Thus, we have shown that physiologically and immunologically relevant molecules can enhance the expression of virus in chronically infected U1 cells, and that cells of monocyte lineage that are noncytopathically infected with HIV-1 can be induced to express virus by these molecules. These findings have important implications in our understanding of the mechanisms by which an HIV-1–infected individual may progress from an asymptomatic carrier state to a state of immunosuppression leading to clinical AIDS.

Multiple cytokines have been reported to activate monocytes and modulate their function (*19*). Two of these, GM-CSF and IFN-γ, have been reported to inhibit the replication of HIV-1 in U937 cells (*14*). Since the study of the latter was carried out with randomly infected cells, the results probably reflect the net effect of these cytokines on the total population of infected cells. The present study, with a single clone, reflects what one would expect to see from a single cell isolated from an infected culture. It is reasonable to believe that infected cells would respond to various cytokines by either up-regulation or down-regulation of HIV-1 infection, depending on the type of cytokine used for induction and on the genomic integration site of the HIV-1 provirus. The up-regulation of HIV-1 expression by cytokines, specifically GM-CSF, may be a result of the induction of a cellular gene that in turn induces the promoter of HIV-1 either through a cis mechanism that depends on the integration site of the provirus or by transactivation via a DNA-binding protein. In this regard, a DNA-binding protein (NF-kB) has been described that binds to the HIV-1 LTR in infected T cells and up-regulates virus expression (*20*).

Interleukin-1 is a well-characterized molecule with many physiological properties, including the induction of fever and other acute phase responses (*21*). This cytokine also has immunoregulatory functions on T and B cells (*22*). Recent reports have indicated that IL-1 may exert much of its effect at the membrane level (*23*). Our finding of enhanced expression of membrane-bound IL-1β after cytokine induction in the U1 clone suggests the possibility that, under certain circumstances, infected monocytes can activate T cells via IL-1 and thus increase the susceptibility of the T cells to infection with HIV-1. It is also possible that enhanced monocyte production of IL-1 may serve an autocrine function (*24*) enabling the monocyte to remain activated and thus support viral replication.

The effect of HIV-1 infection on expression of IL-1 remains to be clarified. However, it is possible that the HIV-1 *tat* gene product (*25*) either directly or indirectly regulates IL-1 gene expression via DNA-binding proteins that bind to sites within the IL-1 promoter region. Alternatively, as mentioned above, the uniqueness of the U1 clone could relate to the integration site of the proviral DNA into the cellular genome and thus represent a clone atypical to infected monocytes in general.

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Biological Invasion by *Myrica faya* Alters Ecosystem Development in Hawaii

PETER M. VITOUSEK, LAWRENCE R. WALKER,*
LOUIS D. WHITEAKER,† DIETER MUELLER-DOMBOIS,
PAMELA A. MATSON

The exotic nitrogen-fixing tree *Myrica faya* invades young volcanic sites where the growth of native plants is limited by a lack of nitrogen. *Myrica* quadruples the amount of nitrogen entering certain sites and increases the overall biological availability of nitrogen, thereby altering the nature of ecosystem development after volcanic eruptions.

BIOLOGICAL INVASIONS BY EXOTIC species can alter the composition of natural and agricultural communities substantially (*1, 2*). Analyses of such effects have been used to test theories in population and community ecology (*3*) and have contributed to discussions of potential environmental effects of releases of genetically altered organisms (*4*). A demonstration that biological invasions by exotic species can also alter fluxes of energy, water, and nutrients could be similarly valuable; it would illustrate that whole ecosystems can be regulated by the populations and properties of individual species (*5*). A more general understanding of such effects would also be useful to conservation biology—exotic species that alter ecosystem-level properties not only compete with or consume native species, but also alter the underlying nature of the area they invade.

Recent reviews (*5, 6*) show that some biological invasions (especially by animals) alter ecosystems, but systematic studies have been few. We studied ecosystem-level consequences of invasion by *Myrica faya*, a small tree with a nitrogen-fixing symbiosis, into ecosystems developing in young volcanic substrates in Hawaii Volcanoes National Park. Such sites contain no native plants with nitrogen-fixing symbioses. Indeed, the actinorrhizal symbionts (*7*) that *Myrica* pos-

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P. M. Vitousek and L. R. Walker, Department of Biological Sciences, Stanford University, Stanford, CA 94305.
L. D. Whiteaker and D. Mueller-Dombois, Department of Botany, University of Hawaii, Honolulu, HI 96822.
P. A. Matson, Ecosystem Science and Technology Branch, NASA-Ames Research Center, Moffett Field, CA 94035.

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*Present address: Department of Biology, University of Puerto Rico, Rio Piedras, PR 00931.
†Present address: Resource Management, Everglades National Park, Homestead, FL 33034.

Table 1. Diameter increment (in millimeters per year, with standard errors in parentheses) of control and fertilized individuals of the native tree *Metrosideros polymorpha* in young, intermediate-aged, and old sites. Fertilizer treatments, application rates, and statistical design are in (*11*). No *Myrica faya* was present on any plot.

Site	Control	Nitrogen-fertilized	Significance level	Effect of other nutrients
1959 ash	6.6 (0.8)	11.6 (0.9)	$P < 0.001$	NS*
1790 ash	0.4 (0.1)	0.8 (0.1)	$P < 0.01$	NS*
Old ash	4.4 (0.7)	5.5 (0.9)	NS*	
Open canopied†	0.6 (0.1)	2.4 (0.3)	$P < 0.001$	

*NS, not significant ($P > 0.05$). †Many canopy trees and all of the understory were eliminated by volcanic cinder from a 1959 eruption; measurements were made on the surviving canopy trees.

Table 2. Sources of nitrogen (in kilograms per hectare per year) in open-canopied sites with and without populations of the exotic nitrogen-fixer *Myrica faya*.

Source	No *Myrica*	With *Myrica*
Rainfall (*16*)	5	5
Native nitrogen fixation (*17*) by		
Leaf litter	0.2	0.3
Decaying wood	0.1	<0.1
Lichens	0.2	0.2
Bryophyte mats	<0.1	<0.1
Nitrogen fixation by *Myrica faya* (*14*)	0	18
Total	5.5	23.5

sesses were absent from the native Hawaiian flora, although the better known legume-rhizobium symbiosis was widespread there.

Myrica faya is native to the Azores and Canary Islands; it was originally brought to Hawaii by immigrants from Portugal late in the 19th century. *Myrica* was first observed in Hawaii Volcanoes National Park in 1961. By 1977, it covered 600 ha in the park despite intensive control efforts. Control was abandoned shortly thereafter, and by 1985 the still-expanding *Myrica* population covered 12,200 ha in the park and 34,365 ha in the Hawaiian Islands (*8*). *Myrica* occurs in sites ranging from recent volcanic cinder areas to closed-canopy native forests, but it is most abundant in pastures, native forests thinned by volcanic eruptions, and open-canopied seasonal montane forests (*9*).

We examined whether invasion by *Myrica faya* has increased the amount and biological availability of fixed nitrogen in young volcanic sites and thereby altered these native forest ecosystems. This statement has three components—nitrogen must limit plant growth in these sites, the fixation of nitrogen by *Myrica* must increase overall inputs of biologically available nitrogen from all sources, and the nitrogen fixed by *Myrica* must enter readily into the biological nitrogen cycle.

Primary succession, the development of a biological community on a wholly new substrate, generally involves a substantial increase in both total and available nitrogen (*10*). It seems reasonable to expect that plant growth would be nitrogen-limited early in primary succession, particularly because recent volcanic material contains most nutrient elements that plants require except for nitrogen. We tested this assumption in communities that developed after recent (1959) and intermediate-aged (1790) eruptions by fertilizing sites with nitrogen, phosphorus, and all other nutrients (*11*) in factorial combination. Additions of nitrogen, and only of nitrogen, significantly increased plant growth (Table 1). Added nitrogen also significantly increased tree growth where a native forest had been thinned but not destroyed by cinder-sized ejecta from a 1959 eruption; it had no significant effect in an older (1000- to 2000-year old) site (Table 1). Nitrogen is clearly the limiting soil-derived resource in these young volcanic sites.

We also tested whether the invasion of *Myrica* has substantially altered inputs of fixed nitrogen into these sites. Fixation of nitrogen by *Myrica faya* was estimated in several sites by using a four-step process based on the acetylene reduction assay for nitrogenase, which is the critical enzyme in nitrogen fixation (*12*). We measured the amount of $^{15}N_2$ fixed per unit of acetylene reduced, the amount of acetylene reduced per gram of root nodule (*13*), the mass of nodules per individual *Myrica* of different sizes, and the population and size distribution of *Myrica* (*14*). The product of these yielded an areal estimate of nitrogen fixation by *Myrica*. Acetylene reduction activity was measured over annual and diurnal cycles in three contrasting situations (unshaded *Myrica* on volcanic cinder, partially shaded *Myrica* under open-canopied *Metrosideros* forests thinned by volcanic cinder, and *Myrica* under closed-canopy rain forest). Acetylene reduction activity per gram of nodule varied little in these different situations, but the mass of nodules per individual varied substantially (*15*).

These results were put into context by estimating inputs of combined nitrogen in precipitation (*16*), biological nitrogen fixation by lichens, and nonsymbiotic biological nitrogen fixation (*17*). The overall importance of *Myrica* in sites where it is abundant can best be summarized by comparing nitrogen inputs in two open-canopied forests, both of which were thinned by cinder from a 1959 eruption. Control of *Myrica* during the 1970s had been ineffective in one site, which had 300 individual *Myrica* trees per hectare in 1974 (*18*) and now has 1050 trees per hectare. *Myrica* had been eliminated from the other site; it is now colonizing vigorously, but we are maintaining an area free of *Myrica*. Annual inputs of nitrogen are summarized in Table 2; they total 23.5 kg ha^{-1} year^{-1} in the site with *Myrica faya* and 5.5 kg ha^{-1} year^{-1} in the site without it. Invasion by *Myrica faya* has clearly altered the nitrogen budget of the heavily colonized site.

Finally, we determined the effect of *Myrica* on the biological availability of nitrogen. Extractable inorganic nitrogen (ammonium plus nitrate) in the heavily colonized site averaged 0.7 μg/g in soil under isolated individuals of *Metrosideros polymorpha*, the dominant native tree, and 2.6 μg/g under *Myrica faya* (which was partially shaded by *Metrosideros*). More importantly, the net release of biologically available nitrogen from organic forms was 5.6 μg g^{-1} month^{-1} under *Myrica* and was slightly negative under isolated *Metrosideros* ($P < 0.01$) (*19*).

All three components of our test were established; therefore, we conclude that *Myrica faya's* ability to support nitrogen-fixing symbionts and the population-level processes that control its dispersal and establishment interact to alter ecosystem-level characteristics in Hawaii Volcanoes National Park. The longer term consequences of this alteration remain to be determined. *Myrica faya* may dominate these sites for many years, replacing native species; it may coexist with natives, perhaps increasing their growth rate and the overall rate of primary succession; or it may be replaced by other species as succession proceeds. Even if *Myrica* is replaced, it is unlikely that the effects of the nitrogen it fixes will disappear. Many exotic species in Hawaii (*20*) and elsewhere (*21*) only invade sites with relatively fertile soils; *Myrica* fertilizes developing Hawaiian ecosystems with nitrogen, the only major nutrient they lack.

More generally, biological invasions are likely to have ecosystem-level consequences where they add a new biological process (for example, nitrogen fixation) to a region, or where they allow the maintenance of such a process in a new environment. In this case, the capacity to fix atmospheric nitrogen is widespread in the Hawaiian flora, but *Myrica faya* appears unique in its ability to establish populations in young volcanic sites (*9*). Similar effects of biological invasions on ecosystem dynamics are likely to prove most common on oceanic islands; their native biota is relatively depauperate, and successful invasions are frequent (*1, 2*). Biological invasions of continents are less common, but they can be equally disruptive (*6, 22*).

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Discovery of Transposable Element Activity Among Progeny of Tissue Culture–Derived Maize Plants

VIRGINIA M. PESCHKE, RONALD L. PHILLIPS, BURLE G. GENGENBACH

Tissue culture–derived plants of many species have often been observed to possess both genetic and cytogenetic abnormalities. A high frequency of structurally altered chromosomes in maize (*Zea mays* L.) plants regenerated from tissue culture led to the prediction that newly activated transposable elements could be detected in regenerated plants. Testcrosses of 1200 progeny from 301 regenerated maize plants confirmed that ten regenerated plants from two independent embryo cell lines contained an active *Ac* transposable element. No active *Ac* elements were present in the explant sources. Recovery of transposable element activity in regenerated plants indicates that some tissue culture–derived genetic variability may be the result of insertion or excision of transposable elements, or both.

ORIGINALLY, THE TISSUE CULTURE of plants was assumed to be a means of asexually propagating many genetically identical individuals. However, heritable changes are frequently recovered in regenerated plants and their progeny. In maize, more than 45 tissue culture–induced mutant phenotypes have been observed, including defective kernel mutants, dwarfs, albinos, many kinds of leaf striping and variegation, and changes from Texas cytoplasmic male sterility to fertility (*1–5*). Cytological aberrations are commonly observed in regenerated maize plants. Interchanges and deletions, which require chromosome breakage, are the most frequent types of rearrangements (*2–4, 6*). In some cases, phenotypic variation is coincident with cytological aberrations (*7*), but usually the phenotypic variation cannot be explained solely on the basis of detectable changes in chromosome structure or number (*2, 3*). The observation that visible changes in chromosome number or structure can account for only a portion of the variation observed in regenerated maize lines suggests that other mechanisms must be involved. Larkin and Scowcroft (*8*) have proposed a number of alternatives, including the release or activation of transposable genetic elements.

Transposable elements in maize cause a variety of changes in gene expression and chromosome structure. McClintock (*9*) discovered transposable elements in the progeny of self-pollinated plants that had undergone a cycle of chromosome breakage, joining of broken ends, and rebreakage (*10*). Chromosome breakage initiated by special chromosomal stocks, ultraviolet light, and x-rays can cause the release or activation of transposable elements (*11, 12*). Such studies indicated that transposable elements exist in an inactive form within the "normal" maize genome and can be released under unusual circumstances. This prediction was confirmed by DNA analysis that revealed four to eight copies of an *Activator*-like sequence in several maize inbreds lacking the transposable element activity characteristic of the *Activator-Dissociation* (*Ac-Ds*) system (*13*).

McClintock (*14, 15*) ascribed the release or activation of transposable elements by chromosome breakage to the "genomic stress" that a broken chromosome causes within a cell. She speculated that such stresses may lead to a variety of genetic alterations on which natural or artificial selection might

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Department of Agronomy and Plant Genetics, University of Minnesota, St. Paul, MN 55108.