

Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming

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Abstract

Question: Have recent increases in temperature caused a decline in arctic-alpine plants at the southern margin of their range?

Location: Above tree line; Glacier National Park, Montana, western USA.

Methods: We monitored the abundance of seven arctic-alpine vascular plants at or near the southern limits of their ranges at three sites in Glacier National Park, Montana from 1989 through 2002. In addition we recorded canopy cover of all plant species in sample plots once at the beginning and again at the end of the study.

Results: Mean summer temperature during this period averaged 0.6 °C higher than the previous four decades. Results of ordinations with non-metric multidimensional scaling suggested that vegetation moved toward the dry end of a moisture gradient at two sites during the course of the study. At the same time four of the peripheral arctic-alpine indicator species demonstrated 31-65% declines in abundance, while none increased.

Conclusions: We cannot rigorously infer causality from our descriptive study; however, changes in both indicator species and the vegetation matrix were consistent with predictions of climate-induced extirpation of high-elevation species and the northern migration of floras. Our results also suggest that species responded to the decade of warming individualistically with little relationship to growth form.

Keywords: Biogeography; Climate change; Glacier National Park; Global warming; Peripheral population; Migration; Montana; Tundra.

Nomenclature: Lesica (2002) for vascular plants; Esslinger & Egan (1995) for lichens; Anderson et al. (1990) for mosses.

Introduction

Climate is among the most important influences on the pattern of species occurrences over the earth (Good 1974). Fossil records have been used to infer gradual changes in the ranges of species in response to past climate changes (Cronin & Schneider 1990; Wright et al. 1993; Williams et al. 2001). These studies have demonstrated that organisms invade into areas of favorable environment, while range contractions occur in the face of deteriorating conditions. Directional migrations of sedentary organisms like plants are the result of dispersal and extirpation and are usually slow because plants are often long-lived and have short dispersal distances. Plant migrations have rarely been observed except where ruderal species are introduced outside their native range (Sauer 1988). The causes of range contraction and expansion are often inferred but rarely known with certainty because most biogeographical methods are descriptive.

The processes of dispersal and extinction in response to environmental change are thought to result in interpretable patterns. Indeed, this has been the basis of historical biogeography (Rosen 1988). Migration in response to past climate change has been inferred from patterns of peripheral rarity, especially disjunction; however, the cause of disjunct patterns is often debatable. For example, disjunct patterns in the Icelandic flora have been explained by long-distance dispersal as well as survival on ice-age nunataks (Rundgren & Ingolfsson 1999). Outlying populations of *Saxifraga aizoides* in the foothills of the Swiss Alps may be glacial relicts or recently founded following post-glacial dispersal (Lutz et al. 2000). Vicariance hypotheses are often favoured over those proposing long-distance dispersal (Brundin 1988), although solid evidence for either is usually lacking (Simberloff et al. 1981). Molecular genetic studies and cladistic analysis are beginning to shed light on these problems (Humphries et al. 1988; Stehlik 2002; Tribsch et al. 2002).

Models of range expansion and contraction in response to climate change predict that abundance will change rapidly at the margin of the species' geographical or ecological range (Parshall 2002). At equilibrium, the range of an organism is determined by its tolerance to stress in areas where environmental factors become limiting. Stressful conditions are generally more common in peripheral populations (Siikamäki & Lammi 1998). Consequently species will be most sensitive to environmental change at the periphery of their range (Cain 1944; Parsons 1990). For example, demographic stochasticity and extinction probability were higher for a perennial herb and a shrub at the northern margin of their range in Quebec (Nantel & Gagnon 1999). More populations of the fen plant *Swertia perennis* in Switzerland have been extirpated at the periphery compared to the centre of the range in the past century (Lienert et al. 2002). The impacts of herbivory on the willow *Salix arizonica* were greater at the southern margin of its range than in the center (Machinski 2001). Geographically peripheral populations often have reduced genetic variation (Lesica & Allendorf 1995) which may lead to increased chances of extinction (Huenneke 1991). However, if peripheral populations are on the leading edge of an invasion front, they are expected to be stable or increasing rather than declining (Nekola 1999).

There is widespread agreement that increasing levels of atmospheric carbon dioxide and other greenhouse gases will result in global warming and widespread alteration of rainfall patterns during the next 50 yr (Henderson-Sellers 1990; Houghton et al. 2001). Comparable but less rapid changes that occurred during the Pleistocene altered the ranges of many species (Webb 1992; Graham & Grimm 1990). High-latitude floras are of relatively recent origin and are thought to provide a more sensitive indicator of climate change (Spicer & Chapman 1990). Arctic-alpine species at the southern limit of their range and tundra communities should be among the most sensitive indicators of the effects of global warming.

Many arctic-alpine plants are at or near the southern limit of their range in Glacier National Park, Montana (Lesica et al. 1984). Among these are seven species of vascular plants that occur in moist tundra above timberline in the center of the Park. These species and their tundra communities should be a sensitive bioassay of the changes in regional climate predicted to occur during the next 50 yr. Monitoring this system will provide information on how different members of these communities respond to climate-induced stress. In 1989 we established permanent monitoring plots for disjunct or peripheral populations of arctic-alpine plants and the composition of the associated tundra vegeta-

tion (Lesica & Steele 1996). In this paper we document changes that occurred in these indicator species and the tundra vegetation during a period of climatic warming that occurred over the past decade. Specifically we tested the hypothesis that climate warming causes a decline of northern species at the southern edge of their range. In addition, we sought to determine how the matrix plant communities changed over the same period. Our results can be used to address the origin of these rare plant populations and hypotheses of migration and range contraction.

Study site

Glacier National Park is located in northwest Montana, USA along the main range of the Rocky Mountains just south of the Canadian border. The Park encompasses approximately 4000 km², nearly all of which is mountainous terrain. The mountain ranges rise to elevations of 2450 - 3050 m and trend northwest to southeast. The Continental Divide runs along the crest of the mountains through the middle of the Park (Fig. 1).

Continuous long-term climatic data for Glacier National Park are available only for stations on the periphery. Shorter-term annual precipitation at Sperry Glacier, at 2440 m and 8 km south of Logan Pass, exceeded 250 cm (Choate & Habeck 1967). At higher elevations most precipitation occurs as snow or rain on snow between November and June (Finklin 1986). Summer climate is cool and moist; during the 1959 growing season, average daily temperature and relative humidity at Logan Pass were 10 °C and 74% (Choate & Habeck 1967); however, little precipitation falls during the growing season of July and August (Finklin 1986).

Moist tundra vegetation at the Lunch Creek and Mount Reynolds sites was similar, dominated by the prostrate shrubs *Dryas octopetala* and *Salix reticulata*, the sedge *Carex scirpoidea*, and *Polygonum viviparum*. *Carex capillaris*, *Silene acaulis* and *Solidago multiradiata* were common at Lunch Creek, while *Carex rupestris* and *Kobresia simpliciuscula* were common at Mount Reynolds. Lichens and bryophytes were sparsely distributed compared to vascular plants. *Brachythecium frigidum*, *Bryum* spp. and *Campylium stellatum* were common bryophytes; *Cladonia pocillum* was a frequent lichen. However, mean canopy cover never exceeded 5% for any bryophyte or lichen species (Lesica & McCune unpubl.). Vegetation at the Akaiyan Lake site was dominated by colonies of the dwarf shrubs *Phyllodoce glanduliflora*, *Salix arctica* and *Kalmia microphylla* interspersed with patches of *Carex paysonis*. Bryophytes were less diverse but more abundant at the Akaiyan Lake site compared to Lunch Creek and Mount Reynolds. *Sphagnum russowii*,

Paraleucobryum enerve and *Polytrichum juniperinum* were the common species.

Permanent monitoring transects were established at Lunch Creek (36 microplots) and Mount Reynolds (35 microplots), just east of the Continental Divide in the centre of Glacier National Park (48°41' N, 113°42' W). Both sites are above timberline and separated by 5 km. The Lunch Creek site is at 2164 m on a gentle, south-facing slope on the rim of a headwall separating the upper and lower cirque basins. The Mount Reynolds site is at 2285 m on a gentle south-facing slope just below the steep south face of Mount Reynolds. Both sites are sub-irrigated throughout the growing season by snowmelt originating upslope. Soils are predominantly organic with areas where mineral substrate has been exposed by erosion. These are the only readily accessible sites known to us that harbor several rare alpine species in a small area. Transects were located to cross the center of habitat where these species occurred together. A third study site of 22 microplots was established on stony benches below Akaiyan Lake at 2344 m, 7 km southwest of Mount Reynolds (48°37' N, 113°46' W). Parent materials in the Logan Pass area are limestones and argillites of the Precambrian Belt Series (Raupp et al. 1983).

Methods

Sampling indicator species

Six species of vascular plants with arctic-alpine distributions occur at or near the southern periphery of their continuous geographic range at the Lunch Creek and Mount Reynolds sites: *Draba macounii*, *Euphrasia arctica*, *Juncus triglumis*, *Kobresia simpliciuscula*, *Pinguicula vulgaris* and *Tofieldia pusilla*. A seventh species, *Gentiana glauca*, occurs at the remote Akaiyan Lake site. A brief description of each species and how it was measured follows.

Draba macounii (*Brassicaceae*) forms one to many rosettes from a root crown that branches below the soil surface. *Draba macounii* occurs from Alaska south to British Columbia, Alberta and northwest Montana with disjunct stations in Colorado. In Montana it is known only from the Logan Pass area of Glacier National Park where it occurs in wet microsites as well as mesic tundra. Number of rosettes was recorded in 20 0.25-m² microplots at the Mount Reynolds site.

Euphrasia arctica (*Scrophulariaceae*) is the only annual among the indicator species. *Euphrasia arctica* is



Fig. 1. Location of Glacier National Park and the three study sites. A = Lunch Creek; B = Mount Reynolds; C = Akaiyan Lake.

found in Scandinavia, Greenland, and in North America south to Maine, Michigan, Minnesota and northwest Montana. Glacier National Park is the only location for this plant in the western continental USA. It occurs in mesic tundra vegetation. Number of plants was recorded in 24 0.1-m² microplots at the Lunch Creek site.

Gentiana glauca (*Gentianaceae*) forms loose mats of small rosettes from creeping stems. It is found from Alaska and adjacent Asia south to northern Washington and northwest Montana. Glacier Park is the only known location for *G. glauca* in the U.S. Rocky Mountains. It occurs in shallow organic soil of moist rock ledges and was recorded in 19 0.5-m² microplots at Akaiyan Lake.

Juncus triglumis var. *albescens* (*Juncaceae*) forms clusters of basal rosettes from fibrous roots. It is found from Greenland to Alaska, south through Canada and in widely separated locations in the Rocky Mountains of Montana, Wyoming, Colorado and Utah. In Montana *J. triglumis* var. *albescens* is known only from the Beartooth Mountains and Glacier National Park. It is most abundant in very wet microsites. Number of plants (clusters of leaf rosettes) was recorded in 18 1-m² microplots at Lunch Creek and Mount Reynolds.

Kobresia simpliciuscula (*Cyperaceae*) is a small tussock-forming sedge with a circumboreal distribution and widely separated populations in the mountains of Montana, Idaho, Wyoming, Utah and Colorado. In Montana *K. simpliciuscula* is known from Glacier Park and several nearby low-elevation peatlands. It occurs in mesic tundra vegetation. Tussocks were recorded in 64 0.1-m² microplots at Lunch Creek and Mount Reynolds.

Pinguicula vulgaris (*Lentibulariaceae*) is carnivorous and forms clustered rosettes on a branching rootcrown. It has a circumboreal distribution and is found south to Oregon, northwest Montana, Michigan and New York. In the Rocky Mountains *P. vulgaris* occurs as far south as Glacier National Park. It often occurs in wet, open microsites as well as mesic tundra vegetation. Number of rosettes was recorded in 22 0.25-m² microplots at the Lunch Creek site.

Tofieldia pusilla (*Liliaceae*) forms clusters of small, flattened rosettes from short rhizomes. It has a circumboreal distribution, south to most of Canada and northwest Montana; Glacier National Park is the only location in the continental USA. *T. pusilla* occurs in mesic tundra vegetation. Number of rosette clusters was recorded in 61 0.25-m² microplots at Lunch Creek and Mount Reynolds.

Hereafter indicator species will be referred to by genus name only.

Sampling vegetation

We sampled 0.1-m² microplots located along permanently marked transects. Canopy cover of all vascular plants, mosses and lichens was estimated to the nearest 5% (1% for cover \leq 2%) once at all sites during the first sampling period (1989-1991) and once during the second sampling period (2000-2002). *Gentiana* was sampled only once (1988) in the first sampling period and twice (2000 and 2002) during the second period due to the remoteness of the site. All six other indicator species were measured in all six years of the two sampling periods. Sampling was conducted during the first two weeks of August. Further details on the study design were reported by Lesica & Steele (1996).

Analysis of indicator species

We used univariate repeated measures analysis of variance followed by predetermined contrasts to assess within-subjects changes in species abundances. Site was included as a factor in the ANOVA for *Juncus*, *Kobresia* and *Tofieldia*. Probability values for time and site effects and interactions were adjusted using the conservative Greenhouse-Geisser procedure (Von Ende 2001). We tested for a decline in target species abundance over the course of the study in two ways. An orthogonal first-order polynomial contrast tested for a linear trend across the 14 years of the study. A second contrast tested the significance of the difference between the three yrs of the first sampling period and those of the second period. Abundance of a species at the two sites was analysed separately in the one case where the time \times site interaction term was significant (*Tofieldia*; $P < 0.05$). For each target species, only microplots that contained at least one plant in at least one yr were included in the analysis.

Analysis of vegetation

Lichen and bryophyte cover was sparse at the Lunch Creek and Mount Reynolds sites, so we had only a weak ability to detect changes in community composition. Furthermore, many of the changes appeared to result from local patch dynamics caused by soil disturbance or the movement of rocks (Lesica & McCune unpubl.). Consequently, we included lichens and bryophytes in analysis of community-level changes only at the Akaiyan Lake site.

Differences in composition among sites were assessed with non-metric multi-response permutation procedure (MRPP; McCune & Mefford 1999). MRPP (Mielke 1984) provides a nonparametric multivariate test of differences between groups. The test was non-metric because we rank-transformed the distance matrix

before calculating the test statistic. Group differences are shown with the *A* statistic, the 'chance-corrected within-group agreement' ($A = 0$ is the expectation under the null model; $A = 1$ when all members of each group are identical within groups; positive *A*-values indicate groups more different than the random expectation). We used Bray-Curtis distance (the quantitative version of Sorensen distance) as a dissimilarity measure (Bray & Curtis 1957; McCune & Grace 2002, p. 48). Canopy cover values were log-transformed before analysis. Numbers of species were 56, 34 and 23 for Lunch Creek, Mount Reynolds and Akaiyan Lake, respectively.

Changes in vegetation between sampling periods were evaluated in two ways.

1. We employed blocked MRPP (Mielke 1984; McCune & Mefford 1999) using Euclidean distance to test for a difference in species composition between sampling periods. Blocked MRPP is to regular MRPP as a paired-sample *t*-test is to an independent-sample *t*-test. Individual plots were defined as blocks, years were defined as groups, and comparisons were made within plots but across yrs. Blocked MRPP yields an *A*-statistic and *p*-value, similar in interpretation to regular MRPP (see above).

2. We compared plot scores from non-metric multidimensional scaling (NMS) ordinations between the two sampling periods in order to determine whether study sites had become drier between sampling periods. NMS ordination is an iterative search for the positions of species and plots on few dimensions (axes) that minimizes the departure from monotonicity in the association between distance (dissimilarity) in the original data and ordination space (Kruskal & Wish 1978). We followed methods outlined by McCune & Grace (2002). Dissimilarity matrices were constructed using Sørensen distance, and canopy cover values were log-transformed before analysis. Three-dimensional solutions were derived in all cases and final instability was < 0.0001 . We used random starting configurations and 40 real data runs. We rotated the solution to select the axis that most closely represented a moisture gradient at Lunch Creek and Mount Reynolds based on the position of species and previous knowledge of them along similar gradients in nearby alpine areas (Choate & Habeck 1967; Achuff & Corns 1982; Cooper et al. 1997). Species were superimposed as points on the ordination by a single weighted averaging step (McCune & Grace 2002). Plot scores were compared between the two sampling periods with a one-tailed, paired-sample *t*-test to test the hypothesis that vegetation did not become more xeric. Axis rotation was not required for the Akaiyan Lake ordination, and we used a two-tailed test. Analyses were conducted separately for each of the three sites because MRPP

indicated they differed in vegetation (see Results).

Canopy cover estimation is dependent to some extent on the observer. This source of error was minimized by having the same recorder perform estimations during both recording periods. Nonetheless, our power to reliably detect trends in the matrix vegetation by estimating canopy cover once per period is not as great as for the indicator species that were measured by counts three times per period.

Analysis of climate data

Climate data are limited because all long-term weather stations are located on the periphery of the Park, and these have been in operation only since ca. 1950. We chose to analyse published data (Western Regional Climate Center; www.wrcc.dri.edu) from West Glacier, established in 1950, because it is closest to our study sites (20 - 30 km) and has the most complete record.

Results

Indicator species

Four of the seven indicator species declined significantly between the two sampling periods, while none increased (Table 1, Fig. 2). The density of *Draba* rosettes declined by 64% ($P = 0.026$); the number of *Euphrasia* plants declined by 65% ($P < 0.001$); the density of *Gentiana* rosettes declined by 44% ($P = 0.048$); and the number of *Kobresia* tussocks declined by 31% ($P < 0.001$). There were significant negative linear trends between 1989 and 2002 for all four species (Table 1). We did not detect any statistically significant changes for *Juncus*, *Pinguicula* or *Tofieldia* between the two sampling periods. However, there was a strong trend for increased number of *Tofieldia* rosette clusters at Mount Reynolds ($P = 0.08$), while a weaker reverse trend was observed at Lunch Creek (Table 1, Fig. 2).

Vegetation

Vascular vegetation differed in composition among the three sites (MRPP; $A = 0.50$, $P < 0.001$). Consequently subsequent analyses were performed separately for each site. The difference between Lunch Creek and Mount Reynolds ($A = 0.25$) was smaller than that between either of these sites and Akaiyan Lake ($A > 0.45$).

Vascular vegetation changed between sampling periods at Lunch Creek (Blocked MRPP; $A = 0.008$, $P = 0.033$) and Mount Reynolds ($A = 0.023$, $P < 0.001$). Some of this change was attributable to a shift from wet- to mesic-site species (Fig. 3). We used NMS to ordinate

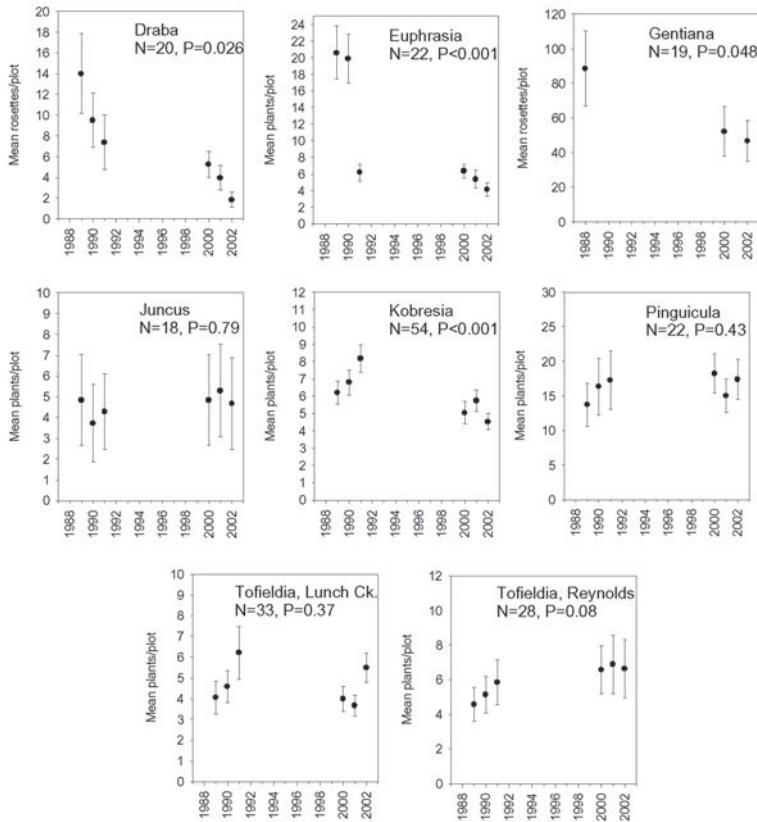


Fig. 2. Density of plants or rosettes for seven arctic-alpine indicator species (\pm SE). Effect of time determined by repeated measures ANOVA followed by contrast between the two three-year sampling periods. Results for *Tofieldia* are given separately for the two sites because of the significant time \times site interaction.

sample plots and subjectively identified an axis associated with a moisture gradient for each site based on species scores (Table 2). At both sites this axis accounted for more variation than either of the other two axes. Mean NMS axis scores shifted toward the drier end of the moisture gradient at both sites (paired *t*-test; $P < 0.05$; Table 2) due to a tendency for species with modal positions at the dry end of the gradient to increase between sampling periods, while those at the wet end

tended to decline (Fig. 3).

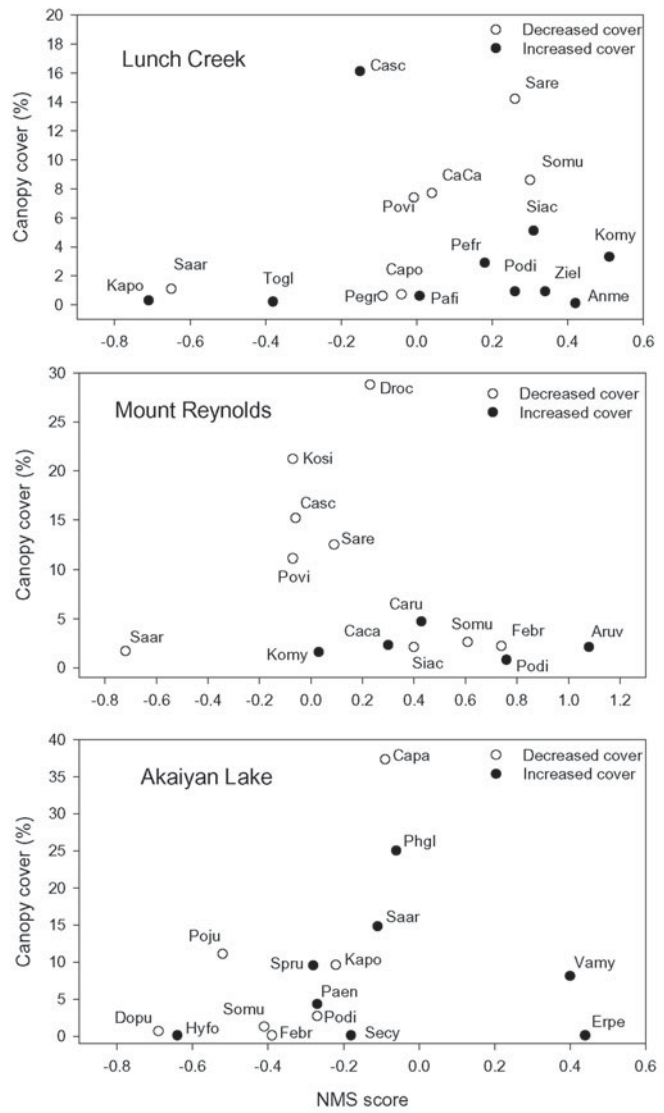
The change in vegetation between sampling periods was greater at Akaiyan Lake than the other two sites ($A = 0.080$, $P < 0.001$). The dominant NMS axis at the Akaiyan Lake site appeared to correspond to a successional gradient of increasing productivity with mosses and low-growing herbaceous vascular plants on one end and more productive herbs and shrubs on the other (Fig. 3). NMS scores shifted toward the higher

Table 1. Within-subject effects of time and time \times site interaction by repeated measures ANOVA followed by linear contrast and between-period contrast tests. Contrasts for *Tofieldia* are given separately for the two sites because of the significant time \times site interaction (see Methods).

Species	ANOVA effects						Contrast effects						
	df	Error MS	Time <i>F</i>	<i>P</i>	Time \times site <i>F</i>	<i>P</i>	df	Error MS	Linear trend <i>F</i>	<i>P</i>	Period Error MS	<i>F</i>	<i>P</i>
<i>Draba</i>	5,95	76	4.98	0.014	one site		1,19	234	6.53	0.019	1341	5.85	0.026
<i>Euphrasia</i>	5,105	60	21.16	< 0.001	one site		1,21	158	25.49	< 0.001	850	24.08	< 0.001
<i>Gentiana</i>	3,36	2213	4.44	0.047	one site		1,18	4191	4.69	0.044	25726	4.51	0.048
<i>Juncus</i>	5,80	34	0.16	0.729	0.16	0.728	1,16	2511	0.06	0.807	939	0.07	0.791
<i>Kobresia</i>	2,260	8	9.33	< 0.001	2.41	0.057	1,52	16	17.36	< 0.001	100	18.58	< 0.001
<i>Pinguicula</i>	5,100	55	1.16	0.308	one site		1,20	207	0.27	0.609	1342	0.19	0.664
<i>Tofieldia</i>	5,295	8	3.30	0.033	3.33	0.031							
Lunch	5,160	8	4.17	0.021	one site		1,32	542	0.34	0.563	3719	0.82	0.373
Reynolds	5,135	9	2.62	0.081	one site		1,27	30	3.47	0.074	178	3.24	0.083

Fig. 3. Mean percent canopy cover (1989) and position on NMS-determined moisture gradient of common (mean canopy cover $\geq 0.1\%$) species that increased and decreased between 1989 and 2001 at the three study sites. Those not changing were omitted. Species abbreviations are:

- | | |
|---|--|
| <i>Antennaria media</i> (Anme) | <i>Arctostaphylos uva-ursi</i> (Aruv) |
| <i>Carex capillaris</i> (Caca) | <i>Carex paysonis</i> (Capa) |
| <i>Carex podocarpa</i> (Capo) | <i>Carex rupestris</i> (Caru) |
| <i>Carex scirpoidea</i> (Casc) | <i>Dodecatheon pulchellum</i> (Dopu) |
| <i>Dryas octopetala</i> (Droc) | <i>Erigeron peregrinus</i> (Erpe) |
| <i>Festuca brachyphylla</i> (Febr) | <i>Hypericum formosum</i> (Hyfo) |
| <i>Kalmia polifolia</i> (Kapo) | <i>Kobresia myosuroides</i> (Komy) |
| <i>Kalmia simpliciuscula</i> (Kosi) | <i>Paraleucobryum enerve</i> (Paen) |
| <i>Parnassia fimbriata</i> (Pafi) | <i>Pedicularis groenlandica</i> (Pegr) |
| <i>Pentaphylloides fruticosa</i> (Pefr) | <i>Phyllodoce glanduliflora</i> (Phga) |
| <i>Polygonum viviparum</i> (Povi) | <i>Polytrichum juniperinum</i> (Poju) |
| <i>Potentilla diversifolia</i> (Podi) | <i>Salix arctica</i> (Saar) |
| <i>Salix reticulata</i> (Sare) | <i>Senecio cymballarioides</i> (Secy) |
| <i>Silene acaulis</i> (Siac) | <i>Solidago multiradiata</i> (Somu) |
| <i>Sphagnum rusowii</i> (Spru) | <i>Tofieldia glutinosa</i> (Togl) |
| <i>Vaccinium myrtillus</i> (Vamy) | <i>Zigadenus elegans</i> (Ziel) |



productivity end of the axis ($P < 0.001$; Table 2) due to a tendency for species at the more productive (late-seral) end of the gradient to increase between sampling periods, while those at the less productive end tended to decline (Fig. 3).

Climate

Climate at West Glacier was warmer during the decade following our first recording period than in the preceding four decades (Fig. 4). Mean annual tempera-

Table 2. Results of NMS ordinations for three study sites and paired-sample *t*-tests comparing scores between 1989 and 2001.

Site	N	NMS ordination			Paired <i>t</i> -test		
		Final stress	Axis R^2	Total R^2 (3 axes)	Mean change in axis scores	<i>t</i>	<i>P</i>
Akaiyan	44	11.56	0.35	0.90	0.335	4.08	0.001
Lunch	72	14.63	0.33	0.85	0.146	2.19	0.018
Reynolds	70	14.41	0.36	0.87	0.113	2.02	0.026

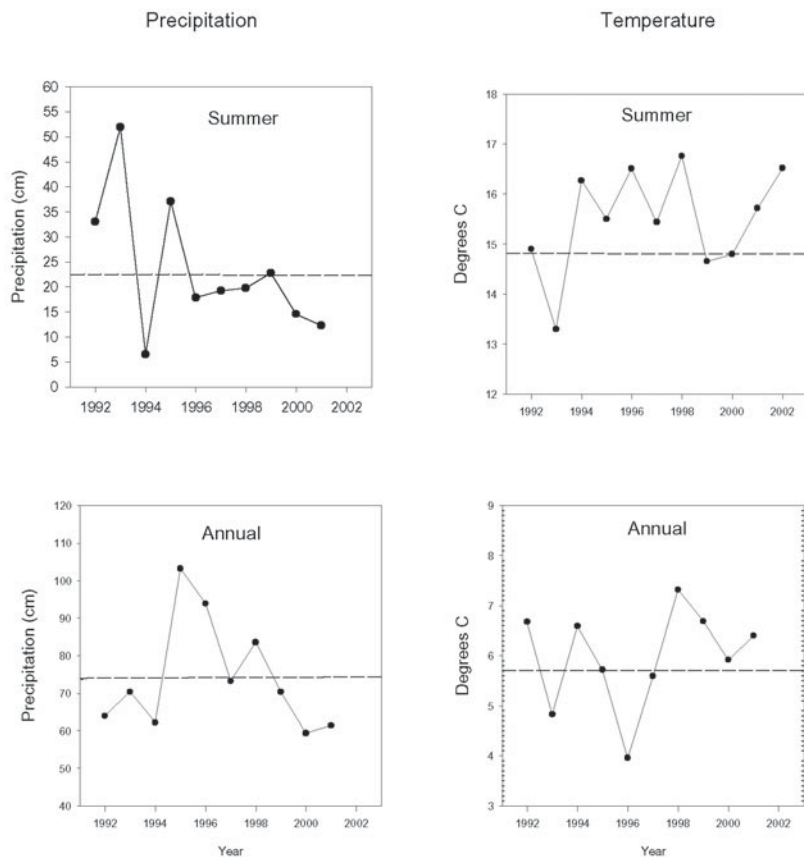


Fig. 4. Mean summer (June-September) and annual temperature and precipitation at West Glacier for 1992-2002. Horizontal lines represent the pre-study means (1950-1991).

ture for 1992-2001 was 6.0 °C, compared to 5.6 °C for 1950-1991. Mean summer temperature (June-September) for 1992-2002 was 15.4 °C, while the 1950-1991 mean was 14.8 °C. Mean annual precipitation was 742 mm for 1992-2001 and 746 mm for 1950-1991. Mean summer precipitation was 236 mm for the study period but 228 mm for the preceding four decades. A warm period was also experienced in Glacier National Park in the 1930s (Finklin 1986).

Discussion

Four of the seven arctic-alpine indicator species showed a significant decline during the past decade, while none increased. If these trends continue, some of these species could be locally extirpated in the future. These changes coincided with a prolonged period of climatic warming; mean annual and growing season temperatures during this period were 0.4 and 0.6 °C respectively higher than the preceding four decades. Warming of this magnitude is thought to be biologically significant for many organisms and ecological systems (McCarty 2001). There was no large change in precipitation during this same period, consistent with predictions of current models of global warming (Houghton et al. 2001).

Results from our study are descriptive in nature rather than experimental, so we cannot rigorously infer that climatic warming caused the decline of the indicator species. However, this hypothesis is supported by the concomitant shift of the tundra matrix vegetation toward a drier species composition at two of the study sites. The role of climate in the observed vegetation changes at the Akaiyan Lake site is less clear; however,

similar increases in shrubs are predicted for arctic tundra in response to climatic warming (Epstein et al. 2000). It is possible that observed changes at Akaiyan Lake resulted from successional processes related to soil accumulation rather than climate. However, the drying trends observed at Lunch Creek and Mount Reynolds are in the wrong direction to be successional but rather suggest a diminution of the hydrologic regime.

Our results are consistent with models of climatic warming that predict an upward shift in the distribution of montane plants with eventual extirpation of those at the highest elevations (Peters & Darling 1985; Bartlein et al. 1997; Saetersdal & Birks 1997). There is some other empirical evidence for recent upward movement. Beech trees (*Nothofagus* spp.) have recently established above the limits of mature trees in the mountains of New Zealand (Wardle & Coleman 1992). Grabherr et al. (1994) documented an increase in species richness at high-elevation sites in the Swiss and Austrian Alps over the past 40 - 90 yr that they attributed to upward migration of the alpine flora in response to global warming. There has been an upward shift in recruitment of several tree species in the mountains of west-central Sweden since 1988 (Kullman 2002). However, there has been no detectable altitudinal change in alpine tree line in Glacier National Park, Montana (Klasner & Fagre 2002) although there has been a rapid retreat of glaciers (Key et al. 2002).

There are surprisingly few reports of declines for peripherally rare arctic-alpine species in North America. To our knowledge, ours is the only study that rigorously documents such declines. Several high-elevation species have disappeared from remote and pristine sites in the Appalachian Mountains of eastern North America over the past century (Zika 1992, 1993). The reported changes cannot be conclusively linked to climatic warming, but they are consistent with model predictions.

Our results are partially consistent with theory that predicts movement of floras and vegetation in response to climate change (Davis & Zabinski 1992; Webb 1992). Species are predicted to be more sensitive to environmental change at the periphery of their range because environmental factors are more limiting and levels of stress higher (Cain 1944; Parsons 1990; Saetersdal & Birks 1997; Siikamaki & Lammi 1998). Several species of plants have been shown to be more prone to local extinction at the edge of their geographic range (Siikamaki & Lammi 1998; Nantel & Gagnon 1999; Lienert et al. 2002). There is evidence that the southern limit of arctic plants is determined by high summer temperatures (Dahl 1951; Gauslaa 1984). Tundra plants often have high base metabolic rates and respire at a detrimentally high rate in abnormally warm environments (Billings & Mooney 1968; Spomer & Salisbury 1968; McNulty et al. 1988; but see Korner 1999, p. 192).

Thus an arctic plant's range should contract first at the southern periphery if warm temperatures are limiting. Our study may be documenting the beginning of range contraction for *Draba*, *Euphrasia*, *Gentiana* and *Kobresia*. Warming of ca. 3 °C with concomitant declines in soil moisture is predicted for temperate regions during the next century (Schneider et al. 1992).

Our results are more consistent with the vicariance origin of these isolated populations of arctic plants rather than from long-distance dispersal. All seven indicator species failed to increase over the past decade, and four declined. Peripheral populations established by recent long-distance dispersal are on an invasion front and expected to be growing or at least not declining (Nekola 1999; Parshall 2002). Vicariance theory predicts that ranges become fragmented as the environment deteriorates and the species is extirpated from less favorable portions of the range first but survives, although often still declining, in the best sites. Stagnant or declining population growth rates are more consistent with isolated populations of arctic plants in Glacier National Park being remnants of formerly more continuous distributions that extended farther south during the Pleistocene glacial periods (Weber 1965).

Multivariate analysis of tundra vegetation at Lunch Creek and Mount Reynolds demonstrated a small but discernable trend toward more xeric composition between 1989 and 2001. These vegetation shifts could have been the result of smaller late summer snowfields, greater evapotranspiration or both. Such changes are consistent with those predicted for global warming (Peters & Darling 1985; Guisan et al. 1998), where changes of just a few degrees centigrade during the growing season can be associated with a 30-40% decline in soil moisture in north-temperate regions (Schneider et al. 1992). Such changes may be sufficient to cause a shift from moist tundra to dry turf or alpine grassland (Brubaker et al. 1983, Chapin et al. 1996). Experimental warming of Colorado subalpine meadows resulted in drier soil compared to controls and was associated with the decline of some species (DeValpine & Harte 2001).

Ecosystem models of arctic tundra suggest that climatic warming will result in an increase in shrubs and a decline in sedges (Chapin et al. 1996, Epstein et al. 2000). Our short-term results from alpine tundra at Lunch Creek and Mount Reynolds do not support this prediction. We found no evidence that any particular growth form was favored with climatic warming. The shrub, *Pentaphylloides fruticosa*, increased while dwarf willows (*Salix* spp.) decreased. One sedge (*Kobresia simpliciuscula*) declined, while another (*Carex rupestris*) increased. Of the indicator species, *Draba macounii*, *Gentiana glauca*, *Pinguicula vulgaris* and *Tofieldia*

pusilla are all rosette-forming herbaceous perennials; the former two declined, while the latter two did not. On the other hand, dwarf shrubs *Vaccinium myrtillus* and *Phyllodoce glandulifera* did increase at the Akaiyan Lake site, and there was a shift toward more productive vegetation. Our limited data suggest that species responded to the decade of warming individually with little relationship to growth form. Field studies and theoretical models also predict this individualistic response (Chapin & Shaver 1985; Woodward 1993). Our results are consistent with the dynamic community hypothesis which predicts that individual species in a community respond differently rather than cohesively to changes in the environment (Gleason 1926; Graham & Grimm 1990). Rather than migrating as a unit, communities will change species composition in response to directional climate change. Given the speed of climate change predicted for the near future (Schneider et al. 1992; Houghton et al. 2001), we might expect rapidly changing community composition resulting in reduced opportunities for co-evolution (Thompson 1994).

Three of four declining indicators (*Draba*, *Euphrasia*, *Kobresia*) were most common in crowded turf vegetation, while two of three stable indicators (*Juncus*, *Pinguicula*) were most abundant in wet, open microsites. This association, although weak, may indicate that competitive interactions play a role in how rare species responded to climatic warming. In some cases it may be competitive effects, such as shading by grass or shrubs, that will cause the decline of smaller tundra species (Chapin et al. 1996; Epstein et al. 2000). Choler et al. (2001) found that competition played a more important role in limiting alpine plant abundance at the lower (warmer) compared to the upper limits of distribution. Competition is predicted to structure the response of some boreal vegetation types to global warming (Woodward 1992).

In the event of a continued warm climate, we predict that moist tundra will be replaced by drier turf or grassland communities. Subordinate species of closed turf may be more sensitive to climate change than dominant species. Continued declines and eventual extirpation of *Draba*, *Euphrasia*, *Gentiana* and *Kobresia* from Glacier National Park might be expected if the trend for warmer, drier climate of the past decade persists.

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