The Effects of Bioturbation on Soil Processes and Sediment Transport

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Key Words   soil production, tree throw, geomorphology, burrowing, landscape evolution

■ **Abstract**   Plants and animals exploit the soil for food and shelter and, in the process, affect it in many different ways. For example, uprooted trees may break up bedrock, transport soil downslope, increase the heterogeneity of soil respiration rates, and inhibit soil horizonation. In this contribution, we review previously published papers that provide insights into the process of bioturbation. We focus particularly on studies that allow us to place bioturbation within a quantitative framework that links the form of hillslopes with the processes of sediment transport and soil production. Using geometrical relationships and data from others' work, we derive simple sediment flux equations for tree throw and root growth and decay.

INTRODUCTION

In its infancy, the field of geomorphology focused on the form and identification of landscape features. The early 1970s, however, witnessed the emergence of studies on landscape processes and sediment transport (Saunders & Young 1983). With this new direction, geomorphologists began to formalize the relationships between process and form. For example, the evolution of a one-dimensional soil-mantled hillslope can be expressed analytically as (Dietrich et al. 1995)

$$\rho_s \frac{\partial h}{\partial t} = -\rho_s \frac{dq_{sx}}{dx} - \rho_b \frac{\partial e}{\partial t}, \tag{1}$$

where ρ_s, ρ_b are the bulk density (M/L^3) of soil and bedrock, respectively; h is the soil depth (L); t is time (T); q_{sx} is the sediment flux in the horizontal direction

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(L^3/LT); and e is the elevation (L) of the soil-bedrock interface. Note that q_{sx} represents a volume of sediment crossing a unit contour width of slope.

This equation states that the change in soil depth at any point on a hillslope is a function of the divergence of the sediment flux and the rate of conversion of bedrock to soil. Hidden within this simple equation lies a rich and complex suite of processes. Soil production occurs at the nexus of chemical weathering, the physical disturbance of bedrock, and hydrology. Soil can be transported by various processes, such as shallow landsliding, overland flow, and the shrinking and swelling of clays. Understanding the controls on hillslope sediment transport and soil production, as well as the functional relationship between hillslope characteristics and these processes, are important goals in geomorphological research.

Bioturbation plays an important role in both sediment transport and soil production on hillslopes. Bioturbation is generally defined as "the churning and stirring of sediment by organisms" (Bates & Jackson 1984). Historically, bioturbation studies have been the province of sedimentologists and stratigraphers, whereas the role of bioturbation in geomorphological processes has not been consistently appreciated. For example, Carson & Kirkby (1972) dismissed bioturbation as an important contributor to soil creep, and Young & Saunders (1986) categorized sediment transport by bioturbation as a "fringe process." In contrast, Davis & Snyder [(1898) as cited in Selby (1993)] attributed soil creep to soil animals and plant roots, Lehre (1987) found that biogenic creep is more important than inorganic creep, and Caine (1986) concluded that "sediment movement rates are increased by one or two orders of magnitude" in bioturbated areas on Alpine slopes.

Although we are most familiar with the animate world that lives above ground, many plants and animals are substantially invested in obtaining resources (e.g., nutrients, water, and mates) in the soil or seeking the protection of the soil from predators, consumers, or environmental variability. To do so, they must penetrate the soil vertically and horizontally. Consequently, they can have strong direct influences on the soil as they generate spaces by excavation or pushing soil aside. These, in turn, yield indirect effects on water movement patterns and soil biogeochemistry.

Plants, as primary producers, send roots into the soil to obtain water and nutrients. Their penetration is passive (i.e., not excavation, per se, but rather pushing aside the soil), although the pressure they exert can be immense. Between 20% and 85% of a plant's biomass may lie below ground. The highest belowground proportions are in the tundra, whereas the lowest proportions are in forests, where large amounts of biomass are tied up in dead wood (Jackson et al. 1996). In addition to soil transport, root growth and decay also leave behind macropores that may become preferential pathways for subsurface water flow (Beasley 1976, Mosley 1979, Montgomery & Dietrich 1995).

Animals consume the biomass produced by plants or consume other animals that eat plants. Many animals spend most or all of their lives below ground seeking food, shelter, and mates. Other animals may conduct most of their activity above ground, but live in dens constructed below ground. Generally, larger animals excavate soil

to construct dens or more elaborate burrow systems (Reichman & Smith 1990). The soil may be displaced to the surface or moved to unused portions of their tunnels. Smaller animals, including small snakes, worms, and other invertebrates, usually push their way through the soil, displacing particles for short distances away from their bodies.

Studies on the geomorphic impact of bioturbation have been extensively reviewed elsewhere (e.g., Butler 1995, Hole 1981, Viles 1988). In this contribution, we focus our attention on the main forms of bioturbation by plants and on the extensive excavation made by fossorial mammals, and we adopt Equation 1 as our guiding principle in developing quantitative approaches to understanding sediment transport and soil production by bioturbation.

PLANTS

Root Growth and Decay

OVERVIEW   Plants can mix soil by several processes: "(i) root expansion during growth; (ii) decay and infilling of former root channels; (iii) settling of the soil due to water extraction by roots; (iv) agitation of the plant during storms, which promotes root movement; and (v) uprooting" (Schaetzl et al. 1989). Here, we consider the processes for which there are quantitative observations: the first two and the last.

Bioturbation by roots has a profound impact on the soil. Roots penetrate the soil by growing from an area of rapidly proliferating cells at their tip. The root tip, called the apical meristem, is covered by a root cap, which is a protective layer of cells that are constantly ablated away as the root pushes into the soil. The growth occurs by the addition of cells and increases in the size of individual cells. As roots elongate, they may also expand in diameter through the proliferation of cells in the lateral meristems (primarily the vascular cambium). This vascular cambium, formed by differentiation from the apical meristem, forms a cylindrical sheath around the root. As the cells increase in number and size, the root swells, pushing away soil. The proliferation of cells is a function of the growth regime of the plant, which depends on day length, season, temperature, nutrients, and growth hormones. The increase in cell size is promoted by the imbibition of water, which can exert enormous pressures on the soil. Radial pressures can reach 0.91 MPa and axial pressures can be as high as 1.45 MPa (Bennie 1991).

These pressures are sufficient to break up bedrock. Tiny roots enter cracks in the bedrock where minute amounts of moisture and nutrients have accumulated. Root hairs first penetrate cracks as small as 100 μm (Zwieniecki & Newton 1995). Fine particles pack in around the root, providing surface contact for the absorption of water and nutrients and transferring the pressure of the growing root to the walls of the crack. The roots inexorably increase in length and girth, slowly splitting the rock apart (Matthes-Sears & Larson 1995). In general, roots only enter the softest of rock matrix through small cracks. However, there is evidence that roots can also

initiate intrusion through mineral dissolution (Stothoff et al. 1999). This effect is enhanced by mineral weathering, which in turn is affected by bioturbation and its influence on water flow (Hinsinger & Gilkes 1997, Kelly et al. 1998). Finally, Lutz (1960) reports that roots of Ponderosa pine have been seen at depths of 6–7 m in fractured granite.

HYDROLOGY   Live roots, and those that have recently died, occupy the spaces they have produced in the soil. When a root dies it begins to desiccate and contract, leaving some space in the soil tube it has formed. Eventually, when the root decomposes, it leaves macropores approximately the size of the root. The macropores left behind by plant roots can affect the infiltration of water. In a comprehensive study, Devitt & Smith (2002) investigated the effect of root channel macropores on the downward movement of water in the Mojave Desert. Using plots that had contained a creosotebush plant (*Larrea tirdentata*) in the past and plots that had not, they followed the movement of water into the soil under various watering regimes. Their results revealed that water moved deeper and more quickly in plots where these woody shrubs had grown. Furthermore, the pattern of movement was more heterogeneous in plots with the shrubs, indicating that water was moving along the macropores rather than as a uniform wetting front. Finally, the rate at which water moved through the soil was positively correlated with the size of the shrub when it was alive, suggesting that more roots of larger sizes promote the downward movement of water. Similarly, Williams & Vepraskas (1994) found that liquid dye markers penetrated a saprolite cap on a waste disposal site only 14 cm without bioturbation by roots, but 40 cm when roots had penetrated the saprolite.

Conceptually, a general relationship between macropores generated by roots and water movement is simple to envision, but quantifying it is more difficult. Noguchi et al. (1999) characterized macropores, most of which were associated with roots from forest trees. Their results indicate that although the macropores are not particularly long (ranging from 2.0 to 61.8 cm, with a mean of 11.6 cm), they interconnect with each other and other features of the soil matrix (soil horizons, bedrock, and fissures in the bedrock) to yield complex, preferential paths for water flow. The relative contribution of root macropores to the transport of subsurface flow should be strongly related to their persistence in the soil because, over time, these macropores will collapse. We are not aware of any study that has specifically addressed the issue of the longevity of intact root macropores; however, it might be reasonable to suggest that macropores will persist longer in cohesive soils and in soils that are subjected to lower rates of bioturbation.

SEDIMENT TRANSPORT   Although tree throw, the uprooting of trees, provides a dramatic example of bioturbation by plants, roots do not have to be ripped out of the ground to move sediment. The prosaic but unremitting process of root growth and decay also contributes to a downslope flux of soil. The mechanics of sediment transport by this process are similar to shrink-swell in clays and frost heave, where there is an initial expansion normal to the ground surface, followed by a vertical

collapse (Carson & Kirkby 1972). In the case of roots, expansion is provided by root growth that can apply axial pressures up to 1.45 MPa and radial pressures up to 0.91 MPa (Bennie 1991). These pressures are substantial and suggest that root growth could push up a column of soil approximately 100-m thick (assuming, of course, no internal deformation within the soil). When the root decays through the continual process of root turnover, the void left by the root is eventually filled by soil caving in from above.

A general slope-dependent equation for the horizontal volumetric flux of sediment (q_{sx}) by root growth and decay can be formulated as

$$q_{sx} = \frac{xr\tau}{\rho_r},\tag{2}$$

where x (m) is the net horizontal displacement of soil, r (kg m^{-2}) is the root mass per unit area, τ (year^{-1}) is the root turnover rate, and ρ_r (kg m^{-3}) is the density of root material.

A simple physical model can be constructed for transport by root growth and decay; the geometrical relationships between hillslope angle and transport distance are shown in Figure 1. Determination of the transport distance, x, in the manner shown requires that two assumptions be made. First, we assume that the soil is rigid and that none of the root growth strain is accommodated by changes in the bulk density of the soil. This removes the complication of root growth pressure locally compacting the soil rather than displacing it. Similarly, this assumption guarantees that the soil that falls in vertically to fill in the root void moves down
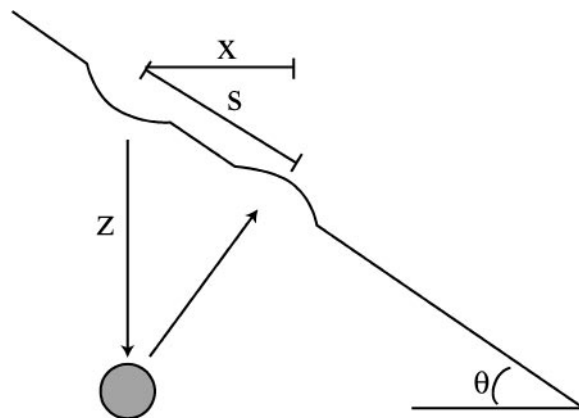
Figure 1   Illustration of geometrical relationships in the calculation of the horizontal distance of soil transport in the process of root growth and decay. The grey circle represents a cross-sectional view of a root. During root growth, soil is pushed in a direction normal to the soil surface. After the root dies, the soil collapses vertically into the root hole.

like a plug. In reality, a portion of the strain is probably accommodated by local density changes and it is likely that the proportion of strain leading to density changes increases with depth. Second, we assume that deformation during root growth acts along a slope-normal path, which, all things being equal, should be the path of least resistance. With these two assumptions, the following analysis therefore represents the maximum soil displacement possible.

From Figure 1, x can be calculated as a function of rooting depth with

$$x = z_c \sin \theta \cos \theta, \tag{3}$$

where z_c (m) is the vertical distance from the soil surface to the center of mass of the roots. Rooting depth, z (m), can be determined with

$$z = \frac{\log(1 - Y)}{100 \text{*} \log \beta}, \tag{4}$$

where Y is the cumulative root fraction from the surface to z and β is a fitted parameter that varies according to plant type (Gale & Grigal 1987). Root turnover, τ, is defined by Gill & Jackson (2000) as

$$\tau = \frac{annual\ belowground\ production}{maximum\ belowground\ standing\ crop}, \tag{5}$$

so that values of τ vary between 0 and 1 year^{-1}. For example, if all of a plant's roots die at the end of the growing season, the turnover rate would be 1 year^{-1} (Gill & Jackson 2000).

Inserting Equations 3, 4, and 5 into Equation 2 and setting Y to 0.5 to represent the center of mass of the roots, Equation 2 can be recast as

$$q_{sx} = \frac{-0.003r\tau}{\rho_r \log \beta} \sin \theta \cos \theta. \tag{6}$$

With a value of 800 kg m^{-3} for ρ_r and measured values for r, τ, and β, a slope-dependent flux equation can be determined for trees, shrubs, and grasses (Table 1). Figure 2 compares the form of the functional relationship between flux in the horizontal direction and hillslope angle with other processes discussed in this

TABLE 1 Parameter values for sediment flux by root growth and decay

Vegetation	β	r (kg m^{-2})	τ (year^{-1})	q_{sx} (m^3 m^{-1} year^{-1})
Temperate grassland	0.943	1.4	1.00	$2.1 \times 10^{-4} \sin \theta \cos \theta$
Sclerophyllous shrubs	0.964	4.8	0.60	$6.8 \times 10^{-4} \sin \theta \cos \theta$
Temperate forest	0.976	4.4	0.56	$8.8 \times 10^{-4} \sin \theta \cos \theta$

Notes: Values for β and r come from Jackson et al. (1996). Turnover rates are from a compilation in Gill & Jackson (2000) for a climate with a mean annual temperature of 20°C.
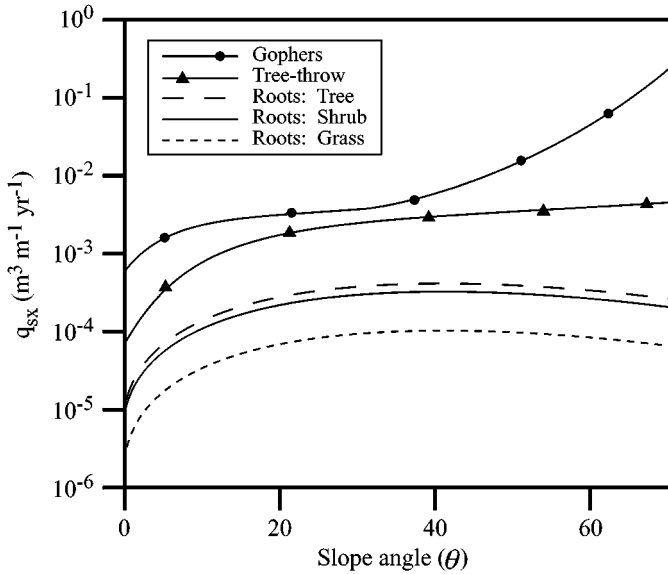
Figure 2   Comparison of the different forms of the relationship between sediment flux in the horizontal direction and slope angle. Functions for tree throw and root growth-and-decay are derived in this paper, whereas the function for the gopher bioturbation was developed in Gabet (2000).

paper. Gill & Jackson (2000) have demonstrated that turnover rates increase with increasing temperature, suggesting that the sediment flux by root growth and decay could increase with global warming.

We present sediment fluxes as fluxes in the horizontal direction (i.e., dq_{sx}/dx) because we are interested in the effects of bioturbation on hillslope evolution. Total sediment flux may also be of interest, for example, to predict sediment delivery into the fluvial network. The flux equations that we examine throughout this paper can be converted to predict total sediment flux with

$$q_s = \frac{q_{sx}}{\cos\theta}, \tag{7}$$

where q_s is the total volumetric sediment flux (m³ m⁻¹ year⁻¹), q_{sx} is the flux in the horizontal direction (m³ m⁻¹ year⁻¹), and θ is the hillslope angle (°).

Finally, Brimhall et al. (1991) investigated the vertical mixing of soil. They performed experiments with a pseudoroot made of surgical tubing buried vertically in a sandy matrix. They found that cyclic inflation and deflation of the pseudoroot caused material on the surface of the matrix to become mixed within the soil column. They also found that the mixing depth increased with the number of inflation-deflation cycles.

Tree Throw

SEDIMENT TRANSPORT   A tree is uprooted when the lateral forces on the crown and trunk exceed the ability of the roots and soil to hold it in place (Putz et al. 1983). Strong winds are often responsible for toppling trees (e.g., Kotarba 1970), although other causes may include overloading by snow, root decay of dead trees, and being knocked down by other falling trees [these are reviewed by Schaetzl et al. (1989)]. When a tree is uprooted and falls over, the root mass that binds soil and rock is rotated up, leaving a pit (Figure 3). As the roots' grip on the soil weakens
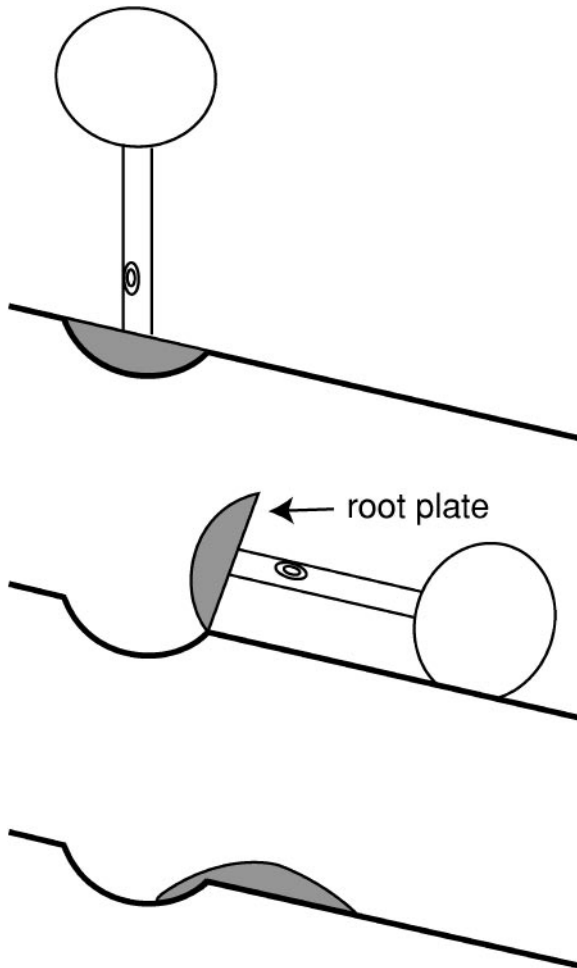
Figure 3   Illustration of the creation of pit and mound topography when a tree topples over.

through decay, the uprooted soil collects underneath, forming a mound. Schaetzl & Follmer (1990) estimated that this may take 5–10 years in the upper Midwest region of the United States; the rate may be higher in areas of greater rainfall. Mounds may be up to 1-m high (Norman et al. 1995); in planar view, they may be circular or elliptical, with the major axis perpendicular to the tree and radii of two to seven meters (Denny & Goodlett 1956). The relief of pit and mound features becomes more diffuse with time, although mounds may take several thousand years to completely disappear (Schaetzl & Follmer 1990). In a maple forest, Denny & Goodlett (1956) found that the rate of pit-filling is quicker than mound-flattening, and Putz (1983) made similar observations in a tropical forest in Panama. In the same forest, Putz (1983) measured pit-filling rates of up to 8.1 cm year^{-1}. Pit and mound pairs have been reported to cover over 40% of the land surface in northern temperate forests (Denny & Goodlett 1956), whereas covering only 0.09% of the surface in a tropical forest (Putz 1983).

One of the first systematic studies on soil transport by tree-throw was motivated by the effects of this process on soil morphology. Lutz & Griswold (1939) mapped the soil profiles of pit-and-mound features and documented the disruption caused by tree fall, such as an A horizon sandwiched between two B horizons. Denny & Goodlett (1956) were the first to quantify amounts of soil disturbed by tree throw.

Although others have also calculated rates of soil transport by tree-throw (Mills 1984, Reid 1981), no studies have derived an equation for predicting the sediment flux as a function of hillslope characteristics. We propose, therefore, a physical model to explore the relationship between sediment flux and hillslope angle. Two basic assumptions, supported by field observations, are required. First, we assume that trees topple over in a simple hinge fall (Beatty & Stone 1986) where the axis of rotation is at the downhill edge of the pit. Beatty & Stone (1986) report that this type of failure accounted for 70% of the uprooted trees that they observed. Second, we assume that after the tree is uprooted the root plate comes to rest at approximately right angles to the soil surface (Schaetzl et al. 1989). Figure 3 illustrates these two assumptions.

The sediment flux (q_s) by a process that occurs as discrete events can be calculated with

$$q_s = \frac{vol}{event} \times \frac{distance}{event} \times \frac{events}{area} \times \frac{events}{time}. \qquad (8)$$

The distance that soil is transported during an uprooting event can be predicted as a function of hillslope angle. The paths followed by the centroid of the root plate are shown in Figure 4 for a tree that falls directly uphill or downhill. We place the centroid of the root plate halfway between the soil surface and the pit depth (D). The center of mass of a similarly shaped object with uniform density would be closer to the flat edge (i.e., the ground surface), but this should be approximately compensated by the unequal distribution of lighter wood near the top and denser soil near the bottom. From the geometrical relationships in Figure 4, a tree falling directly uphill will displace the centroid of the root plate a horizontal distance, x_u,
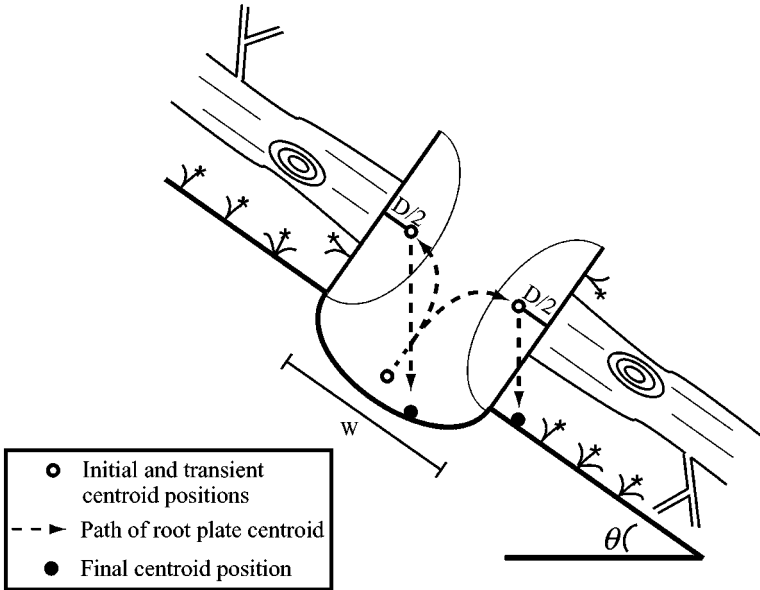
Figure 4 Diagram illustrating the geometrical relationships in calculating the transport distance of the center of mass of the root plate. A tree that has fallen uphill and one that has fallen downhill are both represented. Although the trees shown here appear to have grown normal to the soil surface, this is a simplification. In reality, trees will grow approximately straight up so that the angle between the uphill side of the trunk and the soil surface is 90-θ.

determined by

$$x_u = \frac{W}{2}(\cos\theta - \sin\theta) - \frac{D}{2}(\cos\theta + \sin\theta), \tag{9a}$$

where W is the width of the root plate. A tree falling directly downslope will transport the root plate centroid a horizontal distance, x_d, determined by

$$x_d = \frac{W}{2}(\cos\theta + \sin\theta) + \frac{D}{2}(\sin\theta - \cos\theta). \tag{9b}$$

Although, to our knowledge, there are no published measurements of center of mass transport distances, a distance of 1.7 m on a 4° slope can be estimated from Figure 30 in Denny & Goodlett (1956) for a tree that appears to have fallen directly downslope. With values of W and D estimated from the same figure, Equation 9b predicts a distance of 1.8 m, a reasonably close match.

Averaged over time and space, the net distance that soil is displaced is the difference between the transport caused by trees falling uphill and those falling downhill. We make the simplifying assumption that, over time, an equal number of trees fall in every direction. If α is the angle formed between a topographic
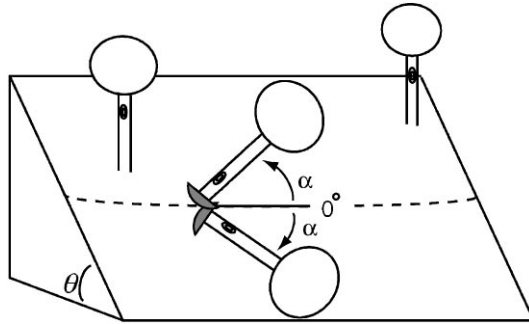
Figure 5 Alpha is the angle formed between a topographic contour line and the trunk of a downed tree.

contour line and the trunk of a downed tree (Figure 5), the mean values of x_u and x_d (Boas 1983) are

$$\overline{x_u} = \frac{2}{\pi} x_u \int_0^{\pi/2} \sin \alpha \, d\alpha = \frac{2}{\pi} x_u \qquad (10a)$$

and

$$\overline{x_d} = \frac{2}{\pi} x_d \int_0^{\pi/2} \sin \alpha \, d\alpha = \frac{2}{\pi} x_d, \qquad (10b)$$

respectively. Combing Equations 9a, 9b, 10a, and 10b, the long-term net horizontal transport distance is then

$$x_n = \overline{x_d} - \overline{x_u} = \frac{2}{\pi}(W + D) \sin \theta. \qquad (11)$$

A further elaboration on the transport distance would account for the downslope travel of particles after hitting the ground (Gabet 2002); however, this is beyond the scope of this review paper. This additional transport is supported by Norman et al. (1995), who observed that the downslope portion of mounds tend to be long and thin at steeper slopes.

With the transport distance calculated as a function of slope angle, a slope-dependent equation for the sediment flux can now be determined based on Equation 8 and data published by others. From data provided by Norman et al. (1995) for a deciduous forest, we choose values of 4 m for W and 0.7 m for D. The values for W and D are on the high end of pit measurements from Norman et al. (1995), but they were chosen because they most likely represent the original dimensions before the pits begin to fill. Root plate volumes estimated from pit volumes range from 0.2–5 m^3 (Norman et al. 1995), 0.3–10 m^3 (Putz 1983), and averages of

1.8 (Mills 1984) and 4.8 m^3 (Denny & Goodlett 1956). Reid (1981) directly measured root plate volumes and reported an average of 4.0 m^3 and a range of 1–15 m^3. For consistency with the root plate width, we choose one of the larger volumes from Norman et al. (1995), 4 m^3, and assume that volumes are not slope-dependent. Although Schaetzl & Follmer (1990) and Norman et al. (1995) report that pit volumes increase with slope, this is likely a result of more soil falling back into the pit on gentler slopes (Norman et al. 1995). In areas of thin soils, rooting depth may be limited by soil depth, and thus pit volume might depend on topographic position. For simplicity, we assume that soils are sufficiently deep. We also assume that uprooting events are uniformly distributed in time and space. Published estimates of uprooting rates include 8–13 trees ha^{-1} year^{-1} in a lime and hornbeam forest (Falinski 1978), 0.13–0.21 trees ha^{-1} year^{-1} in a sugar maple and beech forest (Brewer & Merritt 1978), 8 trees ha^{-1} year^{-1} in a Northern hardwood forest (Mills 1984), and 0.84 trees ha^{-1} year^{-1} in an oak forest [Naka (1982) as cited by Schaetzl et al. (1989)]. Substituting Equation 11, a pit width of 4 m, a pit depth of 0.7 m, a mound volume of 4 m^3, and an uprooting rate of 4 trees ha^{-1} year^{-1} into Equation 8, the sediment flux equation is

$$q_{sx}(m^3\,m^{-1}\,yr^{-1}) = 4.8 \times 10^{-3} \sin\theta. \qquad (12)$$

Equation 12 predicts a horizontal flux of 8×10^{-4} m^3 m^{-1} year^{-1} on a 10° slope. For comparison, Reid (1981) estimated a total flux of 9.6×10^{-4} m^3 m^{-1} year^{-1} in a coniferous forest, and data from Denny & Goodlett (1956) can be used to estimate a total flux of 9.8×10^{-4} m^3 m^{-1} year^{-1} in a maple forest [Denny & Goodlett (1956) made an error in calculating mound volumes (Mills 1984), so the flux presented here is based on the corrected volumes]. From data presented by Kotarba (1970), a horizontal flux of 0.11 m^3 m^{-1} can be calculated for a 4-hr period of high winds in the Tatra Mts. in Poland. The flux from tree throw calculated from Equation 12 is compared to fluxes by other bioturbation processes in Figure 2.

There is a strong relationship between root plate volume and the diameter of the trunk (Mills 1984, Putz 1983, Reid 1981), and Putz (1983) reports that root plate volume is proportional to the trunk diameter squared. Changes in the forest composition or the age distribution of trees through land management strategies or climate change, therefore, could alter rates of sediment flux and sediment delivery. For example, Denny & Goodlett (1956) note that pit volumes in a second growth forest are significantly smaller than in the original forest. Furthermore, smaller trees are more likely to be snapped rather than uprooted (Putz et al. 1983).

Changes in climate may affect the mechanics of tree-throw. Peltola et al. (1999) found that frozen soils help to prevent trees from toppling over during windy, winter storms. Warmer winters at high latitudes will lead to a decrease in soil freezing that will reduce the soil's ability to anchor tree roots when root support is most needed (Peltola 1999). Finally, as an interesting side-note, Denny & Goodlett (1956) found that pit-and-mound features trend toward the prevailing wind direction on level land. This layer of soil slowly creeping after the wind challenges the assumption of no flux at zero gradient for slope-dependent processes.
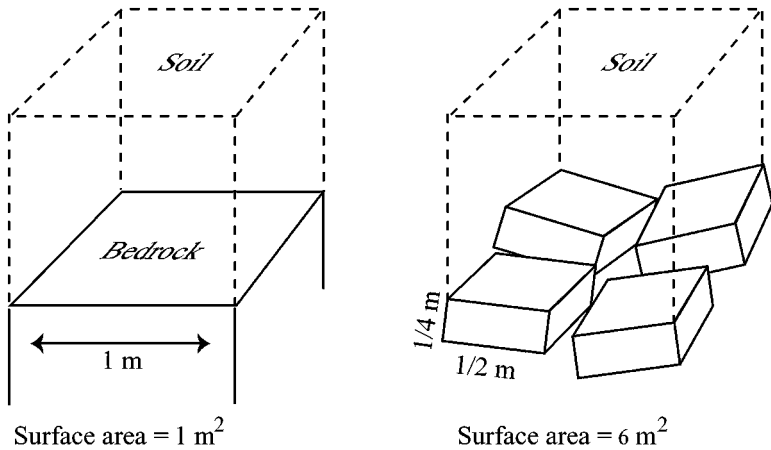
Figure 6   The mechanical disruption of bedrock increases the surface area available to chemical weathering. On the left, the available surface area on the unbroken bedrock is the plane between the soil and the bedrock. On the right, mechanical break-up of the bedrock to a depth of 0.25 m yields a sixfold increase in the surface area exposed to chemical weathering.

SOIL PRODUCTION   The production of soil involves the mechanical break-up as well as the chemical weathering of bedrock. Positive feedbacks between these processes can greatly increase soil production rates. For example, chemical weathering may weaken bedrock and render it more vulnerable to mechanical disturbance, whereas the break-up of large blocks of bedrock into smaller, more "digestible" pieces will increase rates of chemical weathering. Fragmented bedrock weathers more rapidly than an equivalent volume of intact bedrock because chemical weathering processes act on exposed surfaces (Sverdrup & Warfvinge 1988). An increase in exposed surface area by mechanical break-up is illustrated in Figure 6.

Lutz (1960) and Mills (1984) give examples of bedrock being broken up and unearthed by tree throw. Lutz (1960) noted many instances where fresh rock was torn out of bedrock and found two bedrock fragments measuring 1.4 m^3 that had been moved nearly 2 m. Lutz (1960), Mills (1984), and Ruel (2000) report that trees on shallow soils are more likely to fall over than those on deeper soils; Lutz (1960) attributes this to a paucity of bracket roots in trees growing in thin, rocky soils. In bouldery areas nearly devoid of soil, however, Mills (1984) found that trees were less likely to fall over because of the secure anchoring provided by the rock.

The observations by Lutz (1960), Mills (1984), and Ruel (2000) reported above suggest an interesting relationship between soil depth and mechanical disturbance of bedrock by tree throw. On surfaces with little soil, trees will have difficulty becoming established (Childs 1981, Helgerson 1981) but those that do are not likely
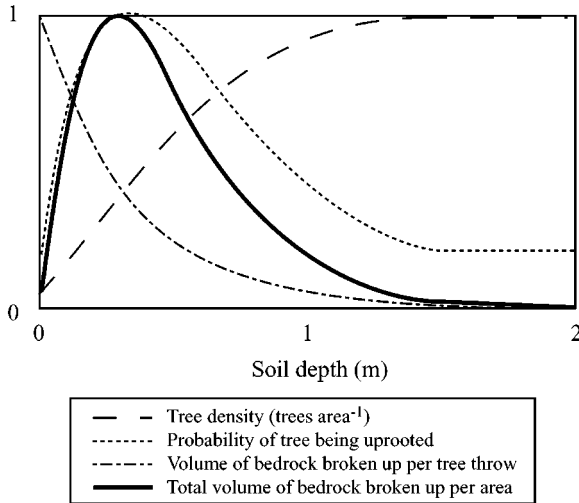
Figure 7 The relationship between soil depth and the volume of bedrock disturbed by tree throw is a product of three other relationships: (*a*) the number of trees per area, (*b*) the probability of trees being uprooted, and (*c*) the volume of bedrock disturbed during a tree throw event. These hypothetical functions have been normalized so that unity represents the maximum.

to blow over and rip out bedrock (Mills 1984). Rates of mechanical disturbance by tree throw, therefore, will be low (Figure 7). As soils thicken, trees are more likely to become established and the roots will be anchored to a greater proportion of soil, increasing the likelihood of being blown over and disturbing bedrock. As soils become even deeper, fewer roots are able to anchor themselves to bedrock and the rates of mechanical disturbance by tree throw should decline. The functional relationship between soil depth and mechanical disturbance represented in Figure 7 implies both positive and negative feedbacks if we assume that the mechanical break-up of bedrock is a limiting process in soil production. At soil depths to the left of the maximum in Figure 7, mechanical disturbance by tree throw increases with increasing soil depths, and increasing soil depths raise the likelihood of mechanical break-up. At soil depths to the right of the maximum, increases in soil depth will decrease the amount of bedrock broken up by tree throw. The shape of the function in Figure 7 is similar to the one proposed by Carson & Kirkby (1972) for the relationship between the rate of bedrock weathering and soil depth and also similar to the one suggested by Dietrich et al. (1995) for the relationship between soil production rate and soil depth, where the biota is an important factor in the mechanical disruption of bedrock.

SOIL DEVELOPMENT   The overturning of soil by tree-throw recognized by Lutz & Griswold (1939) was studied in greater detail by Bormann et al. (1995). Bormann

et al. (1995) concluded that tree-throw in Alaskan spruce and hemlock forests homogenizes soil and that, in its absence (e.g., because of logging), horizonation increases. In particular, they found that without the churning of soil, nutrients accumulate in the O and Bh horizons. Additionally, after 250–300 years, roots become confined to the O horizon because the Bh becomes relatively impermeable to water. Once the tree roots are restricted to the O horizon, any tree-throw that may occur will only mix the organic layer, and this "may cause the site to become excessively organic and reduce the productive potential of the soil" (Bormann et al. 1995). Ulanova (2000), working in boreal spruce forests in Russia, found that soils disturbed by shallow-rooted tree throws recovered to background soil characteristics in 100–200 years, whereas deeper uprootings took 200–300 years to recover. Before fully recovering, throw sites experience significant heterogeneity in local soil processes. For example, Millikin et al. (1996) measured CO_2 fluxes on pits, mounds, and adjacent control microsites and found that the fluxes from the pits were approximately 50% less than on undisturbed sites. They attribute the difference to changes in organic matter, root distribution, and soil microclimate.

ANIMALS

Invertebrates

Soil provides a rich medium in which invertebrate animals live. Many of the invertebrates that live underground (e.g., earthworms, beetle larvae, mites, and nematodes) move through the soil by pushing particles aside as they wedge into the interstices. Other common groups, such as termites and ants, actually excavate large quantities of soil. In either case, the animals physically alter the soil through bioturbation. Furthermore, some animals consume organic matter underground, further affecting soil structure and biogeochemistry.

The abundance of soil invertebrates is staggering (Viles 1988). The numbers of individuals range from tens to tens of millions per m^2, representing biomasses of 10–15,000 kg ha^{-1} (Coleman & Hendrix 2000). Reports indicate that earthworms may move between 5.4×10^{-4}–0.01 m^3 m^{-2} $year^{-1}$ of soil, ants may move 4.5×10^{-6}–1.8×10^{-3} m^3 m^{-2} $year^{-1}$, and termites may move 1.3×10^{-5}–4.1×10^{-4} m^3 m^{-2} $year^{-1}$ (Michell 1988, Whitford 2000) (note that these are volumes of soil displaced per unit area and are not sediment fluxes because they do not consider net transport in any particular direction). Clearly, the number of burrows made by these animals and the amount of soil they excavate potentially have significant influences on the soil. In addition, the specific activities of the various taxa generate characteristic impacts.

Earthworms are large, abundant, and active, and hence their effects on soil have been well studied. Earthworms excavate tunnels (∼5 mm for the large species) in the soil that may collapse or retain some of their form from mucilage excreted as they dig (Edwards & Shipitalo 1998). The macropores generated can increase soil porosity by 3–10-fold (Edwards & Bohlen 1996). The macropores reduce surface

runoff, increase infiltration of water into the soil adjacent to the pore walls, and promote aeration of the soil.

Earthworms consume soil, significantly altering its biochemical makeup and altering soil particle size as ingested particles are broken down during digestion. The casts (feces) left by earthworms are often compact and nutrient-poor. As the soil passes through an earthworm, the casts are bound together by internal secretions of the worm, plant and fungal fibers eaten by the worm, bacterial gums produced as byproducts of the ingestion of bacteria, and the formation of organo-mineral bonds (Edwards & Bohlen 1996). Casts generally decrease the rate of typical soil processes, such as decomposition and biochemical reactions (Edwards & Shipitalo 1998). The amount of cast material varies by species and soil type, but it can range from 3.9×10^{-4}–$9.2 \times 10^{-3} \, \text{m}^3 \, \text{m}^{-2} \, \text{year}^{-1}$ (Edwards & Bohlen 1996). The vertical mixing resulting from cast deposition on the soil surface inhibits soil profile formation.

Earthworm casts left on the soil surface are also an easily transported supply of sediment. Sharpley et al. (1979) showed that pastures with earthworms exhibited sediment runoff loads of $1.1 \times 10^{-4} \, \text{m}^3 \, \text{m}^{-2} \, \text{year}^{-1}$, whereas areas from which earthworms had been removed delivered only $2.9 \times 10^{-5} \, \text{m}^3 \, \text{m}^{-2} \, \text{year}^{-1}$. Although sediment loss by overland flow increased in the presence of earthworms, phosphorus and nitrogen loss was less in plots with earthworms because of the increased infiltration capacity of the soil.

Ants are social insects that can exist in large colonies that construct complicated burrows deep into the ground. In the process, they move tremendous amounts of soil (see above). Ants tend to be absent in very fine-grained soil, and are selective in the grain sizes that they move about. This has the effect of increasing the spatial heterogeneity in soil grain size (Whitford 2000). In general, ants appear to decrease soil bulk density (de Bruyn & Conacher 1994).

Ant burrows are complicated and extensive, forming a network of macropores underground. The macropores tend to be most concentrated near nest openings, and hence hydraulic conductivity is highest in these areas (Whitford 2000). Eldrige & Pickard (1994) found up to 37 nest entrances per m^2 and measured infiltration rates of 140 cm h^{-1} (almost four times the background infiltration rates) in Australia. The effect of ant mounds and burrows on infiltration is complex, with the openings promoting infiltration, whereas the packing of soil around mound openings may promote runoff (de Bruyn & Conacher 1994).

In addition to the effects of ants on the physical structure of soil, they also alter soil chemistry. Ants often carry dead plant or animal material below ground, where it decomposes. As the decomposed material mixes with the soil it is redistributed in less concentrated locations. Although this may increase soil carbon and nitrogen, the increases may not be significant (de Bruyn & Conacher 1994).

Termites have many of the same effects on soils as ants. Termites excavate large galleries below ground and in some cases build large, indurate towers of soil above ground. The soil mass moved by termites ranges from 1 to 10^6 g ha^{-1} year^{-1},

with surface accumulations ranging from 0.0125 to 2 mm year^{-1} (de Bruyn & Conacher 1994).

Vertebrates

Many species of mammals burrow into and through the soil (Reichman & Smith 1990). Most excavate dens that serve as refugia when the animals are not active above ground. Although dens can be extensive, they are usually stable through time with relatively few extensions or modifications. Fossorial mammals, however, spend virtually their entire lives below ground, where they search for food and mates. Thus, they are constantly producing new burrows, generating a much greater impact on the soil than those species that simply construct dens.

Moles, insectivorous burrowing mammals, generally push soil aside with powerful forelimbs. Although little is known about their effect on soils, Mellanby (1971) indicated that European moles increased soil porosity and affected soil microtopography. Schaefer & Sadlier (1981) found similar effects and noted that moles tended to decrease soil bulk density while increasing soil moisture and earthworm densities, an interesting interaction between moles and another prominent bioturbator.

Although herbivorous fossorial mammals occur on all continents except Antarctica and Australia [although Australia hosts a marsupial mole that burrows through sand dunes (Nevo 1979)], relatively little is known about the influence of most species on soils except for the North American geomyids (pocket gophers). Gophers occur over much of the North American continent west of the Mississippi River and in the Southeast. Their impacts on soil can be profound (Reichman & Seabloom 2002). The rodents excavate long burrows and place the loose soil on the surface as mounds or pack it into abandoned burrows (at a bulk density lower than the surrounding matrix). Digging burrows through the soil is very costly [300–3400 times as expensive as walking a similar distance (Vleck 1979)] and thus the animals must eat substantial amounts of vegetation.

The biomass of roots decreases with depth, so an animal foraging on roots would have the greatest success at the shallowest depths. This is countered by the requirement that the burrows be sufficiently deep to maintain their structural integrity. Optimal depth varies with soil type, but generally burrows occur from 10–30 cm below the surface (Miller 1957, Thorn 1978, Vleck 1981) with dens extending down to approximately 1 m (Mielke 1977). Burrow diameters are very close to the diameter of the rodents (5–25 cm) and lengths range from a few meters to almost 100 m [(Reichman & Smith 1990); note that African naked mole-rats, which are social and live in large colonies, can have burrows more than 1 km long (Sherman et al. 1991)]. Smallwood & Morrison (1999) analyzed the burrow excavation dynamics of six species of gophers from North America. The amount of soil excavated ranged from 3.4 to 57.4 m^3 ha^{-1} year^{-1} with an average of 17.8 m^3 ha^{-1} year^{-1} across all species. Burrows may underlay 7.5% of an area, whereas mounds can cover 5%–8% of an area at any one time (Reichman &

Seabloom 2002). The soil associated with the disturbances around burrows and in and around mounds is biogeochemically different from the background soil matrix. Depending on the original conditions and such features as soil type and rainfall, the disturbed soil may be higher or lower in nutrient content, moisture, cations, or pH (Reichman & Seabloom 2002). Gophers are also thought to be responsible for the formation of a stone zone in some areas. These are layers of stone larger than gophers can transport through their burrows that accumulate at a depth just below the bottom of a typical burrow (Johnson 1989). Gradually, bioturbation by gophers leaves behind these larger stones, forming a layer that is nongeological and postdepositional in nature.

The net effect of gophers is to mix soil vertically and generate patchy soil conditions horizontally. Mixing takes place when gophers bring soil to the surface and when burrows collapse. Lateral heterogeneity is generated by the patterns of burrows [highly uniform (Reichman et al. 1982)] and mounds [clustered (Klaas et al. 2000)]. Plant biomass is usually decreased in burrows (due to consumption) and mounds (covering and killing plants), further promoting heterogeneity. Gopher excavation also accelerates physical processes, such as downslope soil movement (Gabet 2000), movement of water (Montgomery & Dietrich 1995), and even gully formation (Swanson et al. 1989) to the extent that the magnitude of the effects constitute a major factor in soil movement (Black & Montgomery 1991).

SEDIMENT TRANSPORT   It is difficult to walk along a hillslope inhabited by pocket gophers without suspecting that they must be a dominant mover of sediment. Gophers displace soil while burrowing underground to eat plant roots (Vleck 1981). Ellison (1946) and Thorn (1978, 1982) estimated the rates of soil disturbance by gophers in Alpine environments, and Black & Montgomery (1991) calculated flux rates in the coastal ranges of northern California. Two of these studies (Black & Montgomery 1991, Thorn 1978) found that gopher activity was the dominant mode of sediment transport.

Gabet (2000) developed a slope-dependent sediment transport equation for gopher bioturbation on the basis of field measurements. Gabet measured subsurface and surface transport distances, mound volumes, and mound production rates. He found that the sediment flux could be predicted as a function of slope so that

$$q_{sx} = 0.018(\tan\theta)^3 - 0.019(\tan\theta)^2 + 0.007\tan\theta + 0.003(\tan\theta)^{0.4}. \quad (13)$$

This function is complex because it incorporates both burrowing behavior and the physics of soil particles rolling down a slope. In Figure 8, the function represented by Equation 13 is compared to a function that represents the physical process of particles rolling down a rough surface (Gabet 2002). The difference between these two curves can be explained by burrowing behavior. The net subsurface transport distance is nearly constant at all slopes (Gabet 2000, Seabloom et al. 2000) so that the shape of the bioturbation curve in Figure 8 is almost entirely due to changes in the surface transport distance.

On a flat surface, the mound is donut-shaped with the tunnel outlet in the middle. If the creation of the mound were a purely physical process, the distance
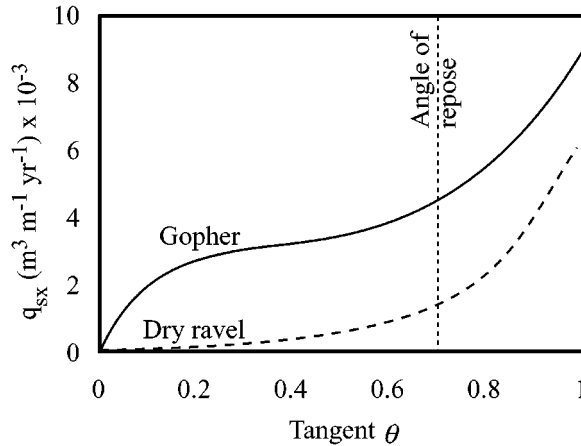
Figure 8 Sediment flux by gopher bioturbation compared to the flux by a purely physical process. At low gradients, the bioturbation flux is strongly controlled by burrowing behavior. At steeper gradients, the physical processes dominate, such that the relationship between sediment flux and gradient for bioturbation is similar to the raveling of particles down a rough surface.

between the center of the donut and the tunnel outlet would gradually increase as slopes became steeper. It is more bioenergetically efficient, however, to push the soil out of the downhill side of the tunnel outlet rather than the uphill side such that, as the slopes begin to increase beyond zero, the majority of the mound material is being pushed directly downhill (Seabloom et al. 2000). Pushing the sediment out of the downhill side also prevents it from falling back into the burrow. This behavior, then, causes the steep rise in flux from 0 to 0.2 (Figure 8). At gradients greater than 0.2, the physical processes dominate and the two curves resemble each other as the fluxes increase sharply beyond the angle of repose. Whereas it might be expected that the sediment flux would go to infinity as it approaches the angle of repose, vegetation and surface topography inhibits the downslope movement of the sediment. The relationship between flux and slope angle for gopher bioturbation is compared to other forms of bioturbation in Figure 2.

MIMA MOUNDS   The origin of Mima mounds has mystified scientists for decades. Generally found in the western United States, these circular mounds of dirt can reach up to 2 m high with a diameter of 25–50 m (Cox 1984). Of the many hypotheses proposed to explain their creation, the fossorial rodent hypothesis (Dalquest & Scheffer 1942, Scheffer 1947) has been the one most investigated and its chief proponent has been Cox (1984, 1990, Cox & Allen 1987). Cox has presented convincing evidence that pocket gophers maintain, and may create, Mima mounds. In two separate investigations, Cox (1984, 1987) used metal markers to determine that gophers at a Mima mound site preferentially moved soil towards the

center of the mounds. This finding indicates that the gophers were moving soil uphill, which is surprising considering Gabet's (2000) results, which indicate a net downhill movement of soil from gopher activity. This discrepancy suggests that, for the Mima mound gophers, the advantages of creating the mounds outweigh the increased bioenergetic costs of moving soil uphill rather than downhill. Mima mounds often occur in areas where the soils are waterlogged (Cox 1984), so the construction of the mounds may be an adaptive behavior to create better living conditions or to enhance plant growth (Dalquest & Scheffer 1942, Mielke 1977).

SOIL PRODUCTION   Because gophers are efficient bioturbators, it is natural to hypothesize that they may be instrumental in converting bedrock to soil (e.g., Heimsath et al. 1999). An examination of their foraging strategy as well as the bioenergetic costs associated with shearing soil suggests, however, that gophers may only play a minor role in the mechanical breakup of bedrock. Pocket gophers mainly burrow 10–30 cm below the soil surface (Miller 1957, Thorn 1978, Vleck 1981) to eat underground plant parts (Vleck 1979); therefore, they are unlikely to tunnel into bedrock or saprolite that is either too deeply buried or too coherent to contain the fine roots favored by the gophers. Gophers occasionally build nests that are up to 1 m deep (Mielke 1977); however, these are semipermanent features that occupy only a minute portion of the landscape. Further, Vleck (1979) has shown that the bioenergetic costs of shearing soil increase rapidly with soil cohesion and bulk density so that the energy required to shear clay is 10 times greater than sand. Extrapolating those results would suggest that the high energy costs would preclude any significant burrowing in saprolite or bedrock.

Mountain beavers (Family Aplodontidae) have also been hypothesized to be significant actors in the breakup of saprolite and bedrock (Heimsath et al. 2001), but their role is also probably a minor one. Not only do mountain beavers forage for food above ground (Beier 1989, Steele 1989) so that their tunneling activity is less than the gophers, but, similar to gophers, the main burrow network is generally no deeper than 30 cm, except for the deeper nesting chambers (Steele 1989) that may occasionally reach depths of 2 m (Nolte et al. 1993). Additionally, Fitts (1996) notes that mountain beavers "live in soft soils that permit efficient burrowing," another indication that mountain beavers may not dig much into bedrock and saprolite. Whereas they may not greatly affect rates of soil production by mechanical disturbance, fossorial mammals may indirectly accelerate the chemical weathering of bedrock by decreasing the bulk density of the soil, thereby increasing its hydraulic conductivity and bringing already-fragmented pieces of bedrock closer to the soil surface (Heimsath et al. 2001) where weathering rates may be higher; however, we are not aware of any research on this topic. Although the available evidence suggests that these fossorial mammals may not be important contributors to the breakup of bedrock, there is clearly a need for detailed studies of this issue.

BIOTIC INTRUSIONS INTO WASTE SITES

Bioturbation has important consequences in the natural processes of all ecosystems as plants and animals penetrate and mix soil. Although these effects are characteristic of ecological systems, they can cause significant disruptions in the burial of hazardous wastes where the intention is to maintain a set of conditions below ground. When wastes are buried, the goal is that the material not be mixed in with the soil (and particularly not be brought to the surface) and that the waste material not seep into the water table. As shown, mixing and increases in infiltration capacity are two of the most common results of bioturbation.

A number of studies have been conducted to identify and quantify the effects of biointrusion into waste sites (Smallwood et al. 1998). In a thorough review of the effects of plants and animals, Bowerman & Redente (1998) documented the role of biointrusion as a factor in disrupting the integrity of stored hazardous wastes.

Plants are often an integral part of planning for waste storage because they generally reduce erosion. However, roots both alter soil profiles and can penetrate putative barriers. Bowerman & Redente (1998) reviewed a number of barrier types and concluded that none are sufficient to preclude root intrusion.

In their review of ants and termites, Bowerman & Redente (1998) found a number of studies suggesting that these invertebrates penetrate barriers and concentrate wastes (in this case radioactive wastes) in the surface mounds. Bowerman & Redente's (1998) review also includes the burrowing effects of mice, kangaroo rats, pocket gophers, ground squirrels, and prairie dogs, and the authors conclude that these burrowing mammals dig deep enough to encounter most barriers. Furthermore, all of the types of barriers studied, which included materials such as gravel, cobble, tuff, crushed rock, and asphalt, were vulnerable to penetration. In those few cases in which the actual spread of radioactive wastes was studied, radionuclide concentrations were much higher among animals that penetrated the barriers compared to controls. In addition to the direct intrusion by animals, their burrows can provide entry sites for roots, exacerbating the problem.

The Bowerman & Redente's summary concludes that prairie dogs, deeply penetrating roots, and harvester ants present the greatest threat to barrier integrity. The greatest effects of biointruders are indirect and mediated through changes in soil bulk density, macropore size and abundance, and water infiltration rates (Bowerman & Redente 1998). They caution that barrier design must include consideration of normal ecological processes as well as engineering criteria.

CONCLUSION

In this contribution, we have reviewed previously published papers that provide insights on bioturbation. We have focused primarily on studies that shed light on the link between the processes of sediment transport and soil production and the form of hillslopes. Bioturbation is, undeniably, a key geomorphological factor in

many landscapes and we hope that this review may stimulate others to investigate it while using the continuity equation as a guiding principle.

ACKNOWLEDGMENTS

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