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Original article

The soil structural stability of termite nests: role of clays in *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mound soils

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Abstract

Fungus-growing termites enrich their nest structures with clays and can modify the mineralogical properties of silicate clays. In order to determine the role of clay in soil structural stability of mounds, we measured the physico-chemical properties and the water behaviour of termite mound soil. Two opposing tendencies control the structural stability of termite mound soil: (i) the increase of clay content in the mound leading to a decrease of pore sizes and rate of water diffusion; and (ii) the swelling of 2:1 clay types when water penetrates into the soil leading to a breakdown of the mound soil. Although soil organic matter (SOM) is usually considered as a cement ensuring the soil structural stability of mound soil, this study shows that SOM has a negligible role and that clay can be considered as a key component to understand the structural stability of *Macrotermes* mound soil.

Keywords: Fungus-growing termites; *Macrotermes bellicosus*; Soil structural stability; Clay

1. Introduction

Some large soil invertebrates have significant effects on soil structural properties, the most important being earthworms, termites and ants [16]. They build organo-mineral structures of different stability such as galleries, casts, sheetings, fungus-comb chambers and mounds. Termites, particularly fungus-growing species (Termitidae, subfamily Macrotermitinae), are often the dominant invertebrate group in tropical and subtropical habitats. Through their actions, fungus-growing termites greatly modify their immediate environment by increasing the clay content and decreasing the organic matter content and porosity in soil [2,13,14,19] in soil [13,14]. The proportion of clay in termite nests is always higher than in the bulk soil, often highest in the royal cell and lowest in the outer wall. Jouquet et al. [15] showed that soil handling by termite workers can modify the mineralogical properties of silicate clays, creating expandable clay minerals. On the other hand, Leprun and Roy-Noël [20] showed that termites are very sensitive to the type of clay and a significant relationship was found between soil clay mineralogy and the presence of some termite species. Therefore, these studies suggest that clay may play a key role in the termite building activity, and then in the properties of termite-built structures.

Soil structural properties, particularly soil organic matter (SOM) and clay content and quality, play key roles in controlling soil structural stability through their influence on water sorptivity and repellency as well as on the strength of bonds between particles [3,22]. Rainfall is the main natural agent responsible for the breakdown of soil aggregates and its effect is threefold: (i) raindrop impact destroys aggregation; (ii) splash detaches soil aggregates and particles; and (iii) runoff removes soil [3]. The susceptibility of a soil to these effects is often evaluated with measurements of aggregate stability. Most results indicate that the aggregates of termite mound soils are only slightly more stable than surface soil in the vicinity of the mound [8,11]. Observations

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that the structure of fungus-growing mounds can last for many decades [9], despite the violent rainfall events that occur in tropical and subtropical climates, would appear to be in contradiction with aggregate stability measurements.

The aim of this study was to investigate this apparent contradiction and to determine the role of clay in the soil structural stability of fungus-growing termite mound soils. First we determined the physical and chemical properties of control and termite mound soils and second, we examined their effects on water retention and movement.

2. Materials and methods

2.1. Study site and data collection

Soil samples were collected in Côte d'Ivoire, near the Lamto Ecological Station (6°13′N, 5°02′W) at the margin of the rain forest [21] in the Guinean bioclimatic zone (rainfall ≈ 1200 mm per year). The study site was a plantation of *Cocos nucifera* where *Macrotermes bellicosus* (Isoptera, Macrotermitinae) is one of the dominant fungus-growing termite species, making conspicuous epigeous nests. Three samples (cubes, 10 cm side) were randomly taken from the base of the external *M. bellicosus* mound wall. Three active mounds of approximately the same size (2 m high) were sampled. Three samples of the control adjacent soils (0–10 cm depth) (without visible termite activity) were collected approximately 5 m from each mound sampled. Soils were stored at field humidity in hermetic boxes.

2.2. Physical and chemical parameters

Soil pH was determined in soil/water suspension and SOM was assessed by total organic C and N concentration using an elemental analyser (NA 1500 Series 2, Fisons). Soils were sieved to obtain five particle size fractions (AFNOR, NFX 31107): clay (<2 µm), fine (2–20 µm) and coarse (20–50 µm) silts, fine (50–200 µm) and coarse (200–2000 µm) sands.

The cation exchange capacity (CEC) and the exchangeable cations (calcium, magnesium, potassium and aluminium) were determined by exchange with cobaltihexamine cation (CEC_{Co}) at natural soil pH [7] (AFNOR NFX 31130). The percentage of cation saturation (*S:T*) was determined from the CEC value and the content of Ca^{2+}, Mg^{2+} and K^{+}. The CEC at pH 7 was determined using ammonium acetate method (Metson method, AFNOR NF X 31130) (CEC_{metson}).

2.3. Measurement of structural stability

The aggregate stability was assessed using the mean weight diameter (MWD) according to Le Bissonnais [18]. This parameter measures three types of alteration in the soil structural stability: (1) a breakdown (fast wetting) simulating the behaviour of dry material under heavy rain, (2) a slow wetting testing the behaviour of dry, or slightly damp materials, when subjected to moderate rain, and (3) a disaggregation test (mechanical breakdown) to analyse the behaviour of damp materials.

- Fast wetting test: 5 g of 3–5-mm diameter air-dried aggregates were immersed in de-ionised water for 10 min. After removing the water with a pipette, the soil material was gently transferred to a 0.05 mm sieve previously immersed in ethanol. The fraction <0.05 mm was recovered by gentle sieving and then oven dried. The remainder fraction >0.05 mm was oven dried and its size distribution was measured by dry sieving using sieves with apertures of 2, 1, 0.5, 0.2, 0.1 and 0.05 mm.
- Slow wetting test: the air-dried aggregates were capillary wetted for 30 min before immersion in water. The procedure for obtaining the different aggregate size fractions was then as above.
- Mechanical breakdown: the air-dried aggregates were wetted with ethanol. The ethanol was removed with a pipette, 200 cm^3 of de-ionised water were added and the flask was agitated end over end 10 times. The aggregate size fractions were then as above.

The aggregate size distribution was determined for the three treatments and the MWD, which is the sum of the quantities of soil remaining on the sieve, multiplied by the mesh size, was calculated using the following equation:

$$MWD = [3(\% >2\ mm) + 1.5(\%\ 1\text{–}2\ mm) + 0.75(\%\ 0.5\text{–}1\ mm) + 0.35(\%\ 0.2\text{–}0.5\ mm) + 0.15(\%\ 0.1\text{–}0.2\ mm) + 0.075(\%\ 0.05\text{–}0.1\ mm) + 0.025(\%\ 0.05\text{–}0\ mm)]/100$$

2.4. Soil structure and water retention properties

The soils were saturated and equilibrated at different soil matric potentials Ψ of –3.2, –32 and –1600 kPa, using pressure membrane equipment. For each pressure, soil volume fractions occupied by water and air were determined. The sum of the volume fractions occupied by air (e_a) and by water (e_w) correspond to the total soil porosity (e_p). The percentage soil shrinkage (ΔV) between Ψ = –3.2 kPa and Ψ = –1600 kPa was calculated from the equation:

$$\Delta V = 100(e_{p\ -3.2\ kPa} - e_{p\ -1600\ kPa})/e_{p\ -3.2\ kPa}$$

The proportion of water in soil according to the matric potentials provides information about the size of the pores. Water is retained in pore sizes <50 µm when subjected to Ψ = –3.2 kPa, <5 µm for Ψ = –32 kPa and <0.1 µm for Ψ = –1600 kPa. The proportion of water in pores up to each maximum pore size was calculated.

2.5. Wettability measurement on aggregates

The wettability of 3–5-mm aggregates was assessed with the water drop penetration time (WDPT) test [6]. Drops of

0.2 µl de-ionised water were deposited with a micro-syringe on the surface of individual air-dried aggregates (3–5 mm diameter), and the time required for a drop to penetrate into the aggregate recorded.

2.6. Statistical methods

The termite mound is the experimental unit, so the three samples obtained have been mixed to obtain a representative sample for each mound. Differences in soil properties between mound external wall and the control soil were analysed through an analysis of variance (ANOVA).

3. Results

3.1. Soil properties

Results are shown in Table 1. Whereas the organic carbon content was greater ($P = 0.036$) in the control soil than in the termite mound soil, there was no significant difference in the nitrogen content ($P = 0.129$). Consequently, the C:N ratio was significantly less in the mound ($P = 0.049$). Although both soils were acid, the pH was lesser in the control soil than in the external wall of *M. bellicosus* mound ($P = 0.029$). The CEC of the termite mound soil was significantly greater than of the control soil ($P < 0.001$) but no difference occurred between the two methods ($P = 0.531$).

The level of exchangeable Mg^{2+} and K^+ were greater in the termite mound soil (Table 2) ($P = 0.003$ for Mg^{2+} and $P = 0.04$ for K^+). Conversely, the concentration of Al^{3+} was greater in the control soil than in the mound ($P = 0.012$). The level of Ca^{2+} did not differ significantly ($P = 0.072$). Conspicuously, the percentage of cation saturation (*S:T*) in the major elements (Ca^{2+}, Mg^{2+}, K^+) was greater in the termite mound than in the control soil ($P = 0.019$).

The termite mound soil was enriched in clay as compared to the control soil ($P = 0.001$). Conversely, control soil has more coarse silt ($P = 0.019$) and fine and coarse sands than the termite mound soil ($P = 0.002$ for the fine sand fraction and $P = 0.001$ for the coarse sand fraction) (Table 3). No difference in the fine silt fraction occurs between the two soil types ($P = 0.304$).

3.2. Soil structure and water retention properties

The porosity at the least potential ($\Psi = -3.2$ kPa) was not significantly different ($P = 0.585$) between the termite mound soil and the control soil (Fig. 1). However, at the two greater potentials, the porosity in termite mound soil was significantly less in the control soil: $e_p = 0.54$ (S.E.: 0.01) and 0.61 (S.E.: 0.02) $cm^3\ g^{-1}$ ($P = 0.002$), respectively, in the termite mound and the control soil for $\Psi = -32$ kPa; and $e_p = 0.49$ (S.E.: 0.01) and 0.58 (S.E.: 0.02) $cm^3\ g^{-1}$ ($P = 0.002$), respectively, in the termite mound and in the control soil for $\Psi = -1600$ kPa.

The difference in porosity between the matric potentials illustrates the shrinkage of the soils. Although both soils had the same porosity when wet ($\Psi = -3.2$ kPa), the mound soil gained more porosity than the control soil as the soil matric potential decreased. The shrinkage of the control soil was only 7.1% while it was 19.2% for termite mound soil.

The two soils had similar water contents at the least potential ($\Psi = -3.2$ kPa): $e_w = 0.44$ (S.E.: 0.03) and 0.40 (S.E.: 0.02) $cm^3\ g^{-1}$ ($P = 0.248$), respectively, in the termite mound and the control soils. However, water retention was greater in the termite mound than in the control soil for the two greater potentials : $e_w = 0.29$ (S.E.: 0.04) and 0.22 (S.E.: 0.01) $cm^3\ g^{-1}$ ($P = 0.03$) for $\Psi = -32$ kPa, and $e_w = 0.18$

Table 1
Soil physical and chemical parameters for the control soil (control) and termite mound soil (mound) are: C and N content (%), pH, CEC at pH 7 and CEC at soil pH. ($n = 3$, S.E. in parentheses)

	C (%)	N (%)	pH	C:N	$CEC_{pH\ 7}$ (cmol kg^{-1})	CEC_{soil} (cmol kg^{-1})
Control	0.68 (0.03)	0.05 (0.01)	4.92 (0.13)	14.88 (0.02)	3.33 (0.09)	3.27 (0.06)
Mound	0.58 (0.02)	0.04 (0.01)	5.38 (0.12)	13.87 (0.44)	4.82 (0.58)	5.37 (0.81)

Table 2
Concentration of Ca^{2+}, Mg^{2+}, K^+ and Al^{3+} (cmol kg^{-1}) and the degree of saturation of the cationic exchange capacity (*S:T*) in the control soil (control) and termite mound soil (mound). ($n = 3$, S.E. in parentheses)

	Ca^{2+} (cmol kg^{-1})	Mg^{2+} (cmol kg^{-1})	K^+ (cmol kg^{-1})	Al^{3+} (cmol kg^{-1})	*S:T*
Control	1.52 (0.06)	0.68 (0.08)	0.15 (0.02)	0.09 (0.02)	0.70 (0.05)
Mound	2.72 (0.65)	1.18 (0.09)	0.24 (0.02)	0.06 (0.01)	0.84 (0.07)

Table 3
Particle size distribution (g per 100 g soil) of the control soil and the termite mound soil. ($n = 3$, S.E. in parentheses)

	Clay	Fine silt	Coarse silt	Fine sand	Coarse sand
Control	10.0 (0.2)	6.4 (0.1)	4.6 (0.2)	23.3 (0.1)	55.8 (0.1)
Mound	20.8 (1.8)	6.3 (0.5)	4.4 (0.1)	17.5 (1.3)	51.1 (2.5)

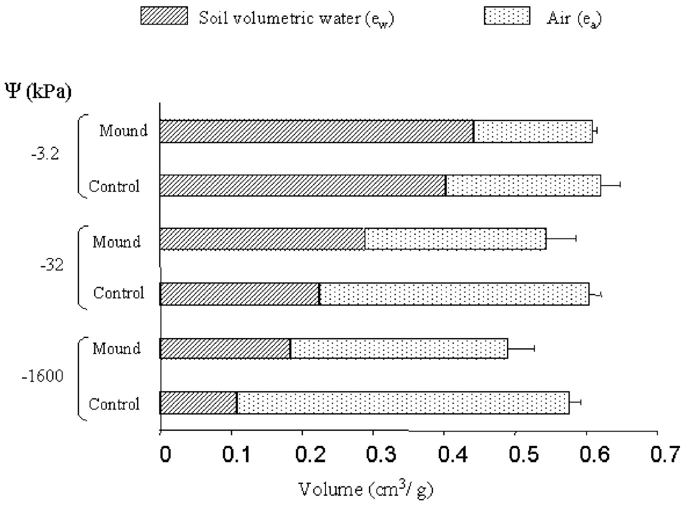

Fig. 1. Soil volumetric water (e_w) and air (e_a) content (cm^3 g^{-1}) at matric potentials of –3.2, –32, and –1600 kPa. Porosity is the sum of volume occupied by air plus volume occupied by water: $e_p = e_w + e_a$. ($n = 3$, bars are S.E.).

(S.E.: 0.01) and 0.11 (S.E.: 0.01) cm^3 g^{-1} (P = 0.08) for Ψ = –1600 kPa, respectively.

As evidenced on Fig. 2, the mound soil had significantly more pores of the smallest size class (<1 µm) than the control (51.3% vs. 28.8%; S.E.'s of 4.9 and 0.9, respectively). The relation was reversed for the two larger size classes (0.1–5 and 5–50 µm) where the control soil had significantly more pores than the mound soil (28.4% vs. 21.2%, S.E.'s of 3.8 and 4.9, respectively, for the 0.1–5 µm class, and 42.8% vs. 27.4%, S.E.'s of 3.9 and 4.1, respectively, for the 5–50 µm class).

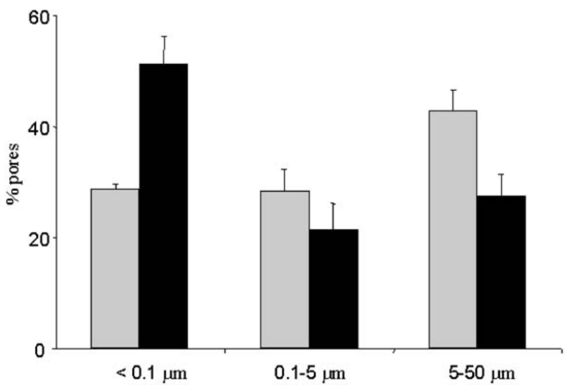

Fig. 2. Percentage of all pores that were smaller than 0.1 µm, from 0.1 to 5 µm and from 5 to 50 µm for either the control soil (in grey) or the termite mound soil (in black). ($n = 3$, bars are S.E.).

3.3. Soil structural stability

The soil aggregate stability treatments provided strong discrimination between the mound and control soils (Table 4). Each of the three wetting/disaggregation treatments resulted in significantly greater MWD for the control soil ($P < 0.001$ for treatments 1 and 2; $P = 0.009$ for treatment 3).

As evidenced on Table 4, the control soil was most disaggregated by the fast wetting of dry soil (test 1); MWD being significantly less than gained from treatment two ($P = 0.011$) and three (P = 0.008) which did not significantly differ (P > 0.05). The aggregate size distribution (Fig. 3) led to similar conclusion: we found similar distribution after the second and the third test and macroaggregates (aggregates more than 2000 mm in size) were lesser after the first test than after test 2 and 3 ($P < 0.001$ in both cases). Conversely, the proportion of aggregates between 100 and 2000 mm in size were greatest after the first treatment (P = 0.031 and 0.049 for aggregates from 100 to 200 mm, respectively, with the second and third treatments; P < 0.001 for all the other aggregate size classes and both treatments).

For the mound soil, MWD value was similar after the first and the second treatments (P = 0.952), whereas treatment 3 gave a significant (P < 0.001) greater MWD (Table 4). However, as shown in Fig. 3, the mound soil was not equally disaggregated by the first and the second tests. The first treatment led to a greater proportion of aggregates between

Table 4
MWD (mm) was assessed using three tests: treatment 1, fast wetting; treatment 2, slow wetting and treatment 3, mechanical breakdown. ($n = 3$, S.E. in parentheses)

	Treatment 1	Treatment 2	Treatment 3
Control	0.19 (0.03)	0.25 (0.01)	0.25 (0.01)
Mound	0.06 (0.01)	0.07 (0.01)	0.19 (0.03)

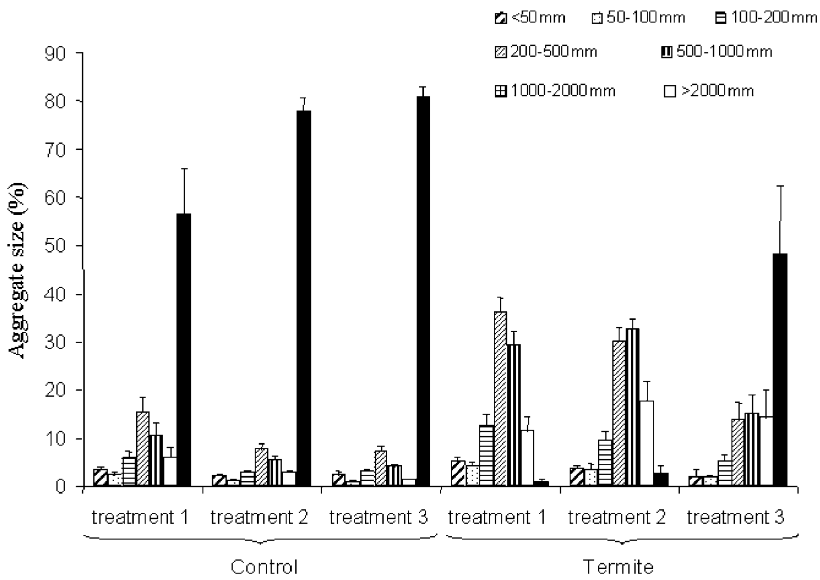

Fig. 3. Aggregate size distribution (%) of the control soil and the termite mound soil for the three tests: fast wetting (treatment 1), slow wetting (treatment 2), and mechanical breakdown (treatment 3). Samples were 3–5-mm control soil aggregates or termite mound soil aggregates. ($n = 3$, bars are S.E.).

100 and 200, 200–500 and a lesser proportion of aggregates between 1000 and 2000 mm in size ($P = 0.020$, 0.004 and 0.027, respectively); the other aggregate size classes being significantly similar ($P > 0.05$). Termite handled soil was least disaggregated by the mechanical breakdown test (treatment 3) and the proportion of macroaggregates was greatest ($P < 0.001$) while aggregates lesser than 2000 mm in size were least ($P < 0.001$ and 0.014 for aggregates <50 mm, respectively, for test 1 and 2; $P < 0.001$ and 0.011 for aggregates between 50 and 100 mm, respectively, for test 1 and 2; $P < 0.001$ for the other aggregate size class, and for both treatments).

3.4. Time requisited to penetrate into the soil

The time required for a drop of water to penetrate into the soils (WDPT) was significantly greater for the mound soil than for the control soil (16.29 vs. 4.76, S.E.'s of 1.24 and 0.18, respectively, $P < 0.001$).

4. Discussion

4.1. Properties of soils

The nest structures of fungus-growing termites are known to be enriched in finer particles, as compared to the surrounding top soil [10,13]. We found that the proportion of fine silt was similar in the control and mound soils and that the percentage of clay increased in the mound soil while the proportions of coarse silt and sand decreased. This action of termites is coupled with increases in the cation content and cation saturation in the mound material. This increased saturation state is inversely related to soil acidity and indicates a tendency toward neutrality [3]. Consequently, the increase in the cation content in termite mound explain the greater pH in the mound soil.

Several authors have found that *Macrotermes* spp. mound soils have less organic matter and greater CEC than soils without termite activity [4,8]. Our results indicated that there was no difference between CEC at soil pH and CEC at pH 7. Therefore, we conclude that the CEC was not pH dependent and charges were mainly permanent without significant variable charges [3]. Our results are unexpected because tropical savannah soils usually have a greater proportion of kaolinite (1:1-type clay) and oxides and these minerals are reported to have exclusively pH dependent charges [1]. Consequently, our results suggest that the content of 1:1-type clay and oxides were too small to influence the results. If clay charges were not pH influenced it means that the clay mineral composition was predominantly 2:1-type clay [1]. The structural stability of soils, and particularly 2:1 clay-dominated soils, is usually correlated with their SOM content [5,17,23]. However, SOM also has mainly pH dependent charges [3]. Although researchers have focused on the role of SOM content and quality [8,12] for determining the mechanisms responsible of the structural stability of *Macrotermes* nests, our study illustrates that SOM may play a negligible role in the value of CEC. The 2:1 clay types are therefore responsible for the CEC value as well as the shrink–swell behaviour of soil.

Despite the clay content of the termite mound soil being twice that of the control soil, we found that the CEC value was less and ΔV was greater than twofold. Therefore, clay minerals in the termite mound soil have different cationadsorbing capacity and shrinkage behaviour than those in the control soil. In addition, the composition of the parent material is probably different to that of the mound soil. Jouquet et al. [15] postulated that the presence of different clays in the wall of the termite mound, relative to the control soil, can be explained by two processes. The first process is the enrichment in fine particles in the nest, and the second process results from modifications of clay properties by the termites of 2:1 minerals, especially after K-extraction [15].

4.2. Influence of clay on soil stability

It has been previously shown that soil from *Macrotermes* mound is only slightly more stable than control soil taken in the vicinity of the nest [8,11]. Our results showed that, using the MWD, termite mound soil can be even less stable than the control soil.

The increase of the proportion of 2:1-type clay leads to two opposing tendencies. First, the increase of the CEC leads to the enhancement of cohesive forces between the particles, and thus the stability of the aggregates [24,25]. The total porosity decreases and the proportion of pores with a diameter smaller than 0.1 µm increases, limiting the diffusion of water. This latter result is illustrated by the greater time required for water to penetrate the soil handled by termites. However, the increase of 2:1-type clays leads to the enhancement of the swelling capacity of soil and, at great matric potentials, the soil is not saturated with water and air trapped within the soil pores under pressure can cause slaking. Therefore, in the stability test, when water penetrates into the pores of the mound soil (first and second tests), the soil swells and the interactions between particles decrease, leading to the slaking of soil aggregates. This property of termite mound soil is enhanced by the lack of SOM in soil for stabilising the aggregates. The mechanical breakdown test (third treatment) caused less disaggregation because water does not penetrate into the pores of termite mound soil and instead only releases particles from the surface of the aggregates [18]. We suggest that the greater stability of the control soil can be explained by the weaker shrinkage behaviour of this kind of soil and by the greater SOM content.

Although water drops probably do not, or only slowly, penetrate into the mound, tests of structural stability are useful to study the behaviour of soil aggregates when they are immersed in water. MWD index can thus be considered as an insufficient parameter for explaining the structural stability of *M. bellicosus* mound soil and a better view would require a deeper investigation of processes at work in the field. We suggest that mound soil is not very structurally stable but disappears only slowly because water only penetrates slowly so that slaking of the surface is a slow process. We speculate that another important factor is that raindrops impact at very acute angle on termite mounds and, therefore, dissipate much less energy/unit area than when hitting flat soil surfaces. They also tend to bounce off and cannot build up an erosive volume of flow on surfaces that are so short and steep.

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