Coupling between Biota and Earth Materials in the Critical Zone

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The surface of our planet is the result of billions of years of feedback between biota and Earth materials. The chemical weathering of soils and the resulting stream and ocean chemistry bear the signature of the biological world. Physical shaping of the Earth's surface in many regions is a biologically mediated process. Given the pervasiveness of life, it is challenging to disentangle abiotic from biotic processes during field observations, yet it is of paramount importance to quantify these interactions and their feedbacks as the human impact on climate and ecosystems becomes more profound. Here we briefly review the fascinating connection between rocks and life and highlight its significance to science and society.

KEYWORDS: chemical weathering, erosion, soils, biosphere

INTRODUCTION

The Earth has an average surface temperature of about 15°C, which is, in terms of planetary conditions suitable for life, the equivalent of winning the cosmic lottery. Yet, without an atmosphere filled with biological waste gases capable of retaining heat (O_2, N_2O, CH_4, CO_2), the average temperature of the planet would be about –18°C (Smil 2002), making the present diversity and abundance of life virtually impossible. Thus, since the evolution of prokaryotic heterotrophic organisms early in the Archean some 4 billion years ago, the Earth's Critical Zone has evolved as a dynamic and generally self-sustaining system. The interplay between biotic and abiotic components of the planet has directed the pace of evolution and shaped the climate of the Earth. This complex system containing life and Earth materials was first termed the *biosphere* in 1875 by the Austrian geologist Eduard Suess, but it remained for the Russian scientist Vladimir Vernadsky in 1926 to articulate the concept as a scientific paradigm. The processes that control the biosphere are now gaining attention, as one species, *Homo sapiens*, enters its third century of massive alteration of the planet. A looming issue at this critical juncture in geological and human time is to understand how resilient this system is to human activities.

"The Earth is not just an ordinary planet!"
– Antoine de Saint-Exupéry
The Little Prince

The Critical Zone is the portion of the biosphere that lies at the interface of the lithosphere, atmosphere, and hydrosphere (FIG. 1), and it encompasses soils and terrestrial ecosystems. While many processes occur within this system, we focus here on how biota and Earth materials interact during chemical weathering and landscape evolution. Because of their impact on society, these processes are important areas of research in Earth sciences. The biotic–abiotic feedback system in the Critical Zone is poorly understood but is important for predicting the near-term habitability of our planet.

BIOTA AND CHEMICAL WEATHERING

Chemical weathering is the aqueous alteration of minerals that is coupled to the release of soluble weathering products and the formation of new minerals. This process impacts global water composition (Gaillardet et al. 2004), soil formation, ecosystem nutrient availability, and atmospheric CO_2 levels (Berner 2003), but until recently, it has been viewed primarily as a set of inorganic reactions (e.g. Berner et al. 2004). Over the past few decades, progress has been made in determining the rates of chemical weathering at the watershed and regional scales (e.g. Gaillardet et al. 1999; Dupré et al. 2003). However, the direct role of life is not easy to separate from the role of climate, because biota is so strongly affected by water and heat. Thus, the search for the specific role of plants and fungi on chemical weathering has intensified (Lucas 2001; Berner et al. 2004; Richter et al. 2007). The evolution of land plants and animals in the distant past had profound effects on the rate of mineral weathering and ultimately on the global climate and atmospheric chemistry—effects that continue today.

Plants are geochemical pumps that remove bio-essential elements from the soil solution, use them in metabolic processes, temporarily store them in tissue, and return them to the soil via litterfall, root decay, and decomposition after death (FIG. 2). Plants mediate these cycles, affecting the chemical availability and physical distribution of rock-derived nutrients in a unique manner. The cycling of lithospheric elements, such as P, Ca, K, and Si, by plants often leads to an upward transport that causes a surface enrichment of these elements that cannot be explained by abiotic

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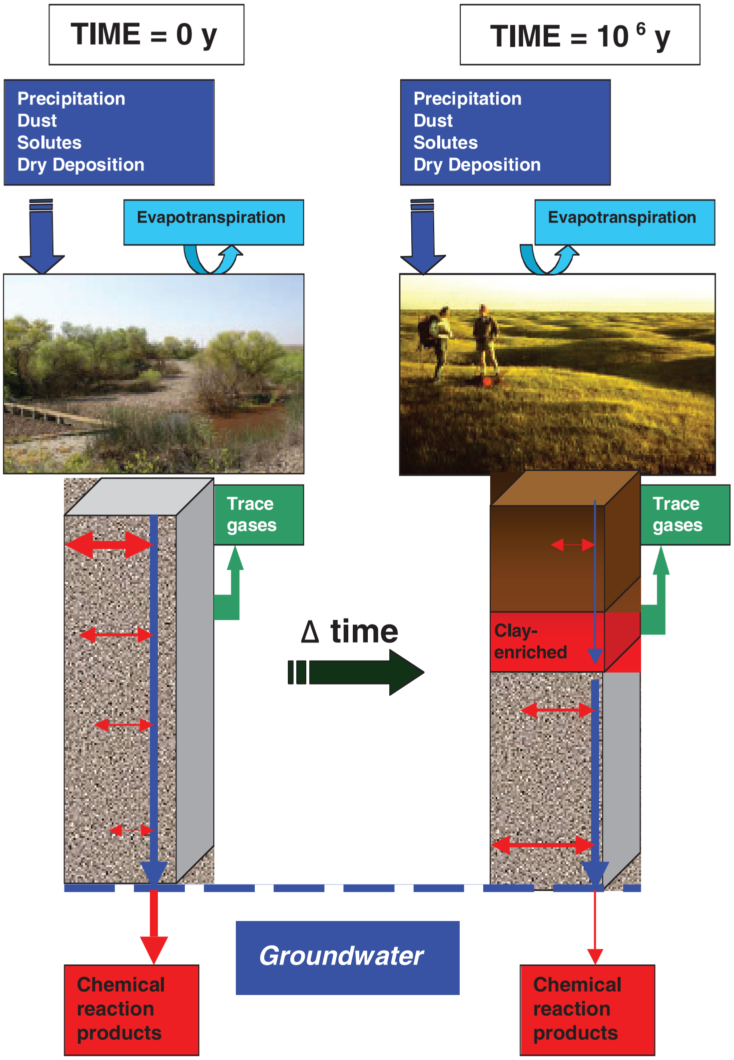

FIGURE 1 Cartoon illustrating hypothesized changes in Critical Zone hydrology, biogeochemical processes, and landscape evolution with time. The sediment column on the left represents a fluvial deposit on a floodplain at time = 0. Following river incision or meandering, the floodplain is abandoned, vegetation is established, and the landscape is physically stabilized. After river incision, long-term soil formation processes ensue, and after 10^5 or more years, chemical weathering (enhanced by the presence of life) and advective transport help to form element-depleted layers near the surface and soil horizons enriched in clay (red layer in right column). Biological mixing stirs organic matter into the soil surface creating a darkened surface horizon. Biota also move soil laterally, creating low mounds, as shown in the photograph on the right. The rates of all processes may change with time. This schematic is representative of soil biogeochemical processes in California's San Joaquin Valley.

processes (Lucas 2001; Jobbágy and Jackson 2004). Biological uplift of Si has been proposed as the mechanism for the unanticipated kaolinite-rich soil horizons that overlie oxide-rich horizons in the warm, humid tropics (Lucas 2001). The release of Si from litterfall is greater than the Si released by mineral weathering, thereby maintaining a near-surface, Si-rich mineral assemblage that would otherwise be impossible under abiotic conditions.

Plants enhance weathering. Plant roots contribute nearly 50% of total soil respiration [soil respiration = 0.15 to 1.5 kg C (in CO_2) m^{-2} y^{-1}; Sanderman et al. 2003]; the balance is from microbial respiration. This biologically derived soil CO_2 drives concentrations in soil gas to levels several orders of magnitude higher than in the atmosphere and forms carbonic acid, which attacks silicate and carbonate minerals. The *rhizosphere* is the immediate region around actively growing roots. It is a millimeter-thick volume in which a locally extreme chemical environment alters weathering rates (Richter et al. 2007). Plants take in solutes in the rhizosphere via ionic exchange (the release of H^+ for Ca^{2+}, Mg^{2+}, Na^+, and NH_4^+), driving pH as low as 3 (Berner et al. 2004) and greatly increasing mineral decomposition rates. In addition, roots exude organic chelates such as oxalate, which form soluble complexes with Al, Fe, and other metals, significantly increasing mineral solubility. Plant-derived humic substances have been found that temporarily store and transfer electrons, thereby mediating oxidation and reduction reactions with redox-active metals.

In conifers and many dicots, symbiotic relationships are formed with ectomycorrhizal fungi, which acquire C compounds for energy use in "exchange" for supplying these plants with essential nutrients such as P. The organic acids produced by these fungi allow them to burrow into silicate rock in order to extract P from apatite. These elements are passed to the host directly, bypassing the soil solution, thus greatly increasing their uptake (Berner et al. 2004). In nutrient-poor soils, some plants use cluster roots to scavenge essential elements. Nutrient uptake is facilitated by an enlarged surface area of root mass and a variety of exudates, including carboxylate anions, acid phosphatases, phenolics, etc.

The biotic impact on soil weathering is translated to the composition and reactivity of streams and oceans. Rivers reflect the biogeochemical fractionation in the Critical Zone. Biota increases the dissolved chemical load in rivers through production of organic acids and ligands that complex dissolved species, greatly increasing their solubility relative to abiotic conditions (Gaillardet et al. 2004). Gaillardet et al. (2004) noted that the organic speciation of many metals in river waters has been poorly documented because these molecules are large and difficult to characterize. Nevertheless, correlations between major elements and dissolved organic carbon have been reported, suggesting that organic matter enhances chemical weathering (Viers et al. 1997).

Novel applications of isotope and element ratios are beginning to reveal that biotic controls on element cycling have strong global signals. The Earth's crust is about 90% silicate minerals and the most abundant cation is Si. It is well known that Si moves from soil minerals to plant tissue by the active intervention of plants. Ge/Si ratios have been used to understand Si behavior during weathering, because while both are released from primary minerals at similar rates, their susceptibility to biological cycling in soils differs greatly, with Ge being largely excluded by plant cycling. Analyses of the Ge/Si ratio of river water generally reveal ratios that differ from, and are considerably lower than, those of the primary minerals in the watersheds. Initial interpretation attributed this phenomenon to the retention of high Ge/Si in secondary phyllosilicates in soils. However, the biological connection suggests that opal (a glass-like mineral that forms in the leaves and other tissues of plants following plant uptake of Si from the soil solution) serves as a Si-rich reservoir (Derry et al. 2005). Following leaf loss, opal is rapidly dissolved, providing silica for subsequent plant uptake; some is released to surface water, contributing to the observed low Ge/Si ratios. In highly weathered soils, this biogenic Si pool is the major source of biologically available Si. Thus, the biotically mediated terrestrial Si cycle translates its Ge/Si signal to rivers and oceans. Silicon isotope ratios ($^{30}Si/^{28}Si$) in Hawaiian soils reveal that plant uptake of Si causes an enrichment of ^{30}Si in the remaining dissolved Si in the soil solution (Ziegler et al. 2005), matching trends in stream water. An extreme case, where soils develop on volcanic ash, is a 15 cm thick surface layer

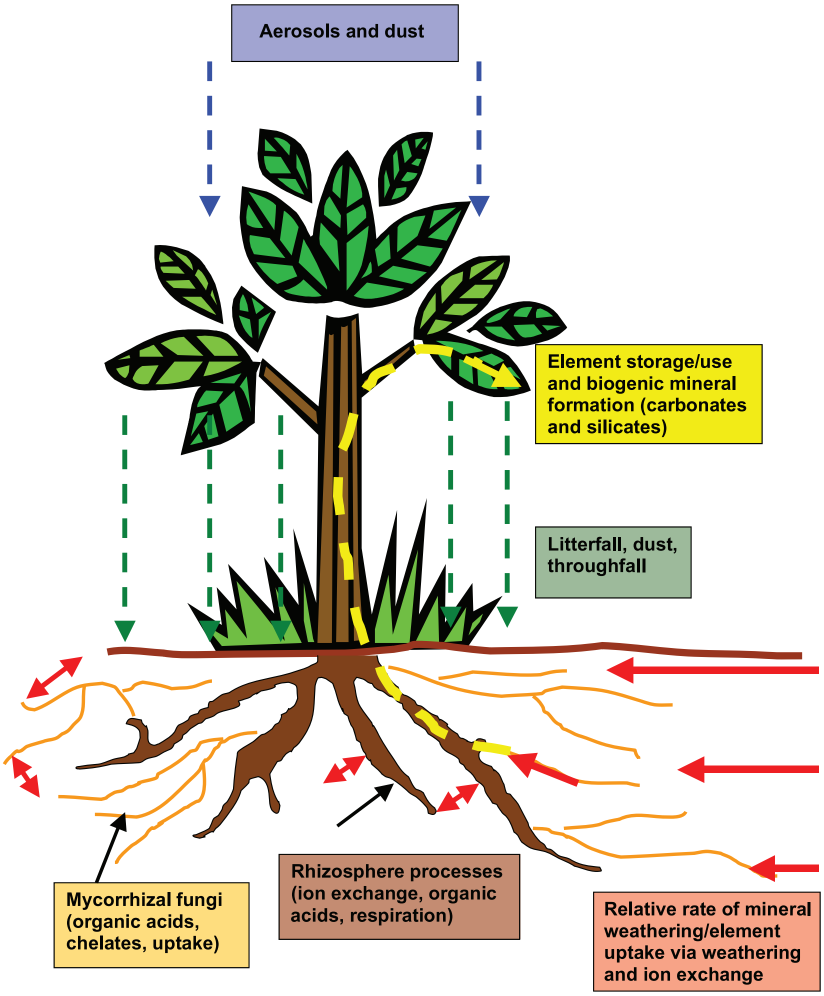

FIGURE 2 Diagram illustrating plant and fungal controls on soil mineral weathering and element cycling. Silicate dust and aerosols from local and distant sources are deposited on leaves and the land surface. Water partially dissolves them and transports the material into the soil. The reactivity of the resulting solution with soil minerals generally declines with depth as waters approach equilibrium, represented by red arrows. Roots passively and actively (via ion exchange) take up dissolved ions from the soil water (indicated by the two-way red arrows). Additionally, roots enhance water–mineral reactions through release of organic molecules capable of increasing mineral solubility. Mycorrhizal fungi, through symbiosis with roots, provide additional avenues of mineral weathering by releasing organic acids and chelating agents that significantly increase the solubility of important nutrients such as P and Ca. Mineral-derived elements accumulate in plant tissue in various forms, serving both structural and physiological functions. Some elements, such as Ca and Si, may form biologically mediated minerals within the plant (carbonates, oxalates, amorphous silica), which are released to the soil following death of the tissue (MODIFIED FROM BERNER ET AL. 2004).

formed almost entirely of biogenic opal produced by the Si bio-accumulator *Nastus borbonicus*. Such soil accumulations decrease Si loss to streams and rivers (Meunier et al. 1999).

Silicon is just one of a growing list of elements observed to reveal the fingerprint of biology. A number of other elements have a strong affinity for organic matter complexation, and isotope and element ratios help reveal these biotic processes. Many "new" isotopic systems are being developed that will serve as fingerprints for life processes: B (contributing to tissue rigidity and transport of sugar); Ca (required for calcification); Mg (necessary for photosynthesis); Cu, Zn, and Mo (components of major enzymes); and Fe. However, separating the biotic from the abiotic effects in these isotope systems is still in its infancy.

That there is a "geochemical signature of life"— a signature that helps to define the rates and degree of chemical alteration at the Earth's surface—is not a new concept. Massive marine limestone deposits, composed of the carbonate hard parts of marine phytoplankton, are the most obvious testimonial. However, this brief review of weathering in the Critical Zone demonstrates that few chemical reactions escape the influence of living organisms.

BIOTA AND GEOMORPHIC MODIFICATION OF LANDSCAPES

The land surface is inhabited by plants and animals that grow through or burrow in the soil. Thus, geomorphic processes are mediated by biota. Bioturbation is so pervasive that it has even led to questions about whether a "topographic signature of life" is observable on the planet (Dietrich and Perron 2006). Although this remains a matter of debate, it is clear that biota affects physical processes (Johnson 1990; Paton et al. 1995). As an illustration, we focus on soil-mantled hillslopes (see Anderson et al. 2007 this issue). In these landscapes, the soil mantle represents a "conveyor belt" of sediment that is slowly driven downslope by random, diffusion-like processes, such as gopher (or other ground-dwelling animals), termite, and earthworm burrowing. Charles Darwin recognized the volume of earth moved by earthworms in his last major work, which he concluded by stating, "It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organised creatures" (Darwin 1881). This biotically powered soil conveyor belt, or biomantle (Johnson 1990), receives its replacement material by the physical transformation of underlying rock and the transfer of the weathered product to the overlying soil column (termed "soil production") and from sediment accumulated by erosion from upslope locations. These processes are described by a "conservation of mass" equation, which describes how the rate of change in the land surface is controlled by the difference between uplift and incision and the transfer of material over the bedrock (FIG. 3):

$$\frac{\partial z}{\partial t} = U - P - \nabla(-K\nabla z) \qquad (1)$$

where z represents the elevation of the land surface, t is time, U is the uplift rate of the landscape, P is the conversion rate of bedrock to soil, and $-K\nabla z$ is the volume flux of sediment per unit slope contour length, a process explicitly dependent on slope, ∇z (Dietrich and Perron 2006). While there is discussion about whether the Earth's biota, through modifying climate and rainfall, can affect uplift rates (Dietrich and Perron 2006), it is now well known that biota contributes significantly both to soil production (P) and to slope-dependent transport ($K\nabla z$).

Gilbert (1877) proposed that soil production must be depth dependent, with rates declining with increasing soil thickness because of the decreasing physical disaggregation processes with depth. He also suggested that the maximum rate of soil production should occur under a shallow (rather than zero) soil thickness. A shallow soil layer allows biota to exist and to interact with the underlying bedrock, causing high soil production rates. This "soil production function" is now being quantified using cosmogenic radionuclides.

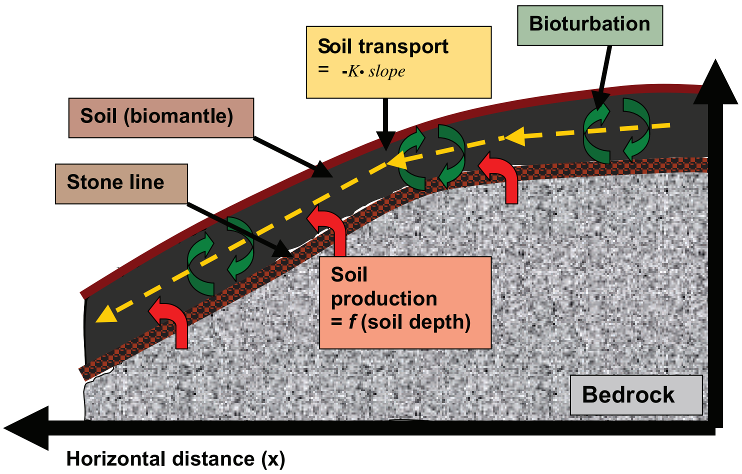

FIGURE 3 Schematic diagram illustrating soil production and slope-dependent transport on a hillslope dominated by biotically driven diffusive sediment transport (modified from Heimsath et al. 1997). A soil biomantle (commonly the dark A horizon, rich in organic matter) is mixed by burrowing animals, insects, and plants on timescales of ~10^2 yrs. This random mixing, combined with a gravity gradient, drives net downslope transport. This is quantified by a "diffusion coefficient," *K*, multiplied by slope. The physical mixing of fine particles by burrowing animals, worms, etc. commonly causes stones and archeological artifacts to "settle" at the base of the mixed layer, forming "stone lines." On landscapes at or near steady state, as the soil mantle thins through erosion, biological and physical processes release material from the underlying rock (soil production), which then become part of the overlying soil. The rate of soil production commonly decreases with increasing soil thickness primarily because biological and physical mixing processes decline with soil depth.

They reveal that maximum soil production rates may sometimes occur under thin soil, and in other cases, where no soil is present (Humphreys and Wilkinson 2007).

The realization that soil movement from hillslopes is controlled by both slope and biota is arguably attributable to Darwin (1881). Darwin counted the annual flux of worm casts that passed across a unit length of a hillslope contour line and he measured the slope, implying that he intuitively recognized that sediment flux is slope dependent. These data allow one to calculate the value of the coefficient *K* in equation 1, a term that implicitly encompasses the effect of biology on sediment transport. Up to now, few attempts have been made to measure the biotic influence on sediment flux (e.g. the value of *K*).

Recently, several groups have begun to question whether slope-dependent transport is linear, as suggested by equation 1, or non-linear, as a result of interplay between biota and Earth materials. Because burrowing soil animals require a minimum soil thickness, there must be some feedback between soil erosion and soil thickness. This has been suggested for burrowing by the North American pocket gopher (e.g. Yoo et al. 2005). As soil thickness increases, gopher burrowing and erosion rates increase (thinning the soil), but as soil thickness declines, burrowing and erosion also decline, allowing soil thickness to slowly increase. In contrast, a quite different pattern is observed in soils where gopher burrowing is minimal or absent (Yoo et al. 2005). In effect, gopher-populated landscapes buffer against rapid changes in soil thickness through feedback, and over long periods this causes a more spatially homogeneous rate of erosion on biotically modified hillslopes than on those modified abiotically. This implies that regional hillslope topography may be preserved longer on gopher-populated landscapes than on landforms undergoing depletion by mechanisms not involving bioturbation. While pocket gophers are peculiar to North America, the same principles may apply, in a somewhat modified way, to other burrowing organisms. Thus, there *may* be a "topographic signature of life," but understanding the mechanisms, rates, and mathematics of the processes is still elusive.

FUNCTION OF THE CRITICAL ZONE WITHOUT LIFE

Given the tenacity of life, the biotic imprint on Earth materials is global and extends to remarkable depths. The pervasiveness of living forms raises the question, "How would Earth surface processes differ in the absence of biota?" One approach is to run the Earth's geological clock backwards into the early Precambrian, prior to the evolution of photosynthesizing organisms. Free O_2 and the ozone layer were lacking, completely changing the redox balance at the Earth's surface, and land-based life was absent. The result would have been a "proto–Critical Zone," an environment completely different from the biota-dominated world we inhabit.

The records of these past geochemical processes are embedded in sedimentary sequences and paleosols. It has recently been proposed that the appearance of biota is reflected in the clay mineral composition of mudstones, which show an increase in the abundance of secondary phyllosilicates (expandable smectites and kaolinite) since the late Precambrian (Kennedy et al. 2006). This increase is coincident with the first appearance of metazoans (multicelled, oxygen-breathing animals), implying a corresponding increase in atmospheric O_2. Kennedy et al. (2006) proposed that the colonization of land surfaces by fungi and other organisms stabilized soil cover, created longer groundwater residence times, added organic acids and chelating agents, and drastically enhanced secondary mineral formation, i.e. a "clay factory." Clays, because of their high surface area and charge, have a strong affinity for organic molecules. The erosion of clay/C-rich soils enhanced the global burial of C, thereby increasing O_2 concentrations in the atmosphere by decreasing the availability of organic material as a CO_2 source (e.g. Berner 2003). The O_2-rich atmosphere that developed was conducive to the evolution of large-bodied organisms. Though debate exists about Earth's early atmosphere, it is clear that strong connections exist between the evolution of life and the function of the Critical Zone. Whether this approaches a biotically self-sustaining Earth, as proposed by the Gaia hypothesis (Lovelock and Margulis 1973), is yet to be demonstrated.

On our current biota-dominated planet, we cannot conduct field research to study a Precambrian-like environment. Yet, there are places on Earth where rainfall (Atacama Desert) and temperature (Dry Valleys of Antarctica) extremes allow us to examine processes and their change at the margins of life. With declining rainfall and temperature, where organism populations become minimal, Critical Zone processes pass through thresholds. For example, the model of the processes controlling soil thickness on hillslopes (equation 1) suggests that as rainfall declines to near zero soil production should also approach zero, and rare precipitation events would erode hillslopes to bedrock. Yet, the reverse occurs in the Atacama Desert, where mean annual precipitation is about 1 to 2 mm per year. Hillslopes are mantled with salts and dust derived from the atmosphere (Ewing et al. 2006), and these remain on slopes because the biotic and abiotic erosion processes are ineffective (Dietrich and Perron 2006). Similar processes occur in the dry Antarctic. In the Atacama Desert, as rainfall declines to 0, soil geochemical processes cross a boundary from net element loss, resulting from biotically enhanced weathering, to large element gain, caused by accumulation of highly soluble chlorides, sulfates, and nitrates derived from the atmosphere (Fig. 4; Ewing et al. 2006). In fact, the lack of active microorganisms is so pronounced that soils accumulate NO_3 because there is no effective biological process to reduce it to N_2. Such a disruption of the N cycle is one of several possible mechanisms for the slow loss of N_2 from the Martian atmosphere (Capone et al. 2006). The impacts of aerosols and dust on the Critical Zone are further discussed by Derry and Chadwick (2007 this issue).

BIOSPHERE RESILIENCE AND THE IMPORTANCE OF CRITICAL ZONE RESEARCH

Because of the rapid changes that have occurred on Earth since the beginning of the Industrial Revolution, Crutzen (2002) argued that humans have steered the Earth into a new geological epoch—the Anthropocene (~250 y BP to present). Large and sudden changes in the biological record form the basis of major divisions in the geological timescale, and based on these criteria the Anthropocene is encompassing one of the most pronounced changes in Earth history by any measurement scale one chooses: extinction rates, extent of climate change, etc. These changes affect other global processes in ways that are only beginning to be quantified. For example, human activity has increased the rate of sediment transport by rivers (2.3×10^9 Mg y^{-1}) as a result of accelerated soil erosion, yet less sediment reaches flood plains and coastal margins (1.4×10^9 Mg y^{-1}) because it accumulates in reservoirs created by dam construction (Syvitski et al. 2005). In turn, enhanced physical erosion is associated with a corresponding increase in the chemical weathering rate (Gaillardet et al. 1999). Another well-documented example is the increase in atmospheric CO_2, which augments the efficiency with which plants use water; this has been cited as a mechanism behind the global increase in river runoff over the past 50 years (Gedney et al. 2006). The increase in runoff in the Mississippi River basin is, in turn, associated with increases in the rate of chemical weathering (Raymond and Cole 2003). Thus, the immense human impacts on one global cycle (erosion, for example) provoke pronounced changes in other cycles (such as chemical weathering). Understanding the human role in a given geochemical cycle, and the corresponding feedback into other systems, is a challenging task (see Brantley et al. 2007 this issue).

Given the severity of human impact on the Earth's biosphere, is the Critical Zone capable of surviving and sustaining our species? In the ecological sciences, the term *resilience* refers to the ability of a system to maintain its function even under disturbance. How resilient are Critical Zone processes? How much disturbance can biotic and abiotic systems withstand before they cease to function in a manner conducive to human survival? To avoid a global, one-time, unrepeatable experiment with our biosphere, it is imperative that the Earth science community embark on an integrated effort to understand the interaction between humankind and life, rocks, air, and water.

In that light, Critical Zone research must focus on the imprint of humans on the planet. The geographical extent of agriculture, for example, with its intensive physical mixing, addition of strong acids, and accelerated erosion, is as great as the landmass scoured by the last glacial advance. Agricultural practices add massive quantities of fertilizers (derived from rocks), such as P and K, and lime to highly weathered soils. Agriculture, forestry, and grazing, combined with extensive urbanization, make the "human biome" the largest land-based ecosystem on the planet. When agricultural and urban lands are overlaid on soil maps of the United States, for example, many areas show an abundance of soil types that are endangered, or even extinct, because these lands have been commandeered for various human uses (Amundson et al. 2003). One goal of Critical Zone research must be to assist in preserving undisturbed segments of the types of landscapes that have been seriously affected. These will serve as scientific benchmarks—reference locations for geochemical comparison with adjacent cultivated landscapes.

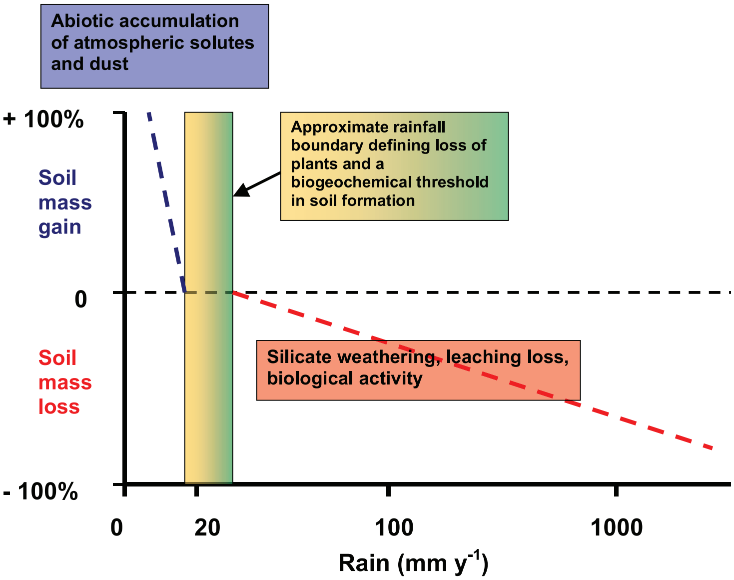

FIGURE 4 Schematic diagram of trends in the variation of total soil mass with rainfall for soils of comparable age (~10^6 y) and temperature (16°C). Where humidity is high, soils undergo large loss of most rock-forming elements through biotically mediated weathering and element cycling. As rainfall declines, net loss also decreases. At the broad boundary between arid (plant-supporting) and hyperarid (plant-inhospitable) climates, soil formation no longer includes element loss, and there is a net soil gain via atmospheric deposition. The rate of gain increases with increasing aridity (Ewing et al. 2006).

In summary, our planet displays the results of an unintentional, multibillion-year experiment between biota and Earth materials. One of the exciting frontiers in the geosciences is the investigation of how biota impacts chemical and physical processes in the Critical Zone. Understanding the feedbacks between life and Earth materials is important for society as well, because humans, a relatively recent addition to the Earth's biota, are increasingly testing the resilience of the Critical Zone. The response of Critical Zone processes to these stresses will ultimately impact the whole of the Earth's biosphere, and thereby, humans themselves.

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