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Quantifying Vegetation Response to Recreational Disturbance in the North Cascades, Washington

Abstract

The purpose of this study was to (1) describe vegetational response to various levels of controlled recreational trampling and (2) explore variation in response between different vegetation types and species. Better information on the ability of vegetation to resist and recover from damage is needed by park and wilderness managers to minimize impacts caused by recreationists. Four vegetation types were trampled at intensities that ranged from 25 to 700 times. Responses shortly after trampling and after one year of recovery were documented. Vegetational response varied significantly both with trampling intensity and between vegetation types. A sedge meadow dominated by black alpine sedge was about 25 times more resistant to trampling damage than a subalpine forb meadow, in which Sitka valerian was the most abundant species. Recovery during the year that followed trampling was greatest in the forb meadow; it was lowest in the two vegetation types dominated by woody species—heather and mountain boxwood. The resistance and resilience of individual species was also assessed. Species resistance appears to be determined primarily by the stature, arrangement, and toughness/flexibility of aerial tissues. Resilience appears to be determined by the location and toughness of perennating tissues and by the growth rate of regenerating tissues. These results have immediate application to recreation managers and also increase our basic understanding of disturbance ecology.

Introduction

The nature of disturbance in natural communities has generated considerable interest among ecologists (Souza 1984). Much basic research has been conducted on vegetational responses to natural disturbance agents such as fire, wind, landslides, and volcanic eruptions (White 1979). Applied ecologists have complemented this work with studies of human-caused disturbances, from relatively localized disturbances such as oil spills (Hutchinson and Freedman 1978) and the construction of winter seismic trails (Felix and Reynolds 1989), to more widespread disturbances such as livestock grazing and logging (Vale 1982).

One disturbance agent that has become increasingly important in recent decades is the recreationist. Substantial quantities of land have been set aside as national parks and wilderness for the purpose of nature preservation. Such places are also available for recreational use, however, and recreational use of these wildlands has increased dramatically. This use commonly compromises preservation goals. One of the most serious types of recreational impact is damage to vegetation caused by trampling at campsites and along trails. Park and wilderness managers often seek to control such impacts by restricting amount of use or by attempting to channel use onto the vegetation types that are most durable. To do this effectively,

managers need information about vegetation response to different levels of trampling stress, as well as about the relative durability of different vegetation types.

The objective of this paper is to describe the effects of recreational trampling on vegetation in the northern Cascade Mountains of Washington. Specifically, it reports the results of experiments in which carefully controlled levels of trampling are applied to vegetation plots. Several experimental trampling studies have already been conducted in the mountains of western Washington. Bell and Bliss (1973) and Schreiner (1974) studied the initial trampling responses of alpine and subalpine meadow communities in the Olympic Mountains. Singer (1971) studied the trampling response of an alpine community on Mt. Rainier. This paper extends this research by describing the results of trampling experiments in four vegetation types from the northeastern Cascade Mountains. Compared with earlier work, this study examined a broader range of vegetation types, from montane forest to alpine meadow, and included both initial damage and subsequent recovery.

Methods

Study Sites

The four study sites were located on the Okanogan National Forest, along the crest and east slope

of the Cascade Mountains. One site (denoted by the generic name of the most abundant understory plant, *Pachistima*) was located at an elevation of about 760 m along the upper Methow River. It was characterized by a moderately dense tree canopy (50-75% cover) entirely of Douglas-fir (*Pseudotsuga menziesii*), with a relatively sparse understory entirely of Douglas-fir. Associated groundcover plants were only moderately dense and consist primarily of shrubs, particularly mountain boxwood (*Pachistima myrsinites*) (Table 1). Nomenclature follows Hitchcock and Cronquist (1973).

Two of the other vegetation types occurred intermixed with each other in a mosaic of subalpine forest and meadow near Harts Pass; elevation was about 1750 m. Both had an overstory of subalpine

fir (*Abies lasiocarpa*), with a smaller number of large Engelmann spruce (*Picea engelmannii*). The groundcover of one type (*Phyllodoce*) was dominated by a dense cover of low shrubs, particularly heather (*Phyllodoce empetriformis*) and huckleberry (*Vaccinium membranaceum*). The other type (*Valeriana*) was characterized by a dense cover of tall broad-leaved herbs, of which valerian (*Valeriana sitchensis*) was most abundant. These groundcovers occurred both under and away from the forest canopy. Most of the experimental units were in small openings, but adjacent to forest.

The final type (*Carex*) was a sedge meadow, located on the slopes of Slate Peak at an elevation of about 2000 m. The sites were located in swales where snowmelt is unusually late; the dominant species was black alpine sedge (*Carex nigricans*).

TABLE 1. Initial frequency and mean percent cover of the more abundant species in each of the four vegetation types.¹

Species	Vegetation type							
	<i>Pachistima</i>		<i>Phyllodoce</i>		<i>Valeriana</i>		<i>Carex</i>	
	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover
<i>Pachistima myrsinites</i>	98	46						
<i>Amelanchier alnifolia</i>	70	9						
<i>Phyllodoce empetriformis</i>			100	81				
<i>Vaccinium membranaceum</i>			93	15				
mosses	13	+	58	7	74	20	73	9
<i>Ligusticum grayi</i>			38	3	28	6		
<i>Valeriana sitchensis</i>			25	2	96	40		
<i>Lupinus latifolius</i>			18	2	13	3		
<i>Arnica mollis</i>			23	2				
<i>Potentilla flabellifolia</i>			28	2	48	8	45	7
<i>Aster alpigenus</i>			25	2	43	6		
<i>Erigeron peregrinus</i>			35	2	18	2		
<i>Trollius laxus</i>			8	1	58	19		
<i>Mitella breweri</i>					67	16		
<i>Senecio triangularis</i>					57	12		
<i>Thalictrum occidentale</i>					41	11		
<i>Carex spectabilis</i>			8	+	25	5	28	5
<i>Hieracium lanatum</i>					18	5		
<i>Equisetum palustre</i>			3	+	35	5		
<i>Osmorhiza purpurea</i>					26	5		
<i>Luzula hitchcockii</i>					22	5	8	1
<i>Veratrum viride</i>					7	2		
<i>Phleum alpinum</i>			5	+	16	2		
<i>Carex nigricans</i>							100	87
<i>Juncus drummondii</i>							43	9
<i>Veronica cusickii</i>					1	+	55	6
<i>Hieracium gracile</i>							45	4

¹Only species with mean cover of at least 2% are included. Frequency is the percent of the forty 30 X 50-cm subplots in which the species was found. A + indicates cover <0.5%.

Field Methods

Four replicate sets of experimental trampling lanes were established in each vegetation type. Each set consisted of five lanes, each 0.5 m wide and 1.5 m long. Where the lanes occurred on a slope, they were oriented parallel to contours. Treatments were randomly assigned to lanes. One lane was a control and received no trampling. The other lanes received either 25, 75, 200, or 500 passes in three of the four vegetation types. In the fourth type (*Carex*), which was highly resistant to impact, treatments were 75, 200, 500, and 700 passes. A pass was a one-way walk, at a natural gait, along the lane. The weight of the trampers was about 70 kg and trampers wore lug-soled boots.

Measurements were taken on each lane in two adjacent 30 X 50-cm subplots. In each subplot, the cover of each vascular plant species, and of lichens and mosses, was estimated. Trampling treatments were administered in July 1988. Initial measurements were taken immediately before trampling. Followup measurements were taken about two weeks after trampling occurred and again one year after trampling.

Data Analysis

The primary response variable for each vegetation type was relative vegetation cover, a measure of the proportion of original vegetation that survives trampling, adjusted for changes on controls. It was calculated by (1) summing the covers of all individual species to obtain total cover and then (2) calculating relative vegetation cover as:

$$\frac{\text{surviving cover on trampled subplots}}{\text{initial cover on trampled subplots}} \times cf \times 100\%$$

$$\text{where } cf = \frac{\text{initial cover on control subplots}}{\text{surviving cover on control subplots}}$$

Relative vegetation cover after trampling and after one year of recovery was calculated for each trampling treatment.

For the most widespread individual species it was also possible to calculate relative cover. For most species, however, it was only possible to discuss their response in qualitative terms.

Results and Discussion

Response of Vegetation Types

The immediate response of vegetation cover to trampling differed significantly both with amount

of trampling and with vegetation type (analysis of variance, $p < 0.001$). The interaction between these two main effects was also significant, but the magnitude of this interaction effect was negligible compared with the main effects.

The relationship between relative vegetation cover and amount of trampling for the four vegetation types is illustrated in Figure 1. Mean relative vegetation cover and standard errors are given for measurements after trampling and after one year of recovery. With only one exception, vegetation cover declined with each successive increase in number of passes. In the *Carex* type, no vegetation cover was lost until the trampling intensity reached 200 passes. With the exception of the *Valeriana* type, the relationship between relative cover and amount of trampling was generally linear. In the *Valeriana* type, substantial vegetation was lost at low levels of trampling, but additional increments of trampling caused successively less damage. This curvilinear relationship is more similar to that reported elsewhere (Cole 1985).

The most resistant vegetation type was clearly the *Carex* type. Seventy-five passes resulted in no cover loss and, even on the 200-pass lane, only a trained observer would have noticed the trampling impact. Relative cover was still 62 percent after 500 passes. The *Pachistima* type was also quite resistant. Cover loss occurred more rapidly than in the *Carex* type, although the difference between the types was not statistically significant. Relative cover on this type was 81 percent after 75 passes and 55 percent after 500 passes. Of more importance, however, was the fact that damage was much more apparent in the *Pachistima* type. Broken branches and stripped leaves on shrubs were apparent after just 75 passes, and a path was readily apparent after 200 passes.

The other two vegetation types were significantly less resistant. The *Phyllodoce* type had a relative cover of 67 percent after 75 passes and only 6 percent after 500 passes. An obvious path had developed after only 75 passes. The *Valeriana* type was significantly more fragile than even the *Phyllodoce* type. Relative cover was reduced by more than 50 percent after just 25 passes; 500 passes eliminated all but a few plants (2% relative cover). An obvious path had developed after just 25 passes and, after 75 passes, all upright stems had been eliminated.

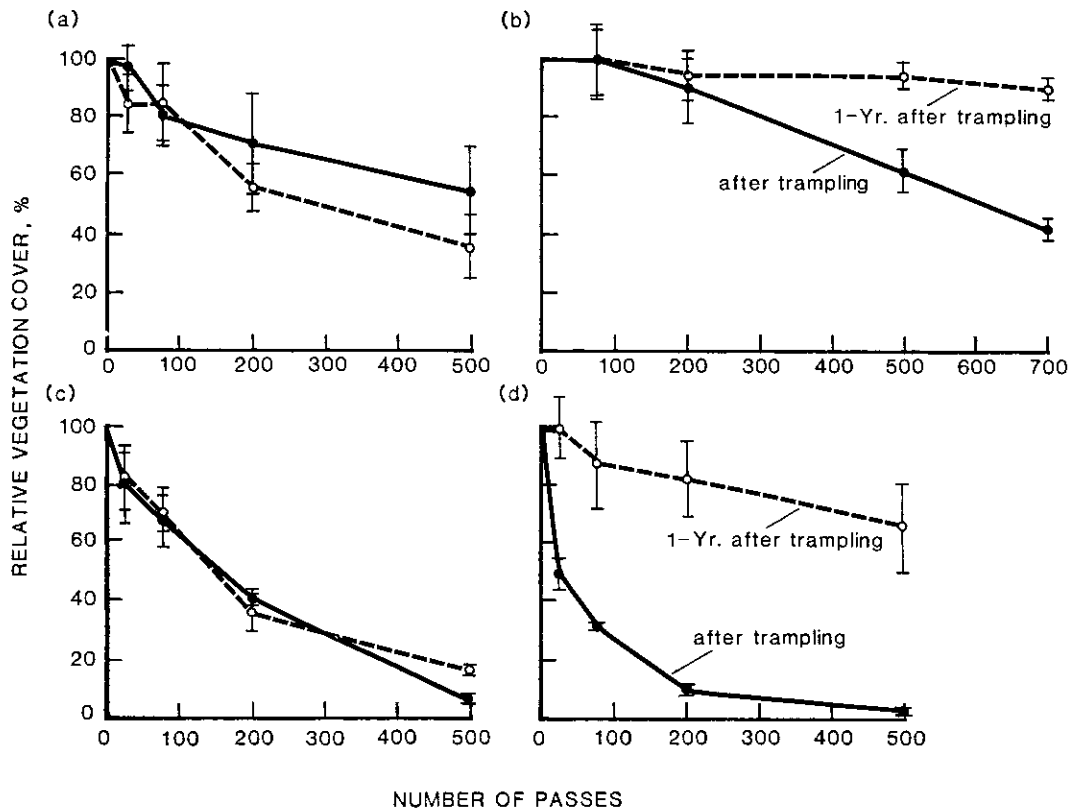


Figure 1. The relationship between vegetation cover and amount of trampling in the (A) *Pachistima*, (B) *Carex*, (C) *Phyllodoce*, and (D) *Valeriana* vegetation types. Bars are one standard error.

Differences between vegetation types and trampling treatments declined somewhat in the year following trampling; however, both main effects—vegetation type and amount of trampling—were highly significant ($p < 0.001$). The interaction between the two was not.

One year after trampling, disturbance was difficult to detect on all but the most heavily trampled lanes in both the *Carex* and *Valeriana* types. Both of these types recovered substantially during the year after trampling was curtailed. In the *Carex* type, relative cover was 62 percent after 500 trampling passes; one year later, relative cover had increased to 95 percent. In the case of the *Valeriana* type, the amount of recovery that occurred over the year was even more dramatic. Relative cover increased from two percent after 500 passes, to 66 percent one year later. These two types, which differed most in their initial

response to trampling, were not significantly different after one year of recovery.

The *Phyllodoce* and *Pachistima* types remained significantly more damaged than the other types after the year of recovery. In each of these types, the 75-pass lane remained obviously damaged even after a year without disturbance. The relative cover of these two types was not significantly different, but their response over the year of recovery was different. The *Phyllodoce* type, which had been more substantially damaged initially, remained relatively unchanged over the year of recovery. Only the lane trampled 500 times experienced an increase in cover of more than five percent. On this type it was primarily forbs that recovered—not *Phyllodoce empetriformis*. Cover on the *Pachistima* type actually declined. Many shrub branches survived trampling damage for a short time, but died during the following winter. Relative

cover after 500 passes was 55%, but after one year of "recovery," cover had declined to just 36%.

The durability of any vegetation type is a reflection of both its ability to resist being disturbed by trampling and its ability to recover from trampling disturbance. The terminology used when describing these two properties is confusing. We follow Cole (1988), Kelly and Harwell (1990), and Sun and Liddle (1991) in using the term *resistance* when referring to the ability of an ecosystem to resist change when subjected to disturbance. This property has also been called inertia by Orians (1975), Cairns and Dickson (1977), Westman (1978) and Grime (1979). Resistance to trampling was assessed with data on immediate responses to trampling. We follow Westman (1978), Grime (1979), Cole (1988), and Kelly and Harwell (1990) in using the term *resilience* when referring to the ability of an ecosystem to recover rapidly following disturbance. Resilience was assessed by comparing relative vegetation cover immediately after trampling with cover after one year of recovery. This property is similar to that defined as elasticity by Orians (1975) and Westman (1978) and as recovery by Sun and Liddle (1991).

We also find it useful to characterize the ability of a vegetation type to both resist and recover from trampling—a property that we term *tolerance*. Tolerance was assessed by comparing vegetation cover after one year of recovery from trampling with cover prior to the trampling treatments. A measure of tolerance provides a single overall indication of durability, but it does not indicate, for example, whether a high level of tolerance results

from an ability to resist damage, an ability to recover from damage, or both.

The four vegetation types vary greatly in all three of these properties. At one extreme is the *Carex* type, which is highly resistant, resilient, and tolerant. The *Valeriana* type exhibits low resistance but high resilience; consequently, tolerance is also relatively high. The *Pachistima* and *Phyllodoce* types are moderately resistant, but not at all resilient; consequently, their tolerance is low.

Response of Individual Species

It was possible to calculate relative cover for nine vascular species and for mosses, as a group. The other species were too sparse or irregularly distributed to provide meaningful results. The responses of individual species to trampling are more diverse than the response of entire assemblages of species (Table 2). A plot of initial response to light trampling (25 passes) on one axis and response to heavy trampling (500 passes) on the other axis reveals three general types of response (Figure 2). *Carex nigricans* and *Pachistima myrsinites* are generally resistant to trampling. Four species—*Trollius laxus*, *Valeriana sitchensis*, *Potentilla flabellifolia*, and *Mitella breweri*—are generally susceptible to trampling disturbance. The others—*Senecio triangularis*, *Vaccinium membranaceum*, *Phyllodoce empetriformis*, and mosses—resist light trampling but are susceptible to heavy trampling.

In a similar plot of cover after the year of recovery (Figure 3), groupings are less discrete. At one

TABLE 2. Relative cover¹ of abundant species after trampling and after one year recovery.

Species	After trampling					After one year recovery				
	Number of passes					Number of passes				
	25	75	200	500	700	25	75	200	500	700
<i>Carex nigricans</i>	—	96	96	78	53	—	106	104	104	95
mosses	95	100	37	12	—	143	136	135	108	—
<i>Pachistima myrsinites</i>	89	71	68	62	—	68	68	43	22	—
<i>Phyllodoce empetriformis</i>	99	90	54	11	—	90	71	26	7	—
<i>Vaccinium membranaceum</i>	93	54	6	0	—	69	46	44	40	—
<i>Mitella breweri</i>	67	50	20	1	—	116	113	99	60	—
<i>Potentilla flabellifolia</i>	58	31	15	16	—	86	86	75	79	—
<i>Senecio triangularis</i>	86	36	1	0	—	119	115	59	65	—
<i>Trollius laxus</i>	43	37	11	5	—	74	69	55	73	—
<i>Valeriana sitchensis</i>	58	26	5	2	—	102	74	69	70	—

¹Relative cover is the proportion of original cover that survives trampling, adjusted for changes on controls.

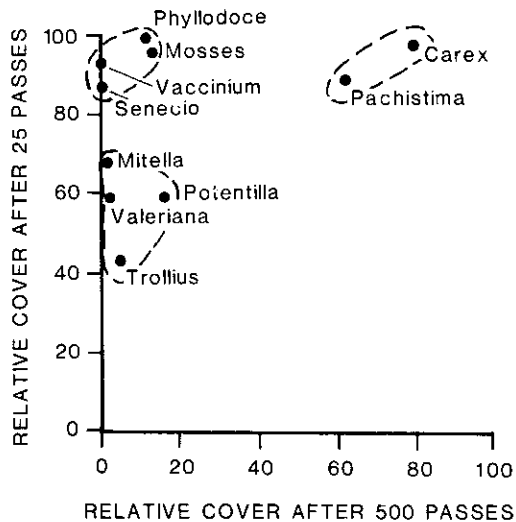


Figure 2. Mean relative cover of abundant species after light and heavy trampling.

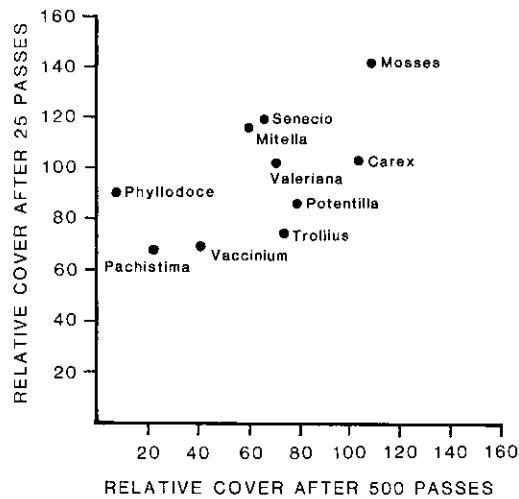


Figure 3. Mean relative cover of abundant species after one year of recovery following light and heavy trampling.

extreme are the highly tolerant mosses and *Carex nigricans*. Following one year of recovery, relative cover exceeds 100 percent, regardless of how heavily they were trampled. At the other extreme are the three shrub species, which have relative cover values of less than 100 percent at all levels of trampling, and cover values of 40 percent or less on the lanes trampled 500 times.

In an effort to assess the resistance and tolerance of less common species, we prepared tables

of mean cover before trampling, immediately after trampling, and one year after trampling, for each level of trampling intensity. From these tables it was possible to identify the trampling levels that clearly caused substantial cover loss. We used these data to develop a simple classification of the resistance and tolerance of less common species. Species were considered resistant if more than 50 percent cover survived after 75 passes. Species were considered tolerant if cover exceeded about 75 percent of original cover one year after trampling on lanes trampled at least 200 times.

Four groups of species can be identified. Species that were both resistant and tolerant included *Antennaria lanata*, *Carex nigricans*, *Carex spectabilis*, *Hieracium gracile*, *Juncus drummondii*, *Leparrhena pyrolifolia*, *Luzula hitchcockii*, *Veronica cusickii*, *Viola orbiculata*, and mosses. These are all low growing plants that have either a tufted growth form or leaves in basal whorls that grow flat against the ground. All of the graminoids species fall into this category. A smaller group of species were resistant but intolerant: *Pachistima myrsinites*, *Phyllodoce empetriformis*, *Vaccinium membranaceum*, and *Vaccinium scoparium*. These four woody shrub species lack resilience, so they are unable to tolerate even moderate levels of trampling.

The largest group of species were nonresistant but tolerant: *Arnica mollis*, *Equisetum palustre*, *Hieracium lanatum*, *Ligusticum grayi*, *Lupinus latifolius*, *Mitella breweri*, *Saxifraga arguta*, *Senecio triangularis*, *Thalictrum occidentale*, *Trollius laxus*, *Valeriana sitchensis*, and *Veratrum viride*. These were all broad-leaved herbaceous plants with upright stems. This growth form has little capacity to resist trampling damage, but these species are able to regenerate rapidly from subsurface adventitious buds that escape damage.

The final group are species that are both nonresistant and intolerant: *Abies lasiocarpa* seedlings, *Caltha bicolor*, *Gentiana calycosa*, *Osmorhiza purpurea*, *Parnassia fimbriata*, *Pedicularis bracteosa*, and *Viola glabella*. The tree seedlings were somewhat resistant to low levels of trampling. Once they were damaged, however, they usually died and their loss was not offset by establishment of new seedlings. The other species—all broad-leaved herbs—are all relatively uncommon species that were highly fragile. Their aerial parts were generally entirely eliminated after as few as 25 passes. Apparently their regenerative tissues were damaged as well, making recovery from damage slow.

Three broad-leaved herbaceous species were unique in that their response varied between vegetation types. *Aster alpigenus*, *Erigeron peregrinus*, and *Potentilla flabellifolia* are all sensitive to trampling disturbance in the generally sensitive *Valeriana* vegetation type. In the more resistant *Phyllodoce* and *Carex* types, however, they are all resistant. Apparently resistant associates protect these species to some extent, so that higher levels of trampling are required to eliminate them. All species found in more than one vegetation types were more resistant in the type that was generally more resistant, although only these three were classified differently.

Factors That Influence Resistance and Resilience

A number of factors may influence the durability of vegetation types. High-elevation ecosystems, particularly those above tree line, are often characterized as being highly fragile (e.g., Leonard *et al.* 1981). It is interesting to note that these data do not support that conclusion. The most resistant vegetation types were the ones at the highest and lowest elevations—*Carex* and *Pachistima*. As has been reported elsewhere (Cole 1985), the resistance of vegetation types to damage is generally unrelated to elevation.

It has also been suggested, however, that higher elevation ecosystems are likely to have little resilience because their growing seasons are so short (Cole 1987). Again, the data do not support this conclusion. The least resilient vegetation type was the lowest elevation type (*Pachistima*) and intermediate vegetation types, *Phyllodoce* and *Valeriana*, varied greatly in their resilience. Perhaps if the intensity of damage had been more severe, the higher elevation types would have required more lengthy recovery periods. For example, we suspect that if *Carex nigricans* was trampled enough to eliminate all cover and kill all roots that recovery would have occurred only very slowly.

The factors that appear to best explain durability are morphological characteristics of constituent species. The primary strategies for resisting trampling damage are to avoid being stepped on, to be cushioned against impact, or to have tough

or flexible aerial parts. Therefore, characteristics that promote resistance include short stature, large size (too large to be stepped on), tufted or bunched habits of growth, stems that are woody or wiry and flexible, and leaves that are tough and/or growing in basal rosettes. Moreover, the resistance of any species will be increased by growing (1) in proximity to other plants that are taller and more resistant (e.g., *Potentilla flabellifolia* in the *Phyllodoce* type) or (2) on a substrate that cushions the impact of trampling (e.g., *Veronica cusickii* growing in a *Carex* turf). Resistant vegetation types tend to be dominated by either tall, tough, woody shrubs (e.g., *Pachistima myrsinites*) or graminoids that grow in bunches or as a turf (e.g., *Carex nigricans*). Low, woody species with brittle stems (e.g., *Phyllodoce empetrifolms*) resist low levels of trampling but are sensitive to high levels. Sensitive vegetation types tend to be dominated by broad-leaved herbaceous species with erect, caulescent stems (e.g., *Valeriana sitchensis*).

The primary strategy of resilient species is the ability for rapid regrowth from perennating tissues that can survive trampling. The characteristics that promote resilience are perennating tissues at or below the ground surface that are tough enough to survive trampling or are hidden or cushioned from trampling impact. Resilient vegetation types tend to be dominated by fast-growing broad-leaved herbaceous species (e.g., *Valeriana sitchensis*) or by tufted or turf-producing graminoid species (e.g., *Carex nigricans*).

Trampling by recreationists can be a significant disturbance agent, particularly in parks and wilderness areas where nature preservation is a primary objective. Vegetation types vary greatly both in the ease with which they are damaged and in their ability to recover from damage. Generally the most durable types are dominated by graminoids. Shrubby understories are often resistant to damage, but once damaged, recovery can occur slowly. Broad-leaved herbaceous understories are readily damaged, but capable of rapid recovery. Individual species within the same vegetation type may vary greatly in durability. Land managers need to keep these various capabilities in mind when trying to plan for visitor use.

Literature Cited

- Bell, K. L., and L. C. Bliss. 1973. Alpine disturbance studies: Olympic National Park, U.S.A. *Biol. Conserv.* 5:25-32.
- Cairns, J. Jr., and K. L. Dickson. 1977. Recovery of streams and spills of hazardous materials. In J. Cairns Jr., K. L. Dickson, and E. E. Herricks (eds.) *Recovery and restoration of damaged ecosystems*. University of Virginia Press, Charlottesville, VA. Pp. 24-42.
- Cole, D. N. 1985. Recreational trampling effects on six habitat types in western Montana. USDA Forest Service Res. Pap. INT-350, Ogden, UT. 43 p.
- . 1987. Research on soil and vegetation in wilderness: a state-of-knowledge review. In R. C. Lucas (comp.) *Proceedings—national wilderness research conference: issues, state-of-knowledge, and future directions*. USDA Forest Service Gen. Tech. Rep. INT-220, Ogden, UT. Pp. 135-177.
- . 1988. Disturbance and recovery of trampled montane grassland and forests in Montana. USDA Forest Service Res. Pap. INT-389, Ogden, UT. 37 p.
- Felix, N. A., and M. K. Reynolds. 1989. The effects of winter seismic trails on tundra vegetation in northeastern Alaska, U.S.A. *Arc. Alp. Res.* 21:188-202.
- Grime, J. P. 1979. *Plant strategies and processes*. John Wiley & Sons, Chichester. 222 p.
- Hitchcock, C. L., and A. Cronquist. 1973. *Flora of the Pacific Northwest*. University of Washington Press, Seattle. 730 p.
- Hutchinson, T. C., and W. Freedman. 1978. Effects of experimental crude oil spills on subarctic boreal forest vegetation near Norman Wells, N.W.T., Canada. *Can. J. Bot.* 56:2424-2433.
- Kelly, J. R., and M. A. Harwell. 1990. Indicators of ecosystem recovery. *Environ. Manage.* 14:527-545.
- Leonard, R. E., E. L. Spencer, and H. J. Plumley. 1981. *Backcountry facilities: design and maintenance*. Appalachian Mountain Club, Boston, MA. 214 p.
- Orians, G. H. 1975. Diversity, stability and maturity in natural ecosystems. In W. H. van Dobben and R. H. Lowe-McConnell (eds.) *Unifying concepts in ecology*. Junk, The Hague. Pp. 139-150.
- Schreiner, E. G. 1974. *Vegetation dynamics and human trampling in three subalpine communities of Olympic National Park, Washington*. M.S. thesis, Univ. Wash., Seattle, WA. 150 p.
- Singer, S. W. 1971. *Vegetation response to single and repeated walking stresses in an alpine ecosystem*. M.S. thesis, Rutgers Univ., New Brunswick, NJ. 69 p.
- Souza, W. P. 1984. The role of disturbance in natural communities. *Ann. Rev. Ecol. Syst.* 15:353-391.
- Sun, D., and M. J. Liddle. 1991. Field occurrence, recovery, and simulated trampling resistance and recovery of two grasses. *Biol. Conserv.* 57:187-203.
- Vale, T. R. 1982. *Plants and people: vegetation change in North America*. Association of American Geographers, Washington, DC. 88 p.
- Westman, W.E. 1978. Measuring the inertia and resilience of ecosystems. *Bioscience* 28:705-710.
- White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. *Bot. Rev.* 45:229-299.

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