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## The influence of pocket gophers on the status of nutrients in Alpine soils

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## Abstract

Soil and soil solutions from the Martinelli Slope Experiment on Niwot Ridge, Front Range, Colorado (40°3'N, 105°36'W) were studied to evaluate the influence of pocket gophers (*Thomomys talpoides*) on nutrient cycling in the alpine soil environment. Concentrations of total C, N, exchangeable Ca and K were significantly lower in gopher mound soils ( $P < 0.05$ ), whereas available  $\text{NO}_3^-$  and nitrogen fluxes were significantly higher in these soils ( $P < 0.001$ ). Silt and clay contents were significantly higher ( $P < 0.01$ ) in the surface horizons compared with the subsurface horizons of the intermounds, whereas particle size distributions exhibited more homogenous profile in the mounds. This pattern was explained by the mixing activity of the pocket gophers. The biological homogenization strongly influenced particle size distribution, bulk density, the availability of nutrients, and especially modified the N cycle within the alpine soil environment.

## 1. Introduction

The importance of fossorial small mammals in soil genesis, nutrient cycling, and consequently the entire ecosystem has been demonstrated by many workers (e.g., Turner et al., 1973; Hole, 1981). The activities of these mammals greatly modify the physicochemical characteristics of soils through mound formation, mixing and restructuring of soil horizons, modification of movement of solution, particulate matter and air in soil, and alteration of biogeochemical cycles in the soil environment (Hole, 1981). Of all the small mammal species, pocket gophers are particularly important in soil genesis, especially in the western United States. Pocket gophers have been implicated as the causal agent in mima mound

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formation (Cox, 1984; Scheffer, 1958; Scheffer and Kruckeberg, 1966) and may shape the topography for hundreds of square kilometers (Ross et al., 1968). Huntly and Inouye (1988) showed that pocket gophers affect the entire ecosystem through cascading mechanisms which modulate microtopography, soils, plants, and the behavior of other animals.

Northern pocket gophers (*Thomomys talpoides*) are common in the alpine zone of the Colorado Rocky Mountains, and they play an important role in alpine geomorphic processes. Population estimates vary from 10.6/ha to 40–46/ha (Burns, 1979; Thorn, 1978). Estimates of soil brought to the surface vary from 1.5 to 10.2 t ha<sup>-1</sup> yr<sup>-1</sup> (Thorn, 1978). Physical disturbance to the soil as well as direct consumption of vegetation results in large changes in the amount and types of vegetation found in the alpine (Thorn, 1982; Davies, 1994). Changes in plant–soil interactions due to these changes can further modify soil characteristics.

Although the importance of these mammals as geomorphic agents has been recognized for years, there is little information concerning their influence on the nutrient status of alpine soils. Because much of the alpine tundra is nitrogen limited (Shulls and Mancinelli, 1982; Bowman et al., 1993), the mixing and mounding activities of gophers may facilitate nutrient recycling. The objective of this investigation was to study the influence of pocket gophers on the status of nutrients in alpine soils and to assess the gopher influence on the alpine ecosystem.

## 2. Study area

The study site is located 35 km west of Boulder, Colorado, on the south slope of Niwot Ridge (40°3'N, 105°36'W) which is adjacent to a semi-permanent snowbank at about 3500 m altitude (Fig. 1). This site was named the Martinelli Slope Experiment site and is part of the Long-Term Ecological Research project of the University of Colorado. During the autumn of 1986 a small incursion of pocket gophers began which turned into a massive invasion during the summer of 1987 and has continued in this area disrupting a planned long-term trampling and denudation experiment. Estimates for the volume of single mounds in the Martinelli slope experiment varied in size from 6100 cm<sup>3</sup> to 48,400 cm<sup>3</sup>, and individual gophers may move approximately 48,000 cm<sup>3</sup> in a 24 hour period. Mean mound volume in 1987 was 23,500 cm<sup>3</sup> and the mean volume in 1988 was 10,200 cm<sup>3</sup> with an average of 10 mounds over the 250 m<sup>2</sup> study area. Hence, the proposed experiment was abandoned before the experiment was initiated and replaced by a long-term study of the effects of pocket gophers on alpine soil processes and plant succession.

The major geomorphic feature of this site is the Martinelli snowfield (~8 ha). A turf bank with hummocky topography to the east of this snowfield was chosen as the major site for our experiments (Fig. 1). Burns (1980) classified this site as an early melting snowbank soil complex. Soils on this site have a pachic-like epipedon which include Oe, A1, A2 and occasionally A3 horizons and 2Bw and 2BC subsurface horizons (Table 1). The soils are classified as Typic Cryumbrepts. The site is near the upper limit of tree growth, with scattered krummholz (tree island) conifers. The area of the experiments is a relatively homogeneous stand of alpine tundra classified by Komarkova and Webber (1978) as *Caricetum elynoidis*. This association is limited primarily to south-facing slopes and is often associated with

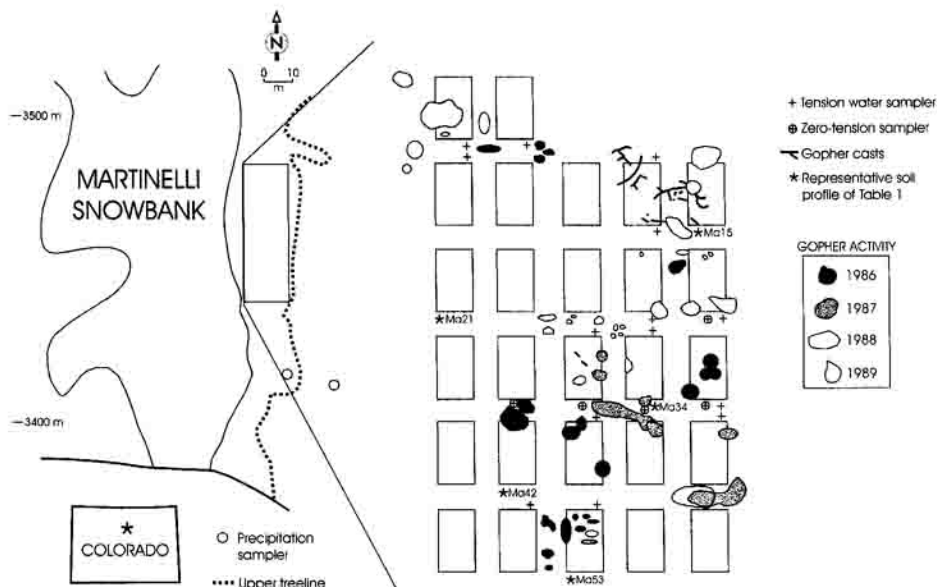


Fig. 1. The Martinelli Slope Experiment.

pocket gopher activity. The turf-forming sedge *Carex elynoides* dominates the vegetation, but this species does not occur on the gopher mounds and is apparently a late successional species in this system. Other important species include *Acomastylis rossii*, *Trifolium parryi*, *Erigeron simplex*, *Pedicularis parryi*, *Achillea lanulosa*, *Artemisia scopulorum*, and *Bistorta bistortoides* (Walker et al., 1993).

### 3. Field and laboratory methods

A Latin square design of  $5 \times 5$  plots was constructed (Fig. 1) to accommodate the initial research experiment of trampling and denudation. Plot dimensions are 2 m by 1.5 m with approximately 1.5 m between adjacent plots and 6 m between the rows. Two additional plots were added later to compensate for vegetational heterogeneity in Row 3.

To examine soil properties in detail, a soil pit adjacent to but outside of the southern (downslope) boundary of each plot (25 total) was excavated to a depth of 1 m. Field descriptions and soil classification were performed according to the guidelines established by the Soil Survey Staff (1975, 1993). On the basis of field observations of the 25 soil pits, 5 representative soil profiles, one from each row (Fig. 1), were collected for detailed chemical and physical characterization. After the gophers had invaded the site, soil samples were collected in August 1988 from all of the mounds, which varied in age of formation (see Fig. 1). Older mounds and mounds outside of the original plots were not sampled. The sampling of mounds was conducted in approximately 10 cm depth intervals to a depth of 50 cm with a 7 cm diam bulk auger.

Soil matric potentials were determined by portable tensiometers during the summer of 1989 at two depths in most intermound and mound sites. The intermound sites were areas

Table 1  
Selected morphological and physical properties of the soils from selected intermound sites in the study area

Horizon <sup>a</sup>	Depth (cm)	Color (moist)	Texture <sup>b</sup>	Structure	Boundary
<i>Ma15<sup>c</sup></i>					
Oe	4–0	10YR 2/1	SL	m	g
A	0–32	10YR 3/3	SL	1,m,sbk	g
2Bw1	32–50	5YR 3/4	LS	1,m,sbk	g
2Bw2	50–78	7.5YR 4/6	LS	1,m,sbk	
<i>Ma21</i>					
Oe	6–0	10YR 3/3	SL	m	c
A1	0–20	7.5YR 3/3	SL	m	g
A2	20–38	5YR 2/3	SL	1,m,sbk	g
A3	38–56	7.5YR 3/4	SL	1,m,sbk	g
2Bw1	56–72	7.5YR 4/4	LS	2,m,sbk	g
2Bw2	72–84 +	7.5YR 4/6	LS	1,f,sbk	
<i>Ma34</i>					
Oe	0–3	10YR 3/2	SL	m	c
A1	0–14	10YR 3/3	SL	m	g
A2	14–50	7.5YR 3/3	SL	1,m,sbk	g
2Bw1	50–70	10YR 4/6	LS	1,m,sbk	g
2Bw2	70–76	7.5YR 5/8	SL	2,m,sbk	g
2BC	76–85 +	7.5YR 4/6	LS	1,f,sbk	
<i>Ma42</i>					
Oe	6–0	10YR 3/2	SL	m	c
A1	0–17	10YR 3/3	SL	m	g
A2	17–47	10YR 3/4	SL	1,m,sbk	c
2Bw	47–66	7.5YR 4/6	LS	1,f,sbk	g
2BC	66–76 +	10YR 4/6	LS	1,f,gr	
<i>Ma53</i>					
Oe	3–0	10YR 2/2	SL	m	c
A1	0–14	7.5YR 3/3	SL	1,m,sbk	g
A2	14–35	7.5YR 3/4	SL	1,m,sbk	c
2Bw1	35–57	7.5YR 4/6	LS	1,f,sbk	g
2Bw2	57–80 +	7.5YR 4/6	LS	1,f,sbk	

<sup>a</sup>Soil horizons nomenclature followed Guthrie and Witty (1982).

<sup>b</sup>Texture: SL = sandy loam, LS = loamy sand; Structure: m = massive, sbk = subangular blocky, m = medium, f = fine, l = weak peds; Boundary: c = clear, g = gradual, d = diffuse.

<sup>c</sup>Ma15, Ma21, Ma34, Ma42, and Ma53 are identification codes for soil pits (see Fig. 1).

in the original plots that were at least 2 m from the center of a mound. There was no evidence of gopher activity in the intermound areas.

Bulk densities of intermound and the mound soils were determined by clod and core methods, respectively (Blake and Hartge, 1986). Exchangeable Ca and K were determined from 1 M NH<sub>4</sub>OAc (pH 5.5) extracts. The content of organic C was determined by dichromate titration (Allison, 1965). Total N was determined by Kjeldahl digestion using a block digester (Nelson and Sommers, 1980); digests were analyzed colorimetrically using a Lachat flow injection analyzer. Available nitrate + nitrite were extracted by 2 M KCl and

determined by a Dionex ion chromatograph after chloride removal with on-guard Ag-exchange column. Extractable  $\text{NO}_3^-$  was obtained from 1:5 soil water suspensions using a Dionex ion chromatograph. Results from the two  $\text{NO}_3^-$  extractions were virtually identical. Extractable Fe was determined using dithionite–citrate–bicarbonate (FeCBD) solution (Jackson et al., 1986).

The natural abundance of  $^{15}\text{N}$  in *Trifolium parryi*, the only plant at this site known to be associated with the symbiotic N-fixer *Rhizobium*, was compared against that of *Achillea lanulosa*, a non-fixing species. Two composite samples consisting of 50 to 60 individual plants of each species were prepared from intermound sites. Two composite samples consisting of all the individual plants of *Trifolium parryi* and *Achillea lanulosa* from several mounds were prepared. Thus, the  $^{15}\text{N}$  ratio obtained for the mounds is for the entire population in these mounds. Five soil humus samples (0–5 cm) and five mineral soils at depths of 5–10 cm and 10–20 cm from the intermound and two surface soils (0–5 cm) from the mound areas were collected for  $^{15}\text{N}$  determination. Soils were sampled immediately beneath each of the plant species. The sample preparation procedure followed the suggestions given by Shearer and Kohl (1986). Isotopic compositions of the plant and soil samples were determined on a Finnigan MAT 251 mass spectrometer.

To evaluate nutrient losses from gopher activities, soil solutions were collected by tension (35 kPa applied for 24 h) and zero-tension samplers. Throughout this report the word sampler was used to avoid the ambiguity associated with the term lysimeter (Litaor, 1988). One-hundred and eight tension samplers and 25 zero-tension samplers were installed at various depths to collect soil solutions from the humus/soil (O/A horizon) interface and the weathered parent material horizons. Soil solution samplers were left in the soil for one year before sampling began. Zero-tension samplers (ZTS) were troughs designed to collect freely flowing water (0 to –5 kPa matric potential) (Litaor, 1988). Freely flowing water within the alpine soil system is a common phenomenon during snow melt and intense summer precipitation events (Litaor, 1992). The water flux in the soil was obtained by measuring the volume collected by the ZTS divided by the surface area of the sampler. The solute flux per  $\text{m}^2$  was obtained by multiplying solute concentration by the water flux adjusted to the appropriate area size. Sampling of soil interstitial water was performed during the snow melt season (June) in 1988, 1989, 1991, and 1992.

The soil solution samplers were installed to the north (upslope) and south (downslope) each of the 25 plots (Fig. 1). To interpret differences among soil solutions, it was necessary to determine which samplers had been affected by gopher activity. The maximum radial distance for which soil solutions can be collected by the tension samplers was computed according to the equation given by Warrick and Amoozegar-Fard (1977). During the 1989 season it became clear that their equation was inadequate for our situation, probably because of the formation of macropores by the rodents. Thus, an empirical approach was adopted based on field classification of the samplers as affected (<20 cm from the center of a mound), or unaffected (>150 cm from the center of a mound) by the gopher activities. The few samplers between 20 and 150 cm from the center of a mound were classified as possibly affected and were not included in the data analysis. This classification scheme was independent of the observed solute concentrations in the interstitial waters.

Pocket gophers invaded the site in the middle of the 1987 season which complicated assessment of the rodent impact on soil solution chemistry during that summer. Therefore,

a comparison between the mound and intermound sites was carried out only for the 1988, 1989, 1991, and 1992 seasons.

Soil solutions for inorganic constituent determinations were collected in acid washed-polypropylene bottles. Conductivity and pH were determined in the field by a conductivity/pH combination meter that automatically compensates for varying temperatures. Samples for major dissolved nutrients were filtered in the laboratory through 0.45 mm Nucleopore® filters. Nutrient concentrations ( $\text{NO}_2^-$ ,  $\text{NO}_3^-$ ,  $\text{SO}_4^{2-}$ ) were analyzed by ion chromatography on a Dionex system 2110i interfaced to a Spectra-Physics SP4270 integrator. Ammonium and orthophosphate were determined colorimetrically using a Lachat flow injection analyzer.

## 4. Results and discussion

### 4.1. Physical attributes

The particle size distribution (PSD) of the mounds and intermounds are summarized in Table 2. Sand, silt, and clay contents in the intermounds varied significantly ( $P < 0.01$ ) between the genetic horizons. The Oe, A1 and A2 exhibited higher silt and clay contents compared with the 2Bw horizons. The increased silt and clay contents in the A2 horizon (Table 2) is accompanied by increased FeCBD content (241 mmol/dm<sup>3</sup> in A2, 18 mmol/dm<sup>3</sup> in Oe, 151 mmol/dm<sup>3</sup> in A1, and 154 mmol/dm<sup>3</sup> in 2Bw horizons), and probably resulted from in-situ weathering. Sand, silt, and clay contents in the mounds exhibited little variations within and between depth classes (Table 2).

Bulk density varied significantly ( $P < 0.001$ ) with depth of the intermound (Table 2), increasing from  $< 1$  g/cm<sup>3</sup> in some Oe horizons to more than 2.5 g/cm<sup>3</sup> in most 2Bw2

Table 2  
Summary statistics of particle size distribution, bulk density, and matric potential in mound and intermound soils

Depth (cm)	Sand (%)		Silt (%)		Clay (%)		Bulk density (g/cm <sup>3</sup> )		Matric potential (kPa)		
	X	SD	X	SD	X	SD	X	SD	X	SD	n
<i>Mound</i>											
0–10	71.2	0.9	17.5	1.0	11.2	0.9	0.89	0.009	41.1	18.3	9
10–20	71.7	1.2	16.7	0.9	11.5	1.0	0.96	0.02	42.6	17.0	9
20–30	70.1	1.8	18.0	1.6	12.1	0.2	1.15	0.14	43.4	16.9	9
30–40	70.6	2.0	18.8	3.5	11.8	0.5	1.3	0.16	45.8	11.6	9
<i>Intermound</i>											
Oe–A1	75.6	2.2	14.1	1.0	10.9	1.0	1.02	0.07	33.3	19.2	11
A2	71.3	2.6	15.4	1.5	13.2	1.0	1.29	0.29	36.1	18.7	11
2Bw1	79.6	4.0	12.6	2.7	7.8	2.4	1.7	0.42	38.2	17.1	11
2Bw2	83.9	7.2	11.3	4.8	4.6	2.5	2.13	0.37	33.1	20.1	11



horizons. The mean bulk density in the upper 10 cm of the mounds was significantly lower ( $P < 0.001$ ) than the Oe horizon of the intermounds. Values as low as  $0.87 \text{ g/cm}^3$  were recorded. The bulk density of the mounds increased significantly with depth, but not as much as was observed for the intermounds (Table 2).

Matric potential profiles of the mounds and the intermounds are summarized in Table 2. There was no significant differences with depth of sampling, however the mounds exhibited higher matric potential than the intermounds.

The results of the physical attributes suggested that the mixing activities of the pocket gophers homogenized the soil and strongly altered the physical attributes of the mound areas. For example, the distinct PSD with depth observed in the intermounds was completely homogenized by the digging and mixing activities of the pocket gophers. The change in bulk density and the drier conditions in the mounds increased their susceptibility to wind erosion. Volume measurements of the mounds during the summer of 1988, showed a volume decrease of one of the mounds from  $23,947 \text{ cm}^3$  to  $10,416 \text{ cm}^3$  in less than 3 months. The volume decrease also constituted a reduction in elevation of the mound by up to 12 cm. The volume change in the mounds coupled with the drier conditions may have long lasting effects on this *Carex elynoides* community in terms of species composition and extent. Moreover, the pocket gopher activity may have also impacted on this plant community for quite some time. Back-filled voids (krotovinas) were found in three soil pits out of the five excavated at the Martinelli Experiment Site prior to the current gopher invasion. Organic matter from a gopher krotovina on the Niwot Ridge, Saddle site (500 m NE of the Martinelli Site) was dated by  $\text{C}^{14}$  and found to be  $4074 \pm 170 \text{ yr B.P}$  (J. Halfpenny, unpubl. data).

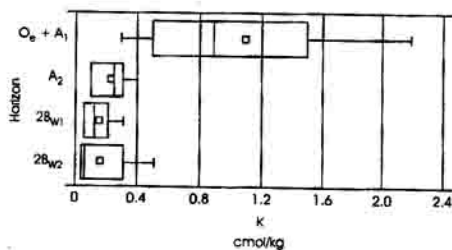
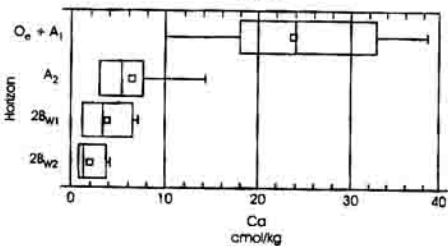
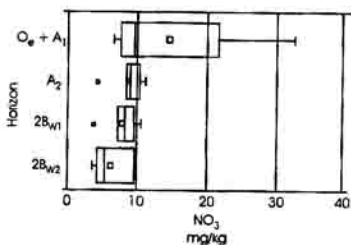
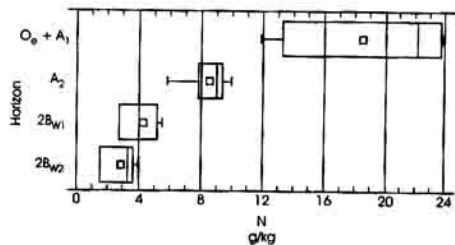
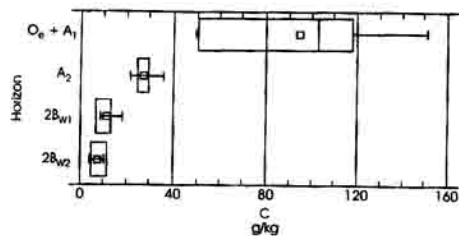
#### 4.2. Nutrient distribution

The concentrations of the major nutrients in the mounds and intermound areas are illustrated in Fig. 2. The vertical distribution of total C in the Oe and A1 horizons exhibited typical high carbon values (varied between 49.1 to 151 g/kg, with a mean of 94.8 g/kg) with sharp decrease with depth. The vertical profile of total C in the mounds showed significant lower values in the upper section of the mound (varied between 27.2 to 56.1 g/kg, with a mean of 41.0 g/kg) than the intermounds and more homogeneous distribution with depth (Fig. 2). The concentration of total N in the Oe and A1 horizons varied between 11.9 and 23.9 g/kg, with a mean of 18.6 g/kg and also exhibited sharp decrease in total N with depth. The vertical profile of total N in the mounds showed significant lower values in the upper section of the mound (varied between 2.7 to 4.2 g/kg, with a mean of 3.3 g/kg) than the intermounds and more homogeneous distribution with depth (Fig. 2). Similar vertical distributions were observed for exchangeable Ca and K (Fig. 2).

The concentrations of  $\text{NO}_3^-$  in the mounds varied between 17 to 78.5 mg/kg with a mean of 44.8 mg/kg (Fig. 2). A further increase in  $\text{NO}_3^-$  concentrations was observed with depth of the mounds, where the concentration of  $\text{NO}_3^-$  at the 10 to 20 cm sampling interval varied between 31 to 81 mg/kg with a mean of 54.5 mg/kg. The concentrations of  $\text{NO}_3^-$  in intermound soils varied between 6.0 to 32.9 mg/kg with a mean of 14.3 mg/kg. Because plant and microbial communities inhabiting the alpine tundra appear to be nitrogen limited (Shulls and Mancinelli, 1982; Mancinelli, 1984; Mancinelli, 1986; Jaeger and Monson, 1992; Bowman et al., 1993), available  $\text{NO}_3^-$  in the soil is rapidly utilized by the microbial



## Intermound Soils



## Mound Soils

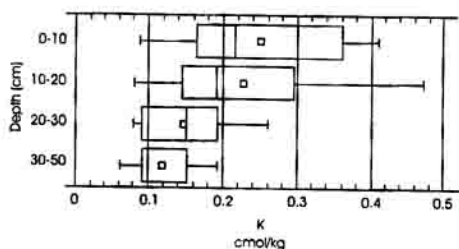
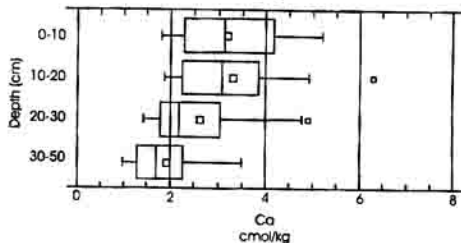
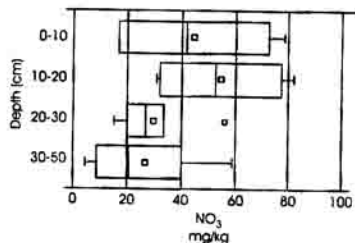
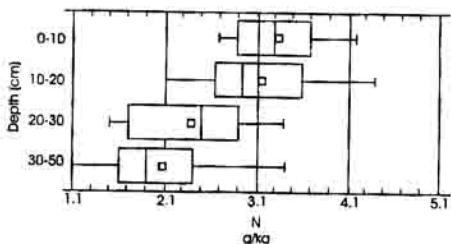
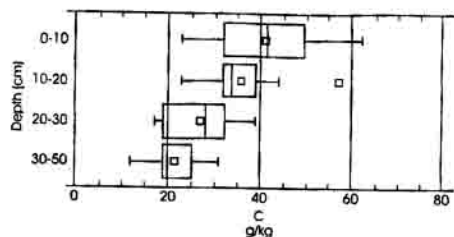


Fig. 2. The concentration of selected nutrients in mound and intermound soils. The boxplot depicts the limits quartiles, median ( $\mid$ ), mean ( $\square$ ), and outliers.

community (Mancinelli, 1986). This was reflected by the low level of available  $\text{NO}_3^-$  in the intermound soils (Fig. 2). In contrast, the mounding and mixing activities of the pocket gophers have substantially increased the concentrations of available  $\text{NO}_3^-$  throughout the mounds. The increase of available  $\text{NO}_3^-$  associated with gopher activity greatly affected the nitrogen cycling rates in the mound soils. For example, Mancinelli and White (1989) showed that the biological fixation rate of  $\text{N}_2$  was reduced by approximately 90% on a yearly basis, from  $\sim 7 \text{ mg N fixed/m}_2/\text{yr}$  in intermound to  $< 1 \text{ mg N fixed m}^{-2} \text{ yr}^{-1}$  in mounds. With the decrease in biological  $\text{N}_2$  fixation, plant and microbial communities must rely on available  $\text{NO}_3^-$  in the soil as their primary N source.

Further evidence of reduced biological N fixation within the mounds was found by comparison of natural  $^{15}\text{N}$  abundances in plants and soils from mound and intermound sites (Table 3). The mean  $\delta(^{15}\text{N})$  value for the only known N-fixing plant species at the study site (*Trifolium parryi*) was fairly similar to that for the non-fixers on the intermound soils. In contrast, the  $\delta(^{15}\text{N})$  value of the non fixer (*Achillea lanulosa*) on the mound was  $\sim 3.4\%$  heavier in its isotopic N composition than the same species on the intermound soils. This shift in  $\delta(^{15}\text{N})$  value suggests that the major source of N for the non-fixing plants on mounds was derived from the soil. There are two plausible explanations for the observed shift in  $\delta(^{15}\text{N})$ . First, soil mixing by the gophers brought to the surface mineralized soil horizons with higher  $\delta(^{15}\text{N})$  values (Table 3). Second,  $^{15}\text{N}$  fractionation occurred due to enhanced nitrification rates in the well aerated mound soils. The latter interpretation is partially supported by 50 percent decrease in denitrification rates (Mancinelli and White, 1989) and significant enrichment of  $\text{NO}_3^-$  in the mound soils (Fig. 2).

Mielke (1977) studied the biogeochemical effects of mound building on the fertility of an alpine soil along the Uncompahgre Plateau in western Colorado. He found that gopher mounds contained higher concentrations of total K, Mg and organic carbon than the intermound soils. These findings contrast those of the present study. Contradictory results have

Table 3  
The  $^{15}\text{N}/^{14}\text{N}$  ratios for *Trifolium parryi* (N-fixer), *Achillea lanulosa*, humus layer and mineralized horizons in mound and intermound sites

Location	$\delta^{15}\text{N}/^{14}\text{N}$		n
	X	SD	
<b>Mound</b>			
<i>Trifolium parryi</i>	-0.07		a
<i>Achillea lanulosa</i>	2.4		a
Surface soil	4.4	0.3	3
<b>Intermound</b>			
<i>Trifolium parryi</i>	-0.8	0.1	2 <sup>b</sup>
<i>Achillea lanulosa</i>	-1.0	0.2	2 <sup>b</sup>
Humus (Oe horizon)	0.0	0.5	5
Mineralized horizon (A1)	3.2	0.3	5
Mineralized horizon (2Bw)	4.4	0.3	5

<sup>a</sup>Samples consisted of all the individual plants in 3 mounds.

<sup>b</sup>Samples contained more than 13 plants for *Trifolium parryi* and 60 plants for *Achillea lanulosa* in two replicates.

been reported for studies of nutrient distributions within mound and intermound soils of different ecosystems or even within the same ecosystem (Huntly and Inouye, 1988). Although the reasons for these inconsistencies are currently unknown, the pre-disturbance soil conditions and the disturbance history of each site are likely reasons for the cited contradictory results.

#### 4.3. Soil solutions

Freely flowing water (0 to 5 kPa) that was intercepted by the zero-tension samplers showed no significant differences in volume and specific conductance values between mound and intermound sites (Table 4). However, the mean leaching rates of  $\text{NO}_3^-$  were significantly greater ( $P < 0.05$ ) at the mound soils than the intermound sites (Table 4). Freely flowing water is usually characterized by short residence times in the alpine soil (Litaor, 1992). Hence, these nitrogen fluxes represent a pulse of nitrogen concentration that leave the soil system. The increased nitrogen fluxes in the mounds probably resulted from the higher available  $\text{NO}_3^-$  content in soils affected by the mixing activity of the pocket gophers (Fig. 2). The highest leaching rates were observed in early and mid June which is the end of the snowmelt season, when plant uptake is still somewhat limited.

Nutrient concentrations in soil interstitial water flowing at matric potentials greater than gravitational force ( $-5$  to  $-40$  kPa) are summarized in Table 5. These soil solutions are usually characterized by longer residence time in the soil and exhibited increased concentrations of  $\text{NH}_4^+$  in the intermound soils compared to mound soils. The reverse distribution

Table 4  
Summary statistics of  $\text{NO}_3^-$  leaching rate, volume and specific conductance recorded at gopher mound and intermound sites

Location	$\text{NO}_3^-$ <sup>a</sup> (mg m <sup>-2</sup> week <sup>-1</sup> )			Volume (ml)			Spec. conductance (S/m)		
	X	Range	SD	X	Range	SD	X	Range	SD
Mounds ( $n=55$ )	35.4	0.03–332	56	525	12–1200	351	2.7	0.4–7.6	1.3
Intermound ( $n=46$ )	16.8	0.04–113	25	544	4–1000	323	2.4	0.2–5.0	1.3

<sup>a</sup>Kruskal Willis test = 3.36,  $P < 0.05$ .

Table 5  
Summary statistics of nutrients concentrations in soil solutions collected at matric potential of  $-5$  to  $-40$  kPa

Location	$\text{NH}_4^+$ <sup>a</sup> ( $\mu\text{g/l}$ )			$\text{NO}_3^-$ <sup>a</sup> (mg/l)			Spec. conductance (S/m)		
	X	Range	SD	X	Range	SD	X	Range	SD
Mounds ( $n=53$ )	23.0	0.7–87	23.8	1.66	0.01–20	3.9	17.2	1.0–63	9.2
Intermound ( $n=41$ )	34.1	0.6–109	31.8	0.58	0.01–5	1.1	17.3	3.8–50	10

<sup>a</sup>Represents significance level of 0.01.

was observed for  $\text{NO}_3^-$  (Table 5). Ammonium is the nitrogen ion preferred by many organisms and plants in soils (Paul and Clark, 1989). If not immediately assimilated by the soil biota the  $\text{NH}_4^+$  will be subjected to volatilization, nitrification, and fixation by clays and organic matter. Mixing by gophers creates well aerated areas which probably enhance volatilization and nitrification and thus minimize the concentration of  $\text{NH}_4^+$  and increase  $\text{NO}_3^-$  in soil solutions. If nitrogen is a limiting nutrient for microbes in this system (Mancinelli, 1986), then microbial activity will increase significantly with the increased availability of  $\text{NH}_4^+$ . The rate of fixed nitrogen assimilation by the microbiota is relatively rapid, and its effects on the microbial community can be detected within 1–3 days (Mancinelli, 1986). If the leaching rate of  $\text{NH}_4^+$  and  $\text{NO}_3^-$  is less than the assimilation rate of  $\text{NH}_4^+$  then the majority of the available  $\text{NH}_4^+$  will be assimilated rather than leach through the system. This will tend to increase the organic-N content and may aid in recolonization of the mounds by plants.

## 5. Conclusions

Pocket gophers have been instrumental in altering the physicochemical environment of the alpine tundra. The mixing activities of the gophers lowered the concentrations of total C, N, exchangeable Ca, and K in the mounds compared with the surface horizons of the intermounds. Nitrate and ammonium distribution in soil and soil interstitial water suggested that the pocket gophers greatly increased N cycling rates and enhanced the nitrification rates in well-aerated soils. These findings provide further evidence for the role of gophers as keystone species in ecosystems and in particular as important geomorphic agents in alpine tundra.

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