Journal of Applied Ecology 1995, 32. 215-224

Experimental trampling of vegetation. II. Predictors of resistance and resilience*

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Summary

1. Experimental trampling was conducted in 18 vegetation types in five separate mountain regions in the United States. Each type was trampled 0-500 times and vegetation response was assessed 2 weeks and 1 year after trampling

2. The response of vegetation to trampling is expressed terms of three indices: resistance, tolerance and resilience. Resistance and tolerance are determined from the vegetation surviving 2 weeks and 1 year after trampling, respectively. Resilience compares the change over the remainder of the year that during the first 2 weeks after trampling.

3. Plant morphological characteristics explained more of the variation in response to trampling than the site characteristics that were assessed: altitude, overstorey canopy cover or total groundlayer vegetation cover.

4. Resistance was primarily a function of vegetation stature, erectness and whether plants were graminoids, forbs or shrubs. The most resistant plants were caespitose or matted graminoids; the least resistant plants were erect forbs.

5. Resilience was primarily a function of whether plants were chamaephytes, with perennating buds located above the ground surface. Chaemaephytes were much less resilient than other plants.

6. Tolerance, which measures the ability of vegetation to withstand a cycle of disturbance and recovery, was correlated more with resilience than resistance Consequently, the least tolerant plants were the chamaephytes. The most tolerant plants were caespitose, matted and rosette hemicryptophytes and geophytes.

7. The resistance and resilience of individual species were negatively correlated, particularly for chamaephytes and graminoids. For herbaceous species with perennating tissues located at or below ground level, tolerance was more highly correlated with resilience than with resistance. For chamaephytes, tolerance was more highly correlated with resistance.

Key-words: plant morphology, recreation impact, tolerance, vegetation impact.

Journal of *Applied Ecology* (1995) 32, 215-224

Introduction

Students of recreation ecology have been particularly interested in understanding the variability of vegetational responses to trampling and factors that explain this variability (Liddle 1991). Beginning with the early work of Bates (1935), numerous studies have documented substantial variation in the ability of different species to tolerate trampling. Explanations for this variation have focused primarily on characteristics of plant morphology that promote durability. Regarding the location of perennating buds, Bates (1935) identified cryptophytes, such as *Poa pratensis*, as the most resistant life form; others have found hemicryptophytes to be most resistant (Hall & Kuss 1989; Liddle & Greig-Smith 1975). Studies also report greater resistance of plants with caespitose, matted, and rosette habits of growth (Naito 1969; Liddle & Greig-Smith 1975; Rogova 1976; Cole 1987a). Finally, woody species have been variously reported as more or less resistant than herbaceous species (Weaver & Dale 1978: del Moral 1979) and, among herbaceous species, graminoids generally have been reported to be particularly resistant (Wagar 1964; Cole 1988).

Broad generalizations about differences in the vulnerability of vegetation to trampling damage remain elusive for two reasons. First, each individual study has examined only a narrow range of vegetation types. Secondly. each study has employed a unique research design. Most studies have derived conclusions by comparing the vegetation of trampled sites with the vegetation of untrampled sites. Others have more effectively isolated the effects of trampling by applying controlled trampling in an experimental design. In all cases, variation in disturbance characteristics (amount, type, timing) and in field measurement techniques makes it difficult to compare results. The study reported here minimized these problems by applying standard experimental trampling treatments to 18 different vegetation types. An earlier paper (Cole 1995) described these vegetation types, their responses to different levels of trampling stress, and variation in these responses. This paper evaluates the extent to which the variation can be explained by characteristics of plant morphology.

Materials and methods

FIELD METHODS

Eighteen experimental study sites were established in five different mountainous regions of the United States. Site characteristics are summarized in Table 1. More detail is given by Cole (1995).

Four replicate sets of experimental trampling lanes were established in each vegetation type. Each set comprised five lanes, each 0.5 m wide and 1.5m long. Where the lanes occurred on a slope, they were orientated parallel to contours. Treatments were randomly assigned to lanes. One lane was a control and received no trampling, the other lanes usually received 25, 75, 200 and 500 passes. The two types in Montana used a different progression of treatments, namely 10, 50, 100, 250 and 500 passes. A pass was a one-way walk, at a natural gait, along the lane. The weight of tramplers was about 70kg and tramplers wore lug-soled boots with incised treads.

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 mosses and lichens was estimated. Vegetation stature was measured to the nearest 1 cm at 50 systematically placed points in each subplot, with a point quadrat frame. Trampling treatments were administered in early summer, after vegetative cover approached its annual peak. Initial measurements were taken immediately before trampling occurred. Follow-up measurements were taken about 2 weeks after trampling and 1 year after trampling.

RESPONSE VARIABLES

The primary response variable for each vegetation type was relative vegetation cover (Bayfield 1979). a measure of the fraction (%) of original vegetation that survives trampling, adjusted for changes on controls. Application of a correction factor *(F)* for changes on controls separates the effects of trampling from other factors that affect change. It was calculated by (1) summing the covers of all individual species to obtain total cover and then (2) calculating relative vegetation cover as

$$\frac{\text{surviving cover on trampled subplots}}{\text{initial cover on trampled subplots}} \times F \times 100, \qquad \text{eqn 1}$$

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

Relative vegetation cover 2 weeks after trampling and after 1 year of recovery was calculated for each trampling treatment. Analyses were based on plot means to avoid pseudoreplication. Relative cover was also calculated for the most abundant individual species.

The general concept of vulnerability was separated into the more specific attributes of resistance, resilience and tolerance. Indices of resistance, resilience and tolerance were calculated for each vegetation type. Resistance refers to the ability of a vegetation type to resist change when trampled. The resistance index used (I_s) is the mean relative vegetation cover (%), 2 weeks after trampling, for all possible trampling intensities between 0 and 500 passes (Cole & Bayfield 1993). Although only five trampling intensities were applied, the resultant responses define a curve of interpolated relative cover values for every number of passes between 0 and 500 (refer to the curves in Fig. 1 of Cole 1995). This index has a number of desirable attributes. It utilizes all the data collected to provide a single index of response to the range of treatments from 0 to 500 passes.

Resilience refers to the ability of a vegetation type to recover following the cessation of trampling. Tolerance refers to the ability of a vegetation type to tolerate a cycle of disturbance and recovery. The tolerance index (I_T), analogous to I_s, is the mean of interpolated relative vegetation cover values (%) for all levels of trampling between 0 and 500 passes, 1 year after trampling. The resilience index (I_L) is the change in relative vegetation cover during the year after trampling, expressed as a fraction (%) of the change in cover that occurred 2 weeks after trampling. Again, these are based on both measured and estimated (by interpolation) values for all trampling intensities between 0 and 500 passes:

$$I_L = \frac{I_T - I_s}{100 - I_s} \times 100 \qquad \text{eqn 2}$$

Table 1. Characteristics of the 18 vegetation types

Vegetation type	State[1]	Altitude (m)	Overstorey canopy cover (%)	Under-storey) vegetation cover (%)	Mean vegetation stature (cm)	Morphological characteristics[2] Phgsiognomic type	Perennating bud location	Leaf-stem architecture
Pachittima myrsinires	WA	760	65	80	25	s	c	e
Phyllodoce empetriformis	WA	1750	30	99	16	s	c	m (e)
Valeriana sitchensis	WA	1750	30	98	14	f	h	e
Carex nigricans	WA	2000	0	99	3	g	g (h)	c
Cornus canadensis	MT	1200	90	80	15	f	h (c)	e
Vaccinium scoparium B	MT	2100	60	65	6	s	c	m
Geranium richardsonii	CO	2650	70	97	19	f	h	e
Vaccinium scoparium A	CO	3350	50	82	7	s	c	m
Trifolium parryi	CO	3350	0	89	3	f (g)	h	m (c)
Kobresia myosuroides	CO	3450	0	98	7	g	h	c
Maianthemum canadensis	NH	450	85	85	10	f	h	e
Leersia oryzoides	NH	450	70	96	31	f (g)	h (g)	e
Lycopodium lucidulum	NH	1050	70	90	13	f	h (c)	m (r)
Carex bigelowii	NH	1600	0	95	15	g	g	c
Poientilla simplex	NC	700	25	88	24	f(g)	h	e
Amphicarpa bracteata	NC	700	90	83	15	f	h	e (m)
Carex pensylvanica	NC	1375	95	50	15	g	g	e
Dryopteris campyloptera	NC	1800	65	95	47	f	g	e

[1] States and floras are: WA = Washington (Hitchcock & Cronquist 1973); MT = Montana (Hitchcock & Cronquist 1973): CO = Colorado (Weber 1976); NH = New Hampshire (Gleason & Cronquist 1963); NC = North Carolina (Radford. Ahles & Bell 1968).
[2] Morphological characteristics of the most abundant species. If a substantial minority (>25% cover) possess another characteristic, this is included in parentheses. Classes are: for physiognomic type, s = shrub, g = graminoid, f = forb; for perennating bud location, c = chamaephyte. h = hemicryptophyte, g = geophyte; for leaf-stem architecture, e = erect, m = matted/creeping, r = rosette, c = caespitoselturf-forming.

Relative cover values were also calculated for the 49 individual species that were sufficiently abundant to analyse separately. Resistance, resilience and tolerance indices were calculated for each species, applying the procedures just described for vegetation types.

STATISTICAL ANALYSIS

The primary analysis objective was to assess which plant morphology and site characteristics are most important in explaining variation in vegetational response to trampling. Because there is no fully satisfactory statistical technique for determining the relative importance of different independent variables (Snedecor & Cochran 1980), three different approaches were taken. Two involved multiple regression analyses based on the response of entire vegetation types. The first approach used an unrestricted model specification in which all plant morphology and site characteristics were simultaneously considered for inclusion as independent variables. The second approach used a restricted model specification. Only plant morphology attributes were considered and each of the three plant morphology classifications was tested individually. The final approach used analysis of covariance based on the response of individual species, with all plant morphology and site characteristics as independent variables.

Multiple regression analysis based on the unrestricted model specification used site characteristics and attributes of plant morphology as independent variables and resistance, resilience and tolerance indices of each vegetation type as dependent variables. Site variables were altitude (transformed to regional equivalents as the elevation above the alpine timberline, to the nearest 100m); mean overstorey canopy cover (ocularly estimated to the nearest l0%)), and mean vegetation cover prior to trampling. Attributes of plant morphology were mean vegetation stature prior to trampling and the proportion of the total vegetation cover in different life and growth form classes. Three versions of life and growth form classifications were used. Each species in each vegetation type was classified according to (1) location of perennating buds as chamaephyte, hemicryptophyte, or geophyte (Raunkiaer 1934); (2) leaf-stem architecture as erect, matted/creeping, rosette or caespitose/turf-forming (turf-forming graminoids were lumped with the caespitose growth form, although they are not truly caespitose); and (3) physiognomic type whether shrub, graminoid, or forb (the last including ferns and fern allies).

Problems arising from collinearity among morphological attributes were reduced through a principal

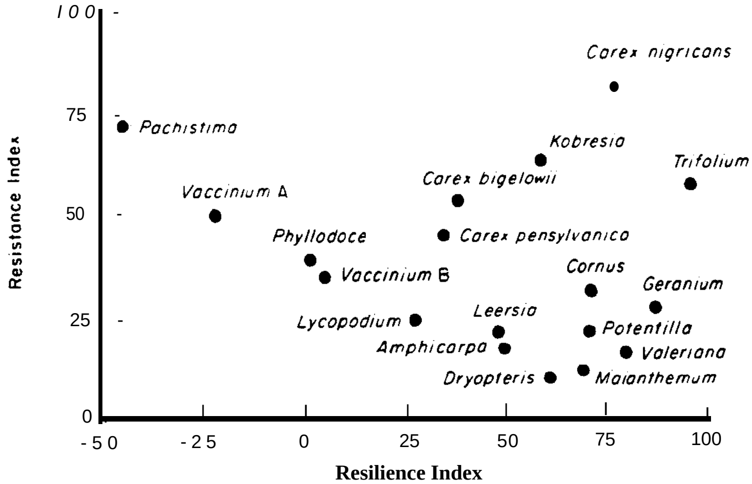

Fig. 1. Resistance (I,) and resilience (I_L) indices (%) for the 18 vegetation types. Resistance index is mean relative cover after O-500 passes. Resilience index is mean increase in cover during the year after trampling, as a percentage of the cover *loss* recorded 2 weeks after O-500 passes.

components analysis of these attributes. The principal components were then treated as independent variables. The process for selecting variables to include in the multiple regression analysis involved a modification of standard stepwise procedures. The independent variable most highly correlated with the dependent variable was entered in the first step. In succeeding steps, the remaining independent variable that was most highly correlated with the dependent variable was entered, after consideration of collinearity. This continued until the addition of new independent variables resulted in either minimal increase in variation explained or substantial problems with collinearity (as reflected in large increases in variance inflation factors).

In the multiple regression analyses based on the restricted model specification, the dependent variables (the resistance, resilience and tolerance indices) were regressed on each plant morphology classification. Thus, the independent variables were the fraction of vegetation cover in each class (chamaephyte, hemicryptophyte or geophyte; erect, matted, rosette or caespitose; and shrub, graminoid or forb). One class was discarded from each analysis to avoid collinearity. The purpose of these analyses was to understand better which of the three plant morphology classifications was most effective in explaining variation in vegetational response to trampling.

Analysis of covariance was used to assess which plant morphology and site characteristics are most important in explaining variation in the response of individual species to trampling. Each species was classified on the basis of each of the three morphological classifications. The resistance. resilience and tolerance indices of individual species were treated as dependent variables: the three different morphological classifications as independent factors: and vegetation stature. overstorey canopy cover and altitude as metric covariates. The significance of differences in response, between morphological classes, was evaluated using least-squares estimates of marginal means (Searle, Speed & Milliken 1980).

Results

The 18 vegetation types varied greatly both in their immediate and in their prolonged responses to trampling. Resistance indices varied from 85% in the *Carex nigricans** type to 10% in the *Dryopteris campyloptera* type (Fig. 1). In the *Carex nigricans* type, substantial cover was lost only on the 500-pass lanes. In the *Dryopteris campyloptera* type, just 25 passes reduced relative cover to 33%. Resilience indices varied from 98% (virtually complete recovery on all lanes) in *Trifolium parryi* to -45% in *Pachisfima myrsinites.* Cover declined during the year following trampling on all lanes in the *Pachistima Myrsinites* type. Tolerance indices varied from 99% in *Trifolium parryi* to about 38% in the two *Vaccinium scoparium* types.

VARIABLES THAT EXPLAIN VARIATION AMONG VEGETATION TYPES

The principal components analysis reduced the plant morphology attributes to three components that explained 86% of the total variation. Loading values for each component suggest that they are defined by (1) the abundance of shrubs and chamaephytes, (2) vegetation stature and the abundance of erect plants and (3) the abundance of caespitose graminoids and geophytes, respectively (Table 2).

Resistance

The unrestricted regression model. judged to explain variation in resistance to trampling best.

* Scientific names conform with those in Tables 1 and 7.

Table 2. Principal components. with rotated loadings for each morphological attribute

Morphological attribute	Principal component 1	2	3
Mean stature	- 1	88	3
Shrub	90	- 9	-34
Graminoid	-18	-34	87
Forb	-73	37	-39
Chamaephyte	90	-12	-37
Hemicryptophyte	-86	-26	-36
Geophyte	2	31	82
Matted	63	-52	-35
Erect	-23	85	-16
Caespitose	-10	-60	71
Variance explained (%)	34	26	26

Table 3. Effects of plant morphology and site characteristics on resistance to trampling. Principal components (PC) l-3 consist of interrelated plant morphological attributes. PC 1-3 arc defined largely by the abundance of shrubs and chamaephytes, by vegetation stature and erectness, and by the abundance of caespitose graminoids and geophytes. respectively. Sequential $r^2 (r^2_{seq})$ shows the increase in 'variation explained' with the addition of each independent variable

Source of variation	df	Mean square	F	P	r^2
Regression model	5	3212.9	21·8	<0·001	0·59
Error	66	193.6			

Variable	Coefficient	SE	t ratio	P	r^2_{seq}
Constant	35•05	2.9	12.2	<0•001	
PC2	-13•51	2.1	-6.6	<0•001	0.23
PC 3	13•10	1.9	6.8	<0•001	0.22
PC 1	9•87	1.9	5.1	<0•00l	0.11
Altitude	-1•26	0.5	-2.5	0•013	0.02
Vegetation cover	0•30	0.1	2.0	0•054	0.01

included the three plant morphology components together with altitude and vegetation cover (Table 3). These five independent variables explained about 60% of the variation in resistance. The use of principal components was successful in reducing most of the collinearity; variance inflation factors for the model were all below 2.5. The coefficients of determination showed that plant stature-erectness and graminoid-geophyte components both explained much of the variation in resistance (r^2 of 0•23 and 0.22, respectively). Additional variation was explained by adding the shrub-chamaephyte component (r^2 increment of 0•ll), altitude (r^2 increment of 0•02) and vegetation cover (r^2 increment of 0•01) for a final r^2 of 0•60. Resistance to trampling was positively related to the abundance of caespitose graminoids, geophytes, shrubs and chamaephytes, and to total vegetation cover; it was negatively related to vegetation stature, the abundance of erect plants and altitude.

There was one exception to the stepwise analysis procedure used to build this model. Overstorey canopy cover was the variable that explained the most variation in resistance index; however, canopy cover was highly collinear with altitude, vegetation cover and plant morphology. Previous research has reported that more densely forested vegetation types tend to be more fragile than more open ones (Marion & Merriam 1985; Schreiner & Moorhead 1979), but the effect of canopy cover is considered to be indirect. Morphological characteristics that are beneficial to growth in environments with low illumination often offer little resistance to trampling stress (Cole 1979). Given that canopy cover was considered to be indirect in its effect and is highly collinear with the morphological attributes, it was added to the model after the principal components that described those attributes. Canopy cover did not explain much variation in resistance once the variation explained by these other variables was accounted for.

When resistance was regressed on each of the three morphological classifications independently (Table 4), physiognomic type (the fraction of vegetation cover that was shrub, graminoid or forb) explained the most variation in resistance (r^2 = 0.59). Resistance was positively related to cover of shrubs and graminoids and negatively related to cover of forbs. Leaf-stem architecture (the fraction of vegetation cover that was erect, caespitose, matted or with basal rosettes) also explained much of the variation in resistance (r^2 = 0•51). Resistance was positively related to cover of caespitose, matted and rosette plants, and negatively related to cover of erect plants. The location of perennating tissues

Table 4. Relationship of three plant morphological classifications to the resistance, resilience and tolerance to trampling of different vegetation types

	Resistance		Resilience		Tolerance	
	P	r^2	P	r^2	P	r^2
Location of perennating tissues	0•06	0.05	<0•001	0•64	<0•001	0•48
Leaf-stem architecture	<0•001	0.51	<0•001	0•28	<0•001	0•41
Physiognomic type	<0•001	0.59	<0•001	0•57	<0•00l	0•38

(the fraction of cover that was chamaephytes. hemicryptophytes and geophytes) did not explain much variation in resistance (P = 0.06; r^2 = 0.05).

Resilience

The unrestricted regression model, judged to explain variation in resilience best, contained only two independent variables: the shrub-chamaephyte principal component and altitude (Table 5). The shrub-chamaephyte component explained most of the variation in resilience (r^2 = 0•59). The addition of altitude to the model increased r^2 by 0•02, to a final r^2 of 0•61. Resilience was negatively related to the abundance of shrubs and chamaephytes, and to altitude.

When resilience was regressed on each of the three morphological classifications independently (Table 4), the fraction of vegetation cover that was chamaephyte, hemicryptophyte or geophyte explained the most variation in resilience (r^2 = 0•64). The fraction that was shrub, graminoid or forb also had considerable explanatory power (r^2 = 0•57). Resilience was positively related to the cover of hemicryptophytes, geophytes, graminoids and forbs; it was negatively related to the cover of chamaephytes and shrubs. The fraction of the vegetation with an erect, matted, caespitose or rosette growth form was also significantly related to resilience (*P* < 0•000), but had relatively low explanatory power (r^2 = 0•28).

Tolerance

The unrestricted regression model, judged to explain variation in tolerance best, contained three independent variables: the shrub-chamaephyte principal component, overstorey canopy cover and the caespitose graminoid-geophyte principal component (Table 6). The shrub-chamaephyte component explained most of the variation in tolerance (r^2 = 0.43). The addition of canopy cover increased r^2 by 0.08

Table 5. Effects of plant morphology and site characteristics on resilience following trampling. Principal component (PC) 1 is defined largely by the fraction of cover consisting of shrubs and chamaephytes. Sequential r^2 (r^2_{seq}) shows the increase in 'variation explained' with the addition of each independent variable

Source of variation	df	Mean square	*F*	*P*	r^2
Regression model	2	41584	55.9	<0•00l	0.61
Error	69	745			

Variable	Coefficient	SE	ı ratio	P	r^2_{seq}
Constant	49•2	4•5	11•0	<0•00l	
PC 1	-34•8	3•3	-10•6	<0•001	0.59
Ahitudc	-1•4	0•7	-2•1	0•042	0.02

Table 6. Effects of plant morphology and site characteristics on tolerance of trampling. Principal components (PC) 1 and 3 are defined largely by the fraction of shrubs and chamaephytes. and by the fraction of caespitose graminoids and geophytes, respectively. Sequential r^2 (r^2_{seq}) shows the increase in 'variation explained' with the addition of each independent variable

Source of variation	df	Mean square	*F*	*P*	r^2
Regression model	3	5225	27.3	<0•00l	0.53
Error	68	191			

Variable	Coefficient	SE	*t* ratio	*P*	r^2_{seq}
Constant	58.4	4.1	14.2	<0•001	
PC 1	-12.2	1.7	-7.2	<0•001	0•33
Canopy cover	5.4	2.3	2.3	0•026	0•48
PC3	34	1.9	I.8	0.075	0•43

and the addition of the graminoid-geophyte component increased r^2 another 0•02, for a final r^2 of 0•53. Tolerance was negatively related to abundance of shrubs and chamaephytes, and positively related to overstorey canopy cover, and to the abundance of caespitose graminoids and geophytes.

When tolerance was regressed on each of the three morphological classifications independently, all three explained considerable variation (Table 4). The fraction of vegetation cover that was chamaephyte, hemicryptophyte, or geophyte explained the most variation in tolerance (r^2 = 0.48). The fraction that was matted, rosette, caespitose or erect explained 41% of the variation and the fraction that was shrub, graminoid or forb explained 38% of the variation. Tolerance was positively related to abundance of caespitose graminoids and geophytes and negatively related to abundance of shrubs and chamaephytes, particularly those that are matted.

VARIABLES THAT EXPLAIN VARIATION AMONG INDIVIDUAL SPECIES

The 49 most abundant individual species varied substantially in their resistance, resilience, and tolerance (Table 7). Analyses of covariance were conducted using the resistance, resilience and tolerance of these species as dependent variables, the three morphological classifications as independent factors, and vegetation stature, overstorey canopy cover and altitude as covariates.

These independent variables explained 68% of the variation in resistance between species (Table 8). However, the only significant independent variables were vegetation stature and physiognomic type (whether species were shrubs, graminoids or forbs). Resistance was negatively related to vegetation stature and was significantly greater for graminoids than for forbs.

These independent variables explained 74% of

Table 7. Resistance. resilience and tolerance of 49 abundant species

Species[*]	Morphological characteristics[‡]				Index[§] (%) of		
	State[†]	Physiognomic type	Perennating bud location	Leaf-stem architecture	Resistance	Resilience	Tolerance
Mitella breweri	WA	f	h	r	35	95	97
Carex nigricans	WA	g	g	C	86	60	94
Senecio triangularis	WA	f	h	e	31	86	90
Potentilla flabellifolia	WA	f	h	e	30	74	82
Valeriana sitchensis	WA	f	h	e	23	73	79
Trollius laxus	WA	f	h	e	24	58	68
Pachisiima myrsinites	WA	S	c	e	73	-92	50
Vaccinium membranaceum	WA	S	c	e	38	19	50
Phyllodoce empetriformis	WA	s	c	m	64	-42	49
Cornus canadensis	MT	f	h	e	37	100	100
Berberis repens	MT	s	c	e	69	16	74
Linnaea borealis	MT	f	c	m	48	8	52
Vaccinium scoparium	MT	s	c	m	31	6	35
Trifolium parryi	CO	s	h	m	64	100	100
Acomastylis rossii	CO	f	h	r	49	98	99
Fragaria ovalis	CO	f	h	r	44	96	98
Potentilla diversifolia	CO	f	h	r	49	92	96
Aster laevis	CO	f	h	e	25	92	94
Carex rossii	CO	g	h	c	89	36	93
Danthonia intermedia	CO	g	h	c	57	81	92
Trifolium dasyphyllum	CO	f	h	m	52	83	92
Thermopsis divaricarpa	CO	f	h	e	9	90	91
Achillea lanulosa	CO	f	h	e	22	86	89
Kobresia myosuroides	CO	g	h	C	68	59	87
Sibbaldia procumbens	CO	f	h	m	56	64	84
Geranium richardsonii	CO	f	h	e	23	64	72
Viola canadensis	CO	f	h	e	19	65	72
Vaccinium scoparium	CO	s	c	m	45	-40	23
Rubus pubescens	NH	f	c	m	13	93	94
Leersia oryzoides	NH	g	h	e	45	73	85
Carex bigelowii	NH	g	g	C	62	50	81
Maianrhemum canadensis	NH	f	h	e	16	74	78
Viola pallens	NH	f	h	e	36	64	77
Dryopteris austriaca	NH	f	g	e	10	64	68
Panicum boscii	NC	g	h	e	15	96	97
Thaspium trifoliata	NC	f	h	e	16	88	90
Holcus lanatus	NC	g	h	e	32	78	85
Geranium maculatum	NC	f	h	e	8	79	81
Dryopteris campyloptera	NC	f	g	e	5	75	76
Viola papilionacea	NC	f	h	e	18	66	72
Clintonia borealis	NC	f	g	e	11	63	67
Carex swanii	NC	g	h	e	43	33	62
Carex pensylvanica	NC	g	g	e	49	22	60
Potentilla simplex	NC	f	h	e	18	43	53
Phlox stolonifera	NC	f	C	m	40	13	48
Oxalis montana	NC	f	h	e	9	26	33
Amphicarpa bracteata	NC	f	h	m	11	22	31

[*] Nomenclature follows Hitchcock & Cronquist (1973) (WA. MT); Weber (1976) (CO); Gleason & Cronquist (1963) (NH); Radford et al. (1968) (NC).

[†] States are: WA = Washington: MT = Montana: CO = Colorado; NH = New Hampshire: NC = North Carolina.

[‡] Classes are: for physiognomic type. s = shrub, g = graminoid, f = forb; for perennating bud location. c = chamaephyte. h = hemicryptophyte. g = geophyte: for leaf-stem architecture, e = erect. m = matted/creeping. r = rosette, c = caespitose/turf-forming.

[§] Indices of: resistance = mean relative cover after 0-500 passes; resilience = mean increase in relative cover during the year after trampling, as a percentage of cover loss that occurred after 0-500 passes: tolerance = mean relativc cover 1 year after 0-500 passes.

the variation in resilience; however, the location of perennating buds (whether individual species were chamaephytes, hemicryptophytes or geophytes) was the only significant independent variable (Table 8). Resilience was significantly greater for hemicryptophytes and geophytes than for chamaephytes.

The independent variables explained 61% of the variation in tolerance (Table 8). Significant variables

Table 8. Effects of plant morphology and site characteristics on resistance. resilience and tolerance of individual plant species

		Resistance				Resilience				Tolerance			
	df	Mean square	*F*	*P*	r^2	Mean square	*F*	*P*	r^2	Mean square	*F*	*P*	r^2
Source of variation													
Model	10	1514	8•0	<0•00l	0.68	6205	10•5	<0•00l	0•74	1210	5•8	<0•001	0•61
Error	31	189				590				209			
Variable													
Physiognomic type	2	657	3•5	0•04		572	1•0	0•39		104	0•5	0•61	
Perennating bud location	2	196	1•0	0•36		5678	9•6	<0•00l		1357	6•5	<0•00l	
Leaf-stem architecture	3	297	1•6	0•21		627	1•1	0•38		626	3•0	0•04	
Vegetation stature	1	716	3•8	0•05		380	0•6	0•43		185	0•9	0•35	
Canopy cover	1	201	1•1	0•31		27	0•1	0•83		73	0•4	0•56	
Elevation	1	3	0•1	0•90		97	0•2	0•69		301	1•4	0•24	

Physiognomic type	Mean resistance (% ± SE)	Perennating bud location	Mean resilience (% ± SE)	Mean tolerance (% ± SE)	Leaf-stem architecture	Mean tolerance (% ± SE)
Graminoid	60±7a*	Hemicryptophyte	74 ± l0a*	92±6 a*	Caespitose	88± l0a*
Shrub	51 ± 10 ab	Geophyte	62± 15 a	84±9a	Rosette	84±9a
Forb	39±5b	Chamaephyte	-11± 13 b	51±8b	Matted	70±7 ab
					Erect	61±5b

* Growth forms with the same letter are not significantly different; *P*> 0.05.

were leaf-stem architecture (whether species were erect, matted, caespitose or rosette) and location of perennating buds (whether species were chamaephytes, hemicryptophytes or geophytes). Tolerance was significantly greater for caespitose and rosette species that for erect species, and significantly greater for hemicryptophytes and geophytes than for chamaephytes.

Among chamaephytes there was substantial variation in response, particularly in resistance. Resistance was positively correlated with the mean diameter of stems (r = 0.76; P= 0.01); however, neither resilience nor tolerance was significantly correlated with stem diameter. The brittleness of stems, which is probably related to stem diameter, has been identified as contributing to susceptibility (Cole 1987b). In contrast to graminoids and forbs, plant stature was positively, but not strongly correlated with resistance (r = 0.47; P = 0.20).

Among graminoids, variation in resistance was negatively correlated with plant stature (r = -0.74; P = 0.01). Moreover, the five erect graminoids were all less resistant than the five caespitose and matted graminoids (Fig. 2). Plant stature and erectness were not correlated with either resilience or tolerance. There were also significant differences between the responses of the cyperaceous and graminaceous species. The cyperaceous species were significantly more resistant (r^2= 0.42; P = 0.04) and less resilient (r^2= 0.71; P = 0.002) than the graminaceous species. Differences in tolerance were not significant.

Among forbs, variation in resistance was negatively correlated with plant stature (r = -0.72; P < 0.001) and all 22 erect forbs were less resistant than the eight forbs with a matted or rosette growth form (Fig. 2). As with graminoids, stature and erectness were not correlated with either resilience or tolerance. Among the erect forbs there was marked variation in resilience and tolerance that could not be explained by the plant morphology and site characteristics assessed in this study.

For all species, resistance and resilience were negatively correlated (r = -0.34; P = 0.02). Tolerance was strongly correlated with resilience (r = 0.82; P< 0.00l) and weakly correlated with resistance (r = 0.14; P = 0.35). The sign and strength of these correlations varied with plant morphological type, however. For chamaephytes, none of these correlations were significant at the 95% confidence level. The strongest correlation was between resistance and resilience (r = 0.58; P= 0.l0), and the correlation between resilience and tolerance (r = 0.31; P= 0.42) was weaker than the correlation between resistance and tolerance (r= 0.54; P= 0.13). The correlation between resistance and resilience was also weak and negative for graminoids (r = -0.47; P = 0.17); for forbs there was no correlation between resistance and resilience (r = 0.02: P = 0.92). The correlation between resilience and tolerance was strong for both graminoids (r = 0.72; P= 0.02) and forbs (r = 0.93; P< 0.00l), while the correlation between resistance and tolerance was weak for both graminoids (r = 0.19, P = 0.60) and forbs (r = 0.29; P = 0.09).

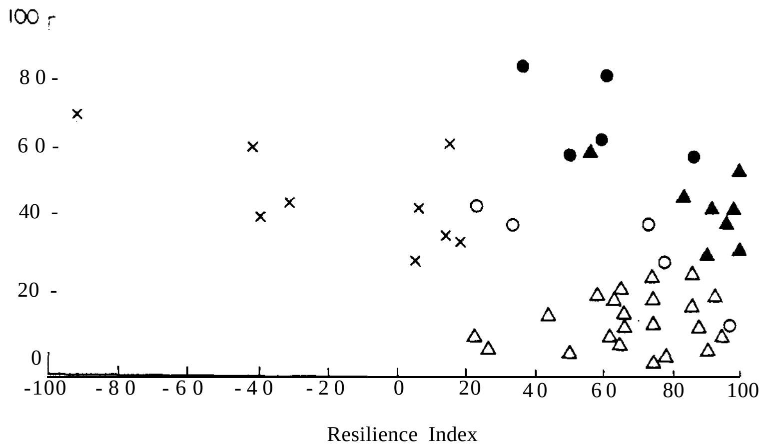

Fig. 2. Resistance and resilience indices (%) for the individual species in Table 7, classified by morphology as chamaephytes (x), erect graminoids (o). non-erect graminoids (•), erect forbs (△) and non-erect forbs (▲). Resistance index is mean relative cover after 0-500 passes. Resilience index is mean increase in cover during the year after trampling, as a percentage of the cover loss recorded 2 weeks after 0-500 passes.

Discussion

Variation in vegetation response to trampling was determined more by plant morphology than by the site characteristics that were assessed in this study, namely altitude, overstorey canopy cover and total vegetation cover. It is possible that site characteristics that were not assessed, such as soil fertility or moisture, might have explained more variation than those site characteristics that were assessed: however, variation in plant morphology explained more than 50% of the variation in resistance, resilience and tolerance. It is also possible that site characteristics would have a more pronounced effect on the response of vegetation to prolonged and repeated trampling, in contrast to the short-term responses to a single trampling event that were studied here.

Resistance was primarily a function of the erectness of plants and physiognomic type (whether the plants were shrubs, graminoids, or forbs). The most resistant species were graminoids, particularly those that were matted or caespitose (Fig. 2). Matted and rosette forbs and woody plants were moderately resistant, while the least resistant plants were the erect forbs. Resilience was primarily a function of woodiness and whether or not perennating buds are located above the ground surface. Chamaephytes, particularly those that were woody, were substantially less resilient than hemicryptophytes and geophytes.

Tolerance, a reflection of both resistance and resilience, was a function of many morphological characteristics. Tolerance was correlated more with resilience of the vegetation than with resistance. Consequently, the most important determinant of tolerance was whether or not the plants were chamaephytes. The least tolerant plants were the chamaephytes, while the most tolerant were the non-erect hemicryptophytes and geophytes.

These findings suggest some reasons for divergent findings about the relative vulnerability of vegetation types to trampling damage. Characteristics that promote the ability initially to resist trampling damage differ from those that enable plants to recover quickly. In fact, resistance was often negatively correlated with resilience. Moreover, combinations of characteristics are more helpful in explaining response than individual characteristics. For example, plant stature and erectness contribute to resistance in woody plants, but detract from resistance in herbaceous plants.

The sizable variation in vegetation response to trampling suggests that managers of natural areas can minimize damage by confining recreational use to vegetation types that can tolerate trampling. Managers can obtain a first approximation of vegetation vulnerability simply by assessing the fraction of chamaephytes, erect herbs and herbs that are caespitose, matted or form rosettes. Vegetation types that are predominantly erect herbs will probably be damaged readily by trampling, but these types should also recover rapidly. Vegetation types that are predominantly chamaephytes will be somewhat more resistant, but damage is likely to be more long-lasting. Vegetation types that are predominantly non-erect herbs are the types that are most stable when subjected to trampling.

There will undoubtedly be exceptions to these generalizations: however. these conclusions were obtained from studies of vegetation types distributed across a wide altitudinal and geographical range. They suggest relatively consistant findings that should apply well at least to the mid-latitudes of North America.

Acknowledgements

The author appreciates field assistance provided by Lisa Campbell, Bart Johnson, Burnham Martin. Deborah Overton and Susan Trull. Computer assistance was provided by John Daigle and Michael Niccolucci.

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Received 23 February 1993; revision received 11 March 1994