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BIOLOGICAL INVASION BY *MYRICA FAYA* IN HAWAI'I: PLANT DEMOGRAPHY, NITROGEN FIXATION, ECOSYSTEM EFFECTS[1]

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Abstract. *Myrica faya,* an introduced actinorhizal nitrogen fixer, is invading young volcanic sites in Hawaii Volcanoes National Park. We examined the population biology of the invader and ecosystem-level consequences of its invasion in open-canopied forests resulting from volcanic cinder-fall. Although *Myrica faya* is nominally dioecious, both males and females produce large amounts of fruit that are utilized by a number of exotic and native birds, particularly the exotic *Zosterops japonica.* In areas of active colonization, *Myrica* seed rain under perch trees of the dominant native *Metrosideros polymorpha* ranged from 6 to 60 seeds$\cdot$m$^{-2}\cdot$yr^{-1}; no seeds were captured in the open. Planted seeds of *Myrica* also germinated and established better under isolated individuals of *Metrosideros* than in the open. Diameter growth of *Myrica* is >15-fold greater than that of *Metrosideros,* and the *Myrica* population is increasing rapidly.

Rates of nitrogen fixation were measured using the acetylene reduction assay calibrated with ^{15}N. *Myrica* nodules reduced acetylene at between 5 and 20 μmol$\cdot$g$^{-1}\cdot$h^{-1}, a rate that extrapolated to nitrogen fixation of 18 kg$\cdot$ha$^{-1}\cdot$yr^{-1} in a densely colonized site. By comparison, all native sources of nitrogen fixation summed to 0.2 kg$\cdot$ha$^{-1}\cdot$yr^{-1}, and precipitation added <4 kg$\cdot$ha$^{-1}\cdot$yr^{-1}. Measurements of litter decomposition and nitrogen release, soil nitrogen mineralization, and plant growth in bioassays all demonstrated that nitrogen fixed by *Myrica* becomes available to other organisms as well. We conclude that biological invasion by *Myrica faya* alters ecosystem-level properties in this young volcanic area; at least in this case, the demography and physiology of one species controls characteristics of a whole ecosystem.

Key words: biological invasion; colonization; Hawai'i; invasibility; Myrica faya; *^{15}N; nitrogen cycling; nitrogen fixation; primary succession; seed dispersal; volcano.*

INTRODUCTION

Human-caused invasions by exotic species are a world-wide phenomenon, but they are particularly frequent and significant on isolated oceanic islands and archipelagos (Bramwell 1979). The greater invasibility of islands relative to continents has long been recognized (Wallace 1880, Campbell 1920, Elton 1958), although the reasons for this pattern continue to be debated (cf. Loope and Mueller-Dombois, *in press*). Prior to human colonization, oceanic islands were characterized by a biota that lacked major elements of continental biotas (such as grazing mammals), and by rates of evolution and speciation in excess of rates of immigration in many of the lineages that did colonize. The latter led to the development of unique and interpretable species complexes like the Galapagos finches (Grant 1986) and the Hawaiian *Drosophila* (Carson 1987).

The Hawaiian Islands are the most isolated archipelago on Earth. The native flora of Hawai'i contained ≈1200 species, >90% of them endemic (Loope and Mueller-Dombois, *in press*). Approximately 1500 yr ago, Polynesian colonizers brought ≈30 more plant species and several animals (Nagata 1985). European contact late in the 18th century marked the beginning of an extraordinary increase in biological invasion as European and Asian colonists from a variety of cultures brought and established their own agricultural, domestic, medicinal, weedy, and ornamental plants and animals. Approximately 4600 exotic species of plants are now found in Hawai'i (Smith 1985); at least 800 of these have established breeding populations, and at least 86 are considered serious threats to native populations and communities (Smith 1985, Wester, *in press*). In Hawai'i, as elsewhere, most invaders colonize human-disturbed sites most successfully (Allan 1936, Egler 1942, Ewel 1986, Crawley 1987, Sukopp and Trepl 1987). Nevertheless, many sites in Hawai'i which have not experienced recent human disturbance contain aggresively expanding populations of exotic species.

While biological invasions are a serious threat to endemic island biota, they also represent an unparalleled opportunity for ecological studies (Vitousek et al. 1987*a*). For example, Moulton and Pimm (1983, 1986) suggested that diffuse competition among exotic birds affects the probability of successful invasion by subsequent colonists, and there is some evidence that com-

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petition between exotic and native birds adversely affects the natives (Mountainspring and Scott 1985). There is considerably more evidence that introduced grazers, predators, and diseases have caused the decline and/or extinction of a number of endemic species of plants and animals on islands (Mueller-Dombois and Spatz 1975, Hadfield and Mountain 1980, Van Riper et al. 1986, Savidge 1987).

Biological invasions of oceanic islands provide a useful system for examining the effects of individual species on ecosystem-level phenomena as well (Vitousek 1986, Ramakrishnan and Vitousek, *in press*). Many studies have addressed the ecosystem-level significance of particular species by determining the amount or proportion of energy, water, or nutrients they utilize at critical times (such as after disturbance, after snowmelt) (Marks and Bormann 1972, Marks 1974, Muller and Bormann 1976, Foster et al. 1980, Boring and Swank 1984*a*, Gholz et al. 1985). Fewer studies, and those mainly of animals, have examined ecosystem-level consequences of species additions and removals (cf. Carpenter et al. 1987).

Invasions by exotic species offer an opportunity to determine the effects of individual species unambiguously. If an invader alters ecosystem-level characteristics (such as productivity, hydrology, nutrient cycling, or disturbance regime) of the area it invades, then it clearly controls aspects of the structure and functioning of that ecosystem. Moreover, where such effects can be demonstrated, they can be used to examine how population- and ecosystem-level processes interact. Studies of the biological perturbation represented by invasions could then be used to understand ecosystems in the same way that studies of other kinds of perturbations (clearcutting, fire) have been central to the understanding of other aspects of ecosystem dynamics (Bormann and Likens 1979, Vitousek and Matson 1985).

We examined invasion by the actinorhizal nitrogen-fixer *Myrica faya* Ait. (Myricaceae) into young volcanic sites in Hawaii Volcanoes National Park. There, *Myrica* invades primary successional sites that hitherto had been nearly or wholly dominated by native species. Moreover, nitrogen deficiency would be expected in such sites; lava flows and volcanic ash, like most substrates for primary succession, lack combined nitrogen but contain most of the other elements that organisms require. Walker and Syers' (1976) analysis of soil development and the many discussions based on it (cf. Cole and Heil 1981, McGill and Cole 1981, Vitousek and White 1981, Melillo and Gosz 1983, Walker et al. 1983, Vitousek and Walker 1987) conclude that nitrogen is in short supply relative to other elements early in soil development, and that nitrogen fixers should therefore dominate some stage of primary succession. Early studies of soil chronosequences (Jenny 1941, Crocker and Major 1955) emphasized nitrogen accumulation, and more recent theoretical treatments (cf. Tilman 1982, 1986) have interpreted primary succession in terms of a gradient from low to high nitrogen availablity.

There is substantial evidence that soil nitrogen availability does increase during primary succession in Hawai'i (Vitousek et al. 1983), as it does elsewhere (cf. Robertson and Vitousek 1981, Vitousek et al. 1989*b*). This pattern of increase could be caused by the dominance of a symbiotic nitrogen fixer at some early stage of succession (cf. Stevens and Walker 1970, Van Cleve et al. 1971, Reiners 1981, Tilman 1982), but no nitrogen-fixing native species occurs in early primary succession in Hawaiian rainforest (or indeed in some primary seres on continents).

Where vascular plants with nitrogen-fixing symbioses dominate an early stage of primary succession, they can accumulate up to 200 $kg \cdot ha^{-1} \cdot yr^{-1}$ of nitrogen within the system (Van Cleve et al. 1971, Binkley et al. 1984). In contrast, primary seres without symbiotic nitrogen fixers must acquire it from precipitation and non-symbiotic fixation; $\approx$2–5 $kg \cdot ha^{-1} \cdot yr^{-1}$ enter terrestrial ecosystems by these pathways in most areas that are not affected by anthropogenic fixed nitrogen (Galloway et al. 1982). *Myrica faya* in Hawai'i is invading a sere that lacks a native symbiotic nitrogen fixer; it therefore has the potential to alter the nitrogen budget of the invaded area substantially.

We evaluated this invasion by determining what allows *Myrica* to be successful as a biological invader, by examining what makes the area invasible by *Myrica*, and by determining the effects of *Myrica* on the inputs and biological availability of nitrogen. The first of these involved a study of the demography of colonizing populations of *Myrica*, including fruit production, seed dispersal, germination, establishment, and growth. The second (invasibility) involved an analysis of the environmental characteristics of sites where *Myrica* invasion is successful. Finally, the amount and biological availability of nitrogen fixed by *Myrica* were compared with those of native nitrogen fixation (by lichens and in decaying organic material) and inputs in precipitation.

BIOLOGY AND HISTORY OF *MYRICA FAYA* IN HAWAI'I

Myrica faya is a small evergreen tree native to the Canary Islands, Azores, and Madeira in the North Atlantic (Melville 1979). It appears to be wind pollinated, but in Hawai'i it is also visited by introduced honeybees (*Apis mellifera*). *Myrica faya* is considered dioecious, but nominally male plants generally produce some fruit and female plants a few male inflorescences (Gardner 1985). The fruit is an edible drupe that contains a stony endocarp; it is believed to be bird-dispersed in its native range (Bannerman 1922) and can be dispersed by birds or feral pigs (*Sus scrofa*) in Hawai'i (Smathers and Gardner 1979, LaRosa et al. 1985).

In its native habitat *Myrica faya* is codominant on lava flows that are several hundred years old (Hodges and Gardner 1985) between 100 and 500 m elevation and on older substrates at higher elevations (Humphries 1979). It was brought to Hawai'i by Portuguese immigrants in the late 1800s, probably as an ornamental or medicinal plant. *Myrica* was planted extensively by the Territorial Department of Forestry for watershed reclamation in the 1920s and 1930s, but these plantings were abandoned when its ability to colonize aggressively and to dominate pastures was recognized (Fosberg 1937). However, by then *Myrica* was established on five of the six largest islands in the Hawaiian archipelago (Whiteaker and Gardner 1985).

The first individuals of *Myrica* were reported in otherwise undisturbed areas of Hawaii Volcanoes National Park (HAVO) in 1961. By 1973, the population was large enough that control efforts were initiated. However, despite the removal of 92 000 individuals between 1973 and 1977, moderate-density *Myrica* populations covered 609 ha of HAVO in 1977. Control was then abandoned (except in a few small areas), and by 1985 *Myrica* covered 12 200 ha in HAVO and was continuing to spread rapidly (Whiteaker and Gardner 1985).

In HAVO a few individuals of *Myrica faya* occur as early colonizers of little-vegetated volcanic cinder resulting from recent (<20-yr-old) eruptions; more are found as suppressed individuals growing in the understory of closed-canopy rainforest. However, the most rapid and successful invasion has taken place in open-canopied sites dominated by scattered individuals of the native tree *Metrosideros polymorpha*. Such sites occur extensively in the water-limited seasonal submontane forest zone (Mueller-Dombois et al. 1981) and in rainforest sites where *Metrosideros* stands have been thinned but not eliminated by volcanic cinderfall from lava fountain-type eruptions (MacDonald et al. 1983).

In its native range *Myrica faya* is an actinorhizal nitrogen fixer (Miguel and Rodrigues-Barrueco 1974, Mian et al. 1976). While such species are notable as colonizers of low-nitrogen sites in the temperate zone and montane tropics worldwide (Tjepkema et al. 1986), the actinorhizal symbiosis apparently was absent from the native flow of Hawai'i, and it is not known when or how the symbiont (*Frankia*) became established. Nonetheless, *Myrica faya* (and exotic *Casuarina*) are now infected with *Frankia* wherever they have been observed, even as small seedlings and ephiphytes (Turner and Vitousek 1987). The *Myrica* nodules are much-branched *Alnus*-type nodules that range in size from <0.1 cm to at least 10 cm in diameter; *Frankia* are confined to cells in a ring near the outer edge of each lobe (J. Whitbeck, *personal communication*), as has been observed for *Myrica faya* in Portugal (Miguel and Rodrigues-Barruceo 1974). All of the nodules examined in Hawai'i lack spores (C. Schwintzer, *personal communication*).

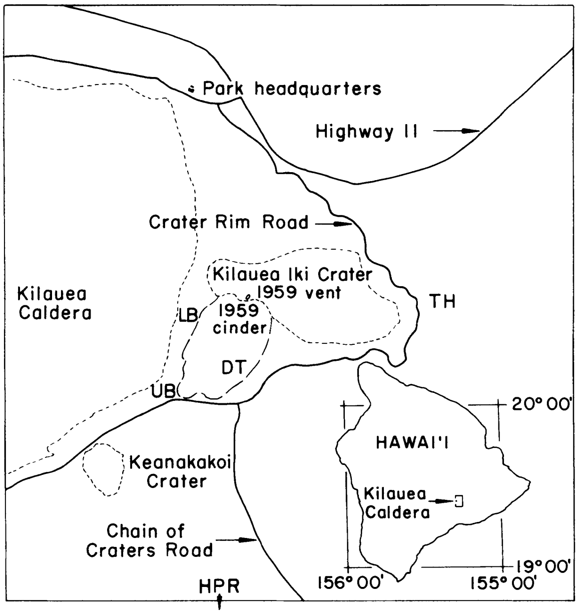

FIG. 1. Locations of the study sites in Hawaii Volcanoes National Park, Hawai'i. UB and LB are the open-canopied Upper Byron's Ledge and Lower Byron's Ledge sites, DT is the 28-yr-old successional Devastation Trail site, TH is the 200-yr-old Thurston Lava Tube site, and HPR is the open-canopied seasonal submontane Hilina Pali Road site. Inset map at lower right is the Island of Hawai'i.

STUDY AREA

This research was carried out in Hawaii Volcanoes National Park (HAVO), between 1100 and 1250 m elevation at and near the summit of Kilauea Volcano (19°20′ N, 155°15′ W) on the island of Hawai'i (Fig. 1). Our measurements were focused on an area affected by cinder from a 1959 eruption from Kilauea Iki Crater. The lava fountain from Kilauea Iki reached 600 m in height, and a 444-ha area downwind was covered by cinder (Smathers and Mueller-Dombois 1974).

We concentrated our reserach on areas in which a several-hundred-yr-old *Metrosideros polymorpha* forest that predated the 1959 eruption had been thinned but not wholly covered or killed by 1–2 m of cinderfall (Habitat area 5 of Smathers and Mueller-Dombois 1974; 125 ha). One such area on the wet side of the 1959 cinder plume had been sampled in 1978 by Smathers and Gardner (1979). It then contained 300 individual *Myrica*/ha, although by 1987 it had over 1000 individuals/ha (L. D. Whiteaker and D. Mueller-Dombois, *personal communication*). The larger *Myrica* are now >20 cm in basal diameter and 8–10 m tall; *Myrica* is codominant with *Metrosideros* in the canopy. We termed this the Lower Byron's Ledge (LB) site. Another area on the southwest side of the plume had a similar *Metrosideros* canopy structure, but *Myrica* invasion was at a very early stage when we initiated the study in 1985. Accordingly, we were able to prevent colonization in a 1-ha plot and monitor it in two others.

We termed this the Upper Byron's Ledge (UB) site. Additional measurements were made in an area where all vegetation had been killed by cinder from the 1959 eruption (Devastation Trail, or DT, site), in closed-canopy montane rainforest dating from a 1790 eruption of Kilauea (Thurston lava tube, or TH, site), and in open-canopied seasonal submontane *Metrosideros* forest (Hilina Pali Road, or HPR, site).

The climate of the major study area is montane tropical. At the nearby Park Headquarters mean annual precipitation is ≈2400 mm, mean January temperature is 14°C, and mean July temperature is 17°. Frost occurs in low-lying areas once every few years. The area is at the edge of the rain shadow that Kilauea Volcano casts in the predominant northeast trade winds; rainfall gradients are steep; and the southwest edge of the area is somewhat drier and warmer than the remainder (Smathers and Mueller-Dombois 1974). There is no distinct dry season. All of the substrates in the study area have been dated and mapped (Smathers and Mueller-Dombois 1974, Holcomb 1987); all are young, and there has been little or no soil profile development.

METHODS

Fruiting phenology and dispersal of Myrica.—Two different pathways *Myrica* reproduction were examined. Seeds can drop under the parent *Myrica,* leading to growth of the population by nucleation (Yarranton and Morrison 1974). Alternatively, some are dispersed away from the parent tree, primarily by birds.

The timing of flowering and fruiting was determined by Whiteaker and Gardner (1987), who made detailed observations on ten individual *Myrica* near the LB site from March 1983 through March 1985. They also measured fruit drop under *Myrica* canopies in 10 1 × 1 m traps which were collected biweekly from April 1983 through April 1984.

We evaluated avian use of *Myrica* canopies and fruit by selecting 1–3 individual *Myrica,* determining the abundance of mature fruit on each, and then keeping track of all avian visitors for 30 min. The species of visitor, length of each visit, feeding activity, flight pattern following each visit, and, where possible, the number of seeds consumed were recorded. Another 1–3 trees were then selected and observed; blocks of observations were made from dawn to sunset in all weather. A total of 234 h, or 402 tree-hours, of observation were accumulated between July and December 1987 in the LB and UB sites. There was some question whether the most frequent visitor (*Zosterops japonica*) actually consumed *Myrica* fruit (LaRosa et al. 1985), so 46 individuals were captured by mist netting and their feces examined for *Myrica* seed (S. Woodward, *personal communication*).

Seed disperal away from parent trees was measured from November 1985 to October 1987 using 0.5 × 1 × 0.1 m deep seed traps with a nylon mesh liner 0.1 m above the ground surface. Thirty traps were placed in the LB site, 10 under *Metrosideros polymorpha* crowns, 10 under standing dead *Metrosideros,* and 10 in the open. Twenty traps were established in the UB site, 10 under *Metrosideros* and 10 in the open. Finally 30 traps were established under *Metrosideros* along a 10-km transect in seasonal submontane forest at the HPR site; the transect extended from a dense *Myrica* stand through an invasion front to 5 km ahead of that front. *Myrica* seeds were collected monthly from all traps (except bimonthly at HPR), sorted and counted, and sown on vermiculite-filled pots in a greenhouse to determine seed viability.

The buried seed pool of *Myrica* was examined by twice collecting a large soil sample (0.3 × 0.3 × 0.1 m) from under each of four *Metrosideros* trees in the UB site. One set of four was collected in September 1986, maintained intact and well-watered in the greenhouse for 1 yr, and monitored for emerging seedlings. A second set was collected in March 1987 and sorted carefully for *Myrica* seeds.

Germination and establishment.—Seed longevity and the factors controlling seed germination were determined by Walker (*in press*) under laboratory and greenhouse conditions. In addition, two field experiments were undertaken to examine the influence of substrate, litter cover, and light on *Myrica* germination in the UB site. We were particularly interested in determining whether the observed concentration of *Myrica* under potential perch trees reflects only greater seed rain there, or if unvegetated cinder represents an unfavorable site for *Myrica* germination and/or establishment.

In the first experiment, *Myrica* seeds were collected in October 1985 and stored at room temperature. In April 1986, 200 seeds with known viability were scarified mechanically using a soil sieve and sown in each of 60 perforated plastic trays 51 × 25 × 5.4 cm deep. Fifteen pairs of trays were filled with volcanic cinder and placed in the open; one in each pair was covered with 2 cm of *Metrosideros* litter. The other 15 pairs of trays were filled with soil and forest floor from under *Metrosideros* canopies and placed under *Metrosideros.* One tray in each pair retained the original 2 cm deep leaf litter layer; litter was removed from the other tray, and any subsequent litterfall was removed every other week. All trays were set into the ground so that the edge of the tray was flush with the ground surface. *Myrica* seeds were sown on the surface, and an additional 0.5 cm of *Metrosideros* litter was then added to the trays with litter. Emergence and survival of seedlings were followed for 64 wk.

Seeds for the second experiment were collected in October 1986. In December 1986, 150 seeds were sown in each of 75 slightly larger trays (55 × 28 × 5.4 cm). Sixty of the trays were placed into the field in the same treatments as in the earlier experiment. An additional 15 trays were filled with cinder and established in the open under a double layer of optically neutral 80% shade cloth to test the effect of reducing heating and surface drying on seed germination and establishment. The shade cloth was held in place by a metal frame 0.6 × 0.3 × 0.18 m tall; there was a 2-cm space between the bottom edge of the shade cloth and the ground surface to allow air circulation. Ninety rat traps were set near these trays and reset weekly to reduce rodent predation on *Myrica* seeds. Measurements of seedling emergence and survival in this experiment continued for 48 wk.

Germination in these experiments was defined as emergence above the ground surface; survival of the seedlings was then monitored as long as each experiment continued. All trays were examined biweekly, and all seedlings were marked as they emerged. At the end of the first experiment, 20 *Myrica* seeds were removed from each tray and sown in vermiculite in a greenhouse to determine seed viability.

Seed predation.—Predation on *Myrica* fruit and seeds was evaluated by placing them in petri dishes in the field and monitoring weekly the number of intact seeds remaining for 2 mo during the period of maximum fruit drop in October–November 1987. Seeds were placed out in a complete factorial design, with four replicates per cell. The factors examined were the presence or absence of pulp, initial density of seeds (1 or 20 per dish), density of *Myrica* in the site (UB or LB), and canopy cover (under *Myrica* or *Metrosideros*).

Growth and survival.—The size structure and growth of colonizing *Myrica* populations were measured in several plots in the UB and LB sites. The basal diameter, height, and survival of each individual *Myrica* (including recent germinants) were recorded bimonthly from September 1986 to September 1987 in a 1-ha plot (Plot I) in the UB site; each plant was permanently marked with a numbered aluminum tag. All *Myrica* were removed from a second 1-ha plot (Plot II) in September 1986, and new arrivals were censused and removed in September 1987. The size distribution of *Myrica* was censused once on a 1-ha plot with a denser population (Plot III), and basal diameters of 30 large *Myrica* (2–10 m tall) were remeasured bimonthly for a year in or near that plot. Additionally, basal diameters of 10 large *Myrica* near the UB site were measured biweekly from May 1986 to August 1987 using nickel alloy dendrometer bands that had been protected from acid corrosion (Walker and Whiteaker 1988). In the LB site, each *Myrica* was marked and its basal diameter measured in November 1986 in four 20 × 20 m plots; these plots were then resurveyed for growth and survival after 13 mo.

Growth of *Myrica* as a function of light was measured in shade boxes with six levels of shade cloth, nominally representing 0%, 30%, 55%, 63%, 80%, and 96% reduction of ambient light. Twenty-four 4-L pots were placed in each box, filled with cinder soil, and sown with *Myrica* seeds in July 1986. A handful of soil from under field-grown *Myrica* was added to each pot to encourage nodulation. Seedlings were thinned to five individuals per pot and fertilized biweekly with 100 mL of $\frac{1}{10}$ strength Hoaglands nutrient solution (including nitrogen). After 6 mo two seedlings per plot were harvested and separated into shoots, roots, and nodules; the remaining seedlings were harvested after 1 yr.

Nitrogen fixation by Myrica faya.—Nitrogen fixation was estimated using a three-part process based on the acetylene reduction assay for nitrogenase, the critical enzyme in nitrogen fixation (Bergersen 1980). We measured acetylene reduction activity (ARA) per gram of nodule, ^{15}N fixation per unit of ARA, and nodule biomass per hectare.

ARA was measured on nodules that had been detached from the plants but which remained attached to a short (≈5 cm) section of root (Boring and Swank 1984*b*). First, clusters of nodules on five individual *Myrica* (two clusters on one of the individuals) were excavated but left attached to the plant. All six clusters of nodules (plus attached root) were then collected as rapidly as possible and sealed in 40-cm^3 serum vials. Three cubic centimetres of acetylene that had been generated from calcium carbide in the field were injected into five of these vials and into a sixth without nodules; the remaining vial with nodules (from the plant from which two clusters of nodules had been collected) was incubated without added acetylene. Vials were buried in the soil at the approximate depth at which nodules had been collected, and gas samples (0.35 cm^3) were withdrawn from each vial with disposable syringes after 3, 6, 9, and 12 min. Syringes were then inserted into rubber stoppers and transported to the laboratory. After repeated measurements failed to detect any ethylene in the vials with acetylene but no nodules or those with nodules but no acetylene, we collected and analyzed gas samples from those vials only after 12 min.

Analyses for ethylene were carried out on 0.25-cm^3 gas samples within 2–4 h of collection. We used a Shimadzu (Columbia, Maryland) Mini-2 gas chromatograph with flame ionization detector; Poropak Q columns were maintained at 46°C, and the detector temperature was 80°.

ARA per unit mass of *Myrica* nodule was determined by calculating ethylene production per minute during the linear portion of ethylene accumulation within the vials; this most often extended to 9 but not 12 min. Viable nodules were then separated from dead nodules, root, and soil material; nodule mass was determined by drying for 48 h at 70°.

Measurements of ARA were carried out over an annual cycle for *Myrica* in full sun in the DT site, partially in the shade of isolated individual *Metrosideros* in the UB site, and under the shade of a closed rainforest canopy in the TH site. The six regular seasonal measurements each consisted of two sets of determinations like that described above on separate days in each site. Additional measurements were made in the LB and

HPR sites, on two diel cycles in the DT site, and immediately before and after a 2-d cloudy and rainy period in the UB site.

The amount of ^{15}N fixed per unit of acetylene reduced was determined in the field. Two clusters of nodules plus attached root were isolated from each of six trees and placed in serum vials. Forty cm^3 of commercially prepared gas containing 80% N_2 (99% enriched in ^{15}N) and 20% O_2 (Prochem, Inc., Summit, New Jersey) were added to one vial in each pair, mixed thoroughly with a syringe, and then 40 cm^3 of the mixture was removed. After 9 min the nodule clusters were removed and separated into viable nodules and attached tissue. Each component was dried and then digested using a sulfuric acid/persulfate procedure in a block digestor. The resulting ammonium was diffused into HCl, evaporated to dryness at 90°C (Adamson and Reeder 1983, Reeder 1984), and shipped to Isotope Services, Inc. (Los Alamos, New Mexico) for ^{15}N determination on an isotope ratio mass spectrometer. The other vial in each pair received acetylene as described above. After 9 min gas samples were removed for determination of ARA.

Nodule mass in the sites was determined by harvesting complete root systems of *Myrica* (Turner and Vitousek 1987). Viable nodules were separated and weighed, and regressions relating stem basal area to nodule mass were calculated. These regressions were combined with the population–size distribution measurements described above to yield nodule mass per hectare. We then calculated nitrogen fixation on the basis of ^{15}N fixed per unit ARA, ARA per gram of nodule, and grams of nodules per hectare.

Nitrogen fixation calculated in this way was compared with measurements of ^{15}N natural abundance (Shearer and Kohl 1986) in *Myrica* and *Metrosideros*. Leaf samples were collected in the LB site; these were dried, ground, and shipped to Washington University for analysis by the procedure of Shearer and Kohl (1986).

Other nitrogen inputs.—Nitrogen fixation by *Myrica* was placed in context by measuring other pathways of nitrogen inputs into these sites. Exploratory work with ARA established that the major native sources of nitrogen fixation in young volcanic sites in HAVO are algae associated with liverwort mats, lichens with blue-green cephalodial phycobionts (*Stereocaulon vulcani* and *S. ramulosum*) and their epiphytes (Fritz-Sheridan and Portécop 1987), and bacteria or algae associated with leaf litter and decomposing wood. Although free-living blue-green algae have been identified as primary colonizers of volcanic cinder in Hawai'i (Doty 1967, Smathers and Mueller-Dombois 1974), we were not able to detect any ARA in cinder without visible lichens.

Only lichens, litter, and wood were important sources of ARA in the UB and LB sites. Lichen activity was measured by collecting material from 20 10-cm^2 plots of cinder substrate in areas with dense and sparse lichen cover, and incubating it in serum vials with added acetylene as described above. Leaf litter was collected from 25 random quadrats in each plot, and 2–3 g (dry mass) sample from each quadrat was incubated with added acetylene. Woody material intercepted by five 40-m transect lines in each plot was collected; 10 subsamples were incubated to determine ARA.

All incubations were carried out for 24 h in the laboratory; lichen samples received 12 h of light during this period. Linearity of ARA over this period was established by sampling a subset of vials at 6 or 14 h. Assays were generally carried out on moist (sometimes moistened) samples; little activity was detectable in dry substrates.

We estimated nitrogen fixation by combining ARA with measurements of ^{15}N fixation and of the amount of each substrate per area. ^{15}N fixation was measured for lichens and leaf litter as described for *Myrica* nodules, except that the incubation period was 24 h and samples were analyzed by natural abundance procedures at Washington University (Shearer and Kohl 1986). We assumed that the ratio of ^{15}N to ARA was the same in wood as in leaf litter. The amount of substrate was determined by estimating the cover of *Metrosideros* and *Myrica* canopies, *Metrosideros* litter, and dense and sparse lichen canopies at 400 points arranged along five 40-m transects in both LB and UB, by measuring the mass of leaf litter in 25 randomly placed 0.25 × 0.1 m quadrats in each site, and by calculating the volume of woody debris (stems and branches) intercepted by five 40-cm transects in each site. Samples of woody debris were collected, dried, and weighed to determine wood density.

The other major source of nitrogen is precipitation. Harding and Miller (1982) reported weighted mean nitrate concentrations and deposition for several sites in the area. In addition, we measured ammonium, nitrate, and organic nitrogen in precipitation in 19 weekly samples from a funnel collector in the open in the UB site.

Nitrogen availability and cycling.—The effect of the nitrogen fixed by *Myrica faya* on the availability and cycling of nitrogen was examined in several ways. The extent to which nitrogen availability limits primary production of native overstory *Metrosideros* was determined by fertilizing 30 trees in the UB site with nitrogen. Nitrogen was applied as a 1:1 mixture of urea and ammonium sulfate; fertilizer application extended to a radius of 3 m from the target tree. The initial nitrogen application was 10 g/m^2; thereafter 2.5 g/m^2 were added twice each year. Growth of the 30 target trees and 30 unfertilized controls was monitored bimonthly with nickel alloy dendrometer bands. In addition, a complete factorial fertilization with nitrogen, phosphorus, and all other nutrients (minus N and P) was carried out at the DT and TH sites (Vitousek et al. 1987*b*).

Effects of *Myrica* on total soil nitrogen were determined by sampling forest floor and soil under five pairs of isolated *Metrosideros polymorpha* in the UB site. One tree in each pair stood alone; the other, which was matched in size and canopy morphology, had a large *Myrica* under and intermingled within its canopy. The area covered by litter from these trees was measured, and nine cores of forest floor and three of soil (both 6 cm in diameter, the soil cores to a depth of 10 cm) were collected according to a spatially stratified random design from the area covered by litter. The samples were composited by horizon and tree, and each composite was oven-dried, weighed, acid-digested, and analyzed for total nitrogen using a Technicon AutoAnalyzer.

Nitrogen release from decomposing leaves of *Myrica* and *Metrosideros* was measured using tethered leaves (Swift et al. 1979). Senescent leaves of each species were collected by plucking easily removed, discolored leaves from trees in August 1985; the leaves were then air-dried for 10 d. A subsample of each species was weighed, oven-dried at 70°C, and reweighed to determine the ratio of air-dry to ovendry weight. The oven-dried leaves were then analyzed for initial N, P, Ca, Mg, K, cellulose, and lignin concentrations (Van Soest and Wine 1968, Reiners and Reiners 1970, Technicon Instrument Systems 1976); mature green leaves were also analyzed for nitrogen and phosphorus on a leaf-area and leaf-weight basis so that nutrient retranslocation during leaf senescence could be determined. The remaining air-dried leaves were weighed individually and their petioles were tied with fishing line into strings of five leaves; the strings were then placed in the field under *Myrica* and under *Metrosideros* in the UB site. Three strings of each type from each habitat were collected after 1, 3, 6, 12, 18, and 24 mo, and the leaves were oven-dried, weighed individually, combined by string, and analyzed for N and P. Decomposition was calculated as final divided by initial dry weights (using strings as sampling units); proportional nutrient release was calculated from final nutrient content (concentration times mass) divided by initial nutrient content.

The influence of *Myrica* on net nitrogen mineralization was estimated by sampling soils under *Myrica* and *Metrosideros* in the UB and LB sites. The measurements followed the procedure of Matson et al. (1987); 10 samples, each consisting of two cores 6 cm in diameter and 15 cm deep, were collected in each site. One core in each pair was placed in a polyethylene bag and replaced in the soil; the other was returned to the laboratory, mixed thoroughly, and a subsample was extracted in 100 mL of 2 mol/L of KCl for determination of initial ammonium and nitrate concentrations. After 14 d field cores were collected, mixed, and extracted in the same way. Soil extracts were analyzed colorimetrically for ammonium- and nitrate-N on a Technicon AutoAnalyzer at Stanford University. Net nitrogen mineralization was calculated as final ammonium-N plus nitrate-N (after incubation) minus initial ammonium-N plus nitrate-N (Matson et al. 1987).

Finally, the growth rate of seedlings in soil collected from under *Myrica* was conpared with that in soil from *Metrosideros*. Seeds of *Metrosideros polymorpha* and of the introduced tree *Psidium cattleianum* (strawberry guava), an aggressive invader of rainforest sites in Hawai'i (Smith 1985), were planted and seedlings were grown to the same initial size. Seedlings of each were then planted two per pot into soil collected from under *Myrica* and *Metrosideros* in the UB site. These pots were kept under a misting system in the greenhouse; they were not fertilized. After 12 mo the seedlings were harvested, and height, shoot mass, and root mass were determined.

Statistical analyses.—One-way analysis of variance was used to detect treatment differences; percentages were arcsine-transformed and chemical data log-transformed prior to analyses. Student-Newman-Keuls multiple range tests were then used to compare individual treatments when a significant treatment effect was detected, except that Scheffés multiple contrast was used for the shade experiment where sample sizes were not equal. SAS was used for all statistical analyses (SAS 1982); all results reported as significant were determined at the 5% level.

RESULTS

Demography of the invader

Fruiting and dispersal.—*Myrica faya* seed-rain under the parent tree ranged from 4000 to 37 000 fruit/m^2 under male and female trees, respectively (Whiteaker and Gardner 1987). Fruit production was strongly seasonal, peaking between September and December. We calculated overall fruit drop per hectare on a 1-ha plot (Plot III) in the UB site based on the area covered by adult *Myrica* of each sex; approximately 4 600 000 seeds/ha fell under parent trees in an area with only 21 adult *Myrica*/ha.

The capture of dispersed *Myrica* seeds in seed traps under *Metrosideros* was also strongly seasonal (Fig. 2), but such dispersal continued for several months following the peak of fruiting and fruit drop. No *Myrica* seeds were captured in 2 yr in 10 m^2 of seed traps in the open, and traps under live *Metrosideros* crowns captured 100 times as many as those under dead crowns. A mean (±SE) of 60 ± 12 seeds$\cdot$m$^{-2}\cdot$yr^{-1} was captured under live *Metrosideros* in the LB site and 6 ± 2 seeds$\cdot$m$^{-2}\cdot$yr^{-1} in the UB site. The pulp had been removed from 98% of these seeds, presumably during passage through birds; only the stony endocarp remained. We found no viable buried seed in eight 0.3 × 0.3 × 0.1 m litter/soil samples collected under *Metrosideros* in the UB site.

Slightly more than 40% of the ground surface was covered by *Metrosideros* canopy in both sites. Using

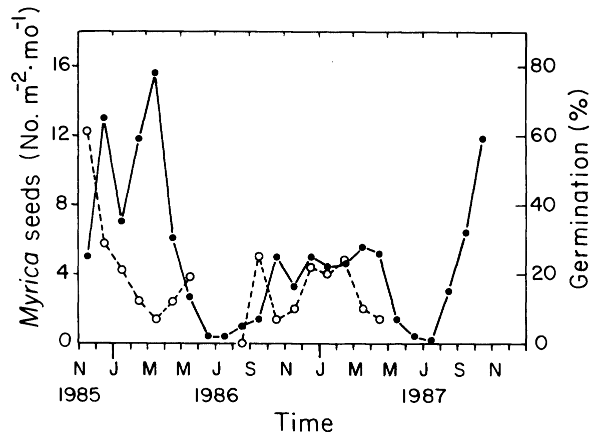

FIG. 2. Dispersal of *Myrica faya* seeds to under *Metrosideros polymorpha* canopies in the LB site (—●—), and germination of the seeds captured under *Metrosideros* (– – o – –). Germination is not reported when <5 seeds/mo were captured in seed traps.

measured seed rain under *Metrosideros* canopies, we calculated the areal inputs of *Myrica* seeds dispersed away from the parents as ≈254 400 and ≈23 700 seeds·ha^{-1}·yr^{-1} in LB and UB, respectively. In the UB site seed dispersal to under *Metrosideros* represents ≈0.5% of the seed drop under *Myrica.*

Bird use of *Myrica* was monitored in UB and LB from July through December 1987. In all, 871 visits were recorded in 402 tree-hours (234 total hours) of observation. The most frequent visitor to *Myrica* was the exotic mejiro or Japanese White-eye *Zosterops japonica,* which accounted for 85% of the visits at LB and 87% at UB. It had been suggested that *Zosterops* do not consume *Myrica* seed in the field (LaRosa et al. 1985). However, we observed *Zosterops* removing seeds and even taking them to a nest, and *Myrica* seed were recovered in the feces of 36% of 46 *Zosterops* captured (Woodward et al., *unpublished manuscript*). The second most common visitor was the native 'apapane (*Himatione sanguinea*); it was never observed feeding on *Myrica* fruit. A number of other native and exotic birds (nine species in all) were observed in *Myrica* trees at the UB and LB sites; several of the infrequent visitors (Table 1) were observed feeding on fruit, and exotic House Finches (*Carpodacus mexicanus*) consumed many fruit in a human-disturbed site near the Park (S. A. Woodward et al., *unpublished manuscript*).

TABLE 1. Birds observed visiting *Myrica faya* in the Upper Byron's Ledge (UB) and Lower Byron's Ledge (LB) sites in Hawaii Volcanoes National Park. Values are the proportion of 258 visits observed in 126 tree-hours in the UB site and 613 visits in 276 tree-hours in the LB site.

Site	Species	Native or exotic	Proportion of total visits
UB	*Zosterops japonica* (mejiro)	Exotic	.87
	Himatione sanguinea ('apapane)	Native	.07
	Lophura leucomelana (kalij)	Exotic	.02
	Cardinalis cardinalis (cardinal)	Exotic	.02
	Hemignathus virens ('amakihi)	Native	.01
	Phaeornis obscurus ('oma'o)	Native	<.01
	Garrulax canoris (laughing thrush)	Exotic	<.01
LB	*Zosterops japonica*		.85
	Himatione sanguinea		.09
	Lophura leucomelana		.02
	Cardinalis cardinalis		.01
	Carpodacus mexicanus (house finch)	Exotic	.01
	Chasiempsis sandwichensis ('elepaio)	Native	.01
	Garrulax canoris		<.01
	Phaeornis obscurus		<.01

TABLE 2. Field germination and seedling survival calculated from *Myrica faya* seeds sown in trays with or without *Metrosideros* litter in the open-canopied UB site on two dates.* NA indicates not applicable.

Treatment	Planting date	Germination (%)	Seedling survival (%)	GT_{50}† (wk)
Metrosideros canopy				
Litter	Apr 1986	0.33 ± 0.05^{ab}	51‡	35
	Dec 1986	1.02 ± 0.07^{b}	95§	22
No litter	Apr 1986	4.32 ± 0.10^{c}	17	12
	Dec 1986	4.61 ± 0.12^{c}	94	18
No canopy				
Litter	Apr 1986	0.12 ± 0.01^{a}	0	39
	Dec 1986	0.00 ± 0.00^{a}	na	na
No litter	Apr 1986	0.10 ± 0.02^{a}	0	41
	Dec 1986	0.00 ± 0.00^{a}	na	na
Shade	Dec 1986	0.01 ± 0.01^{a}	0	22

* Germination is expressed as the percentage of viable seeds sown; survival is a percentage of the maximum number of seeds that germinated (mean ± SE, n = 15). Germination percentages followed by the same letter are not significantly different (P > .05). Values were arcsine-transformed prior to stratistical analyses.

† GT_{50} is the time in weeks to reach 50% of final germination.

‡ Survival after 64 wk.

§ Survival after 48 wk.

Despite the frequency of bird visits, it appears that most dispersal of seed away from parents is relatively short range. In a transect across an invasion front in the HPR site, we found 4.7 ± 2.3 seeds·m^{-2}·mo^{-1} under *Metrosideros* in a dense *Myrica* stand, 1.8 ± 0.9 at the invasion front, and none >0.5 km ahead of the front. Nonetheless, occasional long-distance disperal up to 5 km ahead of a front has been observed (Whiteaker and Gardner 1985).

Germination and establishment.—Approximately 70–80% of *Myrica* seed germinated under greenhouse conditions (Walker, *in press*); greenhouse values for the seeds planted into the field in April and December

TABLE 3. Predation on *Myrica faya* fruit and seeds. Values are the mean (±SE) number of intact seeds remaining after the specified time interval. Results are combined for the UB and LB sites, Hawaii Volcanoes National Park, and for seeds under *Myrica* and *Metrosideros* canopies.

Time interval (mo)	Fruit density High (20/dish)	Fruit density Low (1/dish)	Seed density High (20/dish)	Seed density Low (1/dish)
1	11.8 ± 1.5	.94 ± .06	12.1 ± 1.2	.69 ± .12
2	8.3 ± 1.6	.69 ± .12	5.4 ± 1.5	.19 ± .10

1986 were 75.2% and 75.0%, respectively. However, germination of *Myrica* seeds in the field was much less (Table 2). The germination that did occur in the field was both favored and inhibited by *Metrosideros*. Seeds planted under a *Metrosideros* canopy had significantly greater germination than those in the open (Table 2). Extreme soil surface temperatures reached 61°C in the open and 37° under *Metrosideros* canopy, and mean maximum monthly temperature was 47° in the open and 32° in shade. However, the observed difference in germination was not solely due to temperature; seeds planted into volcanic cinder under shade cloth had no greater germination than those in the open, despite soil-surface temperatures comparable to those under a *Metrosideros* canopy. The observed lack of *Myrica* colonization in open sites could be due to its inability to establish in such sites as well as to the lack of seed inputs there.

Under a tree canopy, seeds planted into trays with *Metrosideros* litter had significantly lower and slower germination rates than those planted into trays without litter (Table 2). This effect was also observed under greenhouse conditions (Walker, *in press*). The survival of seedlings that did germinate was also greater under a canopy than in the open. In the April experiment, survival was also greater in the trays with litter than those without, but there was no effect of litter in the December experiment. None of the ungerminated seeds recovered from the trays at the end of the experiments could be germinated in the greenhouse.

Myrica seedlings became established in two different habitats in the UB site—under *Myrica* and under *Metrosideros* canopies. Of 508 seedlings <1-yr-old in Plot III of the UB site, 195 were under *Myrica* and 313 under *Metrosideros*. We measured distances from parent *Myrica* to those seedlings under *Myrica*; seedlings were clustered around the edge of the canopy of the parent, and surviving larger seedling were farther from the parent than were most new germinants. This pattern of growth and survival allows for horizontal expansion (nucleation) of clumps of *Myrica*. However, the number of seedlings established under *Myrica* was <0.01% of calculated seed rain there, while first-year seedlings represented 1.3% of seed rain under *Metrosideros*.

Seed predation.—Approximately 60% of seeds placed out in Petri dishes remained intact after 1 mo in the field; <40% remained intact in 2 mo (Table 3). There was no significant effect of site (UB vs. LB), canopy (*Myrica* vs. *Metrosideros*), or the presence or absence of pulp, on seed survival. We observed exotic Kalij Pheasants (*Lomphura leucomelana*) taking *Myrica* fruit from the ground, and found tracks of exotic black rats (*Rattus rattus*) in fine sand placed around Petri dishes in which seeds were fragmented.

Growth and survival.—The growth of *Myrica* in the LB and UB sites varied as a function of individual size (Table 4). The mean diameter growth of adult *Myrica* in UB (1.5 ± 0.2 cm/yr) was much more rapid than that of *Metrosideros* in the same site (0.09 ± 0.01 cm/yr for unfertilized individuals; see Effects of *Myrica faya* on Nitrogen Availability and Cycling: Nitrogen Limitation, below). Growth rates of adult *Myrica* were even greater in a nearby site equipped with dendrometers (2.9 ± 0.2 cm/yr); no seasonal pattern in *Myrica* diameter growth was detectable. Diameter growth in 62 similarly large individuals (>6 cm basal diameter) was less (0.8 ± 0.1 cm/yr) in the denser LB site.

Under shadehouse conditions the growth of *Myrica* was strongly dependent on the availability of light (Table 5). There was no significant difference in growth between full sun and 30% shade, but ≥55% shade significantly reduced biomass accumulation after 6 mo or 1 yr. Growth was virtually zero although survival was high at 96% shade, a level similar to that observed under *Myrica* crowns or in a closed-canopy *Metrosideros* forest. Nodules represented a significantly larger proportion of overall plant biomass at higher light levels, as Turner and Vitousek (1987) observed in the field.

Survivorship was assessed in permanent plots in the UB and LB plots. The survival of seedlings to 1 yr was 81% in the permanently marked plot I at the UB site. We observed no natural mortality of individuals >1-yr-old, although 3.2% of the reproductive individuals in the LB plot lost most of their foliage during 13 mo of observation. Three pre-reproductive individuals in the UB site and one in the LB site were pulled up during our observation period in ad hoc control efforts.

TABLE 4. Diameter growth rates of *Myrica faya* in the UB and LB sites, Hawaii Volcanoes National Park. Diameter classes are those at the beginning of a year of growth; both single- and multiple-stemmed *Myrica* are included. All of the groups reported represent 25 or more individuals except those of diameter <1 cm at LB; only 10 individuals were sampled there.

Basal diameter class (cm)	Diameter growth rate (cm/yr) UB site $\bar{X}$	UB site (SE)	LB site $\bar{X}$	LB site (SE)
<1	0.7	(0.1)	0.7	(0.1)
1–3	1.4	(0.1)	0.8	(0.2)
3–6	1.0	(0.1)	1.2	(0.2)
>6	1.5	(0.2)	0.8	(0.1)

TABLE 5. Weight at harvest (1 yr) of *Myrica faya* seedlings grown under different densities of shade cloth. Within plant parts, values with the same letter are not significantly different ($P > .05$).

		Harvest dry mass per pot (g)							
		Shoot		Root		Nodule		Total	
Percent shade	N	$\bar{X}$	SE	$\bar{X}$	(SE)	$\bar{X}$	(SE)	$\bar{X}$	(SE)
0	24	18.0	(1.4)^{ab}	3.4	(0.3)^{a}	0.6	(0.05)^{a}	22.0	(1.7)^{ab}
30	23	21.6	(1.8)^{a}	4.0	(0.4)^{a}	0.7	(0.08)^{a}	26.2	(2.2)^{a}
55	24	12.4	(1.3)^{bc}	1.9	(0.2)^{b}	0.3	(0.03)^{b}	14.6	(1.5)^{c}
63	24	12.9	(1.2)^{bc}	1.8	(0.2)^{b}	0.3	(0.03)^{b}	15.0	(1.4)^{bc}
80	23	8.8	(0.9)^{c}	1.4	(0.2)^{b}	0.1	(0.02)^{bc}	10.3	(1.0)^{c}
96	19	0.1	(0.02)^{d}	$<$0.01^{c}		$<$0.001^{c}		0.1	(0.02)^{d}

Population growth.—Information on seed production, dispersal, growth, and survival for a cohort of *Myrica faya* was summarized for the fully censused Plot III in the recently colonized UB site. Age at first reproduction was estimated at 6 ± 2 yr based upon observations of height at first reproduction (3 m) and height growth rate. Seed production was taken from Whiteaker and Gardner's (1987) measurements near the LB site, and seed rain and seedling establishment under *Metrosideros* were measured directly in Plot III. Survival of germinants to 1 yr was monitored on the permanently marked Plot I in the UB site, and survivorship to reproductive age was calculated including human-caused mortality (a small but pervasive loss to accessible *Myrica* populations in HAVO). This information (summarized in Fig. 3) suggests that the seeds produced during 1 yr by 21 adult *Myrica* would give rise to >150 mature individuals.

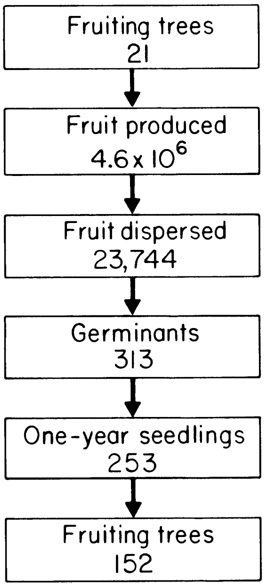

FIG. 3. Flowchart for the demography of one year-class of *Myrica faya* in Plot III of the UB site, Hawaii Volcanoes National Park. Calculated as described in Methods from measured seed rain, population size distribution, and the growth and survival of marked individuals in the UB site.

Effects of the invader on nitrogen inputs and availability

Nitrogen fixation by Myrica faya.–Acetylene reduction activity (ARA) was measured over an annual cycle in *Myrica* nodules collected from trees growing in full sun (DT site), partial shade of isolated *Metrosideros* (UB site), and full shade of *Metrosideros-Cibotium* rainforest (TH site). Most values fell between 5 and 20 $\mu mol \cdot g^{-1} \cdot h^{-1}$, with little difference among sites (Fig. 4). Occasional measurements in the LB site and the seasonal submontane HPR site yielded results in the same range. We observed a distinct summer maximum for ARA in all sites in 1986 (Fig. 4). ARA in a temperate *Myrica gale* population had a much more pronounced seasonal cycle and higher maximum ARA (Schwintzer 1979, Schwintzer et al. 1982); other reported values for *Myrica* are on a fresh-mass (Miguel and Rodrigues-Barrueco 1974, Morris et al. 1974) or per-lobe (Sprent et al. 1978) basis, and hence difficult to compare directly.

In addition to seasonal measurements, we determined ARA over two diurnal cycles. ARA was <2 $\mu mol \cdot g^{-1} \cdot h^{-1}$ after sunset or before dawn; it generally remained within the normal 5–20 $\mu mol \cdot g^{-1} \cdot h^{-1}$ range from shortly after sunrise through sunset, although there was a suggestion of a midday depression in one set of observations. Finally, one set of measurements carried out after 2 d of continuous heavy cloud cover and rain yielded mean (±SE) results indistinguishable from those immediately before the rain (14.3 ± 3.1 $\mu mol \cdot g^{-1} \cdot h^{-1}$ before vs. 13.1 ± 1.6 $\mu mol \cdot g^{-1} \cdot h^{-1}$ after).

ARA was calibrated using $^{15}N_2$ fixation; we determined a molar ratio of 3.5 (±0.7):1 of ARA : $^{15}N_2$. This value is close to the theoretical value of 3.0 (Hardy et al. 1968), which we used in our calculations. The nodule biomass in each site was calculated from regressions of nodule mass on the basal area of individual *Myrica* (Turner and Vitousek 1987); separate equations were used for full-sun, partially shaded, and fully shaded plants.

Areal rates of nitrogen fixation were estimated by multiplying the ratio of ^{15}N fixed : ARA times the overall mean ARA per gram of nodule mass times nodule mass per hectare (times the molecular mass of N_2 times

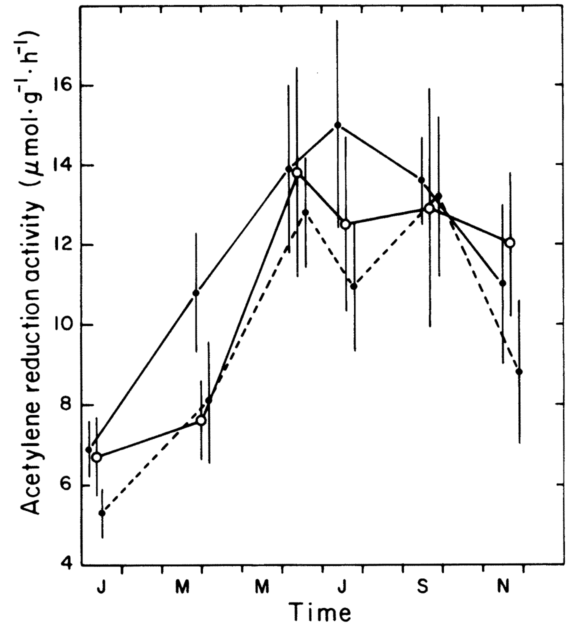

FIG. 4. Seasonal pattern of acetylene reduction activity in *Myrica faya* nodules collected in the open-canopied DT site (—●—), the partially shaded UB site (—○—), and the closed-canopy TH (— —●— —) in Hawaii Volcanoes National Park. Values are means (±SE) of 10 determinations at each time.

12 h/d, 365 d/yr). Nodule mass in the dense LB site was estimated at 39 200 g/ha based on the regressions and four fully enumerated 20 × 20 m plots; nitrogen fixation was calculated at 18.5 kg·ha^{-1}·yr^{-1}. The corresponding values in plot I of the more recently colonized UB site were 393 g/ha and 0.2 kg·ha^{-1}·yr^{-1} for nodule mass and nitrogen fixation, respectively (Tables 6, 7). The estimated nitrogen fixation at LB was reasonably close to that reported for other species of *Myrica* elsewhere—about half that for dense, nearly monospecific stands of *Myrica gale* in Massachusetts and Scotland (Sprent et al. 1978, Schwintzer et al. 1982), and greater than that for *Myrica cerifera* in the southeastern United States (Permar and Fisher 1983).

TABLE 7. Annual nitrogen inputs (kg/ha)into the UB and LB sites, Hawaii Volcanoes National Park. Values for nitrogen fixation are calculated from ARA (Table 6) as described in Results: Nitrogen Fixation by *Myrica faya* and Other Nitrogen Inputs.

Source	LB	UB
Fixation by *Myrica faya*	18.5	0.2
Native N fixation		
Lichens	.02	.06
Litter	.12	.16
Decaying wood	.05	.03
Precipitation		
NH_4-N + NO_3-N	1.0	1.0
Organic N	2.8	2.8
Total inputs	22.5	4.2

We measured the natural abundance of ^{15}N in *Myrica* and *Metrosideros* in an attempt to develop an independent estimate of the fraction of its nitrogen that *Myrica* derives from fixation (Shearer and Kohl 1986). Natural ^{15}N abundance is expressed as $\delta^{15}N$, the part-per-thousand (‰) ^{15}N excess or depletion relative to a standard. The standard is taken at the ^{15}N abundance in the atmosphere (0.3663%). In the LB site *Myrica* had $\delta^{15}N$ of −1.0‰, close to that of the atmosphere (as would be expected of a plant deriving most of its nitrogen from fixation). Most non-nitrogen fixers have positive $\delta^{15}N$, but *Metrosideros* at the LB site had −8.5‰, and a similar pattern was observed for nitrogen-fixers and non-fixers in many other sites in Hawai'i (Vitousek et al. 1989*a*). These negative values are unusual; until they are better understood, we believe that natural abundance can provide only corroborative evidence for the presence of nitrogen fixation in these sites.

Other nitrogen inputs.—The major sources of nitrogen prior to *Myrica* invasion of these sites were precipitation and nitrogen fixation; additionally, some nitrogen was transferred from buried soil horizons to the surface by deep-rooted plants. The major sources of native nitrogen fixation were the lichen *Stereocaulon*

TABLE 6. The amount of substrate and acetylene reduction activity (ARA) of *Myrica faya* and of native sources of nitrogen fixation in the UB and LB sites, Hawaii Volcanoes National Park.

	LB		UB		ARA*	
Source	$\bar{X}$	(SE)	$\bar{X}$	(SE)	$\bar{X}$	(SE)
Myrica faya nodules (g/m^2)	3.9	(.7)	0.04†		11.6	(1.1)
Lichens (mostly *Stereocaulon volcani*)						
Dense (% cover)	1	(.4)	4	(2)	3.6	(1.6)
Sparse (% cover)	32	(4)	35	(3)	0.05	(.05)
Metrosideros leaf litter (g/m^2)	406	(75)	581	(115)	16	(4)
Decaying wood (g/m^2)	206	(51)	150	(41)	12	(6)

* ARA values for *Myrica* are in μmol·g^{-1}·h^{-1} on a nodule dry-mass basis; for wood and litter in nmol·g^{-1}·d^{-1} on a dry-mass basis; for lichens in nmol·cm^{-2}·d^{-1} on a surface-area basis. On a dry-mass basis, ARA of *Stereocaulon vulcani* was 108 (14) nmol·g^{-1}·d^{-1}.

† There is no SE for nodule biomass at UB because the value was derived from a complete enumeration of a single 1-ha plot (Plot I).

vulcani, *Metrosideros* leaf litter, and decaying wood. We estimated nitrogen inputs from these sources using the same three-step process used for *Myrica*.

Measurements of the mass (or cover) and ARA of each of the major substrates in the UB and LB sites are summarized in Table 6. We determined a mean (±SE) molar ratio of ARA to $^{15}N_2$ fixed of 3.1 ± 1.0 for *Stereocaulon vulcani* and 5.4 ± 2.1 for *Metrosideros* leaf litter; we used the theoretical value of 3.0 for *Stereocaulon* and 5.5 for leaf litter. Nitrogen inputs by fixation were then calculated by assuming: (1) that the ARA : ^{15}N ratio is the same for decaying wood as for litter; and (2) that ARA was constant year-round (24 h/d for litter and wood, 12 h/d for lichens). We do not know how reasonable the first assumption is; the second overstates fixation because the ARA assays were carried out at temperatures and moisture contents at the high end of field values. ARA of lichens in particular is highly sensitive to water content (Huss-Daniel 1977). Even with this generous assumption, however, nitrogen fixation by sources other than *Myrica* adds little to overall nitrogen inputs (including precipitation) in these sites (Table 7). The lack of substantial nitrogen fixation by lichens contrasts with their importance, and that of their blue-green algae epiphytes, in other volcanic seres (Henriksson et al. 1972, Fritz-Sheridan and Portécop 1987).

Nitrate in precipitation at HAVO was measured by Harding and Miller (1982); they reported a weighted mean concentration of 20 μg/L of nitrate-N plus nitrite-N. With annual precipitation of 2400 mm, annual deposition is 0.5 $kg \cdot ha^{-1} \cdot yr^{-1}$. We determined concentrations and deposition of nitrogen in 19 precipitation samples over a 5-mo period; our weighted mean concentrations were below detection limits (10 μg/L) for nitrate-N plus nitrite-N and ammonium-N, while the weighted mean concentration of organic-N was 0.12 mg/L. These low values are characteristic of precipitation in remote areas (Galloway et al. 1982). Using Harding and Miller's nitrate-N plus nitrite-N, an ammonium/nitrate ratio of 1, and our measurements of organic N, we calculate annual nitrogen deposition of approximately 3.8 $kg \cdot ha^{-1} \cdot yr^{-1}$, >70% of it organic. Precipitation appears to have been the major natural source of nitrogen prior to *Myrica* invasion of these sites (Table 7); *Myrica* is now the largest source where it is abundant.

Effects of Myrica faya *on nitrogen availability and cycling.*—We examined the potential effects of the nitrogen fixed by *Myrica* in three ways: (1) we determined whether nitrogen actually limits primary production; (2) we evaluated whether the nitrogen fixed by *Myrica* is detectable by an increase in total soil nitrogen under *Myrica*; and (3) we determined whether the nitrogen fixed by *Myrica* is potentially available to other organisms in these ecosytems. The last of these involved several approaches, including measurements of litter decomposition and nutrient release, pool sizes of ammonium and nitrate, net nitrogen mineralization and nitrification, and plant growth in biassays.

1. *Nitrogen limitation.*—In the UB sites, mean (± SE) diameter growth of *Metrosideros* trees that had been fertilized with nitrogen was 0.33 ± 0.04 cm/yr in the 2 yr following initiation of fertilization, compared with 0.09 ± 0.01 cm/yr for unfertilized controls. The difference was highly significant ($P < .001$); nitrogen limited tree growth in this site. Factorial fertilization in the DT and TH sites demonstrated that nitrogen alone limited diameter growth of *Metrosideros* in the 1st yr following fertilization there; phosphorus and other nutrients had no main or interactive effects (Vitousek et al. 1987*b*).

2. *Effects on total soil nitrogen.*—There was significantly more total nitrogen in the forest floor plus soil under individual *Metrosideros* which were associated with large *Myrica* than under paired *Metrosideros* without *Myrica* ($P < .05$, rank test). The mean difference between the pairs was 631 ± 305 g of nitrogen. The difference reflected both higher concentrations of nitrogen and greater pool sizes of organic matter in the forest floor and soil under *Myrica–Metrosideros* pairs.

3. *Decomposition and nutrient release.*—The initial chemistry of senescent leaves of *Myrica* and *Metrosideros* differed substantially; *Myrica* had higher lignin (32% vs. 21%) and nitrogen (1.33% vs. 0.56%) concentrations and much lower cellulose (27% vs. 41%) and phosphorus (0.006% vs. 0.052%) concentrations than *Metrosideros* (Table 8). These differences reflect

TABLE 8. Retranslocation of nitrogen (N) and phosphorus (P) during senescence of *Myrica faya* and *Metrosideros polymorpha* leaves; based on mature and senescent leaves collected in the UB site, Hawaii Volcanoes National Park.

	Concentration basis (mg/g)					Leaf-area basis (g/m²)				
	Mature		Senescent		Retrans-location	Mature		Senescent		Retrans-location
	$\bar{X}$	(SE)	$\bar{X}$	(SE)	(%)	$\bar{X}$	(SE)	$\bar{X}$	(SE)	(%)
Metrosideros										
N	6.6	(.1)	5.6	(.2)	15	1.52	(.04)	1.34	(.08)	12
P	0.7	(.3)	0.52	(.04)	26	0.16	(.01)	0.12	(.02)	25
Myrica										
N	15.2	(.4)	13.3	(.5)	12	2.10	(.12)	1.88	(.14)	10
P	0.32	(.02)	0.06	(.01)	81	0.044	(.004)	0.008	(.001)	82

both the higher foliar nitrogen and lower phosphorus concentrations in live leaves of *Myrica,* and the slightly lesser retranslocation of nitrogen and much greater retranslocation of phosphorus during leaf senescence in *Myrica* (Table 8).

Tethered leaves of both *Myrica* and *Metrosideros* were placed under their own and each other's canopies. By the end of 2 yr, decomposition of *Myrica* was significantly faster than that of *Metrosideros* in both situations, and *Myrica* leaves decomposed more rapidly under *Myrica* canopies than under *Metrosideros* (Fig. 5A). Net nitrogen release from decompoising *Myrica* litter took place earlier than that from *Metrosideros*; *Metrosideros* litter immobilized nitrogen for between 18 and 24 mo, while *Myrica* litter under a *Myrica* canopy began releasing nitrogen between 6 and 12 mo (Fig. 5B). This pattern was reversed for phosphorus; *Myrica* litter immobilized substantial amounts of phosphorus early during decomposition while *Metrosideros* litter mineralized it (Fig. 5C).

These results are consistent with nitrogen being an excess resource to *Myrica.* Foliar nitrogen was retained within plants by retranslocation much less effectively than was phosphorus, and nitrogen was not immobilized within decomposing litter.

4. *Effects on available nitrogen.*—Pool sizes of available nitrogen (ammonium and nitrate) were greater under *Myrica* than under *Metrosideros* in the UB, LB, and DT sites (Table 9); the effect was significant ($P <$ .05) in DT and LB. In the recently colonized UB site there was net immobilization of nitrogen during field incubations under both species, although less under *Myrica.* However, in the LB and DT sites there was a highly significant increase in potential net nitrogen mineralization during incubation under *Myrica.*

5. *Effects on plant growth.*—Seedlings of both *Metrosideros polymorpha* and *Psidium cattleianum* accumulated more biomass when grown in soil from under *Myrica* in the UB site than when grown in soil from under *Metrosideros.* This effect was highly significant ($P <$ .01) for *Psidium* (Table 10). The relative allocation of biomass to roots was greater for both species when they were grown in soil from under *Metrosideros* (Table 10).

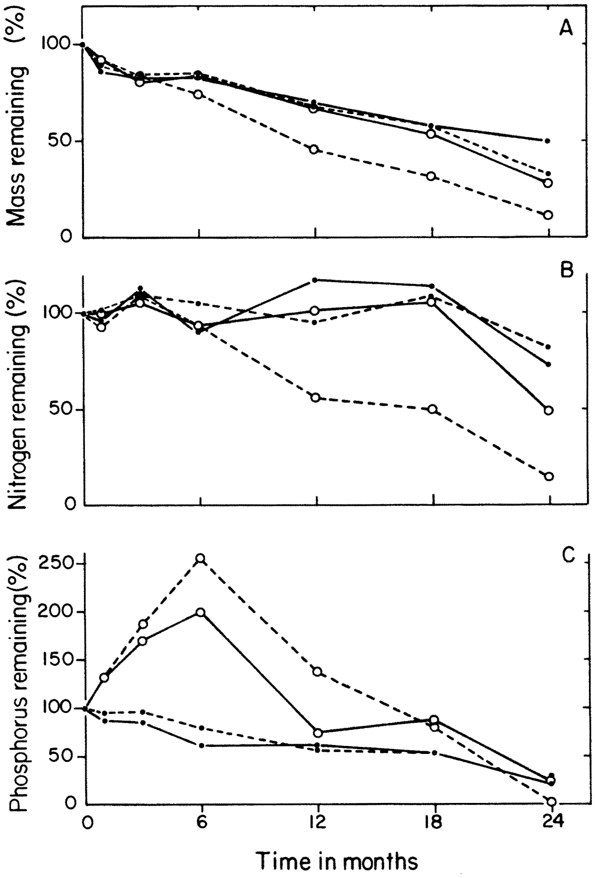

FIG. 5. Decomposition and nutrient release of senescent leaves of *Metrosideros polymorpha* and *Myrica faya* under their own and each others' canopies in the UB site, Hawaii Volanoes National Park. The initial chemical quality of the leaves is summarized in Table 8 and in Results: Decomposition and nutrient release. ●: *Metrosideros* leaves; O: *Myrica* leaves. ——: leaves of either species under *Metrosideros* canopies; – – –: those under *Myrica* canopies. (A) Percent of original mass remaining. (B) Percent of original nitrogen content remaining. (C) Percent of the original phosphorus content remaining.

DISCUSSION

In order for an exotic species to alter ecosystem-level characteristics of an area, the characteristics of the

TABLE 9. Pool sizes of ammonium- and nitrate-nitrogen and net mineralization/nitrification potentials for soils under *Myrica faya* and under *Metrosideros polymorpha* in three sites within Hawaii Volcanoes National Park. Values are in μg/g.

		Initial concentrations				14-d field incubation			
		NH_4-N		NO_3-N		Mineralization		Nitrification	
Site	Soil from	$\bar{X}$	(SE)	$\bar{X}$	(SE)	$\bar{X}$	(SE)	$\bar{X}$	(SE)
UB	*Metrosideros*	2.2	(.4)	0		−1.9	(.4)	0	
	Myrica	2.9	(.8)	0		−0.7	(1)	0	
LB	*Metrosideros*	0.6	(.2)	0		−0.3	(.2)	0	
	Myrica	2.4	(.6)	0		2.6	(2.1)	0	
DT	*Metrosideros*	1.9	(.7)	0.2	(.1)	2.8	(1.5)	0.4	(.1)
	Myrica	12.6	(4.7)	2.8	(.8)	17.6	(15.2)	4.2	(1.7)
	Open	1.1	(.5)	0.2	(.1)	1.3	(0.9)	0.3	(.2)

TABLE 10. Dry mass (g) and shoot height (cm) of *Metrosideros polymorpha* and *Psidium cattleianum* seedlings grown in the greenhouse on soil collected from under *Metrosideros* and from under *Myrica faya* in the UB site, Hawaii Volcanoes National Park. Values are those of seedlings from 12–14 pots, each with two seedlings.

		Dry mass (g/seedling)						Shoot height (cm)	
		Shoot		Root		Total			
Species	Soil source	$\bar{X}$	(SE)	$\bar{X}$	(SE)	$\bar{X}$	(SE)	$\bar{X}$	(SE)
Metrosideros polymorpha	*Myrica*	0.77	(.11)	0.22	(.04)	0.99	(.15)	9.3	(1.0)
	Metrosideros	0.55	(.04)	0.18	(.02)	0.73	(.06)	8.0	(0.8)
Psidium cattleianum	*Myrica*	0.74	(.08)	0.38	(.04)	1.12	(.12)	13.0	(0.8)
	Metrosideros	0.35	(.01)	0.23	(.01)	0.58	(.02)	8.1	(0.4)

species itself must promote colonization. Even on oceanic islands, most propagules fail to establish a breeding population (Simberloff 1986, Ehrlich 1986). In addition, the area must be invasible; every successful invasion represents an interaction of species and site (Myers 1983, Ewel 1986, Orians 1986, Crawley 1987). Finally, the invader must have the capacity to alter ecosystem-level characteristics such as productivity, hydrology, or nutrient cycling. Not every successful invader does so; many supplant native species without changing ecosytem-level properties meaningfully. We will examine each of these facets of invasion by *Myrica faya,* then discuss the ecosystem-level effects of biological invasion more generally.

What makes Myrica faya *a good invader?*—Many aspects of its biology interact to make *Myrica* capable of rapid invasion. It can be wind-pollinated, and so is not dependent on biological pollen-vectors. While nominally dioecious, almost every adult that we have examined produces both male and female flowers, so a population probably can be founded by a single colonizer. Fruit production is prolific; an average adult male produces more than 40 000 fruits/yr, while an average adult female produces more than 400 000 (Whiteaker and Gardner 1987).

Unlike many congeners (Fordham 1983), *Myrica faya* seeds do not require passage through birds to germinate (LaRosa et al. 1985, Walker, *in press*). Nonetheless, its fruits are used by a broad range of birds (Table 1), especially the exotic passerines mejiro (*Zosterops japonica*) (in our sites) and House Finch (*Carpodacus mexicanus*) (LaRosa et al. 1985, S. A. Woodward et al., *unpublished manuscript*). We have also observed the native 'oma'o (*Phaeornis obscurus*) and 'amakihi (*Hemignathus virens*) using *Myrica* fruit, but it is uncertain that *Myrica* could invade successfully with just the current native birds as vectors. Thus there may be a species interaction in which each exotic partner facilitates the other that is invading. Seed dispersal by birds is a common feature of woody exotics in Hawaii (Smith 1985) and elsewhere (Glyphis et al. 1981); bird dispersal may be particularly important to nitrogen fixers in that relatively large seed reserves may be required to establish the symbiosis.

Myrica faya grows rapidly in open-canopied sites; its diameter growth can exceed that of the native dominant *Metrosideros polymorpha* by >15:1. Moreover, the growth of *Myrica* is relatively plastic; it can grow at a wide range of light availability (Table 5) and survive at very low light. Like *Schinus terebenthifolius* in Florida (Ewel 1986), *Myrica* can persist in the understory of a closed-canopy native-dominated forest, and then grow rapidly if tree-fall or stand-level dieback (Mueller-Dombois 1987) increases light availability.

Perhaps most importantly, *Myrica* has a symbiotic association with *Frankia* with the capacity to fix atmospheric nitrogen; this ability is responsible for its rapid growth relative to that of non-fixing natives. The distribution and/or dispersal of *Frankia* (the symbiont) does not appear to limit *Myrica* colonization, although the actinorhizal symbiosis is not native to Hawaii. A similarly wide distribution of *Frankia* far from actinorhizal hosts has been observed in northern Sweden (Huss-Daniel and Frej 1986). This symbiosis is another way in which it is an interacting pair of species that is invading.

What makes these ecosystems invasible?—*Myrica faya* invades a range of sites in the Hawaiian Islands, but it is most successful in open-canopied forests where a combination of several conditions favors colonization by *Myrica.* First, there are perch trees and alternate food sources (nectar, foliage insects) for the passerine birds that are the major dispersers of *Myrica* seed. Second, the ground surface is partially shaded, allowing more successful germination and establishment of *Myrica* (Table 4). Finally, substantial light remains at ground level, allowing rapid growth and nitrogen fixation (Table 5). This combination of conditions occurs in HAVO in the seasonal submontane environment (Mueller-Dombois et al. 1981), where low rainfall prevents canopy closure by *Metrosideros,* and also in sites that have been thinned but not killed by volcanic cinder-fall (Smathers and Mueller-Dombois 1974). Additionally, human-disturbed sites with similar conditions (for example, partially tree-covered pasture) are colonized heavily by *Myrica.*

The nitrogen status of the soil may be equally important. Early primary successional ecosystems in general (Walker and Syers 1976, Robertson and Vitousek 1981, Vitousek et al. 1989*b*), and young volcanic sites in HAVO in particular (Vitousek et al. 1983, Vitousek 1987*b*), are low in available nitrogen. Nitrogen fixers would be expected to have a substantial competitive advantage in such sites (Walker and Syers 1976, Vitousek and White 1981), and indeed they are often dominant at some early stage of primary succession (Stevens and Walker 1970, Gorham et al. 1979, Reiners 1981). However, native vascular plants with symbiotic nitrogen fixers were absent from young volcanic sites in the rain-forest or seasonal submontane zones in HAVO, and a nitrogen fixer with the ability to disperse to and establish within them could therefore be expected to do well.

How does Myrica faya *change ecosystem properties?*—Three requirements must be satisfied in order to demonstrate that the nitrogen fixed by *Myrica* alters these ecosystems in a meaningful way (Vitousek et al. 1987*b*): (1) nitrogen must be a limiting resource, (2) *Myrica* must alter nitrogen inputs significantly, and (3) the nitrogen fixed by *Myrica* must become available to other organisms. All three of these can be demonstrated in open canopied sites thinned by volcanic cinder-fall. First, diameter growth of the native dominant *Metrosideros polymorpha* was more than tripled by fertilization with nitrogen (alone) in the open-canopied UB site. Other nutrients were not applied there, but a factorial experiment demonstrated that only nitrogen limited growth of *Metrosideros* in other young volcanic sites in HAVO (Vitousek et al. 1987*b*).

Second, *Myrica* increases total nitrogen inputs substantially in sites where it is abundant, adding more than four times more nitrogen than all other sources combined (Table 7). Even where colonization is in a very early stage, *Myrica* adds as much nitrogen as all other biological sources together—and its rapid population growth suggests that it will become increasingly important in the future.

Third, a number of lines of evidence demonstrate that nitrogen fixed by *Myrica* is available to other organisms. *Myrica* leaf litter contains large quantitites of nitrogen, and it decomposes and releases that nitrogen much more rapidly than does *Metrosideros* litter (Fig. 5). The availability of soil nitrogen (as indicated by pool sizes or mineralization potentials) is significantly greater under *Myrica* than *Metrosideros* (Table 9). Finally, greenhouse-grown plants in soil from under *Myrica* accumulate more biomass than those in soil from under *Metrosideros* (Table 10).

Biological consequences of ecosystem change.—A fourth component of any successful invasion that alters ecosytem properties is the physiological-, population-, and community-level response to the ecosystem-level change; such responses can then feed back to cause further changes in ecosystems. As yet, we can only speculate about these feedbacks for *Myrica* in HAVO. However, one reasonable prediction is that if *Myrica* is eventually replaced during primary succession (as are most symbiotic nitrogen-fixers elsewhere), the nitrogen fixed by *Myrica* will ultimately favor invasion by a broader range of exotic species. Sites with fertile soils are invaded more successfully by a broader range of species than are sites with infertile soils in Hawai'i (Gerrish and Mueller-Dombois 1980) and elsewhere (Bridgwater and Backshall 1981, Pickard 1984). *Myrica* increases soil fertility substantially by providing young volcanic sites with nitrogen, the one nutrient that they lack. Rapid growth by seedlings of the aggressive exotic tree, strawberry guava (*Psidium cattleianum*), in soil that had been collected under *Myrica* (Table 10), suggests one possible long-term consequence of invasion by *Myrica.*

Why were native nitrogen-fixers absent from these sites?—The successful invasion and rapid growth of *Myrica faya* in HAVO demonstates that symbiotic nitrogen fixation can be advantageous to a colonizer there. Why have native legumes not filled this role in primary succession in Hawai'i and in other seres elsewhere in which exotic nitrogen-fixers are highly successful invaders (Glyphis et al. 1981, Wheeler et al. 1987)? This question is unanswerable as stated, but we can speculate reasonably about why two widespread, native, woody legumes, *Acacia koa* and *Sophora chrysophylla,* fail to colonize the study sites despite the presence of natural populations within 5 km.

We believe that characteristics of their seeds are sufficient to explain the lack of colonizing ability by *Acacia* and *Sophora.* Both have seeds that are much larger than those of *Myrica,* neither has fleshy fruit, and both have seeds borne in pods that are large and non-edible when the seeds are mature. Although the unripe pods and seeds of *Sophora* are the major food source of the endemic passerine palila (*Loxioides bailleui*), birds do not pass intact *Sophora* seeds through their digestive system (C. van Riper, *personal communication*). Both legumes appear to be dispersed primarily by gravity and secondarily by water; neither has a mechanism for longer distance dispersal into newly created sites, although both grow rapidly when planted into open-canopied rainforest sites on young volcanic cinder. Given these characteristics, it is not clear to us how *Acacia* and *Sophora* dispersed naturally to Hawai'i and to many other Pacific islands.

BIOLOGICAL INVASION AND ECOSYSTEM PROCESSES

We have demonstrated that invasion by *Myrica faya* can alter ecosystem-level properties in volcanic sites in Hawai'i. This ability is not unique to *Myrica* or to Hawai'i; it is equally clear that exotic pigs (*Sus scrofa*) alter nutrient cycling and/or loss in otherwise-undisturbed ecosystems in the Great Smoky Mountains National Park (Singer et al. 1984) and Hawai'i (Vitousek 1986), and that feral goats (*Capra hircus*) affect soil erosion in Hawai'i and elsewhere (Stone 1985, Stone et al., *in press*). There is also evidence that exotic saltcedars (*Tamarix* spp.) alter water budgets in the semiarid southwestern United States (Neill 1983), as does *Andropogon virginicus* in Hawai'i (Mueller-Dombois 1973); that the ice-plant (*Mesembryanthemum crystallinum*) decreases soil fertility in California and Australia (Vivrette and Muller 1977, Kloot 1983); that the exotic nitrogen-fixers *Acacia cyclops* and *Acacia selignathus* alter soils in South African fynbos (Witkowski and Mitchell 1987); and that a variety of exotic species affect fire frequency in many areas (Parsons 1972, Smith 1985, van Wilgen and Richardson 1985).

Vitousek (*in press*) suggested that there are at least three means by which exotic species can alter ecosystems—invaders can cause changes in overall resource availability, in the trophic structure of an area, or in disturbance frequency or intensity. *Myrica faya* is an example of the first of these; exotic nitrogen-fixing *Acacia* in South Africa (Glyphis et al. 1981) and Scotch broom (*Cytisus scoparius*) in the northwestern United States (Wheeler et al. 1987) may be as well. Lampreys (*Petromyzon marinus*) in Lake Superior (Avon and Smith 1971, Kitchell and Carpenter 1987), goats in Hawai'i, and introduced predators in New Zealand (King 1984), are examples of the second, while fire-enhancing and fire-responsive exotic C_4 grasses exemplify the third (Smith 1985). Feral pigs in Hawai'i and elsewhere are agents of both trophic alteration and disturbance.

Where biological invasions alter ecosystem-level characteristics, they represent an unambiguous demonstration that the properties of individual species matter at the level of whole ecosystems. Moreover, such invasions offer the raw material with which to integrate the methods and approaches of population biology and ecosystem studies directly. In such cases population processes are integral to ecosystem processes, and it should be possible to trace the factors affecting ecosystem-level dynamics from the demography of individual species to whole-system characteristics such as nutrient cycling and back to populations again.

An understanding of biological invasions that change ecosystem-level properties also could be useful in the field of conservation biology. Species that alter ecosystems change the ground rules of existence for all of the organisms in an area; they are therefore worth more intensive management effort than most other species (MacDonald et al., *in press*). This problem is particularly important in parks and preserves on oceanic islands (Loope, *in press*, Loope and Mueller-Dombois, *in press*), but the effects of pigs in the Great Smoky Mountains National Park (Singer et al. 1984) and saltcedar in Death Valley National Monument (Neill 1983) demonstrate that the phenomenon is not unique to islands.

CONCLUSIONS

1) Invasion by the exotic nitrogen-fixer *Myrica faya* is promoted by its prolific seed production, effective dispersal by exotic birds, and rapid growth rates.

2) *Myrica* preferentially invades open-canopied sites in Hawaii Volcanoes National Park; these sites are colonized due to their combination of perch trees for birds, suitable sites for germination and establishment, and relatively high light levels at the ground surface.

3) Nitrogen is limiting to primary production in young volcanic sites in Hawai'i.

4) In sites where it is abundant, *Myrica* fixes >four times more nitrogen annually than is added by all other sources. Moreover, *Myrica* increases the overall biological availability of nitrogen in the stands it invades.

5) Biological invasions that alter ecosystems represent unambiguous evidence that population-level processes can control ecosystem-level properties and processes. They can thereby provide the raw material for integration of the techniques and approaches of population biology and ecosystem studies.

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