SMALL-SCALE COMMUNITY ANALYSES OF ALPINE RIDGE VEGETATION IN THE CENTRAL SIERRA NEVADA

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Abstract

Most studies of alpine vegetation communities focus on the variation occurring across large scales, in which diverse environmental habitats are assessed across the landscape and detailed plant associations are described. However, community patterns occurring at more intricate scales are easily concealed by such a broad perspective. To complement large-scale studies, we assessed smaller-scale patterns occurring at the extremes of moisture and exposure gradients in an alpine environment. We studied the variation in plant community composition among and within seven ridges extending down two rocky metamorphic peaks in Yosemite National Park. Species cover and environmental factors (proximity to a summit, elevation, aspect, slope, and substrate size) were sampled in 281 2 × 2-meter plots. Variation among ridges was primarily determined by differences in aspect. Within the ridges, although the physical environment in which we sampled was seemingly homogenous, ordinations identified two distinct vegetation types: (1) high diversity and high cover vegetation (HD), dominated by cushion plants and (2) low diversity and low cover vegetation (LD), dominated by plants in large clumps or small rosettes. In general, LD vegetation was found nearer to the summit and was highly variable in its component species, while HD vegetation was found farther along the ridgeline and was relatively uniform. This non-intuitive pattern in which cushion plants do not dominate the most exposed habitat occurred independent of elevation. Instead, our data suggest that along with changes in rock size and aspect, proximity to a summit is a meaningful factor governing alpine community structure. We discuss the water limited conditions imposed by the absence of smaller rock structure at the summit and how this may allow for only the sparse LD vegetation to persist there.

Key Words: alpine plant communities, environmental gradients, ordination, scale, Yosemite National Park, Sierra Nevada.

Alpine plant communities have been analyzed and classified for decades with studies that usually operate across broad geographic scales and include diverse habitats (e.g., Douglas and Bliss 1977; Kirkpatrick and Bridle 1998; Wiser 1998). These studies often (1) establish broad inventories of co-occurring alpine plant species and (2) identify primary environmental factors that control these patterns (e.g., Taylor 1984; Urbanczyk and Henderson 1994). The resulting alpine vegetation patterns have consisted of well-defined groups of species, which are governed primarily by moisture availability (e.g., Major and Taylor 1988). Moisture availability has been assessed using surrogate factors such as aspect, exposure, and temperature to assess vegetation patterns (Mark et al. 2000). However, it is unclear whether or not these factors carry the same importance at finer scales.

Patterns at different scales often elucidate different ecological processes (Turner 1989). However, only fairly recently has this question of scale begun to be evaluated and applied to alpine vegetation studies (Kirkpatrick and Bridle 1998; Mark et al. 2000). One study from the North Carolina piedmont confirms that examining patterns at a smaller

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scale can be useful in detecting locally important processes, which would normally be masked by more widely varying factors in large-scale studies (Reed et al. 1993). In addition, Mohler (1983), in a theoretical simulation study, showed that intense sampling at gradient extremes produces more accurate autecological species descriptions. Along with distinguishing patterns that may be related to local ecological processes, appropriately-scaled alpine community analyses can provide important baseline data for monitoring and predicting future vegetation dynamics that may result from climate changes (Gottfried et al. 1998; Mark et al. 2000).

Our study uses a classical community ordination approach with a contemporary consideration of scale to analyze alpine vegetation in the central Sierra Nevada. We chose a relatively homogenous habitat (rocky metamorphic ridges), to limit overpowering patterns originating from extensive variation in moisture and exposure, which are often primary factors involved in governing alpine plant communities. Ridges represent an extreme xeric environment because of their broad contact with drying winds and intense solar radiation (Billings 2000). This is especially true in the Sierra Nevada, where much of the alpine flora is more closely related to adjacent eastern high desert species rather than traditional arctic-alpine taxa (Chabot and Billings 1972; Major and Taylor 1988). Because of the

TABLE 1. GENERAL CHARACTERISTICS FOR THE SEVEN RIDGES EXTENDING OFF OF MT. DANA AND MT. GIBBS, YOSEMITE NATIONAL PARK. Numbers in parentheses represent the percentage of the total plots sampled on that ridge that contained vegetation.

Peak	Ridge	Elevation range (m)	Aspect	Length (m)	Total plots	Vegetated plots
Dana	1	3980–3360	NW	1120	56	43 (77%)
Dana	2	3980–3785	E	480	24	9 (38%)
Dana	3	3785–3755	NE	520	26	20 (78%)
Gibbs	4	3890–3600	WNW	960	48	37 (77%)
Gibbs	5	3890–3700	ESE	640	32	25 (78%)
Gibbs	6	3890–3765	NNE	760	38	18 (47%)
Gibbs	7	3890–3655	SW	1140	57	47 (82%)
All ridges					281	199 (71%)

almost desert-like habitat found on ridges, our samples were effectively taken at the extreme end of a montane moisture gradient. In addition, aspect could be an important factor determining plant communities at high altitudes (Pinder et al. 1997). However, on high altitude ridges, we predicted that the degree to which aspect would govern community composition would be minimal because all ridges are exposed to sun and precipitation to a similar degree, unlike their adjacent slopes. In addition to receiving similar exposure, the substrate on our study ridges was overwhelmingly composed of large metamorphic rocks, which have the tendency to break into small irregular fragments, allowing for very minimal moisture retention (Taylor 1984). Since different substrates often harbor very different plant communities (Johnson and Billings 1962; Bamberg and Major 1968), we hoped that minimizing the variation in different rock types might reveal more subtle patterns in the vegetation.

The primary objectives of our study were to describe the rocky alpine ridge-top vegetation patterns occurring at small scales and to relate these patterns to variation in the physical environment. Specifically, we sought to describe the variation in species composition and abundance among and within the ridges. By relating these patterns to measured abiotic variables (i.e., proximity to a summit, elevation, aspect, slope, and rock size), we hoped to discern the primary environmental factors controlling plant composition and abundance in this relatively homogenous habitat. Finally, we wished to examine how the vegetative patterns and governing factors in our small-scale study compared with those identified in larger-scale studies.

METHODS

Study Areas

The two peaks we studied (Mt. Dana and Mt. Gibbs) are located in the central Sierra Nevada on the border between the Yosemite Wilderness and the Ansel Adams Wilderness in Mono County, California. Mt. Dana (3983 m; 37°57'59"N, 119°13'13"W) has two distinct ridges, one of which we divided and analyzed as two different ridges

because the second half takes a distinct jagged turn, separating it from the first part of the ridge. Mt. Gibbs (3890 m; 37°52'38"N, 119°12'40"W) has four distinct ridges extending off its summit. The substrate on both peaks is metamorphic in origin. The climate in this region consists of long cold winters, short dry summers, and frequent strong winds. This creates an environment where plants must tolerate low temperature extremes, periodic heat stress, and high rates of evapotranspiration (Körner 2003).

Data Collection

The data for this study were collected in July and August of 2001 while biomass production was at its peak. This particular summer was relatively dry, so species abundances should be considered only as a relative description of what can be found on these ridges.

The study included seven ridges, each containing 24–57 sampling plots (Table 1). Sampling for each ridge began at the summit and moved down the ridge. The plots were located in a line that was defined as the highest point along the ridge. Thus, the line was able to curve with the ridge as it descended downward at various aspects. Plots were each 2 × 2 meters and were placed at random distances between 15 and 25 meters apart, down the length of the ridge. We stopped sampling when the defining apex of the ridge was no longer apparent. This point was reached when the angle of the slopes descending off each side of the ridge were roughly horizontal.

At each plot, we measured distance from the summit, elevation, aspect, slope, species composition, and rock size composition. Each plot was divided into four 1 × 1-meter subplots. In each subplot, vegetation and substrate were classified and quantified using standard relevé techniques. Each distinct clump of vegetation was classified into one of five size classes based on the clump's basal diameter: 1–2.5 cm, 2.5–5 cm, 5–10 cm, 10–20 cm, and 20–30 cm. For each species in the plot, we recorded its frequency at each size class. These were transformed into percent cover values by dividing total basal area by plot area. We estimated

that each clump was roughly a circle and used the median diameter for each size class to calculate the basal area covered by each size class. To determine rock size composition we visually estimated the percent cover of rocks of different diameters: soil–1 cm, 1–5 cm, 5–30 cm, 30–60 cm, and >60 cm. The "major substrate size" was defined as the size class taking up the greatest proportion of the plot. We identified plant species in the field or in the Yosemite National Park research station in Tuolumne Meadows, using Hickman (1993), Weeden (1996), and Botti (2001).

Data Analysis

We preformed Bray-Curtis ordinations with the software PC-Ord 4.0 (McCune and Mefford 1999) to assess patterns in vegetation composition. To avoid effects that can result from rare occurrences, we included only those species that were found in >5% of the plots. We transformed our data with Beal's smoothing function, a robust technique used to blend information from a large number of small sample units, where many species have minimal cover (McCune 1994). Using the ordination solution on two axes, we used both Pearson correlations and linear regressions to analyze relationships among environmental factors and species composition. Finally, we used Multi-Response Permutation Procedures (MRPP) in PC-Ord 4.0 (McCune and Mefford 1999) to evaluate differences in composition between ridges.

RESULTS

We found a total of 36 plant species, 19 of which occurred in >5% of the plots (Table 2). Although individual species were found in up to 50% of the vegetated plots on an individual ridge, vegetation was very sparse; 30% of the 281 plots sampled were completely void of vegetation (Tables 1 and 2). Individual ridges contained between 8 and 24 species (Table 2). Of the vegetated plots, mean richness per ridge ranged from 1.9 to 5.9 species. This variation in richness was not significantly correlated with ridge length (effective sample area) ($R^2 = 0.396$, $P = 0.130$). Thus, species richness was affected by some other factor besides sample area.

Variation Among Ridges

Species composition and abundance varied among ridges. MRPP showed that nearly all ridges were significantly different from one another in their species composition (Table 3). The only non-significantly different pairs of ridges were 4–6 and 5–6 ($P = 0.09$ and $P = 0.27$). This variation may largely be an artifact of the differences in aspect among ridges. For example, Figure 1 shows vertical separation among different ridges along Axis 2. The ridges toward the top of the ordination are facing between NW and E (which includes Ridges 1, 2, 3, and 6; Fig. 1 and Table 1). Plots on the lower side of the ordination are mostly dominated by Ridges 4, 5, and 7, with ESE to WNW aspects (Fig. 1, Table 1). Ridge 7 (Gibbs) was especially divergent from ridges 1, 2, and 3 (Dana) ($P = 0.003$, 0.00003, and $< 1.0 \times 10^{-6}$, respectively). Finally, vertical separation among plots was also related to the abundance of *Calyptridium umbellatum* and the amount of small (1–5 cm) rocks. As the amount of small rocks increased, so did *C. umbellatum* cover ($R^2 = 0.443$, $P < 0.001$).

Variation Within Ridges

Patterns of species composition and abundance also varied within ridges. Ordination analyses revealed that plots were distributed along a somewhat linear continuum (Fig. 1); most of the variation in species composition was explained by Axis 1 (first eigenvalue $R^2 = 0.836$). On the left side of the ordination, vegetation was characterized by high cover, high species richness, and an abundance of cushion plants (hereafter HD = high diversity vegetation; Table 4). For example, the occurrence of plants such as *Podistera nevadensis*, *Phlox pulvinata*, *Astragalus kentrophyta* var. *danaus*, and *Eriogonum ovalifolium* var. *nivale* had a strong negative correlation with Axis 1 (Table 4). The high cover of these dominant plant species increased the tightness of their clustering since the ordination takes into consideration both composition and abundance. These mat-forming species were joined by fine upright graminoids such as *Poa stebbinsii*, *Trisetum spicatum*, and *Festuca brachyphylla* subsp. *breviculmis*. On the right side of the ordination, vegetation was characterized by low cover, low species richness, robust upright plants, and occasionally by sparse minute plants (hereafter LD = low diversity vegetation; Table 4). Instead of plots with rich clustered mats, plots on the right side of the spectrum often contained solitary patches of single or relatively few associated species. These species, such as *Polemonium eximium*, robust *Carex* species, and *Hulsea algida*, have greater aboveground biomass than the HD cushion species, even though they may provide less total cover (basal area). Plots with LD vegetation also may contain smaller species such as *Muhlenbergia filiformis*, *Draba breweri*, and mosses.

The distinction between HD and LD vegetation is related to the distance plots were located from the summit, which was negatively correlated with Axis 1 (Table 4). Richness and vegetative cover were positively correlated with plot distance from the summit (richness: $R^2 = 0.186$, $P < 0.001$, vegetative cover: $R^2 = 0.144$, $P < 0.001$). While LD vegetation was common within 200 m of the summit, HD vegetation extended down the length of the ridge (Fig. 2). However, as in most systems, the involved species were not strictly partitioned. For example, while *Carex* species were most common near the summit, they were also found farther down

TABLE 2.
species w

Code
ANME
ANSE
ARLE
ASKE
CAHE
CALE
CANA
CARO
CAUM
CAVE
DRBR
DRLE
ERCO
ERDI
ERIN
EROV
ERVA
FEBR
HECO
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IVLY
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($R^2 = 0.036$, P

TABLE 2. LIST OF SPECIES FOUND, WITH SPECIES CODES AND FREQUENCIES OF OCCURRENCE ON EACH RIDGE. Bolded species were found in greater than five percent of the plots.

| | | Frequency | | | | | | |
| | | Dana | | | Gibbs | | | |
Code	Species	1	2	3	4	5	6	7
ANME	*Antennaria media* E. Greene	3	0	0	0	1	0	1
ANSE	*Androsace septenrionalis* L. subsp. *subumbellata* G. Robb.	4	0	0	0	0	0	0
ARLE	*Arabis lemmonii* S. Watson	1	0	2	0	0	0	0
ASKE	**Astragalus kentrophyta** (A. Gray **var. danaus** (Barneby) Barneby	19	0	3	4	2	0	2
CAHE	**Carex heteroneura** W. Boott **var. heteroneura**	10	3	13	10	5	3	2
CALE	**Carex leporinella** Mackenzie	5	0	10	2	11	7	7
CANA	*Castilleja nana* Eastw.	4	0	2	0	0	0	1
CARO	*Carex rossii* Boott	1	0	0	0	0	0	0
CAUM	*Calyptridium umbellatum* (Torrey) E. Greene	0	0	0	9	2	3	10
CAVE	*Carex vernacula* L. Bailey	1	0	0	0	0	0	0
DRBR	**Draba breweri** S. Watson	17	3	3	0	2	2	6
DRLE	*Draba lemmonii* S. Watson	2	0	1	0	0	0	0
ERCO	**Erigeron compositus** Pursh	24	1	2	5	6	8	3
ERDI	*Ericameria discoidea* (Nutt.) G. Nesom	0	0	0	1	0	0	11
ERIN	**Eriogonum incanum** Torrey & A. Gray	11	0	3	3	2	0	15
EROV	*Eriogonum ovalifolium* Nutt. **var. nivale** (Canby) M. E. Jones	5	0	0	3	0	0	3
ERVA	**Erigeron vagus** Payson	0	0	0	0	0	0	1
FEBR	**Festuca brachyphylla** Schultes & Schultes **subsp. breviculmis** S. Frederiksen	22	0	7	13	10	6	18
HECO	*Hesperostipa comata* (Trin. & Rupr.) Barkworth subsp. *comata*	1	0	0	0	0	0	0
HUAL	**Hulsea algida** A. Gray	2	0	4	0	1	3	0
IVLY	*Ivesia lycopodioides* A. Gray subsp. *lycopodioides*	2	0	2	0	0	0	1
JU1	*Juncus* sp. 1	0	0	1	0	0	0	0
JU2	*Juncus* sp. 2	0	0	0	0	0	0	1
MOSS	**acrocarpous moss species**	15	6	10	4	3	2	3
MUFI	**Muhlebergia filiformis** (Thurber) Rydb.	8	1	0	0	0	0	1
OXDI	*Oxyria digyna* (L.) Hill	0	1	0	0	0	0	0
Penst	*Penstemon* sp.	0	0	0	0	0	0	2
PHDI	*Phlox pulvinata* (Wherry) Chronq.	2	0	0	0	0	0	0
PHPU	**Phlox diffusa** Benth.	25	0	5	8	11	5	26
POEX	**Polemonium eximium** E. Greene	5	1	1	7	0	0	0
PONE	**Podistera nevadensis** (A. Gray) S. Watson	18	1	2	9	10	3	21
POPS	*Potentilla pseudosericea* Rydb.	5	0	0	0	0	0	0
POST	**Poa stebbinsii** R. Soreng	18	0	7	7	7	1	19
RASC	**Raillardella scaposa** (A. Gray) A. Gray	0	0	0	0	0	0	7
TOSC	**Townsendia scapigera** Eaton	0	0	5	10	7	0	24
TRSP	**Trisetum spicatum** (L.) Richter	24	0	4	22	16	5	42
	Total Plots with Vegetation	43	9	20	37	25	18	47
	Total Plots without Vegetation	13	15	6	11	7	20	10
	Total Species Richness	27	8	20	16	16	12	24
	Average Species Richness per Plot	6	2	4	3	4	3	5

the ridge (Fig. 2). Similarly, *Podistera nevadensis* was characteristic of HD vegetation, but was also found within 200 m of the summit (Fig. 2). While these two species ranged along the entire ridges, when found near the summit, they occurred in plots with low richness and low cover. Plots with these species farther down the ridge had high richness and high cover. Thus, the community characteristics of richness and cover, rather than particular species identities, gave more consistent descriptions of the patterns identified by the ordination analyses. Rock size also varied with the distance from the summit. Rocks in the two smaller size classes (soil-1 cm and 1–5 cm) increased farther down the ridge ($R^2 = 0.036$, $P = 0.0014$ and $R^2 = 0.027$, $P =$

0.0063, respectively). Distance from the summit was not confounded by elevation. Elevation varied little among plots (Table 1) and showed little to no correlation with either ordination axis (Table 4).

DISCUSSION

In general, the individual species we identified on the ridges that extend off of Mt. Dana and Mt. Gibbs were similar to those found in detailed surveys of alpine vegetation from Yosemite National Park (Pemble 1970; Taylor 1984). While studies such as these describe xeric ridge species collectively as one general vegetation type, our study further partitioned that one type by evaluating the pat-

TABLE 3. RESULTS FROM THE MULTI-RESPONSE PERMUTATION PROCEDURES TESTING FOR DIFFERENCES IN SPECIES COMPOSITION AMONG RIDGES AND PEAKS. Test-statistic values (T) and significance levels (* $P < 0.05$, *** $P < 0.001$) are shown for differences (A) between individual ridges, (B) among groups of ridges, and (C) between peaks.

	2	3	4	5	6	7
A.						
1	−5.71*	−0.962***	−5.037*	−2.82*	−2.86*	−16.1***
2		−2.37*	−4.73*	−8.19***	4.23*	−21.1***
3			−4.32*	−7.51***	−3.29*	−22.6***
4				−2.32*	−1.12ns	−9.97***
5					−0.606ns	−3.57*
6						−11.2***
B.						
1, 2, 3	−9.23***					
4, 5, 6, 7	−8.43***					
C.						
Dana-Gibbs	−13.5***					

TABLE 4. CORRE[...]

PONE	
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ASKE	
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ERIN	
TOSC	
DRBR	
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CAUM	
CALE	
MOSS	
HUAL	
MUFI	
CAHE	

terns at a finer scale. We found that there was not only variation among ridges of this same habitat type but also within each ridge. In contrast with large-scale analyses that characterize vegetation types based on common member species, the patterns we found within ridges were more readily described by variation in richness and cover.

Variation Among Ridges

Surprisingly, we found that variation among ridges was most strongly controlled by aspect. Regardless of aspect, all ridges are overwhelmingly exposed to wind and sun. Thus, we assumed that aspect would have little bearing on micro-climatic conditions along ridges. Nevertheless, aspect may

indeed help explain the significant compositional differences among the ridges confirmed by the MRPP analyses as it has in large-scale alpine studies (Mark et al. 2000; Glew 1994). Overall, the ridges varied little in most of the abiotic factors we measured, except for differences in aspect (Table 1). Changes in aspect can be accompanied by changes in moisture availability, solar radiation, wind, and snow-pack, all of which contribute to alpine plant community composition at large scales (Pinder et al. 1997). Since we did not measure these specific variables, aspect may still have served as a representation for changes in the combinations of these three factors.

We hypothesize that additional differences may

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□ Ridge 1 (Mt. Dana)
× Ridge 2 (Mt. Dana)
△ Ridge 3 (Mt. Dana)
⊞ Ridge 4 (Mt. Gibbs)
● Ridge 5 (Mt. Gibbs)
▲ Ridge 6 (Mt. Gibbs)
+ Ridge 7 (Mt. Gibbs)

FIG. 1. Results of a Bray-Curtis ordination showing patterns for seven ridges on Mt. Dana (1–3) and Mt. Gibbs (4–7), Yosemite National Park. Plots do not cluster into distinct groups based on species composition. Instead, correlations along Axis 1 (explaining 83.6% of the variation) correspond to community characteristics of richness and total vegetative cover (see Table 4). In the loosely clustered plots, vertical variation is roughly separated by different ridge identity.

FIG. 2. Percent cover
from the summit.

TABLE 4. CORRELATION VALUES FOR SPECIES (GIVEN BY CODE) AND ENVIRONMENTAL FACTORS WITH ORDINATION AXES.

Species			Environmental Factors, Richness, and Cover		
	Axis 1	Axis 2		Axis 1	Axis 2
PONE	−0.939	−0.054	Species Richness	−0.522	0.11
PHPU	−0.922	0.039	Total Vegetative Cover	−0.447	0.051
POST	−0.904	−0.015	Distance from Summit	−0.366	0.124
TRSP	−0.904	−0.407	Elevation	−0.009	0.007
ASKE	−0.894	0.083	Major Substrate Size	0.012	0.083
EROV	−0.826	−0.099	5–30 cm	0.027	−0.277
FEBR	−0.707	0.449	30–60 cm	0.039	0.315
ERCO	−0.601	0.302	1–5 cm	0.11	−0.507
ERIN	−0.576	−0.351	>60 cm	0.138	0.238
TOSC	−0.573	−0.486	Slope	0.165	0.351
DRBR	−0.274	0.389	soil-1 cm	0.222	0.242
ERVA	0.041	0.253	Aspect	0.291	0.286
POEX	0.165	0.344			
CAUM	0.196	−0.838			
CALE	0.306	0.285			
MOSS	0.424	0.465			
HUAL	0.435	0.326			
MUFI	0.503	0.524			
CAHE	0.947	0.225			

also be attributed to the micro-topography of the surface rocks and the sub-surface rock architecture on different ridges. *Calyptridium umbellatum,* for example, was tightly correlated with one particular rock size (1–5 cm). The prevalence of smaller rock sizes decreased toward the summit. The eco-physiological effect of different rock sizes may be related to the plant's ability to penetrate into a moisture supply, its ability to establish in an area relatively free of organic matter or soil, and the shelter it receives by large rocks (Körner 2003).

Variation Within Ridges

Both community characteristics (richness and cover) as well as individual species present varied along the length of each ridge. The strongest environmental factor correlated with these patterns was proximity to the summit (i.e., HD vegetation was farther from the summit than LD vegetation;

Table 4 and Fig. 2). Wind in exposed alpine areas can limit plant growth (and indirectly plant distributions) by increasing evaporation and reducing insular heating close to the ground (Körner 2003). Studies have shown that exposure to harsh winds can explain major differences in plant communities (Hoare et al. 2000), especially on a macro-scale level (Mark et al. 2000). While all plants on exposed ridges generally experience severe mechanical wind stress, at a smaller-scale, near-by rocks and plants can provide shelter from these stresses (Körner 2003). An increase in wind toward the summit, which we did not measure directly but noticed while sampling ridges, might help explain the distribution of HD and LD vegetation. While most studies compare the effects of winds at very different topographical features (e.g., slope versus ridge, Billings 2000), our study suggests that there may also be notable variation in wind effects within these features.
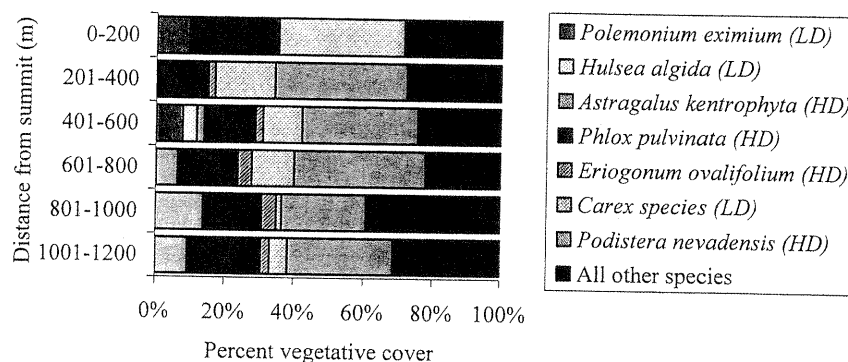

FIG. 2. Percent cover of High Diversity/Cover (HD) and Low Diversity/Cover (LD) species at increasing distances from the summit.

One might expect only the low-growing cushion plants to survive the harsh winds of the exposed summit. Counter to this intuition, however, our study showed that the most common species near the summit included large robust species (e.g., *Carex heteroneura*, *Polemonium eximium*, and *Hulsea algida*) and few low-growing species (e.g., *Calyptridium umbellatum*). If the wind is indeed fiercer at the summit, then how do these large plants that produce much of their above-ground biomass anew every year survive near the summit, and why aren't they found farther down?

Based on the physical architecture of the species found in HD and LD vegetation, we hypothesize that variation in the ability to colonize and persist may explain the divergence of these vegetation types. Conditions near the summit include fewer small rocks and possibly fiercer winds. These conditions may demand that the plant establish quickly and independently, using larger root systems and fueled by greater energy-collection from the above-ground portion of the plant. Farther from the summit, plants may take advantage of facilitative "nurse mats." Such mats formed by cushion species provide a warm protected shelter for smaller incoming species (Arroyo et al. 2003). In return, the new species would contribute nutrients and biomass to the micro-habitat and thus encourage increased colonization (Carlsson and Callaghan 1991). While it is generally assumed that abiotic physical attributes are by far the most important factors that govern alpine plant distributions (Crombie 1947; Körner 2003), these subtle biotic interactions might also be involved since the level of species diversity strongly helped define the vegetation patterns.

In summary, our data suggest that even at the relatively small scale limited to xeric alpine ridges, definable patterns of species composition and abundance do exist. The patterns we found were better defined by variation in species richness and cover (i.e., HD and LD vegetation) rather than solely groups of species defined by frequent co-occurrence. The ultimate governing factors defining these patterns may still be moisture availability and shelter from the wind, quantified in our study by aspect, rock size, and proximity to the summit. However, micro-habitat variation may be working at a much finer scale, which is less easily measured (e.g, sub-surface rock architecture). Our study has shown, that in order to fully understand the distributions and abundances of alpine plant communities, it is helpful to examine compositional patterns at a small scale.

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