

# Vascular plant species richness in Alaskan arctic tundra: the importance of soil pH

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## Summary

**1** Species diversity in the Arctic varies dramatically across abiotic gradients, including topography, moisture, pH and nutrient availability. We hypothesized that vascular plant species density, richness and diversity in Alaskan tundra would be correlated with: (i) site age, (ii) soil pH, (iii) above-ground productivity and biomass, and (iv) spatial heterogeneity. We sampled moist tussock, snowbed and watertrack communities in three sites that differed in substrate age (11 000–4.5 million years since deglaciation) for a variety of environmental and vegetation data over one growing season.

**2** Productivity, biomass and heterogeneity were not consistently correlated with species density. However, variation in canopy height was correlated with species density and richness in a unimodal fashion, suggesting that heterogeneity of the light regime may be important for maintaining higher species numbers.

**3** The 11 000-year-old site supported more vascular plant species than the two older sites, primarily due to greater numbers of forb species on the youngest site.

**4** Soil pH was significantly positively correlated with species richness ( $R^2 = 0.82$ ) and species density ( $R^2 = 0.61$ ). In general the species found on acidic substrates (pH < 5.5) also occurred on non-acidic substrates (pH > 5.5).

**5** This pattern of higher richness with higher pH occurs across other tundra types throughout the Arctic, suggesting that soil pH is an important filter of the regional species pool within northern regions, although other factors may become more important at local scales.

*Keywords:* biomass, landscape age, spatial heterogeneity, species density, species diversity

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## Introduction

The harsh environmental conditions present in northern regions of the globe require arctic plants to possess evolutionary adaptations to cold and frequently saturated soils, low nutrients, and short growing seasons (Billings & Mooney 1968; Chapin & Shaver 1985; Billings 1992; Bliss & Matveyeva 1992; Shaver 1995). These factors limit the total number of species found in this biome, while other environmental variables, in particular topography, snow cover, soil moisture and soil pH, have been

correlated with plant species richness at both regional and local scales (Walker 1985; Matveyeva 1988; Walker *et al.* 1994; Walker 1995; Gould & Walker 1999). The mechanisms behind these correlations have not been examined in detail, although several biotic factors acting at local, ecological scales have also been investigated for their relationship with species richness. For example, the role of competition in natural tundra vegetation has been studied, but its importance in influencing community structure is unclear as removal experiments have produced mixed results (Jonasson 1992; Hobbie *et al.* 1999). Vertebrate herbivory may also affect arctic plant communities significantly at local scales (Jefferies *et al.* 1994). Therefore, at local scales, factors affecting either regional species pools (i.e. growing season length, soil parent material) or acting at

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a finer-scale (i.e. competition) may control species diversity and richness, and both sets of factors need to be taken into account to understand fully patterns in plant species distributions (Zobel 1992, 1997; Ricklefs & Schluter 1993; Gough *et al.* 1994).

The goal of this study was to describe variation in vascular plant species richness and diversity in relation to environmental variables in three plant community types on three different landscapes in the northern foothills of the Brooks Range, Alaska. We used three different measures of species numbers, mean species density (number of species in 1-m<sup>2</sup> plots), species richness (number of species in the community) and species diversity (incorporates evenness, the distribution of abundance of individuals among species), to examine how different variables may affect species numbers at different scales, and may also affect community structure. The plant communities in this region have been classified into several broad vegetation types, dry heath, moist tussock, wet sedge and riparian shrub, of which moist tussock tundra is the most common in northern Alaska (Bliss & Matveyeva 1992). Soil moisture is generally used to discriminate among vegetation types at this scale, and the communities also differ in terms of snow cover, which is influenced by height of the vegetation, slope, aspect and exposure. As well as tussock tundra, we focused on two other common vegetation types that have been less well studied. These are watertracks (areas of water flow down hillsides where species numbers can be very low) and snowbeds (sites usually on north-facing hillslopes that retain snow for up to 4 weeks later into the growing season than typical tussock and watertrack sites). These allowed us to test our hypothesis that vascular plant species density, species richness and species diversity would be correlated with four site variables: (i) site age, (ii) soil pH, (iii) above-ground productivity and biomass, and (iv) local scale spatial heterogeneity.

Based on previous research in this region of Alaska (Walker *et al.* 1994; Walker *et al.* 1995), we hypothesized that a younger surface (deglaciated in the past 11 000 years) would harbour more species than older sites (deglaciated 66 000 years ago and up to 4.5 million years ago) for two reasons. First, we expected less pronounced dominance and a less developed shrub canopy, and therefore less light competition, in younger vegetation assemblages. The light regime may be a vital component of more diverse communities because most of the diversity on younger substrates is composed of forb species; a less developed canopy allowing more light to the soil surface could promote initial germination and establishment by many species. Secondly, as these surfaces age they tend to become more acidic because of increased organic acid accumulation and increased abundance of *Sphagnum* (Walker *et al.*

1995). *Sphagnum* species acidify the soil surface (Clymo & Hayward 1982), maintain low pH and high moisture content of the soil, and may prevent germination or establishment of vascular plants by preventing roots from reaching the soil. Low pH restricts nitrification rates and increases concentrations of certain elements known to be toxic to many plants (e.g. aluminium). However, soil pH does not simply reflect the age of the substrate. Circumneutral soils may be maintained on very old surfaces by inputs of loess from rivers (Walker & Everett 1991) and by other forms of disturbance, including dust input from gravel roads (Auerbach *et al.* 1997). Thus we also hypothesized that lower soil pH would be correlated with fewer species, regardless of site age.

The third variable we examined was above-ground biomass and productivity. The generally expected pattern between biomass and species richness is a hump-shaped curve (recently reviewed in Grace 1999), and various mechanisms have been proposed regarding the control of species numbers, including competitive exclusion at high biomass levels (Grime 1979). Although data from other ecosystems have shown the expected pattern (Grace 1999), arctic data collected to date have demonstrated little to no correlation between biomass and species richness (Fox 1985; Waide *et al.* 1999).

Finally, we hypothesized that increased spatial heterogeneity at a local scale (both horizontal and vertical) would allow increased richness by creating more niches for additional species to coexist. In particular, freeze–thaw action in arctic tundra soils can cause the formation of frost boils, areas where the surface is bare mineral soil. Frost boils may be important sites for germination and establishment (Gartner *et al.* 1983) and may maintain greater species diversity by creating new areas for secondary succession (Johnson & Neiland 1983; Matveyeva 1988). Vertical heterogeneity in the plant canopy could also be important by providing a heterogeneous light environment and allowing smaller species to survive, or by influencing microclimate (snow cover, wind exposure or temperature). Evaluating these four variables should lead to greater understanding of controls on plant species density, richness and diversity in arctic tundra, and provide new hypotheses that can be investigated experimentally.

## Methods

### STUDY SITES

The three sites examined in this study were all located in the vicinity of the Arctic Long-Term Ecological Research (LTER) site at Toolik Lake (68°38'N, 149°36'W, 760 m a.s.l.) on the North Slope of the Brooks Range, Alaska. Three landscapes were selected that differed in glacial history,

based on the maps of Hamilton (1994), as well as in soil acidity. A non-acidic site was located approximately 500 m from the north-west shore of Toolik Lake on a young surface deglaciated approximately 11 000 years ago. One of the acidic sites (Toolik) included the area used for ongoing LTER experimental plots (on the south shore of the Lake), and was deglaciated approximately 66 000 years ago, while the other (near Sagwon) was located approximately 100 km north of Toolik Lake (69°27'N, 148°38'W, 380 m a.s.l.), on the northern edge of the foothills. The Sagwon area has not been glaciated for at least 4.5 million years (Hamilton 1994).

Areas of three community types (moist tussock, watertrack and snowbed) were identified at each site. Moist tussock tundra communities are distinguished by the presence of the tussock-forming sedge *Eriophorum vaginatum* L. and are quite common throughout the North Slope and the circumpolar Arctic (Bliss & Matveyeva 1992). Watertracks, which are dominated by sedges and deciduous shrubs, occur on hillslopes where water drains downslope, providing greater water movement and nutrient flow. Watertracks frequently have higher productivity than tussock communities (Chapin *et al.* 1988; Gebauer *et al.* 1996). Finally, snowbeds occur on the leeward side of slopes, usually north-facing, where snow remains present later into the growing season than in surrounding areas. Productivity is generally low, and the communities are dominated by dwarf shrubs and lichens (Walker *et al.* 1994).

All communities selected had a similar north-facing aspect. Eight randomly located 3 × 3 m plots were established in early or mid-June 1997, following snowmelt in each community at each site ( $n = 8$  replicate plots × 3 communities × 3 sites = 72), with one corner randomly chosen in each plot for harvesting, point quadrat sampling and as the location of the initial quadrat for nested species-area determination (see below).

## SOILS

### *Chemical analyses*

At three times during the growing season of 1997, 5.2-cm diameter soil cores (up to 30 cm long, depending on depth of thaw) were taken from six locations outside the permanent plots at each community within each site. At the second sampling in July 1997, a 5-g subsample of the homogenized organic horizon of each soil core was shaken with 25 ml of 0.01 M CaCl<sub>2</sub> solution, and the pH of the solution was measured. We defined soils with pH > 5.5 as non-acidic, while acidic soils had pH < 5.5 (Soil Taxonomy Survey 1975). At all three dates, 2N KCl-extractable NO<sub>3</sub> and NH<sub>4</sub> and 0.025 N HCl-extractable PO<sub>4</sub> were determined following

the methods of Giblin *et al.* (1991). NH<sub>4</sub> and PO<sub>4</sub> samples were analysed colorimetrically on a spectrophotometer at the Toolik Field Station; NO<sub>3</sub> samples were frozen and shipped to the Ecosystems Center, Woods Hole, MA, for analysis with an autoanalyser. We do not report the results of these analyses in detail here, but rather mention them as they relate to our hypotheses concerning species richness.

### *Spatial heterogeneity*

To quantify vertical and horizontal heterogeneity in thickness of the organic horizon and thaw depth, four randomly located 6-m long transects were laid out at each site. At the tussock and snowbed sites the transects were parallel to the slope; at watertrack sites transects were placed perpendicularly to the slope across the width of the watertrack itself. At all sites, metal rods were inserted into the soil at each end of the transect. A string was tied to the rods and levelled above the transect to serve as a stable, level reference point for measurements. At the tussock sites, the transect was dug so that the border between the upper organic and lower mineral soil horizons was clearly visible. At 7.5-cm intervals ( $n = 80$ ) along each transect, distance from the reference string to the top of the plant canopy, the top of the moss layer, the top of the organic soil surface, and the top of the mineral horizon was measured. At each interval, depth of thaw was measured by inserting a narrow steel rod into the soil until it could not be pushed deeper. Horizontal heterogeneity was calculated as the coefficient of variation of the mean of depth of thaw and organic horizon depth, and by examining the trench profiles (see the Results). Frost boils were indicated by deeper thaw and a very thin or absent organic horizon where the mineral soil had pushed up to the soil surface. Similar trenches were dug at the snowbed sites, but depth of thaw could not be measured accurately because of the many rocks in the soil. A representative soil pit was dug to permafrost at each snowbed site, but there was no replication for depth of thaw. At the watertrack sites, only thaw depth was measured because water on the soil surface prevented examination of the horizons across the length of the transect.

## VEGETATION SAMPLING

### *Species density and richness*

In June 1997, all plots were surveyed for the presence of vascular plant species. A square 0.04-m<sup>2</sup> quadrat was placed in one corner of each plot. Larger quadrats of 0.36-, 1-, 4- and 9-m<sup>2</sup> areas were examined, each larger quadrat including the smaller ones by being based in the same corner. Plots were revisited in August 1997 to ensure that later-flower-

ing species had not been missed. These data were used to generate species–area curves. Both plot area and species numbers were log-transformed and regressed to determine the constant and slope of the species–area relationship for each community within each site, and determine adequate plot sizes at which the communities should be compared. Species density (the number of species per unit area,  $D$ ) was determined within each community at each scale as the mean number of species encountered at each quadrat size, including all species recorded in the smaller plots. Species richness ( $S$ ) was determined as the cumulative number of species encountered within all plots examined for that particular scale [e.g. over an area of  $72\text{ m}^2$  for each community within each site ( $8\text{ plots} \times 9\text{ m}^2$ )]. We assume  $S$  at the largest scale to be a good representative of the number of species present in the community within each site, based on previous studies of similar areas (Walker *et al.* 1994).

#### *Species diversity and canopy heterogeneity*

In late June and early July 1997, one  $0.56\text{-m}^2$  area in each plot was sampled with the point quadrat method (Mueller-Dombois & Ellenberg 1974; Walker 1996) to assess canopy structure and species diversity. A square aluminium frame,  $0.75\text{ m}$  on each side, was placed over the plot. A double layer of strings was placed  $7.5\text{ cm}$  apart to create a  $10 \times 10$  grid and used to insert a pin vertically into the vegetation at 100 evenly spaced sampling points. The distance from the frame to the first contact with vegetation, to the top of the moss layer, and to the ground surface was recorded. Each hit was categorized regarding surface type (e.g. tussock, moss mat, open water, etc.). The identity and number of contact points for each vascular species in contact with the pin were recorded. The number of vascular hits per pin was calculated as an indication of the layers of the canopy (canopy structure). Moss and lichen species were also recorded, but only once per pin as individuals could not be estimated. However, we were uncertain of our identification of many of the moss species and limit our documentation in this paper to vascular plant species. To calculate vascular diversity, the number of contacts for each species summed over the eight replicate plots was divided by the total number of contacts of all species over the eight plots to obtain proportional abundance ( $p_i$ ). The equation for the Shannon–Weiner diversity index ( $H'$ ) is:

$$H' = - \sum p_i \ln(p_i)$$

This measure incorporates evenness and therefore describes the distribution of individual abundance among the species in addition to the number of species in a plot (Magurran 1988).

#### *Biomass and productivity*

Biomass was determined with a clip harvest conducted between 25 July and 1 August 1997. A  $20 \times 20\text{-cm}$  quadrat was located in the same corner as was used as the basis for species–area sampling and point quadrat sampling. Above-ground vegetation within the quadrat was clipped and removed from each plot. Samples were returned to the laboratory and separated into vascular plant material, mosses and lichens. Vascular plants were separated by species, and further divided into new (current year's growth) and old tissues. Mosses were separated by species in half ( $n = 4$ ) of the quadrats, while lichens were separated by genus in all samples. Plant material was dried at  $60^\circ\text{C}$  for at least 72 h and weighed. Above-ground net primary productivity (ANPP) was estimated by adding the mass of new tissue plus an estimate of new stem secondary growth (wood production), calculated as a percentage of old stem mass. Secondary stem growth rates had been obtained previously for the woody species present in these plots (Shaver 1986; Chapin *et al.* 1995). Biomass was the sum of the mass of all plant material present.

#### ANALYSIS

SAS (Version 6.12; SAS Institute, Cary, NC) was used for all statistical analyses. Regressions of pH with other variables were performed using PROC REG, and adjusted  $R^2$  values are reported. ANOVA was performed using PROC GLM with site and community type as the main effects of interest. Variances were examined for homogeneity with residual plots, and normality was checked with the Shapiro–Wilks statistic. ANPP and biomass data were log-transformed prior to analysis to obtain homogeneous variances. If log-transforming other variables did not correct for lack of normality, Scheffé's pair-wise test was used to compare means, as it is generally robust to model violations. Significance was indicated by a  $P$ -value less than 0.05.

#### Results

One plot at the Toolik acidic site was eliminated from the analysis because of fertilizer leaching in from an adjacent fertilized plot; thus the sample size for vegetation data was 71 plots.

#### DIFFERENCES AMONG SITES AND COMMUNITIES

Species–area curves (data not presented) showed that the community types were distinguishable from one another at the  $1\text{-m}^2$  scale, with differences remaining consistent at larger scales. This scale was

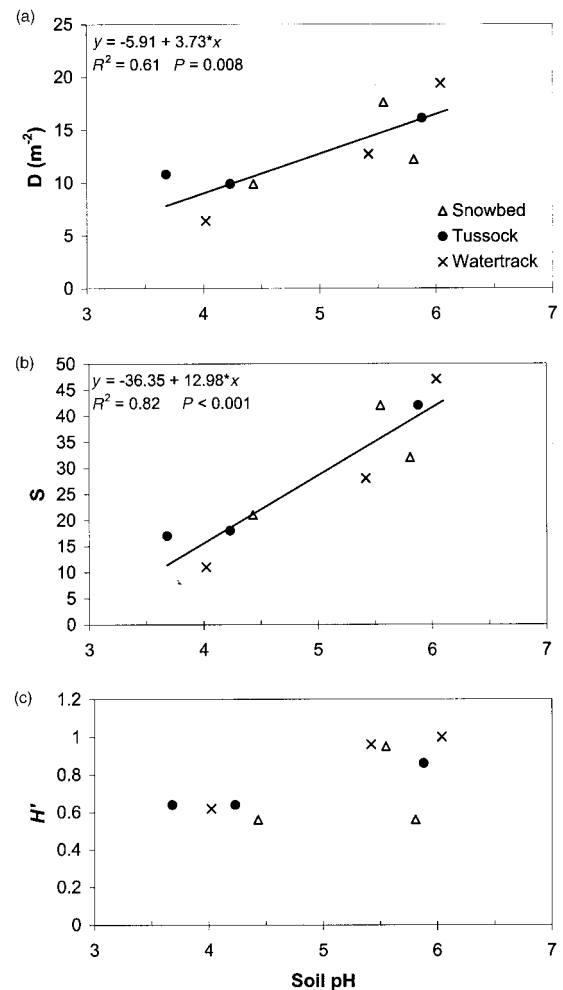
therefore used for species density ( $D$ ) in all subsequent analyses. Species density, richness and diversity varied both within and across community types and sites (for  $D$  there was a site–community interaction:  $F_{4,62} = 21.4$ ,  $P < 0.01$ ; Table 1). Although these variables also differed across sites (for  $D$ :  $F_{2,62} = 21.2$ ,  $P < 0.01$ ), community type alone was not a consistent source of variation ( $P > 0.05$ ; Table 1).

#### SITE AGE

More vascular plant species occurred on the younger surface than the other two surfaces at all scales examined, with significant differences among sites detected at the 1-m<sup>2</sup> scale. The two older sites did not differ significantly in species numbers at any scale (Table 1).

#### SOIL PH

Soil pH was not clearly correlated with site age (site–community interaction:  $F_{4,41} = 14.4$ ,  $P = 0.0001$ ). Soil pH ranged from 3.4 to 6.9 (Table 1), with the mean values for non-acidic being  $5.9 \pm 0.1$ , for Toolik acidic  $4.5 \pm 0.2$  and for Sagwon acidic  $4.6 \pm 0.1$  ( $n = 18$ ; site  $F_{2,41} = 62.6$ ,  $P = 0.0001$ ). The community means also differed from one another, with the tussock sites overall having lower pH values than the snowbed and water-track sites (community:  $F_{2,41} = 11.2$ ,  $P = 0.0001$ ). The relationship between mean soil pH and  $D$ , and mean soil pH and  $S$ , for each community within each site was significantly positive and linear (Fig. 1). The relationship between pH and  $H'$  was marginally significant ( $P = 0.06$ ; Fig. 1c). Soil pH explained 82% of the variance in species richness and 61% of the variance in mean species density (Fig. 1).



**Fig. 1** Relationship between site/community mean soil pH and (a) mean vascular plant species density per m<sup>2</sup> ( $D$ ); (b) species richness per 72m<sup>2</sup> ( $S$ ); and (c) Shannon–Weiner diversity index per 72m<sup>2</sup> ( $H'$ ).

#### PRODUCTIVITY AND BIOMASS

ANPP varied among community types within and among sites, with a significant interaction between

**Table 1** Vascular plant species density, richness and diversity, and soil pH, for each community and site, related to site age. Mean values with different superscript letters are significantly different ( $P < 0.05$ ) from other means within the same row based on pair-wise comparisons. Community abbreviations: S, snowbed; T, tussock; W, watertrack

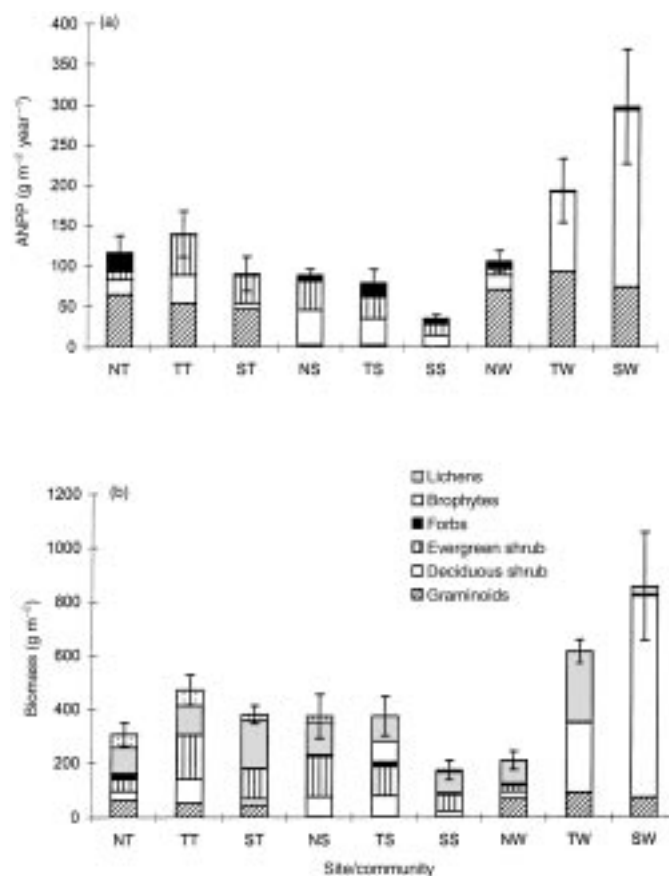
Non-acidic	Toolik acidic		Sagwon acidic			S			
	T	W	Site S	T	W				
Community									
Site									
Approximate years since deglaciation		11 k			66 k	4.5 m			
Species richness ( $S$ , 216 m <sup>2</sup> )		69			51	40			
Mean species density ( $D$ , 1 m <sup>2</sup> )		15.9 <sup>a</sup>			11.6 <sup>b</sup>	10.6 <sup>b</sup>			
Community									
Species richness ( $S$ , 72 m <sup>2</sup> )	42	47	32	17	11	42	18	28	21
Mean species density ( $D$ , 1 m <sup>2</sup> )	16.1 <sup>ab</sup>	19.4 <sup>a</sup>	12.2 <sup>bc</sup>	10.8 <sup>cd</sup>	6.4 <sup>d</sup>	17.6 <sup>a</sup>	9.9 <sup>cd</sup>	12.7 <sup>bc</sup>	9.9 <sup>cd</sup>
Shannon–Weiner diversity index ( $H'$ )	0.86	1.01	0.56	0.64	0.62	0.95	0.64	0.96	0.56
Soil pH (organic horizon)	5.9 <sup>a</sup>	6.0 <sup>a</sup>	5.8 <sup>a</sup>	3.7 <sup>c</sup>	4.0 <sup>c</sup>	5.6 <sup>a</sup>	4.2 <sup>b</sup>	5.2 <sup>ab</sup>	4.4 <sup>bc</sup>

site and community ( $F_{4,62} = 8.2$ ,  $P = 0.001$ ; Fig. 2a). There were significant differences among all three community types, with watertracks having the greatest ANPP and snowbeds the least ( $F_{2,62} = 28.3$ ,  $P = 0.001$ ), while sites were not significantly different from one another ( $P > 0.05$ ). Plant growth form composition also differed in ANPP among communities and sites, particularly in terms of the abundance of deciduous and evergreen shrubs. Forbs contributed substantially to ANPP only in three of the most diverse sites (non-acidic tussock, non-acidic watertrack and Toolik snowbed; Fig. 2a and Table 1). The variation in above-ground community biomass was similar to that of ANPP (site–community interaction:  $F_{4,62} = 7.3$ ,  $P = 0.001$ ; community main effect:  $F_{2,62} = 3.8$ ,  $P = 0.03$ ; Fig. 2b), although site differences were also significant as a main effect, with the non-acidic site having lower biomass than the other two sites ( $F_{2,62} = 7.13$ ,  $P = 0.002$ ).

Examining vascular biomass separately produced the same results (main effects and interaction significant at  $P < 0.05$ ).

Neither ANPP nor biomass were correlated with D (Fig. 3). There was a great deal of scatter in the points and no consistent pattern within or among community types. Means by community within site for ANPP and biomass showed no relationship with D, S or  $H'$  (data not shown;  $P > 0.05$  for all regressions).

No relationships were found between species density or richness and soil nitrogen availability (all regressions:  $P > 0.10$ ; data not shown). Weak correlations between  $\text{PO}_4$  and D ( $R^2 = 0.26$ ,  $P = 0.09$ ), and  $\text{PO}_4$  and S ( $R^2 = 0.27$ ,  $P = 0.08$ ) indicated a trend towards more species with higher soil phosphate concentrations. This relationship was confounded by a positive correlation between soil  $\text{PO}_4$  concentration and pH ( $R^2 = 0.32$ ,  $P = 0.06$ ).



**Fig. 2** (a) Above-ground net primary productivity (ANPP) of vascular plants and (b) biomass of all plants and lichens plotted by growth form for each site and community. Error bars are  $\pm 1$  SE for total ANPP or biomass, respectively ( $n = 8$  except TT where  $n = 7$ ; see Results). Site/community abbreviations are: NT, non-acidic tussock; TT, Toolik acidic tussock; ST, Sagwon acidic tussock; NS, non-acidic snowbed; TS, Toolik acidic snowbed; SS, Sagwon acidic snowbed; NW, non-acidic watertrack; TW, Toolik acidic watertrack; SW, Sagwon acidic watertrack.

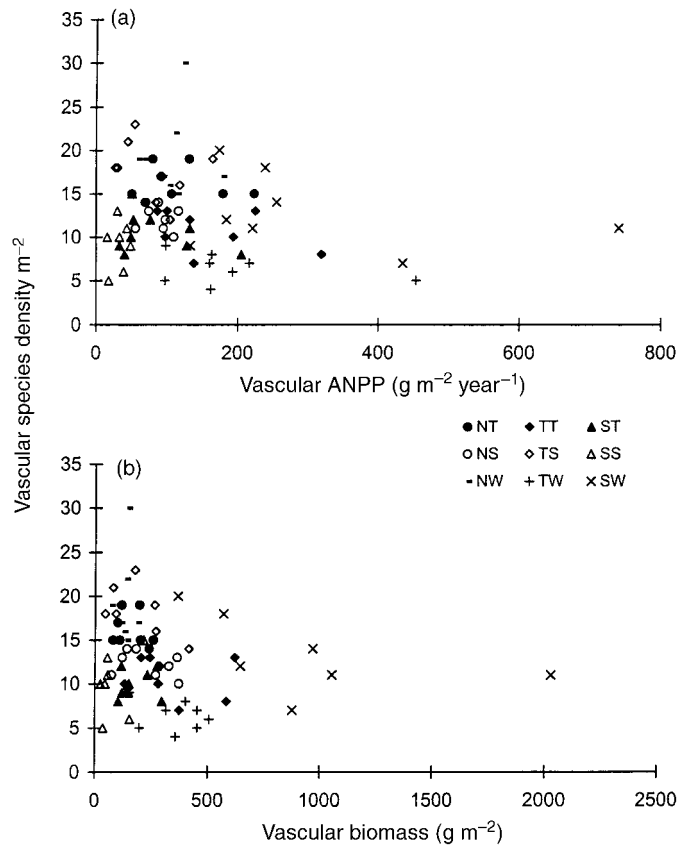


Fig. 3 Species density (per m<sup>2</sup>) vs. (a) ANPP and (b) biomass (vascular plants only). Site/community abbreviations as in Fig. 2.

#### SPATIAL HETEROGENEITY

##### *Below-ground characteristics*

By examining variation in the thickness of the organic horizon and thaw depth, we could detect below-ground frost heaving and frost boils in the tussock communities. Larger variation in horizon thickness and thaw depth indicates greater amounts of cryoturbation, as frost boils cause the organic layer to be pushed away from the surface, thus increasing depth of thaw because of lack of insulation by plants and organic matter. The organic horizon was much thicker in the tussock communities than in the snowbeds (Table 2). Organic horizon thickness did not vary in a predictable way with species richness among the communities and sites, as Toolik acidic had the greatest variation in thickness but fewest species. Snowbeds were most deeply thawed (because of the thin organic horizon providing little insulation), followed by watertracks and then tussock communities (Table 2). Within each community there was variation in mean and variance of depth of thaw, but the mean and coefficient of variation of thaw depth were not correlated with species density or richness (all regressions  $P > 0.05$ ).

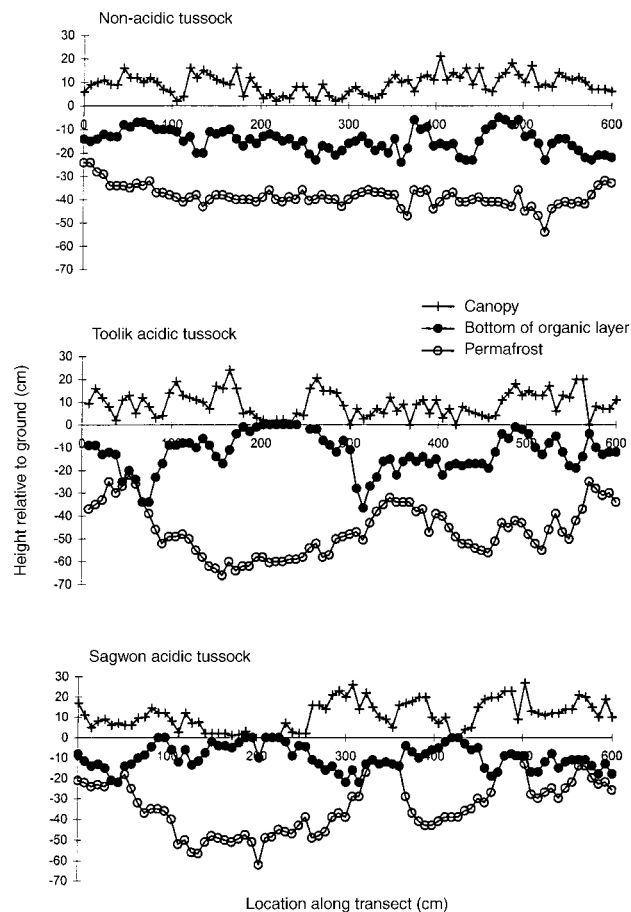
Three representative trench profiles (Fig. 4) demonstrated variation in organic horizon thickness among the soils of the three tussock communities, and differences in degree of cryoturbation. The profiles were corrected for position relative to the ground surface (boundary between the base of the living moss and top of the organic horizon) so that hummocks would not be visible. The non-acidic tussock site had the least evidence of frost boil action, as indicated by the relatively constant organic horizon thickness and thaw depth (Fig. 4 and Table 2). The two acidic sites were more variable, with frost boils evident where depth of thaw was greatest and the organic horizon was very thin or absent.

##### *Above-ground characteristics*

The point quadrat data allowed us to examine several different aspects of both vertical and horizontal heterogeneity within each site and community. Differences in mean percentage cover of the plots by vascular plants, mosses, lichens and litter were not consistent across sites or communities, and showed little relation to species density, richness or diversity (data not shown).

**Table 2** Mean ( $\pm 1$  SE) and coefficient of variation (CV) of below-ground characteristics and mean and CV of above-ground characteristics for each site and community ( $n = 480$  for below-ground and  $n = 800$  for above-ground). Different superscripts indicate means were significantly different within each column. Standard errors are given for below-ground variables because missing cells made statistical comparisons difficult (see the Methods). There was no replication of thaw depth measurements for snowbed sites

Community	Site	Below-ground				Above-ground			
		Organic horizon thickness (cm)		Thaw depth (cm)		Canopy height (cm)		Number of hits/pin	
		Mean	CV	Mean	CV	Mean	CV	Mean	CV
Tussock	Non-acidic	15.5 $\pm$ 0.4	0.47	38.4 $\pm$ 0.5	0.21	8.1 <sup>c</sup>	0.59	3.0 <sup>cd</sup>	0.91
	Toolik acidic	13.4 $\pm$ 0.5	0.72	38.8 $\pm$ 0.8	0.36	13.2 <sup>c</sup>	0.50	6.2 <sup>a</sup>	0.73
	Sagwon	13.3 $\pm$ 0.3	0.47	28.4 $\pm$ 0.6	0.38	11.3 <sup>d</sup>	0.46	3.3 <sup>c</sup>	0.84
Watertrack	Non-acidic	–	–	55.5 $\pm$ 0.7	0.22	8.1 <sup>c</sup>	0.64	2.2 <sup>ef</sup>	0.82
	Toolik acidic	–	–	63.7 $\pm$ 0.3	0.08	23.3 <sup>b</sup>	0.48	2.7 <sup>de</sup>	0.83
	Sagwon	–	–	50.4 $\pm$ 0.4	0.13	31.0 <sup>a</sup>	0.48	4.8 <sup>b</sup>	0.62
Snowbed	Non-acidic	4.4 $\pm$ 0.1	0.35	119	–	3.1 <sup>f</sup>	0.93	1.5 <sup>gh</sup>	1.12
	Toolik acidic	9.6 $\pm$ 0.3	0.48	75	–	4.2 <sup>f</sup>	0.75	1.9 <sup>fg</sup>	0.94
	Sagwon	2.0 $\pm$ 0.1	0.61	86	–	2.8 <sup>f</sup>	0.87	1.1 <sup>h</sup>	1.42



**Fig. 4** Representative trench profiles for the three tussock sites demonstrating topography of plant canopy, organic/mineral soil horizon boundary and permafrost depth. All measurements are relative to the ground, which is represented by the x-axis.



Mean vascular plant canopy height was calculated from the point quadrat data, along with the mean number of contacts per pin (indication of layers of the plant canopy). Canopy height differed among sites and communities (Table 2), but with no relationship to species richness. The variation in canopy height within each plot was significantly curvilinearly correlated with species numbers, so that the peak in  $D$ ,  $S$  and  $H'$  occurred at intermediate levels of variation in canopy height (for  $D$ :  $R^2 = 0.56$ ,  $P = 0.04$ , second order polynomial; Fig. 5). Mean canopy layer structure and variation in canopy structure were not correlated with  $D$ ,  $S$  or  $H'$  ( $P > 0.05$ ; Table 2).

## Discussion

### NO CLEAR CORRELATION BETWEEN SITE AGE AND SOIL PH

Two of the areas, Toolik snowbed and Sagwon watertrack, had higher pH than was expected based on the site location (Table 1). The Toolik acidic snowbed located on the edge of Toolik Lake may have been scoured during the most recent deglaciation, so that the soils there were less weathered and less acidic. Also, loess may have been deposited by wind along with snow, thus increasing soil pH. The Sagwon watertrack appeared to be draining a gravel quarry located upslope, which may explain its higher pH. Both of these areas had higher species numbers than expected based on site age, but the values were correlated with the higher pH, giving further evidence that higher richness occurs on higher pH sites regardless of the mechanism influencing acidity.

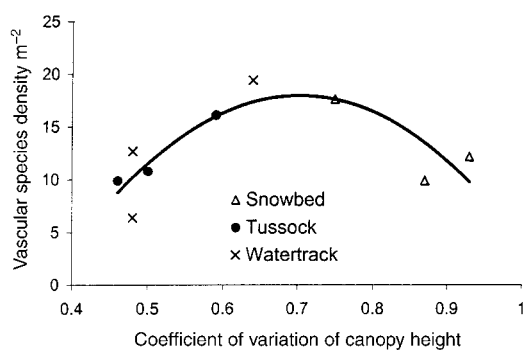


Fig. 5 Relationship between coefficient of variation of canopy height determined from point quadrat data and vascular species density for each site/community.

### PRODUCTIVITY, BIOMASS AND HETEROGENEITY NOT CLEARLY CORRELATED WITH RICHNESS

Neither productivity nor biomass was correlated with species density, richness or diversity in this study. We found a similar degree of scatter in an earlier examination of productivity, biomass and species density from sites at Toolik Lake and also in literature reports of data from across the Arctic (Waide *et al.* 1999). Several authors have suggested that a hump-shaped relationship should be visible across community types (Moore & Keddy 1989; Guo & Berry 1998), but we did not detect it in this data set. The lack of a clear pattern between these two variables is common in natural vegetation (e.g. G.G. Mittelbach *et al.*, unpublished manuscript) and suggests that different factors regulate these variables at different sites in different ecosystems so that productivity and biomass do not affect species numbers in any consistent way (see also Grace 1999). For the Arctic, this result implies that, despite the harshness of the environment, many different species and species assemblages are capable of achieving similar productivity and biomass; adaptations to environmental conditions have therefore not restricted productivity or biomass consistently.

The relationship between species richness, density and diversity and various measures of spatial heterogeneity also showed little pattern. Horizontal heterogeneity at the plot or transect level, in particular in terms of the percentage of the substrate covered by vascular plants, mosses or bare ground, did not appear to affect species numbers at the local scale, despite what others have found at larger scales (Matveyeva 1988; Walker 1995). Also, degree of cryoturbation was not clearly correlated with species density, richness or diversity consistently across community types, although frost-heaved areas in a subarctic alpine heath had higher species numbers in a Swedish study (Jonasson & Sköld 1983). Bockheim *et al.* (1998) have suggested that cryoturbation may be more important on non-acidic, loess-dominated areas than acidic areas, but we found no active or subsurface frost boils at the young, non-acidic tussock site studied here. Average cover of the plots by mosses or lichens was not correlated with species density, richness or diversity. Differences may exist, however, in the influence of *Sphagnum* and non-*Sphagnum* mosses on the vascular community, as almost no *Sphagnum* was encountered at the non-acidic sites, while most of the mosses present at acidic sites were *Sphagnum* species (Carroll 1998).

Heterogeneity of the height of the canopy was correlated with species density, richness and diversity, indicating that heterogeneity of the light regime may influence species diversity in arctic plant communities. Most of the species responsible for the

diversity of the non-acidic sites are forbs with relatively short life cycles, and these data therefore suggest that a heterogeneous light environment may be one factor important for establishment of many of these species. Variation in vegetation height may also affect snow cover depth and duration, trapping of seeds, and loess input. Experimental work is needed before a causal relationship can be established.

#### MORE PLANT SPECIES ON YOUNGER SITE

Fewer vascular plant species coexist on the two older landscapes in our study, suggesting decreased vascular species richness with increased site age (Matthews 1992). However, this difference only existed between the youngest site and the two older sites; millions of years did not appear to affect species numbers between the intermediate-aged and oldest site examined here, possibly because of simultaneous development of tussock tundra on the two older sites approximately 7000 years ago (Walker *et al.* 1995). It is therefore difficult to interpret site differences in species richness as differences in successional stage. Two possible mechanisms behind this observed difference are discussed here: (i) decreased soil pH with age (see below), and (ii) increased light competition due to increased canopy closure by shrubs at the older sites. Woody shrub species in arctic tundra are long-lived, mostly clonal, and take many years to develop a full canopy. The mean age of individual dwarf birches, *Betula nana* L., at the Toolik acidic tussock site is 150 years (S. Bret-Harte, unpublished data). Long-term nutrient additions at the acidic tussock LTER site have increased canopy development of *B. nana* and decreased vascular species richness; similar changes are developing more slowly in long-term warming experiments at the same site (Chapin *et al.* 1995; L. Gough & G.R. Shaver, unpublished data). Most of the species lost in these manipulated plots were forbs. These results indicate the potential importance of a dense canopy in eliminating low-stature, less long-lived species.

#### SOIL PH EXPLAINS MOST VARIATION IN SPECIES RICHNESS

For many years plant ecologists have documented high plant species numbers on calcareous soils (Grime 1979; Grubb 1986). Decades ago, several researchers investigated this 'calicicole-calcifuge problem' from a physiological perspective (Clymo 1962; Grubb *et al.* 1969). Aluminium toxicity or calcium deficiency in acidic soils may prevent germination or survival and explain why some species occur only on more basic soils (Rorison 1960). However, the more general reasons behind community differences

on soils of different pH remain to be investigated thoroughly.

In the Arctic, higher plant species numbers on non-acidic substrates have been described on different-aged landscapes, on loess deposition areas, and in riparian tundra (Walker *et al.* 1994; Shaver *et al.* 1996; Gould & Walker 1997, 1999). Thus factors beyond soil parent material affect soil pH. Our results provide further evidence that pH is related directly to species richness regardless of the driving force behind soil acidity or base content. Most of the differences in species richness among sites are due to increased numbers of relatively sparse forb species on non-acidic sites, while the dominant species at acidic sites tend to be still present but less abundant at non-acidic sites (Walker *et al.* 1994; Shaver *et al.* 1996).

Soil pH is known to vary over short distances in arctic tundra, and although the biogeochemical causes of this variation have been studied (Valentine & Binkley 1992) the implications for the plant communities are not yet completely understood. Recent investigations in tundra treat pH as a variable of interest in ordinations, often finding that it explains a significant amount of variation among communities and species assemblages (van Raamsdonk 1988; Timoney *et al.* 1993; Walker *et al.* 1994; Heikkinen 1996; Heikkinen & Neuvonen 1997). When we examined pH and species numbers within relatively homogeneous communities, we found a stronger correlation with species richness than species density, implying that other factors in addition to pH may be acting at the local scale to reduce species numbers. One crucial element may be the role of *Sphagnum* mosses. *Sphagnum* is known to acidify the soil and to insulate the soil surface, restricting depth of thaw, and may prevent germination of some vascular plant species because of the thickness of the moss mat. *Sphagnum* is found almost exclusively on acidic substrates in this region (Walker *et al.* 1994).

#### COMPLEX COMBINATION OF BIOTIC AND ABIOTIC FACTORS CAUSE HIGHER PH SOILS TO SUPPORT MORE SPECIES

We believe that the correlation between soil pH and species richness represents a series of complex mechanisms interacting to determine species diversity, including soil nutrient availability, abiotic factors such as element toxicity (e.g. aluminium), and biotic factors such as the influence of moss mats on germination of vascular species. Some of these factors act at the regional scale, restricting the species pool based on environmental tolerances and adaptations of individual species, while other factors act at the local scale (e.g. interspecific competition) to decrease species numbers further (Ricklefs &

Schluter 1993; Zobel 1997). Recently Walker *et al.* (1998) suggested that non-acidic and acidic tundra may behave differently in terms of carbon storage and carbon cycling, partially caused by differences in plant composition, especially woody shrubs. Clearly we need further research into these processes to understand what underlies the pattern with pH, but we can make some initial hypotheses from the data already collected.

We hypothesize that nutrient availability is greater and more heterogeneous (in terms of forms of nutrients present) on non-acidic soils. Recent evidence has demonstrated that arctic tundra plants partition limited soil nutrients. The various dominant vascular species take up different forms of nitrogen in the field, including amino acids (Michelsen *et al.* 1996; Nadelhoffer *et al.* 1996; Schimel & Chapin 1996). This evidence suggests that coexistence on a very limited soil nitrogen supply is maintained in part by partitioning of nitrogen uptake by chemical form, perhaps by time of year, and by rooting depth, and that selective uptake may be facilitated by mycorrhizal associations (Michelsen *et al.* 1998). Additional amino acids are available at circumneutral pH levels (Kielland 1994), possibly providing alternative nitrogen sources for certain species on non-acidic soils. Our data show slightly higher phosphate and nitrate levels on the non-acidic substrate (data not shown), but mineralization rates and pool sizes are needed to assess differences in nutrient availability among sites.

The importance of abiotic factors restricting growth of individual species on both acidic and non-acidic substrates needs further investigation. Although several possible mechanisms can be proposed to explain the absence of many species from acidic soils, including aluminium toxicity, calcium deficiency and possible effects of *Sphagnum*, mechanisms preventing germination and survival on non-acidic soils are more difficult to describe. Because many of the differences among tundra communities in terms of productivity and biomass are driven by presence or absence of woody species, both deciduous and evergreen, we need experiments designed to enable independent assays of the multiple abiotic and biotic variables affecting shrub dispersal and survival, to allow these site differences to be teased apart.

In conclusion, it is remarkable that 82% of the variance in vascular species richness among sites could be explained by just one abiotic variable, soil pH. This correlation has been documented in other ecosystems (e.g. European chalk grasslands) and implies strong restriction of the species pool based on factors associated with pH. The fact that the variance in species numbers explained by soil pH decreased when the dependent variable was the number of species within a 1-m<sup>2</sup> plot implies that

other factors, possibly biotic, are also reducing species richness at the local scale (Gough *et al.* 1994; Partel *et al.* 1996). Heterogeneity of the canopy was correlated with species numbers, possibly demonstrating one local biotic component. This study provides further evidence that factors controlling the species pool must be taken into account when studying local coexistence, and that biotic mechanisms important at finer scales cannot be ignored in arctic tundra plant communities.

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### References

- Auerbach, N.A., Walker, M.D. & Walker, D.A. (1997) Effects of roadside disturbance on substrate and vegetation properties in arctic tundra. *Ecological Applications*, **7**, 218–225.
- Billings, W.D. (1992) Phytogeographic and evolutionary potential of the arctic flora and vegetation in a changing climate. *Arctic Ecosystems in a Changing Climate* (eds F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda), pp. 91–109. Academic Press, New York, NY.
- Billings, W.D. & Mooney, H.A. (1968) The ecology of arctic and alpine plants. *Biological Review*, **43**, 481–529.
- Bliss, L.C. & Matveyeva, N.V. (1992) Circumpolar arctic vegetation. *Arctic Ecosystems in a Changing Climate* (eds F.S. Chapin III, R.L. Jefferies, J.F. Reynolds, G.R. Shaver & J. Svoboda), pp. 59–90. Academic Press, New York, NY.
- Bockheim, J.G., Walker, D.A., Everett, L.R., Nelson, F.E. & Shiklomanov, N.I. (1998) Soils and cryoturbation in moist nonacidic and acidic tundra in the Kuparuk River Basin, arctic Alaska, USA. *Arctic and Alpine Research*, **30**, 166–174.
- Carroll, J. (1998) *Controls over bryophyte diversity in Alaskan arctic tundra*. BA Thesis. Tulane University, New Orleans, USA.
- Chapin, F.S. III & Shaver, G.R. (1985) Arctic. *Physiological Ecology of North American Plant Communities* (eds B.F. Chabot & H.A. Mooney), pp. 16–40. Chapman & Hall, London, UK.

- Chapin, F.S. III, Fetcher, N., Kielland, K., Everett, K.R. & Linkins, A.E. (1988) Productivity and nutrient cycling of Alaskan tundra: enhancement by flowing soil water. *Ecology*, **69**, 693–702.
- Chapin, F.S. III, Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. (1995) Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.
- Clymo, R.S. (1962) An experimental approach to part of the calcicole problem. *Journal of Ecology*, **50**, 707–731.
- Clymo, R.S. & Hayward, P.M. (1982) *The Ecology of Sphagnum* (ed. A.J.E. Smith), pp. 229–290. Chapman & Hall, London, UK.
- Fox, J.F. (1985) Plant diversity in relation to plant production and disturbance by voles in Alaskan tundra communities. *Arctic and Alpine Research*, **17**, 199–204.
- Gartner, B.L., Chapin, F.S. III & Shaver, G.R. (1983) Demographic patterns of seedling establishment and growth of native graminoids in an Alaskan tundra disturbance. *Journal of Applied Ecology*, **20**, 965–980.
- Gebauer, R.L.E., Tenhunen, J.D. & Reynolds, J.F. (1996) Soil aeration in relation to soil physical properties, nitrogen availability, and root characteristics within an arctic watershed. *Plant and Soil*, **178**, 37–48.
- Giblin, A.E., Nadelhoffer, K.J., Shaver, G.R., Laundre, J.A. & McKerrow, A.J. (1991) Biogeochemical diversity along a riverside toposequence in arctic Alaska. *Ecological Monographs*, **61**, 415–435.
- Gough, L., Grace, J.B. & Taylor, K.L. (1994) The relationship between species richness and community biomass: the importance of environmental variables. *Oikos*, **70**, 271–279.
- Gould, W.A. & Walker, M.D. (1997) Landscape-scale patterns in plant species richness along an arctic river. *Canadian Journal of Botany*, **75**, 1748–1765.
- Gould, W.A. & Walker, M.D. (1999) Plant communities and landscape diversity along an arctic river. *Journal of Vegetation Science*, **10**, 537–548.
- Grace, J.B. (1999) The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology, Evolution and Systematics*, **2**, 1–28.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, New York, NY.
- Grubb, P.J. (1986) Problems posed by sparse and patchily distributed species in species-rich plant communities. *Community Ecology* (eds J. Diamond & T.J. Case), pp. 207–225. Harper & Row, New York, NY.
- Grubb, P.J., Green, H.E. & Merrifield, R.C.J. (1969) The ecology of chalk heath; its relevance to the calcicole-calcifuge and soil acidification problems. *Journal of Ecology*, **57**, 175–212.
- Guo, Q. & Berry, W.L. (1998) Species richness and biomass: dissection of the hump-shaped relationship. *Ecology*, **79**, 2555–2559.
- Hamilton, T.D. (1994) Late Cenozoic glaciation of Alaska. *The Geology of Alaska G-1* (eds G. Plafker & H.C. Berg), pp. 813–844. Geological Society of America, Boulder, CO.
- Heikkinen, R.K. (1996) Predicting patterns of vascular plant species richness with composite variables: a meso-scale study in Finnish Lapland. *Vegetatio*, **126**, 151–165.
- Heikkinen, R.K. & Neuvonen, S. (1997) Species richness of vascular plants in the subarctic landscape of northern Finland: modeling relationships to the environment. *Biodiversity and Conservation*, **6**, 1181–1201.
- Hobbie, S.E., Shevtsova, A. & Chapin, F.S. III (1999) Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos*, **84**, 417–434.
- Jefferies, R.L., Klein, D.R. & Shaver, G.R. (1994) Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos*, **71**, 193–206.
- Johnson, A.W. & Neiland, B.J. (1983) An analysis of plant succession on frost scars 1961–1980. *Permafrost: Fourth International Conference Proceedings, 17–22 July 1983, Fairbanks, AK*, pp. 537–542. National Academy Press, Washington, DC.
- Jonasson, S. (1992) Plant responses to fertilization and species removal in tundra related to community structure and clonality. *Oikos*, **63**, 420–429.
- Jonasson, S. & Sköld, S.E. (1983) Influences of frost-heaving on vegetation and nutrient regime of polygon-patterned ground. *Vegetatio*, **53**, 97–112.
- Kielland, K. (1994) Amino acid absorption by arctic plants: implications for plant nutrition and nitrogen cycling. *Ecology*, **75**, 2373–2383.
- Magurran, A.E. (1988) *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- Matthews, J.A. (1992) *The Ecology of Recently Deglaciated Terrain. A Geoecological Approach to Glacier Forelands and Primary Succession*. Cambridge University Press, New York, NY.
- Matveyeva, N.V. (1988) The horizontal structure of tundra communities. *Diversity and Pattern in Plant Communities* (eds H.J. During, M.J.A. Werger & J.H. Willems), pp. 59–65. SPB Academic Publishing, The Hague, the Netherlands.
- Michelsen, A., Quarmby, C., Sleep, D. & Jonasson, S. (1998) Vascular plant <sup>15</sup>N natural abundance in heath and forest tundra ecosystems is closely correlated with presence and type of mycorrhizal fungi in roots. *Oecologia*, **115**, 406–418.
- Michelsen, A., Schmidt, I.K., Jonasson, S., Quarmby, C. & Sleep, D. (1996) Leaf <sup>15</sup>N abundance of subarctic plants provides field evidence that ericoid, ectomycorrhizal and non- and arbuscular mycorrhizal species access different sources of nitrogen. *Oecologia*, **105**, 53–63.
- Moore, D.R.J. & Keddy, P.A. (1989) The relationship between species richness and standing crop in wetlands: the importance of scale. *Vegetatio*, **79**, 99–106.
- Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and Methods of Vegetation Ecology*. John Wiley and Sons, New York, NY.
- Nadelhoffer, K., Shaver, G., Fry, B., Giblin, A., Johnson, L. & McKane, R. (1996) <sup>15</sup>N natural abundances and N use by tundra plants. *Oecologia*, **107**, 386–394.
- Partel, M., Zobel, M., Zobel, K. & van der Maarel, E. (1996) The species pool and its relation to species richness: evidence from Estonian plant communities. *Oikos*, **75**, 111–117.
- van Raamsdonk, L.W.D. (1988) Principal component analysis of ecological indicator values of Swiss alpine flora. *Botanica Helvetica*, **98**, 195–205.
- Ricklefs, R.E. & Schluter, D. (1993) Species diversity: regional and historical influences. *Species Diversity in Ecological Communities* (eds R.E. Ricklefs & D. Schluter), pp. 350–364. University of Chicago Press, Chicago, IL.
- Rorison, I.H. (1960) Some experimental aspects of the calcicole-calcifuge problem. I. The effects of competition and mineral nutrition upon seedling growth in the field. *Journal of Ecology*, **48**, 585–599.
- Schimel, J.P. & Chapin, F.S. III (1996) Tundra plant uptake of amino acid and NH<sub>4</sub><sup>+</sup> nitrogen in situ:

- plants compete well for amino acid N. *Ecology*, **77**, 2142–2147.
- Shaver, G.R. (1986) Woody stem production in Alaskan tundra shrubs. *Ecology*, **67**, 660–669.
- Shaver, G.R. (1995) Plant functional diversity and resource control of primary production in Alaskan arctic tundras. *Arctic and Alpine Biodiversity* (eds F.S. Chapin III & C. Körner), pp. 199–211. Springer-Verlag, New York, NY.
- Shaver, G.R., Laundre, J.A., Giblin, A.E. & Nadelhoffer, K.J. (1996) Changes in live plant biomass, primary production, and species composition along a riverside toposequence in arctic Alaska, USA. *Arctic and Alpine Research*, **28**, 361–377.
- Soil Taxonomy Survey (1975) Soil taxonomy. *A Basic System of Soil Classification for a Making and Interpreting Soil Surveys*. USDA Handbook 436. US Government Printing Office, Washington, DC.
- Timoney, K.P., La Roi, G.H., Zoltai, S.C. & Robinson, A.L. (1993) Vegetation communities and plant distributions and their relationships with parent materials in the forest-tundra of northwestern Canada. *Ecography*, **16**, 174–188.
- Valentine, D.W. & Binkley, D. (1992) Topography and soil acidity in an arctic landscape. *Soil Science Society of America Journal*, **56**, 1553–1559.
- Waide, R.B., Willig, M.R., Mittelbach, G., Steiner, C., Gough, L., Dodson, S.I., Juday, G.P. & Parmenter, R. (1999) The relationship between primary productivity and species richness. *Annual Review of Ecology and Systematics*, **30**, 257–300.
- Walker, D.A. (1985) *Vegetation and Environmental Gradients of the Prudhoe Bay Region, Alaska*. CRREL Report 85–14. US Army Cold Regions Research and Engineering Laboratory, Hanover, NH.
- Walker, D.A. & Everett, K.R. (1991) Loess ecosystems of northern Alaska: regional gradient and toposequence at Prudhoe Bay. *Ecological Monographs*, **61**, 437–464.
- Walker, D.A., Auerbach, N.A., Bockheim, J.G., Chapin, F.S. III, Eugster, W., King, J.Y., McFadden, J.P., Michaelson, G.J., Nelson, F.E., Oechel, W.C., Ping, C.L., Reeburg, W.S., Regli, S., Shiklomanov, N.I. & Vourlitis, G.L. (1998) Energy and trace-gas fluxes across a soil pH boundary in the Arctic. *Nature*, **394**, 469–472.
- Walker, D.A., Auerbach, N.A. & Shippert, M.M. (1995) NDVI, biomass, and landscape evolution of glaciated terrain in northern Alaska. *Polar Record*, **31**, 169–178.
- Walker, M.D. (1995) Patterns and causes of arctic plant community diversity. *Arctic and Alpine Biodiversity* (eds F.S. Chapin III & C. Körner), pp. 1–20. Springer-Verlag, New York, NY.
- Walker, M.D. (1996) Community baseline measurements for ITEX studies. *ITEX Manual*, edn 2 (eds U. Molau & P. Mølgaard), pp. 39–41. International Tundra Experiment, Danish Polar Center, Copenhagen, Denmark.
- Walker, M.D., Walker, D.A. & Auerbach, N.A. (1994) Plant communities of a tussock tundra landscape in the Brooks Range foothills, Alaska. *Journal of Vegetation Science*, **5**, 843–866.
- Zobel, M. (1992) Plant species coexistence – the role of historical, evolutionary and ecological factors. *Oikos*, **65**, 314–320.
- Zobel, M. (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology and Evolution*, **12**, 266–269.

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