AN ABSTRACT OF THE THESIS OF

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Dr. Bruce P. McCune

The goal of this thesis is to develop a better understanding of the ecology of the vascular and nonvascular vegetation in the caldera of Mt. Aniakchak, Alaska by identifying important environmental gradients and examining the distribution of plant communities in relationship to them. A three-step approach was taken: (1) prior to examining vegetation patterns, it was necessary to determine whether the vascular and nonvascular strata exhibited a strong enough correlation with one another to be combined for overall analysis. Separate ordinations showed that both strata responded to the same primary gradient (proximity to water). Regression of Axis 1 vascular and nonvascular ordination scores against one another revealed a strong correlation between the strata (r^2=0.77). A similar analysis, performed on Axis 2 scores, indicated that the strata were unrelated to one another along the secondary gradient (r^2=0.01) because the vascular stratum responded to slope (r^2=0.34), while the nonvascular stratum did not. The importance of slope to the vascular stratum may reflect the role of steep slopes in sloughing ash, thereby enhancing survivorship of relict vascular plant species after an eruption in 1931. The absence of a similar slope-response in the nonvascular stratum may be due to the ability of nonvascular plants to quickly recolonize disturbed areas, whether flat or sloping. Thus the different secondary gradients exhibited by the strata may reflect disturbance colonization in the caldera.

(2) Based on the strength of correlation observed between strata relative to the primary environmental gradient, data from both strata were combined into a single data set and analyzed collectively to detect vegetation patterns with respect to environmental gradients. Nonmetric multidimensional scaling ordination revealed proximity to water as the primary environmental gradient. Communities were related to presence of rock (i.e. basalt outcrops, lava fields) as the secondary gradient, and to steepness of slope as the tertiary. Seven vegetation groups were identified with cluster analysis. Discriminant analysis was then used to identify the distinguishing ecological factors and characteristic species associated with each group. The abundance of nitrogen fixing taxa, which accounted for 73% of the total lichen cover, was discussed with regard to their potential role as facilitators of primary succession. A list of 343 vascular and nonvascular species is presented.

(3) The extent to which vegetation layers are correlated with one another has been the subject of much debate. The Aniakchak data set was used to show that the strength of correlation observed between strata is dependent in part on the scale at which the observations are made. This was demonstrated by subdividing the data set into progressively more homogeneous units, recalculating correlations (r^2), and plotting strength of correlation as a function of scale. These analyses underscored the importance of carefully considering the scale (heterogeneity) at which a study was conducted when making comparisons among results.

Vascular and Nonvascular Vegetation of the Caldera of Mt. Aniakchak, Alaska

by

Linda M. Hasselbach

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Linda M. Hasselbach, Author

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Finally, while this thesis is all about the 'science' of Aniakchak, I cannot close without acknowledging the power of that strange and wild place. We are fortunate as a society to be able to set aside such places in recognition of their intrinsic value, and I am fortunate to have had the opportunity to experience the beauty of such an incredible place.

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Chapter I. Introduction

Situated on the central Alaska Peninsula, midway between the Pacific Ocean and the Bering Sea, Mt. Aniakchak is one of a long chain of volcanoes forming the backbone of the Aleutian Range. First "discovered" in 1922, the 35 km^2 caldera of Mt. Aniakchak was believed to be one of the largest in the world. Father Bernard Hubbard, then head of the Geology Department at Santa Clara University, launched an exploratory trek into the area in 1930. Upon reaching Aniakchak caldera he discovered a "wonderland" of which he wrote enthusiastically: "The amount and variety of life astonished us... the fish, game, and bird life was even surpassed by the variety and profusion of flowers, particularly orchids..." (Hubbard 1931, p. 332). It was during this expedition that Hubbard began to suspect that Mt. Aniakchak was not a dead volcano as commonly assumed, but active to the point of imminent eruption. The proof came on May 1, 1931 when Aniakchak erupted through a side vent in the caldera floor. The eruption lasted 10 days, sending a continuous stream of gases, pumice, rocks and ash into the air.

> The earth shook, flame and smoke rose thousands of feet high, and the pyrotechnic display of individual lava bombs hurtling through the air combined with the lightening forming in the clouds to make a truly fear-inspiring sight. Thunder added its din to the almost constant explosions of the erupting volcano, and the sides of the mountain reverberated to the crash of falling rocks (Hubbard 1932, p. 56).

Sixty miles to the south, at Chignik, the volume of ashfall was estimated as "a pound per hour to the square foot" (Hubbard 1932). Ashfall was even heavier to the north. On Kodiak Island, Katmai National Monument and points more than 250 km distant, a centimeter of ash covered everything (Hubbard 1932). Within the caldera, ash accumulated to depths of 60 cm (Hubbard 1932).

Hubbard returned to Aniakchak caldera in the weeks following the eruption and wrote:

> There was a new Aniakchak, but it was the abomination of desolation, it was the prelude of hell. Black walls, black floor, black water, deep black holes and black vents...no streams coarsed through flower strewn meadows, no grassy slopes led up to former volcanic vents; no glistening glaciers or snowfields broke the monotony of huge crater walls... Beautiful Surprise Lake, nestled under the northern rim, was choked and muddy and black were its shores, and filled its coves... (Hubbard 1932, p. 61).

Obviously a disturbance of this magnitude would be expected to have a profound impact on plant communities within the caldera. Direct references to vegetation effects are scarce in Hubbard's documents, limited to passing comments such as: "we were going through a valley of death in which not a blade of grass or a flower or a bunch of moss broke through the thick covering of deposited ash..." (Hubbard 1932, p. 60).

No further biological investigation occurred until a 1967 reconnaissance that recognized the flora as being "of great interest to botany" (Alaska Search 1967) and resulted in the nomination of Aniakchak caldera as a National Natural Landmark (NNL). Aniakchak was incorporated into the National Park Service in 1978. In 1992 and 1993, with the assistance of funding from the NNL program, a study of the vegetation was undertaken, the goal of which was to better understand the ecology of the vascular and nonvascular vegetation of Aniakchak caldera as it currently existed, 63 years after the eruption.

The inclusion of nonvascular plants in this study is noteworthy. Too often nonvascular plants are excluded from such endeavors due to their small stature and the taxonomic difficulty associated with their identification. Yet in Aniakchak caldera, as in many arctic, subarctic and alpine habitats, nonvascular plants are extremely important in terms of ecosystem functioning (see Chapter III). Furthermore, from a floristic standpoint, the inclusion of nonvascular plants in this study fills a void in the existing knowledge of species distribution on the Alaska Peninsula.

Two vegetation strata (or layers) are easily recognized in Aniakchak caldera. The nonvascular strata ranges in height from 1 to 6 cm and is typically appressed to the substrate. It is composed of a variety of moss, liverwort and lichen species. The vascular strata, which seldom exceeds 60 cm in height, consists of a variety of herbs and dwarf willow species. In designing this study, a decision as to how to incorporate the nonvascular strata into the analyses had to be made. This decision was complicated by the fact that it was not known whether the vegetation layers in Aniakchak were correlated to one another, or not. If the composition of one layer (e.g. nonvascular) could be predicted based on the composition of another layer (e.g. vascular), then the layers are said to be "correlated", and could be combined for subsequent analyses. However, if the vascular strata responds to different factors than the nonvascular strata, or if the strata are structured differently in some other way, then the layers are "uncorrelated", and would have to be described separately. This study was designed to first resolve the issue of correlation among layers in Aniakchak, and then let these results guide the subsequent analysis strategy. The resulting document is divided into two complimentary chapters, which are presented in manuscript form:

I. *Correlation between vascular and nonvascular strata in Aniakchak caldera, Alaska with emphasis on the importance of scale.*

Objectives:

1. to determine the strength of the correlation between the vascular and nonvascular strata in Aniakchak caldera, Alaska; and

2. to determine whether the strength of correlation observed between strata is dependent in part on the scale at which the observations are made.

II. *Patterns of vascular and nonvascular vegetation with respect to environmental gradients in Aniakchak caldera, Alaska.*

Objectives:

1. to describe the vegetation of Aniakchak caldera by identifying major vegetation groups and their component species;

2. to determine the environmental factors most important in the separation of the vegetation groups; and

3. to identify important environmental gradients and examine the distribution of plant communities to them.

A total of 343 species were documented in Aniakchak as a result of this study. Of these, 302 species (including 164 vascular and 138 nonvascular species) were encountered on the sample plots. Raw data, in compact format (McCune 1992), are presented in Appendices IV and V.

The decision to organize this thesis into manuscripts had the effect of generating a certain amount of redundancy in this document. The reader should keep in mind that the following chapters are constructed to ultimately stand alone as publishable manuscripts and are artificially combined in this document to fulfill university thesis requirements.

Chapter II. Correlation Between Vascular and Nonvascular Strata in Aniakchak caldera, Alaska with Emphasis on the Importance of Scale

ABSTRACT

The extent to which vegetation strata (e.g. bryophyte, shrub, herb) are correlated to one another has been the subject of much debate. In Aniakchak caldera, separate ordinations showed that both vascular and nonvascular strata responded to the same primary environmental gradient (proximity to water). Regression of Axis 1 vascular and nonvascular ordination scores against one another revealed a strong correlation between the strata (r^2=0.77). A similar analysis, performed on Axis 2 scores, showed that the strata were not correlated with one another along the secondary gradient because the vascular stratum responded to steepness of slope, while the nonvascular stratum did not. The importance of slope to the vascular stratum may reflect the role of steep slopes in sloughing ash, thereby enhancing survivorship of relict vascular plant species after an eruption in 1931. The absence of a similar slope-response in the nonvascular stratum may be due to the ability of nonvascular plants to quickly recolonize disturbed areas, whether flat or sloping. Thus the different secondary gradients exhibited by the strata may reflect disturbance colonization in the caldera.

The strength of correlation observed between strata is dependent in part on the scale at which the observations are made. This was demonstrated by subdividing the Aniakchak data set into progressively more homogeneous units, recalculating correlation (r^2), and plotting strength of correlation as a function of scale. In one analysis average dissimilarity (distance in species space) was the measure of scale. In another analysis beta diversity was the measure of scale. Both analyses revealed that correlation between strata increased as the scale (heterogeneity) of the data set increased.

INTRODUCTION

The extent to which vegetation strata (e.g. bryophyte, herb, shrub) are correlated with one another has long been debated among ecologists. Several early workers argued that the strata were independent (DuRietz 1930, Lippmaa 1933, Cain 1936) based on subjective observation. More recently, quantitative research on the relationship between strata has yielded conflicting results, some suggesting that correlation between strata is weak (McCune & Antos 1981a, Herben 1987, Rogers 1987) and others maintaining that strata, particularly adjacent ones, are indeed correlated (delMoral & Watson 1978, Roberts & Christensen 1988, Host & Pregitzer 1992). There are many potential explanations for this disagreement among researchers. Assessing the validity of the arguments for and against correlation among strata is further complicated by the multiplicity of methods that have been used to approach the problem.

In an effort to clarify the issue of correlation between vegetation layers we divided the relevant questions into two categories: (1) those questions that are "unanswerable," or extremely difficult to substantiate given practical limitations; and (2) those questions that are both "answerable" and useful in an applied way. "Unanswerable" questions tend to concern causation or mechanistic aspects such as: "Why are (or are not) the layers correlated? Do they simply respond directly to the same gradient or do species interactions drive the correlation?" Attempts to address such questions using non-manipulative, non-experimental approaches can only be expected to generate hypotheses. On the other hand, even if experiments establish a causative factor in one circumstance, it is unlikely that this factor will be generally applicable to other systems. "Answerable" questions consider such aspects as "To what extent are vegetation layers correlated with one another?" They are answerable because correlations can be calculated, and they are useful for management or classification purposes. For example, quite often sampling is restricted to selected layers (e.g. tree or herb) with the assumption that other layers (e.g. bryophyte) are correlated with them. Whether or not this assumption is valid is what we address as a useful and answerable question in this paper.

One potential cause of apparent differences in the strength of correlation is, however, testable because we can manipulate it after-the-fact by partitioning data sets. The strength of correlation observed may be dependent in part on the scale at which the observations were made (McCune & Antos 1981a; Hermy 1988). "Scale" as used here refers not to spatial scale, but rather to the spread of sampling points in species space, where each dimension of the space represents abundance of a particular species. Since increasing scale also implies increasing environmental heterogeneity, and since beta diversity (ß) is a measure of heterogeneity, the argument can be restated to suggest that as the ß of a sample increases, so should the correlation between vegetative layers. Proposed by McCune and Antos (1981a) as a possible reconciliation of their results with those of delMoral and Watson (1978), the idea of scale dependence has been discussed, and at times misunderstood, by other researchers. Some have argued against scale-dependence as though it were proposed as the main or overriding factor (Roberts & Christensen 1988); others have agreed in theory (Bee et. al 1989; Hermy 1988). Hermy (1988) addressed this when he compared stratal relationships of deciduous forests along a gradient from temporarily flooded to dry sandy soils (high ß) with a subset of more homogeneous riverine plots (low ß) and concluded that indeed "correspondence between compositional patterns in different layers increases with beta diversity" (p. 77).

The objectives of this paper were: (1) to determine the strength of the correlation between vascular and nonvascular strata in Aniakchak caldera, Alaska; and (2) to determine whether the strength of correlation observed between strata is dependent in part on the scale at which the observations are made.

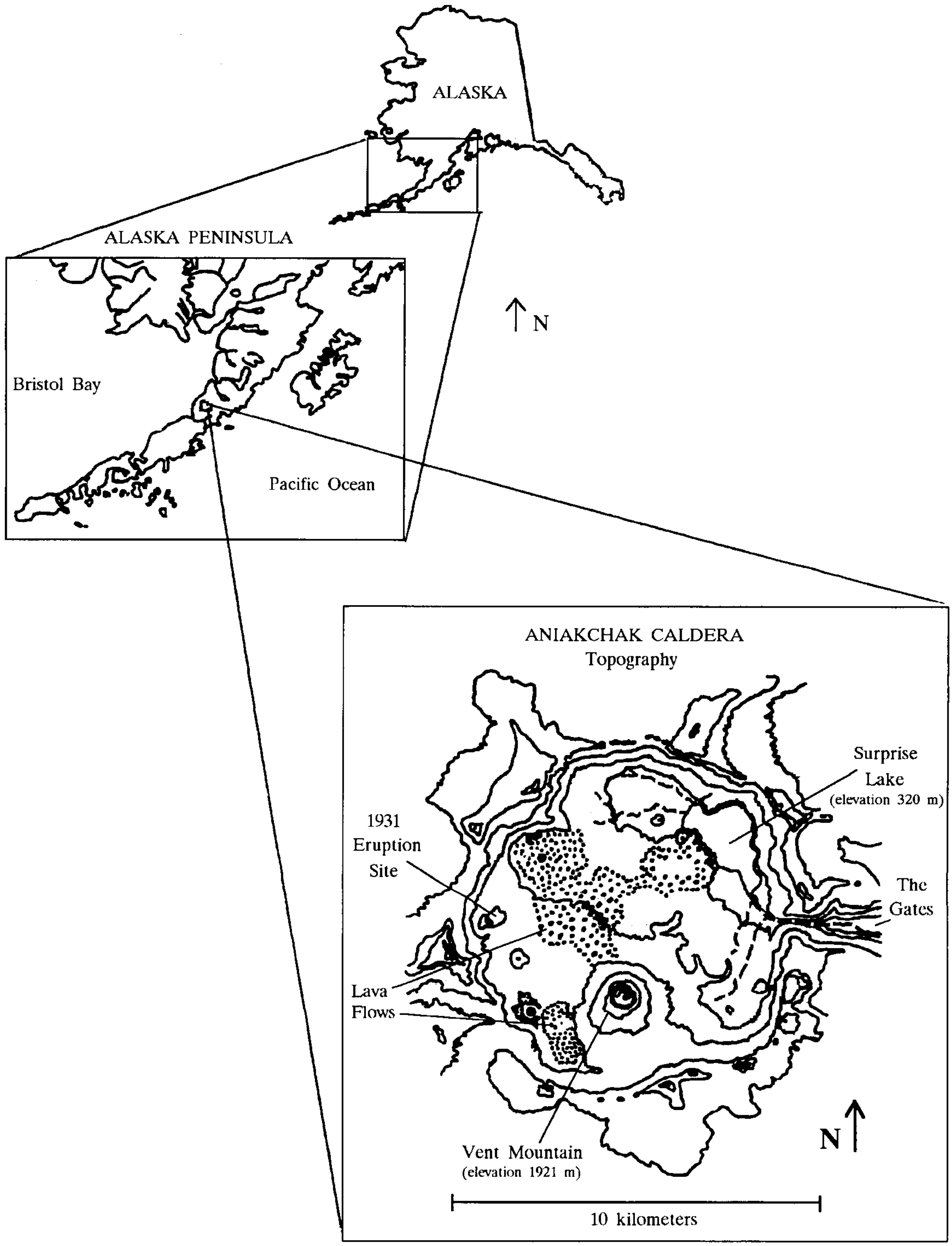
STUDY SITE DESCRIPTION

Situated on the central Alaska Peninsula, midway between the Pacific ocean and the Bering Sea, Mt. Aniakchak (56.88°N, 158.17°W) is one of a long chain of volcanoes forming the backbone of the Aleutian Range (Figure II.1). The caldera of Mt. Aniakchak, formed approximately 3400 years ago by the collapse of the andesitic stratovolcano (Miller 1990), is 9.5 km in diameter and encompasses an area of approximately 35 km^2. The lowest point on the caldera floor is 320 m in elevation. The rim averages 1000 m in elevation with the highest point reaching 1341 m. Post-formation volcanic activity within the caldera has resulted in the emplacement of numerous lava domes, maars, eruption pits and lava flows. The caldera remains thermally active as evidenced by the presence of several warm springs, as well as areas with ground temperatures of 85°C at depths of 25 cm (Miller 1990). The most recent eruption occurred in 1931 from a side vent in the caldera floor. This event blanketed the caldera with up to 60 cm of volcanic ash (Hubbard 1932) and had a significant impact on the vegetation within the caldera (Hubbard 1932). Soils, most of which are derived from ashfall, are well developed and acidic (pH=4.8-5.2).

A deep lake filled much of the caldera at one time (McGimsey et al. 1995). This lake eventually breached the caldera rim eroding a deep cleft through soft sandstone deposits in the northeast portion of the caldera wall (Cameron 1992). Surprise Lake, a large (275 ha) lake located along the northeast edge of the caldera floor, is a relict of the ancient lake. Surprise Lake drains 80% of the caldera and is fed by 11 surface inlets and numerous warm and cold springs (Cameron 1992).

Due to its position on the crest of the Aleutian Range, the caldera is affected by both the Pacific Coast and Bristol Bay climatic regimes. The Pacific coast has a maritime climate characterized by high precipitation and moderate temperatures; Bristol Bay has a more

Figure II.1. Location map (modified from Cameron (1992).



continental climate with lower precipitation and wider temperature ranges. Weather inside the caldera is affected by shifting air currents that carry weather from the two climate zones, as well as by its own topography. Low cloud ceilings, rain, and high winds are common, even when the weather is relatively calm outside the caldera. Meteorological data for Aniakchak caldera is limited to weather observations recorded daily for the duration of this study (June 23 to August 23, 1993). During this period, average daily maximum and minimum temperatures were 59°F and 47°F respectively. Measurable precipitation was recorded on 32 days for a cumulative total of 29.4 cm. Maximum recorded wind speed was 100+ km/hr. Winter snow accumulation data is unavailable for the caldera, but ranges from 74 cm at Port Heiden on the Bristol Bay Coast to 150 cm at Chignik on the Pacific Coast (in Cameron 1992).

There are no trees, and relatively few tall shrubs, in Aniakchak caldera. Most of the vegetative biomass is concentrated around Surprise Lake. The lake inlet area has three perennial streams and supports a large subarctic lowland wet sedge meadow (Carex lyngbyaei; vascular plant nomenclature: Hultén 1968). The lake outlet area contains a large lowland herb wet meadow with areas of wet bryophytes (Philonotis fontana; bryophyte nomenclature: Anderson et al. 1990). The lush headlands and terraces around the lake support bluejoint meadows (Calamagrostis canadensis), open low willow stands (Salix alaxensis and S. barclayi) and mesic mixed herb communities (Lupinus nootkatensis, Epilobium angustifolium, etc.). These areas tend to have high vegetative cover and a diverse flora. Crowberry tundra (Empetrum nigrum) is also well represented on low slopes around the perimeter of the lake (vegetation community nomenclature as used above follows Viereck et al. 1992).

Much of the remainder of the caldera consists of rugged windswept ash fields supporting comparatively few species. The moss Racomitrium ericoides forms large mats, and the dwarf willow, Salix stolonifera is also common. Basaltic outcrops support a complex of lichen species including Melanelia stygia, Pseudephebe minuscula, Parmelia saxatilis and several species of Umbilicaria (lichen nomenclature: Thomson 1984). A cryptogamic crust consisting primarily of liverwort species (e.g. Cephaloziella spp, Marsupella alpina, Pleuroclada albescens; liverwort nomenclature: Schuster 1966) covers large portions of the ash flows. Lava flows and eruption pits are dominated by nonvascular species including thick carpets of Racomitrium ericoides and R. lanuginosum. Stereocaulon vesuvianum, a lichen with nitrogen-fixing cephalodia, is abundant on lava rock throughout the caldera.

Two vegetation strata are easily recognized in the caldera. The nonvascular layer ranges in height from 1 to 6 cm and is typically appressed to the substrate. It is composed of a wide variety of moss, liverwort, and lichen species. The vascular layer, which seldom exceeds 60 cm in height, consists of a variety of herbs and dwarf willow species.

METHODS

Field Methods

Observations were made on a total of 52 plots from June through August, 1993. Using knowledge of Aniakchak caldera vegetation from an earlier pilot study (Hasselbach 1992), 18 separate geomorphic features were chosen to represent the widest possible range of diversity within the caldera. Three 0.10 hectare (1000 m^2) circular plots were placed within each geomorphic unit with the exception of two smaller units which had two plots apiece.

General site information, including slope, aspect, elevation, topographic position, presence of surface water (m^2), distance-to-water (1=water on plot, 2=water within 100 m of plot, 3=water greater than 100 m from plot), presence of rock (%), cryptogamic crust (%), overall vegetative cover (%), relative vascular cover (%) and relative nonvascular cover (%) was recorded for each plot. Overall vegetative cover on the plots was recorded as an absolute value ranging from 0 to 100%. Vascular and nonvascular cover were designed to reflect the relative abundance of these plants and, as such, always added to 100% (e.g. a plot with overall vegetative cover of 60% may have relative vascular and nonvascular cover values of 25% and 75% respectively).

Cover for both vascular and nonvascular species was estimated using the following cover classes: 1=single individual, 2=two individuals to 1%, 3=2-5%, 4=6-25%, 5=26-50%, 6=51-75%, 7=76-100%. A whole-plot method was chosen for recording both vascular and nonvascular cover. Whole-plot estimates of cover yield higher species capture than sampling with many small subplots, especially when vegetation is sparse or patchy (McCune & Lesica 1992) as it is in many areas of the caldera.

Data Analysis

Correlation between strata Due to the broad range of total abundance values among the areas sampled, the primary data matrices were relativized by plot totals, expressing species abundances as relative proportions, to give equal weight to all plots. This transformation had the added benefit of improving the spread of points in the ordinations. Species with fewer than 4 occurrences were deleted.

Ordinations, using the quantitative version of the Sørenson index (Beals 1984) as the distance measure, were performed on the relativized data with nonmetric multidimensional scaling (NMS) (Kruskal 1964; Mather 1976; implemented in McCune 1993). Vascular and nonvascular strata were ordinated separately. Initial ordinations revealed a group of nine sparsely vegetated plots of similar make-up that were forcing the remainder of the plots to be clustered into a tight, uninterpretable mass. These nine plots were removed from the matrix. Three additional plots were identified as outliers (average distance to other plots > 2.00 standard deviations from the overall average distance) and were removed to improve the spread and interpretability of the ordination. Ordination of the final data matrices (vascular = 40 plots x 111 species; nonvascular = 40 plots x 72 species) yielded two interpretable axes for each strata. The appropriateness of using two axes was confirmed by an examination of stress in NMS as a function of dimensionality. First and second axis ordination scores for each stratum were then related to each other by correlation analysis.

The importance of scale The second group of analyses, aimed at determining the effect of scale of observation on the strength of correlation observed, was performed on the complete data set of 52 plots for each strata, followed by a series of partitioned data sets of increasing homogeneity. The correspondence between strata (r^2) was plotted against two measures of scale (or heterogeneity of the data): average dissimilarity (distance) among plots, and beta diversity (ß). Each of these is explained in detail below.

The frequency distribution of dissimilarity values for each stratum showed that distances for nonvascular plants were more evenly distributed than distances for vascular plants along the full range of dissimilarity values between 0 and 1. Therefore, the nonvascular plants were used as the basis for partitioning the data in the analyses that follow.

Prior to the series of analyses, a dissimilarity matrix was generated (as described below) and vascular and nonvascular dissimilarities were regressed against one another (overall r^2= 0.36). Examination of the scatter plot revealed that the distribution of data points was skewed toward an excess of high dissimilarity values for both strata. This results from the loss of sensitivity of distance measures at high distances which in turn results from the "zero truncation problem" (Beals 1984). To counteract this problem we transformed the dissimilarity matrices by squaring each value. The resulting frequency distributions were less skewed and the bivariate correlation between layers improved for the full data set (r^2=0.45).

Dissimilarity method Dissimilarity values were plotted against r^2 to determine if correlation increased with increasing scale in multi-dimensional species space. To this end, separate stand dissimilarity matrices, based on species cover for each strata, were constructed. The quantitative form of the Sørenson coefficient was chosen as the distance measure. To avoid division by zero when two plots were empty for a given stratum, an arbitrary small number (0.001) was added to each value in each raw data matrix. The two dissimilarity matrices were then compared with a series of 19 regressions which were performed in the following manner: 1) dissimilarity values < 1.00 (i.e. all dissimilarity values because 1 is maximum) were regressed against one another and the coefficient of determination (r^2) recorded; 2) all plot pairs with nonvascular dissimilarity < 0.95 were selected and the r^2

between nonvascular and vascular distances recorded once again, and so on, at intervals of 0.05 until a dissimilarity of 0 was reached; 3) finally, the r^2 values were plotted against the dissimilarity used as the selective criterion.

Beta diversity method In a related analysis, a series of regressions used beta diversity (ß) as a criterion for partitioning the data. Beta diversity as used here is an indication of the overall rate of species change in a multidimensional environment (Whittaker 1972), rather than the rate of species change along a single gradient. ß was calculated by dividing the total number of species on all plots by the average number of species on a single plot (Whittaker 1960, 1972). The nonvascular data were again used as the basis of partitioning the data. These analyses proceeded as follows: (1) as in the above analysis, a Sørenson dissimilarity matrix was generated, correlation analysis performed, and an r^2 for the initial ß was obtained. 2) PC-ORD program ROWCOL (McCune 1993) was used to identify five farthest outlying plots at a time, using as a criterion the average distance to other plots; these plots were removed and ß was re-calculated. (3) This process was repeated until only 3 plots (i.e. 3 dissimilarity values) remained. The sequential removal of outlying plots decreased beta diversity, as each step diminishes the heterogeneity of the data set. (4) Finally, as above, r^2 values were plotted against ß.

Note that by using dissimilarity matrices for these analyses a large number of data points are acquired, but the number of independent observations (i.e. plots in this case) is actually much smaller (e.g. for the full data set of 52 plots, there are 1326 data points (dissimilarity values) and 51 degrees of freedom). Therefore, in both of the above analyses, a cut-off value of 17 plots (16 degrees of freedom) was arbitrarily determined as the value below which too few plots remained to generate a viable regression. This problem could have been avoided by increased sampling intensity at low ß.

RESULTS AND DISCUSSION

Correlation between strata in Aniakchak caldera

Separate NMS ordinations were performed for vascular and nonvascular strata. Both ordinations had similar coefficients of determination: Axis 1 accounted for approximately 57% of the total variation in each ordination, while Axis 2 accounted for approximately 18%.

Axis 1 For both vascular and nonvascular ordinations, Axis 1 is interpreted as a strong moisture (proximity to water) gradient. A related paper discusses this gradient analysis in greater detail as part of an overall Aniakchak vegetation description (Chapter III; Hasselbach & McCune, in prep.).

Regression of Axis 1 ordination scores of plots in vascular and nonvascular species space against one another revealed a strong correlation between the strata (r^2=0.77). While such a high correlation suggests a strong similarity in each stratum's response to the predominant moisture gradient, there are other possible interpretations. For instance, the vascular stratum may respond strongly and directly to the moisture gradient, while the nonvascular stratum is being heavily influenced by species interactions with the vascular strata (e.g. shading, etc.) and thus only indirectly responded to the moisture gradient as well. These, and more complex causal linkages, would be impossible to establish through correlative methods alone.

Axis 2 A similar analysis was performed for Axis 2 by regressing vascular and nonvascular ordination scores against one another. This regression indicated that correlation between the strata is essentially non-existent along the secondary compositional gradients (r^2=0.01). An examination of both vascular and nonvascular ordinations and correlation coefficients corroborates the regression results. Although both strata were similarly related to presence of rock as a secondary gradient (r^2=0.32 for each), the vascular strata exhibited a correlation to slope (r^2=0.34), while the nonvascular stratum was unrelated to slope (r^2=0.01).

The strong relationship between nonvascular species and rock is easily explained as an expression of the importance of rock as a substrate for certain lichen and moss species. But why are the strata responding differently to slope? There are many reasons to expect vascular and nonvascular plants to respond differently to environmental gradients (Slack 1977; During 1979; Lee and LaRoi 1979). Nonvascular plants have no roots and lack a well developed vascular system. Consequently they are unable to draw upon substrate resources in periods of drought (During 1979). Their growth is largely controlled by moisture conditions that may fluctuate widely (Herben 1987). Thus they respond more rapidly than vascular plants to changes in water availability (During 1979; Herben 1987). Furthermore, due to their small size, it has been suggested that nonvascular plants respond to smaller scale environmental variation so that a wider range of substrates are available for their use (i.e. they experience greater habitat heterogeneity) (McCune & Antos 1981b). Similarly, a greater range of microclimatic conditions are available to them, at least in forests (McCune & Antos 1981b).

In Aniakchak, however, the differential response of layers may be linked more directly to the history of the site. The 1931 eruption blanketed the entire area with up to 60 cm of ash (Hubbard 1932). Steeper slopes would tend to slough the ash more readily, enhancing survivorship of relict individuals. These survivors have been shown to be important to post-eruption recovery for vascular plants (Zobel & Antos 1992). Plants of flatter surfaces would likely die (Antos & Zobel 1985), resulting in low survivorship of vascular plants in such places. So one could reasonably expect a positive correlation between abundance of vascular plants and slope.

Many nonvascular plants are considered "pioneer" or "early successional" species (Longton 1992). The absence of a similar slope response by nonvascular plants may be due to their ability to quickly colonize disturbed areas. In the caldera, the nonvascular biomass is dominated by species of the genus Racomitrium (Hasselbach & McCune, in prep.) which is particularly adept at colonizing disturbed or "immature substratum" (Tallis 1959). Therefore, following the high mortality associated with the 1931 eruption (Hubbard 1932), it is likely that nonvascular plants, Racomitrium species in particular, quickly recolonized both flat and sloping areas, in addition to surviving on the slopes where ash was sloughed off. Thus the different relationships of the strata may be a reflection of disturbance colonization in the caldera.

An alternative, or perhaps contributing, explanation for the differential response of the strata to slope in Aniakchak caldera concerns the scale at which the slope parameter was measured. Numerous basaltic outcrops with near-vertical faces are found in relatively flat areas within the caldera. These outcrops support a variety of saxicolous lichen and moss species. Ash would have sloughed readily from these steep surfaces, presumably enhancing survivorship of resident species; the slope, however, was measured at a plot-wide scale (0.10 ha) which is not reflective of the smaller scale variation represented by the rock faces.

While these analyses indicate that correlation between layers is fairly strong along the moisture gradient in Aniakchak, it is not strong enough to be used in a predictive fashion. To do so would be to miss stratum-specific patterns such as those demonstrated by the different responses of the strata to slope.

The effect of scale on correlation observed between layers

The Aniakchak results, as discussed above, illustrate some of the pitfalls associated with attaching causation to the existence of correlation among vegetative layers. But if the more important question is of the extent to which correlation exists, then the scale at which the question is addressed becomes important. We used a series of partitions of the Aniakchak data set (nonvascular stratum ß=8.5; vascular stratum ß=6.6; overall ß=7.3) to demonstrate the scale dependence of correlation. Figure II.2 uses distance as a measure of the heterogeneity of the data set. This is consistent with Hermy (1988, p. 79) who stated that "percent dissimilarity may be considered here as a measure of ß; as the length of the environmental gradient increases, the percent dissimilarity between communities will increase." Figure II.2 shows a positive relationship between the observed correlation and the dissimilarity, or heterogeneity, of the data set. For example, had we confined our study to a narrower ecological range with maximum dissimilarity of 0.4, our reported coefficient of determination (r^2) would have been 0.01 rather than the 0.45 we observed along the entire gradient.

Although the use of average dissimilarity as a descriptor of the extent or scale of the data set on the horizontal axis is effective, it has two main drawbacks: (1) it is seldom reported, making comparisons between studies difficult; and (2) distance measures tend to lose sensitivity as the heterogeneity of the data set increases (Beals 1984). For these reasons, a different analysis was performed using ß on the horizontal axis (Figure II.3). Beta diversity is easily calculated as the total number of species found on all plots divided by the average number of species on a single plot (Whittaker 1960, 1972). This analysis further corroborates the scale dependency of correlation between layers by displaying an increase in correlation with increasing ß. The effect is significant when one considers the increase in r^2 from 0.20 to 0.45 gained with increasing ß from 4.0 to 8.5. The main limitation of the Aniakchak data set for this application became apparent at low ß (<4.0) when the number of plots remaining for calculation was too small for adequate representation.

Figure II.2. Increase in correlation between strata with dissimilarity as a measure of heterogeneity.

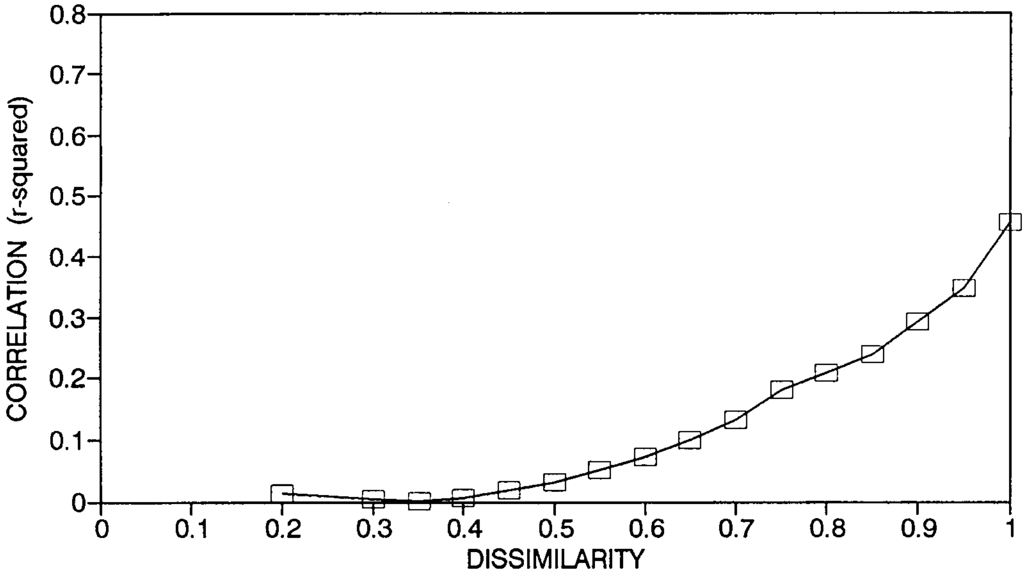
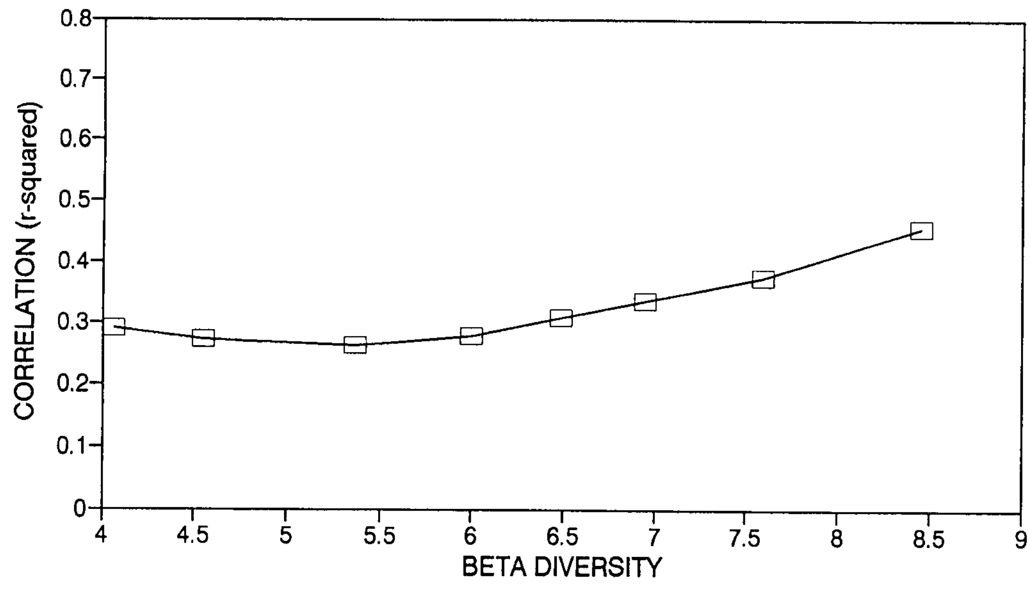


Figure II.3. Increase in correlation between strata with beta diversity as a measure of heterogeneity.



These results lend an element of clarity to the overall problem of correlation in the following way. Consider an attempt to reconcile results from a study (McCune and Antos 1981a, 1981b) indicating extremely low correlations between bryoid and herb layers in Swan Valley, MT (r^2=0.06, ß=5.8 for bryoid) with those presented in this paper indicating high correlation between layers in Aniakchak caldera, AK (r^2=0.45, ß=8.5 for bryoid layer). Ignoring methodological differences between the studies for a moment, Figure II.3 indicates a higher correlation in Aniakchak simply by virtue of the higher ß. That the graph in Figure II.3 does not accurately reflect the actual ß found in Swan Valley is an indication that indeed other factors in addition to scale contribute to the strength of correlation observed. Also, since our sampling scheme was designed to represent the greatest amount of environmental variation possible in Aniakchak, sampling intensity was low in homogeneous areas. This had the effect of undersampling at low ß.

Note that the overall correlation observed between layers in Aniakchak using raw dissimilarity matrix-based analyses is weaker (r^2=0.45) than that observed using ordination axis-based analyses (r^2=0.77) because ordinations tend to filter noise (Gauch 1982). Finally, while it is true that one would expect increased correlation with expanding "scale" in any positive linear regression, this fact is sometimes overlooked when making comparisons between studies. These analyses attempt to underscore the importance of carefully considering the scale at which a study was conducted; specifically, the spread of sample points in species space. For this reason, it is strongly recommended that ß values always be reported to facilitate such comparisons.

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Chapter III. Patterns of Vascular and Nonvascular Vegetation with Respect to Environmental Gradients in Aniakchak Caldera, Alaska

ABSTRACT

Vascular and nonvascular vegetation was sampled on 52 plots representing the widest possible range of geomorphic variation in Aniakchak caldera, Alaska. Data from these plots were analyzed to detect vegetation patterns with respect to environmental gradients. Nonmetric multidimensional scaling ordination revealed proximity to water as the primary environmental gradient. Plant communities were related to presence of rock (i.e. lava flows, basalt outcrops) as the secondary gradient, and to slope as the tertiary. Seven vegetation groups were identified with cluster analysis. Discriminant analysis was then used to identify the distinguishing ecological factors and characteristic species associated with each group. The abundance of nitrogen-fixing taxa, which accounted for 73% of the total lichen cover, was discussed with regard to their potential role as facilitators of primary succession.

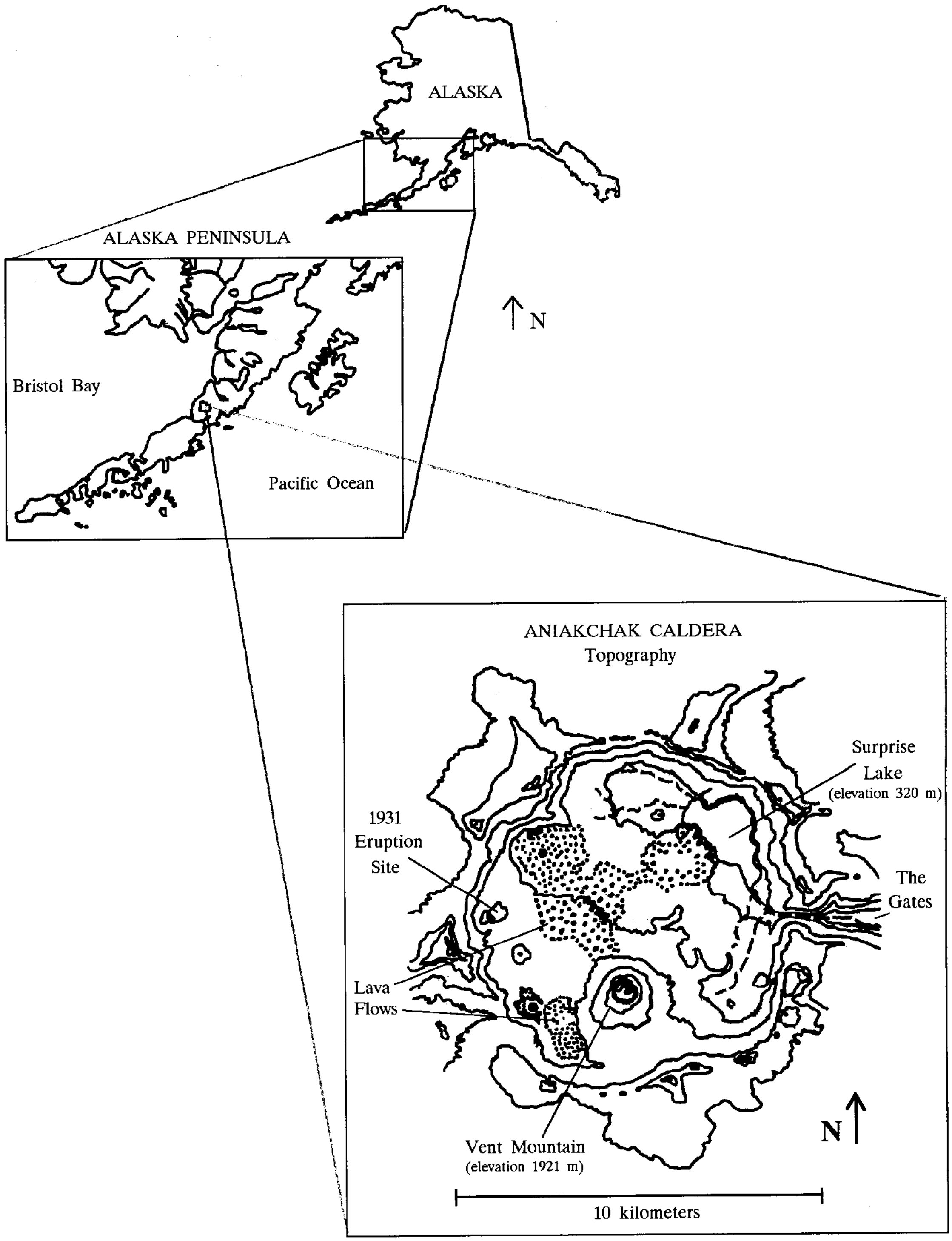
INTRODUCTION

Mt. Aniakchak contains one of the largest active calderas in Alaska and, as such, is of considerable scientific interest. Situated on the central Alaska Peninsula, midway between the Pacific Ocean and the Bering Sea, Aniakchak (56.88°N, 158.17°W) is one of a long chain of volcanoes forming the backbone of the Aleutian Range (Figure III.1). Although progress has been made in understanding the vegetation ecology of volcanic areas in many regions of the world (Tagawa et al. 1985, Tsuyuzaki 1987, delMoral & Wood 1988), very little is known about such areas in Alaska, specifically on the Alaska Peninsula. Existing vegetation research on the volcanic peninsula primarily consists of work at Katmai National Park's Valley of Ten Thousand Smokes after the eruption of Novarupta Volcano in 1912 (Griggs 1919 a,b). As both a National Monument and a National Natural Landmark, Aniakchak offers an excellent opportunity to study the natural patterns of an ecosystem unaltered by human impact.

The prominence of mosses and lichens in Aniakchak caldera is readily apparent (Bosworth 1987, Hasselbach 1992). Nonvascular plants are extremely important to the functioning of many plant communities. For example, mosses aid in water retention, nutrient cycling, soil development and stabilization, and provide microsite sheltering for propagules (Longton 1992). Lichens function as nitrogen fixers, provide important forage for caribou and other animals, and also aid in soil development through physical and chemical weathering (Longton 1992). Despite the significance of nonvascular plants, knowledge of these taxa on the Alaska Peninsula is extremely limited, the nearest published work originating at Amchitka Island (Persson 1968, Thomson & Sowl 1989), 700 km southwest of Aniakchak.

Our research in Aniakchak caldera was designed to address both the lack of understanding of the vegetation ecology in volcanic landscapes of the Alaska Peninsula, and the lack of distributional data for lichens and mosses. The objectives were: (1) to describe the vegetation of Aniakchak caldera by identifying major vegetative groups and their component species, (2) to determine the environmental factors most important in the separation of the vegetation groups, and (3) to identify important environmental gradients and examine the distribution of plant communities in relation to them. A separate paper addresses the strength of correlation between the vascular and nonvascular strata in Aniakchak (Hasselbach & McCune, in prep.).

Figure III.1. Location map (modified from Cameron 1992).



STUDY SITE DESCRIPTION

Aniakchak caldera was formed approximately 3400 years ago by the collapse of an andesitic stratovolcano (Miller 1990). It is 9.5 km in diameter and encompasses an area of approximately 35 km^2. The lowest point on the caldera floor is 320 m in elevation. The rim averages 1000 m in elevation with the highest point reaching 1341 m. Post-formation volcanic activity within the caldera has resulted in the emplacement of numerous lava domes, maars, eruption pits and lava flows (Miller 1990). The caldera remains thermally active as evidenced by the presence of several warm springs, as well as areas with ground temperatures of 85°C at depths of 25 cm (Miller 1990). The most recent eruption occurred in 1931 from a side vent in the caldera floor. This event blanketed the caldera with up to 60 cm of volcanic ash (Hubbard 1932) and had a significant impact on the vegetation within the caldera (Hubbard 1932). Soils, most of which are derived from ashfall, are well-drained and acidic (pH = 4.8-5.2).

A deep lake filled much of the caldera at one time (McGimsey et al. 1995). This lake eventually breached the caldera rim eroding a deep cleft through soft sandstone deposits in the eastern portion of the caldera wall (Cameron 1992). Surprise Lake, a large (275 ha) lake located along the northeast edge of the caldera floor, is a relict of the ancient lake. Surprise Lake drains 80% of the caldera and is fed by 11 surface inlets and numerous warm and cold springs (Cameron 1992).

Due to its position on the crest of the Aleutian Range, the caldera is affected by both the Pacific Coast and Bristol Bay climatic regimes. The Pacific coast has a maritime climate characterized by high precipitation and moderate temperatures; Bristol Bay has a more continental climate with lower precipitation and wider temperature ranges. Weather inside the caldera is affected by shifting air currents that carry weather from the two climate zones (in

Cameron 1992), as well as by its own topography. Low cloud ceilings, rain, and high winds are common, even when the weather is relatively calm outside the caldera. Meteorological data for Aniakchak caldera is limited to weather observations recorded daily for the duration of this study (June 23 to August 23, 1993). During this period, average daily maximum and minimum temperatures were 59°F and 47°F respectively. Measurable precipitation was recorded on 32 days for a cumulative total of 29.4 cm. Maximum recorded wind speed was 100+ km/hr. Winter snow accumulation data is unavailable for the caldera, but ranges from 74 cm at Port Heiden on the Bristol Bay Coast to 150 cm at Chignik on the Pacific Coast (in Cameron 1992).

There are no trees, and relatively few tall shrubs, in Aniakchak caldera. Most of the vegetative biomass is concentrated around Surprise Lake. The lake inlet area has three perennial streams and supports a large subarctic lowland wet sedge meadow (Carex lyngbyaei). The lake outlet area contains a large lowland herb wet meadow with areas of wet bryophytes (Philonotis fontana). The lush headlands and terraces around the lake support bluejoint meadows (Calamagrostis canadensis), open low willow stands (Salix alaxensis and S. barclayi) and mesic mixed herb communities (Lupinus nootkatensis, Epilobium angustifolium, etc.). These areas tend to have high vegetative cover and a diverse flora. Crowberry tundra (Empetrum nigrum) is also well represented on low slopes around the perimeter of the lake (vegetation community nomenclature as used above follows Viereck et al. 1992).

Much of the remainder of the caldera consists of rugged windswept ash fields supporting comparatively few species. The moss Racomitrium ericoides forms large mats, and the dwarf willow Salix stolonifera is also common. Basaltic outcrops support a complex of lichen species including Melanelia stygia, Pseudephebe minuscula, Parmelia saxatilis and several species of Umbilicaria. A cryptogamic crust consisting primarily of liverwort species (e.g., Cephaloziella spp., Marsupella alpina, Pleuroclada albescens) covers large portions of the ash flows. Lava flows and eruption pits are dominated by nonvascular species including thick carpets of Racomitrium ericoides and R. lanuginosum. Stereocaulon vesuvianum, a lichen with nitrogen-fixing cephalodia, is abundant on lava rock throughout the caldera.

METHODS

Field Methods

Observations were made on 52 plots from June through August, 1993 (Appendix I). Using knowledge of Aniakchak caldera vegetation from an earlier pilot study (Hasselbach 1992), 18 separate geomorphic features were chosen to represent the widest possible range of diversity within the caldera. Three 0.10 hectare (1000 m^2) circular plots were placed within each geomorphic unit with the exception of two smaller units which had two plots apiece.

General site information, including slope, aspect, elevation, topographic position, presence of surface water (m^2), distance-to-water (1=water present on plot, 2=water within 100 m of plot, 3=water greater than 100 m from plot), percent rock, percent cryptogamic crust, percent overall vegetative cover, relative vascular cover (%), and relative nonvascular cover (%) was recorded for each plot. Overall vegetative cover on the plots was recorded as an absolute value ranging from 0 to 100%. Vascular and nonvascular cover were designed to reflect the relative abundance of these plants and, as such, always added to 100% (e.g. a plot with an overall vegetative cover of 60% may have relative vascular and nonvascular cover values of 25% and 75% respectively).

Cover for both vascular and nonvascular (moss, liverwort, and macrolichen) species was estimated using the following cover classes: 1=single individual, 2= two individuals to 1%, 3=2-5%, 4=6-25%, 5=26-50%, 6=51-75%, 7=76-100%. A whole-plot method was chosen for recording both vascular and nonvascular cover. Whole-plot estimates of cover yield higher species capture than sampling with many small subplots, especially when vegetation is sparse or patchy (McCune & Lesica 1992) as it is in many areas of the caldera. The disadvantage of the whole-plot method is that it sacrifices a degree of quantitative accuracy (McCune & Lesica

1992). Since little is known about the nonvascular plants of the Alaska Peninsula from a floristic perspective, we wanted to produce the most complete species inventory possible.

Nomenclature of vascular plants follows Hultén (1968). Nomenclature for lichens, mosses, and liverworts follows Thomson (1984), Anderson et al. (1990), and Schuster (1966) respectively. Vouchers of all species were collected for residence in the University of Alaska herbarium in Fairbanks.

Data Analysis

Diversity Measures Gamma diversity (γ) was recorded as the total number of species encountered on the plots. Beta diversity (ß) was calculated by dividing the total number of species on all plots by the average number of species on a single plot (Whittaker 1960, 1972). Used in this fashion, ß is an indication of the overall amount of species compositional change (or heterogeneity) between plots (Whittaker 1972) rather than the rate of species change along a single gradient. Species richness (S) was measured as the number of species occurring on a plot. Species diversity, which incorporates both S and the evenness with which species are distributed, was computed using the Shannon-Weaver index (H'; Shannon & Weaver 1949; as implemented in McCune 1993). Although there are problems with all diversity indices (Peet 1974), the use of H' is appropriate as a means of comparing diversity between the different vegetation groups within the caldera. The entire primary data matrix (52 plots x 302 species) was used in all of the above calculations.

Ordinations Elsewhere (Hasselbach & McCune, in prep.), we examined the relationship between the vascular and nonvascular strata in Aniakchak and determined that they exhibited a relatively high degree of correlation with respect to the primary moisture gradient. For the purposes of this paper the vascular and nonvascular strata were combined into a single data set and analyzed collectively.

Prior to analysis, species with fewer than 4 occurrences were removed from the data set. Ordinations, using the quantitative version of the Sørenson index (Beals 1984) as the distance measure, were performed on the unrelativized data with nonmetric multidimensional scaling (NMS) (Kruskal 1964; Mather 1976; as implemented in McCune 1993). Initial ordinations revealed a group of 9 sparsely vegetated plots of similar make-up that were forcing the remainder of the plots to be clustered into a tight, uninterpretable mass. Since 8 of these plots also grouped together in the cluster analysis, we removed them from the main ordination and described them separately in the classification section (see group 7). Three additional plots were identified as outliers (average distance to other plots > 2.00 standard deviations from the overall average distance) and were removed to improve the spread and interpretability of the ordination. Ordination of the final data matrix (40 plots x 158 species) yielded three interpretable axes.

Classification Seven vegetation groups were defined through cluster analysis of 49 plots. Three empty plots were removed to avoid division by zero. Ward's method, an hierarchical agglomerative polythetic procedure (CLUSTR in PC-ORD; McCune 1993), was used to form the groups. To equalize the weighting of the plots, relative Euclidean distance measure was chosen. Discriminant analysis was then used to evaluate the adequacy of this classification by identifying misclassified plots.

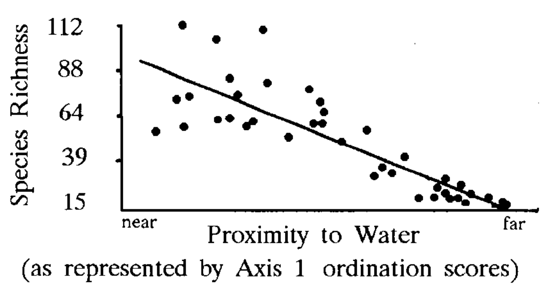
Discriminant Analysis (DA) is a statistical method for examining membership of predefined groups based on a set of predictors (e.g. environmental variables). This technique was used to determine which ecological factors were most important in the separation of the seven groups. In a separate analysis, DA was used to identify characteristic species for each group. To distinguish ecological factors most important in separating groups, the ecological variables for each of the seven vegetation groups were entered simultaneously (Method = DIRECT in SPSS; Norusis 1990), group means for each ecological variable were calculated, and means were compared to determine differences among groups. The ecological variables included elevation, slope, aspect, rock (%), cryptogamic crust (%), overall vegetative cover (%), nonvascular cover (%), standing water (m^2), flowing water (m^2), and distance-to-water. This procedure was repeated to determine characteristic plant species for each group by simultaneously entering species data.

RESULTS AND DISCUSSION

Diversity/Floristics

A total of 343 species were documented in Aniakchak caldera as a result of this study (Appendix II). Of these, 302 species (including 164 vascular and 138 nonvascular species) were encountered on the sample plots. Nonvascular plants were underestimated as a result of the omission of crustose lichens from the data set due to their taxonomic difficulty. The number of species present (S) ranged from 0 to 112 on individual plots, with an average of 41 species per plot (standard deviation=0.87). Figure III.2 demonstrates the decline in species richness with distance from Surprise Lake (see Axis 1 ordination results for explanation of horizontal axis). Overall beta diversity (ß) was 7.4 indicating a fairly high degree of heterogeneity between plots. Beta diversity for vascular and nonvascular components separately was 6.7 and 8.5 respectively. Overall species diversity values (H') were similar for vascular and nonvascular plants (Table III.1).

Figure III.2. Species richness as a function of proximity to water.



A total of 43 species (19 vascular and 33 nonvascular) were encountered only once in the sampling of 52 plots (Appendix II). Typically, these "rare" taxa occurred on either headlands or in eruption pits. The 16 most frequent taxa (i.e. those occurring on 50% or more of the plots) are noted in Appendix II. A total of 22 range extensions were recorded for vascular plants (Appendix III). Range extension information is difficult to ascertain for nonvascular plants due to the general lack of distributional information on the Alaska Peninsula.

Table III.1. Mean species diversity indices for plot data set.

	Gamma Diversity (γ)	Species Richness (S)	Beta Diversity (ß)	Shannons Diversity Index (H')
all species	302	41	7.4	3.10
vascular species	164	25	6.7	2.53
nonvascular species	138	16	8.5	2.30

Environmental Gradients

Nonmetric multidimensional scaling (NMS) ordination of 40 plots yielded 3 interpretable axes. The first axis displayed strong correlations with several interrelated factors which, when considered together, were indicative of a single environmental gradient (Table III.2, Figure III.3, III.4). Percent vegetation, a measure of the overall vegetative cover on each plot, demonstrated a strong positive relationship with Axis 1, while distance-to-water, a categorical measure of the proximity of a plot to surface water, demonstrated a strong negative relationship. Taken together, these results reflect the concentration of vegetation in and near areas with surface water in Aniakchak. Furthermore, the first axis displayed a strong negative correlation with elevation. In Aniakchak caldera an increase in elevation implies an increase in distance from Surprise Lake at the caldera lowpoint. Thus, the availability of surface water decreases dramatically with elevation, an effect compounded by the porous, well drained

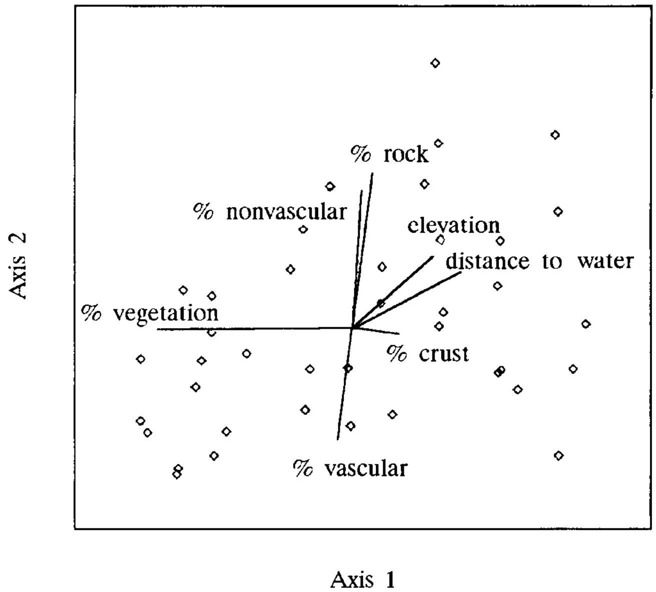
Table III.2. Varience explained by the three ordination axes and correlations (r) between those axes and selected variables.

	Axis 1	Axis 2	Axis 3
Varience explained (%)	49.7	29.2	7.3
		r	
elevation	-0.516	0.584	0.152
slope	0.183	-0.237	0.454
aspect	-0.204	0.057	0.140
rock cover (%)	-0.220	0.792	0.312
cryptogamic crust cover (%)	-0.440	-0.069	0.155
overall vegetative cover (%)	0.868	-0.154	-0.035
nonvascular cover (%)	-0.190	0.661	0.325
vascular cover (%)	0.190	-0.661	-0.325
standing water (m^2)	0.304	-0.102	0.166
flowing water (m^2)	0.262	-0.323	-0.102
distance to water (ordered categorical)	-0.645	0.501	0.039

nature of the ashy soils (Bosworth 1987). Therefore, the first axis is interpreted as a moisture (or proximity to water) gradient. This interpretation is corroborated by the positive correlation of such mesophytic species as the moss Philonotis fontana (r=0.35) and the herb Stellaria calycantha (r=0.61) to Axis 1, as well as by negative correlations of such relatively xerophytic species as the moss Racomitrium ericoides (r= -0.79) and the herb Luzula arcuata (r= -0.67). The amount of surface water was also positively correlated with this axis but perhaps not as strongly as expected since the method of recording this variable (i.e. area of standing and flowing water measured separately on each plot) was not truly indicative of water availability.

Percent cover of cryptogamic crust also exhibited a negative correlation to Axis 1. Cryptogamic crusts develop at soil surfaces and usually consist of some combination of tiny mosses, liverworts, lichens, algae (brown, green, blue-green) and fungi (West 1990). Cryptogamic crusts are common in climatically extreme environments (e.g. desert and tundra) and are known to occur on new volcanic surfaces (West 1990). In Aniakchak caldera, cryptogamic crusts were well developed on comparatively dry surfaces in the mid and upper portions of the caldera. This pattern is consistent with the Axis 1 interpretation.

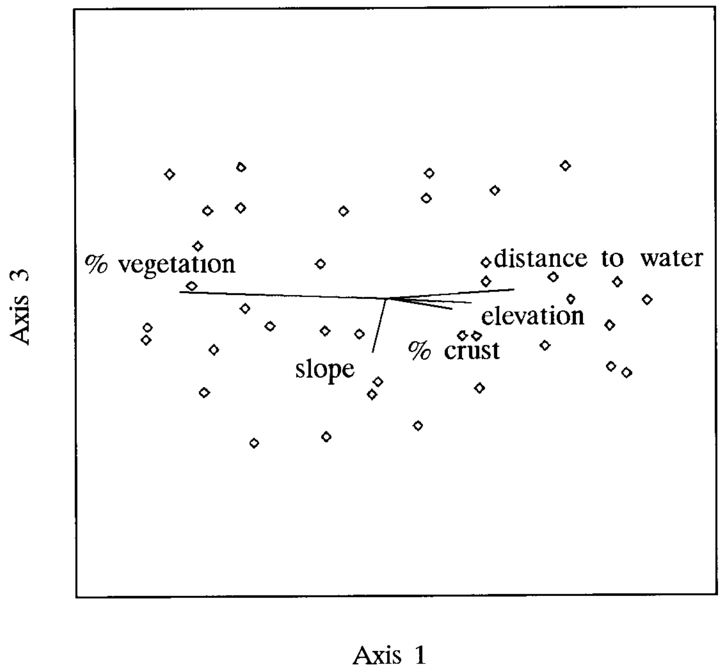
Figure III.3. Nonmetric multidimensional scaling ordination of plots in species space. Axes 1 and 2. Radiating lines from the centroid of the point cluster indicate the direction and relative strengths of the correlations with the named variables (cutoff for inclusion of vector: r= 0.40).



The separation of plots along the second axis was most strongly related to the amount of rock present (i.e. basalt outcrops, lava flows). On this axis, cover of rock is strongly correlated to the relative cover of nonvascular species (Table III.2, Figure III.3) reflecting the presence of many epilithic moss and lichen species. Data supporting this interpretation included positive correlations of such rock dwelling species as the lichen Allantoparmelia alpicola (r=0.43) and the moss Andreae rupestris (r=0.46) to Axis 2, and negative correlations of ground dwelling species such as the liverwort Pleuroclada albescens (r= -0.36) and the lichen Peltigera scabrosa (r= -0.37).

Axis 3 showed slope emerging as a gradient (Table III.2, Figure III.4). Although this axis explained only 7.3% of the total variation, it is ecologically meaningful in light of the potential importance of steep slopes in sloughing off ash from the 1931 eruption, thereby facilitating the survivorship of relict vascular species which are known to be important to post-disturbance recovery. This is discussed in detail in Hasselbach & McCune (in prep.).

Figure III.4. Nonmetric multidimensional scaling ordination of plots in species space. Axes 1 and 3. Radiating lines from the centroid of the point cluster indicate the direction and relative strengths of the correlations with named variables (cutoff for inclusion of vector: r= 0.40).



Vegetation Groups

Seven vegetation groups were distinguished from a cluster analysis of 49 plots (Figure III.5). Partitioning the dendrogram at the seven group level provided both distinct and interpretable groups. The separation of these groups is illustrated by placement of plots in ordination space (Figure III.6). Overall, lower elevation, wet plots occupied the lower left portion of the ordination; higher elevation plots with lingering snow occupied the central upper portion; high, rocky plots such as lava flows and eruption pits occupied the righthand portion; less rocky, mid-elevation plots with greater cryptogamic crust cover occupied the lower righthand portion. The central lower section is occupied by dry, steep plots. Discriminant analysis was used to evaluate the adequacy of this classification by using the species data as predictors of group membership. No misclassifications were encountered.

Figure III.5. Cluster Analysis.

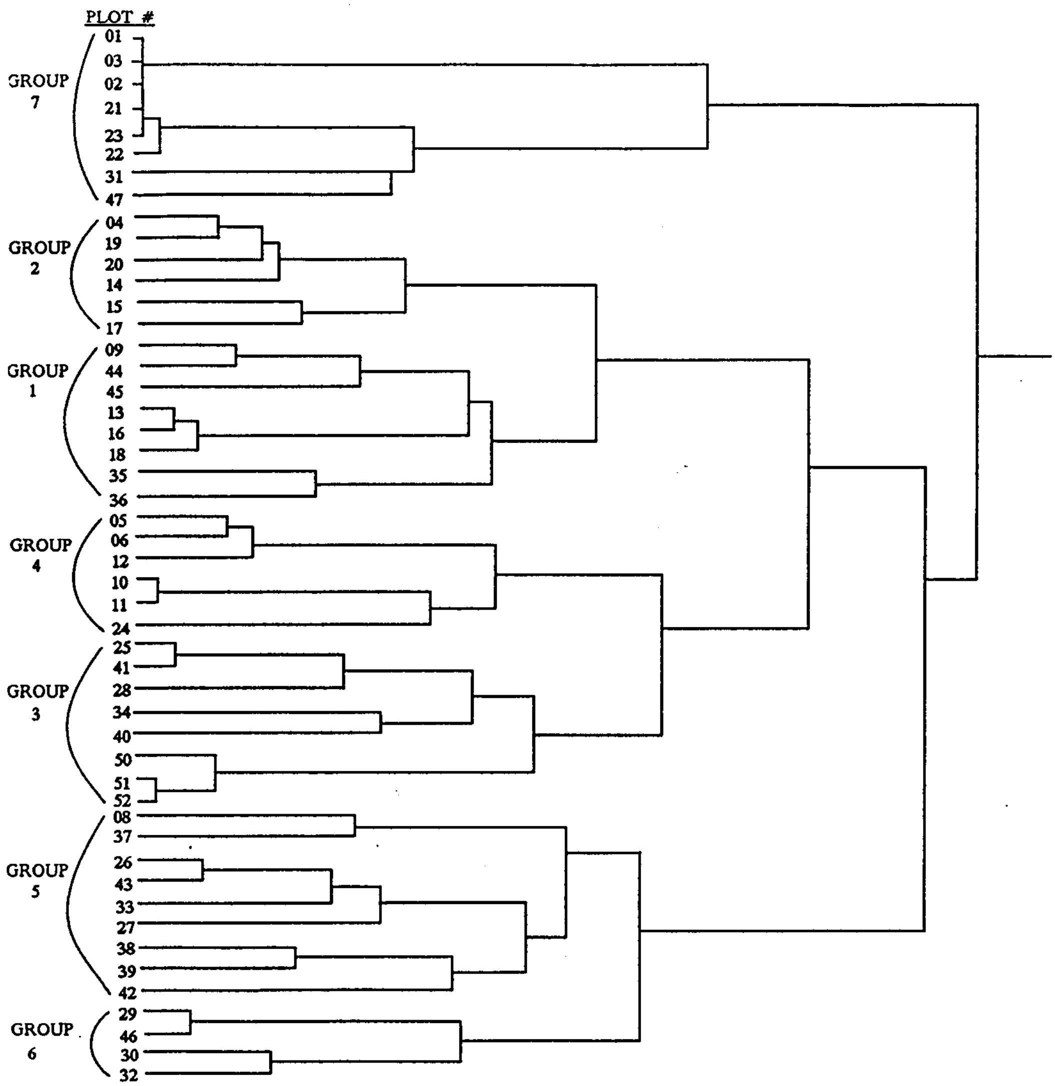
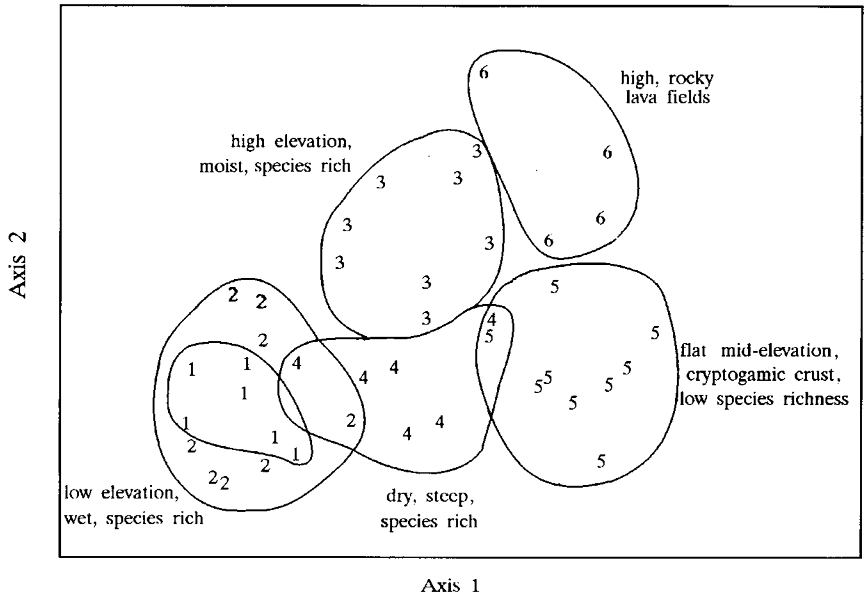


Figure III.6. Placement of vegetation groups (as defined by cluster analysis) in NMS ordination space. Vegetation Group 7 (flat, windswept, barren plots) is absent as explained in text (p.34).



Description of groups Discriminant analysis (DA) revealed that 94% of the plots could be correctly classified as to vegetation group based on the environmental variables alone. The first two discriminant functions expressed 80% of the variation among the seven groups. Of the 10 environmental factors considered, 7 differed significantly ($p<0.05$) among groups, although crust was borderline ($p=0.04$). Aspect, standing water, and flowing water did not differ among the groups. The insignificance of the latter two factors is likely a reflection of the inadequacy of surface water measurement techniques used. DA was also used to identify characteristic species for each vegetation group. Vegetation groups are presented below (Table III.3) in order of their position on the first axis, a moisture gradient (i.e. Group 1 is most strongly influenced by water; Group 7 is least).

Table III.3. Characteristics of the seven vegetation groups as determined by discriminant analysis.

Vegetation Group	Characteristic Vascular Species	Characteristic Nonvascular Species	Typical Sites	Distinguishing Ecological Factors	Overall Vegetative Cover (%)	Average Species Richness	Shannon-Weiner Diversity Index
1	*Lupinus nootkatensis* *Salix alaxensis* *Angelica lucida* *Arabis lyrata* *Arctagrostis latifolia* *Carex macrochaeta*	*Philonotis fontana* *Brachythecium frigidum* *Rhytidiadelphus squarrosus* *Marchantia polymorpha* *Peltigera membranaceae* *Peltigera scabrosa*	inlet meadows, base of caldera walls	gentle slopes low elevation 5% rock 2% black crust	89	61	3.9
2	*Lupinus nootkatensis* *Rhododendron camtschaticum* *Salix barclayi* *Heracleum lanatum* *Saxifraga punctata* *Solidago multiradiata*	*Aulacomnium palustre* *Sanionia uncinata* *Stereocaulon tomentosum* *Cladonia borealis* *Peltigera aphthosa* *Psoroma hypnorum*	headlands, lakeside areas	steep slopes low elevation 6% rock 3% black crust	87	93	4.3
3	*Salix stolonifera* *Salix rotundifolia* *Carex pyrenaica* *Cystopteris fragilis*	*Stereocaulon vesuvianum* *Solarina crocea* *Polytrichum piliferum* *Dicranum spadiceum* *Arctoa fulvella* *Racomitrium ericoides*	eruption pits, high relief lava	gentle slopes high elevation lingering snow 74% nonvascular cover 37% rock 15% black crust	64	44	3.6
4	*Empetrum nigrum* *Vaccinium uliginosum* *Salix stolonifera* *Antennaria pallida* *Arnica lessingii* *Aster sibiricus*	*Pleurozium schreberi* *Racomitrium ericoides* *Racomitrium lanuginosum* *Nardia scalaris* *Allantoparmelia alpicola* *Lobaria linita* *Pseudephebe pubescens*	lava domes, midslope of caldera walls	steep slopes mid elevation 12% rock 22% black crust	48	63	3.9

Table III.3. Cont.

5	*Salix stolonifera* *Minuartia macrocarpa* *Trisetum spicatum* *Sibbaldia procumbens*	*Racomitrium ericoides* *Racomitrium fasciculare* *Oligotrichum hercynicum*	pyroclastic flows, tuff cones	gentle slopes mid elevation 10% rock 27% black crust	9	24	3.0
6	*Cardamine bellidifolia* *Luzula wahlenbergii*	*Stereocaulon vesuvianum* *Racomitrium lanuginosum* *Conostomum tetragonum* *Pogonatum urnigerum*	eruption pits, blocky lava	gentle slopes high elevation 89% nonvascular cover 55% rock 3% black crust	38	22	3.0
7	*Deschampsia caespitosa* *Sagina intermedia*	*Placopsis gelida*	alluvial plains, flat ridgetops	gentle slopes mid elevation 1% rock 3% black crust	2	5	1.7

Group 1 *Flat areas in water-collection zones.* Distinguished by low slopes, Group 1 had high overall vegetative cover (89%) and high species richness. Topographically, plots in this group were found in water collection zones such as toe-slopes and low lying areas subject to seasonal inundation by snow-melt. Some of the areas had saturated or shallowly flooded soils. Presence of rock and cryptogamic crust was minimal. These sites supported lush mesic mixed forb and lowland herb wet meadow communities dominated by herbs (Lupinus nootkatensis), mosses (Rhytidiadelphus squarrosus, Philonotis fontana) and widely scattered shrubs (Salix alaxensis). Typical sites include inlet and outlet meadows and the bases of caldera walls in some cases (Figure III.7a,b).

Group 2 *Steep, low elevation slopes near lakeside.* While similar to Group 1 in its high overall vegetative cover (87%), low elevation, and proximity to water, Group 2 is distinguished by steep slopes. Species richness and diversity were greatest in this group, possibly due to a combination of water availability and the ash-sloughing effect of steep slopes that enhanced survivorship of relict plants after the 1931 eruption (Hasselbach & McCune, in prep.). In addition, the desiccating effect of wind on low growing plants may be mitigated by the sheltering effect provided by the presence of tall shrubs and umbels, and by the overall high biomass which are characteristic of this group. Presence of rock and cryptogamic crust was minimal. Plant communities include mesic mixed herb and open tall willow communities dominated by a variety of shrubs (Salix barclayi, S. arctica), herbs (Heracleum lanatum, Saxifraga punctata, Solidago multiradiata), mosses (Sanionia uncinata) and lichens (Peltigera aphthosa, Stereocaulon tomentosum). Typical sites include headlands and lakeside areas (Figure III.8).

Group 3 *High elevation, flat, species rich sites protected from wind.* Although surface water was not present, these sites tended to hold snow longer due to the effect of both topographic shading and north-facing exposures. Species richness was high, perhaps as a result of increased moisture availability from lingering snow melt. This group was distinguished from other waterless, high elevation sites by the higher overall vegetative cover (64%) which may be a result of wind protection from high relief lava fields. In addition, there was a strong rock/nonvascular component on the lava flows associated with this group reflecting the presence of subdominant amounts of the lichen Stereocaulon vesuvianum as well as a variety of bryophyte species. Vascular plants were uncommon. Presence of cryptogamic crust was minimal. Typical sites include bottoms of eruption pits and well-vegetated, high relief lava fields (Figure III.9).

Group 4 *Mid-elevation sites on dry, steep slopes.* These sites were windy and exposed yet still supported an average of 48% overall vegetative cover. Species richness values were noticeably high. That the two most species rich groups (Groups 2 and 4) were correlated most strongly with steep slopes is another indication of the importance of steep slopes in sloughing ash and enhancing vascular plant recovery as discussed in Hasselbach and McCune (in prep.). A well developed cryptogamic crust consisting primarily of liverwort species (e.g., Cephaloziella spp., Marsupella alpina) was prominent. A moderate amount of rock was present. Vascular and nonvascular plants were equally represented in the alpine herb (Salix stolonifera, Arnica lessingii, Racomitrium ericoides) and Empetrum tundra (Empetrum nigrum, Vaccinium uliginosum, Lobaria linita) communities characteristic of this group. Typical sites include lava domes and midslope portions of caldera walls (Figure III.10).

<u>Group 5</u> *Mid-elevation sites in dry, flat areas.* This group was distinguished from Group 4 by lower slopes, greatly reduced overall vegetative cover (9%), and decreased species richness. These areas were wind-swept and ash covered. Cryptogamic crust was well developed and little rock was present. Plant communities consisted of widely spaced <u>Salix stolonifera</u>, patches of <u>Racomitrium ericoides</u> and scattered herbs. Typical sites include pyroclastic flows and tuff cones (Figure III.11).

<u>Group 6</u> *Rocky, flat, dry, high elevation sites with some degree of wind protection.* This group is similar to Group 3 in that it consisted of protected eruption pit and lava flow sites with moderate species richness. Unique in its high rock content and the associated dominance of nonvascular plants (89% of vegetation present), this group had moderate overall vegetative cover (38%) and little cryptogamic crust. Typical sites include eruption pits (e.g. the 1931 eruption site) with blocky lava blanketed by <u>Stereocaulon vesuvianum</u> (Figure III.12).

<u>Group 7</u> *Flat, dry, wind-swept, barren.* Expansive areas of loose, unconsolidated material subject to desiccating winds. Overall vegetative cover was extremely low (2%) consisting primarily of crustose lichen species and a few tiny moss sprigs established in the shelter of small rocks. Little rock or cryptogamic crust was present. Typical sites include flat, open ridgetops and large alluvial fans (Figure III.13).

Figure III.7a. Surprise Lake.

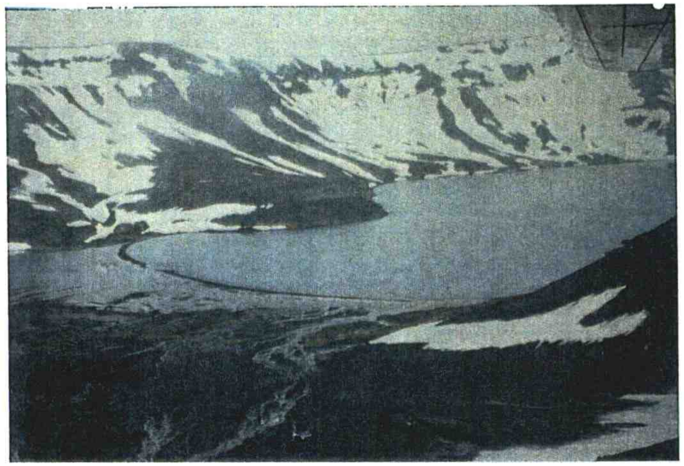


Figure III.7b. Vegetation Group 1.

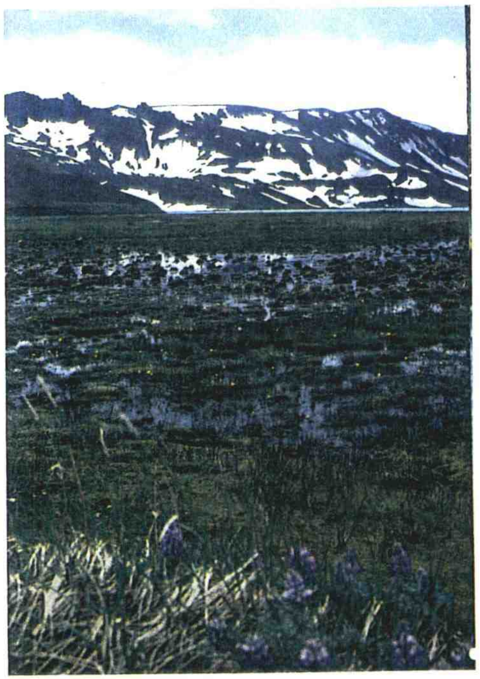


Figure III.8. Vegetation Group 2.

Figure III.9. Vegetation Group 3.

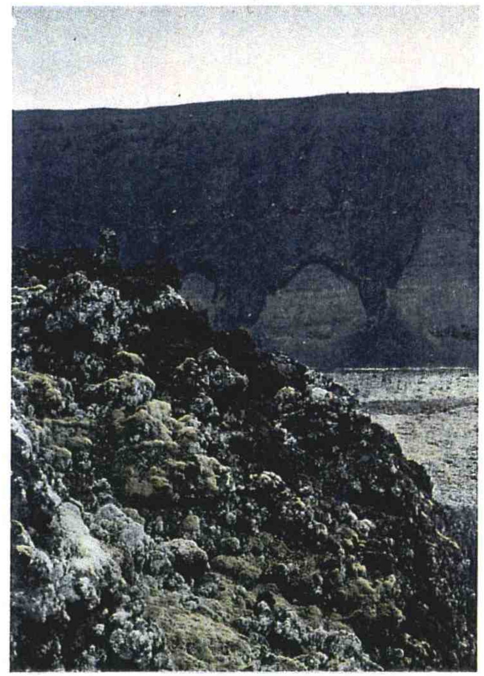


Figure III.10. Vegetation Group 4.

Figure III.11. Vegetation Group 5.

Figure III.12. Vegetation Group 6.

Figure III.13. Vegetation Group 7.

Additional Observations

The 1931 eruption in Aniakchak caldera buried the previous plant communities under up to 60 cm of ash, providing a new substratum in many places for primary succession. Development of early successional vegetation in volcanic areas is often limited by the lack of fixed nitrogen in the ash (Vitousek & Walker 1987). In severe environments such as Aniakchak, the process of facilitation, whereby colonizing species improve the environment for later successional species, is believed to be important (Chapin et al. 1994). The prevalence of nitrogen-fixing taxa may directly enhance the growth of associated species in primary succession (del Moral & Wood 1993). In Aniakchak nitrogen-fixing taxa are exceedingly common, especially in the higher ashfields . The most abundant lichen in the caldera, Stereocaulon vesuvianum (9% of the overall lichen abundance), has nitrogen-fixing cephalodia and is known to colonize relatively young lava flows (Thomson 1984). Placopsis gelida is another ubiquitous nitrogen-fixing lichen in the caldera, as are Peltigera species and Lobaria linita. In total, 73% of the lichen cover (or 44% of the species present) was composed of nitrogen-fixing species. And although we have no specific data, it is possible that some of the mosses present in the caldera also contribute to nitrogen fixation by hosting epiphytic cyanobacteria (Longton 1992). Finally, Lupinus nootkatensis, the sixth most abundant vascular plant in the caldera, is also notable for its nitrogen-fixing ability.

It is of interest to note the absence of nitrogen-fixers in the cryptogamic crust, which is known to contain cyanobacteria in arid regions (West 1990). The absence of cyanobacteria in Aniakchak crust can probably be attributed to the high acidity of the ashy soils (Belnap pers. comm., in West 1990).

CONCLUSION

This study provided a better understanding of the vegetation ecology of Aniakchak caldera. In addition to fulfilling our objectives of examining environmental gradients, identifying major vegetation groups, and determining the environmental factors most important in the separation of the groups, our research has underscored two areas of potential concern for managers of Aniakchak National Monument:

(1) Aniakchak caldera supports areas of remarkably high species richness and diversity particularly in the immediate vicinity of Surprise Lake (Figure III.2). The three most species rich plots were located on the headlands which separate protected coves from one another. Due to the rugged terrain and extreme wind exposure of most areas of the caldera, potential camp sites are limited to these coves. Soils in this area are derived from ashfall and are of sandy texture with inherently poor cohesion and therefore are susceptible to disturbance. In the event of increased visitorship in the caldera, these rich and fragile areas would be negatively impacted. Considering the slow recovery of caldera vegetation in the 64 years since the last eruption, such damage may have long-term effects.

(2) The presence of large amounts of cryptogamic crust is also of interest to resource managers. The crust is inconspicuous and often occurs in high elevation, apparently barren portions of the caldera. Such areas are naturally well suited to foot travel by visitors. While the role of cryptogamic crusts in ecosystem processes is poorly understood at present (West 1990), many scientists believe they perform valuable functions. Crusts may enhance soil moisture by increasing interception and infiltration of rain water, slow erosion by water and

wind, increase nutrient input and retention, aid in seed lodgement, add organic matter and contribute to soil development (see West 1990 for review).

The impact of human footprints on cryptogamic crust is unknown, although research indicate that most crusts are susceptible to mechanical damage by livestock grazing (Rogers & Lange 1971). Furthermore, some crusts are slow to recover from disturbance, at least in desert regions (Webb et al. 1988). If Aniakchak is to continue to function as an intact ecosystem, human impact to these areas should be minimized.

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Chapter IV. Summary

1. Species composition in the vascular and nonvascular strata in Aniakchak caldera were both strongly correlated to the same primary gradient: proximity to water gradient.
2. Vascular and nonvascular strata showed no correlation along the secondary gradient because the vascular stratum responded to steepness of slope while the nonvascular stratum did not. The importance of slope to the vascular stratum may reflect the role of steep slopes in sloughing ash, thereby enhancing survivorship of relict vascular plant species after an eruption in 1931. The absence of a similar slope-response in the nonvascular stratum may be due to the ability of nonvascular plants to quickly recolonize disturbed areas, regardless of the degree of sloping. Thus the different secondary gradients exhibited by the strata may reflect disturbance colonization in the caldera.
3. The strength of correlation observed between strata in Aniakchak increased as the scale (heterogeneity) of the data set increases. This relationship was demonstrated using both dissimilarity and beta diversity as measures of heterogeneity.
4. With respect to the combined data set, proximity to water was the primary environmental gradient, presence of rock (i.e. lava flows, basalt outcrops) was the secondary gradient, and slope was the tertiary.
5. Vegetation in Aniakchak caldera can be divided into seven distinct groups. These groups were distinguished on the basis of environmental factors and characteristic species.
6. Aniakchak caldera supports areas of remarkably high species richness and diversity particularly in the immediate vicinity of Surprise Lake. In addition, large amounts of

cryptogamic crust are present in mid and upper portions of the caldera floor. Human impact to these areas should be minimized.

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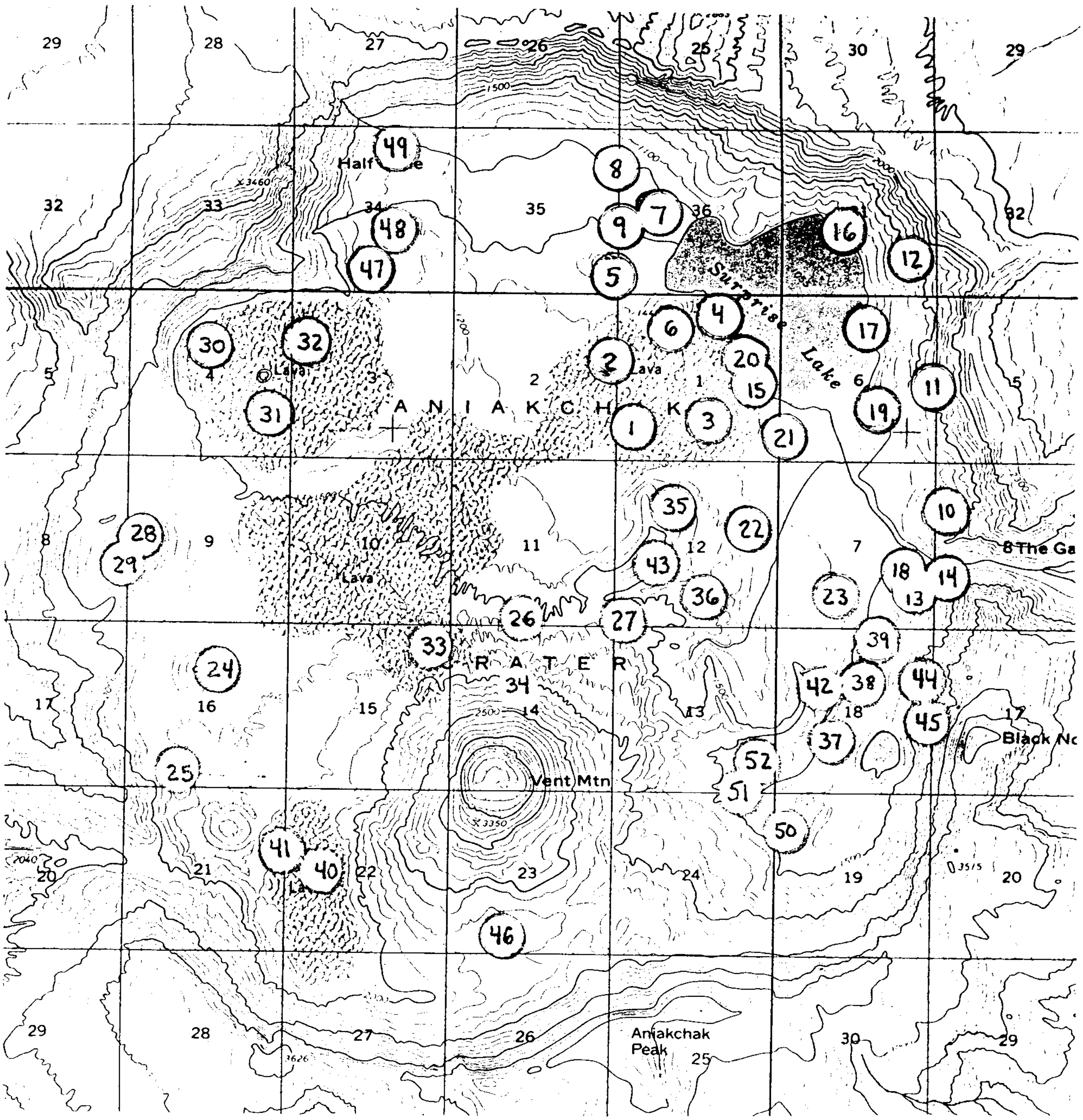
APPENDICES

Appendix I. Plot locations.

Geomorphic Feature	**Plot Number**
Old Lava Ridgetop	1, 2, 3
Headlands	4, 15, 20
Lava Domes	5, 6, 24
Inlet Meadow	7, 8, 9
Midslope Caldera Walls	10, 11, 12
Gates Meadow	13, 14, 18
Lower Slope - Lakeside	16, 17, 19
Outlet Alluvium	21, 22, 23
Inlet Alluvium	47, 48, 49
Eruption Pits	25, 28, 29
Vent Mtn. Pyroclastic Flow	26, 27, 33
Half Cone Lava Flow	30, 31, 32
Gully	34, 35, 36
Maar Lake Lava Flow	37, 38, 39
Tuff Cones	42, 43
Vent Mtn. Lava Flow	40, 41, 46
Naknek Toeslope	44, 45
Lava Outwash Plain	50, 51, 52

Appendix I. Cont. Plot locations.



Appendix IIa. Vascular Plant Species.
* indicates species observed on a single plot
** indicates frequency of occurrence is greater than 50%

Achillea borealis **
Agrostis alaskana
Agrostis borealis
Angelica lucida
Antennaria alpina (L.) Gaertn. var. compacta
Antennaria monocephala var. monocephala
Antennaria pallida
Arabis lemmoni
Arabis lyrata ssp. kamchatica
Arctagrostis latifolia var. latifolia
Arctagrostis latifolia var. arundinacea *
Arnica chamissonis
Arnica lessingii ssp. lessingii **
Artemisia arctica ssp. arctica
Artemisia borealis
Artemisia globularia *
Artemisia tilesii
Aster sibiricus
Athyrium filix-femina
Botrychium boreale *
Botrychium lunaria
Botrychium lanceolatum
Calamagrostis canadensis
Caltha palustris ssp. arctica
Campanula lasiocarpa ssp. lasiocarpa
Cardamine bellidifolia
Cardamine umbellata
Carex bigelowii
Carex dioica ssp. gynocrates
Carex enanderi
Carex glareosa
Carex kelloggii
Carex lachenalii
Carex lyngbyaei
Carex macrochaeta
Carex nesophila
Carex pyrenaica ssp. micropoda
Carex rariflora
Carex spectabilis
Cassiope lycopioides
Cassiope stelleriana
Cerastium beeringianum var. beeringianum
Cerastium beeringianum var. grandiflorum
Chrysosplenium wrightii
Coeloglossum viride ssp. bracteatum
Corallorrhiza trifida
Cryptogramma crispa
Cystopteris fragilis
Deschampsia beringensis
Deschampsia caespitosa **
Diapensia lapponica
Draba alpina *
Draba crassifolia
Draba nivalis *
Dryas octopetala ssp. octopetala
Dryopteris dilatata ssp. americana
Elymus arenarius
Empetrum nigrum
Epilobium anagallidifolium
Epilobium angustifolium ssp. macrophyllum
Epilobium behringianum
Epilobium glandulosum
Epilobium hornemannii
Epilobium latifolium **
Epilobium leptocarpum
Epilobium luteum
Equisetum arvense
Equisetum palustre
Equisetum silvaticum
Equisetum variegatum
Eriophorum angustifolium
Eriophorum scheuchzeri
Euphrasia mollis
Festuca altaica
Festuca brachyphylla
Festuca rubra
Gentiana aleutica
Gentiana amarella ssp. acuta
Gentiana tenella
Geranium erianthum
Geum macrophyllum ssp. macrophyllum
Geum rossii
Gymnocarpium dryopteris *
Heracleum lanatum
Heuchera glabra *
Hieracium triste

Hierlochloe odorata
Hippuris vulgaris
Hordeum brachyantherum
Juncus arcticus
Juncus castaneus
Juncus drummondii
Juncus mertensianus
Koenigia islandica
Lagotis glauca
Ledum palustre ssp. decumbens
Leptarrhena pyrolifolia
Listera cordata
Loiseleuria procumbens
Luetkea pectinata
Lupinus nootkatensis
Luzula arcuata ssp. unalaschcensis **
Luzula multiflora
Luzula parviflora
Luzula tundricola
Luzula wahlenbergii ssp. piperi
Lycopodium alpina
Lycopodium annotinum var. annotinum
Lycopodium clavatum
Lycopodium sabinaefolium var. sitchense *
Lycopodium selago
Menyanthes trifoliata
Minuartia macrocarpa
Montia fontana ssp. fontana *
Oxyria digyna
Papaver alaskanum
Parnassia kotzebuei
Parnassia palustris
Pedicularis capitata
Pedicularis kanei
Pedicularis langsdorffii ssp. langsdorffii
Pedicularis sudetica
Pedicularis verticillata
Petasites hyperboreus
Petasites frigidus
Phleum commutatum ssp. americanum
Phyllodoce aleutica ssp. aleutica
Platanthera dilatata var. chlorantha
Platanthera dilatata var. dilalata
Platanthera obtusata
Poa alpina
Poa arctica ssp. arctica **
Poa arctica ssp. longiculmis
Poa palustris
Poa paucispicula
Polemonium acutiflorum
Polemonium boreale
Polygonum viviparum
Polypodium vulgare ssp. columbianum *
Potamogeton praelongus
Potentilla palustris *
Potentilla villosa
Primula cuneifolia ssp. saxifragifolia
Pyrola asarifolia *
Pyrola minor
Pyrola secunda *
Ranunculus eschscholtzii
Ranunculus hyperboreus ssp. hyperboreus *
Ranunculus trichophyllus
Rhododendron camtschaticum ssp.camtschaticum
Romanzoffia sitchensis
Rubus arcticus ssp. stellatus
Rumex graminifolius
Sagina intermedia
Salix alaxensis ssp. alaxensis
Salix arctica ssp. crassijulis
Salix barclayi
Salix phlebophylla
Salix pulchra
Salix reticulata
Salix rotundifolia
Salix sitchensis
Salix stolonifera **
Sanguisorba stipulata
Saxifraga bronchialis ssp. funstonii
Saxifraga caespitosa *
Saxifraga foliolosa var. foliolosa
Saxifraga hirculus
Saxifraga lyallii
Saxifraga nivalis
Saxifraga oppositifolia ssp. oppositifolia
Saxifraga punctata ssp. nelsoniana **
Saxifraga rivularis ssp. flexuosa
Saxifraga serpyllifolia
Saxifraga unalaschcensis
Sedum rosea ssp. integrifolium
Sibbaldia procumbens **
Silene acaulis ssp. acaulis
Solidago multiradiata var. multiradiata
Solidago multiradiata var. arctica *
Spiranthes romanzoffiana
Stellaria calycantha ssp. isophylla

Stellaria crassifolia *
Stellaria monantha
Stellaria ruscifolia ssp. aleutica *
Taraxacum ceratophorum
Thelypteris phagopteris
Trientalis europaea ssp. arctica
Trisetum spicatum **
Vaccinium ovalifolium
Vaccinium uliginosum
Vaccinium vitis-idaea ssp. minus
Vahlodea atropurpurea
Veronica serpyllifolia ssp. humifusa *
Veronica stelleri
Viola epipsila ssp. repens
Viola langsdorffii

Appendix IIb. Bryophyte Species.
* indicates species observed on a single plot
** indicates frequency of occurrence is greater than 50%

Andreaea rupestris
Arctoa fulvella
Aulacomnium palustre
Aulacomnium turgidum *
Barbilophozia hatcheri
Bartramia ithyphylla
Brachythecium albicans
Brachythecium asperrimum
Brachythecium frigidum
Brachythecium plumosum *
Brachythecium reflexum var. pacificum
Brachythecium starkei var. starkei
Bryoerythrophyllum recurvirostre
Bryoxiphium norvegicum *
Bryum bicolor
Bryum weigelii *
Calliergon stramineum
Ceratodon purpureus
Conostomum tetragonum
Cratoneuron filicinum
Dichodontium pellucidum *
Dicranella palustris *
Dicranella subulata
Dicranowesia crispula
Dicranum angustum *
Dicranum scoparium
Dicranum spadiceum
Dicranum tauricum
Didymodon vinealis
Diplophyllum albicans
Diplophyllum taxifolium
Distichium capillaceum
Ditrichum flexicaule *
Drepanocladus aduncus
Eurhynchium pulchellum *
Grimmia donniana *
Grimmia torquata var. torquata *
Gymnomitrion obtusum
Hylocomium splendens
Hypnum lindbergii *
Isopterygium pulchellum *
Kiaeria falcata *

Lophozia sudetica
Marchantia polymorpha var. polymorpha
Marsupella alpina
Marsupella ustulata
Mnium ambiguum *
Moerckia blyttii
Nardia scalaris
Oligotrichum hercynicum
Paludella squarrosa
Philonotis fontana var. fontana
Plagiomnium affine
Plagiothecium cavifolium
Pleuroclada albescens
Pleurozium schreberi
Pogonatum urnigerum **
Pohlia cruda
Pohlia wahlenbergii
Polytrichastrum alpinum
Polytrichum commune
Polytrichum juniperinum
Polytrichum piliferum
Polytrichum sexangulare
Pseudoleskea radicosa var. denudata *
Pseudoleskea stenophylla
Pseudotaxiphyllum elegans *
Ptilidium ciliare
Racomitrium ericoides **
Racomitrium fasciculare **
Racomitrium lanuginosum
Racomitrium sudeticum
Rhizomnium punctatum
Rhytidiadelphus loreus *
Rhytidiadelphus squarrosus
Rhytidialelphus triquetrus
Sanionia uncinata
Schistidium apocarpum
Schistidium rivulare var. rivulare
Sphagnum girgensohnii
Sphagnum russowii
Sphagnum squarrosum
Sphagnum teres *
Splachnum sphaericum

Splachnum vasculosum *
Tetraplodon mniodes
Timmia austriaca
Tortula ruralis
Warnsdorfia exannulata var. exannulata

Appendix IIc. Lichen Species.
* indicates species observed on a single plot
** indicates frequency of occurrence is greater than 50%

Allantoparmelia alpicola
Cetraria islandica ssp. orientalis
Cladina arbuscula *
Cladina mitis *
Cladonia bellidiflora *
Cladonia chlorophaea
Cladonia borealis (=C. coccifera)
Cladonia cornuta
Cladonia pyxidata
Cladonia scabriuscula
Cladonia stricta
Cladonia sulphurina *
Cladonia verticillata
Lobaria linita
Melanelia stygia
Nephroma bellum *
Omphalodiscus virginis
Pannaria pezizoides
Parmelia omphalodes *
Parmelia saxatilis
Parmelia sulcata *
Peltigera aphthosa
Peltigera canina *
Peltigera collina
Peltigera degenii
Peltigera didactyla
Peltigera didactyla var. extenuata
Peltigera horizontalis
Peltigera kristonssonii *
Peltigera membranaceae
Peltigera polydactylon sens. str. *
Peltigera praetextata
Peltigera scabrosa
Peltigera rufescens
Peltigera venosa
Physcia caesia *
Pilophorus robustus
Placopsis gelida **
Pseudephebe minuscula
Pseudephebe pubescens
Psoroma hypnorum
Solarina crocea **
Sphaerophorus fragilis *
Sphaerophorus globosus
Stereocaulon alpinum
Stereocaulon glareosum
Stereocaulon rivulorum
Stereocaulon tomentosum
Stereocaulon vesuvianum **
Thamnolia vermicularis
Umbilicaria arctica *
Umbilicaria cylindrica *
Umbilicaria hyperborea var. hyperborea
Umbilicaria hyperborea var. radicicula
Umbilicaria proboscidea
Umbilicaria torrefacta
Xanthoria candelaria
Xanthoria elegans *

Appendix III. Range extensions according to Hultén (1968).

Asteraceae
- Antennaria pallida
- Artemisia borealis
- Hieracium triste

Caryophyllaceae
- Stellaria crassifolia
- Stellaria ruscifolia spp. aleutica
- Stellaria calycantha ssp. isophylla

Cyperaceae
- Carex bigelowii
- Carex pyrenaica ssp. micropoda
- Carex rariflora

Equisetaceae
- Equisetum variegatum

Ericaceae
- Vaccinium ovalifolium

Gentianaceae
- Gentiana tenella

Juncaceae
- Juncus drummondii

Orchidaceae
- Listera cordata

Poaceae
- Poa alpina
- Poa paucispicula

Pyrolaceae
- Pyrola secunda ssp. secunda

Salicaceae
- Salix phlebophylla
- Salix sitchensis

Saxifragaceae
- Parnassia palustris
- Ranunculus eschscholtzii

Scrophulariaceae
- Pedicularis langsdorffii ssp. langsdorffii

Appendix IVa. Raw data for combined data set (i.e. vascular and nonvascular species) in compact data format for analysis in PC-ORD (McCune 1992). The 3 digit number represents the species code (see Appendix I.1b); the subsequent single digit represents abundance (see Methods Section for cover class codes).

PLOT01
149 1 138 1 200 1 155 3 100 1 254 1 278 1 199 2 259 2 368 1 355 1 436 2/
PLOT02
149 1 254 1 268 1 138 2 155 2 355 2 368 2 436 2/
PLOT03
155 1 100 1 199 2 149 1 280 1 200 1 134 1 254 1 368 2 355 2 436 2/
PLOT04
199 3 257 5 156 4 293 3 250 3 197 2 100 2 280 2 162 2 278 2 277 9
215 2 106 2 105 2 224 2 262 2 113 1 158 2 104 3 275 2 219 2 174 1 211 9
149 1 171 1 294 1 266 2 125 1 217 1 252 2 200 2 276 1 209 1 273 8
147 1 117 3 138 2 110 1 144 1 291 1 242 1 121 1 163 2 120 1 256 2 258 9
141 1 284 1 127 1 227 1 289 2 297 1 288 1 182 2 226 2 245 2 175 1 299 8
264 2 155 1 225 1 254 1 143 1 122 1 165 1 366 4 360 2 380 3 338 3 365 3 371 3 372 2 330
2 342 2 356 2 368 3 386 2 307 2 303 2
381 1 331 3 347 2 379 2 325 8 373 1 334 1 507 2 501 2 505 1 508 1 353 3
415 3 440 2 447 2 434 2 436 2 430 3 422 2 454 2 439 9
411 2 457 2 408 2 420 1 446 2 428 1/
PLOT05
156 6 257 5 277 2 113 2 293 4 106 2 250 4 174 2 219 2 211 2 266 9
237 2 231 2 138 3 114 2 203 2 275 2 242 2 100 2 273 2 291 1 286 1 253 8
125 1 215 2 197 2 276 1 173 1 217 2 180 1 294 2 280 2 259 1 218 1 107 8
224 1 118 1 245 1 110 1 284 1 149 1 262 1 366 4 372 4 353 4 368 5 380 2 331 1 304 2 302
1 354 3 374 2 338 2 332 3 307 1 365 3
379 1 321 1 371 3 359 2 509 8 360 1 415 4 430 3 446 3 448 2 440 2 453 2 454 3 400 1 436
2 434 2 447 9 425 2 441 2 457 4 408 2 420 2 405 1 422 2 432 1/
PLOT06
156 5 257 4 197 4 174 2 106 2 218 2 280 2 211 2 293 4 125 2 250 1
277 2 138 2 113 2 201 2 291 2 100 2 237 2 162 1 215 2 107 2 271 1 242 8
149 2 219 1 224 1 266 2 273 1 200 1 275 2 231 1 272 1 253 2 173 1 259 9
217 1 141 1 180 1 165 1 276 1 368 6 366 4 365 3 353 2 356 3 307 1 331 1 355 2 357 1 380
1 300 9
364 1 339 1 338 1 511 1 457 4 447 3 453 2 454 3 440 2 445 2 422 2 415 4 448 2 430 3
418 8 439 1 433 1 408 2 417 2 452 2 400 3 437 2 442 1 419 1 436 2 425 1/
PLOT07
133 5 186 3 124 3/
PLOT08
129 4 124 3 148 2 248 2 241 2 192 3 212 1 135 3 165 1 188 2 259 8
133 1 284 2 261 2 351 3 336 4 325 2 337 4 375 1 324 3 359 1/

PLOT09
199 4 155 3 165 3 258 2 104 3 259 4 162 2 174 2 215 3 188 1
201 2 100 2 280 2 277 2 149 2 110 1 257 3 273 2 288 1 161 2 118 2 134 9
132 2 190 2 224 2 286 1 253 1 227 1 270 1 256 3 267 1 171 1 109 8
231 2 293 2 191 1 225 1 158 1 278 1 368 4 355 3 371 4 351 5 338 3 369 2 325 2 328 2 311
3 359 1 378 2 353 2 303 3 377 2 509 2 508 1 415 2 430 4 425 2 423 2 444 1 432 3
422 2/
PLOT10
259 3 266 2 275 2 106 2 279 2 180 3 138 2 293 3 219 2 211 2 277 9
271 1 240 2 125 2 200 2 230 1 291 1 115 2 143 1 173 1 254 1 149 2 113 9
250 3 253 1 141 1 257 2 237 1 278 2 156 3 280 1 272 1 368 4 355 2 307 1 365 2 300 1 366
3 415 2 430 3 436 3 422 2 445 2 410 2 439 1 457 2
440 1 453 2 447 1 438 2 400 2/
PLOT11
266 2 162 2 211 2 275 2 259 4 277 2 180 2 278 2 272 2 138 2 173 9
115 2 100 2 141 2 253 2 252 1 149 2 254 1 271 2 240 2 214 2 219 2 113 9
143 2 125 2 193 1 291 2 200 2 286 1 114 2 236 2 237 1 215 1 118 9
273 1 106 1 174 1 250 2 257 2 147 1 231 1 152 1 156 2 368 4 355 2 342 2 338 2 366 3 308
2 364 2 306 1 356 1 307 1 445 2 436 3 439 2 430 3
415 2 422 3 440 2 457 2 453 1 433 1/
PLOT12
257 4 259 4 180 2 250 3 219 2 277 2 162 2 116 2 125 2 211 2 138 9
200 2 106 2 174 2 275 2 270 2 113 2 197 2 291 1 149 2 156 2 293 2 253 9
266 2 278 2 273 2 254 1 272 1 114 2 100 1 255 1 240 2 252 1 204 2 158 8
256 1 237 1 193 1 231 1 368 4 366 3 355 3 326 2 301 1 300 3 361 2 365 2 360 1 440 2 445
2 436 2 415 3 447 3 411 2 439 2 430 3 422 3 438 9 453 2 457 2 400 2 408 2 418 1 437 1
420 1/
PLOT13
256 3 199 4 252 4 277 2 104 3 110 4 100 2 162 2 258 3 264 2 245 9
224 2 273 2 159 2 127 2 134 3 188 2 155 2 225 2 113 2 259 3 135 2 274 8
231 2 129 2 278 2 165 2 257 2 117 1 244 2 262 1 203 1 221 1 132 8
237 1 247 1 288 1 144 1 147 1 371 6 359 3 338 2 330 1 325 1 367 2 377 1 351 3 369 2 336
9 505 1 415 2 410 1 430 3 427 2 432 1/
PLOT14
256 3 199 3 155 4 104 4 134 3 221 2 156 2 266 2 162 2 113 2 211 9
259 2 118 2 286 2 215 2 100 2 277 2 174 2 110 2 231 2 291 2 230 2 222 9
127 2 160 2 161 2 293 2 273 2 278 2 284 2 109 2 141 2 148 2 252 9
102 1 253 2 125 2 254 2 173 1 242 2 115 2 275 2 132 2 245 2 258 3 200 9
279 1 338 6 371 4 352 2 359 2 357 1 330 2 355 2 368 2 365 2 342 2 366 9
379 2 500 2 430 3 446 2 426 2 415 2 436 2 439 2 414 2 422 2 457 1 408 8
453 1 447 1/
PLOT15
256 3 199 4 250 4 156 3 257 5 201 2 107 2 291 2 280 2 197 2 174 9
277 2 100 2 252 2 125 2 113 2 101 2 215 2 220 2 175 1 135 4 121 1 295 9
114 2 222 2 227 1 225 2 245 2 293 2 158 2 258 2 237 2 231 2 110 4 262 8

200 1 219 1 209 1 123 1 299 2 122 2 290 2 144 1 297 2 161 2 284 2 165 9
119 2 195 2 127 2 117 1 254 1 147 1 242 2 288 1 273 2 106 1 162 1 155 8
271 1 148 1 159 1 278 1 338 4 368 3 359 2 366 3 360 2 371 4 355 2 344 2 331 2 302 9
356 2 372 2 353 1 380 2 352 2 348 2 384 2 365 2 332 2 307 1 330 2 300 9
305 2 351 2 306 2 342 3 381 3 335 2 341 2 334 2 349 8
303 1 322 2 505 2 504 2 445 2 414 2 415 2 422 1 432 1 430 3 427 3 439 3 418 9
426 2 420 3 408 1 437 1 447 2/
PLOT16
256 3 258 4 199 4 111 4 134 3 100 2 113 2 277 2 293 2 281 2 104 9
158 2 252 3 259 4 257 2 174 2 231 2 155 2 156 3 221 2 222 2 284 1 165 9
253 1 291 2 135 1 278 1 162 2 161 2 148 1 182 2 127 2 245 2 225 9
125 1 109 1 141 1 103 1 371 5 338 4 325 1 368 2 359 3 379 1 366 2 308 1 348 1 505 1 415
2 430 4 446 1 432 1 428 1 443 1 439 1 436 1 411 1 409 1/
PLOT17
156 4 257 4 293 4 250 3 277 2 114 2 113 2 222 2 290 2 194 2 252 9
221 2 231 1 199 3 201 2 174 2 200 2 165 2 155 2 148 2 134 2 100 2 158 8
110 2 104 2 256 2 258 3 175 1 237 2 280 2 284 1 298 1 245 1 182 2 123 8
160 2 161 2 117 1 197 2 162 2 294 2 125 2 135 2 219 1 278 1 291 1 101 8
242 2 286 1 225 1 171 1 192 2 259 2 366 4 331 3 372 2 371 3 338 4 353 2 314 1 365 3 359
1 356 9 355 1 330 1 381 1 325 2 511 1 408 1 455 1 421 1 420 1/
PLOT18
156 3 199 3 256 3 293 3 104 3 222 2 182 2 118 2 277 2 225 2 165 1
179 2 273 2 113 2 252 3 221 2 237 2 142 2 204 2 278 2 215 2 110 2 130 9
231 2 134 3 245 2 297 2 100 2 259 2 262 2 288 2 174 2 253 2 162 3 127 9
201 2 235 2 291 1 275 1 250 2 200 1 269 8
258 3 220 1 188 1 160 2 270 2 296 2 192 1 227 1 148 1 129 2 255 2 211 8
117 1 284 1 195 1 155 1 371 4 338 4 359 2 352 2 368 2 376 2 369 2 311 4 303 2 375 1
324 2 505 3 430 3 415 3 422 2 439 1 432 1/
PLOT19
256 3 155 4 280 2 259 3 199 2 156 2 278 2 293 2 252 2 100 2 245 9
162 2 215 2 125 2 118 2 182 2 222 2 113 2 277 2 258 3 101 2 117 2 174 9
134 2 298 1 110 2 104 2 102 1 157 2 161 2 231 2 284 2 175 2 291 2 225 9
123 3 135 2 141 2 276 2 149 2 154 2 115 2 109 2 201 2 190 2 192 2 273 8
253 1 200 1 275 1 211 2 173 1 257 3 242 2 197 2 106 1 266 1 372 5 359 2 338 4 348 2 357
2 365 3 303 1 342 1 325 3 366 2 368 2
360 2 379 1 505 2 446 3 415 2 432 2 408 1 410 1 404 1 403 1 439 2 422 2 436 9
430 2 440 1/
PLOT20
197 2 250 3 125 2 162 2 222 2 280 2 257 5 100 2 205 2 156 5 246 9
165 2 293 4 199 3 252 2 237 2 291 2 245 2 155 2 278 2 219 2 175 2 134 9
231 2 104 2 295 2 159 2 215 2 225 2 264 2 101 2 258 2 147 1 182 2 259 9
171 1 201 2 113 2 262 2 107 2 299 2 106 2 242 2 277 2 200 2 174 2 273 9
227 1 118 1 217 1 211 2 209 1 115 1 275 2 294 2 114 2 194 1 286 1 272 8
284 1 368 4 366 4 331 3 359 2 371 3 372 2 338 3 307 2 380 2 355 9
357 2 330 3 300 2 360 1 342 3 356 2 379 1 384 2 305 1 344 2 334 8

312 2 348 1 369 1 303 2 351 2 311 2 323 2 343 1 373 1 445 1 415 3 439 2 430 2 440 2
411 2 432 3 408 3 436 2 447 9 454 2 451 2 438 2 420 3 431 2 442 2 422 2 403 2 407 2 425
1 456 1/
PLOT21
368 1 506 2 502 1 508 2 436 2/
PLOT22
149 1 368 1 436 1/
PLOT23
368 1 436 2/
PLOT24
138 3 259 4 278 3 125 2 263 3 277 2 102 2 200 2 253 2 173 9
106 2 158 1 257 2 291 2 165 2 162 2 276 2 130 2 254 2 211 2 273 2 204 9
242 1 213 1 234 2 113 1 288 1 149 3 231 1 368 3 365 2 355 2 360 2 367 2 326 2 356 1 307
2 509 2 418 1 447 3 440 2 436 2 457 2/
PLOT25
273 2 278 2 204 2 263 3 163 2 275 2 291 2 254 2 119 2 158 1 162 9
274 1 173 2 276 2 200 2 198 3 146 1 147 2 213 2 258 2 126 1 143 1 259 8
184 1 113 1 224 1 154 1 136 1 360 2 355 2 366 4 368 4 330 2 359 2 332 3 358 2 356 2 364
9/
301 1 382 2 503 2 502 2 509 2 504 1 447 5 446 3 409 3 436 2 408 3 406 2 407 2 439 2
418 9 451 1 432 2 433 1/
PLOT26
259 3 293 2 114 2 277 2 220 2 135 2 149 2 253 2 125 2 113 2 278 9
200 2 211 1 291 2 107 1 101 1 280 1 106 1 368 3 365 2 326 1 355 2 300 2 447 3 451 2 438
2 436 2 440 2/
PLOT27
259 3 200 2 149 2 275 2 125 2 211 2 135 2 291 1 250 1 293 2 220 9
253 2 368 2 301 1 300 1 360 1 355 1 443 2 436 2 440 2 438 2 453 2/
PLOT28
158 2 291 2 209 2 259 2 101 2 268 2 119 2 278 2 202 2 273 2 234 9
207 2 147 2 161 2 126 2 125 2 154 2 102 2 141 1 146 1 113 1 107 1 224 8
286 2 162 2 156 2 263 2 275 2 258 2 200 2 238 1 181 1 231 1 149 1 366 6 359 2 365 3 360
2 355 2 326 3 353 2 331 2 358 1 345 1 332 9 338 2 368 2 374 1 309 1 370 1 305 2 356 1
504 2 502 2 501 2 447 4 457 2 422 2 440 3 436 1 408 2 432 3 437 2 415 9
445 2 439 2 418 2 413 2 412 2 414 2 407 1/
PLOT29
273 1 198 1 147 2 204 2 154 2 510 2 326 1 366 4 358 2 332 3 501 2 365 3 356 2 355 2 330
2 447 5 409 2 408 2 436 2 430 1 440 1 411 1/
PLOT30
126 2 162 2 213 1 273 2 254 2 149 1 204 2 231 2 276 2 259 1 109 1 368 2 365 2 355 2 366
2 307 1 300 2 326 1 509 2 436 2 447 2 440 1/
PLOT31
162 1 213 1 149 1 200 1 368 2 355 1 436 1/
PLOT32
162 2 155 2 259 1 173 1 254 1 200 2 273 1 231 2 126 2 257 1 101 8

278 2 242 1 149 1 365 3 355 2 366 2 368 2 300 2 326 2 307 1 360 1 509 1 503 2 447 3 440 2 417 1 436 2 454 1 452 2/

PLOT33

259 3 211 2 291 2 200 2 149 2 275 2 253 2 254 2 276 1 278 1 355 2 350 2 368 2 365 2 509 1 440 2 457 2 436 2 444 1 451 2 453 2/

PLOT34

198 3 204 3 226 3 189 2 209 2 134 3 163 2 140 2 100 2 245 2 219 9
277 2 113 2 184 2 114 2 205 1 135 2 237 2 293 2 125 2 149 2 278 2 259 1
162 2 106 2 107 2 295 2 136 2 222 2 211 2 291 2 200 2 275 2 101 1 358 2 301 3 332 3 326 2 368 4 371 2 360 2 353 2 365 2 307 1 380 8 510 1 504 1 457 2 453 2 443 2 440 2 436 1 415 2 430 2 439 2 432 2 422 2 447 9 408 1/

PLOT35

198 5 195 3 250 3 226 3 156 3 280 2 158 2 100 2 114 2 293 2 225 9
155 2 184 2 104 2 113 2 125 2 259 3 295 2 163 3 291 2 101 2 229 2 202 9
197 2 264 2 175 1 207 2 134 2 277 2 257 2 245 2 258 1 119 1 205 1
162 2 105 1 200 1 359 2 355 3 360 2 368 3 301 2 338 3 332 2 353 2 331 2 357 8
313 1 307 1 371 2 440 2 439 2 411 1 415 2 422 3 432 3 407 1 443 3/

PLOT36

198 5 195 4 226 3 202 2 237 2 184 2 100 2 278 2 199 2 101 9
134 2 159 2 114 2 277 2 156 2 259 2 207 2 208 2 206 2 291 2 293 3 205 9
125 2 245 2 231 2 284 2 119 1 162 2 196 1 250 2 140 2 113 2 224 1 220 9
110 2 256 2 147 2 189 2 155 1 107 1 225 1 257 1 295 1 309 2 314 1 307 2 359 2 368 3 332 3 360 2 383 1 385 1 356 8 326 1 380 2 371 2 446 2 415 2 422 2 440 2 430 1 432 3 447 2/

PLOT37

259 4 113 2 118 2 278 3 200 2 149 1 102 1 261 1 202 2 263 1 135 9
100 1 256 1 368 3 365 2 367 3 301 2 330 2 436 2 443 2 447 2/

PLOT38

149 2 200 2 278 2 162 2 100 2 276 1 135 2 254 2 259 3 231 2 250 8
211 1 287 1 273 2 368 2 365 3 367 2 366 2 307 1 355 2 350 2 300 2 447 3 436 2 457 1 440 1 451 1/

PLOT39

259 3 155 2 211 2 278 2 149 2 101 2 200 2 100 2 135 2 125 2 199 9
113 2 257 2 162 2 273 2 263 2 250 1 276 1 156 1 368 3 365 2 300 2 332 2 301 1 355 2 307 1 326 1 447 2 440 2 436 2 451 2 457 2 450 1/

PLOT40

200 2 162 2 263 1 231 1 147 2 198 1 273 1 158 1 136 2 126 1 293 8
259 1 278 1 355 2 326 2 366 3 350 2 365 3 360 2 332 4 368 3 330 1 358 9
301 2 367 4 510 3 447 5 440 3 436 1/

PLOT41

273 2 162 2 202 2 158 2 200 2 147 2 275 1 263 2 291 1 276 1 259 8
213 1 368 3 365 3 326 2 350 2 366 3 332 3 330 2 367 2 355 1
361 2 360 1 510 3 447 5 451 1 440 4 412 1 408 2 418 2 457 2 432 2 436 1/

PLOT42
149 2 200 2 258 1 278 2 213 1 155 2 231 2 141 2 100 2 259 1 125 8
118 1 162 2 174 1 198 1 199 1 276 1 355 2 368 2 365 2 436 2/
PLOT43
211 2 125 2 149 2 259 2 200 2 235 1 135 2 278 2 291 2 173 1 253 9
113 2 100 1 231 1 118 1 293 1 368 2 365 2 369 2 355 2 447 2 436 2 440 2 443 2/
PLOT44
199 5 259 4 100 3 278 2 225 2 231 2 161 2 202 2 295 2 284 1 253 9
162 2 110 2 134 2 127 2 254 1 230 2 276 1 214 1 118 1 200 2 115 1 109 8
245 2 256 2 291 1 156 1 226 1 263 2 275 2 277 2 113 2 273 1 155 1 102 8
101 1 224 1 198 1 368 5 338 3 355 2 330 2 357 1 359 3 313 2 325 1 439 2 443 2 436 2 415
1 430 3 422 2/
PLOT45
259 4 199 5 202 2 263 3 100 2 258 3 278 2 273 2 262 2 134 2 245 9
119 2 231 2 275 2 240 2 256 3 285 1 110 2 277 2 109 2 147 2 274 2 264 9
162 2 272 1 125 1 226 2 297 2 198 2 250 2 195 2 257 1 183 2 213 1 206 8
205 1 161 2 252 1 140 2 155 2 154 2 158 2 209 1 113 1 126 1 217 2 247 1
330 4 368 4 359 2 332 4 338 4 307 2 309 2 371 2 355 2 380 1 445 3 440 2
439 2 422 2 430 2/
PLOT46
126 2 200 2 273 2 355 2 365 2 367 4 368 2 326 2 366 2 332 2 504 2 447 6 440 3 451 2 457
1/
PLOT47
155 1/
PLOT48
999 0/
PLOT49
999 0/
PLOT50
259 4 278 2 162 2 198 4 113 2 202 2 189 2 156 1 231 1 226 2 161 9
100 2 135 2 273 1 256 1 155 1 136 2 184 1 367 3 368 4 365 2 330 1 301 4 355 2 332 2 359
2 509 2 447 3 440 3 436 2 430 2 449 2 415 2 422 2/
PLOT51
259 4 278 2 113 2 155 1 162 2 200 2 198 3 189 2 184 2 224 1 202 9
273 1 149 2 136 1 365 3 355 2 368 4 367 3 360 2 332 2 301 2 330 3 440 3 443 3 436 2 447
3 415 3 437 2/
PLOT52
198 4 259 4 202 3 289 2 125 2 113 2 205 2 278 2 162 2 100 2 136 9
155 2 134 2 184 2 149 2 293 1 273 1 180 1 110 1 156 1 200 2 291 1 365 4 355 2 367 2 330
2 360 2 368 4 332 2 301 3 415 2 440 3 445 2 422 2 439 2 436 2
446 2 431 2/

Appendix IVb. Species codes for all vascular and nonvascular species in Aniakchak caldera.

100	ACHBOR	Achillea borealis
101	AGRALA	Agrostis alaskana
102	AGRBOR	Agrostis borealis
104	ANGLUC	Angelica lucida
105	ANTALP	Antennaria alpina
106	ANTMON	Antennaria monocephala var. monocephala
107	ANTPAL	Antennaria pallida
108	ARALEM	Arabis lemmoni
109	ARALYR	Arabis lyrata ssp. kamchatica
110	ARCLAT	Arctagrostis latifolia var. latifolia
111	ARCLA2	Arctagrostis latifolia var. arundinacea
112	ARNCHA	Arnica chamissonis
113	ARNLES	Arnica lessingii ssp. lessingii
114	ARTARC	Artemisia arctica ssp. arctica
115	ARTBOR	Artemisia borealis
116	ARTGLO	Artemisia globularia
117	ARTTIL	Artemisia tilesii
118	ASTSIB	Aster sibiricus
119	ATHFIL	Athyrium filix-femina
120	BOTBOR	Botrychium boreale
121	BOTLUN	Botrychium lunaria
122	BOTLAN	Botrychium lanceolatum
123	CALCAN	Calamagrostis canadensis
124	CALPAL	Caltha palustris ssp. arctica
125	CAMLAS	Campanula lasiocarpa ssp. lasiocarpa
126	CARBEL	Cardamine bellidifolia
127	CARUMB	Cardamine umbellata
128	CARDIO	Carex dioica ssp. gynocrates
129	CARENA	Carex enanderi
130	CARGLA	Carex glareosa
131	CARKEL	Carex kelloggii
132	CARLAC	Carex lachenalii
133	CARLYN	Carex lyngbyaei
134	CARMAC	Carex macrochaeta
135	CARNES	Carex nesophila
136	CARPYR	Carex pyrenaica ssp. micropoda
137	CARRAR	Carex rariflora
138	CARSPE	Carex spectabilis
139	CASLYC	Cassiope lycopioides
140	CASSTE	Cassiope stelleriana
141	CERBEE	Cerastium beeringianum var. beeringianum

142	CERBE2	Cerastium beeringianum var. grandiflorum
143	CHRWRI	Chrysosplenium wrightii
144	CEOVIR	Coeloglossum viride ssp. bracteatum
145	CORTRI	Corallorrhiza trifida
146	CRYCRI	Cryptogramma crispa
147	CYSFRA	Cystopteris fragilis
148	DESBER	Deschampsia beringensis
149	DESCAE	Deschampsia caespitosa
150	DIALAP	Diapensia lapponica
151	DRACRA	Draba crassifolia
152	DRANIV	Draba nivalis
153	DRYOCT	Dryas octopetala ssp. octopetala
154	DRYDIL	Dryopteris dilatata ssp. americana
155	ELYARE	Elymus arenarius
156	EMPNIG	Empetrum nigrum
157	EPIANA	Epilobium anagallidifolium
158	EPIANG	Epilobium angustifolium
159	EPIBEH	Epilobium behringianum
160	EPIGLA	Epilobium glandulosum
161	EPIHOR	Epilobium hornemannii
162	EPILAT	Epilobium latifolium
163	EPILEP	Epilobium leptocarpum
164	EPILUT	Epilobium luteum
165	EQUARV	Equisetum arvense
166	EQUPAL	Equisetum palustre
167	EQUSIL	Equisetum silvaticum
168	EQUVAR	Equisetum variegatum
169	ERIANG	Eriophorum angustifolium
170	ERISCH	Eriophorum scheuchzeri
171	EUPMOL	Euphrasia mollis
172	FESALT	Festuca altaica
173	FESBRA	Festuca brachyphylla
174	FESRUB	Festuca rubra
175	GENALE	Gentiana aleutica
176	GENAMA	Gentiana amarella ssp. acuta
177	GENTEN	Gentiana tenella
178	GERERI	Geranium erianthum
179	GEUMAC	Geum macrophyllum ssp. macrophyllum
180	GEUROS	Geum rossii
181	GYMDRY	Gymnocarpium dryopteris
182	HERLAN	Heracleum lanatum
183	HEUGLA	Heuchera glabra
184	HIETRI	Hieracium triste
185	HIEODO	Hierlochloe odorata
186	HIPVUL	Hippuris vulgaris

187	HORBRA	Hordeum brachyantherum
188	JUNARC	Juncus arcticus
189	JUNDRU	Juncus drummondii
190	JUNCAS	Juncus castaneus
191	JUNMER	Juncus mertensianus
192	KOEISL	Koenigia islandica
193	LAGGLA	Lagotis glauca
194	LEDPAL	Ledum palustre ssp. decumbens
195	LEPPYR	Leptarrhena pyrolifolia
196	LISCOR	Listera cordata
197	LOIPRO	Loiseleuria procumbens
198	LUEPEC	Luetkea pectinata
199	LUPNOO	Lupinus nootkatensis
200	LUZARC	Luzula arcuata ssp. unalaschcensis
201	LUZMUL	Luzula multiflora
202	LUZPAR	Luzula parviflora
203	LUZTUN	Luzula tundricola
204	LUZWAH	Luzula wahlenbergii
205	LYCALP	Lycopodium alpina
206	LYCANN	Lycopodium annotinum var. annotinum
207	LYCCLA	Lycopodium clavatum
208	LYCSAB	Lycopodium sabinaefolium var. sitchense
209	LYCSEL	Lycopodium selago
210	MENTRI	Menyanthes trifoliata
211	MINMAC	Minuartia macrocarpa
212	MONFON	Montia fontana ssp. fontana
213	OXYDIG	Oxyria digyna
214	PAPALA	Papaver alaskanum
215	PARKOT	Parnassia kotzebuei
216	PARPAL	Parnassia palustris
217	PEDCAP	Pedicularis capitata
218	PEDKAN	Pedicularis kanei
219	PEDLAN	Pedicularis langsdorffii ssp. langsdorffii
220	PEDSUD	Pedicularis sudetica
221	PEDVER	Pedicularis verticillata
222	PETHYP	Petasites hyperboreus
223	PETFXH	Petasites frigidus X hyperboreus
224	PETFRI	Petasites frigidus
225	PHLCOM	Phleum commutatum
226	PHYALE	Phyllodoce aleutica ssp. aleutica
227	PLADI2	Platanthera dilatata var. chlorantha
228	PLADIL	Platanthera dilatata var. dilalata
229	PLAOBT	Platanthera obtusata
230	POAALP	Poa alpina
231	POAARC	Poa arctica ssp. arctica

232	POAAR2	Poa arctica ssp. longiculmis
233	POAPAL	Poa palustris
234	POAPAU	Poa paucispicula
235	POLACU	Polemonium acutiflorum
236	POLBOR	Polemonium boreale
237	POLVIV	Polygonum viviparum
238	POLVUL	Polypodium vulgare ssp. columbianum
239	POTPRA	Potamogeton praelongus
241	POTPAL	Potentilla palustris
242	POTVIL	Potentilla villosa
243	PRICUN	Primula cuneifolia ssp. saxifragifolia
244	PYRASA	Pyrola asarifolia
245	PYRMIN	Pyrola minor
246	PYRSEC	Pyrola secunda
247	RANESC	Ranunculus escholtzii
248	RANHYP	Ranunculus hyperboreus ssp. hyperboreus
249	RANTRI	Ranunculus trichophyllus
250	RHOCAM	Rhododendron camtschaticum ssp. camtschaticum
251	ROMSIT	Romanzoffia sitchensis
252	RUBARC	Rubus arcticus ssp. stellatus
253	RUMGRA	Rumex graminifolius
254	SAGINT	Sagina intermedia
256	SALALA	Salix alaxensis ssp. alaxensis
257	SALARC	Salix arctica ssp. crassijulis
258	SALBAR	Salix barclayi
259	SALOVA	Salix stolonifera
260	SALPHL	Salix phlebophylla
261	SALPUL	Salix pulchra
262	SALRET	Salix reticulata
263	SALROT	Salix rotundifolia
264	SALSIT	Salix sitchensis
265	SANSTI	Sanguisorba stipulata
266	SAXBRO	Saxifraga bronchialis ssp. funstonii
267	SAXCAE	Saxifraga caespitosa
268	SAXFOL	Saxifraga foliolosa var. foliolosa
269	SAXHIR	Saxifraga hirculus
270	SAXLYA	Saxifraga lyallii
271	SAXNIV	Saxifraga nivalis
272	SAXOPP	Saxifraga oppositifolia ssp. oppositifolia
273	SAXPUN	Saxifraga punctata ssp. nelsoniana
274	SAXRIV	Saxifraga rivularis ssp. flexuosa
275	SAXSER	Saxifraga serpyllifolia
276	SAXUNA	Saxifraga unalaschcensis
277	SEDROS	Sedum rosea ssp. integrifolium
278	SIBPRO	Sibbaldia procumbens

279	SILACA	Silene acaulis ssp. acaulis
280	SOLMUL	Solidago multiradiata var. multiradiata
281	SOLMU2	Solidago multiradiata var. arctica
282	SPIROM	Spiranthes romanzoffiana
284	STECAL	Stellaria calycantha ssp. isophylla
285	STECRA	Stellaria crassifolia
286	STEMON	Stellaria monantha
287	STERUS	Stellaria ruscifolia ssp. aleutica
288	TARCER	Taraxacum ceratophorum
289	THEPHA	Thelypteris phagopteris
290	TRIEUR	Trientalis europaea ssp. arctica
291	TRISPI	Trisetum spicatum
292	VACOVA	Vaccinium ovalifolium
293	VACULI	Vaccinium uliginosum
294	VACVIT	Vaccinium vitis-idaea ssp. minus
295	VAHATR	Vahlodea atropurpurea
296	VERSER	Veronica serpyllifolia ssp. humifusa
297	VERSTE	Veronica stelleri
298	VIOEPI	Viola epipsila
299	VIOLAN	Viola langsdorffii
300	ANDRUP	Andreaea rupestris
301	ARCFUL	Arctoa fulvella
303	AULPAL	Aulacomnium palustre
304	AULTUR	Aulacomnium turgidum
306	BARVIN	Didymodon vinealis
307	BARITH	Bartramia ithyphylla
308	BRAALB	Brachythecium albicans
309	BRAASP	Brachythecium asperrimum
311	BRAFRI	Brachythecium frigidum
312	BRAPLU	Brachythecium plumosum
313	BRAREF	Brachythecium reflexum var. pacificum
314	BRASTA	Brachythecium starkei var. starkei
305	BRYREC	Bryoerythrophyllum recurvirostre
316	BRYNOR	Bryoxiphium norvegicum
319	BRYBIC	Bryum bicolor
322	BRYWEI	Bryum weigelii
324	CALSTR	Calliergon stramineum
325	CERPUR	Ceratodon purpureus
326	CONTET	Conostomum tetragonum
362	CRAFIL	Cratoneuron filicinum
302	DICPEL	Dichodontium pellucidum
328	DICPAL	Dicranella palustris
385	DICSUB	Dicranella subulata
330	DICCRI	Dicranowesia crispula

386	DICANG	Dicranum angustum
331	DICSCO	Dicranum scoparium
332	DICSPA	Dicranum spadiceum
387	DICTAR	Dicranum tauricum
334	DISCAP	Distichium capillaceum
335	DITFLE	Ditrichum flexicaule
336	DREADU	Drepanocladus aduncus
337	DREEXA	Warnsdorfia exannulata var. exannulata
338	DREUNC	Sanionia uncinata
382	EURPUL	Eurhynchium pulchellum
339	GRIDON	Grimmia donniana
341	GRIALP	Schistidium rivulare var. rivulare
342	GRIAPO	Schistidium apocarpum var. stricta
343	GRITOR	Grimmia torquata var. torquata
344	HYLSPL	Hylocomium splendens
323	HYPLIN	Hypnum lindbergii
345	ISOELE	Pseudotaxiphyllum elegans
346	ISOPUL	Isopterygium pulchellum
347	LESRAD	Pseudoleskea radicosa var. denudata
348	LESSTE	Pseudoleskea stenophylla
349	MNIAMB	Mnium ambiguum
350	OLIHER	Oligotrichum hercynicum
351	PHIFON	Philonotis fontana var. fontana
352	PLAAFF	Plagiomnium affine
384	PLACAV	Plagiothecium cavifolium
353	PLESCH	Pleurozium schreberi
354	POGALP	Polytrichastrum alpinum
355	POGURN	Pogonatum urnigerum
356	POHCRU	Pohlia cruda
357	POHWAH	Pohlia wahlenbergii
358	POLCOM	Polytrichum commune
359	POLJUN	Polytrichum juniperinum
360	POLPIL	Polytrichum piliferum
361	POLSEX	Polytrichum sexangulare
364	RACCAN	Racomitrium ericoides
368	RACERI	Racomitrium ericoides
365	RACFAS	Racomitrium fasciculare
366	RACLAN	Racomitrium lanuginosum
367	RACSUD	Racomitrium sudeticum
369	RHIPUN	Rhizomnium punctatum
370	RHYLOR	Rhytidiadelphus loreus
371	RHYSQU	Rhytidiadelphus squarrosus
372	RHYTRI	Rhytidialelphus triquetrus
373	SPHGIR	Sphagnum girgensohnii
374	SPHRUS	Sphagnum russowii

375	SPHSQU	Sphagnum squarrosum
376	SPHTER	Sphagnum teres
377	SPLSPH	Splachnum sphaericum
378	SPLVAS	Splachnum vasculosum
379	TETMNI	Tetraplodon mniodes
380	TIMAUS	Timmia austriaca
381	TORRUR	Tortula ruralis
400	ALLALP	Allantoparmelia alpicola
403	CETISL	Cetraria islandica ssp. orientalis
404	CLAARB	Cladina arbuscula
405	CLAMIT	Cladina mitis
406	CLABEL	Cladonia bellidiflora
407	CLACHL	Cladonia chlorophaea
408	CLABOR	Cladonia borealis
409	CLACOR	Cladonia cornuta
410	CLAPYX	Cladonia pyxidata
411	CLASCA	Cladonia scabriuscula
412	CLASTR	Cladonia stricta
413	CLASUL	Cladonia sulphurina
414	CLAVER	Cladonia verticillata
415	OLBLIN	Lobaria linita
457	MELGRP	Melanelia stygia group
416	NEPBEL	Nephroma bellum
417	OMPVIR	Omphalodiscus virginis
418	PANPEZ	Pannaria pezizoides
419	PAROMP	Parmelia omphalodes
420	PARSAX	Parmelia saxatilis
421	PARSUL	Parmelia sulcata
422	PELAPY	Peltigera aphthosa
423	PELCAN	Peltigera canina
424	PELCOL	Peltigera collina
425	PELDID	Peltigera didactyla
427	PELHOR	Peltigera horizontalis
428	PELKRI	Peltigera kristonssonii
430	PELMEM	Peltigera membranaceae
431	PELPRA	Peltigera praetextata
432	PELSCA	Peltigera scabrosa
433	PELVEN	Peltigera venosa
434	PILROB	Pilophorus robustus
435	PHYCAE	Physcia caesia
436	PLAGEL	Placopsis gelida
437	PSEMIN	Pseudephebe minuscula
438	PSEPUB	Pseudephebe pubescens
439	PSOHYP	Psoroma hypnorum

440	SOLCRO	Solarina crocea
441	SPHFRA	Sphaerophorus fragilis
442	SPHGLO	Sphaerophorus globosus
443	STEALP	Stereocaulon alpinum
444	STEGLA	Stereocaulon glareosum
445	STERIV	Stereocaulon rivulorum
446	STETOM	Stereocaulon tomentosum
447	STEVES	Stereocaulon vesuvianum
448	THEVER	Thamnolia vermicularis
449	UMBARC	Umbilicaria arctica
450	UMBCYL	Umbilicaria cylindrica
451	UMBHYP	Umbilicaria hyperborea var. hyperborea
452	UMBHY2	Umbilicaria hyperborea var. radicicula
453	UMBPRO	Umbilicaria proboscidea
454	UMBTOR	Umbilicaria torrefacta
455	XANCAN	Xanthoria candelaria
456	XANELE	Xanthoria elegans
500	BARHAT	Barbilophozia hatcheri
501	DIPALB	Diplophyllum albicans
502	DIPTAX	Diplophyllum taxifolium
503	GYMOBT	Gymnomitrion obtusum
504	LOPSUD	Lophozia sudetica
505	MARCHA	Marchantia polymorpha
506	MARALP	Marsupella alpina
507	MARUST	Marsupella ustulata
508	MOEBLY	Moerckia blyttii
509	NARSCA	Nardia scalaris
510	PLEALB	Pleuroclada albescens
511	PTICIL	Ptilidium ciliare
999	EMPTY	EMPTY PLOT

Appendix Va. Raw data for nonvascular strata in compact data format for analysis in PC-ORD (McCune 1993). The 3 digit number represents the species code (see Appendix I.1b); the subsequent single digit represents abundance (see Methods Section for cover class codes).

PLOT01
368 1 355 1 436 2/
PLOT02
355 2 368 2 436 2/
PLOT03
368 2 355 2 436 2/
PLOT04
366 4 360 2 380 3 338 3 365 3 371 3 372 2 330 2 342 2 356 2 368 3 386 2 307 2 303 2 381 1 331 3 347 2 379 2 325 8 373 1 334 1 507 2 501 2 505 1 508 1 353 3
415 3 440 2 447 2 434 2 436 2 430 3 422 2 454 2 439 9 411 2 457 2 408 2 420 1 446 2 428 1/
PLOT05
366 4 372 4 353 4 368 5 380 2 331 1 304 2 302 1 354 3 374 2 338 2 332 3 307 1 365 3 379 1 321 1 371 3 359 2 509 8 360 1 415 4 430 3 446 3 448 2 440 2 453 2 454 3 400 1 436 2 434 2 447 9 425 2 441 2 457 4 408 2 420 2 405 1 422 2 432 1/
PLOT06
368 6 366 4 365 3 353 2 356 3 307 1 331 1 355 2 357 1 380 1 300 9
364 1 339 1 338 1 511 1 457 4 447 3 453 2 454 3 440 2 445 2 422 2 415 4 448 2 430 3 418 8 439 1 433 1 408 2 417 2 452 2 400 3 437 2 442 1 419 1 436 2 425 1/
PLOT07
999 0/
PLOT08
351 3 336 4 325 2 337 4 375 1 324 3 359 1/
PLOT09
368 4 355 3 371 4 351 5 338 3 369 2 325 2 328 2 311 3 359 1
378 2 353 2 303 3 377 2 509 2 508 1 415 2 430 4 425 2 423 2 444 1 432 3 422 2/
PLOT10
368 4 355 2 307 1 365 2 300 1 366 3 415 2 430 3 436 3 422 2 445 2 410 2 439 1 457 2 440 1 453 2 447 1 438 2 400 2/
PLOT11
368 4 355 2 342 2 338 2 366 3 308 2 364 2 306 1 356 1 307 1 445 2 436 3 439 2 430 3 415 2 422 3 440 2 457 2 453 1 433 1/
PLOT12
368 4 366 3 355 3 326 2 301 1 300 3 361 2 365 2 360 1 440 2 445 2 436 2 415 3 447 3 411 2 439 2 430 3 422 3 438 9 453 2 457 2 400 2 408 2 418 1 437 1 420 1/
PLOT13
371 6 359 3 338 2 330 1 325 1 367 2 377 1 351 3 369 2 336 9
505 1 415 2 410 1 430 3 427 2 432 1/

PLOT14
338 6 371 4 352 2 359 2 357 1 330 2 355 2 368 2 365 2 342 2 366 9
379 2 500 2 430 3 446 2 426 2 415 2 436 2 439 2 414 2 422 2 457 1 408 8
453 1 447 1/
PLOT15
338 4 368 3 359 2 366 3 360 2 371 4 355 2 344 2 331 2 302 9
356 2 372 2 353 1 380 2 352 2 348 2 384 2 365 2 332 2 307 1 330 2 300 9
305 2 351 2 306 2 342 3 381 3 335 2 341 2 334 2 349 8
303 1 322 2 505 2 504 2 445 2 414 2 415 2 422 1 432 1 430 3 427 3 439 3 418 9
426 2 420 3 408 1 437 1 447 2/
PLOT16
371 5 338 4 325 1 368 2 359 3 379 1 366 2 308 1 348 1 505 1 415 2 430 4 446 1 432 1 428
1 443 1 439 1 436 1 411 1 409 1/
PLOT17
366 4 331 3 372 2 371 3 338 4 353 2 314 1 365 3 359 1 356 9 355 1 330 1 381 1 325 2 511
1 408 1 455 1 421 1 420 1/
PLOT18
371 4 338 4 359 2 352 2 368 2 376 2 369 2 311 4 303 2 375 1 324 2 505 3 430 3 415 3 422
2 439 1 432 1/
PLOT19
372 5 359 2 338 4 348 2 357 2 365 3 303 1 342 1 325 3 366 2 368 2
360 2 379 1 505 2 446 3 415 2 432 2 408 1 410 1 404 1 403 1 439 2 422 2 436 9
430 2 440 1/
PLOT20
368 4 366 4 331 3 359 2 371 3 372 2 338 3 307 2 380 2 355 9
357 2 330 3 300 2 360 1 342 3 356 2 379 1 384 2 305 1 344 2 334 8
312 2 348 1 369 1 303 2 351 2 311 2 323 2 343 1 373 1 445 1 415 3 439 2 430 2 440 2 411
2 432 3 408 3 436 2 447 9 454 2 451 2 438 2 420 3 431 2 442 2 422 2 403 2 407 2 425 1
456 1/
PLOT21
368 1 506 2 502 1 508 2 436 2/
PLOT22
368 1 436 1/
PLOT23
368 1 436 2/
PLOT24
368 3 365 2 355 2 360 2 367 2 326 2 356 1 307 2 509 2 418 1 447 3 440 2 436 2 457 2/
PLOT25
360 2 355 2 366 4 368 4 330 2 359 2 332 3 358 2 356 2 364 9
301 1 382 2 503 2 502 2 509 2 504 1 447 5 446 3 409 3 436 2 408 3 406 2 407 2 439 2 418
9 451 1 432 2 433 1/
PLOT26
368 3 365 2 326 1 355 2 300 2 447 3 451 2 438 2 436 2 440 2/
PLOT27
368 2 301 1 300 1 360 1 355 1 443 2 436 2 440 2 438 2 453 2/

PLOT28
366 6 359 2 365 3 360 2 355 2 326 3 353 2 331 2 358 1 345 1 332 9
338 2 368 2 374 1 309 1 370 1 305 2 356 1 504 2 502 2 501 2
447 4 457 2 422 2 440 3 436 1 408 2 432 3 437 2 415 9
445 2 439 2 418 2 413 2 412 2 414 2 407 1/
PLOT29
510 2 326 1 366 4 358 2 332 3 501 2 365 3 356 2 355 2 330 2 447 5 409 2 408 2 436 2 430
1 440 1 411 1/
PLOT30
368 2 365 2 355 2 366 2 307 1 300 2 326 1 509 2 436 2 447 2 440 1/
PLOT31
368 2 355 1 436 1/
PLOT32
365 3 355 2 366 2 368 2 300 2 326 2 307 1 360 1 509 1 503 2 447 3 440 2 417 1 436 2 454
1 452 2/
PLOT33
355 2 350 2 368 2 365 2 509 1 440 2 457 2 436 2 444 1 451 2 453 2/
PLOT34
358 2 301 3 332 3 326 2 368 4 371 2 360 2 353 2 365 2 307 1 380 8
510 1 504 1 457 2 453 2 443 2 440 2 436 1 415 2 430 2 439 2 432 2 422 2 447 9
408 1/
PLOT35
359 2 355 3 360 2 368 3 301 2 338 3 332 2 353 2 331 2 357 8
313 1 307 1 371 2 440 2 439 2 411 1 415 2 422 3 432 3 407 1 443 3/
PLOT36
309 2 314 1 307 2 359 2 368 3 332 3 360 2 383 1 385 1 356 8
326 1 380 2 371 2 446 2 415 2 422 2 440 2 430 1 432 3 447 2/
PLOT37
368 3 365 2 367 3 301 2 330 2 436 2 443 2 447 2/
PLOT38
368 2 365 3 367 2 366 2 307 1 355 2 350 2 300 2 447 3 436 2 457 1 440 1 451 1/
PLOT39
368 3 365 2 300 2 332 2 301 1 355 2 307 1 326 1 447 2 440 2 436 2 451 2 457 2 450 1/
PLOT40
355 2 326 2 366 3 350 2 365 3 360 2 332 4 368 3 330 1 358 9 301 2 367 4 510 3 447 5 440
3 436 1/
PLOT41
368 3 365 3 326 2 350 2 366 3 332 3 330 2 367 2 355 1 361 2 360 1 510 3 447 5 451 1 440
4 412 1 408 2 418 2 457 2 432 2 436 1/
PLOT42
355 2 368 2 365 2 436 2/
PLOT43
368 2 365 2 369 2 355 2 447 2 436 2 440 2 443 2/
PLOT44
368 5 338 3 355 2 330 2 357 1 359 3 313 2 325 1 439 2 443 2 436 2 415 1 430 3 422 2/

PLOT45
330 4 368 4 359 2 332 4 338 4 307 2 309 2 371 2 355 2 380 1 445 3 440 2 439 2 422 2 430 2/
PLOT46
355 2 365 2 367 4 368 2 326 2 366 2 332 2 504 2 447 6 440 3 451 2 457 1/
PLOT47
999 0/
PLOT48
999 0/
PLOT49
999 0/
PLOT50
367 3 368 4 365 2 330 1 301 4 355 2 332 2 359 2 509 2 447 3 440 3 436 2 430 2 449 2 415 2 422 2/
PLOT51
365 3 355 2 368 4 367 3 360 2 332 2 301 2 330 3 440 3 443 3 436 2 447 3 415 3 437 2/
PLOT52
365 4 355 2 367 2 330 2 360 2 368 4 332 2 301 3 415 2 440 3 445 2 422 2 439 2 436 2 446 2 431 2/

Appendix Vb. Raw data for vascular strata in compact data format for analysis in PC-ORD (McCune 1993). The 3 digit number represents the species code (see Appendix I.1b); the subsequent single digit represents abundance (see Methods Section for cover class codes).

PLOT01
149 1 138 1 200 1 155 3 100 1 254 1 278 1 199 2 259 2/
PLOT02
149 1 254 1 268 1 138 2 155 2/
PLOT03
155 1 100 1 199 2 149 1 280 1 200 1 134 1 254 1/
PLOT04
199 3 257 5 156 4 293 3 250 3 197 2 100 2 280 2 162 2 278 2 277 9
215 2 106 2 105 2 224 2 262 2 113 1 158 2 104 3 275 2 219 2 174 1 211 9
149 1 171 1 294 1 266 2 125 1 217 1 252 2 200 2 276 1 209 1 273 8
147 1 117 3 138 2 110 1 144 1 291 1 242 1 121 1 163 2 120 1 256 2 258 9
141 1 284 1 127 1 227 1 289 2 297 1 288 1 182 2 226 2 245 2 175 1 299 8
264 2 155 1 225 1 254 1 143 1 122 1 165 1/
PLOT05
156 6 257 5 277 2 113 2 293 4 106 2 250 4 174 2 219 2 211 2 266 9
237 2 231 2 138 3 114 2 203 2 275 2 242 2 100 2 273 2 291 1 286 1 253 8
125 1 215 2 197 2 276 1 173 1 217 2 180 1 294 2 280 2 259 1 218 1 107 8
224 1 118 1 245 1 110 1 284 1 149 1 262 1/
PLOT06
156 5 257 4 197 4 174 2 106 2 218 2 280 2 211 2 293 4 125 2 250 1
277 2 138 2 113 2 201 2 291 2 100 2 237 2 162 1 215 2 107 2 271 1 242 8
149 2 219 1 224 1 266 2 273 1 200 1 275 2 231 1 272 1 253 2 173 1 259 9
217 1 141 1 180 1 165 1 276 1/
PLOT07
133 5 186 3 124 3/
PLOT08
129 4 124 3 148 2 248 2 241 2 192 3 212 1 135 3 165 1 188 2 259 8
133 1 284 2 261 2/
PLOT09
199 4 155 3 165 3 258 2 104 3 259 4 162 2 174 2 215 3 188 1
201 2 100 2 280 2 277 2 149 2 110 1 257 3 273 2 288 1 161 2 118 2 134 9
132 2 190 2 224 2 286 1 253 1 227 1 270 1 256 3 267 1 171 1 109 8
231 2 293 2 191 1 225 1 158 1 278 1/
PLOT10
259 3 266 2 275 2 106 2 279 2 180 3 138 2 293 3 219 2 211 2 277 9
271 1 240 2 125 2 200 2 230 1 291 1 115 2 143 1 173 1 254 1 149 2 113 9
250 3 253 1 141 1 257 2 237 1 278 2 156 3 280 1 272 1/
PLOT11
266 2 162 2 211 2 275 2 259 4 277 2 180 2 278 2 272 2 138 2 173 9

115 2 100 2 141 2 253 2 252 1 149 2 254 1 271 2 240 2 214 2 219 2 113 9
143 2 125 2 193 1 291 2 200 2 286 1 114 2 236 2 237 1 215 1 118 9
273 1 106 1 174 1 250 2 257 2 147 1 231 1 152 1 156 2/
PLOT12
257 4 259 4 180 2 250 3 219 2 277 2 162 2 116 2 125 2 211 2 138 9
200 2 106 2 174 2 275 2 270 2 113 2 197 2 291 1 149 2 156 2 293 2 253 9
266 2 278 2 273 2 254 1 272 1 114 2 100 1 255 1 240 2 252 1 204 2 158 8
256 1 237 1 193 1 231 1/
PLOT13
256 3 199 4 252 4 277 2 104 3 110 4 100 2 162 2 258 3 264 2 245 9
224 2 273 2 159 2 127 2 134 3 188 2 155 2 225 2 113 2 259 3 135 2 274 8
231 2 129 2 278 2 165 2 257 2 117 1 244 2 262 1 203 1 221 1 132 8
237 1 247 1 288 1 144 1 147 1/
PLOT14
256 3 199 3 155 4 104 4 134 3 221 2 156 2 266 2 162 2 113 2 211 9
259 2 118 2 286 2 215 2 100 2 277 2 174 2 110 2 231 2 291 2 230 2 222 9
127 2 160 2 161 2 293 2 273 2 278 2 284 2 109 2 141 2 148 2 252 9
102 1 253 2 125 2 254 2 173 1 242 2 115 2 275 2 132 2 245 2 258 3 200 9
279 1/
PLOT15
256 3 199 4 250 4 156 3 257 5 201 2 107 2 291 2 280 2 197 2 174 9
277 2 100 2 252 2 125 2 113 2 101 2 215 2 220 2 175 1 135 4 121 1 295 9
114 2 222 2 227 1 225 2 245 2 293 2 158 2 258 2 237 2 231 2 110 4 262 8
200 1 219 1 209 1 123 1 299 2 122 2 290 2 144 1 297 2 161 2 284 2 165 9
119 2 195 2 127 2 117 1 254 1 147 1 242 2 288 1 273 2 106 1 162 1 155 8
271 1 148 1 159 1 278 1/
PLOT16
256 3 258 4 199 4 111 4 134 3 100 2 113 2 277 2 293 2 281 2 104 9 158 2 252 3 259 4 257
2 174 2 231 2 155 2 156 3 221 2 222 2 284 1 165 9 253 1 291 2 135 1 278 1 162 2 161 2
148 1 182 2 127 2 245 2 225 9 125 1 109 1 141 1 103 1/
PLOT17
156 4 257 4 293 4 250 3 277 2 114 2 113 2 222 2 290 2 194 2 252 9
221 2 231 1 199 3 201 2 174 2 200 2 165 2 155 2 148 2 134 2 100 2 158 8
110 2 104 2 256 2 258 3 175 1 237 2 280 2 284 1 298 1 245 1 182 2 123 8
160 2 161 2 117 1 197 2 162 2 294 2 125 2 135 2 219 1 278 1 291 1 101 8
242 2 286 1 225 1 171 1 192 2 259 2/
PLOT18
156 3 199 3 256 3 293 3 104 3 222 2 182 2 118 2 277 2 225 2 165 1
179 2 273 2 113 2 252 3 221 2 237 2 142 2 204 2 278 2 215 2 110 2 130 9
231 2 134 3 245 2 297 2 100 2 259 2 262 2 288 2 174 2 253 2 162 3 127 9
201 2 235 2 291 1 275 1 250 2 200 1 269 8 258 3 220 1 188 1 160 2 270 2 296 2 192 1 227
1 148 1 129 2 255 2 211 8 117 1 284 1 195 1 155 1/
PLOT19
256 3 155 4 280 2 259 3 199 2 156 2 278 2 293 2 252 2 100 2 245 9
162 2 215 2 125 2 118 2 182 2 222 2 113 2 277 2 258 3 101 2 117 2 174 9

134 2 298 1 110 2 104 2 102 1 157 2 161 2 231 2 284 2 175 2 291 2 225 9
123 3 135 2 141 2 276 2 149 2 154 2 115 2 109 2 201 2 190 2 192 2 273 8
253 1 200 1 275 1 211 2 173 1 257 3 242 2 197 2 106 1 266 1/
PLOT20
197 2 250 3 125 2 162 2 222 2 280 2 257 5 100 2 205 2 156 5 246 9
165 2 293 4 199 3 252 2 237 2 291 2 245 2 155 2 278 2 219 2 175 2 134 9
231 2 104 2 295 2 159 2 215 2 225 2 264 2 101 2 258 2 147 1 182 2 259 9
171 1 201 2 113 2 262 2 107 2 299 2 106 2 242 2 277 2 200 2 174 2 273 9
227 1 118 1 217 1 211 2 209 1 115 1 275 2 294 2 114 2 194 1 286 1 272 8
284 1/
PLOT21
999 0/
PLOT22
149 1/
PLOT23
999 0/
PLOT24
138 3 259 4 278 3 125 2 263 3 277 2 102 2 200 2 253 2 173 9 106 2 158 1 257 2 291 2 165
2 162 2 276 2 130 2 254 2 211 2 273 2 204 9 242 1 213 1 234 2 113 1 288 1 149 3 231 1/
PLOT25
273 2 278 2 204 2 263 3 163 2 275 2 291 2 254 2 119 2 158 1 162 9
274 1 173 2 276 2 200 2 198 3 146 1 147 2 213 2 258 2 126 1 143 1 259 8
184 1 113 1 224 1 154 1 136 1/
PLOT26
259 3 293 2 114 2 277 2 220 2 135 2 149 2 253 2 125 2 113 2 278 9
200 2 211 1 291 2 107 1 101 1 280 1 106 1/
PLOT27
259 3 200 2 149 2 275 2 125 2 211 2 135 2 291 1 250 1 293 2 220 9 253 2/
PLOT28
158 2 291 2 209 2 259 2 101 2 268 2 119 2 278 2 202 2 273 2 234 9
207 2 147 2 161 2 126 2 125 2 154 2 102 2 141 1 146 1 113 1 107 1 224 8
286 2 162 2 156 2 263 2 275 2 258 2 200 2 238 1 181 1 231 1 149 1/
PLOT29
273 1 198 1 147 2 204 2 154 2/
PLOT30
126 2 162 2 213 1 273 2 254 2 149 1 204 2 231 2 276 2 259 1 109 1/
PLOT31
162 1 213 1 149 1 200 1/
PLOT32
162 2 155 2 259 1 173 1 254 1 200 2 273 1 231 2 126 2 257 1 101 8
278 2 242 1 149 1/
PLOT33
259 3 211 2 291 2 200 2 149 2 275 2 253 2 254 2 276 1 278 1/
PLOT34
198 3 204 3 226 3 189 2 209 2 134 3 163 2 140 2 100 2 245 2 219 9

277 2 113 2 184 2 114 2 205 1 135 2 237 2 293 2 125 2 149 2 278 2 259 1
162 2 106 2 107 2 295 2 136 2 222 2 211 2 291 2 200 2 275 2 101 1/
PLOT35
198 5 195 3 250 3 226 3 156 3 280 2 158 2 100 2 114 2 293 2 225 9
155 2 184 2 104 2 113 2 125 2 259 3 295 2 163 3 291 2 101 2 229 2 202 9
197 2 264 2 175 1 207 2 134 2 277 2 257 2 245 2 258 1 119 1 205 1
162 2 105 1 200 1/
PLOT36
198 5 195 4 226 3 202 2 237 2 184 2 100 2 278 2 199 2 101 9
134 2 159 2 114 2 277 2 156 2 259 2 207 2 208 2 206 2 291 2 293 3 205 9
125 2 245 2 231 2 284 2 119 1 162 2 196 1 250 2 140 2 113 2 224 1 220 9
110 2 256 2 147 2 189 2 155 1 107 1 225 1 257 1 295 1/
PLOT37
259 4 113 2 118 2 278 3 200 2 149 1 102 1 261 1 202 2 263 1 135 9
100 1 256 1/
PLOT38
149 2 200 2 278 2 162 2 100 2 276 1 135 2 254 2 259 3 231 2 250 8
211 1 287 1 273 2/
PLOT39
259 3 155 2 211 2 278 2 149 2 101 2 200 2 100 2 135 2 125 2 199 9
113 2 257 2 162 2 273 2 263 2 250 1 276 1 156 1/
PLOT40
200 2 162 2 263 1 231 1 147 2 198 1 273 1 158 1 136 2 126 1 293 8
259 1 278 1/
PLOT41
273 2 162 2 202 2 158 2 200 2 147 2 275 1 263 2 291 1 276 1 259 8
213 1/
PLOT42
149 2 200 2 258 1 278 2 213 1 155 2 231 2 141 2 100 2 259 1 125 8
118 1 162 2 174 1 198 1 199 1 276 1/
PLOT43
211 2 125 2 149 2 259 2 200 2 235 1 135 2 278 2 291 2 173 1 253 9
113 2 100 1 231 1 118 1 293 1/
PLOT44
199 5 259 4 100 3 278 2 225 2 231 2 161 2 202 2 295 2 284 1 253 9
162 2 110 2 134 2 127 2 254 1 230 2 276 1 214 1 118 1 200 2 115 1 109 8
245 2 256 2 291 1 156 1 226 1 263 2 275 2 277 2 113 2 273 1 155 1 102 8
101 1 224 1 198 1/
PLOT45
259 4 199 5 202 2 263 3 100 2 258 3 278 2 273 2 262 2 134 2 245 9
119 2 231 2 275 2 240 2 256 3 285 1 110 2 277 2 109 2 147 2 274 2 264 9
162 2 272 1 125 1 226 2 297 2 198 2 250 2 195 2 257 1 183 2 213 1 206 8
205 1 161 2 252 1 140 2 155 2 154 2 158 2 209 1 113 1 126 1 217 2 247 1/
PLOT46
126 2 200 2 273 2/

PLOT47
155 1/
PLOT48
999 0/
PLOT49
999 0/
PLOT50
259 4 278 2 162 2 198 4 113 2 202 2 189 2 156 1 231 1 226 2 161 9
100 2 135 2 273 1 256 1 155 1 136 2 184 1/
PLOT51
259 4 278 2 113 2 155 1 162 2 200 2 198 3 189 2 184 2 224 1 202 9
273 1 149 2 136 1/
PLOT52
198 4 259 4 202 3 289 2 125 2 113 2 205 2 278 2 162 2 100 2 136 9
155 2 134 2 184 2 149 2 293 1 273 1 180 1 110 1 156 1 200 2 291 1/