Landscape Ecology vol. 6 no. 4 pp 269-278 (1992)
SPB Academic Publishing bv, The Hague

Trail corridors as habitat and conduits for movement of plant species in Rocky Mountain National Park, Colorado, USA

Mary Benninger-Truax, John L. Vankat and Robert L. Schaefer
Institute of Environmental Sciences, Department of Botany, and Department of Mathematics and Statistics, Miami University, Oxford, OH 45056

Keywords: disturbance, edge, exotic species, vegetation

Abstract

Ground-layer vegetation was sampled along selected trail corridors to determine whether corridors provide habitat for certain species and act as conduits for species movement. Patterns of plant species composition were analyzed in relation to distance from trail edge, level of trail use, and distance from trailheads, junctions, and campgrounds. Species composition was significantly affected by distance from trail edge and level of trail use, as species were favored or inhibited by the corridor, depending upon their growth habits. Species composition was also affected by distance from trailheads. These findings, along with the presence of exotic species, indicate that trail corridors in Rocky Mountain National Park function as habitat and conduits for movement of plant species.

1. Introduction

The desire to allow public access into natural areas has resulted in construction of trails for pedestrian and equestrian use. Trails are examples of line corridors caused by disturbance, and this type of corridor is characterized by a central portion devoid of biota due to continued inputs of energy (Bayfield 1973; Cole 1978; Forman and Godron 1986). Adjacent to the barren center may be corridor edge communities which can exhibit distinct zonation (Clements 1928; Bates 1935; Dale and Weaver 1974; Hall and Kuss 1989) and contain both native and non-native species (Westhoff 1967; Cole 1978, 1981; Forman and Godron 1981; Bright 1986). Colonization by exotic species is often facilitated by the ongoing disturbance characteristic of trails (Forman and Godron 1986; Hammitt and Cole 1987). In addition to being necessarily disturbance-resistant, exotic and native species occupying the corridor edge also may be favored by its microenvironment (Bates 1935; Dale and Weaver 1974; Liddle and Greig-Smith 1975; Cole 1978; Hall and Kuss 1989).

Along with providing habitat for certain species, corridors may function as conduits of movement for plants and animals (Getz *et al.* 1978; Wegner and Merriam 1979; Baudry 1984; Forman and Godron 1986; Verkaar 1988; Harris and Gallagher 1989). Intersecting line corridors such as trail systems form networks which may enhance this movement by providing numerous pathways and sources of species inputs (Forman and Godron 1981, 1986; Baudry 1984).

These possible effects of line corridors, *i.e.*, maintenance of edge habitat and movement of species, are major concerns of resource managers responsible for natural areas. Although others have studied the effects of trail corridors on plant species composition (e.g., Bates 1935; Dale and Weaver

1974; Liddle and Greig-Smith 1975), only one study considered distance from source populations (Bright 1986) and none approached both the habitat and conduit functions from a landscape ecology perspective.

Our objective was to determine whether trail corridors functioned as habitat and conduits for movement of plant species in Rocky Mountain National Park (RMNP). We focused on patterns of plant species composition in relation to distance from the trail edge, degree of trail use, and distance from trailheads, junctions, and campgrounds.

2. Study area

Rocky Mountain National Park is located in north-central Colorado, USA between 42” 10’ and 40°32′ north latitude and 105°31′ and 105°41′ west longitude. The park encompasses 1060 km^2 of the Front and Mummy Ranges of the Rocky Mountains, and elevations range from 2377 m on the eastern slopes to 4345 m at the summit of Longs Peak.

The vegetation in RMNP is divisible into montane, subalpine, and alpine elevational zones. This study investigated trailside vegetation in coniferous forests of the montane (2400-2700 m) and subalpine (2700-3400 m) zones. These forests are composed of mosaics of stands of different ages created by fire, wind, and insect disturbance (Peet 1981, 1988). They may be classified into several forest types based on elevation and moisture gradients (Peet 1981, 1988; Vankat 1990). With increasing elevation, the montane zone forests include a ***Pinus ponderosa*** forest type, a ***Pinus ponderosa-Pseudotsuga menziesii*** type, and a mixed type of ***Picea engelmannii, Abies lasiocarpa, Pseudotsuga menziesii,*** and ***Populus tremuloides*** (nomenclature follows Weber 1976). The dominant subalpine forest is a ***Picea engelmannii-Abies lasiocarpa,*** and a *Pinus flexilis* type occurs on dry sites above 2800 m. Two successional forests, a *Pinus contorta* type and a ***Populus tremuloides*** type, can be found at all elevations.

3. Methods

From United States Geological Survey topographic maps we determined the locations and lengths of trails in RMNP. We transposed the trails onto vegetation maps (provided by the park's research office) to determine which traversed the various elevational zones and the most common coniferous forest types, particularly the ***Pinus ponderosa, Pinus contorta,*** and ***Picea engelmannii-Abies lasiocarpa*** types. Using information in the RMNP Trail Plan (1982), we selected two trails in each of three use types: heavy pedestrian and equestrian, moderate pedestrian and equestrian, and light pedestrian and no equestrian (Benninger 1989). With regard to equestrian use, heavy and moderate were defined as annual use by $\geq$ 3000 and $<$ 500 horses, respectively. Pedestrian use was defined qualitatively in the RMNP Trail Plan (1982) and verified by our field observations. We could find no suitable trails with other combinations of pedestrian and equestrian use.

In June-August 1988, we used a distance-measuring wheel to divide each trail into 50 equal segments with one sample site each. Sample sites were equidistant, and we randomly selected the distance from the trailhead to the first site and the side of the trail for each site. Potential sites located in meadows or other non-forested areas were not sampled. At each forested sample site, we placed two 0.5 x 1 m contiguous plots (to cover a 0.5 x 2 m area) along and perpendicular to the trail edge and a 0.5 x 1 m plot perpendicular to the trail and 5 m into the forest. The 5 m distance represented forest interior conditions. These plot positions are referred to as Edge 1, Edge 2, and Interior. Within each plot, we identified all herbaceous and woody species $\leq$ 1 m in height and estimated their cover using cover classes: O-5, 6-20, 21-40, 41-60, 61-80, and 81-100%.

Our sampling design was intended to provide data at enough combinations of site factors (slope, aspect, topography, etc.) for the effects of these factors to average out across the plot positions and trail-use types. We employed two-way analysis of variance (ANOVA) to determine effects of plot position and trail use on species richness, total plot

Table 1. Results of two-way ANOVA tests examining the effects of plot position and trail use on species richness, plot cover, and average species cover for **(A)** all species and (B) exotic species.

	Plot position		Trail use		Position*use	
	F-value	p-value	F-value	p-value	F-value	p-value
A)						
Richness	2.96	.0521	5.31	.0051	0.45	.7705
Plot cover	47.16	.0001	15.95	.0001	0.36	.8340
Avg. species cover	24.71	.0001	11.83	.0001	1.21	.3032
B)						
Richness	8.43	.0007	2.31	.1092	0.98	.4273
Plot cover	1.27	.2888	0.61	.5168	0.13	.9695
Avg. species cover	1.70	.1923	0.38	.6888	0.22	.9253

cover, and average cover of species. Least square means (LSM) was used to determine where significant differences occurred. Because few species occurred at all combinations of plot position and trail use, we used one-way ANOVA to determine effects of these factors on cover of individual taxa. Chi-square tests were employed to determine effects of plot position and trail use on frequency of occurrence of individual taxa. We used correlation analysis to determine whether richness, plot cover, and average species cover were related to distances from trailheads, junctions, and campsites for each plot position and along each trail-use type. Alpha = 0.05 for all analyses.

4. Results and discussion

4.1. Trail corridors as habitat

Our findings demonstrate that trail corridors in RMNP provide habitat for vegetation different from the forest interior. For example, 52 (29%) of the total of 178 taxa sampled at the 291 sites were restricted to one of the plot positions (30 restricted to Edge 1, 12 to Edge 2, and 10 to the Interior). In addition, two-way ANOVA suggested (p = .0521) that plot position affected species richness (Table 1A), and LSM showed that richness was significantly greater in plot position Edge 1 than Interior (Fig. 1A). Also, plot cover and average species cover were lower in Edge 1 and 2 than in the Interior plot position (Table 1A, Figs. 1B and 1C).

Since the pioneering work of Bates (1935), differences in the composition of vegetation between the trail corridor and the matrix have been observed in coniferous forests (Dale and Weaver 1974; Cole 1978, 1981), deciduous forests (Hall and Kuss 1989), woodlands (Burden and Randerson 1972; Bright 1986), grasslands (Bates 1935; Chappell et *al.* 1971; Burden and Randerson 1972), and sand dunes (Liddle and Greig-Smith 1975). There is a gradient from constant to rare disturbance from the center of the corridor into the matrix, and different plant species are favored at different positions along this gradient. In addition to stress imposed on the vegetation via direct trampling, floristic differences between the trail corridor and the matrix have been attributed to differences in light intensity (Bates 1935; Dale and Weaver 1974; Cole 1978; Hall and Kuss 1989), direct precipitation (Dale and Weaver 1974), grazing pressure (Dale and Weaver 1974; Cole 1981), soil density (Bates 1935), soil moisture (Bates 1935; Burden and Randerson 1972; Liddle and Greig-Smith 1975), and root competition (Dale and Weaver 1974).

Insight into species' responses to trail corridors is gained by considering the growth form of species

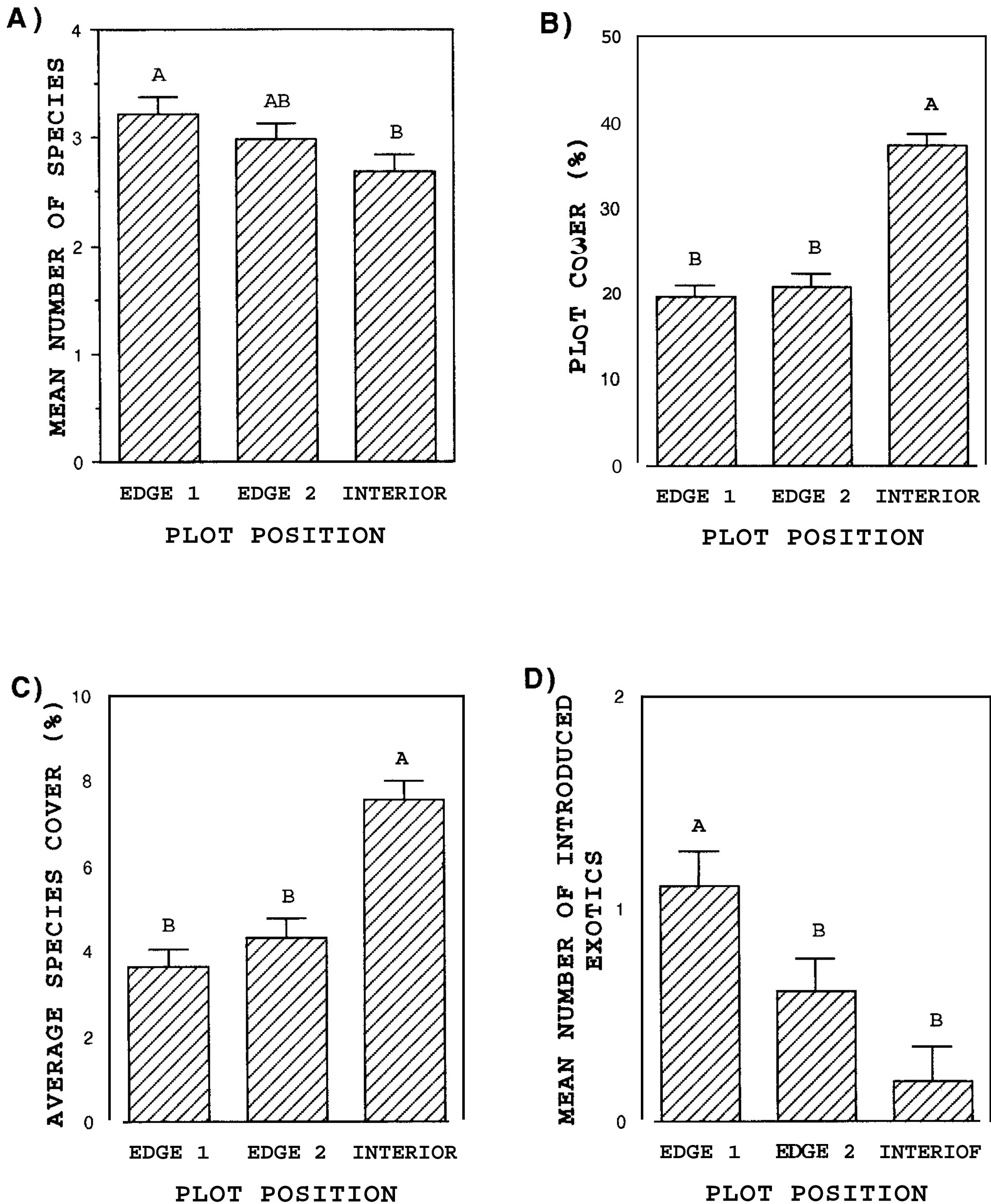

Fig. 1. Results of ANOVA and LSM showing the effects of plot position on **A)** species richness, B) plot cover, **C)** average species cover, and D) richness of exotic species. In each graph, bars with different letters represent means that are significantly different.

whose abundance differed among plot positions. Chi-square tests on species whose abundance was sufficient for statistical testing showed that three (6%) of 48 taxa differed in number of occurrences (Table 2A) and 16 (12%) of 135 taxa differed in average cover among plot positions (Table 2B). These taxa generally occurred less frequently or had greater cover with greater distance from the trail edge, paralleling the general trends noted for species richness and cover above. Taxa more abundant along the trail edge included *Antennaria spp.* (*parvifolia* and *rosea), Heterotheca fulcrata, Taraxacum officinale, Aster campestris,* and *Astragalus parryi,* all of which have traits, such as

Table 2. Species with significant differences in (A) number of occurrences and (B) cover among plot positions Edge 1 (E1), Edge 2 (E2), and Interior (INT). In B, values in same row with letters in common are not significantly different.

A)

Species	p-value	X^2 (df)	Number of occurrences		
			E1	E2	INT
Antennaria spp. (rosea and parvifolia)	.017	8.161	24	26	10
Heterotheca fulcrata	.029	7.115	16	19	6
Taraxacum officinale*	.008	9.735	14	7	2

B)

	ANOVA			LSD			
Species	p-value	F-value	R^2	Mean cover E1	Mean cover E2	Mean cover INT	Stand. Dev.
Arnica cordifolia	.0001	12.95	.1188	2.3 b	3.3 b	7.9 a	0.8
Aster campestris	.0270	7.00	.7000	0.6 a	0.2 b	–	0.1
Astragalus parryi	.0020	20.90	.8745	2.1	–	–	0.3
Bromopsis porteri	.0083	5.49	.2336	1.1 b	1.0 b	5.7 a	1.1
Carex heliophila	.0238	4.19	.2027	1.1 b	0.8 b	4.8 a	1.1
Chamerion angustifolium	.0002	9.41	.1327	0.9 b	1.4 b	4.4 a	0.6
Chimaphila umbellata	.0023	84.04	.9825	1.3 b	0.3 b	13.0 a	0.8
Drymocallis fissa	.0227	3.90	.0557	3.7 ab	2.1 b	5.4 a	0.8
Festuca saximontana	.0414	3.44	,1467	1.2 b	2.1 ab	6.0 a	1.4
Juniperus communis	,0096	4.82	.0711	4.6 b	12.7 a	16.1 a	2.7
Koeleria macrantha	.0145	4.56	.1380	1.8 b	2.4 b	7.2 a	1.4
Muhlenbergia montana	.0038	8.26	.5240	5.5 b	6.0 b	22.5 a	3.4
Populus tremuloides	.0086	5.16	,1467	2.1 b	0.1 b	7.6 a	1.6
Rosa woodsii	.0266	3.73	.0559	2.7 b	3.9 ab	6.4 a	1.0
Thermopsis divaricarpa	.0243	3.83	.0573	4.2 b	5.0 b	8.6 a	1.2
Vaccinium spp. (myrtillus and scoparium)	.0001	24.52	.0994	10.2 b	12.0 b	22.4 a	1.3

* Introduced to RMNP
– Absent

small ground-level leaves or vegetative reproduction at or below the ground, which reportedly enable them to survive in disturbed areas (cf. Bates 1935; Dale and Weaver 1974; Liddle 1975; Liddle and Greig-Smith 1975). *Antennaria parvifolia* and *Astragalus parryi* have matted caespitose growth forms; *Antennaria rosea* and *Aster campestris* reproduce vegetatively by runners and rhizomes, respectively; *Heterotheca fulcrata* may have a spreading habit; and *Taraxacum officinale* bears a rosette of basal leaves (Harrington 1964; Weber 1976).

The importance of growth form to the distribution of species is further suggested by the observation that these same characteristics apparently provide some species with the capability of colonizing trampled areas outside their normal elevational range (Benninger 1989). Examples include *Agropyron albicans, Carex heliophila, C. pachystachya,* and *Symphoricarpos occidentalis,* all of which are densely caespitose or have shallow perennating tissue.

Other species lack traits adaptive to the disturbance of trail corridors. In fact, most of the taxa

Table 3. Exotic species sampled in plot positions Edge 1 (E 1), Edge 2 (E 2), and Interior (INT) and along trail-use types heavy (H), moderate (M), and light (L).

Species	Plot position			Trail use		
Acetosella vulgaris		E 2	INT		M	
Bromus tectorum	E 1				M	
Machaeranthera pattersonii	E 1			H		
Nepeta cataria	E 1	E 2	INT		M	
Phleum pratense	E 1	E 2			M	
Poa pratensis	E 1	E 2	INT	H	M	
Taraxacum officinale	E 1	E 2	INT	H	M	L

which differed among plot positions had greater cover in the interior, away from trampling. These species included *Vaccinium* spp. (*myrtillus* and *scoparium)* which are common as ground cover in *Picea engelmannii-Abies lasiocarpa* forests. In this forest type, as well as the *Pinus contorta* type, the undergrowth is dominated by shade-resistant forbs characterized by large leaf area and supportive tissue, a growth form particularly susceptible to disturbance (Cole 1981).

Findings for exotic species also support the conclusion that trail corridors provide habitat for certain species, as all seven exotics occurred in one or both of Edge 1 and 2 and three (43%) were restricted to the edge plot positions (Table 3). These and several other exotic plants (*e.g.*, *Cirsium arvense* and *Trifolium pratense)* were often observed along trails. However, only *Taraxacum officinale* was sampled often enough for statistical testing, and it occurred most often in the Edge 1 position (Table 2A). Two-way ANOVA and LSM showed that species richness of the exotics was significantly greatest in the Edge 1 plot position (Table 1B, Fig. 1D). However, plot cover and average species cover were unaffected by distance from trail edge (Table 1B). Cole (1981), Kuss and Graefe (1985), Forman and Godron (1986), and Hammitt and Cole (1987) also concluded that trail corridors are important in the distribution of disturbance-resistant exotic plants. In theory, as habitats are modified by trampling stress, opportunistic exotic species are able to invade and colonize (Kuss and Graefe 1985).

The composition of trailside plant communities was also affected by trail use. Ninety-eight (55%) of the 178 taxa were restricted to one of the trail-use categories (29 restricted to light-use trails, 49 to moderate, and 20 heavy). Two-way ANOVA and LSM showed that species richness was significantly greater along light- and moderate-use trails than along heavy-use trails (Table 1A, Fig. 2A), and plot cover and average species cover were greatest along moderate-use trails (Table 1A, Figs. 2B and 2C). The high cover values along moderate-use trails may be due to intermediate levels of stress promoting the invasion of aggressive, opportunistic species without excluding less competitive individuals (Westhoff 1967; Grime 1973; Liddle and Greig-Smith 1975). Greater stress, such as along heavy-use trails, decreases species richness as disturbance-sensitive taxa are lost.

Trail use was important to some of the taxa whose abundance permitted statistical testing. Although no taxa differed significantly in average cover among trail-use types, 25 (71%) of 35 taxa showed significant differences in number of occurrences (Table 4). None of these taxa were restricted to one trail-use type, but seven (28%) occurred most often on heavy-use trails, eight (32%) on moderate, and 10 (40%) on light.

Only one of the seven exotic species occurred at all levels of trail use, the rest were restricted to one or both of the heavy- and moderate-use trail types (Table 3). Two-way ANOVA showed no significant effect of trail use on the richness, plot cover, or average species cover of the exotics (Table 1B). Least square means, however, showed species richness to be significantly greater along moderate- than along light-use trails (Fig. 2D).

4.2. *Trail corridors as conduits for species movement*

Our finding that trail use affects species composition along trails suggests that trail corridors function as conduits for species movement. This is supported by our determination that species richness and average species cover were affected by distance from trailheads. For example, with all trail-use types and all plot positions combined, richness was significantly negatively correlated with distance

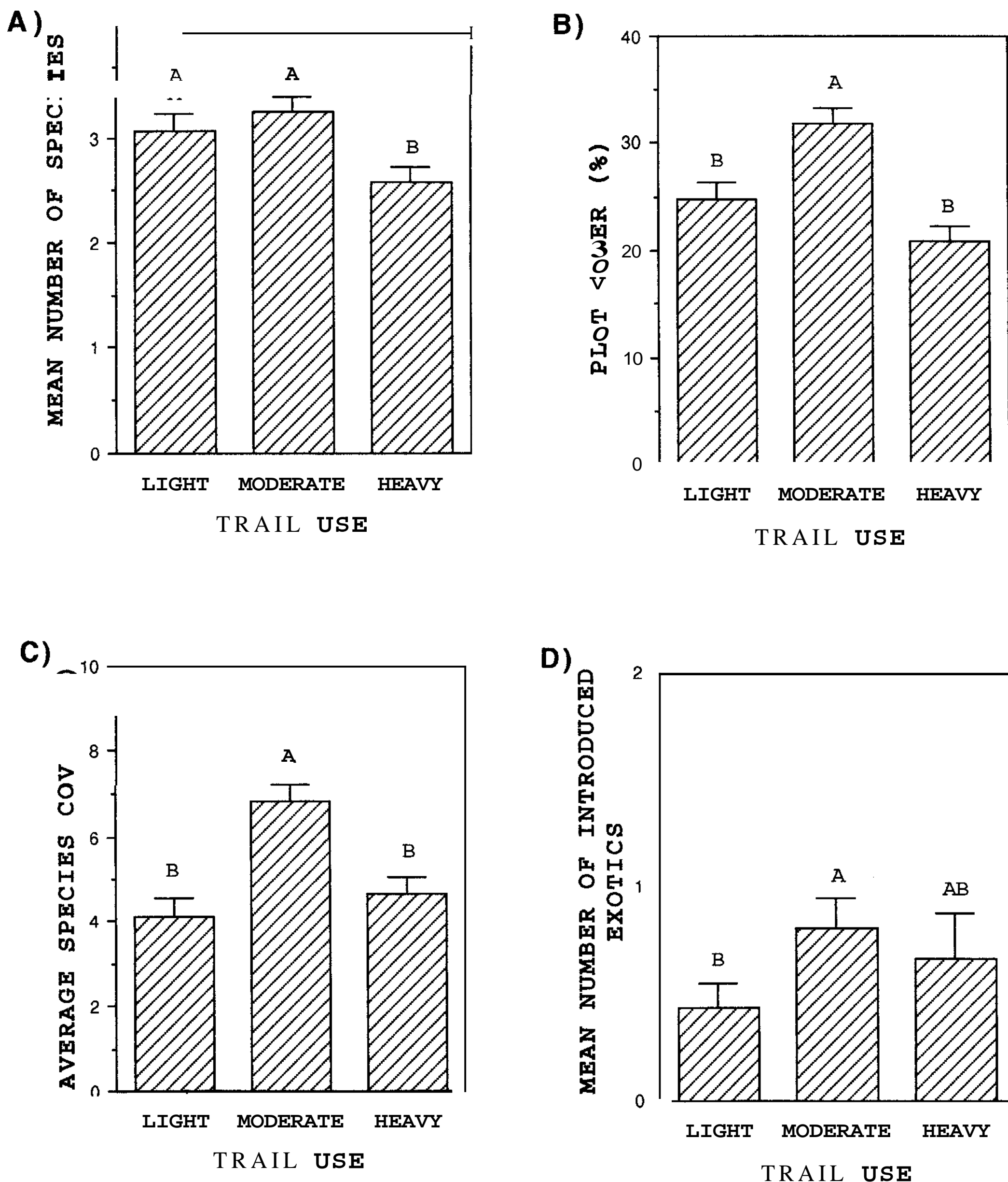

Fig. 2. Results of ANOVA and LSM showing the effects of trail use on A) species richness, B) plot cover, C) average species cover, and D) richness of exotic species. In each graph, bars with different letters represent means that are significantly different.

from the trailhead (Table 5A). This relationship was also significant for the Edge 1 plot position when all trail-use types were combined and for all three plot positions along the heavy-use trails. No other trail-use category exhibited a consistent, statistically-significant relationship for all three plot positions (or even for an edge plot position; Benninger 1989).

With all trail-use types combined, average species cover was significantly positively correlated with distance from trailheads for all plot positions combined and for all plot positions treated separately (Table 5B). This relationship was also significant for moderate-use trails for all plot positions combined and for both edge positions when treated separately.

Table 4. Species with significant differences in number of occurrences among trail-use types heavy (H), moderate (M), and light (L).

Species	p-value	X^2	Number of occurrences H	M	L
Abies lasiocarpa	.000	24.92	6	29	6
Achillea lanulosa	.032	6.90	11	14	20
Antennaria spp. (parvifolia and rosea)	.000	17.31	5	12	21
Arnica cordifolia	.000	36.18	7	43	15
Artemisia frigida	.024	5.07	11	3	0
Artemisia ludoviciana	,027	4.88	14	5	0
Aster foliaceus	.006	7.59	1	10	0
Bromopsis porteri	.014	6.08	0	3	10
Calamagrostis purpurascens	.001	14.42	14	1	13
Carex foenea	.016	8.27	4	16	12
Carex rossii	.000	60.39	3	4	31
Chamerion angustifolium	.004	11.14	7	15	20
Drymocallis fissa	.003	9.06	16	0	2
Erigeron eximius	.015	5.90	3	0	10
Festuca saximontana	.034	6.78	10	3	2
Fragaria ovalis	.000	16.81	2	14	1
Koeleria macrantha	.019	5.50	16	0	4
Penstemon virens	.001	14.10	17	6	21
Pyrola minor	.050	3.86	0	12	3
Rosa woodsii	.000	32.91	4	32	7
Senecio fendleri	.008	7.12	16	0	3
Solidago spathulata	.000	30.04	10	11	31
Taraxacum officinale*	.012	8.88	2	5	10
Thermopsis divaricarpa	.000	24.26	13	5	25
Vaccinium spp. (myrtillus and scoparium)	.000	125.84	18	98	33

* Introduced to RMNP

Table **5.** Correlation coefficients relating (A) species richness and (B) average species cover to distance from trailhead.

	N	Pearson correlation coefficients (R) All plots	Edge 1	Edge 2	Interior
A)					
All trails	291	−.1448*	−.1346*	−.1094	−.1025
Heavy use	103	−.4053**	−.3530**	−.2548**	−.3220**
Moderate use	105	−.1508	−,1356	−.1657	−.1445
Light use	83	−.2216*	−.1691	−.1488	−.2548*
B)					
All trails	291	.2972**	.3415**	.1729**	.2100**
Heavy use	103	.1537	.0940	.1312	.1106
Moderate use	105	.3575**	.3955**	.2191*	.1774
Light use	83	.0964	.1431	.0317	.0965

* $p < .05$
** $p < .01$

Nip-van der Voort *et al.* (1979) and Bright (1986) also observed that distance from source populations effected plant species composition, but their studies were in non-mountainous areas. As with most montane regions, trails in RMNP usually increase in elevation and pass through different forest types with greater distance from the trailhead. However, if elevation or changes in forest type accounted for the decrease in species richness and increase in average species cover we observed with distance from trailheads, our findings would have been statistically significant for each of the trail-use categories. Instead, significance was observed only when trail use was moderate (average species cover) or heavy (species richness).

We expected that distances from trail junctions and trailside campgrounds also affected species richness and cover. In theory, intersecting corridors form networks which enhance migration by providing alternative pathways for movement (Forman 1981, 1984; Forman and Godron 1981, 1986). Baudry (1984) observed that plant species richness and the frequency of occurrence for many species in hedgerows were significantly higher near intersections. Also, campgrounds theoretically could act as nodes or sources of disturbance-related species. For example, Cole (1981) observed that plant cover and the presence of certain species were affected by disturbance in campgrounds. However, correlations between all three parameters (*i.e.*, richness, plot cover, and average species cover) and distances from trail junctions and campgrounds, as well as between plot cover and distance from trailheads, were inconsistent (Benninger 1989).

Although exotic species showed no significant correlations with any distance parameter, their presence along trail corridors of RMNP, indicates that they use the corridors as a means of migration into natural areas. Furthermore, the presence of four of the seven exotics in the interior plot position suggests that trail corridors can facilitate the invasion of exotic species into the forests of RMNP. Preliminary study indicates that some exotic species are dispersed in horse scat (Benninger 1989).

5. Conclusions

Our findings that plant species composition was affected by distance from trail edge and level of trail use and that exotic species are present along trails show that trail corridors in RMNP provide habitat for certain species. Species are favored or inhibited by disturbance and microenvironment associated with the trail corridor, depending on their adaptive characteristics.

Our documentation that species composition was affected by level of trail use and distance from trailheads and that exotic species occur along trails indicate that trail corridors function as conduits for movement of species. The evidence is inferential because our study was short-term and pattern-based. Direct evidence for the conduit function awaits long-term study of the dispersal process itself, because plant dispersal, as a saltatory or step-by-step process (Baudry 1984; Forman and Godron 1986), often involves long periods of time.

Acknowledgments

We thank the Rocky Mountain Nature Association for funding; Curt Bucholtz, David Stevens, and Richard Keigley for assistance at RMNP; Michael Vincent for plant identifications; and Andrew Truax for assistance with sampling.

References

Bates, G.H. 1935. The vegetation of footpaths, sidewalks, cart-tracks and gateways. J. Ecol. 23: 463–487.

Baudry, J. 1984. Effects of landscape structure on biological communities: The case of hedgerow network landscapes. *In* Proceedings of the first international seminar of the International Association of Landscape Ecology. Vol. 1, pp. 55–65. Edited by J. Brandt and P. Agger. Roskilde University Centre, Roskilde, Denmark.

Bayfield, N.G. 1973. Use and deterioration of some Scottish hill paths. J. Appl. Ecol. 10: 635–644.

Benninger, M.C. 1989. Trails as conduits of movement for plant species in coniferous forests of Rocky Mountain National Park, Colorado. Masters thesis, Miami University, Oxford, Ohio.

Bright, J.A. 1986. Hiker impact on herbaceous vegetation along

trails in an evergreen woodland of central Texas. Biol. Conserv. **36: 53–59.**

Burden, R.F. and Randerson, P.F. **1972.** Quantitative studies of the effects of human trampling on vegetation as an aid to the management of semi-natural areas. J. Appl. Ecol. **9: 439–457.**

Chappell, H.G., Ainsworth, J.F., Cameron, R.A.D. and Redfern, M. **1971.** The effect of trampling on a chalk grassland ecosystem. J. Appl. Ecol. **8: 869–882.**

Clements, F.E. **1928.** Plant succession and indicators. H.W. Wilson Company, New York.

Cole, D.N. **1978.** Estimating the susceptibility of wildland vegetation to trailside alteration. J. Appl. Ecol. **15:** 281–286.

Cole, D.N. **1981.** Vegetational changes associated with recreational use and fire suppression in the Eagle Cap Wilderness, Oregon: Some management implications. Biol. Conserv. **20:** 247–270.

Dale, D. and Weaver, T. **1974.** Trampling effects on vegetation of the trail corridors of north Rocky Mountain forests. J. Appl. Ecol. 11: **767–772.**

Forman, R.T.T. 1981. Interactions among landscape elements: A core of landscape ecology. *In* Proceedings of the International Congress organized by the Netherlands Society for Landscape Ecology, Veldhoven, The Netherlands. pp. **35–48.** Edited by S.P. Tjallingii and A.A. de Veer. Centre for Agricultural Publishing and Documentation, Wageningen.

Forman, R.T.T. **1984.** Landscape ecology principles and landscape function. *In* Proceedings of the first international seminar of the International Association of Landscape Ecology. Vol. 5, pp. **4–5.** Edited by J. Brandt and P. Agger. Roskilde University Centre, Roskilde, Denmark.

Forman, R.T.T. and Godron, M. **1981.** Patches and structural components for a landscape ecology. Bioscience **31:** 733–**740.**

Forman, R.T.T. and Godron, M. **1986.** Landscape ecology. John Wiley & Sons, New York.

Getz, L.L., Cole, F.R. and Gates, D.L. **1978.** Interstate roadsides as dispersal routes for *Microtus pensylvanicus*. J. Mammal. **59:** 208–212.

Grime, J.P. **1973.** Control of species density in herbaceous vegetation. J. Env. Manag. 1: 151–167.

Hall, C.N. and Kuss, F.R. **1989.** Vegetation alteration along trails in Shenandoah National Park, Virginia. Biol. Conserv. **48: 211–227.**

Hammitt, W.E. and Cole, D.N. **1987.** Wildland recreation. John Wiley & Sons, New York

Harrington, H.D. **1964.** Manual of the plants of Colorado. Swallow Press, Chicago.

Harris, L.D. and Gallagher, P.B. **1989.** New initiatives for wildlife conservation: The need for movement corridors. *In* defense of wildlife: Preserving communities and corridors. pp. **11–34.** Edited by G. Mackintosh. Defenders of Wildlife, Washington, DC.

Kuss, F.R. and Graefe, A.R. **1985.** Effects of recreation trampling on natural area vegetation. J. Leisure Research **17: 165–183.**

Liddle, M.J. **1975.** A selective review of the ecological effects of human trampling on natural ecosystems. Biol. Conserv. **7: 17–36.**

Liddle, M.J. and Greig-Smith, P. **1975.** A survey of tracks and paths in a sand dune ecosystem. J. Appl. Ecol. **12: 909–930.**

Nelson, R.A. **1982.** Plants of Rocky Mountain National Park. Fifth edition, Rocky Mountain Nature Association, Boulder, Colorado.

Nip-van der Voort, J., Hengefeld, R. and Haeck, J. **1979.** Immigration rates of plant species in three Dutch polders. J. Biogeogr. **6: 301–308.**

Peet, R.K. **1981.** Forest vegetation of the Colorado Front Range. Vegetatio **45: 3–75.**

Peet, R.K. **1988.** Forests of the Rocky Mountains. *In* North American terrestrial vegetation. pp. **63–101.** Edited by M.G. Barbour and W.D. Billings. Cambridge University Press, Cambridge, England.

Rocky Mountain National Park Trail Plan. **1982.** Denver Service Center, National Park Service, U.S. Department of the Interior.

Vankat, J.L. **1990.** A classification of the forest types of North America. Vegetatio **88: 53–66.**

Verkaar, H.J. **1988.** The possible role of road verge and river dykes as corridors for the exchange of plant species between natural habitats. *In* Proceedings of the 2nd international seminar of the International Association for Landscape Ecology. pp. **79–84.** Edited by Karl-Friedrich Schreiber. Schoningh, Paderborn.

Weber, W.A. **1976.** Rocky mountain flora. Fifth edition, Colorado Associated University Press, Boulder, Colorado.

Wegner, J.F. and Merriam, H.G. **1979.** Movements by birds and small mammals between a wood and adjoining farmland habitats. J. Appl. Ecol. **16: 349–358.**

Westhoff, V. **1967.** The ecological impact of pedestrian, equestrian and vehicular traffic on vegetation. Proceedings and Papers of the Tenth Technical Meeting of I.U.C.N. **10: 218–223.**