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Experimental trampling of vegetation. I. Relationship between trampling intensity and vegetation response*

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DAVID N. COLE

Aldo Leopold Wilderness Research Institute, Forest Service, US Department of Agriculture, PO Box 8089, Missoula, MT 59807, USA

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. Response to trampling was assessed by determining vegetation cover 2 weeks after trampling and 1 year after trampling.

2. Response varied significantly with trampling intensity and vegetation type. Trampling intensity and vegetation type explained more of the variation in vegetation cover 2 weeks after trampling than they did 1 year after trampling.

3. For most vegetation types, the relationship between vegetation cover after trampling and trampling intensity was best approximated by a second order polynomial of the form $Y = A - BX + CX^2$. The relationship was linear in a few vegetation types.

4. The curvilinearity of the relationship between trampling intensity and surviving vegetation cover decreased with increases in resistance, tolerance and species diversity of the vegetation type.

Key-words: recreation impact, regression analysis, vegetation impact.

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Introduction

Over the past few decades, concerns about adverse impacts associated with outdoor recreation have increased greatly. In national parks, wilderness areas and other natural areas, managing agencies are asked simultaneously to preserve natural conditions and allow for recreational use. To find optimal balances between these competing goals, land managers need better information about recreational impacts on the environment. This need has spurred development of the science of recreation ecology (Cole 1987b; Liddle 1991).

Students of recreation ecology have been particularly interested in the effects of human trampling on natural vegetation and many studies have documented deleterious effects of trampling. One common research approach has been to use experimental designs to separate the effects of trampling intensity on vegetation response from other confounding variables. This approach makes it possible to model the relationship between trampling intensity and vegetation response. It is also possible to assess variation in response among different vegetation types.

The results of most previous experimental trampling studies suggest a curvilinear relationship between trampling intensity and vegetation response (e.g. Bayfield 1971; Bell & Bliss 1973; Liddle & Thyer 1986). In only two studies was this relationship described mathematically. For an *Empetrum nigrum* sand dune ecosystem in Denmark, Hylgaard & Liddle (1981) approximated the relationship with a logistic model of the general form

$$Y = \frac{A + B}{1 + \exp(C + DZ)} \qquad \text{eqn 1}$$

where $Z = \log(X + 1)$ and X = number of passes. For six different vegetation types in Montana, USA, Cole (1987a) approximated the relationship with an asymptotic model of the general form

$$Y = A - B\exp(-CX) \qquad \text{eqn 2}$$

where X = number of passes. He also reported that degree of curvilinearity appeared to decrease as vegetation resistance increased. No explanation for these relationships was offered.

The research reported in this paper expands on previous trampling research by applying a standard

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experimental procedure in 18 different vegetation types. This provides a unique opportunity to evaluate the consistency of response and differences between vegetation types. The primary objectives of this paper are (i) to describe vegetational response to different levels of trampling, and (ii) to assess variation in response between vegetation types. A subsequent paper (Cole 1995) will evaluate the extent to which variation in response can be explained by characteristics of plant morphology.

Materials and methods

Eighteen experimental study sites were established in five different mountainous regions of the United States, namely the Cascade Mountains (Washington), the northern Rocky Mountains (Montana), the central Rocky Mountains (Colorado), the northern Appalachian Mountains (New Hampshire) and the southern Appalachian Mountains (North Carolina). Four different vegetation types were studied in each location except Montana, where only two types were studied. Common vegetation types, at various elevations and of differing physiognomy, were selected for study (Table 1). For discussion purposes, these types will be referred to by the name of the most abundant groundcover species. The Appendix gives more details on floristic composition.

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 usually received 25, 75, 200 and 500 passes. A pass was a one-way walk, at a natural gait, along the lane. The weight of tramplers was about 70 kg and tramplers

Table 1. Classification of the 18 vegetation types based on schemes developed by Mueller-Dombois & Ellenberg (1974) and Vankat (1990) and on dominant life forms of the groundcover vegetation. Locations and floras are **WA**, (Washington, Hitchcock & Cronquist 1973); **MT**, (Montana, Hitchcock & Cronquist 1973); **CO**, (Colorado, Weber 1976); **NH**, (New Hampshire, Gleason & Cronquist 1963); and **NC**, (North Carolina, Radford, Ahles & Bell 1968)

- Closed forests
  - Evergreen coniferous forests
    - *Picea rubens–Abies* subalpine forest
      - *Picea–Abies balsamea/Lycopodium lucidulum* (clubmoss-forb-fern), **NH**
      - *Picea–Abies fraseri/Dryopteris campyloptera* (erect fern-forb), **NC**
    - *Picea engelmannii–Abies lasiocarpa* subalpine forest
      - *Picea–Abies/Vaccinium scoparium* A (matted shrub), **CO**
      - *Picea–Abies/Cornus canadensis* (erect forb), **MT**
      - *Pinus contorta/Vaccinium scoparium* B (matted shrub), **MT**
    - *Pseudotsuga menziesii*–mixed conifer upper montane forest
      - *Pseudotsuga/Pachistima myrsinites* (erect shrub), **WA**
  - Cold-deciduous forest with evergreen trees admixed
    - *Acer saccharum–Fagus grandifolia–Betula alleghaniensis* forest
      - Northern hardwood/*Leersia oryzoides* (erect forb–fern–grass), **NH**
      - Northern hardwood/*Maianthemum canadensis* (erect forb–fern), **NH**
      - Gray beech/*Carex pensylvanica* (erect graminoid), **NC**
    - *Populus tremuloides* forest
      - *Populus/Geranium richardsonii* (erect forb), **CO**
  - Cold-deciduous forest without evergreen trees
    - Cove hardwood/*Amphicarpa bracteata* (erect and trailing forb), **NC**

- Dwarf-scrub communities
  - Evergreen dwarf scrub
    - *Phyllodoce empetriformis* subalpine heath (matted shrub), **WA***

- Terrestrial herbaceous communities
  - Meadow and grasslands
    - Below timberline (man-induced)
      - *Potentilla simplex* old-field (erect forb-graminoid), **NC***
    - Above timberline
      - *Carex bigelowii* meadow (matted graminoid), **NH**
      - *Carex nigricans* turf (matted graminoid), **WA**
      - *Kobresia myosuroides* turf (caespitose graminoid), **CO**
      - *Trifolium parryi* meadow (matted forb-caespitose graminoid), **CO**
  - Perennial forb communities
    - *Valeriana sitchensis* subalpine meadow (erect forb), **WA***

* Some of the plots in the *Phyllodoce* and *Valeriana* types have an open overstorey of *Picea engelmannii* and *Abies lasiocarpa*. The *Potentilla* old-field is reverting to a deciduous forest.

wore boots with incised treads (lug soles). In two resistant vegetation types, *Carex nigricans*[1] and *Kobresia myosuroides*, 500 passes caused relatively little vegetation loss, so the 25-pass lane was replaced by a 700-pass lane. For these two vegetation types, only the data from the 75-, 200- and 500-pass lanes were included in the analyses reported here. The two types in Montana, *Vaccinium scoparium* B and *Cornus canadensis*, used a different progression of treatments, namely 10, 50, 100, 250 and 500 passes.

Measurements were taken on each lane in two adjacent 30 × 50-cm subplots. In each subplot, the cover of each vascular plant species, and of mosses and lichens, was estimated. 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.

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

$$\frac{\text{surviving cover on trampled subplots}}{\text{initial cover on trampled subplots}} \times F \times 100\%, \qquad \text{eqn 3}$$

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

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.

Results

VARIATION IN VEGETATION RESPONSE TO TRAMPLING

Analyses of variance were used to test the effect of trampling intensity and vegetation type on relative vegetation cover. Relative vegetation cover was transformed to ranks in order to meet assumptions of normality and homogeneity of variance. Results from the two vegetation types in Montana were excluded from the analysis of variance because they received a unique set of trampling treatments.

Relative vegetation cover 2 weeks after trampling varied significantly with both trampling intensity and vegetation type (Table 2). The interaction between these two main effects was also highly significant. Consequently, analysis of the effect of different trampling intensities was done separately for each vegetation type. Relative cover 1 year after trampling also varied significantly with both trampling intensity and vegetation type (Table 2). The interaction was significant again. One year after trampling, variation in relative cover was less pronounced than it was 2 weeks after trampling, and trampling intensity and vegetation type explained less of the variation in relative cover.

Vegetation types varied greatly in their immediate response to trampling and in the amount of recovery that occurred during the year that followed trampling (Fig. 1). In the vegetation type that lost the least cover, *Carex nigricans* (alpine sedge turf), relative cover after 500 passes exceeded 60%. In the type that lost the most cover, *Dryopteris campyloptera* (subalpine forest with erect fern understorey), relative cover was 33% after just 25 passes and only 2% cover survived after 500 passes. The vegetation type that recovered the most during the year following trampling was *Geranium richardsonii* (montane forest with erect forb understorey). In this type, relative cover 2 weeks after 200 passes was 10%; 1 year after 200 passes, relative cover was 89%. In the type that recovered least, *Vaccinium scoparium* A (subalpine forest with matted shrub understorey in Colorado), relative cover on 200-pass lanes declined from 51% 2 weeks after trampling to 35% 1 year later.

The magnitude of differences in response can be quantified in various ways. Liddle (1975) has suggested the number of passes needed to effect a 50% reduction in vegetation cover as an index of relative vulnerability. This index would be about 600 passes in *Carex nigricans* and about 20 passes in *Dryopteris campyloptera*, suggesting a 30-fold difference in vulnerability. Pronounced differences in vulnerability can occur over short distances. For example, the *Phyllodoce empetriformis* vegetation type is about 10 times less vulnerable than the *Valeriana sitchensis* type, with which it is typically intermixed.

One year after trampling, fewer vegetation types differed significantly in relative cover. In many of the vegetation types that lost substantial cover 2 weeks after trampling, cover increased to levels found in types that were never severely affected by trampling. A few of the vegetation types did not recover, however, and a few lost cover over the year. Consequently, the magnitude of difference between the most and least vulnerable vegetation types remained as great 1 year after trampling as 2 weeks after trampling.

The vegetation type that was least affected by trampling 1 year after the trampling treatments was

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[1] Scientific names conform with those in the Appendix and Table 1.

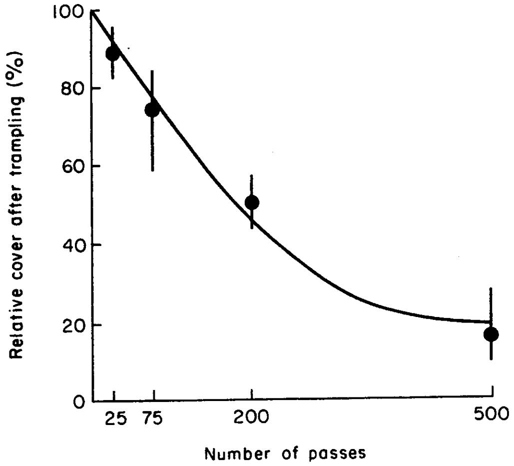

Fig. 2. Relative vegetation cover after trampling in relation to number of passes for the *Vaccinium scoparium* A vegetation type in Colorado. The best fit equation was $Y = 100 - 0{\cdot}339X + 0{\cdot}00036X^2$, $r^2 = 0{\cdot}93$. Mean and range of four replications shown.

less than 0·69. Neither the logistic model suggested by Hylgaard & Liddle (1981) nor the asymptotic model suggested by Cole (1987a) provided such good fits for any of these vegetation types as the models chosen here.

For the seven vegetation types that lost the most cover when trampled, the curvilinearity of the relationship was partially an artifact of the research design. In *Dryopteris campyloptera* and *Maianthemum canadensis*, relative cover was less than 20% after 75 passes. Consequently, the amount of cover these types could lose as trampling intensity increased to 500 passes was low. In *Valeriana sitchensis*, *Amphicarpa bracteata*, *Leersia oryzoides*, *Potentilla simplex* and *Geranium richardsonii*, relative cover was less than 20% after 200 passes.

For these seven types, piecewise regression was used to determine whether curves would best be considered to consist of two separate parts, differentiated at the point where there is no longer much cover to lose (<20%). For all of these types, with the exception of *Geranium richardsonii*, these piecewise regressions provided a better fit to the data ($r^2 = 0{\cdot}77 - 0{\cdot}94$) than a single second-order polynomial. However, only in the *Maianthemum canadensis* and *Dryopteris campyloptera* types was the increase in r^2 substantial (>0·08).

For the six types with curves that are best treated as two separate curves, linear and curvilinear regression models were fitted to that portion of the curve where relative cover exceeded 20%. In all cases, second-order polynomials provided the best fit ($r^2 = 0{\cdot}81 - 0{\cdot}95$).

Influences that may affect the general form of these models are first, a decline in potential for vegetation loss as cover decreases; secondly, variation in vulnerability between different species within the same vegetation type; and thirdly variation in vulnerability within the same species or individual.

The rate of change in vegetation cover with increased trampling should be a function of the vegetation loss per unit of trampling pressure and of the effective pressure exerted by each trampling pass. The effective pressure exerted by a trampling pass should decline at a constant rate as surviving cover declines, because fewer tramples then fall on intact plant tissue. If the susceptibility of plant tissue remains constant as trampling intensity changes, the rate of cover loss should decrease at a constant rate as trampling intensity increases. Therefore, the model that describes the relationship between vegetation cover and trampling intensity should have a first derivative that is a negative linear function of number of passes. The models that possess this attribute are second-order polynomials.

For the relationship between vegetation cover and trampling intensity to deviate from this expected model, susceptibility of the vegetation must vary with trampling intensity. If a vegetation type comprises both resistant and non-resistant species, susceptibility should decline as trampling intensity increases, because most of the fragile species will have been eliminated. This suggests that for vegetation types with species that vary greatly in vulnerability, the curvilinearity of models should be even greater than in the predicted second-order polynomials. It also suggests the testable hypothesis that curvilinearity should increase as vegetation diversity increases.

For curvilinearity to be less than in the predicted second-order polynomials, as it was in at least four of the vegetation types, the vulnerability of plants must increase as trampling intensity increases. This might occur in highly resistant plants that are capable of resisting low levels of trampling, but are damaged by high levels of trampling. This suggests a second testable hypothesis, namely that curvilinearity of the model should decrease as resistance to trampling increases.

These two hypotheses were tested with a multiple regression analysis, with degree of curvilinearity as the dependent variable, and resistance index and Simpson's (1949) index of species diversity as independent variables. Degree of curvilinearity was estimated using the absolute value of the coefficient associated with the quadratic term in the polynomial equations for each vegetation type. Curvilinearity decreases as this coefficient approaches zero. Resistance index is defined as mean relative cover 2 weeks after trampling for all levels of trampling between 0 and 500 passes (Cole 1995). The two vegetation types in which curvilinearity was substantially accentuated by the research design, *Maianthemum canadensis* and *Dryopteris campyloptera*, were excluded from the analysis.

The multiple regression analysis supported both hypotheses (Table 4). Curvilinearity decreased as resistance index increased and as species diversity decreased. These two variables explained 92% of the variation in linearity of the data.

Effects of trampling after 1 year

In most vegetation types, the magnitude of relative cover differences between trampling intensities were less pronounced 1 year after trampling than 2 weeks after trampling. For four vegetation types (*Trifolium parryi*, *Carex nigricans*, *Geranium richardsonii* and *Potentilla simplex*), the relationship between trampling intensity and relative cover was not significant. With the exception of the last, these types had essentially recovered, regardless of trampling intensity. For the 14 other vegetation types, a second-order polynomial generally provided the closest fit to the data, although r^2 values varied between 0·92 and 0·09. Again, linear functions provided equally good fits in some vegetation types and relatively poor fits in others.

Related to these models, two hypotheses were advanced: first, that curvilinearity of the data should decrease as vegetation tolerance increase and, secondly, that curvilinearity should increase as species diversity increases. Curvilinearity and species diversity were operationalized as before. Tolerance was assessed as the mean relative cover 1 year after trampling for all intensities between 0 and 500 passes (Cole 1995). One year after trampling, species diversity was not significantly correlated with curvilinearity of the data (P = 0·72) and was deleted from the model. Tolerance was significantly and negatively correlated with curvilinearity, but explained only 40% of the variation in linearity (Table 5).

Table 5. Relationship between curvilinearity of the trampling intensity/vegetation cover model and tolerance of the vegetation, 1 year after trampling. Curvilinearity is the coefficient of the quadratic term in the model × 10^4

Source of variation	df	Mean square	F	P	r^2
Regression model	1	21·7	9·6	0·009	0·40
Error	12	2·3			

Variable	Coefficient	SE	t ratio	P
Intercept	7·94	1·66	4·8	<0·001
Tolerance index	−0·08	0·03	−3·1	0·009

Discussion

Both the rate of change in vegetation cover with increased trampling and the consistency of this rate of change, at different trampling intensities, varied greatly between vegetation types. These two characteristics of response were related. Those vegetation types that changed the least 2 weeks after trampling and 1 year after trampling (e.g. *Kobresia myosuroides*) had the most constant rates of vegetation loss. In contrast, in those vegetation types with low resistance and tolerance (e.g. *Amphicarpa bracteata*), the relationship between vegetation cover and trampling intensity was highly curvilinear.

Table 4. Relationship between curvilinearity of the trampling intensity-vegetation cover model and the resistance and species diversity of the vegetation, 2 weeks after trampling. Curvilinearity is the coefficient of the quadratic term in the model × 10^4. Species diversity is based on Simpson's (1949) index

Source of variation	df	Mean square	F	P	r^2
Regression model	2	62·5	92·1	<0·001	0·92
Error	13	0·7			

Variable	Coefficient	SE	t ratio	P
Intercept	8·10	1·20	6·7	<0·001
Resistance index	−0·12	0·01	−8·4	<0·001
Species diversity	2·39	1·15	2·1	0·05

Most previous experimental trampling research has reported a highly curvilinear relationship between trampling intensity and vegetation response (Bell & Bliss 1973; Hylgaard & Liddle 1981; Cole 1987a; Kuss & Hall 1991). This curvilinearity should be expected, given that the amount of vegetation that can be affected declines as trampling intensity increases. The results of this study indicate, however, that the relationship can be linear, particularly in the most resistant and tolerant vegetation types. This suggests that certain vegetation types have thresholds of vulnerability. They are capable of resisting damage as long as trampling intensity is low. Once trampling intensities exceed these thresholds, damage occurs and increases as trampling increases.

Several of these findings have significant implications for the management of natural vegetation types subjected to recreational use. Vegetation types vary substantially in their vulnerability to trampling damage. Some of the vegetation types examined in this study were at least 30 times more vulnerable than others. This suggests that there is great potential to reduce the impacts of recreational trampling on vegetation by controlling the spatial distribution of use. Traffic can be directed onto more durable vegetation types and away from more vulnerable types.

Vegetation types vary both in their ability to resist being damaged by trampling and in their ability to recover from trampling damage. The appropriateness of management strategies will vary with both of these properties. In this study, the vegetation types that were least able to tolerate a complete cycle of damage and recovery were those that recovered least, rather than those that were damaged most initially. Some of the most resistant vegetation types can tolerate a certain amount of trampling, as long as trampling intensities do not exceed threshold levels. Managers could maintain trampling impacts at negligible levels by keeping the trampling intensities below these thresholds. Additional research might lead to more precise identification of these thresholds.

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Appendix

Table A1. Initial frequency and mean percentage cover of the more abundant species in each of the four Washington Cascade Mountain vegetation types*

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

* Only species with mean cover of at least 2% are included. Frequency is the fraction (%) of 40 subplots of 30 × 50 cm in which the species was found. +, cover less than 0·5%. Nomenclature follows Hitchcock & Cronquist (1973).

Table A2. Initial frequency and mean percentage cover of the more abundant species in each of the two Montana Rocky Mountain vegetation types*

	Vegetation type					Vegetation type			
	Vaccinium B		*Cornus*			*Vaccinium* B		*Cornus*	
Species	Freq.	Cover	Freq.	Cover	Species	Freq.	Cover	Freq.	Cover
Vaccinium scoparium	100	54			*Fragaria virginiana*			75	5
Carex geyeri	31	4			*Equisetum arvense*			31	4
Pedicularis racemosa	15	2			*Symphoricarpos albus*			23	3
Cornus canadensis			90	25	*Clintonia uniflora*			21	3
Berberis repens			79	19	*Senecio pseudaureus*			33	3
Bromus vulgaris			60	7	*Calamagrostis rubescens*			29	2
Smilacina stellata			52	7	*Galium triflorum*			44	2
Linnaea borealis			60	6	*Antennaria racemosa*			15	2
Osmorhiza chilensis			83	5	Mosses	67	5	44	12
Viola canadensis			40	5	Lichens	92	13	8	+
Thalictrum occidentale			40	5					

* Only species with mean cover of at least 2% are included. Frequency is the fraction (%) of 48 subplots of 30 × 50 cm in which the species was found. +, cover less than 0·5%. Nomenclature follows Hitchcock & Cronquist (1973).

Table A3. Initial frequency and mean percentage cover of the more abundant species in each of the four Colorado Rocky Mountain vegetation types*

	Vegetation type							
	Trifolium		*Kobresia*		*Vaccinium* A		*Geranium*	
Species	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover
Trifolium parryi	100	20						
Danthonia intermedia	95	17						
Sibbaldia procumbens	88	12						
Potentilla diversifolia	100	10						
Erigeron melanocephalus	90	7						
Deschampsia caespitosa	30	4						
Kobresia myosuroides			100	65				
Acomastylis rossii			85	7				
Trifolium dasyphyllum			73	5				
Vaccinium scoparium					100	60		
Carex rossii					76	5		
Aster laevis							73	22
Fragaria ovalis							98	17
Geranium richardsonii							100	17
Viola canadensis							90	14
Thermopsis divaricarpa							73	12
Achillea lanulosa							98	10
Galium boreale							95	7
Bromopsis porteri							85	6
Carex norvegica							70	4
Thalictrum fendleri							20	4
Trisetum spicatum	13	1	40	2			23	4
Taraxacum officinale							45	4
Arnica cordifolia							45	3
Mosses	53	5	80	3	36	2		
Lichens	38	1	90	4	59	5		

* Only species with mean cover of at least 2% are included. Frequency is the fraction (%) of 48 subplots of 30 × 50 cm in which the species was found. +, cover less than 0·5%. Nomenclature follows Weber (1976).

Table A4. Initial frequency and mean percentage cover of the more abundant species of the four New Hampshire White Mountain vegetation types*

	Vegetation type							
	Carex bigelowii		*Leersia*		*Lycopodium*		*Maianthemum*	
Species	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover
Carex bigelowii	100	65						
Arenaria groenlandica	55	14						
Vaccinium uliginosum	35	5						
Juncus trifidus	23	3						
Leersia oryzoides			100	24				
Viola pallens			85	12				
Onoclea sensiblis			35	12				
Aster acuminatus			40	11	40	11	6	1
Rubus pubescens			53	10				
Carex crinita			43	9				
Dryopteris austriaca			20	9	60	14	58	22
Impatiens pallida			43	9				
Osmunda cinnamomea			5	3				
Oxalis acetosella†			30	3	98	45	55	18
Scutellaria lateriflora			18	3				
Dryopteris phegopteris			23	3			1	+
Maianthemum canadensis			25	3			100	51
Lycopodium lucidulum					98	47	19	4
Abies balsamea					30	3	13	1
Trientalis borealis			8	+			62	5
Dryopteris disjuncta			10	1			14	3
Lichens	60	20						
Mosses	50	19	45	3	8	+	24	4

* Only species with mean cover of at least 2% are included. Frequency is the fraction (%) of 40 subplots of 30 × 50 cm in which the species was found. +, cover less than 0·5%. Nomenclature follows Gleason & Cronquist (1963).

† *Oxalis acetosella* is named *O. montana* in the flora by Radford *et al.* (1968) in the Great Smoky Mountains.

Table A5. Initial frequency and mean percentage cover of the more abundant species of the four North Carolina Great Smoky Mountain vegetation types*

	Vegetation type							
	Carex pensyl.		*Potentilla*		*Amphicarpa*		*Dryopteris*	
Species	Freq.	Cover	Freq.	Cover	Freq.	Cover	Freq.	Cover
Carex pensylvanica	100	45						
Medeola virginiana	35	4						
Rubus canadensis	18	3	48	6	2	+		
Holcus lanatus			88	17				
Potentilla simplex			93	17	4	+		
Panicum boscii			60	17				
Carex swanii			85	12				
Chrysanthemum leucanthemum			75	7				
Agrimonia parviflora			35	6				
Fragaria virginiana			73	6	2	+		
Luzula echinata			18	5				
Solidago gigantea	3	+	35	5				
Prunella vulgaris			65	5				
Lespedeza procumbens			8	5				
Solidago sp.			25	4				
Parthenocissus quinquefolia			28	4	52	5		
Clematis virginiana			33	3				
Amphicarpa bracteata			28	3	96	28		
Phlox stolonifera					92	16		
Thaspium trifoliata					71	15		
Geranium maculatum					57	12		
Viola papilionacea	15	+	10	+	68	5		
Aster divaricatus	5	+			33	4		
Laportea canadensis					39	4		
Dryopteris campyloptera							98	82
Clintonia borealis					6	+	50	17
Athyrium asplenioides					2	+	23	16
Oxalis montana[†]							78	3
Cacalia rugelii							13	3
Mosses			13	1	43	4	75	9

* Only species with mean cover of at least 2% are included. Frequency is the fraction (%) of 40 subplots 30 × 50 cm in which the species was found. +, cover less than 0·5%. Nomenclature follows Radford *et al.* (1968).

[†] *Oxalis montana* is named *O. acetosella* in the flora by Gleason & Cronquist (1963) in the White Mountains.