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Calcium carbonate in termite galleries – biomineralization or upward transport?

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Abstract Termites and soil calcium carbonate are major factors in the global carbon cycle: termites by their role in decomposition of organic matter and methane production, and soil calcium carbonate by its storage of atmospheric carbon dioxide. In arid and semiarid soils, these two factors potentially come together by means of biomineralization of calcium carbonate by termites. In this study, we evaluated this possibility by testing two hypotheses. Hypothesis 1 states that termites biomineralize calcium carbonate internally and use it as a cementing agent for building aboveground galleries. Hypothesis 2 states that termites transport calcium carbonate particles from subsoil horizons to aboveground termite galleries where the carbonate detritus becomes part of the gallery construction. These hypotheses were tested by using (1) field documentation that determined if carbonate-containing galleries only occurred on soils containing calcic horizons, (2) $^{13}C/^{12}C$ ratios, (3) X-ray diffraction, (4) petrographic thin sections, (5) scanning electron microscopy, and (6) X-ray mapping. Four study sites were evaluated: a C_4-grassland site with no calcic horizons in the underlying soil, a C_4-grassland site with calcic horizons, a C_3-shrubland site with no calcic horizons, and a C_3-shrubland site with calcic horizons. The results revealed that carbonate is not ubiquitously present in termite galleries. It only occurs in galleries if subsoil carbonate exists within a depth of 100 cm. $^{13}C/^{12}C$ ratios of carbonate in termite galleries typically matched $^{13}C/^{12}C$ ratios of subsoil carbonate. X-ray diffraction revealed that the carbonate mineralogy is calcite in all galleries, in all soils, and in the termites themselves. Thin sections, scanning electron microscopy, and X-ray mapping revealed that carbonate exists in the termite gut along with other soil particles and plant opal. Each test argued against the biomineralization hypothesis and for the upward-transport hypothesis. We conclude, therefore, that the gallery carbonate originated from upward transport and that this $CaCO_3$ plays a less active role in short-term carbon sequestration than it would have otherwise played if it had been biomineralized directly by the termites.

Keywords Atmospheric carbon dioxide · Arid and semiarid soils · Carbon isotopes · Carbon sequestration · Chihuahuan Desert · Pedogenic carbonate

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Introduction

Carbon dioxide in vast quantities moves continually into soil by root respiration and microbial decomposition of photosynthetic tissue and moves out of soil and re-enters the atmosphere by mass flow and diffusion. Although much carbon can be stored in roots, most carbon in soil is stored as soil organic carbon and, in dryland regions, calcium carbonate. The global amount of soil organic carbon is estimated to be 1,550 Pg, while the global amount of soil carbonate carbon is estimated to be 750–950 Pg (Schlesinger 1985; Eswaran et al. 2000). Because of rising concentrations of atmospheric CO_2, many studies have been initiated to better understand the role that both soil organic and carbonate carbon plays in the global C cycle and ways to sequester more carbon in cropland soils (Lal et al. 1998), forest soils (Kimble et al. 2003), and grazing land soils (Follett et al. 2001).

Grazing land soils, which are the focus of this study, are common in arid and semiarid climates characterized by annual precipitation amounts less than 500 mm (Sobecki et al. 2001; Monger et al. 2005). Although both organic carbon and carbonate carbon occur in arid and semiarid soils, carbonate carbon typically exceeds organic carbon by a factor of 10 or more (Schlesinger 1982; Grossman et al. 1995). About 50–66 Pg of carbonate C occurs in U.S. soils alone (Monger and Martiñez-Rios 2001), which is roughly double the amount of aboveground biomass C in U.S. forests (26.3 Pg, Birdsey and Lewis 2003).

Termites, like pedogenic carbonates, are ubiquitous in arid and semiarid soils of the tropics and subtropics. Termite population densities in these areas can reach 2,000 individuals per m^2 (Lee and Wood 1971a). Termites dig tunnels, transport particles, consume major amounts of plant debris, and affect the nutrient status of soils (Thorp 1967; Gile 1975; Whitford 2002). Termites also produce major amounts of global methane (Khalil et al. 1990), accounting for approximately 11% of the global methane emissions from natural sources (Houghton 2004). In many arid and semiarid regions of the subtropics termites build mounds that rise from 1 to 4 m above the land surface (Lee and Wood 1971a). In other dryland regions
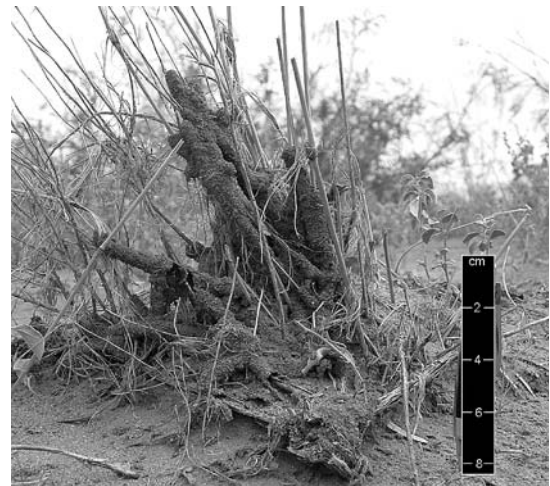

Fig. 1 Aboveground termite gallery in the study area. The galleries, built of soil particles, are constructed around plant stems and leaves which the termites consume

termites construct their nests belowground with aboveground galleries that encase the plant materials they consume (Whitford 1991; Fig. 1). In general, soils that are modified by termite activity have higher amounts of $CaCO_3$ than neighboring unmodified soils (Milne 1947; Lee and Wood 1971a, b; Arshad 1981; Moore and Picker 1991; Asawalam et al. 1999). This is
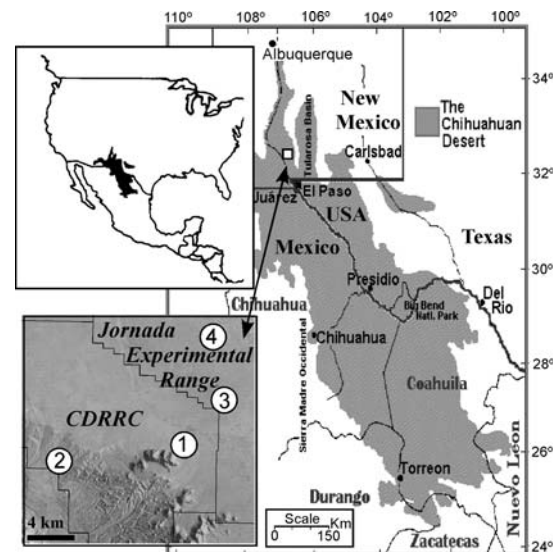

Fig. 2 Location of the Chihuahuan Desert. Insert on lower left locates the four study areas in the Jornada Experimental Range and the Chihuahuan Desert Rangeland Research Center (CDRRC) in southern New Mexico

especially true for the large termite mounds of the semiarid subtropics (Lal 1987).

In the Chihuahuan Desert (Fig. 2), many termite galleries that encase stems, twigs, leaves, seeds, cattle dung, and wooden fence poles were found to react (i.e., effervesce) with hydrochloric acid despite the fact that surrounding soil was non-effervescent (Monger and Gallegos 2000). In addition, thin sections of the effervescent termite galleries revealed a matrix of silt-size carbonate particles that engulfed and formed bridges between sand grains (Fig. 3A). Thin sections of the termites themselves revealed a continuous stream of silt-size crystals with optical properties (i.e., birefringence) similar to calcite extending from

their abdomens, through their thoraxes, and to their mandibles. Other evidence that suggested the presence of intra-termite calcite were (1) the termites themselves effervesced with HCl after being air dried and ground to a powder and (2) the ground termite bodies yielded calcite peaks when analyzed with X-ray diffraction.

Since some insects are known to make carbonate minerals by biomineralization (Lowenstam and Weiner 1989), the possibility arose that termites might biomineralize carbonate for use as a cementing agent. If termites are biomineralizing carbonate for the construction of their galleries, then because of their global abundance, they would be an important agent for terrestrial

Fig. 3 Microscopy of termite gallery and termites. (A) Petrographic thin section of effervescent termite gallery showing carbonate matrix. (B and C) Composite X-ray image of termite of which Ca concentration is shown below in (D) and (E). (F) Scanning electron micrograph of crystals concentrated along the edge of termite body, located by square in (C). (G) Composite X-ray image of crystals shown in SEM image to left. (H) Chemical map of image to left showing that potassium, rather than Ca, exists in greatest abundance
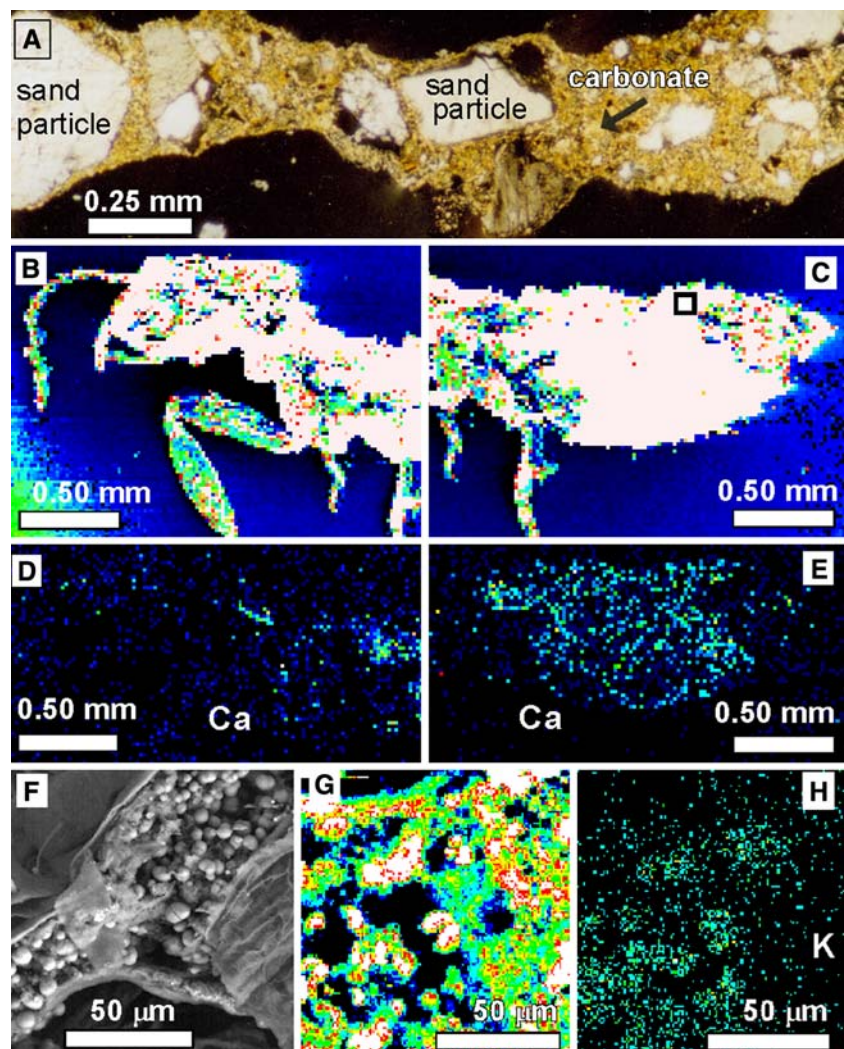
carbon sequestration in arid and semiarid climate. Thus, the objective of this study was to investigate the origin of the calcium carbonate in aboveground termite galleries in the northern Chihuahuan Desert. To this end, two hypotheses were tested: (1) termites are transporting calcium carbonate particles from subsoil carbonate horizons and (2) termites are biomineralizing carbonate.

Methods

Study sites and sample collection

This study was conducted at the New Mexico State University's Chihuahuan Desert Rangeland Research Center and the adjoining U.S. Department of Agriculture Jornada Experimental Range (http//:usda-ars.nmsu.edu). Both are located in the northern Chihuahuan Desert (Fig. 2) approximately 40 km NNE of Las Cruces, New Mexico. Historically, this region was mostly semiarid grassland, but shrub invasion during the past century has transformed large areas of grassland into desert shrublands (Buffington and Herbel 1965; Conley et al. 1992; Gibbens et al. 2005).

The experimental design consisted of four sites. Each site was 500×500 m and contained three sub-site replications (pedons) whose distance from each other was greater than 300 m. The sites were chosen based on their plant communities and soil properties, namely the dominant plant photosynthetic pathway, so $\delta^{13}C$ values could be used as tracers, and the existence of calcic horizons (Soil Survey Staff 1999). The grasslands consist of grasses that use the C_4 photosynthetic pathway and the shrublands are dominated by woody shrubs that use the C_3 photosynthetic pathway (Syvertsen et al. 1976; Monger 2003).

Site 1 ($B_{w/o}$) was in an area dominated by black grama [*Bouteloua eriopoda* (Torrey) Torrey] without a calcic horizons in the underlying soil (i.e., "$B_{w/o}$" stands for black grama without carbonate). This grassland includes sparse creosotebush [*Larrea tridentata* (Sess. & Moc. Ex DC.) Cov.], soaptree yucca (*Yucca elata* Engelm), mormon tea (*Ephedra trifurca* Torr.) and sparse

amounts of cactus (*Opuntia phaeacantha* Engelm). The soil at this site is a coarse-loamy, mixed, thermic Ustic Haplargid (Gile et al. 2003). Although the soil has an argillic horizon, it is a very weak horizon with loamy sand textures and an eluvial/illuvial clay increase of 3%. The soil is mostly non-calcareous except for a zone of carbonate filaments whose upper depths in the three pedons are 68, 100, and 110 cm below the land surface.

Site 2 ($M_{w/o}$) was in an area dominated by mesquite (*Prosopis glandulosa* Torrey) on soil without calcic horizons with low densities of creosotebush, broom snakeweed [*Gutierrizia sarothrae* (Pursh) Britt. & Rusby], and mormon tea. The soil is a mixed, thermic Typic Torripsamment. The soil is mostly non-calcareous except for a zone from 15 to 25 cm, which contains thin pebble coatings of carbonate and some inter-pebble carbonate filaments.

Site 3 (B_w) was in an area dominated by a black grama grassland on soil with a calcic (and in some areas a petrocalcic horizon) with sparse mesa dropseed [*Sporobolus flexuosus* (Trb. Ex Vasey) Rydb.], red threeawn [*Aristida purpurea Var. longiseta* (Steud.) Vasey], snakeweed, and a few soaptree yucca. The soil is a coarse-loamy, mixed, thermic Typic Calciargid, although one of the pedons is a Petronodic Calciargid. The soil has carbonate filaments beginning at depths ranging from 9 to 17 cm and extending to a calcic or petrocalcic horizon with its upper boundary between 42 and 68 cm in the three pedons. The calcic horizon is a stage III plugged horizon (Gile et al. 1966), which is characterized by the engulfment of the soil fabric by calcium carbonate. The petrocalcic horizon is a laterally discontinuous stage IV horizon.

Site 4 (M_w) was in an area dominated by mesquite on soil with a calcic horizon. Scattered soaptree yucca and broom snakeweed are minor component of this mesquite coppice dune site. The soil is a coarse-loamy, mixed, thermic Typic Calciargid. The soil has carbonate filaments beginning at depths ranging from 12 to 22 cm and extending to a calcic horizon with its upper boundary between 50 and 119 cm in the three profiles. Like site 3, the calcic horizon occurs as a stage III plugged horizons.

Soil horizons were differentiated based on their morphological characteristics (Soil Survey Staff 1993). Soil samples were collected from each soil horizon at 10–15 cm depth intervals from the center of the horizon. Termite galleries were collected randomly within 5–50 m from the pedons in September and November 2001. Termites themselves were collected from the four study sites in October 2001 and May 2002 and put into labeled glass bottles with 85% ethyl alcohol. Galleries were collected from around the stems of yucca, shrubs, and grasses (Liu 2002).

Analytical techniques

Carbon isotopic ratios ($^{13}C/^{12}C$) of carbonate in galleries and soil samples were obtained by dissolving carbonate with 100% phosphoric acid, cryogenically purifying CO_2 (Boutton 1991), and analyzing the CO_2 with a dual-inlet mass spectrometer. The $^{13}C/^{12}C$ ratios are expressed as $\delta^{13}C$ values in per mil (‰) notation with respect to the PDB standard (Craig 1957) using the following relationship:

$$\delta^{13}C\,(\text{‰}) = [(^{13}C/^{12}C)\ \text{sample}/(^{13}C/^{12}C)\ \text{standard} - 1] \times 1,000$$

X-ray diffraction (XRD) analysis was conducted with a Rigaku Geigerflex instrument (Tokyo, Japan) on samples pulverized to a fine powder using CuK$_\alpha$ radiation of $\lambda = 1.54178$ Å at 40 mA and 1,000 counts min^{-1} at a $2\theta/\theta$ scale. Three sets of air-dried termite gallery samples were analyzed with XRD from each study site. Soil samples analyzed with XRD were taken from soil pits at depths 44–50, 50–70, and 70–85 cm. A group of termite bodies from each study site were oven dried at 70°C for 30 min and ground to fine powder for XRD analysis.

Petrographic thin sections were made of unbroken termite galleries and termite bodies after embedding with low-viscosity epoxy resin (Liu 2002). To confirm the presence of calcium carbonate in termite bodies, 10% HCl acid was dropped on the thin section slides and observed under a dissecting microscope. Biological thin sections of termite bodies were observed with

scanning electron microscopy (SEM) using a Hitachi S3200N (Pleasant, CA). Crystalline materials within termite bodies were analyzed by spot, line, and area X-ray scan analysis with a Thermo Noran energy dispersive spectrophotometry analyzer.

Results and discussion

Field documentation

Field documentation was used to test the two hypotheses as follows: If termites are *transporting* carbonate particles from subsoil horizons to the land surface where they use carbonate in the construction of galleries, then galleries containing carbonate particles should only occur on soils with calcic or petrocalcic horizons. If, on the other hand, termites are *biomineralizing* carbonate, all galleries would contain carbonate regardless of its presence or absence in the subsoil.

Three of the four sites had galleries that contained carbonate: Site 2 ($M_{w/o}$), Site 3 (B_w), and Site 4 (M_w). Only Site 1 ($B_{w/o}$) did not have carbonate in the galleries. Although Site 2 ($M_{w/o}$) has no calcic horizon, it does have carbonate filaments, but so does Site 1 ($B_{w/o}$) whose galleries did not contain carbonate. The main difference between Site 1 ($B_{w/o}$) and Site 2 ($M_{w/o}$) is the depth of the carbonate filaments. At Site 1 ($B_{w/o}$), the zone of carbonate filaments is one meter deep or deeper. At Site 2 ($M_{w/o}$), the zone of filaments is 15–30 cm.

Based on field documentation of carbonate in galleries and soils, calcic or petrocalcic horizons per se are not a precondition for calcareous galleries. Soils with minor amounts of carbonate in the form of subsoil filaments will suffice for the production of calcareous termite galleries. However, the filaments must exist above a depth of one meter.

Stable carbon isotopes

$\delta^{13}C$ values were used to test the two hypotheses as follows: If termites are *transporting* carbonate to aboveground galleries, $\delta^{13}C$ values of carbon-

ate in the galleries should match those in subsoil carbonate horizons. If termites are *biomineralizing* carbonate, then the $\delta^{13}C$ values would not necessarily match the subsoil carbonate.

Figure 4 shows a comparison of the $\delta^{13}C$ values of carbonates in termite galleries with the $\delta^{13}C$ values of underlying soil carbonate for Sites 2, 3, and 4 (Site 1 was not included because there was no carbonate in its galleries). At Site 2 ($M_{w/o}$), the gallery $\delta^{13}C$ values ranged from –5.0 to –3.0‰. Soil carbonate within this range of $\delta^{13}C$ values exists at depths ranging from 20 to 90 cm at two of the pedons, while the third pedon (Pedon $M(_{w/o})$#1) falls slightly outside the range. The uppermost $\delta^{13}C$ samples at Pedon $M(_{w/o})$#2 and Pedon $M(_{w/o})$#3 are notably different than the galleries. At Site 3 (B_w), the $\delta^{13}C$ values of galleries ranged from –3.8 to –2.0‰. Soil carbonate

within this range exists at various depths ranging from 10 to 150 cm. At Site 4 (M_w), the $\delta^{13}C$ values of galleries ranged from –4.5 to –2.2‰. Soil carbonate within this range exists at various depths between 10 and 150 cm for the three pedons.

At eight of the 9 pedons, galleries had carbonate $\delta^{13}C$ values with corresponding soil carbonate $\delta^{13}C$ values at some depth. The one exception was Pedon $M(_{w/o})$#1 whose gallery $\delta^{13}C$ values were very near (within 0.13‰) the values of the galleries (Liu 2002). If the gallery carbonate $\delta^{13}C$ had been consistently different than soil carbonate $\delta^{13}C$, then that would have been evidence for the biomineralization hypothesis. Based on isotopic analysis, however, termites appear more likely to have transported carbonate particles to the land surface for use in the construction of their galleries.
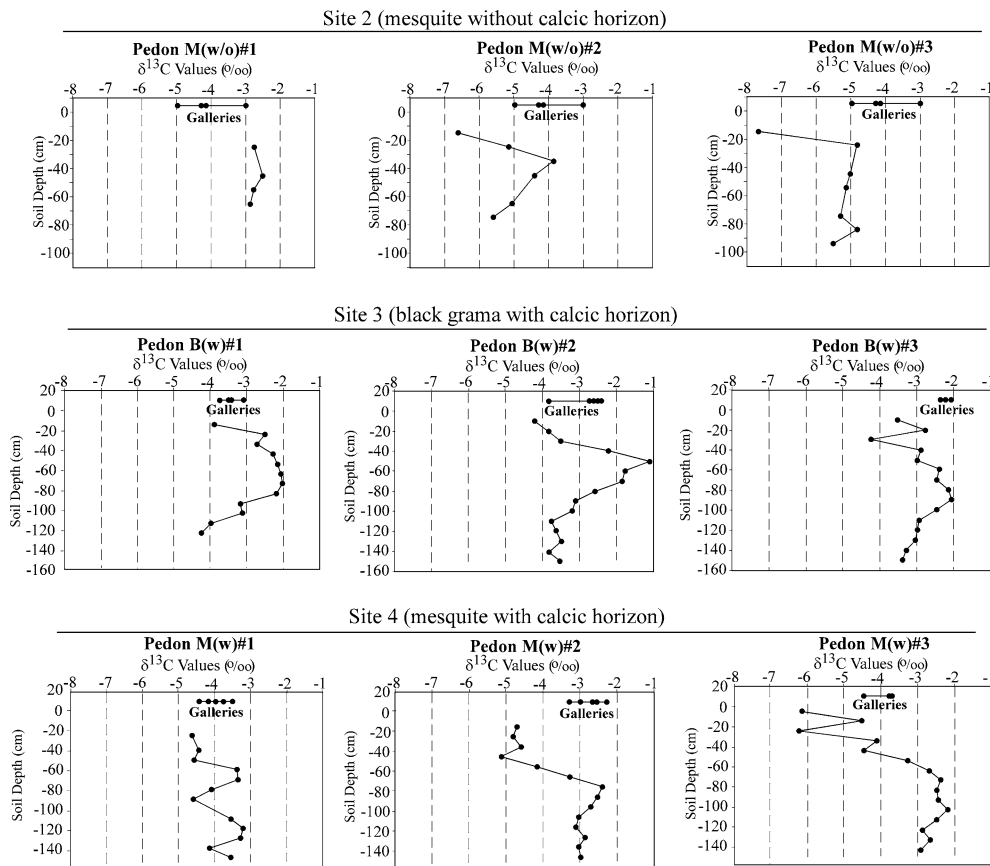

Fig. 4 Comparison of carbonate $\delta^{13}C$ values in galleries and underlying soil for the three sites having calcareous termite galleries

X-ray diffraction

X-ray diffraction was used to test the hypotheses as follows: If termites are *transporting* carbonate particles to the galleries, then carbonate mineralogy in the galleries should match the carbonate mineralogy of the carbonate subsoil horizons. If the termites are *biomineralizing* carbonates, then the carbonate mineralogy might consist of different carbonate minerals, such as vaterite (Lowenstam and Weiner 1989).

Based on XRD analysis, carbonate in all the galleries as well as in all the subsoil samples was calcite (Liu 2002). At Site 2 ($M_{w/o}$), calcite concentrations are low in both termite galleries and soils. At Site 3 (B_w), the calcite concentrations are lower in termite galleries than soils. However, at Site 4 (M_w), the calcite concentrations are higher in termite galleries than in soil.

At all 9 pedons, the carbonate mineralogy matched the carbonate mineralogy of the underlying soil carbonate. In all cases the carbonate was calcite with no evidence of Mg substitution in these soils or neighboring soils (Kraimer et al. 2005). If the mineralogy of gallery carbonate had been vaterite or some other carbonate mineral, then that would have been evidence for the biomineralization hypothesis. Based on this analysis, however, termites appear more likely to have transported particles from the subsoil to the surface.

Microscopy and X-ray mapping

Petrographic thin sections, scanning electron microscopy, and X-ray analysis were used to test the hypotheses as follows: If termites are *biomineralizing* carbonate, then carbonate should be generated in the termite bodies at specialized sites capable of making crystals (Simkiss and Wilbur 1989; Lowenstam and Weiner 1989; Weiner and Dove 2003). If termites are transporting carbonate, no such biomineralizing sites are required. Instead, the termites would be carrying carbonate in their guts.

Petrographic thin sections of termite bodies indicate an abundance of crystals that appear to be calcite within each termite body for all four sites. These crystals are mainly distributed along

the edges of termite abdomens, but also extend through their thoraxes, necks, and into their heads. Optically, these crystals have a birefringence similar to calcite (0.172). However, when 10% HCl was applied to the crystals under a dissecting microscope, no effervescence was observed.

Moreover, X-ray chemical maps of termites revealed that Ca is not necessarily concentrated at the sites of these crystals along the edges of the termite bodies. Instead, Ca is most concentrated throughout the abdomen in general (Fig. 3B–E). This supports the HCl test, which indicated that the crystals along the edge of the termite bodies are not calcite. A closer view of the crystals along the edge of the termite bodies reveal that the crystals are round (Fig. 3F) and contain high concentrations of potassium rather than calcium based on X-ray mapping (Fig. 3G, H) and X-ray spot analysis (Liu 2002).

Still, the existence of calcite within termite bodies was confirmed by analyzing the termites with XRD (Fig. 5). However, based on the Ca
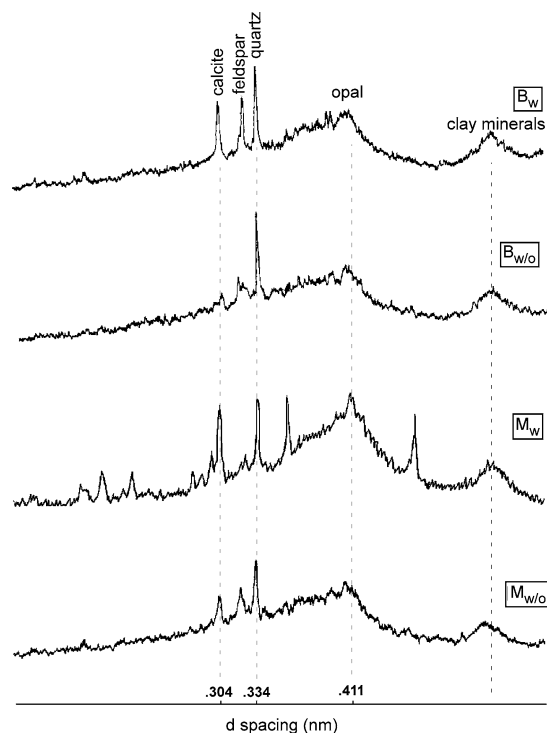

Fig. 5 X-ray diffraction patterns of termite bodies collected from the four study sites

map (Fig. 3D, E), the calcite must be located in the gut. There also the termites would carry phytolith opal, quartz, feldspars, and other soil minerals detected by XRD (Fig. 5). The phytolith opal would be obtained from ingesting plants, mainly grasses, which contain notorious amounts of biogenic silica (Monger and Kelly 2002).

Although termites contain abundant crystals throughout their bodies that have a birefringence similar to calcite, analysis of these crystals with HCl and X-ray chemical analysis reveal that they are not calcite. Instead, calcite is carried in the termite's gut, along with other soil minerals. Based on microscopy and chemical mapping, therefore, termites are not biomineralizing calcite, but are transporting calcite particles to the land surface.

Conclusions

The objective of this study was to determine the origin of carbonate particles in termite galleries. The field documentation test of the hypotheses argues against the biomineralization hypothesis because carbonate did not occur in all galleries regardless of the presence or absence of subsoil carbonate. The carbon isotope test could not explicitly disprove the biomineralization hypothesis because it is possible that termites could have precipitated carbonate with the same δ^{13}C values as the underlying soil carbonate. However, the isotope test did provide evidence for the transport hypothesis since the majority of galleries had carbonate δ^{13}C values that matched the underlying soil carbonate δ^{13}C values at some depth.

The X-ray diffraction test, like the previous test, did not explicitly exclude the biomineralization hypothesis because termites could have biomineralized calcite. However, this test did provide evidence for the transport hypothesis because the calcite XRD peaks in the galleries matched the calcite XRD peaks in the underlying soil horizons. The microscopy and X-ray mapping tests provided the strongest evidence for the exclusion of the biomineralization hypothesis. There was no evidence of in situ calcite production in the termite bodies. Instead, calcite existed

in the guts of termites, along with other soil minerals, which support the transport hypothesis.

It is concluded, therefore, that the carbonate in the aboveground termite galleries of the Chihuahuan Desert study area originated from the upward transport of carbonate particles by termites and that biomineralized $CaCO_3$ is not the cementing agent, which instead is probably saliva or excrement (Lee and Wood 1971a; Whitford 2002). Therefore, the role that termites play in the carbon cycle and carbon sequestration of this region is probably less significant than a role termites would have otherwise played had they biomineralized $CaCO_3$ directly.

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