HOW SOIL NUTRIENT AVAILABILITY AFFECTS PLANT SEXUAL REPRODUCTION AND SEEDLING RECRUITMENT IN ALASKAN DRY HEATH TUNDRA: IMPLICATIONS FOR RESPONSE TO CLIMATE CHANGE

by

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ABSTRACT

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The harsh growing conditions of the arctic biome, in particular low temperatures and soil nutrient availability, restrict the growth and reproduction of arctic plant species. Recent and ongoing changes in climate are increasing air and soil temperatures in these ecosystems, thus affecting decomposition rates of arctic soils. As decomposition increases, nutrients that are currently immobilized in the soil organic layer become available to nutrient-limited tundra plants. Plant species within the tundra communities then compete for the newly available nutrients, potentially causing a shift in community composition. As an important component of plant life cycles, seeds provide new individuals and genetic diversity to future adult communities, but little is known about the role that seeds play in arctic ecosystems where most species are also capable of producing new individuals vegetatively. My research focused on how experimentally adding soil nutrients for 12 years affected reproduction, seedling recruitment (dispersal and germination) and seedling establishment in dry heath plant communities in northern Alaska.

Fertilizer addition significantly shifted adult community composition by decreasing lichens and evergreen shrub species and increasing abundance of the grass, *Hierochloe alpina*. Flowering and fruiting abundance also shifted among species with nutrient addition, reflecting the increase in *H. alpina* and a deciduous dwarf shrub, *Betula nana*, and the loss of lichens and dwarf evergreen shrubs in the adult community. Dispersal of seeds was greater with nutrient additions, particularly for *B. nana*, although dispersal of seeds within species, suggesting unequal distribution into the arctic landscape. Significant changes in species composition of germinated seed in soil seed banks occurred with greater nutrient availability, with the germinated seedlings reflecting the adult communities seen in the field. Few established seedlings were observed in both experimentally manipulated and control plots in the field, suggesting that recruitment from seed and subsequent seedling establishment is rare and most likely limited by space within the community. Certain plant species are better adapted to greater nutrient availability, thus resulting in the shift from an evergreen-dominated community to a grass-dominated community. Seeds from these species are continually being produced in current nutrient amended communities, and their role in maintaining that adult community may become important if disturbances, such as the removal of litter or adult vegetation by herbivores, occur. These disturbances may create conditions favorable for new seedling recruitment. Because higher soil nutrients favor different plant species, changes in plant communities in the Arctic could be greatly affected by climate change.

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INTRODUCTION

1.1 Plant Adaptations to Arctic Climates

The arctic tundra, located in the northernmost latitudes, can be characterized into particular tundra types according to the plant community composition and prevailing environmental conditions, such as wet sedge or dry heath tundra. Common growth forms within arctic plant communities include tussock-forming grasses and sedges, dwarf evergreen shrubs, and dwarf deciduous shrubs (Billings and Mooney 1968; Chapin and Shaver 1985a; Walker et al. 1994). Most of the plants in the Arctic, including lichens and mosses, are slow-growing perennials, some of which have developed some form of food storage system, such as large root or rhizome systems, in response to abiotic limitations, in particular low temperatures and soil nutrient availability (Billings 1987). Temperature limits plant growth and development in arctic systems because plant metabolic processes, such as photosynthesis and respiration, are hindered by low temperatures characteristic of arctic climates (Warren Wilson 1957; Bliss 1962; Billings 1987, 1992). As a result, a majority of the plants are small and close to the ground. Temperatures at 1 cm above ground level have been documented as warmer and more stable than temperature measurements at 1 m above ground level (Wilson 1957; Bliss 1962). This suggests that low stature of arctic plants is actually advantageous, since slight increases in temperature during the arctic growing season actually enhance these processes enough so that growth and development, although slow, do occur (Wilson 1957; Bliss 1962). A typical growing season in arctic ecosystems lasts 9-14 weeks, when the ground is snow free (Billings and Mooney 1968; Chapin and Shaver 1985). Carbohydrates and starches made during the short growing season are stored in extensive roots or rhizome structures of the plants, which then enable plants to develop tissues and structures before the next growing season (Billings and

Mooney 1968; Chapin and Shaver 1985a). In many arctic species, the leaves are developed one season, and then overwinter in an advanced state of development to take advantage of favorable conditions to break dormancy the following spring (Billings and Mooney 1968; Bliss 1962).

Plant growth and development in the Arctic is also limited by nutrient availability. The combination of low precipitation, soil moisture extremes (e.g. flooded or dry) and low mean annual temperature affects the input of nitrogen (N) and phosphorus (P) into arctic ecosystems (Babb and Whitfield, 1977; Chapin et al. 1978, 1987; Ellis 1980). Soil temperature is influenced by both the low mean annual air temperature from above and the presence of the permafrost layer from below, a trait that helps define tundra ecosystems. Permafrost is permanently frozen ground, made up of soil and bedrock, and is a result of both low annual solar radiance and negative mean annual air temperature (Chapin and Shaver 1985a). In certain parts of the tundra, the permafrost layer can reach depths up to 400 m in thickness (Bliss et al. 1973). The combination of soil moisture extremes and low soil temperatures restricts decomposition of soil organic matter in the Arctic, as these conditions are not favorable to the metabolic processes of soil microbial organisms (Bliss 1962; Clein and Schimmel 1995; Mikan et al. 2002). Therefore N and P are bound in large proportions within the soil, which in turn restricts plant growth and biomass (Shaver and Chapin 1986; Billings 1987; Chapin et al. 1995).

Specific adaptations enable some plant species to overcome low nutrient availability. Some graminoid, or grass-like, species have been shown to elongate their leaves the following season if those leaves were produced late in the previous season, instead of producing entirely new leaves (Chapin and Shaver 1985a). Other plants keep their leaves year round and can photosynthesize longer than other plants if environmental conditions allow, which is typical of evergreen species (Starr and Oberbauer 2003). Because arctic plant growth and development is greatly reduced by the combination of low temperatures and soil nutrient availability, plant sexual reproduction may also be delayed due to the same limitations.

1.2 Reproductive Efforts

Since the growing season lasts only a few weeks, arctic plants must adapt their reproductive efforts to account for the shortened growing period. Many arctic plants are capable of reproducing both clonally, in the form of rhizomes, bulbils, and other means (Bliss 1958; Billings 1987), and sexually, although flowering varies greatly from year to year (Chapin and Shaver 1985a; Shaver et al. 1986). Some arctic and alpine species rarely reproduce sexually, and instead direct energy into clonal growth (Chester and Shaver 1982a; Alsos et al. 2003). The amount of nutrients available may also play a role in whether or not arctic plants reproduce sexually. Since plant growth and biomass is nutrient-limited, the growth and development of reproductive structures, such as flowers and pollen, may be nutrient-limited as well. Because production of reproductive structures requires more nitrogen than vegetative growth (Bazzaz et al. 1987), plants in the Arctic may likely spend more energy reproducing clonally than sexually (Callaghan 1984; Headley et al. 1988; Jonsdottir and Callaghan 1988; Jonsdottir et al. 1996).

Despite the prevalence of asexual reproduction, evidence of genetic diversity has been documented in both the arctic and alpine ecosystems. Bauert (1996) found high levels of genetic diversity within populations of a predominantly asexual plant species, *Polygonum viviparum*, suggesting that sexual reproduction must occur. Studies on *Saxifraga cernua*, an arctic-alpine clonal plant, show that widespread, locally abundant arctic populations have high levels of genetic diversity as well (Gabrielsen and Brochmann 1998), although in highly isolated alpine populations, no genetic diversity was found in this species (Bauert et al. 1998). *Geum reptans*, an alpine plant that reproduces both sexually and asexually, can establish from seed in years that have favorable environmental conditions, thus adding to the diversity of the adult population (Weppler et al. 2006). Repeated, long-distance colonization of plant species from multiple source locations also increases genetic diversity, as shown in a study by Alsos et al. (2007) on Svalbard, a remote arctic archipelago. Seed dispersal by wind and drifting sea ice from various locations brought in new genetic diversity to the Svalbard plant communities (Alsos et al. 2007). This and other studies indicate that sexual reproduction does occur, introducing genetic diversity into the plant populations.

The development of reproductive structures prior to the growing season may be beneficial for arctic plants. Flower buds of some species begin developing early in the growing season a year before the plant flowers (Billings and Mooney 1968; Bliss 1962, 1971; Sorensen 1941; Bell and Bliss 1980). This adaptation allows plants to acquire the resources necessary to produce flowers over the length of one growing season. The buds are protected throughout the harsh arctic winters by other vegetative structures (Bliss 1971). Flowering is then dependent upon the air temperature and photoperiod during the flowering year, and the last snowmelt that season (Billings and Mooney 1968; Kudo 1993). For example, flowering of plant species on a polar desert in Canada was significantly restricted in years following cold growing seasons (Bliss and Gold 1999). In favorable growing seasons, flowering in tundra ecosystems can occur rapidly and in synchrony, due to the formation of the flower bud the previous year (Bliss 1971). Many of the common tundra plants have been shown to have relatively similar reproductive efforts (Chester and Shaver 1982b); however pollination and subsequent fertilization may or may not occur, depending on environmental conditions.

Pollination of flowers in these ecosystems either occurs by self-pollination or by insect pollinators. In both arctic and alpine habitats, butterflies, moths, bumblebees, and flies are the main floral pollinators (Billings and Mooney 1968; Bliss 1971; Kevan 1972). Pollinators are important because they provide the opportunity for cross pollination, helping introduce genetic diversity into the population (Bliss 1962). However if visitation from pollinators does not occur, some plants are able to self-pollinate. This becomes an important mechanism specifically in the extreme arctic environments where the chance of pollination from a pollinator is low (Bliss 1962). A study by Molau (1993) looked at the relationship between flowering phenology and life history strategies in arctic plants. Species that flower early in the season are typically dioecious, where an individual plant has either male or female reproductive structures, and rely on pollination (Molau 1993). Species that flower later in the season tend not to depend on pollinators, utilize clonal growth, and may produce seeds via apomixis, which is a form of seed production without meiosis or fertilization (Billings and Mooney 1968; Bliss 1971; Billings 1987; Molau 1993). Early flowering species are more likely to produce viable seeds since there is a greater opportunity for pollination to occur. Non-viable seed formation has been documented in some arctic plant species. *Carex bigelowii, Betula nana,* and *Ledum palustre* had the highest proportion of aborted embryos between fruit formation and seed dispersal, suggesting that many seeds dispersed from these plants are not viable (Chester and Shaver 1982b). Berry-forming plants, such as *Vaccinium uliginosum, V. vitis-idaea*, and *Empetrum nigrum*, mostly aborted their embryos between flower formation and fruit formation (Chester and Shaver 1982b), which often resulted in small, underdeveloped fruits. However despite the large proportions of aborted seeds found in these studies, tundra plants do produce many viable seeds which are then dispersed into the tundra landscape (Billings and Mooney 1968; McGraw and Vavrek 1989).

1.3 Seed Ecology

Seeds play an important role in plant community dynamics. Fertilization, dispersal, germination and establishment of seeds are all important processes that allow plant communities to maintain community structure, introduce variability within populations and communities, and colonize disturbed sites (Figure 1.1; Baskin and Baskin 2001). Seeds in the Arctic usually ripen toward the end of the growing season, between late July and September, after which they are dispersed (Billings and Mooney 1968). Seed dispersal is attributed to either wind or animal dispersal. In alpine habitats, wind is an important “agent” of seed dispersal, although deposited seed distance from the nearest parent plant was restricted to a 50 cm radius due to the low stature of the adult plants and the reduction in wind speed closer to the ground surface (Marchand and Roach 1980). In arctic landscapes, wind-dispersed seeds are small and light-weight, and usually have appendages that foster dispersal by wind (Gartner 1983; Welling et al. 2005; Jakobsson et al. 2006). Small-seeded arctic species are generally better dispersers than larger-seeded species (Welling et al. 2005), although larger-seeded species may move longer distances horizontally across the surface since they are less likely to be trapped by soil particles (Chambers et al. 1991). Fleshy fruits, such as those of the arctic plants *Rubus chamaemorus* and *Vaccinium uliginosum*, are usually dispersed by mammalian herbivores and birds (Gartner 1983). Herbivore consumption is an important mechanism of seed dispersal in arctic ecosystems since many animals are migratory. Musk oxen and barnacle geese are two herbivores that have been shown to disperse ingested seed long distances within arctic communities (Bruun et al. 2008). Arctic foxes have also been documented as long distance seed dispersers; however seed viability is dependent upon the amount of time spent in the gut (Graae et al. 2004).

Soil seed banks are important because they provide both new individuals and potential genetic diversity to future adult plant communities. Arctic and alpine soil seed banks, once thought to be small compared to other biomes, are often dense and diverse (McGraw 1980; Fox 1980; McGraw and Vavrek 1989; Diemer and Prock 1993; Alsos et al. 2003; Cooper et al. 2004; Welling et al. 2004). However, species composition and abundance of arctic soil seed banks have been shown to not entirely represent that of the adult community (Fox 1980; Chang et al. 2001; Diemer and Prock 1993; McGraw 1980; Molau and Larsson 2000; Welling et al. 2004). The absence of particular plant species may be due to seed production or dispersal limitations or an inability of seeds to persist in arctic soils (Alsos et al. 2003; Cooper et al. 2004). Studies suggest that seeds of certain species, in particular graminoids, are able to persist longer in arctic soils than others, germinating when exposed to the right environmental conditions (Billings and Mooney 1968; McGraw 1980). The ability to survive in a state of dormancy over long periods of time is highly beneficial, since it may protect seeds from mortality. Seeds of certain arctic species, mostly herbaceous forbs, have physical dormancy, caused by seed-coat inhibition, and need to be scarified in order to germinate (Billings and Mooney 1968; Baskin and

Baskin 2001). Other species, such as *Betula nana* and *Ledum palustre*, have physiological dormancy, where seeds are able to germinate after undergoing a period of cold stratification (Baskin and Baskin 2001). Seeds of twenty-eight *Vaccinium* species, which have physiological dormancy, persisted an average of 8 years in arctic soils, with five species persisting as long as 15-17 years (Hill and Vander Kloet 2005). Climatic factors and reproductive variables accounted for much of the variation in seed longevity (Hill and Vander Kloet 2005), suggesting that persistence is dependent upon both biotic and abiotic factors. In general, dormancy enables seeds to persist in the harsh arctic environment, and studies of soil seed banks document seed persistence.

Like growth of the adult plant community, germination of seeds in the Arctic is limited by biotic and abiotic factors under current climate conditions. Germination studies have shown that while viable seeds are often produced, seedlings themselves are in low abundance (Bliss 1958; Diemer and Prock 1993; Cooper et al. 2004). Low air temperature may inhibit seed germination. Arctic seeds generally have optimal germination temperatures ranging between 20-30℃ (Billings and Mooney 1968; Bliss 1971; Gartner 1983), while mean air temperature in July ranges between 5-16℃ (Maxwell 1992). Laboratory experiments on germination of arctic species support the fact that current arctic temperatures most likely limit germination in the field since high levels of germination do occur under controlled conditions (Bell and Bliss 1980; Cooper et al. 2004). Low soil moisture can inhibit seed imbibition, a requirement for germination. Results from studies involving moisture and germination suggest seeds in drier soils germinate less due to low moisture content as well as low soil temperatures (Bell and Bliss 1980). Competition for space may also inhibit germination. With the presence of vegetatively spreading adult plants, areas for seed germination are limited; however, ‘safe sites’ or gaps in vegetation within the landscape provide areas where seeds can germinate and establish (McGraw and Shaver 1982; Eskelinen and Virtanen 2005; Gough 2006; Cooper et al. 2004). Lichen and moss mats may also offer suitable growing conditions for seeds because they provide small amounts of moisture and protection from wind and seed predation (Bell and Bliss 1980). Disturbances that remove plant material from bare ground may also open areas for seeds to germinate and establish (Gartner et al. 1986). Frost boils are small, natural disturbances formed by frost heaves exposing the mineral layer in arctic soils, providing areas to colonize within a bare ground limited landscape (McGraw and Vavrek 1989; Walker et al. 1994; Walker et al. 2004; Gough 2006). Vegetation removal and simulated herbivory experiments also show increased germination of seeds in disturbed arctic and alpine communities (Chang et al. 2001; Gough 2006; Lindgren et al. 2007; Olofsson and Shams 2007). Desiccation cracks may provide a suitable environment for seeds to germinate and establish, since cracks can provide moisture, protection and access to mineral soil (Bell and Bliss 1980). Increasing day length does affect germination, but usually only after seeds receive a period of cold stratification, characteristic of the arctic spring season (Densmore 1997). Therefore, germination and subsequent seedling establishment are often limited by soil moisture, nutrients, available space, and ultimately whether or not viable seeds are present in or can be dispersed into the seed bank.

1.4 Climate Change Observations and On-going Studies

Because the effects of climate change are most evident at higher latitudes, scientists may detect biological responses there over shorter time scales than in other areas (Shaver et al. 1992). Warming of air temperatures has already been observed in many parts of the Arctic (Chapman and Walsh 1993; Serreze et al. 2000). Ocean-atmospheric general circulation models predict that with air temperature increases, the thickness of the permafrost layer in the northern most parts of the Arctic will become discontinuous (Maxwell 1992; Anisimov and Nelson 1996). As a result, the soil active layer above the permafrost may thicken, releasing soil microbial processes from temperature limitation and affecting nutrient mineralization (Maxwell 1992; Nadelhoffer et al. 1992; Anisimov et al. 1997). An increase in available nutrients under warmer air conditions could potentially release arctic plants from nutrient limitations which would then lead to increased plant biomass and productivity (Chapin and Shaver 1985b; Chapin et al. 1995). Models based on these potential nutrient increases suggest that the current plant communities in the northwest North American Arctic could be replaced with new, stable plant communities, composed of different species, within 200 years (Epstein et al. 2000). Changes in plant communities, in particular regional increases in shrub abundance as a result of increasing air temperatures, have already been documented in the Arctic using aerial photography (Sturm et al. 2005), and remote sensing (Hope et al. 2003). As a result, many climate change studies have focused on manipulating increasing temperatures, nutrients or a combination of both.

Experimental manipulations involving temperature have been designed determine the outcome of increased air temperature on growth and flowering in arctic plants. The International Tundra Experiment (ITEX) was designed to study the response of vascular plants to increased air temperature, and is set up in multiple locations throughout the Arctic (Molau and Molgaard 1996). Open-top chambers (OTC), hexagonal fiberglass structures, were designed and used to increase ground level air temperature (Molau and Molgaard 1996; Marion et al. 1997; Wahren et al. 2005). Other long term studies have incorporated clear plastic greenhouses designed to raise the air temperature between the last snow-melt and fall senescence (Chapin and Shaver 1985b). Data compiled from studies at various arctic field sites suggest that both photosynthesis and respiration of plants begin earlier under warmer conditions than control, increasing aboveground net primary production and biomass of certain species and lowering species diversity (Chapin and Shaver 1996; Hobbie and Chapin 1998a; Wahren et al. 2005; Oberbauer et al. 2007).

Other studies show that an increase in air temperature allows plants to flower earlier in the season, as well as increase the number of flowers produced. Results from a meta-analysis from 13 different ITEX sites indicate that leaf bud burst and flowering occurred earlier in plots experiencing warmer temperatures (Arft et al. 1999). Results also suggest that reproductive efforts and success of the plant species increased around the fourth year of temperature manipulations (Arft et al. 1999). Aerts et al. (2004) showed that flowering phenology of two arctic species, *Andromeda polifolia* and *Rubus chamaemorus*, was highly responsive to changes in climate, advancing the onset of flowering by 1-4 days in response to increased temperatures. Warming of the air temperature in the OTCs by almost 3℃ significantly affects timing and development of flowers of *Silene acaulis*, resulting in an increase in seed production (Alatalo and Totland 1997). A study by Aerts et al. (2006) reviewed the general responses of cold, northern ecosystems to climate change. The review indicated that changes in plant phenology have occurred with recent climate warming, including a range shift of plant species to northern regions. They suggest that the structure and dynamics of high-latitude ecosystems may be disrupted as plant distributions shift northward with climate warming (Aerts et al. 2006).

Direct warming manipulations of soils alter soil processes, most importantly soil respiration. A meta-analysis looking at experimental ecosystem warming showed that across all sites and years, warming of air or soil temperatures by 0.3-6.0℃ significantly increased soil respiration by 20% (Rustad et al. 2001). Results by Aerts et al. (2006) also support the idea that increases in soil temperature enhances soil respiration, which increases N-mineralization, therefore leading to higher nitrogen availability in tundra sites. If soil temperature is raised by 9℃ in a laboratory incubation, nitrogen mineralization has been shown to increase due to greater organic matter decomposition by soil microbes (Nadelhoffer et al. 1991). The inorganic forms of nitrogen, along with other nutrients, then become available to nutrient-limited plant species (Chapin et al. 1995).

The addition of N and P to experimental tundra plots is designed to test how increased soil nutrients affect arctic plant communities. Studies show that there is an increase in net primary production (NPP) in tundra communities when nutrients are added (Chapin et al. 1995; Shaver and Jonasson 1999; Johnson et al. 2000; Bret-Harte et al. 2001, 2002; Shaver et al. 2001; Gough and Hobbie 2003; Hobbie et al. 2005). At Moist Acidic Tussock tundra (MAT), the increase in NPP is mostly due to increases in woody production in the deciduous dwarf shrub, *Betula nana* (Bret-Harte et al. 2001, 2002; Shaver et al. 2001; Hobbie et al. 2005). Biomass however did not change with increased nutrient availability because of a change in dominant species, e.g. evergreen, lichen and moss biomass decreased while deciduous and graminoid biomass increased (Chapin et al. 1995; Chapin and Shaver 1996; Bret-Harte et al. 2002, 2008). In MAT, the increase in secondary growth when exposed to increased nutrients enables *B. nana* to outcompete other species for resources, particularly light (Bret-Harte et al. 2001). Inflorescence production also increased under increased nutrient availability for *B. nana* (Bret Harte et al. 2001), which suggests that plants will increase sexual reproduction if conditions are favorable. Increased nutrients were shown to increase flower bud size in the tussock forming grass, *Eriophorum vaginatum*, at MAT (Shaver et al. 1986). These results suggest that more resources are allocated to flower bud formation when nutrients are not limited (Shaver et al. 1986). The observed increase in flower production indicates the importance of sexual reproduction, and subsequent seed dispersal into the Arctic landscape, which may become important under a changing climate.

1.5 Characteristics of Dry Heath Tundra

Dry heath (DH) tundra is a relatively common type of tundra vegetation found in North America, Greenland, Europe and Asia (Bliss and Matveyeva 1992; Shaver and Jonasson 1999). The majority of plant species that occur in DH are dwarf evergreen shrubs in the heath family, Ericaceae, including *Empetrum nigrum*, *Vaccinium vitis-idaea*, *Cassiope tetrogona*, *Ledum palustre*, and *Loiseleuria procumbens* (Muller 1952; Jonasson 1982; Bliss and Matveyeva 1992). Lichens are also found in great abundance, while mosses, deciduous dwarf shrubs, grasses and sedges are less common (Jonasson 1982; Bliss and Matveyeva 1992). Scandinavian heath tundra systems at Abisko, Sweden, are predominantly composed of one heath species, *C. tetragona* (Shaver and Jonasson 1999), while in Finland, *E. nigrum* and *Vaccinium myrtillus* dominate heath tundra (Welling and Laine 2002). Alaskan heath tundra systems at Toolik Lake, my study site, are composed mainly of *L. procumbens*, *L. palustre*, and

V. vitis-idaea, the deciduous shrub, *Arctostaphylos alpina,* and lichens, and are characterized by thin, dry soils over exposed, well-drained areas with low nutrient availability (Shaver and Chapin 1991; Shaver and Jonasson 1999; Gough et al. 2002; Olofsson 2006). Although located at similar latitudes, the climate at Abisko is milder than Toolik Lake due to its closeness to the Atlantic Ocean (Hartley et al. 1999). As a result, above-ground vascular biomass in Scandinavian heath communities is 6 times higher than that in Alaskan heath tundra communities (Shaver and Jonasson 1999).

1.6 Climate Studies in Heath Tundra

Experiments that manipulate nutrient availability are currently ongoing in heath tundra systems. In Alaskan DH, experimentally added N and P significantly increased NPP and abundance of two relatively rare species, *B. nana*, a deciduous dwarf shrub, and *Hierochloe alpina*, a tussock forming grass (Gough et al. 2002). Total community biomass decreased significantly in nutrient-amended plots compared to control plots because of the reduction of evergreen species and the loss of their woody tissues (Gough et al. 2002; Gough unpublished data). In Sweden, abundance of all plant species, in particular the arctic grass, *Calamagrostis lapponica,* increased in response to added nutrients, while above-ground biomass did not show a significant response (Press et al. 1998). Both studies however showed a marked decrease in species richness following fertilizer addition, particularly with the loss of non-vascular plant species (Press et al. 1998; Cornelissen et al. 2001; Gough et al. 2002, 2008).

Plant litter accumulation from grasses under increased nutrient levels have been documented in both Alaskan and Swedish heath tundras (Press et al. 1998; Gough et al. 2002, 2008), suggesting a higher turnover of plant material than in CT. Increased plant litter could possibly shade the understory dwarf evergreen shrubs and lichens, leading to less abundance of these particular growth forms. Increased plant litter abundance, along with greater soil nutrient availability, may be possible causes for the observed shift from a lichen and evergreen, dwarf shrub-dominated community to a grass-dominated community.

Climate change may also affect sexual reproduction in heath tundra plants. Current research shows that a temperature increase of about 3° C would significantly affect the reproductive efforts of arctic plants in heath tundra systems (Alatalo and Totland 1997; Klanderud 2005). Flowering time of *Silene acaulis*, a cushion-forming arctic plant, occurred sooner in OTCs in heath tundra in Sweden because the microhabitat around the plants thawed out earlier than controls (Alatalo and Totland 1997). Because the *Silene* flowers reached maturation earlier, these plants also had significantly more mature seeds than control plants (Alatalo and Totland 1997). Gough et al. (2007) documented an increase in *H. alpina* flowers in Alaskan heaths under increased nutrient availability. Since inflorescence abundance increased in *H. alpina* in DH communities, and *B. nana* in MAT communities (see Bret-Harte et al. 2001), dispersal from these species will most likely increase as well. Since seeds of both species are dispersed by wind, dispersal should not be limited, potentially reaching all areas within the dry heath tundra landscape. The observed shift in plant communities of arctic tundra as nutrient availability increases with climate change may be a result of increased flowering and subsequent seed production. Greater production of seeds and dispersal of seeds into the landscape may play important roles in community dynamics since the seeds could potentially be adapted to the new, changing environments. However few studies have looked at how soil nutrient availability affects plant sexual reproduction and seedling recruitment in heath tundra communities.

1.7 Study Objectives

By examining sexual reproduction and recruitment in heath tundra communities, I hope to identify the role of seeds in community changes associated with increasing soil nutrients and increasing temperature. In particular, I hope to identify how important reproduction from seed is in maintaining the dominance of *H. alpina* and *B. nana* in nutrient-amended treatments, therefore supporting the changes seen in the adult community over the years of treatment. Based on previous studies looking at nutrient manipulations on adult dry heath tundra communities, I tested the following hypotheses regarding the role of sexual reproduction and recruitment in plots that had received added soil nutrients for 12 years, focusing first on the entire community, and then specifically evaluating the response of the two plant species that come to dominate the fertilized plots, *H. alpina* and *B. nana* (See Figure 1.1 for different hypotheses on each life cycle stage).

First, I expected the number of flowers and fruits to be greater for all plant species, including *H. alpina* and *B. nana*, in fertilized plots compared to control plots (H1). Second, I expected that the dispersal of any particular seed of all species would be the same in both treatments. Underlying this hypothesis was an assumption that dispersal ability by wind of all plant species within the community is not going to change under increased nutrient availability (H2). Third, I expected there to be greater seed germination of all species in response to elevated nutrient levels when compared with controls (H3). Finally, I expected the species richness and number of seedlings in both fertilized treatments and passively warmed treatments in the field to be greater than the species richness and seedling numbers in the control treatments (H4). To test these four hypotheses I used a combination of field observations and greenhouse experiments, some of which focused exclusively on *H. alpina* and *B. nana*. Evaluating these hypotheses allowed me to clarify what has happened to these experimental treatments over the past 12 years and also to make predictions regarding future changes in dry heath tundra in Alaska with climate warming and associated increased soil nutrient availability.

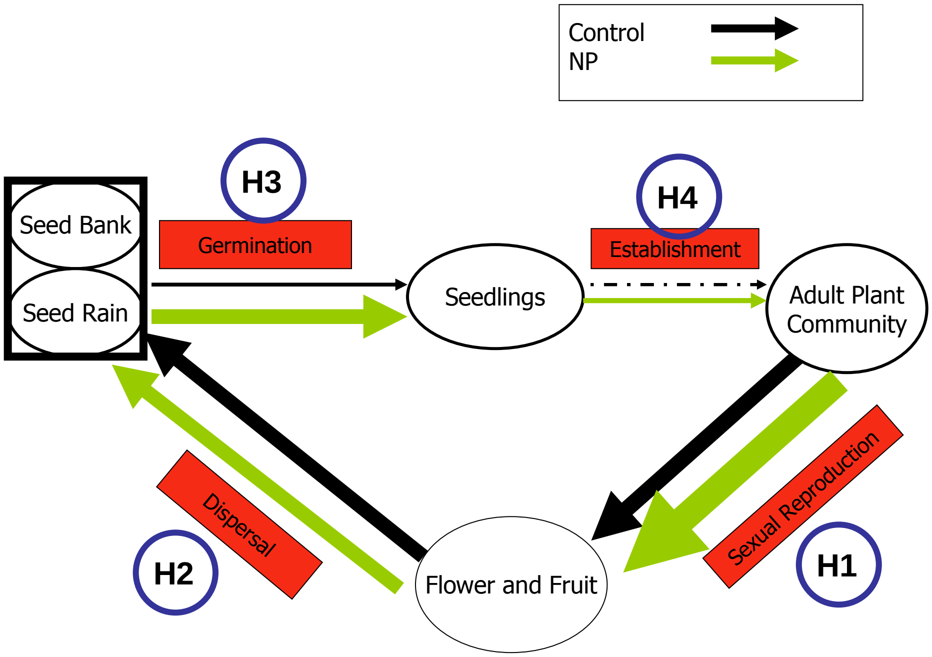

Figure 1.1 Conceptual diagram showing expectations from increased nutrient availability compared to ambient conditions on *H. alpina* and *B. nana* species only in the dry heath tundra at Toolik Field Station. Green arrows indicate fertilizer addition treatments. Thickness of arrows refers to the importance of that process under field treatments.

CHAPTER 2

METHODS

2.1 Field Studies

2.1.1. Study Site

Field studies were conducted at plots maintained by the Arctic Long Term Ecological Research (LTER) project and the International Tundra Experiment (ITEX) project at Toolik Lake, Alaska (68°38'N, 149°43'W, elevation 760 a.s.l.). The Arctic LTER Dry heath (DH) tundra plots are located near the north end of Toolik Lake (Shaver and Chapin 1991; Gough et al. 2002). The tundra is dominated by lichens, deciduous dwarf shrubs, including *Arctostaphylos alpina*, *Vaccinium uliginosum*, and *Salix phlebophylla*, and evergreen dwarf shrub species, including *Empetrum nigrum*, *Ledum palustre*, *Loiseleuria procumbems* and *Vaccinium vitis-idaea* (Nomenclature follows Hultén 1968). Graminoid species, such as *Hierochloe alpina* and *Carex microchaeta*, and the dwarf deciduous shrub, *Betula nana*, are rare but present. Three blocks of ten 5 x 20 m replicate plots were initially established in 1989 as part of the LTER (Table 2.1; see http:/ecosystems.mbl.edu/ARC). Control (CT) and N plus P (NP89, NP96) treatments were randomly assigned within the block design. Annual spring (early June) application of both N (10 g/m^2 as NH_4NO_3) and P (5 g/m^2 as P_2O_5) started in 1989 for NP89 plots, and 1996 for NP96 plots.

The ITEX heath plots are located south of Toolik Lake (Walker et al. 1999, 2006; Table 2.1). The community is also dominated by lichens and both deciduous and evergreen dwarf shrub species similar to the LTER DH. In 1994 a 60 m long by 3 m high snow fence was erected perpendicular to prevailing winter winds, and was designed for snow cover manipulations. The leeward side of the fence was divided into five zones, each containing three control and three warming plots. Open-top chambers (OTC; 0.4 m tall by 1 m diameter fiberglass open-top hexagon) were used for warming treatments (Marion et al. 1997).

2.1.2. Statistical Analysis

All statistical analyses were carried out using SAS v. 9.1.3 for Windows (SAS Inst., Cary, NC, USA). Data were transformed as necessary to meet model assumptions. All statistical analyses differences were considered significant at the 0.05 level. Statistical models used are specified in the sections below.

2.1.3. Percent Cover

Aerial percent cover was estimated in all three blocks of the CT, NP96, and NP89 treatment plots of the LTER DH in mid- to late-July 2007 and 2008. Permanent monitoring plots in the non-destructive sections of each treatment were established in 1998. A 1 m^2 quadrat, divided into 20 x 20 cm sub-quadrats, was placed 0.25 m inside the edge of the plot. Percent cover of moss, lichen and all vascular plant species was estimated visually, with additional estimates of litter and animal activity. The quadrat was then moved to the next 1m^2 area, so that observations were repeated eight times. Relative percent cover of growth forms was calculated by dividing the summed cover of individuals in a growth form by the total plant cover (sum of all non-vascular and vascular species) for that 1 m^2 plot.

Flower and fruit counts of all plant species were taken during the percent cover estimates in both 2007 and 2008. Eight 0.2 m^2 quadrats were sampled per treatment per block. In 2008, flower and fruit counts of *H. alpina* were made on a per tussock basis.

Community composition was compared between fertilization treatments at the LTER DH site using a MANOVA including a block factor to reflect the experimental design; each 1 m^2 quadrat was nested within block. I only report data analysis from 2008 to focus on the longest-running data; patterns in 2007 were quite similar. The data were grouped into the following 8 dependent variables: bare ground, deciduous shrubs, evergreen shrubs, graminoids, lichen, litter, moss and animal category. Animal category included all observed and quantified animal activity (i.e. animal feces, animal litter, etc.) within each treatment. Data were arcsine-square-root transformed prior to analysis to meet assumptions of normality. Differences between fertilization treatments were examined using Wilk’s Lambda as the test statistic.

Species richness was analyzed using an ANOVA to test for fertilizer effect with block and quadrat as described above. Because of concerns about meeting parametric model assumptions, I used the more conservative Scheffe’s test for pairwise differences. To test whether there were differences in number of flowers and fruits between fertilization treatments, I used a Chi square test of independence on the 2007 flower and fruit data, where flowers and fruits were summed for each species to represent total number of reproductive units for that year.

2.1.4. Seedling Surveys

Non-destructive seedling censuses were conducted in late July at the LTER DH site during the collection of percent cover in 2007 and 2008, and at the ITEX heath site in 2007. A seedling was defined as a single, one- to two-leafed, individual separate from similar surrounding species.

At the LTER DH site, CT, NP96, and NP89 were surveyed for seedling numbers. Eight 0.2 m^2 quadrats were sampled per treatment per block. Different quadrats were surveyed each year so duplicate seedlings would not be recorded. Litter and canopy vegetation was shifted, but not removed during searches, which may have underestimated the total number of seedlings recorded. Seedlings were counted and identified to species when possible. If identification to species was impossible, seedlings were grouped by growth form as graminoid, ericaceous, deciduous, or forb.

At the ITEX heath site, seedlings were surveyed in the control and OTC plots in each of the five zones. Each zone was considered a block for this experiment. Sample areas were located by randomly tossing a 20 x 20 cm square into the plot. Only one square was examined in each plot. Seedlings were searched for, counted and identified similar to the LTER seedling census. These data were not analyzed statistically because so few seedlings were found.

2.1.5. Seed Rain Experiment

In late July 2007, a 3 by 3 plot control gradient was set up 35 m north of the three blocks at the LTER DH site to study seed dispersal (Figure 2.1). Three rows were set up 10 m apart from each other, with CT-1 closest to the DH treatment blocks. Within each row, three 2 x 2 m plots were set up 12 m away from each other. Plots were labeled with treatment, year, and plot number (i.e. CT 07 P1-P9). Within the LTER DH blocks (NP89-1 through 4), four 2 x 2 m plots were set up around the NP89 plots (one in each cardinal direction; Figure 2.1). Each plot was labeled with treatment, year, block, and plot number (i.e. NP 89 B1 P1-P4).

In early August 2007, seed rain traps were placed in each plot of the dispersal control gradient grid and the dispersal NP89 set up following Molau (Figure 2.1; Molau and Molgaard 1996, Molau and Larsson 2000). The traps thus collected fall and winter seed dispersal. In each plot, three 0.25 m^2 artificial turf mats were placed in a triangle with the "point" pointing south. Each mat was placed 1 m from the other within the 2 x 2 m plot. The mats were then fixed to the ground using 13 cm nails in two opposing corners. The coordinates of the plots were determined using GPS, and the mats were left out over winter.

On 11 June 2008, the final snowmelt of the spring, each mat was placed in pre-labeled plastic white trash bags. Mats were identified by treatment, block (at NP only), plot, and mat number (1-3). Mats were then sealed in the bags and transported horizontally to an empty lab where bags were opened to allow the seeds to air dry.

On 21 July 2008, mats were processed individually by shaking the contents onto a clean, white surface. Tweezers were used to remove seeds and debris stuck in the trap. Using a clean paintbrush, the contents were swept into a labeled paper bag and placed in a 40° C drying oven for seven days. Samples were transported back to UT Arlington on 30 July 2008. A reference collection of seeds and fruits used for identification was collected from dry heath, moist acidic and moist non-acidic tussock tundra sites in the summer of 2007.

Individual seed trap samples were separated using four different mesh soil sieves (#18, #35, #60 and #170 mesh). Seeds and berries were identified and counted in the lab using an Olympus SZ30 stereo microscope. Caribou feces were also counted if found in the samples.

To determine effects of proximity to the experimental plots on seed dispersal patterns, I first analyzed seed number for the CT plots only with a one-way ANOVA with "block" as the factor of interest reflecting distance from the experimental plots for total seeds and *Betula* separately, including mat and replicate nested in mat to reflect the sampling design. I then analyzed the seed rain results as a one-way ANOVA with fertilization treatment as the main effect, and included block as a blocking factor, mat as a subsample, and replicate nested within mat.

2.2 Greenhouse Studies

2.2.1 Seed Bank Experiments

2.2.1.1 2006 Seed Bank

On 3 August 2006 soil cores were taken from undisturbed locations in the LTER DH site using a 5-cm diameter corer. In each of the three blocks, four cores were randomly located in an area designated for destructive sampling in the NP96 plot, and in the walkway directly to the south of the CT plot (n = 12 cores per treatment; total DH N = 24). Cores were taken to a depth of 5 cm and were then placed in gallon sized plastic bags labeled with date, site, block, treatment, and soil core numbers (1-4). The cores were then shipped to UT Arlington and placed in cold storage (4℃) for 6 months. In February 2007, soil cores were removed and each bag was placed on individual brown craft paper. The four cores from each treatment and block combination were homogenized, removing live mosses, vascular plants, roots, rhizomes, and rocks greater than 1 cm in diameter. Clear plastic deli cups (4.3 cm deep by 11.7 cm diameter) with three drainage holes were filled half way with a mixture of equal parts potting soil and sand. Each deli cup was labeled with the treatment and block (ex. NP-B1), and a replicate number 1 through 8; the homogenized sample was thus used to generate 8 replicates. A 1 cm layer of homogenized soil was placed on top of the potting soil mix. Eight deli cups with the soil mixture were used as blanks for the project. This allowed for identification of non-target seedlings in the greenhouse.

The deli cups were placed in the greenhouse facility at UT Arlington on 2 February 2007. Temperature was set to follow a 20℃ maximum daily temperature and a 15℃ minimum nightly temperature (day/night: 16/8 hour) cycle. To simulate a 24-hour growing season photoperiod, supplemental lighting was provided during both day and night by overhead fluorescent lighting. Replicates were watered with tap water three to four times a week, and monitored daily until the first seed germinated. Replicates were rotated randomly each week to avoid possible temperature gradients within the greenhouse.

Seedlings were monitored weekly for eight weeks and marked using colored toothpicks. Non-target seedlings were removed once identified. Target seedlings were gently removed and repotted in a potting soil mixture for further identification. Transplanted seedlings that dried up prior to identification to species were categorized as graminoid, ericaceous, or unknown.

2.2.1.2 2007 Seed Bank

In late July 2007, prior to setting out the seed rain mats, four soil cores were taken and sampled within each 2 x 2 m plot from the dispersal control gradient grid and the NP89 dispersal set up. The same procedure was followed in sampling and processing as for the 2006 samples. The soils were homogenized according to each treatment and plot combination, and then divided into 5 replicates cups. The experiment began on 25 January 2008 and monitored weekly for eight weeks.

Data from both seed bank experiments were analyzed using the total number of seeds only. A one-way ANOVA was used in both experiments, with fertilization as the main effect, and including block and plot nested in block in the model. The replicates within each plot were averaged prior to analysis.

2.2.2 Germination Experiment

Catkins from *B. nana* and seed heads from *H. alpina* were collected from randomly-located adult plants in dry heath tundra outside of the experimental plots on 26-27 July 2008. These two species were used because both respond to increased nutrient addition in experimental plots (Gough et al. 2002). Seeds were then transported to UT Arlington and placed in a 0℃ freezer on 2 September 2008 for 30 days. On 1 October 2008, seeds were then transferred to zip lock bags with moistened, sterile paper towels and placed in a 4℃ cold room for 15 days for stratification.

Seeds of each species were then separated into 21 groups, one group in one Petri dish, of 10 seeds each. Each group was assigned to one of three treatments: control, half nutrients, and full nutrients (7 groups per treatment). Green Light® water-soluble all purpose (20-20-20) plant food was used as the nutrient source. Full nutrient concentration consisted of 0.71 g/L N (0.29 g/L as NH_3 and 0.39 g/L as $(NH_2)_2CO$) and 0.71 g/L P (as P_2O_5), while the half nutrient concentration consisted of 0.36 g/L N (0.14 g/L as NH_3 and 0.2 g/L as $(NH_2)_2CO$) and 0.36 g/L P (as P_2O_5).

The experiment was run in the greenhouse facility at UT Arlington starting 1 October 2008. Temperature was set to follow a 24℃ maximum daily temperature and a 16° C minimum nightly temperature (day/night: 16/8 hr) cycle. To simulate a 24-hour growing season photoperiod, supplemental light was provided during both day and night by overhead fluorescent lighting. Replicates were watered twice a week with the solution treatment. Data on seed germination were recorded once a week for four weeks. At the end of the experiment, seeds were examined under a dissecting scope for presence of seeds, embryos, and radicles or cotyledons. This was done to determine the number of viable seeds, and if any germination went undetected.

Table 2.1. Summary of field manipulations at Arctic LTER and ITEX DH field sites. CT = Control, NP96 = Nitrogen plus Phosphorus since 1996, NP89 = Nitrogen and phosphorus since 1989; OTC = Open Top Chambers.

	Treatment	**Year Started**	**# of Blocks**
LTER	CT	1996	3
	NP96	1996	3
	NP89	1989	3
ITEX	CT	1994	5
	OTC	1994	5

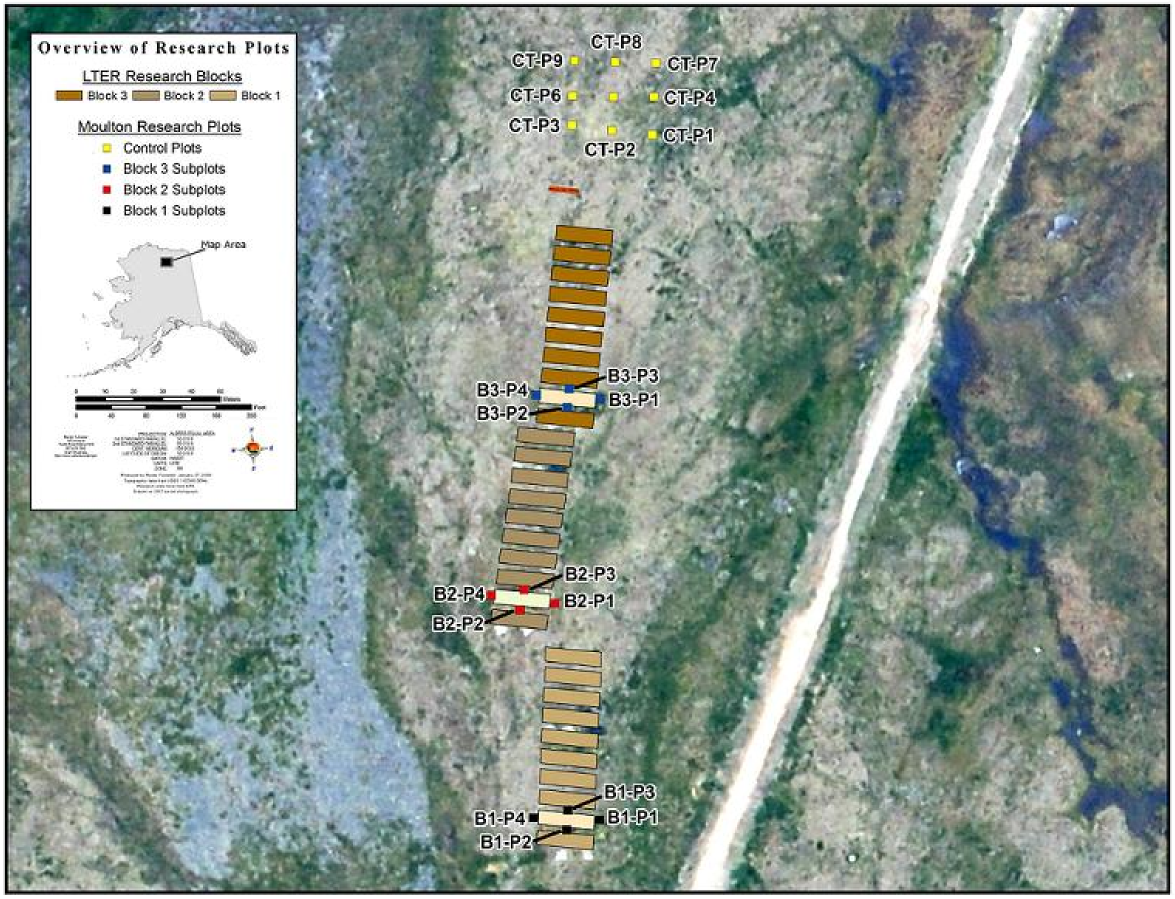

Figure 2.1. GIS map of seed rain and 2007 seed bank plots at the dry heath experimental site, Toolik Field Station. GIS map courtesy of R. Fulweber and J. Stuckey, University of Alaska, Fairbanks.

CHAPTER 3

RESULTS

3.1 Field Results

3.1.1. Percent Cover

Community composition shifted significantly with fertilization, as indicated by an overall significant treatment effect in the MANOVA ($F_{16,78}$=39.08, P<0.0001). Cover of certain growth forms responded significantly to fertilization treatments. Moss, litter and graminoid cover increased significantly with nutrient addition (Figure 3.1). Moss and litter seemed to stabilize after 12 years of treatment, while graminoids, continued to increase cover with continued nutrient manipulation, though not significantly different between the fertilizer treatments. *Hierochloe alpina*, although rare in control plots, had the greatest abundance out of all graminoids observed in fertilized plots (Table 3.1). Both lichen and evergreen cover decreased significantly with the addition of nutrients. *Vaccinium vitis-idaea*, *L. procumbens* and *L. palustre* composed the majority of the evergreen cover in CT plots, but were either rare or eliminated from fertilized plots (Table 3.1). Deciduous cover did not change significantly with fertilization; however, a shift from *A. alpina* to *B. nana* occurred when fertilizer was added (Table 3.1). Bare ground and animal activity also did not differ among the treatments. Species richness decreased significantly in the fertilized plots with a clear indication that more species were lost with additional years of nutrient addition (F = 2.64, *p* = 0.002; Table 3.3). Although not statistically analyzed, community diversity tends to decrease over time with fertilizer addition. The CT community has more species present and the species are more evenly distributed than those in both NP communities. This suggests that species diversity is decreasing as soil nutrient availability increases (Table 3.3).

Flower and fruit data for the following four species are reported here: *B. nana,* and *H. alpina,* because of their presence in the fertilized adult community, and *L. palustre* and *L. procumbens,* because of their high seed number in the seed rain. Other species were excluded in this analysis because they did not show a trend in total dispersed seed numbers. In 2008, flowers were surveyed per tussock for *H. alpina*, instead of 0.2 m^2 for each block by treatment combination as in 2007. Because of the difference in sampling area of *H. alpina* between the two years and to provide comparable data with the other species, I only analyzed the flower and fruit data from the 2007 census. The χ^2 test of independence showed that there was an effect of fertilizer on flowering and fruiting of the targeted plant species ($\chi^2_6 = 2413.60$, $p < 0.0001$). *Ledum palustre* and *L. procumbens*, both evergreen dwarf shrubs, had greater numbers of flowers and fruits per m^2 in the control plots than in the NP96 plots (Table 3.4). Flowers and fruits of these species were absent in the NP89 plots for both years because the adults were either rare or absent in the fertilized community. In contrast, *B. nana* and *H. alpina* had greater numbers of flowers and fruits in both NP96 and NP89 treatments than CT. *Hierochloe alpina* was present, but rare in the 2008 cover data (Table 3.1). *Betula nana*, although not present in the 2008 cover data, has been previously recorded in small quantities in CT plots from biomass harvests, and is quite patchily distributed in CT plots (Gough et al. 2002; Gough unpublished data). Climate conditions were cold and wet in 2006, and may have contributed to low flower bud formation for some species that year (Table 3.2). In 2007 climate conditions were warmer, but dry, which may have affected flower bud formation in 2007 (Table 3.2). No obvious trend between climate conditions and flower and fruit abundance was observed.

3.1.2. Seedling Surveys

Seedling numbers at both field sites and in both years were extremely low, however slightly more seedlings were encountered on a per m^2 basis at the ITEX DH site than at the LTER DH site (Table 3.5). At the LTER DH site, one unknown ericaceous seedling was recorded from 24 plots in CT, and one unknown graminoid seedling was recorded from 24 plots in NP89 in 2007; no seedlings were encountered in any of the surveyed plots in 2008, which may have been affected by the warm, dry growing season in 2007 (Table 3.2, 3.5). Seedling counts from a 2006 biomass harvest of DH showed one *E. nigrum* seedling in CT, and one *H. alpina* seedling in NP96 plots (Gough unpublished data).

At the ITEX DH site, both CT and OTC plots were littered with deposited seeds of various species (personal observation); however observed seedling counts were still extremely low. In CT plots, one unknown ericaceous seedling and one unknown graminoid seedling were recorded. In the OTC plots, two unknown graminoid seedlings, one *L. procumbens* seedling and one *V. vitis-idaea* seedling were recorded (Table 3.5).

3.1.3. Seed Rain

The artificial turf mats design described by Molau and Molgaard (1996) for the ITEX manual worked well in collecting seeds that had been dispersed. The mats are best for capturing seeds 0.3 mm or larger, which includes seeds of all the species reported here (Molau and Larsson 2000).

Seeds recovered from both CT and NP89 seed traps were similar in species composition. *Betula nana, L. procumbens* and *L. palustre* were the most abundant species, and were collected in almost all plots in both treatments (Figure 3.2). No differences were found between total seed numbers collected from control mats and those close to fertilized plots, although there was a suggestion of more *B. nana* seeds on mats adjacent to fertilized plots ($F_{1,48} = 3.37$, $P = 0.07$; Figure 2.1, 3.2). When total seeds and *B. nana* seeds were analyzed for control plots only, a significant effect of “block” or distance from the experimental plots was found: more total seeds ($F_{2,16} = 3.70$, $P = 0.05$) and more *B. nana* seeds ($F_{2,16} = 4.61$, $P = 0.03$) were collected closer to the plots than farther away. The number of *B. nana* seeds recorded was higher in the dispersal gradient closest to the NP89 plots (CT-1: max = 502, min = 1) than in the rows further away (i.e. CT-2: max = 26, min = 2).

Within the NP89 treatments, the number of *B. nana* seeds varied greatly in two of the three blocks (NP89-2: max = 5835, min = 3; NP89-3: max = 4161, min = 10), driving the high variance in total seeds among the blocks. The “other” category consisted of the remainder of the species recorded in the seed traps. In NP89-1, seeds of the grass, *Calamagrostis canadensis*, made up a majority of the “other” category (173 seeds out of 184 total “other” seeds). *C. canadensis* seeds were also present in NP89-2, but were fewer in number. *H. alpina* seeds were slightly greater in number in the NP89 mats, but only accounted for a small percentage of the “Other” category, and were not examined separately statistically. Seeds of the boreal species of fireweed, *Epilobium angustifolium*, were present in low numbers in both CT and NP89 seed traps (Table 3.1). Adults of this plant species are found in the NP89 adult community and along the side of the road adjacent to the study site.

3.2 Greenhouse Results

3.2.1. Seed Bank Experiment

3.2.1.1 2006 Seed Bank

In both seed bank experiments, stray, non-target seedlings germinated in the deli cup replicates. These were removed and not counted in the analysis. In the 2006 soil seed bank, more seedlings emerged overall from fertilized soil cores when compared with control cores collected the same year ($F_{1,22} = 5.48$, $P = 0.03$; Table 3.6). The germination of seeds in both the graminoid and ericaceous categories was higher in soils after 12 years of fertilization. *Hierochloe alpina* only germinated in the nutrient-amended soils. No *B. nana* seeds germinated in the 2006 seed bank experiment, although adults were present in both treatments. The presence of *H. alpina* seedlings in the fertilized soils likely reflects the high relative abundance of the adults in fertilized plots and the increased abundance of *H. alpina* seeds in the soil seed bank.

3.2.1.2 2007 Seed Bank

Contrary to the 2006 seed bank results, total number of germinated seeds in 2007 did not significantly differ between the total germinated seeds in CT and NP89 (130 ± 39 seedlings/m^2 and 83 ± 30 seedlings/m^2, respectively). *Hierochloe alpina* and *B. nana* only emerged from the fertilized soil cores, and were absent in the control soil cores (Table 3.1). This pattern is similar to the composition of the adult community of the two treatments. Two ericaceous species (Ericaceous sp1 and Ericaceous sp2) emerged only in the control soils (Figure 3.3). Ericaceous sp 1 seedlings were small in size (1-2 mm across length of cotyledons) and generally sprouted in clusters. Ericaceous sp 2 seedlings were also small in size (3-5 mm across length of cotyledons) and had grey-green, lance-shaped cotyledons. These two unknowns did not germinate in the blank replicates therefore are considered native Alaskan seedlings.

Within the dispersal control gradients, seedling totals increased with distance from the NP plots which was the inverse of the pattern in the seed rain results (see Figure 3.2 and 3.3). However the differences in total seedlings among the control gradients were not significant because of the variability within the dataset (Figure 3.3). *Betula nana* seeds were abundant in the seed rain in the gradient row closest to the NP plots, but did not germinate in the seed bank from that row, suggesting that this species is not dispersal limited. The graminoids that germinated in the seed bank did not appear to follow the pattern of the seed rain, which had an overall low number of seeds dispersed by graminoids. In the seed bank, more graminoid seeds germinated in soils from each CT gradient than were accounted for in the CT seed rain. The graminoids that germinated in the NP soils may reflect the seed rain from NP plots, since more graminoid seeds were dispersed from NP plots than CT.

3.2.2. Germination

In the greenhouse germination experiment, *H. alpina* seeds did not germinate in any treatment. Seeds were kept in the husk for the duration of the experiment, which may have restricted germination. Out of 210 caryopses used, 66 seeds were viable but showed no indication of germination. Forty-nine seeds were not viable (i.e. no fully developed embryo, deformed seed, etc.), and the remaining 93 had no seed present in the caryopsis.

All *B. nana* seeds had embryos present, and germination occurred in all three treatments. Germination was greatest in control conditions, with 37 (±5) % of the seeds germinating. Half nutrient conditions had 10 (±4) % of the seeds germinate, and only 3 (±2) % of the seeds germinated under full nutrient conditions.

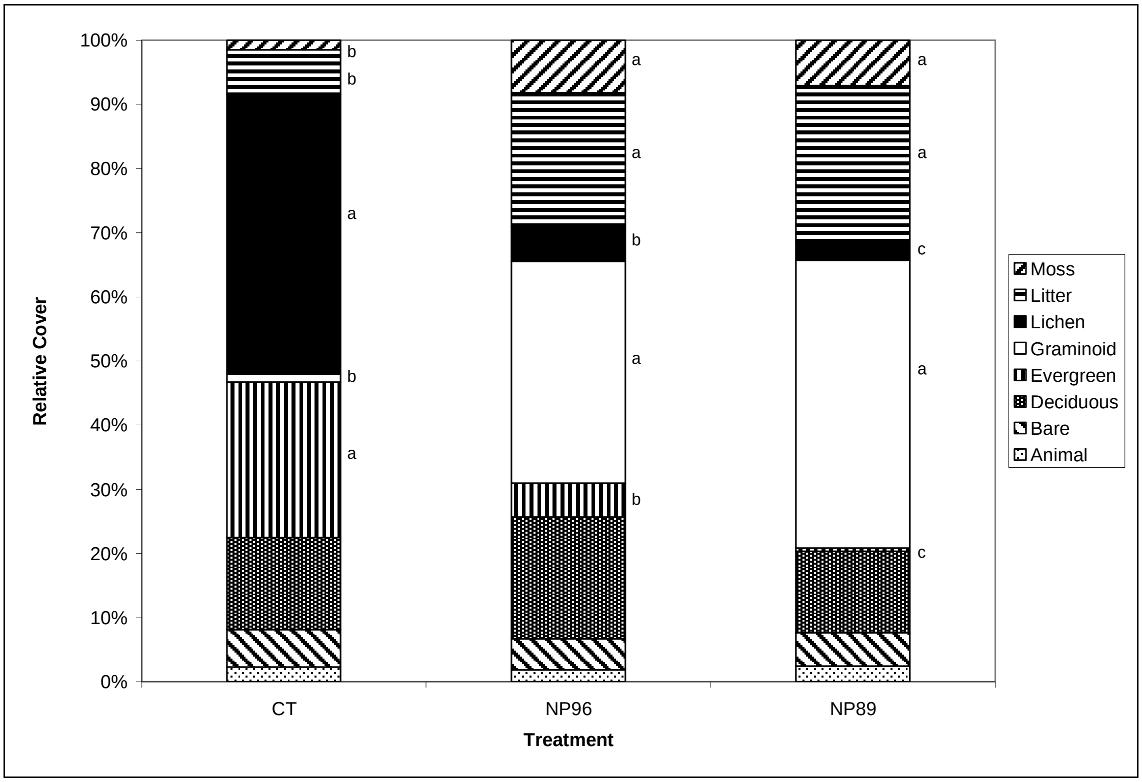

Figure 3.1. Relative cover of the adult dry heath tundra community in 2008. Different letters indicate significant differences within a particular growth form. No letters indicate differences are not significant.

Table 3.1 Summary of plant species at dry heath (DH) tundra near the Arctic LTER at Toolik Lake, AK. Nomenclature follows Hultén (1968). Quantities are mean ± SE per m^2.

		Adult % cover			Seed Rain		Seed Bank				Seedlings (field)		
Growth Form	Species	CT	NP96	NP89	CT	NP89	CT 2006	CT 2007	NP96	NP89	CT	NP96	NP89
Graminoid	Unknown Graminoid	-	-	-	-	-	13 ± 4	44 ± 15	29 ± 19	20 ± 10	0.2 ± 0.2	-	0.2 ± 0.2
	Hierochloe alpina	0.01± 0	0.42 ± 0.08	0.57 ± 0.06	1 ± 1	16 ± 3	-	-	50 ± 19	3 ± 3	-	-	-
	Carex microchaeta	-	0.04 ± 0.03	0.01 ± 0	4 ± 2	8 ± 5	-	-	-	-	-	-	-
	Arctagrostis latifolia	-	0.03 ± 0.02	0.04 ± 0.02	4 ± 3	1 ± 1	-	-	-	-	-	-	-
	Calamagrostis canadensis	-	-	-	1 ± 1	29 ± 20	-	-	-	-	-	-	-
	Poa pratensis	-	-	-	-	1 ± 1	-	-	-	-	-	-	-
	Carex spp.	-	-	0.03 ± 0.03	-	-	-	-	-	-	-	-	-
Evergreen	Unknown Ericaceous	-	-	-	-	-	17 ± 7	36 ± 7	25 ± 18	56 ± 23	-	-	-
	Ericaceous SP1	-	-	-	-	-	-	41 ± 21	-	-	-	-	-
	Ericaceous SP2	-	-	-	-	-	-	9 ± 9	-	-	-	-	-
	Empetrum nigrum	0.04 ± 0.01	-	-	2 ± 2	2 ± 1	-	-	-	-	-	-	-
	Ledum palustre	0.07 ± 0	0.02 ± 0.01	-	204 ± 62	190 ± 22	-	-	-	-	-	-	-
	Loiseleuria procumbens	0.09 ± 0.01	-	-	597 ± 124	419 ± 110	-	-	-	-	-	-	-
	Vaccinium vitis-idaea	0.09 ± 0.01	0.05 ± 0.03	0.01 ± 0	6 ± 3	3 ± 1	-	-	-	-	-	-	-
Deciduous	*Arctostaphylos alpina*	0.15 ± 0.05	0.01 ± 0	-	-	-	-	-	-	-	-	-	-
	Betula nana	-	0.18 ± 0.09	0.15 ± 0.04	194 ± 158	1584 ± 714	-	-	-	3 ± 2	-	-	-
	Vaccinium uliginosum	0.02 ± 0.01	0.06 ± 0.02	0.01 ± 0	-	-	-	-	-	-	-	-	-
Forb	*Epilobium angustifolium*	-	-	0.04 ± 0.04	1 ± 0.4	3 ± 1.3	-	-	-	-	-	-	-
Moss	moss	0.02 ± 0.01	0.12 ± 0.02	0.11 ± 0.03	-	-	-	-	-	-	-	-	-
Lichen	lichen	0.51 ± 0.04	0.08 ± 0.04	0.04 ± 0.02	-	-	-	-	-	-	-	-	-
Totals					253 ±85	554 ±143	29 ±8	115 ±29	104 ±51	82 ±28			

Table 3.2 Climate summaries for temperature (℃) and precipitation from the central weather station at the Arctic LTER at Toolik Lake. Temperatures were measured at a height of 1 m until September 2008 when the sensor shifted to a height of 3 m. These data are found at http://ecosystems.mbl.edu/ARC/weather/tl/index.shtml.

		Temperature (℃)						Precipitation (mm)				
Year	Month	May	June	July	Aug	Sept		May	June	July	Aug	Sept
1988-2008	T_{mean}	-1.1	8.8	11.2	7.3	-0.2		16.1	42	78.2	62.2	30.4
2006	T_{max}	1.6	14.1	24.3	16.8	17.1						
	T_{mean}	-4.7	9.6	10.1	5.5	4.8		9.3	20.2	27.4	20.7	10.4
	T_{min}	-11.3	4.9	-1.9	-3.7	-4.6						
2007	T_{max}	13.1	26.2	23	21	8.7						
	T_{mean}	-3.2	11.4	13.1	10.1	3.1		2	8.9	20.8	11.3	1.1
	T_{min}	-20.6	-2.8	0.4	-2.3	-3.3						
2008	T_{max}	2.2	15	14.9	8.8	2.3						
	T_{mean}	-2.3	9.6	10.6	4.3	-1.8		7.7	25.8	37.4	5.8	6.1
	T_{min}	-7.4	3.7	5.4	-0.8	-6.2						

Table 3.3 Species richness (S) and Diversity (H') in LTER DH 2008 cover/m^2. Results reported as mean ± SE. Different superscript letters indicate significant differences between treatments.

	S	H'
CT	7.5 ±0.4^{a}	1.3 ±0.03
NP96	6.3 ±0.5^{b}	1.2 ±0.06
NP89	4.9 ±0.4^{c}	0.9 ±0.03

Table 3.4 Number of fruit and flower totals per m^2 at LTER DH over two years. In 2008 *H. alpina* data is reported as mean ±SE number of flowers per tussock per m^2.

	CT		96NP		89NP	
SPECIES	2007	2008	2007	2008	2007	2008
B. nana	0	0	93 ±48	166 ±135	82 ±69	51 ±19
H. alpina	0	0	106 ±18	16 ±8	99 ±28	14 ±6
L. palustre	11 ±8	13 ±11	1±1	10 ±10	0	0
L. procumbens	125 ±31	126 ±73	2 ±2	0	0	0

Table 3.5 Number of seedlings recorded per m^2 at LTER DH and ITEX DH over two years. Results reported as mean ± SE.

		LTER Dry Heath			ITEX Dry Heath	
YEAR	SPECIES	CT	NP96	NP89	CTL	OTC
2007	Ericaceous	0.2 ±0.2	0	0	1.7 ±1.7	0.0
	Graminoid	0	0	0.2 ±0.2	1.7 ±1.7	3.3 ±3.3
	L. procumbens	0	0	0	0.0	1.7 ±1.7
	V. vitis-idaea	0	0	0	0.0	1.7 ±1.7
	TOTAL	0.2 ±0.2	0	0.2 ±0.2	3.4 ±3.4	6.7 ±4.1
2008	Ericaceous	0	0	0	▨	▨
	Graminoid	0	0	0	▨	▨
	TOTAL	0	0	0	▨	▨

Table 3.6 Number of seedlings per m^2 in 2006 seed bank. Results reported as mean ± SE.

SPECIES	CT	NP96
Ericaceous	17 ±7	25 ±18
Graminoid	13 ±4	29 ±19
H. alpina	0	50 ±19
TOTAL	29 ±8	104 ±51

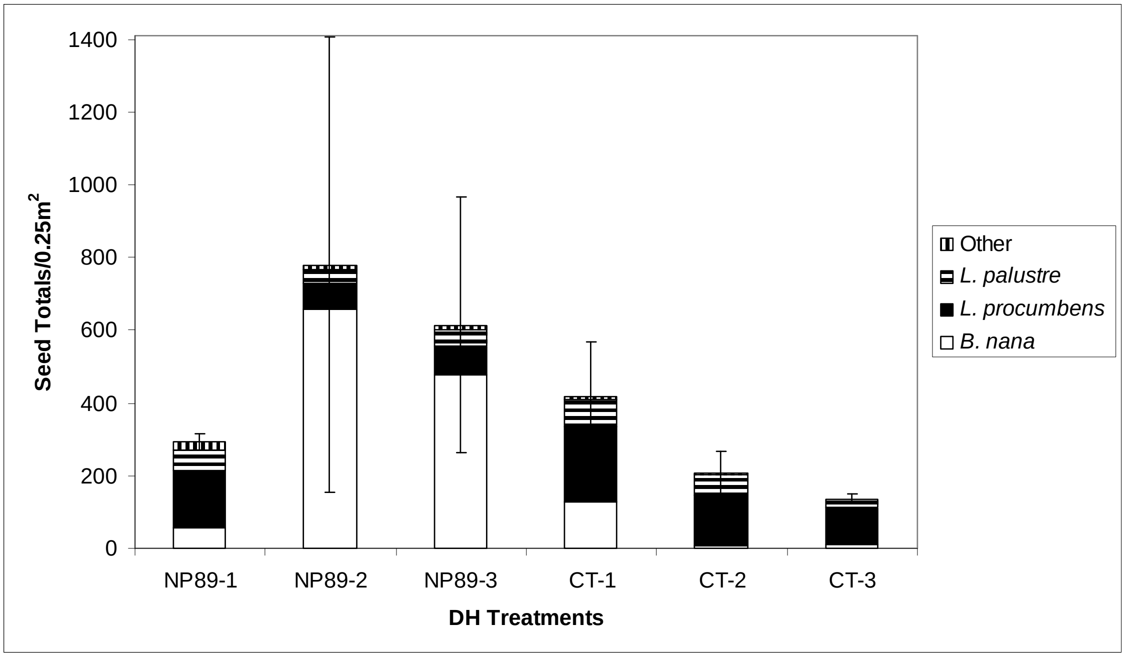

Figure 3.2 Total number of seeds dispersed per 0.25 m^2 separated by species. Error bars represent ±1 SE of total number of seeds collected.

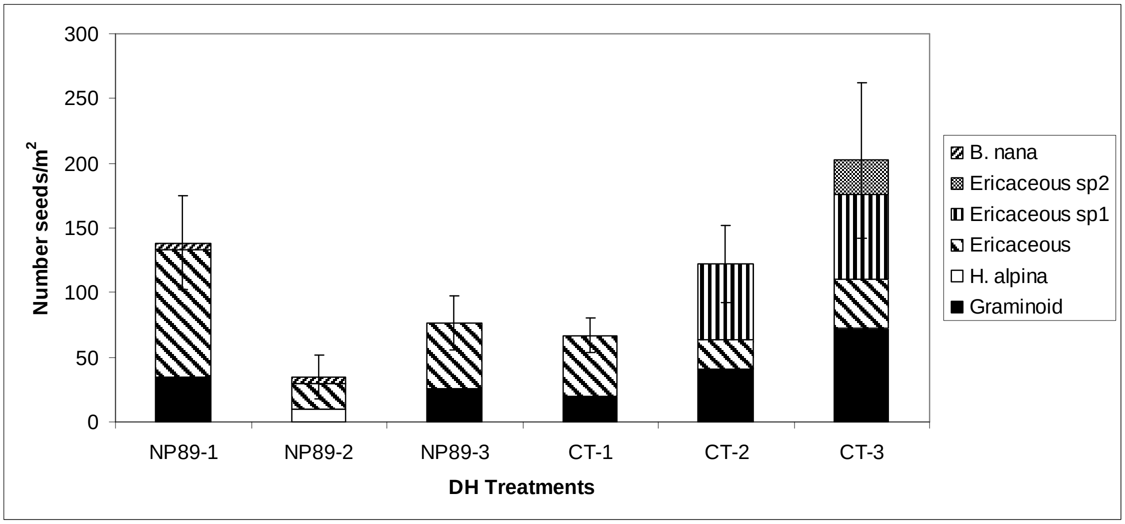

Figure 3.3 Number of seeds germinated in 2007 seed bank experiment. Error bars represent ±1 SE of total number of seeds germinated.

CHAPTER 4

DISCUSSION

4.1 Adult Community

After 12 years of nutrient addition to the dry heath tundra plots, I saw similar changes in species composition as documented in an earlier study at the same site examining the effects of fertilization after 9 years (Gough et al. 2002). Community composition of the adult vegetation shifted from an evergreen dwarf heath shrub and lichen dominant community to one dominated by the grass, *H. alpina*. A shift in deciduous dwarf shrub species from *A. alpina* to *B. nana* occurred after 12 years of fertilizer addition. *Betula nana* is present, but rare, within the control dry heath community and is taller and shrubbier compared to *A. alpina*. When released from nutrient limitation, *B. nana* is able to increase production of branches that develop into a larger canopy (Bret-Harte et al. 2001, 2002). This canopy likely shades the understory, limiting light resources to *A. alpina*.

The change in species composition with nutrient additions shown here follows that of other fertilization experiments on dry heath tundra (Press et al. 1998; Grellman 2002; Cornelissen et al. 2001; Richardson et al. 2002), as well as the natural shift from heathlands to grasslands in northern Europe as a result of atmospheric nitrogen deposition (Roelofs 1986; Berendse et al. 2001; Heijmans et al. 2001; Aerts and Berendse 1988; Vitousek et al. 1997). In habitats with low nutrient availability, evergreen plants are able to establish and thrive because (a) they continue to photosynthesize and accumulate biomass longer than deciduous plants during the growing season (Chapin and Shaver 1989), and (b) they conserve nutrients better than other deciduous plants because their leaves have low nutrient concentrations and longer life spans (Aerts 1995). However, when nutrients become more readily available in the ecosystem, other plant growth forms, such as graminoids and deciduous dwarf shrubs, are able to maximize growth and outcompete the evergreens and lichens. The observed shift from evergreen dwarf shrubs and lichens to graminoids and deciduous dwarf shrubs in heath tundra systems after 12 years of nutrient addition may become more pronounced with continued nutrient addition. After 19 years of nutrient addition, evergreen shrubs become even rarer within the community, suggesting potential local extinction of those species in dry heath tundra communities.

The increase in plant litter abundance observed in nutrient amended heath communities is also consistent with other studies at dry heath under increased nutrient availability (Gough et al. 2002, 2008), as well as in other tundra communities (Bret-Harte et al. 2008; Aerts and Berendse 1988; Press et al. 1998). At dry heath tundra systems, senescent *H. alpina* leaves contribute most of the of plant litter. This increase most likely played a role in the community shift by possibly shading out existing evergreen dwarf shrubs and lichens. This idea is supported by a study by Jensen and Gutekunst (2003) that detected a decrease in light levels under plant litter accumulation in a fen grassland community. Studies examining the effects of plant litter on vegetation suggest that litter can have positive aspects in plant communities, such as trapping moisture during dry seasons (Fowler 1968) and providing nutrients upon decomposition (Facelli and Pickett 1991). However, the overall effect of plant litter in communities is negative because of the large role litter plays in how plant communities are structured, specifically by affecting species richness (Foster and Gross 1998; Xiong and Nilsson 1999).

Overall, there was an effect of nutrient addition on fruits and flowers for all four species examined, providing mixed support of my first hypothesis because fruits and flowers increased for some species and decreased for others (H1; Figure 4.1). The two evergreen species that were examined, *L. procumbens* and *L. palustre*, had fewer flowers and fruits in fertilized plots than control because these species became less abundant in the fertilized adult community. Flower and fruit numbers of *H. alpina* and *B. nana* were greater under increased nutrient levels, most likely an effect of greater relative abundance within the fertilized adult community. Flowering within these two species is most likely an effect of increased soil nutrient availability. Gough et al. (2007) found a significant increase in *H. alpina* flowering measured on individual plants under fertilized conditions in dry heath compared to control conditions. Similarly, a trend toward greater flowering of *B. nana* due to increased nutrient availability at dry heath tundra was observed on individual plants, although this data analysis was not significant (D.R. Johnson unpublished data). Similar studies of increasing flowering structures were noted in *B. nana* at moist acidic tussock tundra communities at the Arctic LTER. *B. nana* increased the number of inflorescences per individual plant when exposed to increased nutrients (Bret-Harte et al. 2001).

4.2 Seed Rain

Species composition of dispersed seeds was similar in nutrient-treated and control plots, but the abundance of seeds of many species differed between the two treatments, causing me to reject my second hypothesis (H2). The underlying assumption that seeds of different species do not differ in dispersal ability is also rejected. Within the treatments, the number of total seeds varied among the blocks, suggesting that seeds are not dispersing equally into the landscape. There was a decrease in total seed abundance, in particular *B. nana* seeds, across the control gradient. This decrease in seed abundance suggests there is a correlation between proximity to fertilized plots and *B. nana* seed dispersal. This correlation implies that the experimental plots at DH could potentially be a seed source of for this species, and under naturally increasing soil nutrient availability, the dispersed *B. nana* seeds could potentially help shift other parts of the tundra. The presence of higher seed abundance of *L. palustre* and *L. procumbens* in control plots was probably due to their increased presence in the adult community. Fruits of both species are dehiscent dry fruits, where the walls of the fruit break open, allowing seeds to disperse into the landscape (Raven et al. 2005). *Ledum palustre* seeds are 0.2-2 mm long with a loose, elongate testa, or seed coat, which aids in wind dispersal (Karlin and Bliss 1983; Densmore 1997). *Loiseleuria procumbens* seeds are 0.4-0.6 mm long and smooth (Aiken et al. 1999). Seeds of these two species are most likely wind dispersed, although my results suggest that the seeds dropped to the ground near the parent plants, instead of dispersing into the landscape, causing high numbers of seeds in the seed rain.

Although rare in the adult community, *H. alpina* and *C. canadensis* seeds were found in low numbers in the control seed traps. Fruits of both species are one-seeded, dry, indehiscent fruits, where the seed stays in the fruit after dropping from parent plant (Raven et al. 2005). *Hierochloe alpina* seeds are 2.8-3 mm long, while *C. canadensis* seeds are 1.6-2 mm long (Aiken et al. 1995, 1999). Fruits of these two species are most likely wind dispersed due to their small size. Dispersal from fertilized plots could have contributed to these seeds found in the traps, since both species increase their presence in nutrient amended soils, increasing the chance of seeds dispersing into the landscape.

Among the fertilized blocks, variability was mainly driven by the presence of *B. nana* seeds. The high output of *B. nana* seed in fertilized plots may be a result of increased inflorescence abundance under nutrient-amended conditions (Bret-Harte et al. 2001). The small size and low weight of the seeds make them well-suited for dispersal over long distances, which could explain why large numbers of seeds were recorded in the control gradient closest to the fertilized plots, but does not explain the high variability within fertilized plots. In a seed rain experiment conducted in Northern Sweden, wind-dispersed seeds, including a *Betula* species, were recorded in large numbers and found beyond their known distribution (Molau and Larsson 2000), suggesting that certain seeds can reach long distances within the landscape via wind dispersal. *Calamagrostis canadensis* also did not disperse equally in the fertilized treatment landscape. The seeds of this species seemed to disperse only short distances (1-5 m) since seed numbers varied among the blocks. Although not recorded in the area sampled in 2008, *C. canadensis* has been documented as the second most abundant grass in arctic dry heath fertilized plots, although still relatively low (Gough et al. 2002), and supports the presence of their seeds in the seed rain.

Epilobium angustifolium seed presence in the seed rain suggests that immigration of plant species is occurring into this plant community when soil nutrients are increased. *Epilobium angustifolium* has been recorded in dry heath plots that have received nutrient addition for almost 20 years, as well as in other experimental plots in different, nearby tundra communities (Gough, unpublished data). This species was seeded into the former oil pipeline construction camp at Toolik Field Station as an attempt to revegetate the gravel pad, and has maintained populations in the disturbed areas, but is not seen in tundra with ambient soil nutrients (Hultén 1968). The seeds of this species have plumes which aid in wind dispersal (personal observation). Therefore the seeds could very easily travel from the camp to the adjacent tundra, where they are dispersed into the landscape each year, and then germinate when conditions become favorable. This species is present in plots that have received NP for 19 years. It was not recorded in the community composition survey because it is patchy within those plots, but seems to have become more present in those plots in the past several years.

4.3 Germination

4.3.1 Greenhouse Germination

The results from the greenhouse germination experiment did not support my third hypothesis (H3). The lack of germination in *H. alpina* could be attributed to several factors, including the short stratification period it received prior to the experiment. *Hierochloe alpina* seeds are physiologically dormant, requiring a cold stratification period to facilitate germination (Baskin and Baskin 2001). A stratification period of 15 days at 4℃ may have been too short to break seed dormancy. The low presence of viable seeds suggests that *H. alpina* seed production in 2008 was low, probably due to the warmer, drier growing season in 2007 when flower buds were formed (Table 3.2).

The stratification period of 15 days was enough to break seed dormancy of *B. nana.* This species, also physiologically dormant, requires only 14 days of cold stratification to break dormancy (Baskin and Baskin 2001). Although some germination did occur, overall, increased nutrient solutions appeared to inhibit germination of *B. nana* seeds. However I do not think the results for this species are enough to reject my third hypothesis. One study looking at nutrient addition and germination found that germination increased with nutrient availability (Pons 1989), which is contradictory to my findings. Therefore this experiment should be repeated on *B. nana* seeds, one using filter paper to retest these results, and another using sterile soil/growing medium. I would also use a growth chamber instead of a controlled greenhouse, since light and temperature are better controlled. The concentrations of the nutrient solutions should stay the same to test for the effects of increased nutrients on germination.

4.3.2 Seed Banks

Germination from seed banks varied in abundance and species composition between the two soil treatments and between years, providing mixed support for my third hypothesis (H3). The abundance of germinated seeds in nutrient amended plots was greater than from control plots in the 2006 experiment, but not the 2007 experiment. This could have occurred because the 2007 nutrient-treated soil cores were collected from the seed rain plots surrounding the fertilized treatments, and not from the actual soils that have been receiving 20 years of nutrient addition. I assumed that leaching of applied fertilizer pellets would also reach into the 1 m buffer surrounding each 5 x 20 m treatment, but I did not test soil nutrient levels. Therefore I focus on the 2006 results below because I know these soils received the nutrient treatment.

Species composition in the nutrient-treated soils reflected the changes in the adult community. The presence of *H. alpina* seedlings in nutrient-amended soil seed banks suggests that this species is being dispersed and incorporated into the soil and is adapted to increased nutrient availability. The lack of *B. nana* seed germination in the 2006 fertilized seed bank contradicts the results from the seed rain experiment. Because of the high seed abundance of this species in the seed rain, *B. nana* seeds may have been present in the seed bank experiment, but did not germinate. The reason these two species were not seen in the 2006 control soil seed bank could be attributed to the low abundance in the adult community, low seed dispersal into the control plots, and lower soil nutrient availability.

The lack of other species in the 2006 fertilized seed bank may be because the seeds of other species may lose viability over time, and if dispersal into the fertilized plots is low, then they are not reincorporated into the seed bank. If seeds of other species had dispersed into the fertilized treatments, the presence of plant litter and mosses may have hindered their incorporation into the soil, leaving the seeds to rest on top. I removed the plant litter and moss layer from the soil prior to the experiment, which may have resulted in removing these species that had dispersed into the fertilized plots.

The 2007 soil samples were collected from plots designed to look at seed dispersal from the adult communities. The data from the 2007 seed bank show the reverse pattern from the 2006 seed bank and there was more variability among the treatments in this year. The 2007 control seed bank had more seeds germinate than the 2007 fertilized seed bank. *Betula nana* and *H. alpina* seeds were present in soils from seed banks adjacent to the nutrient amended plots, indicating dispersal from the adult community. The lack of these species in the control seed bank suggests that a) seeds are not being produced from adults in the control plots, b) seeds are being produced but are not incorporating into the soil, or c) seeds are being produced and are incorporating into the soil, but are not viable or germinating. *Hierochloe alpina* seeds, if present in the control soil seed bank in 2007, most likely were not viable, based on the low numbers of viable seeds observed in my germination experiment. Low viability may also be why so few *H. alpina* seeds germinated from seed banks adjacent to the nutrient amended plots, although seeds were probably more abundant there than in control soils based on the flower and fruit abundance in the adult NP vegetation. Although *B. nana* seeds are dispersing into parts of these control plots, the seeds may not be integrating into the soil. Low incorporation of seeds of all species into the seed bank may be a result of soil particle size, which may or may not increase trapping of seeds (Chambers et al. 1991), or exposure to high winds on dry heath tundra, which cause wind dispersed seeds to move further distances (Chambers 1995).

4.3.3 Seedling Surveys

Numbers of seedlings were low in both experimentally manipulated plots and control plots in dry heath tundra, so my test of my fourth hypothesis was inconclusive (H4). These results are important because they suggest that the current role of seedling establishment is low in both ambient and nutrient-amended soils. However, initial recruitment from seed must have been a part of the community transition. Had the transition been solely by vegetative growth, the cover of *H. alpina* and *B. nana* after 12 years of nutrient addition would not be as pronounced as it is currently. Multiple seedlings must have established within the plots, which then increased abundance by clonal growth.

Seedling counts from a 2006 biomass harvest from dry heath tundra were also very low and did not differ significantly between fertilized and control treatments, although germinated species were different: *E. nigrum* in the control and *H. alpina* in the fertilized (Gough unpublished data). In the nutrient-amended treatments, low seed germination and establishment in the field may be a result of the presence of plant litter. Increases in plant litter production may negatively affect seed germination and seedling emergence (Bosy and Reader 1995; Foster and Gross 1998; Xiong and Nilsson 1999). However, plant litter has been shown to increase water moisture in dry habitats (Fowler 1986), which may be beneficial in dry heath tundra where moisture content in the soil is low. Since the overall number of recorded seedlings was low, seedling establishment appears to be limited by abiotic and biotic interactions: low nutrients and temperature, and competition for space in control plots, and competition for space due to increased plant litter accumulation and larger plants in fertilized plots.

More seedlings were encountered on a per m^2 basis in the warming treatments at the ITEX heath site than at the LTER dry heath site, suggesting that air temperature increases may contribute to greater seed germination. If seedling survey sample size increased in warming treatments, perhaps the trend toward increasing seedling establishment could be identified. Although warming increases production of flowers and seeds (Alatalo and Totland 1997; Aerts et al. 2006), little is known about recruitment under warming conditions. Large numbers of seeds were observed at the dry heath ITEX site both inside and outside of the OTC plots (personal observation). The OTCs may be restricting dispersal of seeds to the outside landscape, which could potentially increase the number of seeds available for germination. Large numbers of seeds from the tussock-forming sedge *Eriophorum vaginatum* were also observed in plastic greenhouse warming experiments of the moist non-acidic tussock tundra at the Arctic LTER (Gough personal communication). These structures may increase the probability of seed germination due to the fact that dispersal is restricted. The seeds located outside of the OTCs were most likely deposited over the winter in the snow drifts on the leeward side of the snow fence. Overall, very few seedlings were recorded in all treatments.

4.4 Synthesis

My results suggest that the adult community in fertilized treatments most likely came from a combination of seedling recruitment and vegetative reproduction. As expected, nutrient addition increases flower and fruit abundance for those species that are more abundant as adults, particularly *H. alpina* and *B. nana* (Figure 4.1). Dispersal of seeds was greater with nutrient availability, particularly for *B. nana* species because of its greater abundance in the adult fertilized community. Dispersal into the community varied greatly among the plant species suggesting that seeds are unequally dispersed into the landscape. Germination from nutrient amended soil seed banks also increased, in particular with seeds of *H. alpina* and *B. nana*. Buried seed of these two species in nutrient-amended soils most likely comes from the seed rain from the adult plants in fertilized treatments. The fact that these two were absent in control seed banks suggest that these species are limited in seed rain, that seed production of the rare adult plants in the control plot is very low, or that there are no viable seeds of these species in control soils. Seedling establishment was not greater under increased nutrient availability compared to ambient conditions, implying that seedling recruitment in the field is very rare.

Nutrient availability affects each process in the plant life cycle, enabling the “new” *H. alpina* community to develop (Figure 4.1). Earlier in the transition to the grassland community, this species was able to take advantage of the available nutrients to produce reproductive structures and germinate from seed, possibly increasing clonal growth as the seedlings became established. However currently under nutrient-amended conditions, recruitment from seed is less important, most likely due to lack of available areas to germinate. Plant litter most likely plays a large role in dictating seedling establishment by reducing resources such as light and suppressing establishment of germinated seedlings. Disturbances such as the removal of litter or adult vegetation by herbivores may create conditions where germination can occur.

If nutrients in tundra communities become more readily available as climate change continues, species that are better adapted to the new soil conditions could potentially outcompete the current dominant plant species, as shown in these manipulative experiments. Immigration by seed of species not currently found in tundra communities, such as *Epilobium angustifolium*, could potentially flourish due to their ability to take advantage of the increased nutrients. Possible northward advancement of the boreal treeline could also become an issue if climate continues to warm and alter nutrient levels in the soil. Hobbie and Chapin (1998b) found that *Picea glauca* seedlings grew well and survived in treatments that increased air temperature and nutrient availability in arctic tundra. Their results suggest that conditions associated with climate change may allow treeline species to invade, which may significantly affect ecosystem processes. Geographic barriers, such as the Brooks Range in northern Alaska, have impeded seed dispersal from the lower latitudes into the tundra. However accidental dispersal into the tundra by mammals, birds and humans may allow immigrant species of seed to lie dormant until favorable growing conditions arise.

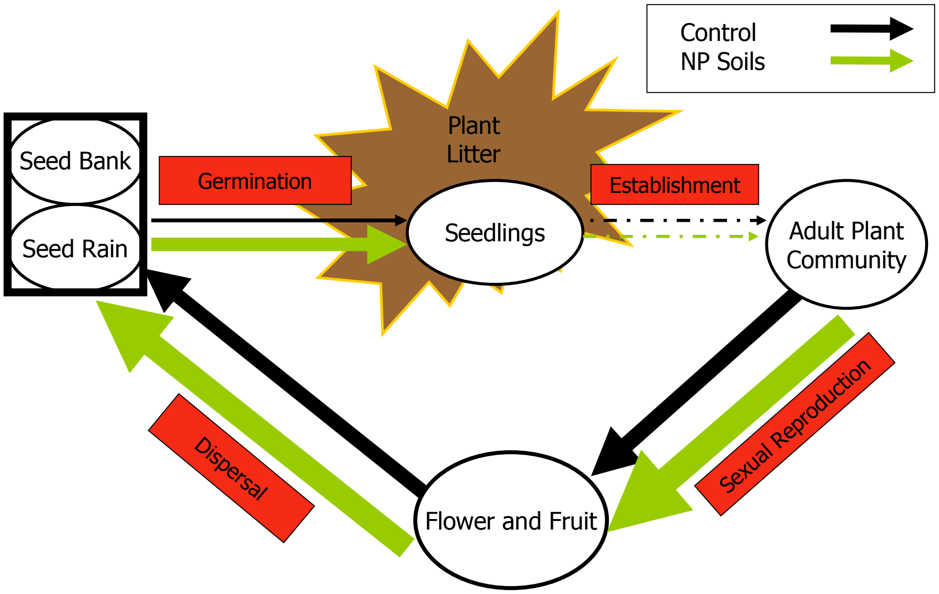

Figure 4.1 Conceptual diagram showing results from nutrient addition treatments compared to ambient conditions on *H. alpina* and *B. nana* species only. Green arrows indicate nutrient addition treatments, while yellow arrows indicate nutrient addition plus the presence of plant litter in the community. Thickness of arrows refers to the importance of that process under those condition.

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BIOGRAPHICAL INFORMATION

Carol Ann Moulton was born and raised in Beverly, Massachusetts, a coastal suburb north of Boston. She received a B.S. in Ecology from Unity College, Maine, in 2004 under the supervision of Dr. Edward Beals. After graduating, Carol worked with small mammals, insects and song birds in various seasonal jobs before enrolling into the graduate program at UT Arlington under the supervision of Dr. Laura Gough in 2006. Her research interests include the ecology of arctic and alpine ecosystems, the effects of climate change on those plant communities, plant invasion ecology, and ornithology. Carol is at peace when working in the outdoors, and hopes to share her knowledge and love for nature with everyone she encounters.