Understory Succession Following a Dieback of *Myrica faya* in Hawai'i Volcanoes National Park[1]

PETER B. ADLER,[2] CARLA M. D'ANTONIO,[2] AND J. TIMOTHY TUNISON[3]

ABSTRACT: Studies of invasion by the introduced nitrogen-fixing tree *Myrica faya* Aiton in Hawai'i Volcanoes National Park have led to predictions that the nitrogen-rich soil *M. faya* creates will promote invasion by nonindigenous plant species. An insect-caused dieback of *M. faya* that began in the late 1980s provides an opportunity to test this hypothesis. We compared percentage cover and density of all plant species under live and dead *M. faya*, as well as total nitrogen in soil and plant tissue. Mean percentage cover of four common species increased significantly, and no species decreased in cover after dieback. Cover of native shrubs and herbs increased from 4.8 to 15.2%, largely due to the spread of *Carex wahuensis* C.A. Mey, and introduced grasses increased from 2.3 to 14.1%. Density of native shrubs did not differ beneath live and dead *M. faya*, but immature introduced grass individuals were significantly more numerous beneath dead *M. faya*. We found no differences in total nitrogen in soil or plant tissue collected beneath live versus dead *M. faya*. Beneath dead *M. faya*, cover of *C. wahuensis* increased with total soil N, and introduced grass cover decreased. This surprising result may be the legacy of shading effects from the live *M. faya* canopies, for which total soil N may be an indicator. Success of grass seedlings compared with failure of native shrubs to recruit from seed suggests that dieback promotes nonnative grass species. Replacement of *M. faya* with introduced grasses may greatly increase fire risk.

NITROGEN-FIXING PLANTS can increase total and available nitrogen in an ecosystem (e.g., Vitousek et al. 1987, Witkowski 1991). Elevated nitrogen levels may cause changes in community composition and, ultimately, in successional pathways. Specifically, nutrient enrichment may favor invasive introduced plants, many of which are capable of responding to high nutrient status with rapid growth (Maron and Connors 1996). Studies of artificial fertilization and atmospheric nitrogen deposition have shown that an increase in nutrients often lowers plant species richness (e.g., Goldberg and Miller 1990, Huenneke et al. 1990, Hobbs and Huenneke 1992). Two studies report increased invasion by introduced earthworms in sites dominated by introduced nitrogen-fixing plants (Aplet 1990, Zou 1993). Yet until recently, no example existed of a plant invasion facilitated by nitrogen elevated as a result of fixation.

Recently, Maron and Connors (1996) directly linked nitrogen fixed by a native bush lupine (*Lupinus arboreus* Sims.) to decreases in plant species diversity in a California coastal prairie. After germination, lupine plants grow rapidly, suppressing vegetation under their dense canopies. When insect herbivory kills the lupine after a few years, a nitrogen-rich opening is created. One growing season after lupine death, 57% fewer native species grew on the dead lupine sites compared with surrounding grassland. Repeated cycles of lupine establishment and mortality

[2] Department of Integrative Biology, University of California, Berkeley, California 94720 (direct correspondence to Carla D'Antonio).
[3] Resources Management, P.O. Box 52, Hawai'i Volcanoes National Park, Hawai'i 96718.

create high-productivity, low-diversity sites dominated by weedy introduced annual plants (Maron and Connors 1996).

In Hawai'i Volcanoes National Park on the island of Hawai'i, the introduced nitrogen-fixing tree *Myrica faya* Aiton fixes four times more nitrogen than all existing sources combined in the sites it invades (Vitousek et al. 1987, Vitousek and Walker 1989). *Myrica faya* invades wildland plant communities on young lava flows that are low in available and total nitrogen, leading Vitousek and Walker (1989) to make the prediction that if *M. faya* is eventually replaced during primary succession (as are most symbiotic nitrogen fixers elsewhere), the nitrogen that it has fixed will favor invasion by a broader range of nonindigenous species. Because *M. faya* tree canopies suppress almost all understory species (Tunison et al. in press *b*), the trees must senesce before invasion can occur (Walker and Vitousek 1991). Likewise, Maron and Connors (1996) found that live lupines suppressed all understory species, and introduced grasses and forbs responded most effectively to elevated nitrogen after lupine mortality.

Previous studies have not demonstrated conclusively that introduced species gain an advantage over native species as a result of *M. faya* invasion. In comparisons of understory composition beneath isolated *Metrosideros polymorpha* Gaud. and live *Metrosideros/M. faya* pairs in an open dryland forest and a shrubland, cover of introduced grasses was two-fold lower beneath *M. faya* compared with *Metrosideros,* and native shrub density decreased three-fold. Native herb cover did not differ significantly between treatments, and the cover of one native sedge was actually higher under *M. faya* than under *Metrosideros* alone (Tunison et al. in press *b*). Understory suppression of both native and introduced species also occurs in a range of much wetter communities that *M. faya* has invaded successfully (Tunison and Loh in press). One community classification approach found no preferential association of introduced plant species with *M. faya* on another young volcanic surface in Hawai'i (Mueller-Dombois and Whiteaker 1990), but

a second classification study found a positive association of *M. faya* with four other species (Aplet et al. 1991). Finally, Aplet et al. (in press) reported increased numbers of introduced species in patches formerly occupied by *M. faya* only after trees were manually killed and physically removed from the sites. Killing the trees and leaving them standing did not result in increases in introduced species. Other studies have focused on competitive effects of *M. faya,* such as changes in *Metrosideros* germination and productivity in the presence of *M. faya,* rather than succession (Walker and Vitousek 1991, Vitousek and Walker 1989).

In 1988, the introduced leafhopper *Sophonia rufofascia* (Kuoh & Kuoh) began causing *M. faya* dieback (Yang et al. in press). Tree mortality is extensive, and over 1000 ha of woodland, previously heavily invaded by *M. faya,* contains stands of dead and decaying *M. faya* trees. Dieback is concentrated in the seasonal submontane zone of Hawai'i Volcanoes National Park and radiates out from a central area of severe dieback where more than 80% of trees are dead. When dieback occurs, ecosystem nitrogen inputs decline: *M. faya* litter begins releasing nitrogen after 6 to 12 months, and 85 to 90% of the nitrogen is released within 2 yr (Vitousek and Walker 1989). Available nitrogen may remain elevated for years, but we do not know how much nitrogen will stay in the cycling pool. This dieback offers the opportunity to examine the hypothesis that nitrogen fixed by *M. faya* favors the invasion of these ecosystems by a "wide range of exotic species" (Vitousek and Walker 1989).

In seasonally dry habitats in Hawai'i, introduced C_4 grasses have become a substantial component of the understory vegetation. *Schizachyrium condensatum* (Kunth) Nees and *Andropogon virginicus* L., both grasses from the mainland Americas, are already well established in sites invaded by *M. faya,* although Aplet et al. (1991) found both species to be negatively associated with *M. faya.* We suspect that this association is the result of the very low light levels in mature stands of *M. faya* (C. Lipp, unpubl. data) but that these grasses may benefit from *M. faya*

dieback and eventual decay. In unburned woodland in the absence of *M. faya*, introduced grasses can reduce the growth of native woody species (C.M.D., Hughes, Mack, Hitchcock, and Vitousek, unpubl. data). But the most dramatic effect of grass invasion is the positive feedback cycle between grass and fire: these grasses promote fire (Smith and Tunison 1992), recover quickly from it, and substantially reduce light availability, thereby inhibiting shrub reestablishment (Hughes and Vitousek 1992).

This paper specifically addresses the impact of *M. faya* dieback on understory composition in an area where propagules of both introduced and native species are abundant. We attempted to determine whether the *M. faya* dieback is promoting introduced species rather than native species, and we discuss the importance of nitrogen fixed by now dead *M. faya* in potentially causing species change.

Study Area

The study area is located at 980 m elevation in the seasonal submontane zone of Hawai'i Volcanoes National Park on the island of Hawai'i, within the central area of *M. faya* dieback (Tunison et al. in press *a*). It is bounded on the west and east by the Hilina Pali Road and 'Āinahou Ranch, respectively, and on the south by Kalanaokuaiki Pali. The 250- to 350-yr-old Koko'olau pāhoehoe lava flows form the substrate, overlain by cinder and ash soils ranging from under 10 to over 30 cm in depth, with outcroppings of exposed pāhoehoe. Annual rainfall totals approximately 2000 mm/yr, with typically dry summers. *Metrosideros polymorpha* ('ōhi'a) trees form a discontinuous canopy 5 to 10 m high. *Dodonaea viscosa* Jacq. ('a'ali'i) and *Styphelia tameiameiae* (Cham. & Schlechtend) Muell. (pūkiawe) compose the shrub layer, with occasional *Osteomeles anthyllidyfolia* (Sm.) Lindl., *Vaccinium reticulatum* Sm., *Dubautia cilioata* (DC) D. Keck, and *Wikstroemia phillyreifolia* A. Gray. The most common native herb is *Carex wahuensis* C.A. Mey followed by *Machaerina angustifolia* (Gaud.) Koyama. A nearly continuous layer of the introduced grasses *Andropogon vir-* *ginicus* (broomsedge) and *Schizachyrium condensatum* (beardgrass) fills the spaces between shrub and *M. faya* canopies. *Myrica faya*, scattered and in groups, grows to 7 m. The first signs of *M. faya* dieback appeared in early 1988, and by 1993 an 80-ha area of severe dieback (80% of trees dead) was surrounded by over 1000 ha with progressively lower mortality (Tunison et al. in press *a*).

MATERIALS AND METHODS

From a randomly chosen point near the center of the dieback in an area with approximately 60% *M. faya* mortality, transects were walked in the cardinal directions. Plots were established under 27 live and 27 dead *M. faya* trees (one plot per tree) meeting the following criteria, in the order they were encountered: sampled trees had to have a canopy large enough to cover one 2 m by 2 m square plot, no unusual geologic features such as cracks or pāhoehoe tumuli, and an adjacent reproductively mature *Metrosideros* at least 4 m tall. The live *M. faya* sampled had no more than 10% leaf loss, whereas dead trees were totally defoliated and had been dead between 4 and 6 yr.

In each 2 m by 2 m plot, percentage cover of all species was estimated using a modified line intercept as in Tunsion et al. (in press *b*). PVC pipes, 2 m long and 1.6 cm diameter, marked at 5-cm intervals, were placed at ground level beneath the low-growing *M. faya* branches, and the distance along the transect occupied by each species <20 cm high was recorded and converted into percentage cover. To analyze the spatial distribution of the understory, cover also was recorded in 3-cm intervals along one 150-cm transect extending outward from the base of each *M. faya* trunk along a random azimuth. Also all woody plants within each plot were counted and recorded in four height classes (0–10, 10–50, 50–100, and >100 cm). Immature grasses, defined as any individual without an inflorescence, were also censused.

With a 0.6-cm steel rod/soil probe, three soil depth measurements were taken at random locations within each plot. We also

measured basal diameters for all *M. faya* stems belonging to the study tree. Basal diameters were converted to basal areas and then summed for each plot. Although we did not create a decay index, partial to complete collapse of sampled dead *M. faya* was noted where present.

Two soil cores 5 cm wide by 10 cm deep were taken within each plot, and the soil was sieved through a 2-mm mesh, dried, and ground for analysis of total nitrogen. Mature leaves from *C. wahuensis, S. condensatum,* and *D. viscosa* were collected from beneath live and dead *M. faya* and the location of the sample relative to the trunk of the *M. faya* was recorded. The plant tissue was dried at 70°C, ground to a fine powder, and, along with the soil samples, analyzed for total carbon and nitrogen in a Fisons NA1500.

Student's *t*-tests were performed to compare mean percentage cover and plant density between live and dead *M. faya* plots, as well as mean soil depth and total nitrogen. Model I analysis of variance (ANOVA) was used to analyze the effect of distance from *M. faya* on percentage cover. Least-squares regression was used to show relationships between total soil nitrogen and vegetation cover. All results are significant at $P < .05$, unless otherwise noted.

RESULTS

Cover

Carex wahuensis, D. viscosa, A. virginicus, and *S. condensatum* all increased in mean percentage cover under dead *Myrica faya* trees (Table 1). These four species composed 74% of total cover under live *M. faya* and 91% under dead *M. faya.* Mean native vegetation increased from 4.8 to 15.2%, more than two-thirds of which was accounted for by *C. wahuensis.* Introduced grasses increased from 2.3 to 14.1%.

Cover was not distributed uniformly but depended on distance from the *M. faya* bole. Under live *M. faya,* cover of *D. viscosa, S. tameiameiae,* and *S. condensatum* was lowest

TABLE 1

PERCENTAGE COVER OF VEGETATION UNDER LIVE AND DEAD *Myrica faya*

| | LIVE | | DEAD | | |
SPECIES	MEAN	SE	MEAN	SE	P^a
Carex wahuensis	3.0	0.7	10.6	1.6	**
Dodonaea viscosa	0.3	0.1	2.0	0.4	**
Elaphoglossum sp.	0.0	0.0	0.0	0.0	
Machaerina angustifolia	0.4	0.2	0.1	0.1	
Metrosideros polymorpha	0.5	0.2	0.6	0.2	
Styphelia tameiameiae	1.1	0.3	1.8	0.3	
Vaccinium reticulatum	0.0	0.0	0.0	0.0	
Total native cover	4.8	0.8	15.2	1.4	**
Andropogon virginicus	1.0	0.3	5.5	1.3	*
Schizachyrium condensatum	1.3	0.3	8.6	1.6	**
Total alien grass cover	2.3	0.4	14.1	2.4	**
Total cover	7.2	0.9	29.3	2.5	**

^{a}Using Student's *t*-test: *, $P < .05$; **, $P < .01$; $n = 27$.

closest to the *M. faya* base and highest farther from the base (Table 2). This pattern was not apparent beneath dead *M. faya.* It is worth noting that the distribution of *C. wahuensis* showed a trend toward the opposite gradient: under dead trees cover was higher near the bole of the tree, and under live trees cover was evenly distributed.

Soil depth was not associated with changes in cover or density of any plant species. The extent of decay of the dead *M. faya* trees, as assessed by comparing the average cover under completely collapsed versus standing dead trees, also had no effect on understory plant cover or density.

Density

Overall, densities of woody plants in our plots were very low and there were no differences in woody plant densities between live and dead *M. faya* plots (Table 3). The density of immature introduced grasses, however, was significantly higher under dead than under live *M. faya. Andropogon virginicus* increased from 0.2 to 1.6 plants per plot, and *S. condensatum* increased more dramatically, from 0.2 to 3.3 plants per plot

TABLE 2

CHANGES IN PERCENTAGE COVER WITH DISTANCE FROM THE BASE OF LIVE AND DEAD *Myrica faya* TREES

M. faya	A. virginicus	S. condensatum	C. wahuensis	D. viscosa	S. tameiameiae
Alive					
0–50 cm	0.2a	0.4a	4.4a	0.0a	0.6a
50–100 cm	0.5a	2.1ab	4.4a	0.1a	0.6a
100–150 cm	1.0a	6.4b	3.3a	1.3b	3.8b
Dead					
0–50 cm	6.2a	8.9a	13.5a	0.7a	2.9a
50–100 cm	9.0a	14.7a	7.0a	2.3a	3.0a
100–150 cm	11.7a	2.0a	6.0a	1.9a	4.0a

NOTE: Means that share the same letter do not differ significantly, using Tukey post hoc comparisons ($P < 0.10$). Comparisons are within live and within dead across distance classes but not between live and dead.

TABLE 3

NATIVE WOODY PLANT DENSITY (PER 4-m^2 PLOT) UNDER LIVE AND DEAD *Myrica faya*

SPECIES	LIVE		DEAD	
	MEAN	SE	MEAN	SE
Dodonaea viscosa				
<10 cm	0.0	0.0	0.1	0.1
10–50 cm	0.0	0.0	0.2	0.1
50–100 cm	0.1	0.1	0.2	0.1
>100 cm	0.3	0.1	0.1	0.1
Subtotal	0.4	0.1	0.5	0.1
Metrosideros polymorpha				
<10 cm	0.0	0.0	0.0	0.0
10–50 cm	0.0	0.0	0.0	0.0
50–100 cm	0.1	0.1	0.0	0.0
>100 cm	0.3	0.2	0.1	0.1
Subtotal	0.4	0.2	0.1	0.1
Styphelia tameiameiae				
<10 cm	0.0	0.0	0.1	0.1
10–50 cm	0.3	0.1	0.5	0.2
50–100 cm	0.9	0.2	0.9	0.2
>100 cm	1.2	0.2	0.7	0.2
Subtotal	2.4	0.3	2.1	0.4
Vaccinium reticulatum				
<10 cm	0.0	0.0	0.0	0.0
10–50 cm	0.1	0.1	0.3	0.1
50–100 cm	0.0	0.0	0.1	0.1
>100 cm	0.0	0.0	0.0	0.0
Subtotal	0.2	0.1	0.3	0.2
Total density	3.0	0.4	3.0	0.5

NOTE: None significant at $P < .05$ using Student's t-test; $n = 27$.

($P < .01$). Small plants, less than 50 cm, were more numerous beneath dead than live *M. faya*, but the density of larger individuals did not differ significantly.

Total Nitrogen

A range in percentage N in soil was found and there was no significant difference between soil from under live versus dead *M. faya* trees. Amount of plant tissue N also did not differ between individuals collected from under live versus dead trees for any of the species tested (Table 4). However, the levels of tissue nitrogen were quite high (>1%) compared with those from a nearby submontane site with very little *M. faya* where values are typically 0.2 to 0.3% lower (C.M.D., unpubl. data). Within the dead treatment, soil N was weakly associated with *M. faya* stem basal area (slope = 3.82, $R^2 = 0.13$, $P = .067$). Multiple regression showed soil N to be a better predictor of both *C. wahuensis* and introduced grass cover under dead *M. faya* ($P = 0.033$ and 0.062, respectively) than stem basal area ($P = 0.156$ for *C. wahuensis* and 0.356 for grass). Univariate regression using soil N alone (Figure 1) showed that *C. wahuensis* cover increased with soil N (slope = 15.0, $R^2 = 0.25$, $P = .009$), and grass cover decreased (slope = -8.8, $R^2 = 0.10$, $P = .110$). Percentage N in *C. wahuensis* tissue from beneath dead *M. faya* increased weakly but significantly with

TABLE 4

PERCENTAGE C AND N (BY WEIGHT) FROM SOIL AND PLANT TISSUE COLLECTED UNDER LIVE AND DEAD *M. faya* TREES

COLLECTION SITE	TREATMENT	C		N		C:N	
		MEAN	SE	MEAN	SE	MEAN	SE
Soil	Dead	7.37	0.79	0.41	0.05	18.11	0.57
	Live	6.79	0.58	0.36	0.03	19.28	0.65
C. wahuensis	Dead	44.70	0.34	1.15	0.06	40.21	2.50
	Live	44.37	0.26	1.21	0.08	37.96	2.39
S. condensatum	Dead	46.12	0.29	1.43	0.07	32.92	1.66
	Live	46.39	0.29	1.35	0.05	34.8	1.14
D. viscosa	Dead	51.04	0.33	1.78	0.06	28.97	0.94
	Live	49.59	0.42	1.69	0.10	30.16	1.80
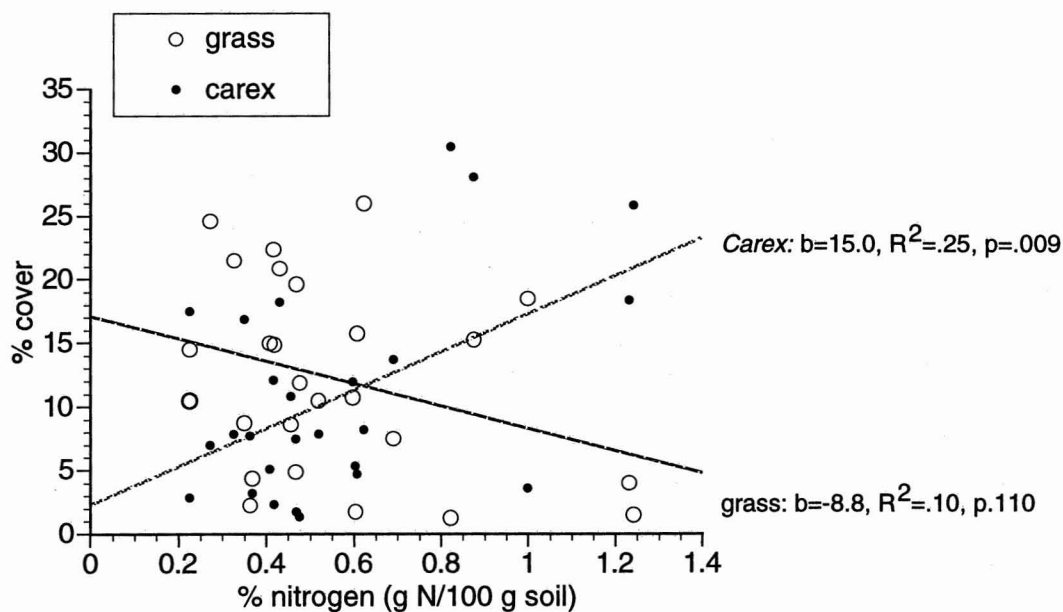
FIGURE 1. Regression of cover of introduced grasses and *Carex wahuensis* cover on soil N under dead *Myrica faya*.

soil N (slope $= 0.40$, $R^2 = 0.30$, $P = .052$ [see Figure 2]). None of these associations was found in the live *M. faya* treatment.

DISCUSSION

Grass Invasion

Whether dieback promotes introduced grasses depends on both relative growth rates and recruitment, estimated in our study by changes in percentage cover and plant density. Although the changes in cover offer little evidence of an advantage for *A. virginicus* and *S. condensatum* over native species, the density data do suggest that *M. faya* dieback favors the introduced grasses.

Introduced and native species made virtually equal gains in cover of 11.8 and 10.4%, respectively, but over two-thirds of the native increase was due to *C. wahuensis*, which was
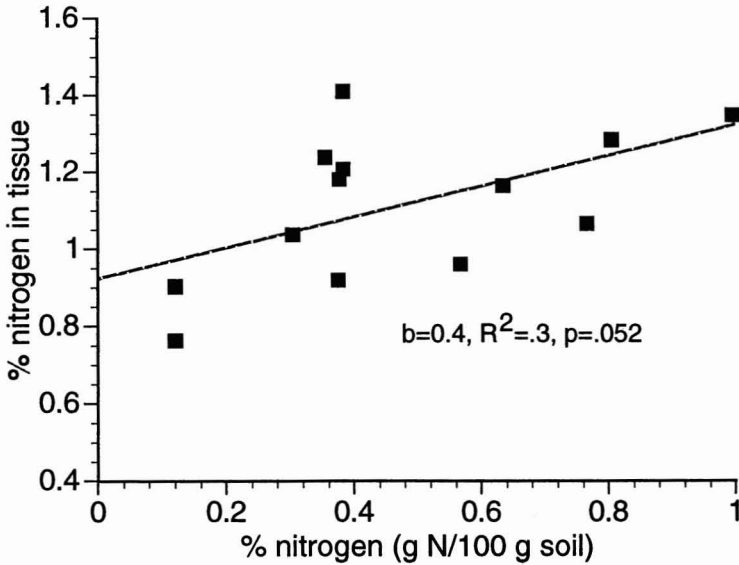
FIGURE 2. Percentage nitrogen in *Carex wahuensis* tissue as a function of soil percentage nitrogen under dead *Myrica faya.*

relatively more common in the area close to the *M. faya* base and can spread vegetatively. As introduced grass continues to spread into the gaps created by the *M. faya* canopies, it may eventually outcompete *C. wahuensis* because both *A. virginicus* and *S. condensatum* grow considerably taller and faster than the sedges. Because *C. wahuensis* increased during both *M. faya* invasion and dieback, it could decline (losses to competition) considerably and still remain more abundant than it was before *M. faya* invasion. The grasses, on the other hand, may have just recovered to their preinvasion levels: the relative increases in cover of *S. condensatum* and *A. virginicus* within our dieback study plots are similar to the decreases of the same species observed earlier by Tunison et al. (in press *b*) during *M. faya* invasion in a similar nearby area.

The lack of native shrub recruitment, compared with the success of grass seedlings under dead *M. faya*, does support the hypothesis that dieback promotes nonnative species. Grasses are beginning to come back extensively from seed but may also be resprouting: we found many young individuals growing attached to mats of old grass litter. These appear to be resprouts from plants that were presumably suppressed by the live *M. faya* canopy. Shrub regeneration, at this point, is limited to growth release following *M. faya* death. In the few plots we encountered with substantial cover of native shrubs, the cover was the result of branches from large plants rooted outside the plot, beyond the edge of the canopy. If grasses can gain an advantage over native shrubs with *M. faya* dieback, as it appears, the long-term prospects for native shrubs are poor because grasses suppress growth and recruitment of native species in similar unburned woodland sites nearby (C.M.D., Hughes, Mack, Hitchcock, and Vitousek, unpubl. data).

Although the introduced grasses, already present in these sites, may benefit from the *M. faya* dieback, we found no evidence of an increase in the richness of nonnative species growing beneath dead *M. faya* trees. *Rubus argutus* Link. might have been expected to invade, because it grows within the study area and expanded rapidly after experimental removal of *M. faya* canopy in a mesic forest nearby (Aplet et al. in press). Yet not once

did we find *R. argutus* beneath *M. faya* trees. Given more time, perhaps other nonnative species will colonize these sites if the competitive advantage of the grasses is not too great to overcome.

Managers should give careful consideration to the potential effects on the fire regime caused by the replacement of *M. faya* with introduced grasses. Although we have not measured changes in fuel biomass after *M. faya* dieback, we observed many places near our plots where *S. condensatum* individuals were up to 2 m tall or where large clumps of the fire-promoting African grass *Melinis minutiflora* P. Beauv. now surround the base of dead trees. Live *M. faya* does not burn well; thus, a forest of live *M. faya* is not nearly as great a fire hazard as a grassland or *Metrosideros* forest with a continuous tall *S. condensatum* understory. The replacement of live *M. faya* first by dead *M. faya* and then by introduced grasses would favor the spread of fires and, consequently, further reduce shrub cover and native shrub and tree reestablishment.

Nitrogen Analysis

Finding no difference in total soil nitrogen between treatments is not surprising. The tremendous amount of nitrogen fixed by *M. faya*—four times the nitrogen fixed by all native vegetation (Vitousek et al. 1987)—becomes part of total soil N as roots turn over and leaves decompose. Soil N should therefore be a function of tree age and size, as the regression of soil N on stem basal area indicates. The large variation in soil N is partially accounted for by tree size.

The lack of between-treatment (live versus dead) differences in plant tissue N for *S. condensatum* and *D. viscosa* suggests either that nitrogen availability is similar between live and dead *M. faya* soils or that plants are not able to utilize the potentially high N conditions under dead *M. faya*. Light limitation may continue for several years after *M. faya* death before stems and branches decay and may prevent colonizing plants from taking advantage of available N. Unfortunately, we have no quantitative estimates of light

availability in our plots. No between-treatment differences were found in *C. wahuensis* tissue either, but within the plots under dead *M. faya*, percentage N in the sedge tissue increased with soil N. This is in contrast to *C. wahuensis* individuals under live *M. faya*, which showed no change in tissue N with soil N. *Schizachyrium condensatum* and *D. viscosa* leaf N never showed a response to soil N. Perhaps *C. wahuensis* is less limited by light under dead *M. faya* than are *S. condensatum* and *D. viscosa*.

A legacy of light limitation, rather than the influence of nitrogen, may also explain the relationship between soil N and sedge and grass cover. *Carex wahuensis*, the only species to increase in cover with *M. faya* invasion, can persist and expand effectively in shade, whereas grasses are suppressed. If total soil N under dead *M. faya* is an indicator of extent or intensity of shade while the *M. faya* was alive (high leaf area), sites with high soil N would favor *C. wahuensis* but offer poor places for grass establishment. Stem basal area had a similar relationship to sedge and grass cover as soil N, but was not as good a predictor in regressions.

Despite the remarkable similarity of *M. faya* invasion and dieback to the bush lupine cycle described by Maron and Connors (1996), our results contrast markedly with theirs. One fundamental difference is the much greater size and longevity of *M. faya* trees compared with bush lupine. The greater size and leaf area of *M. faya*'s canopy and larger amount of woody material, compared with bush lupine, creates a much different light environment and could affect the trajectory of succession even after complete removal of leaves. Another important distinction is that although many generations of bush lupine have come and gone, affecting nitrogen status over a wide area, this is the first cycle of *M. faya* invasion and dieback, with correspondingly limited effects.

Conclusions

Vitousek and Walker (1989) proposed that the nitrogen-enriched soil produced by *M. faya* invasion would promote invasions by

nonindigenous species following *M. faya* dieback. Although our results show that the introduced grass *S. condensatum* has increased in density after *M. faya* dieback while native woody species have not, we could not identify elevated available nitrogen as the principal cause. In fact, elevated soil N was negatively correlated with introduced grass cover and positively associated with cover of a native sedge. We attribute this phenomenon to the legacy of light limitation under live *M. faya*. As dieback continues over the next decade and dead trees decay, we suspect that the ecological opportunities for introduced species will increase. The fire-promoting introduced grasses *A. virginicus* and *S. condensatum* have already begun to exploit these opportunities. Once established, they may exclude other species, native and introduced, by themselves limiting light at the soil surface. Because both of these species respond rapidly to high soil nitrogen conditions in greenhouse and field studies (C.M.D., unpubl. data), fuel accumulation in these sites over the next decade or more could be enormous.

LITERATURE CITED

APLET, G. H. 1990. Alteration of earthworm community biomass by the alien *Myrica faya* in Hawai'i. Oecologia (Berl.) 82: 414–416.

APLET, G. H., S. J. ANDERSON, and C. P. STONE. 1991. Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park. Vegetatio 95: 55–62.

APLET, G. H., R. L. LOH, J. T. TUNISON, and P. M. VITOUSEK. Experimental restoration of a dense *M. faya* stand. Coop. Natl. Park Resour. Study Unit Univ. Hawaii Tech. Rep. (in press).

GOLDBERG, D., and L. MILLER. 1990. Effects of different resource additions on species diversity in an annual plant community. Ecology 71: 213–225.

HOBBS, R. J., and L. F. HUENNEKE. 1992. Disturbance, diversity, and invasion: Implications for conservation. Conserv. Biol. 6: 324–337.

HUENNEKE, L. F., S. P. HAMBURG, R. KOIDE, H. A. MOONEY, and P. M. VITOUSEK. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71: 478–491.

HUGHES, F., and P. M. VITOUSEK. 1992. Barriers to shrub reestablishment following fire in the seasonal submontane zone of Hawaii. Oecologia (Berl.) 93: 557–563.

MARON, J. L., and P. G. CONNORS. 1996. A native nitrogen fixing tree facilitates weed invasion. Oecologia (Berl.) 105: 302–312.

MUELLER-DOMBOIS, D., and L. D. WHITEAKER. 1990. Plants associated with *M. faya faya* and two other pioneer trees on a recent volcanic surface in Hawaii Volcanoes National Park. Phytocoenologia 19: 29–41.

SMITH, C. W., and T. TUNISON. 1992. Fire and alien plants in Hawai'i: Research and management implications for native ecosystems. Pages 394–408 *in* C. P. Stone, C. W. Smith, and T. Tunison, eds. Alien plant invasion in Hawai'i: Management and research in native ecosystems. University of Hawai'i Press, Honolulu.

TUNISON, J. T., and R. L. LOH. The invasion of *M. faya* in five plant communities: A baseline study, 1994. Coop. Natl. Park Resour. Study Unit Univ. Hawaii Tech. Rep. (in press).

TUNISON, J. T., L. S. CASTRO, and R. L. LOH. in press *a*. *M. faya* dieback: Distribution, demography, and associated ecological factors. Coop. Natl. Park Resour. Study Unit Univ. Hawaii Tech. Rep.

TUNISON, J. T., S. CARLBERG, and R. L. LOH. in press *b*. Effect of *M. faya* on understory at an early stage of invasion in two com-

munities. Coop. Natl. Park Resour. Study Unit Univ. Hawaii Tech. Rep.

VITOUSEK, P. M., and L. R. WALKER. 1989. Biological invasion by *M. faya faya* in Hawai'i: Plant demography, nitrogen fixation, and ecosystem effects. Ecol. Monogr. 59:247–265.

VITOUSEK, P. M., L. R. WALKER, L. D. WHITEAKER, D. MUELLER-DOMBOIS, and P. A. MATSON. 1987. Biological invasion by *M. faya* alters ecosystem development in Hawaii. Science (Washington, D.C.) 238:802–804.

WALKER, L. R., and P. M. VITOUSEK. 1991. Interactions of an alien and a native tree during primary succession in Hawaii Vol-canoes National Park. Ecology 72:1449–1455.

WITKOWSKI, E. T. F. 1991. Effects of invasive alien acacias on nutrient cycling in the coastal lowlands of the Cape fynbos. J. Appl. Ecol. 28:1–15.

YANG, P., D. FOOTE, and V. JONES. Preliminary investigations of the effect of the two-spotted leafhopper, *Sophonia rufofascia* (Kuoh and Kuoh), on faya tree. Coop. Natl. Park Resour. Study Unit Univ. Hawaii Tech. Rep. (in press).

ZOU, X. 1993. Species effects on earthworm density in tropical tree plantations in Hawai'i. Biol. Fertil. Soils 15:35–38.