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Effects of the northern pocket gopher (*Thomomys talpoides*) on alpine soil characteristics, Niwot Ridge, CO

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Abstract. Effects of the northern pocket gopher (*Thomomys talpoides*) on surface soil characteristics were examined at the alpine site of Niwot Ridge, CO. We measured erosion of soil from gopher mounds and compared the characteristics of gopher mound (disturbed) and undisturbed soils in two major plant community types. Our measurements of erosion indicate long-term susceptibility of gopher-disturbed soils to redistribution by water and/or wind in this ecosystem. Ecosystem heterogeneity introduced by the gopher is reflected in significantly lower SOM in gopher mounds than in surrounding undisturbed soils, a characteristic which appears to be causally associated with other effects of gopher disturbance including changes in soil texture and significantly lower clays, total C, total N, total P, and labile P. In contrast to plant-available P, NO_3^- was higher and steadily increased for the short term in both gopher mound soils and those beneath the mounds. These pools of NO_3^- then decreased to pre-disturbance levels by the following spring. Collectively our results indicate that, through the physical manipulation of soil and subsequent effects on soil resources, the northern pocket gopher functions as an agent of increased ecosystem heterogeneity and soil mass and nutrient redistribution at Niwot Ridge.

Introduction

The effects of disturbance on soil characteristics and ecosystem processes have been well-documented for fire (e.g. Christensen et al. 1989), wind (e.g. Bormann & Likens 1979), forest clearcuts (e.g. Vitousek & Reiners 1975), and other large-scale perturbations (e.g. Romme & Knight 1982; Sousa 1984). The impacts of smaller disturbances on ecosystem structure and function have received considerably less attention, however, or are viewed as intrinsic properties of the ecosystems themselves. For example, forest tree gaps caused by the death of a single tree (e.g. Runkle 1997), bison wallows

(Knapp et al. 1999) and the burrowing and mounding activities of prairie dogs (Whicker & Detling 1988) or gophers (Huntly & Inouye 1988) represent small-scale disturbances that are not measured using traditional ecosystem metrics. Other small-scale processes such as insect herbivory may, however, be recognized as ecosystem disturbances when their levels reach a measurable threshold (e.g. Swank et al. 1981).

We documented the effects of a biological agent of small disturbance, the northern pocket gopher (*Thomomys talpoides*), on the characteristics of alpine soils at Niwot Ridge, CO. Pocket gophers introduce ecosystem heterogeneity by the excavation of subterranean burrows and deposition of soil on the tundra surface. The resulting gopher mound is a new soil surface with little or no plant biomass, higher incident light (Inouye et al. 1987; Huntly & Inouye 1988), and higher soil temperatures (Cortinas & Seastedt 1996). These altered microenvironmental conditions of gopher mounds are disparate from surrounding soils and may subsequently influence related ecosystem processes such as energy and nutrient dynamics.

Responses of soil characteristics to pocket gopher disturbance vary depending on the ecosystem (McDonough 1974; Laycock & Richardson 1975; Mielke 1977; Grant et al. 1980; Inouye et al. 1987; Koide et al. 1987). Changes in soil organic matter (SOM), total nitrogen, and total phosphorus are parallel, however (Mielke 1977; Killham 1994), suggesting that changes in the latter two may be predicted with observations of SOM. At the alpine site of Niwot Ridge, total soil C and N are lower in areas heavily-impacted by gopher activity (Cortinas & Seastedt 1996; Litaor et al. 1996). The gopher has also been described as a major geomorphic agent at Niwot Ridge through its excavation of large volumes of soil which are then susceptible to accelerated erosion (Thorn 1978; Burns 1979).

We compared erosion, decomposition, and physical and biogeochemical soil parameters between gopher-disturbed and undisturbed areas at Niwot Ridge. Because N and P are co-limiting nutrients in the alpine tundra (Bowman et al. 1993), these were of primary interest in the context of gopher disturbance. We expected to find higher availabilities of N in gopher mounds due to stimulated mineralization in response to disturbance (Birch 1958; Johnson et al. 1995; Cortinas & Seastedt 1996) and substantial organic substrate of belowground plant biomass (Webber and Ebert-May 1977; May and Webber 1982) in excavated soils. Phosphorus occurs in a variety of plant-available and -unavailable forms that are highly sensitive to changes within the soil milieu, whether physical or biogeochemical (Reddy et al. 1980; Easterwood & Sartain 1990; Hue 1991; Tiessen & Moir 1993; Iyamuremye et al. 1996; Staunton & Leprince 1996; Gressel & McColl 1997). The sensitivity of P fractions to so many environmental factors complicates their measurement and interpretation, but we hypothesized that soils brought up from depth with gopher burrowing would harbor pools of greater available P than undisturbed soils due to the same factors controlling available N. Lastly, we expected to measure higher N and P availability in the moist meadow than in the dry meadow due to greater total nutrient capital in the former (Fisk 1995).

Study area

Niwot Ridge (40°03' N, 105°35' W) is about 35 km west of Boulder, Colorado, on the eastern slope of the Rocky Mountain Front Range. At ~3500 m, Niwot Ridge is the alpine representative of the NSF's Long-Term Ecological Research Program. The mean annual temperature at a long-term monitoring station ~200 m above the study sites is –3.7 °C and annual precipitation, predominantly snow, averages 930 mm (Greenland 1989). Prevailing winds are from the northwest with a mean annual velocity of 10.3 m/s and gusts over 45 m/s (Barry 1973; Isard 1986). Landscape position influences microenvironmental conditions, as actual precipitation inputs to any point on the tundra are further modified by snow redeposition (e.g. Walker et al. 1993).

Measurements of soil loss from gopher mounds were taken at the Martinelli Slope (15–20°; 3400 m a.s.l.) on the south slope of Niwot Ridge. This is an area of sustained gopher disturbance which has been monitored since 1987. Soil A horizons at Martinelli are sandy loams overlying mostly loamy sand B horizons. See Table 1 for further characteristics.

Soil collections were from two community types at Niwot Ridge (Table 1). Dry meadows, dominated by the sedge *Kobresia myosuroides*, are exposed to high winter winds and retain little snowcover. Dry meadow soils for the most part are very rocky, with a finely-textured A horizon (umbric epipedon), likely deposited from aeolian processes, overlying a cambic B horizon (Burns 1980). Pocket gopher activity is moderate in the dry meadows but considerably more concentrated in the moist meadow community type (Burns 1980; Thorn 1982). The soils of the moist meadow community retain a larger snowpack than the dry meadows and are dominated by the forb *Acomastylis rossii*. Pocket gopher activity and/or downslope movement have thickened the A horizon in some areas to > 40 cm (Burns 1980), and these overlie cambic B horizons. Our moist meadow soil collections were from areas with an average A horizon depth of 28 cm (Seastedt 2001) and all corresponding disturbed and undisturbed samples were taken from the same soil type (Table 2). Decomposition studies were exclusively in the dry meadow, which yielded more equivalent activity on the north and south slopes than did the moist meadow, to allow for a comparison of topographic effects.

Table 1. Selected soil characteristics of the three major plant communities studied, Niwot Ridge, CO. Burns (1980) recognizes three different A horizon thicknesses in the moist meadow, the deepest being "overthickened" by pocket gopher activity and/or downslope soil movement. Our soil collections were from Typic and Pachic Cryumbrepts with an average A horizon depth of 28 cm (Seastedt 2001). Data are unavailable for B horizon thickness for the dry and moist meadows

Community	Soil classification[a]	A horizon thickness (cm) and/or texture	B horizon thickness (cm) and/or texture	A horizon Carbon (g/kg)	A horizon Nitrogen (g/kg)
Martinelli	Pergelic Cryochrepts	32–56 (sandy loam)[b]	76–85 (loamy sand)[b]	∼37[b]	∼9[b]
Dry Meadow	Pergelic Cryumbrepts	18[a]		129[c]	10[c]
Moist Meadow	Dystric Cryochrept	18[a]			
	Typic Cryumbrept	18–40[a]		142[c]	11[c]
	Pachic Cryumbrepts	>40[a]			

[a]Burns 1980, [b]Litaor et al. 1996, [c]Fisk & Schmidt 1995.

Table 2. Bulk densities (unsieved), organic matter contents, and % total C and N of disturbed and undisturbed soils in two different meadow types at Niwot Ridge, CO. None of these parameters manifested seasonal change

	Bulk density (g/cc)		SOM (%)		% C		% N	
Meadow type:	Dry	Moist	Dry	Moist	Dry	Moist	Dry	Moist
Disturbed soil	1.10 ± 0.02	0.71 ± 0.02	7.00 ± 0.14	15.99 ± 0.71	3.76 ± 0.13	7.91 ± 0.47	0.29 ± 0.01	0.63 ± 0.04
Undisturbed soil	1.80 ± 0.05	1.22 ± 0.06	11.11 ± 0.38	24.31 ± 0.62	6.26 ± 0.32	11.67 ± 0.36	0.45 ± 0.03	0.87 ± 0.03

Methods

Erosion

We used semicylindrical troughs to measure the loss of soil from gopher mounds at the Martinelli Slope Experiment site. Twenty-four troughs were constructed of sheet aluminum sealed at each end by a halved PVC cap. The troughs were 25 cm long $\times$ 15 cm in diameter, and along the length of each was 3 cm of extra sheet metal forming a lip. In September 1995, 24 troughs were placed downslope of 24 gopher mounds: six troughs were placed at 0 m (immediately) below six gopher mounds, six were placed at 0.5 m below six gopher mounds, six at 1 m, and six at 2 m. Eleven control troughs were placed downslope of areas that exhibited no signs of recent disturbance. All troughs were placed so that the 3 cm lip was oriented uphill. Upon snowmelt in June 1996, 1997, and 1998, all soil that had accumulated in the troughs was collected, dried, and sieved (2 mm), and both size fractions (< 2 mm and > 2 mm) were weighed. Troughs remained in their original positions throughout the measurement period and measured soil loss from the same disturbances. Each size fraction and the sum of their masses were analyzed using two-way ANOVAs with year and distance below the gopher mound as factors.

The < 2 mm size fraction collected in the summer of 1996 was tested for percent total carbon (%C) and nitrogen (%N) using a Fisons CHN Elemental Analyzer (Beverly, MA). Data were log-transformed to meet normality assumptions and then tested for significant differences among distances from the disturbance using a one-way ANOVA.

Measurements of erosion were pooled across all years for presentation here, as the soils collected downslope of gopher mounds showed no differences among years for either size fraction nor for total mass.

Physical and biogeochemical characteristics

We collected soils from fresh gopher mounds in the moist and dry meadows as soon as possible after gopher disturbance in June 1996, 1997, and 1998, and sampled monthly from the same disturbances until snowfall. We sampled 6–11 gopher mounds in each community type, depending on the level of activity. Soils for biogeochemical analysis were obtained by coring the top 10 cm of the mound with a plastic 3 cm dia. auger. Samples for bulk density and textural analysis were taken from the midregion of the gopher mound with an aluminum tin after scraping away a portion of the mound to expose the volume interior. For each mound, we took a corresponding sample of undisturbed soil (> 1 m from the mound) by coring to 10 cm with a steel

1.5 cm dia. auger. Soil compaction did not occur due to the unstructured nature of gopher mound soils and the sharpness of the corers. Different corers were used for mounds and undisturbed tundra because the plastic corer used for gopher mounds was not strong enough for the undisturbed, vegetated soil surface, and the 1.5 cm steel corer, which is manipulated with a "T-bar" handle, was too cumbersome for the friable gopher mound soils. In the 1998 field season, we expanded sampling to include soils beneath gopher mounds ("submound" soils) by inserting the 1.5 cm steel corer through the hole that was made with the 3 cm plastic corer and taking a sample from the tundra soil beneath the gopher mound.

All soils were sieved (2 mm) except those used to measure bulk density. In 1996 and 1998, we extracted inorganic N with 2N KCl within 12 hours of collection. The extracts were analyzed for NH_4^+ and NO_3^- using a flow-injection colorimetric autoanalyzer (Lachat Instruments, Mequon, Wisconsin).

Soils collected in 1996 were analyzed for SOM with loss on ignition and for %C and %N. Soil texture was determined by the hydrometer method at the Soil, Water and Plant Testing Laboratory, Fort Collins, CO. We assumed that bulk density and texture of undisturbed soils are seasonally static and so used measurements only from those collected in June.

Soils collected in 1996 were analyzed at the University of Denver for plant-available P using a modification of the Hedley fractionation (Hedley et al. 1982; Tiessen & Moir 1993), a sequential process that extracts P fractions in decreasing order of plant availability. We measured the first two fractions only, resin-extractable (P_r) and a bicarbonate-extractable fraction. P_r is freely-exchangeable and is the most available for plant nutrition. The bicarbonate-extractable fraction is comprised of both organic (P_o) and inorganic (P_i) components which reflect P that is moderately available through root respiration and the conversion of CO_2 to bicarbonate in soil solution (Tiessen & Moir 1993; Nziguheba et al. 1998). Total soil P contains other organic and inorganic forms but our focus was on "plant-available" or "labile" P and therefore exclusive to the first two Hedley fractions (Cross & Schlesinger 1995).

The 1997 soil samples were analyzed for Bray P (Bray & Kurtz 1945), another index of available P, and for total P using a nitric-perchloric acid digest and Inductively-Coupled Plasma Optical Emission Spectroscopy, at the Soil, Water and Plant Testing Laboratory (Fort Collins, CO). Soil pH was measured using a 1:1 slurry of soil and water within 12 hours of collection. Because pH is a logarithmic index, all pH values were converted to H^+ concentrations for data analysis.

We used repeated-measures ANOVAs with month as the within-subjects factor to test the effects of disturbance and meadow type on each soil parameter. Because Hedley P fractions are extracted sequentially and are highly collinear, these data were analyzed as a combined variate in a repeated-measures MANOVA. Within-factor means were used as dummy variables for missing P_i data to meet homogeneity-of-variance assumptions. Because missing inorganic N data were too numerous to allow a robust repeated-measured ANOVA, conventional ANOVAs were used with meadow type, treatment (undisturbed, gopher mound, and submound soils), and month as main factors.

Landscape and decomposition

Our third assessment of pocket gopher effects on ecosystem characteristics was an examination of the interacting effects of topography and disturbance on litter decomposition in the dry meadows of Niwot Ridge. This was a more detailed examination of the litter archive remaining from Cortinas and Seastedt (1996). As the dominant plant species in the dry meadow, *K. myosuroides* is the species most commonly buried by gopher mounds in this community type. *K. myosuroides* foliage was collected, oven-dried at 60 °C, and partitioned in $\sim$2 g samples among 160 8 $\times$ 15 cm litterbags of 0.3 mm polyester mesh. Six fresh gopher mounds were selected on both the north and the south slopes to contain the litterbags. Eight bags were buried in each gopher mound at the interface of the mound and the original O horizon, and 48 corresponding bags were fixed on undisturbed soils near each of these mounds. Initial placement was in June 1993. Two litterbags were collected at 3, 12, 14, and 25 months, oven-dried at 80 °C for 24 hr, and the litter removed from the bags and weighed. Litter weight loss was calculated to estimate decomposition rates. We analyzed the litter from the last 3 harvests for total C and N. Initial nutrients were not measured by Cortinas and Seastedt (1996); we therefore assumed initial %C to be 50% and initial %N values were taken from Fisk and Schmidt (1996). All data were tested for significant differences among slope, date of harvest, and treatment (mound vs. surface) with 3-way ANOVAs.

Results

Erosion

Downslope transport of soil was significantly greater to areas in the immediate vicinity of the disturbance than it was to distances 0.5 m or greater, which did not differ from control designations (Figure 1a; F = 28.31; $p < 0.001$). Soil N and C trends were opposite that of mass, with significant differences between 0 m and all other distances, including the control (Figures 1b&c). Total soil nutrient transport (the product of soil mass and % total C and N) paralleled soil mass (Figure 1a); these short-range soils therefore represent the greatest net displacement of nutrients from gopher mounds on a mass basis.

There were no differences in the soil C:N ratio with distance, nor between disturbed and control soils (average C:N 12.67 ± 0.29; all values reported are mean ± standard error).

Physical characteristics

Differences in bulk density were significant between disturbed and undisturbed soils and between community types (Table 2; F = 299.l08 and 193.69, respectively; $p < 0.001$), and the interaction between these two factors was also significant (F = 6.76; $p < 0.05$). There was no seasonal change in bulk density in disturbed soils, but there was considerable change in soil texture across the season (Figure 2). In both meadow types, undisturbed and newly-disturbed soils are sandy loams. Over the course of the 1996 growing season, however, there was a progressive loss of the finer soil fractions from gopher mounds, and by October the clay fraction was undetectable. Gopher mound soils at the end of the growing season were classified as sand in the dry meadow and loamy sand in the moist meadow.

Biogeochemical characteristics

Organic matter and total nutrients
Soil organic matter, %C, and %N are all highly correlated (Table 3) and manifest parallel trends between meadow types and between disturbed and undisturbed soils (Table 2). SOM, %C, and %N are significantly lower in disturbed soils than in undisturbed soils (F = 45.19, 33.36, and 21.11, respectively; $p < 0.001$), and are significantly higher in the moist meadow than in the dry meadow (F = 104.30, 53.37, and 48.13, respectively; $p < 0.001$). None of these parameters exhibited seasonal trends. C:N ratios also were significantly lower in disturbed soils (F = 42.73, $p < 0.001$) but there were no C:N differences between the two community types.

Plant-available N
Pools of extractable NO_3^- changed significantly over time, between communities, and among soil treatments; interactions among these factors were also significant (Table 4, Figure 3a). Similar to the patterns of SOM And

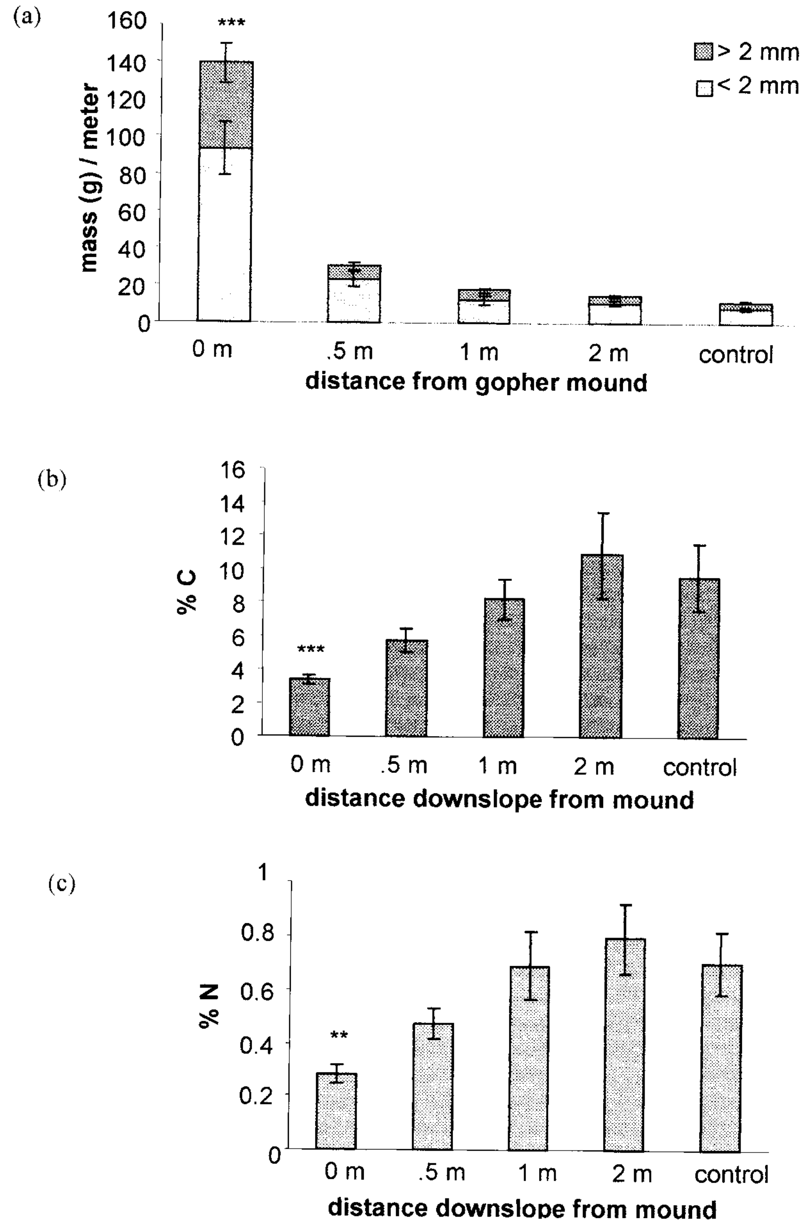

Figure 1. Mass and nutrients of soil collected downslope of gopher mounds following snowmelt, Martinelli Snowfield, Niwot Ridge, CO. Significant differences, indicated by asterisks, are between soils at 0 m and all other distances, including the control placement. (a) Mass of two size fractions. Values are per meter of trough length. Data are pooled across 1996–1998. Standard error bars are respective to each size fraction. $^{***}p < 0.001$ for the total weight of each distance as well as for each size fraction. (b) Mean ± SE %C. Data are from 1996. F = 6.7548 and $p = 0.0005$. (c) Mean ± SE %N. Data are from 1996. F = 5.6554 and $p = 0.0016$.

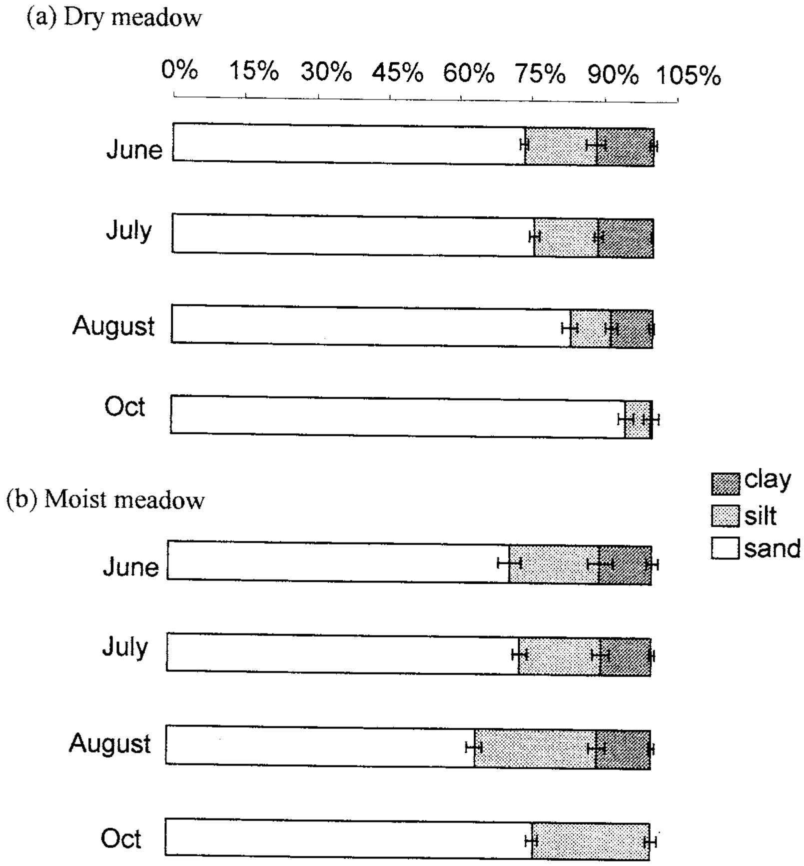

Figure 2. Sequence over the 1996 growing season of texture changes in gopher mound soils, Niwot Ridge. (a) Texture classifications in the dry meadow progressed from sandy loam in June to loamy sand in August, then to sand in October. (b) In the moist meadow, texture progressed from sandy loam in June to loamy sand in October.

%N, NO_3^- levels in the moist meadow are higher than in the dry meadow. Unlike SOM and %N, however, the quantities of NO_3^- in fresh gopher mounds are higher than in undisturbed areas, increase over the growing season, and drop back to near-pre-disturbance levels the following spring. A parallel increase in submound NO_3^- pools occurred in the moist meadow, but stopped in the submound soils of dry meadow by mid-summer (Figure 3a).

NH_4^+ pools were more erratic than those of NO_3^-, but similarly decreased between October and the following June (Figure 3b). The strongest dynamics of NH_4^+ were in dry meadow submound soils (Figure 3b, Table 4), with higher pools within the first two months after disturbance and significantly lower pools thereafter.

Table 3. Correlation coefficients of soil parameters measured for soils collected in 1996. D_B refers to bulk density. See text for explanation of P fractions

	% clay	D_B	% C	% N	NH_4^+	NO_3^-	P_i	P_o	P_r
D_B	0.21								
% C	0.06	–0.30**							
% N	0.00	–0.36**	0.99***						
NH_4^+	–0.16	–0.38***	0.49***	0.51***					
NO_3^-	–0.41***	–0.40***	–0.07	0.00	0.36***				
P_i	0.12	–0.42***	0.66***	0.66***	0.39***	0.02			
P_o	–0.11	–0.64***	0.66***	0.69***	0.35***	0.14	0.65***		
P_r	0.25**	–0.07	0.75***	0.74***	0.37***	–0.16*	0.65***	0.52***	
SOM	0.03	–0.39***	0.93***	0.92***	0.57***	–0.03	0.69***	0.67***	0.78***

***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

Table 4. F statistics and significance of 3-way ANOVAs testing the effects of meadow type, soil treatment (mound, submound, or undisturbed soils), and month on inorganic nitrogen pools

	NO_3^-	NH_4^+
Meadow	5.65*	17.84***
Month	3.74**	1.19
Treatment	42.29***	1.86
Meadow × Month	2.73*	2.20
Meadow × Treatment	4.40*	0.20
Month × Treatment	5.30***	3.50**
Meadow × Month × Treatment	0.97	0.58

***$p < 0.001$, **$p < 0.01$, *$p < 0.05$.

Phosphorus

The Hedley indices of available P ("fractionation P") showed strong, positive correlations with SOM, %C, and %N (Table 3). Multiple regressions of each P fraction on SOM and soil clay content indicate that SOM is more important in determining the quantities of fractionation P in these alpine soils (Table 5). The sum of the three P fractions was not significantly different between disturbed and undisturbed soils, and the only seasonal change was an August increase in disturbed soils of the dry meadow (Figure 4a). However, considering the three fractions as a collinear variate, repeated-measures MANOVA indicated that disturbance and meadow type, both independently and inter-

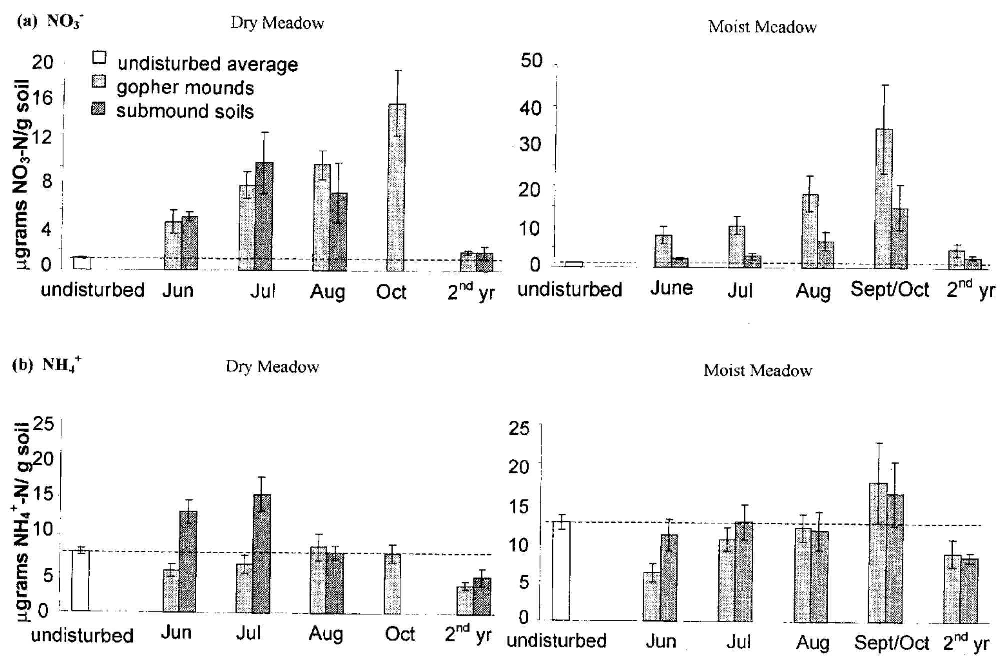

Figure 3. NO_3^- and NH_4^+ dynamics in gopher mound soils, soils beneath gopher mounds, and undisturbed controls in the dry and moist meadows of Niwot Ridge. Undisturbed controls are averaged over all measurements. (a) NO_3^-. Note the difference in scale between the two community types. Considering each meadow separately and excluding undisturbed soils, two-way ANOVAs yielded a significant effect of month only in the dry meadow (F = 10.07; $p < 0.001$) and of both month (F = 3.72; $p = 0.007$) and treatment (F = 7.75; $p = 0.006$) in the moist meadow. (b) NH_4^+. Considering the two meadow types individually, there were no significant effects of month, treatment, or their interaction in the moist meadow. All of these, however, were significant in the dry meadow (F = 4.85, 14.02, and 5.06, respectively; $p < 0.01$).

actively, have significant effects on fractionation P (Table 6). There were also detectable changes in the variate across the season, primarily attributable to P_r and P_i (Figure 4a).

Bray-extractable phosphorus differed significantly between meadow types (17.33 $\pm$ 0.65 μg/g in the dry meadow, 19.84 $\pm$ 0.51 μg/g in the moist meadow), but not in response to disturbance nor across the season (Table 6). Total P was significantly greater in undisturbed soils of the dry meadow, was greater in the moist meadow than the dry, and changed significantly over time (Table 6; Figure 4b).

pH

Soil pH was significantly reduced in disturbed soils (Figure 5; F = 8.75; Pillai's $p = 0.009$). Statistically there were no seasonal nor community differences, nor was there any interaction between these variables (F = 2.73, Pillai's $p = 0.083$), but pH in the moist meadow decreased suddenly between June and July while changes in the dry meadow were comparatively moderate (Figure 5).

Decomposition

The net effect of gopher mound burial is increased decomposition, as indicated by significantly greater cumulative litter decay in gopher mounds compared to that on the tundra surface (F = 108.78, $p < 0.001$; Figure 6a). After 25 months in the field, buried and surface litterbags had lost an average of 56.8% and 50.2% of their initial mass, respectively. Instantaneous decay rates between individual collection dates steadily declined for litter on the tundra surface but varied seasonally for buried litter. Aspect did not affect decay rates.

Proportions of N in decomposing litter were consistently higher for that buried in gopher mounds than for the litter on the undisturbed tundra surface, but the carbon percentage of litter in the two different treatments converged after 25 months in the field (Figure 6b). The total mass of litter N (mass $\times$ %N), an estimate of the nutrient retention of decomposing litter, appears to be unchanged for that buried in gopher mounds over the second year of decomposition, while that of surface litter clearly decreased (Figure 6c). By the 25th month in the field, the two treatments had equivalent values of total N mass. In contrast, the total mass of litter C decreased consistently in both treatments, that buried in gopher mounds significantly more so than on the surface (F = 91.02, $p < 0.001$).

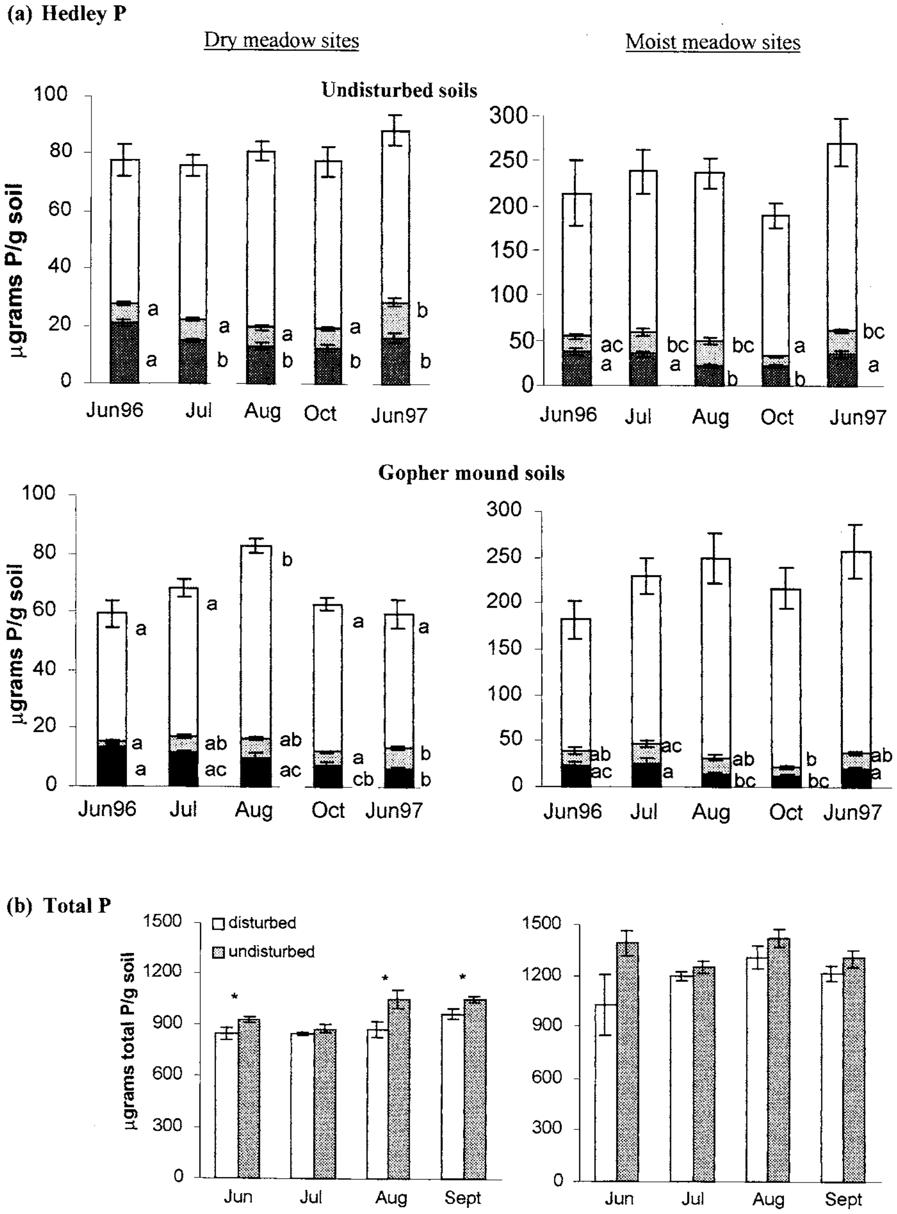

Figure 4. Phosphorus dynamics in dry and moist meadow soils. (a) Sequence of P_r (bottom fraction), P_i (middle) and P_o (top) in disturbed and undisturbed soils, 1996. Within each fraction, different letters indicate significant differences ($p < 0.05$). P_o remained constant over the season in all but dry meadow gopher mounds. Note the difference in scale between community types. (b) Total P, 1997. $^*p < 0.05$ between disturbed and undisturbed soils.

Table 5. Results of multiple regression of each available P fraction on SOM and soil clay content

	Resin P (P_r)			Bicarb-inorganic (P_i)			Bicarb-organic (P_o)		
Multiple R	0.81			0.69			0.69		
R^2	0.66			0.48			0.47		
Adj. R^2	0.66			0.47			0.46		
Std. Error	6.58			6.97			62.65		
ANOVA F	111.43***			52.72***			50.45***		
	B ± s.e.	β	T	B ± s.e.	β	T	B ± s.e.	β	T
SOM	1.18 ± 0.08	0.77	14.20***	0.89 ± 0.09	0.68	10.10***	7.86 ± 0.79	0.68	9.92***
% clay	0.59 ± 0.14	0.23	4.21***	0.23 ± 0.15	0.10	1.55	–2.54 ± 1.35	–0.13	–1.89
Constant	–4.22 ± 1.83		–2.31*	–2.33 ± 1.93		–1.21	29.75 ± 17.40		1.71

***$p < 0.001$, *$p < 0.05$.

Table 6. Results of repeated-measures ANOVAs testing the effects of disturbance and meadow type on indices of soil phosphorus. Month of sampling was defined as the within-subjects factor. Hedley P results (Pillai's Trace statistics and powers, data from 1996) are from multivariate ANOVA testing factors on the variate created with three plant-available P fractions. Bray and total P F statistics are from 1997 data

Source	Hedley P		Bray P	Total P
	Pillai's Trace	Power		
Between subjects				
Disturbance	0.73***	1.00	0.33	19.62***
Meadow	0.83***	1.00	4.79*	277.36***
Disturbance × Meadow	0.36*	0.80	2.87	0.48
Within subjects				
Month	0.96***	1.00	0.91	10.11***
Month × Disturbance	0.49	0.37	1.27	2.13
Month × Meadow	0.74*	0.88	0.02	1.82
Month × Disturbance × Meadow	0.49	0.38	1.07	1.96

***$p < 0.001$, *$p < 0.05$.

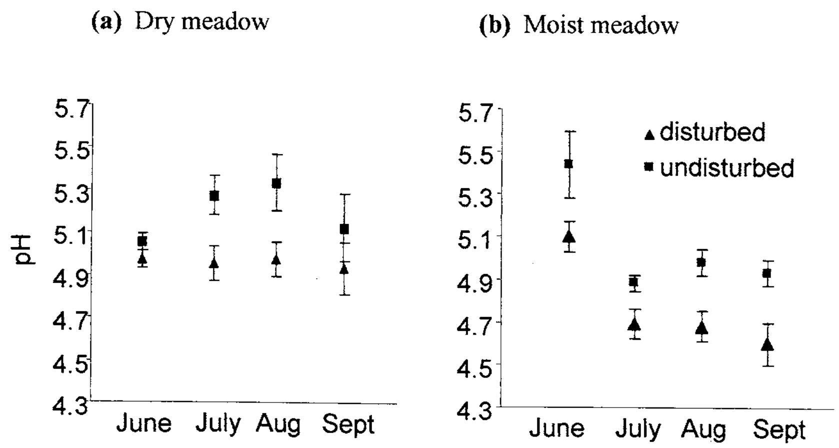

Figure 5. Soil pH in dry (a) and moist (b) meadows, Niwot Ridge, CO.

Discussion

Through its burrowing and mounding activities, the pocket gopher creates microsites of distinct physical, biological, and biogeochemical conditions with the potential of impacting other plant and microbial species. The lower

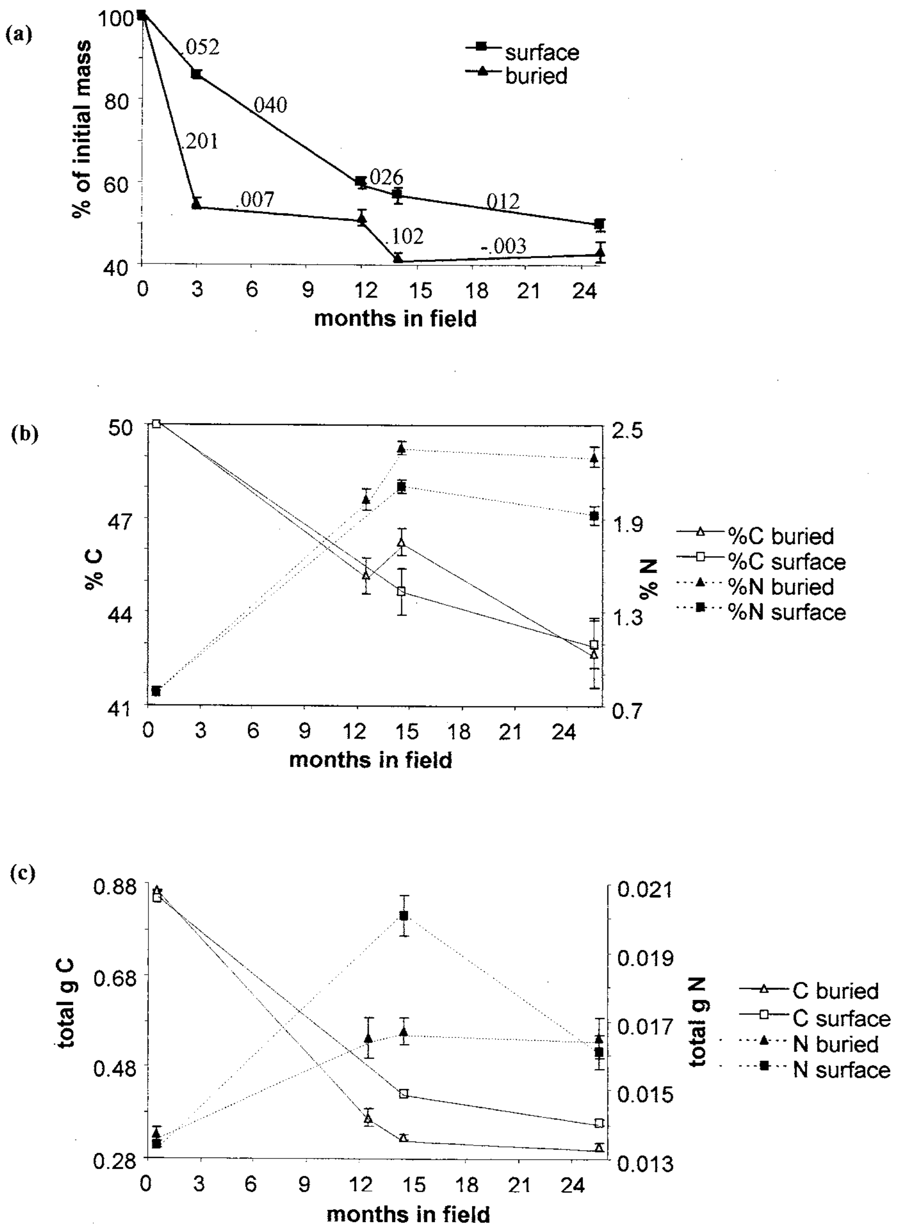

Figure 6. (a) Decomposition of *Kobresia* foliage over time. Months 0–3, 12–15, and 24–25 are summer months. Numbers refer to k, the decomposition constant. Data from the first four harvests are from Cortinas and Seastedt (1996). (b) % C and % N of decomposing litter. (c) Total mass of C and N in *Kobresia* litterbags calculated as the product of litter mass and the percent content of that nutrient.

quantities of organic matter in disturbed soils (Table 2) appear to be causally related to several other effects of the pocket gopher on Niwot Ridge soils, including significant changes in texture and lower quantities of nutrients. 'Selective' excavation by the pocket gopher, i.e. partitioning out edible root material before depositing the more mineral soil on the surface, may account for lower SOM in gopher mounds. Due to the necessity of food acquisition, it is improbable that gophers burrow below the bulk of the rooting zone of alpine plants ($\sim$15 cm for dry and $\sim$10 cm for moist meadows; Webber & Ebert-May 1977), although depth of burrowing may account for lower C:N ratios in gopher mound soils (Table 2; Coleman et al. 1989; Joergensen & Scheu 1999).

Our measurements of soil collected downslope of gopher mounds at Martinelli demonstrate the susceptibility of disturbed soils to erosion in the alpine tundra, supporting Thorn's (1978) and Burns' (1979) observations that the pocket gopher is a geomorphic agent in this ecosystem. Because collections of eroded soil were made immediately following snowmelt, we consider it most likely that snowmelt was the medium of soil transport as opposed to rain, which usually occurs in the summer as brief, convective events, or wind, from which the Martinelli site is well-sheltered. In more exposed areas of the alpine, however, such as on ridgetops or windswept dry meadows, strong aeolian forces (Barry 1973; Burns 1980) are a likely means of transporting gopher mound soils.

Gopher-induced erosion at Niwot Ridge is not short-lived, indicated by the consistent quantities of soil collected over the course of three years. This protracted temporal component is in contrast to the smaller spatial component of the erosion, as indicated by the relatively short distance of soil transport (Figure 1a). Gopher-induced erosion at Martinelli therefore impacts the ecosystem at the microsite or community level, but may not be detectable at the watershed scale unless gopher mound densities reach a critical threshold and induce larger-scale erosion as an aggregate.

In contrast to the trends of mass, eroded soil nutrient contents increase with increasing distance downslope of pocket gopher mounds (Figure 1b&c), indicating that the soils transported the furthest from gopher disturbances are also the highest in organic matter. This is likely due to depletion of the soils' heavier mineral components with downslope movement, and easier transport of lighter organic fractions. Thorn (1978) and Burns (1979) estimated that pocket gophers unearth between 1134 and 5800 kg soil $ha^{-1}yr^{-1}$ at Niwot Ridge. Based on our measurements of the nutrient content of eroded soils at Martinelli (Figure 1b,c) and of the dry and moist meadows, we calculate that areas experiencing these disturbance intensities could redistribute 37.8–

459.0 kg C ha^{-1} and 3.2–36.5 kg N ha^{-1} over the course of at least three years.

Gopher-induced erosion at Niwot Ridge is also manifested in the decline of clay fractions in gopher mound soils (Figure 2). Whether they infiltrate to the original soil surface with precipitation or are carried off-site by wind, their removal from surface horizons result in local decreases of cation exchange capacity. Concomitant increases of sand proportions in these surface soils will decrease the soil pH buffering capacity which, along with apparent increases in nitrification (Figure 3a) and production of organic acids during decomposition, likely contributes to the lower pH observed in gopher mounds (Figure 5).

Lower SOM in gopher mounds than in undisturbed soils (Table 2) accounts for similar differences in total C, total N, and total and labile P, a conclusion supported by positive, significant correlations (Table 3) and results of multiple regression (Table 5). Because much plant-available P in surface soils is derived from soil organic matter (Smeck 1985; Walbridge et al. 1991; Jobággy & Jackson, in press), lower organic material in these soils would directly preclude any higher available P.

Although in surface soils both N and P are associated with soil organic matter, plant-available N trends were contrary to those of SOM and plant-available P and, in the case of NO_3^-, steadily increased over the first growing season following disturbance (Figure 3a). These data corroborate Litaor et al. (1996) and are similar to the findings of Holland and Detling (1990) in prairie dog colonies and Tardiff and Stanford (1998) in bear digs. We attribute the differences between NO_3^- and labile P in disturbed soils primarily to the lower bulk density of gopher mound soils (Table 2), which facilitates soil aeration and nitrification (Litaor et al. 1996) but would not affect conversions of organic P. Greater microbial activity has been documented in gopher mounds in the Colorado shortgrass steppe (L. Dempse, pers. comm.), and our data reflecting lower pH (Figure 5) and C:N ratios (Table 2) are consistent with greater net mineralization and nitrification rates (Steltzer & Bowman 1998). Also, overall biotic uptake of NO_3^- is assumed to be negligible within the mound area due to microbial preference for NH_4^+ (Jones & Richards 1977; Kaye & Hart 1997) and the general absence of vegetation on fresh gopher mounds. This latter characteristic also has an indirect effect on NO_3^- pools because there is no plant-microbe competition for NH_4^+, allowing greater substrate availability for autotrophic nitrifiers. Minimal NO_3^- uptake is probably also the reason for the steady NO_3^- increase in gopher mounds over the growing season (Figure 3a) and indirectly contributes to NO_3^- losses from these soils the following spring (Vitousek et al. 1981).

Disturbance generally produces greater short-term nutrient availability (Vitousek 1985; Litaor et al. 1996), and the potential to exploit this higher availability varies among ecosystems. Vegetation that can utilize higher nutrient availabilities will generally yield greater net primary production (NPP) (e.g. Grant et al. 1980; Reichman et al. 1993; Cortinas & Seastedt 1996) and in this way will retain more nutrients within the ecosystem. In ecosystems that cannot exploit greater nutrient availabilities, NPP in disturbed areas is lower (Foster & Stubbendieck 1980; Grant & McBrayer 1981; Inouye et al. 1987; Hobbs et al. 1988) and the chances of system-wide nutrient loss are greater (Vitousek et al. 1981). Although the NO_3^- pools at Niwot Ridge apparently leach from gopher mounds with spring runoff, observations of greater plant productivity on south-facing slopes with gopher mounds (Cortinas & Seastedt 1996) suggest nonetheless that the flora are plastic enough to use these short-term nutrient increases, and in this way support ecosystem-wide nutrient retention.

Litter decomposition is initially faster within gopher mounds than on the tundra surface (Cortinas & Seastedt 1996; Figure 6) owing to disparate conditions between the two treatments: burial of substrate by a gopher mound affords greater surface area available to decomposers; soil disturbance stimulates microbial processes (Birch 1958; Johnson et al. 1995); and the gopher mound is a warmer and potentially moister microclimate, particularly during the growing season (Cortinas & Seastedt 1996).

Months 14–25 exhibited an apparent suspension of mass loss of litter in gopher mounds (Figure 6), consistent with Bryant (1996). Decreasing C:N ratios of litter (Figure 6b) and its C mass, but not N mass (Figure 6c), during this period suggest an approaching labile-carbon limitation of microbial decomposers in gopher mounds. Indeed, because detrital nitrogen levels appear fairly constant during this period, most detrital losses from gopher mounds appear to be restricted to carbon, which is presumably respired.

Ecosystem implications

Through the physical manipulation of soil and subsequent effects on soil resources, the northern pocket gopher functions not only as an agent of disturbance but as one of increased ecosystem heterogeneity and mass and nutrient redistribution of the soils of the Niwot Ridge alpine tundra. The net ecosystem effects of pocket gopher activity include lower surface organic matter content and decreasing clays which presumably affect soil CEC. The higher short-term nitrogen availability and sustained microbial activity of these scattered microsites may directly benefit local vegetation (Cortinas & Seastedt 1996) in spite of diminished available P. Estimates of pocket gopher concentrations range from 10.6 to 46 animals ha^{-1}, depending on the community type and the year (Thorn 1978; Burns 1979; Halfpenny & Southwick 1982; Thorn 1982; Halfpenny et al. 1984; Davies 1994; Sherrod 1999), each gopher unearthing an average of 100,940 cm^3 soil annually (Burns 1979). Particularly at the higher population concentrations, which is ultimately a function of topography (Sherrod 1999), the net ecosystem effects of the northern pocket gopher warrant consideration of this animal as a control of ecosystem processes in this alpine ecosystem.

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