Soil and Ecosystem Development Across the Hawaiian Islands

Peter M. Vitousek, Department of Biological Sciences, Stanford University, Stanford, CA 94305
Oliver A. Chadwick, Department of Geography, University of California, Santa Barbara, CA 93106
Timothy E. Crews, Department of Biological Sciences, Stanford University, Stanford, CA 94305
James H. Fownes, Department of Agronomy and Soils, University of Hawaii—Manoa, Honolulu, HI 96822
David M. Hendricks, Department of Soil and Water Science, University of Arizona, Tucson, AZ 85721
Darrell Herbert, Department of Agronomy and Soils, University of Hawaii—Manoa, Honolulu, HI 96822

ABSTRACT

Biological and geologic processes interact to drive the development of soils and ecosystems across a well-defined 4.1 m.y. sequence of rainforest sites in the Hawaiian Islands. Weathering of the parent rock is the major source of most plant nutrients in young sites, but the more readily weathered minerals are depleted by 20,000 yr, and soil fertility declines in the oldest sites. The supply of biologically available nitrogen limits plant production early in the sequence, while phosphorus supply limits production in the oldest site. The geologic processes of weathering, mineral transformation, and leaching set boundary conditions for terrestrial systems and interact with shorter term biological processes and feedbacks that control plant production, carbon storage, and nutrient cycling.

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INTRODUCTION

Biological and geochemical processes interact to drive the development of soils and ecosystems. Over tens of thousands to millions of years, they shape the characteristics as disparate and important as the development and degradation of soil fertility, the structure and dynamics of landscapes, and the role of terrestrial systems as a source or sink for atmospheric carbon dioxide. Understanding how biological and geochemical processes interact is inherently complex; it is further complicated by the fact that the underlying processes occur on very different time scales, and are studied by different communities of scientists.

A broad-brush understanding of the development of soils and ecosystems on wholly new substrates has been synthesized from studies carried out at widely different scales and summarized in several conceptual models (Walker and Syers, 1976; Jenny, 1980; Fox et al., 1991; Van Breeman, 1993). In humid areas, we recognize three broad phases of development.

1. Building, which begins with a new substrate deposited by receding glaciers, volcanic eruptions, or other geologic processes. The chemical weathering of primary minerals in this new substrate releases elements into soluble and biologically available forms, from which they can be used by organisms, lost via water percolating through the soil, or retained in secondary minerals in the soil. Plant growth during the building phase is constrained by slow dispersal of plants to newly exposed sites, by often-harsh physical and microclimatic conditions, and/or by the supply of fixed nitrogen (which alone among essential plant nutrients is absent from most new substrates).

2. Sustaining, during which the most soluble primary minerals have been depleted, but weathering of more resistant minerals continues to contribute elements to soluble pools and to buffer atmospheric and biological acidity. Clay particles that form as secondary minerals within the soil retain relatively mobile cations like Ca, Mg, and K by ion exchange. Atmospherically derived N and less mobile rock-derived elements such as P reach their maximum biological availability.

3. Degrading, by which virtually all primary minerals have been depleted, or are too deep in the soil to contribute to ecosystems. Atmospheric and biological acidity are no longer buffered by weather-
ing: soils acidify and the solubility of toxic Al increases. Even relatively immobile P has been lost, or bound up in recalcitrant, insoluble, and/or physically protected forms that organisms cannot use. Biological activity is constrained by the low availability of P and/or other rock-derived elements—and unless new geologic activity (volcanism, glaciation, erosion) rejuvenates the soil, only continued degradation can be anticipated.

While many of these features of long-term soil and ecosystem development have been observed in field studies, the nature and consequences of interactions between ecological processes (on time scales of months to decades) and pedological processes (with time scales of centuries to millions of years) are little known—in large part because few places contain well-preserved landforms of vastly different ages that are underlain by similar substrates, and influenced by similar climates and biotic communities.

Crews et al. (1995) described a developmental sequence of sites in the Hawaiian Islands that offer the opportunity to integrate ecological, pedological, and geochemical approaches to understanding long-term soil and ecosystem development. We are analyzing this developmental sequence, with the aims of (1) describing the underlying patterns and processes of soil and ecosystem development, over hundreds to millions of years, (2) determining how interactions between biological and geochemical processes shape the dynamics of soils and ecosystems, and (3) evaluating their regional and global implications.

**Sequence of Sites**

Several features of the Hawaiian Islands make them particularly suitable for studies of long-term soil and ecosystem development. First, the Hawaiian Islands result from the movement of the Pacific tectonic plate over a stationary “hot spot” in the mantle (Hawaii Scientific Drilling Project Team, 1996). Distance from the currently active volcanoes at the southeast extreme of the archipelago closely corresponds to substrate age (Fig. 1), and ages of the different surfaces have been characterized well on both short and long time scales (Clague and Dalrymple, 1987; Wolfe and Morris, 1996). Second, other variables can be held nearly constant. The substrate in which soil and ecosystem development begins is all mantle-derived lava, with relatively little chemical variation in space or time (Wright and Helz, 1987). The maritime tropical environment reduces the impact of Pleistocene climate change, precluding glaciation (which would reset soil and ecosystem development) except at the highest elevations. Topographic position can be kept constant by selecting sites on the well-defined constructional surfaces of the shield volcanoes, which persist as remnants into the oldest sites (MacDonald et al., 1983). Even the dominant organisms can be kept constant—the Hawaiian Islands are the most isolated archipelago on Earth, and the few species that colonized naturally have radiated to occupy an extremely broad range of environments and soils (Carlquist, 1980).

Crews et al. (1995) selected six forested sites arrayed across the Hawaiian Islands; the ages of the underlying tephra substrates are approximately 300, 2100, 20,000, 150,000, and 1,400,000 yr, and 4.1 m.y. Landforms associated with the four youngest sites are illustrated in Figure 1. All six sites are near 1200 m elevation, with 16 °C mean annual temperature, and all currently receive approximately 2500 mm of precipitation annually. All support intact rain-forest vegetation dominated by the native tree *Metrosideros polymorpha* (Kitayama and Mueller-Dombois, 1995).

The sequence is not perfect—no attempt to trade space for time can be. For example, Pleistocene climatic variations are known to have occurred in Hawaii, if in a dampened form relative to continental and temperate areas, and so sites older than 14,000 yr have undergone much of their development in conditions that differ from those of the present (Gavenda, 1992; Hotchkiss and Juvik, 1993). Other sources of variation include isostatic subsidence of the islands (Moore and Clague, 1992), differences in lava chemistry between shield-building and postshield volcanic phases (Wright and Helz, 1987), subtle effects of surface erosion, varying inputs of atmospheric dust from Asia (Fox et al., 1991), and the recent introduction of plant and animal species from outside Hawaii (Vitousek and Walker, 1989). Nevertheless, environmental variation that could affect soils and ecosystems can be constrained in Hawaii to an extent that cannot be matched elsewhere.
RESULTS AND DISCUSSION

Weathering and Mineral Transformations

Immediately after a volcanic eruption, the lava substrate is composed primarily of glass, olivine, clinopyroxene, feldspar, and magnetite-ilmenite. These minerals weather rapidly in the high-rainfall rain-forest environment, particularly after plants become established (Cochran and Berner, 1997). We calculated the absolute loss of each element from the soil relative to an immobile component, using mass-balance procedures that take into account the initial state of the lava, volume change during soil formation, and additions of atmospheric dust. Between four and six soil profiles at each site were sampled by genetic horizon and analyzed for total element concentrations using plasma emission spectroscopy on a borate sample matrix and X-ray fluorescence spectroscopy for Zr.

Elemental loss or gain relative to initial conditions for total element concentrations was calculated following Brimhall et al. (1992):

$$\delta_{i,w} = (p_w C_{i,w} (e_{i,w} + 1)) - (p_p C_{i,p})/100.$$

where $p$ refers to parent material, $w$ refers to weathered soil, $i$ refers to an immobile element, $j$ refers to mobile elements, $p$ is bulk density, $C$ is elemental concentration in wt%, and volume change, $e_{i,w} = (p_{i,p} C_{i,p})/(p_{i,w} C_{i,w}) - 1$ (Chadwick et al., 1990). Here we used Zr as the immobile element; Nb was similarly conservative, in contrast to mobile elements such as Ca (Fig. 2). Mass-loss values were calculated on a whole-soil basis, integrated by horizon over the top 1 m of soil (Chadwick et al., 1990). Major elements contributed by rainout of continental dust (Jackson et al., 1971; Dymond et al., 1974) were quantified on the basis of quartz and mica contents, and subtracted prior to mass-balance analysis.

As Figure 3, parts A and B show, K, Ca, Mg, and Si are leached rapidly; <10% of their initial quantities remain after 20,000 yr. Al and P are less mobile, in that >25% of initial contents remain within the soil after >1 m.y. Compared to other studies (e.g., Merritts et al., 1992; White, 1995), these rates of weathering and loss are relatively rapid, because of both the wet tropical climate and the reactive nature of lava substrate. Volume-change calculations using Zr as the immobile index element show that soil formation initially dilates the substrate by >100% (Fig. 3C), due primarily to addition of organic carbon (see below). Following this rapid dilution, there is a gradual decline in volume due to leaching losses, leading to a 50% collapse (relative to the initial substrate) by 150,000 yr. At the oldest site, 10 m of the original substrate has weathered to produce the top 1 m of soil. Soil thickness at the first five sites remains constant at about 1 m, indicating that a dynamic balance exists between atmospheric addition, weathering-driven collapse, and surface erosion for >1 m.y. On Kauai, weathering depths are greater, probably exceeding 5 m.

Figure 3. Weathering, mineral transformations, and plant-available nutrients during soil and ecosystem development in Hawaii. A: The fraction of parent material Ca (red), Mg (black), and K (blue) remaining in soils across the sequence. B: Fractions of parent material Si (red), Al (black), and P (blue) remaining. C: Dilution and collapse of soils due to organic matter additions and element leaching. D: The relative contribution of the primary mineral feldspar (fel.; red), of noncrystalline secondary minerals (non; black), and of crystalline kaolin and sesquioxides (cry.; blue) to soil mineralology. E: The fraction of total soil P in the forms of the primary mineral apatite (apt.; red), organic P (org.; blue), and recalcitrant or physically protected P (rcl.; black) (Crews et al., 1995). F: Exchangeably bound Ca (green), Mg (black), and K (blue) (shown here x10), and Al (red). G: Resin-extractable (biologically available) inorganic N (red) and P (black) (shown here x10) in soils (Crews et al., 1995).
30% H$_2$O$_2$, noncrystalline minerals were determined by means of selective dissolution by acid ammonium oxalate in the dark. The residue of this dissolution was treated with Na-dithionite and Na-citrate, and the Blakemore et al. (1987) procedure was used to determine crystalline sesquioxides. Poorly crystalline minerals were then determined when this residue was treated with 0.5 M NaOH. Finally, the residue of this procedure was heated to 500 °C, followed by dissolution in 0.5 M NaOH of the collapsed lattice, to determine kaolin; X-ray diffraction of the <2 μm fraction confirmed that the kaolin fraction was primarily halloysite. Feldspar and atmospherically derived quartz and mica were determined on the residue of these treatments (Jackson et al., 1986).

The dominant soil minerals change dramatically along the sequence, the rapidly weatherable olivine and glass and relatively weatherable plagioclase being completely consumed by congruent weathering processes before 20,000 yr. Noncrystalline minerals (primarily ferrihydrite, allophane, and imogolite) then form a pedogenic mineral assemblage that persists for 1 m.y. or more. Allophane, imogolite, and ferrihydrite are metastable, X-ray amorphous minerals characterized by a high degree of hydration and short-range crystal order; their formation is favored over crystalline clay minerals in young soils derived from volcanic ash sources (Shoji et al., 1993). Finally, secondary kaolinite and crystalline sesquioxide minerals characteristic of highly weathered tropical soils accumulate slowly, but in the two oldest soils these minerals begin to dominate the <2 μm fraction (Fig. 3D). The change from allophane-imogolite-ferrihydrite to kaolin-sesquioxide is important because the former minerals have large and reactive surface areas that bind cations, phosphorus, and soil organic matter more effectively than the latter minerals (Wada, 1989; Schwertmann and Taylor, 1989).

Transformations and losses of P are particularly significant during long-term soil and ecosystem development, both because of P's biological importance and because its inputs from the atmosphere are very small. We measured the chemical forms and hence long-term biological availability of P in these soils following Tiessen and Moir (1993). As P is lost from soil (Fig. 3B), its forms change systematically from primary minerals in the young soils, to organic P in the 20,000- and 150,000-yr-old sites, and then on to insoluble or physically protected (and hence biologically unavailable) Fe- and Al-bound P in the oldest sites (Fig. 3E).

### Soil Nutrient Availability and Plant Nutrient Pools

A small fraction of each element in soil is present in solution or in readily exchangeable forms that organisms can use. Exchangeable pools of Ca and Mg decline from young to intermediate-aged substrates, and remain low thereafter—while exchangeable Al, which can inhibit root growth at high concentrations, increases across most of the sequence (Fig. 3F). Available pools of inorganic N (ammonium plus nitrate) and P both are low in the youngest site and increase into the intermediate-aged sites; P declines thereafter, while N availability remains high (Fig. 3G). Other measures of N availability yield a similar pattern (Riley and Vitousek, 1995). The low availability of P

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early reflects the fact that most P remains in primary minerals in young soils (Fig. 3E); the decline in available P late reflects both an absolute loss of P and the fact that the majority of residual P is in insoluble or physically protected Fe and Al oxyhydroxide-bound forms (Fig. 3, B and E).

Concentrations of elements in live tree leaves generally reflect available nutrient pools in the soil, for both the dominant tree Metrosideros polymorpha (Fig. 4, A and B) and for eight other species sampled across the sequence (Vitousek et al., 1995). Cation concentrations are high early and decline by 20,000 yr, while P and N concentrations increase to a peak in the intermediate-age sites and decline thereafter. Nitrogen concentrations in leaves in the older sites follow soil P availability more closely than they do soil N availability (Figs. 3G and 4B).

**Plant Production, Decomposition, and Nutrient Cycling**

Net primary production (NPP) of forests was determined at five sites across the sequence (Herbert, 1995). Production peaks in the intermediate-aged sites, later in the sequence than do soil or plant nutrients (Fig. 4C), and variation in NPP is small (~15%) relative to variation in other plant and soil properties. Rates of decomposition of leaf litter (senescent leaves) dropped by the dominant Metrosideros trees were measured at four sites, by using litter bags as described in Crews et al. (1995). Litter decomposes much more rapidly (up to threefold faster) in the intermediate-aged sites compared to either the youngest or the oldest site (Fig. 4D), despite the constancy of both precipitation and temperature across the sequence. Live leaves in these intermediate-aged sites are relatively enriched in N and P (Fig. 4B), and the trees in those sites withdraw less N and P from leaves before dropping them than do the trees in the youngest and oldest sites (Riley and Vitousek, 1995; Herbert, 1995).

This relatively efficient within-tree cycling of N and P in the youngest and oldest sites, coupled with increased leaf longevity there, maintains relatively high NPP despite low nutrient availability (Herbert, 1995). However, by reducing N and P concentrations in leaf litter, it slows rates of nutrient cycling between soil and plants. Leaf litter in the youngest and oldest sites decomposes slowly—and it is decomposition that transforms organically bound nutrients back into forms available to plants. We determined the fraction of the N and P present in freshly fallen leaf litter that remains within decomposed litter or its associated microbes (and hence not available to plants) after 2 yr of decomposition. There was little net release of plant-available N or P in the youngest and oldest sites—indeed, in some cases microbes accumulate additional nutrients from soil or solution. However, 70%–90% of the N and P in leaf litter from more fertile intermediate-aged sites has been cycled back into plant-available forms within two years (Fig. 4E).

This difference in the regeneration of available nutrients in fertile vs. infertile sites can drive a positive feedback between plants and soil. Plants drawing upon high levels of available nutrients in soil produce tissue and litter with relatively high nutrient concentrations (Fig. 4, A and B); these decompose more rapidly than litter from infertile sites, and they regenerate available nutrients much more rapidly (Fig. 4, D and E), thereby maintaining high levels of available nutrients. Conversely, plants in infertile sites produce low-nutrient leaves that decompose and regenerate nutrients slowly, thereby accentuating low nutrient availability in soil (Vitousek, 1982; Wedin and Tilman, 1990).

**Implications for Nutrient Limitation**

The observed changes in nutrient availability and cycling across this Hawaiian developmental sequence are consistent with conceptual models suggesting that a low supply of N constrains biological activity on young substrates, while a low P supply does so on very old sites; the supply of N and P should be greater, and more or less in balance, in intermediate-aged sites (Walker and Syers, 1976). We evaluated this pattern experimentally in three sites on the sequence—the youngest (300 yr), the relatively fertile 20,000-yr-old site, and the oldest (4.1 m.y.) (Vitousek et al., 1993; Herbert and Fownes, 1995; Vitousek and Farrington, 1997). In each site, we fertilized with N, P, and a combined treatment that included all essential elements other than N and P, applying the nutrients to replicated plots, singly and in all factorial combinations, for at least 2 yr, as described in Vitousek and Farrington (1997).

Additions of elements other than N and P did not affect plant growth in any site. As predicted by the Walker and Syers (1976) model, additions of N stimulated growth in the youngest site, while P had no effect there. In contrast, P additions stimulated growth in the oldest site, where N had no significant effect. Neither N nor P alone increased tree growth substantially on the intermediate-aged site, although in combination they nearly doubled it (Fig. 5), suggesting that the supply of N vs. P has more or less equilibrated in this site.

**Sinks for Atmospheric Carbon Dioxide**

Soils and ecosystems can represent sinks for atmospheric CO$_2$ in three major ways. First, plants take up CO$_2$ and store it in accumulating biomass; wood in particu-
sphere between 300 and 20,000 yr, but the average rate of removal decreases substantially after 300 yr (Fig. 4G), to less than 1% of forest production. After 20,000 yr, there is no further net C storage; an increase in the weathering sink is offset by a decrease in net C storage in plants and particularly soils (Fig. 4F), the latter reflecting reduced binding of organic C by the highly weathered secondary minerals present in the oldest sites (Torn et al., 1997). Long-term C sinks are largely confined to building systems; they occur at times and in regions where geologic disturbances such as glaciation and volcanic eruptions reset soils and ecosystems to early stages of development.

**IMPLICATIONS**

This sequence of sites across the Hawaiian Islands represents a relatively simple set of systems within which geologic and biological processes involved in soil and ecosystem development, and their interactions and regulation, can be evaluated more or less straightforwardly. While the processes underlying long-term soil and ecosystem development here are general ones, the rates and some of the details of change in this sequence cannot be applied globally. The transitions from the building to the sustaining phase probably occur more rapidly in these Hawaiian sites than in many places, due to abundant rainfall, relatively warm temperatures year-round, and easily weathered primary minerals. Later, the alteration of secondary minerals from metastable noncrystalline allophane (and others) to crystalline kaolin and sesquioxide that occurs on non-volcanic substrates may be delayed due to additional N.

**REFERENCES CITED**

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Global Learning and Observations To Benefit the Environment (GLOBE)

Because a large percentage of GSA members are involved in education, the Global Learning and Observations to Benefit the Environment program (GLOBE) is the subject of this month’s Washington Report, especially given that a National Science Foundation (NSF) Announcement of Opportunity for Science/Education Teams (NSF 97-129) for GLOBE is available. GLOBE is a network of K–12 students, teachers, and scientists from around the world working together to learn more about our environment. The GLOBE program is designed to increase scientific understanding of Earth, student achievement in science and mathematics, and environmental awareness of individuals.

The GLOBE program, which is championed by vice-president Al Gore, last requested proposals in 1994. The deadline for responding to the latest request is October 15, 1997.

In addition to NSF, the National Oceanic and Atmospheric Administration (NOAA) and the National Aeronautics and Space Administration (NASA) cooperate on GLOBE. Projects supported by the GLOBE program currently include kindergarten through twelfth-grade students at more than 1,500 schools. These students and their teachers make environmental observations following established research protocols. Data are reported via the Internet to the GLOBE Student Data Archive. More than 2,000 additional schools and other educational venues have also committed to following these same protocols. Data collected through GLOBE are publicly available.

GLOBE also supplies training to teachers and teacher-trainers in the implementation of this program, taking its measurements, and using its learning activities, which complement the measurements. Various information resources are provided on-line, including visualizations of some data and GLOBE-mail, a Web-based mail system that allows program participants around the world to communicate with one another. A tour of the GLOBE program and additional information about the announcement can be found at the GLOBE Web site at http://www.globe.gov.

It is anticipated that 20 to 50 proposals, including international participants on a no-exchange-of-funds basis, will be selected for the GLOBE program. Approximately 20 awards to U.S. institutions are expected to total approximately $3.6 million per year in combined funding from the three agencies, depending on the quality of the proposals received and the availability of funds.

The NSF announcement indicates that GLOBE is seeking proposals in five specific areas:

1. Scientific Involvement in GLOBE and Its Measurements. Proposals for this area are provided on-line, including visualizations of some data and GLOBE-mail, a Web-based mail system that allows program participants around the world to communicate with one another. A tour of the GLOBE program and additional information about the announcement can be found at the GLOBE Web site at http://www.globe.gov.

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