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CONTROLS OVER NUTRIENT FLOW THROUGH PLANTS AND
MICROBES IN ARCTIC TUNDRA

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Summary Report

We successfully developed a series of models to explore the importance of species differences in phenologies of growth and nitrogen uptake to competitive interactions in upland tussock tundra. We developed growth models for 4 major tussock tundra species, based on observed growth rates and phenologies. We found that differences in phenology and nutrient use strategy could permit coexistence of some, but not all of the tundra plants modeled. The plant that was the best competitor, because of its rapid growth rate and superior ability to retranslocate nitrogen, may be naturally limited in its competitive ability by its tussock growth form. The mechanisms behind this limitation, and the contributions of patterns of mortality to observed production, will be explored in future modeling and experimental studies. In addition, our models point out that our understanding of the dynamics of nitrogen supply is still inadequate.

Background

Tussock tundra is a simple ecosystem where 8 species of plants make up over 90% of the biomass (Shaver and Chapin 1991), and where several different species are co-dominant. It has been shown previously that nitrogen is the main factor limiting plant productivity in this system (Shaver and Chapin 1980, 1986), and all species almost invariably respond to added nitrogen with increased growth when grown in the laboratory (Shaver and Kummerow 1992). However, in the intact community, added nitrogen sometimes promotes the growth of all species (Shaver and Chapin 1980), but at other times promotes the growth of some species, while decreasing the growth of others (Chapin and Shaver 1985, Chapin et al. in press). This implies competition for nitrogen. Because plants are mostly very low in stature, with relatively open canopies, and because experiments shading communities do not cause reduction in growth except for the overstory species (Chapin and Shaver 1985), we hypothesized that competition for nitrogen is the main plant interaction.

Tundra plants differ substantially in their inherent maximum relative growth rates, in their nitrogen content of biomass, especially of leaves, and in their ability to retranslocate nitrogen out of senescing leaves. Because the capacity to take up soil nutrients is often tied to the physiological demands of growth, species with higher inherent growth rates probably have higher uptake capacity for soil nitrogen. We wondered how species with low nitrogen content of biomass and slow growth rates could coexist with faster-growing species with higher nitrogen content of biomass. We hypothesized that differences in the phenology of growth and uptake of nitrogen might permit slow-growing species to avoid competition, by beginning growth earlier in the season, and growing later in the season, than their fast-growing neighbors.

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Model Development

To investigate these hypotheses, we wrote simulation models for the growth and competition for nitrogen of four common species of tundra plants (*Ledum palustre*, *Betula nana*, *Eriophorum vaginatum*, and *Hylocomium splendens*) with quite different inherent growth rates and nitrogen contents. We assumed that competition for nitrogen was their only significant interaction, that ability to take up nitrogen was correlated with internal demand for nitrogen, and that all of the species had access to the same nitrogen pool (fig.1). Their growth was based upon observed rates (Chapin et al. 1980, Shaver and Chapin 1991) and phenologies of growth in the field (fig. 2; Chapin et al. 1980, Shaver and Kummerow 1992), but could be reduced if nitrogen was not sufficient to maintain the nitrogen content of biomass. Nitrogen availability was calculated from observed rates of net nitrogen mineralization in tussock tundra (Kielland 1990). We chose a time step of 1 week for the model, because that was short enough to incorporate significant phenology, but not so short that we could not find growth data on that scale. We modeled the growth of aboveground biomass, keeping track separately of old and new leaves and old and new stem material, and each plant had a nitrogen storage pool. Because these arctic plants primarily reproduce clonally, not by seed, and because they are extremely long-lived, we defined success by persistent increase in biomass, and did not model the plants as populations of individuals.

Model Results

A first significant result of the model is that the observed rates of net nitrogen mineralization are not sufficient to support observed aboveground plant biomass, even when storage is taken into account. This has been observed in several systems, and indicates that microbial mineralization measured in the absence of living plant roots does not accurately reflect plant-available nitrogen.

If each of the species in the model is grown in the absence of any competition, the observed growth pattern reflects the observed within-season phenology of growth (fig. 3). Over many seasons, each species increases until it reaches a stable equilibrium (e.g. fig. 4). The value at equilibrium depends on the nitrogen content of biomass, while the speed of the approach to equilibrium depends mainly on the maximum relative growth rate.

If two species are grown together, relatively long-term coexistence is possible if they have very different phenologies of growth and similar overall uptake capacity (fig. 5). We did not find much evidence in the literature for big differences in the phenology of uptake, although the data on this question is sketchy. Addition of a weaker competitor does not significantly change the dynamics of the interaction between the other competitors (fig. 6). However, *Eriophorum vaginatum* is such a good competitor in the model that it achieves competitive exclusion in about 10 years (fig. 7), which does not correspond to reality. In the model, *Eriophorum*'s success results from its rapid relative growth rate (it makes very little support tissue), and its superior ability to retranslocate nitrogen from senescing leaves.

The model assumes that all species have access to the same nitrogen pool. This is clearly not true for the moss species, which does not have roots. In addition, it is likely that the roots of *Eriophorum vaginatum* do not have access to the entire soil volume, as *Eriophorum* grows in discrete tussocks, and its roots grow straight down without branching, unlike the roots of all the other species. Allowing the moss priority access to nitrogen from atmospheric deposition and restricting *Eriophorum* to the proportion of the nitrogen pool represented by the fraction of surface area occupied by tussocks results in relatively long-term coexistence (fig. 8). The equilibrium biomass of the moss *Hylocomium splendens* in the model is similar to that observed in the field, but is much less than the entire biomass of all mosses supported, indicating again that our understanding of the sources of nitrogen for plant growth are inadequate.

It seems likely that heterogeneity in nitrogen supply, either spatial or chemical, may be necessary to explain coexistence, if competition for nitrogen is the main plant interaction in tussock tundra. It has recently been observed that different species preferentially use different chemical forms of added nitrogen (McKane, personal communication). In addition, it is of interest to understand why *Eriophorum* grows in discrete tussocks, and why these expand outward in area so relatively slowly. It has been observed that tillers in the center of the tussock grow more vigorously than those on the edges, but the mechanisms behind this difference are not clear. Another important data gap revealed by the model is that we lack good understanding of mortality and biomass turnover in these long-lived clonal plants. Over the long-term this knowledge is just as important as knowledge of growth for understanding current distributions and community interactions and for predicting future performance. Experimental studies are being set up to address these issues.

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Model Structure

For each species , N uptake = N factor * [X]dem

Phenology