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M. H. Nash · W. G. Whitford

# Subterranean termites: regulators of soil organic matter in the Chihuahuan Desert

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**Abstract** Soil organic matter and the abundance of subterranean termites were measured at 89 locations spaced at 30-m intervals from the bottom to the top of a small desert watershed. There was no correlation between soil organic matter content and topographic position on the watershed. Analysis by autocorrelogram demonstrated that the soil organic matter content was randomly distributed on the watershed. There was a highly significant negative correlation between termite abundance and soil organic matter, $r = -0.97$. Soils characterized by horizon in soil pits within each vegetation type (soil type) showed some relationships to erosion-deposition areas on the watershed, with surface organic matter contents varying between 3.4% in the playa basin where termites were absent to 0.4% in a sparse shrubland on erosional soils. In the northern Chihuahuan Desert, subterranean termites appear to be responsible for most of the variation in soil organic matter.

**Key words** Autocorrelation · Chihuahuan Desert · Keystone species · Soil organic matter · Spatial analysis Subterranean termites · Watershed

MH. Nash[1]
Department of Agronomy and Horticulture,
New Mexico State University,
Las Cruces, NM 88003, USA

W. G. Whitford (✉)[2]
Department of Biology,
New Mexico State University,
Las Cruces, NM 88003, USA

*Present addresses:*
[1]USGS/FEC Hydrology Program,
Mercury, NV 89023, USA
[2]US-EPA, Environmental Monitoring and Assessment Laboratory,
PO Box 93478, Las Vegas,
NV 89193, USA

## Introduction

The organic matter content is an important soil property, especially in arid regions, because of its beneficial effects on nutrient availability, soil structure, and water retention (Franzmeier et al. 1985). The low concentrations of organic matter in desert soils have been attributed to the low rates of net primary production, which result in low rates of organic matter input. If the concentration of soil organic matter is a function of net primary production, then there should be direct relationships between soil organic matter and plant production across the landscape, topography, and wind and water flow.

In the Chihuahuan Desert, a large fraction (>50%) of the potential inputs to soil organic matter may be consumed by termites (Johnson and Whitford 1975; Whitford et al. 1982; Whitford et al. 1988). Organic matter is more rapidly metabolized and more completely metabolized by the gut microflora of termites than is organic matter that is processed in soil by free-living microflora and fauna (Lee and Wood 1971; Butler and Buckerfield 1979). The small quantities of organic matter found in termite excreta with little or no humic materials in the feces show that subterranean termites return little of the organic matter that they consume to the soil. Therefore, if the consumption of organic inputs by termites is a primary determinant of the soil organic matter concentration, there should be a negative relationship between termite abundance and soil organic matter.

In arid ecosystems, plant litter, animal feces, etc. are redistributed on a watershed by overland flow during intense rain and wind storms. The soil of the lower slopes that receive the run-on of organic materials as overland flow velocity decreases should therefore have higher concentrations of soil organic matter.

The design of the Jornada LTER (long-term ecological research) program, which consists of a series of plots along a 3-km transect traversing a desert watershed, provided an opportunity to examine patterns of soil organic matter distribution in relationship to landscape position, net primary production, and the abundance of termites. Here we report the results of studies of the abundance of subterranean termites and soil organic matter in relation to topographic position on a Chihuahuan Desert watershed.

## Materials and methods

The study was conducted on the New Mexico State University Ranch approximately 40 km NNE of Las Cruces, Doña Ana County, New Mexiko. The climate is arid with an average of 230 mm precipitation annually; more than 60% of the rainfall occurs in July through September. Summer maximum temperatures reach 40 °C and winter minimum temperatures are frequently below 0 °C. Data were collected along a 2700-m transect extending from an ephemeral dry lake (playa) upslope to the base of a mountain. Prevailing winds flow from the base of the mountain towards the dry lake (essentially the same direction as the water flow). The dominant vegetation along the transect includes a mixed grass-shrub community, a creosotebush (*Larrea tridentata*) community, and a black grama (*Bouteloua eriopoda*) community.

The transect comprised 89 sites spaced at 30-m intervals. At each site, four soil cores were taken to a depth of 120 cm with a 7-cm diameter bucket auger. The cores were taken at 0–30 cm, 30–60 cm, 60–90 cm, and 90–120 cm, for a total of 356 samples. The percent organic C by weight was determined by reduction of potassium dichromate (Nelson and Sommers 1982). Organic matter was assumed to be 1.724×the organic C content. Organic matter in the four depths at each location was averaged to obtain a single value for the regression and autocorrelation analyses. The abundance/activity of termites was measured as the numbers of termites removed from rolls of toilet tissue used as baits (Johnson and Whitford 1975). Four tissue rolls, covered with aluminum foil to prevent damage due to wetting, were placed at the corners of a 1-m square at each sampling location on the transect. Baits were placed in the field in March 1984 and retrieved in November 1984. Rolls were checked at 2-week intervals from April until November. Termites feeding in a bait were shaken into a pan, counted, and released. This provided a measure of the active population at the time the sample was taken; hence, it is only an index of population size and feeding intensity. The numbers of termites in the baits at each station along the transect were summed to obtain an estimate of abundance/activity. A single figure for abundance/activity was obtained by summing the numbers at each station for all sample dates during the year.

An additional set of data was obtained from soil pits dug to a depth of 100–120 cm in each of the seven soil mapping units on the watershed. Samples of soil were collected from each horizon and soil organic matter measured as described above.

The soil organic matter data were initially analyzed by constructing an autocorrelogram. An autocorrelogram represents the relationship between the autocorrelation coefficient (a measure of the correlation between a spatial series and the same series at distance $h$, or lag $h$). If observation $z$ at location $i$ and observation $z$ at location $i+h$ are highly correlated, then the correlogram is dependent (Fig. 1). As the distance $h$ is increased, the covariance decreases gradually until it becomes zero when there is no correlation or spatial dependence between the two series. A typical correlogram for observations that are spatially correlated exhibits a decline to zero (Fig. 1 a). If the observations are random, the decline to zero is abrupt (Fig. 1 b). If soil organic matter varies as a function of position on the watershed as a result of fluvial transport and deposition of organic material, then the autocorrelogram should exhibit a smooth decline to zero, a dependent correlogram.

The data were also subjected to analysis by linear regression of soil organic matter and termite activity.

## Results

The distribution of soil organic matter along the 2700-m transect appeared to be random (Fig. 2). There was no readily apparent pattern attributable to position on the watershed except that some of the highest values were obtained at the base of the watershed. When these data were subjected to autocorrelation analysis, the random nature of the soil organic matter content was confirmed (Fig. 1).

The termites in the bait rolls were mostly *Gnathamitermes tubiformans*, with a small number (<5%) of *Amitermes wheeleri*. There was a highly significant negative correlation between termite abundance/activity and soil organic matter: $r = -0.97$.

The regression for soil organic matter as a function of termite abundance/activity was:

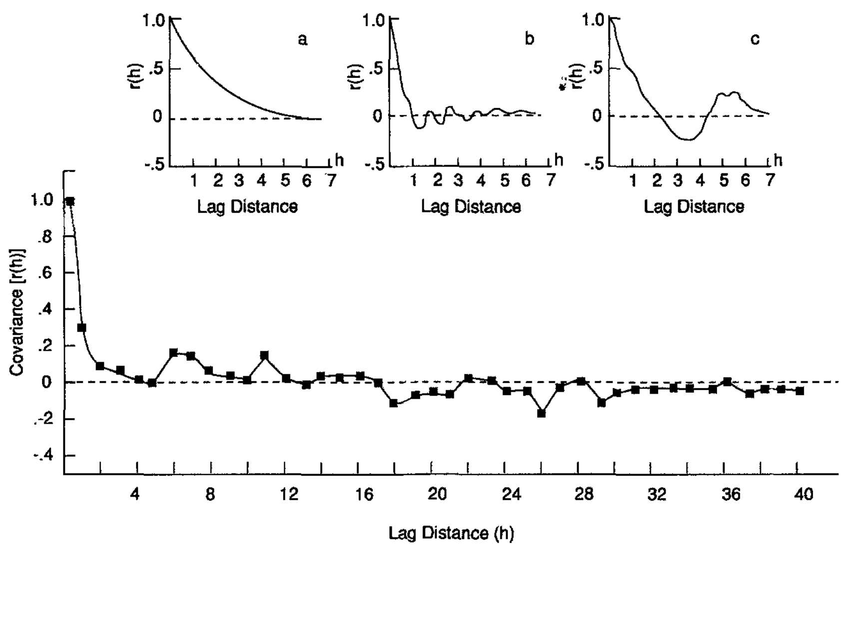


**Fig. 1** The autocorrelogram (*lower panel*) for the spatial distribution of soil organic matter on a small watershed in the northern Chihuahuan Desert in New Mexico, U.S.A. Reference autocorrelograms in the upper panel show good spatial autocorrelation (**a**), completely random pattern (no autocorrelation) (**b**), and some spatial autocorrelation (**c**)

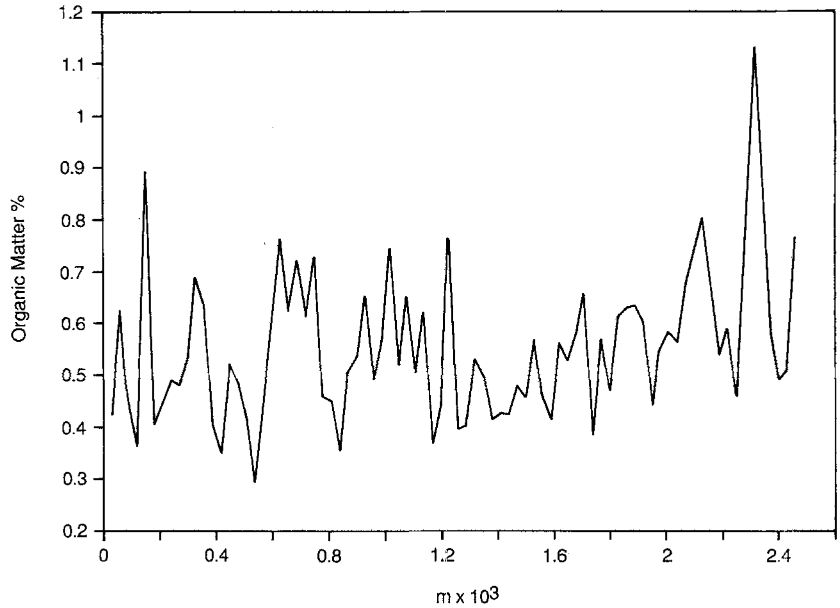


**Fig. 2** Variation in percent organic matter at 30-m intervals along a 2.5-km transect on a small watershed in the northern Chihuahuan Desert in New Mexico

Percent organic matter = 0.82 − 0.0076 termite abundance/activity index ($F = 56.7$, $P < 0.005$).

Soil organic matter measured in the soil pits provided a general pattern of lowest values in the erosional sparse shrub community, and higher values in the depositional areas at the base of the watershed. However, the soil organic matter content in the perennial grassland community with a highly vegetative cover (>50%) was not different from the soil organic matter content in the mixed shrub-herbaceous-perennial grass community (Fig. 3). The highest soil organic matter content in the watershed was in the upper 5 cm of the ephemeral lake soils (Fig. 3). There were no subterranean termites in the ephemeral lake soils.

## Discussion

Termites are known to affect the chemistry of soils, especially soils in semi-arid tropical regions where mound-building termites are abundant (Watson 1962; Arshad 1981; Holt 1987; Jones 1990). Jones (1990) hypothesized that the density of termites and their litter-harvesting behavior should noticeably influence the soil nutrient status and C cycling on a regional scale. The data from our study supports her hypothesis on a watershed scale.

The most surprising result of our study was the lack of any spatial pattern in the distribution of soil organic matter on the watershed. Downslope transport of leaf litter, rabbit feces, and small pieces of wood is a regular occurrence during the intense convectional rains that are characteristic of this region in summer. Given the quantities of organic matter transported downslope, soil organic matter should be elevated at the base of the watershed where the slopes are less than 1%. Litter accumulations are frequently riddled with termite galleries and are filled with termites in both the galleries and litter, especially in late summer (W. G. Whitford, personal observations). In the northern Chihuahuan Desert, subterranean termites are known to consume large quantities of plant litter (Whitford et al. 1982), roots of grasses and herbaceous plants (Whitford et al. 1988), and to consume ani-

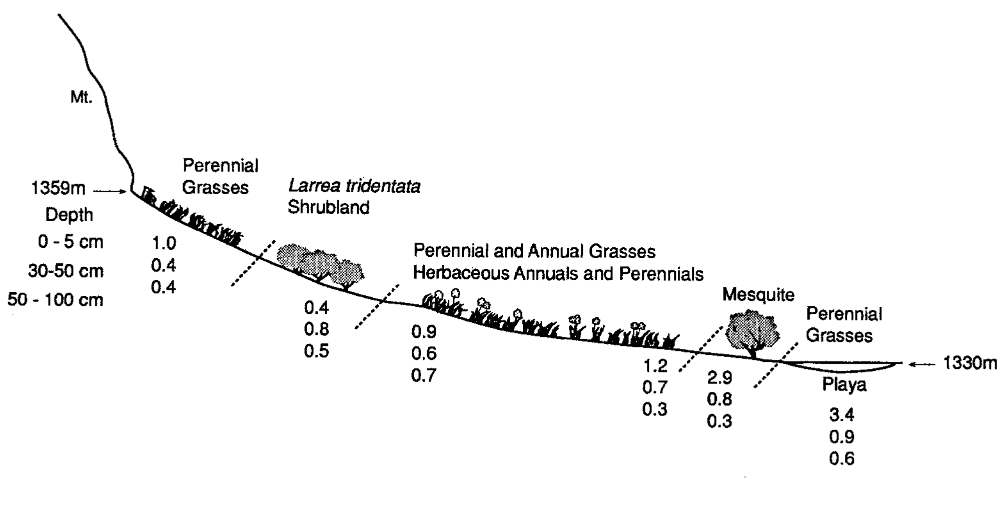


**Fig. 3** The pattern of soil organic matter distribution from soil horizons in pits dug at the midpoint of each soil mapping unit or vegetation community

mal dung and woody debris (Whitford 1991). Thus materials that accumulate at the base of the watershed represent rich food sources which are quickly exploited by subterranean termites. Subterranean termite galleries and nest chambers were found at depths of 10 m in an excavation on this watershed. The small quantities of fecal material produced by subterranean termites are generally used in the cementing materials of gallery walls and nest chamber walls. The mineralization of organics within the gut of termites, plus the deposition of fecal organics deep in the soil in gallery-wall cement, remove most of the organic C ingested by termites from the surface soils and the rooting zone of most plants. The absence of any organic matter pattern coupled with the highly significant negative correlation with termite abundance provides strong evidence that subterranean termites are primarily or even solely responsible for variations in soil organic matter.

The direct linkage between the soil organic matter content and the N mineralization potential of these desert soils (Fisher et al. 1990) further implicates subterranean termites as "keystone" species affecting many key properties of Chihuahuan Desert ecosystems. The abundance of subterranean termites in tropical and subtropical regions suggests that these soil animals may be important in those ecosystems as well. Indeed, the low soil organic matter contents of soils in subtropical semi-arid regions is probably largely the result of termite activity, as suggested by Jones (1990) and as demonstrated n the present study.

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