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Badger (*Taxidea taxus*) Mounds Affect Soil Hydrological Properties in a Degraded Shrub-Steppe

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ABSTRACT.—Overgrazing, weed invasion and wildfire have resulted in the conversion of large areas of shrub steppe to exotic annual grassland in the western United States. This has been accompanied by reduced habitat for native plants and animals, and altered water and nutrient flows. In these landscapes, badgers increase landscape heterogeneity by creating a mosaic of foraging pits and mounds over extensive areas while preying on fossorial animals. The effects of badger-produced mounds on infiltration and surface physical properties were examined in a mixed sagebrush (*Artemisia*) – winterfat (*Krascheninnikovia*) site in west-central Idaho. Recently constructed mounds were physically degraded (*i.e.*, more compacted, poorly aggregated, few macropores, erodible by wind) and vascular plant and cryptogamic crust cover increased as mounds aged. Infiltration through younger mounds was about half that through older mounds or inter-mounds. The results indicate that mounds function as water shedding sites, suggesting that the area around the base of the mounds will be moisture-rich, and may be important for recruitment of shrub-steppe plant species.

INTRODUCTION

The burrowing and foraging activities of many animals are known to lead to dramatic changes in soil and ecological processes in drylands (*e.g.*, Whitford and Kay, 1999). Soil disturbance by animals is a form of bioengineering (Jones *et al.*, 1994) that alters the physical and chemical arrangement of soil patches (Huntly and Inouye, 1988; Mun and Whitford, 1990; Schooley *et al.*, 2000). Animal-induced disturbances create physically- and chemically-distinct patches compared with the surrounding soil matrix, contributing to landscape heterogeneity. Biophysical changes associated with these disturbances often substantially affect plant community structure (Guo, 1996; Boeken *et al.*, 1995), creating safe sites for germinating plants and typically leading to increases (but sometimes declines) in patch- and landscape-level plant and animal diversity and abundance (Krogh *et al.*, 2003).

In the western United States, the American Badger (*Taxidea taxus*) is a significant predator of semi-fossorial animals such as ground squirrels (*Spermophilus* spp.) and burrowing owls (*Athene cunicularia*). Badgers create pits up to 15 cm across and 30 cm deep, and large fan-shaped mounds up to 1 m long and 0.5 m high at the pit entrance (Platt, 1975; Green and Anthony, 1989; Eldridge, 2004). In the Snake River Birds of Prey National Conservation Reserve (BOPNCR) in west-central Idaho, badger mounds account for 8% of the soil cover, and the effects of their digging are thought to persist for several decades after disturbance (Platt, 1975).

We have previously reported on the extent of badger digs and mounds in the western United States (Eldridge, 2004) and their effects on biogeochemical processes (Eldridge and Whitford, 2009). Here we report on a study of the effect of mounds on soil hydrological processes. The effects of burrows and tunnels constructed by semi-fossorial rodents on soil water flow is generally well-known (*e.g.*, Hakonson, 1999; Whitford and Kay, 1999). For

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example, areas of ground squirrel burrows have greater rates of infiltration (Laundré, 1993). In the Mojave Desert in Nevada, infiltration was greater in soils with small mammal burrows, particularly under shrubs compared with inter-burrow soils (Soholt and Irwin, 1976). Similarly, Hakonson (1999) showed that soils with pocket gophers (*Thomomys bottae*) had 75% less runoff than soils where gophers were absent. Hakonson's (1999) work has important implications not only for the transport of water, but for the movement of radionuclides in the soil.

Few studies, however, have examined infiltration directly on the mounds of fossorial animals (Whitford and Kay, 1999). The generally accepted view is that most animal-produced mounds have higher infiltration rates compared with adjacent mound-free soils, mainly due to lower levels of bulk density and therefore greater soil porosity (Whitford and Kay, 1999). Hongo *et al.* (1993) demonstrated greater rates of infiltration through the mounds of the Cansu Mole Rat (*Myospalax cansus*) in a shrub-steppe environment in China's Loess plateau. However, no differences in infiltration were observed between sites with mounds of the Northern Pocket Gopher (*Thomomys talpoides*) and mound-free areas, though this may have been due to the gophers' habit of plugging up large sections of their burrows beneath the mounds (Zaitlin *et al.*, 2007). Indeed the hydrological effects of mounds may be the most significant impact of pocket gopher activities (Kerley *et al.*, 2004). Moorehead *et al.* (1988) and Mun and Whitford (1990) demonstrated significantly lower soil moisture in *Dipodomys spectabilis* mounds compared with inter-mound soils, though they did not measure infiltration directly. Lower soil moisture could result from a faster rate of soil drying, ultimately leading to patches of dry soil in the landscape (Cortinas and Seastedt, 1996; Whitford and Kay, 1999).

We measured infiltration with disc permeameters (infiltrometers), enabling us to separate out the effects due solely to mounds from the combined and interactive effect of mounds and their associated sub-surface burrows. The small scale of the permeameter measurements ($\sim 380 \text{ cm}^2$) enabled us to measure the effects of mounds alone. We predicted that badger mound surfaces would (1) be physically and biologically depauperate compared with the inter-mound matrix and (2) have few biologically-derived macropores, and given their compacted surface, would therefore conduct less water than the inter-mound soil matrix. These hypotheses are important, as we argue that the result of mound formation by badgers is the creation of a radically altered surface type with different resource levels compared with the inter-mound area. The second hypothesis suggests that, if macropores are absent from mound soils, then saturated water flow through the mounds will be substantially reduced. Therefore, any precipitation on the mounds would be redistributed as runoff to the annular zone surrounding the mound.

METHODS

THE STUDY SITE

The study was conducted in a sagebrush shrub-steppe community in the BOPNCR on the western Snake River Plain, west-central Idaho, about 40 km south-west of Boise (43°27' N, 116°26' W, 884–914 m above sea level). The soils are predominantly fine silty Xerollic Haplargids (Aridisols; Collett, 1980) formed on loess and sedimentary deposits covering basalt lava flows (Hironaka *et al.*, 1983). Soils in the area show substantial declines in silt and increases in sand (mainly fine sand) with depth. Between the mounds, soils are characterized by increasing concentrations of soluble cations, particularly after 40 cm depth, and rapid declines in total nitrogen. The climate is semi-arid, with hot, dry summers and cool, wet winters. Annual precipitation ranges from 178–305 mm, with less than 35% of

the moisture occurring between April and September (Hironaka *et al.*, 1983). Mean daily temperatures range from -1 C in January to 24 C in July. The topography of the area is generally flat, with small basalt outcrops or remnants of volcanic activity. The study was conducted at a mixed Wyoming big sagebrush (*Artemisia tridentata*) – winterfat (*Krascheninnikovia lanata*) community near Initial Point west of Kuna in west-central Idaho. The site was unburned and covered an area of about 10,000 ha. Although the site was dominated by Sandberg's bluegrass (*Poa secunda*), it still supported a variable cover of cheatgrass (*Bromus tectorum*).

Surface physical characteristics.—The physical and soil hydrological properties of mound and inter-mound soils (soil surface strength, dry aggregate stability, bulk density, wet aggregate stability, surface morphology, infiltration capacity) were measured within three microsites; 'crusted' mounds, 'recovering' mounds and inter-mounds. Ten replicates of each microsite were measured. Each replicate location consisted of a cluster of two mounds and an adjacent non-mound.

Soil surface strength was measured with a GeotesterTM portable penetrometer. Ten measurements were taken (and averaged) at each microsite at each of the 10 locations. Dry aggregate stability, a measure of the erodibility of the surface by wind, was assessed using the method described by Leys *et al.* (2002). Three sub-samples were taken (and averaged) for each surface type at the ten locations. Bulk density was measured using a soil corer of diameter 47 mm and depth 50 mm on each of the three surface types. Soil samples were oven-dried at 105 C for 24 h. Three sub-samples were taken (and averaged) from each surface type. Wet aggregate stability of surface aggregates from each of the three microsites was assessed by immersing aggregates of about 7 mm in diameter in a Petrie dish with deionised water and recording the time taken for aggregates to disperse. Values represent the average of three sub-samples.

The morphology of the soil surface was assessed using a line-intercept method. A 1 m micro-transect was placed in a pre-determined location on each of the three microsites and the surface described in terms of the proportion of micro-morphological features (*i.e.*, micro-scarps, micro-depressions and micro-flats) along the micro-transect. Surface cover was further classified on the micro-flats and micro-depressions as either bare soil, cryptogamic crust or litter (including dung) to the nearest millimetre. Measurements were made in areas devoid of vascular plants in order to maximise the ability to detect surface morphological types. Crusts were different on the three surface types. They ranged from a mixture of physical (raindrop-impacted) crusts, sometimes invaded by smooth, dark-colored cyanobacterial crusts on the surface of the 'crusted' mounds, to a diverse community of cryptogamic crusts dominated by mosses, lichens and cyanobacteria on the recovering mounds (Eldridge, 2004).

Infiltration through the mounds.—Both sorptivity ($\text{mm h}^{-0.5}$) and steady-state infiltration (mm h^{-1}) were measured with disc permeameters (CSIRO, 1988) at supply potentials of -40 mm (tension) and $+10$ mm (ponded; Perroux and White, 1988). When a negative pressure or tension is applied to the soil using the disc permeameter, flow is restricted to the matrix pores only and water is prevented from entering macropores. At a tension of -40 mm tension, flow is restricted to pores < 1 mm in diameter (Wilson and Luxmore, 1988). However, when flow is measured with a positive pressure, water flows through both macropores and matrix pores. The ratio of sorptivity under ponded conditions to sorptivity under tension is a useful index of the relative contribution of macropores to total water flow given that the two tensions measure the contribution by different pore sizes. This ratio is extremely informative, as macropores are indicative of healthy, highly conductive soils. A

TABLE 1.—Soil physical properties and cover component data for the surface soils of the three microsites. Mean values (\pm standard error) within a row followed by a different letter are significantly different at $P=0.05$. #Mean values are back-transformed after \log_{10} transformation prior to ANOVA

Attribute	Mound					
	Crusted		Recovering		Inter-mound	
	Mean	SEM	Mean	SEM	Mean	SEM
Crust strength (kg cm^{-2})#	16.8 ^a	0.90	22.0 ^b	2.20	26.5 ^b	2.20
Dry aggregate stability (%>0.84 mm)	56.2 ^a	4.08	69.6 ^b	3.66	69.4 ^b	3.76
Bulk density (Mg m^{-3})	1.35 ^a	0.02	1.32 ^a	0.04	1.35 ^a	0.04
Micro scarp cover (%)	7.2 ^a	3.43	7.3 ^a	2.71	4.0 ^a	0.84
Micro flat cover (%)	55.2 ^a	12.3	61.2 ^a	8.95	63.4 ^a	12.2
Micro depression cover (%)	37.6 ^a	14.7	31.5 ^a	9.00	32.6 ^a	12.7

loss of ecosystem function in terms of water flow, can be attributed in a large part to a loss of this macroporosity.

At each of the 10 locations, water flow under ponding and tension was measured on each of the crusted and recovering mounds and the adjacent inter-mound surface. The ponded permeameter was placed on a steel ring of 220 mm internal diameter which was gently pressed into the soil to a depth of about 7–10 mm and sealed with moistened soil along the outside edge to prevent leakage of water. Both permeameters were placed alongside each other and run for approximately 30 min, by which time steady-state had been achieved. At each supply potential, sorptivity was calculated according to the method of Cook and Broeren (1994) and steady-state infiltration according to White (1988).

DATA ANALYSES

A two-way ANOVA was used for all analyses with sites as blocks, where a site corresponded to a cluster of one each of crusted, recovering and inter-mound microsite, and tested for significance between microsites by using the sites (blocks) \times microsite interaction as the residual mean square ($df=18$). Data subjected to ANOVA were first checked for homogeneity of variance using Levene's test (Minitab, 2003) and diagnostic tools within the Minitab (2003) statistical program and transformed, where necessary, to stabilise the variance before undertaking ANOVA.

RESULTS

Physical structure of the mounds.—The proportion of micro-scarps, flats and depressions did not differ significantly between the three microsites ($P>0.05$; Table 1). For the flat and depression categories, the cover of cryptogams increased ($F_{2,18}=12.89$, $P<0.001$) and bare soil decreased ($F_{2,18}=36.48$, $P<0.001$) from crusted, through recovering mounds to inter-mound surfaces, but there was no significant trend in litter cover between the three surfaces (Fig. 1). Crusted mounds were about 30% more erodible by wind ($F_{2,18}=13.0$, $P<0.001$) and less resistant to penetration ($F_{2,18}=12.6$, $P<0.001$; Table 1) than recovering mounds or inter-mounds. Soil aggregates from crusted mounds dispersed after 0.7 min, compared with 1.6 min for recovering mounds and 4.9 min for inter-mound surfaces ($F_{2,18}=38.6$, $P<0.001$). There were no differences in bulk density between the three mound microsites ($P=0.79$; Table 1).

Infiltration capacity of the mounds.—Ponded infiltration through crusted or recovering mounds was 53% less than that through inter-mound surfaces ($F_{2,18}=8.47$, $P=0.003$; Fig. 2).

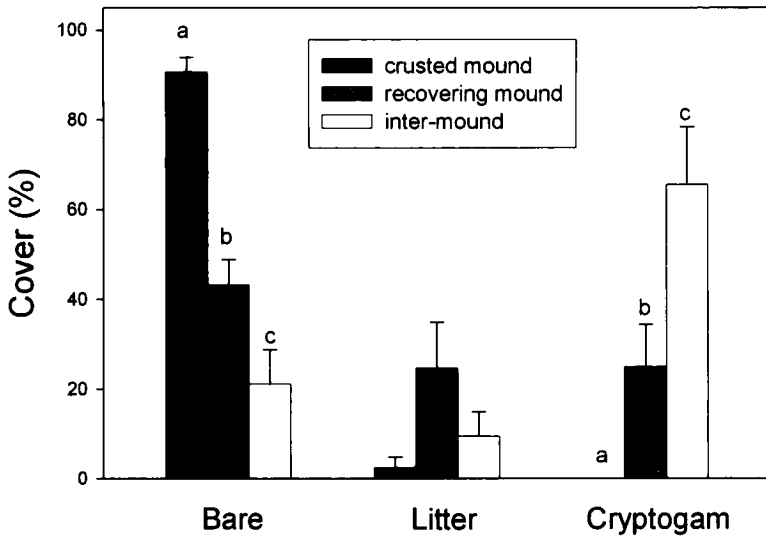


FIG. 1.—Mean (\pm SEM) cover (%) of bare soil, litter and cryptogams on the flat and depressed microsites from crusted mounds, recovering mounds and inter-mound surfaces. Different letters within a surface type indicate a significant difference between microsites at $P=0.05$

Furthermore, the macropore index, the ratio of sorptivity under ponding (+10 mm) to sorptivity under tension (−40 mm), was significantly greater in the recovering (2.6:1) and inter-mound (3.0:1) surfaces compared with the crusted surfaces (1.2:1; $F_{2,18}=10.3$, $P=0.001$ on \log_{10} -transformed data). This indicates substantially lower levels of macroporosity in the mound soils. Sorptivity under tension (−40 mm) was significantly greater on the crusted mounds ($62.0 \text{ mm h}^{-0.5}$) compared with recovering mounds ($42 \text{ mm h}^{-0.5}$) or inter-mound surfaces ($35 \text{ mm h}^{-0.5}$, $F_{2,18}=12.8$, $P<0.001$; Fig. 2).

DISCUSSION

Soil disturbance by mammals is a key ecosystem process that contributes to the development of resource-rich patches in otherwise nutrient-poor environments (Kinlaw, 1999; Whitford and Kay, 1999). In this study however, badger mounds were physically degraded and characterized by a lower resistance to penetration, a greater cover of bare soil and reduced cover of vascular plants and cryptogams compared with inter-mound surfaces. The direct effect of digging was also to increase the erodibility of the soil by wind, and increase seven-fold the speed at which surface aggregates disperse in water compared with inter-mound surfaces.

Infiltration through badger mound soils was always less than that through inter-mound surfaces, contrary to that observed for other animal mound types (Whitford and Kay, 1999). Differential rates of infiltration on animal-disturbed patches have been demonstrated in a range of desert and semi-desert environments, though most studies have concentrated on burrow systems rather than mounds. For example, Cox (1987) demonstrated substantially greater infiltration on abandoned gerbil colonies in Namibia. Similarly, unpublished data from the semi-arid woodlands of eastern Australia indicated an 85% greater rate of steady-state infiltration on intact and physically disturbed (ripped) mounds (warrens) created by

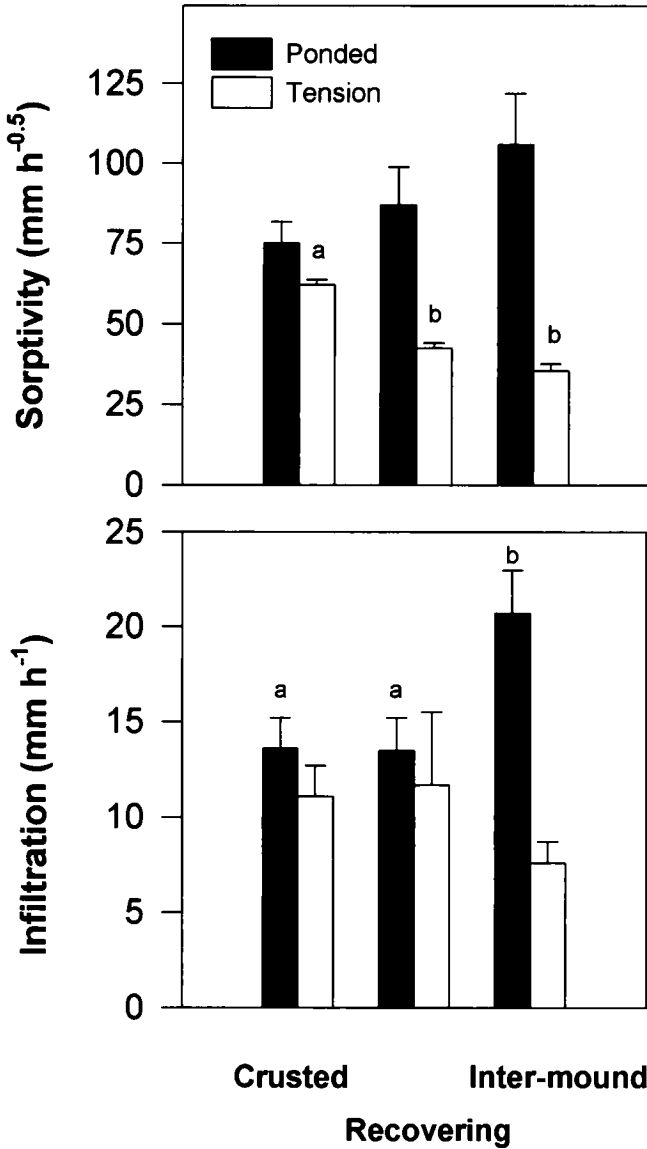


FIG. 2.—Mean sorptivity (mm h^{-0.5}) and steady-state infiltration (mm h⁻¹) under ponding (+10 mm) and tension (-40 mm) in relation to the three microsites. For water flow under either ponded or tension conditions, different letters indicate a significant difference at P<0.05. Bars without letters are not significantly different. Bars indicated standard error of the mean

the European rabbit (*Oryctolagus cuniculus*) compared with non-warren surfaces (Birnbaum, 2007).

The substantially lower sorptivity ratio for the crusted mounds (1.2:1) compared with the recovering mounds (2.6:1) or inter-mounds (3.0:1) suggests that differences in infiltration

are due to lower levels of macroporosity in younger, but not older, mounds. Despite the marked differences in steady-state infiltration under ponding, there were no differences under tension, *i.e.*, when flow was restricted to matrix pores, the small interstitial spaces between individual soil particles. This suggests that infiltration rates, at least in mound soils, are largely driven by matrix pores, probably due to the compacted nature of mound soils with their low levels of biologically-derived macropores (produced by plant root and faunal holes). In the absence of macropores therefore, mound soils are probably relatively homogeneous, giving them similar inherent abilities to conduct water.

Reduced infiltration on silt-rich soils can also be due to surface sealing resulting from structural disintegration of the soil surface (Poesen, 1992). On crusted mounds, fine particles released by disaggregation of surface aggregates will likely block surface pores, resulting in the formation of a surface seal, or reinforcing the physical crust (*sensu* Valentin and Bresson, 1992), further restricting infiltration. Aggregates from crusted mounds dispersed in less than a minute compared with 5 min in the inter-mound surfaces. Surface sealing on badger mounds is likely intensified by low levels of vegetation cover and exacerbated by the fact that soil on the mound surface originates from a depth of 40–80 cm and is inherently poorly aggregated. This compares with inter-mound surfaces where raindrop energy is moderated by vascular plants and biological soil crusts (Wainwright *et al.*, 1999).

Recently excavated mounds remain erodible until the first rains or heavy frost hardens the surface into a physical, raindrop-impacted crust. Observations during wind storms indicate that the powder-like surface of recently excavated, unconsolidated mounds is extremely erodible by wind due to a lack of stable aggregates or protective plant cover. Although wind storms probably winnow fine material (<250 μm) from mound soils, data suggest that these particle sizes accumulate in the pits (Eldridge and Whitford, 2009), which in frequently burned sites probably represent the only substantial resource traps. Indeed, the smooth, concave surface of the mounds would have failed to trap appreciable resources.

Water-repellant, crusted mound surfaces will therefore generate runoff water, which can only be redistributed to the inter-mound areas. The paucity of litter on the mounds will mitigate against the retarding or ponding of water, further reducing infiltration and enhancing runoff. Increased runoff is also likely to entrain sediment (and adsorbed nutrients), contributing to local soil nutrient and moisture pools around the base of the mounds. Much of this runoff is likely to infiltrate at the base of the mounds where macropores, plant cover and biological activity are greatest, analogous to zones of enhanced infiltration around ground squirrel burrows (Laundré, 1993). Enhanced soil-water accumulation around pocket gopher mounds is believed responsible for higher cover and biomass of herbaceous annuals in the Chihuahuan Desert (Kerley *et al.*, 2004).

Results from a broader study (Eldridge and Whitford, 2009) demonstrate a depletion of essential resources (sediment, nutrients) on mounds compared with either the pits or inter-mound surfaces. Badger mounds and their associated pits provide the only substantial structure in post-fire sagebrush steppe, where shrubs and their associated hummocks have largely been eliminated. Pits associated with mounds also trap water and are likely sites of fungal decomposition (Cortinas and Seastedt, 1996; Sherrod and Seastedt, 2001). Preliminary observations suggest that the density and biomass of the alien annual grass cheatgrass are substantially lower on mounds and around the periphery of the mounds compared with the areas between the mounds (D.J. Eldridge, pers. obs.), and that the areas around older recovering mounds are sites of reestablishment of perennial native shrubs and grasses such as winterfat and Sandberg's bluegrass. Native plants may be advantaged on the

edge of the mounds where water is being redistributed and where the C:N ratio of the soil is relatively high (~25:1), indicative of the immobilization of nitrogen (Eldridge and Whitford, in review).

The work reported here suggests that badger mounds are important regulators of soil water in semi-arid shrub steppe communities. Given that mounds occupy up to 8% of the surface area of shrub steppe environments, their effects are likely to have landscape-wide implications. The work also reinforces the view of Neave and Abrahams (2001) that the pedoturbatory activities of semi-fossorial animals must be taken into account when modelling rainfall-runoff relationships in arid and semi-arid environments.

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