The Hawaiian Islands as a Model System for Ecosystem Studies[1]

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ABSTRACT: The Hawaiian Islands encompass an extraordinary range of variation in climate and soil age in a small area; the younger volcanoes are also extraordinary for their lack of variation in relief or topography, parent material, and biota (before widespread invasions by alien species). Consequently, in Hawai'i the independent and interactive effects of temperature, precipitation, and soil age on ecosystem structure and function can be evaluated with a power that is beyond the reach of studies elsewhere. Not only are extreme conditions well represented in Hawai'i, but there are also complete gradients between the extremes, allowing the determination of the relationships as well as the differences among sites. My colleagues and I have established two sets of sites that make use of these gradients: the Mauna Loa Environmental Matrix, a set of lava flows ('a'ā versus pāhoehoe, old versus young) that cover a broad elevational range on the wet east versus dry northwest flank of Mauna Loa; and a chronosequence of sites that reaches from Kīlauea ($\sim$300 yr old) to Kaua'i ($\sim$4,100,000 yr old) at 1200 m elevation, 2500 mm annual precipitation. These sites are being used to determine climatic and developmental controls of ecosystem function. I report some of the early results here.

A NUMBER OF BIOLOGICAL, geological, and climatic features combine to make the Hawaiian Islands a unique system for ecosystem studies. In fact, I suggest that Hawai'i can be to ecosystem studies what *Escherichia coli* has been to molecular genetics or the Hawaiian *Drosophila* to population genetics: a relatively well-defined model system in which fundamental mechanisms can be identified, understood, and tested.

Hawai'i is useful for ecosystem studies in part because environmental factors vary across an extraordinarily broad but extraordinarily well-defined range of conditions. Jenny (1941, 1980) proposed that the characteristics of soils and ecosystems are determined by a small number of variables that he termed "state factors" (climate, relief, parent material, organisms, time, etc.). This ap-

proach represents a powerful framework for determining ultimate controls on ecosystem structure and function, and Jenny and his successors (including many Hawaiian soil scientists) have applied it widely. Except under unusual circumstances, however, analyses based solely on state factors cannot determine the regulation of ecosystem dynamics. The state factors interact strongly with each other, and there are often several layers of mechanisms and feedbacks between these ultimate controls and the proximate mechanisms that regulate ecosystem structure and function. Nonetheless, an explicit combination of the context provided by state factors with the insight developed from detailed process studies (together with the conceptual and mathematical models that integrate them) remains the most productive way to analyze proximate as well as ultimate controls on ecosystems.

In this paper, I review several theories that relate the time, climate, and organism state factors to the control of ecosystem properties and processes, and show how each of the major factors varies in Hawai'i. I then dis-

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cuss how the wide, well-defined, continuous, and *independent* variation in these factors makes the Hawaiian Islands an extraordinary resource for the development and testing of ecosystem theory and its application.

THE STATE FACTORS

Time

T. W. Walker and Syers (1976) combined empirical work on soil phosphorus in a number of New Zealand chronosequences with an understanding of soil formation to develop a coherent theory for biogeochemical cycling during soil development. To oversimplify a bit, they pointed out that most newly deposited primary substrates (volcanic material, glacial debris, etc.) contain almost all of the rock-derived nutrients (particularly P) that they will ever have, but almost no nitrogen. Weathering of the more labile minerals in primary substrates causes a relatively rapid increase in the availability of P (and Ca, Mg, K); therefore the availability of nitrogen should limit primary production, biomass accumulation, and possibly microbial activity early in primary succession (Vitousek and Howarth 1991). Consequently, nitrogen-fixing organisms should have a substantial competitive advantage once they reach a site, and their activity should in turn increase the amount and availability of nitrogen in the system as a whole (Stevens and Walker 1970, Gorham et al. 1979, Binkley et al. 1984, Boring et al. 1988).

As soil development proceeds further, phosphorus release from primary minerals declines as the more labile minerals are exhausted. Most of the phosphorus released by weathering should be retained on-site, because chemical processes make P nearly immobile in most soils (Cole and Heil 1981, Uehara and Gillman 1981, Cole et al. 1989), and uptake of P by plants and soil microorganisms also can be rapid (Wood et al. 1984, Walbridge and Vitousek 1987). However, each time P cycles through the available pool, a small amount can be bound in wholly unavailable forms (physically or chemically

protected), and a little could be lost to the site. T. W. Walker and Syers (1976) emphasized P loss; subsequent discussions have emphasized irreversible P adsorption or physical protection (Cole and Heil 1981, Sollins et al. 1988). Over many millennia, most of the residual phosphorus comes to reside in protected inorganic and recalcitrant organic forms, and the system comes to a "terminal steady state" of low productivity and strong P limitation (T. W. Walker and Syers 1976).

A number of modifications of this theory have been proposed. In particular, J. Walker et al. (1981) emphasized the increasing depth of the B horizon during soil development, McGill and Cole (1981) and Hunt et al. (1983) discussed the implications of biochemical mineralization of ester-bonded P (by exoenzymes) versus biological mineralization of carbon-bonded N, and Lajtha and Schlesinger (1988) demonstrated that little P accumulates in recalcitrant inorganic fractions in arid ecosystems. All of these modifications are reasonable; none alters the overall conclusions. The theory is broadly consistent with observed patterns of nutrient cycling versus soil age. For example, N:P ratios in leaves, roots, and litter are larger in tropical ecosystems on old, deeply leached oxisols than in those on younger soils (Vitousek and Sanford 1986), and there is a coarse-scale association between the extent of soil weathering and low P availability (Smeck 1985). The approach has been incorporated into long-term process models of ecosystem-level biogeochemistry (Parton et al. 1987), and it has been used to explain community processes such as forest dieback (J. Walker et al. 1983). However, only pieces of the theory have been tested experimentally, and none of these through a full developmental sequence.

The Hawaiian Islands offer an outstanding opportunity to test nutrient dynamics during soil development. The Islands result from the movement of the Pacific tectonic plate over a stationary convective plume ("hot spot") in the mantle; the plume is now centered under the southeast edge of the chain, with progressively older islands to the northwest. Two of the volcanoes at the southeast end (Mauna Loa and Kīlauea)

erupt frequently, giving rise to a well-replicated age series of lava flows and ash deposits. These surfaces have been dated using historical records and ^{14}C dating of buried organic matter (Lockwood and Lipman 1980), and they have been mapped in detail (Holcomb 1987, Lockwood et al. 1988). On Mauna Loa, almost every flow and every *kīpuka* (island of older lava surrounded by younger flows) has been mapped. Relative ages have been assigned to all, and absolute ages (by ^{14}C dating) are available for many. Older surfaces and soils (from <5000 to ca. 5 million yr old) occur on older mountains on the island of Hawai'i and the older Islands to the northwest; these surfaces have been dated using K-Ar (Clague and Dalrymple 1987). Overall, geological research (and the geological situation) provides ecological studies with a finely resolved set of young sites, and a well-defined age gradient from Kīlauea Volcano on the southeast edge of the archipelago to Kaua'i and Ni'ihau on the northwest.

Climate

Globally, the climate factor accounts for more of the variation in ecosystem structure and function than any other factor; indeed, temperature and precipitation independently may be more important than any other factor. At a time when the scale of human activity is becoming sufficiently large to alter climate regionally and globally, it is particularly important that the influence of this factor be understood.

Within the Tropics, temperature varies primarily with elevation. Lower temperatures at higher elevations reduce both primary production and decomposition, but generally decomposition is affected more than is production. Consequently, carbon and nitrogen pools are larger at higher elevations (to some limit) (Post et al. 1982, 1985), but their turnover is slower. Low rates of decomposition at high elevation (Tanner 1981) can lead to reduced nutrient availability; that in turn can lead to reduced carbon quality and nutrient concentrations in litter, which feed back to a further reduction in decomposition. Also, the systematic increase in leaf thickness and decrease in nutrient concentrations observed in

high-elevation plants (Grubb 1977, Friend et al. 1989, Vitousek et al. 1992) could itself cause slower decomposition and nutrient cycling. Both possibilities are consistent with observations of lower N circulation, lower N mineralization, and greater ^{15}N immobilization by microorganisms in tropical montane sites (Marrs et al. 1988, Vitousek and Matson 1988, Vitousek et al. 1988b, Heaney and Proctor 1989, Veneklaas 1991).

Patterns of biogeochemical cycling along tropical moisture gradients are less well described (Murphy and Lugo 1986). The reduced intensity of leaching in drier sites means lower nutrient losses; indeed, that may be part of the reason for the success of long-term human occupancy of seasonally dry tropical sites. Nutrient concentrations in vegetation and litterfall are rather high in the few dry tropical forests (ca. 1200–1800 mm/yr) studied to date (Raman 1975, Arnason and Lambert 1982, Lugo and Murphy 1986, Vitousek et al. 1992). Interpretation of tropical moisture gradients is complicated greatly by the transition from forest to savanna, because these systems differ sharply in growth form, dominant photosynthetic pathway (C_3 versus C_4), and microclimate and fire regime (both of which are in part biologically controlled) (Goldammer 1990).

Gradients of moisture and temperature are striking and substantially orthogonal in the Hawaiian Islands (Mueller-Dombois et al. 1981). The climate is maritime, so daily and seasonal temperature variation is moderate (the record high in Hilo is 32°C; the record low is 12°C). Mean annual air temperature varies from 24°C at sea level to 10°C at 2500 m, and this variation follows an environmental lapse rate of 5.7°/1000 m closely (Atlas of Hawaii 1983).

The Islands are in the northeast trade winds for most of the year. Precipitation varies with elevation, but the windward northeast sides of the high Islands are generally moist to extremely wet from sea level to nearly 2000 m elevation. In contrast, the leeward southwest side of each mountain is generally dry, with as little as <250 mm annual rainfall (Giambelluca et al. 1986). Consequently, there is a substantial temperature gradient from sea level to treeline on both the

wet northeast and the dry southwest side of each high Island.

This simple picture becomes more complicated on the Big Island of Hawai'i and to a lesser extent on Maui. There, areas are above the trade wind inversion and in contact with very dry air, leading to very high rates of potential evaporation above 2000 m (Juvik et al. 1978). In addition, the mass of Mauna Loa Volcano is sufficient to establish a land-sea breeze cycle on its leeward southwest flank during the summer, leading to substantial summer rains in Kona. Consequently, the windward east flank of Mauna
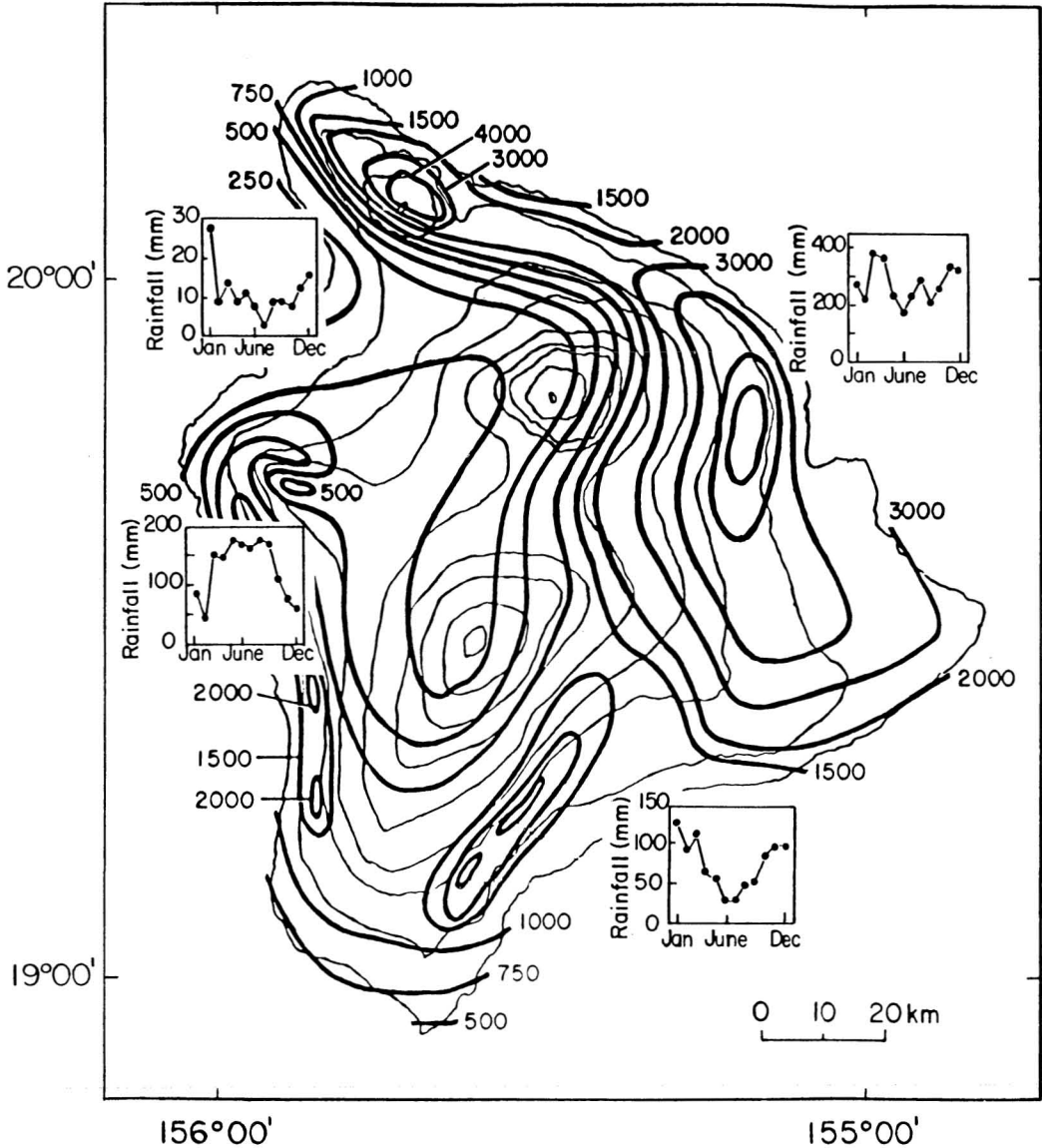

FIGURE 1. Mean annual rainfall for the island of Hawai'i (from Giambelluca et al. 1986). Climate diagrams showing the seasonality of precipitation in the east (wet year-round), northwest (dry nearly year-round), southwest (summer wet), and southeast (winter wet) quadrants of the island are superimposed.

Loa is wet year-round, the southeast experiences winter rain (the normal leeward wet season), the southwest receives summer rain caused by the sea-breeze cycle, and the northwest flank (which is in the lee of Mauna Kea and the Kohala Mountains) is arid (Figure 1).

Organisms

Although it is widely recognized that "the biota" as a whole regulates ecosystem-level biogeochemistry, there is less information on the ecosystem-level importance of individual species. In part, this lack of information may be a consequence of the divergent paths followed by population biology and ecosystem studies for the past decades. This dichotomy is breaking down; some population-based approaches are incorporating ecosystem concepts in a much-improved way (Mueller-Dombois 1988a, Tilman 1988), and some ecosystem models include increasingly reasonable feedbacks among species composition, resource quality, and nutrient cycling (Pastor and Post 1986, Pastor et al. 1987). Another reason why consideration of the organism factor has lagged may be that its analysis provides conceptual difficulties more severe than those for other factors. To quote Jenny (1980): "The real bugbear was the biotic factor. Like everyone else, I could see that vegetation affects the soil and that soil affects the vegetation, the very *circulus vitiosis* that I was trying to avoid." Jenny's solution was to identify the regional flora (and fauna), the potential occupants of a site, as the factor of interest.

Biological invasions by alien species represent a change in the organism factor, and their study provides a way in which the ecosystem-level effects of individual species can be demonstrated unequivocally (Vitousek 1986). The majority of such invasions probably do not alter ecosystem properties, however serious their effects on native biota. However, for those invasive species that do alter ecosystems, the causal connections leading from the demography of the invader to alterations in the biogeochemistry of the system can be demonstrated clearly.

In an earlier paper, I discussed the circumstances under which alien species could regulate ecosystem-level phenomena (Vitousek 1990). Species effects can be identified where:

(1) The invader alters resource availability. The nitrogen-fixer *Myrica faya* Aiton (Vitousek et al. 1987a, Vitousek and Walker 1989, Walker and Vitousek 1991) increases system-level nitrogen availability in Hawai'i; the common ice plant (*Mesembryanthemum crystallinum*) causes soil salinization and erosion in California and Australia (Vivrette and Muller 1977, Kloot 1983); the hydrologic cycle is altered by *Andropogon virginicus* L. in Hawai'i (Mueller-Dombois 1973) and *Tamarix* spp. in the southwestern United States and Australia (Neill 1983).

(2) Invasion alters trophic structure. Adding or removing a top carnivore can change ecosystems dramatically (Carpenter et al. 1987). Such effects are well documented in aquatic ecosystems (Avon and Smith 1971, Kitchell and Carpenter 1987); they may also underlie the devastation wrought by feral ungulates on isolated oceanic islands (Stone 1985, Merlin and Juvik 1992).

(3) The invader alters disturbance frequency or intensity. Effects of this sort are diverse; they include the influence of feral pigs on soil properties, nutrient transformations, and even watershed-level nutrient losses (Singer et al. 1984, Vitousek 1986), as well as effects of plant invasion on fire frequency and intensity (Parsons 1972, Smith 1985, Mack 1986, Hughes et al. 1991, Witkowski 1991, D'Antonio and Vitousek 1992).

The Hawaiian Islands are a useful system for determining species effects on ecosystems for two reasons. First, Hawai'i is the most isolated archipelago on Earth. In consequence, the native flora and fauna are depauperate, and the few successful colonists often have undergone extensive adaptive radiation over a broad range of habitats (Carlquist 1980). One striking example is the dominant native tree *Metrosideros polymorpha* Gaud. (Myrtaceae). On young soil

(<4000 yr old), *Metrosideros* dominates natural ecosystems from treeline to sea and from extremely wet (>6000 mm/yr) to quite dry (<500 mm/yr) sites. It is often the first woody colonist on young volcanic sites, and in rain forest it retains its dominance on the oldest substrates in Hawai'i (ca. 5,000,000 yr).

Metrosideros is not the same everywhere. The specific epithet *"polymorpha"* is accurate in implying a highly variable species, and there is evidence that successional varieties have evolved along the soil-age gradient (Stemmermann 1983). The "organism factor" nevertheless varies relatively little across a broad range of Hawaiian ecosystems, in comparison with the substantial variation in the continental Tropics, and this lack of variation adds power to examinations of the other state factors.

Second, the Hawaiian Islands host an exceptional array of successful alien species. The native vascular flora included about 1200 species, and more than 4600 exotic species are now known, of which more than 800 are well established and more than 90 are considered serious threats to native biota (Smith 1985, Loope and Mueller-Dombois 1989, Wester 1992). Exotic species dominate many lowland areas (except on young volcanic substrates), but at higher elevations (>800 m) many native systems are more or less intact. Consequently, it remains possible to observe and to manipulate biological invasions and their ecosystem-level consequences (Vitousek et al. 1987a,b; Vitousek and Walker 1989).

Parent Material and Relief

Both parent material and relief or topography can control ecosystem structure and function. However, relatively little ecological work with these factors has been done in Hawai'i, and I will not describe their influences in detail here. Rather, I will discuss how their variation and lack of variation in Hawai'i can affect analyses of the effects of other state factors.

As discussed above, the Hawaiian Islands result from the movement of the Pacific tec-tonic plate over a stationary plume or "hot spot" in Earth's mantle. As a consequence, the chemical composition of Hawaiian volcanic parent material is remarkably constant. During the shield-building stage of volcanism, this material is tholeiitic basalt or its close relatives. The products of different eruptions differ in the mixing ratio of magnesium and to a lesser extent because of differentiation during residence in magma reservoirs (Wright and Helz 1987), but the differences are small in comparison with those in any continental situation.

The chemistry of parent material differs to a greater extent later in the evolution of a shield volcano, when more alkalic lavas emerge. Still more alkalic lavas are produced during a brief rejuvenation of volcanic activity that often occurs when the formation of a new shield volcano to the southeast causes the uplift of a dormant volcano (Clague and Dalrymple 1987). Soils derived from material erupted during the shield phase can nonetheless be located on all of the major Islands. The initial texture of parent material ranges from massive *pāhoehoe* lava flows (smooth, ropy textured, often with large cooling-related cracks) to *'a'ā* flows (clinker-type lava) to tephra deposited by lava fountains and the rare explosive eruptions. This variation influences initial water-holding capacity, sites for seedling establishment, and the surface area accessible to chemical weathering; therefore it also affects the initiation and rate of primary succession (Smathers and Mueller-Dombois 1974) and longer-term forest dynamics (Jacobi et al. 1983). There is little association between parent material texture and parent material chemistry.

The importance of relief or topography varies as a function of substrate age and climate in Hawai'i. Aggrading shield volcanoes like Mauna Loa and Kīlauea are built up by lava flow piled upon lava flow; they are remarkably lacking in coarse-scale topography. Older shield volcanoes become subject to water erosion with time; the oldest are strikingly dissected, especially on the wet east and northeast sides (Macdonald et al. 1983). This relief has substantial effects on native communities and presumably ecosystem proper-

ties (Mueller-Dombois 1988b). It is possible, nevertheless, to locate undissected shield remnants on all of the high Islands, even in wet areas.

ECOSYSTEM STUDIES IN HAWAI'I

Temperature, precipitation, and substrate age vary independently and largely orthogonally over much of Hawai'i, but parent material, relief, and organisms can be held constant to a substantial extent. Consequently, sites that differ very widely from each other can be compared in a small geographical region—and more important, the existence of complete gradients between extremes allows the relationships as well as the differences among sites to be investigated. Moreover, these gradients provide a background against which the ecosystem consequences of biological invasions can be evaluated.

Portions of the environmental gradients in Hawai'i have been studied for many years, including Forbes's (1912), Skottsberg's (1941), Atkinson's (1970), and Eggler's (1971) studies of primary succession; Sherman and Ikawa's (1968) and Yost et al.'s (1982) work on soil sequences; the Island Ecosystems IBP research in Hawai'i Volcanoes National Park (Mueller-Dombois et al. 1981); extensive studies of 'ōhi'a forest dynamics (Mueller-Dombois 1986, 1987, 1990); and agronomic studies on the MauiNET climatic gradients on Maui (cf. George et al. 1987). My colleagues and I have focused our work in two areas: controls of energetics and nutrient cycling on a matrix of lava flows that we call the Mauna Loa Environmental Matrix, and the effects of invasions in Hawai'i Volcanoes National Park. Research is now expanding into an age gradient of sites from Kīlauea to Kaua'i (Riley 1992) and to elevation/precipitation gradients on older volcanoes.

Mauna Loa Environmental Matrix

The collection of lava flows mapped by Lockwood et al. (1988) on Mauna Loa rep-

resents an extraordinarily valuable resource for ecosystem studies. Each flow is an ecologist's dream—a single-age, single-substrate transect reaching from above treeline toward, and often to, the sea. Moreover, otherwise nearly identical flows of different ages occur side by side across the elevational range, flows of the same age occur on different sides of Mauna Loa and therefore experience wholly different precipitation regimes, and there is even true replication of similar-age flows on the same side of Mauna Loa.

We selected nine of these flows for detailed study (Figure 2). These include a young (<140 yr old) versus an old (>2800 yr old) flow of 'a'ā versus pāhoehoe on the wet east (2000–6000 mm/yr) versus the dry northwest (300–600 mm/yr) flank of Mauna Loa, plus an additional young pāhoehoe flow on the east flank. All of these have been sampled across the elevational range from the lower edge of native vegetation (often near 600 m) to 2000–2500 m. In sum, these flows represent a complete matrix of sites that vary markedly and independently in temperature, precipitation, age, and parent material texture.

This matrix has been used to evaluate controls of carbon isotope fractionation during photosynthesis (Vitousek et al. 1990), foliar and soil nutrient concentrations (Vitousek et al. 1988a, 1992), vegetation composition and biomass (Aplet and Vitousek 1994; Aplet, Hughes, and Vitousek, unpubl. data), primary production (Raich, Russell, and Vitousek, unpubl. data), and litter decomposition and nutrient release (Vitousek et al. 1994); it is also being used to test models of ecosystem structure and function (cf. Parton et al. 1989). Perhaps the most interesting results of studies completed to date are the following:

(1) All else being equal (as it is to a remarkable extent on Mauna Loa), low temperatures inhibit decomposition more than they do photosynthesis. Low rates of decomposition mean that carbon and nutrient pools accumulate to a greater extent at high than at low elevation on older flows; slow decomposition also
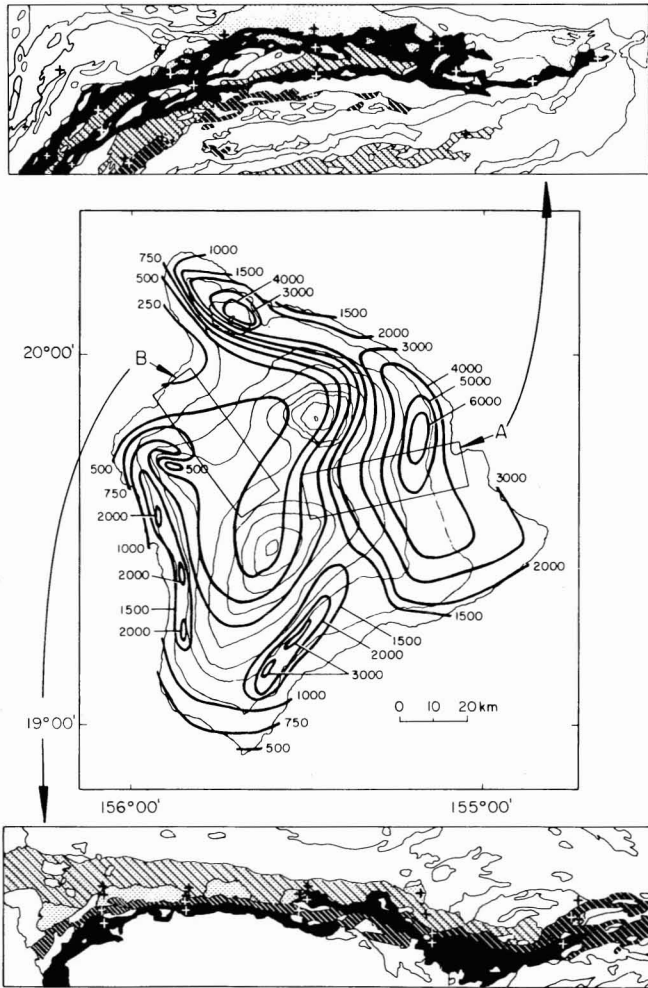
FIGURE 2. (*Center*) A rainfall map of the island of Hawai'i (Giambelluca et al. 1986). (Top) A partial map of the lava flows in rectangle A; (*bottom*) a similar map of rectangle B (from Lockwood et al. 1988). The darker shadings represent the younger flows sampled (1852, 1855, 1859, 1881); the lighter shadings the older flows (Kanikū, Punahoa, and unnamed flows >3500 yr old). 'A'ā flows are indicated with diagonal lines; *pāhoehoe* flows are black; sampling sites for soils are marked with a +. Leaf chemistry was sampled in additional sites (not shown). (From Vitousek et al. 1992, reproduced with permission.)

slows nutrient release and causes high-elevation communities to be limited by nutrient availability to a greater extent than those at low elevations, at least to several thousand years of age (Vitousek et al. 1992).

(2) All else being equal, low precipitation has the opposite effect, reducing primary production (and hence plant demand for nutrients) more than it does decomposition (and hence nutrient supply). Consequently, both soil nutrient availability and tissue nutrient content are greater in dry than in paired wet sites on Mauna Loa (Vitousek et al. 1992). Leaf litter produced in dry sites also is inherently

more decomposable than that produced in wet sites (Vitousek et al. 1994).

Biological Invasions and Ecosystem Consequences

My colleagues and I have examined the ecosystem-level consequences of two biological invasions by alien species—that of *Myrica faya* into young volcanic sites in Hawai'i Volcanoes National Park (HAVO) and that of alien grasses into the seasonal submontane zone of HAVO. *Myrica faya* is an actinorrhizal nitrogen-fixer from the Canary Islands (Whiteaker and Gardner 1985). We have suggested that *Myrica* invasion could alter ecosystem function by adding atmospheric nitrogen to otherwise nitrogen-deficient young volcanic sites (which lack a native symbiotic nitrogen-fixer).

The consequences of *Myrica* invasion

(Figure 3) were demonstrated by showing that:

(1) Nitrogen is the only soil nutrient that limits tree growth in young volcanic sites (Vitousek et al. 1987a).
(2) In heavily invaded sites, *Myrica* fixes enough nitrogen to more than quadruple overall inputs on the ecosystem level (Vitousek and Walker 1989).
(3) The nitrogen fixed by *Myrica* becomes available to other organisms relatively rapidly (Vitousek and Walker 1989).
(4) Myrica invasion affects populations and growth rates of other organisms (Aplet 1990, L. R. Walker and Vitousek 1991).

This project also examined how the biology of *Myrica faya* and the characteristics of invaded communities interact to promote *Myrica* invasion. One interesting result that illustrates the potential importance of species interactions during invasion is that *Myrica*
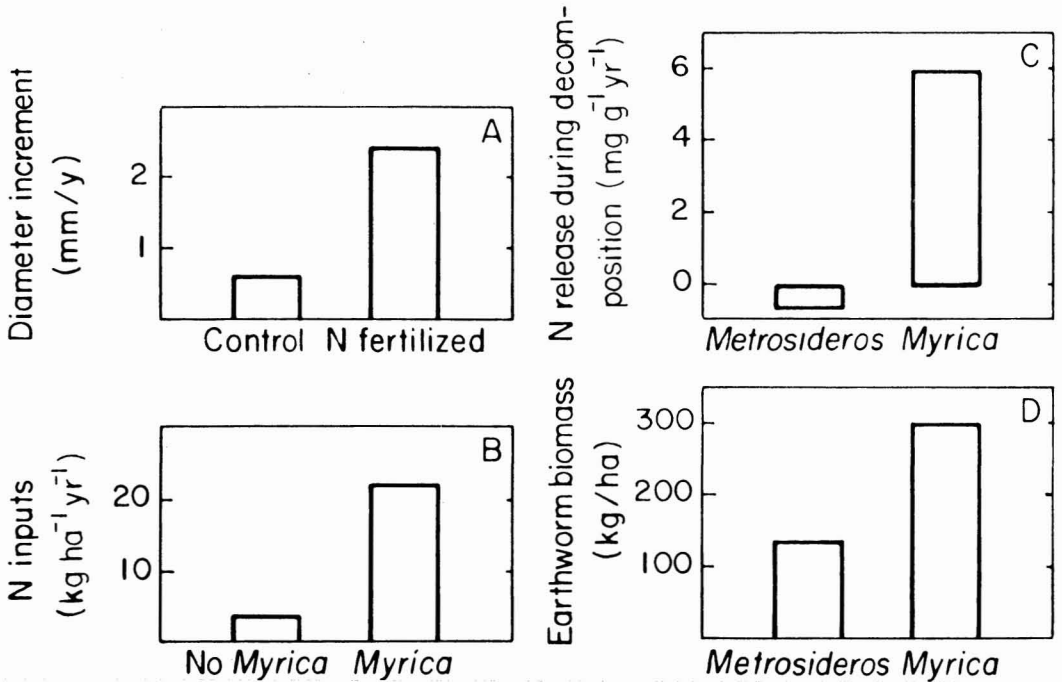

FIGURE 3. Effect of invasion by the alien tree *Myrica faya* on primary successional ecosystems in Hawai'i Volcanoes National Park. A, Nitrogen amendments demonstrate that nitrogen is limiting to growth of native *Metrosideros*. B, *Myrica* fixes enough nitrogen to increase total annual inputs of nitrogen more than 4-fold. C, The nitrogen fixed by *Myrica* becomes available in the soil, where it can be obtained by other organisms. D, *Myrica* colonization affects populations of alien earthworms in the sites it dominates. (From Vitousek [1994], reproduced with permission.)

invasion is facilitated by the alien bird *Zosterops japonicus* (white-eye) (Vitousek and Walker 1989, Woodward et al. 1990).

More recently, effort has been focused on invasion by the perennial C_4 grasses *Schizachyrium condensatum* (Kunth) Nees and *Melinis minutiflora* P. Beauv. in dryland forest in HAVO. The initial invader of otherwise undisturbed native systems is *Schizachyrium*; it adds sufficient fine fuel to permit fires to spread in areas that previously did not burn (Hughes et al. 1991, Smith and Tunison 1992). Most native species are eliminated by fire, but *Schizachyrium* recovers rapidly after fire and the even more flammable *Melinis* invades. The increased dominance of grasses further increases flammability, and subsequent fires lead to nearly monospecific stands of *Melinis* (Hughes et al. 1991, Hughes and Vitousek 1993). This grass-fire positive feedback cycle (involving *Pennisetum setaceum* [Forssk.] Chiov. and *Cenchrus ciliaris* L. in other sites, as well as the two species we studied) is the most serious threat to the remaining Hawaiian dryland forests; it also threatens the maintenance and restoration of dry tropical forests in continental as well as island areas worldwide (D'Antonio and Vitousek 1992).

Research on Hawaiian ecosystems offers the opportunity to understand controls on ecosystem structure and function in a relatively simple, well-defined set of ecosystems. That understanding can then be applied as the basis for understanding more complex continental systems. In this sense, the ecosystems of Hawai'i are a globally significant resource, as are the Hawaiian populations and species. This value provides another motivation for extraordinary effort to preserve, protect, and restore Hawaiian ecosystems.

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