Ants as a powerful biotic agent of olivine and plagioclase dissolution

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ABSTRACT

The biotic enhancement of Ca-Mg silicate weathering has helped maintain Earth's habitability over geological time scales by assisting in the gradual drawdown of atmospheric CO_2. 25 years of in-situ measurements of Ca-Mg silicate mineral dissolution by ants, termites, root mats, bare ground, and a control reveals ants to be one of the most powerful biotic weathering agents yet recognized. Six sites in Arizona and Texas (USA) indicate that eight different ant species enhance mineral dissolution by ~50×–300× over controls. A comparison of extracted soil at a 50 cm depth in ant colonies and adjacent bare ground shows a gradual accumulation of $CaCO_3$ content for all eight ant species over 25 yr. Ants, thus, have potential to provide clues on how to enhance contemporary carbon sequestration efforts to transform Ca-Mg silicates and CO_2 into carbonate. Given that ants underwent a great diversification and biomass expansion over the Cenozoic, a speculative implication of this research is that ant enhancement of Ca-Mg silicate dissolution might have been an influence on Cenozoic cooling.

INTRODUCTION

Earth's habitability over geological time scales requires the slow drawdown of atmospheric CO_2 despite increasing solar irradiance (Schwartzman, 2002) through the Urey reaction (Urey, 1952) generalized as:

$$CO_2 + CaSiO_3\,(\text{Ca-silicate, e.g., plagioclase}) \rightarrow CaCO_3\ (\text{limestone}) + SiO_2\ (\text{e.g., clays}), \tag{1}$$

and

$$CO_2 + MgSiO_3\ (\text{Mg-silicate, e.g., olivine}) \rightarrow MgCO_3\ (\text{dolomite}) + SiO_2\ (\text{e.g., clays}). \tag{2}$$

CO_2 drawdown largely depends on the time that water remains in contact with undissolved Ca-Mg silicates and rates of dissolution (Maher and Chamberlain, 2014), and this drawdown is countered by volcanic outgassing, oxidation of reduced carbon in sediments (Schwartzman, 2002), sulfide oxidation, and carbonate dissolution (Torres et al., 2014). Biotic enhancement of Ca-Mg-silicate mineral decay has been vital in keeping Earth's temperature habitable for low-temperature life through CO_2 drawdown (Drever, 1994; Moulton et al., 2000; Schwartzman, 2002; Schwartzman and Volk, 1989).

Researchers increasingly use field measurements to better understand weathering (Brantley, 2005; Navarre-Sitchler and Brantley, 2007; Swoboda-Colberg and Drever, 1993; White and Brantley, 2003). Several field-based approaches analyzed the solute load of rivers to estimate the biological enhancement of weathering (BEW). For example, a BEW of 2×–5× occurs for conifers compared to lithobiont-covered drainages in Iceland (Moulton et al., 2000); 4× for pine trees over a deforested drainage (Arthur and Fahey, 1993); and 8× for trees over bare ground/meadow in alpine drainages (Drever and Zobrist, 1992). The dissolved load of rivers, however, could end up overestimating or underestimating chemical weathering rates (Bouchez and Gaillardet, 2014).

Strategies other than river solute, however, reveal similar BEWs: cosmogenic nuclide and geochemical mass-balance methods indicate a BEW of 2× for trees compared to scrub vegetation above tree line (Riebe et al., 2004); using digital image processing of backscattered electron microscope imagery, 3×–20× under lichens as opposed to abiotic sites (Brady et al., 1999); 10×–18× for pines in sandboxes (Bormann et al., 1998); and 8× for microorganisms in glaciated systems (Montross et al., 2013). No prior research, however, has yet examined the BEW of over 10^{13} ants on Earth (Holldobler and Wilson, 1990) or of termites, which could have a higher world population than ants (Zimmerman et al., 1982).

METHODS SYNOPSIS

The general research strategy employed here places completely foreign mineral material—sand-sized particles of ground-up Hawaiian basalt—in the midst of potential weathering agents (ant nests; termite nests; root mats of angiosperms and gymnosperms) and away from these agents at bare soil spots and inside plastic pipes receiving only infiltrating precipitation to serve as a control. Step 1 involved collection of basalt from the A.D. 1800–1801 Kaupulehu flow of Hualalai volcano (Hawaii) and measuring the initial state of intra-crystal porosity for 200 Ca-plagioclase grains at 0.002% ± 0.002% and for 200 Mg-olivine grains at 0.001% ± 0.001%.

Step 2 involved crushing basalt, sieving 1φ basalt sand grains (0.5 mm), and transporting grains to four sites in the Catalina Mountains of Arizona at elevations of 1000 m (32.311°N, 110.779°W), 1500 m (32.339°N, 110.681°W), 2000 m (32.367°N, 110.676°W), and 2500 m (32.428°N, 110.801°W). The Catalina sites range from desert scrub at 1000 m, to oak-grassland at 1500 m, to oak-chaparral at 2000 m, to a mixed pine-oak forest at 2500 m. Two sites within 300 m of each other at Palo Duro Canyon of Texas (34.809°N, 101. 397°W) at 760 m host a semi-arid ecoregion including *Prosopis glandulosa* and *Juniperus monosperma*.

Step 3 placed the foreign basalt grains into ant and termite nests in five auger holes ~50 cm deep, into bare-ground sites in five auger holes ~50 cm deep, and into root mats of different trees at these sites (*Cercidium microphyllum, P. juliflora, Quercus turbinella, Cercocarpus montanus, Q. emoryi, Pinus ponderosa, Q. hypoleucoides, P. glandulosa, J. monosperma*).

Step 4 repeated every 5 yr with an auger-facilitated extraction of basalt grains from each weathering agent. Using these extracted grains, backscattered electron microscopy of randomly selected Ca-plagioclase and Mg-olivine minerals imaged intra-crystal porosity. In-situ dissolution was then measured using digital image processing to calculate the percent intra-crystal porosity (Dorn, 1995). The cumulative dissolution after 25 yr allows a direct comparison of various ant, termite, and plant agents versus controls on 100 Ca-plagioclase grains and 100 Mg-olivine grains collected after 5, 10, 15, 20, and 25 yr from these field sites. The GSA Data Repository[1] provides further details on these methods.

Then, in order to assess temporal trends in carbonate abundance, material extracted every 5 yr from ant colonies and adjacent bare-ground patches from depths of 50 cm was subject to loss on ignition, with the carbonate content determined by multiplying weight loss between 550 °C and 1000 °C by 1.36 (Dean, 1974).

ANTS AS A POWERFUL WEATHERING AGENT

Mean and median metrics of central tendency for ants, termites, root mats, and bare ground are placed in a ratio where the denominator is the value measured for grains sitting within the plastic pipe at each of the sites for 25 yr (Fig. 1). The Data Repository provides the full data set used to construct Figure 1, including dissolution measurements on each mineral grain.

Metrics of central tendency reveal a clear pattern of biotic enhancement of Ca-Mg sili-

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[1] GSA Data Repository item 2014278, supplementary data (method details, summary data, and a series of data tables for dissolution measurements on individual crystals), is available online at www.geosociety.org/pubs/ft2014.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.

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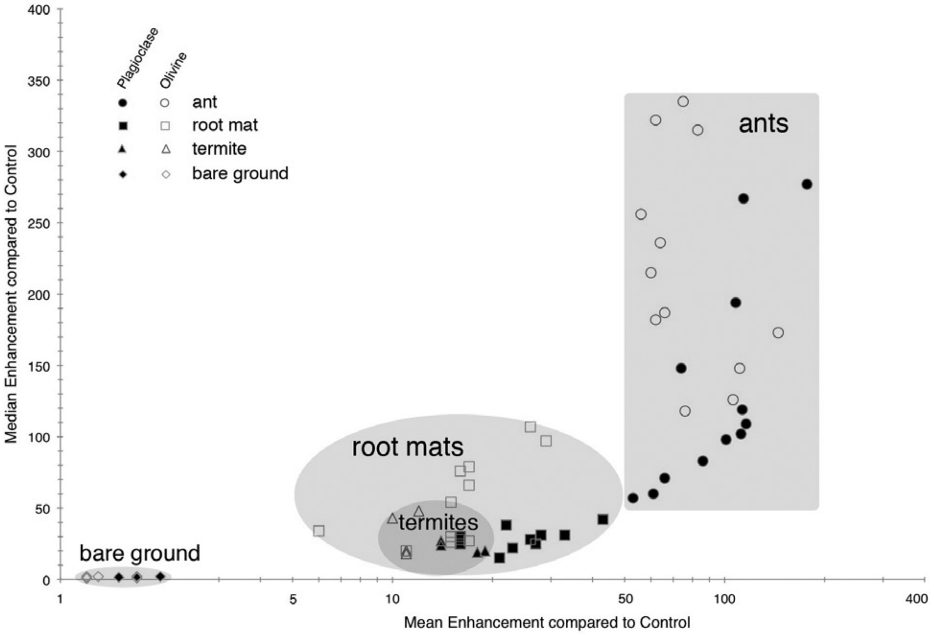

Figure 1. Mineral dissolution enhancements for 25 yr at six field settings in west Texas and the Catalina Mountains of Arizona (USA). Samples of emplaced basalt grains containing plagioclase and olivine were extracted from ant nests, termite nests, root mats of trees, bare-ground settings, and a control consisting of basalt grains in plastic pipes exposed only to infiltrating precipitation. Dissolution measurements on individual minerals and summary data are available in the Data Repository (see footnote 1).

cates exposed to mineral decay agents for 25 yr (Fig. 1): ants >> root mats > termite colonies >> bare ground > control minerals in plastic pipes. Values for abiotic mineral decay rates in the control setting of plastic pipes experiencing only infiltrating water are similar to other abiotic rates of in-situ dissolution (Brady et al., 1999). Bare-ground sites showed only a slight enhancement above minerals in the plastic pipes.

Average biotic enhancements by the root mats of different woody species range from 11× to 43× (Fig. 1). The highest observed root-mat enhancements are at 2500 m in Arizona's Catalina Mountains for *P. ponderosa* (43× for plagioclase) and *Q. hypoleucoides* (33× for plagioclase). Root-mat enhancements measured here (Fig. 1) are considerably higher than those of other field-based studies (Taylor et al., 2009); however, minerals in previous studies included already weathered surfaces as reaction sites. In contrast, this study only analyzed fresh surfaces of minerals that remained in the midst of porous root mats for the entire 25 yr. Thus, these measurements are best interpreted as maximum BEWs of Ca-Mg mineral dissolution for the studied species and in these particular ecoregion settings.

Ants have been identified previously as an agent of soil mixing that enhances weathering rates (Schwartzman, 2002), and termites are also known to alter elements (Sarcinelli et al., 2009) and clay minerals (Jouquet et al., 2007) around colonies. No prior research, however, has quantified the impact of ants or termites on the dissolution of Ca-Mg silicates. For the termite genus *Reticulitermes* at two sites in the Catalina Mountains and two sites in west Texas, termites enhanced the average dissolution of olivine by ~10×–12× and plagioclase by 14×–19× .

For eight different ant species, mean enhancement of plagioclase ranges from 66× to 177× (Fig. 1). Mean enhancement of olivine ranges from 53× to 75× . Using the median, the enhancement of plagioclase ranges from 98× to 277× and olivine ranges from 76× to 335× . These high BEWs are seen at all elevations (climates) in the Catalina Mountains in Arizona, for all species of ant at the different sites in Arizona and Texas, and for both Mg- and Ca-silicate minerals. Ants are ~3×–10× more powerful decay agents than nearby tree roots, and have ~5× the effect of termites and ~50×–100× the effect of mineral dissolution observed in adjacent bare soil.

While the basalt sand grains remained in direct proximity to root mats for the entire 25 yr, the exact history of the randomly extracted basalt grains from ant and termite colonies remains uncertain. It is unlikely that the basalt grains remained in close proximity to ant or termite BEW agents (e.g., ant glands, in fungal gardens) for the entire 25 yr—leading to interpretation that these BEWs for ant and termite colonies are best interpreted as minimum BEWs.

While the randomly selected grains from ant colonies experienced average dissolution rates on the order of 0.01%/yr, some emplaced basalt sand grains fell apart (crumbled) upon handling. Electron microscope examination of these highly decayed minerals reveals extensive pitting on mineral surfaces and hollowing of the center of grains (Fig. 2). It is possible that these highly decayed grains spent more time in contact with ant weathering agent(s) over 25 yr.

Processes responsible for the BEW of tree roots and associated mycorrhizal fungi relate to photosynthate transported from shoots to roots, mycelial networks acidifying the immediate root environment to extract nutrients from altered minerals, and releasing low-molecular-weight organic chelators and other associated processes (Taylor et al., 2009). In contrast, the processes by which ants and termites might enhance mineral decay, other than increased bioturbation (Schwartzman, 2002), remain unstudied.

$CaCO_3$ PRECIPITATION IN ANT COLONIES

Mandel and Sorenson (1982) reported higher concentrations of $CaCO_3$ in ant colonies compared to adjacent undisturbed soils—an observation replicated in this 25 yr study. Loss on ignition (Dean, 1974) measured carbonate abundance in sediment extracted from ant colonies and adjacent bare ground sites. The material derived from a depth of 50 cm reveals a clear trend: all sampled ant colonies accumulated calcium carbonate over time, whereas adjacent bare ground sites did not (Fig. 3).

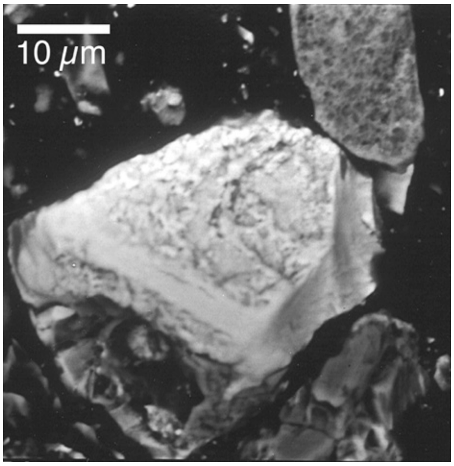

Figure 2. Backscattered electron (BSE) microscope image of olivine and plagioclase minerals pitted and hollowed in an ant nest. The random sampling strategy used to obtain a statistical understanding of the impact of ants on mineral decay does not address the extreme decay observed in just 25 yr for some minerals, as viewed by BSE for minerals that fell apart while handling a sand grain from the *Dorymyrmex bicolor* colony at the Catalina 1500 m site. The brighter grain showing pitting and hollowing of the core is olivine. The darker grains showing pitting (upper right) and hollowing (lower right) are plagioclase.

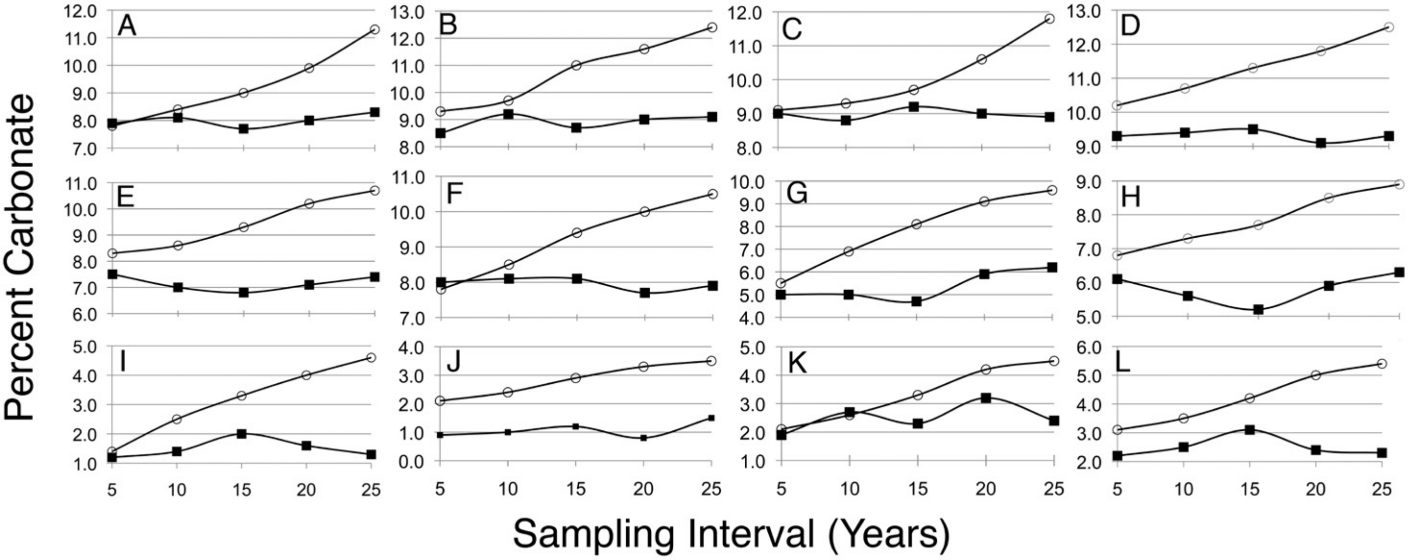

Figure 3. Carbonate accumulation in ant nests (open circles), compared to adjacent bare ground (solid squares), over a 25 yr period. Both sample types were collected from a depth of 50 cm every 5 yr. A: *Pogonomyrmex rugosus* at Palo Duro, Texas (PD, USA), site 1. B: *P. rugosus*, PD site 2. C: *P. barbatus*, PD site 1. D: *P. barbatus*, PD site 2. E: *Dorymyrmex bicolor*, Catalina Mountains, Arizona (CM), at 1000 m elevation. F: *Forelius pruinosus*, CM 1000 m. G: *D. bicolor*, CM 1500 m. H: *F. pruinosus*, CM 1500 m. I: *Liometopum luctuosum*, CM 2000 m. J: *Tapinoma sessile*, CM 2000 m. K: *Formica neogagates*, CM 2500 m. L: *Camponotus vicinus*, CM 2500 m.

The source of the calcium for this carbonate accumulation is important, because drawdown of atmospheric CO_2 would occur if the observed $CaCO_3$ accumulation (Mandel and Sorenson, 1982) (Fig. 3) resulted from the Ca from silicates combining with soil bicarbonate. The precipitation of $CaCO_3$ around plagioclase grains (Fig. 4) provides speculative support for the hypothesis that plagioclase could be a source for at least some of the calcium. However, ants could also be scavenging $CaCO_3$ from the adjacent soil, and Ca could come from soil water derived from atmospheric dust (Naiman et al., 2000).

A second uncertainty associated with the accumulation of carbonate involves the processes taking place in the eight observed ant species that promote carbonate accumulation. Possible explanations include: enhanced pCO_2 in the pores of ant nests (Tschinkel, 2013) that could result in calcite precipitation once Ca^{2+} became available; and the hydrolysis of urea catalyzed by urease (Hammad et al., 2013) that occurs in association with ant microbes (Zientz et al., 2005).

POTENTIAL IMPLICATIONS OF HIGH ANT BEW

Current research on ways to reduce atmospheric CO_2 through weathering includes olivine, where 1 kg could sequester approximately 1 kg of CO_2 (Cressey, 2014), and storage as carbonate in underground basalt (Gislason and Oelkers, 2014). Given observed high BEW of ant colonies, an understanding of the geobiology of ant-mineral interactions might offer a line of research on how to geoengineer accelerated CO_2 consumption by Ca-Mg silicates. Similarly, ants might also provide clues on geoengineering efficient pathways of $CaCO_3$ precipitation to sequester atmospheric CO_2.

Earth's climate has cooled significantly over the past 65 m.y., likely from hydrologic regulation (Maher and Chamberlain, 2014), vegetation change (Dutton and Barron, 1997; Retallack, 2001), and interactions related to tectonism (Raymo and Ruddiman, 1992) in part mediated by Ca-Mg silicate mineral dissolution (Maher and Chamberlain, 2014; Torres et al., 2014; Willenbring and von Blanckenburg, 2010) that draws down CO_2. Although speculative, the timing of the expansion in the variety and number of ants in the Paleogene and the Neogene (Brady et al., 2006; LaPolla et al., 2013) suggests that ant BEW could potentially be a part of the puzzle of Cenozoic cooling.

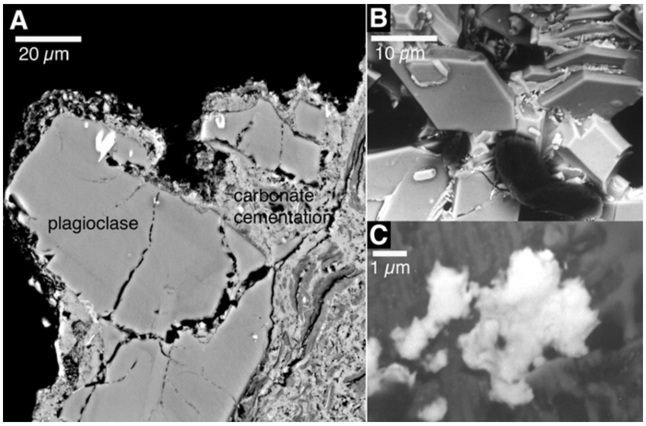

Figure 4. Backscattered electron (BSE) images of accumulation of calcium carbonate on plagioclase grains in an ant nest at Palo Duro site 2 (Texas, USA). Energy dispersive X-ray spectrometry distinguished plagioclase from calcium carbonate deposits. A: In wall of tunnel of ant nest infused with epoxy, carbonate rims and cements plagioclase grains that were not emplaced but derived from local granitic bedrock. B: Carbonate occurs as bright spots deposited on heavily fragmented plagioclase grains of emplaced basaltic sand grain. C: Close-up of carbonate deposit from B.

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