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SOIL ORGANISMS AND RANGELAND SOIL HYDROLOGICAL FUNCTIONS

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ABSTRACT

Soil organisms control water distribution in rangelands by creating macropores which rapidly conduct water into the soil, by generating stable soil aggregates which prevent crusting and increase water holding capacity, and by controlling litter decomposition. Ants, termites and earthworms have all been shown to increase infiltration capacity; anecdotal evidence suggests that macropore formation by a variety of other macroinvertebrates may have equally dramatic effects. Macroinvertebrates generate aggregates in the form of fecal pellets. Lichens, mycorrhizal fungi, cyanobacteria and other microorganisms also contribute to aggregate formation and soil surface stabilization. The direct effects of rapid litter decomposition on infiltration and soil water storage in arid and semi-arid rangelands is generally negative: litter removal exposes the surface to raindrop impact, which leads to the formation of physical crusts, and increases evaporation from the soil surface. These negative impacts are balanced by the creation of surface-connected macropores and the incorporation of soil organic matter, resulting in the formation of stable aggregates.

Keywords: hydrology, infiltration, soil water, available water holding capacity, invertebrate, ant, termite, earthworm, fungi, rangeland, soil structure, aggregate, soil organic matter

INTRODUCTION

Biomass production in most North American rangelands is limited by soil moisture availability during at least part of the year. Annual precipitation is low, variable often arrives during periods which are unsuitable for plant growth. As a result, monthly potential evapotranspiration (the amount of water which could be lost to the atmosphere from a free water surface) may exceed precipitation by a factor of100 or more during periods when temperatures are high enough to support plant production (Hargreaves and Samani 1991).

These limitations are compounded on some parts of the landscape by high runoff rates. In closed-basin systems, this water is conserved in lower parts of the landscape, while in open systems it is effectively lost. These losses are not necessarily negative from a regional perspective, as the runoff supports riparian systems and is frequently collected in reservoirs for urban and agricultural uses. Losses from the rooting zone may also contribute to groundwater recharge. High rates of runoff, however, are rarely supported as a management objective.

Water redistribution also occurs at much smaller scales. Redistribution at the scale of tens of meters has been cited to explain patterns of banded vegetation in many arid ecosystems (Tongway and Ludwig 1994). Schlesinger and others (1990) suggested that water and nutrient redistribution at the level of the individual plant are associated with the transition of grasslands to shrublands.

In addition to redistribution, the capacity of the soil to store water also varies across the landscape. The volume of plant-available water which can be stored at any particular point and depth in the profile depends on complex plant-soil interactions. In general, however, more highly structured soils have a higher capacity to store water at tensions at which it is accessible to plants, and provide conditions which favor root exploration of a larger soil volume.

Soil organisms can affect water redistribution, soil water holding capacity and the accessibility of water to plants through a variety of mechanisms. They modify soil structure, alter the form and spatial distribution of above- and below-ground detritus and, ultimately, change the relative growth rates of different plants and therefore plant cover and community composition. The objective of this paper is to review the role of soil organisms in altering rangeland soil hydrology through aggregate and macropore formation. Microbiotic crusts are only briefly considered here. For a more extensive discussion of their role please see recent reviews by Warren (1995), Ladyman and Muldavin (1996), the NRCS (1997), Belnap (this volume) as well as a forthcoming book in the Advances in Ecology series. Recent papers by Eldridge and Greene (1994) and

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Eldridge and others (1997) have explored the effects of these crusts on soil surface hydrology in Australia.

SOIL WATER INFILTRATION

The volume of water which enters the soil profile at a particular point on the landscape is a function of (1) supply or the depth of water which is available for infiltration, (2) residence time, or the amount of time which water is resident on the soil surface, and (3) infiltration characteristics. Hydrologists often describe soil water infiltration in terms of *sorptivity*, which is related to the initial rate of water movement into a dry soil, and the *saturated hydraulic conductivity*, or the rate of water movement into the soil after it has become saturated. Soil organisms affect both residence time and infiltration characteristics. They can also affect the water supply at one location by modifying the soil surface in adjacent patches, or at other locations higher in the landscape.

Supply

Water available for infiltration is a function of both total precipitation and run-on. The unique plant communities associated with riparian zones and playa lakes owe their existence to supplemental water from higher parts of the landscape. Most studies focus on the effects of soil organisms at a single point and down-slope effects of changes in the populations and activity of soil organisms are rarely considered.

Residence Time

Soil biota affect residence time by modifying surface roughness and the distribution of litter on the soil surface. Both soil surface roughness and the presence of litter slow the movement of water across the landscape. In some cases, small "ponds" may be formed by litter dams (Ludwig and Tongway 1995) or by micro-depressions formed by surface features stabilized by microbiotic crusts (West 1990). Increases in residence time by litter can be important in rangelands which depend on brief, high-intensity storms. Ponds, even if only 10-25 millimeters deep, can be locally significant: 25 millimeters is equivalent to over 10 percent of the average annual precipitation in much of the western United States and northern Mexico.

Soil organisms affect litter distribution and residence time through at least four processes: stabilization, shredding, burial, and consumption. Fungi can temporarily stabilize litter and limit redistribution by wind and water by binding it to the soil surface. Shredders, including both vertebrates and invertebrates, modify the susceptibility of litter to both redistribution and further degradation by reducing fragment size. Litter is removed from the surface through both burial and consumption. Ants tend to bury material in their nests, where it may later be consumed directly or used to culture fungi. Anecic species of earthworms, such as *Lumbricus terrestris*, drag litter into burrows, while epigeic species consume material at the surface (Edwards and Bohlen 1996). A third group (the endogeic species) function solely in the mineral soil and do not contribute to removal of litter from the surface. Dung beetles exhibit an even wider variety of behaviors. Some species bury dung in the soil directly below dung patches (paracoprids), others roll dung balls to another location where it is buried (telecoprids), while a third group lays eggs directly inside the dung patch, leaving the larvae to consume at the soil surface (Bornemissza 1969). Most other important species consume material at the surface and may deposit fecal material both above- and belowground.

While high levels of soil biotic activity are normally viewed as an indicator of a healthy system, the direct effects on infiltration of litter removal from the soil surface are generally negative. In addition to slowing runoff, litter protects the soil surface from raindrop impacts. This limits the formation of soil physical crusts. This is particularly important in arid and semiarid rangelands where vegetative canopy cover is generally much lower than 100 percent.

The net impact of direct and indirect effects of litter decomposition on infiltration depend on complex interactions with a number of other processes including the formation of soil structure by the decomposers and changes in soil microtopography. For example, Trojan and Linden (1992) reported that infiltration was deepest where earthworm burrows were located at the bottom of depressions in the soil surface.

Infiltration Characteristics

Infiltration depends on the density, size distribution, and continuity of soil pores. It also depends on the degree of repulsion between soil and water (hydrophobicity), particularly in the early stages of precipitation events. Soil organisms form pores through two basic processes: excavation and aggregation. A third process, root decomposition, also results in the development of new voids.

Pore formation by excavation–Excavation generally results in the formation of transmission pores, or those pores which transmit water during infiltration. These pores are > 30μ in diameter (Marshal and others 1996) and are commonly classified as mesopores (30 - 75μ) and macropores (> 75μ) (Soil Science Society of America 1997). Earthworms, ants and termites are arguably the three groups of invertebrates responsible for the majority of biopore formation in rangeland soils. Direct observations during rainstorms indicate that a number of other species including burrow-forming vertebrates such as pocket gophers (Family Geomyidae), prairie dogs (*Cynomys spp.*) and kangaroo rats (*Spectabilis spp.*) are probably locally important.

Lee and Smettem (1995) state that, "[Earthworm] burrows are the most numerous and most important macropores of animal origin in nearly all soils." Earthworms form burrows by forcing their bodies through the soil, and by swallowing soil to be later excreted as casts either elsewhere in the soil, or at the soil surface. These burrows may range from one to over ten millimeters in diameter. Anecic worms, or those which move between the surface and the subsoil, have been shown to be particularly effective at improving infiltration capacity. Up to 2,000 burrow entrances per square meter have been reported (Lee and Foster 1991). Even much lower densities can dramatically increase infiltration due to the fact that the burrows frequently connect the surface to much deeper layers of soil.

The relative importance of earthworms in rangelands has not been evaluated, however. A recently revised book by Edwards and Bohlen (1996) provides a comprehensive review of the role of earthworms in soils, but contains few references to non-arable systems. The key anecic species are virtually absent from many arid and semi-arid rangelands, including the Chihuahuan (Whitford 1996) and Namib Deserts (Crawford and others 1993). They do occur in moister parts of the Chilean Arid Zone where coastal fogs appear to maintain higher levels of soil moisture in spite of annual rainfall of less than 200mm (Crawford and others 1993). The lack of earthworms in many rangeland ecosystems suggests that other species, including ants and termites, dominate biological macropore formation.

Rangeland termites can be divided into two groups based on whether or not they build mounds. Only soil-dwelling termites (non-mound builders) are found in North America, occurring throughout the southwestern United States and Mexico. They form extensive near-surface galleries and tunnels which extend deep into the soil. Most are detritivores, feeding on dead material below the soil surface. Those which have the highest direct impact on infiltration feed on litter and standing dead vegetation at the surface. Some, like *Gnathamitermes tubiformans* form protective sheaths around vegetation, while others, including *Amitermes wheeleri* feed directly at the surface during periods when evaporation rates are minimal. Soil-dwelling termites can generate very high densities of surface-connected macropores, particularly under concentrated sources of organic matter such as cattle dung. Infiltration rates in a Costa Rican pasture were over twice as high (71 mm/h) under dung patches which had been decomposed primarily by termites than they were in adjacent control plots (34 mm/h) (Herrick and Lal, 1995).

The positive impact of termites on infiltration through macropore development may be balanced by the negative effects of high rates of litter decomposition. This is illustrated by a comparison of two studies in which termites were eliminated with the use of the insecticide, Chlordane. Rainfall simulation was used in both cases to measure infiltration capacity. Four years after termite removal from a Chihuahuan Desert creosote shrubland, infiltration rates had declined by over 40 percent relative to control in areas with less than 5 percent perennial cover. In plots centered on creosote bushes (*Larrea tridentata*), there was no change (table 1; Elkins and others 1986). In a shortgrass prairie in Texas, cumulative infiltration actually increased relative to control plots two to three years after termites were removed (table 2; Spears and others 1975). This increase was associated with a 50 percent increase in organic carbon in the top 1 centimeter of soil and an 80 percent increase in litter mass.

Table 1—Final measured infiltration rates (mean ± S.E.) based on rainfall simulation on 1m^2 plots on a Chihuahuan Desert bajada four years after termite exclusion (data from Elkins and others 1986).

	Termites excluded	Termites present
	mm/hour	
No shrub; < 5 percent *Erioneuron pulchellum*	51.3 ± 6.8	88.4 ± 5.6
Larrea tridentata canopy	106.4 ± 9.7	100.6 ± 6.1

In Australia, subterranean termites (*Drepanotermes spp.*) increase the density of surface-connected macropores and reduce it in others, leading to redistribution of water at the patch (1 meter) scale. These termites form a cap of up to 2 meters in diameter directly above their nests, and macropores lead to the surface in the area surrounding the nest. Eldridge (1994) reported that ponded infiltration rates into the nest margins were over 16 times higher than in the caps. Rates in control areas were similar to slightly lower than those recorded in the nest margins. In one of the few studies in which soil-dwelling termite activity has been evaluated as a potential management tool, Mando (1997) found that infiltration into a bare, crusted soil was increased by termite activity, and that there was a strong positive interactive effect of mulch and termite treatments on both infiltration and soil water storage. Subsequent microscopic and computerized image analysis confirmed that 60 percent of the macroporosity in the top 10 centimeters could be attributed to termite tunnels and chambers (Mando and Miedema 1997). Enhanced termite activity has also been shown to increase macropore flow in two degraded soils in the Chihuahuan Desert (unpublished data).

Table 2—Characteristics of plots two to three years after initiation of termite exclusion from a shortgrass prairie (data from Spears and others 1975).

	Termites excluded	Termites present
	– mm/40 minutes --	
Cumulative infiltration	18.5	15
	– percent --	
Organic carbon: top 0 - 1 cm	1.8	1.2
	– g/m^2 –	
Litter	63	35

Ants create extensive networks of voids and macropores in many rangeland ecosystems. Whitford and DiMarco (1995) calculated that they move one centimeter of soil to the surface per 100 years in a Chihuahuan Desert grassland. Assuming that most of the soil was derived from the top meter, this represents a porosity increase of 1 percent, or a 2 percent addition to the typical pore volume for a sandy loam soil. At nature reserve in New South Wales, Australia, funnel ants (*Aphaenogaster barbigula*) alone cover 2.5 percent of the soil surface per year with their mounds, which they move approximately every 9 months (Eldridge and Pickard 1994). The authors calculate that up to 92.5 percent of the soil surface would be affected after 100 years, resulting in a net transport to the surface of 2.8 centimeters of soil.

Infiltration around entrances has been measured for only a few species. Several Australian studies suggest that ant activity has a generally positive impact on infiltration, at least when the entrance is included. Ponded rates were four (sandy loam) and eight (loam) times higher over funnel ant (*A. barbigula*) nests (Eldridge 1993, 1994). Infiltration was positively correlated with nest entrance diameter on both soils. A study by Lobry de Bruyn and Conacher (1994) indicates that these effects probably depend on ant species, soil type and land use. Water infiltration under ponded or near-ponded (5 millimeter tension) conditions was higher under *Pheidole sp.* nests located on a sandy loam in a woodland and on farmland (fig. 1a, b), while nests of a *Camponotus* species apparently had no effect in the woodland (fig. 1c). Two species of *Rhytidoponera* also had no effect on infiltration into a shrub-dominated sand (fig. 1d) (Lobry de Bruyn and Conacher 1994).

The high variability in nest morphology of different species and even within species suggests that effects on infiltration should also vary. Some authors have speculated that while infiltration is increased at nest entrances, it may be reduced in the surrounding area due to vegetation removal (Lobry de Bruyn and Conacher 1990) or by the generation of impermeable caps by species such as *Trachymyrmex smithii* and *Pogonomyrmex maricopa* (Whitford 1993) or *Pogonomyrmex maricopa* (W.G. Whitford pers. commun.).

Where ant nests do increase infiltration, their importance is magnified by the fact that they are able to conduct water deep into the profile (Eldridge 1993) where it is protected from rapid evaporative loss. This is a function of both the diameter and the continuity of the macropores in the nests. Soil moisture content under harvester ant nests (*Pogonomyrmex wheeleri*, Cole) in a southeastern Idaho sagebrush-grassland was less than or equal to that in control areas to a depth of 40 cm. From 60 to 100 cm, however, soil moisture content was higher under nests (Laundré 1990).

Pore formation by aggregation–Pores are formed each time three or more soil particles are linked together as aggregates. These intra-aggregate pores tend to be much smaller than those formed by excavation, and are more likely to be involved in water storage (Hindell and others 1994), while pores formed between individual aggregates are more likely to contribute to water transmission. Stable aggregates at the soil surface also help maintain infiltration capacity by limiting physical crusting and blockage of surface-connected macropores during storms.

A general hierarchical model of aggregate structure and formation has been proposed by Tisdall and Oades (1982) and refined by Oades and Waters (1991). This model is based on the assumption that soil macroaggregates (> 250μ in diameter) are formed from more stable microaggregates (50 – 250μ) and that different binding mechanisms are dominant at each scale (table 3). Elliott (1986) found that the model could be applied to a Nebraska soil which had been under sod for the previous 14 years. More recent studies have confirmed that the form of soil organic matter is at least as important as total content in the formation of stable aggregates (reviewed in Herrick and Wander 1998).

Soil organisms contribute to soil aggregation directly by forming fecal pellets, by re-arranging particles during

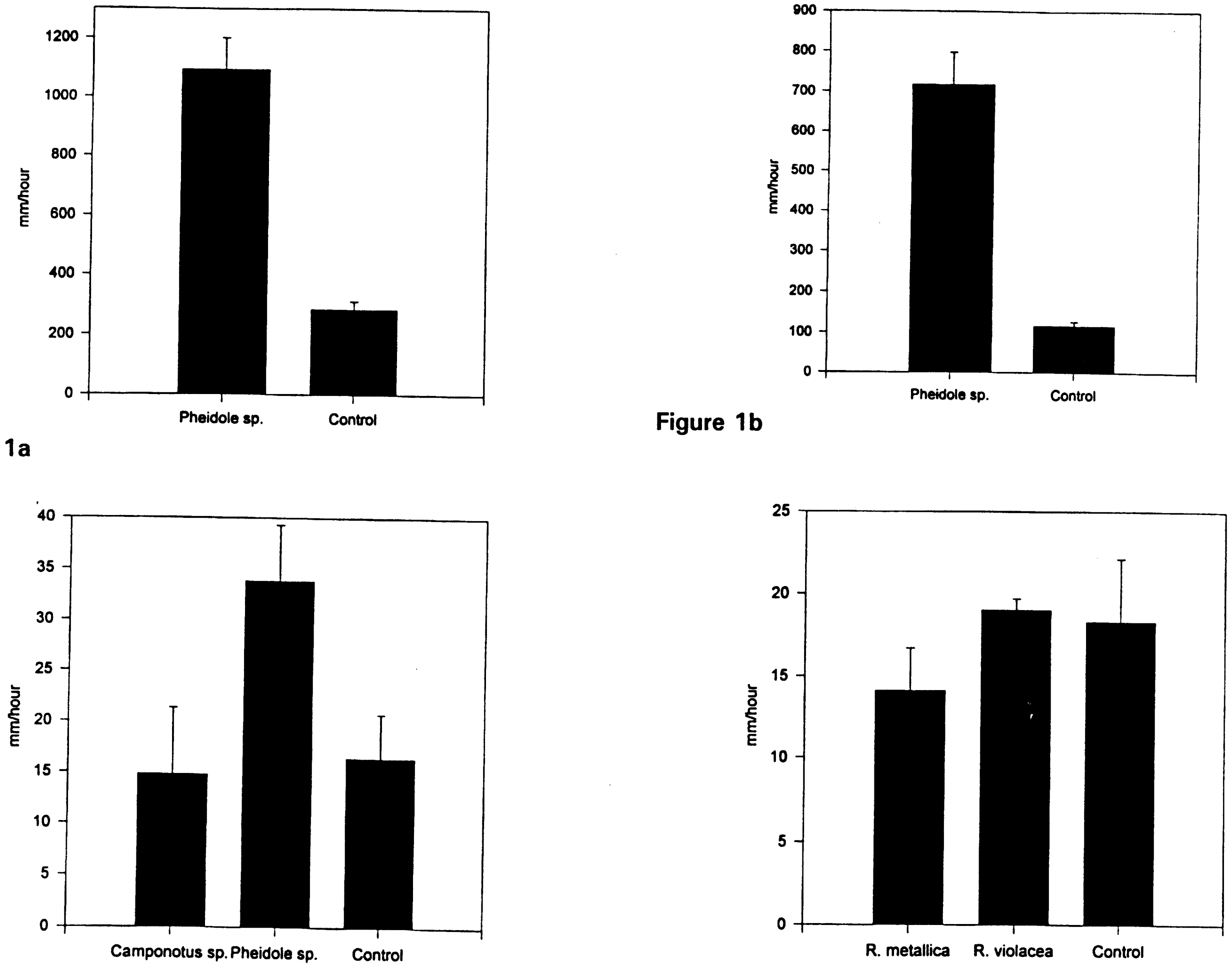

Figure 1a

Figure 1b

Figure 1c

Figure 1d

Figure 1—Effects of *Pheidole sp.* nests on ponded steady state infiltration into a yellow sand (a) and grey sandy loam (b) in farmland, of *Camponotus sp.* and *Pheidole sp.* into a grey sandy loam in a woodland (c), and of two *Rhytidoponera* species into a yellow sand under heath (d) in Western Australia. Data from Lobry de Bruyn and Conacher (1994).

movement through the soil, by cross-linking particles with their bodies (fungal hyphae, for example) and by generating products such as mucilages which act as binding agents. Fecal pellets are formed in a wide variety of shapes and sizes. Microarthropods produce pellets which are generally less than 1 millimeter in diameter (Lee and Foster 1991), while earthworm casts can be well over one hundred times that size (Edwards and Bohlen 1996). As fecal pellets tend to be relatively concentrated sources of energy and nutrients, they are rapidly colonized or consumed by other organisms in the detrital food web. In cattle dung patches colonized by both dung beetles and termites, fecal pellets produced by dung beetle larvae are rapidly attacked by termites (Herrick and Lal 1995). Some pellets, however, persist to form the nucleus for long-term stable aggregates. Earthworm casts, which are predominantly inorganic and therefore less susceptible to attack, may account for over 50 percent of the soil mass in some grassland soils (Lee and Foster 1991).

Table 3—Primary binding agents for aggregates of different diameters. Note that larger aggregates may be formed from smaller aggregates and/or from primary particles such as sand grains.

Aggregate Diameter (*μ*)	Primary binding agents
200 - 2000	Roots
	Hyphae
	Fecal pellets
20 - 200	Hyphae
	Bacteria
	Decomposition products
2 - 20	Persistent organic materials
<2	Primarily inorganic

The presence of fungal hyphae has been shown to promote stable aggregate formation in many grassland soils (Tisdall 1991; Degens and others 1996; Chantigny and others 1997). Organic amendments including manure lead to rapid increases in hyphal length density (Roldán and others 1996; Degens and others 1996). The impact of these amendments on aggregate formation appears to depend on environmental factors controlling extension of the hyphae away from the organic substrate into the surrounding soil (Degens and others 1996).

SOIL WATER HOLDING CAPACITY

Soil organisms affect soil water holding capacity through effects on pore volume and size distribution and on the content and form of soil organic matter. Increases in soil organic matter generally increase soil water holding capacity (Hudson 1994) both because of its high absorptive potential and because of its role in the formation and maintenance of soil structure. The water holding capacity of organic matter varies widely depending on its form. Carbon in the form of plant lignin holds relatively little water, but microorganisms can convert this to polysaccharides, which can retain many times their weight in water.

The most important pores for water retention are those located within soil aggregates. Water is held more tightly in small pores than in large pores and water in the smallest pores is unavailable to plants. Clay soils hold much more water than loamy soils, but much of this water is never extracted because it is tightly bound in microscopic pores. Information on soil water content is difficult to interpret without information on the tension of the water. The smallest pores inhabited by bacteria are on the order of 0.2 μ in diameter (Hassink and others 1993). This is the minimum pore diameter from which it is assumed that most plants can extract water (Marshall and others 1996), although there are reports of rangeland plants continuing to transpire at much lower (more negative) tensions.

RELATIONSHIPS TO VEGETATION

Soil hydrology, soil biota and vegetation are intimately linked in rangelands. While the discussion here emphasizes direct impacts of soil biota on infiltration, it is essential to consider the positive and negative feedbacks between soil biota, changes in the soil water regime and vegetative cover, composition and spatial distribution (fig. 2). Increases in plant production generally follow an improvement in the soil water regime in water-limited environments. Higher primary production means more material to support the soil food web, leading to a positive feedback loop. Other papers in this volume describe interactions between soil biota and vegetation. Plant canopy cover is frequently cited as the single most important factor controlling infiltration on rangelands (Spaeth and others 1996). Much of the strength of this relationship is probably due to the association of soil biotic activity with plants, as described above. However, plant canopies also directly enhance infiltration by protecting the soil surface from destructive raindrop impacts. Plant bases increase residence time by increasing tortuosity, slowing the movement of water across the landscape.

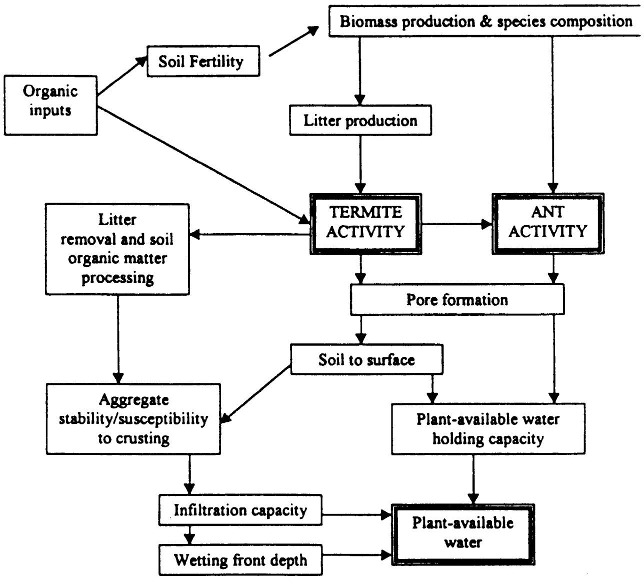

Figure 2—Simplified illustration of relationships between ant and termite activity, and changes in plant-available water.

Different types of soil organisms alter the hydrologic regime in different ways, affecting both the amount and vertical distribution of water in the profile. For example, anecic earthworms and deep-burrowing harvester ants may favor shrubs by rapidly conducting water to deeper soil layers, while epigeic worms and the smaller Dolichoderine ants would tend to concentrate water in the upper layers of the profile. Similarly, colonization of litter by different species of fungi will change the relative hydrophobicity of the soil surface, altering water redistribution patterns at the surface. Few of these soil organism-vegetation feedbacks have been explored and even fewer tested.

RESILIENCE

The contribution of soil organisms to the resilience of hydrologic functions following disturbance has received relatively little attention. Rangeland soils are constantly subjected to structural degradation caused by raindrop impact, overland flow, wind and the activities of both native and domesticated animals. These processes ultimately lead to physical crusting and compaction. Physical crusts limit infiltration at the surface. This type of crust is distinguished from biologically-stabilized crusts which can enhance infiltration in many cases (Belnap in this volume). Compaction reduces movement of water to deeper layers and can limit surface infiltration during prolonged storms.

The balance between structural degradation and recovery is a function of both biological and physical processes. The importance of biological processes increases in coarse-textured soils. In fine-textured soils charged clay particles bind to each other and to other particles when they are brought into contact by wet-dry and freeze-thaw cycles. In some cases, information on the contribution of soil organisms may be used to promote recovery of degraded systems (DePuit and Redente 1988; Whisenant 1996; Herrick and others 1997). There is a high potential to change the quantity and distribution of plant water availability in rangelands by manipulating soil organism populations through changes in disturbance regimes and organic matter inputs (Lee and Smettem 1995). However, with the exception of studies on earthworms in croplands, the inclusion of *Rhizobium* with seed, the addition of mycorrhizal fungi to extremely degraded mineland (Allen 1988), and the work on termites by Mando (1997), there have been few attempts to develop management tools which directly incorporate soil organisms.

The studies cited in this review, along with preliminary results from recently established studies in southern New Mexico (unpublished data) indicate that recovery of soil structure in a variety of rangeland ecosystems following both small and large disturbances depends on soil organism activity. Resilience is believed to increase with the number of species per functional group (Naeem 1998). Species redundancy appears to be extremely low for hydrologic functions in at least some rangeland ecosystems. For example only two species of termites (*Gnathamitermes tubiformans* and *Amitermes wheeleri*) contribute significantly to macropore formation in the northern Chihuahuan desert. The impacts of removing or limiting the activity of just these two species can be quite dramatic, as illustrated by the termite removal study described above (Elkins and others 1986).

SUMMARY AND CONCLUSIONS

Soil organisms have significant impacts on hydrologic processes and may play a key role in controlling water redistribution on the landscape across a broad range of rangeland ecosystems. These impacts vary across functional groups, microsites, plant communities and regions. Larger macroinvertebrates are responsible for macropore formation and for the breakdown and incorporation of litter, controlling the residence time on the soil surface. Smaller invertebrates, bacteria and fungi contribute to aggregate formation and thereby soil water storage capacity. An understanding of soil biology and the direct and indirect (through vegetation) effects on hydrology can already be used in some areas to direct or guide management practices involving soil surface disturbance and the removal or incorporation of organic matter.

ACKNOWLEDGMENTS

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QUESTIONS FROM THE FLOOR

Q: What is the relative importance of hydrophobicity for water infiltration in more xeric rangeland environs?

A: Hydrophobicity varies widely across both space and time in rangeland environments. It is commonly associated with the accumulation of decomposing litter under shrubs, but can also occur in interspaces between plants. In some rangeland environments it can be extremely important during at least part of the year, while in others it is scarcely evident.

Q: Do bacteria & fungi play a bigger role in infiltration rates with black grama (Bouteloua eriopoda) grasslands that are not degraded when compared to ants and termites?

A: I am not aware of any studies which have directly compared the relative contribution of these soil organisms to soil structure in black grama grasslands. All appear to be important. Shrub invasion of black grama grasslands is generally associated with a decline in soil lichen cover. The lichens are frequently replaced by cyanobacteria, which are less apparent, but more resilient. Fungal density is correlated with both live roots and with organic matter inputs. As the system moves from grass- to shrub-domination, these distribution of these resources become more patchy at the decimeter to meter scale. Ants and termites are ubiquitous throughout both degraded and non-degraded systems.

Q: You described binding agents for various size aggregates. Are these representative binding agents, in all ecosystems and if not, what agents occur in different ecosystems or soil types?

A: The binding agents which I described for various size classes of aggregates have been found to occur in all ecosystems. Elliott (1986) found that the basic model described here applies at least in general to a Nebraska prairie soil. However, the relative importance of each type of binding agent does vary across both ecosystems and soil types. Very little information is currently available, particularly for low-organic matter perennial-dominated rangeland soils. A USDA-University of Illinois study was initiated in 1998 to address this issue for the Chihuahuan Desert at the Jornada Experimental Range.

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