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Effects of Gray-tailed Vole Activity on Soil Properties

Abstract

Voles are well-known crop pests, especially when peak populations are present, but their role in soil fertility and impacts on agricultural sustainability are not well understood. Five months after the abrupt disappearance of a peak in a gray-tailed vole (*Microtus canicaudus*) population, we examined burrow structure, determined concentrations of trace elements, carbon and nitrogen in the soil immediately surrounding vole burrows, and compared soil chemical properties to a depth of 90 cm between areas with prior vole activity and areas of no activity. Vole tunneling activity was confined to the top 10 cm of the soil profile and was coincident with the majority of root biomass. Soil NH_4^+, NO_3^-, extractable organic carbon, and soil organic matter were greater below vole tunnels than above; however, due to small sample sizes, differences were not significant. There were no differences in trace elements with respect to position around vole tunnels. Vole activity was associated with increased soil nitrate concentrations and decreased soil pH to a depth of 90 cm, indicating that nitrification might be enhanced by vole activity, and that this effect continues after vole populations crash. Greater inorganic nitrogen could have long-term effects on ecosystem productivity. The effects voles have on soil processes that influence carbon and nutrient cycle requires further investigation.

Introduction

Soil is the product of both biotic and abiotic processes, including the actions of soil-dwelling animals. Although invertebrates make up the greatest biomass of animals in soil, fossorial vertebrates such as gophers, voles and mice have been recognized for their role in soil mixing and nutrient enhancement (Grinnell 1923, Hole 1981, Huntley and Reichman, 1994, Pastor et al. 1996, Reichman and Seabloom 2002, Bakker 2003, Clark et al. 2005). Small herbivorous mammals can play an important role in the nutrient cycling of an ecosystem by increasing the rate of release of carbon and nutrients tied up in plant biomass. The nutrients stored in their fecal matter can turn over rather quickly; the mean residence time of fecal nitrogen of meadow voles and red-backed voles ranged from only 0.7 to 1.5 weeks (Pastor et al. 1996). High densities of burrowing rodents have been associated with high soil nitrate concentrations (Jorgensen 2002) and nitrogen mineralization rates (Bakker 2003). Clark et al. (2005) found that the fecal and urinary nitrogen output of small rodents in perennial grassland represented a flux of 3.7 kg nitrogen ha^{-1} yr^{-1} and Bakker (2003) estimated vole fecal outputs to amount to as much as 47 kg nitrogen ha^{-1} yr^{-1}. These animals can add to local soil fertility not only through their excretion of wastes but also through storage of food caches and nesting materials (Woodmansee 1978). In addition to direct nutrient inputs, they can indirectly affect soil nutrient cycling by changing plant community composition (Canals et al. 2003, Howe et al. 2006) and/or by changing the microclimate of soils (Bakker 2003). Sirotnak and Huntly (2000) showed that although voles increased nitrogen mobility during and right after population peaks, over the long term, nitrogen mineralization decreased on these sites. They found that selective herbivory of plants with high nitrogen content created plant communities with lower carbon-to-nitrogen ratios. The burrowing action of these animals can loosen and increase the aeration status of the soil (Bakker 2003), which can significantly affect the rate of soil processes such as nitrogen mineralization.

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Voles are small, herbivorous, fossorial rodents best known for their tendency to fluctuate in numbers by several orders in magnitude within a relatively short period of time (Elton 1942, Hornfeldt et al. 1986, Lambin et al. 2000, Korpimaki et al. 2004). Although they feed extensively aboveground, some vole species frequently excavate and maintain extensive burrow networks. They use these networks for travel to foraging areas (Liro 1974), nesting, and storing food. Voles do not move the large volumes of soil that gophers do, and it appears that burrow networks are maintained by generations of voles and thus may be semi-permanent features of the soil profile. Excavations of these burrows have revealed a complex, interconnected network that can span an area up to 4 m^2 and to depths ranging from 5 to 20 cm (Cassidy 2002; the authors, unpublished data). Some parts of the network have been associated with regions of low bulk density, highly aggregated soil, and greater densities of burrows created by invertebrates such as earthworms (Cassidy 2002). The degree to which soil texture and/or plant root depth might control burrow depth is still under investigation.

Voles can also influence the hydrology of the sites they colonize. Their runways and tunnels intercept surface runoff and redirect flow to burrow entrances, increasing infiltration of water into the soil profile (Cassidy 2002). Greater infiltration of water was noted in soil adjacent to ground squirrel burrows, with burrow density increasing the amount of water retained in the soil profile (Laundré 1993). The role that the presence of voles may play in the hydrologic and biologic soil function is complicated by the dramatic population fluctuations that these mammals frequently undergo. In western Oregon, the gray-tailed vole (*Microtus canicaudus*) may reach densities of thousands of individuals per ha (Edge et al. 1995). Burrow densities in excess of 10 entrances per m^2 were recorded during the 2005 irruption of gray-tailed voles in the Willamette Valley, Oregon (J. A. Gervais, Oregon State University, unpublished data). As is characteristic of these outbreaks, local populations within the Willamette Valley underwent abrupt declines during the winter and spring of 2006. In many areas, voles had apparently completely disappeared; however, their burrows remained intact in some areas for at least a full year following the population crash.

This study was conducted in a perennial grass system in the Willamette Valley to better understand vole burrow structure and the impact that vole activity has on soil moisture and chemical properties. It was performed in the spring of 2006, five months after the abrupt disappearance of a gray-tailed vole population following a significant irruption. This irruption was particularly noteworthy due to the millions of dollars of losses to the grass seed, plant nursery, and wine industries. Based on other fossorial mammals' impacts on nutrient cycling and carbon and nitrogen availability, we hypothesized that concentrations of soil carbon, nutrients, trace elements, and moisture would be greater directly below vole burrows than above or away from the burrows. We also hypothesized that soil that had supported vole populations would have greater amounts of soil organic matter, greater concentrations of carbon and nitrogen, and greater soil moisture than soil with no vole activity. The objectives of this study were therefore to: (1) examine vole burrow structure in a perennial grassland system; and (2) explore the influence of burrows on pH, organic matter and carbon, soil moisture, and soil nutrients.

Methods

Research was conducted at the Oregon State University Hyslop Field Research Laboratory located in Benton County, Oregon, U.S.A. (44° 38′ N, 123° 11′ W) on the well-drained Woodburn silt loam (fine-silty, mixed, superactive, mesic Aquultic Argixerolls). The study site included 24 gated enclosures made of metal flashing extending approximately 1 m above and below ground to prevent voles from immigrating or emigrating. Each enclosure was 45 x 45 m (0.2 ha). The enclosures were installed in the early-mid 1990s and were used in previous studies of gray-tailed vole population biology and behavior (Edge et al. 1995, Wolff et al. 1997, Wang et al. 2001). Enclosures were planted with mixed pasture grasses in the early 1990s, including fawn tall fescue (*Festuca arundinacea*), perennial ryegrass (*Lolium perenne*), annual ryegrass (*Lolium multiflorium*), and Potomac orchardgrass (*Dactylis glomerata*) (Wang et al. 1999). Annual grasses and weedy herbaceous plants became established and currently dominate the vegetation. Following completion of a series of projects in 2000, the enclosures have been mowed annually and spot-treated for woody invasive weeds such as blackberry (*Rubus armeniacus*). They have otherwise remained undisturbed and with their gates open since 2000, allowing animals to move in and out of the enclosures. Vole populations within the enclosures therefore have been free to fluctuate in conjunction with those in the region, and clearly reached very high densities in the fall of 2005. Signs of living voles disappeared entirely by February 2006 (J. A. Gervais, Oregon State University, unpublished data).

Three field studies were performed in May 2006. One examined vole burrow structure, another analyzed soil chemical properties in the immediate vicinity, above and below vole burrows, and the third measured differences in soil chemical properties from the surface to a depth of 90 cm between an area of previous vole activity and an area devoid of vole activity.

Burrow Structure Study

In May 2006, we selected an area within an enclosure with a very high density of vole burrows for a study of burrow structure. We mixed approximately 135 liters of plaster of Paris to a thin consistency following Cassidy (2002) and poured it into a series of burrows within 5 m of each other. Burrows were filled until no additional plaster could enter the system and began to pool upon the surface. The plaster was allowed to set for several days. A backhoe then excavated an access trench along the side of the plot allowing the excavation of burrow systems by hand tools. Working in the direction of the plaster-filled burrow systems, soil was carefully removed by hand in 10-cm increments to the depth of the burrow network. The plaster casts of excavated burrows were photographed and measured for depth from the surface, diameter and the presence or absence features such as nesting burrows and food caches.

Burrow Vicinity Study

Twelve soil samples were collected as the plaster burrows were being excavated to determine if there were relationships between soil nutrients and proximity to vole burrows. Four soil samples were taken directly above (within 5 cm) a burrow and five were taken from directly below (within 5 cm) a burrow. Additional samples were collected at a distance of 25 cm from a burrow in soil that appeared to be undisturbed. Two of these samples were collected "below and away" from the burrow and one was collected "above and away" from the burrow. All samples were stored in plastic bags at 4 °C prior to analysis.

Soil samples collected from the burrow vicinity study were analyzed for a series of trace elements as well as other chemical constituents. The concentrations of total Al, B, Ba, Ca, Cu, Fe, K, Mg, Mn, P, S, Si, and Zn in soil were determined by microwave-assisted HF/HNO_3 acid digestion (EPA method 3052) using an Ethos D microwave station (Milestone Inc., Monroe, CT) and subsequent analysis on an inductively coupled plasma optical emission spectrometer (ICP-OES) (Perkin-Elmer Life and Analytical Sciences, Shelton, CT). Soil samples were also analyzed for extractable total N (ETN), extractable organic carbon (EOC), nitrate-N (NO_3^-), ammonium-N (NH_4^+), percent soil organic matter (SOM), moisture concentration, and pH. Soil samples (25 g) were extracted with 100 mL of 0.5 M K_2SO_4 and shaken for 30 min at 350 rpm. After shaking, samples were allowed to settle and were then filtered through Whatman Qualitative No. 1 filters (Florham Park, NJ) that had been washed 3 times with 1% H_2SO_4 (v/v) and 0.5 M K_2SO_4. Soil ETN and EOC concentrations were determined on the soil extracts using a Shimadzu total organic C analyzer with a total N analyzer attachment (Shimadzu Scientific Instruments Inc., Baltimore, MD). The filtrate was also analyzed colorimetrically for NO_3^- (QuickChem method 12-107-04) and NH_4^+ (QuickChem method 12-107-06) on a Lachat flow injection autoanalyzer (Hach Co., Loveland, CO). Soil organic matter was determined by loss on ignition at 500 °C after 4 h. Soil gravimetric moisture concentration, or percentage water to soil, was determined after drying 25 g of soil for 24 h at 105 °C. Soil pH was determined on a 1:2 soil/H_2O slurry using a pH meter equipped with a glass-body electrode (HANNA Instruments, Inc., Ann Arbor, MI).

Soil Profile Study

Five additional enclosures were chosen randomly for a study on the effects of vole activity on soil nutrient chemistry to a depth of 90 cm. Within each enclosure, an area of 1 m^2 with no burrow entrances was identified by following a random compass bearing until such a spot was encountered. If the enclosure edge was encountered first, then a new compass bearing was randomly chosen and the process repeated until a suitable plot was found. In addition, a 1 m^2 plot with the greatest density of burrow entrances was identified and marked within each enclosure. Two soil depth cores (3.2 cm diameter), were collected from 0 to 90 cm in each of the paired plots using a JMC Environmental soil probe (ESP-Plus, Clements Associates, Newton, IA) for a total of four cores per enclosure. Cores were capped and stored in their plastic sheaths at 4 °C prior to processing. These intact soil cores were divided into the following depths: 0 to 5, 5 to 10, 10 to 15, 15 to 30, 30 to 60, and 60 to 90 cm. Soil samples from each depth class were homogenized and subsamples were analyzed in a manner similar to the samples from the burrow vicinity study for ETN, EOC, NO_3^-, NH_4^+, SOM, moisture concentration, soil pH and conductivity.

Statistical Analyses

No statistics were calculated for the first study, that of burrow structure. Geometric means and 90% confidence intervals (Zar 1984) were calculated for comparison of trace elements and other properties of soil samples collected from the second study, the burrow vicinity study. Small sample sizes precluded further analyses and no statistical comparisons were performed.

For the third study, paired t-tests were performed on the differences in ETN, EOC, NO_3^-, NH_4^+, SOM, moisture concentration, soil pH and conductivity between vole and no-vole soil cores collected from each enclosure for each depth class (0-5, 5-10, 10-15, 15-30, 30-60, and 60-90 cm). Original data for all variables except pH were log-transformed to improve data distribution and equalize variances. Median differences between vole and no-vole plots and 90% confidence intervals were calculated from the transformed data for each of the five pairs of cores for each depth class (Ramsey and Shafer 1997). The back-transformed median difference is an indication of how many times greater the vole values were than the no-vole values. We calculated *P*-values for these comparisons according to Ramsey and Schafer (1997) and selected P=0.10 as the alpha level given the small sample sizes and desire to minimize Type II errors.

Results

Burrow Structure Study

Plaster of Paris proved to be a very effective tool to visualize and evaluate the structure of the vole burrow systems. Average burrow diameter was approximately 3 cm and most burrows appeared to be compressed and somewhat rectilinear in cross section. The maximum depth of a burrow was 10 cm and length varied between roughly 10 to 100 cm before reaching the surface again. One excavated burrow network covered an approximate area of 2 m^2 and another network covered 1 m^2. Burrows were shallower than seen at the study site of Cassidy (2002) and appeared to be coincident with the rooting depth of field grasses and close to the depth (8 cm) at which there was a significant increase in clay content of the soil from 20 to 34% (William Austin, Dept. Crop and Soil Science, Oregon State University, personal communication). Burrows appeared at two distinct depths, 5 and 10 cm. Some burrows progressed to a depth of approximately 5 cm for about 50 cm then suddenly dropped to a 10 cm depth for another 50 cm. Only one burrow was seen to go up at an incline and it was not clear if a new outlet was being dug. No food caches or nests were located.

Burrow Vicinity Study

We hypothesized that soil moisture would be highest in the “below” compared to the “above” or “away” positions due to preferential flow of precipitation and surface water into burrows. Mean soil moisture was roughly 25% greater in the “below” position. We also hypothesized that soil organic matter, carbon and nitrogen would be significantly greater in the “below” position due to the accumulation of vole waste/nest/food products in the soil below their activity. Soil NH_4^+, NO_3^-, ETN, EOC, and SOM were consistently greater in the “below” position; however, there were no clear differences for these variables (Table 1). There were also no obvious differences in pH among positions. The small sample size in this study and the high natural heterogeneity of soil likely contributed to the lack of discernable pattern in cases (NH_4^+, NO_3^- and ETN) where differences may have been detectible with increased sample size. Values for trace elements in this part of the study (Table 2) were within ranges reported in the literature (Bowie and Thornton 1985, Stevenson and Cole 1999). Unlike the carbon and nitrogen data, there were no consistent trends between position and concentrations of trace elements. In fact, there were only two instances where confidence intervals did not overlap: Ca in the “above” posi-

TABLE 1. Geometric means and 90% confidence limits (in parentheses) of soil parameters from the vole burrow vicinity study. “Above” refers to soil samples taken within 5 cm above burrows, “below” refers to soil samples taken from within 5 cm below burrows, samples from “above away” were taken 25cm above a burrow and “below away” were taken 25 cm below a burrow. Units are mg N kg^{-1} dry soil for nitrate (NO_3^-), ammonium (NH_4^+), and extractable total nitrogen (ETN), mg C kg^{-1} dry soil for extractable organic carbon (EOC) and percentages for soil organic matter (SOM) and gravimetric soil moisture (GSM).

Soil Parameter	Above (n=4)	Below (n=5)	Above Away (n=1)	Below Away (n=2)
pH	5.34 (5.17-5.52)	5.55 (5.27-5.83)	5.60	5.67 (4.33-7.01)
NH_4^+ (mg/kg)	1.32 (0.84-1.81)	13.1 (-10.8-37.0)	1.36	1.10 (1.00-1.20)
NO_3^- (mg/kg)	0.84 (0.70-0.99)	1.17 (0.69-1.65)	0.96	0.90 (0.24-1.55)
ETN (mg/kg)	8.49 (6.84-10.2)	18.0 (-1.58-37.6)	8.42	7.71 (5.94-9.48)
EOC (mg/kg)	54.3 (49.0-59.7)	67.5 (48.1-86.9)	60.6	54.2 (42.6-65.8)
SOM (%)	3.64 (2.81-4.47)	3.91 (3.38-4.44)	3.28	3.19 (2.21-4.18)
GSM (%)	16.1 (15.1-17.2)	21.5 (19.7-23.3)	14.7	16.3 (13.0-19.6)

TABLE 2. Geometric means and 90% confidence limits (in parentheses) of soil trace elements from the burrow vicinity study. “Above” refers to soil samples taken within 5 cm above burrows, “below” refers to soil samples taken from within 5 cm below burrows, samples from “above away” were taken 25 cm above a burrow and “below away” were taken 25 cm below a burrow. Units are in mg kg^{-1} soil.

Trace Element	Above (n=4)	Below (n=5)	Above Away (n=1)	Below Away (n=2)
Aluminum	25069 (24506-25632)	24715 (23793-25691)	25435	25778 (20174-31381)
Barium	225 (217-233)	229 (223-236)	242	234 (206-262)
Boron	336 (118-553)	302 (111-494)	637	575 (-71-1221)
Calcium	5534 (4510-6558)	5814 (4331-7296)	4381	4391 (4301-4481)
Copper	14 (13-16)	14 (13-15)	14	16 (14-17)
Iron	29420 (28731-30109)	28750 (28022-29478)	30225	30128 (25282-34973)
Magnesium	5422 (5317-5527)	5335 (5206-5463)	5559	5533 (4658-6407)
Manganese	1213 (1141-1286)	1110 (1048-1171)	1189	1183 (1096-1270)
Phosphorus	1431 (1339-1522)	1488 (1403-1572)	1355	1356 (1314-1397)
Potassium	4008 (3927-4088)	4196 (3864-4528)	4547	4010 (3252-4768)
Sulfur	2817 (1637-3998)	3239 (2726-3753)	1298	2682 (1688-3676)
Silicon	1763 (1495-2031)	1769 (1605-1932)	2146	1976 (361-3590)
Zinc	116 (113-119)	117 (114-121)	110	118 (107-129)

tion was greater than “below away” and P in the “below” position was greater than “below away”. It is difficult to say if these differences are due to vole activity or to depth in the soil profile because of the confounded nature of depth and position in relation to vole tunnels.

Soil Profile Study

The effects of vole activity on soil characteristics varied by parameter and by depth (Table 3). There were no significant differences in gravimetric soil moisture (GSM) between the vole and no-vole plots at any depth (Figure 1). GSM was moderate (24-25%) in the surface soil (0-5 cm) and decreased to 21% at 10 to 15 cm. Below this depth, soil moisture increased with depth with the maximum GSM of 30% occurring at 90 cm. Soil profile GSM was representative of what might be expected in May, a time of year in the Willamette Valley when the water table is still relatively high (< 1 m) at the end of the seasonal wet period. Moisture data from Davis et al. (2008) showed that 30% GSM in the

TABLE 3. Ratios (and ranges) of differences between vole plots and no-vole plots for soil profile characteristics including pH, NH_4^+, NO_3^-, total nitrogen (TN), total carbon (TC), organic matter (OM) and soil moisture. Ratios were back-transformed from the logged mean differences. The variable pH was not transformed as it already represents a log value. The back-transformed median difference is an indication of how many times greater the vole values were than the no-vole values. Negative differences indicate the no-vole plot values were greater than the vole plots. The 90% confidence intervals for the ratios are in parentheses. Sample size is five pairs of cores in all cases. Letters represent significant differences between vole and no-vole plots (*a* significant at $P \leq 0.05$; *b* significant at $P \leq 0.10$).

Depth (cm)	pH	NH_4^+	NO_3^-	TN	TC	OM	Moisture
0-5	-0.14	1.28^b	2.89^a	1.13	0.93	1.01	0.96
	(-0.28-0.01)	(1.01-1.63)	(1.35-6.21)	(0.94-1.36)	(0.84-1.03)	(0.95-1.08)	(0.89-1.04)
5-10	-0.23^b	1.13	2.71^a	1.26^b	1.04	0.99	0.99
	(-0.43-(-0.02))	(0.98-1.31)	(1.41-5.24)	(1.01-1.57)	(0.97-1.11)	(0.92-1.07)	(0.92-1.05)
10-15	-0.30	1.09	2.17^a	1.22	1.05	0.97	0.98
	(-0.71-0.110)	(0.44-2.70)	(1.50-3.16)	(0.89-1.66)	(0.96-1.16)	(0.88-1.08)	(0.94-1.02)
15-30	-0.46^a	0.84	2.25^a	1.20^b	1.07	0.96^b	1.00
	(-0.80-(-0.12))	(0.50-1.41)	(1.51-3.37)	(1.00-1.43)	(0.93-1.24)	(0.93-0.99)	(0.97-1.03)
30-60	-0.37^b	1.49	1.79^a	1.33	1.00	0.99	0.99
	(-0.71-(-0.04))	(1.01-2.21)	(1.17-2.73)	(0.99-1.78)	(0.90-1.12)	(0.90-1.09)	(0.97-1.02)
60-90	-0.08	1.12^b	1.60^a	1.24^a	1.06	0.97	1.00
	(-0.41-0.26)	(1.00-1.25)	(1.13-2.26)	(1.08-1.43)	(1.00-1.12)	(0.89-1.05)	(0.97-1.03)

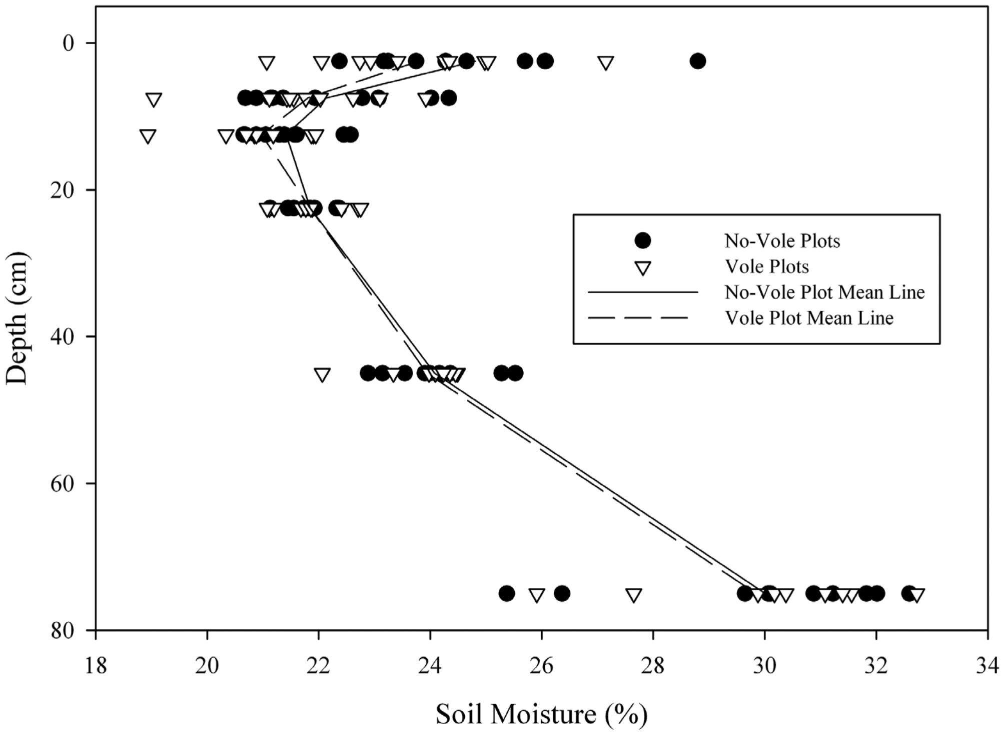

Figure 1. Relationship between soil moisture and soil depth in plots with and without vole activity in the Willamette Valley, Oregon in May 2005. Lines connect means for each soil depth class (0-5, 5-10, 10-15, 15-30, 30-60, and 60-90 cm). Differences between no-vole and vole plots were not significant at any depth ($P > 0.10$). Raw untransformed data are presented.

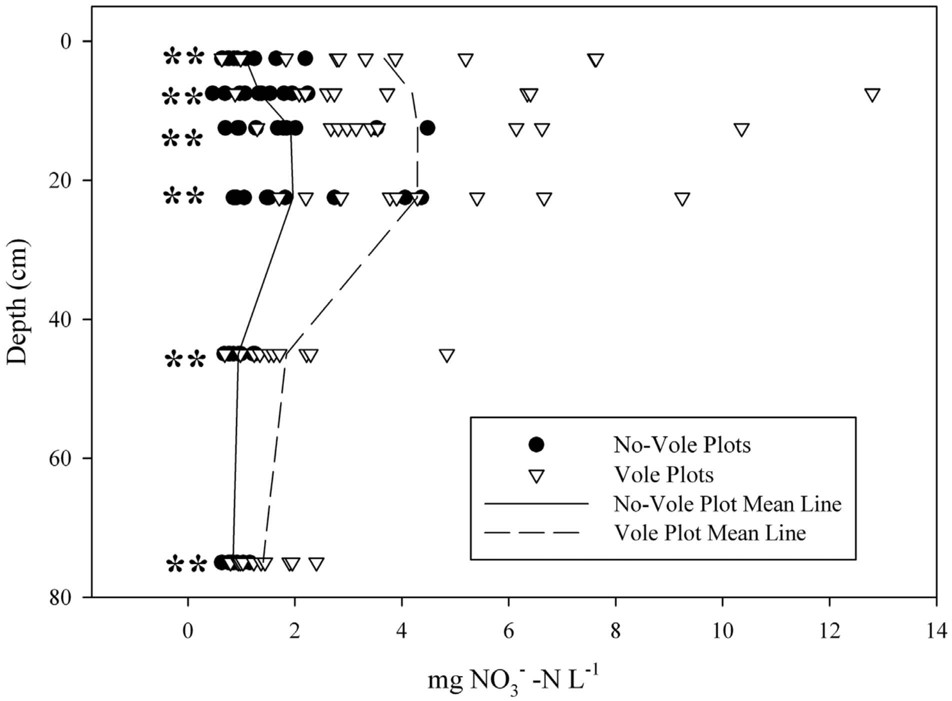

Figure 2. Relationship between soil depth and soil NO_3^- in plots with and without vole activity in the Willamette Valley, Oregon in May 2005. Lines connect means for each soil depth class (0-5, 5-10, 10-15, 15-30, 30-60, and 60-90 cm). Differences between no-vole and vole plots were significant at all depths ($P \leq 0.10$). The untransformed raw data are presented. Significance is denoted at $P \leq 0.10$ by * and at $P \leq 0.05$ with **.

subsoil of a poorly drained Holcomb soil in same region indicated saturated conditions (water table) whereas the surface was saturated at 40 to 50% GSM. Data from the present study indicated that some drying out of the surface soil had occurred (21-25%) at the time of sampling creating similar moisture conditions within the surface soil of the vole and no-vole plots.

The most consistent trend in the study was in soil nitrate. Soil NO_3^- concentrations were consistently greater in the vole plots compared to the No-Vole plots at all depths (Figure 2). Concentrations of NO_3^- were generally greater in the surface soils (< 30 cm) than in the subsoil. Nelson et al. (2006) showed that the seasonality of precipitation in the Willamette Valley was related to relatively predictable patterns of soil NO_3^- concentrations. Soil NO_3^- tends to be highest in fall after soil nitrogen has been mineralized and nitrified over the warm dry summer. Soil NH_4^+ concentrations ranged from 0.54 to 3.37 mg nitrogen kg^{-1} with the only difference occurring in the surface soil (0-5 cm; $P = 0.09$) where the vole plots had greater concentration than the no-vole plots. Extractable total nitrogen (ETN) is a measure of both inorganic and organic forms of soil nitrogen. Concentrations of ETN decreased with depth and were significantly greater in the vole (3.5 mg N kg^{-1}) compared to the no-vole (2.8 mg N kg^{-1}) plots at the 60 to 90 cm depth ($P = 0.03$). However, after subtracting inorganic nitrogen (NO_3^- and NH_4^+) concentrations from ETN concentrations at this depth, it became evident that the organic fraction of ETN was quite similar between the vole and no-vole plots (1.5 mg N kg^{-1}). Therefore, differences in ETN at this depth were due to differences in inorganic nitrogen rather than organic nitrogen.

Soil pH was significantly greater in the no-vole compared to the vole plots at depths of 5 to 10 cm ($P = 0.08$), 15 to 30 cm ($P = 0.05$), and 30 to 60 cm ($P = 0.08$) (Figure 3). Values of pH were within range of those reported for a nearby Woodburn soil (5.2) by Nelson et al. (2006).

There were no significant differences in EOC at any depth between the vole and no-vole plots ($P > 0.10$). Extractable organic carbon decreased

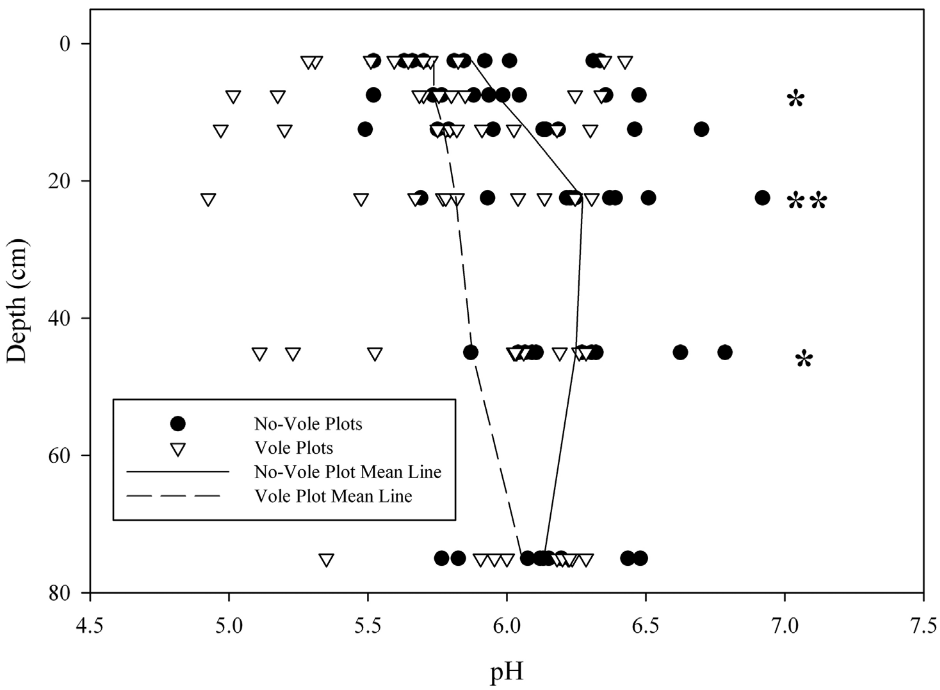

Figure 3. Relationship between soil depth and soil pH in plots with and without vole activity in the Willamette Valley, Oregon in May 2005. Lines connect means for each soil depth class (0-5, 5-10, 10-15, 15-30, 30-60, and 60-90 cm). Differences between no-vole and vole plots were significant at depths 15-30 cm and 5-10 cm and 30-60 cm ($P \leq 0.10$). The untransformed raw data are presented. Significance is denoted at $P \leq 0.10$ by * and at $P \leq 0.05$ with **

from the surface (76.3 mg C kg soil^{-1}) to a depth of 30 cm (55.3 mg C kg soil^{-1}) and was relatively constant (51-57 mg C kg soil^{-1}) from 30 to 90 cm. Surface soil levels of EOC were close to those reported for a perennial ryegrass seed cropping system soil (0-15 cm; 65.2 mg C kg soil^{-1}) in the Willamette Valley (Davis et al., 2008). Soil organic matter (SOM) ranged from 4.7% in the surface (0-5cm) soil to 3.1% in the subsoil (> 30 cm). The only significant difference in SOM was at 15 to 30 cm where the no-vole plots had greater SOM than vole plots ($P = 0.06$).

Discussion

Vole activity was associated with significantly increased soil nitrate concentrations to a depth of 60-90 cm in the present study. This trend is consistent with other studies showing greater soil nitrate with greater densities of rodents (Jorgensen 2002, Clark et al. 2005) and increased nitrogen mobility during and after population peaks (Sirotnak and Huntly 2000). Voles increased nitrification rates 1.5 times (Bakker 2003), due to the addition of feces and urine to the soil and changes in microclimate factors such as aeration and temperature (Pastor et al. 1996, Baker 2003, Martin 2003).

Because nitrogen is normally a limiting nutrient for plant growth in most unmanaged ecosystems, the availability of nitrogen for plant uptake could impact plant community structure. Studies have shown that plant communities with greater nutrient availability tend to have lower diversity (Hart 1994). Greater inorganic nitrogen combined with selective herbivory by voles (Howe et al. 2006) could have long-term effects on ecosystem productivity and needs further investigation, even though many processes affect nitrogen availability in ecosystems.

In the finer-textured soils and wet winters of the Willamette Valley, soil processes such as mineralization and nitrification in undisturbed soil may be limited by the diffusion of O_2 into the soil profile. Sumbera et al. (2004) showed that mole-rat burrows had an O_2 status that was only slightly lower (1-2 %) than ambient air. In the present study, greater aeration with vole burrows may have promoted mineralization and nitrification especially in the late winter and early spring and allowed more NO_3^- to accumulate than in the soil without vole burrows. Because NO_3^- is a highly mobile anion, groundwater can easily move NO_3^- produced in the surface soil into the subsurface. Concentrations of NO_3^- tend to decrease over the wet winter as the mobile anion moves with groundwater where it is diluted, incorporated into plants, microbes or soil organic matter or is removed from the soil through denitrification in wet soils (Davis et al. 2008). Davis et al. (2008) reported average soil NO_3^- concentrations of 1.25 mg NO_3^- kg soil^{-1} in April of 1998 under a third-year perennial ryegrass crop. These values are close to the concentrations found in the present study in May.

Canals et al. (2005) suggested that increased concentrations of inorganic nitrogen in gopher mounds could partly be due to the lack of plant uptake on bare mound soil. In the present study, no visible differences in plant cover were noted between the vole and no-vole plots. Lower pH in the soils with vole activity and greater soil NO_3^- concentrations supported the conclusion that nitrification was greater in the vole plots. The oxidation of NH_4^+ during nitrification releases hydrogen ions and can cumulatively decrease soil pH over time (Pierzynski et al. 1994).

Data from the burrow structure study indicated that the direct effects of vole activity on soil were confined to the top 10 cm of the soil profile. The depth of the vole activity was coincident with the majority of root biomass and was just above a significant increase in clay content from 20 to 34% at about 8 cm. Consequently, effects of vole activity parameters on soil below 10 cm would be indirect and due to the movement of nutrients and carbon into the soil profile with gravity and the flow of soil water. Vole burrow systems remained intact for at least six months and in many instances for even longer, suggesting that their effects on soil may also be persistent, even as the impacts of their herbivory fluctuate with population density.

Laundré (1993) found that small mammal burrows increased the amount of water that entered the soil profile and the depth to which water infiltrated. We therefore hypothesized that vole activity would increase moisture in the soil profile. Although there was a difference in soil moisture in the "below burrow" position in comparison to "above", "above away", and "below away", data from the soil profile study showed no difference in soil moisture between vole and no-vole plots. This finding was surprising, especially in the surface soils where it was thought that burrows would direct more water into the soil profile. The difference in soil moisture among these positions in the vicinity study therefore appears to be an effect of soil depth rather than position relative to a vole burrow.

Soil moisture status and water table dynamics in the Willamette Valley exhibit strong seasonal patterns that are unique to the region. The climate is characterized by cool, wet winters where water tables can be at or close to the soil surface and warm dry summers where the soil becomes dry and cracked and the water table drops below 1.5 m. Fall and spring are times of transition between wet and dry conditions. Samples in the present study were collected in May, when the frequency and duration of precipitation events tend to decrease and the upper profile begins to dry out. Greater soil moisture at the surface (0-5 cm) compared to the 5 to 30 cm depths indicated that recent precipitation events had occurred but were not substantial enough to increase soil moisture below 5 cm, the zone of burrow influence. It is likely that the impact of vole burrows on soil moisture would be greatest in the fall when the dry soil is first wetting up or during infrequent summer precipitation events.

Questad and Foster (2007) found that vole burrows had greater total carbon than the surrounding soil matrix. We hypothesized that soil disturbance and accumulation of plant biomass by voles would increase turnover of SOM and increase EOC and extractable organic nitrogen (EON) concentrations. Vole activity was actually associated with lower organic matter at 15 to 30 cm and surprisingly, did not produce any consistent trends in soil EOC or extractable organic nitrogen. Values of SOM were within the range of those reported for the same Woodburn soil (4%) by Nelson et al. (2006). The turnover of organic carbon and nitrogen is controlled by many factors including temperature, moisture, and aeration status, all of which may be affected by vole activity. It is possible that if vole activity did produce more EOC and EON, increased microbial activity from greater aeration and soil disturbance would have increased consumption of these pools as well. The fact that no nesting materials or food caches were found in the burrows after five months provides some evidence that organic matter decomposed rapidly in the burrows.

Voles are well known for their cyclic or irruptive population dynamics and the damage that these high-density populations may inflict on cropland, forests, or grasslands (Spencer 1958, Myllymaki 1977, Romakow and Grala 1995). In contrast, the ecological consequences of vole population spikes have hardly been explored beyond their effects on predator populations (e.g., Korpimaki and Norrdahl 1991, Sundell et al. 2004, Gervais et al. 2006). To our knowledge, this is the first attempt to quantify the effects of voles on soil properties beyond nitrogen. It is important to identify the role that voles play in soil ecosystems because these impacts may change dramatically in coming decades as world climate shifts and ecosystems subsequently change. For example, the widely recognized population cycles of the Fennoscandia voles appear to have disappeared or at least shifted in recent decades (Hornfeldt 2004, Brommer et al. 2009). It remains to be seen how much the vole populations have shaped both the soil and the plant communities at these higher latitudes, and what their disappearance will mean to these ecosystems. Whether voles may actually provide some benefit to agriculture that might offset the occasionally substantial damage has not yet been determined, but in natural grasslands, these animals may contribute to soil formation and maintenance in a manner quite different from the mound-creating activities of gophers and moles.

Conclusions

This study is the first to elucidate the signature of vole activity on soil in a perennial grassland ecosystem in the Willamette Valley of Oregon. Vole activity had the greatest impact on the production of NO_3^- in these soils. Greater concentrations of NO_3^- and decreased pH extended to depths of 60-90 cm in areas with previous burrowing activity, even though the burrows appeared to be largely confined to the top 10 cm of soil. Soil NH_4^+, NO_3^-, extractable organic carbon, and soil organic matter tended to be greater below burrows than above them. Nitrification may be enhanced by vole activity, and this effect outlasts the population spikes that create the characteristic extensive burrow network.

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