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Trampling Disturbance of High-Elevation Vegetation, Wind River Mountains, Wyoming, U.S.A.

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Abstract

Trampling experiments were conducted in five high-elevation plant communities in the Wind River Mountains. In one experiment (simulating infrequent acute disturbance), plots were trampled once and recovery was followed for 3 yr. In another experiment (simulating chronic disturbance), plots were trampled for three successive years and recovery was followed for one year. Yearly trampling intensities were 0 to 500 passes (up to 800 and 1000 in two communities). Structural responses (reductions in cover and height) were more pronounced than compositional responses. Low levels of trampling caused substantial reductions in cover and height, but rates of change decreased as trampling intensity increased. The ability of different plant communities to tolerate trampling disturbance varied by at least an order of magnitude, suggesting that impacts can be reduced by directing use to more tolerant plant communities. Moreover, tolerance can be gauged on the basis of readily observable plant characteristics. Plant communities with groundcover dominated by chamaephytes (primarily low, woody shrubs) or by erect, caulescent forbs were less resistant than those with groundcovers dominated by turf-forming or caespitose graminoids, or by forbs with matted, caespitose or rosette growth forms. Plant communities with woody, chamaephytic groundcover were less resilient than other plant communities.

Introduction

Recreational use and tourism are increasing throughout high-mountain ecosystems of the world. Particularly in parks and wilderness areas, where management objectives emphasize minimal human disturbance, recreational trampling causes impacts that are substantial enough to require a managerial response. Rigorous studies of trampling effects on mountain vegetation date from the late 1960s (Bayfield, 1971; Bell and Bliss, 1973), when the potential for recreation to adversely affect these ecosystems was recognized. Early studies described the more readily observable effects of trampling, particularly reductions in vegetation cover and height, as well as shifts in the relative abundance of individual species (e.g., Bayfield, 1971; Burden and Randerson, 1972). The ultimate and most damaging effects of trampling include the extirpation of rare species (Zika, 1991), the creation of bare ground, and the acceleration of erosion processes.

Subsequent studies of trampling effects on plant physiology and morphology have revealed more about the processes of vegetation response to trampling. Trampling can break off plant parts and rip entire plants out of the ground. More subtle effects of trampling include reductions in the area of individual leaves, the number of leaves per shoot, flower density, and seed production per flower (Liddle, 1975; Hartley, 1976; Bratton, 1985). Goryshina (1983) reported that reductions in leaf area result more from inhibition of cell division than of cell elongation. Stem length is often reduced and prostrate branching tends to increase as a result of frequent damage to terminal buds (Liddle, 1997). Reductions in photosynthetic area can result in depleted carbohydrate reserves (Hartley, 1976) and reduced plant vigor. Reproduction and establishment of seedlings can be limited by both the lack of a diaspore bank and the lack of safe sites for

germination and juvenile development (Klug et al., 2002, this issue). The nature and magnitude of these responses vary greatly between species, however, resulting in pronounced shifts in species composition. Under moderate trampling pressure, some species increase in abundance (e.g., *Juncus trifidus*, Pryor, 1985) and others reproduce profusely (e.g., *Poa supina*, Klug et al., 2002, this issue), in contrast to the majority of species which have little ability to tolerate trampling.

Trampling studies have contributed to both our general understanding of disturbance ecology and more effective management of recreation (see recent reviews: Liddle, 1997; Yorks et al., 1997). Particularly helpful, conceptually, have been controlled trampling experiments (Bayfield, 1979; Sun and Liddle, 1991). Such studies isolate the effect of trampling from confounding variables, making it possible to (1) describe the relationship between trampling intensity and vegetation response and (2) assess the relative vulnerability of different plant species and communities.

A study of the effect of experimental trampling on 18 plant communities, in five different mountainous regions of the United States, provided an opportunity to assess the consistency of the relationship between trampling intensity and vegetation response (Cole, 1995a) and the extent to which variation in vegetation response to trampling can be predicted on the basis of plant morphology (Cole, 1995b). In most plant communities, the relationship between trampling intensity and vegetation response was curvilinear and best approximated by second-order polynomials. However, the curvilinearity of models decreased with trampling resistance of the vegetation; in the most resistant plant communities a linear model provided as good an approximation as the polynomial (Cole, 1995a).

The resistance and resilience of different plant communities

varied substantially, with much of this variation being explained by morphological characteristics of the vegetation (Cole, 1995b). Resistance was largely a function of vegetation stature, erectness, and physiognomic type. The most resistant plants were caespitose and matted graminoids, and forbs that are caespitose, matted, or that formed rosettes. The least resistant plants were erect, caulescent forbs. Resilience could be predicted largely on the basis of woodiness and the location of perennating buds. Woody chamaephytes, with perennating buds located above-ground, were least resilient. Tolerance, the ability to return to a state approximating original conditions after disturbance and a recovery period (Cole and Bayfield, 1993), was correlated more with resilience than with resistance.

Cole's (1995a, 1995b) study—and most experimental studies (Yorks et al., 1997)—only assessed response to a single application of trampling, however. This limits the management application of results, because trampling disturbance is typically chronic rather than acute. The objectives of this paper are to assess the degree to which vegetation response to chronic trampling is comparable to vegetation response to acute trampling and to test whether the general models and predictive relationships described by Cole (1995a, 1995b) apply in five plant communities in the subalpine and lower alpine zones of the Wind River Mountains, Wyoming, U.S.A. Specific questions addressed in regard to trampling response are (1) what is the nature of the relationship between trampling intensity and vegetative response? (2) do two and three years of trampling cause more disturbance than a single year? (3) are recovery rates following two and three years of trampling less than those following one year? (4) are plant communities with groundcover dominated by turf-forming graminoids or by matted or low-growing forbs without caulescent leaves more resistant to trampling than communities of erect, caulescent forbs? and (5) are plant communities with groundcover dominated by woody chamaephytes less resilient than herbaceous communities?

Study Area

The Wind River Mountains contain the most extensive zone of upper subalpine and alpine vegetation in Wyoming. An area about 45 km wide, extending 180 km from Togwotee Pass in the northwest to South Pass in the southeast, rises above 2900 m. Vegetation is a mosaic of forest and meadow in the upper subalpine, grading into alpine vegetation, typically at elevations of about 3200 m. Although not as world-renowned as nearby Yellowstone and Grand Teton National Parks, the Wind River Mountains are a magnet for recreation use, particularly for backpackers and horse packers. Over 400,000 ha of land—most of the upper subalpine and alpine zone—are protected in three contiguous Forest Service wilderness areas, the Bridger, Fitzpatrick, and Popo Agie, and a portion of the Wind River Indian Reservation that is managed as *de facto* wilderness. Heavy recreation use leaves many places devoid of vegetation and often with serious soil erosion problems. Although the most severely impacted places are localized, most of the popular destinations are in the upper subalpine and lower alpine zones, noted for outstanding scenery and abundant lakes.

Trampling studies were conducted at five sites in the Wind River Range. One site was located in the northwest portion of the range, at Togwotee Pass, where the Wind River and Absaroka Ranges abut. The four other sites were in the southeastern portion of the range, within the Popo Agie Wilderness south of Lander, in the watersheds of Stough and Basco Creeks, headwater tributaries of the Middle Fork of the Popo Agie River.

Study sites were located in plant communities that were representative of common vegetation types, that collectively were physiognomically diverse but individually were physiognomically homogeneous, and that had substantial groundcover. Each of the five communities, denoted by abundant groundcover species, is described below and in the Appendix. Nomenclature follows Dorn (1992).

FOREST WITH *EPILOBIUM ANGUSTIFOLIUM*–*ARNICA CORDIFOLIA* UNDERSTORY

This plant community was located at an elevation of 2925 m at Togwotee Pass, 43°45'30"N, 110°03'45"W. Vegetation was a mosaic of dense tree clumps in a matrix of herbaceous vegetation. Trampling plots were located between tree clumps, rather than underneath trees. Trees occupied about 20% of the ground surface. *Picea engelmannii*, *Abies lasiocarpa*, and *Pinus albicaulis* were all common. The largest trees were *Picea engelmannii*, 1 m in diameter, but *Pinus albicaulis* was most abundant in the mature tree, sapling, and seedling size classes. The density of mature trees (>5 cm dbh) was 300 stems/ha, while the density of tree reproduction (<1.5 m tall) was 730 stems/ha. Understory vegetation was diverse and multilayered, but discontinuous. Erect, caulescent forbs comprised over 90% of the groundcover. *Epilobium angustifolium*, *Arnica cordifolia*, *Lupinus argenteus*, *Achillea millefolium*, and *Agoseris glauca* var. *dasycephala* were the most abundant species. Graminoids and mosses each accounted for about 5% cover. Shrubs were not present. Mean bare ground (the proportion of plots not covered by vegetation) was 25%. Mean understory vegetation height was 11 cm.

FOREST WITH *VACCINIUM SCOPARIUM* UNDERSTORY

This site is located at an elevation of 3100 m in the Popo Agie Wilderness, 42°41'00"N, 109°00'30"W. The plant community is subalpine coniferous forest with groundcover dominated by the low-growing shrub *Vaccinium scoparium*. Although forest canopy cover was about 20%, trees were denser, smaller, and more evenly distributed than in the forests with the *Epilobium angustifolium*–*Arnica cordifolia* understory. *Pinus contorta* and *Pinus albicaulis* were the most abundant mature tree species, although *Picea engelmannii* and *Abies lasiocarpa* were common in flats where thicker soils accumulate. The largest trees were typically about 0.5 m in diameter. The density of mature trees around the study plots was 1050 stems/ha, while the density of tree reproduction was 1800 stems/ha. About 80% of the tree reproduction was *Pinus albicaulis*, although *Abies lasiocarpa* was also reproducing consistently. Understory vegetation was low-lying and discontinuous, with substantial exposed rock and litter between plants. *Vaccinium scoparium* accounted for more than 90% of the groundcover vegetation, with *Erigeron peregrinus*, *Arnica cordifolia*, and *Hieracium gracile* the most widely distributed and abundant associates. Mean understory vegetation height was 9 cm, with mean bare ground of 18%.

DESCHAMPسيا CESPITOSA–ANTENNARIA CORYMBOSA MEADOW

This plant community is located at an elevation of 3125 m in the Popo Agie Wilderness, 42°40'15"N, 109°02'30"W. It is a riparian meadow surrounded by subalpine forest. Such meadows, while wet immediately after snowmelt, dry as summer progresses and become prime sites for camping and for grazing recreational pack stock. This meadow contained a dense, diverse as-

semblage of graminoids and forbs. Forbs were more abundant than graminoids. The most abundant forbs, *Antennaria corymbosa*, *Caltha leptosepala*, and *Potentilla diversifolia*, were matted or had mostly basal leaves. Caespitose graminoids, *Deschampsia cespitosa*, *Agrostis humilis*, *Phleum alpinum*, *Juncus drummondii*, and various species of *Carex*, were all common. Mean moss cover was 12%; there were no shrubs. Mean bare ground was 9%, while mean vegetation height was 5 cm.

ELYMUS TRACHYCAULUS–FESTUCA IDAHOENSIS TURF

This site is located immediately above timberline on the flank of Roaring Fork Mountain in the Popo Agie Wilderness, at an elevation of 3230 m, 42°40'30"N, 109°00'00"W. The plant community is a dense turf codominated by the grasses *Elymus trachycaulus* and *Festuca idahoensis*. Despite the dominance of these two grasses, many other graminoid and forb species were present on the site. The most abundant forb associates are *Achillea millefolium*, *Taraxacum ceratophorum*, and *Stellaria longipes*. There were no shrubs or mosses. Mean bare ground was 2%, while mean vegetation height was 15 cm.

GEUM ROSSII–TRIFOLIUM NANUM TURF

This site is located in a saddle on Roaring Fork Mountain in the Popo Agie Wilderness, at an elevation of 3245 m, 42°39'15"N, 108°59'30"W. The plant community is transitional between fellfield and turf. While much of the saddle consisted of rocky soils, occupied predominantly by the cushion plants indicative of fellfields, we purposively located our plots in patches of denser vegetation more characteristic of alpine turf. Between exposed rocks, vegetation cover was dense and diverse. Although both grasses and forbs were well represented, forbs were more abundant. Matted forbs, *Geum rossii* and *Trifolium nanum*, were most abundant. Other prominent forbs included *Potentilla diversifolia* and *Artemisia scopulorum*. The most abundant graminoids were *Carex elynoides*, *Carex scirpoidea*, *Carex atrata* var. *chalciolepis*, and *Deschampsia cespitosa*. Mosses were present, but not abundant, and shrubs were absent. Mean bare ground was 6%, while mean vegetation height was 4 cm.

Methods

FIELD METHODS

Experimental design followed the protocols of Cole and Bayfield (1993). Four replicate blocks of trampling lanes were established in each plant community. Each block consisted of nine lanes, each 0.5 m wide and 1.5 m long. Blocks were located on flat sites without evidence of previous human impact, in visually homogeneous vegetation. Where the ground had any slope, lanes were oriented parallel to contours. Treatments were randomly assigned to lanes. Treatments varied both intensity of trampling per year and the number of years that trampling occurred. One lane was a control and received no trampling. Four lanes were trampled once at different intensities to simulate infrequent acute disturbance. The other four were trampled yearly for three successive years at different intensities to simulate chronic disturbance. In three plant communities, the trampling intensities applied were 25, 75, 200, and 500 passes per year. However, in the resistant *Geum rossii*–*Trifolium nanum* and *Elymus trachycaulis*–*Festuca idahoensis* communities, the 25-pass treatment was replaced with 800- and 1000-pass-per-year treat-

ments, respectively. A pass was a one-way walk, at a natural gait, along the lane. Trampers staggered starts from three locations across the 0.5-m width of the lane so that the entire width was trampled uniformly. Trampers wore lightweight boots with lug soles and averaged 65 kg. Previous research indicates that neither shoe type nor weight of trampler has a substantial effect on vegetation response to trampling (Cole and Bayfield, 1993).

Trampling treatments were applied when biomass first approached near-maximum levels, typically in late July and early August. All lanes within a plant community were trampled within a few days of each other and treatments within a block were almost always applied on the same day. Initial measurements were taken immediately before trampling. Post-trampling measurements were taken either immediately after trampling (vegetation height) or 2 wk after trampling (vegetation cover), when it was easier to distinguish between dead plants and plants that were damaged but still living.

The lanes that were trampled once were measured before and after trampling in year one and once per year for the following three years. This permitted an assessment of both short-term (1 yr) and longer-term (3 yr) recovery following an acute disturbance event (a single application of trampling). The lanes that were trampled for three consecutive years were measured before and after trampling for each of those three years, as well as 1 yr after the final application of trampling. This permitted an assessment of the effect of chronic disturbance (successive years of trampling), as well as the magnitude of seasonal recovery (the amount of recovery that occurred during the year between trampling applications) and the effect of successive years of trampling on seasonal recovery. Short-term (1 yr) recovery from chronic disturbance was assessed, but longer-term recovery was not.

Measurements were taken in two adjacent 30- by 50-cm subplots located in the center of each lane, with long axes parallel to the long axis of the lane. Within each subplot we estimated canopy cover of each individual species, and of mosses and lichens. Cover was recorded as 0 if absent and as 0.2% if less than 0.5% cover. Otherwise it was recorded as the closest of the following values: 1, 5, 10, 15, 20, 30, 40, 50, 60, 70, 80, 90, or 100%. We used a point quadrat frame, with 5 pins each 5 cm from the next, to estimate vegetation height. The frame was placed 10 times, systematically, along the length of each subplot. Pins were dropped to the ground. When the pin hit live vegetation, the height of the pin strike was recorded to the nearest 1 cm. If the pin hit a live plant at less than 0.5 cm, 0.2 cm was recorded. When no living plants were hit, a zero was recorded.

DATA ANALYSIS

From these measured parameters we calculated three index variables of change in plant community attributes. Both subplots in each trampling lane were combined, so that there are four replicates of each treatment in each plant community. Relative vegetation cover (Bayfield, 1979) is the proportion of original vegetation cover that remains after trampling, adjusted for changes on controls. We summed the cover of all individual species to obtain (1) initial cover on trampled lanes (IC_t), (2) surviving cover on trampled lanes (SC_t), (3) initial cover on controls (IC_c), and (4) surviving cover on controls (SC_c). From these we calculated relative vegetation cover (RVC) as:

$$RVC = [(SC_t \div IC_t) \div (SC_c \div IC_c)] \times 100\% \quad (1)$$

The relative vegetation cover of common and abundant individual species was calculated in an analogous manner.

Relative vegetation height is mean vegetation height after trampling, as a proportion of original vegetation height, adjusted for changes on controls. It was calculated by (1) summing the heights of all the pin hits and dividing by the number of nonzero values to obtain mean vegetation height and (2) substituting mean height values for the cover values in equation 1.

To assess the effect of trampling on species composition, we calculated floristic dissimilarity, the difference between pre-treatment and post-treatment species composition, on each plot. Related to Sorensen's similarity indices (Mueller-Dombois and Ellenberg, 1974), floristic dissimilarity (FD) is calculated as:

$$FD = 0.5 \sum |p_1 - p_2| \quad (2)$$

where p_1 is relative cover of a species prior to treatment (the cover of that species as a proportion of the cover of all species) and p_2 is relative cover of the same species after treatment. Insights about compositional change resulting from trampling were gained by comparing floristic dissimilarity on controls with floristic dissimilarity on trampled plots.

We used detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) (McCune and Mefford, 1999) to further explore the magnitude of compositional change resulting from trampling. We used DCA to generate ordinations of species and plots and then evaluated the correlation, for each plot, between trampling intensity and scores on the first and second axes of the ordinations. With CCA, trampling intensity was used as a single environmental variable. The ratio of the eigenvalue for trampling intensity to total variance was used as an indication of the degree to which trampling disturbance affected composition.

We assessed the resilience of these plant communities by examining (1) seasonal (1 yr) recovery following chronic disturbance and (2) longer-term (3 yr) recovery following a single acute disturbance. Lanes trampled three successive years had 1 yr to recover between applications of trampling. On these lanes, seasonal recovery (SR) is the difference in relative vegetation cover (RVC) immediately after trampling and after the seasonal recovery period (immediately before the next application of trampling), as a proportion of the cover lost as a result of trampling. It was calculated as

$$SR = \frac{(RVC \text{ after recovery} - RVC \text{ after trampling})}{(100 - RVC \text{ after trampling})} \quad (3)$$

Only lanes receiving at least 200 passes/year were included in the analysis to avoid problems with assessing resilience following minimal disturbance. Longer-term recovery was assessed, over a period of 3 yr, on lanes that received a single application of trampling.

We used ANOVA (GLM Repeated Measures, SPSS, Ver 9.0) to assess whether the magnitude of response to trampling varied with trampling intensity, years of trampling, or plant community. We employed the Type IV sum-of-squares method because we had an unbalanced design with empty cells. Seven different trampling intensities were used in the experiment (counting the control), but each plant community had only five intensities. Typically interactions between factors were statistically significant, making it necessary to conduct separate analyses for each plant community and for the acute and chronic disturbance experiments.

In these analyses, we were interested in whether additional years of trampling caused additional vegetation impact or reduced short-term resilience (seasonal recovery) of the vegeta-

tion. Effects of additional years were tested using within-subject contrasts. We were also interested in how many years were required for vegetation to completely recover from an acute trampling event. Recovery was considered complete when relative vegetation cover and relative vegetation height were not significantly different from 100% (one-sample t -test) and when floristic dissimilarity on trampled plots and controls were not significantly different (Dunnett's test). For all tests we used $\alpha = 0.05$.

Linear and curvilinear regression analyses were performed to identify the mathematical models that best approximated the relationship between trampling intensity and relative vegetation cover. Alternate models were evaluated on the basis of their coefficient of determination (r^2) and the distribution of residuals.

Results

VEGETATION COVER

Trampling caused pronounced reductions in vegetation cover. The magnitude of response varied with trampling intensity (repeated measures ANOVA, $F = 58.7$, $df = 6$, $P < 0.001$), years of trampling ($F = 20.1$, $df = 2$, $P < 0.001$), and among plant communities ($F = 57.7$, $df = 4$, $P < 0.001$). Interactions between all these factors were also statistically significant, making it necessary to conduct separate repeated measures analyses for each plant community. All three nonforested plant communities (*Geum rossii*-*Trifolium nanum* turf, *Deschampsia cespitosa*-*Antennaria corymbosa* meadow, and *Elymus trachycaulus*-*Festuca idahoensis* turf) were resistant to cover loss resulting from trampling. In each of these communities, relative cover declined significantly with trampling intensity (repeated measures ANOVA, $P < 0.05$) but not with successive years of trampling (Fig. 1).

Relative cover also decreased significantly with trampling intensity in the two forested plant communities. These communities were less resistant than the nonforested communities and cover decreased significantly with successive yearly applications of trampling. In forests with the *Epilobium angustifolium*-*Arnica cordifolia* understory, relative cover was significantly less after three yearly applications of trampling than after two applications (repeated-measures ANOVA, within-subject contrasts, $F = 11.7$, $df = 1$, $P = 0.05$). In the forest with *Vaccinium scoparium* understory, relative cover was significantly less after two yearly applications of trampling than after one application ($F = 167.5$, $df = 1$, $P < 0.001$); a third yearly application of trampling had no additional effect ($F = 1.1$, $df = 1$, $P = 0.32$).

The mathematical models that best fit the relationship between trampling intensity and relative vegetation cover were generally second-order polynomials, but the curvilinearity of models decreased with trampling resistance of the vegetation. For *Elymus trachycaulus*-*Festuca idahoensis* turf, the most resistant plant community, a linear model provided as good an approximation as the polynomial. Regression models, where Y is relative vegetation cover and X is number of passes, for each plant community from most to least resistant, were as follows: *Elymus trachycaulus*-*Festuca idahoensis* turf ($Y = 96 - 0.03X + 0.00001X^2$, $r^2 = 0.58$), *Geum rossii*-*Trifolium nanum* turf ($Y = 102 - 0.103X + 0.000065X^2$, $r^2 = 0.68$), *Deschampsia cespitosa*-*Antennaria corymbosa* meadow ($Y = 101 - 0.119X + 0.0001X^2$, $r^2 = 0.65$), forest with *Epilobium angustifolium*-*Arnica cordifolia* understory ($Y = 99 - 0.503X + 0.0007X^2$, $r^2 = 0.78$), and forest with *Vaccinium scoparium* understory ($Y = 92 - 0.660X + 0.001X^2$, $r^2 = 0.80$).

The magnitude of seasonal recovery, between yearly appli-

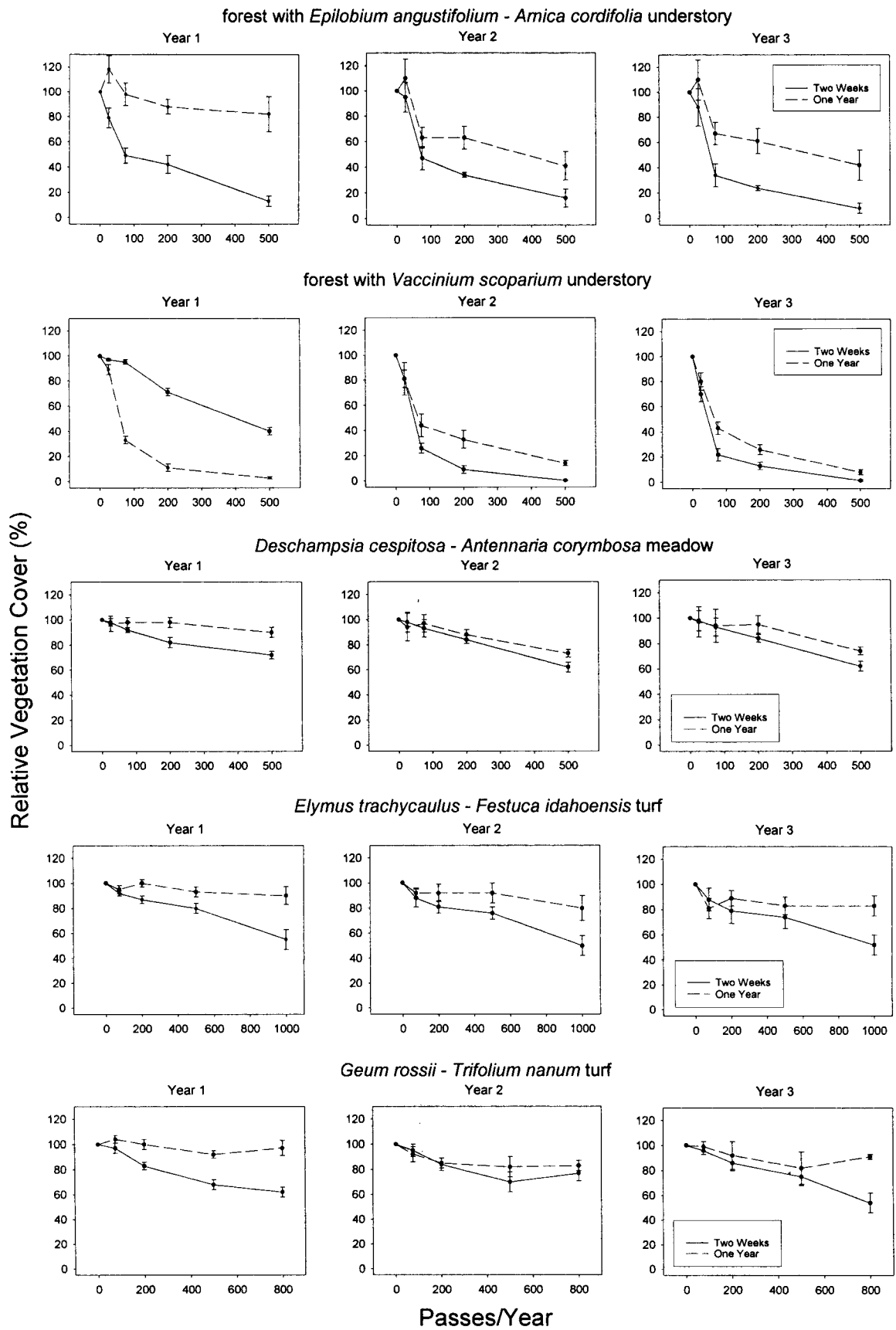


FIGURE 1. Relative vegetation cover (mean \pm 1 SE, n = 4) of five plant communities, two weeks and one year after one, two, and three yearly applications of trampling at various intensities.

TABLE 1

Seasonal recovery^a (mean \pm 1 SE, n = 4) of vegetation cover in five plant communities following one, two, and three yearly applications of trampling

Plant community	Years of trampling		
	One	Two	Three
<i>Epilobium angustifolium</i> – <i>Arnica cordifolia</i> understory	76 \pm 7	37 \pm 8	44 \pm 8
<i>Vaccinium scoparium</i> understory	-152 \pm 32	20 \pm 5	12 \pm 2
<i>Deschampsia cespitosa</i> – <i>Antennaria corymbosa</i> meadow	64 \pm 9	33 \pm 10	30 \pm 16
<i>Elymus trachycaulus</i> – <i>Festuca idahoensis</i> turf	71 \pm 6	46 \pm 9	52 \pm 9
<i>Geum rossii</i> – <i>Trifolium nanum</i> turf	75 \pm 6	28 \pm 13	43 \pm 18

^a 100% recovery indicates recovery to predisturbance conditions, while negative resilience values indicate loss of cover during the yearlong "recovery" period.

cations of trampling, varied with years of trampling (repeated measures ANOVA, $F = 8.9$, $df = 2$, $P < 0.001$) and among plant communities ($F = 31.6$, $df = 4$, $P < 0.001$). Interactions between these factors were also statistically significant ($F = 32.9$, $df = 8$, $P < 0.001$), making it necessary to analyze each plant community separately. Seasonal recovery following the first year of trampling was high (mean recovery of 64 to 76%) in the four plant communities with herbaceous groundcover—forest with *Epilobium angustifolium*–*Arnica cordifolia* understory, *Deschampsia cespitosa*–*Antennaria corymbosa* meadow, *Elymus trachycaulus*–*Festuca idahoensis* turf, and *Geum rossii*–*Trifolium nanum* turf (Table 1). In forest with *Epilobium angustifolium*–*Arnica cordifolia* understory, for example, relative vegetation cover increased from 13% 2 wk after the first application of 500 passes to 82% 1 yr after trampling (Fig. 1). In each of these herbaceous plant communities, the magnitude of seasonal recovery decreased significantly after the second yearly application of trampling (repeated measures ANOVA, within-subject contrasts, $P < 0.05$), but differences in recovery after the second and third applications were not significant. In the forest with *Vaccinium scoparium* understory, in contrast, resilience was significantly greater after the second yearly application of trampling than after the first or third yearly applications of trampling.

The substantial resilience of the four plant communities with herbaceous groundcover was also reflected in how rapidly

they recovered from acute trampling disturbance. In these plant communities, relative vegetation cover one year after trampling was not significantly different from 100% (one sample *t*-test), regardless of the trampling intensity applied. In the forest with *Vaccinium scoparium* understory, however, recovery was much slower. Lanes that received just 25 passes recovered within one year. However, lanes trampled 75 or more times had not recovered completely even after three years (Fig. 2).

VEGETATION HEIGHT

In addition to reducing the density and cover of vegetation, trampling also reduced vegetation height. Magnitude of response varied with trampling intensity (repeated measures ANOVA, $F = 74.0$, $df = 6$, $P < 0.001$), years of trampling ($F = 4.2$, $df = 2$, $P = 0.02$), and among plant communities ($F = 24.4$, $df = 4$, $P < 0.001$). Interactions between all these factors were also statistically significant. Except in the forest with *Vaccinium scoparium* understory, trampling had a more pronounced effect on vegetation height than on vegetation cover.

Relative vegetation height decreased with trampling intensity in all five plant communities (Fig. 3). The three nonforested plant communities were more resistant than the forested communities. *Geum rossii*–*Trifolium nanum* turf was initially most resistant; however, vegetation height decreased significantly with each successive year of trampling. In *Elymus trachycaulus*–*Festuca idahoensis* turf and *Deschampsia cespitosa*–*Antennaria corymbosa* meadow, the first yearly application of trampling reduced height substantially, but subsequent applications had less effect.

The *Epilobium angustifolium*–*Arnica cordifolia* understory, dominated by erect herbs, was particularly vulnerable to height reduction. Just one application of 25 passes reduced relative height to 26% (Fig. 3). Height decreased with trampling intensity but did not vary significantly with successive years of trampling. The *Vaccinium scoparium* understory was initially resistant to trampling. However, vegetation height decreased significantly with trampling intensity, as well as with each successive year of trampling.

The magnitude of seasonal recovery in vegetation height was generally greater than seasonal recovery of vegetation cover, particularly after the second and third yearly applications of trampling. Again, recovery varied with years of trampling (repeated measures ANOVA, $F = 3.4$, $df = 2$, $P < 0.008$) and among plant communities ($F = 37.5$, $df = 4$, $P < 0.001$) and the interaction between these factors was statistically significant ($F = 4.4$, $df = 8$, $P < 0.001$).

Seasonal recovery following the first application of trampling was high in *Deschampsia cespitosa*–*Antennaria corymbosa*

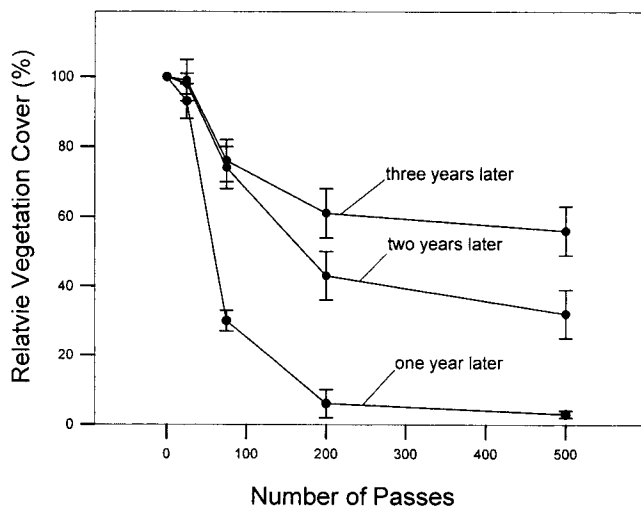


FIGURE 2. Relative vegetation cover (mean \pm 1 SE, n = 4) of the forest with *Vaccinium scoparium*-dominated understory, one, two, and three years after a single application of 0–500 passes.

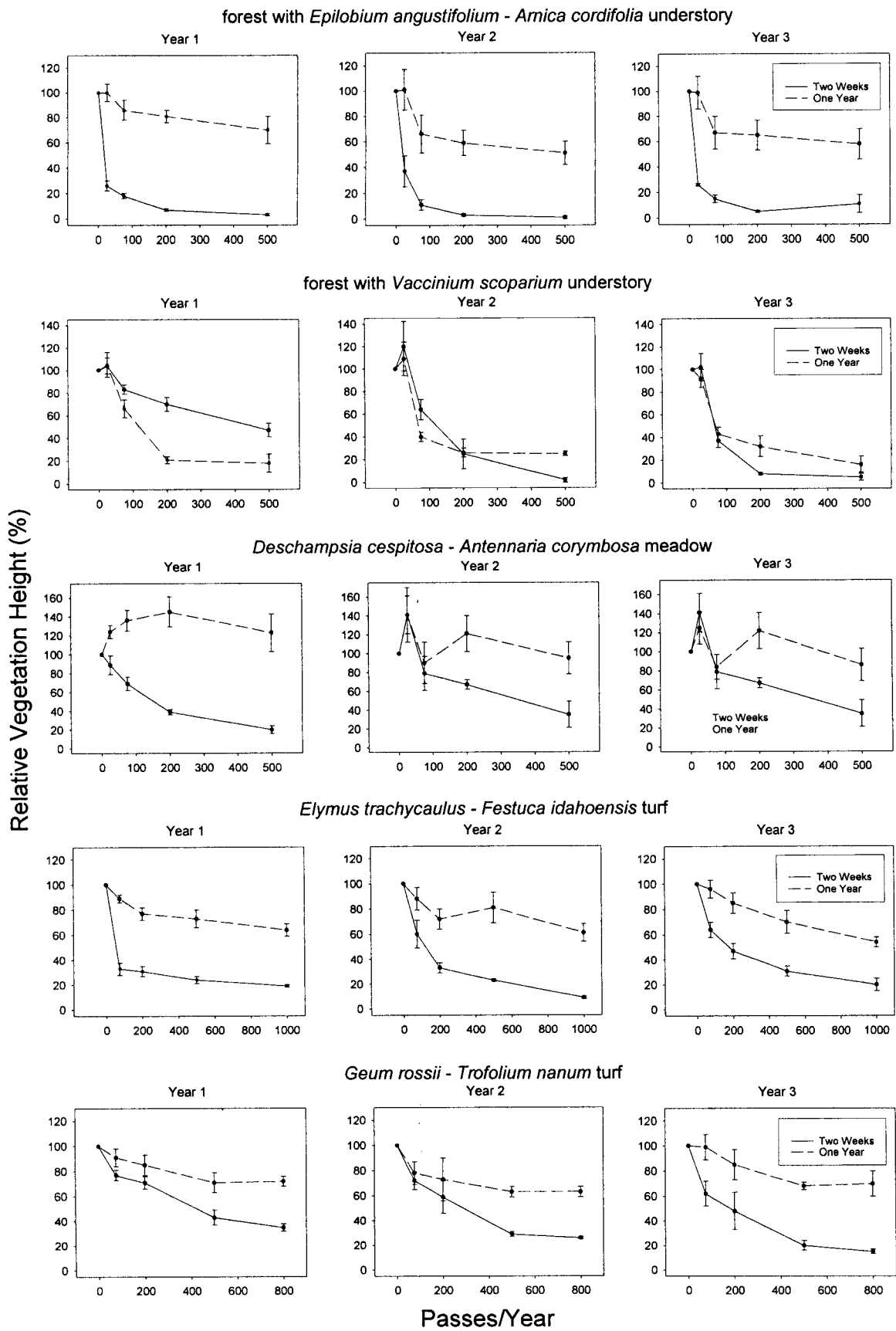


FIGURE 3. Relative vegetation height (mean \pm 1 SE, n = 4) of five plant communities, two weeks and one year after one, two, and three yearly applications of trampling at various intensities.

meadow (92%), forest with *Epilobium angustifolium*–*Arnica cordifolia* understory (73%), and *Elymus trachycaulus*–*Festuca idahoensis* turf (61%). Seasonal recovery was lower in the *Geum rossii*–*Trifolium nanum* turf (41%) and in the forest with *Vaccinium scoparium* understory (–63%), where height continued to decline. In the forest with *Epilobium angustifolium*–*Arnica cordifolia* understory and *Deschampsia cespitosa*–*Antennaria corymbosa* meadow, seasonal recovery was significantly lower after the second yearly application of trampling than after the first. In *Elymus trachycaulus*–*Festuca idahoensis* turf, seasonal recovery was similar after each of the three successive years of trampling. In *Geum rossii*–*Trifolium nanum* turf and forest with *Vaccinium scoparium* understory, seasonal recovery increased with each successive yearly application of trampling. Seasonal recovery after the third yearly application of trampling was 58 to 79% in all plant communities other than the *Vaccinium scoparium* understory, where mean recovery was only 23%.

Recovery of plant stature following infrequent acute disturbance occurred rapidly, regardless of trampling intensity, in *Deschampsia cespitosa*–*Antennaria corymbosa* meadow. Within 1 yr of the cessation of trampling, mean relative vegetation height varied between 114% (on 25-pass lanes) and 156% (on 200-pass lanes); trampling disturbance may have stimulated growth in this community. However, in other plant communities, complete recovery of plant height took longer than recovery of plant cover. In *Elymus trachycaulus*–*Festuca idahoensis* turf, vegetation height had not recovered completely within 1 yr of the cessation of trampling on any of the treatments. Complete recovery took 2 yr, regardless of trampling intensity. In the forest with *Epilobium angustifolium*–*Arnica cordifolia* understory and *Geum rossii*–*Trifolium nanum* turf, lanes that received 200 passes or more did not recover completely until 3 yr after the cessation of trampling. In the forest with *Vaccinium scoparium* understory, lanes that received 75 passes or more had not recovered completely even three years after the single application of trampling.

SPECIES COMPOSITION

Compositional change resulting from trampling was assessed as the difference in species composition on trampled plots, before and after trampling (floristic dissimilarity), in comparison to differences on control plots. As was the case with vegetation cover and height, trampling caused detectable changes in species composition. Magnitude of change varied with trampling intensity (repeated measures ANOVA, $F = 27.3$, $df = 6$, $P < 0.001$), years of trampling ($F = 4.1$, $df = 2$, $P = 0.02$), and among plant communities ($F = 38.3$, $df = 4$, $P < 0.001$) and interactions between all these factors were statistically significant.

The three nonforested plant communities did not experience substantial compositional change resulting from trampling (Fig. 4). In *Geum rossii*–*Trifolium nanum* turf and *Elymus trachycaulus*–*Festuca idahoensis* turf, after the first application of trampling, floristic dissimilarity was significantly higher on plots that received 500 or more passes than on control plots. However, in neither community were there significant differences between controls and any of the trampled lanes after either the second or third yearly applications of trampling. The resistance of all of the more abundant species in these two plant communities, primarily turf-forming or caespitose graminoids, and forbs that are matted, creeping, or that form rosettes, was high and roughly equivalent.

In *Deschampsia cespitosa*–*Antennaria corymbosa* meadow,

although trampling initially caused little composition change, magnitude of change increased significantly after the second and third yearly applications of trampling. The less resistant species were forbs with erect stems. After three yearly applications of 500 passes, the mean relative cover of *Antennaria corymbosa*, *Caltha leptosepala*, and *Potentilla diversifolia* (the most abundant forbs) was 28 to 49%. In contrast, mean relative cover of the most common graminoids, *Carex* spp., *Agrostis humilis*, and *Deschampsia cespitosa*, was 82 to 103%. The mat-forming forb, *Sibbaldia procumbens*, also little affected by trampling, had a mean relative cover of 118% after three yearly applications of 500 passes.

In the forest with *Vaccinium scoparium* understory, compositional change was more pronounced and increased with successive yearly applications of trampling. Compositional change was most pronounced after the second yearly application of trampling. In this community, although none of the groundcover species were resistant to trampling, the dominant subshrub, *Vaccinium scoparium*, was less resistant than its forb associates. After three yearly applications of 500 passes, mean relative cover of *Vaccinium scoparium* was <1%, while mean relative cover of *Erigeron peregrinus* and *Arnica cordifolia* was 22 to 30%.

The composition of groundcover vegetation in the forest with *Epilobium angustifolium*–*Arnica cordifolia* understory changed most rapidly in response to trampling. Mean floristic dissimilarity on 500-pass lanes was 52% greater than on controls after just one season of trampling. Mean relative cover of the most abundant forbs, *Epilobium angustifolium*, *Arnica cordifolia*, *Lupinus argenteus*, *Achillea millefolium*, and *Agoseris glauca*, was 0 to 11% after 500 passes. In contrast, mean relative cover of the most abundant graminoids, *Poa nervosa* and *Carex rossii*, was 57 to 68%. Floristic dissimilarity remained substantially higher on heavily trampled lanes than on controls after the second and third yearly applications of trampling.

Multivariate ordinations (DCA and CCA) suggest that the magnitude of compositional change resulting from trampling was modest, even in the least resistant plant communities. In the CCA analyses, the first axis of ordinations is constrained to the effect of the only environmental variable we assessed, trampling intensity. Even after three yearly trampling applications, eigenvalues for the first CCA axis—indicative of the variation in species data due to trampling intensity—were low (0.03–0.16), particularly in relation to eigenvalues for the unconstrained second CCA axis (0.20–0.40) or for the unconstrained first axis in DCA ordinations (0.22–0.42). Correlations (Spearman's rho) between trampling intensity and first axis DCA scores ranged from –0.01 in *Elymus trachycaulus*–*Festuca idahoensis* turf to 0.43 in forest with *Vaccinium scoparium* understory. We used ANOVA to assess the extent to which first axis DCA scores varied with trampling intensity and block. DCA scores varied significantly with trampling intensity in the forest with *Vaccinium scoparium* understory ($F = 5.9$, $df = 4$, $P = 0.001$), the forest with *Epilobium angustifolium*–*Arnica cordifolia* understory ($F = 3.2$, $df = 4$, $P = 0.02$) and the *Geum rossii*–*Trifolium nanum* turf ($F = 8.8$, $df = 4$, $P = 0.001$); however, F values were greater for block effects than for trampling intensity effects except in the *Vaccinium scoparium* understory. Visual examination of the DCA ordinations show that plots were clustered more according to block than trampling treatment, suggesting that initial variation in composition between blocks exceeded variation resulting from differences in trampling intensity.

In the forest with *Epilobium angustifolium*–*Arnica cordifolia* understory and *Geum rossii*–*Trifolium nanum* turf, composition recovered completely (i.e., floristic dissimilarity was not

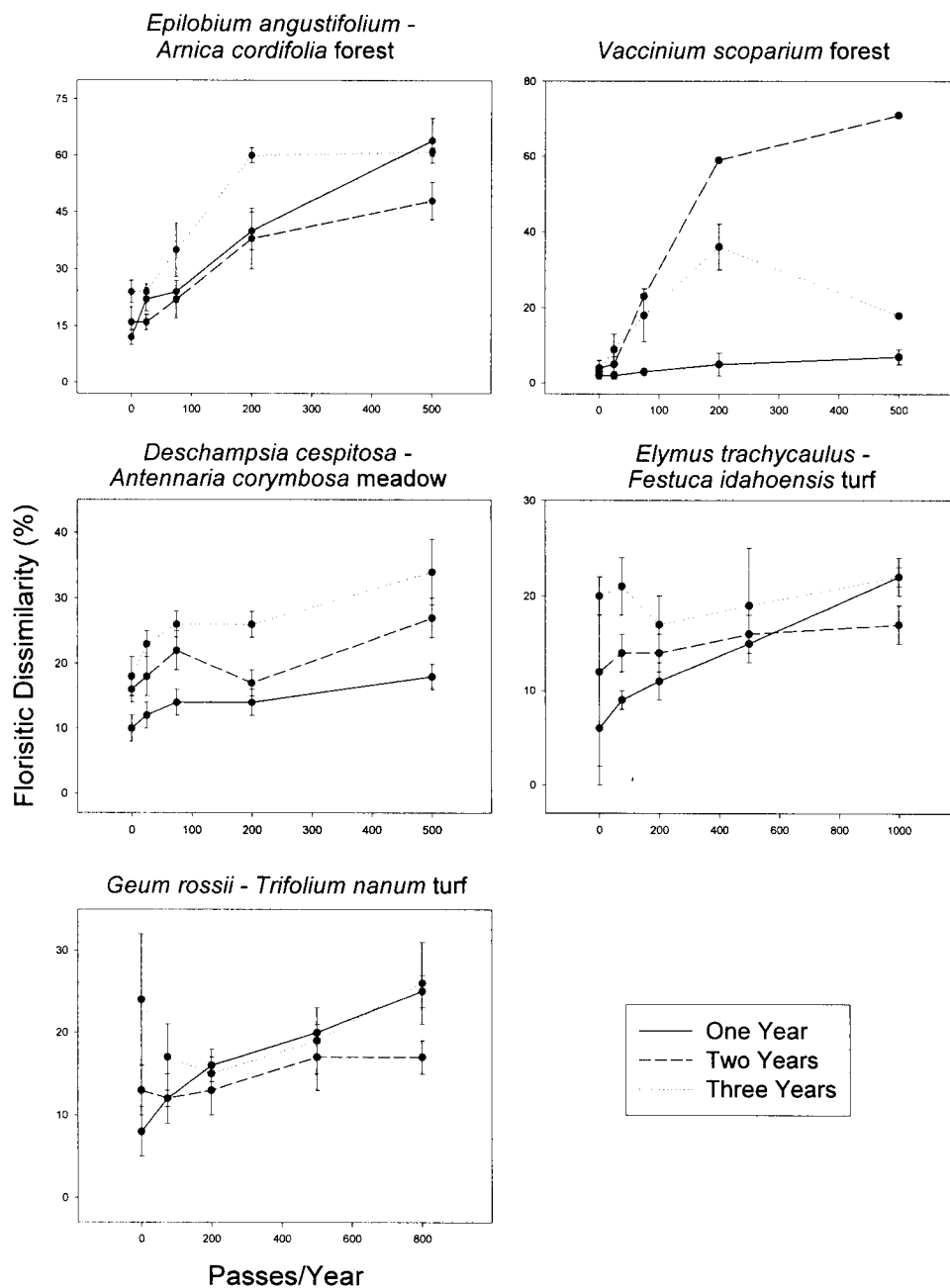


FIGURE 4. Floristic dissimilarity (difference in pre- and post-treatment species composition) (mean \pm 1 SE, n = 4) of five plant communities, 2 wk after one, two, and three yearly applications of trampling at various intensities.

significantly greater on trampled lanes than on controls) between yearly applications of trampling, regardless of trampling intensity. In the three other communities, both the magnitude of seasonal recovery and the effect of successive yearly applications of trampling on seasonal recovery were variable. In *Elymus trachycaulus*-*Festuca idahoensis* turf and the forest with *Vaccinium scoparium* understory, seasonal recovery increased with each successive year of trampling. In *Elymus* turf, composition did not recover completely during the year that followed the first application of 1000 passes; but it did recover completely during the year that followed the second and third yearly applications. In *Vaccinium* understory, composition continued to change during the winter following the first application of trampling but recovered somewhat after the second and third yearly applications. In *Deschampsia cespitosa*-*Antennaria corymbosa* meadow, little seasonal recovery occurred after any of the yearly applications of trampling. Because each successive application of trampling caused further compositional change, *Deschampsia*

cespitosa-*Antennaria corymbosa* meadow was the community most compositionally altered at the end of the experiment—after three successive yearly applications of trampling and periods of recovery.

Complete compositional recovery from one application of trampling occurred within 1 yr on all lanes in the forest with *Epilobium angustifolium*-*Arnica cordifolia* understory, and on lanes that received less than 75 passes in the forest with *Vaccinium scoparium* understory, less than 200 passes in *Geum rossii*-*Trifolium nanum* turf, less than 500 passes in *Deschampsia cespitosa*-*Antennaria corymbosa* meadow, and less than 1000 passes in *Elymus trachycaulus*-*Festuca idahoensis* turf. In all plant communities, complete recovery occurred within 2 yr of the cessation of trampling, regardless of trampling intensity.

Discussion and Conclusions

These high-elevation plant communities, in the Wind River Mountains of Wyoming, responded compositionally and struc-

turally to trampling disturbance. Compositional changes were more modest than decreases in the abundance (cover) and stature (height) of vegetation. Particularly in the most resistant plant communities, the most pronounced effect of trampling at the intensities applied was a reduction in vegetation height. Modest compositional change is, in part, an artifact of our selection of plant communities that were physiognomically homogeneous. In physiognomically diverse communities, individual species are more likely to vary in trampling tolerance and, therefore, composition is more likely to change substantially. Theoretically, the magnitude of compositional change should be related more to the diversity of trampling tolerance among different species in a plant community than the mean tolerance of the species in the community.

Results support Cole's (1995a) findings that (1) the mathematical models that best fit the relationship between trampling intensity and relative vegetation cover are generally second-order polynomials and (2) the curvilinearity of models decreases with resistance of the vegetation. Relatively low levels of trampling typically caused substantial impact.

Trampling resistance varied an order of magnitude among plant communities, however, and variation in resilience and tolerance were even greater. As predicted on the basis of earlier work (Cole, 1995b), plant communities with groundcover dominated either by (1) turf-forming graminoids (*Elymus trachycalus*–*Festuca idahoensis* turf) or (2) matted and low-growing forbs without caulescent leaves, with caespitose graminoids intermixed (*Geum rossii*–*Trifolium nanum* turf and, to a lesser degree, *Deschampsia cespitosa*–*Antennaria corymbosa* meadow), were substantially more resistant to infrequent acute trampling disturbance than the community dominated by erect forbs (forest with *Epilobium angustifolium*–*Arnica cordifolia* understory). The plant community with groundcover dominated by woody chamaephytes (forest with *Vaccinium scoparium* understory) was less resilient than the herbaceous communities. Tolerance was more highly correlated with resilience than with resistance. Consequently, 1 yr after one application of trampling, the primary difference was between the *Vaccinium scoparium* understory and the more resilient plant communities. These generalizations hold whether the response variable is vegetation cover, vegetation height, or species composition.

When comparing the effects of chronic disturbance to those of infrequent acute disturbance, there is little difference in the nature of the relationship between trampling intensity and vegetation response or in the plant morphological characteristics that best predict resistance and resilience. Differences in response, between chronic and acute disturbance, were most pronounced in the forest with *Vaccinium scoparium* understory. In *Vaccinium* understory, cover loss was modest 2 wk after the first trampling application, but cover decreased substantially during the subsequent year of "recovery" (before the next trampling application). Cover loss after the second trampling application was substantially greater than loss immediately following the first application, and seasonal recovery was much greater after the second application than after the first.

This suggests—in contrast to the other plant communities—that chronic disturbance causes a substantial reduction in resistance and increase in resilience in the forest with *Vaccinium scoparium* understory. This interpretation is misleading, however. Both effects are artifacts of the lengthy time lag between the first application of trampling and the death of many *Vaccinium scoparium* shrubs. Many *Vaccinium scoparium* shrubs damaged by the first application of trampling did not die until the following winter. Delayed damage, first reported by Bayfield

(1979), is particularly common in ericaceous shrubs. The time lag between trampling and plant death means that estimates of resistance, based on cover 2 wk after the initial application of trampling, are overstated, while estimates of resilience, based on change between measures taken at this time and one year later, are understated. With the insights gained from both acute and chronic trampling experiments, it is clear that the *Vaccinium scoparium* understory is neither resistant nor resilient when subjected to either infrequent acute or chronic disturbance.

With chronic disturbance, temporal variation in the response of vegetation cover to trampling disturbance declines. Additional years of trampling have little additional effect on cover loss but resilience declines with successive years of trampling. Vegetation height, in contrast, continues to vary more temporally, particularly in the herbaceous plant communities. In particular, resilience does not decline as much with successive years of trampling. Variation in the resilience of different plant communities does decline with chronic disturbance, however. Consequently, a plant community's tolerance of chronic trampling increasingly becomes defined more by its resistance than by its resilience. This contrasts with Cole's (1995a) conclusion, for a single acute disturbance, that tolerance is correlated more with resilience than with resistance.

These findings have significant implications for management of plant communities subjected to recreational use, particularly in wildernesses and national parks, where objectives emphasize minimizing human disturbance. Plant communities growing in close proximity to each other can vary an order of magnitude or more in their trampling tolerance. Consequently, managers can keep impacts to a minimum by directing recreational use to more tolerant plant communities. In the more common situation, where disturbance is chronic, the most tolerant communities are those with high resistance. Where disturbance is infrequent but acute, the more resilient communities are most tolerant.

Moreover, the resistance and resilience of many plant communities can be roughly gauged on the basis of readily observable characteristics. Where resilience is the primary concern, use should be directed away from plant communities with a groundcover of chamaephytes, particularly low-growing shrubs. Where resistance is the concern, use should be directed away from communities with groundcovers of chamaephytes, as well as those with groundcovers of erect, caulescent forbs. The more resistant plant communities include those dominated by caespitose or turf-forming graminoids or by matted or low-growing forbs with leaves that are mostly basal or in rosettes. Managers might attempt to teach recreationists to gauge resistance and resilience in the hope that, armed with such knowledge, they can avoid stepping on vegetation that is intolerant of trampling.

If trampling intensity is sufficient, all vegetation will be eliminated regardless of the resistance or resilience of vegetation. In such cases, confinement of use and impact to as small an area as possible is the most useful management strategy. We also recognize that trampling tolerance is only one of several characteristics to consider when distributing use and impact. There are undoubtedly situations where a lesser degree of impact to a rare or highly valued plant community should be considered much more costly than a greater degree of impact to a common community.

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Ms submitted June 2001

APPENDIX

Pretreatment frequency (% of 72 subplots of 30 × 50 cm in which the species was found) and cover (%) of the more abundant species in each plant community

Species	Freq	Cover
Forest with <i>Epilobium angustifolium</i> – <i>Arnica cordifolia</i> understory		
<i>Epilobium angustifolium</i>	100	25
<i>Arnica cordifolia</i>	75	22
<i>Lupinus argenteus</i>	60	10
<i>Achillea millefolium</i>	65	7
<i>Agoseris glauca</i> var. <i>dasycephala</i>	71	6
<i>Geranium viscosissimum</i>	42	4
<i>Solidago multiradiata</i> var. <i>scopulorum</i>	32	4
<i>Pedicularis racemosa</i>	47	4
<i>Aster foliaceus</i> var. <i>apricus</i>	36	3
<i>Senecio crassulus</i>	24	2
<i>Poa nervosa</i> var. <i>wheeleri</i>	40	2
<i>Carex rossii</i>	35	2
<i>Frasera speciosa</i>	6	2
<i>Aster integrifolius</i>	25	2
<i>Erigeron ursinus</i>	25	2
<i>Festuca idahoensis</i>	15	1
<i>Pedicularis bracteosa</i>	8	1
<i>Castilleja miniata</i>	13	1
Moss	42	5
Forest with <i>Vaccinium scoparium</i> understory		
<i>Vaccinium scoparium</i>	100	79
<i>Erigeron peregrinus</i>	32	3
<i>Arnica cordifolia</i>	28	1
<i>Hieracium gracile</i>	25	1
Moss	19	1
<i>Deschampsia cespitosa</i> – <i>Antennaria corymbosa</i> meadow		
<i>Deschampsia cespitosa</i>	93	23
<i>Antennaria corymbosa</i>	97	19
<i>Caltha leptosepala</i>	96	17
<i>Carex</i> spp.	93	17
<i>Agrostis humilis</i>	90	15
<i>Potentilla diversifolia</i>	90	12
<i>Sibbaldia procumbens</i>	43	8
<i>Erigeron peregrinus</i>	74	7
<i>Veronica wormskjoldii</i>	64	6
<i>Juncus drummondii</i>	72	6
<i>Viola adunca</i>	50	5
<i>Phleum alpinum</i>	85	4
<i>Danthonia intermedia</i>	29	3
<i>Agoseris aurantiaca</i>	46	3
<i>Epilobium clavatum</i>	54	1
<i>Polygonum bistortoides</i>	43	1
<i>Senecio cymbalarioides</i>	17	1
Moss	61	12
<i>Elymus trachycaulus</i> – <i>Festuca idahoensis</i> turf		
<i>Elymus trachycaulus</i>	100	38
<i>Festuca idahoensis</i>	100	31
<i>Achillea millefolium</i>	92	19
<i>Taraxacum ceratophorum</i>	67	14
<i>Stellaria longipes</i> var. <i>longipes</i>	71	13

APPENDIX

(Cont.)

Species	Freq	Cover
<i>Deschampsia cespitosa</i>	63	12
<i>Polemonium viscosum</i>	85	10
<i>Agoseris glauca</i>	57	10
<i>Potentilla diversifolia</i>	75	5
<i>Polygonum bistortoides</i>	54	4
<i>Carex elynoides</i>	67	4
<i>Poa secunda</i> var. <i>incurva</i>	49	3
<i>Cymopterus longilobus</i>	39	3
<i>Phlox hoodii</i>	21	3
<i>Besseyia wyomingensis</i>	32	2
<i>Cerastium beeringianum</i>	25	2
<i>Elymus scribneri</i>	8	1
<i>Agrostis scabra</i>	7	1
<i>Trisetum spicatum</i>	11	1
<i>Aster foliaceus</i> var. <i>apricus</i>	8	1
<i>Geum rossii</i> - <i>Trifolium nanum</i> turf		
<i>Trifolium nanum</i>	100	38
<i>Geum rossii</i>	100	31
<i>Potentilla diversifolia</i>	92	19
<i>Carex elynoides</i>	67	14
<i>Artemisia scopulorum</i>	71	13
<i>Carex scirpoidea</i>	63	12
<i>Deschampsia cespitosa</i>	85	10
<i>Carex atrata</i> var. <i>chalciolepis</i>	57	10
<i>Polygonum bistortoides</i>	75	5
<i>Phlox hoodii</i>	54	4
<i>Sedum lanceolatum</i>	67	4
<i>Trisetum spicatum</i>	49	3
<i>Festuca ovina</i> var. <i>brevifolia</i>	39	3
<i>Calamagrostis purpurascens</i>	21	3
<i>Poa alpina</i>	32	2
<i>Taraxacum ceratophorum</i>	25	2
<i>Carex phaeocephala</i>	8	1