures. *Physiologia Plantarum* 20: 458–464.
- Sturm, M., C. Racine, and K. Tape, 2001. Climate change: Increasing shrub abundance in the Arctic. *Nature* 411: 546–547.
- Tenhunen, J.D., O.L. Lange, S. Hahn, R. Siegwolf, and S.F. Oberbauer, 1992. The ecosystem role of poikilohydric tundra plants. In: F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver, and J. Svoboda, eds. *Arctic Ecosystems in a Changing Climate: An Ecophysiological Perspective*. Academic Press, San Diego, CA, pp. 213–237.
- Tieszen, L.L., 1973. Photosynthesis and respiration in arctic tundra grasses: field light intensity and temperature responses. *Arctic and Alpine Research* 5: 239–251.
- Tissue, D.T. and W.C. Oechel, 1987. Response of *Eriophorum vaginatum* to elevated CO<sub>2</sub> and temperature in the Alaskan tussock tundra. *Ecology* 68: 401–410.
- van Wijk, M.T., K.E. Clemmensen, G.R. Shaver, M. Williams, T.V. Callaghan, F.S. Chapin III, J.H.C. Cornelisen, L. Gough, S.E. Hobbie, S. Jonasson, J.A. Lee, A. Michelsen, M.C. Press, S.J. Richardson, and H. Rueth, 2003a. Long-term ecosystem level experiments at Toolik Lake, Alaska, and at Abisko, Northern Sweden: generalizations and differences in ecosystem and plant type responses to global change. *Global Change Biology* 10: 105–123.
- van Wijk, M.T., M. Williams, L. Gough, S.E. Hobbie, and G.R. Shaver, 2003b. Luxury consumption of soil nutrients: a possible competitive strategy in aboveground and belowground biomass allocation for slow-growing arctic vegetation? *Journal of Ecology* 91: 664–676.
- Walker, M.D., D.A. Walker, and N.A. Auerbach, 1994. Plant communities of a tussock tundra landscape in the Brooks Range Foothills, Alaska. *Journal of Vegetation Science* 5: 843–866.
- Walker, M.D., C.H. Wahren, R.D. Hollister, G.H.R. Henry, L.E. Ahlquist, J.M. Alatalo, M.S. Bret-Harte, M.P. Calef, T.V. Callaghan, A.B. Carroll, H.E. Epstein, I.S. Jønsdøttir, J.A. Klein, B. Magnusson, U. Molau, S.F. Oberbauer, S.P. Rewa, C.H. Robinson, G.R. Shaver, K.N. Suding, C. Thompson, A. Tolvanen, Ø. Totland, P.L. Turner, C.E. Tweedie, P.J. Webber, and P.A. Wookey, 2006. Plant community response to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences* 103: 1342–1346.
- Warren Wilson, J., 1966. An analysis of plant growth and its control in arctic environments. *Annals of Botany* 30: 383–482.

- Weintraub, M.N. and J.P. Schimel, 2005. The seasonal dynamics of amino acids and other nutrients in Alaskan Arctic tundra soils. *Biogeochemistry* 73: 359–380.
- Welker, J.M., P.A. Wookey, A.P. Parsons, T.V. Callaghan, M.C. Press, and J.A. Lee, 1993. Comparative responses of subarctic and high arctic ecosystems to simulated climate change. *Oikos* 67: 490–502.
- Wookey, P.A., J.M. Welker, A.N. Parsons, M.C. Press, T.V. Callaghan, and J.A. Lee, 1994. Differential growth, allocation and photosynthetic response of *Polygonum viviparum* to simulated environmental change at a high arctic polar semi-desert. *Oikos* 70: 131–139.
- Wookey, P.A., C.H. Robinson, A.N. Parsons, J.M. Welker, T.V. Callaghan, and J.A. Lee, 1995. Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high Arctic polar semi-desert, Svalbard. *Oecologia* 102: 478–489.
- Zhou, L., C.J. Tucker, R.K. Kaufman, D. Slayback, N.V. Shabanov, and R.B. Myneni, 2001. Variations in northern vegetation activity inferred from satellite data of vegetation index during 1981 to 1999. *Journal of Geophysical Research* 106: 20069–20084.

