

**PATTERNS OF DIVERSITY IN HIGH ARCTIC SNOWBED PLANT COMMUNITIES  
AT ALEXANDRA FIORD, ELLESMERE ISLAND, CANADA**

**by**

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## ABSTRACT

This study examines the patterns of diversity within three natural snowbeds and one manipulated snowbed at Alexandra Fiord, Ellesmere Island in the Canadian High Arctic. Recent predictions of climate change in the Arctic suggest that not only will temperature increase, but also snowmelt will be earlier leading to a longer growing season. Experimental manipulations of snowmelt were begun in 1992 in a late-lying snowbed in order to determine the response of species to longer and shorter growing seasons.

To measure the biomass of each species within the manipulated snowbed without destructively harvesting the vegetation, the point quadrat method of estimating total species area (TSA) was employed. Simple linear regressions of TSA and biomass for each species were constructed and were used to estimate biomass from only TSA data. For most species the variance explained ( $R^2$ ) was very high ranging, from 0.311 to 0.943. When diversity indices were calculated, there was essentially no difference between the values as calculated from real or from estimated biomass. The best fitting relative abundance distribution model for each quadrat was also consistent, regardless of whether actual or estimated biomass was used. Therefore, this method offers an efficient alternative to destructively harvesting a large number of quadrats for relatively simple communities and allows a non-destructive means to follow biomass changes in permanent quadrats over time.

Ordination using redundancy analysis (RDA) showed that gradients of biomass, soil pH, moss cover and snow meltdate were found strongly related to the community structure within the natural and manipulated snowbeds. Total quadrat biomass was found to be the most important variable in the RDA at explaining the variation of species data and was significantly related to diversity. All measures of alpha diversity decreased with increasing biomass. When the three natural snowbed communities are included with other arctic communities, a hump shaped relation between species richness and biomass is observed, with a peak in diversity at moderate biomass. These results offer indirect evidence that biological interactions, namely competition, may be important in structuring these high arctic communities.

Patterns of alpha diversity within the natural snowbeds were not significantly related to snowmelt, although there were more graminoid species in the earliest melting plots, with the longest growing season, and more forbs species in the last plots to melt. The manipulated snowbed, with snow removal, snow addition and control plots, also had more graminoid species in the plots where snow had been removed. The lowest species richness was found in the snow

addition plots while greatest richness was found in the removal plots. However, evenness increased in both the addition and removal plots. This suggests that the graminoid species will likely become more abundant in the short term if the growing season length increases as a result of climate change. The importance of this work is that it is the first evidence that snowmelt changes will alter the structure of arctic communities, although more research is necessary to determine the resultant functional changes that will likely accompany structural changes in these and other arctic tundra ecosystems.



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# 1. INTRODUCTION

## 1.1 GENERAL INTRODUCTION

Significant changes in global climate are predicted to occur within decades, and the most pronounced changes are likely to occur at the polar latitudes (Cattle and Crossley 1995, Maxwell 1992). Aside from the well known predicted increase in temperature, increases in snowfall, accompanied by a faster snowmelt leading to a longer growing season, are also likely to occur (Maxwell 1992). These changes will likely shift species distributions significantly (Chapin and Körner 1995, Robinson et al. 1998, Starfield and Chapin 1996) although the consequences for specific ecosystem functions are unclear (Shaver et al. 1997).

Experimental warming treatments have shown that arctic species respond significantly, especially in terms of reproductive and vegetative phenology (Arft et al. 1999, Callaghan and Jonasson 1995, Chapin et al. 1995a, Chapin and Shaver 1996, Henry and Molau 1997, Hobbie et al. 1999, Robinson et al. 1998). Similar experimental studies have not yet been completed to determine the response of species to altered snowmelt and growing season length in the Arctic, although some manipulative work has been completed in alpine tundra in Colorado (Galen and Stanton 1993, Galen and Stanton 1995). Natural gradients of snowmelt are known to be important in determining the structure of communities in arctic and alpine tundra (Billings and Bliss 1959, Kudo and Ito 1992, Philipp 1978, Reznicek and Svoboda 1982, Schaefer and Messier 1995, Stanton et al. 1994, Walker et al. 1993) and may offer insights as to the changes that may occur under differing climate change scenarios. Changes in diversity within snowbeds have only been commented on in a qualitative manner, with suggestions that diversity tends to decrease in the plots with the shortest growing season (Billings and Bliss 1959, Galen and Stanton 1995, Kudo and Ito 1992) and that the species that are found in these plots tend to be either graminoid or forb species (Billings and Bliss 1959, Galen and Stanton 1995, Kudo and Ito 1992, Stanton et al. 1994, Walker et al. 1993).

The role that diversity plays in communities and ecosystems has been incredibly controversial (Johnson et al. 1996, Lawton 1994, Tilman 1999), although, in general, ecologists agree that diversity is important in the structure and function of ecosystems (Schläpfer and

Schmid 1999, Schlöpfer et al. 1999). Ecologists believe that ecosystem process rates, such as nutrient cycling and productivity, and diversity are strongly correlated (Schlöpfer et al. 1999). The term biodiversity is also controversial since it encompasses all levels of diversity from genetic variability within species to variations between entire ecosystems. Usually species diversity is the primary level of interest, as in my work presented here.

Given the potential for climatic change in the Arctic and the lack of experimental studies on the consequences to vegetation, my work examines patterns of diversity within natural and manipulated snowbeds at Alexandra Fiord, Ellesmere Island, in the Canadian High Arctic. In order to sample species abundances effectively without destructively harvesting plots, the point quadrat method was employed in the snow manipulation plots. Abundance can be measured in cover, frequency, biomass or productivity. These measurements are not the same and in certain methods there are preferable abundance measures (Hengeveld 1979). For estimates of diversity, biomass or productivity seems to be the advocated abundance measurement (Chiarucci et al. 1999, Guo and Rundel 1997, Whittaker 1965). The method of estimation of biomass from point quadrat data (Jonasson 1988) is evaluated in Chapter 2 by comparing estimated biomass to actual biomass values. In Chapter 3, patterns of species and functional group diversity in response to meltdate are studied for three natural gradients of snowmelt and for one manipulated snowbed. All diversity indices are not formulated equally and therefore specific rationales for choosing diversity indices are outlined in Appendix A. Because diversity will also change in response to other environmental factors such as soil moisture, temperature, pH, moss cover, and, in particular, biomass (Grime 1979, Huston 1979, Tilman 1988), multivariate techniques are used to determine the most important variables in affecting community structure. A summary of the conclusions reached in Chapters 2 and 3 are presented in Chapter 4.

## **1.2 STUDY SITE DESCRIPTION**

Research was conducted during the summer of 1998 at three separate natural snowbed communities within the Alexandra Fiord lowland, Ellesmere Island (78°53'N; 75°55'W) (Figure 1.1). The lowland is a high-arctic oasis of approximately 8 km<sup>2</sup> that gently slopes to the north, towards Alexandra Fiord, and is bound to the east and west by steep and high rock cliffs and to the south by ice of an outlet glacier (Figure 3.1). The meltwater from snow and ice during the summer months provide more available moisture to the lowland than in the surrounding upland areas, and gives the area features of a hydrologic oasis (Freedman et al. 1983). Also, the general

climatic conditions characteristic of Alexandra Fiord, namely the close proximity of the Greenland high-pressure system and the arctic circumpolar vortex (which is influenced by the flow over arctic islands), make the lowland have greater levels of incoming solar radiation than surrounding regions (Labine 1994). Bordering topography, which may reflect sunlight and emit long-wave radiation, and is referred to as the "oven-effect", as well as the reflected light from the glacial and sea ice, increase the net radiation to more favorable values for plant growth relative to the surrounding uplands (Freedman et al. 1983, Labine 1994). These contribute to dense vegetation cover on the lowland with nearly 90% of its area covered by vegetation, which is much higher than the surrounding upland areas (Freedman et al. 1994). At least 96 vascular plant species are found on the lowland (Ball and Hill 1994). Productivity and standing crop are also higher in the lowlands than the adjacent uplands and is also greater here than in the majority of the regions in the High Arctic, making it more comparable to southern regions of the Arctic (Freedman et al. 1994). Due to its remote location, the lowland is very infrequently used by muskoxen or caribou and is therefore essentially free from the effects of major herbivores (Henry et al. 1990).

The soils of the lowland are young having been covered by ice as recently as 4000-6000 years ago and are characteristically poorly developed, classified as Regosolic Cryosols, and are very spatially heterogeneous (Muc et al. 1994b). The soils associated with the sites used in this study were primarily gravels and sands of alluvium or glacial till and are typical of arctic soils, in that they are relatively nutrient poor (Marion et al. 1997, Muc et al. 1994b). More details of the environmental conditions of the lowland, and the research completed at Alexandra Fiord, can be found in Svoboda and Freedman (1994).



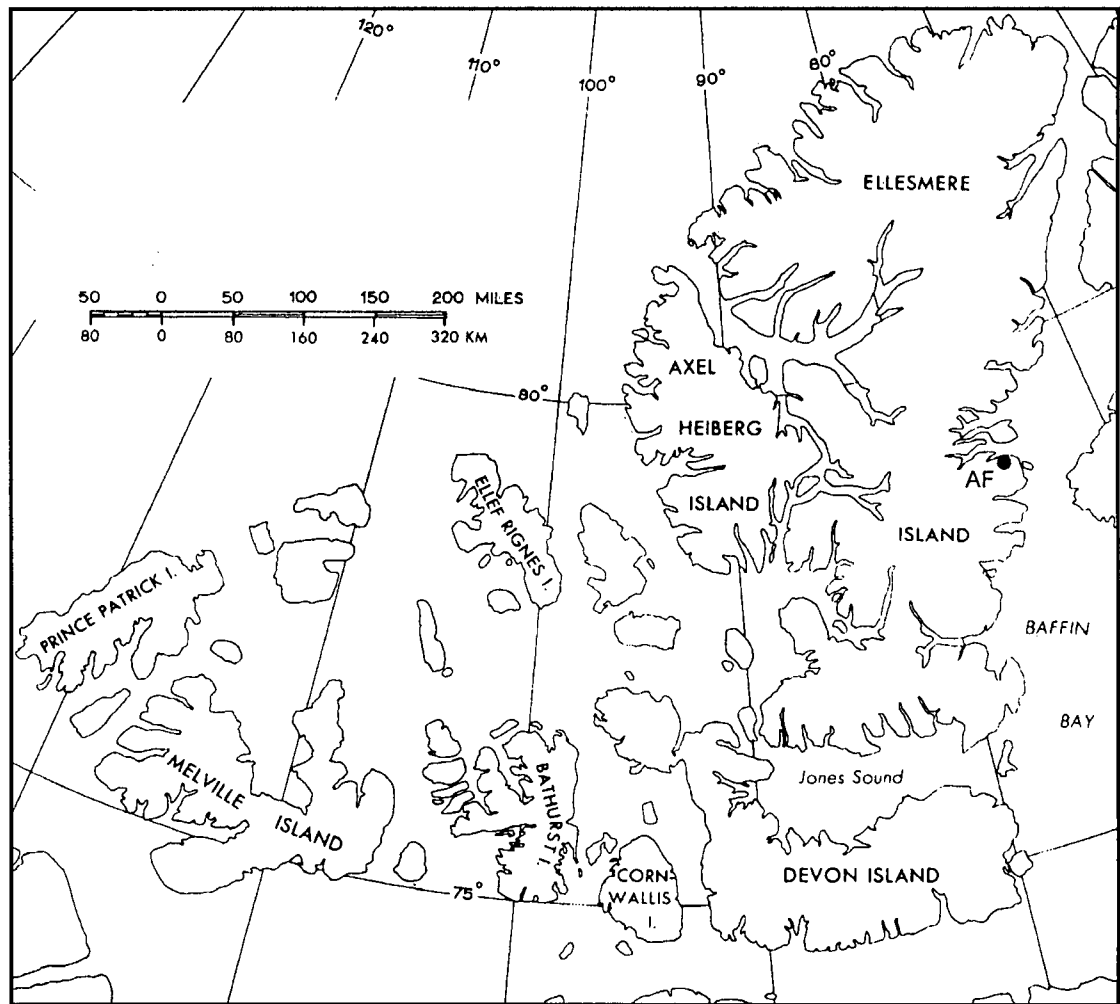


Figure 1.1. Map of Queen Elizabeth Islands, in the Canadian High Arctic, showing the location of Alexandra Fiord (AF). Modified from Henry (1998).

## **2. BIOMASS ESTIMATION USING POINT QUADRATS**

### **2.1 INTRODUCTION**

Studies of diversity in plant communities are usually based on either cover or biomass estimations of species abundance. Recent work has suggested that cover and biomass will give different results (Chiarucci et al. 1999, Guo and Rundel 1997), leading to the suggestion that biomass should be the preferred method of abundance estimation in diversity studies, although it has also been recommended the best method of estimating species abundance is production (Whittaker 1975).

Unfortunately, destructive harvesting to estimate the biomass of a species can be problematic due to the great deal of time required to complete the harvest and to sort species (Bullock 1996). Also, biomass harvests can be very damaging to the ecosystem examined, especially in areas where succession and regrowth is slow. These problems have lead some to the conclusion that biomass harvests should only be done if it is essential (Bullock 1996) while others have developed methods of estimating biomass, which minimize impact (Catchpole and Wheeler 1992). One such method is the use of point quadrats to estimate cover and relate this value to biomass using simple linear regression (Goodall 1952, Jonasson 1988). This method is also called the point intercept method (Jonasson 1988) or double sampling (Catchpole and Wheeler 1992).

Previous research has indicated that point quadrats can be used effectively to estimate the biomass of specific species (Jonasson 1988); however, this method has not been applied to all species in the community in order to determine the diversity using estimated biomass. Using the low growing high arctic vegetation of Alexandra Fiord, the objectives of my study are: 1) to determine if the use of cover versus biomass in diversity studies can lead to different conclusions, 2) to determine if regressions of an estimate of cover and biomass can be useful for estimating biomass, and 3) to determine if estimated biomass used in diversity studies will give the same results as actual biomass.

## 2.2 METHODS

### 2.2.1 General Site Description

Three snowbed communities were chosen for a diversity study (see Chapter 3) within the Alexandra Fiord lowland (78°53'N; 75°55'W)(Figure 1.1). A description of the lowland is given in Chapter 1. Detailed descriptions of the lowland, and the studies that have taken place there, can be found in Svoboda and Freedman (1994). The glacier river snowbed community (GRSB) is located on a river slope facing east and is dominated by *Cassiope tetragona* (an evergreen dwarf shrub and heath species) and *Dryas integrifolia* (an evergreen dwarf shrub). The second site, the beach ridge snowbed (BRSB), is a raised beach ridge dominated by *Cassiope tetragona*, *Dryas integrifolia* and *Salix arctica* (a deciduous dwarf shrub). Another raised beach ridge, the camp snowbed (CPSB), was also sampled and is dominated by *Salix arctica*, *Dryas integrifolia*, and *Saxifraga oppositifolia* (a perennial mat).

### 2.2.2 Field Sampling

The three communities were sampled using a stratified random design, with the strata based on the snowmelt date of the quadrat. Because the plots were sampled randomly, they were pooled such that each set of plots represents replicate samples of the community from which they were sampled. The GRSB community contained 20 quadrats, the BRSB community had 40 quadrats, and there were 50 quadrats in the CPSB community. More detailed descriptions of the sampling methodology are given in Chapter 3.

Each quadrat was 0.5 m × 0.5 m and both cover and biomass were recorded. Cover was estimated using the point quadrat method (Bullock 1996) with a density of 100 points/0.25m<sup>2</sup>. The point quadrat used was constructed of ¾" PVC tubing with monofilament fishing line strung in a grid fashion such that the points were uniformly spread over the area. The fishing line was wrapped around the PVC tubing and at each grid point the line passed at two elevations separated by approximately 2 cm. This gave a quadrat frame with two identical grids on each side of the tubing. The quadrat frame was leveled at a height just above all vegetation within

the quadrat and at each point the species 'hits' were observed from above by lining up the two intersection points. If the same species was hit multiple times at the same point, the total number of hits was tallied. After all cover data were collected, all vegetation was harvested to ground level, sorted to species and air dried to prevent spoiling during shipping to Vancouver, BC. All material was dried at 80 °C for 48 hours before being weighed.

During subsequent analysis cover data were computed using two different methods. Because at each point a single species could be hit more than once, the data as measured actually described the total area of leaves, stems and inflorescences for each species. For the purpose of this study, this value was called the total species area (TSA). Percent cover usually represents the total horizontal area occupied by a single species and does not exceed 100% (Bullock 1996), whereas TSA for a single species can theoretically achieve values higher than 100 hits per 100 points. In dense vegetation with complex, layered canopies the total cover can exceed 100% for all species combined. Therefore, data were re-tabulated such that for each point, a species that was hit more than once was only counted as a single hit per point. This value will be called cover and has a maximum value of 100 hits per quadrat (100% cover).

### **2.2.3 Analysis Methods**

For all species the non-parametric Spearman rank correlation coefficient ( $r_s$ ) was calculated between the biomass and cover values, biomass and TSA values, and cover and TSA values across the quadrats. This method was used since it gives the correlation based on the rank of species abundance in the quadrats rather than the correlation of the actual values as calculated with the Pearson product-moment correlation coefficient (Zar 1984).

Diversity indices were calculated for each quadrat with the biomass, cover and TSA values using the program ECOLOGICAL METHODOLOGY (Krebs and Kenney 1998). The most commonly used diversity indices, Shannon's diversity index ( $H'$ ) and Simpson's index ( $\lambda$ ), as well as the recommended diversity indices (Krebs 1999), the exponential form of Shannon's diversity index ( $N_1$ ) and the reciprocal of Simpson's diversity index ( $1/\lambda$ ), were calculated along with the evenness indices most recently advocated (Smith and Wilson 1996) including Camarago's  $E'$ , Simpson's  $E_{1/\lambda}$ , and Smith and Wilson's  $E_q$  and  $E_{var}$  indices. Detailed descriptions and the equations of the diversity and evenness indices are found in Appendix A.

The Spearman correlation coefficient ( $r_s$ ) was calculated for the diversity and evenness estimates from the biomass and cover values, biomass and TSA values, and cover and TSA values. The communities were compared using the diversity and evenness values obtained from each abundance measure separately using analysis of variance, ANOVA (Zar 1984). If the ANOVA indicated that there was a statistically significant difference between the mean diversity or mean evenness value, Tukey's "honestly significant difference test" (Zar 1984) was used as a multiple comparison procedure to determine which community or communities differed from the others. ANOVA results for each diversity and evenness index were compared between the biomass, cover and TSA methods of estimating abundance to determine if results were consistent regardless of the method used.

Using the methods described by Wilson (1991), the relative abundance distribution (RAD) for each quadrat was fitted for the four most common RAD models: the broken stick, geometric, general lognormal and the Zipf-Mandelbrot (Magurran 1988) using the biomass, cover and TSA data. This was done using a program provided by J. B. Wilson (University of Otago), called DomDimXX, which determines the sum of squares deviance between the actual data and the models predictions; therefore, the best fitting model is the one with the smallest sum of squares deviance. The best fitting model for each method of estimating abundance was compared to determine if results were consistent. This method treats each plot as a separate replicate within a community and compares the fitting of each model to each plot (Wilson 1991); however, many researchers use all quadrats combined to give an average community RAD (Magurran 1988, Tokeshi 1993). This was also done with each community type to determine if the best fitting model remained constant.

Because previous researchers have found good correspondence between cover and biomass data (Chiarucci et al. 1999, Frank and McNaughton 1990, Jonasson 1988), traditional least-squares regression was used to examine the relation between cover and biomass and between TSA and biomass for all species that were present in enough quadrats to fit a regression line. Before this was done, analysis of covariance (ANCOVA) was used to compare the regressions of cover and biomass or TSA and biomass for each species the community (GRSB, BR SB and CPSB) treated as a treatment or block to determine if the slopes of the regression line for each community were statistically different (Zar 1984). If the slopes for each community were the same, the data were pooled when calculating the regression line. Some researchers have found that the growth form of the plant species may be important in determining the relation between cover and biomass (Frank and McNaughton 1990). The abundance values for all plant species

within the same functional group, as defined previously (Chapin et al. 1996), were pooled in each quadrat to give a sum of all the biomass, cover and TSA values for all plots. The relation between cover and biomass and between TSA and biomass was then determined for all growth forms. For all regression lines the least significant number (LSN) was also calculated. This is the number of random observations necessary to obtain a regression with a statistically significant slope given the parameters associated with the power as calculated.

To test the value of using either cover or TSA to estimate biomass, the data were split equally in a stratified random design that was stratified according to community. The first data set was used to estimate the regression model and the second set was used to test the correspondence between the estimated biomass and the actual biomass of each species within the plot. This method avoids the problem of using the same data in both the model generating and testing stages, which is statistically invalid and over-estimates the fit.

With the test-subset of the data, the estimated biomass of each species was computed. The Spearman correlation coefficient ( $r_s$ ) was then used to determine if the species rank is consistent between the estimated and actual biomass. The diversity and evenness indices were also calculated as previously and were tested using the Spearman correlation coefficient ( $r_s$ ) as before. To determine if diversity and evenness values obtained from the estimated biomass method was comparable to the actual biomass in absolute terms, a paired t-test was completed for each diversity and evenness index. The RAD for each plot in the test data set was also determined and compared between the estimated biomass and the actual biomass to examine the consistency of the best fitting model using the methods previously described.

All statistical tests were preformed using the program JMP (SAS 1995) except where previously noted. Statistical significance was at  $\alpha = 0.05$ , except where noted.

## **2.3 RESULTS**

### **2.3.1 Individual Species Abundance**

The correlations of species rank across quadrats between the different methods of estimating abundance were high for most species and are given Table 2.1. There was no relation between

the strength of the correlation and which functional group the plant species belong to. The correlations for all species found in more than 11 plots were statistically significant (Table 2.1).

Table 2.1. Spearman correlation coefficients ( $r_s$ ) between different methods of estimating abundance (cover, TSA, and mass) for species rank across all quadrats. Functional groups are those of Chapin et al. (1996). N = number of quadrats in which the species occurred out of 110.  $r_s$  was not calculated for species which were not hit a minimum of 4 times using the point quadrat method (note that this is not the same as N since some species were not hit with the point quadrat method even though they were present).

| Functional groups and species   | N   | Mass and TSA<br>$r_s$ | $P$    | Cover and TSA<br>$r_s$ | $P$    | Mass and Cover<br>$r_s$ | $P$    |
|---------------------------------|-----|-----------------------|--------|------------------------|--------|-------------------------|--------|
| <b>Deciduous Shrubs</b>         |     |                       |        |                        |        |                         |        |
| <i>Salix arctica</i>            | 107 | 0.9325                | <.0001 | 0.9479                 | <.0001 | 0.9398                  | <.0001 |
| <b>Evergreen Shrubs</b>         |     |                       |        |                        |        |                         |        |
| <i>Cassiope tetragona</i>       | 58  | 0.9227                | <.0001 | 0.9669                 | <.0001 | 0.8802                  | <.0001 |
| <i>Dryas integrifolia</i>       | 94  | 0.9028                | <.0001 | 0.9857                 | <.0001 | 0.9194                  | <.0001 |
| <b>Forbs</b>                    |     |                       |        |                        |        |                         |        |
| <i>Cardamine bellidifolia</i>   | 7   |                       |        |                        |        |                         |        |
| <i>Draba</i> species            | 23  | 0.4671                | 0.0246 | 1.0000                 | <.0001 | 0.4671                  | 0.0246 |
| <i>Equisetum variegatum</i>     | 2   |                       |        |                        |        |                         |        |
| <i>Lycopodium selago</i>        | 6   |                       |        |                        |        |                         |        |
| <i>Minuartia rubella</i>        | 5   |                       |        |                        |        |                         |        |
| <i>Oxyria digyna</i>            | 44  | 0.7540                | <.0001 | 0.9761                 | <.0001 | 0.7850                  | <.0001 |
| <i>Papaver radicum</i>          | 23  | 0.6974                | 0.0002 | 0.9956                 | <.0001 | 0.6943                  | 0.0002 |
| <i>Pedicularis</i> species      | 23  | 0.4847                | 0.0164 | 1.0000                 | <.0001 | 0.4947                  | 0.0164 |
| <i>Polygonum viviparum</i>      | 15  | 0.7586                | 0.0010 | 0.9987                 | <.0001 | 0.7617                  | 0.0010 |
| <i>Saxifraga cernua</i>         | 7   |                       |        |                        |        |                         |        |
| <i>Saxifraga nivalis</i>        | 12  |                       |        |                        |        |                         |        |
| <i>Saxifraga oppositifolia</i>  | 85  | 0.7718                | <.0001 | 0.9911                 | <.0001 | 0.7721                  | <.0001 |
| <i>Silene acaulis</i>           | 8   |                       |        |                        |        |                         |        |
| <i>Stellaria longipes</i>       | 26  | 0.4449                | 0.0288 | 0.9997                 | <.0001 | 0.4452                  | 0.0227 |
| <b>Graminoids</b>               |     |                       |        |                        |        |                         |        |
| <i>Arctagrostis latifolia</i>   | 3   |                       |        |                        |        |                         |        |
| <i>Carex aquatilis</i>          | 5   | 0.8208                | 0.0886 | 0.9211                 | 0.0263 | 0.6669                  | 0.2189 |
| <i>Carex maritima</i>           | 1   |                       |        |                        |        |                         |        |
| <i>Carex misandra</i>           | 42  | 0.8603                | <.0001 | 0.9736                 | <.0001 | 0.8445                  | <.0001 |
| <i>Carex nardina</i>            | 1   |                       |        |                        |        |                         |        |
| <i>Carex rupestris</i>          | 1   |                       |        |                        |        |                         |        |
| <i>Eriophorum angustifolium</i> | 6   | 0.8286                | 0.0416 | 0.9429                 | 0.0048 | 0.7714                  | 0.0724 |
| <i>Festuca brachyphylla</i>     | 11  | 0.5994                | 0.0513 | 0.9918                 | <.0001 | 0.6346                  | 0.0360 |
| <i>Juncus biglumis</i>          | 2   |                       |        |                        |        |                         |        |
| <i>Luzula arctica</i>           | 73  | 0.7042                | <.0001 | 0.9797                 | <.0001 | 0.6980                  | <.0001 |
| <i>Luzula confusa</i>           | 52  | 0.7696                | <.0001 | 0.9763                 | <.0001 | 0.7729                  | <.0001 |
| <i>Poa arctica</i>              | 18  | 0.6088                | 0.0073 | 0.9985                 | <.0001 | 0.6195                  | 0.0061 |

### 2.3.2 Diversity and Evenness Indices

All correlations of diversity and evenness values between the different methods of estimating abundance were statistically significant (Table 2.2). The correlations between

cover and TSA were higher than either correlation of mass and TSA or mass and cover, although all correlations of diversity were high (Table 2.2). The  $E_{var}$  and  $E_q$  correlations of TSA and mass and cover and mass were much lower than any other, although these were still significant correlations.

Table 2.2. Spearman correlation coefficients ( $r_s$ ) between diversity and evenness values as calculated from different methods of estimating abundance.

| Index       | Mass and TSA |        | Cover and TSA |        | Mass and Cover |        |
|-------------|--------------|--------|---------------|--------|----------------|--------|
|             | $r_s$        | $P$    | $r_s$         | $P$    | $r_s$          | $P$    |
| $\lambda$   | 0.8242       | <.0001 | 0.9630        | <.0001 | 0.8002         | <.0001 |
| $1/\lambda$ | 0.8254       | <.0001 | 0.9716        | <.0001 | 0.8067         | <.0001 |
| $H'$        | 0.8189       | <.0001 | 0.9776        | <.0001 | 0.7894         | <.0001 |
| $N_1$       | 0.8199       | <.0001 | 0.9781        | <.0001 | 0.7899         | <.0001 |
| $E'$        | 0.6811       | <.0001 | 0.9601        | <.0001 | 0.6490         | <.0001 |
| $E_{var}$   | 0.2460       | 0.0096 | 0.8911        | <.0001 | 0.3493         | 0.0002 |
| $E_{1/D}$   | 0.6761       | <.0001 | 0.9679        | <.0001 | 0.6404         | <.0001 |
| $E_q$       | 0.2391       | 0.0119 | 0.8354        | <.0001 | 0.2600         | 0.0061 |

The mean diversity and evenness values in each community are presented in Table 2.3. Cover always gave the highest diversity or evenness, followed by TSA, with mass giving the lowest values. For all diversity indices, the GRSB community was significantly less diverse than either BRSB or CPSB, regardless of the method of estimating abundance, with the only exception being the Shannon-Weiner  $H'$  and its exponential derivative,  $N_1$ , which gave different conclusions when cover was used. The results from the evenness indices differed depending on the index used and the method of abundance estimation employed. Results for the indices  $E'$ ,  $E_{1/D}$  and  $E_q$  were consistent (no significant difference) for both the cover and mass data, whereas for the TSA data, a significant difference between the three communities existed, although the conclusions across the indices were different. The results for  $E_{var}$  index were different for each method of estimating abundance.



Table 2.3. Mean ( $\pm$  SE) predicted diversity and evenness in the three communities for the three abundance estimation methods. Values with different letters in the same row are significantly different ( $\alpha=0.05$ ; Tukey-Kramer HSD test).

| Index           | Estimation<br>Method | GRSB<br>(N = 20)    | BRSB<br>(N = 40)    | CPSB<br>(N = 50)   | F ratio | P value |
|-----------------|----------------------|---------------------|---------------------|--------------------|---------|---------|
| $\lambda$       | mass                 | 0.184 $\pm$ 0.045a  | 0.347 $\pm$ 0.311b  | 0.348 $\pm$ 0.029b | 5.361   | 0.0060  |
|                 | TSA                  | 0.286 $\pm$ 0.044a  | 0.496 $\pm$ 0.031b  | 0.433 $\pm$ 0.028b | 7.695   | 0.0008  |
|                 | cover                | 0.335 $\pm$ 0.042a  | 0.537 $\pm$ 0.030b  | 0.454 $\pm$ 0.026b | 7.851   | 0.0006  |
| $1/\lambda$     | mass                 | 1.259 $\pm$ 0.136a  | 1.739 $\pm$ 0.096b  | 1.731 $\pm$ 0.086b | 5.031   | 0.0082  |
|                 | TSA                  | 1.436 $\pm$ 0.193a  | 2.323 $\pm$ 0.137b  | 2.083 $\pm$ 0.122b | 7.070   | 0.0013  |
|                 | cover                | 1.552 $\pm$ 0.204a  | 2.503 $\pm$ 0.144b  | 2.167 $\pm$ 0.129b | 7.281   | 0.0011  |
| $H'$            | mass                 | 0.544 $\pm$ 0.118a  | 1.031 $\pm$ 0.084b  | 0.969 $\pm$ 0.075b | 6.140   | 0.0030  |
|                 | TSA                  | 0.819 $\pm$ 0.122a  | 1.474 $\pm$ 0.087b  | 1.231 $\pm$ 0.077b | 9.566   | 0.0002  |
|                 | cover                | 0.948 $\pm$ 0.122a  | 1.619 $\pm$ 0.087b  | 1.280 $\pm$ 0.077a | 10.644  | <.0001  |
| $N1$            | mass                 | 1.476 $\pm$ 0.176a  | 2.203 $\pm$ 0.125b  | 2.118 $\pm$ 0.111b | 6.219   | 0.0028  |
|                 | TSA                  | 1.789 $\pm$ 0.229a  | 2.992 $\pm$ 0.162b  | 2.562 $\pm$ 0.145b | 9.251   | 0.0002  |
|                 | cover                | 1.956 $\pm$ 0.239a  | 3.278 $\pm$ 0.169b  | 2.664 $\pm$ 0.151c | 10.578  | <.0001  |
| $E'$            | mass                 | 0.255 $\pm$ 0.019a  | 0.237 $\pm$ 0.013a  | 0.272 $\pm$ 0.012a | 1.846   | 0.1629  |
|                 | TSA                  | 0.394 $\pm$ 0.030a  | 0.407 $\pm$ 0.021a  | 0.481 $\pm$ 0.019b | 4.798   | 0.0101  |
|                 | cover                | 0.424 $\pm$ 0.030a  | 0.445 $\pm$ 0.022a  | 0.498 $\pm$ 0.019a | 2.835   | 0.0631  |
| $Evar$          | mass                 | 0.107 $\pm$ 0.016ab | 0.150 $\pm$ 0.012a  | 0.105 $\pm$ 0.010b | 4.662   | 0.0115  |
|                 | TSA                  | 0.294 $\pm$ 0.035a  | 0.352 $\pm$ 0.025ab | 0.399 $\pm$ 0.022b | 3.391   | 0.0373  |
|                 | cover                | 0.352 $\pm$ 0.037a  | 0.434 $\pm$ 0.026a  | 0.429 $\pm$ 0.024a | 1.866   | 0.1597  |
| $E_{1/\lambda}$ | mass                 | 0.253 $\pm$ 0.021a  | 0.226 $\pm$ 0.015a  | 0.271 $\pm$ 0.013a | 2.450   | 0.0912  |
|                 | TSA                  | 0.379 $\pm$ 0.036a  | 0.393 $\pm$ 0.036a  | 0.478 $\pm$ 0.023b | 4.246   | 0.0168  |
|                 | cover                | 0.408 $\pm$ 0.038a  | 0.422 $\pm$ 0.028a  | 0.496 $\pm$ 0.024a | 2.988   | 0.0546  |
| $E_q$           | mass                 | 0.077 $\pm$ 0.006a  | 0.089 $\pm$ 0.004a  | 0.079 $\pm$ 0.004a | 2.466   | 0.0897  |
|                 | TSA                  | 0.127 $\pm$ 0.021a  | 0.143 $\pm$ 0.015ab | 0.185 $\pm$ 0.013b | 3.982   | 0.0215  |
|                 | cover                | 0.141 $\pm$ 0.017a  | 0.161 $\pm$ 0.012a  | 0.182 $\pm$ 0.011a | 2.361   | 0.0992  |

### 2.3.3 Relative Abundance Distributions

The Zipf-Mandelbrot model was the best fitting model for the RADs in most quadrats in the three communities regardless of the method used to estimate abundance (Table 2.4). Because the program used to fit the RADs requires at least 4 species per quadrat, and species richness as observed from the cover or TSA method could be lower than observed with the mass estimation of abundance (due to some species not measured or not hit with the point frame), those quadrats with fewer than 4 species observed using cover or TSA were excluded from the analysis. There were no significant differences in the number of times different RAD models fit best for the different abundance estimation methods (Table 2.4) in either the GRSB community ( $\chi^2 = 3.14$ ,  $df = 4$ ,  $P = 0.53$ ) or in the BRSB community ( $\chi^2 = 5.16$ ,  $df = 6$ ,  $P = 0.52$ ). There was a significant difference in the number of times the models fit best between the different abundance estimation methods in the CPSB community ( $\chi^2 = 15.12$ ,  $df = 6$ ,  $P = 0.02$ ). These conclusions were consistent if the mass data previously excluded were included in the analysis for the BRSB community ( $\chi^2 = 4.73$ ,  $df = 6$ ,  $P = 0.58$ ) and for the CPSB community ( $\chi^2 = 15.22$ ,  $df = 6$ ,  $P = 0.02$ ) but not for the GRSB community ( $\chi^2 = 9.93$ ,  $df = 4$ ,  $P = 0.04$ ), which indicated a significant difference in the number of times the different RAD models fit for the different abundance estimation methods.

Table 2.4. Number of quadrats that fit each RAD model in the three communities for cover, TSA, and mass data. Plots with less than 4 species were not fitted and are listed. For each column and community the number of quadrats that fit each RAD model and those that were excluded will sum to the total number of quadrats sampled in the community (N). The quadrats that were not fitted using cover or TSA were initially excluded from the analysis for the mass data, although the numbers of quadrats fitting each model for the entire mass data set are given in parentheses.

| Community        | RAD model         | Cover | TSA | Mass    |
|------------------|-------------------|-------|-----|---------|
| GRSB<br>(N = 20) | Geometric         | 0     | 0   | 1 (4)   |
|                  | Broken-Stick      | 0     | 0   | 0 (0)   |
|                  | General Lognormal | 0     | 1   | 1 (3)   |
|                  | Zipf-Mandelbrot   | 15    | 14  | 13 (13) |
|                  | No model fitted   | 5     | 5   | 5 (0)   |
| BRSB<br>(N = 40) | Geometric         | 3     | 4   | 4 (4)   |
|                  | Broken-Stick      | 0     | 1   | 0 (0)   |
|                  | General Lognormal | 4     | 5   | 9 (9)   |
|                  | Zipf-Mandelbrot   | 31    | 28  | 25 (27) |
|                  | No model fitted   | 2     | 2   | 2 (0)   |
| CPSB<br>(N = 50) | Geometric         | 7     | 6   | 10 (12) |
|                  | Broken-Stick      | 1     | 2   | 0 (0)   |
|                  | General Lognormal | 2     | 1   | 9 (11)  |
|                  | Zipf-Mandelbrot   | 27    | 28  | 18 (24) |
|                  | No model fitted   | 13    | 13  | 13 (3)  |

The RAD model that fit the average species abundance best was not consistent across the different abundance estimation methods (Table 2.5). Because the best fit was often only marginally better than other models, the standardized sum of squares deviance (model sum of squares deviance minus the best fitting model sum of squares deviance) are presented as well (Table 2.6). The broken-stick was consistently the worst fitting RAD model while the General-Lognormal or the Zipf-Mandelbrot was usually the best fitting model. There were strong species rank correlations between the different species abundance estimation methods (Table 2.7), meaning that the species ranks were consistent regardless of the estimation method used for the species abundance when they are averaged over all quadrats.

Table 2.5. Best fitting RAD model for the average species abundance in each community for the different species abundance estimation methods.

| Community | Mass              | TSA             | Cover             |
|-----------|-------------------|-----------------|-------------------|
| GRSB      | Zipf-Mandelbrot   | Zipf-Mandelbrot | Geometric         |
| BRSB      | General-Lognormal | Zipf-Mandelbrot | Zipf-MandelBrot   |
| CPSB      | General-Lognormal | Zipf-Mandelbrot | General-Lognormal |

Table 2.6. Standardized sum of squares deviance for each RAD model of average species abundance in three communities using different species abundance estimation methods.

| Community | RAD Model         | Mass   | TSA    | Cover  |
|-----------|-------------------|--------|--------|--------|
| GRSB      | Geometric         | 1.037  | 0.933  | 0      |
|           | Broken-Stick      | 54.769 | 19.001 | 12.836 |
|           | General-Lognormal | 0.911  | 1.710  | 0.169  |
|           | Zipf-Mandelbrot   | 0      | 0      | 0.011  |
| BRSB      | Geometric         | 8.769  | 0.643  | 0.402  |
|           | Broken-Stick      | 70.619 | 20.123 | 13.686 |
|           | General-Lognormal | 0      | 0.354  | 0.128  |
|           | Zipf-Mandelbrot   | 0.018  | 0      | 0      |
| CPSB      | Geometric         | 11.100 | 1.289  | 1.155  |
|           | Broken-Stick      | 78.416 | 21.291 | 15.412 |
|           | General-Lognormal | 0      | 0.487  | 0      |
|           | Zipf-Mandelbrot   | 1.879  | 0      | 0.179  |

Table 2.7. Spearman rank correlation coefficients ( $r_s$ ) for average species abundance between the different methods of estimating abundance for three communities. All correlations are significant ( $P < 0.0001$ ).

| Community | Mass and TSA | Mass and Cover | Cover and TSA |
|-----------|--------------|----------------|---------------|
| GRSB      | 0.9817       | 0.9542         | 0.9815        |
| BRSB      | 0.8853       | 0.8833         | 0.9986        |
| CPSB      | 0.8793       | 0.8790         | 0.9962        |

### 2.3.4 Regression Analysis Between Mass and Cover or TSA

For each species, regressions between mass and cover or mass and TSA were compared between communities to determine if it was appropriate to pool data across communities using ANCOVA to verify equality of slopes (Table 2.8). Only 9 species had sufficient observations in each community to test equality of slopes and nearly half of the regressions tested indicated species data could not be pooled across communities. The results indicate regressions should not be calculated with data pooled across communities for *Carex misandra* using cover data, for *Saxifraga oppositifolia* using TSA data and for *Dryas integrifolia*, *Luzula arctica*, and *Papaver radicatum* for either cover or TSA data (Table 2.8).

The regression of each species' mass with cover and TSA are given in Table 2.9 and Table 2.10, respectively. The regression lines generally explained a high proportion of the observed variance in the species mass with  $R^2$  ranging from 0.311 to 0.954 for the regressions using cover data (Table 2.9) and from 0.311 to 0.943 for TSA data (Table 2.10). The  $R^2$  tended to be higher with TSA than with cover data with the most common species observed, such as *Cassiope tetragona* (0.841 vs. 0.745), *Salix arctica* (0.767 vs. 0.740), *Saxifraga oppositifolia* (0.630 vs. 0.616), although *Dryas integrifolia* had a higher fit with cover (0.727) than with TSA (0.617). There was little difference in the LSN between the regressions using cover or TSA data, which ranged from 4 to 15 random observations needed to detect a statistically significant line (Table 2.9, Table 2.10).

Table 2.8. ANCOVA results for species regression lines of mass and cover (CVR) or mass and TSA for 3 communities. The number of quadrats that had the species present in each community is also listed along with the F value for equality of slopes;  $F_c$  is the critical value of F.

| Species                        | Abundance<br>Estimation<br>Method | GRSB<br>(N=20) | BRSB<br>(N=40) | CPSB<br>(N=50) | F     | $F_c$ | Same<br>Slope? |
|--------------------------------|-----------------------------------|----------------|----------------|----------------|-------|-------|----------------|
| <i>Carex misandra</i>          | CVR                               | 0              | 15             | 26             | 4.54  | 4.12  | No             |
|                                | TSA                               | 0              | 15             | 26             | 0.28  | 4.12  | Yes            |
| <i>Cassiope tetragona</i>      | CVR                               | 20             | 31             | 7              | 0.34  | 3.18  | Yes            |
|                                | TSA                               | 20             | 31             | 7              | 0.61  | 3.18  | Yes            |
| <i>Dryas integrifolia</i>      | CVR                               | 18             | 36             | 40             | 7.14  | 3.11  | No             |
|                                | TSA                               | 18             | 36             | 40             | 4.60  | 3.11  | No             |
| <i>Eriophorum triste</i>       | CVR                               | 0              | 3              | 3              | 0.02  | 18.5  | Yes            |
|                                | TSA                               | 0              | 3              | 3              | 0.05  | 18.5  | Yes            |
| <i>Luzula arctica</i>          | CVR                               | 9              | 33             | 31             | 4.05  | 3.15  | No             |
|                                | TSA                               | 9              | 33             | 31             | 11.06 | 3.15  | No             |
| <i>Luzula confusa</i>          | CVR                               | 14             | 25             | 13             | 1.60  | 3.20  | Yes            |
|                                | TSA                               | 14             | 25             | 13             | 2.65  | 3.20  | Yes            |
| <i>Papaver radicatum</i>       | CVR                               | 4              | 12             | 7              | 4.44  | 3.59  | No             |
|                                | TSA                               | 4              | 12             | 7              | 4.94  | 3.59  | No             |
| <i>Salix arctica</i>           | CVR                               | 17             | 40             | 50             | 1.08  | 3.09  | Yes            |
|                                | TSA                               | 17             | 40             | 50             | 1.00  | 3.09  | Yes            |
| <i>Saxifraga oppositifolia</i> | CVR                               | 15             | 26             | 44             | 1.60  | 3.13  | Yes            |
|                                | TSA                               | 15             | 26             | 44             | 3.60  | 3.13  | No             |

Table 2.9. Regression results of species mass and cover for all quadrats. Regression lines were calculated for all quadrats and for each community separately for those species as suggested from the ANCOVA results (Table 2.8) that indicated statistically different regression slopes for each community (meaning communities should not be pooled). The number of observations in each regression line are given as N, F-ratios are of regression mean square to residual mean square, Y is the mean response, RMSE is the root mean square error,  $R^2$  is the coefficient of determination, a is the regression intercept,  $S_a$  is the standard error of the intercept estimate, b is the regression slope,  $S_b$  is the standard error of the slope estimate and LSN is the least significant number. All regressions were statistically significant ( $P < 0.05$ )

| Species                        | Site | N   | F-ratio | Y      | RMSE   | $R^2$ | a      | $S_a$ | b     | $S_b$ | LSN   |
|--------------------------------|------|-----|---------|--------|--------|-------|--------|-------|-------|-------|-------|
| <i>Carex misandra</i>          | ALL  | 43  | 220.560 | 0.800  | 0.712  | 0.843 | -0.335 | 0.133 | 0.461 | 0.031 | 3.92  |
|                                | BRSB | 15  | 71.379  | 0.326  | 0.197  | 0.846 | 0.026  | 0.062 | 0.250 | 0.030 | 3.98  |
|                                | CPSB | 26  | 146.733 | 1.134  | 0.844  | 0.859 | -0.546 | 0.216 | 0.496 | 0.041 | 3.85  |
| <i>Cassiope tetragona</i>      | ALL  | 58  | 28.674  | 79.370 | 28.674 | 0.745 | -0.043 | 7.263 | 1.856 | 0.145 | 4.51  |
| <i>Draba species</i>           | ALL  | 23  | 9.481   | 0.152  | 0.181  | 0.311 | 0.098  | 0.041 | 0.306 | 0.099 | 12.03 |
| <i>Dryas integrifolia</i>      | ALL  | 94  | 245.342 | 13.671 | 13.078 | 0.727 | -3.435 | 1.736 | 2.777 | 0.177 | 4.61  |
|                                | GRSB | 18  | 53.201  | 18.834 | 16.018 | 0.769 | 0.321  | 4.549 | 3.875 | 0.531 | 4.45  |
|                                | BRSB | 36  | 105.441 | 14.802 | 14.518 | 0.756 | -7.002 | 3.219 | 2.973 | 0.290 | 4.46  |
|                                | CPSB | 40  | 479.626 | 10.331 | 4.302  | 0.927 | -1.960 | 0.882 | 2.147 | 0.098 | 3.43  |
| <i>Eriophorum triste</i>       | ALL  | 6   | 10.600  | 0.503  | 0.145  | 0.726 | 0.184  | 0.114 | 0.066 | 0.020 | 5.25  |
| <i>Festuca brachyphylla</i>    | ALL  | 11  | 11.967  | 0.083  | 0.092  | 0.571 | 0.018  | 0.033 | 0.065 | 0.019 | 6.50  |
| <i>Luzula arctica</i>          | ALL  | 73  | 103.794 | 0.707  | 0.0586 | 0.594 | 0.079  | 0.092 | 0.214 | 0.021 | 5.74  |
|                                | GRSB | 9   | 30.521  | 1.611  | 0.703  | 0.813 | 0.594  | 0.298 | 0.327 | 0.059 | 4.29  |
|                                | BRSB | 33  | 56.842  | 0.916  | 0.513  | 0.647 | 0.131  | 0.137 | 0.188 | 0.025 | 5.30  |
|                                | CPSB | 31  | 19.785  | 0.223  | 0.221  | 0.406 | 0.070  | 0.053 | 0.099 | 0.022 | 8.84  |
| <i>Luzula confusa</i>          | ALL  | 52  | 30.731  | 0.402  | 0.336  | 0.381 | 0.136  | 0.067 | 0.072 | 0.013 | 9.30  |
| <i>Oxyria digyna</i>           | ALL  | 44  | 39.707  | 0.135  | 0.107  | 0.486 | 0.033  | 0.023 | 0.064 | 0.010 | 7.18  |
| <i>Papaver radicum</i>         | ALL  | 23  | 20.214  | 0.168  | 0.126  | 0.490 | 0.066  | 0.035 | 0.147 | 0.033 | 7.28  |
|                                | GRSB | 4   | 13.719  | 0.265  | 0.134  | 0.873 | -0.087 | 0.116 | 0.351 | 0.095 | 4.28  |
|                                | BRSB | 12  | 11.126  | 0.174  | 0.100  | 0.527 | 0.106  | 0.035 | 0.102 | 0.031 | 7.07  |
|                                | CPSB | 7   | 2.283   | 0.104  | 0.114  | 0.308 | 0.029  | 0.066 | 0.130 | 0.087 | 14.73 |
| <i>Pedicularis species</i>     | ALL  | 23  | 16.997  | 0.023  | 0.018  | 0.447 | 0.017  | 0.004 | 0.030 | 0.007 | 8.06  |
| <i>Poa arctica</i>             | ALL  | 18  | 31.181  | 0.102  | 0.074  | 0.661 | 0.046  | 0.020 | 0.056 | 0.010 | 5.29  |
| <i>Polygonum viviparum</i>     | ALL  | 15  | 272.528 | 0.108  | 0.036  | 0.954 | 0.027  | 0.010 | 0.058 | 0.004 | 3.29  |
| <i>Salix arctica</i>           | ALL  | 107 | 299.522 | 13.195 | 9.321  | 0.740 | -2.776 | 1.290 | 0.888 | 0.051 | 4.52  |
| <i>Saxifraga oppositifolia</i> | ALL  | 85  | 133.253 | 2.359  | 2.076  | 0.616 | -0.048 | 0.307 | 0.802 | 0.070 | 5.51  |
| <i>Stellaria longipes</i>      | ALL  | 26  | 37.926  | 0.062  | 0.055  | 0.612 | 0.029  | 0.012 | 0.065 | 0.011 | 5.67  |

Table 2.10. Regression results of species mass and TSA for all plots. Symbols and details are as described in Table 2.9. All regressions were significant ( $P < 0.05$ ).

| Species                        | Site | N   | F-ratio | Y      | RMSE   | R <sup>2</sup> | a      | S <sub>a</sub> | b     | S <sub>b</sub> | LSN   |
|--------------------------------|------|-----|---------|--------|--------|----------------|--------|----------------|-------|----------------|-------|
| <i>Carex misandra</i>          | ALL  | 43  | 500.554 | 0.800  | 0.495  | 0.924          | -0.132 | 0.086          | 0.216 | 0.009          | 3.45  |
| <i>Cassiope tetragona</i>      | ALL  | 58  | 297.908 | 79.370 | 22.582 | 0.842          | 2.384  | 5.356          | 0.974 | 0.056          | 3.92  |
| <i>Draba</i> species           | ALL  | 23  | 9.481   | 0.152  | 0.181  | 0.311          | 0.098  | 0.041          | 0.306 | 0.099          | 12.03 |
| <i>Dryas integrifolia</i>      | ALL  | 94  | 148.333 | 13.671 | 15.494 | 0.617          | -1.674 | 2.035          | 1.237 | 0.102          | 5.49  |
|                                | GRSB | 18  | 36.500  | 18.834 | 18.390 | 0.695          | 2.464  | 5.112          | 1.786 | 0.296          | 5.00  |
|                                | BRSB | 36  | 50.078  | 14.802 | 18.697 | 0.596          | -4.608 | 4.151          | 1.333 | 0.188          | 5.79  |
|                                | CPSB | 40  | 337.606 | 10.331 | 5.050  | 0.899          | -1.214 | 1.106          | 0.968 | 0.053          | 3.60  |
| <i>Eriophorum triste</i>       | ALL  | 6   | 13.584  | 0.503  | 0.132  | 0.773          | 0.146  | 0.111          | 0.063 | 0.017          | 4.81  |
| <i>Festuca brachyphylla</i>    | ALL  | 11  | 10.586  | 0.083  | 0.095  | 0.540          | 0.020  | 0.035          | 0.050 | 0.015          | 6.93  |
| <i>Luzula arctica</i>          | ALL  | 73  | 100.551 | 0.707  | 0.592  | 0.586          | 0.140  | 0.089          | 0.115 | 0.011          | 5.82  |
|                                | GRSB | 9   | 28.444  | 1.611  | 0.723  | 0.803          | 0.591  | 0.308          | 0.200 | 0.037          | 4.37  |
|                                | BRSB | 33  | 60.681  | 0.916  | 0.502  | 0.662          | 0.204  | 0.127          | 0.100 | 0.013          | 5.18  |
|                                | CPSB | 31  | 53.778  | 0.223  | 0.170  | 0.650          | 0.066  | 0.037          | 0.062 | 0.009          | 5.29  |
| <i>Luzula confusa</i>          | ALL  | 52  | 54.827  | 0.402  | 0.293  | 0.523          | 0.121  | 0.056          | 0.049 | 0.007          | 6.60  |
| <i>Oxyria digyna</i>           | ALL  | 44  | 36.948  | 0.135  | 0.109  | 0.468          | 0.031  | 0.024          | 0.058 | 0.010          | 7.47  |
| <i>Papaver radiculatum</i>     | ALL  | 23  | 25.461  | 0.168  | 0.119  | 0.548          | 0.070  | 0.031          | 0.119 | 0.024          | 6.44  |
|                                | GRSB | 4   | 108.471 | 0.265  | 0.051  | 0.982          | -0.037 | 0.038          | 0.242 | 0.023          | 3.16  |
|                                | BRSB | 12  | 9.947   | 0.174  | 0.103  | 0.499          | 0.110  | 0.036          | 0.077 | 0.024          | 7.53  |
|                                | CPSB | 7   | 2.283   | 0.104  | 0.114  | 0.308          | 0.029  | 0.066          | 0.130 | 0.087          | 14.73 |
| <i>Pedicularis</i> species     | ALL  | 23  | 16.997  | 0.023  | 0.018  | 0.447          | 0.017  | 0.004          | 0.030 | 0.007          | 8.06  |
| <i>Poa arctica</i>             | ALL  | 18  | 30.707  | 0.102  | 0.074  | 0.657          | 0.043  | 0.021          | 0.051 | 0.009          | 5.32  |
| <i>Polygonum viviparum</i>     | ALL  | 15  | 215.779 | 0.108  | 0.040  | 0.943          | 0.030  | 0.012          | 0.043 | 0.003          | 3.361 |
| <i>Salix arctica</i>           | ALL  | 107 | 345.052 | 13.195 | 8.837  | 0.767          | -1.522 | 1.165          | 0.581 | 0.031          | 4.349 |
| <i>Saxifraga oppositifolia</i> | ALL  | 85  | 141.514 | 2.359  | 2.037  | 0.630          | 0.045  | 0.294          | 0.705 | 0.059          | 5.375 |
|                                | GRSB | 15  | 7.330   | 2.860  | 2.706  | 0.361          | 0.279  | 1.181          | 0.968 | 0.357          | 10.62 |
|                                | BRSB | 26  | 80.480  | 1.533  | 0.863  | 0.770          | 0.558  | 0.201          | 0.461 | 0.051          | 4.40  |
|                                | CPSB | 44  | 111.631 | 2.677  | 2.102  | 0.727          | -0.683 | 0.449          | 0.803 | 0.076          | 4.65  |
| <i>Stellaria longipes</i>      | ALL  | 26  | 36.662  | 0.062  | 0.055  | 0.604          | 0.031  | 0.012          | 0.059 | 0.010          | 5.76  |

The regression results for the functional groups listed in Table 2.1 are given in Table 2.11. Results were comparable between cover and TSA with R<sup>2</sup> ranging from 0.454 to 0.762 for cover and from 0.436 to 0.821 for TSA, with TSA tending to have higher R<sup>2</sup> values. LSN ranged between 5 and 8 for both cover and TSA.



Table 2.11. Regressions between cover (CVR) or TSA and mass for functional groups. Symbols and details are as described in Table 2.9. All regressions were significant ( $P < 0.05$ ).

| Group      | Method | F-ratio | Y      | RMSE   | R <sup>2</sup> | a      | S <sub>a</sub> | b     | S <sub>b</sub> | LSN  |
|------------|--------|---------|--------|--------|----------------|--------|----------------|-------|----------------|------|
| Deciduous  | CVR    | 299.522 | 13.195 | 9.321  | 0.740          | -2.776 | 1.290          | 0.888 | 0.051          | 4.52 |
|            | TSA    | 345.052 | 13.195 | 8.837  | 0.767          | -1.522 | 1.165          | 0.581 | 0.031          | 4.40 |
| Evergreen  | CVR    | 362.105 | 60.707 | 28.232 | 0.762          | 1.393  | 4.235          | 1.880 | 0.099          | 4.20 |
|            | TSA    | 435.621 | 60.707 | 26.203 | 0.821          | 1.800  | 3.879          | 0.993 | 0.048          | 4.03 |
| Forbs      | CVR    | 86.466  | 2.117  | 2.334  | 0.454          | -0.239 | 0.340          | 0.595 | 0.064          | 7.60 |
|            | TSA    | 80.249  | 2.117  | 2.373  | 0.436          | -0.059 | 0.335          | 0.499 | 0.056          | 7.95 |
| Graminoids | CVR    | 88.027  | 1.140  | 1.039  | 0.461          | -0.061 | 0.163          | 0.193 | 0.021          | 7.48 |
|            | TSA    | 161.819 | 1.140  | 0.883  | 0.611          | -1.063 | 0.130          | 0.128 | 0.010          | 5.54 |

### 2.3.5 Test of Biomass Estimation

The rank correlations between the actual and estimated biomass from regressed TSA data for the most commonly occurring species, and those that were the highest proportion of the biomass, were all significant (Table 2.12). The species which were significantly correlated between actual and observed biomass accounted for 99.88% of the total biomass of all plots, whereas those species which were uncorrelated accounted for only 0.12% of the total biomass. There was no significant difference between the mean actual biomass and the mean predicted biomass for each species using a paired t-test except for *Saxifraga oppositifolia* (Table 2.12).

Table 2.12. Spearman correlation coefficients ( $r_s$ ) and paired T-test results between estimated biomass and actual biomass for the subset of quadrats used to test the regression estimation method. This included all species that were found in 4 or more quadrats.

| Species                        | N  | $r_s$  | P > $ r_s $ | T      | P > $ t $ |
|--------------------------------|----|--------|-------------|--------|-----------|
| <i>Cardamine bellidifolia</i>  | 4  | 0.7746 | 0.2264      | 2.2714 | 0.1078    |
| <i>Carex misandra</i>          | 13 | 0.8388 | <0.0001     | 1.5087 | 0.1456    |
| <i>Cassiope tetragona</i>      | 29 | 0.9187 | <0.0001     | 0.8700 | 0.3917    |
| <i>Draba</i> species           | 9  | 0.5175 | 0.1536      | 2.0549 | 0.0739    |
| <i>Dryas integrifolia</i>      | 49 | 0.8716 | <0.0001     | 0.5737 | 0.5689    |
| <i>Eriophorum triste</i>       | 5  | 0.9000 | 0.0374      | 1.8736 | 0.1343    |
| <i>Festuca brachyphylla</i>    | 5  | 0.6489 | 0.2362      | 0.4317 | 0.6882    |
| <i>Luzula arctica</i>          | 38 | 0.6950 | <0.0001     | 0.0232 | 0.8172    |
| <i>Luzula confusa</i>          | 28 | 0.7543 | <0.0001     | 0.8491 | 0.4033    |
| <i>Oxyria digyna</i>           | 21 | 0.6131 | 0.0031      | 0.7449 | 0.4650    |
| <i>Papaver radicum</i>         | 9  | 0.6236 | 0.0727      | 1.7014 | 0.1273    |
| <i>Pedicularis</i> species     | 14 | 0.3548 | 0.2132      | 1.0070 | 0.3333    |
| <i>Poa arctica</i>             | 9  | 0.8398 | 0.0046      | 0.7313 | 0.4855    |
| <i>Polygonum viviparum</i>     | 7  | 0.6682 | 0.1009      | 1.2688 | 0.2515    |
| <i>Salix arctica</i>           | 54 | 0.8985 | <0.0001     | 1.4150 | 0.1629    |
| <i>Saxifraga nivalis</i>       | 5  | 0.7071 | 0.1817      | 1.0585 | 0.3495    |
| <i>Saxifraga oppositifolia</i> | 41 | 0.7955 | <0.0001     | 4.5172 | <0.0001   |
| <i>Stellaria longipes</i>      | 13 | 0.6364 | 0.0194      | 0.0753 | 0.9412    |

Within each quadrat, the rank correlation of species abundance as estimated from the regressed TSA data and from the actual biomass averaged 0.841 (SE = 0.027), with all but 12 of 55 plots (22%) showing a statistically significant correlation and the majority showing a very strong correlation (Figure 2.1). The plots that showed no significant correlation had significantly lower species richness (5.67, SE = 0.31) than the plots that showed a significant correlation (7.35, SE = 0.35), as indicated with an independent t-test ( $t = 3.615$ ,  $P < 0.001$ ).

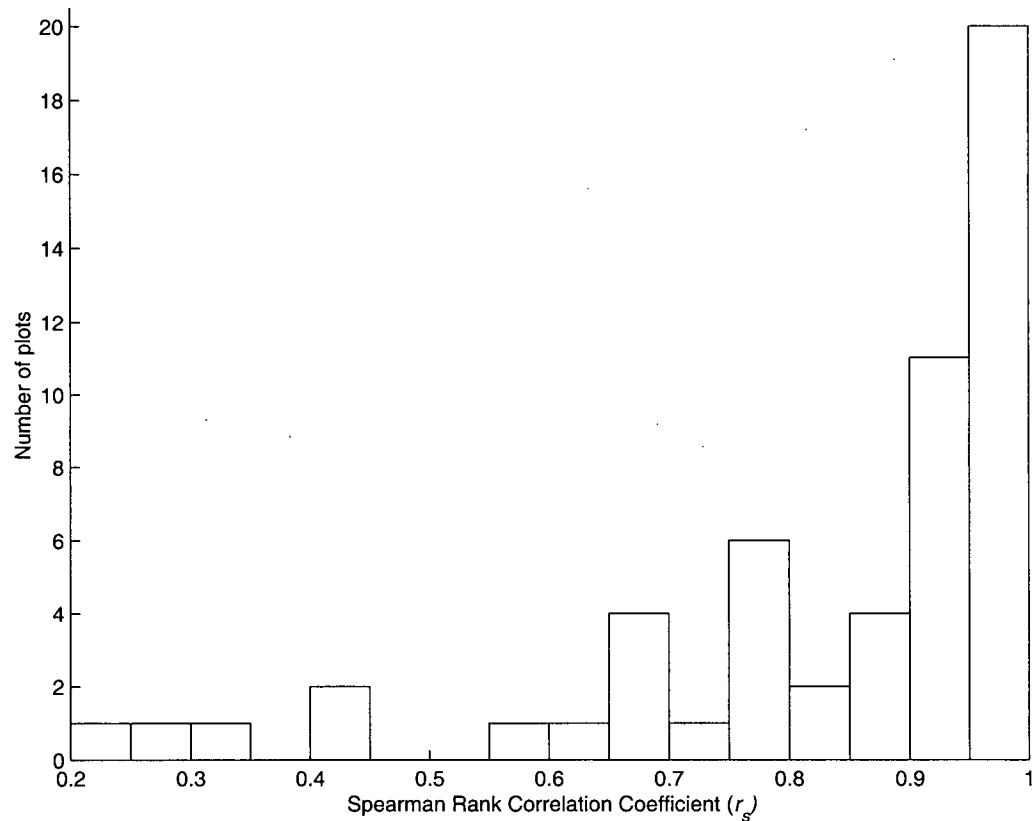


Figure 2.1. Frequency distribution of number of plots and Spearman correlation coefficients ( $r_s$ ) for the correlation across species abundance using regressed TSA data and actual biomass data.

The rank correlations of all diversity and evenness values between the estimated biomass and actual biomass were all strong and significant, although the mean diversity and evenness as calculated from actual biomass data was lower than the mean value as calculated from the estimated biomass for all indices except  $\lambda$  and  $1/\lambda$  (Table 2.13). However, the statistical conclusion that the mean diversity and evenness values were different cannot be made since all of the data sets violate the normality assumption as tested using the Shapiro-Wilk W-Test (SAS 1995). None of the traditional transformations or the Box-Cox transform (Krebs 1999) could transform the data to normal. No significant difference for any of diversity or evenness indices using estimated and actual biomass were detected using the non-parametric Wilcoxon rank scores test, which is equivalent to the Mann-Whitney U Test (Zar 1984).

Table 2.13. Spearman correlation coefficients ( $r_s$ ) and the Wilcoxon test (Z) results between diversity and evenness values as calculated from the actual biomass and the estimated biomass for 55 quadrats.

| Index           | $r_s$ | $P >  r_s $ | Z     | $P >  Z $ |
|-----------------|-------|-------------|-------|-----------|
| $\lambda$       | 0.917 | <0.0001     | 0.520 | 0.603     |
| $1/\lambda$     | 0.917 | <0.0001     | 0.520 | 0.603     |
| $H'$            | 0.931 | <0.0001     | 0.502 | 0.616     |
| $N_1$           | 0.932 | <0.0001     | 0.505 | 0.613     |
| $E'$            | 0.899 | <0.0001     | 0.643 | 0.520     |
| $Evar$          | 0.696 | <0.0001     | 1.815 | 0.070     |
| $E_{1/\lambda}$ | 0.828 | <0.0001     | 0.768 | 0.442     |
| $E_q$           | 0.544 | <0.0001     | 1.381 | 0.167     |

There was no significant difference in the number of times different RAD models fit between the actual biomass and the estimated biomass (Table 2.14;  $\chi^2 = 1.28$ ,  $df = 2$ ,  $P = 0.53$ ). The degree of fit (standardized sum of squares deviance) between actual and estimated biomass was correlated for each RAD model except for the General lognormal model (Table 2.15). Quadrats that fit a particular RAD model using actual biomass data tended to fit the same model using estimated biomass data and this relation was statistically significant (Table 2.16;  $\chi^2 = 16.61$ ,  $df = 4$ ,  $P = 0.002$ ).

Table 2.14. Number of plots which fit different RAD models using actual biomass data and estimated biomass from regressed TSA.

| RAD model         | Actual mass | Estimated mass |
|-------------------|-------------|----------------|
| Geometric         | 0           | 0              |
| Broken-Stick      | 8           | 10             |
| General-Lognormal | 10          | 6              |
| Zipf-Mandelbrot   | 36          | 38             |

Table 2.15. Spearman rank correlation ( $r_s$ ) of the model fit as calculated using the actual and estimated biomass for each RAD model. Model fit is the standardized sum of squares deviance (standardized to 0.0 for best fitting model).

| RAD model         | $r_s$  | P      |
|-------------------|--------|--------|
| Geometric         | 0.5284 | <.0001 |
| Broken-Stick      | 0.6836 | <.0001 |
| General-Lognormal | 0.2323 | 0.0910 |
| Zipf-Mandelbrot   | 0.2952 | 0.0302 |

Table 2.16. Number of quadrats that fit each RAD model with actual mass data and the number of quadrats that fit other models using estimated mass data. For the models G = Geometric, BS is the Broken Stick, GL = General Lognormal, ZM = Zipf-Mandelbrot.

| Estimated mass | Actual mass |    |    |    |
|----------------|-------------|----|----|----|
|                | G           | BS | GL | ZM |
| G              | 5           | 0  | 3  | 2  |
| BS             | 0           | 0  | 0  | 0  |
| GL             | 0           | 0  | 2  | 4  |
| ZM             | 3           | 0  | 5  | 30 |

## 2.4 DISCUSSION

Previous researchers have compared results based on cover and biomass data and have concluded that cover should not be used as a surrogate for biomass (Chiarucci et al. 1999, Guo and Rundel 1997). These judgments were made even though there was little difference between diversity measures based on the comparison of cover and biomass; however, there were differences in the community structure measurements using cover or mass based on the best fitting RAD models (Chiarucci et al. 1999, Guo and Rundel 1997) and for rarefraction curves (Guo and Rundel 1997). My results are generally consistent with those of previous researchers, although I also demonstrate that an estimate of biomass can be made once the relation between

TSA (or cover) and mass has been determined for each species, and that estimated biomass can be used reasonably well as a surrogate for biomass (Catchpole and Wheeler 1992, Jonasson 1988). Estimated biomass can be used to estimate diversity or examine community structure using RAD models and will give very similar results to actual biomass. My data also differ from previous work in that researchers have only been able to compare consistency in results between cover and mass for 2 separate areas (Guo and Rundel 1997) or 35 plots (Chiarucci et al. 1999), whereas my data include comparisons between 3 separate areas with a total of 110 quadrats.

The rank correlations of species between the different abundance estimation methods were generally both high and statistically significant, which is confirmatory to earlier reports (Chiarucci et al. 1999). Diversity values were all strongly correlated between mass and cover data or mass and TSA data, except for some evenness values. However, all correlations for evenness values were statistically significant, but tended to be less so than with diversity. This was especially true for  $E_{var}$  and  $E_q$ , as observed previously by Chiarucci et al. (1999).

When the mean diversity was compared across the three communities, the selection of index and the method of estimating abundance could change the conclusions reached. There are specific rationales for choosing the most appropriate diversity index (Krebs 1999) or evenness index (Smith and Wilson 1996) based on the mathematical properties of the indices. These criteria are summarized in Appendix A.

The best fitting RAD models differed between abundance estimation methods when the replicate quadrats were compared in the manner advocated by Wilson (1991), and when species abundances were averaged across the entire community. The Zipf-Mandelbrot model fit best for all communities and for all abundance estimation methods, although the General Lognormal model fit more frequently with mass data than with cover or TSA data (Table 2.4). Chiarucci et al (1999) stated that this tendency is because the General Lognormal model has a tail that decreases sharply for rare species and biomass is the only estimation method that can adequately represent this. Both cover and TSA have a minimum value of 1, whereas mass is limited to the precision of the balance used to measure the sample. Similarly, the use of cover sets an upper species abundance limit of 100 when measured as a percent, or as in this case where 100 pins were used. This results in boundaries on the RAD, making the value of fitting models questionable or even inadvisable (Wilson 1991). Using TSA circumvents the problem associated with an upper limit, but TSA also suffers from a lower limit problem. In these data the use of TSA rather than cover mostly changes the dominant species, since rare species are

usually only hit once or twice when using the point frame. Dominant species such as *Cassiope tetragona* and *Salix arctica*, which have multiple stems and layered leaf architecture, will likely be hit repeatedly at the same point. Because the dominant species had more hits using TSA than with cover, the diversity index tended to be lower when calculated with TSA than with cover, although it still higher than the values calculated from biomass data.

One of the most common uses of RADs is to determine which biologically based RAD model most closely fits the species abundances (Magurran 1988, Tokeshi 1993). This may be to relate hypotheses of natural environmental patterns or experimental manipulations to the observed RAD. The fit of the different RAD models is "often subtle, making it unsurprising that the abundance measure used should affect the result" (p.40 of Chiarucci et al. 1999). However, the best fitting model is also often only marginally better than others when using sum of squares deviance. To conclude that one model fits better than another, using the methods of Wilson (1991), may not be of assistance to researchers when in fact there is no statistical difference between the different models when using procedures like the  $\chi^2$  test of goodness of fit or the Kolmogorov-Smirnov one-sample test, the procedures advocated by Pielou (1975) and Tokeshi (1993) respectively. This will be especially true if the number of species observed is low, since the differing models will overlap. Unfortunately, there are no clear distinctions among the best methods to fit RAD models. Therefore, it is likely most useful to use the methods advocated by Wilson (1991) and to report the standardized sum of squares deviance so others may observe how close the best fitting models were to each other.

Generally, the relation between TSA and mass or cover and mass was not as good as previous work where  $R^2$  values have been reported as ranging from 0.67 to 0.93 (Jonasson 1988). For species data pooled across all communities, the  $R^2$  ranged between 0.311 to 0.954 for the regressions of cover and mass and between 0.311 and 0.943 for the regressions of TSA and mass. Grouping species of similar life form and calculating a regression with cover or TSA and mass gave  $R^2$  values ranging from 0.436 to 0.821. These values are somewhat less than values listed by previous researchers who reported  $R^2$  values ranging from 0.831 to 0.956 (Frank and McNaughton 1990), although they may still give acceptable estimates of biomass depending on the needs of the researcher. For instance, foresters may only need a quick estimate of understory vegetation biomass for making predictions of fire behavior (Catchpole and Wheeler 1992). The lower  $R^2$  values presented here likely result from the combination of species that have slightly differing life forms (and cover to biomass relations) within the same functional group. An example would be that both *Oxyria digyna*, a small perennial herb with mostly basal

leaves, and *Saxifraga oppositifolia*, a herb found as a loose or dense mat that often has semi-woody stems, are considered forbs with the functional groups used here.

The tests of the biomass estimation method from regressed TSA data indicate this technique performs effectively. TSA was the preferred method to estimate mass for the same reason inclined point quadrats are often used, because the numbers of intercepts are higher (Bullock 1996). The Spearman correlations of biomass and estimated biomass were significant for most of the species and there was no significant difference between biomass and estimated biomass for all species, except *Saxifraga oppositifolia*. This may be due to the morphological variability of this plant, which can be found as a loose or dense mat (Cody 1996, Desrosiers 1991), each with similar cover but differing mass. The rank correlation of species within the quadrats was high and significant in all but 12 of 55 quadrats. Quadrats that did not have a significant rank correlation of species had lower species richness; therefore, this technique may perform better with quadrats with higher species richness.

Rank correlation of the diversity and evenness indices were all strong and significant; however, the indices based on estimated biomass from regressed TSA data tended to be slightly inflated versus the values calculated from the actual biomass. Because these data are strongly skewed to approximately a Poisson distribution, the conclusion reached from a paired t-test is not statistically valid due to the non-normal data structure (Zar 1984). The comparison I would like to have made necessitates the use of a paired t-test, which loses some degrees of freedom, but accounts for the variance between plots (Wilkinson et al. 1992), rather than a t-test based on independent samples or a non-parametric Wilcoxon Test (also called the Mann-Whitney Test). Both of the latter tests indicated no significant difference between the mean diversity or evenness index as calculated from the estimated biomass and actual biomass data, although the Mann-Whitney Test is the only one that is statistically valid.

The number of best fitting RAD models was consistent between the estimated biomass and the actual biomass. There was also a significant relation between which RAD model fit best using biomass and estimated biomass. This was not observed when comparing cover, TSA and biomass data. A problem that was observed with the estimated biomass method was that there was a significant difference in the rank correlation of the degree of fit for the General Lognormal model. This is likely due to the poorer estimation of the rare species abundance. Because rare species were infrequent in the quadrats used to calibrate the regression models, poor abundance data exists to construct regression lines of cover and mass. Therefore, it is not surprising that the fit was poor for the General Lognormal model, which is sensitive to changes



in the rare species that occur in the tail of the RAD, when the estimated biomass is used rather than the actual biomass. Overall, the performance of this method to estimate biomass is excellent, with results very similar to that of actual biomass.

Chiarucci et al. (1999) also used ordination analysis (DCA) to determine if there was a difference between the eigenvalues for the first axis or the gradient length as calculated with cover or biomass. They found that there was little difference between the abundance measures. Since the rank correlation between cover and biomass estimates of species data is very high, there is no reason to expect differences in the gradient length approach of examining diversity, because the peak abundance of cover will occur when biomass peaks. Therefore, the use of DCA, or other ordination techniques, to determine differences between the methods of estimating abundance is ineffective.

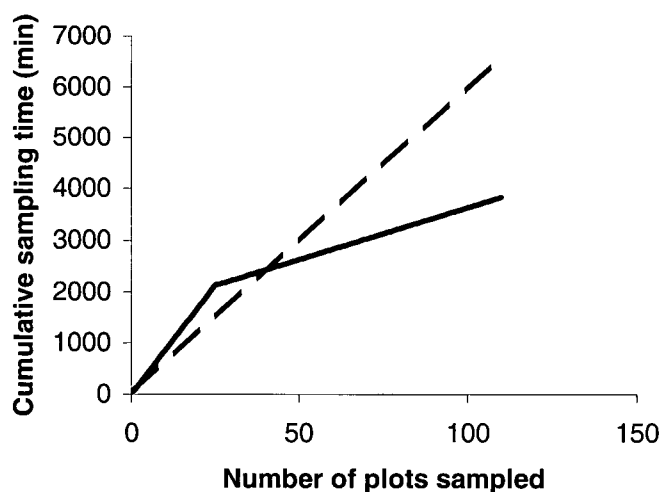


Figure 2.2. Time required to sample plots (or quadrats) assuming that to destructively sample for biomass (dashed line) takes 60 minutes per plot (this is likely an underestimation) and that it takes 20 minutes per plot using point quadrat sampling (solid line) to estimate TSA with 100 points per quadrat. For the point quadrat sampling, the first 20 plots were point quadrat sampled and destructively sampled to calibrate the regression between TSA and biomass and all subsequent plots were sampled using point quadrats only.

The use of estimated biomass from simple linear regressions of TSA could potentially save a great deal of time if a large number of quadrats need to be surveyed, since as few as 4 quadrats are required to determine a significant relation between TSA and mass. A great deal of time could be saved if quadrats were sampled optimally (in terms of minimizing time spent per quadrat). This could be accomplished by sampling quadrats using both point quadrat sampling

and destructive biomass harvests and calculating the regression line after every quadrat until a significant relation is established for each species, and then only sampling with point quadrats. From the data collected for my work, approximately 20 to 25 quadrats would be needed to determine the relation, meaning that if I had optimally sampled I could have completed the entire 110 quadrats in 40 % less time than was actually spent destructively sampling the quadrats (Figure 2.2). This method of estimating biomass could also be useful for permanent plots that cannot be destructively harvested in order to quantify changes in vegetation dynamics (see Chapter 3).

## **2.5 CONCLUSIONS**

Although the differences in the conclusions reached between cover and biomass data were not as large as previous reports, the best fitting RAD model was not identical to the average RAD in each community. Given that biomass is the preferred measure of abundance, and that it is very time consuming to determine, the point quadrat method of estimating TSA was used to quantify the abundance of each species and this value was converted into an estimated biomass from regression lines of TSA and mass. This method was shown to give results that were essentially identical to the results of using actual biomass for diversity, evenness and RADs. This method can be more efficient if a large number of plots are to be sampled and may be especially useful if plots are not to be damaged. Biomass estimation from point quadrat data is a viable alternative to destructive harvesting.

### **3. PATTERNS OF DIVERSITY WITHIN NATURAL AND MANIPULATED SNOWBEDS**

#### **3.1 INTRODUCTION**

General circulation models predict great changes in the world's climate, with the earliest and most intense changes occurring in the high latitude regions (Cattle and Crossley 1995, Maxwell 1992). Predicted changes with particular importance to arctic vegetation include a longer snow-free season (by as much as an extra month), increased soil and air temperature, deeper active soil layer, northern movement of the permafrost boundary and tree line, decreased sea ice cover in summer months and increased winter precipitation with a possible increase in summer soil moisture (Maxwell 1992). Short-term climatic change will likely be more variable and this is predicted to be of more importance than either warming or change in precipitation in driving ecosystem change (Starfield and Chapin 1996). Predictive models of vegetation are further complicated by major regional differences in the potential climate change (both in magnitude and direction) and therefore will need to be location specific (Maxwell 1992). Nonetheless, alteration of arctic ecosystems will likely occur with climate change due to shifts in dominance and a migration of sub-arctic species to the Low Arctic and low arctic species to the High Arctic (Chapin and Körner 1995, Starfield and Chapin 1996) as well as increased vegetation cover in the High Arctic due to higher rates of germination and successful colonization in polar semi-deserts (Robinson et al. 1998).

Ample evidence has already accumulated to suggest that increased surface temperature will affect vegetation from studies throughout the Arctic and Alpine regions (Callaghan and Jonasson 1995, Chapin and Shaver 1996, Chapin et al. 1995b, Galen and Stanton 1993, Galen and Stanton 1995, Henry and Molau 1997, Hobbie et al. 1999, Robinson et al. 1998). Results of particular interest come from the International Tundra Experiment (ITEX), which was established to monitor plant species' response to experimental manipulations of micro-climate and has 26 sites throughout the Arctic and some in the lower latitude Alpine tundra (Henry and Molau 1997). Results of the experiments to date are summarized in a special issue of *Global Change Biology* (Henry 1997) and in Arft et al. (1999). Short-term responses, especially

changes in reproductive and vegetative phenology, to increased temperature have been observed in almost all of the primary target species (Henry and Molau 1997, Murray 1997).

Influence of snow on vegetation is also well documented in natural gradients (Billings and Bliss 1959, Kudo and Ito 1992, Philipp 1978, Schaefer and Messier 1995, Stanton et al. 1994, Walker et al. 1993, Wijk 1986) and in experimentally modified gradients of snowmelt (Galen and Stanton 1993, Galen and Stanton 1995). Most of these studies were conducted in alpine regions, although see Philipp (1978), Reznicek and Svoboda (1982) and Schaefer and Messier (1995). Snowmelt date is studied because as meltdate decreases the length of the potential growing season would increase (Stanton et al. 1994, Walker et al. 1993). Work has primarily focused on specific species responses or on functional group changes as a result of snowmelt patterns. Few studies have examined changes in diversity along this gradient in any more than a simple qualitative examination.

Diversity has become one of the most controversial aspects of recent ecological study; especially the diversity-stability debate and other issues related to the ecosystem functions of diversity (Johnson et al. 1996, Lawton 1994, Tilman 1999). Recent debates have included whether diversity depends on productivity (Grime 1977, Huston 1979, Tilman 1985, Tilman 1990) or productivity depends on diversity (MacNaughton 1993, Naeem et al. 1994, Tilman et al. 1996, Vitousek 1993) or the proper interpretation of studies of biodiversity (Aarssen 1997, Allison 1999, Doak et al. 1998, Huston 1997, Naeem et al. 1994, Tilman 1996, Tilman 1997, Tilman and Dowling 1994, Tilman et al. 1998). If universally accepted conclusions can be reached, and it appears that in general a consensus is being reached among ecologists (Schläpfer and Schmid 1999, Schläpfer et al. 1999), it would seem that species diversity is related to plant production and that within a system as diversity increases, so does ecosystem function. Ecosystem function in the study mentioned (Schläpfer et al. 1999) was described as the ecosystem processes that were important for sustained production in forestry, agriculture and fisheries, or that were directly beneficial to humans; this is a very anthropocentric view of "ecosystem services". The processes identified as important were water catchment, regulation, and groundwater recharge, storage and cycling of nutrients and organic matter, fixation of solar energy, localized climate regulation, accumulation and recycling of human waste and pollution, and the regulation of natural populations including pest species (Schläpfer et al. 1999).

Diversity can be examined at any level, from the genetic to the entire system (Walker 1995), but for the purposes of my research, only species diversity will be discussed. Within arctic ecosystems, diversity has been linked to community structure and ecosystem function (Chapin

et al. 1995a, Chapin et al. 1995b, Henry 1998, Pastor 1995). Species diversity in the Arctic, as elsewhere, is related to the specific scale of interest with numerous filters limiting the number of species (Walker 1995); the most important limiting factor being climate, particularly the effects of temperature (Rannie 1986). Because of these reasons, the Arctic is a particularly interesting place to do research: it has few species and is therefore of a somewhat simpler structure than more southerly locales, has plants of smaller stature facilitating manipulative experiments of entire systems, is functionally diverse (Chapin et al. 1995a), and has a strong potential for change due to climatic change.

The principal focus of my work is to examine the relation between species diversity of vascular plants and meltdate within natural and manipulated snowbeds in the Canadian High Arctic. Patterns of species abundance within the natural snowbeds were compared to changes observed from the experimental gradient of snowmelt date in the manipulated snowbed. Species diversity was also examined as a function of total aboveground biomass per unit area. Other factors could also be responsible for community structure; therefore, numerous other environmental variables were also quantified and examined to determine the principal variables related to species abundance and diversity.

## **3.2 METHODS**

### **3.2.1 Study Sites**

An introduction to the location of the studies, Alexandra Fiord lowland (78°53'N; 75°55'W), and to its general environmental features can be found in Chapter 1. For a comprehensive description of the lowland, see Svoboda and Freedman (1994). Three naturally occurring snowbeds were used as study sites (Figure 3.1) within the lowland, because they were persistent snowbeds. Other snowbeds were also observed on the lowland, but the chosen sites were close together or were sites of previous research projects. One site, the glacial river snowbed (GRSB), was located along an east facing river slope beside the lowland's largest river. This site was characterized by a steeper slope than any of the other research sites and also differed in that it was very hummocky. The dominant vascular plant species were *Cassiope tetragona* and *Dryas integrifolia*. A second research site, the camp snowbed (CPSB), was a raised beach ridge with a northerly aspect and was located within the research camp. This site differed from the

others because it was the only one dominated by a deciduous shrub, *Salix arctica*, although *Dryas integrifolia* and *Saxifraga oppositifolia* were also important. The third natural snowbed was also a raised beach ridge, the beach ridge snowbed (BRSB) and was dominated by *Cassiope tetragona*, *Dryas integrifolia* and *Salix arctica*.

An additional site, which was adjacent to the BRSB (Figure 3.1) and had very similar environmental conditions and vegetation composition, was the snow manipulation snowbed (SMSB). The SMSB was established in 1992, by G. Henry, to examine the effect of snow manipulation and the subsequent alteration in growing season length on the phenology, growth, and composition and density of vegetation. Since the SMSB is within a naturally occurring persistent snowbed, there is still snow early in June when the field season begins. The manipulations include removal of snow off of one set of plots at the beginning of the season to a depth of approximately 5 –10 cm above the surface of the ground, which leads to an earlier onset of the growing season and gives these plots a longer growing season. All removed snow is added to the adjacent plot and is evenly spread such that the plot will have shorter growing season due to the later snow-free date. There is also an adjacent control plot where snow cover is not manipulated. Each plot is approximately 3 m × 3 m and is separated by a 1 m buffer, and there are 3 replicates of each experimental treatment (removal, addition and control), giving a total of 9 plots.

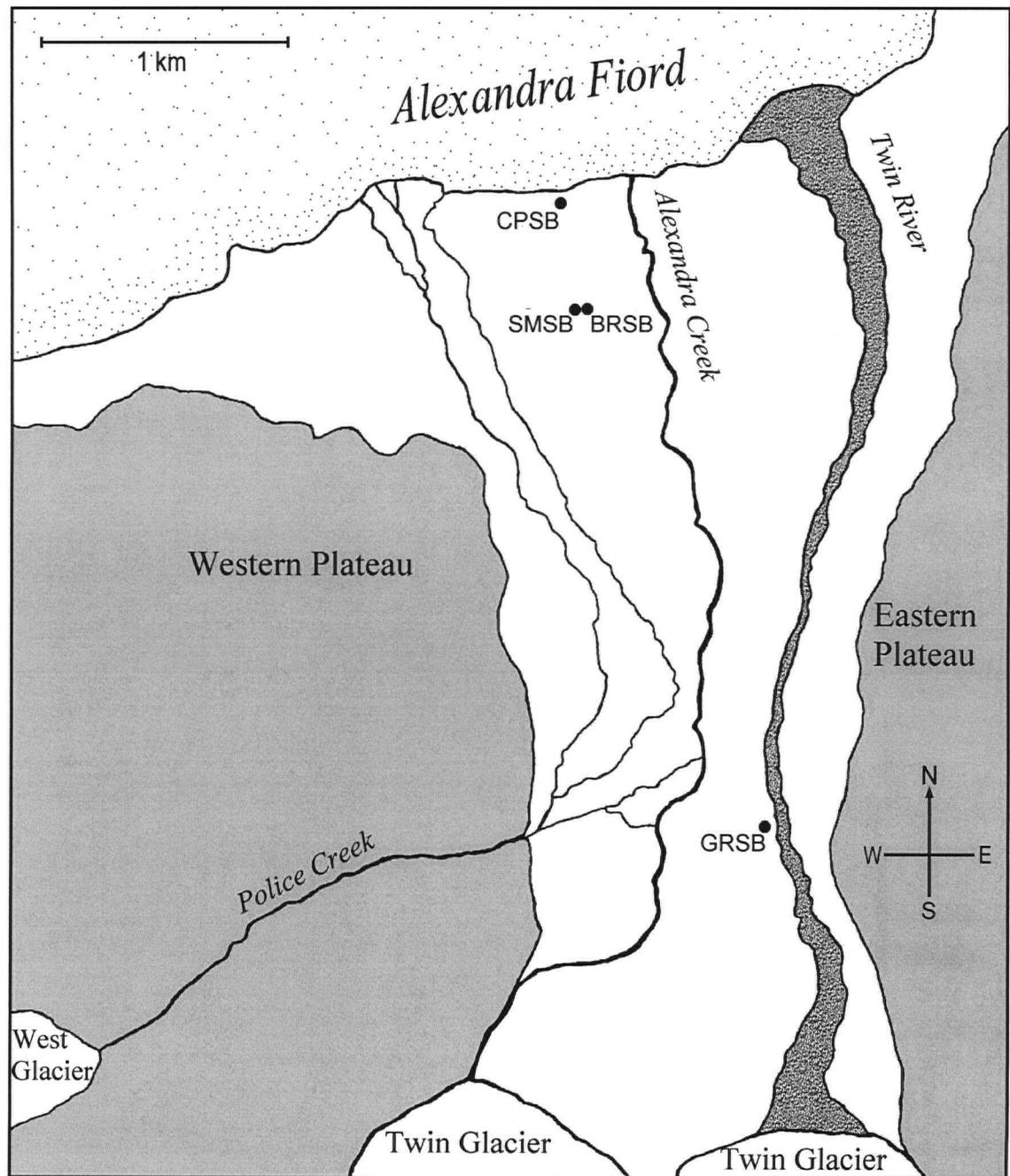


Figure 3.1. Map of the Alexandra Fiord lowland showing the locations of study sites; the Beach Ridge Snowbed (BRSB), the Camp Snowbed (CPSB), the Glacial River Snowbed (GRSB), and the experimental site, called the Snow Manipulation Snowbed (SMSB). The gray areas on each side of the map represent the upland plateaus surrounding the lowland (white area). The Twin River is a braided stream, with stream channels constantly modified, and the dark gray mottled area shown represents the gravel bed. Map modified from Johnstone (1995).

### 3.2.2 Sampling Design

At the beginning of the field season, early June 1998, the perimeter of the 3 natural snowbeds were marked with labeled tent pegs at approximately equidistant intervals of 3-5 m. Every 2 to 3 days, the edge of the snowmelt was marked along transects between the original edge markers. All of the transects ran perpendicular to the snowmelt direction. Within the GRSB there were 7 transects, the BRSB had 11 transects and the CPSB had 16 transects. The snowbeds always have snow persisting longer than the surrounding area and general melt patterns are consistent between years (G. H. R. Henry, personal communication, 1998). Although the absolute date of snowmelt may vary year to year, it is assumed that the meltdate recorded for each plot was indicative of the relative meltdate for that specific plot.

Once all of the snow in the snowbeds melted, plots were assigned within each snowbed in a stratified random design, with meltdate as the strata. Each plot measured 0.5 m  $\times$  0.5 m. A total of 20 plots were assigned in the GRSB, 40 plots in the BRSB and 50 plots in the CPSB. All destructive sampling was done when standing crop peaked for the growing season, at the end of July into early August. At each plot assigned for destructive harvest, the abundance of each species was estimated using the point quadrat method as described earlier (2.2.2 Field Sampling). Each plot was then destructively harvested to ground level and all matter was sorted to the species level in the field. All samples were brought back to the field camp and air-dried to prevent spoilage during shipping to Vancouver, BC. All samples were then sorted to live leaf tissue, live wood tissue, live inflorescences and dead tissue as appropriate for each species to examine relations between biomass allocation patterns. Samples were then dried at 80 °C for 48 hours to constant weight and were weighed to  $\pm 0.001$  g. The sum of each allocation fraction for a single species was the standing crop per plot for that species. The standing crop was regressed to the total species area (TSA) in Section 2.2.3 (Analysis Methods) for each species so that biomass could be estimated for the SMSB plots. The regression lines were given previously in Table 2.10.



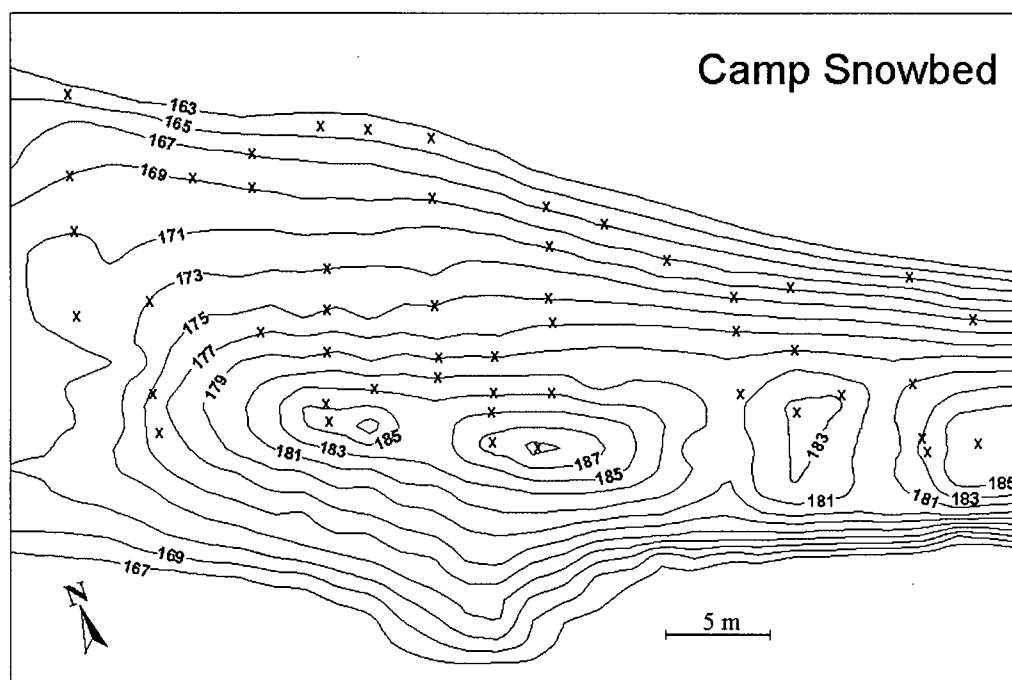


Figure 3.2. Snowmelt patterns and vegetation sampling locations (X) within the Camp Snowbed in 1998. The isoclines represent the extent of the snowbed on that day of the year.

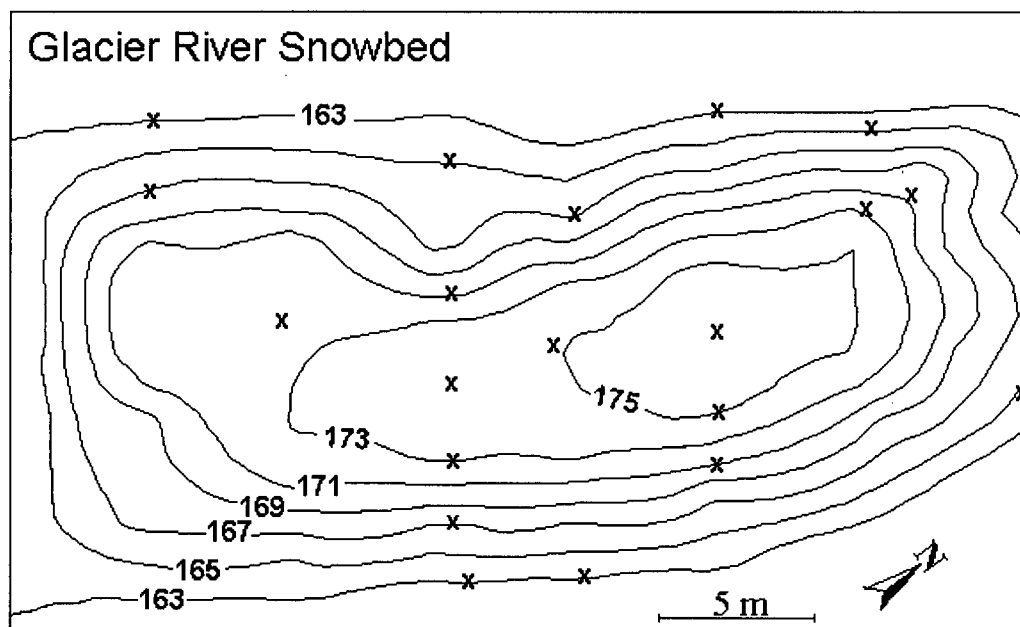


Figure 3.3. Snowmelt patterns and vegetation sampling locations (X) within the Glacier River Snowbed in 1998. The isoclines represent the extent of the snowbed on the day of the year.

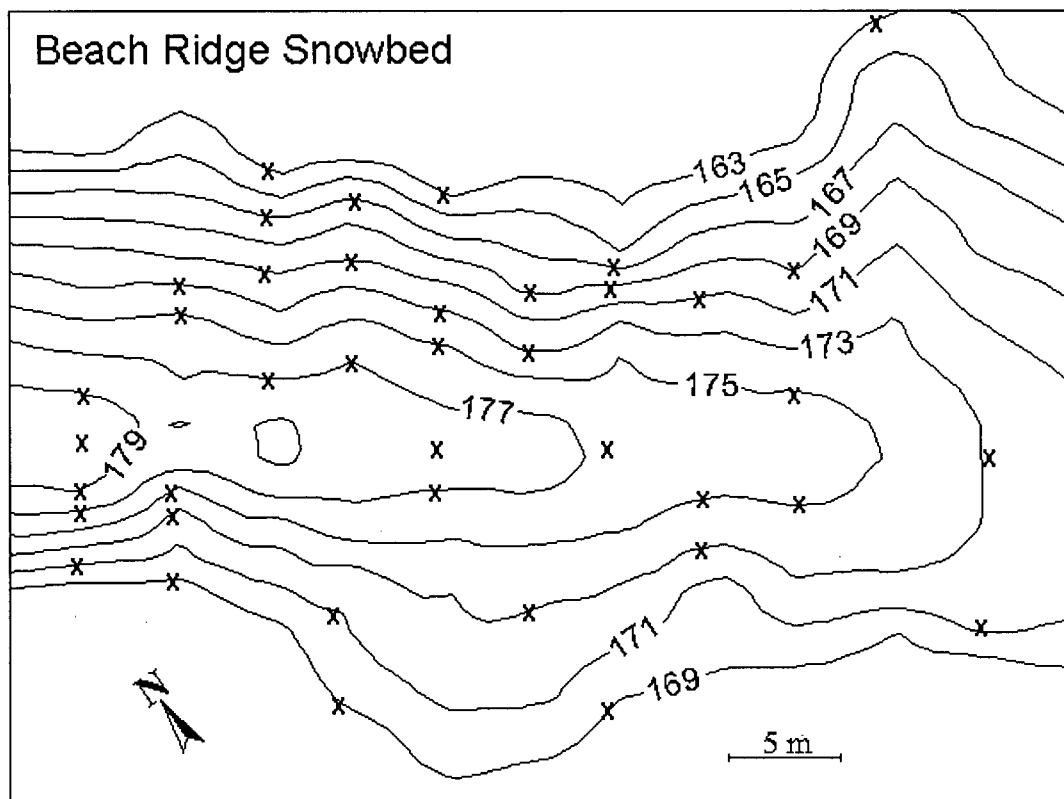


Figure 3.4. Snowmelt patterns and vegetation sampling locations (X) within the Beach Ridge Snowbed in 1998. The isoclines represent the extent of the snowbed on the day of the year. The Snow Manipulation Snowbed (SMSB) is located to the west of this snowbed and would occur within the area of the 177 or 179 isoclines.

The meltdate of each plot in the SMSB was noted and no marking of snowmelt patterns were made to minimize the disturbance. Each plot was essentially clear of snow 1 to 3 days after the onset of a snow-free patch within that plot. This was also observed in a previous study that used these snow manipulation plots (Johnstone 1995). The estimation of species abundance was made at the same time as in the adjacent BRSB. Originally 2 subplots of 0.5 m × 0.5 m each were randomly located within each plot and sampled using the point quadrat method (2.2.2 Field Sampling). To increase the precision of the estimated abundances, this was redone in the following season, 1999, using 3 subplots per treatment plot. The original data, collected in 1998, were not used in this analysis. This gave a total of 27 subplots sampled in 3 replicates plots of the 3 treatments, snow removal, addition and control. For species present in the plots, but not hit using the point quadrat method, the abundance was arbitrarily assigned as 0.5 hits per plot. Using the regression lines calculated previously and shown in Table 2.10, the estimated

standing crop of each species was calculated for each subplot. If the ANCOVA results (Table 2.8) indicated that the regression lines for a particular species were significantly different between the communities, the regression line as calculated from the adjacent BRSB was used to estimate biomass in the SMSB.

### **3.2.3 Environmental Variables**

A number of environmental variables, that previous research in arctic or alpine regions had indicated were related to plant biomass or diversity, were quantified to determine their relation to species abundance and diversity. All variables were quantified at each plot and were continuous variables unless noted below. When more than one measurement was made at a single time or at a series of occasions for the same plot, the values were averaged and the average was used for subsequent analysis. A list of all the environmental variables measured and the mean values for each can be found in Appendix B.

The primary environmental variable of interest in this study was the meltdate of each plot, which was measured before the plots were assigned. All analyses of the natural snowbeds were carried out using meltdate, given as the day of the year, which could range from 1 (for January 1) to 365 (for December 31), while all analyses of the experimental SMSB used the treatment as the grouping factor.

The depth of the active layer was measured every 2-3 days at the onset of the study, and once the depth no longer increased as rapidly, it was measured approximately once per week. This was accomplished using a steel permafrost probe that was pushed into the ground until ice was hit. All measurements were done as close to the marking post as possible for all marked points, until the plots were assigned, at which time only the plots were measured. The maximum active layer depth as measured in cm for each plot was used in subsequent analyses. Since some plots did not have an active layer limited by ice, but were rock limited, this was noted and was used as a categorical variable. The SMSB plots were sampled at the same time as the BRSB, and within each plot, 2 measurements were taken and averaged every time measurements were done. None of the 9 SMSB plots were rock limited.

Soil temperature (°C) was measured at mid-day or early afternoon on 2 occasions for the GRSB and at 3 times for the SMSB, BRSB, and CPSB sites. This was done on days that were sunny and there had been no measurable precipitation for at least 72 hours. Temperatures were taken using copper-constantan thermocouples connected to a portable thermocouple reader

(Digi-Sense®, Cole Palmer) at the soil surface, and at 5 cm and at 10 cm below the surface. Only the soil temperature at a depth of 10 cm was used in the analyses, since it was less likely to show diurnal variation.

Soil moisture was measured in the middle of the growing season once for the GRSB and on 2 occasions for the SMSB, BRSB, and CPSB sites. At each plot soil samples of a known volume (50 cm<sup>3</sup> for the GRSB and 170 cm<sup>3</sup> for all other sites) were taken from the top of the soil surface to a depth of 5 cm. The soils were weighed to  $\pm 0.01$  g and were air dried to prevent spoilage during shipping to Vancouver, BC. The soil samples were then dried at 80 °C for 48 hours to constant weight and were weighed to  $\pm 0.01$  g. Gravimetric water content ( $\theta_{grav}$ , %) was then calculated as

$$\theta_{grav} = \frac{mass_{wet} - mass_{dry}}{mass_{dry}} \times 100\%.$$

Plant water uptake is related to the water potential of the soil (Jones 1992), which can be described using volumetric soil water content ( $\theta_{vol}$ ). Therefore, a more physiologically meaningful measurement of soil moisture would be  $\theta_{vol}$  (%), calculated as

$$\theta_{vol} = \frac{\theta_{grav}}{100} \times \frac{\rho_b}{\rho_w} \times 100\%$$

where  $\rho_b$  (kg m<sup>-3</sup>) is the bulk density of the soil calculated as  $\rho_b = \frac{mass_{dry}}{vol_{soil}}$  and  $\rho_w$  is the density of water (1000 kg m<sup>-3</sup>). A related measure of soil moisture is the percent of saturation ( $\theta_{\%sat}$ , %) calculated as

$$\theta_{\%sat} = \frac{\theta_{vol}}{\theta_{sat}} \times 100\%$$

where  $\theta_{sat}$  is the saturated water content of the soil calculated as  $\theta_{sat} = \left(1 - \frac{\rho_b}{\rho_s}\right) \times 100\%$  and  $\rho_s$  is the particle density of the soil (2650 kg m<sup>-3</sup> for mineral soils and 1300 kg m<sup>-3</sup> for organic soils). For these soils, it was assumed that a  $\rho_b$  of 300 kg m<sup>-3</sup> or less was an organic soil and all others were mineral. The variable  $\theta_{\%sat}$  has a maximum of 100%, meaning that the soil is saturated, whereas the  $\theta_{grav}$  can potentially have values higher than 100%. Also,  $\theta_{vol}$  can have equal values in different plots, but because of different  $\theta_{sat}$ , they are not necessarily equal in terms of plant water uptake. The  $\rho_b$  was also used as an environmental variable in the analyses since it was inversely related to the organic content of the soil.

The dry soil samples were also used for determination of pH, which was done potentiometrically (Accumet Basic pH Meter, Fisher Scientific Ltd., Nepean, Ontario) using the soil-to-solution method (Kalra and Maynard 1991). Replicate samples from each plot were pooled. The soil was sieved through a 2mm screen and 10 g of soil was mixed with either 40 mL of water to give a 1:4 solution for organic soil or was mixed with 20 mL of water for mineral soil giving a 1:2 solution. The pH was then determined after stirring each sample periodically for 30 minutes and then allowing each solution to settle for 30 minutes.

A series of environmental variables were measured when point quadrat data were collected for each plot. The first of these variables was the slope of the plot calculated by measuring the height of each corner to the ground of the point frame, which was leveled, and computed as the average rise over run. A related measurement was a calculation of the surface roughness. This was calculated by measuring the height to the ground of 10 grid points down the middle point frame grid in both vertical and horizontal directions, giving a total 20 height measurements. The variance of these 20 points was used as the measure of surface roughness and was called the soil micro topographic variation (SMTV). Two other variables measured with the point quadrat method was the percent cover of bare ground and of rock.

Other environmental variables collected with the point quadrat method in each plot were of a biological nature. The first of these variables was the percent cover of litter. Another variable collected was the percent cover of black algal micro-biotic crust (likely including *Gymnomitrium corallioides*, although all species were grouped together). Percent cover of *Peltigera* lichen was also estimated with the point quadrat method. No attempt at distinguishing between species was made. Most of the *Peltigera* lichens observed belonged to the species *Peltigera aphthosa*, although other species are found at Alexandra Fiord (Maass and Nams 1994). Lichen and moss species were also estimated using the point quadrat method, with species-specific identification attempted for each species. For the analyses presented here, no distinctions are made to the species level and the cover of each group of species was estimated as the sum of all hits on any lichen or moss species. The final environmental variable estimated for each plot was the plot biomass, the sum of the aboveground biomass of each species in the plot as determined through the destructive harvest discussed above.

### 3.2.4 Analysis Methods

Diversity was quantified at both the alpha and beta levels using total standing crop of each species as the measure of abundance. Alpha diversity was calculated in terms of each of its components, observed species richness per plot, the evenness per plot, and as a combination of these parts using diversity indices. The evenness index used was the Smith and Wilson's  $E_{var}$  (Smith and Wilson 1996), which is independent of species richness, is sensitive to common and rare species, and is applicable to a wide range of datasets (Krebs 1999). The diversity indices used were the exponential form of the commonly used Shannon's  $H'$ , which is  $N_1$ , and the reciprocal of Simpson's index,  $1/\lambda$  (Krebs 1999). All alpha diversity components were calculated using the program ECOLOGICAL METHODOLOGY (Krebs and Kenney 1998). The equations for the indices and more details for the selection of these indices over others are given in Appendix A.

Beta diversity was also used to characterize and compare the different communities. Since beta diversity is based on the differences between communities, it is often described by using similarity measures (Whittaker 1972). The most commonly used similarity measures used on quantitative data, the percentage similarity and the simplified Mortista-Horn coefficient (Krebs 1999), were calculated for comparison of the communities using the program ECOLOGICAL METHODOLOGY (Krebs and Kenney 1998). Percentage similarity ( $P_{sim}$ ) between community 1 and 2 is calculated as

$$P_{sim} = \sum_i \min(p_{1i}, p_{2i})$$

where  $p_{1i}$  is the percentage of species  $i$  in community sample 1 and  $p_{2i}$  is the percentage of species  $i$  in community sample 2 (Krebs and Kenney 1998). The simplified Mortista-Horn index of similarity ( $C_H$ ) is more complicated in its calculation (see Krebs (1999) for equations) than the percentage similarity index, but has the advantage of being nearly independent of sample size. A new similarity index, based on the partitioning of species diversity (using Simpson's diversity index  $D = 1/\lambda$ , Appendix A) into within community diversity and total diversity for all communities pooled (Lande 1996) was also calculated. The Lande community similarity index ( $\Psi_D$ ) was calculated as

$$\Psi_D = \overline{D}_{within} / D_T$$

where  $\overline{D}_{within}$  is the mean Simpson's diversity index,  $D$ , of two communities being compared and  $D_T$  is Simpson's diversity index as calculated with the two communities' species data pooled. This index is not yet commonly used and ranges from 0 to 1. Another method of comparing beta diversity is to calculate the species turnover along gradients (Gauch and Whittaker 1972). Species turnover is related to gradient length, which was calculated using detrended correspondence analysis (DCA) with the program CANOCO (ter Braak and Smilauer 1998).

Overall community characteristics were also calculated and compared. The estimated species richness of each community was calculated using the first and second order jackknife methods and with the bootstrap estimator using simple closed order equations, meaning no iterations were needed (Hellmann and Fowler 1999). These equations are listed in Appendix A. Since the sampling effort was not consistent for each snowbed, rarefaction curves were used to estimate species richness as a function of sampling effort using the Qbasic program rarefrac.qbs (Ludwig and Reynolds 1988).

Dominance-diversity curves, relative abundance distributions (RAD), and importance curves are all names for plots of some measure of species abundance or importance on the ordinal axis with a log scale and species rank, from the most common to the least common species, on the abscissa. These are useful ways to present diversity and the shape of the RAD can be related to specific biological hypotheses (Magurran 1988, Tokeshi 1990, Tokeshi 1993). For each plot, the best fitting RAD model of four most common models (Geometric, Broken Stick, General Lognormal, and Zipf-Mandelbrot) was determined following the method described by Wilson (1991) using the program DomDimXX provided by J. B. Wilson (University of Otago). The best fitting model is the one with the smallest sum of squares deviance. This was done for each plot within each snowbed community as advocated by Wilson (1991), since each plot can be considered replicate samples of fully censused biological space (Smith and Wilson 1996). All plots for each snowbed were combined so the communities could be compared in terms of their overall RAD and the best fitting model was determined using the same method and program.

Relations between the measures of alpha diversity and snow meltdate or biomass were examined using simple linear regression with JMP (SAS 1995). Second order polynomials and transformations were also used to determine if the relations were non-linear. Since environmental variables other than biomass and meltdate are likely important in structuring the community, multiple regression was used to predict the diversity measures. Forward and

backward stepwise regression were used to select the most important environmental variables with the selection criteria based on the maximizing the fit or coefficient of determination ( $R^2$ ) and minimizing Mallows'  $C_p$ , which increases with the number of variables in a model (SAS 1995).

Multivariate relations between the vegetation and meltdates were also examined using multivariate analysis of variance (MANOVA). This was originally accomplished using JMP (SAS 1995) and was then confirmed using the multiple general linear modeling (MGLM) platform in SYSTAT (Wilkinson et al. 1992). Both methods fit the data the same way (with MGLM), but SYSTAT gives some slightly more conservative MANOVA statistics (Scheiner 1993). Since there were insufficient degrees of freedom to test all species at the same time, and doing multiple univariate ANOVAs over-inflate the Type I error rate (Scheiner 1993), species were grouped together for analysis by similar life forms (Stroup and Stubbendieck 1983). The functional groups used were deciduous shrubs, evergreen shrubs, forbs, and graminoids (Chapin et al. 1996). One potential problem with the ANOVA and MANOVA occurs with the analysis of unbalanced data (Scheiner 1993, Shaw and Mitchell-Olds 1993). MGLM handles this efficiently since the estimates are computed with maximum likelihood rather than least squares (Wilkinson et al. 1992).

Allocation patterns were also examined in response to productivity and meltdates. All plants were sorted to the live leaves, live flowers, live stems and attached dead (such as stems, flowers or leaves). The aboveground net production of each species ( $\text{g}/0.25\text{m}^2$ ) was estimated by adding all of the live fractions, such as current season's flowers and leaves. This method was altered for the evergreen shrubs, *Cassiope tetragona* and *Dryas integrifolia*, and for the deciduous shrub, *Salix arctica*. Since *C. tetragona* retains green leaves for approximately 2 years (G. Henry, pers. comm., 1999) at which time it turns red then brown, the live green mass was divided by 2 before flower mass was added. *D. integrifolia* has green leaves for 1.2 years (Chapin et al. 1996), which turn red before dying. Because the harvest was completed at the end of the growing season, the previous year's leaves were primarily red, so care was taken to sort and weigh only fresh green leaves from the current year. For *S. arctica*, the new leaves only come from new wood at growing tips. These new increments of wood growth were also added to the current year's production.

To estimate the total aboveground net primary productivity (ANPP), all production estimates for each species in each plot were added together. Because the species may not peak in their optima for live mass and flower mass at the same position along an environmental gradient, the



absolute values were standardized to relative measures by transforming by the maximum (by dividing by the maximum), which is often called standardizing to maximum (Palmer 1998). For each species, the maximum value of flower mass or live mass in all plots was determined, and this value was divided from the actual value in each of the plots. This relative measure facilitated plotting the live and flower mass on the same graph with ANPP or meltdat and better shows where the maximum values of each species, in terms of live or flower mass, occurs along gradients of ANPP or meltdat. LOWESS (locally weighted regression scatterplot smoothing) smoothed lines were added using SYSTAT to examine where the peak of live or flower mass occurred and if they coincided. This smoothing technique is not employed very frequently in ecology, but is useful if the relation between a dependent and independent variables do not fit any single function well (Trexler and Travis 1993). The basic assumption of this regression technique is that neighboring values of the independent variable are the best predictors of the dependent variable (Trexler and Travis 1993).

The relation between species data and environmental variables were analyzed using redundancy analysis (RDA), which is also known as reduced-rank regression, principal components analysis (PCA) of  $y$  with respect to  $x$ , and two-block mode C partial least-squares (ter Braak and Prentice 1988). RDA is a constrained ordination method, or multivariate direct gradient analysis, and is the canonical form of PCA (Jongman et al. 1995). All species data are fitted to the weighted sums of a few environmental variables that describe the species data by maximizing the total regression sum of squares (ter Braak and Prentice 1988). Therefore, RDA is an ordination of all species data in which the axes are the best fitting linear combinations of the selected environmental variables. Since the species responses to the environmental variables are assumed to be linear with this technique, it is most appropriate to use data sets that are of short gradients, perhaps less than 2 SD (ter Braak and Prentice 1988). For gradients of greater than 4 SD, the species response curves will likely be unimodal or normal (Gauch and Whittaker 1972), and therefore it is necessary to use a method which assumes a unimodal distribution such as canonical correspondence analysis (CCA) or detrended CCA (DCCA).

The ordination diagram resulting from RDA is a biplot, two variables presented on the same diagram, which displays the components of the community variation that can be explained by the environmental variables and also shows the correlation between species variables and environmental variables (ter Braak and Prentice 1988). Both species and environmental variables are presented in a biplot as arrows and sites may also be represented as points in ordination space resulting in a triplot. Examining the cosine of the angle between the species

and environmental arrows gives the correlation between the two variables (Jongman et al. 1995). If the arrows point in a similar direction they are positively correlated, if the angle between the arrows is approximately a right angle, there is almost no correlation and if the arrows point in opposite directions the relation between the variables is highly negative. The length of the arrows also indicates the importance of the variable in the analysis and the confidence of the correlation (ter Braak and Prentice 1988). All ordination work was completed using the program CANOCO (version 4.0; ter Braak and Smilauer 1998).

To determine the best environmental variables in explaining the variance in the species dataset, the automatic forward selection routine was used within CANOCO (ter Braak and Smilauer 1998). This selects the K best variables sequentially to maximize fit. Each model, with K variables, was then tested to determine the statistical significance of the relation between species and environmental variables for both the first ordination axis (the first canonical eigenvalue) and for the sum all 4 axes (all canonical eigenvalues) using Monte Carlo permutation (ter Braak and Smilauer 1998). All of the default settings were retained in the RDA such that scaling was focused on inter-species differences, species scores were post-transformed by dividing by the SD, and centering by species. This gives the most commonly interpreted RDA biplot (ter Braak and Smilauer 1998).

### 3.3 RESULTS

#### 3.3.1 Natural Snowbed Communities

The three natural snowbed communities were primarily composed of the same species, although the abundance of each differed between the communities (Table 3.1). All three are dominated by 2 or 3 species, using the definition of a dominant as a species that has a higher abundance in a community than if all species were equally abundant (Camargo 1995). The GRSB was dominated by *Cassiope tetragona* and *Dryas integrifolia*, which comprised 95.9 % of the total standing crop in the community (Table 3.1). In the BRSB community, the same two species were most abundant, although *Salix arctica* was also a dominant species and all three dominants encompassed 96.5 % of the community's biomass (Table 3.1). The CPSB differed in that its primary dominant species was *Salix arctica*, a deciduous shrub. *Dryas integrifolia* and

*Saxifraga oppositifolia* were also dominant in the CPSB, while the three dominants accounted for 94.5 % of the total community biomass. A similar table of the environmental differences between the natural snowbeds is given in Appendix B (Table B.1).

Table 3.1. Mean biomass ( $\text{g} / 0.25\text{m}^2$ )  $\pm$  1 SE of vascular plant species at the Glacial River Snowbed (GRSB), Beach Ridge Snowbed (BRSB) and Camp Snowbed (CPSB) communities. Species that are dominant in the community, using Camargo's (1995) distinction of dominance, are shown in bold. T = trace are species found in the community but not measured in any quadrats. Total standing crop is the average per quadrat value for the entire site, as is the estimated ANPP.

| Functional Group<br>and Species  | GRSB<br>(N = 20)                  | BRSB<br>(N = 40)                  | CPSB<br>(N = 50)                 |
|--|-----------------------------------|-----------------------------------|----------------------------------|
| <b>Deciduous Shrubs</b>  |                                   |                                   |                                  |
| <i>Salix arctica</i>   | 2.256 $\pm$ 0.557                 | <b>4.008</b> $\pm$ <b>0.748</b>   | <b>24.128</b> $\pm$ <b>3.061</b> |
| <b>Evergreen Shrubs</b>  |                                   |                                   |                                  |
| <i>Cassiope tetragona</i>  | <b>111.230</b> $\pm$ <b>9.451</b> | <b>55.936</b> $\pm$ <b>10.498</b> | 0.923 $\pm$ 1.908                |
| <i>Dryas integrifolia</i>  | <b>16.951</b> $\pm$ <b>7.334</b>  | <b>13.321</b> $\pm$ <b>4.636</b>  | <b>8.264</b> $\pm$ <b>2.307</b>  |
| <b>Forbs</b>   |                                   |                                   |                                  |
| <i>Cardamine bellidifolia</i>  |                                   | 0.002 $\pm$ 0.005                 | 0.0002 $\pm$ 0.0008              |
| <i>Draba</i> species   | 0.029 $\pm$ 0.074                 | 0.038 $\pm$ 0.023                 | 0.028 $\pm$ 0.049                |
| <i>Equisetum variegatum</i>  |                                   |                                   | 0.012 $\pm$ 0.042                |
| <i>Lycopodium selago</i>   |                                   | 0.029 $\pm$ 0.066                 |                                  |
| <i>Minuartia rubella</i>   |                                   | 0.011 $\pm$ 0.018                 |                                  |
| <i>Oxyria digyna</i>   |                                   | 0.145 $\pm$ 0.026                 | 0.002 $\pm$ 0.002                |
| <i>Papaver radicum</i>   | 0.053 $\pm$ 0.082                 | 0.052 $\pm$ 0.031                 | 0.015 $\pm$ 0.022                |
| <i>Pedicularis</i> species   | T                                 | 0.009 $\pm$ 0.006                 | 0.011 $\pm$ 0.016                |
| <i>Polygonum viviparum</i>   | T                                 | 0.036 $\pm$ 0.039                 | 0.003 $\pm$ 0.005                |
| <i>Saxifraga cernua</i>  |                                   |                                   | 0.002 $\pm$ 0.002                |
| <i>Saxifraga nivalis</i>   |                                   | 0.0002 $\pm$ 0.002                | 0.022 $\pm$ 0.033                |
| <i>Saxifraga oppositifolia</i>   | 2.145 $\pm$ 0.794                 | 0.996 $\pm$ 0.313                 | <b>2.355</b> $\pm$ <b>0.577</b>  |
| <i>Silene acaulis</i>  |                                   | 0.042 $\pm$ 0.053                 | 0.026 $\pm$ 0.129                |
| <i>Stellaria longipes</i>  | 0.007 $\pm$ 0.021                 | 0.005 $\pm$ 0.015                 | 0.026 $\pm$ 0.014                |
| <b>Graminoids</b>  |                                   |                                   |                                  |
| <i>Arctagrostis latifolia</i>  |                                   | 0.019 $\pm$ 0.063                 |                                  |
| <i>Carex aquatilis</i>   |                                   |                                   | 0.110 $\pm$ 0.190                |
| <i>Carex maritima</i>  |                                   |                                   | 0.010 $\pm$ 0.068                |
| <i>Carex misandra</i>  | 0.002 $\pm$ 0.006                 | 0.122 $\pm$ 0.085                 | 0.590 $\pm$ 0.329                |
| <i>Carex nardina</i>   |                                   |                                   | 0.004 $\pm$ 0.027                |
| <i>Carex rupestris</i>   |                                   |                                   | 0.001 $\pm$ 0.006                |
| <i>Eriophorum angustifolium</i>  |                                   | 0.047 $\pm$ 0.100                 | 0.023 $\pm$ 0.061                |
| <i>Festuca brachyphylla</i>  | 0.002 $\pm$ 0.005                 | 0.003 $\pm$ 0.010                 | 0.015 $\pm$ 0.026                |
| <i>Juncus biglumis</i>   |                                   |                                   | 0.000 $\pm$ 0.001                |
| <i>Luzula arctica</i>  | 0.725 $\pm$ 0.428                 | 0.756 $\pm$ 0.147                 | 0.138 $\pm$ 0.044                |
| <i>Luzula confusa</i>  | 0.263 $\pm$ 0.085                 | 0.330 $\pm$ 0.096                 | 0.049 $\pm$ 0.033                |
| <i>Poa arctica</i>   | T                                 | 0.006 $\pm$ 0.040                 | 0.032 $\pm$ 0.020                |
| <b>Total Aboveground<br/>Standing Crop</b><br>( $\text{g} / 0.25 \text{m}^2$ ) | 133.66 $\pm$ 8.44                 | 75.91 $\pm$ 9.51                  | 36.79 $\pm$ 3.56                 |
| <b>Est. ANPP</b><br>( $\text{g} / 0.25 \text{m}^2 \text{y}^{-1}$ )             | 12.72 $\pm$ 0.84                  | 7.82 $\pm$ 0.64                   | 8.63 $\pm$ 0.74                  |

The total standing crop for the communities differed, varying with the dominant species present (Table 3.1). The highest standing crop was associated with the heath species, which were dominant in the GRSB and BRSB communities, and the lowest standing crop was in the CPSB, which was dominated by a deciduous species. The similarity indices of the different communities suggest that the GRSB and the BRSB are most similar, while the CPSB tends to be more like the BRSB than the GRSB (Table 3.2). The percentage similarity and simplified Morisita-Horn indices, which relate to species composition similarity between communities (Krebs 1999), indicated that the CPSB is quite different than the GRSB and BRSB communities, which were very similar. When the Lande community similarity index, which compares the similarity of diversity between communities (Lande 1996), was used to compare the communities, this relation was still found, although it was very weak (Table 3.2).

Table 3.2. Percent similarity ( $P_{sim}$ ), simplified Morisita-Horn index of similarity ( $C_H$ ) and Lande community similarity index ( $\Psi_D$ ) between Glacial River Snowbed (GRSB), Beach Ridge Snowbed (BRSB) and Camp Snowbed (CPSB) communities.

| $P_{sim}$ |      |      |      | $C_H$ |      |      |      | $\Psi_D$ |      |      |      |
|-----------|------|------|------|-------|------|------|------|----------|------|------|------|
|           | GRSB | BRSB | CPSB |       | GRSB | BRSB | CPSB |          | GRSB | BRSB | CPSB |
| GRSB      | 100  |      |      | GRSB  | 1.00 |      |      | GRSB     | 1.00 |      |      |
| BRSB      | 90.2 | 100  |      | BRSB  | 0.99 | 1.00 |      | BRSB     | 0.99 | 1.00 |      |
| CPSB      | 19.3 | 27.8 | 100  | CPSB  | 0.11 | 0.19 | 1.00 | CPSB     | 0.60 | 0.68 | 1.00 |

Species diversity within the natural communities differed with the GRSB community consistently having the lowest diversity, the BRSB having intermediary diversity and the CPSB having the highest diversity of all the communities for all species richness estimators, diversity indices and for the evenness index  $E_{var}$  (Table 3.3). The only exceptions to this pattern is the gradient length, which indicated BRSB having the longest gradient length and highest rate of species turnover, with GRSB having a much shorter gradient length than either of the other communities. Since sampling effort between communities was not equal, comparison of the simple species richness estimator, or observed species richness ( $S_o$ ), is problematic. Therefore, rarefaction curves for each community were calculated using biomass as the measure of abundance (Figure 3.5). At any given amount of biomass sampled, the CPSB had highest estimated species richness. The lowest estimated number of species in a sample was always with the GRSB community (Figure 3.5), again confirming that it is the least diverse community.

Table 3.3. Diversity of the three natural communities, the Glacial River Snowbed (GRSB), Beach Ridge Snowbed (BRSB) and the Camp Snowbed (CPSB). Diversity values are observed species richness ( $S_o$ ), first and second order jackknife estimators of species richness ( $J_n^1(S)$  and  $J_n^2(S)$ , respectively), bootstrap estimator of species richness ( $B_n(S)$ ), reciprocal of Simpson's index ( $1/\lambda$ ), exponential form of Shannon's diversity ( $N_1$ ), Smith and Wilson's evenness index ( $E_{var}$ ) and gradient length in SD. See Appendix 1 for the calculation of each.

|                      | GRSB  | BRSB  | CPSB  |
|----------------------|-------|-------|-------|
| $S_o$                | 14    | 22    | 26    |
| $J_n^1(S)$           | 16.93 | 23.95 | 28.94 |
| $J_n^2(S)$           | 17.00 | 24.00 | 29.00 |
| $B_n(S)$             | 14.50 | 23.11 | 27.58 |
| $1/\lambda$          | 1.41  | 1.73  | 2.06  |
| $N_1$                | 1.82  | 2.38  | 2.83  |
| $E_{var}$            | 0.053 | 0.076 | 0.078 |
| Gradient Length (SD) | 1.332 | 2.639 | 2.163 |

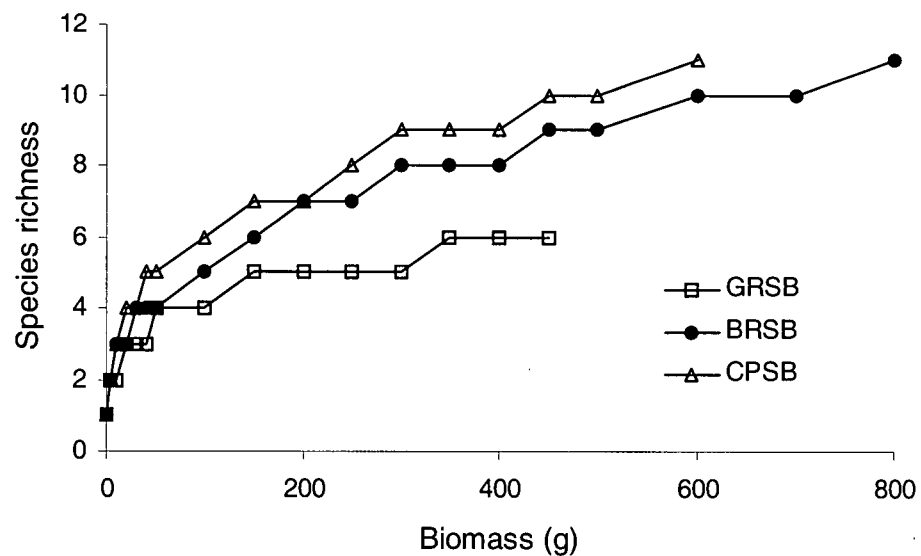


Figure 3.5. Rarefaction curves for the Glacial River Snowbed (GRSB), Beach Ridge Snowbed (BRSB) and Camp Snowbed (CPSB) communities. Species richness is the expected number of species in a sample and biomass is the total biomass of the sample.

The relative abundance distributions (RADs) of the natural snowbed communities also indicate the GRSB was the least diverse community (Figure 3.6). Both the BRSB and the CPSB communities follow similar patterns and visually demonstrate higher evenness as compared to the GRSB (Figure 3.6, Table 3.3). When all plots were combined to get a single average value for each species' abundance, the best fitting model RAD model was the Zipf-Mandelbrot model for the GRSB while the General Lognormal was the best fitting model for the CPSB and BRSB (Table 2.6). There was very little difference between the best fitting RAD model and the next best fitting model or models, especially for the GRSB, which was approximately equally well described by the Zipf-Mandelbrot, General Lognormal and the Geometric models (Table 2.6). The CPSB and BRSB were both described well with the General Lognormal and Zipf-Mandelbrot models. The number of times that each model best fit the RAD of the plot data (as advocated by Wilson, 1991) was not significantly different between communities ( $\chi^2 = 4.9$ ,  $df = 4$ ,  $P = 0.29$ , Table 2.4). The best fitting RAD model was generally the Zipf-Mandelbrot, fitting 60.7 % of plots, followed by the Geometric and General-Lognormal, both fitting 19.6 % of plots.

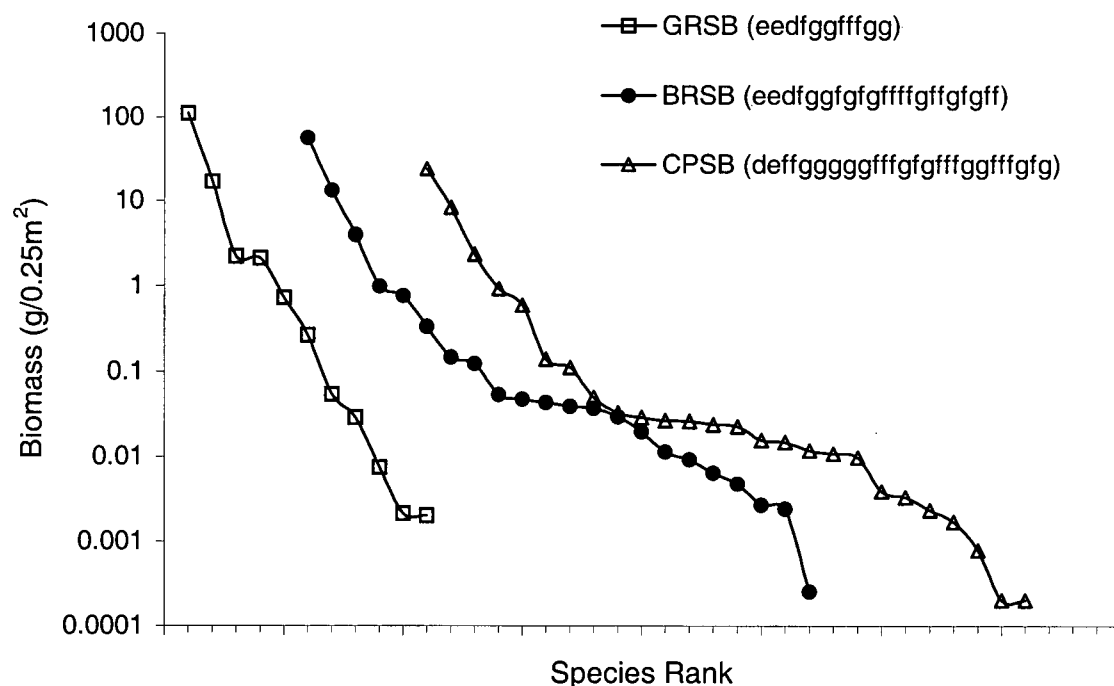


Figure 3.6. Relative abundance distributions (RADs) for the 3 natural snowbed communities, the Glacier River Snowbed (GRSB), the Beach Ridge Snowbed (BRSB) and the Camp Snowbed (CPSB). The measure of abundance is biomass (g/0.25 m<sup>2</sup>) of each species in the plot. Functional groups, deciduous shrubs (d), evergreen shrubs (e), forbs (f) and graminoids (g), are given in parentheses and specific species identities can be found in Table 3.1.

### 3.3.2 Patterns of Diversity Within the Natural Snowbeds

#### 3.3.2.1 Responses to Meltdates

Meltdates ranged from day 164 to 194 for the CPSB, from day 163 to 177 for the GRSB, and from day 163 to 181 for the BRSB. There was no statistically significant relation between any of the diversity measures and the snowmelt date for the pooled data of all communities combined (Figure 3.7, Table C.1). The interaction term between meltdates and snowbed community for all diversity measures was not significant (Table C.1). When each community was examined separately, only the GRSB had a statistically significant relation between meltdates and any diversity measure (Table C.2,  $N_1 = 6.586 - 0.03029 \times \text{MELTDATE}$ ,  $R^2 = 0.32$ ,  $p = 0.009$ ). This suggests that within the GRSB, compositional changes due to snowmelt date or growing season length would most likely be observed with the most common species, since the  $N_1$  index is primarily sensitive to changes in the dominant species (Peet 1974). From an examination of the vegetation data from the GRSB, this pattern appears to occur. The mean biomass per plot of the most dominant plant species, *Cassiope tetragona*, significantly increases ( $R^2 = 0.23$ ,  $P = 0.034$ ) while the second most abundant species, *Dryas integrifolia*, decreases ( $R^2 = 0.21$ ,  $P = 0.042$ ) as meltdates increase. As the most dominant species increases and the second most dominant decreases, the mathematical consequence is that the  $N_1$  index must decrease if the number of species and the evenness among the remaining species stays the same.

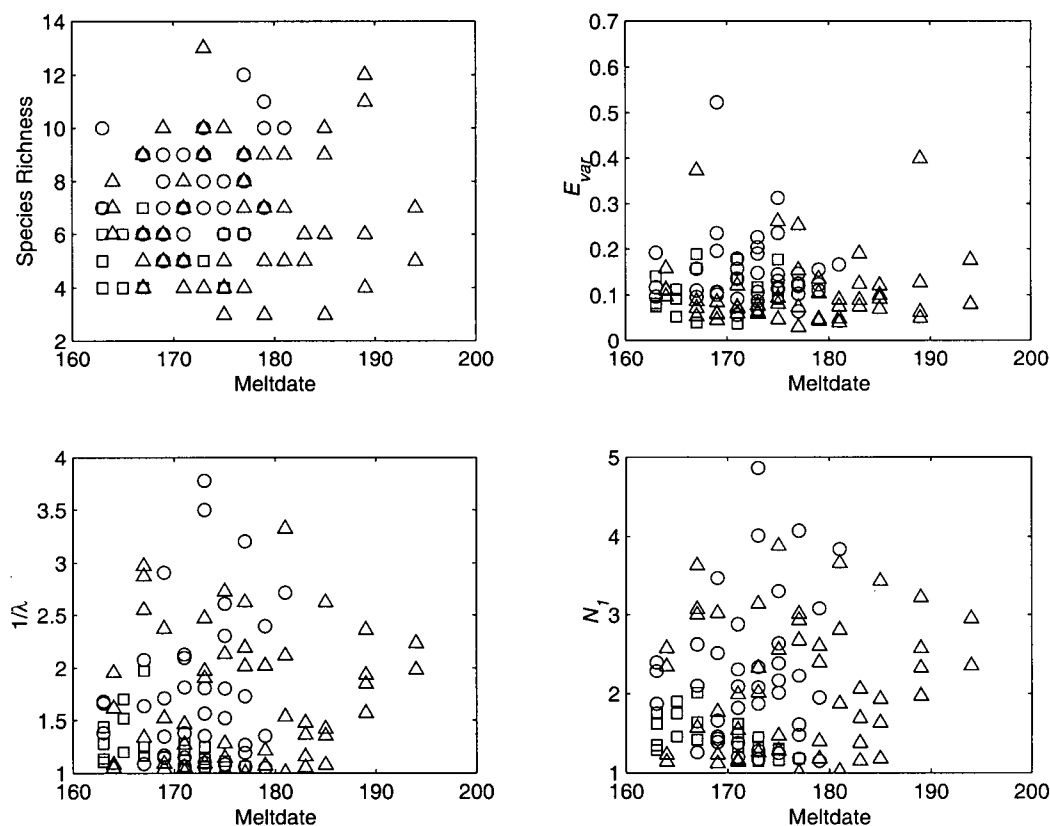


Figure 3.7. Relation between diversity and meltdate for all plots within the GRSB (squares), BRSB (circles), and CPSB (triangles) communities. Diversity measures were for each plot and included species richness, Smith and Wilson's evenness index ( $E_{var}$ ), reciprocal of Simpson's index ( $1/\lambda$ ) and the exponential form of Shannon's  $H'$  index ( $N_1$ ). Meltdate is the day of the year when the plot was clear of snow.

Best fitting relative abundance distribution (RAD) models were somewhat dependent on meltdate. When plots were grouped into early melting, intermediate plots and late melting plots there was a weak tendency for the number of times each model best fit each group of plots to be different (Table 3.4,  $\chi^2 = 7.74$ ,  $df = 4$ ,  $P = 0.10$ ). The best fitting model was always the Zipf-Mandelbrot for all meltdate classes. However, within the later melting plots, there was an increase in the number of plots that were best described by the Geometric model relative to the earlier melting plots.



Table 3.4. Best fitting RAD models for early melting plots (Julian meltdat e  $\leq 170$ , N = 34), intermediate plots (N = 49) and late melting plots (Julian meltdat e  $> 178$ , N = 24).

| MODEL             | Early Meltdat e | Mid-Meltdat e | Late Meltdat e |
|-------------------|-----------------|---------------|----------------|
| General Lognormal | 9               | 7             | 5              |
| Geometric         | 7               | 6             | 8              |
| Zipf-Mandelbrot   | 18              | 36            | 11             |

Analysis of the functional groups using MANCOVA indicated that there was no interaction ( $P = 0.4850$ ; Roy's Max Root) between the independent variables meltdat e and which community the sample came from (Table 3.5). This means that it is appropriate to exclude the interaction term from the MANOVA (Wilkinson et al. 1992). Since the CPSB had snow remaining within the snowbed longer than either of the other communities, the community that the sample came from was also included as an independent variable in the analysis along with meltdat e. This was to statistically control for differences in the abundance of each functional group that may be found in each community. MANOVA results (Model B, Table 3.5) indicate that functional groups were statistically related to both snowbed community ( $P < 0.001$ ) and to meltdat e ( $P = 0.012$ ).

Table 3.5. Multivariate analysis of covariance (MANCOVA) of the effects of snow meltdat and snowbed community on the standing crops of the four functional groups (deciduous shrubs = DEC, evergreen shrubs = EVER, forbs = FORB, and graminoids = GRAM). Total sample size = 110 plots. The non-significant interaction ( $\alpha = 0.05$ ) in model A suggests it is appropriate to test the effects using model B. Source is the model term (source of model variation). Value is the value of the test statistic (Roy's Max Root, although all MANOVA test statistics were the same). F is the F value for the multivariate test. NUM DF is the numerator degrees of freedom. DEN DF is the denominator degrees of freedom. PR> F is the significance probability corresponding to the F ratio.

Model A.

| SOURCE           | VALUE | F     | NUM DF | DEN DF | PR>F  |
|------------------|-------|-------|--------|--------|-------|
| SNOWBED          | 0.035 | 0.890 | 4      | 102    | 0.473 |
| MELTDATE         | 0.042 | 1.049 | 4      | 101    | 0.386 |
| SNOWBED*MELTDATE | 0.034 | 0.870 | 4      | 102    | 0.485 |

Model B.

| SOURCE   | VALUE | F      | NUM DF | DEN DF | PR>F  |
|----------|-------|--------|--------|--------|-------|
| SNOWBED  | 1.252 | 32.553 | 4      | 104    | 0.000 |
| MELTDATE | 0.131 | 3.367  | 4      | 103    | 0.012 |

Univariate ANOVA results of each dependent variable, the functional groups, in the MANOVA with snowbed and meltdat as independent variables (Model B, Table 3.5) are given in Table D.1. Analyzing univariate ANOVA's after a statistically significant MANOVA result is appropriate if  $\alpha$  levels are corrected using the Bonferroni correction (Scheiner 1993). The corrected  $\alpha' = \alpha / \text{number of multiple comparisons}$ . In this case, since there are 4 functional groups  $\alpha' = 0.05 / 4 = 0.0125$ . Given this  $\alpha'$ , only the forbs functional group was significantly related to meltdat, although if the significance level was relaxed to  $\alpha = 0.10$ , the graminoids group was close to being significant (Figure 3.8, Table D.1). The standing crop of forbs increased with meltdat, when snowbed was used as a covariate (Model B, Table 3.5) to control for differences between communities, while graminoids tended to decrease and deciduous and evergreen shrubs did not differ (Figure 3.8). These conclusions were robust to the removal of the covariate such that the conclusions reached were the same. There were statistical differences in the abundance in deciduous and evergreen shrubs between the different snowbed communities when meltdat is used as a covariate ( $P < 0.001$ , Table D.1, Figure 3.9). These conclusions are identical if the covariate is removed. Differences in the abundance of the

functional groups follows the dominant species of each community as already mentioned (Table 3.1). The CPSB has significantly more deciduous shrubs than either the GRSB or BRSB while all communities are different in terms of the abundance of evergreen shrubs with the most in the GRSB and the least in the BRSB (Figure 3.9).

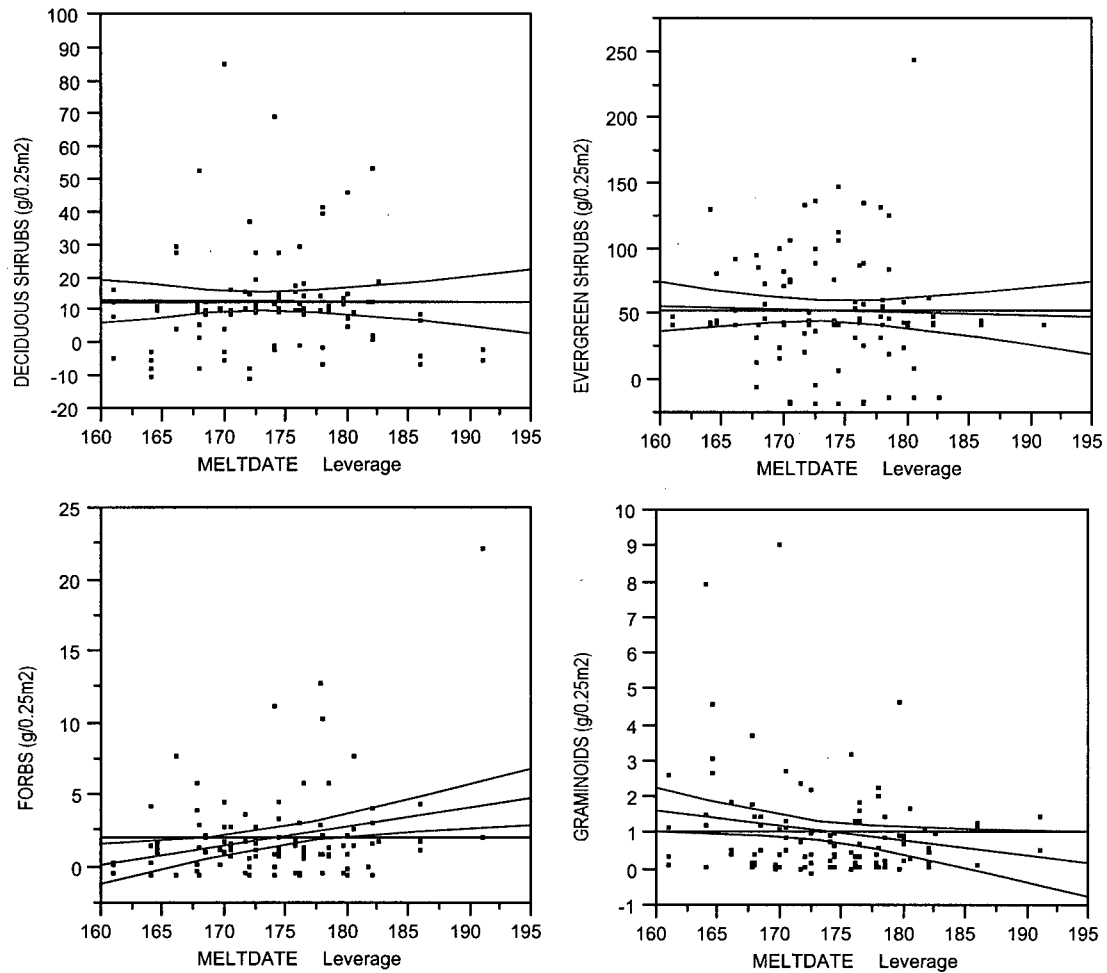


Figure 3.8. Leverage plots of the effect MELTDAT from model B (Table 3.5) for each univariate model (Table D.1.b) of the four functional groups. The sloped line represents the fitted line of the effect with the 95 % confidence limits. The distance of points to the line of fit is the actual residual. The horizontal line represents the model with the effect (MELTDAT) removed and the distance between the points and the horizontal line is the residual error with the effect removed. Only the forbs line is statistically significant ( $P = 0.004$ ) at the Bonferroni corrected  $\alpha' = 0.0125$  (where  $\alpha = 0.05$ ) although the fit line for graminoids ( $P = 0.042$ ) is close to being significant at  $\alpha' = 0.025$  (where  $\alpha = 0.1$ ). Note that the effect line for the deciduous shrubs overlaps with the horizontal line, which represents the model with the effect removed.

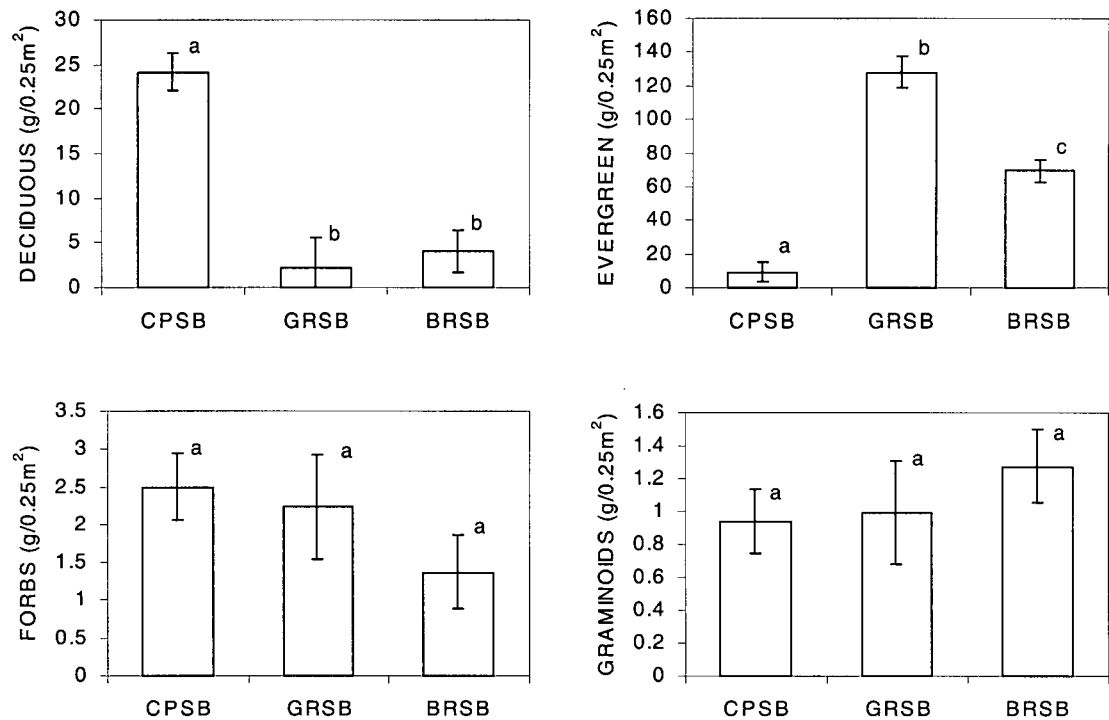


Figure 3.9. Biomass (mean and 1 SE) of each functional group in the natural snowbed communities. There is a statistically significant difference between snowbed communities for the deciduous shrubs ( $P < 0.001$ ) and evergreen shrubs ( $P < 0.001$ ) at the Bonferroni corrected  $\alpha' = 0.0125$ , where  $\alpha = 0.05$  but no difference for forbs or graminoids (Table D.1.a). Values sharing the same letter are not statistically different ( $\alpha = 0.05$ ; Tukey-Kramer HSD test).

### 3.3.2.2 Responses to Biomass

There was a statistically significant decrease in every diversity measure (species richness,  $E_{var}$ ,  $1/\lambda$ , and  $N_1$ ) with an increase in biomass when all 110 plots were examined from all 3 natural snowbed communities (Figure 3.10, Table E.1). Although the regression lines were all statistically significant, all were a relatively poor fit of the data with low  $R^2$  values ranging from 0.05 to 0.21 (Table E.1). When each community was examined separately and the significance level was relaxed to  $\alpha = 0.10$ , the only relations between diversity and biomass occurred in CPSB with  $N_1$ , GRSB with  $E_{var}$  and in BRSB all diversity measures were significant (Table E.2). In all cases, the significant relation was a decrease in the diversity measure with an increase in biomass.

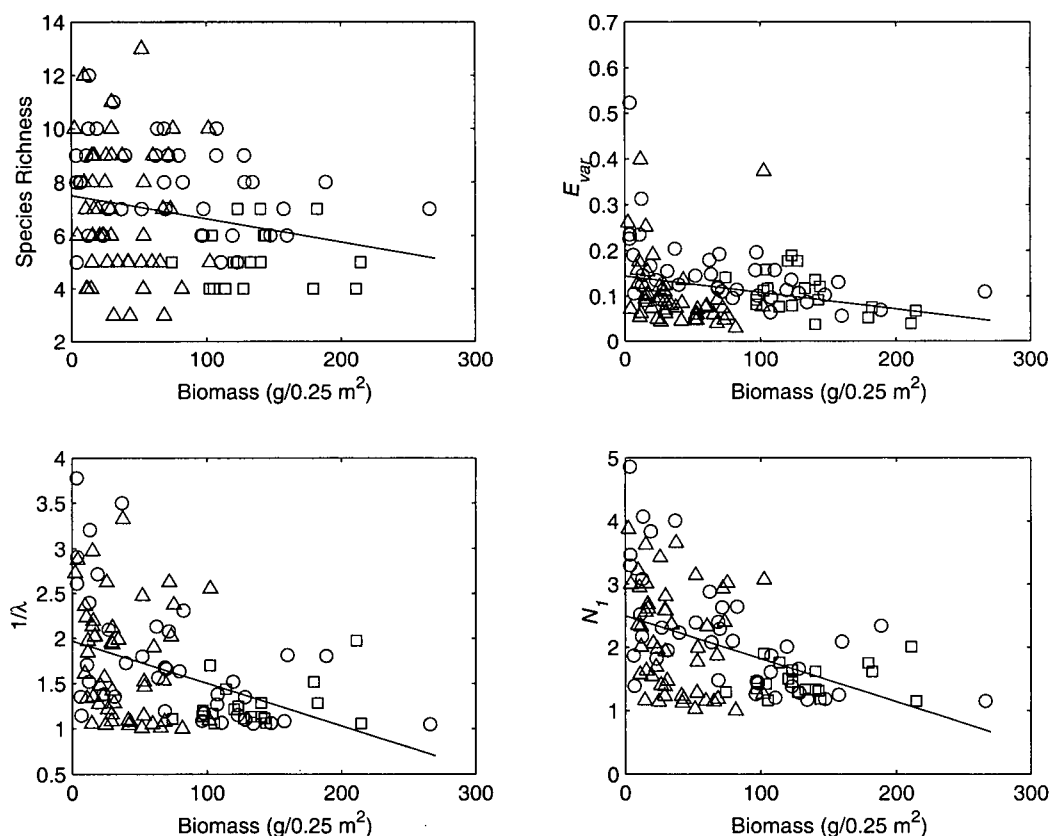


Figure 3.10. Relation between some measures of diversity and biomass (total live plus dead) for all plots in the three natural snowbed communities. Symbols are the same as Figure 3.7. All regression lines are statistically significant (Table E.1).

To improve upon the relatively poor fit between biomass and diversity, as shown in Figure 3.10 (Table E.1), other environmental factors were examined using forward and backward stepwise regression to select for the most important variables in the statistical description of the diversity variables. The best multiple regression models, which were selected on the basis of maximizing  $R^2$  and minimizing Mallows'  $C_p$ , are given in Table 3.6. Fit was lowest with the models which predicted  $E_{var}$  ( $R^2 = 0.239$ ) and species richness ( $R^2 = 0.328$ ), although both were significant ( $P < 0.0001$ ) and were improvements on the models with just biomass as a predictor. The models to predict  $1/\lambda$  and  $N_1$  were also significant ( $P < 0.0001$ ) and had better fits ( $R^2 = 0.528$  and  $R^2 = 0.557$ , respectively), and both used the same predictor variables. Biomass was an important predictor in all 4 multiple regression models (Table 3.6).

Table 3.6. Multiple regression models (forward and backward selection) to predict diversity within the 3 natural snowbed communities (N = 110). The variable in bold is the predicted variable and all others are the predictor variables (environmental variables). All multiple regression models to predict diversity are significant (P < 0.0001).

| Predicted and<br>predictor variables | Coefficient | Std Error | Cumulative R <sup>2</sup> | P     |
|--------------------------------------|-------------|-----------|---------------------------|-------|
| <b>Species Richness</b>              |             |           |                           |       |
| Intercept                            | 15.823      | 2.726     |                           | <.001 |
| pH                                   | -1.768      | 0.426     | 0.079                     | <.001 |
| Biomass                              | -0.013      | 0.004     | 0.211                     | 0.001 |
| Bare ground                          | 0.048       | 0.018     | 0.244                     | 0.011 |
| Lichen                               | -0.039      | 0.018     | 0.267                     | 0.031 |
| Black crust                          | 0.095       | 0.047     | 0.300                     | 0.045 |
| Rock limited                         | -0.772      | 0.365     | 0.314                     | 0.037 |
| Active layer depth                   | 0.032       | 0.021     | 0.328                     | 0.136 |
| <b>1/λ</b>                           |             |           |                           |       |
| Intercept                            | 4.651       | 0.731     |                           | <.001 |
| Biomass                              | -0.004      | 0.001     | 0.172                     | <.001 |
| Moss                                 | -0.013      | 0.003     | 0.289                     | <.001 |
| Litter                               | -0.011      | 0.003     | 0.347                     | 0.001 |
| pH                                   | -0.545      | 0.105     | 0.389                     | <.001 |
| Rock limited                         | -0.242      | 0.629     | 0.433                     | <.001 |
| Lichen                               | -0.016      | 0.005     | 0.465                     | 0.003 |
| $\theta_{grav}$                      | 0.003       | 0.001     | 0.481                     | 0.002 |
| $\rho_b$                             | 0.001       | 0.000     | 0.519                     | 0.004 |
| Soil temperature                     | 0.047       | 0.033     | 0.529                     | 0.159 |
| <b>N<sub>1</sub></b>                 |             |           |                           |       |
| Intercept                            | 6.179       | 0.929     |                           | <.001 |
| Biomass                              | -0.006      | 0.001     | 0.2094                    | <.001 |
| Moss                                 | -0.017      | 0.004     | 0.3144                    | <.001 |
| pH                                   | -0.729      | 0.133     | 0.377                     | <.001 |
| Litter                               | -0.014      | 0.080     | 0.438                     | 0.001 |
| $\theta_{grav}$                      | 0.004       | 0.001     | 0.465                     | 0.001 |
| Rock limited                         | -0.257      | 0.080     | 0.489                     | 0.002 |
| Lichen                               | -0.019      | 0.007     | 0.515                     | 0.005 |
| $\rho_b$                             | 0.001       | 0.000     | 0.549                     | 0.005 |
| Soil temperature                     | 0.055       | 0.041     | 0.557                     | 0.188 |
| <b>E<sub>var</sub></b>               |             |           |                           |       |
| Intercept                            | 0.128       | 0.013     |                           | <.001 |
| Lichen                               | 0.002       | 0.000     | 0.146                     | <.001 |
| Biomass                              | -0.0003     | 0.000     | 0.212                     | 0.005 |
| Slope                                | -0.101      | 0.067     | 0.234                     | 0.134 |

There was a significant interaction in the MANOVA of functional groups with biomass, snowbed community, and biomass $\times$ snowbed as the effect variables (Table F.1). This is not surprising since it is known *a priori* that the CPSB is dominated by deciduous shrubs (Table 3.1). The relation between functional group abundance and biomass are shown for each community (Figure 3.11, Figure 3.12). All three natural snowbed communities had statistically significant MANOVAs of functional groups with biomass as the effect variable (Table F.2). These functional group changes with biomass were primarily due to changes within the dominant functional group of each community. The relation between evergreen shrubs and biomass was significant and had very good fit for all 3 snowbeds, although in the CPSB the relation between deciduous shrubs, the dominant group, was also significant (Figure 3.11, Table F.3). There were no statistical relations between the abundance of forbs and increasing biomass for any of the communities (Figure 3.12, Table F.3). Graminoids increased with an increase in biomass within the CPSB and decreased in the GRSB (Figure 3.12, Table F.3).

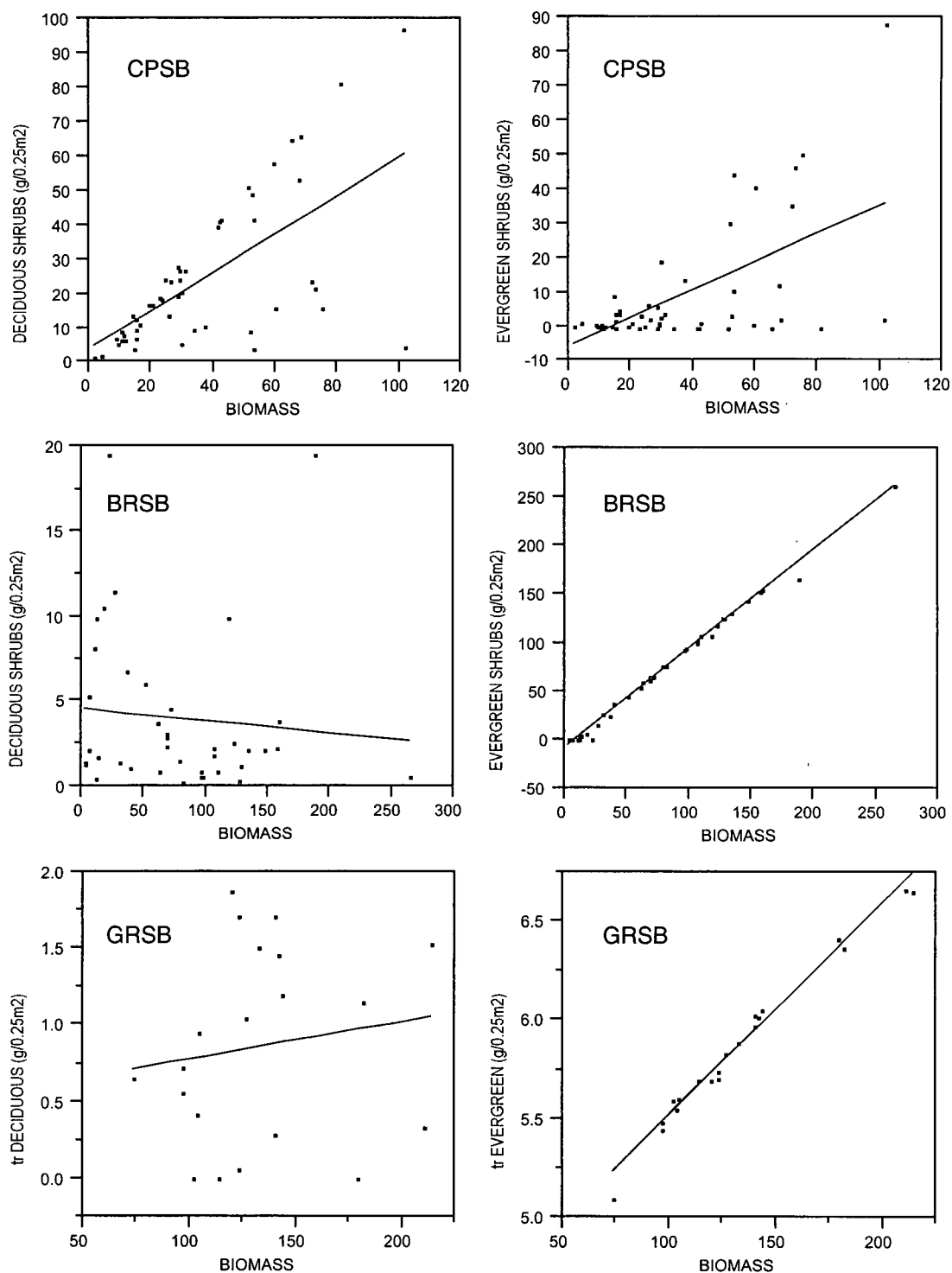


Figure 3.11. Relation between deciduous or evergreen shrubs and biomass in each natural snowbed community. For the GRSB, deciduous and evergreen shrubs were brought closer to a normal distribution using the Box-Cox transformation. No other transformations were performed, since all variables were approximately normally distributed. The regression lines for deciduous shrubs in CPSB and all evergreen lines are statistically significant. All regression statistics are given in Table F.3.



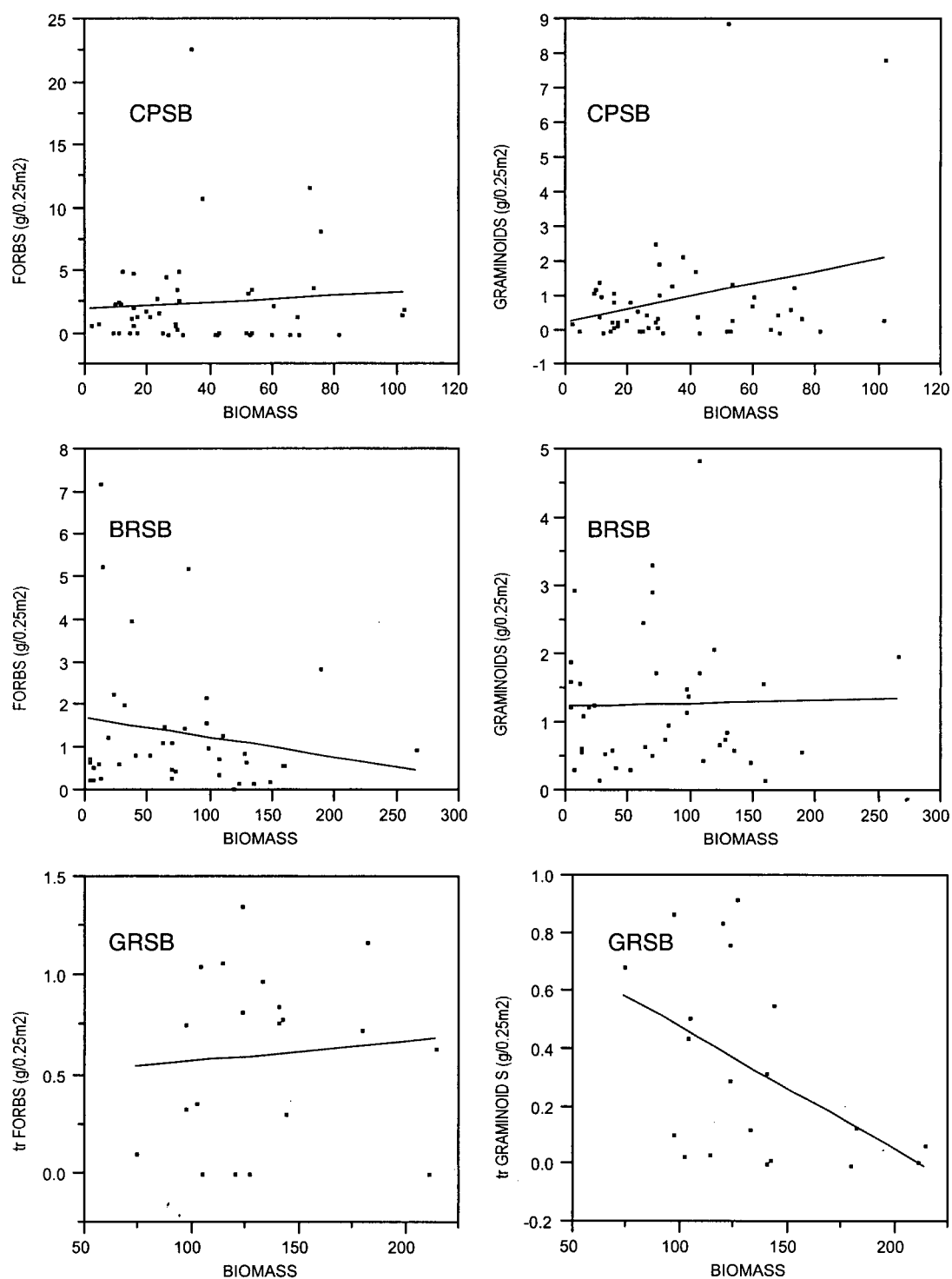


Figure 3.12. Relation between forbs or graminoids and biomass in each natural snowbed community. For the GRSB, forbs and graminoids were brought closer to a normal distribution using the Box-Cox transformation. No other transformations were performed, since all variables were approximately normally distributed. The regression lines for graminoids in CPSB ( $\alpha = 0.10$ ) and in GRSB ( $\alpha = 0.05$ ) are statistically significant. All regression statistics are given in Table F.3.

### 3.3.2.3 Allocation Patterns

There was a significant relation between the estimated aboveground net primary productivity (ANPP) and plot biomass for all 110 plots from all 3 natural snowbed communities ( $ANPP = 0.0571 \text{ BIOMASS} + 4.9532$ ,  $R^2 = 0.41$ ,  $P < 0.001$ ). However, there was also a significant interaction between the relation between ANPP and biomass with the relation between ANPP and snowbed (ANCOVA,  $P = 0.010$ ). This is because the slope of the regression of ANPP and biomass is significantly steeper in the CPSB than in either of the other snowbed communities, although all 3 snowbed communities had a significant relation between ANPP and biomass (Figure 3.13).

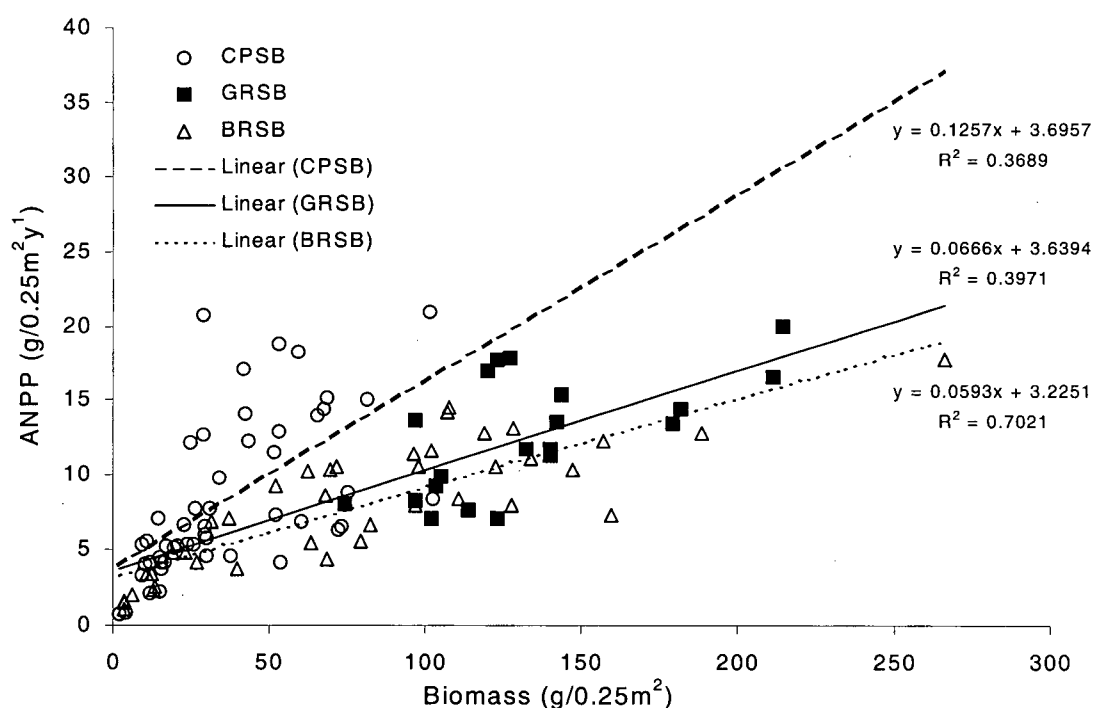


Figure 3.13. Relation between total plot biomass (BIOMASS,  $\text{g}/0.25\text{m}^2$ ) and the estimated plot aboveground net primary productivity (ANPP,  $\text{g}/0.25\text{m}^2\text{y}^1$ ) for the 3 natural snowbed communities. For all regression lines  $x = \text{BIOMASS}$  and  $y = \text{ANPP}$  and all regression lines are statistically significant ( $P < 0.001$ ).

Of the species that had flowers present in more than 6 plots, there existed a strong linear relation between the per plot live biomass and the per plot total standing crop of live plus dead biomass (Table 3.7). The relation between flower and live mass per plot also was significant for

all species except *Draba* species, although the relation was weaker within the deciduous shrub, *Salix arctica*, and evergreen shrubs, *Cassiope tetragona* and *Dryas integrifolia* (Table 3.7).

Table 3.7. Relations between live mass and total mass (standing crop of live plus dead) and between flower mass and live mass for some selected species as measured in g/0.25m<sup>2</sup>. Species were included if they had flowers in more than 6 plots.

| SPECIES                        | MODEL                        | N   | R <sup>2</sup> | P     |
|--------------------------------|------------------------------|-----|----------------|-------|
| <i>Salix arctica</i>           | Live = 0.595 + 0.243 Total   | 107 | 0.821          | <.001 |
|                                | Flower = -0.090 + 0.097 Live | 107 | 0.449          | <.001 |
| <i>Cassiope tetragona</i>      | Live = 2.055 + 0.147 Total   | 58  | 0.879          | <.001 |
|                                | Flower = -0.005 + 0.007 Live | 58  | 0.110          | 0.011 |
| <i>Dryas integrifolia</i>      | Live = 0.275 + 0.074 Total   | 94  | 0.915          | <.001 |
|                                | Flower = 0.007 + 0.020 Live  | 94  | 0.216          | <.001 |
| <i>Carex misandra</i>          | Live = 0.005 + 0.201 Total   | 43  | 0.970          | <.001 |
|                                | Flower = -0.006 + 0.110 Live | 43  | 0.714          | <.001 |
| <i>Luzula arctica</i>          | Live = 0.006 + 0.215 Total   | 73  | 0.935          | <.001 |
|                                | Flower = -0.001 + 0.172 Live | 73  | 0.721          | <.001 |
| <i>Luzula confusa</i>          | Live = -0.003 + 0.318 Total  | 52  | 0.748          | <.001 |
|                                | Flower = -0.032 + 0.443 Live | 52  | 0.621          | <.001 |
| <i>Draba</i> species           | Live = -0.040 + 0.840 Total  | 23  | 0.841          | <.001 |
|                                | Flower = 0.010 + 0.028 Live  | 23  | 0.044          | 0.337 |
| <i>Papaver radicum</i>         | Live = 0.023 + 0.537 Total   | 23  | 0.821          | <.001 |
|                                | Flower = -0.026 + 0.538 Live | 23  | 0.708          | <.001 |
| <i>Polygonum viviparum</i>     | Live = -0.002 + 0.785 Total  | 15  | 0.985          | <.001 |
|                                | Flower = -0.001 + 0.254 Live | 15  | 0.872          | <.001 |
| <i>Saxifraga oppositifolia</i> | Live = -0.002 + 0.007 Total  | 70  | 0.481          | <.001 |
|                                | Flower = -0.002 + 0.051 Live | 70  | 0.660          | <.001 |

Given the relation between flower and live mass for the species listed in Table 3.7, it is not surprising that the flower and live mass for most of these species covary in their relations with ANPP or meltdte (Figure 3.14, Figure 3.15, Figure 3.16). All of these figures show the proportion of the maximum value for both live mass and for flower mass, which is known as standardizing to the maximum, rather than showing the absolute values of each variable. This transformation better shows where the maximum values of each species, in terms of live or

flower mass, occur along the gradients of ANPP or meltdat and highlights the few extremely high values (Figure 3.14, Figure 3.15, Figure 3.16). LOWESS smoothing was used to demonstrate the relation between the mass of each variable and ANPP or meltdat. Only large relative changes in the LOWESS smoothed line are discussed as genuine relations.

The live biomass of the deciduous shrub, *Salix arctica*, increased with ANPP, and the same was found for the evergreen shrub, *Cassiope tetragona* (Figure 3.14). There was no such increase in the mass of flowers with ANPP, although there was a significant relation between flower and live biomass for both of these species (Table 3.7). This indicates that *Salix arctica* and *Cassiope tetragona* grow to a higher biomass per plot where there exists a higher ANPP, but overall flower mass per plot does not tend to increase, or if there were a relation it would be only be a very minor increase (Figure 3.14). No trend existed between *Dryas integrifolia* and ANPP or between any of the shrubs and meltdat for either live or flower mass (Figure 3.14). The decrease in the live mass of *Cassiope tetragona* at the highest meltdat is only due to a single point and may or may not represent a real trend (Figure 3.14).

No major trends were present between live or flower mass and ANPP or meltdat with any of the graminoids, although there appeared to be an increase in *Luzula arctica* biomass with an increase in ANPP (Figure 3.15). The initial decrease in *Luzula confusa* with an increase in meltdat is likely due to a single extreme point.

The live and flower mass of most forbs covaried across the gradients of ANPP or meltdat (Figure 3.16). *Draba* species did not follow this pattern for ANPP, where live mass increased with ANPP and flower mass was high at low and high ANPP and low at mid values of ANPP (Figure 3.16). For the *Draba* species and *Polygonum viviparum*, both live and especially flower mass decreased with an increase in meltdat. *Polygonum viviparum* tended to do best, for both live and flower mass, with intermediate ANPP (Figure 3.16). *Papaver radicum* live and flower mass tended increase initially with an increase in ANPP and then remained constant, whereas live mass peaked with intermediate meltdat (Figure 3.16). No patterns existed in the relation between live or flower mass with ANPP or meltdat for *Saxifraga oppositifolia* (Figure 3.16).

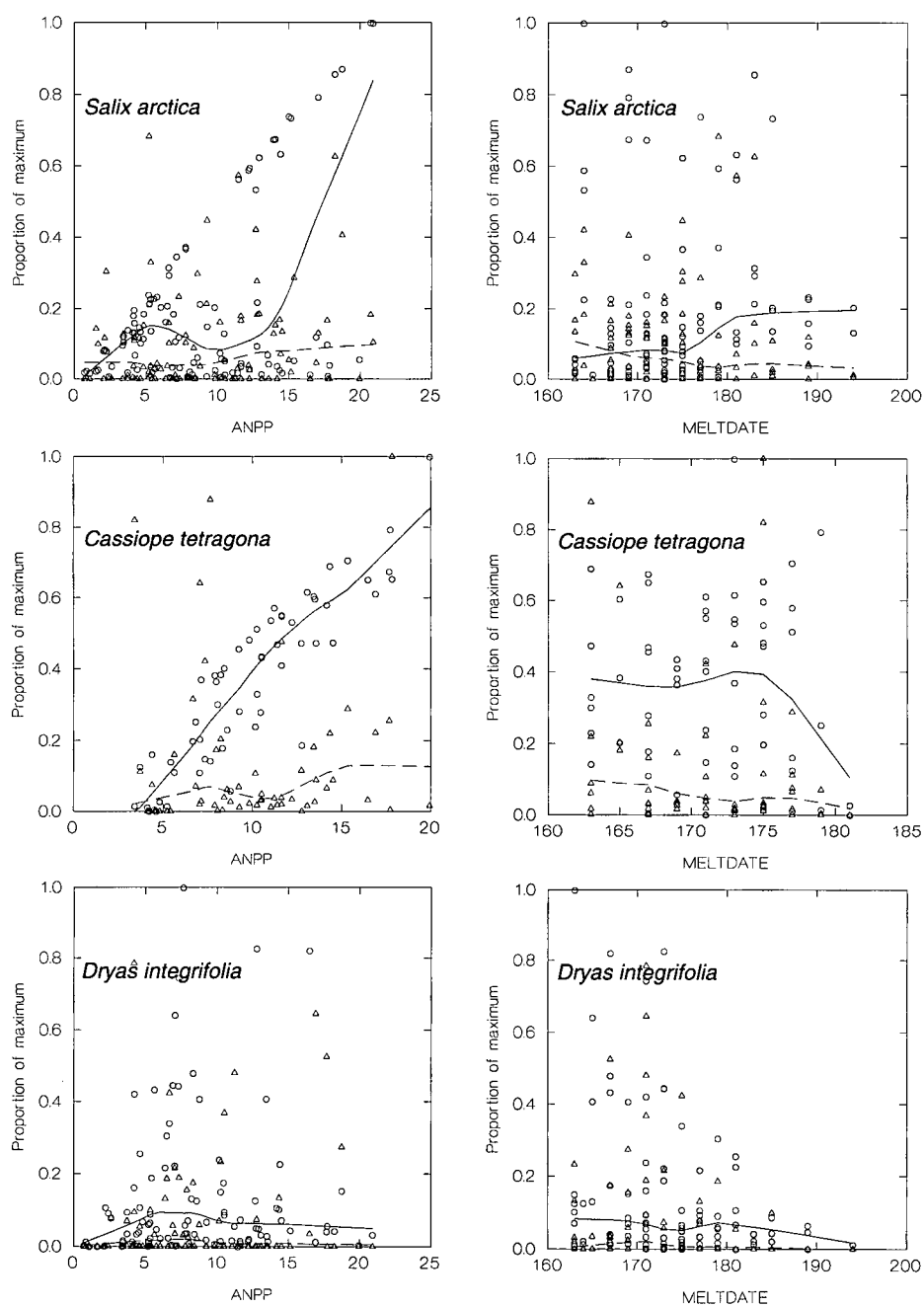


Figure 3.14. Relations between live mass (circles and solid line) or flower mass (triangles and dashed line) and aboveground net primary productivity ( $\text{g}/0.25\text{m}^2\text{y}^{-1}$ ) or meltdates for the deciduous shrub, *Salix arctica*, and evergreen shrubs *Cassiope tetragona* and *Dryas integrifolia*. Live mass or flower mass is measured as the proportion of the maximum mass found in any quadrat (quadrat value divided by the maximum value in any of the quadrats). All lines are LOWESS smoothed lines. See text for details.

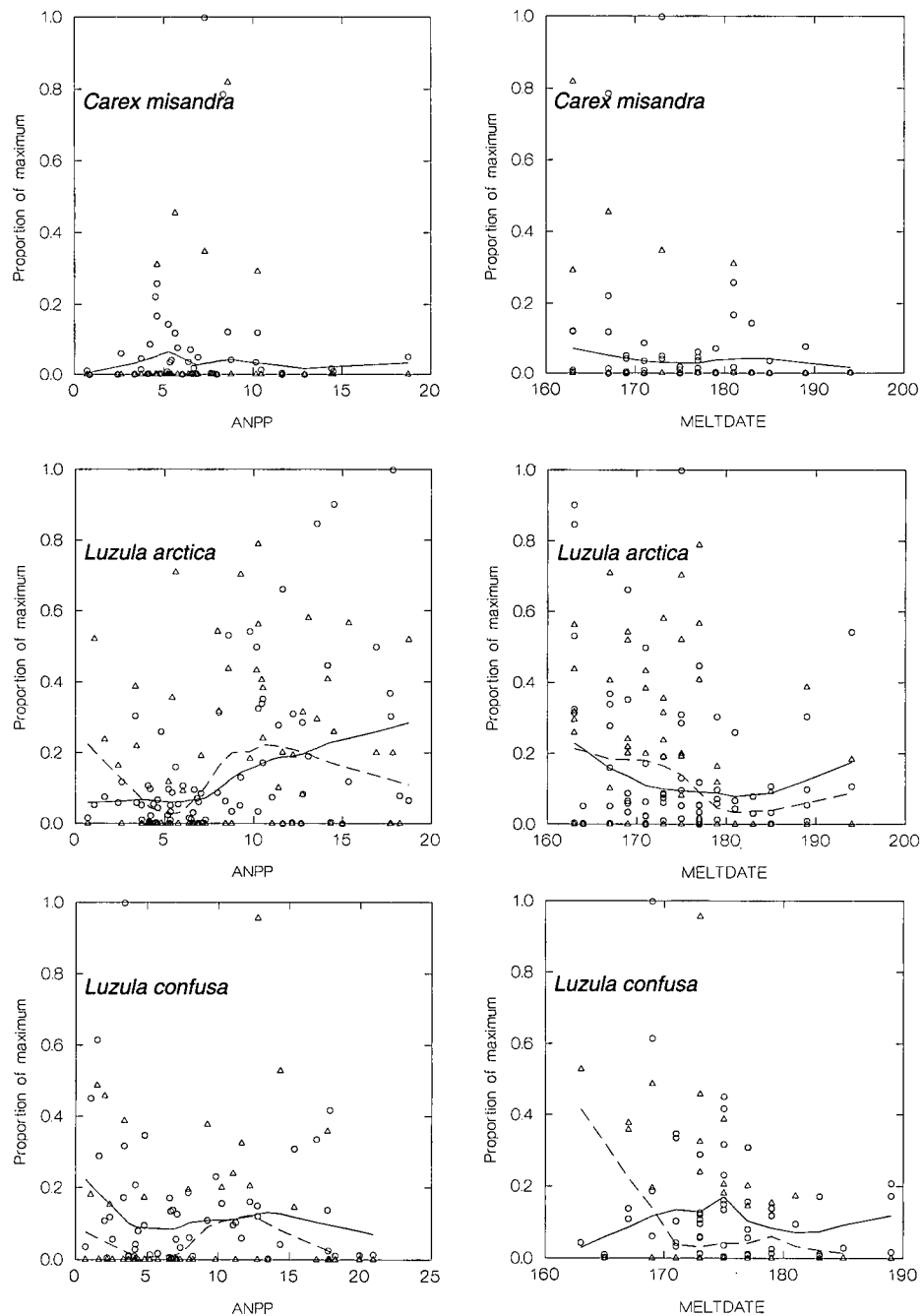


Figure 3.15. Relations between live mass (circles and solid line) or flower mass (triangles and dashed line) and aboveground net primary productivity ( $\text{g}/0.25\text{m}^2\text{y}^{-1}$ ) or meltdate for the graminoid species, *Carex misandra*, *Luzula arctica*, and *Luzula confusa*. Symbols are the same as in Figure 3.14. For more details see text.

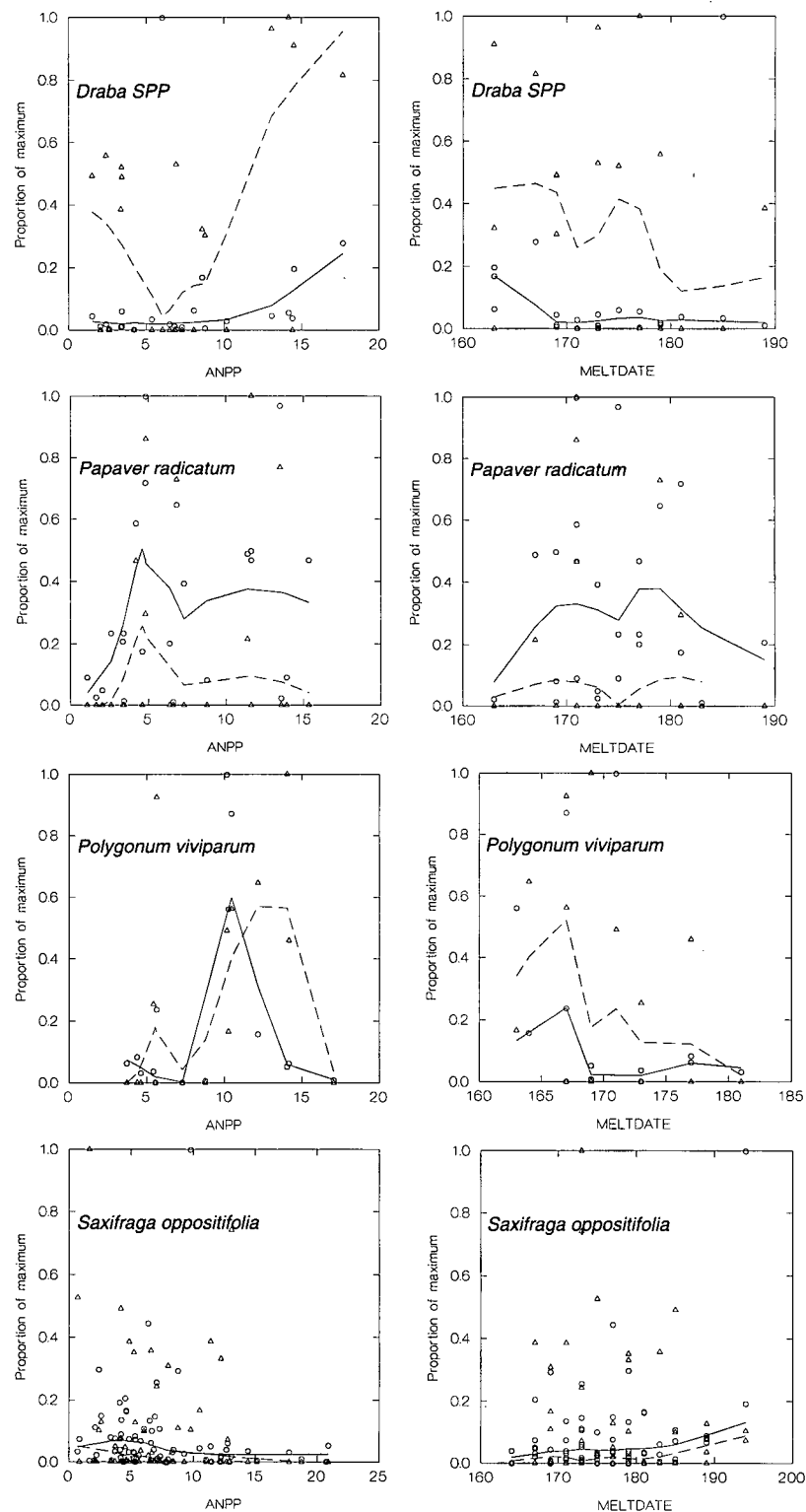


Figure 3.16. Relations between live mass (circles and solid line) or flower mass (triangles and dashed line) and aboveground net primary productivity ( $\text{g}/0.25\text{m}^2\text{y}^{-1}$ ) or meltdate for the forb species, *Draba* species, *Papaver radicatum*, *Polygonum viviparum* and *Saxifraga oppositifolia*. Symbols are the same as in Figure 3.14. For more details see text.

### 3.3.3 Patterns of Diversity within a Manipulated Snowbed

The species found within the snow manipulation snowbed (SMSB) were similar to the BRSB and were dominated by the two evergreen shrubs, *Cassiope tetragona* and *Dryas integrifolia* (Table 3.8). There was no difference in the mean standing crop between the treatments (F ratio = 1.812, P = 0.185). All treatments were very similar in composition with the two manipulated plots, the addition and removal treatments, being the most similar (Table 3.9).

Table 3.8. Mean biomass (g/0.25m<sup>2</sup>)  $\pm$  1 SE of the species found in the 3 treatments within the SMSB. For each treatment the mean is based on 3 replicate quadrat samples in 3 plots (9 quadrats total for each treatment).

| SPECIES                        | ADDITION            | CONTROL              | REMOVE              |
|--------------------------------|---------------------|----------------------|---------------------|
| <i>Arctagrostis latifolia</i>  |                     | 0.025 $\pm$ 0.025    | 0.081 $\pm$ 0.058   |
| <i>Carex misandra</i>          | 0.340 $\pm$ 0.171   | 0.124 $\pm$ 0.104    | 1.079 $\pm$ 0.650   |
| <i>Cassiope tetragona</i>      | 69.542 $\pm$ 13.962 | 113.853 $\pm$ 20.365 | 63.205 $\pm$ 24.146 |
| <i>Dryas integrifolia</i>      | 16.597 $\pm$ 2.806  | 7.834 $\pm$ 1.352    | 8.498 $\pm$ 1.075   |
| <i>Luzula arctica</i>          | 0.498 $\pm$ 0.107   | 0.704 $\pm$ 0.113    | 0.765 $\pm$ 0.140   |
| <i>Luzula confusa</i>          | 0.157 $\pm$ 0.064   | 0.149 $\pm$ 0.043    | 0.192 $\pm$ 0.045   |
| <i>Oxyria digyna</i>           | 0.127 $\pm$ 0.054   | 0.130 $\pm$ 0.050    | 0.156 $\pm$ 0.067   |
| <i>Papaver radicum</i>         | 0.062 $\pm$ 0.033   | 0.046 $\pm$ 0.032    |                     |
| <i>Pedicularis species</i>     |                     |                      | 0.004 $\pm$ 0.000   |
| <i>Poa arctica</i>             | 0.066 $\pm$ 0.045   | 0.032 $\pm$ 0.023    | 0.056 $\pm$ 0.025   |
| <i>Polygonum viviparum</i>     |                     |                      | 0.039 $\pm$ 0.021   |
| <i>Salix arctica</i>           | 3.201 $\pm$ 1.415   | 2.770 $\pm$ 0.794    | 4.678 $\pm$ 1.102   |
| <i>Saxifraga oppositifolia</i> | 1.448 $\pm$ 0.427   | 2.069 $\pm$ 0.319    | 1.469 $\pm$ 0.341   |
| Total Estimated                |                     |                      |                     |
| Biomass                        | 92.038 $\pm$ 13.523 | 127.736 $\pm$ 20.372 | 80.221 $\pm$ 20.378 |

Table 3.9. Percent similarity ( $P_{sim}$ ), simplified Morisita-Horn index of similarity ( $C_H$ ) and Lande community similarity index ( $\Psi_D$ ) between the addition (ADD), control (CONT) and remove (REM) treatments within the SMSB.

| $P_{sim}$ |      |      |     | $C_H$ |      |      |      | $\Psi_D$ |       |       |       |
|-----------|------|------|-----|-------|------|------|------|----------|-------|-------|-------|
|           | ADD  | CONT | REM |       | ADD  | CONT | REM  |          | ADD   | CONT  | REM   |
| ADD       | 100  |      |     | ADD   | 1.00 |      |      | ADD      | 1.000 |       |       |
| CONT      | 86.3 | 100  |     | CONT  | 0.98 | 1.00 |      | CONT     | 0.973 | 1.000 |       |
| REM       | 92.5 | 89.6 | 100 | REM   | 0.99 | 0.99 | 1.00 | REM      | 0.995 | 0.988 | 1.000 |



The best fitting RAD model for each treatment was generally the Zipf-Mandelbrot model, regardless of whether all 27 quadrat samples were examined or if averaged values across the replicate plots or across treatments were analyzed (Table 3.10). There was no significant difference between the treatments in the number of times each model best fit the observed distributions when all 27 quadrats sampled were examined ( $\chi^2 = 2.29$ ,  $df = 4$ ,  $P = 0.68$ ). If the quadrats within each replicate plot were averaged so there were 3 replicates of the 3 treatments, giving a total of 9 plots, there was also no significant difference between the treatments ( $\chi^2 = 2.27$ ,  $df = 2$ ,  $P = 0.32$ ). The best fitting RAD model for each treatment, when all quadrats within each plot and replicate plots were averaged, was the Zipf-Mandelbrot model for the addition and control treatments and the General Lognormal model for the removal treatment (Figure 3.17, Table 3.10).

Table 3.10. Best fitting RAD model for the SMSB when compared for all 27 quadrats sampled (3 quadrats in each of 3 replicate plots of the 3 treatments,  $3 \times 3 \times 3 = 27$ ), in 9 plots (3 quadrats averaged to give a single measurement for each of the 3 replicate plots of the 3 treatments,  $1 \times 3 \times 3 = 9$ ) and for the 3 treatments (3 quadrats averaged and replicate plots average to give a single measurement for each treatment  $1 \times 1 \times 3 = 3$ ).

| MODEL           | 27 quadrats |      |     | 9 plots |      |     | 3 treatments |      |     |
|-----------------|-------------|------|-----|---------|------|-----|--------------|------|-----|
|                 | ADD         | CONT | REM | ADD     | CONT | REM | ADD          | CONT | REM |
| Geometric       | 1           | 0    | 2   | 0       | 0    | 1   | 0            | 0    | 0   |
| Broken Stick    | 0           | 0    | 0   | 0       | 0    | 0   | 0            | 0    | 0   |
| Gen-Lognormal   | 1           | 1    | 1   | 0       | 0    | 0   | 0            | 0    | 1   |
| Zipf-Mandelbrot | 7           | 8    | 6   | 3       | 3    | 2   | 1            | 1    | 0   |

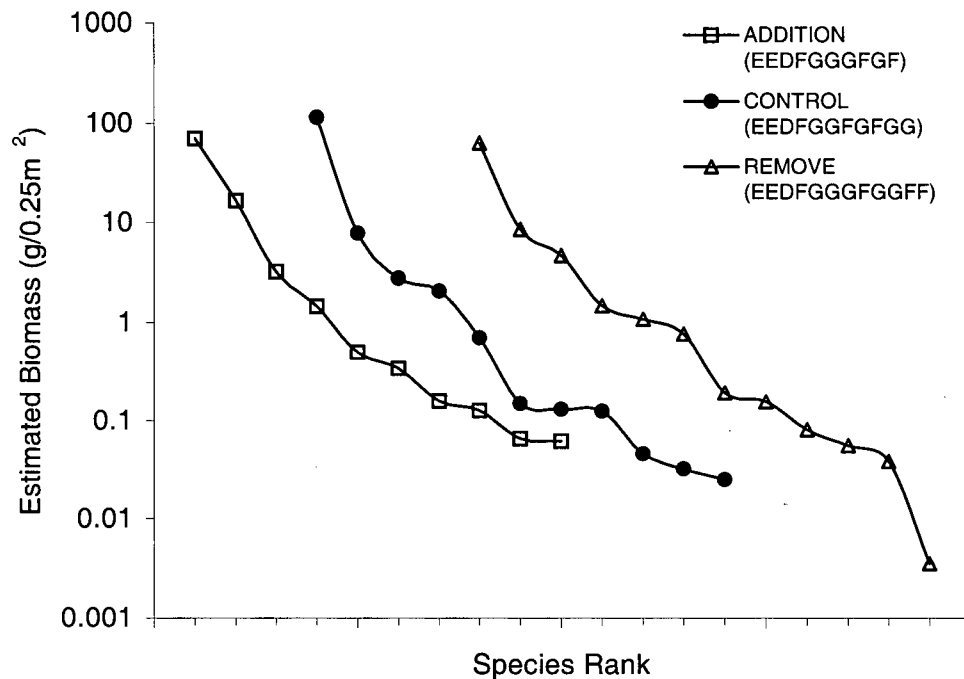


Figure 3.17. Relative abundance distributions (RAD) for the 3 treatments in the SMSB. Estimated biomass (g/0.25 m<sup>2</sup>) is the measure of abundance for each species in the sampled quadrat. Functional groups, deciduous shrubs (D), evergreen shrubs (E), forbs (F) and graminoids (G), are given in parentheses and specific species identities can be found in Table 3.8.

All quadrats sampled within each replicate plot were used in the remaining analyses to increase the sample size to 27, with 9 samples per treatment. There were statistical differences between the treatments for species richness,  $1/\lambda$  and  $N_1$  at  $\alpha = 0.05$  and for  $E_{var}$  at  $\alpha = 0.10$  (Figure 3.18, Table 3.11). Species richness was significantly lower in the addition treatment than in the removal treatment. For the diversity indices,  $1/\lambda$  and  $N_1$ , the control was lower than the removal treatment, although there was also a non-significant increase in the addition treatment (Figure 3.18). When  $\alpha = 0.10$ , the trends in evenness were identical to the trend in the diversity indices. Collectively, these results suggest that snow removal will increase both species richness and evenness, while snow addition will decrease richness and increase evenness.

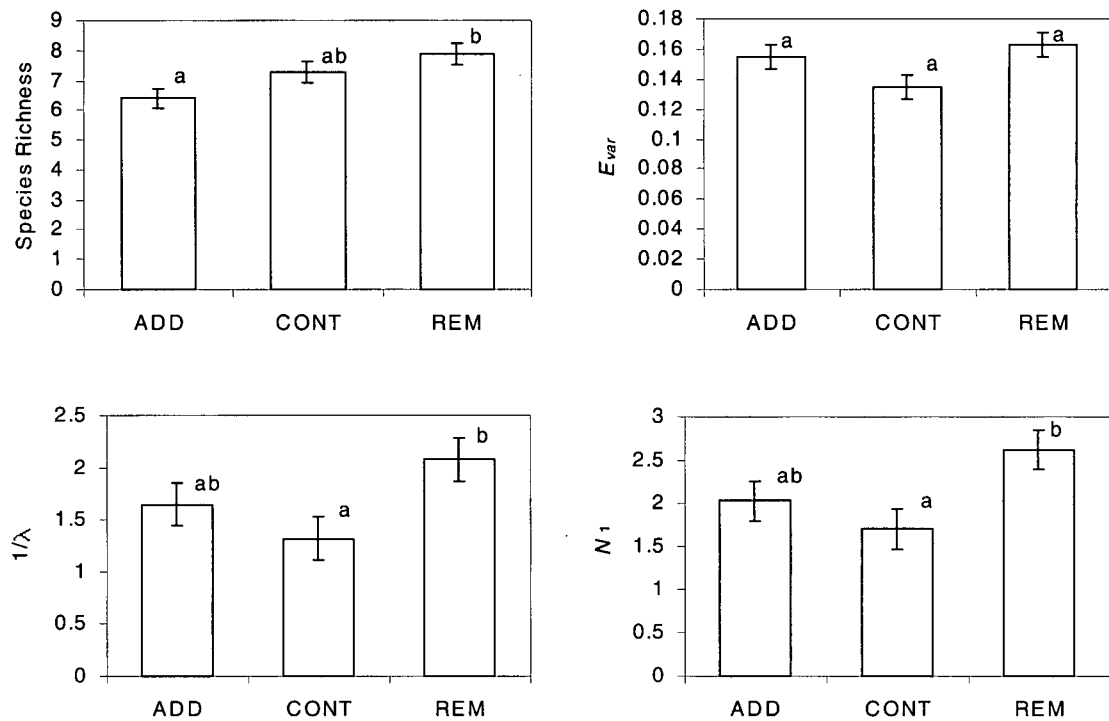


Figure 3.18. Mean diversity values ( $\pm 1$  SE) for each treatment, addition (ADD), control (CONT) and removal (REM), in the SMSB. These values are based on 3 sampled quadrats in 3 replicate plots (giving 9 samples) for each treatment. Values sharing the same letter are not statistically different ( $\alpha = 0.05$ ; Tukey-Kramer HSD test). The removal treatment is statistically different from the control for  $E_{var}$  if  $\alpha = 0.10$ .

Table 3.11. ANOVAs for each measure of diversity with treatment as the independent variable for the SMSB. These data are displayed in Figure 3.18.

| Dependent Variable | SOURCE | SS     | DF | MS    | F ratio | Pr>F  |
|--------------------|--------|--------|----|-------|---------|-------|
| Species Richness   | Model  | 9.556  | 2  | 4.778 | 4.230   | 0.027 |
|                    | Error  | 27.111 | 24 | 1.130 |         |       |
| $1/\lambda$        | Model  | 2.609  | 2  | 1.305 | 3.449   | 0.048 |
|                    | Error  | 9.080  | 24 | 0.378 |         |       |
| $N_1$              | Model  | 3.917  | 2  | 1.958 | 4.109   | 0.029 |
|                    | Error  | 11.438 | 24 | 0.477 |         |       |
| $E_{var}$          | Model  | 0.004  | 2  | 0.002 | 3.088   | 0.064 |
|                    | Error  | 0.014  | 24 | 0.001 |         |       |

MANOVA test results of the functional groups were not consistent among the different multivariate test statistics (Model A, Table 3.12). Roy's Max Root statistic indicated that the interaction between the effect terms TREATMENT and PLOT was significant, while Pillai's Trace statistic was not significant (Table 3.12). The Box-Cox transform was applied to the functional groups, deciduous ( $\lambda = -0.068$ ), evergreen ( $\lambda = 0.504$ ) and graminoids ( $\lambda = -0.350$ ), so that all were normally distributed by themselves (Shapiro-Wilk W Test,  $P < 0.10$ ). Since multivariate normality tests have not been implemented in any of the current statistical programs and because all test results using MANOVA should be viewed with caution when  $0.10 < P < 0.01$  (Scheiner 1993), the more conservative conclusion reached with the Pillai's Trace statistic will be used (Table 3.12).

Table 3.12. MANOVA results for the test of functional groups for models A and B. Two MANOVA tests are given because test results were not consistent. Pillai's trace is more robust to violation of MANOVA assumptions and Roy's Max Root has the best power (Wilkinson et al. 1992). The functional groups were transformed with the Box-Cox transform to meet the assumptions of normality.

| MODEL A          |       |       |        |        |        |
|------------------|-------|-------|--------|--------|--------|
| SOURCE and TEST  | VALUE | F     | NUM DF | DEN DF | Pr > F |
| TREATMENT        |       |       |        |        |        |
| Pillai's Trace   | 0.712 | 2.211 | 8      | 32     | 0.053  |
| Roy's Max Root   | 0.812 | 3.248 | 4      | 16     | 0.040  |
| PLOT             |       |       |        |        |        |
| Pillai's Trace   | 0.671 | 2.020 | 8      | 32     | 0.076  |
| Roy's Max Root   | 0.780 | 3.120 | 4      | 16     | 0.045  |
| TREATMENT * PLOT |       |       |        |        |        |
| Pillai's Trace   | 0.783 | 1.093 | 16     | 72     | 0.376  |
| Roy's Max Root   | 0.653 | 2.938 | 4      | 18     | 0.050  |
| MODEL B          |       |       |        |        |        |
| SOURCE and TEST  | VALUE | F     | NUM DF | DEN DF | Pr > F |
| TREATMENT        |       |       |        |        |        |
| Pillai's Trace   | 0.588 | 2.081 | 8      | 40     | 0.061  |
| Roy's Max Root   | 0.608 | 3.039 | 4      | 20     | 0.041  |
| PLOT             |       |       |        |        |        |
| Pillai's Trace   | 0.593 | 2.107 | 8      | 40     | 0.058  |
| Roy's Max Root   | 0.735 | 3.674 | 4      | 20     | 0.021  |

The MANOVA of the same transformed functional groups, with just treatment and plot as the effects, was statistically significant for both effects (Model B, Table 3.12). The univariate responses of each functional group was not significantly related to meltdat at  $\alpha = 0.05$ , although at  $\alpha = 0.10$  graminoids were significantly different between the treatments (Figure

3.19, Table 3.13). Although all the trends in functional groups with the treatments were slight and were non significant, they are sufficient to explain the statistically significant trends in the relations between diversity and the treatments (Figure 1.1, Table 3.1). Since the abundance of evergreen shrubs tends to be slightly higher in the control relative to the treatments (Figure 3.19), this will lead to a decrease in the evenness and species diversity indices for the control plots as observed in Figure 3.18.

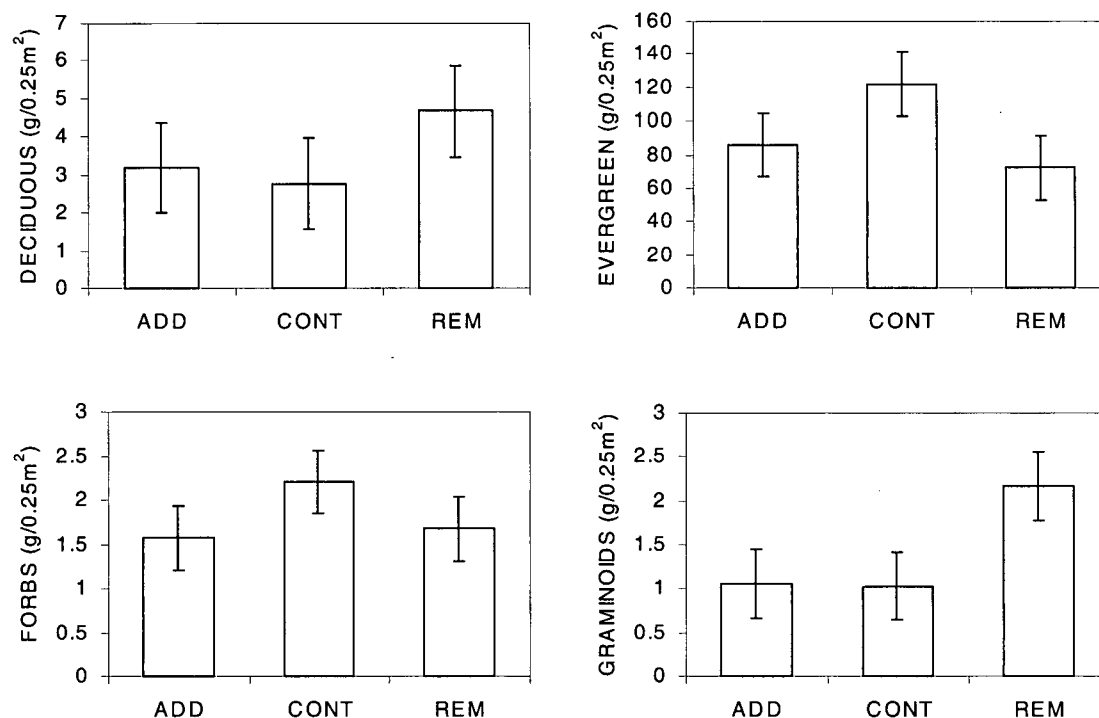


Figure 3.19. Biomass (mean  $\pm$  1 SE) of each functional group in the manipulated snowbed community. There are no statistical differences between the treatments for any functional group at  $\alpha = 0.05$ , although graminoids are different at  $\alpha = 0.10$  (Table 3.13).

Table 3.13. ANOVAs for each functional group with treatment as the independent variable for the SMSB. These data are displayed in Figure 3.19.

| DEPENDENT<br>VARIABLE | SOURCE | SS        | DF | MS      | F ratio | Pr>F  |
|-----------------------|--------|-----------|----|---------|---------|-------|
| Deciduous Shrubs      | Model  | 18.028    | 2  | 9.014   | 0.717   | 0.499 |
|                       | Error  | 301.937   | 24 | 12.581  |         |       |
| Evergreen Shrubs      | Model  | 11911.419 | 2  | 5955.71 | 1.892   | 0.173 |
|                       | Error  | 75551.174 | 24 | 3363.95 |         |       |
| Forbs                 | Model  | 2.046     | 2  | 1.023   | 0.856   | 0.437 |
|                       | Error  | 28.260    | 24 | 1.195   |         |       |
| Graminoids            | Model  | 7.599     | 2  | 3.800   | 2.735   | 0.085 |
|                       | Error  | 33.343    | 24 | 1.389   |         |       |

### 3.3.4 Ordination of Snowbed Communities

The natural snowbed communities generally had short gradients of between 1.332 to 2.639 SD as measured with DCA (Table 3.3). When all 110 plots were analyzed together, the gradient length was only 2.729 SD, which justified the use of linear constrained ordination techniques, namely RDA (ter Braak and Prentice 1988). When the snowbed data were examined with CCA and DCCA (results not presented), the method that described the most species variation was consistently RDA, as is often the case even with longer gradients than traditionally would be examined with the unimodal techniques (Økland 1999). The best environmental variables in explaining the variance in the species dataset were determined using the automatic forward selection routine within CANOCO (ter Braak and Smilauer 1998). Like multiple regression, RDA can be over-fit with extraneous variables adding little to the fit of a particular model. In order to not over parameterize the RDA, forward selection was used to determine the best K variables. The order of selection and the improvement in fit of each variable is given in Table 3.14. The K number of variables in the RDA was then plotted against the cumulative variance of the species data explained in ordination space (Figure 3.20). From this figure it becomes

clear that only marginal improvement in fit occurs after the addition of the first few variables. For the GRSB, after two variables are added there was only minor improvement in fit. This leveling off in improvement of fit occurred with the addition of only a single variable for the entire dataset and the BRSB, although the fit was lower than in the GRSB (Figure 3.20). The CPSB needed many more variables than any of the other datasets, although the increase in fit with added variables seemed to stabilize between 5 and 7 variables (Figure 3.20). Of the 7 most important variables in explaining the variance of species data, only the variables biomass, pH and meltdat were common to the RDA models for each of the three natural snowbed communities and the model of all plots combined (Table 3.14). If the selection was expanded to the 8 most important variables for each model, moss cover is also added to this list of variables common to all models. This exploratory data analysis suggested that the four variables common to all ordinations, biomass, pH, meltdat, and moss cover, were key variables in the description of the structure of the snowbed communities.

Table 3.14. Environmental variables and the cumulative sum of the eigenvalues ( $\lambda$ ) of the ordination axes. The sum of the eigenvalues is the cumulative variance of the species data explained in ordination space. The variables are listed in the order selected with forward selection for each snowbed community and for all snowbeds combined. Figure 3.20 shows the relation between the number of variables in the RDA model and the sum of  $\lambda$ .

| ALL SNOWBEDS |                  | BRSB             |                  | GRSB             |                  | CPSB             |                  |
|--------------|------------------|------------------|------------------|------------------|------------------|------------------|------------------|
| Variable     | Sum of $\lambda$ | Variable         | Sum of $\lambda$ | Variable         | Sum of $\lambda$ | Variable         | Sum of $\lambda$ |
| Biomass      | 0.623            | Biomass          | 0.640            | Biomass          | 0.364            | Biomass          | 0.374            |
| Litter       | 0.658            | Rock             | 0.668            | Bareground       | 0.793            | $\rho_b$         | 0.494            |
| Soil Temp    | 0.692            | Meltdat          | 0.683            | <i>Peltigera</i> | 0.820            | Slope            | 0.546            |
| pH           | 0.713            | Moss             | 0.725            | Blackcrust       | 0.841            | Meltdat          | 0.584            |
| Bareground   | 0.729            | pH               | 0.745            | Meltdat          | 0.852            | Litter           | 0.620            |
| Aspect       | 0.739            | $\rho_b$         | 0.766            | pH               | 0.868            | pH               | 0.634            |
| Meltdat      | 0.749            | Lichen           | 0.791            | Lichen           | 0.886            | Blackcrust       | 0.645            |
| SMTV         | 0.758            | $\theta_{\%sat}$ | 0.799            | Moss             | 0.897            | Moss             | 0.650            |
| Moss         | 0.762            | $\theta_{vol}$   | 0.816            | $\theta_{grav}$  | 0.908            | Soil Temp        | 0.660            |
| Lichen       | 0.768            | Bareground       | 0.821            | Soil Temp        | 0.915            | $\theta_{\%sat}$ | 0.664            |
| All          | 0.786            | All              | 0.844            | All              | 0.993            | All              | 0.709            |
| variables    |                  | variables        |                  | variables        |                  | variables        |                  |

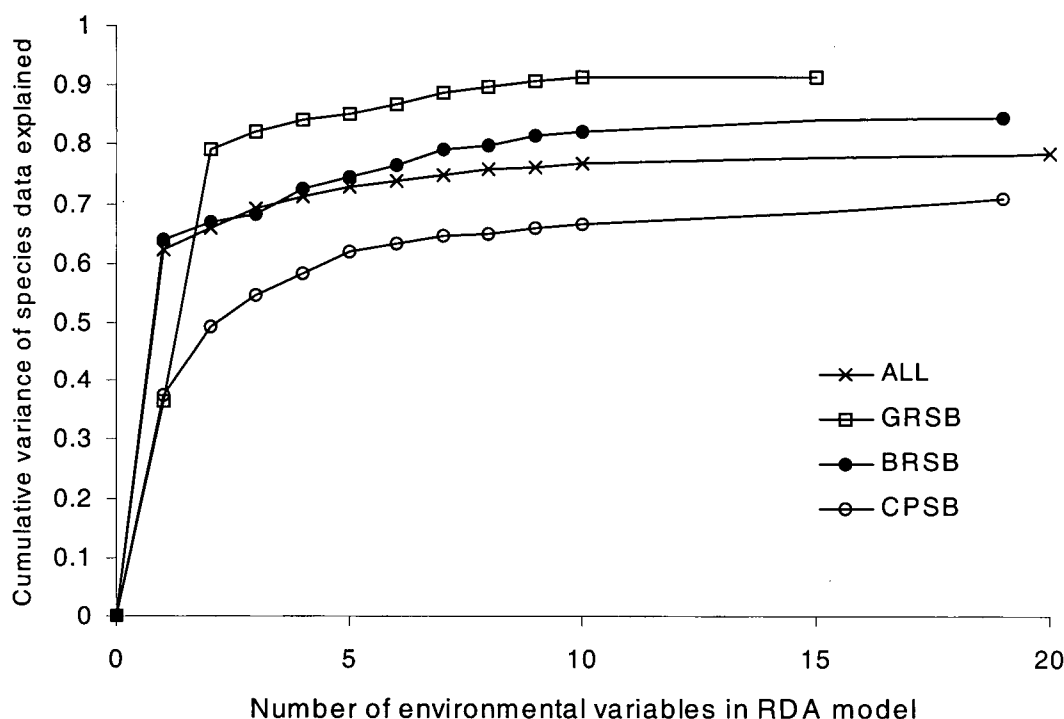


Figure 3.20. Relation between the number of best fitting environmental variables in the RDA model and the cumulative variance of the species data explained in ordination space for all snowbed data combined ( $N = 110$  quadrats sampled), GRSB ( $N = 20$ ), BRSB ( $N = 40$ ) and CPSB ( $N = 50$ ). The variables were added in order of best fit as determined with forward selection. The cumulative variance explained for the first variable is the first eigenvalue for the first axes, the second variable is the sum of the first two axes' eigenvalues, the third variable is the sum of the first three axes' eigenvalues and for the fourth to the  $K$ th variables is the sum of all constrained axes, which is four in CANOCO (ter Braak and Smilauer 1998).

Biomass, pH, meltdate, and moss cover described most of the variation of species data in ordination space for the RDA of all natural snowbed communities combined, with the first 2 axes describing 66.8 % of the variation (Figure 3.21, Table 3.15). This was only a minor decrease in fit when compared with the 4 best variables chosen with forward selection (Table 3.14). Which snowbed the sample belonged to was not used as a variable to determine if the RDA can still accurately describe the species data, although the addition of snowbed identity does slightly increase the fit of the model. The higher biomass plots tended to have less diversity and were from either the GRSB or the BRSB (Figure 3.21). For all the RDA ordinations presented here, the diversity shown is an index combining species richness and evenness within the plot. The index is strongly correlated with  $H'$  (personal observation). The majority of the species were either not related or were negatively correlated to biomass, which



was principally related to increasing *Cassiope tetragona* (Figure 3.21). Biomass was the most important variable in describing the species data for this and all of the communities examined separately, although other variables were also significantly related to the axes (Table 3.15). Meltdat was significantly related to the second axis, but did not seem to be related to the diversity within the plots. The species of similar live form, or of the same functional groups, tended to be grouped together on the RDA (Figure 3.21). The best example is LIST 4 on Figure 3.21, which are all graminoids and are not related to biomass but are strongly negatively correlated with increasing moss.

Within the CPSB, biomass and pH were strongly related to the first and second axes respectively. The overall fit was lower in this snowbed (Figure 3.22, Table 3.16) than in the other sites, or for the combined data. The inclusion of other environmental variables did increase the fit in the RDA of this snowbed (Table 3.14), although the RDA model was still a statistically significant fit of the species data with the first two axes describing 44.1 % of the variation (Table 3.16). Diversity decreased within this snowbed on plots with high biomass and high pH (Figure 3.22). Biomass within this snowbed tended to increase with increases in the species *Salix arctica* and *Dryas integrifolia*, which were not strongly related to each other (Figure 3.22).

The RDA for the GRSB was the best fitting of the natural snowbeds when analyzed alone, with the first two axes describing 75.3 % of the species data (Figure 3.23, Table 3.17). Biomass and moss were the only variables significantly related to the first two axes and unlike the other snowbed communities, diversity tended to increase with an increase in biomass and a decrease in moss cover (Figure 3.23). The overall increase in biomass was strongly correlated to increasing *Cassiope tetragona*.

Both the BRSB and the SMSB show very similar RDA results as would be expected with their close proximity (Figure 3.24, Figure 3.25). Total plot biomass was strongly related to the first axis and moss and meltdat or the snow treatments were related to the both the first and second axes for the BRSB and SMSB (Table 3.18, Table 3.19). The RDA models are very good fits of the species data with the first two axes describing 71.5 % of the species data in the BRSB and 99.6 % in the SMSB (Table 3.18, Table 3.19). For both snowbeds the increase in biomass corresponds with increasing dominance in *Cassiope tetragona* and a decrease in diversity and the abundance of most other species (Figure 3.24, Figure 3.25).

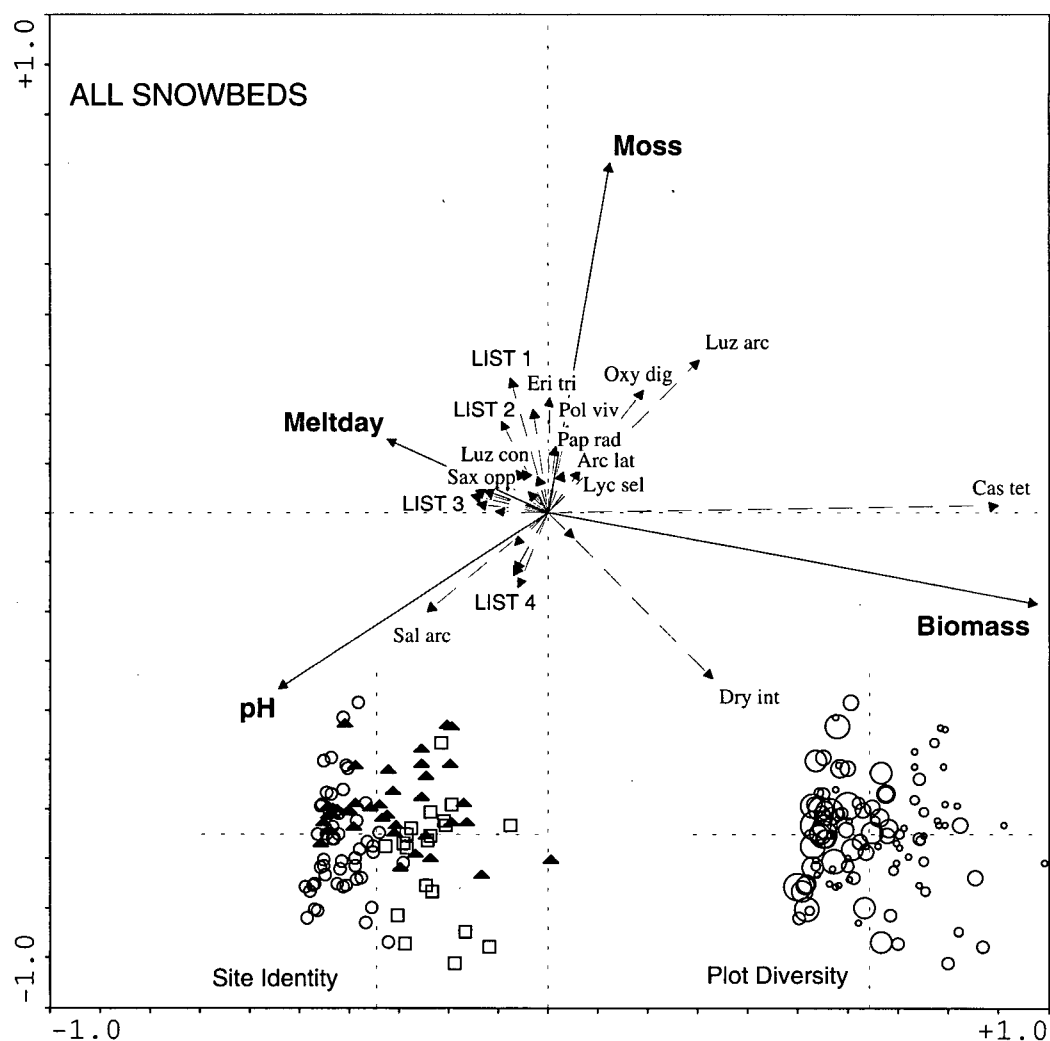


Figure 3.21. RDA biplot of all 3 natural snowbed communities combined (N = 110) showing species (dashed lines) and environmental variables (solid lines). Inset diagrams have the same axes as the larger figure and show the site identity (bottom left; open circles = CPSB, closed triangles = BRSB, open squares = BRSB) and the diversity for each plot (bottom right; each circle represents a single plot and the size of the circle is directly proportional to the diversity). Species too close together to be shown are given by LIST 1 = *Cardamine bellidifolia*, *Equisetum variegatum*, *Saxifraga nivalis*; LIST 2 = *Carex rupestris*, *Draba* species, *Pedicularis* species; LIST 3 = *Carex aquatilis*, *Juncus biglumis*, *Minuartia rubella*, *Saxifraga cernua*, *Silene acaulis*, *Stellaria longipes*; LIST 4 = *Carex maritima*, *Carex misandra*, *Carex nardina*, *Festuca brachyphylla*, *Poa arctica*. All species codes are the first 3 letters of the genus and species names for the species listed in Table 3.1. Summary ordination statistics are shown in Table 3.15.

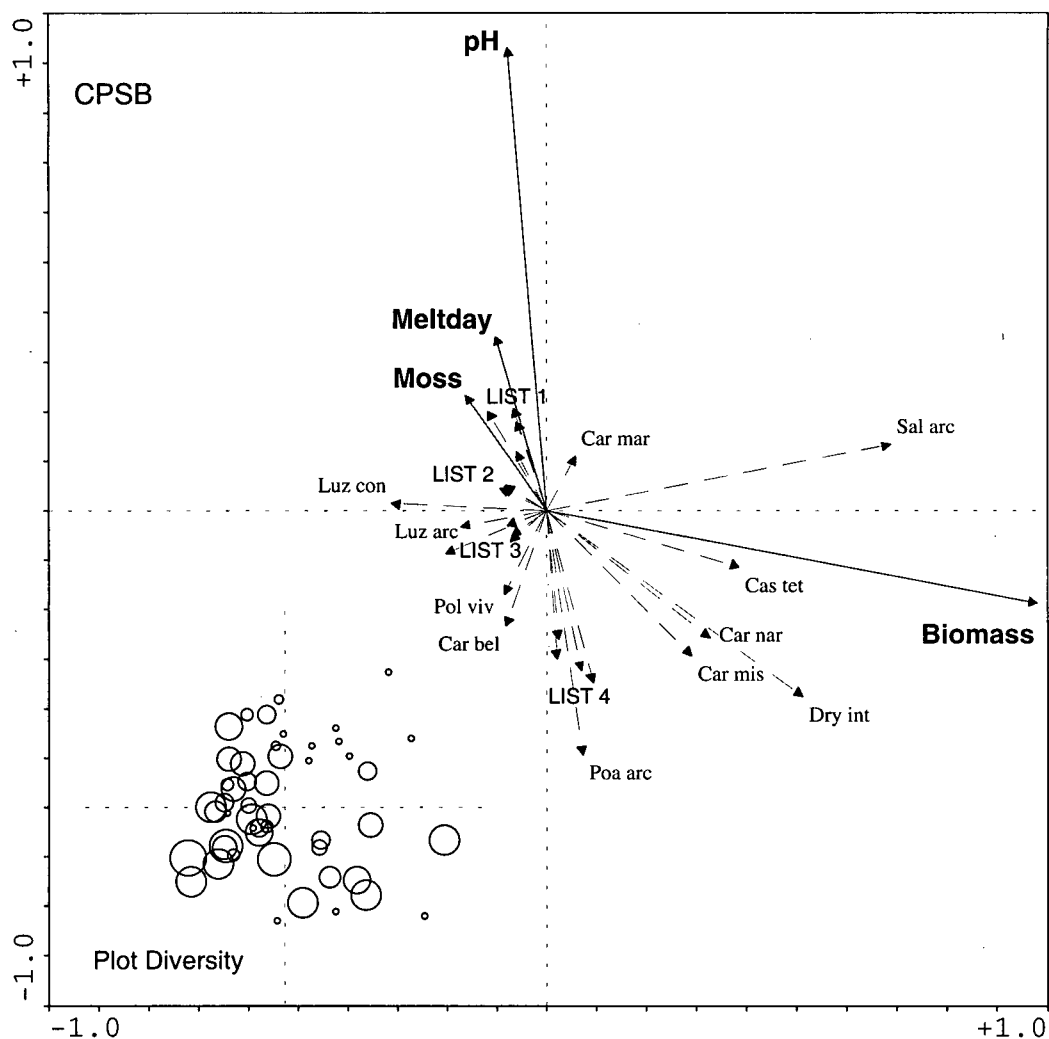


Figure 3.22. RDA biplot of the CPSB (N = 50) showing species (dashed lines) and environmental variables (solid lines). The inset diagram in the lower left has the same axes as the larger figure and shows the diversity for each plot (each circle represents a single plot and the size of the circle is directly proportional to the diversity). Species too close together to be shown are given by LIST 1 = *Carex aquatilis*, *Equisetum variegatum*, *Eriophorum angustifolium*, *Stellaria longipes*; LIST 2 = *Juncus biglumis*, *Pedicularis* species, *Saxifraga nivalis*; LIST 3 = *Carex rupestris*, *Draba* species, *Saxifraga cernua*, *Silene acaulis*; LIST 4 = *Festuca brachyphylla*, *Oxyria digyna*, *Papaver radicum*, *Saxifraga oppositifolia*. All species codes are the first 3 letters of the genus and species names for the species listed in Table 3.1. Summary ordination statistics are shown in Table 3.16.

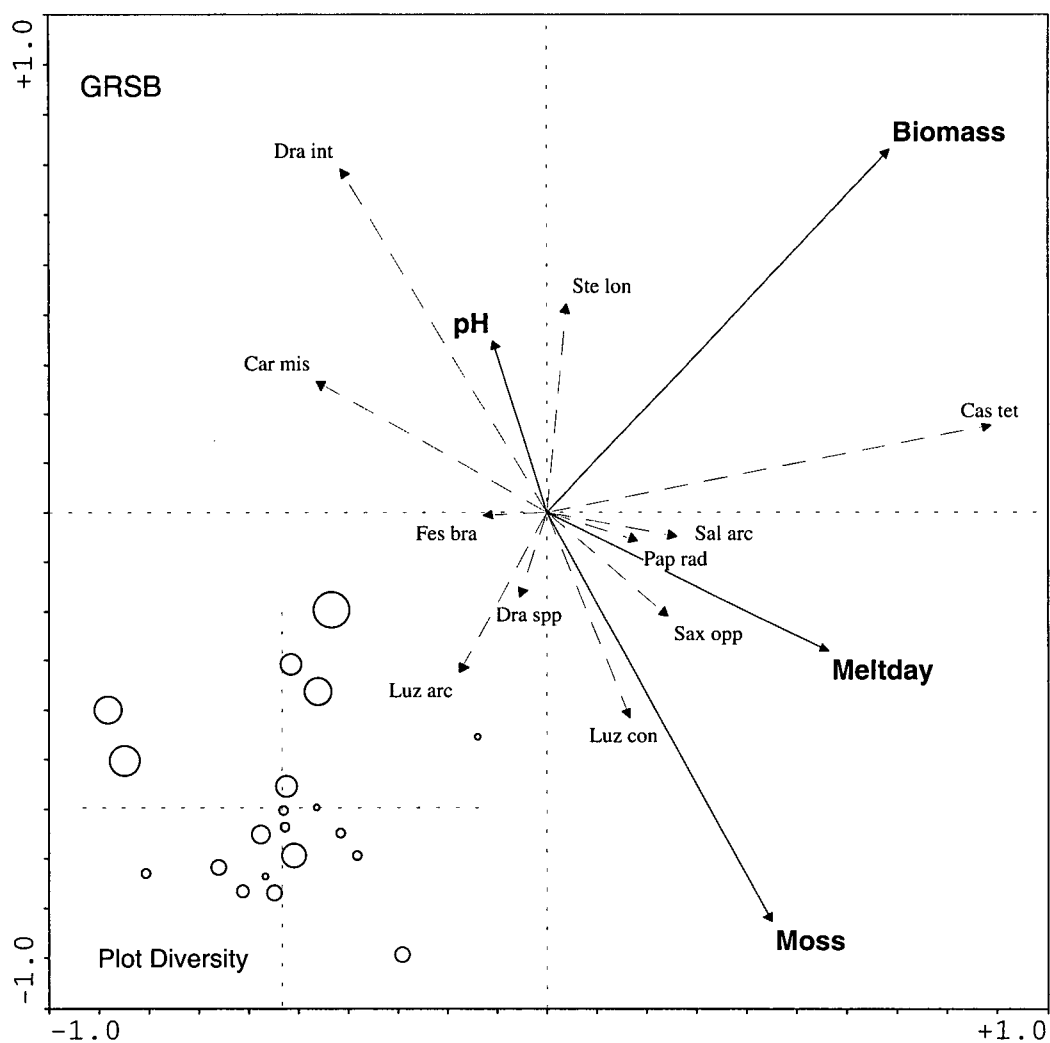


Figure 3.23. RDA biplot of the GRSB (N = 20) showing species (dashed lines) and environmental variables (solid lines). The inset diagram in the lower left has the same axes as the larger figure and shows the diversity for each plot (each circle represents a single plot and the size of the circle is directly proportional to the diversity). All species codes are the first 3 letters of the genus and species names for the species listed in Table 3.1. Summary ordination statistics are shown in Table 3.17.

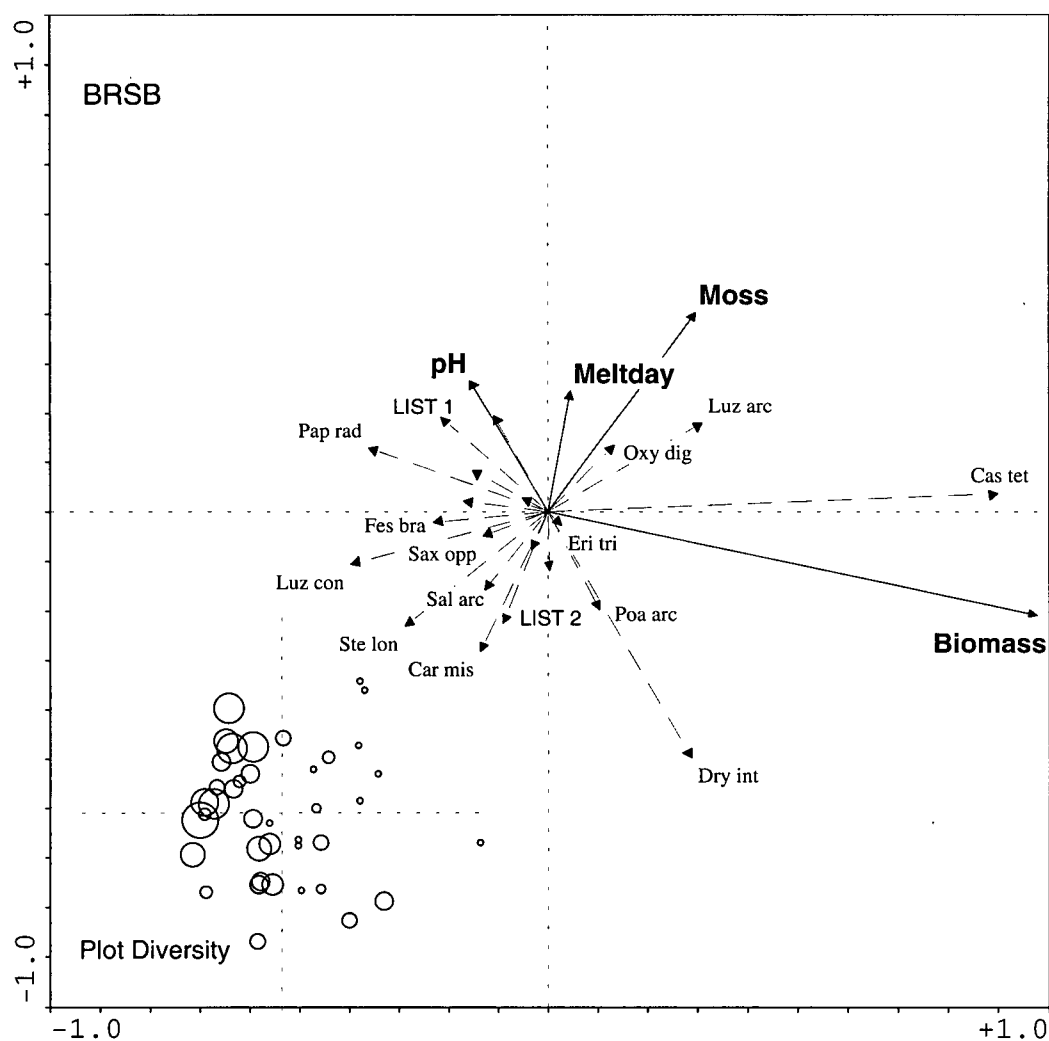


Figure 3.24. RDA biplot of the BRSB (N = 40) showing species (dashed lines) and environmental variables (solid lines). The inset diagram in the lower left has the same axes as the larger figure and shows the diversity for each plot (each circle represents a single plot and the size of the circle is directly proportional to the diversity). Species too close together to be shown are given by LIST 1 = *Cardamine bellidifolia*, *Draba* species, *Minuartia rubella*, *Pedicularis* species, *Saxifraga nivalis*, *Silene acaulis*; LIST 2 = *Arctagrostis latifolia*, *Lycopodium selago*, *Polygonum viviparum*. All species codes are the first 3 letters of the genus and species names for the species listed in Table 3.1. Summary ordination statistics are shown in Table 3.18.

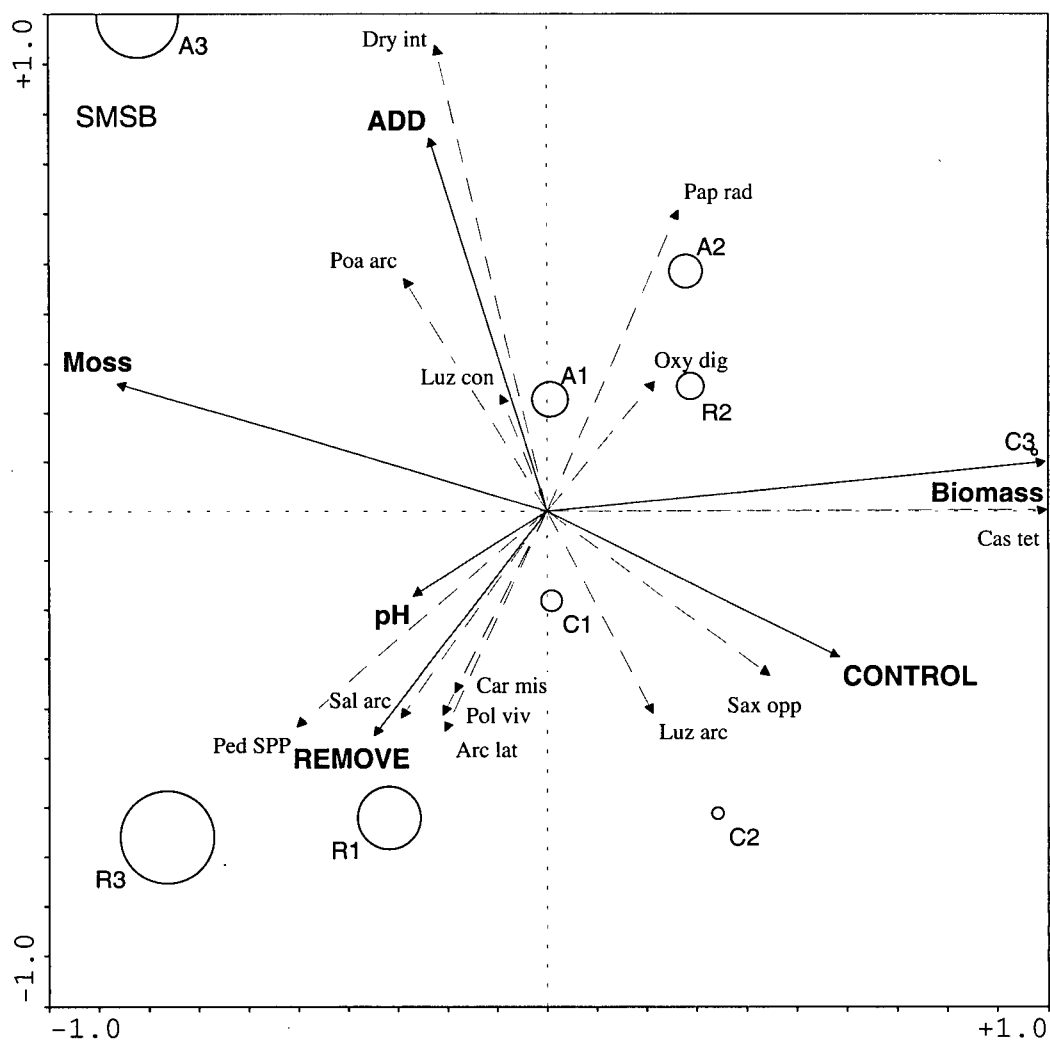


Figure 3.25. RDA triplot of the snow manipulation snowbed, SMSB (N = 9) showing species (dashed lines) and environmental variables (solid lines). The plots are shown as labeled circles and the size of each represents the diversity for each plot (the size of the circle is directly proportional to the diversity). All species codes are the first 3 letters of the genus and species names for the species listed in Table 3.1. Summary ordination statistics are shown in Table 3.19.

Table 3.15. Summary of RDA for all snowbed communities as shown in Figure 3.21. The first canonical axis was significant (F-ratio = 195.029, P = 0.0050) as were all canonical axes combined (F-ratio = 56.823, P = 0.0050). The correlations of environmental variables with each of the species axes are shown in bold if significant at  $t = 1.96$ . This critical  $t$  is indicative of the strength of the correlation (1.96 is the default value in CANOCO).

|                                  | AXIS 1        | AXIS 2        | AXIS 3       | AXIS 4        |
|----------------------------------|---------------|---------------|--------------|---------------|
| Eigenvalues                      | 0.650         | 0.018         | 0.015        | 0.000         |
| Species-environment correlations | 0.913         | 0.374         | 0.426        | 0.234         |
| Parameter: Meltday               | -0.297        | <b>0.056</b>  | <b>0.199</b> | -0.115        |
| Moss cover                       | <b>0.114</b>  | <b>0.262</b>  | <b>0.110</b> | 0.125         |
| Biomass                          | <b>0.893</b>  | -0.069        | <b>0.040</b> | <b>-0.226</b> |
| pH                               | <b>-0.494</b> | <b>-0.133</b> | <b>0.314</b> | 0.167         |

Table 3.16. Summary of RDA for the CPSB as shown in Figure 3.22. The first canonical axis was significant (F-ratio = 28.331, P = 0.0050) as were all canonical axes combined (F-ratio = 9.117, P = 0.0050). The correlations of environmental variables with each of the species axes are shown in bold if significant at  $t = 1.96$ . This critical  $t$  is indicative of the strength of the correlation (1.96 is the default value in CANOCO).

|                                  | AXIS 1        | AXIS 2       | AXIS 3       | AXIS 4 |
|----------------------------------|---------------|--------------|--------------|--------|
| Eigenvalues                      | 0.386         | 0.055        | 0.006        | 0.000  |
| Species-environment correlations | 0.883         | 0.349        | 0.474        | 0.122  |
| Parameter: Meltday               | -0.090        | 0.122        | <b>0.389</b> | -0.032 |
| Moss cover                       | -0.144        | 0.081        | -0.040       | 0.154  |
| Biomass                          | <b>0.867</b>  | -0.065       | 0.019        | -0.235 |
| pH                               | <b>-0.069</b> | <b>0.325</b> | -0.163       | 0.003  |

Table 3.17. Summary of RDA for the GRSB as shown in Figure 3.23. The first canonical axis was significant (F-ratio = 19.606, P = 0.0050) as were all canonical axes combined (F-ratio = 11.440, P = 0.0050). The correlations of environmental variables with each of the species axes are shown in bold if significant at  $t = 1.96$ . Meltday is significant with axes 1,2 and 4 if  $t = 1.65$ , which corresponds approximately to a 10% significance level. This critical  $t$  is indicative of the strength of the correlation (1.96 is the default value in CANOCO).

|                                  | AXIS 1       | AXIS 2        | AXIS 3 | AXIS 4 |
|----------------------------------|--------------|---------------|--------|--------|
| Eigenvalues                      | 0.567        | 0.186         | 0.000  | 0.000  |
| Species-environment correlations | 0.864        | 0.890         | 0.316  | 0.188  |
| Parameter: Meltday               | 0.487        | -0.249        | 0.297  | -0.341 |
| Moss cover                       | <b>0.391</b> | <b>-0.735</b> | -0.048 | -0.360 |
| Biomass                          | <b>0.590</b> | <b>0.649</b>  | 0.020  | -0.345 |
| pH                               | -0.094       | 0.311         | -0.139 | 0.241  |

Table 3.18. Summary of RDA for the BRSB as shown in Figure 3.24. The first canonical axis was significant (F-ratio = 70.034,  $P = 0.0050$ ) as were all canonical axes combined (F-ratio = 21.917,  $P = 0.0050$ ). The correlations of environmental variables with each of the species axes are shown in bold if significant at  $t = 1.96$ . This critical  $t$  is indicative of the strength of the correlation (1.96 is the default value in CANOCO).

|                                  | AXIS 1       | AXIS 2       | AXIS 3 | AXIS 4       |
|----------------------------------|--------------|--------------|--------|--------------|
| Eigenvalues                      | 0.667        | 0.048        | 0.000  | 0.000        |
| Species-environment correlations | 0.926        | 0.469        | 0.365  | 0.046        |
| Parameter: Meltday               | <b>0.043</b> | <b>0.116</b> | -0.337 | 0.022        |
| Moss cover                       | <b>0.276</b> | <b>0.189</b> | 0.291  | 0.232        |
| Biomass                          | <b>0.906</b> | -0.097       | -0.074 | <b>0.791</b> |
| pH                               | -0.146       | 0.125        | -0.155 | -0.091       |

Table 3.19. Summary of RDA for the manipulated snowbed SMSB as shown in Figure 3.25. The first canonical axis was significant (F-ratio = 142.954,  $P = 0.0050$ ) as were all canonical axes combined (F-ratio = 218.772,  $P = 0.0050$ ). The correlations of environmental variables with each of the species axes are shown in bold if significant at  $t = 1.96$ . This critical  $t$  is indicative of the strength of the correlation (1.96 is the default value in CANOCO). Note that the removal treatment is a redundant dummy variable and therefore is not included in the analysis but is still shown on the RDA triplot (Figure 3.25).

|                                  | AXIS 1        | AXIS 2        | AXIS 3        | AXIS 4 |
|----------------------------------|---------------|---------------|---------------|--------|
| Eigenvalues                      | 0.979         | 0.016         | 0.001         | 0.000  |
| Species-environment correlations | 0.999         | 0.962         | 0.969         | 0.639  |
| Parameter: Addition              | <b>-0.236</b> | <b>0.722</b>  | <b>-0.100</b> | 0.161  |
| Control                          | 0.583         | <b>-0.287</b> | <b>0.298</b>  | -0.532 |
| Removal                          | -0.348        | -0.435        | -0.197        | 0.371  |
| Moss cover                       | <b>-0.863</b> | <b>0.252</b>  | <b>-0.143</b> | 0.161  |
| Biomass                          | <b>0.994</b>  | 0.097         | <b>-0.031</b> | -0.146 |
| pH                               | -0.270        | -0.166        | <b>-0.264</b> | -0.352 |

Moss cover likely does not directly affect species abundance, but is a surrogate that probably reflects other environmental variables. Specifically, moss is related strongly to  $H_2O_{grav}$  (Pearson correlation coefficient,  $r = 0.573$ ,  $P < 0.001$ ) and is inversely related to soil temperature ( $r = -0.417$ ,  $P < 0.001$ ). When these variables were substituted in place of moss cover in the RDA of all natural snowbed plots, the overall model was still significant (sum of all canonical axes = 0.668, F-ratio = 41.842,  $P = 0.0050$ ) although the fit was not quite as good (0.683, Table 3.15). The patterns of species abundance and the relations with the axes were identical, suggesting that increasing moss likely represents a gradient of increasing soil moisture and a decrease in soil temperature.



### 3.4 DISCUSSION

Within the natural snowbeds there were no statistical trends between meltdates and any of the alpha diversity measures; however, the maximum species richness and diversity index values were in the middle range of meltdates. Given the peak in the species richness and meltdates relation and no relation between evenness and meltdates, the peaks in the  $1/\lambda$  and  $N_1$  likely reflect changes in the number of species present. Although no trends were observed in the alpha diversity measures, the number of times that the geometric model was the best fitting RAD model in the latest melting plots was higher than in the earlier melting plots. No real importance can be attributed to the predominance of the Zipf-Mandelbrot RAD model in fitting the majority of the plots. The Zipf-Mandelbrot model is usually assumed to be characteristic of early succession communities (Frontier 1985, Gray 1988, Magurran 1988) and is actually the most flexible of all the models used here, so it is to be expected to fit more often (see Wilson (1991) for the equations to the RAD models). The geometric model is usually interpreted as a niche pre-emption model, implying competition (Magurran 1988, Pastor 1995), however it is also characteristic of early succession communities and of communities with few species or of harsh environments (Bazzaz 1975, Whittaker 1965, Whittaker 1975). Since a reduction in the number of species able to survive is expected with an increase in the severity of the environment (Walker 1995), the observed patterns match theory. Decreases in species richness have been observed in alpine snowbed communities with an increase in snowcover, although these have only been qualitative statements with no statistics given (Billings and Bliss 1959, Kudo and Ito 1992, Walker et al. 1993).

Changes in the diversity in the manipulated snowbed plots were observed with a decrease in the species richness in the snow addition plot and an increase in the species richness in the removal plots, relative to the control. This was accompanied by slight and statistically significant increase ( $\alpha = 0.10$ ) in evenness in the two treatment plots versus the control. Diversity indices corresponded to these patterns with the removal having the greatest diversity, the control having the least and the addition being in the middle. The slight increase of the diversity within the addition plots must therefore be attributed to the minor increase in the evenness since there was a reduction in the species richness. No changes were observed in the best fitting RAD models.

Abundance of the functional groups differed depending on the meltdate for both the natural and snow manipulation snowbeds. Within the natural snowbeds, no changes in the deciduous and evergreen shrubs were observed, although forbs increased and graminoids decreased with an increase in meltdate. Contradictory to this, the peak performance of the forbs *Polygonum viviparum* and *Draba* species seemed to be early in the gradient of meltdate, while *Papaver radicatum* peaked in the middle of the gradient. There were no statistically significant trends in the manipulated snowbed for the deciduous shrubs, evergreen shrubs or forbs, but the removal treatment had significantly more graminoids than any other treatment. Therefore, both natural and manipulated snowbeds had proportionally more graminoids in the plots that were snow-free early in the season.

Previous researchers have also observed specific changes in species and functional groups along a snowmelt gradient. Kudo and Ito (1992) sampled alpine vegetation in Japan and found that the dominant vegetation shifted from evergreen and deciduous shrubs in early exposed plots to forbs and finally graminoids in plots that had snow cover the longest in an alpine snowbed. In the plots with the longest snow covered period, no forbs or deciduous shrubs were present (Kudo and Ito 1992). Short growing seasons have also been shown to limit the growth of *Salix herbacea* in an alpine snowbed in northern Scandinavia (Wijk 1986). Similarly, no deciduous or evergreen shrubs were found in the latest melting parts of another alpine snowbed in Wyoming (Billings and Bliss 1959). This pattern is repeated again at another alpine snowbed in Colorado with nothing but graminoids and forbs in the plots with the latest snow meltdate (Walker et al. 1994). Many of the alpine snowbeds examined by previous researchers have been entirely dominated by forbs and herbs (Billings and Bliss 1959, Galen and Stanton 1993, Galen and Stanton 1995, Stanton et al. 1994).

Patterns of diversity observed in the manipulated snowbeds were not a perfect reflection of the natural snowbed patterns. This might be attributed to the disturbance of the manipulated snowbed plots. Primary interest in the SMSB has focused on phenology measurements (G. Henry, pers.comm. 1998), and due to the large size of the plots and the large number of measurements taken every season, a significant amount of disturbance may have occurred. Corroborating evidence comes from the differences between the BRSB and SMSB in terms of increase in cover of bare ground ( $2.94 \pm 0.85$  % and  $9.00 \pm 1.42$  % respectively,  $P = 0.001$ ) and the increase in the bulk density,  $\rho_b$  ( $674.8 \pm 59.8$  kg m<sup>-3</sup> and  $954.3 \pm 99.6$  kg m<sup>-3</sup>,  $P = 0.022$ ). Note that the plots that were dissimilar to the vegetation composition in the SMSB (along the

very top of the snowbed) were excluded in this analysis. This suggests that trampling disturbance may be important in the SMSB.

The length of time to observe a response in the vegetation, as a result of the experimental treatments of snow addition and removal, could also account for the somewhat different results between the manipulated snowbed and the natural snowbeds. When the measurements were taken in 1999, 8 years had passed since the beginning of the snow manipulation experiment. Although the treatment plots did differ in composition and diversity, it is likely that not enough time had elapsed for the vegetation to reach a steady state (if it ever will), and the observed patterns likely reflect the transitional dynamics described by Tilman (1988). Another potential cause of the discrepancy in the observed patterns is that the experimental treatments may not adequately reflect natural snow regimes. The natural snowbed communities represent a gradient of growing season length, mainly due to different snowmelt dates in the early summer. Plots that melt later may also have snow earlier in the fall, which will in turn lead to an even shorter growing season, relative to plots at the extremities of the snowbed. This is not likely the case, since these snowbeds probably occur as a result of the deposition of wind-blown snow, which collects on the leeward side of slopes, as at other snowbed sites (Billings and Bliss 1959, Stanton et al. 1994, Walker et al. 1993). Even if the middle sections of the snowbeds do have an earlier onset of snow cover in the fall, this will not likely have a large effect on the vegetation, since all plants of the same species were observed to undergo senescence at approximately the same time, regardless of their position in the snowbed.

Research completed in an alpine snowbed found that a species' position in a historical snow depth gradient was a poor predictor of the species' response to manipulated snow cover (Galen and Stanton 1995). This was attributed to different processes acting on the plant at different life stages. Factors that affect species abundance and distribution such as colonization and soil features will not necessarily have the same effect as immediate changes in growing season length (Galen and Stanton 1995). Species found in extreme environments are already tolerant of the harsh conditions (Billings and Mooney 1968, Bliss 1971) and when the conditions are ameliorated, the immediate response will not necessarily be alterations in abundance by increased growth, but will be related to reproductive development (Callaghan and Jonasson 1995). Within the SMSB, changes in phenology were noticed for *Cassiope tetragona* after only the second year of the treatments (Johnstone 1995).

Numerous studies have shown that alteration of the environmental conditions in the Arctic will have effects on the plant species and the largest effect is usually observed with the addition

of fertilizer (Callaghan and Jonasson 1995, Chapin et al. 1995b, Henry et al. 1986, Robinson et al. 1998). The supply of nutrients is generally found to be the most important limiting factor for plant growth in arctic ecosystems such as high arctic semi-deserts (Robinson et al. 1998), polar oases (Henry et al. 1986) and low arctic tundra (Chapin and Shaver 1985, Chapin et al. 1995b). Even when combined with other treatments such as increased temperature or precipitation, the greater effect was due to nutrient addition (Chapin et al. 1995b, Robinson et al. 1998).

In general, forbs and graminoids are the first species to respond with increased production to alteration of the nutrient status of the soil, at least initially (Callaghan and Jonasson 1995, Chapin and Shaver 1985, Chapin et al. 1995b, Henry et al. 1986). This has been attributed to a more flexible response in altering morphological and physiological characteristics within the graminoids as compared to other species (Shaver et al. 1997). This flexible response is known as acclimation (Bazzaz 1996). Similarly, herbaceous species respond before and with a greater relative magnitude than other functional groups in response to warming treatments (Arft et al. 1999, Chapin et al. 1995b). The species with the highest potential growth rates, deciduous shrubs, may need time to alter their allocation patterns in order to take advantage of the added nutrients or longer growing season (Shaver et al. 1997). Slowest response will likely be observed in the evergreen shrubs, although if the nutrient supply rates remains constant, eventually the evergreen community may increase to the same productivity and biomass levels as communities dominated by other functional groups (Shaver et al. 1997). Results of the snow manipulation experiment presented here follow these predicted patterns.

Other environmental variables were also shown to be relevant in describing the species abundance and diversity with the natural and manipulated snowbeds. Ordination results suggest that plot biomass, pH, moss cover, and meltdate were important in describing community structure. Moss was not likely directly related to the vascular species abundance, but was more likely a surrogate for the strongly related variables soil moisture and soil temperature. However, there is the possibility that in some communities, such as polar semi-deserts, moss might compete with vascular species (Sohlberg and Bliss 1987). This was mere speculation by the authors, as was the more parsimonious explanation, that microclimatic differences, either resulting from moss cover or correlated with moss cover, were the cause of the observed patterns. These results are not surprising since soil moisture is known to be related to vegetation zonation in arctic tundra (Webber 1978) and temperature, which was negatively correlated to moss cover, is also usually related to increases in species production (Billings and Mooney 1968, Bliss 1971, Chapin et al. 1995b). Unexpectedly, the measurement of soil moisture with

the strongest relation to moss cover was  $\theta_{grav}$  ( $r = 0.574$ ,  $P < 0.0001$ ), but it had no other significant correlations to any measure of species diversity or to biomass by itself. Using multiple regression, other variables were shown to be more important in estimating diversity, meaning soil moisture was either not essential in predicting diversity or an interaction with another variable may be present. Soil pH was related to the vegetation data, as demonstrated in other studies (Gough et al. 2000, Stanton et al. 1994), likely due to its relation with nutrient availability (Hausenbuiller 1985). Plot biomass is widely reported to be related to species diversity (Abrams 1995, Al-Mufti et al. 1977, Gough et al. 1994, Tilman 1993) although the specific relation is somewhat unclear (Waide et al. 1999). This variable is also likely a surrogate of nutrient availability, but may also be related to the potential for biotic interaction. As biomass increases, the potential of competition as a factor important in structuring the community might increase (Grime 1977), although others have suggested competition may be important in unproductive environments as well (Tilman 1990). Also, there may be more facilitation in lower biomass plots, with competition becoming increasingly important as standing crop increases (Belcher et al. 1995, Bertness and Callaway 1994, Brooker and Callaghan 1998). The generality of these hypotheses is unknown, with no clear relation between biotic interaction and productivity when 296 cases from 14 studies were examined with meta-analysis (Goldberg et al. 1999).

There is a certain amount of circular reasoning to the inclusion of biomass and moss as environmental variables (Palmer 1998). Exploratory data analysis often incorporates such surrogate variables since hypothesis testing is not a specific goal. However, since the RDA model was developed with the natural snowbed communities and was applied to the manipulated snowbed afterward, and all models were strongly statistically significant, there is good evidence to suggest that this is a good set of variables in describing the communities. Dissecting the data into two datasets, a model building set and a model testing set, is common in multiple regression (Neter et al. 1985) and in cluster analysis (Romesburg 1984). Other similar methods, recently developed for use with constrained ordination, include variance partitioning or data diving with cross-validation (Hallgren et al. 1999, Økland and Eilertsen 1994).

Biomass for all natural snowbeds was the most important factor in describing the community structure. Within the manipulated snowbed, biomass was also the most important variable in the RDA ordination. Alpha diversity decreased as a simple linear function of biomass for all indices, although the fit was poor. The decrease in evenness might simply be a statistical consequence of the abundance distribution of species within communities (Drobner et

al. 1998, Weiher and Keddy 1999). Similar statements have been made of the relation between species richness and biomass because of the principles of statistical averaging (Doak et al. 1998), but this has been refuted (Tilman et al. 1998). Significant improvement in the fit of the regression models was achieved with the addition of other environmental variables. Similar problems in predicting species richness using plot biomass was observed in Louisiana wetlands leading to the conclusion that community biomass is of limited value in the prediction of species richness across a range of communities (Gough et al. 1994, Marrs et al. 1996).

The three natural snowbed communities described here have a fairly high standing crop and moderately high species richness relative to other communities in the High Arctic (Figure 3.26). The impetus for Figure 3.26 came from Waide et al. (1999) who plotted aboveground net primary productivity (ANPP) with species richness. Species richness on their figure represents the number of species within the community, not based on area. Waide et al. (1999) stated that there was a positive linear relation between species richness and ANPP and reported that  $R^2 = 0.45$  and  $P < 0.001$ . This estimate must have excluded a single high ANPP point shown on their graph with low species richness from Webber (1978). They postulated that the observed relation was because the biomass is very low and therefore light competition was not important. They further suggest that as the environment becomes more favorable, and biomass increases, more species can be found within any given area. Within the Low Arctic sites, no statistical relation was detected, which was attributed to the increase in the importance of biotic interactions (Waide et al. 1999).

When the data presented by Waide et al. (1999) was supplemented by other datasets from the High and Low Arctic other trends became apparent. Most of the data presented by Waide et al. (1999) were included in Figure 3.26, although some sources were not available. The same distinction between high and low Arctic sites (Bliss 1988), as used by Waide et al. (1999), was employed here. The primary changes in the data I present here include the addition of many High Arctic sites, including a particularly a high number of polar desert sites (Lévesque 1997), and some higher productivity sites such the snowbed communities I discussed here, as well as other communities from the Alexandra Fiord lowland (Henry et al. 1990, Nams and Freedman 1994), other sites from Devon Island (Svoboda 1977) not used by Waide et al. (1999) and some from the former USSR (Matveyeva et al. 1975). These sites were added to the data from the High Arctic presented by Waide et al. (1999) (Bliss 1977a, Bliss and Svoboda 1984, Bliss et al. 1984, Muc et al. 1994a, Muc et al. 1994b, Webber 1978). To the low arctic sites already presented by Waide et al. (1999) (Chapin et al. 1995b, Jonasson 1981, Jonasson 1982, Miller

1982, Shaver and Chapin 1991, Shaver et al. 1996), a few other datasets were added (Haag 1974, Stoner et al. 1982, Wielgolaski 1972).

Presented on Figure 3.26 are the upper limits of the scatter (solid lines) to define the maximum values of species richness found for a given ANPP or standing crop. The use of constant lines to define the edges of scatter diagrams is a fairly new addition to quantitative ecology and there definitely problems to be resolved (Guo et al. 1998, Scharf et al. 1998, Thomson et al. 1996). For this reason, and the fact that the current methods are all fairly subjective, the constraint lines on Figure 3.26 are fit by eye using a log-linear increasing function and a simple linear decreasing function. If plotted on a semi-log graph, there is a clear log-linear increase in the species richness of an area with an increase in ANPP (Figure 3.26). Similarly, the linear decreasing function (which appears curved on a semi-log graph) seems to adequately delimit the maximum of the scatter of species richness and ANPP at higher productivity sites. The decreasing line could be moved slightly to fit with only the high arctic sites by retaining the same slope and lowering the intercept value.

There exists a strong and statistically significant relation between ANPP and standing crop (Shaver et al. 1997, Shaver et al. 1996). Within the data presented in Figure 3.26 the overall relation can be described by a simple linear regression ( $R^2 = 0.69$ ,  $P < 0.0001$ ,  $N = 89$ ), although the relation was lower for the High Arctic ( $R^2 = 0.32$ ,  $P < 0.0001$ ,  $N = 65$ ) or for the Low Arctic ( $R^2 = 0.67$ ,  $P < 0.0001$ ,  $N = 24$ ) when analyzed alone. Because it is easier to find datasets with biomass data and that there exists a strong relation between ANPP and biomass, it is appropriate, and perhaps even preferable, to analyze the relation between species richness and biomass (Figure 3.26). When these data are examined, an identical relation to the one found with ANPP becomes apparent (Figure 3.26). There exists a statistically significant increasing linear relation between species richness and standing crop ( $R^2 = 0.20$ ,  $P < 0.0001$ ) or ANPP ( $R^2 = 0.26$ ,  $P < 0.0001$ ) in the High Arctic; however, there is a better fit if a second order polynomial is used to describe the relation ( $R^2 = 0.37$ ,  $P < 0.0001$  for standing crop and  $R^2 = 0.48$ ,  $P < 0.0001$  for ANPP). Waide et al. (1999) would not have observed a similar improvement in fit with the addition of a quadratic term because only one high biomass site with lower species richness was shown on their figure (which was also excluded from their regression, presumably because it was an outlier). Although there is no statistical relation in the Low Arctic, this is likely due to a lack of datasets. There simply are not many datasets from the Low Arctic that show lower productivity sites. Similarly, there are not many sites in the High Arctic that fall in the 10 to 100 g/m<sup>2</sup> range showing reasonably high species richness. These

sites likely exist, but research in the High Arctic tended to focus on either highly productive polar oases (Bliss 1977b, Svoboda and Freedman 1994) or it has focused on polar deserts (Bliss et al. 1984, Lévesque 1997). Intermediate sites have not yet been shown similar interest.

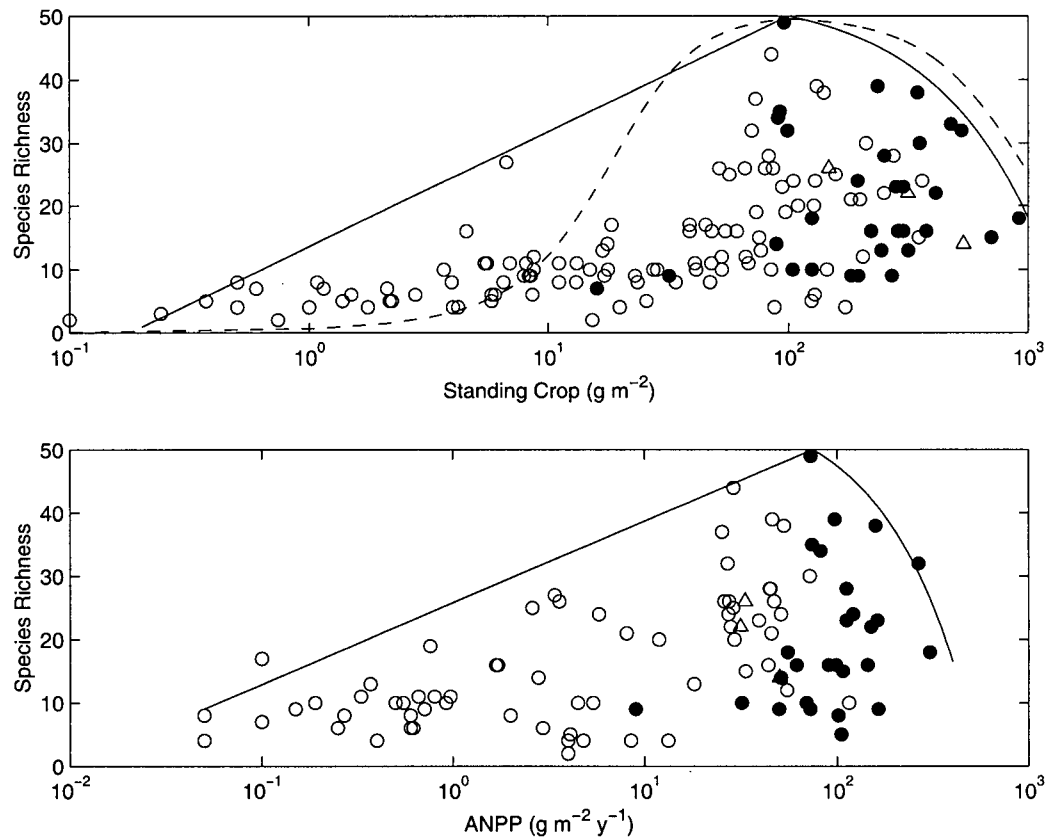


Figure 3.26. Relation between species richness and standing crop (top graph) or aboveground net primary productivity (ANPP, bottom graph). High Arctic sites are open circles, Low Arctic sites are closed circles, and the 3 snowbed communities from this study are open triangles. All data sources are listed in the text. In total, for the standing crop graph (top) there are 109 High Arctic sites and 31 Low Arctic sites and for the ANPP graph (bottom) there are 68 High Arctic sites and 27 Low Arctic sites. The dashed line represents the two equations set by Keddy and Fraser (unpublished manuscript) to describe the upper limit of species richness as a function of aboveground biomass. The solid lines set the upper limit on both graphs and are for the increasing portion a logarithmic increasing line and for the decreasing linear line. These lines are fit by eye. See text for further details.

Since there are many factors other than biomass or ANPP that affect species richness, Keddy and Fraser (unpublished manuscript) developed two equations that set upper constraint lines to species richness in herbaceous plant communities. They theorized that the maximum possible species richness in a community could be calculated from a 'collector curve' (Pielou 1977) of



the number of shoots in a quadrat. The upward constraint line is calculated from the standing crop divided by the mean individual weight to compute the number of individual shoots and from this they calculate the species richness, which asymptotically approaches the species pool, the total number of species in a given community or area. The downward constraint line (from the maximum downward) is based on the self-thinning rule for plants, a fairly controversial subject in ecology (Lonsdale 1990, Weller 1987, Weller 1991, Westoby 1984), which they use to predict the decrease in the number of individuals and the subsequent decrease in richness.

Keddy and Fraser's constraint lines are plotted on Figure 3.26 with the maximum set to the highest species richness found in any arctic community rather than the species pool. Although the limit lines set by Keddy and Fraser were originally intended for species richness (or more accurately species density when limited to a measures based on area) for quadrats of  $1 \text{ m}^2$ , it is not unreasonable to alter the lines to species richness of communities since the peak in the number of species in a pool has been shown to occur at the same standing crop per  $\text{m}^2$  as species density per  $1 \text{ m}^2$  quadrat (Wisheu and Keddy 1996). Arctic sites tend to fall under the limit lines except for values under  $20 \text{ g/m}^2$  (Figure 3.26). The upper limits were developed with a dataset based on higher standing crop, and only accurately represent communities greater than  $20 \text{ g/m}^2$  (Keddy and Fraser, unpublished manuscript). Species richness below that standing crop tends not be related to biomass and Keddy and Fraser suggest that species richness does not exceed 20 for quadrats with biomass less than  $20 \text{ g/m}^2$ . The data from the Arctic seems to fit their overall predictions, although it fits rather poorly for the lower biomass values (Figure 3.26).

Although the plot data presented in Figure 3.10 were best described using a linear regression between species richness and plot biomass and did not fit the humped-back relation as could be expected, the figure was redrawn as a semi-log graph with Keddy and Fraser's curve (Figure 3.27). The limit lines do not accurately portray the limits to the species richness per quadrat in the snowbed communities, although the diversity does appear greatest in the middle of the data scatter (Figure 3.27) as in Figure 3.26. Keddy and Fraser's descriptive model seems to fail in its prediction of very low biomass plots, where species richness can be fairly high, relative to the higher biomass plots. I am aware of only two examples from the Arctic that show the unimodal relation between species richness and biomass. One example comes from Southampton Island (Reznicek and Svoboda 1982) and the other comes from Eagle Summit, Alaska (Fox 1985), although disturbance was also important in the latter example.

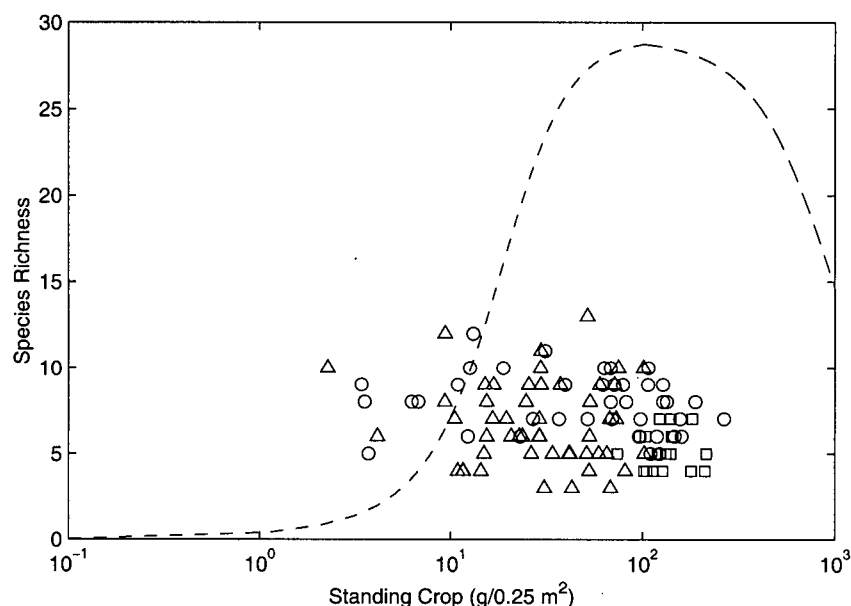


Figure 3.27. Relation between species richness (per 0.25m<sup>2</sup> plot) and the standing crop or biomass per plot (g/0.25m<sup>2</sup>). These are the same data as plotted in Figure 3.10 only this figure is plotted on a semi-log scale with the line representing the equations given by Keddy and Fraser (unpublished manuscript) to set upper bounds on species richness as a function of standing crop. The asymptote of 29 was set as the species pool (the total number of species in the entire dataset, Table 3.1). The triangles = CPSB plots, circles = BRSB, squares = GRSB.

A number of statistical issues were raised with the analyses and results presented here. Multivariate methods were important in determining the patterns of diversity within the snowbeds as a result of meltdate and biomass gradients. Specifically, RDA was employed as an exploratory data analysis method and was very useful in determining underlying environmental gradients. The constrained ordination techniques offer community ecologists a very useful series of tools in the analysis of vegetation patterns (Palmer 1993) although RDA is not one of the more commonly used methods (Jongman et al. 1995, ter Braak and Prentice 1988). Also, MANOVA proved useful in detecting changes within the functional groups. Unfortunately, multivariate methods are generally underutilized in ecology (James and McCulloch 1990), even though they are often the proper method of analysis (Scheiner 1993). Another potential problem with these techniques is that researchers use them incorrectly because they are unaware of the assumptions (Austin 1999), although this can be said of most statistical techniques.

MANOVA is useful for detecting patterns that when analyzed in separate univariate analyses are not observed (Scheiner 1993, Stroup and Stubbendieck 1983). Another alternative to multivariate analysis is to use an aggregate measure of all response variables, in the case

presented here, diversity variables (Scheiner 1993). This approach has been criticized by Scheiner (1993), although the analysis of all response variables is not always possible. My entire dataset here has 29 species and a gradient in meltdates of 31 days (from day 163 to 194) measured every other day. The 110 quadrats sampled do not offer enough degrees of freedom to do a test for all of the data unless some data are grouped together. Grouping similar species together, which may have low frequency or abundance, is the preferred method of combining data for analysis (Stroup and Stubbendieck 1983). Functional groups of species that either use resources or respond to perturbation similarly also offer a useful method of grouping species (Smith et al. 1997).

Functional groups here differed between treatments and in their response the gradients of meltdates and biomass. It must be remembered that whenever data are aggregated there is a resultant loss of information, as with diversity indices. For example, within the GRSB no significant relation was found to occur between evergreen shrub abundance and meltdates ( $R^2 = 0.024$ ,  $P = 0.513$ ). The diversity index  $N_1$  was significantly related to meltdates, indicating that there were changes in the most dominant species, evergreen shrubs. Regressions of *Cassiope tetragona* and *Dryas integrifolia* indicated the former increased with meltdates and the latter decreased, which results in a decrease in the diversity. Within the same functional group the response was very different, with each response canceling out the other in the overall biomass of the group. This is not a major criticism of the classification of the functional groups used here, because they have been used effectively here and elsewhere (Chapin et al. 1996, Shaver et al. 1997). In another example, the forbs as a group tended to increase with meltdates, but when the most common species, *Draba* species, *Papaver radicum*, *Polygonum viviparum* and *Saxifraga oppositifolia*, were examined separately in their response to meltdates, the response was either negative or nonexistent. Therefore, no pattern would have been detected if results were analyzed separately, even though there was an overall tendency for increase with meltdates.

Biomass estimation of each species' abundance within the snow manipulation plots proved to be an accurate method of estimation (Chapter 2) that did not damage the plots. This not only facilitates the continued monitoring of the snow manipulation plots, but also gives an accurate estimate of each species biomass, that can be used to compare with actual biomass data collected from natural snowbeds. Of more serious concern is the issue of pseudoreplication (Hurlbert 1984). Because the snow manipulation plots measured  $9 \text{ m}^2$ , and these are technically the experimental units, the 3 quadrats of  $0.25 \text{ m}^2$  that were sampled within each plot should be pooled to a single estimate with a estimated variance (this is multistage sampling or

“subsampling”, Krebs 1999). However, this greatly reduces the degrees of freedom available for statistical testing since there are only 3 replicate blocks of each treatment. Because the sampling unit was  $0.25 \text{ m}^2$  for both the natural and manipulated snowbeds, and because of the much larger size of the snow manipulation plots ( $9 \text{ m}^2$ ), it seems to be a reasonable violation to analyze each sample quadrat as a replicate unit (giving 27 replicates rather than just 9). Each manipulation plot was then treated as a block, in the statistical sense, such that each is another source of variation. Henry et al. (1986) used a similar approach in a fertilization study at the same site. As a whole these methods and procedures proved very effective in detecting important changes in diversity as a response to meltdate.

### 3.5 CONCLUSIONS

No statistical relation was observed between the alpha diversity measures and snow meltdate within the natural snowbed communities, but there were changes in the abundance of functional groups. However, manipulated snowbeds had significant differences in terms of diversity values and functional groups. Graminoid species had higher abundance in the earliest snow-free plots for both the natural and manipulated snowbeds. Collectively, these results suggest that climatic change resulting in an increase in growing season will alter the composition and diversity of communities in the High Arctic. Short-term responses will likely first be related to phenology and to species such as forbs and graminoids, which may be able to acclimate faster to a rapidly changing environment. This is the first experimental evidence of responses in diversity to snowmelt in the High Arctic. The response of diversity and functional group abundance within the plots to aboveground biomass was also significant, although this was not the only environmental variable important in describing the community structure. Moss cover, pH and meltdate were also important in describing the overall community structure, with biomass the most important factor. These natural snowbed communities have very high standing crop and moderately high species richness relative to other High Arctic communities. As a whole, the relation between maximum species richness and standing crop in the Arctic is best described as a logarithmic increasing curve to the maximum (approximately 50 species in a stand or community), at which point the trend becomes a linear decreasing line. Unimodal responses to biomass have been noted in more southerly (and productive) environments, but this is the first evidence that this relation may occur across the Arctic, a relatively unproductive area.

## 4. CONCLUSIONS

My results suggest that changes in the structure of plant communities are likely to occur in the Canadian High Arctic, at least in the short-term, if we assume a longer growing season due to faster snowmelt. The changes observed in the snow manipulation snowbed (SMSB) included higher estimated graminoid abundance in the plots where snow has been removed compared to both the control plots and plots where snow has been added. A slightly greater abundance of evergreen shrubs and forbs were found in the control plots relative to either manipulative treatment. This suggests that the graminoid species, and to a lesser extent the deciduous shrub, *Salix arctica*, respond favorably to snow removal whereas the other functional groups respond negatively to either an increase or decrease of snow cover. Species richness changes were also observed in the SMSB. Significantly fewer species were found in the snow addition plots relative to the snow removal plots. However, evenness increased in both the snow addition and removal plots. These changes combined to give higher diversity in the removal plots than in the control plots.

Species diversity in the natural snowbeds was not related to meltdates, although diversity seemed to peak in the middle of the snowbeds. Previous research has indicated that the distribution along a historical snowmelt gradient is a poor predictor of response to meltdates perturbations (Galen and Stanton 1995). Although alpha diversity did not follow similar patterns within natural and manipulated snowbeds in this study, functional groups did respond similarly in both types of snowbeds. The natural gradient of snowmelt had a significant increase in forb abundance and a decrease in graminoid abundance with increased meltdates, or a decreased growing season length. Therefore, both natural and manipulated snowbeds have greater graminoid abundance in the plots with the earliest snowmelt. This phenomenon is likely due to the group's faster acclimation than other groups (Shaver et al. 1997), resulting in a higher relative growth rate than other species in the changed environment. Results of my study suggest that if the GCMs are correct in the prediction that the growing season will lengthen (Maxwell 1992), increases in graminoid abundance may have significant impacts on community structure for some ecosystems in the Arctic, at least in the short-term. Future research must therefore concentrate on whether these structural changes will affect attributes of ecosystem function like productivity, nutrient pools and trophic level interactions. In the Low Arctic of Alaska,

functional groups have shown the largest changes in abundance during disturbance, such as warming and nutrient addition (Chapin and Shaver 1996, Chapin et al. 1995b, Hobbie et al. 1999). Since each species has differing functional characteristics, like nutrient use efficiencies and production rates (Chapin et al. 1996, Shaver et al. 1997), ecosystem functions like nutrient cycling and nutrient pools may be altered. In the same system, warming treatments altered functional group abundance, but species interactions buffered against significant changes in productivity and standing crop (Chapin and Shaver 1996). Similar experimental work has not yet been completed with regards to the alteration of snow regimes. Therefore, more research is necessary in order to determine the short and long term functional consequences of structural changes in arctic tundra communities due to climatic perturbations.

Continued monitoring of the snow manipulation plots is possible since no destructive harvests were completed to determine the abundance of each species. Biomass, as estimated from regression lines of total species area (TSA) and biomass from point quadrat data (Jonasson 1988), proved to be a very accurate estimate of abundance. Previous research has indicated that cover and biomass do not necessarily give the same results during analysis, especially in diversity studies (Chiarucci et al. 1999, Guo and Rundel 1997). My work presented here also shows that when diversity was calculated from estimates of abundance, such as cover or TSA, the diversity values were much higher than if biomass was used as the measure of abundance. However, if biomass was estimated from regression lines of TSA and measured biomass, there was essentially no difference between the diversity values calculated from real biomass or estimated biomass. Similar results were observed for the best fitting relative abundance distribution models. Since estimated biomass is far less destructive, is faster if many plots need to be surveyed in a relatively simple system (meaning few species) and gives essentially the same information as measured biomass data, this method provides a useful alternative to destructive harvesting. This is especially true for permanent plots where repeated measures of structural changes in the community are to be undertaken.

Though meltdate was important in determining the community structure in the natural snowbed communities, biomass was the most important environmental factor related to the patterns of diversity or the specific responses of the functional groups. A significant reduction in the diversity within a plot was related to an increase of biomass for all alpha diversity measures: species richness,  $E_{var}$ ,  $1/\lambda$  and  $N_I$ . Redundancy analysis (RDA) highlighted that biomass, soil pH, moss cover and meltdate were important in describing the structure within the

natural and manipulated communities, but biomass was once again the most important determining factor.

The reduction in diversity associated with an increase in biomass could be related to more favorable environmental conditions, such as soil nutrient status, and an increase in the potential for biological interactions, likely competition, as assumed by other researchers for the Low Arctic (Waide et al. 1999). When the three natural snowbed communities were compared to other sites in the Arctic, it became apparent that the aboveground biomass was fairly high, likely due to the favorable growing conditions of Alexandra Fiord (Freedman et al. 1994), but the species richness was found to be somewhat lower than other sites. It appeared that in the High Arctic a hump-backed relation between species richness and biomass, with a peak in richness at moderate biomass levels, best described this relation contrary to the linear increasing relation as previously proposed (Waide et al. 1999). Waide et al. (1999) stated that as biomass increased in the High Arctic it was likely due to more favorable environmental or site conditions, thus giving rise to the reported linear relation. However, they had not included any sites reporting high biomass in the High Arctic, and therefore missed the observed decrease in species richness. The reduction in richness in the Low Arctic studies was attributed to the higher probability that biological interactions may occur. A similar conclusion could be reached in the High Arctic with the inclusion of high biomass sites with low species richness such as these sites at Alexandra Fiord. Collectively, the results from the three natural communities discussed here, and from data gathered from across the Arctic, suggest that biological interactions may be important in determination of species diversity, and hence, community structure.

The results from this research at Alexandra Fiord provide the first evidence that snowmelt changes will alter the structure of arctic communities. Further research is required to investigate the functional changes that will likely accompany structural changes due to environmental change. Evidence from this study also suggests a likely role for biological interactions in structuring these communities. Ultimately, more experimental research is necessary to determine the part that species interactions play in structuring communities in these and other arctic ecosystems.

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## APPENDIX A: DIVERSITY AND EVENNESS INDICES

Whittaker (1972) described different types of diversity in terms of the scale of interest. Alpha diversity is the species diversity within a community and is composed of two components, the species richness, which is the number of species in a sample, and evenness, which is how equally the species are distributed (Pielou 1975). Most of the work on diversity focuses on alpha diversity (Magurran 1988, Pielou 1975) and the rest of this appendix is devoted to the description of this level of diversity. Gamma diversity is usually the sum of all species richness (alpha diversity) for many communities or of geographic units, and therefore has the same dimensional characteristics as alpha diversity, such as species lists or relative importance values (Whittaker 1972). Beta diversity is based on the differences between communities and therefore has a different dimensional character than alpha or gamma diversity. Beta diversity is usually represented as the ratio of gamma diversity to alpha diversity, and is usually calculated as either a similarity index between communities (Krebs 1999, Ludwig and Reynolds 1988, Whittaker 1972) or can be compared between communities with the gradient length, measured in standard deviation units (SD), of the first axis of a detrended correspondence analysis ordination for each community. This gradient length represents the rate of species turnover (Gauch and Whittaker 1972). For example, if two sites differ by greater 4 SD then they are expected to have no species in common because a species is expected to have a unimodal response curve which rises and falls over a gradient length of 4 SD (Hill and Gauch 1980, ter Braak and Prentice 1988).

### *Species richness*

The simplest determination of species richness is a count of the number of different species in a sample (Magurran 1988). Because the concept of communities as discrete units is problematic (Palmer and White 1994), it is useful to think of each quadrat as a “fully-censused piece of biotic space at a particular scale” (Smith and Wilson 1996). The total number of species in an arbitrarily designated community is the observed richness value ( $S_0$ ).  $S_0$  is a simple determination of species richness, however, it is usually an underestimate of the true species richness (Hellmann and Fowler 1999, Palmer 1990). For a sampled community (*sensu* Pielou 1975) the true total richness value can be estimated using jackknife or bootstrap procedures with simple closed form formulae, rather than by iteration, for quadrat-based data (Hellmann and Fowler 1999). The closed-form first-order jackknife estimator of species richness is

$$J_n^1(S) = S_0 + \{r_1(n-1)\}/n$$

where  $S_0$  is the total number of species found in the community,  $r_1$  is the number of species found in exactly one quadrat, and  $n$  is the number of quadrats. The second order jackknife estimator is

$$J_n^2(S) = S_0 + [\{r_1(2n-3)/n\} - \{r_1(n-2)^2\}/\{n(n-1)\}]$$

where  $r_2$  is the number of species in only two quadrats. This could be easily expanded to the  $k$ th-order jackknife (Hellmann and Fowler 1999). The closed-form bootstrap estimate of species richness is

$$B_n(S) = S_0 + \sum_{j=1}^{S_0} (1 - p_j)^n$$

where  $p_j$  is the proportion of quadrats in which species  $j$  is present.

When examining the species richness of a community, and sample size is small, the least biased estimator is the second-order jackknife, followed by the first order jackknife, the bootstrap, and the simple richness indicator (Hellmann and Fowler 1999). As the sampling effort increases the second-order jackknife and the first-order jackknife become positively biased. The simple richness estimator,  $S_0$ , is the most precise estimator, but also gives the largest underestimate of the species richness, regardless of sample size (Hellmann and Fowler 1999). Because all of these estimators are strongly positively correlated, all will yield useful and comparable information (Palmer 1990, Palmer 1991). If sampling effort between communities was not identical, comparison of the species richness (or any other measure of diversity) is problematic because all estimators are dependent on sampling effort (Hellmann and Fowler 1999). Rarefaction curves may need to be constructed so that richness can be compared for unequal sampling effort (Gotelli and Graves 1996, Ludwig and Reynolds 1988), though ideally this method should be used with data measurements based on individuals.

### ***Evenness indices***

Evenness describes the distribution of abundance among the different species in a community or a sample. Evenness indices are not used as frequently as diversity indices. Since alpha diversity is divided into species richness and evenness (Pielou 1977), logic dictates that an evenness index must be mathematically independent of species richness (Smith and Wilson 1996), although similar biological processes may be acting on each component in a similar manner, thus forcing each to be correlated. Given this simple

criterion, only 5 of 14 evenness indices tested by Smith and Wilson (1996) met the condition of independence between species richness and evenness, and only 4 of these met the 4 requirements and 10 other desirable features set by the authors. The first of these 4 indices advocated by Smith and Wilson (1996) is based on Simpson's index (Simpson 1949), which is a diversity index of dominance (see below), and is

$$E_{1/D} = \frac{1}{S(\sum_{i=1}^S p_i^2)}$$

where  $S$  is the number of species present in the sample and  $p_i$  is the proportion of species  $i$  in the sample. Another index (Camargo 1993) is

$$E' = 1 - \sum_{s1=1}^S \sum_{s2=s1+1}^S |p_{s1} - p_{s2}| / S.$$

The index developed by Smith and Wilson (1996) is

$$E_{\text{var}} = 1 - 2/\pi \arctan \left\{ \frac{\sum_{i=1}^S (\ln(n_i) - \sum_{j=1}^S \ln(n_j) / S)^2 / S}{\sum_{i=1}^S \ln(n_i)} \right\}$$

where  $\arctan$  is assumed to provide an angle in radians,  $n_i$  is the number of individuals of species  $i$  and  $n_j$  is the number of individuals of species  $j$ . This index was developed to examine the proportional differences by examining the variance over the log abundances (Smith and Wilson 1996). The final index advocated by Smith and Wilson (1996) is a modified version of a previously developed index (Nee et al. 1992), such that

$$E_q = -2/\pi \arctan(b')$$

where  $b'$  is the slope of the log abundance on the rank of abundance (the slope of the dominance diversity curve) and  $\arctan$  is assumed to provide an angle in radians.

Smith and Wilson (1996) provide clear justification for the use of the indices given above, over other indices, because these indices meet the four requirements of the authors. They also offer guidance on when each index should be used based on two other features, symmetry between minor and abundant species and Molinari shape. To be symmetric, an evenness index must give the same value for a community with many abundant species and one minor species as another community with a single abundant species and many minor species. Molinari shape refers to the response of an index to a replacement series of samples with changes in evenness. For example, a replacement series of 2 species in the following combinations of species 1 and species 2 such as 999 1, 900 100, 800 200, 700 300, 600 400 and 500 500 would have an ideal Molinari shape if the response was a convex curve (Smith

and Wilson 1996). Smith and Wilson (1996) suggest that their new index  $E_{var}$  is the preferred index and they give the following key for choosing an evenness index:

If symmetry between minor and abundant species is not important:

If a good Molinari shape is required or if the index must have a minimum of 0:  $E_{1/\lambda}$

If good mid-range behavior is needed:  $E'$

If symmetry between minor and abundant species is required:

If Molinari shape is not important:  $E_q$

If Molinari shape is important:  $E_{var}$

### ***Diversity indices***

The most commonly used diversity indices are all mathematically related (Hill 1973), and therefore, the choice of index used will make little difference to the conclusions reached if the properties of each index are taken into account in the analysis. All alpha diversity indices are a combination of the species richness and the evenness of sample (Magurran 1988), and are therefore occasionally called heterogeneity indices (Peet 1974).

The first diversity index used in ecology was Simpson's index (Simpson 1949), which represents the probability that two individuals drawn from a sample at random will be the same species (Peet 1974). Simpson's index ( $\lambda$ ) as originally formulated is

$$\lambda = \sum_{i=1}^S p_i^2$$

where  $S$  is the number of species in the sample and  $p_i$  is the proportion of species  $i$  in the sample. Pielou (1975) changed this index (now  $L$ ) for finite populations to

$$L = \sum_{i=1}^s \frac{n_i(n_i - 1)}{N(N - 1)}$$

where  $n_i$  is the number of individuals (or some measure of importance) of species  $i$  and  $N$  is the total number of individuals for all species in the sample. Because Simpson's index varies inversely with heterogeneity, it was reformulated to its more commonly used form, which increases with heterogeneity, by solving for its complement. This gives what is commonly called the Simpson diversity index  $D$  (Whittaker 1972) where

$$D = 1 - \lambda$$

or in its more statistically correct form (Pielou 1975) as

$$\tilde{D} = 1 - L$$



when adjusted for finite populations. Both  $\lambda$  and  $D$  are strongly affected by the first one, two or three species abundances (Whittaker 1972), and are therefore widely recognized as a measure of species dominance (Magurran 1988). The reciprocal of Simpson's index

$$1/\lambda = 1 / \sum_{i=1}^S p_i^2$$

is also used and for clarity should be written as  $1/\lambda$ , although it is usually and incorrectly stated as  $1/D$ . This nomenclature problem is present in the evenness index  $E_{1/D}$ , which is calculated from  $1/\lambda$ , and should be called  $E_{1/\lambda}$ . The usual interpretation of  $1/\lambda$  is the number of equally common species required to give the same value as  $\lambda$  (Peet 1974). The index  $1/\lambda$  is obviously related to  $\lambda$  and  $D$  (Figure A.1), but has statistical features that make it preferable to either  $\lambda$  or  $D$  (MacArthur 1972, Peet 1974), primarily that it is not bound between 0 and 1 like  $\lambda$  and  $D$  (Figure A.2). The index  $1/\lambda$  can range from very small numbers to the value of  $S$ , which is the number of species in the sample (Figure A.2). If evenness is perfect (equal proportions of each species and therefore diversity is higher), the  $\lambda$  index is  $1/S$ ,  $1-\lambda$  (or  $D$ ) is  $1-1/S$  and  $1/\lambda$  is  $S$  (Figure A.2), whereas if evenness is low (and dominance is high and diversity is lower)  $\lambda$  approaches 1 while both  $1-\lambda$  and  $1/\lambda$  approach 0.

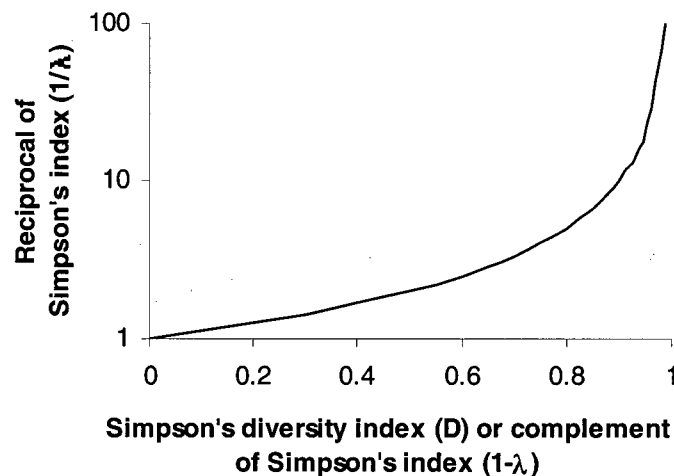


Figure A.1. The relation between the complement of Simpson's index ( $1-\lambda$ ) and the reciprocal of Simpson's index ( $1/\lambda$ ). The relation between Simpson's index ( $\lambda$ ) and the reciprocal of Simpson's index ( $1/\lambda$ ) is not shown, but would follow the same shape except it would decrease from high values of  $1/\lambda$  and low  $\lambda$  to approximately 1 for each index (the curve would be a mirror image).

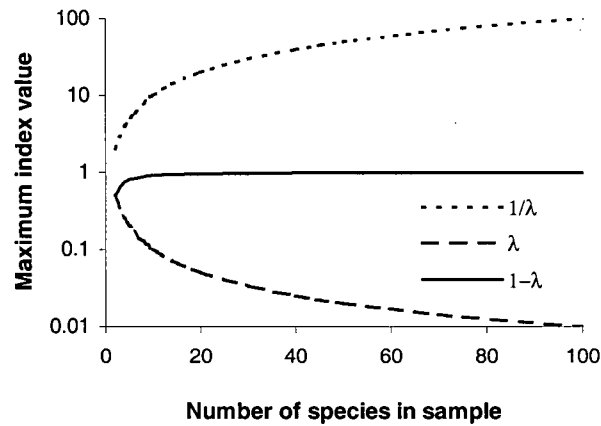


Figure A.2. The maximum index value as a function of the number of species in a sample for Simpson's index ( $\lambda$ ), the complement of Simpson's index ( $1-\lambda$ ) and the reciprocal of Simpson's index ( $1/\lambda$ ). Maximum diversity occurs when all species are equally common. Since diversity is a combination of evenness and richness, the maximum index value depends on the number of species in a sample if all species are equally common.

The other commonly used diversity index in ecology is the Shannon-Weiner diversity index, which is based on information theory (Shannon and Weaver 1949). This index is often falsely attributed to Weaver, who co-wrote the book in which it appeared, and is inappropriately called the Shannon-Weaver index, but was actually independently determined by Shannon and Wiener and therefore should be called the Shannon-Wiener index (Krebs 1994). The Shannon-Wiener index ( $H'$ ) can be determined from the equation

$$H' = \sum_{i=1}^S (p_i)(\ln p_i)$$

where the units for  $H'$  are bits of information/individual. The interpretation of this term is somewhat problematic (Magurran 1988, Peet 1974, Pielou 1975), but is related to the amount of uncertainty in the identity of a random individual drawn from a population. For example, if richness is constant, an increase in evenness will increase the uncertainty of a random individual drawn from the sample (and the diversity of sample) since dominance is decreased. If evenness is constant, an increase in the species richness will increase the uncertainty of the identity of a randomly chosen individual and therefore the diversity also increases. This index is most affected by the abundance of rare species in the sample rather than the dominant species, as in the Simpson's index  $\lambda$  and its derivatives. Because of this tendency, exclusion of rare species (possibly due to sampling) can greatly change the value of the  $H'$  index. A more easily understood index is the exponential Shannon-Wiener index

$$N_1 = e^{H'}$$

which is interpreted as the number of equally occurring species required to give the same value of  $H'$  or as the geometric mean of the proportional abundances (Hill 1973, Peet 1974). These indices are linearly related on a semi-log graph (Figure A.3), although the exponential form is a better index since it is not as narrowly bound as  $H'$  (Figure A.4). Both indices give very low values when evenness is low and when evenness is perfect approach  $\ln S$  and  $S$  for  $H'$  and  $N_1$  respectively (Figure A.4). The exponential form will also suffer from the exclusion of rare species, however, the magnitude of the change will be less in more species rich communities than with  $H'$ .

Hill (1973) demonstrated that  $1/\lambda$  and  $N_1$  are related indices which are just special cases of a more general equation of diversity such that

$$N_a = \left( \sum_{i=1}^S p_i^a \right)^{1/(1-a)}$$

where  $N_a$  is a measure of diversity and  $a$  is any number, although it is most commonly 0, 1, or 2. By substitution, any number of indices can be constructed of which the most common indices (and special cases) are  $N_0$  is the number of species in a sample,  $N_1$  is the exponential form of the Shannon-Wiener index (this is where the commonly used name comes from) and  $N_2$  is the reciprocal of the Simpson index,  $1/\lambda$  (Hill 1973). The flexibility of this equation leads to a vast number of possible indices, although Hill (1973) cautions that it is not necessary to go beyond the most common diversity indices used.

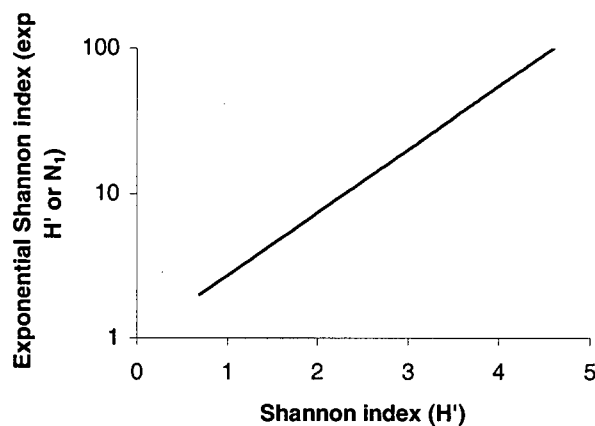


Figure A.3. The relation between Shannon index of diversity ( $H'$ ) and the exponential form of the Shannon index ( $N_1$ ).

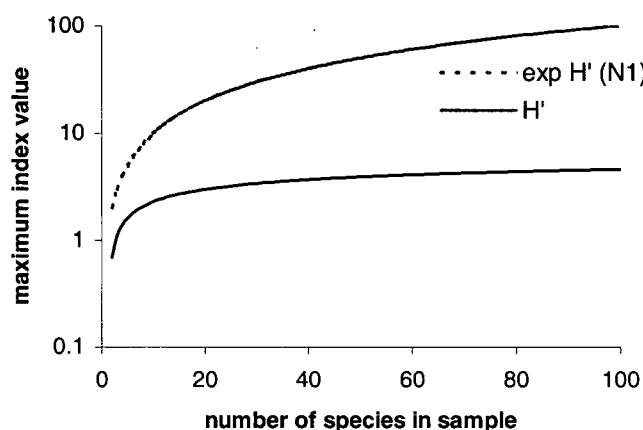


Figure A.4. The maximum index value as a function of species number for Shannon's  $H'$  and the exponential form of Shannon's index,  $N_1$ . Maximum diversity occurs when all species are equally common. Since diversity is a combination of evenness and richness, the maximum index value depends on the number of species in a sample if all species are equally common.

Diversity indices have received a great deal of criticism, with some even suggesting that the use of measures that combine richness and evenness be abandoned (Gotelli and Graves 1996). Others have stated that species diversity is a "nonconcept" (Hurlbert 1971). It has also been widely stated that even R. H. MacArthur felt the use of diversity indices should be abandoned (Gotelli and Graves 1996, Peet 1974), which is indeed an astounding reversal of opinion when it is considered that much of the early development of diversity in ecology was perpetuated by MacArthur (MacArthur 1957, MacArthur 1960, MacArthur 1965). I believe Peet (1974, p. 285) was the first to state that MacArthur (1972) felt that the term diversity had "outlived its usefulness", and from here onward this idea was perpetuated in the literature. This is simply not the case. MacArthur (1972) advocated the use of  $1/\lambda$  diversity index and stated in the introduction to an appendix on the derivation of  $1/\lambda$  that much time was wasted in the study of diversity on "polemics".

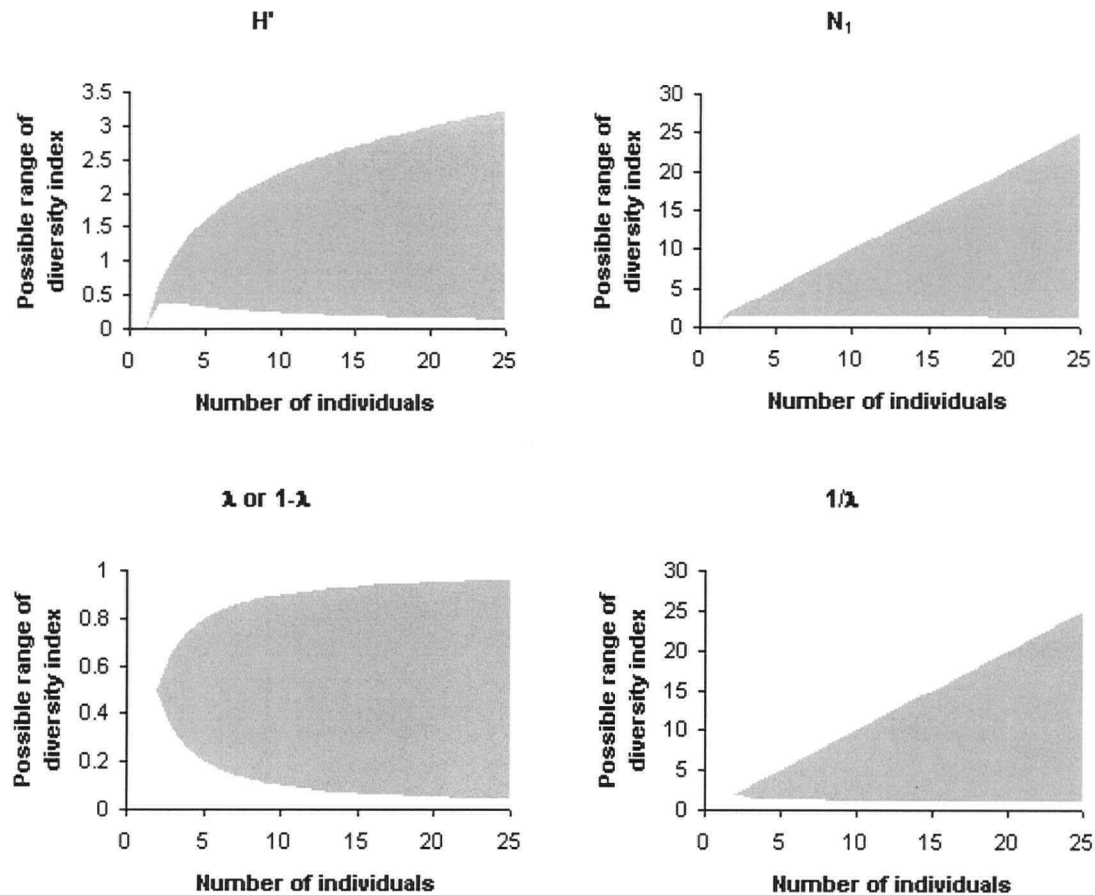


Figure A.5. The possible range of each diversity index when values are calculated from data on individuals. Maximum diversity occurs when each individual is a different species and minimum diversity occurs when all individuals, except one, belong to a single species (therefore there are only 2 species).

One other area of criticism of diversity indices relates to the narrow range of possible diversity values based on using individuals when few species are present (Figure A.5) (Austin 1999). This problem is not overly important in plant ecology, since sampling and the subsequent calculation of diversity are usually based on cover or biomass. If cover or biomass is used as the estimate of abundance, the minimum diversity values approach zero to a greater extent and the maximum values remain the same as shown in Figure A.5, since maximum diversity will occur when evenness between each species is equally abundant. Austin (1999) noted the work on bird diversity by MacArthur and co-workers (MacArthur et al. 1966) was flawed since the possible range of diversity values was very limited due to the low number of species present. This is a valid concern and the researcher must realize the limitations of combining species richness and evenness in examples such as this, where

species richness is low and individuals are used as the estimate of abundance. This can lead to serious logical constraints to interpretation (Austin 1999). If there are no changes in species richness, it may be more appropriate to use one of the useful evenness indices (Smith and Wilson 1996).

There are numerous other diversity indices available (Magurran 1988) although both Whittaker (1972) and Hill (1973) came to the conclusion that the simple and easily understood diversity indices are preferable to those that are more mathematically elaborate. The general consensus in ecology is to use one of the diversity indices based on Shannon's index or on Simpson's index (Smith and Wilson 1996) although Magurran (1988) believes that the Margalef index, the Berger-Parker index or the log-series  $\alpha$  are better indices. Whittaker (1972) stated that the most important measure of diversity is a direct measure, namely  $S$ , and some measure of the slope of the species abundance, such as  $\lambda$  or  $H'$ , should also be given. The  $1/\lambda$  index is described and supported by MacArthur (1972). Other researchers advocate the use of  $1/\lambda$  or  $N_I$  (Hill 1973, Peet 1974) with Krebs (1999) clarifying the issue by giving the advice to use  $1/\lambda$  when it is preferred to place the emphasis on the most common species and to use  $N_I$  when the emphasis is to be placed on the rare species in a sample.

Given all the concerns listed above, it must be noted that the diversity indices are correlated (Table A.1) though the use of a particular index over another can still affect the outcome of the conclusions reached. For example, in this study significant differences between the snowbeds were not always observed depending on the diversity or evenness index used and the abundance estimation method (see Table 2.3). Ultimately, the researcher must be aware of the constraints and limitations each index and justify the use of the index chosen.

Table A.1. Spearman rank correlations for the alpha diversity indices of species richness ( $S$ ), diversity and evenness for the 110 plots surveyed in Chapter 2 and 3. The diversity and evenness indices were calculated with biomass data. All correlations are statistically significant ( $P < 0.001$ ) except those that are underlined ( $P > 0.05$ ).

|                 | $\lambda$ | $1/\lambda$ | $H'$   | $N_1$  | $E'$    | $E_{var}$     | $E_{1/\lambda}$ | $E_q$          |
|-----------------|-----------|-------------|--------|--------|---------|---------------|-----------------|----------------|
| $S$             | 0.4787    | 0.4794      | 0.5539 | 0.5532 | -0.4235 | <u>0.1317</u> | -0.4285         | <u>-0.1168</u> |
| $\lambda$       |           | 1.0000      | 0.9872 | 0.9874 | 0.5200  | <u>0.1750</u> | 0.5255          | 0.2746         |
| $1/\lambda$     |           |             | 0.9873 | 0.9875 | 0.5194  | <u>0.1749</u> | 0.5248          | 0.2742         |
| $H'$            |           |             |        | 0.9999 | 0.4578  | 0.2560        | 0.4436          | 0.3054         |
| $N_1$           |           |             |        |        | 0.4582  | 0.2555        | 0.4442          | 0.3053         |
| $E'$            |           |             |        |        |         | <u>0.1723</u> | 0.9765          | 0.4570         |
| $E_{var}$       |           |             |        |        |         |               | <u>0.0499</u>   | 0.7591         |
| $E_{1/\lambda}$ |           |             |        |        |         |               |                 | 0.3460         |

## APPENDIX B: ENVIRONMENTAL VARIABLES WITHIN EACH SNOWBED

Table B.1. Mean ( $\pm$  SE) of environmental variables (Env. Var.) for the Camp Snowbed (CPSB, N = 50), Glacier River Snowbed (GRSB, N = 20), Beach Ridge Snowbed (BRSB, N = 40) and Snow Manipulation Snowbed (SMSB, N = 9) communities. Symbols are the same as described in Section 3.2.3 except for ALD (active layer depth) and Mass (total plot biomass). Some variables are not presented here because they were not measured (N/M).

| Env. Var.                      | CPSB               | GRSB               | BRSB               | SMSB               |
|--------------------------------|--------------------|--------------------|--------------------|--------------------|
| Meltdate (day of year)         | 176.80 $\pm$ 1.14  | 168.70 $\pm$ 1.03  | 172.35 $\pm$ 0.71  | 178.11 $\pm$ 1.41  |
| Rock cover (%)                 | 14.16 $\pm$ 2.86   | 0.80 $\pm$ 0.47    | 2.20 $\pm$ 0.43    | 1.22 $\pm$ 0.33    |
| Bare ground (% cover)          | 10.86 $\pm$ 1.55   | 9.35 $\pm$ 2.57    | 6.45 $\pm$ 1.33    | 9.00 $\pm$ 2.17    |
| Litter cover (%)               | 42.14 $\pm$ 2.66   | 31.85 $\pm$ 2.61   | 44.90 $\pm$ 2.88   | 43.11 $\pm$ 3.21   |
| Moss cover (%)                 | 25.38 $\pm$ 3.24   | 27.15 $\pm$ 3.45   | 24.68 $\pm$ 2.83   | 22.33 $\pm$ 3.97   |
| Lichen cover (%)               | 2.74 $\pm$ 0.57    | 17.75 $\pm$ 1.90   | 22.98 $\pm$ 2.26   | 12.22 $\pm$ 2.45   |
| <i>Peltigera</i> cover (%)     | 0.64 $\pm$ 0.26    | 0.60 $\pm$ 0.26    | 0.23 $\pm$ 0.14    | 0.33 $\pm$ 0.17    |
| Black crust cover (%)          | 1.44 $\pm$ 0.36    | 2.85 $\pm$ 0.81    | 3.93 $\pm$ 0.84    | 0.074 $\pm$ 0.07   |
| Slope (rise/run)               | 0.13 $\pm$ 0.01    | 0.21 $\pm$ 0.03    | 0.09 $\pm$ 0.01    | N/M N/M            |
| SMTV (cm <sup>2</sup> )        | 7.69 $\pm$ 1.50    | 21.78 $\pm$ 7.41   | 3.93 $\pm$ 0.52    | N/M N/M            |
| Soil temp. (°C)                | 8.25 $\pm$ 0.15    | 8.83 $\pm$ 0.64    | 6.81 $\pm$ 0.19    | 6.75 $\pm$ 0.15    |
| ALD (cm)                       | 12.76 $\pm$ 0.86   | 40.65 $\pm$ 1.34   | 42.38 $\pm$ 3.05   | 63.11 $\pm$ 1.93   |
| $\rho_b$ (kg m <sup>-3</sup> ) | 587.72 $\pm$ 29.31 | 947.13 $\pm$ 37.96 | 770.18 $\pm$ 48.24 | 954.33 $\pm$ 104.1 |
| $\theta_{\text{grav}}$ (% wt)  | 89.75 $\pm$ 14.84  | 29.86 $\pm$ 2.25   | 70.99 $\pm$ 9.53   | 47.03 $\pm$ 5.84   |
| $\theta_{\text{vol}}$ (%)      | 39.68 $\pm$ 2.63   | 27.80 $\pm$ 1.86   | 39.13 $\pm$ 2.97   | 41.12 $\pm$ 2.91   |
| $\theta_{\text{sat}}$ (%)      | 49.86 $\pm$ 2.60   | 44.07 $\pm$ 3.28   | 53.77 $\pm$ 3.40   | 67.16 $\pm$ 7.17   |
| Mass (g/0.25 m <sup>2</sup> )  | 36.79 $\pm$ 3.56   | 133.66 $\pm$ 8.44  | 75.91 $\pm$ 9.51   | 100.00 $\pm$ 13.13 |
| pH                             | 5.89 $\pm$ 0.06    | 5.05 $\pm$ 0.06    | 4.53 $\pm$ 0.03    | 4.55 $\pm$ 0.04    |



## APPENDIX C: RELATION BETWEEN MELTDATE AND DIVERSITY IN NATURAL SNOWBED COMMUNITIES

Table C.1. ANCOVA results (A) for the interaction term SNOWBED\*MELTDATE for each diversity variable to determine if it is appropriate to analyze MELTDATE separately from SNOWBED (all were non-significant) along with regression results (B) for each diversity variable with MELTDATE as the independent variable along with the corresponding ANOVA tables (C). All analyses were for the natural snowbed communities (N = 110).

### A. Separate ANCOVAs for SNOWBED\*MELTDATE for each diversity variable.

| Dependent Variable | SS    | DF | Mean Square | F ratio | Pr>F  |
|--------------------|-------|----|-------------|---------|-------|
| Species Richness   | 1.907 | 2  | 0.953       | 0.235   | 0.791 |
| $1/\lambda$        | 0.570 | 2  | 0.285       | 0.765   | 0.468 |
| $N_1$              | 0.960 | 2  | 0.480       | 0.768   | 0.467 |
| $E_{var}$          | 0.003 | 2  | 0.002       | 0.299   | 0.743 |

### B. REGRESSIONS on each diversity variable.

| MODEL                                     | R <sup>2</sup> |
|---|----------------|
| Species Richness = 1.687 + 0.030 MELTDATE | 0.009          |
| $1/\lambda$ = -0.545 + 0.013 MELTDATE     | 0.020          |
| $N_1$ = -1.186 + 0.019 MELTDATE           | 0.025          |
| $E_{var}$ = 0.133 - 0.00006 MELTDATE      | 0.000          |

### C. ANOVA for each Regression model listed in B above.

| Dependent Variable | SOURCE     | SS      | DF  | Mean Square | F ratio | Pr>F  |
|--------------------|------------|---------|-----|-------------|---------|-------|
| Species Richness   | Regression | 4.848   | 1   | 4.848       | 1.021   | 0.315 |
|                    | Residual   | 513.052 | 108 | 4.750       |         |       |
| $1/\lambda$        | Regression | 0.858   | 1   | 0.858       | 2.188   | 0.142 |
|                    | Residual   | 42.349  | 108 | 0.392       |         |       |
| $N_1$              | Regression | 1.847   | 1   | 1.847       | 2.758   | 0.100 |
|                    | Residual   | 72.311  | 108 | 0.670       |         |       |
| $E_{var}$          | Regression | 0.000   | 1   | 0.000       | 0.004   | 0.953 |
|                    | Residual   | 0.620   | 108 | 0.006       |         |       |

Table C.2. Univariate relation, by simple linear regression, of meltdat as the independent variable with diversity, species richness,  $1/\lambda$ ,  $N_1$  and  $E_{var}$ , as the dependent variable for each snowbed community determined separately. Only the relation  $N_1 = 6.586 - 0.03029 \times \text{MELTDATE}$  ( $R^2 = 0.323$ ,  $P = 0.009$ ) in the GRSB is statistically significant. For CPSB  $N = 50$ , for BRSB  $N = 40$  and for GRSB  $N = 20$ .

| Diversity Index  | CPSB  |       | GRSB  |       | BRSB  |       |
|------------------|-------|-------|-------|-------|-------|-------|
|                  | $R^2$ | P     | $R^2$ | P     | $R^2$ | P     |
| Species Richness | 0.002 | 0.769 | 0.001 | 0.703 | 0.024 | 0.337 |
| $1/\lambda$      | 0.004 | 0.663 | 0.174 | 0.068 | 0.021 | 0.367 |
| $N_1$            | 0.012 | 0.453 | 0.323 | 0.009 | 0.020 | 0.389 |
| $E_{var}$        | 0.008 | 0.548 | 0.019 | 0.562 | 0.000 | 0.683 |

# **APPENDIX D: RELATION BETWEEN MELTDATE AND FUNCTIONAL GROUPS IN NATURAL SNOWBED COMMUNITIES**

Table D.1. Univariate F tests of the effects in Model B from Table 3.5. These correspond to separate ANOVAs on each functional group (deciduous shrubs = DEC, evergreen shrubs = EVER, forbs = FORB, and graminoids = GRAM) with the model effects, SNOWBED community or MELTDATE of each plot, as the independent variables. Assuming a significance level of  $\alpha = 0.05$  the appropriate  $\alpha' = \alpha/4 = 0.0125$  for significance when using the very conservative Bonnferoni correction (Scheiner 1993). Similarly, assuming a significance level of  $\alpha = 0.10$  the appropriate  $\alpha' = 0.025$ .

## **A. Model Effect: SNOWBED**

| SOURCE | SS         | DF  | MS        | F      | P     |
|--------|------------|-----|-----------|--------|-------|
| DEC    | 9843.151   | 2   | 4921.575  | 21.806 | 0.000 |
| Error  | 23923.522  | 106 | 225.694   |        |       |
| EVER   | 174749.130 | 2   | 87374.565 | 49.384 | 0.000 |
| Error  | 187543.169 | 106 | 1769.275  |        |       |
| FORB   | 22.472     | 2   | 11.236    | 1.256  | 0.289 |
| Error  | 948.342    | 106 | 8.947     |        |       |
| GRAM   | 2.323      | 2   | 1.161     | 0.608  | 0.546 |
| Error  | 202.566    | 106 | 1.911     |        |       |

## **B. Model Effect: MELTDAY**

| SOURCE | SS         | DF  | MS       | F     | P     |
|--------|------------|-----|----------|-------|-------|
| DEC    | 0.028      | 1   | 0.028    | 0.000 | 0.991 |
| Error  | 23923.522  | 106 | 225.694  |       |       |
| EVER   | 225.239    | 1   | 225.239  | 0.127 | 0.722 |
| Error  | 187543.169 | 106 | 1769.275 |       |       |
| FORB   | 76.723     | 1   | 76.723   | 8.576 | 0.004 |
| Error  | 948.342    | 106 | 8.947    |       |       |
| GRAM   | 8.060      | 1   | 8.060    | 4.218 | 0.042 |
| Error  | 202.566    | 106 | 1.911    |       |       |

## APPENDIX E: RELATION BETWEEN BIOMASS AND DIVERSITY IN NATURAL SNOWBED COMMUNITIES

Table E.1. ANCOVA results (A) for the interaction term SNOWBED\*BIOMASS for each diversity variable to determine if it is appropriate to analyze BIOMASS separately from SNOWBED (all were non-significant) along with regression results (B) for each diversity variable with BIOMASS as the independent variable along with the corresponding ANOVA tables (C). All analyses were for the natural snowbed communities (N = 110). The regressions in B were all statistically significant and are presented in Figure 3.10.

### A. Separate ANCOVAs for SNOWBED\*BIOMASS for each diversity variable.

| Dependent Variable | SS    | DF | Mean Square | F ratio | Pr>F  |
|--------------------|-------|----|-------------|---------|-------|
| Species Richness   | 1.747 | 2  | 0.873       | 0.219   | 0.804 |
| $1/\lambda$        | 1.593 | 2  | 0.796       | 2.496   | 0.087 |
| $N_1$              | 2.449 | 2  | 1.224       | 2.400   | 0.096 |
| $E_{var}$          | 0.000 | 2  | 0.000       | 0.042   | 0.959 |

### B. REGRESSIONS on each diversity variable.

| MODEL                                    | R <sup>2</sup> |
|--|----------------|
| Species Richness = 7.497 - 0.009 BIOMASS | 0.049          |
| $1/\lambda$ = 1.971 - 0.005 BIOMASS      | 0.172          |
| $N_1$ = 2.498 - 0.007 BIOMASS            | 0.209          |
| $E_{var}$ = 0.145 - 0.0003 BIOMASS       | 0.061          |

### C. ANOVA for each Regression model list in B above.

| Dependent Variable | SOURCE     | SS      | DF  | Mean Square | F ratio | Pr>F  |
|--------------------|------------|---------|-----|-------------|---------|-------|
| Species Richness   | Regression | 25.455  | 1   | 25.455      | 5.583   | 0.020 |
|                    | Residual   | 492.445 | 108 | 4.560       |         |       |
| $1/\lambda$        | Regression | 7.432   | 1   | 7.432       | 22.434  | 0.000 |
|                    | Residual   | 35.775  | 108 | 0.331       |         |       |
| $N_1$              | Regression | 15.529  | 1   | 15.529      | 28.605  | 0.000 |
|                    | Residual   | 58.629  | 108 | 0.543       |         |       |
| $E_{var}$          | Regression | 0.038   | 1   | 0.038       | 7.054   | 0.009 |
|                    | Residual   | 0.582   | 108 | 0.005       |         |       |

Table E.2. Univariate relation, by simple linear regression, of biomass as the independent variable with diversity, species richness,  $1/\lambda$ ,  $N_1$  and  $E_{var}$ , as the dependent variable for each snowbed community determined separately. Statistically significant relations ( $\alpha = 0.05$ ) include for GRSB:  $E_{var} = 0.188 - 0.001 \text{ BIOMASS}$  and for BRSB:  $1/\lambda = 2.216 - 0.006 \text{ BIOMASS}$ ,  $N_1 = 2.885 - 0.090 \text{ BIOMASS}$  and  $E_{var} = 0.201 - 0.001 \text{ BIOMASS}$ . Statistically significant relations ( $\alpha = 0.10$ ) include for CPSB:  $N_1 = 2.411 - 0.089 \text{ BIOMASS}$  and for BRSB:  $\text{SPP RICH} = 8.498 - 0.008 \text{ BIOMASS}$ .

| Diversity Index  | CPSB  |       | GRSB  |       | BRSB  |       |
|------------------|-------|-------|-------|-------|-------|-------|
|                  | $R^2$ | P     | $R^2$ | P     | $R^2$ | P     |
| Species Richness | 0.000 | 0.879 | 0.001 | 0.859 | 0.083 | 0.072 |
| $1/\lambda$      | 0.033 | 0.205 | 0.112 | 0.150 | 0.285 | 0.000 |
| $N_1$            | 0.059 | 0.089 | 0.045 | 0.367 | 0.354 | 0.000 |
| $E_{var}$        | 0.034 | 0.197 | 0.257 | 0.022 | 0.255 | 0.001 |

## APPENDIX F: RELATION BETWEEN BIOMASS AND FUNCTIONAL GROUPS IN NATURAL SNOWBED COMMUNITIES

Table F.1. MANOVA results for the test of functional groups with the independent variables SNOWBED, BIOMASS, and SNOWBED\*BIOMASS. Two MANOVA tests are given because test results were not consistent. Pillai's trace is more robust to violation of MANOVA assumptions and Roy's Max Root has the best power (Wilkinson et al. 1992).

| SOURCE and TEST   | VALUE     | F         | NUM DF | DEN DF | Pr > F |
|-------------------|-----------|-----------|--------|--------|--------|
| SNOWBED           |           |           |        |        |        |
| Pillai's Trace    | 0.086     | 1.141     | 8      | 204    | 0.337  |
| Roy's Max Root    | 0.091     | 2.314     | 4      | 102    | 0.063  |
| BIOMASS           |           |           |        |        |        |
| Pillai's Trace    | 1.000     | 7988213.1 | 4      | 101    | <.001  |
| Roy's Max Root    | 316364.88 | 7988213.1 | 4      | 101    | <.001  |
| SNOWBED * BIOMASS |           |           |        |        |        |
| Pillai's Trace    | 0.592     | 10.730    | 8      | 204    | <.001  |
| Roy's Max Root    | 1.336     | 34.069    | 4      | 102    | <.001  |

Table F.2. Separate MANOVA results for each snowbed community with functional groups as the response variable and biomass as the independent variable. Roy's Max Root is the test statistic presented here, although the P values were identical for all multivariate test statistics. For CPSB N = 50, for BRSB N = 40 and for GRSM N = 20.

| COMMUNITY | VALUE   | F        | NUM DF | DEN DF | Pr > F |
|-----------|---------|----------|--------|--------|--------|
| CPSB      | 99895   | 1123824  | 4      | 45     | <.0001 |
| BRSB      | 2401060 | 21009273 | 4      | 35     | <.0001 |
| GRSM      | 53.5    | 200      | 4      | 15     | <.0001 |

Table F.3. Least-squares regression of the abundance of each functional group (Y, g/0.25 m<sup>2</sup>) and total plot biomass (X, g/0.25 m<sup>2</sup>). The regression lines for the GRSB use Box-Cox transforms of the predicted variable, which were also used in the MANOVA in Table F.2, such that for deciduous shrubs,  $\lambda = -0.123$ , evergreen shrubs  $\lambda = 0.079$ , forbs  $\lambda = -0.579$  and graminoids  $\lambda = -0.826$ . These lines are shown on Figure 3.11 for deciduous and evergreen shrubs and on Figure 3.12 for forbs and graminoids.

| FUNCTIONAL<br>GROUP | CPSB<br>(N = 50)   | BRSB<br>(N = 40)   | GRSB<br>(N = 20)  |
|---------------------|--|--|---|
| Deciduous shrubs    | Y = 3.575 + 0.559 X,<br>R <sup>2</sup> = 0.421, P = <.001  | Y = 4.552 - 0.007 X,<br>R <sup>2</sup> = 0.008, P = 0.576  | Y = 0.539 + 0.002 X,<br>R <sup>2</sup> = 0.020, P = 0.550 |
| Evergreen shrubs    | Y = -5.897 + 0.410 X,<br>R <sup>2</sup> = 0.343, P = <.001 | Y = -7.518 + 1.011 X,<br>R <sup>2</sup> = 0.994, P = <.001 | Y = 4.442 + 0.011 X,<br>R <sup>2</sup> = 0.980, P = <.001 |
| Forbs               | Y = 2.041 + 0.013 X,<br>R <sup>2</sup> = 0.006, P = 0.580  | Y = 1.717 - 0.005 X,<br>R <sup>2</sup> = 0.032, P = 0.270  | Y = 0.466 + 0.001 X,<br>R <sup>2</sup> = 0.008, P = 0.707 |
| Graminoids          | Y = 0.269 + 0.018 X,<br>R <sup>2</sup> = 0.076, P = 0.053  | Y = 1.250 + 0.0004 X,<br>R <sup>2</sup> = 0.000, P = 0.896 | Y = 0.903 - 0.004 X,<br>R <sup>2</sup> = 0.231, P = 0.032 |