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Nodule Biomass of the Nitrogen-Fixing Alien *Myrica faya* Ait. In Hawaii Volcanoes National Park[1]

DOUGLAS R. TURNER AND PETER M. VITOUSEK[2]

ABSTRACT: *Myrica faya* forms a nitrogen-fixing symbiosis in which fixation takes place in specialized root nodules. The biomass of these nodules was greater in open-grown than shaded individuals of *Myrica faya*, and was greater in large than small individuals. All *Myrica faya* examined, including seedlings and those growing epiphytically, had active nodules. Nitrogen fixation by invading *Myrica faya* could alter patterns of primary succession in Hawaii Volcanoes National Park.

Myrica faya AIT. IS AN AGGRESSIVE INVADER of most of the major Hawaiian Islands (Whiteaker and Gardner 1985). It grows rapidly, forms dense, nearly monospecific stands, and can reach 20 m in height (Smathers and Gardner 1979). *Myrica faya* represents a particularly serious problem because it forms a symbiotic association with the nitrogen-fixing actinomycete *Frankia* (Miguel and Rodrigues-Barrueco 1974, Mian et al. 1976) and hence can use nitrogen from the atmosphere rather than the soil. This symbiosis, unlike the better known legume-*Rhizobium* association, apparently was absent from the native Hawaiian flora. *Myrica faya* is considered one of the worst weeds in Hawai'i (Smith 1985) because of its ability to fix nitrogen and its potential to form monospecific stands.

Myrica faya invaded the Hawaii Volcanoes National Park (HAVO) in 1961 (Doty and Mueller-Dombois 1966). By 1978, its range was 600 ha despite strenuous control efforts. Shortly thereafter, park-wide control was abandoned, and *Myrica faya* had occupied 12,000 ha by 1985 and was still expanding (Whiteaker and Gardner 1985). Populations of *Myrica faya* are densest in open seasonal montane forests and pastures, but they are found in the understory of closed *Metrosideros polymorpha* forests, in stands damaged by volcanic ash, and in the open in volcanic ash deposits as young as 10–12 years.

The nitrogen-fixing potential of the *Myrica*/*Frankia* symbiosis is of particular concern in HAVO because young volcanic soils are very low in available nitrogen (Vitousek et al. 1983, Balakrishnan and Mueller-Dombois 1983). Invasion by *Myrica faya* could supplement the slow accumulation of nitrogen from rainfall and nonsymbiotic fixation with more rapid symbiotic fixation. Since susceptibility to invasion of Hawaiian ecosystems is dependent in part on soil fertility (Gerrish and Mueller-Dombois 1980), *Myrica faya* could therefore affect both the productivity and the possibility of further invasions of HAVO ecosystems.

We collected descriptive information on the presence and distribution of nitrogen-fixing root nodules on *Myrica faya* in HAVO and quantitative information on nodule biomass. *Myrica faya* root systems were harvested from plants in three areas–open, partially shaded, and under a *Metrosideros-Cibotium* canopy. The results of the harvests were used to develop regressions relating nodule biomass to basal area of individuals of *Myrica faya*.

STUDY SITES

All study sites were at 1150–1250 m elevation in HAVO, near the summit of Kilauea Volcano on the island of Hawai'i. Mean annual temperature is 17°C, and mean annual precipitation near 2000 mm.

[1] Manuscript accepted February 1987.
[2] Department of Biological Sciences, Stanford University, Stanford, California 94305.

The open site (site #1) is located in Devastation Area, a deep deposit of volcanic cinder resulting from a 1959 eruption of Kilauea Iki Crater. The site is now sparsely colonized by *Metrosideros polymorpha*, *Myrica faya*, and several other native and exotic woody plants; community composition has been sampled repeatedly since the 1960's (Smathers and Mueller-Dombois 1974, Wright 1985).

Adjacent to Devastation Area, much of the *Metrosideros*-dominated forest survived shallower deposits (< 2 m) of cinder in 1959. This area (site #2) is now an open-canopied *Metrosideros* forest, with rapid colonization of *Myrica faya* occurring under and at the edge of *Metrosideros* crowns. Areas of bare cinder remain, and most of the colonizing *Myrica faya* receive some full sunlight each day.

The third site (site #3) is located within a *Metrosideros/Cibotium* forest developed on a 1790 ash deposit near Thurston lava tube. *Myrica faya* is present as scattered individuals in the forest understory; occasional larger individuals reach into the subcanopy.

METHODS

Myrica faya growth form, root systems, and nodules were examined in all of the sites to develop an understanding of ranges of variation. Six or seven individuals were then selected to represent a size range in each site, and diameter and height (of each stem for multiple-stemmed individuals) were recorded. Root systems were then excavated using trowels and spoons; digging usually progressed from the basal area outward, following roots to their branched and numerous tips. Clusters of nodules were removed as they were encountered and stored in polyethylene bags. When a complete root had been unearthed, it was removed to allow access to deeper roots. Nodules were washed in the laboratory, sorted carefully to remove roots and debris, and washed again. Functional nodules were identified by their light-brown to brown color and the presence of vascular connections to roots; dark, dry or partially decomposed nodules did not reduce acetylene effectively and were discarded. The active nodules were dried at 70°C for 72 hours and then weighed. Approximately 100 person-hours were required to harvest and sort the nodules from each of the largest *Myrica faya* sampled.

RESULTS AND DISCUSSION

We observed *Myrica faya* rooting in bare volcanic cinder and in organic soils, establishing in cracks in old pahoehoe lava with a thin veneer of ash, and perched on decaying trunks or epiphytically on the tree fern *Cibotium chamissoi*. Nodules were present on all of the individuals examined, including seedlings < 2 cm tall and epiphytes on *Cibotium* (in which nodules occurred within the outer fibrous trunk of the tree fern). We found nodules up to 13 m away from the base of a tree, and up to 2.2 m deep. Masses of branched nodules up to 15 × 8 cm in size were found, although most clusters ranged from < .5 × .5 cm to 3 × 3 cm. All of the nodules tested actively reduced acetylene to ethylene, indicating the presence of the nitrogen-fixing nitrogenase enzyme system.

The aboveground growth form of *Myrica faya* varied among the sites. Individuals from the forest understory (site 3) were taller in proportion to their diameter (Figure 1) and less branched than open-grown individuals. Below-ground growth forms also differed; roots in the forest understory were noticeably sparser and appeared randomly distributed. In the open and partially shaded sites, *Myrica faya* roots grew and proliferated more actively in the organic-rich soil under plant canopies than in areas of bare cinder. Many roots grew into the organic mat surrounding the trunk of adjacent individuals of *Metrosideros polymorpha*, and some were appressed against the *Metrosideros* trunk. One or two roots of the two largest open-grown individuals reached the previous soil surface, which was buried under more than 2 m of 1959 cinder.

Masses of nodules on different-sized individuals are summarized in Figure 2. For a given basal area, nodule biomass was greater in the open-grown (site 1) than in the partially shaded individuals (site 2), which in turn was greater than under closed canopies (site 3).

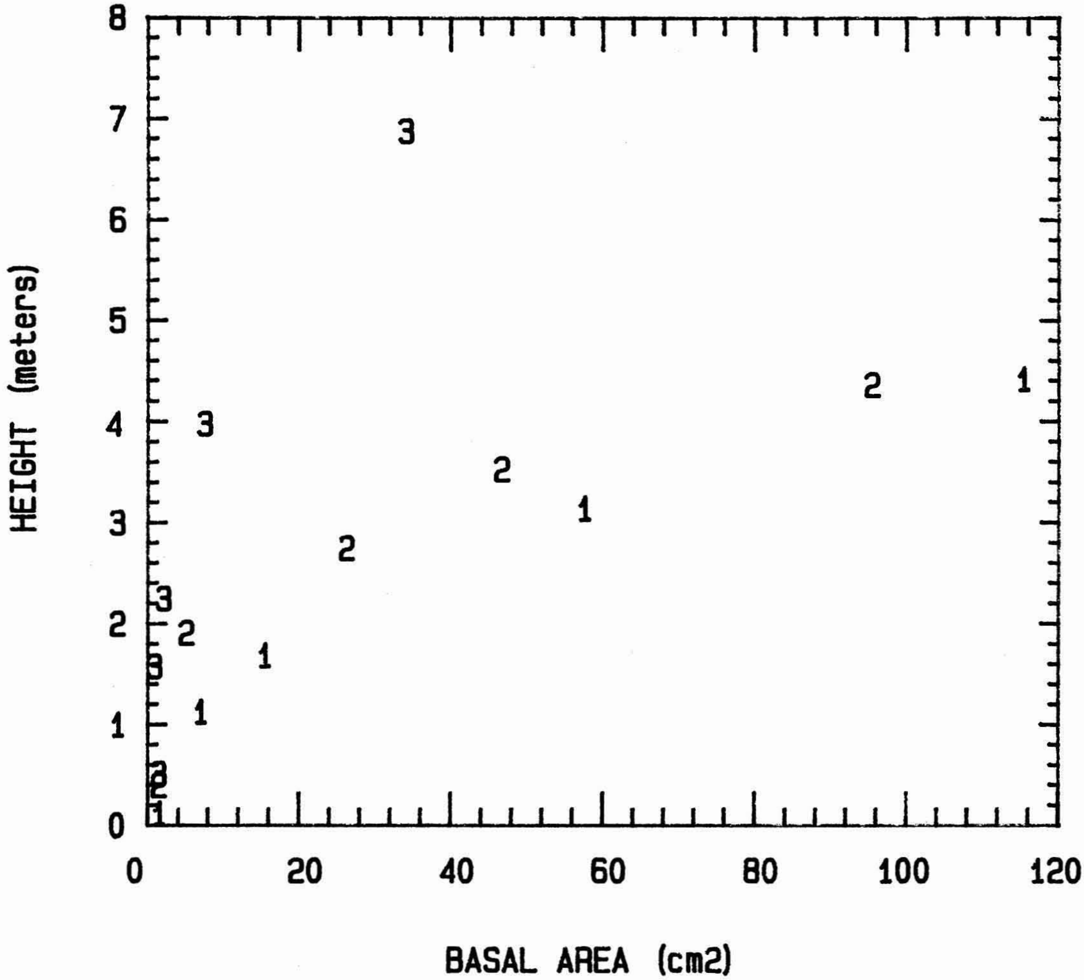

FIGURE 1. Diameter versus height of *Myrica faya* stems grown in the open ("1"), under partial shade ("2"), and under a closed forest canopy ("3").

The relationship between nodule mass and basal area was asymptotic in sites 1 and 2 but linear in site 3. Non-linear regressions of the form

$$Y = \frac{A}{1 + B_1 e^{-B_2 x}}$$

where x is basal area in cm^2, B_1 and B_2 coefficients, A the asymptote, and Y nodule biomass in grams, were fit to the results from site 1 and 2; linear regression was used in site 3 (slope = .33). B_1 and B_2 for site 1 were 27.5 and 0.18, and for site 2 were 58.4 and 0.16 respectively. The proportion of variation explained by the regressions was .99, .94, and .99 in sites 1, 2, and 3 respectively.

The association between canopy cover and nodule biomass reported here (Figure 2) has been observed in other studies of *Frankia*-nodulated plants (Binkley 1981, Bormann and Gordon 1984). This association could be caused by greater energy availability for N_2 fixation in the open-grown plants, or alternatively by slower growth and hence lower demand for fixed nitrogen in shaded plants.

We did not anticipate the strongly asymptotic nature of the relationship between basal

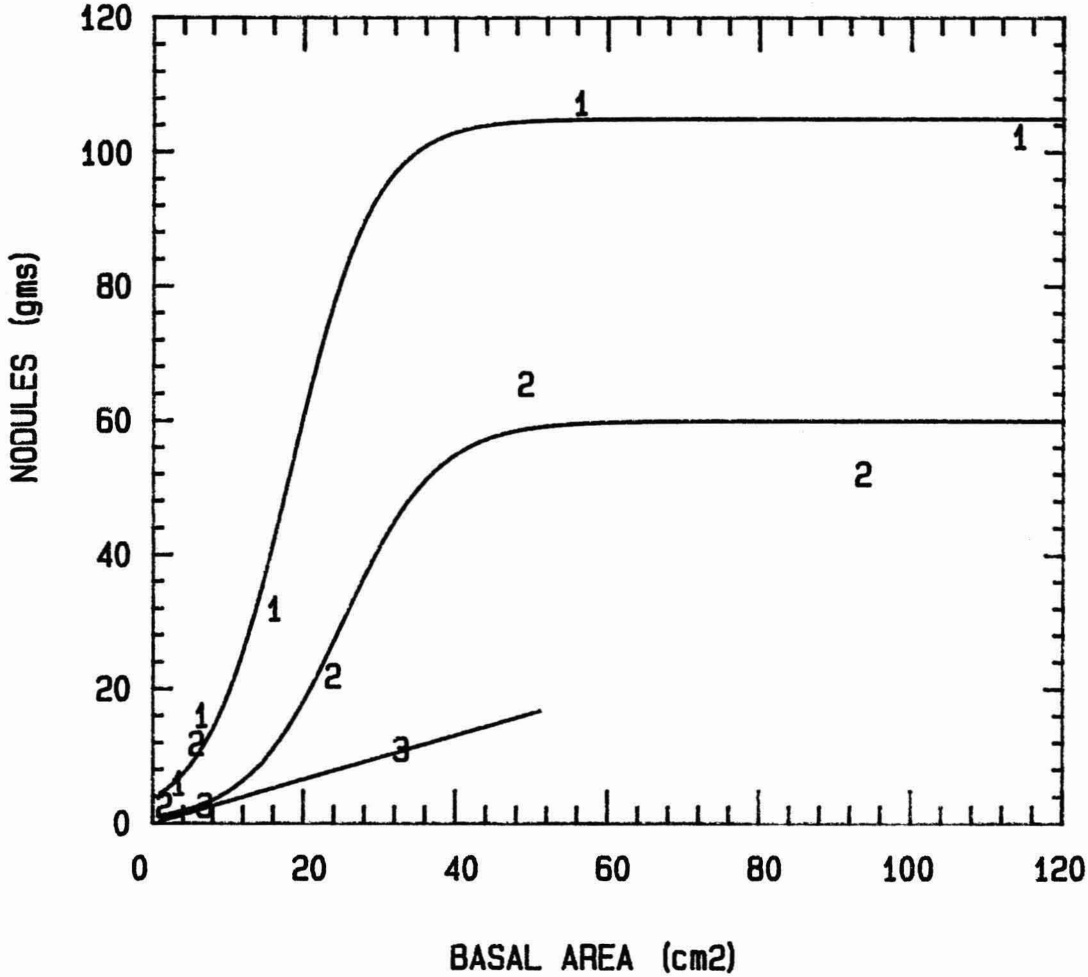

FIGURE 2. Basal area of *Myrica faya* (cm^2) versus nodule biomass in grams. Lines are least-squares regressions (see text). Trees were sampled in the open ("1"), under partial shade ("2"), and under closed forest canopy ("3").

area and nodule biomass in sites 1 and 2. We see three possible causes for the relatively small nodule mass in the largest individuals. First, Smathers and Gardner (1979) identified an inverse correlation between stem diameter and vigor of *Myrica faya*. Second, the availability of fixed nitrogen is elevated in the soil beneath large individuals of *Myrica faya* (P. A. Matson, personal communication), so perhaps they require that less nitrogen be provided by energetically costly nitrogen fixation. Finally, the large individuals may have slower relative growth rates, and hence relatively lower demands for nitrogen.

Overall, the information summarized here demonstrates that invasion by *Myrica faya* could represent a substantial perturbation to primary succession in Hawaii Volcanoes National Park. If *Myrica faya* nodules fix only 1 μM N_2/g/hr (a low rate for the *Frankia* symbiosis), then a single partially-shaded individual could fix 14 g/yr. Populations of *Myrica faya* in a partially-shaded site adjacent to the Devastation Area are approximately 1100 individuals per hectare (Whiteaker, personal communication), representing potential nitrogen fixation of 15 kg/ha/yr. This additional nitrogen represents a substantial modification to primary succession on these nitrogen-deficient young volcanic soils.

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