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Effects of Recreational Traffic on Alpine Plant Communities in the Northern Canadian Rockies

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Abstract

Recreational activities in alpine areas have been increasing in recent decades, creating the need to improve our understanding of the impacts of these activities and how they are best managed. We explored impacts of recreational trail use on dry alpine meadows in the northern Canadian Rockies of Alberta. Data collected in 142 plots (0.5 m × 1 m) were used to compare plant community metrics among (1) a recreational trail, (2) intact tundra meadows (undisturbed), and (3) sparsely vegetated gravel steps formed by frost disturbance (naturally disturbed). As compared to undisturbed tundra, trails had substantially lower cover of vascular plants (4% vs. 35%), lichen (0% vs. 10%), and cryptogamic crust (0% vs. 4%); trails also had lower species richness (7 vs. 11 species per plot), but greater soil compaction (2.75 vs. 1.25 kg cm^{-2}). Trails differed from natural gravel steps, which had three times more biotic cover and different composition. This highlights the difference in effects of human and natural disturbance. Positive feedback effects of trampling in tundra ecosystems may lead to altered environmental conditions, including decreased infiltration capacity and nutrient cycles in soils, and more extreme temperatures at the soil surface. These feedbacks could inhibit regeneration of abandoned trails.

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Introduction

Tundra ecosystems have low productivity because of the short growing season, harsh climate, nutrient-poor soils (Bowman et al., 1993; Bliss, 1962), and waterlogging in areas underlain by permafrost (Munroe and Bockheim, 2001). Such ecosystems are believed to be easily disturbed and slow to recover (Liddle, 1975), and the tundra has long been considered to be fragile and sensitive to human activities. The majority of studies of human disturbance in the Arctic have focused on impacts of large-scale industrial developments such as petroleum exploration and extraction, or diamond mining (e.g., Walker and Walker, 1991; Forbes et al., 2001; Kershaw and Kershaw, 1987; Lawson, 1986). However, the natural beauty and ecological uniqueness of both arctic and alpine ecosystems have been attracting increasing numbers of recreational visitors in recent years (Billings, 1973; Dearden and Sewell, 1985; Parsons, 2002; Forbes et al., 2004). Climate change is also predicted to cause abiotic changes in these ecosystems (Chapin et al., 1995; Wipf et al., 2009; Klanderud, 2008), which may stress both individual species and the ecosystem as a whole. Climate change might also be associated with increased numbers of visitors as the warm season increases in length. Thus, there is a growing need to improve our understanding of how recreational activities impact these communities and how these impacts can best be managed.

Trampling resulting from hiking, horse riding, and all-terrain vehicle (ATV) use reduces plant cover, in turn influencing litterfall, nutrient cycling, and soil temperature (Edwards and Cresser, 1992), and potentially causing increased runoff and erosion (Frissell, 1978). Trampling has been associated with decreased species richness (Gremmen et al., 2003), although this is not always the case (Growcock, 2005; Monz, 2002). One of the key predictors of a species' ability to withstand trampling is its morphological form, and changes in community composition are expected as a result of increases in relative abundance of species with trampling-tolerant growth forms and decreases in species with growth forms that are intolerant of trampling (Cole, 1995b).

Plants that do not tolerate trampling well include brittle woody plants (Price, 1985; Cole, 1978), tall herbaceous plants (Price, 1985; Cole, 1995b), upright growth forms (Cole, 1995b), cushion plants (Whinam and Chilcott, 2003; Gremmen et al., 2003), and chamaephytes (Cole, 1995b; Cole and Monz, 2002). Some morphological groups, including shrubs, forbs, and bryophytes have shown mixed responses to trampling (Cole, 1995b; Whinam and Chilcott, 2003; Gremmen et al., 2003; Grabherr, 1982; Cole and Monz, 2002). Very few studies of recreational impacts have examined how community composition is affected by trampling, but see Cole and Monz (2002), who found only minor effects of trampling on species composition in alpine communities in Wyoming.

Recreational activities can also affect plant litter and cryptogamic soil crusts. In alpine areas, all the plants are low-lying and as a result, litter deposition is quite localized. Thus, on alpine trails where plant cover is sparse, we would expect to see very little litter. Litter is an important source of nutrients that can be recycled back into the soil system (Bryant et al., 1998), thus, a loss of litter could lead to reductions in soil nutrients. Cryptogamic soil crusts are thin crusts made up of mosses, lichens, bacteria, fungi, and/or algae that often form on the soil surface in dry environments, particularly in deserts and tundra (Belnap and Gillette, 1998). Human impacts on cryptogamic crusts have mostly been studied in desert ecosystems (e.g.: Belnap and Gillette, 1998) and have found these crusts to be sensitive to trampling. Because they provide important ecological functions, including nitrogen fixation (Belnap and Gillette, 1998), soil temperature moderation (Gold, 1998), increased nutrient retention (Belnap, 1993), and increased moisture retention (Gold et al., 2001), the loss of soil crusts could have implications for the ecosystem as a whole.

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Our objective was to examine how human traffic associated with recreational activities impacts alpine tundra in the front range of the Canadian Rocky Mountains. We examined the vegetation on, near, and away from trails, as well as abiotic factors such as soil compaction. We addressed the following two questions: (i) How does the vascular plant community on an alpine trail differ from the adjacent tundra (which was presumed to represent a control condition); (ii) How does the plant community on the trail compare to that in a naturally sparsely vegetated alpine area? Naturally barren environments, such as scree slopes and fellfields, are superficially similar to trails (i.e.: rocky, exposed, and supporting only scattered plant life), but the two have never been compared to see how ecologically similar they are.

Methods

STUDY SITE

Fieldwork was carried out at Cardinal Divide, a road-accessible alpine ridge, and at the base of Tripoli Mountain, which lies immediately to the southwest of Cardinal Divide. Both sites are located in the southern portion of Whitehorse Wildland Provincial Park (52°53′N, 117°15′W), in the Nikanassin Range of the Canadian Rockies near the hamlet of Cadomin, in Alberta, Canada. The area is believed by some to be a glacial refugium (Packer and Vitt, 1974; but see Strong, 1999) and is a hotspot for rare and disjunct species (Achuff, 1984). Cardinal Divide is situated at approximately 2000 m a.s.l., and is a dry, exposed ridge underlain by calcareous substrate. The most common plant community along the Divide is dry tundra meadows dominated by *Dryas integrifolia* M. Vahl. Also abundant in this community type are *Carex rupestris* All., *Hedysarum alpinum* L. ssp. *americanum* (Michx.), and *Hedysarum boreale* Nutt. The Divide also supports snowbed communities in depressions and gullies as well as krummholz patches, which are made up of *Picea engelmanii* Parry ex Engelm. and *Abies lasiocarpa* (Hook.) Nutt., and surrounded by heath communities dominated by *Phyllodoce glanduliflora* (Hook.) Coville, *Phyllodoce empetriformis* (Smith) D. Don., and *Cassiope tetragona* (Bong.) D. Don. The plant community found at the Tripoli Mountain site was similar to the *Dryas*-dominated community found on Cardinal Divide.

From the 1970s to the late 1990s Cardinal Divide was open to off-highway vehicle (OHV) users, horseback riders, mountain bikers, and hikers. Since the incorporation of Whitehorse Wildland Park in 1998, only foot traffic has been permissible on the Divide and has been concentrated along two long hiking trails (each 1.5–2 km), one on each side of the access road. This trail network was formalized in large part due to the efforts of the Alberta Native Plant Council (ANPC) which worked with the Alberta government to delineate a path using rock markers aligned with the footprint of the major existing trails. The Cardinal Divide trail received over 2000 visits (passes) in the summer of 2008 (Alberta Parks, unpublished data).

SAMPLING DESIGN

Fieldwork took place during the summers of 2008 and 2009. Data to characterize conditions on trails and on the adjacent tundra were collected in a series of transects perpendicular to the trail on Cardinal Divide. Data on naturally barren alpine environments and on adjacent tundra were collected on naturally formed gravel steps located at the base of Tripoli Mountain, approximately 2 km away from the main trail site on Cardinal Divide.

Sampling of the trail and adjacent tundra on the Divide was conducted on 42 transects in *Dryas*-dominated tundra in a study area beginning at the trailhead and extending 1.5 km along the trail on the west side of the access road. To ensure that the study area was sampled evenly along its length, the 1.5 km length of the trail was divided into five, 300-m-long sections, and eight or nine transects were randomly located within each section. The 0–300 m and 300–600 m sections had nine transects each, while the other three sections (600–900 m, 900–1200 m, and 1200–1500 m) had eight transects each, for a total of 42 transects. Transects were placed a minimum of 5 m apart to avoid issues of autocorrelation.

Each transect started on one side of the trail, crossed it, and then extended 50 m away from the trail edge into the tundra. A coin toss was used to determine in which direction (left or right of the trail) each transect would be established. We placed four 0.5 m × 1 m survey plots along each transect at the following locations: one at the center of the trail, one at the edge of the trail, and one at each of 15 m and 50 m from the trail edge (long axis of plot parallel to trail). The trail edge plot began at the point at which vegetation cover increased markedly. The distance between the trail and edge plots varied with trail width, but was never less than 1 m. A few individual plots were removed from the data set because they were outliers that could potentially skew results, thus, the final data set therefore comprised 36–39 plots from each location.

On a knoll at the base of Tripoli Mountain, where the vegetation was similar to that on the Divide, we sampled naturally occurring gravel steps to assess whether they could be considered natural analogues of trail plant communities and to compare the effects of natural versus anthropogenic disturbance. These steps, which are commonly found on moderate to steep slopes subject to frost disturbance (Nicholson, 1976), are composed of alternating strips of fully vegetated tundra and more sparsely vegetated gravel patches oriented parallel to slope contours. These gravel steps bear superficial resemblance to trails in that they are open and gravely, and support only a sparse plant community. Here we laid out a series of parallel transects, 5 m apart, placed perpendicular to the gravel steps. We walked along each transect until we found a gravel patch that was large enough to accommodate the 1 m × 0.5 m survey plot. We repeated this process until we were able to complete 20 survey plots. We also collected data in five reference plots randomly located on the fully vegetated tundra adjacent to the steps. Reference plots were compared to off-trail plots from Cardinal Divide to ensure that any differences found between the trail and the gravel steps did not simply reflect differences in community composition between the two sites.

In each plot at the trail and gravel step sampling locations, a single observer made visual estimates of cover for each vascular plant species and for rock, bare soil, lichens (all species combined), bryophytes (all species combined), and exposed cryptogamic soil crust (identified by its hard-surfaced, filamentous texture). Soil compaction was quantified in the center of each plot using a Humboldt H-4200 pocket soil penetrometer. Care was taken to avoid rocks at or under the soil surface when measuring soil compaction. If the instrument hit a rock at any point while taking a measurement, a new reading was taken in a different location. Because of equipment problems we were unable to measure soil compaction at the gravel step site.

DATA ANALYSIS

For examination of trail impacts we compared plots on the trail, at the edge, and at 50 m. Because the trail is situated along a ridgetop location, many of the 50 m plots were located at a slightly lower topographic position and on slightly greater slope than was found in the area nearer to the trail. This potentially confounded trampling effects but was unavoidable. However, we compared the 15 m and 50 m plots and found almost no differences. We therefore considered the 50 m plots as the reference condition for assessment of trail impacts. For the sake of brevity we do not report further on the 15 m plots. For analyses focused on the gravel steps we compared the gravel steps, trail plots, the reference plots at the trail site (50 m), and the reference plots from the tundra adjacent to the gravel steps ('gravel step reference').

Total cover per plot was calculated by summing individual species' cover values. We also calculated species richness (# of species), Shannon's Diversity Index, and Shannon's Evenness per plot (Magurran, 2004). In addition, species were assigned to one of five growth forms: caespitose (tufted), rosette (characterized by a rosette of leaves at the base of the plant), mat (plants with a prostrate habit and a tendency for lateral spread), upright (plants with an upright habit and cauline leaves), or cushion (plants with numerous stems tightly packed into a compact cushion form). Species were classified according to the growth form most commonly displayed by individuals of that species (see Appendix 1). We then calculated relative cover for each of these categories by dividing the sum of cover of species in that group by the sum of cover values for all species in the plot. We also examined differences between the trail and adjacent tundra in terms of relative abundance by structural group (herb, shrub, graminoid) and life form (Raunkiaer, 1934), but we do not report those results here because they did not provide much additional insight (Crisfield, 2010).

Univariate analyses used for comparisons of total vascular plant cover; vascular species richness, evenness, and diversity; vascular plant cover by growth form; abiotic and non-vascular cover; and soil compaction were as follows. The effect of location relative to the trail (trail, edge, 50 m) was examined using two paired *t*-tests in order to compare the trail to each of the two off-trail locations. Off-trail plots were statistically compared in a separate analysis but these results are not presented here (see Crisfield, 2010). When data were highly non-normal, Wilcoxon's signed rank tests (Wilcoxon, 1945) were used (total vascular plant cover, richness and evenness; cover of rock, soil, lichen, bryophytes, litter, and cryptogamic crust; and covers by growth form). For comparison of the trail to the gravel steps, two-way analysis of variance (ANOVA) was used with the main effects being: site (trail site vs. gravel step site), plot location (trail/gravel step vs. reference), and their interaction. When data did not conform to the assumptions for ANOVA (this was the case for all response variables except for richness, evenness, and diversity), we used the Scheirer-Ray-Hare extension of the Kruskal-Wallis test (Scheirer et al., 1976). Significant main effects were followed up with pair-wise planned comparisons (in the case of normal data) or Wilcoxon's test for paired two-sample comparisons (in the case of non-normal data) with a Bonferroni adjustment of α. All univariate analyses were conducted using SAS 9.2 (SAS Institute, 2004).

Non-metric multidimensional scaling (NMDS; McCune and Grace, 2002), using the Sørenson (Bray-Curtis) distance measure, was used to visualize patterns in species composition in relation to plot locations. One- to six-dimensional models were created initially and we used stress values to choose the final two-dimensional solution. For statistical comparisons of vascular species composition (cover by species) of trail, edge, and 50 m plots, we used permutational multivariate analysis of variance (perMANOVA) with transect included as a blocking (random) factor (Anderson, 2001). We were unable to use perMANOVA tests for the comparisons involving the gravel steps because sample sizes were highly unequal. We therefore used the multi-response permutation procedure (MRPP), which is another distance-based technique appropriate for comparing among groups using data sets with multiple response variables (McCune and Grace, 2002). We used indicator species analysis (Dufrêne and Legendre, 1997) to find species that characterized different locations (trail vs. adjacent tundra or gravel steps). We considered species with a *p*-value of <0.05 and an indicator value of ≥ 20 as important indicators (McCune and Grace, 2002). All multivariate analyses were conducted using PCOrd v. 5 (McCune and Mefford, 2006).

Results

COMPARISON OF THE TRAIL TO ADJACENT TUNDRA

We found a total of 73 vascular plant species (Appendix 1). The trail was dramatically different from the adjacent tundra for most variables measured, while the plots at the trail edge and 50 m away from the trail were more similar to one another. Vascular plant cover and species richness were significantly lower on the trail than in either of the off-trail locations. In contrast, diversity and evenness were significantly higher on the trail (Table 1). The trail plots were significantly different from the edge and 50 m plots for all six categories of non-vascular and abiotic cover (Table 1). Rock was by far the dominant substrate on the trail, and there was also substantially more exposed soil on the trail than on the edge or 50 m plots. The other four substrates were more abundant off the trail: lichens, bryophytes, and cryptogamic crust all had fairly low cover values off the trail, but were present only in minute traces on the trail. Litter was the most abundant cover type on off-trail plots but was only present in small amounts on the trail. Soil on the trail plots was significantly more compacted than on either the edge or 50 m plots (Table 1).

The trail differed significantly from both the edge and 50 m plot locations in terms of species composition (by perMANOVA; $p < 0.001$ in both cases). Four species were found to be indicators for the trail when compared to both the edge and 50 m locations: two caespitose species, one upright grass, and the cushion plant *Minuartia* spp. (Table 2). Four species were found to be significant indicators for both the edge and 50 m plots, as compared to the trail: two upright shrubs, an upright sedge, and a rosette aster (Table 2). Six species were indicators for the 50 m location only and four

TABLE 1

Mean (standard deviation) or median (5th–95th percentiles) values for vascular plant cover; richness; evenness; Shannon's Diversity index; cover of: rock, bare soil, bryophytes, and lichens; and soil compaction in the alpine tundra.

		Trail	Edge	50m/trail reference	Gravel step	Gravel step reference
Cover (%)	Median	4	32.5*	35*	8*	30
	C.I.	(1–12)	(10–62)	(20–49)	(5–13)	(18–36)
Richness (#sp/plot)	Median	7	9*	11*	11*	13
	C.I.	(3–12)	(6–13)	(8–17)	(8–14)	(10–16)
Evenness	Median	0.86	0.57*	0.61*	0.6*	0.69
	C.I.	(0.68–0.91)	(0.43–0.78)	0.09	(0.46–0.76)	–0.07
Shannon	Mean	1.70	1.34*	1.53*	1.44	1.8 +
	Std. dev.	0.35	0.28	0.27	0.24	0.22
Rock (%)	Median	71	19*	2.5*	77	18 +
	C.I.	(47–85)	(0–63)	(0–32)	(63–85)	(4–39)
Soil (%)	Median	19	5*	0.25*	4*	2 +
	C.I.	(9–85)	(0–26)	(0–3)	(0–7)	(0–3)
Lichen (%)	Median	0	0.25*	10*	0.25*	7
	C.I.	(0–0)	(0–5)	(5–25)	(0–4)	(0–13)
Bryophytes (%)	Median	0	0.25*	0.25*	0.25*	2
	C.I.	(0–0)	(0–3)	(0–5)	(0–0)	(0–4)
Litter (%)	Median	3	32*	49*	9*	35
	C.I.	(0–12)	(12–55)	(29–64)	(4–15)	(0–51)
Crust(%)	Median	0	5*	4*	3*	6
	C.I.	(0–1)	(0–13)	(0–11)	(0–7)	(0–11)
Soil Compaction (kg cm^{-2})	Median	2.75	1.88*	1.25*		
	C.I.	(1–4.5)	(1–3)	(0.7–2)		

*Edge, 50 m or gravel step significantly different from the trail; + gravel step reference significantly different from trail reference.

other species were indicators for only the edge location. The trail was also different from either adjacent location in terms of morphological composition (relative abundance of growth form; Table 3). The trail was characterized by significantly higher relative abundance of caespitose, rosette, cushion, and upright growth forms. The upright form had the highest relative abundance of all growth forms on the trail, comprising nearly half of the trail vegetation. Caespitose plants were also much more abundant on the trail than off. Cushion growth forms were not very abundant on the trail but were nearly absent in off-trail plots. Plants with a mat growth form had significantly higher relative abundance on the off-trail plots, where they made up more than 60% of off-trail vegetation (Table 3).

COMPARISON OF TRAILS TO GRAVEL STEPS

Vascular plant cover and richness were significantly higher on the gravel steps than on the trail (Table 1). In contrast, the gravel steps had significantly lower evenness. There were no significant differences in diversity. The two sets of reference plots differed only for diversity, which was slightly higher on the gravel step reference plots.

Rock was the primary cover type for both trail and gravel step plots and did not differ significantly between these two locations (Table 1). The trail had significantly higher cover of bare soil but significantly lower cover of lichens, bryophytes, litter, and cryptogamic crust than the gravel steps (Table 1). The two sets of reference plots (trail vs. gravel step sites) were similar in their cover of lichen, moss, litter, and cryptogamic crust. In contrast to the results for the trail versus gravel step plots, the gravel step reference plots had higher cover of rock and bare soil than did the trail reference plots (Table 1).

The NMDS (Fig. 1) showed a clear separation of the trail and gravel step plots from the two sets of reference plots. The gravel step plots were more similar to both sets of reference plots, while the trail plots were more strongly separated from these. The reference plots from the two sites were not distinct in terms of composition. Based on the MRPP there were significant differences among the four locations overall. Follow-up tests (pairwise MRPPs) found significant differences between the trail and the gravel steps as well as between the trail reference and gravel step reference plots ($p < 0.0001$ in both cases). However, absolute values of T, which is a measure of effect size, were higher for the comparison of the trail to the gravel steps ($T = -22.86$) than for the trail reference versus gravel step reference ($T = -8.99$). These results suggest the trail is more compositionally dissimilar from the gravel steps than the reference tundra communities were from each other.

The same four species that were indicators of the trail location as compared to the edge and 50 m location (see above) were significant indicators of the trail location as compared to the gravel steps and the two reference locations in this analysis (Table 4). There were six significant indicators for the gravel step location, including two rosette species, two mat species, one cushion species, and one caespitose grass; three of these were also indicators for the step reference location (Table 4). There were five indicators for the trail reference plots, of which two were also indicators for the gravel step reference location. An additional three species were significant indicators for only the gravel step reference location.

TABLE 2

Results of Indicator Species analysis comparing (A) trail plots *versus* edge plots, and (B) trail plots *versus* plots 15 m from the trail. Given are species, along with their Indicator Values for each plot location and the significance. Only species for which $p < 0.05$ and I.V. > 20 in at least one of the comparisons are listed.

(A). Trail vs. edge

	Indicator value (IV)		
Species	**Trail**	**Edge**	***p***
Aster alpinus	3	**29**	0.011
Betula glandulosa	0	**29**	<0.001
Carex rupestris	6	**81**	<0.001
Deschampsia cespitosa	**23**	0	<0.001
Dryas integrifolia	2	**91**	<0.001
Festuca brachyphylla	**18**	0	0.014
Gentiana prostrata	**18**	0	0.014
Hedysarum boreale	0	**84**	<0.001
Kobresia myosuroides	0	**63**	<0.001
Minuartia spp.	**43**	1	<0.001
Poa alpina	**77**	0	<0.001
Polygonum viviparum	8	**86**	<0.001
Salix nivalis	0	**20**	0.005
Trisetum spicatum	**59**	0	<0.001

(B). Trail vs. 50 m

	Indicator Value (IV)		
Species	**Trail**	**50 m**	***p***
Anemone parviflora	0	**27**	<0.001
Aster alpinus	2	**24**	0.038
Betula glandulosa	0	**43**	<0.001
Carex rupestris	13	**46**	<0.001
Deschampsia cespitosa	**22**	0	<0.001
Hedysarum alpinum	0	**32**	<0.001
Minuartia spp.	**46**	0	<0.001
Oxytropis podocarpa	0	**48**	<0.001
Pedicularis lanata	0	**44**	<0.001
Poa alpina	**75**	0	<0.001
Salix nivalis	0	**37**	<0.001
Silene acaulis	0	**27**	0.002
Trisetum spicatum	**53**	1	<0.001
Zigadenus elegans	0	**26**	0.002

TABLE 3

Median (5th–95th percentiles) values for vascular plant cover by growth form in the alpine tundra plots in different locations.

		Trail	**Edge**	**Trail reference (50 m)**	**Gravel step**	**Gravel step reference**
Caespitose (%)	Median	12	0.25*	0.5*	2*	3+
	C.I.	(0–59)	(0–10)	(0–2)	(0–7)	(1–12)
Mat (%)	Median	6	66*	63*	69*	71
	C.I.	(0–55)	(38–80)	(36–79)	(45–89)	(45–80)
Cushion (%)	Median	2	0*	0*	2	1
	C.I.	(0–30)	(0–3)	(0–3)	(0–9)	(0–2)
Rosette (%)	Median	8	1*	2*	6	2
	C.I.	(0–35)	(0–6)	(1–4)	(0–15)	(0–3)
Upright (%)	Median	43	29*	35*	16*	23
	C.I.	(11–76)	(11–58)	(17–58)	(6–38)	(6–47)

*Edge, 50 m or gravel step significantly different from the trail; + gravel step reference significantly different than trail reference

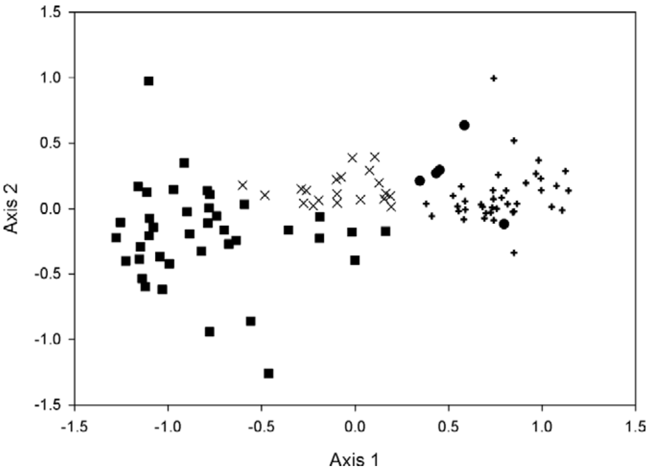

FIGURE 1. Results of the non-metric multidimensional scaling (NMDS) ordination of plant community data showing the locations of sample plots from different locations in species space. Sample plots are coded according to type: ■ = trail; × = gravel step; + = trail reference; ● = gravel step reference (n = 103 plots * 82 species). Distance measure = Bray-Curtis; stress = 15.36, variation explained = 82.2%.

Three of the five growth forms varied in terms of their proportional abundance between the trail and the gravel step locations. Caespitose and upright plants had significantly higher relative abundance on the trail than on the gravel steps. On the other hand, matted plants had significantly higher relative abundance on the gravel steps. Cushion and rosette plants did not differ in relative abundance between locations (Table 3). The dominance of the upright growth form on the trail was mostly attributable to non-caespitose graminoids, while graminoids in general were not a large component of the plant community on the gravel steps. The only significant difference between the trail reference and gravel step reference plots was that the gravel step reference had slightly higher relative abundance of caespitose plants, but relative abundance overall of this group was quite low in both locations (Table 3).

Discussion

The trail at Cardinal Divide was substantially different from adjacent tundra, having lower cover of vascular plants, bryophytes, lichens, and cryptogamic crust but higher diversity and evenness and higher cover of rocks and exposed soil than the surrounding tundra. That the edge and 50 m plots showed similar characteristics suggests that the effects of human traffic do not extend much off the main trail. It was notable, however, that the locations farther away from the trail had higher cover of lichen and litter.

The dramatically lower values for total vascular plant cover on the trail (4% vs. >30%) were no surprise given that the loss of vascular cover is one of the most obvious and well-studied impacts of trampling in tundra ecosystems. This loss of about 88% of vascular cover is greater than the declines of 40–80% which have been previously reported in studies of trampling in tundra communities (Cole, 1995a, 1995b; Cole and Monz, 2002; Monz, 2002; Whinam and Chilcott, 1999, 2003; McDougall and Wright, 2004). These studies focused on a variety of community types, including forb-dominated, shrub-dominated, and graminoid-dominant tundra, so the variation in results might simply be a reflection of differences in trampling tolerance between different tundra community types. Monz (2002), who also studied the effects of trampling on *Dryas*-dominated tundra, found that within 10 days of applying 500 passes of artificial trampling, plant cover declined by 80%. This is just

TABLE 4

Results of Indicator Species analysis comparing trail, gravel step, trail reference, and gravel step reference locations. Given are species, along with their Indicator Values for each plot location and the significance. Bold indicator values indicate significance for this location. Only species for which $p < 0.05$ and I.V. > 20 are listed.

	Indicator value				
Species	**Trail**	**Gravel steps**	**Trail reference**	**Step reference**	***p***
Anemone lithophila	0	2	0	**32**	0.016
Antennaria spp.	1	**35**	2	0	0.007
Arnica angustifolia	1	**25**	1	**33**	0.028
Betula glandulosa	0	0	**59**	0	0.001
Deschampsia caespitosa	**23**	0	0	0	0.027
Dryas integrifolia	1	12	**55**	**31**	0.001
Festuca brachyphylla	7	**26**	0	0	0.022
Hedysarum boreale	0	0	**80**	0	0.001
Kobresia myosuroides	0	0	18	**64**	0.002
Minuartia spp.	**28**	10	0	3	0.031
Oxytropis podocarpa	0	**23**	2	**71**	0.002
Pedicularis lanata	0	0	**41**	0	0.008
Poa alpina	**59**	8	0	2	0.001
Polygonum viviparum	3	8	**27**	**60**	0.001
Potentilla nivea	2	0	2	**47**	0.002
Salix reticulata	0	**21**	10	**41**	0.024
Saxifraga oppositifolia	0	**25**	6	0	0.030
Trisetum spicatum	**49**	1	1	2	0.002

slightly less than the estimated loss on Cardinal Divide from years of human use, including use by ATVs.

The lower species richness on the trail (compared to the adjacent tundra) confirms the findings of Gremmen et al. (2003) in a study of decades-old trails on subantarctic Marion Island. In contrast, Monz (2002) found no significant change in richness due to even the highest level of artificial trampling in *Dryas* tundra in Alaska. Somewhat surprisingly, species diversity and evenness were higher on the trail than on the adjacent tundra. One possible explanation for this is that the heavy dominance of the tundra meadows by *Dryas integrifolia* results in low evenness, and by extension, low diversity. Douglas and Ballard (1971) found a similar result in burned krummholz/heath communities in the Cascade Mountains, where diversity was higher in burned areas 30 years following fire than in unburned sites, and the authors hypothesized that this was driven by the reduced the dominance of *Phyllodoce* spp.

The reduction in cover of cryptogamic crusts on trails has important ecological implications, as it could lead to reduced soil moisture and nutrient levels and more extreme temperatures at the soil surface (Gold, 1998; Belnap and Gillette, 1998; Belnap, 1993; Gold et al., 2001). Trampling does not always negatively affect cryptogamic communities. For example, a study of caribou trampling in tundra found that low-intensity trampling can benefit soil crust organisms as it creates variation in soil microtopography and microenvironments (Csotonyi and Addicott, 2004). However, these microtopographical variations and their benefits to cryptogams are lost when trampling pressure is high, such as it would be on intensively used recreational trails.

Although our finding of higher soil compaction on the trail was not unexpected, this result contrasts with those of Monz (2002), who found that even 500 passes of experimental trampling on *Dryas* tundra in Alaska had no significant effect on soil compaction. He did, however, find that soil compaction increased significantly after trampling in a cottongrass community. Willard and Marr (1970) found that trampling led to patches of bare ground in which finer particles were washed away, leaving behind a gravelly substrate. The absence of cryptogamic crust cover has also been found to be associated with coarser soil texture (Gold et al., 2001). This is further supported by our finding of higher rock cover on the trails.

While the trail community consisted of species that were found in the surrounding tundra, there was a pronounced shift in the relative abundances of those species. With the exception of *Taraxacum officinale*, all the species that were found on the trail were also found in the adjacent tundra, but in many cases species that were common on the trail, such as *Poa alpina* and *Trisetum spicatum*, were only present in trace amounts in the off-trail community. Our results contrast with those of Cole and Monz (2002) who, in a three-year experimental trampling study, found that changes in species composition as a result of trampling in dry alpine meadows were minor. This might be a reflection of differences in community type between their study and ours. The meadows that Cole and Monz (2002) studied included forb-dominated and graminoid-dominated communities, whereas the tundra on Cardinal Divide is dominated by dwarf shrubs, which have been found to be intolerant of trampling (Cole, 1995b). Also, it is possible that the duration or intensity of the trampling in their study was not enough to cause compositional changes.

Our results for differences in relative abundance of different growth forms on the trail versus adjacent tundra mostly confirm what other studies have found about the trampling tolerance of different morphological groups (Cole, 1995b; Cole and Monz, 2002; Kuss, 1986; Price, 1985; Grabherr, 1982; Pounder, 1985; Whinam and Chilcott, 2003; Gremmen et al., 2003). Trail vegetation was dominated by upright and caespitose growth forms, and the majority of indicator species on the trail were grasses (*Poa alpina*, *Trisetum spicatum*, *Deschampsia cespitosa*, and *Festuca brachyphylla*). Another indicator, *Minuartia* spp., is a genus of cushion plant. This was somewhat surprising given that cushions have not been found to be a trampling-tolerant growth form. However, cushion plants possess characteristics that may be advantageous to them in the harsh, exposed trail environment. For example, their closely packed stems and leaves can moderate air temperature within the cushion and they have been found to be able to conserve moisture in the soil beneath them (Körner, 2003). In addition, the cushion life form acts as a litter trap, allowing the plant to access extra nutrients in nutrient-poor environments (Körner, 2003). These characteristics may at least partially explain why cushion plants were found to be relatively more abundant on the trail than off.

While there were superficial similarities between the trail and the gravel steps, the results suggest that trampling leads to the development of a community type that is unique in the context of the surrounding alpine environment on Cardinal Divide, different from both the undisturbed tundra meadows and from naturally disturbed, sparsely vegetated gravel steps. The gravel steps had higher cover of vascular plants, lichens, bryophytes, cryptogamic crust, and litter and higher richness than did the trail. Also, the plant community on the gravel steps was dominated by plants with a mat growth form, similar to undisturbed tundra, and the gravel steps had different indicator species than did the trails. In contrast, the trail plant community was clearly dominated by trampling-resistant species and growth forms. Both trampling and frost disturbance reduced species richness and plant cover in relation to the surrounding tundra, but this effect was more pronounced on the trails. Although trampling and the natural disturbance that forms the gravel steps both cause mechanical damage to plants (frost action can lead to root damage and breakage (Benninghoff, 1952) and trampling causes the breakage of the above-ground organs), the two disturbance types have very different effects on the alpine tundra. This might be because these two disturbance types differ in terms of their effects on soil. Trampling leads to increased soil compaction, while frost heave might loosen soils (Whinam and Chilcott, 2003), resulting in very different conditions for plant growth. It is also difficult to control for trampling intensity in a field setting, and differences in disturbance intensity may account for some of the observed differences.

Unlike lower elevation plant communities, associations between alpine plants are believed to be mainly facilitative (Choler et al., 2001; Callaway et al., 2002). At lower elevations where competition is common, increased space between neighboring plants can be beneficial as it reduces competition between individuals for resources. In contrast, in high alpine communities physical isolation can be a source of stress, as isolated plants are more exposed to the cold, windy conditions of the alpine environment (Choler et al., 2001). Thus, in the alpine, individual plants can benefit from growing in close association with other plants of the same or different species. Plants growing on the trail experience a fairly high degree of physical isolation from their neighbors, and this stress could be selecting for certain species while excluding others from the trail community. Plants on the gravel steps also experience this physical isolation and yet these communities were quite different from those on the trails. Overall our results suggest that the trail community is likely being shaped by trampling pressure rather than by the exposed, harsh environment that results from the greatly reduced plant cover on the trail. Further, the type of plant community on the trail is not found under natural conditions in the tundra (as it differed from both undisturbed and naturally disturbed communities), a conclusion that has important implications in protected areas, which are established to protect native communities.

We hypothesize that the combined effects of reduced plant cover along with soil compaction result in an environment that is extremely inhospitable to plants, with colder, windier, and drier conditions than the surrounding tundra, leading to a series of feedback effects which will inhibit recovery of abandoned trails (Fig. 2). Low amounts of litter and cryptogamic soil crust on the trail could have negative implications for soil nutrient availability. Litter is an important source of nutrients in alpine communities (Körner, 2003), while cryptogamic crust fixes nitrogen, which is believed to be a limiting factor in dry alpine tundra (Bowman et al., 1993). Gold et al. (2001) found that in the absence of cryptogamic crusts, alpine soils had lower levels of both nitrogen and phosphorus. Soil temperatures can become more extreme as a result of the loss of the insulating effects of litter and soil crust (Gold et al., 2001). The microenvironment near and at the soil surface in tundra ecosystems is naturally prone to extreme temperatures and temperature fluctuations (Körner, 2003) and an increase in these fluctuations may be a source of stress for plants growing in denuded areas.

Soil compaction reduces soil porosity and infiltration capacity, inhibits root growth (Liddle, 1997; Pounder, 1985) and aggravates erosion by increasing surface runoff (Batey, 2009). The loss of soil pores can hinder the establishment of seedlings by making it difficult for them to develop sufficient root biomass (Bassett et al., 2005) and can also impede a mature plant's ability to expand its root network (Liddle, 1997). The near complete absence of vegetation on the trail is also of concern because the soil anchoring function that plant roots provide is lost.

Feedback effects such as these could underlie the apparent slow recovery rates for tundra communities that have been damaged by recreational activities (Willard et al., 2007; Ebersole, 2002), and active restoration might be necessary in some cases to reverse these effects and encourage revegetation. They also point to the importance of understanding threshold effects of trampling in tundra ecosystems. If human traffic could be managed so as to avoid the initiation of these feedback effects, long-term damage to tundra plant communities could perhaps be avoided.

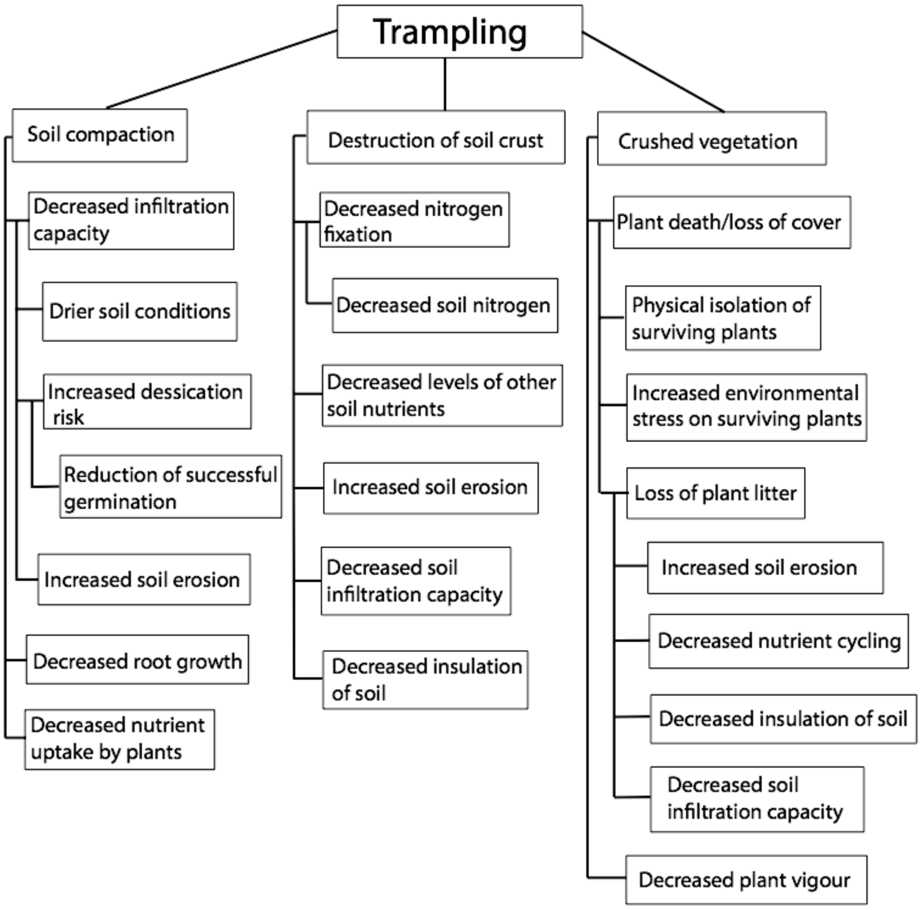

FIGURE 2. Conceptual model of positive feedback effects on alpine plant communities initiated by trampling.

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References Cited

Achuff, P. F., 1984: *Cardinal Divide Area: Resource Description and Comparison with Other Rocky Mountain Areas*. Edmonton: Alberta Energy and Natural Resources, Natural Areas Technical Report No. 23, 75 pp.

Anderson, M. J., 2001: A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26: 32–46.

Bassett, I. E., Simcock, R. C., and Mitchell, N. D., 2005: Consequences of soil compaction for seedling establishment: implications for natural regeneration and revegetation. *Austral Ecology*, 30: 827–833.

Batey, T., 2009: Soil compaction and soil management—A review. *Soil Use and Management*, 25: 335–345.

Belnap, J., 1993: Recovery rates of cryptobiotic soil crusts: assessments of artificial inoculant and methods of evaluation. *Great Basin Naturalist*, 53: 89–95.

Belnap, J., and Gillette, D. A., 1998: Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture and disturbance. *Journal of Arid Environments*, 39: 133–142.

Benninghoff, W. S., 1952: Interactions of vegetation and soil frost phenomena. *Arctic*, 5: 34–44.

Billings, W. D., 1973: Arctic and alpine vegetations: similarities, differences and susceptibility to disturbance. *Bioscience*, 23: 697–704.

Bliss, L. C., 1962: Adaptations of arctic and alpine plants to environmental conditions. *Arctic*, 15: 117–144.

Bowman, W. D., Theodose, T. A., Schardt, J. C., and Conant, R. T., 1993: Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology*, 74: 2085–2097.

Bryant, D., Holland, E. A., Seastedt, T. R., and Walker, M. D., 1998: Analysis of litter decomposition in an alpine tundra. *Canadian Journal of Botany*, 76: 1295–1304.

Callaway, R. M., Brooker, R. W., Choler, P., Kikvidze, Z., Lortiek, C. J., Michalet, R., Paolini, L., Pugnaireq, F. I., Newingham, B., Aschehoug, E. T., Armasq, C., Kikodze, D., and Cook, B. J., 2002: Positive interactions among alpine plants increase with stress. *Nature*, 417: 844–848.

Chapin, F. S., III, Shaver, G. R., Giblin, A. E., Nadelhoffer, K. J., and Laundre, J. A., 1995: Responses of arctic tundra to experimental and observed changes in climate. *Ecology*, 76: 694–711.

Choler, P., Michalet, R., and Callaway, R. M., 2001: Facilitation and competition on gradients in alpine plant communities. *Ecology*, 82: 3295–3308.

Cole, D. N., 1978: Estimating the susceptibility of wildland vegetation to trailside alteration. *Journal of Applied Ecology*, 15: 281–286.

Cole, D. N., 1995a: Experimental trampling of vegetation. I. Relationship between trampling intensity and response. *Journal of Applied Ecology*, 32: 203–214.

Cole, D. N., 1995b: Experimental trampling of vegetation. II. Predictors of resistance and resilience. *Journal of Applied Ecology*, 32: 215–224.

Cole, D. N., and Monz, C. A., 2002: Trampling disturbance of high-elevation vegetation, Wind River Mountains, Wyoming, U.S.A. *Arctic, Antarctic, and Alpine Research*, 34: 365–376.

Crisfield, V. E., 2010: The impacts of recreation on alpine tundra. MSc thesis, University of Alberta, Edmonton, Alberta, Canada.

Csotonyi, J. T., and Addicott, J. F., 2004: Influence of trampling-induced microtopography on growth of the soil crust bryophyte *Ceratodon purpureus* in Jasper National Park. *Canadian Journal of Botany*, 82: 1382–1392.

Dearden, P., and Sewell, W. R. D., 1985: From gloom to glory and beyond: the North American mountain recreation experience. *In* Bayfield, N. G., and Barrow, G. C. (eds.), *The Ecological Impacts of Outdoor Recreation on Mountain Areas in Europe and North America.* Ashford: Wye College Department of Horticulture, Recreation Ecology Research Group, Report no. 9, 1–7.

Douglas, G. W., and Ballard, T. M., 1971: Effects of fire on alpine plant communities in the North Cascades, Washington. *Ecology*, 52: 1058–1064.

Dufrêne, M., and Legendre, P., 1997: Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs*, 67: 345–366.

Ebersole, J. J., 2002: Recovery of alpine vegetation on small, denuded plots, Niwot Ridge, Colorado, U.S.A. *Arctic, Antarctic, and Alpine Research*, 34: 389–397.

Edwards, A. C., and Cresser, M. S., 1992: Freezing and its effect on chemical and biological properties of soil. *In* Stewart, B. A. (ed.), *Advances in Soil Science. Volume 18.* New York: Springer-Verlag, 59–80.

Forbes, B. C., Ebersole, J. J., and Strandberg, B., 2001: Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. *Conservation Biology*, 15: 954–969.

Forbes, B. C., Monz, C. A., and Tolvanen, A., 2004: Ecological impacts of tourism in terrestrial polar ecosystems. *In* Buckley, R. (ed.), *Environmental Impacts of Ecotourism*. Wallingford: CABI Publications, 155–170.

Frissell, S. S., 1978: Judging recreation impacts on wilderness campsites. *Journal of Forestry*, 76: 481–483.

Gold, W. G., 1998: The influence of cryptogamic crusts on the thermal environment and temperature relations of plants in a high arctic polar desert, Devon Island, N.W.T., Canada. *Arctic and Alpine Research*, 30: 108–120.

Gold, W. G., Glew, K. A., and Dickson, L. G., 2001: Functional influences of cryptobiotic surface crusts in an alpine tundra basin of the Olympic Mountains, Washington, U.S.A. *Northwest Science*, 75: 315–326.

Grabherr, G., 1982: The impact of trampling by tourists on a high altitudinal grassland in the Tyrolean Alps, Austria. *Plant Ecology*, 48: 209–217.

Gremmen, N. J. M., Smith, V. R., and van Tongeren, O. F. R., 2003: Impact of trampling on the vegetation of subantarctic Marion Island. *Arctic, Antarctic, and Alpine Research*, 35: 442–446.

Growcock, A. J. W., 2005: Impacts of camping and trampling on Australian alpine and subalpine vegetation and soils. PhD dissertation, Griffith University, Gold Coast, Australia.

Kershaw, G. P., and Kershaw, L. J., 1987: Successful plant colonizers on disturbances in tundra areas of northwestern Canada. *Arctic and Alpine Research*, 19: 451–460.

Klanderud, K., 2008: Species-specific responses of an alpine plant community under simulated environmental change. *Journal of Vegetation Science*, 19: 363–372.

Körner, C., 2003: *Alpine Plant Life: Functional Ecology of High Mountain Ecosystems.* Berlin: Springer-Verlag, 355 pp.

Kuss, F. R., 1986: A review of major factors influencing plant responses to recreation impacts. *Environmental Management*, 10: 637–650.

Lawson, D. E., 1986: Response of permafrost terrain to disturbance: a synthesis of observations from northern Alaska, U.S.A. *Arctic and Alpine Research*, 18: 1–17.

Liddle, M., 1997: *Recreation Ecology: the Ecological Impact of Outdoor Recreation and Ecotourism*. London: Chapman & Hall.

Liddle, M. J., 1975: A theoretical relationship between the primary productivity of vegetation and its ability to tolerate trampling. *Biological Conservation*, 8: 251–255.

Magurran, A. E., 2004: *Measuring Biological Diversity*. Malden: Blackwell Publishing, 256 pp.

McCune, B., and Grace, J., 2002: *Analysis of Ecological Communities*. Gleneden Beach: Mjm Software Design.

McCune, B., and Mefford, M. J., 2006: PC-ORD. Multivariate Analysis of Ecological Data. Version 5. Gleneden Beach: MjM Software.

McDougall, K. L., and Wright, G. T., 2004: The impact of trampling on feldmark vegetation in Kosciuszko National Park, Australia. *Australian Journal of Botany*, 52: 315–320.

Monz, C. A., 2002: The response of two arctic tundra plant communities to human trampling disturbance. *Journal of Environmental Management*, 64: 207–217.

Munroe, J. S., and Bockheim, J. G., 2001: Soil development in low arctic tundra of the northern Brooks Range, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research*, 33: 78–87.

Nicholson, F. H., 1976: Patterned ground formation and description as suggested by low arctic and subarctic examples. *Arctic and Alpine Research*, 8: 329–342.

Packer, J. G., and Vitt, D. H., 1974: Mountain Park: a plant refugium in the Canadian Rocky Mountains. *Canadian Journal of Botany,* 52: 1393–1409.

Parsons, D. J., 2002: Understanding and managing impacts of recreation use in mountain environments. *Arctic, Antarctic, and Alpine Research*, 34: 363–364.

Pounder, E. J., 1985: The effects of footpath development on vegetation at the Okstindan research station in arctic Norway. *Biological Conservation*, 34: 273–288.

Price, M. F., 1985: Impacts of recreational activities on alpine vegetation in western North America. *Mountain Research and Development,* 5: 263–277.

Raunkiaer, C., 1934: *The Life Forms of Plants and Statistical Plant Geography*. Oxford: Clarendon Press, 632 pp.

SAS Institute, 2004: *SAS/STAT 9.1 User's Guide*. Cary, North Carolina: SAS Institute Inc.

Scheirer, C. J., Ray, W. S., and Hare, N., 1976: The analysis of ranked data derived from completely randomised factorial designs. *Biometrics*, 32: 429–434.

Strong, W. L., 1999: Mountain Park area: a plant refugium in the Canadian Rocky Mountains? *Journal of Biogeography*, 26: 413–423.

Walker, D. A., and Walker, M. D., 1991: History and pattern of disturbance in Alaskan arctic terrestrial ecosystems: a hierarchical approach to analysing landscape change. *Journal of Applied Ecology*, 28: 244–276.

Whinam, J., and Chilcott, N., 1999: Impacts of trampling on alpine environments in central Tasmania. *Journal of Environmental Management*, 57: 205–220.

Whinam, J., and Chilcott, N. M., 2003: Impacts after four years of experimental trampling on alpine/sub-alpine environments in western Tasmania. *Journal of Environmental Management*, 67: 339–351.

Wilcoxon, F., 1945: Individual comparisons by ranking methods. *Biometrics Bulletin*, 1: 80–83.

Willard, B., and Marr, J., 1970: Recovery of alpine tundra under protection after damage by human activity in the Rocky Mountains of Colorado. *Biological Conservation*, 3: 181–190.

Willard, B. E., Cooper, D. J., and Forbes, B. C., 2007: Natural regeneration of alpine tundra vegetation after human trampling: a 42-year data set from Rocky Mountain National Park, Colorado, U.S.A.. *Arctic, Antarctic, and Alpine Research*, 39: 177–183.

Wipf, S., Stoeckli, V., and Bebi, P., 2009: Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climatic Change*, 94: 105–121.

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Appendix

Species list indicating the growth form for each. Nomenclature follows Moss (1983).

Species	Growth form
Arctostaphylos rubra (Rehder & Wils.) Fern.	mat
Arctostaphylos uva-ursi (L.) Spreng.	mat
Androsace chamaejasme Host	rosette
Anemone lithophila Rydb.	upright
Anemone parviflora Michx.	upright
Antennaria alpina (L.) Gaertn.	rosette
Antennaria spp.	rosette
Antennaria umbrinella Rydb.	rosette
Arnica angustifolia M. Vahl	rosette
Artemisia norvegica Fries ssp. *saxatilis* (Bess.) H. & C.	upright
Aster alpinus L.	rosette
Astragalus alpinus L.	upright
Betula glandulosa Michx.	upright
Braya purpurascens (R.Br.) Bunge	mat
Bromus inermis Leyss. ssp. *pumpellianus* (Scribn.) Wagnon	upright
Campanula uniflora L.	upright
Carex nardina Fries	caespitose
Carex petricosa Dewey	upright
Carex rupestris All.	upright
Carex scirpoidea Michx. var. *scirpoidea*	upright
Cassiope tetragona (L.) D. Don var. *saximontana* (Small) Porsild.	upright
Cerastium beeringianum Cham. & Schlecht.	mat
Deschampsia cespitosa (L.) Beauv. ssp. *cespitosa*	caespitose
Draba borealis DC.	rosette
Draba cana Rydb.	rosette
Draba spp.	rosette
Dryas integrifolia M. Vahl	mat
Dryas octopetala L. ssp. *hookeriana* (Juz.) Hult.	mat
Elymus innovatus Beal ssp. *innovatus*	upright

(*Continued*)

Appendix

Species list indicating the growth form for each. Nomenclature follows Moss (1983). ***(Continued)***

Species	Growth form
Equisetum scirpoides Michx.	upright
Erigeron compositus Pursh	upright
Erigeron peregrinus (Pursh) Greene spp. *callianthemus* (Greene) Cronq.	upright
Festuca baffinensis Polunin	caespitose
Festuca brachyphylla Schultes	caespitose
Gentiana prostrata Haenke	upright
Gentianella propinqua (Richards.) J.M. Gillett	upright
Habenaria hyperborea (L.) R.Br.	upright
Habenaria viridis (L.) R.Br. var. *bracteata* (Muhl.) Gray.	upright
Hedysarum alpinum L. ssp. *americanum* (Michx.) Fedtsch	upright
Hedysarum boreale Nutt.	upright
Kobresia myosuroides (Vill.) Fiori & Paol.	caespitose
Luzula spicata (L.) DC.	caespitose
Minuartia spp.	cushion
Oxytropis podocarpa A. Gray	mat
Oxytropis sericea Nutt. var. *spicata* (Hook.) Barneby	upright
Pedicularis capitata Adams	upright
Pedicularis flammea L.	rosette
Pedicularis lanata Cham. & Schlecht.	rosette
Phyllodoce glanduliflora (Hook.) Coville	upright
Picea engelmannii Parry *ex* Engelm.	upright
Pinus contorta Loudon ssp. *latifolia* Engelm.	upright
Poa alpina L.	upright
Polygonum viviparum L.	upright
Potentilla diversifolia Lehm.	upright
Potentilla fruticosa L.	upright
Potentilla nivea L.	caespitose
Potentilla ovina Macoun	mat
Pyrola grandiflora Radius	rosette
Salix arctica Pallas	mat
Salix barratiana Hook.	upright
Salix reticulata L. ssp. *nivalis* Löve, Löve & Kapoor	mat
Salix sp. 1	upright
Salix sp. 2	upright
Saxifraga oppositifolia L.	cushion
Senecio lugens Richards.	rosette
Silene acaulis L.	cushion
Smelowskia calycina (Stephan.) C.A. Mey var. *americana* (Rydb.) Drury & Rollins	upright
Solidago multiradiata Ait.	upright
Taraxacum ceratophorum (Ledeb.) DC.	rosette
Taraxacum officinale Weber	rosette
Trisetum spicatum (L.) Richt. ssp. *molle* (Michx.) Hult.	caespitose
Unidentified conifer germinant	upright
Zigadenus elegans Pursh	upright