



Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests

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Abstract

We examined the effects of fertilization on the diversity, abundance, and cover of the understory plant community of two montane wet forests in Hawaii. One site occupies a young substrate, where aboveground tree growth is limited by nitrogen (N), while the other site is on an older substrate, where aboveground tree growth is limited by phosphorus (P). Both sites contained an on-going, long-term factorial fertilization experiment in which plots were fertilized semi-annually with N, P, or N and P in combination. In each fertilization treatment, we measured density of species ≥ 0.5 m tall and percent cover of species < 0.5 m tall. Fertilization with N reduced species richness at the young, N-limited site, but none of the nutrient additions altered species richness at the older, P-limited site. Species diversity and evenness were not affected by fertilization at either site. At the site with low N availability, plots fertilized with NP had higher densities of the non-native ginger *Hedychium gardnerianum*, and at the site with low P-availability, densities of the exotic shrub *Rubus argutus* were higher in P- and NP-fertilized plots. Other effects included declines in moss cover with fertilization at both sites, and reduced abundance of native seedlings in response to N and NP addition at the N-limited site. Continued long-term fertilization could lead to greater dominance of non-native species by encouraging their growth at the expense of native species, which may suffer decreased recruitment as fertilization and increased abundance of the non-native species may reduce suitable substrates for seedling establishment.

Introduction

Fertilization has been demonstrated to increase biomass production in a variety of both natural and managed ecosystems (DiTommaso and Aarssen 1989). Fertilization also causes changes in species composition, dominance, and diversity (Reed 1977; Bakelaar and Odum 1978; Tilman 1987; Hobbs and Huenneke 1992; Chapin et al. 1995), often by facilitating colonization by new species, which in some cases are non-native (Vitousek 1986). For example, fertilization led to invasion and dominance of non-native grasses in serpentine grasslands (Hobbs et al. 1988; Huen-

neke et al. 1990). In nitrogen (N) limited systems, atmospheric N deposition (Wedin and Tilman 1996) or changes in N availability resulting from the activity of N-fixing species (Vitousek and Walker 1989; Maron and Connors 1996; Pelquin and Hiebert 1999) affected establishment or increased dominance of invasive species. However, when fertilization increases the productivity of the native community and disturbance is low, canopy closure can prohibit establishment of invading species (Burke and Grime 1996).

In addition to its effects on the success of invasive species, fertilization often changes the composition of species already present in the community (Vitousek

et al. 1997; Bobbink et al. 1998). One hypothesized mechanism through which nutrients affect the structure of plant communities is by altering competitive interactions among species, a mechanism that has been demonstrated experimentally (Tilman 1987; Gurevitch and Unnasch 1989; Wilson and Tilman 1993). Increased productivity in N-fertilized systems is often associated with decreased species richness (e.g. Bakelaar and Odum (1978); Huenneke et al. (1990); Tilman (1993)). This decline in diversity may be caused by higher rates of species loss associated with increased shading and/or litter production, which can limit seedling establishment (Tilman 1993). In contrast to this general trend, Hobbs and Atkins (1988) found that fertilization (all macronutrients combined) increased species richness of both native and introduced species in five Australian vegetation types.

While changes in species composition and dominance after fertilization have been fairly well-studied in grassland and old-field ecosystems (Tilman 1987; DiTommaso and Aarssen 1989; Huenneke et al. 1990; Bobbink 1991), most fertilization studies in forests have focused on the effects of fertilization on overstory tree growth and have not considered understory communities. Recent studies, however, have begun to examine how fertilization may alter forest understory communities, noting changes in species composition in response to N-fertilization and recognizing the potential for understory vegetation to be used as indicators of N saturation (Rainey et al. 1999; Thomas et al. 1999; van Dobben et al. 1999). In addition, studies that examine the effects of atmospheric nutrient deposition, rather than experimental fertilization, have also begun to focus on understory communities (Liu and Brakenhielm 1996; Tybirk and Strandberg 1999). To date, most of these studies have focused on N due to its importance in temperate ecosystems and concern over how rising N deposition levels might affect temperate forest ecosystems. In tropical forests, however, phosphorus (P) is often in short supply (Vitousek and Sanford 1987), and in some cases, forests may be saturated with respect to N (Vitousek et al. 1997; Hall and Matson 1999). Increased N availability is likely to have less pronounced effects on productivity and species composition in systems where P or another resource is limiting or co-limiting with N (e.g. Huenneke et al. (1990); Morecroft et al. (1994); Matson et al. (1999)). However, even in systems already saturated with N, additional N could reduce productivity and/or diversity through adverse ef-

fects of soil acidification and cation leaching (Bobbink et al. 1998; Matson et al. 1999). We therefore hypothesize that in tropical forests where N is not limiting plant productivity, the effects of fertilization on understory plant communities may differ substantially from those seen in temperate forest ecosystems.

Our study focuses on changes in the understory community after fertilization in two Hawaiian montane forests. The two forests differ greatly in N and P availability, but have similar climate, geology, and species composition of the dominant overstory (Crews et al. 1995). Nutrient limitation to above-ground net primary productivity (ANPP) of the dominant tree species at the sites has been documented through previous fertilization experiments (Herbert and Fownes 1995; Vitousek and Farrington 1997). These nutrient addition experiments demonstrated that N additions enhanced ANPP at the younger site (hereafter N-limited site) and P additions enhanced ANPP at the older site (hereafter P-limited site). This montane forest type, like many other forests in Hawaii, has been invaded by a variety of non-native species (Stone and Pratt 1994). Using plots fertilized with both N and P in a factorial design at the two sites, we examined species diversity, composition, and abundance to test the effects of fertilization on the structure of the forest understory plant community. We expected to see more pronounced changes in understory community composition in plots fertilized with the nutrient that limits overstory productivity than in plots fertilized with the non-limiting nutrient.

Methods

The younger, N-limited site is adjacent to Thurston Lava Tube just outside Hawai'i Volcanoes National Park at an elevation of 1176 m on the island of Hawai'i (19°25' W, 155°15' N). The soil at this site, classified as a Hydric Dystrandept (Riley and Vitousek 1995), consists of 200–400-yr-old coarse tephra deposits (Crews et al. 1995) overlaying an older pahoehoe (smooth) lava flow (Vitousek et al. 1993). While fertilization experiments indicate that ANPP at this site is N-limited (Herbert and Fownes 1995; Vitousek and Farrington 1997), soil and plant measurements indicate that other nutrients are also available in low supply (Table 1). Overstory vegetation at this site is dominated by *Metrosideros* with a conspicuous tree fern understory/sub-canopy of *Cibotium* spp. (Crews et al. 1995). The older, P-limited site is lo-

Table 1. Characteristics of the study sites. Data are mean \pm SE. Sample sizes (n) are given when possible.

	N-limited site	P-limited site
Soil characteristics		
<i>In situ</i> resin bags ($\mu\text{g bag}^{-1} \text{d}^{-1}$) ^a		
NO ₃ -N	0.22 \pm 0.12 (n=5)	10.20 \pm 4.91 (n=6)
NH ₄ -N	3.09 \pm 1.44 (n=5)	4.12 \pm 2.29 (n=6)
P	0.20 \pm 0.08 (n=5)	0.41 \pm 0.17 (n=6)
Total nutrients (upper 100 cm mineral soil) ^b		
N(g kg ⁻¹)	0.10 \pm 0.03 (n=7)	0.53 \pm 0.04 (n=4)
P(g kg ⁻¹)	0.05 \pm 0.01 (n=7)	0.04 \pm 0.02 (n=4)
Gross N mineralization (mg m ⁻² d ⁻²) ^b	195 \pm 70 (n=8)	647 \pm 114 (n=4)
Gross nitrification (mg m ⁻² d ⁻¹) ^b	33 \pm 9 (n=8)	112 \pm 52 (n=4)
pH in H ₂ O ^a	5.02	3.99
Plant characteristics		
Foliar nutrients ^c		
N(%)	0.87 \pm 0.04	0.86 \pm 0.04
P(%)	0.060 \pm 0.006	0.061 \pm 0.002
Litter nutrients ^a		
N(%)	0.40 \pm 0.01	0.37 \pm 0.015
P(%)	0.026 \pm 0.001	0.022 \pm 0.001
ANPP (g m ⁻² yr ⁻¹) ^d	1577 \pm 127	1514 \pm 135

^a data from Crews et al. (1995);

^b data from Riley and Vitousek (1995);

^c foliar nutrients for *Metrosideros polymorpha* leaves (glabrous variety), data from Vitousek et al. (1995);

^d data from Herbert and Fownes (1999).

cated within Na Pali Kona Forest Reserve at an elevation of 1134 m on the island of Kaua'i (22°08' W, 159°37' N). The substrate is so weathered that it is difficult to determine conclusively whether soils here were derived from tephra or lava, but the parent material has been estimated to be 4.1 million years old, and the soil is classified as a Plinthic Acrothox (Riley and Vitousek 1995). While *Metrosideros* is also dominant here, the trees are considerably shorter than at the younger site and *Cibotium* is almost completely absent from study plots. Other ferns, particularly *Elaphoglossum* spp., are common in the understory (Crews et al. 1995). This site was hit by hurricanes in 1982 and 1992 (Herbert et al. 1999). Precipitation at both sites averages 2500 mm per year, and mean annual temperature at the sites is 16 °C (Crews et al. 1995).

Long-term factorial fertilization experiments have been ongoing at the N-limited site since October 1985 (Vitousek et al. 1993) and at the P-limited site since March 1991 (Herbert and Fownes 1995). A 15 \times 15 m area of each plot was fertilized semi-annually at a rate of 100 kg ha⁻¹ yr⁻¹ of N (half as urea, half as ammonium nitrate) or 100 kg ha⁻¹ yr⁻¹ P (as triple

superphosphate) or as combination of N and P at the same rates. Unfertilized plots are referred to as controls (C); each treatment (C, N, P, or NP) had 4 replicate plots.

In order to address changes in understory community structure with fertilization, particularly in relation to non-native species, we measured the plant community at the two sites in 1996. No data on understory species composition were taken before fertilization began, but each plot was randomly assigned a treatment (C, N, P, or NP). Our statistics (F tests) explicitly test for variation within and between treatments, with the control plots representing pre-treatment variation in vegetation composition. In each plot described above, we uniformly established 4 transects of 15 m length. For individuals \geq 0.5 m tall (longer-lived stems such as shrubs and trees), we estimated density by counting all individuals in a 1 m belt along each transect. Multi-stemmed plants with a common trunk or stem were considered one plant. To categorize ground cover and vegetation < 0.5 m tall (shorter-lived herbaceous vegetation and seedlings), we used 0.25 m² quadrats. Five quadrats, stratified randomly every 3 m were placed along each transect, for a total

of 20 quadrats per plot. In each quadrat, we counted seedlings and noted percent cover of all higher plants < 0.5 cm tall, moss, leaf litter, fine woody debris, logs, stems/rhizomes, and bare ground. Because percent cover was estimated for each species and cover class individually and included overlapping canopy layers, total ground cover can exceed 100%.

Changes in community structure were examined using species richness (S), Shannon-Weiner species diversity index ($H' = \sum -\log P_i * P_i$, where P_i is the proportion of individual stems divided by the total number of stems for each species), and evenness (H'/S). Differences among treatments in these variables were analyzed by one-way analysis of variance using JMP (SAS Institute Inc. 1995).

We used forward stepwise discriminant function analyses (Tabachnick and Fidell 1989) to examine whether the control plots could be separated from the fertilized treatment plots based on either density (for species ≥ 0.5 m) or percent cover (for species < 0.5 m and ground cover categories). This procedure allowed us to consider the assemblage of species within a plot rather than performing individual analysis of variance for each species; it uses linear combinations of variables to discriminate among the treatment groups. Individual species were the predictor variables. Settings used in the model were $F_{to\ enter} = 1.00$, $F_{to\ remove} = 0.00$, and tolerance = 0.01. The analysis was run using the 10-15 most abundant species. Cover values were transformed to arc sine square roots before analysis. Data were analyzed using StatSoft Inc. (1997).

Results

Effects on community structure.

A variety of life forms were found at the two sites, summarized in Tables 2 and 3. Most of the species were native, with the notable exceptions of *Hedychium gardnerianum* and *Rubus argutus*, which occurred at high relative densities and frequencies. Fertilization with N decreased species richness at the N-limited site, but none of the nutrient additions significantly altered species richness at the P-limited site. Neither the Shannon-Weiner diversity index nor evenness was affected by fertilization at either site (Table 4).

Effects on density.

Stepwise discriminant function analysis at the N-limited site produced a model in which the four treatment groups could be discriminated along two axes based on the densities of six species (≥ 0.5 m tall; Wilks' Lambda = 0.03, approximate $F_{18,20} = 2.7$, $p < 0.0165$). Based on the eigenvalues, the first two axes described 81.4% and 97.2% of the cumulative variance. N-fertilized plots were significantly different from P, NP, and C plots (Figure 1). Treatments were classified correctly 87.5% of the time. The factor structure of the canonical variables (pooled-within-groups correlations) suggests that the N-fertilizer treatment, which separated most strongly from the other treatments along axis 1, was strongly influenced by the densities of the exotic ginger *Hedychium gardnerianum* and the native *Vaccinium calycinum*, which tended to be lower in the N plots than in the other treatments, and by the density of the native tree fern *Cibotium glaucum*, which tended to be higher in the N plots than in the other treatments (Table 2). While *Hedychium* density at the N-limited site tended to be reduced by N addition alone, it increased dramatically in response to addition of N and P in combination (Table 2).

At the P-limited site, a model using seven species described 75.5% and 97.0% of the cumulative variance along the two axes (Wilks' Lambda = 0.02, approximate $F_{21,17} = 2.7$, $p < 0.0437$). Control plots were significantly different than the N and P plots (Figure 1). Treatments were classified correctly in 93.75% of cases. Separation along axis 1 was positively correlated with the density of the exotic shrub *Rubus argutus* (Table 5), which tended to be higher in the P and NP plots than in the C plots and was negatively correlated with the density of the native tree *Cheirodendron trigynum*, which did not respond to fertilization. Along axis 2, treatment separation was most negatively correlated with density of the native tree *Metrosideros*, which was unaffected by fertilization treatments, and was most positively correlated with density of the native herb *Stenogyne purpurea*, which tended to be higher in the N plots than in the other treatments (Table 5). Interestingly, relative density and importance of the exotic ginger *Hedychium* did not change with fertilization at the P-limited site, in contrast to its response to N and P in combination at the N-limited site.

Table 2. Relative density, relative frequency, and importance value of each species (greater than 0.5 m tall). Fertilizer treatments (n = 4 plots) were unfertilized control (C), Nitrogen addition (N), Phosphorus addition (P), and N and P in combination (NP). Species are listed in descending order of importance value, calculated as the sum of the relative density and relative frequency. Non-native species are listed in bold.

Species	Family	Life form	Relative Density (%)				Relative Frequency (%)				Importance Value (%)			
			C	N	P	NP	C	N	P	NP	C	N	P	NP
N-LIMITED SITE (HAWAII)														
<i>Hedychium gardnerianum</i>	Zingiberaceae	shrub/tree	5.2	1.1	4.5	13.3	2.8	1.4	2.1	2.8	8.0	2.5	6.6	16.1
<i>Sadleria</i> spp.	Blechnaceae	fern	2.2	7.7	2.2	4.5	2.8	2.8	2.8	2.8	5.0	10.5	5.0	7.3
<i>Metrosideros polymorpha</i>	Myrtaceae	shrub/tree	3.2	1.5	4.3	2.9	2.8	2.8	2.8	2.8	6.0	4.3	7.1	5.7
<i>Coprosma</i> spp.	Rubiaceae	shrub/tree	3.1	1.4	2.8	2.9	2.8	2.8	2.8	2.8	5.9	4.2	5.6	5.7
<i>Cibotium glaucum</i>	Dickinsoniaceae	fern	2.0	3.4	2.8	1.8	2.8	2.8	2.8	2.8	4.8	6.2	5.6	4.6
<i>Ilex anomala</i>	Aquifoliaceae	shrub/tree	2.5	1.2	1.7	1.2	2.8	2.8	2.8	2.8	5.3	4.0	4.5	4.0
<i>Vaccinium calycinum</i>	Ericaceae	shrub/tree	2.5	0.4	2.1	2.8	2.8	1.4	2.8	2.8	5.3	1.8	4.9	5.6
<i>Myrsine lessertiana</i>	Myrsinaceae	shrub/tree	0.4	0.3	0.1	0.5	2.1	2.1	0.7	2.1	2.5	2.4	0.8	2.6
<i>Dicranopteris linearis</i>	Gleicheniaceae	fern	3.1	0.0	1.8	0.0	0.7	0.0	1.4	0.0	3.8	0.0	3.2	0.0
<i>Lycopodium</i> sp.	Lycopodiaceae	lycopod	2.7	0.0	0.3	0.0	2.8	0.0	0.7	0.0	5.5	0.0	1.0	0.0
<i>Setaria palmifolia</i>	Poaceae	herb	0.1	0.2	0.8	0.8	0.7	0.7	1.4	1.4	0.8	0.9	2.2	2.2
<i>Machaerina angustifolia</i>	Cyperaceae	herb	0.6	0.0	0.0	0.0	2.1	0.0	0.0	0.0	2.7	0.0	0.0	0.0
<i>Cyrtandra platyphylla</i>	Gesneraceae	shrub/tree	0.2	0.0	0.0	0.2	0.7	0.0	0.0	0.7	0.9	0.0	0.0	0.9
<i>Hedychium</i> sp.	Zingiberaceae	shrub/tree	0.2	0.0	0.0	0.1	0.7	0.0	0.0	0.7	0.9	0.0	0.0	0.8
<i>Rubus argutus</i>	Rosaceae	shrub/tree	0.0	0.1	0.0	0.1	0.0	0.7	0.0	0.7	0.0	0.8	0.0	0.8
<i>Psychotria hawaiiensis</i>	Rubiaceae	shrub/tree	0.0	0.2	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.9	0.0	0.0
<i>Cheirodendron trigynum</i>	Araliaceae	shrub/tree	0.1	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.8	0.0	0.0	0.0
<i>Myrica faya</i>	Myricaceae	shrub/tree	0.0	0.0	0.1	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.8	0.0
<i>Anemone hupehensis</i> var. japonica	Ranunculaceae	herb	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.8
<i>Psidium cattleianum</i>	Myrtaceae	shrub/tree	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.8
<i>Cibotium chamissoi</i>	Dickinsoniaceae	fern	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
P-LIMITED SITE (KAUAI)														
<i>Hedychium gardnerianum</i>	Zingiberaceae	shrub/tree	11.4	10.6	9.5	5.9	1.8	1.8	1.8	1.8	13.2	12.4	11.3	7.7
<i>Rubus argutus</i>	Rosaceae	shrub/tree	0.4	0.1	4.7	10.0	0.4	0.9	1.8	1.8	0.8	1.0	6.5	11.8
<i>Alyxia oliviformis</i>	Apocynaceae	vine	2.5	2.3	2.7	1.5	1.8	1.8	1.8	1.8	4.3	4.1	4.5	3.3

Table 2. Continued.

Species	Family	Life form	Relative Density (%)				Relative Frequency (%)				Importance Value (%)			
			C	N	P	NP	C	N	P	NP	C	N	P	NP
<i>Vaccinium calycinum</i>	Ericaceae	shrub/tree	2.2	2.3	3.5	0.8	1.8	1.3	1.8	1.8	4.0	3.6	5.3	2.6
<i>Metrosideros polymorpha</i>	Myrtaceae	shrub/tree	1.2	1.1	1.7	1.3	1.8	1.8	1.8	1.8	3.0	2.9	3.5	3.1
<i>Cheirodendron trigynum</i>	Araliaceae	shrub/tree	0.5	0.4	0.4	0.2	1.8	1.8	1.8	1.3	2.3	2.2	2.2	1.5
<i>Psychotria</i> spp.	Rubiaceae	shrub/tree	0.4	0.4	0.4	0.2	1.8	1.3	1.8	0.9	2.2	1.7	2.2	1.1
<i>Syzygium sandwicensis</i>	Myrtaceae	shrub/tree	0.7	0.2	0.4	0.3	1.3	1.3	1.8	0.9	2.0	1.5	2.2	1.2
<i>Smilax nelastomifolia</i>	Smilacaceae	vine	0.6	0.3	0.2	0.4	1.8	0.9	1.3	1.3	2.4	1.2	1.5	1.7
<i>Dicranopteris linearis</i>	Gleicheniaceae	fern	5.1	0.0	0.0	0.1	0.4	0.0	0.0	0.9	5.5	0.0	0.0	1.0
<i>Melicope</i> spp.	Rutaceae	shrub/tree	0.3	0.1	0.3	0.3	1.8	0.4	1.8	1.3	2.1	0.5	2.1	1.6
<i>Peperomia</i> spp.	Piperaceae	herb	0.1	0.2	0.4	0.6	0.9	0.4	1.3	1.3	1.0	0.6	1.7	1.9
<i>Dianella sandwicensis</i>	Liliaceae	herb	0.5	1.4	0.1	0.1	0.9	0.9	0.9	0.4	1.4	2.3	1.0	0.5
<i>Stenogyne purpurea</i>	Lamiaceae	herb	0.1	1.4	0.4	0.3	0.9	0.4	1.3	0.4	1.0	1.8	1.7	0.7
<i>Coprosma</i> spp.	Rubiaceae	shrub/tree	0.2	0.5	0.2	0.1	1.3	0.9	1.3	0.4	1.5	1.4	1.5	0.5
Unknown fern #1		fern	0.8	0.4	0.9	0.0	0.4	0.4	0.4	0.0	1.2	0.8	1.3	0.0
Unknown sedge #1	Cyperaceae	herb	0.1	0.3	0.0	0.4	0.9	0.9	0.0	0.4	1.0	1.2	0.0	0.8
<i>Hedyotis terminalis</i>	Rubiaceae	vine	0.2	0.0	0.4	0.1	0.9	0.0	0.9	0.4	1.1	0.0	1.3	0.5
<i>Elaeocarpus bifidus</i>	Tiliaceae	shrub/tree	0.03	0.0	0.0	0.3	0.4	0.0	0.0	1.3	0.4	0.0	0.0	1.6
<i>Styphelia tameiameia</i>	Epacridaceae	shrub/tree	0.03	0.03	0.0	0.2	0.4	0.4	0.0	0.9	0.4	0.4	0.0	1.1
<i>Cheirodendron platyphyllum</i> subsp. <i>kauaiense</i>	Araliaceae	shrub/tree	0.0	0.0	0.2	0.03	0.0	0.0	1.3	0.4	0.0	0.0	1.5	0.4
<i>Labordia</i> sp.	Loganiaceae	shrub/tree	0.1	0.0	0.03	0.03	0.9	0.0	0.4	0.4	1.0	0.0	0.4	0.4
<i>Vikstroemia oahuensis</i>	Thymelaeaceae	shrub/tree	0.0	0.2	0.0	0.0	0.0	0.9	0.0	0.4	0.0	1.1	0.0	0.4
<i>Broussaisia arguta</i>	tydrangeaceae	shrub/tree	0.1	0.1	0.0	0.0	0.9	0.4	0.0	0.0	1.0	0.5	0.0	0.0
<i>Ilex anomala</i>	Aquifoliaceae	shrub/tree	0.0	0.03	0.0	0.3	0.0	0.4	0.0	0.4	0.0	0.4	0.0	0.7
<i>Pittosporum gayanum</i>	Pittosporaceae	shrub/tree	0.1	0.0	0.03	0.0	0.4	0.0	0.4	0.0	0.5	0.0	0.4	0.0
<i>Antidesma platyphyllum</i>	Euphorbiaceae	shrub/tree	0.03	0.03	0.0	0.0	0.4	0.4	0.0	0.0	0.4	0.4	0.0	0.0
<i>Tetraplasandra oahuensis</i>	Araliaceae	shrub/tree	0.0	0.0	0.03	0.03	0.0	0.0	0.4	0.4	0.0	0.0	0.4	0.4

Table 2. Continued.

Species	Family	Life form	Relative Density (%)				Relative Frequency (%)				Importance Value (%)			
			C	N	P	NP	C	N	P	NP	C	N	P	NP
<i>Vaccinium dentatum</i>	Ericaceae	shrub/tree	0.2	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.6	0.0	0.0	0.0
Acacia melanoxylon	Fabaceae	shrub/tree	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.5
<i>Pteridium aquilinum subsp. decompositum</i>	Hypolepidaceae	fern	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.5	0.0	0.0	0.0
<i>Psidium cattleianum</i>	Myrtaceae	shrub/tree	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.5	0.0	0.0	0.0
<i>Cryptomeria japonica</i>	Taxodiaceae	shrub/tree	0.0	0.1	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.5	0.0	0.0
<i>Cyrtandra longifolia</i>	Gesneriaceae	shrub/tree	0.0	0.0	0.0	0.03	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4
<i>Scaveola procera</i>	Goodeniaceae	shrub/tree	0.0	0.03	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0
<i>Cibotium chamissoi</i>	Dickinsoniaceae	fern	0.0	0.03	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0
<i>Ambrosia artemisiifolia</i>	Asteraceae	herb	0.0	0.0	0.0	0.03	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4
<i>Myrica faya</i>	Myricaceae	shrub/tree	0.0	0.0	0.0	0.03	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4
<i>Astelia argyrocoma</i>	Liliaceae	herb	0.0	0.03	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0

Effects on cover and seedlings.

At the N-limited site, a combination of eight variables separated out differences in percent cover of species < 0.5 m tall and ground cover among the fertilization treatments (Wilks' Lambda = 0.005, approximate $F_{24,15} = 3.3$, $p < 0.0102$). Control plots were significantly different from the fertilized plots, but these three treatments were not different from each other (Figure 2). Classifications were correct 93.75% of the time. The first and second axes explained 87.7% and 95.3% of the cumulative variation. The factor loadings of the canonical variables suggests that along axis 1 the control plots separated from the other treatments due mainly to the cover of the native grass *Isachne*, the seedlings of the native tree *Metrosideros*, and logs, all of which tended to be lower in the N-addition plots (Table 6). Percent cover for all variables is presented in Table 3; one notable change is a decline in moss cover with fertilization. There was a trend toward separation of the NP from the N and P plots along axis 2, which was driven mainly by the

cover of fine wood, logs, and cover of *Cibotium glaucum*. While cover of fine wood and logs tended to be higher in the NP plots, that of *C. glaucum* was lower (Table 6).

At the P-limited site, ten variables were involved in the discriminant function analysis for cover (Wilks' Lambda = 0.0003, approximate $F_{30,19} = 4.5$, $p < 0.0110$). The first and second axes explained 51.9% and 96.9% of the cumulative variation. Control plots separated out in between the fertilizer plots and were not significantly different from any of them, but all of the three fertilizer treatments were different from each other (Figure 2). All classifications were correct (100%). Along axis 1, the herb *Peperomia*, bare ground, fine wood, and the fern *Elaphoglossum hirtum var. micans* had the highest negative loadings, while fallen logs had the highest positive loading. Along axis 2, the treatments were separated by bare ground, sedge, log, and fern cover (Table 6).

Seedlings of native species at the N-limited site generally declined in abundance in the N and NP-fertilized plots (Kruskal Wallis test, $X^2 = 9.4$, $p = 0.02$,

Table 3. Means and standard deviations (untransformed data) of percent cover for the species < 0.5 m tall found fertilized plots at both sites. Species found very infrequently (< 0.25%) are not listed here. Fertilizer treatment (n = 4 plots) as in Table 2. Non-native species listed in bold.

	C		N		P		NP	
	mean	sd	mean	sd	mean	sd	mean	sd
N-LIMITED SITE								
leaf litter	87.9	3.9	87.4	4.7	83.0	13.6	87.3	3.1
moss	22.3	8.7	8.2	4.3	17.2	4.9	14.8	4.3
log	16.5	5.1	6.1	5.5	9.5	2.4	13.2	3.8
grass	8.7	11.9	6.3	9.9	11.6	13.9	10.1	6.1
fine wood	5.9	1.6	2.7	2.5	4.3	3.2	8.4	4.3
<i>Isachne distichophylla</i>	4.6	4.2	0.04	0.03	1.6	1.0	0.4	0.5
<i>Sadleria spp.</i>	3.8	4.6	2.7	2.3	2.3	2.2	3.4	3.0
<i>Lycopodium sp.</i>	0.7	0.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Coprosma spp.</i>	0.6	0.4	0.3	0.2	0.6	0.6	0.9	0.9
<i>Cibotium glaucum</i>	0.6	1.1	2.4	2.3	0.0	0.0	0.0	0.0
<i>Vaccinium calycinum</i>	0.6	0.4	0.1	0.1	0.9	0.4	0.5	0.2
<i>Hedychium gardnerianum</i>	0.6	0.6	0.2	0.2	0.5	0.4	0.2	0.1
<i>Metrosideros polymorpha</i>	0.4	0.2	0.1	0.1	0.4	0.3	0.1	0.1
bare ground	0.3	0.3	2.4	3.1	0.2	0.2	0.8	0.6
P-LIMITED SITE								
leaf litter	76.4	12.9	67.7	6.4	83.4	5.5	78.8	8.5
<i>Elaphoglossum spp.</i>	22.9	6.5	15.0	7.8	40.4	12.8	16.6	11.9
log	18.6	8.1	17.0	7.6	18.6	4.5	18.0	7.1
moss	17.6	6.6	18.3	4.7	12.1	2.4	10.4	6.8
<i>Elaphoglossum hirtum</i>	16.3	13.8	2.0	2.4	5.0	4.1	9.8	10.2
<i>Unknown fern # 1</i>	13.1	14.7	2.3	4.0	11.3	9.3	16.4	18.1
<i>Peperomia spp.</i>	4.8	3.6	1.2	2.3	4.9	1.7	8.0	2.7
<i>Nephrolepis sp.</i>	3.8	7.6	6.3	12.5	11.3	22.5	11.8	23.7
bare ground	3.6	1.8	16.8	6.4	9.0	7.3	14.0	6.2
<i>Vaccinium calycinum</i>	2.9	3.4	1.3	2.5	0.5	0.6	0.3	0.5
<i>Rubus argutus</i>	2.6	3.0	1.3	2.5	1.5	1.7	3.9	4.8
fine wood	2.4	4.8	2.4	3.4	5.4	4.3	11.4	16.4
<i>Hedychium gardnerianum</i>	1.9	2.7	2.4	1.6	1.9	2.0	1.3	1.3
<i>Grammitis sp.</i>	1.5	2.4	0.0	0.0	2.5	2.9	0.0	0.0
<i>Cheirodendron trigynum</i>	1.3	2.5	2.8	4.9	0.3	0.5	0.0	0.0
<i>Smilax melastomifolia</i>	1.3	2.5	0.0	0.0	1.3	2.5	0.0	0.0
<i>Unknown fern # 4</i>	1.0	1.4	0.0	0.0	3.9	4.8	0.0	0.0
<i>Unknown sedge # 1</i>	0.9	1.8	0.4	0.7	0.0	0.0	0.9	1.9
<i>Alyxia oliviformis</i>	0.8	1.5	2.5	5.0	0.5	0.6	0.0	0.0
<i>Coprosma spp</i>	0.1	0.1	0.1	0.1	0.0	0.0	0.0	0.0
<i>Unknown fern # 3</i>	0.04	0.1	3.3	6.5	18.8	13.1	8.9	14.3
<i>Stenogyne purpurea</i>	0.0	0.0	3.3	3.9	0.3	0.5	0.0	0.0
<i>Pteridium aquilinum</i>	0.0	0.0	0.3	0.5	0.0	0.0	0.0	0.0
<i>Dicranopteris linearis</i>	0.0	0.0	10.0	20.0	0.0	0.0	0.0	0.0
<i>Myrica faya</i>	0.0	0.0	4.4	8.8	0.0	0.0	1.3	2.5
<i>Ilex anomala</i>	0.0	0.0	0.3	0.5	0.0	0.0	0.0	0.0
Unknown seedling	0.0	0.0	0.5	0.6	0.0	0.0	0.3	0.5
<i>Metrosideros polymorpha</i>	0.0	0.0	1.5	2.4	3.0	4.7	2.0	2.4
<i>Dianella sandwicensis</i>	0.0	0.0	5.1	5.9	0.0	0.0	0.0	0.0
<i>Sphenomeris chinensis</i>	0.0	0.0	0.3	0.6	1.3	2.5	5.0	10.0

Table 4. Species richness, Shannon-Weiner diversity index (H'), and evenness index for the two sites. Data are displayed as means and standard deviations for each treatment ($n = 4$); fertilizer treatments are described in Table 2. Asterisk is significant at $p \leq 0.005$. Letters signify statistically significant differences among fertilization treatments.

	C		N		P		NP		Signif.
	mean	sd	mean	sd	mean	sd	mean	sd	
N-LIMITED SITE									
Species richness	10.75a	1.26	7.5b	1.29	8.75ab	2.22	9.5ab	0.58	*
H'	0.87	0.05	0.70	0.11	0.83	0.08	0.73	0.12	ns
Evenness	0.84	0.05	0.80	0.07	0.90	0.08	0.75	0.11	ns
P-LIMITED SITE									
Species richness	15.5	2.89	12.25	4.11	14.75	2.06	14.25	3.77	ns
H'	0.73	0.29	0.69	0.30	0.78	0.17	0.71	0.28	ns
Evenness	0.62	0.24	0.62	0.20	0.67	0.13	0.61	0.18	ns

Table 5. Factor structure matrix for the discriminant function analysis on density in the fertilized plots at both sites. Values are correlation coefficients that are pooled within groups; numbers refer to the correlation between the component and the axes shown in Figure 1. Species (bold are non-native) are listed in the order they were chosen in the stepwise discriminant function analysis.

Species	Axis 1	Axis 2
N-LIMITED SITE		
<i>Hedychium gardnerianum</i>	0.27	0.48
<i>Vaccinium calycinum</i>	0.21	-0.01
<i>Cibotium glaucum</i>	-0.23	-0.06
<i>Dicranopteris linearis</i>	0.07	-0.32
<i>Ilex anomala</i>	0.09	-0.36
<i>Metrosideros polymorpha</i>	0.13	-0.26
P-LIMITED SITE		
<i>Rubus argutus</i>	0.27	-0.18
<i>Cheirodendron trigynum</i>	-0.20	-0.12
<i>Dicranopteris linearis</i>	-0.14	-0.06
<i>Unknown fern</i>	-0.08	-0.13
<i>Syzygium sandwicensis</i>	-0.10	-0.10
<i>Metrosideros polymorpha</i>	0.06	-0.32
<i>Stenogyne purpurea</i>	0.001	0.21

Table 7), in concert with a decline in moss cover (Table 7). At the P-limited site, however, seedling density of both native and non-native species was unchanged by fertilization (Table 7). Native seedlings included *Coprosma* sp., *Vaccinium* sp., and *M. polymorpha*; non-native seedlings were mainly the ginger *H. gardnerianum*.

Discussion

Fertilization has often been shown to facilitate invasion of opportunistic species that prefer higher soil

resource levels (Hobbs et al. 1988; Huenneke et al. 1990; Maron and Connors 1996; Wedin and Tilman 1996). In the case of the understory of these Hawaiian forests, two of the most abundant non-native species had a significant increase in abundance in fertilized plots. Discriminant function analysis indicated that fertilized plots were significantly different from control plots in terms of both plant density (≥ 0.5 m) and cover composition (< 0.5 m). The species that contributed most strongly to the separation between fertilized and control plots in the density analyses were non-native. At the N-limited site, plots fertilized with NP had higher densities of the non-native ginger *Hedychium gardnerianum*, although it is notable that plots fertilized only with N tended to have lower densities and importance values than control plots (Table 2). While N limits growth of the dominant species at this site, P availability is also low (Crews et al. 1995), and may limit the response of *Hedychium* to N addition. At the P-limited site, densities of the shrub *Rubus argutus* were higher in P- and NP-fertilized plots (Table 2). Thus, addition of the nutrient that limits growth of the dominant tree species (*Metrosideros polymorpha*), especially when applied in combination (NP), appears to increase abundance of these important non-native species in the understory. Rather than new invasions, we suspect that these bird-dispersed non-native species were present at lower densities before fertilization began, but that nutrient addition led to increases in abundance.

It is likely that changes in the abundance of non-native species at the P-limited site were affected by hurricane disturbance, as well as by fertilization. Density of the non-native *Rubus argutus* was noted to increase after the 1992 hurricane (D.A. Herbert, personal communication), and various studies have sug-

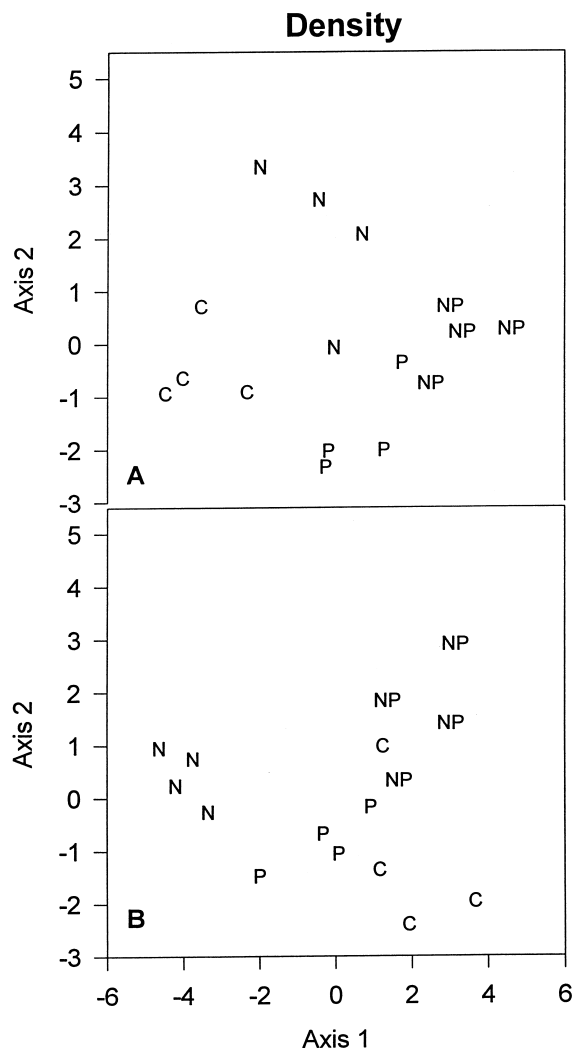


Figure 1. Stepwise discriminant function analysis of understory density of species in plots that either received fertilization with nitrogen (N), phosphorus (P), both elements (NP), or unfertilized control plots (C). A. N-limited site; B. P-limited site.

gested or demonstrated interactions between fertility and disturbance in facilitating invasion (Hobbs and Atkins 1988; Burke and Grime 1996). Furthermore, Herbert et al. (1999) demonstrated in this same P-limited site that P- and NP-fertilized plots tended to have greater reductions in LAI and increased crown damage from the hurricanes, but also recovered more quickly in terms of ANPP than control plots. At this site, we suggest that increased abundance of non-native species is due to a combination of greater hurricane damage and increased nutrient supply.

Although fertilization affected abundance it did not generally have strong effects on species richness, di-

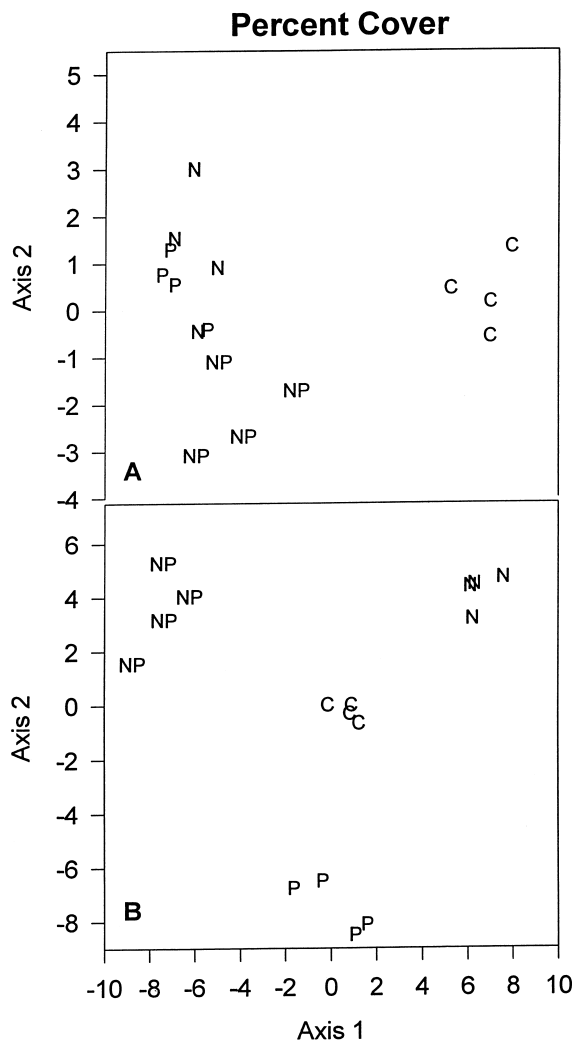


Figure 2. Stepwise discriminant function analysis of understory percent cover of cover types in plots that either received fertilization with nitrogen (N), phosphorus (P), both elements (NP), or unfertilized control plots (C). A. N-limited site; B. P-limited site.

versity, or evenness. It is likely that in ecosystems dominated by long-lived species these changes will occur over longer time periods than alterations of biomass, cover, and density. Milchunas and Lauenroth (1995) found that long-term N fertilization in short-grass steppe did not alter community composition until 7 years following the cessation of fertilization, by which time the treated plots had been invaded at high densities by exotic species. The reduction in species richness in response to N addition at the N-limited site is consistent with the results of fertilization studies in other systems and may be caused by increased shading by a more productive overstory (Vitousek et al. 1993). The lack of change in species richness in

Table 6. Factor structure matrix for the discriminant function analysis on cover in the fertilized plots at both sites. Values are correlation coefficients that are pooled within groups; numbers refer to the correlation between the component and the axes shown in Figure 2. Species (bold are non-native) are listed in the order they were chosen in the stepwise discriminant function analysis. The native grass *Isachne distichophylla* was considered separately from other grasses, which were non-native.

Species	Root 1	Root 2
N-LIMITED SITE		
<i>Isachne distichophylla</i>	0.21	0.14
fine wood	0.08	-0.57
<i>Cibotium glaucum</i>	-0.03	0.39
log	0.16	-0.40
grass	0.001	-0.13
<i>Coprosma spp.</i>	0.05	-0.30
<i>Sadleria spp.</i>	0.02	-0.02
<i>Metrosideros polymorpha</i>	0.16	0.13
P-LIMITED SITE		
<i>Elaphoglossum spp.</i>	0.02	-0.18
<i>Peperomia spp.</i>	-0.16	-0.03
bare ground	0.10	0.14
Unknown fern #4	0.10	-0.06
Unknown fern #3	-0.03	-0.08
fine wood	-0.07	0.004
<i>Elaphoglossum hirtum var. micans</i>	-0.06	0.03
log	-0.01	-0.02
Unknown fern #1	-0.03	-0.02
Unknown sedge #1	-0.01	0.04

Table 7. Median number of seedlings/m² found at the two sites. Fertilizer treatments are described in Table 2. Asterisk is significant at $p \leq 0.05$.

	C	N	P	NP	Significance
N-LIMITED SITE					
Native seedlings	13.6	3.0	4.9	7.8	*
Non-native seedlings	0.4	0.2	0.2	0.8	ns
P-LIMITED SITE					
Native seedlings	18.9	19.0	16.2	24.8	ns
Non-native seedlings	6.6	8.1	6.0	6.4	ns

response to fertilization at the P-limited site may be related to disturbance by hurricanes. Thinning of the canopy by hurricane damage may have counteracted fertilization effects on light infiltration at this site. However, differences between the sites may also be due to differential responses to N and P fertilization. The N-limited site was fertilized for a longer time, and it is possible that plants at the two sites were not experiencing the same degree of nutrient limitation,

either due to time since fertilization or inherent differences in the availability of N and P. For example, P added to old, acidic, weathered soils tends to become fixed by iron and aluminum oxides and can be in forms relatively unavailable to plants, while added N may not undergo the same geochemical constraints (Brady 1990).

At both sites, fertilized plots had a decline of moss cover (Table 3), which may be due to reduced light infiltration, lower cover of logs in fertilized plots (Table 3), or salt stress from the fertilizer since bryophytes lack a cuticle (Kellner 1993; Walker et al. 1996). The reduction in moss cover was most pronounced in N fertilized plots at the N-limited sites, and in P and NP fertilized plots at the P-limited site, suggesting an ecological mechanism, rather than experimental artifact. It is likely that positive fertilization effects on canopy density (Herbert and Fownes 1999; Vitousek et al. 1993) have adversely affected moss cover by reducing light infiltration. Declines in bryophyte cover, frequency, or biomass have been reported in fertilization studies in boreal forest (Kellner (1993); Prescott et al. (1995); Turkington et al. (1998); but see Nordin et al. (1998)), north temperate Douglas fir plantations (Thomas et al. 1999), and in subtropical lower montane elfin forest (Walker et al. 1996). In a wooded meadow in Estonia known for exceptionally high bryophyte diversity (96 species), the decline in cover with fertilization was balanced by an increase in species richness, the opposite of the response commonly seen with vascular plants (Ingerpuu et al. 1998).

This decrease in moss cover may be particularly significant for regeneration in Hawaiian wet forests, as most of the native species in the wet forest germinate on moss-covered fallen logs or on tree ferns (*Cibotium* sp.) but not on mineral soil (Scowcroft 1992). For example, in a fenced enclosure recovering from grazing in a wet forest life zone, approximately 3/4 of the natural regeneration was found on organic material such as decayed wood, moss-covered root mats, or debris-filled pockets of live plants. The number of plants on these organic seedbeds was disproportionate to the total surface area because the substrates accounted for < 2% of total area (Scowcroft 1992). It is hypothesized that these elevated organic substrates provide a more favorable microclimate (e.g., higher temperature and greater water holding capacity) and protection from feral pigs (Burton and Mueller-Dombois 1984). We noted declines in native seedling density with fertilization at the N-limited site (Table 7),

and this observation merits further study. In addition, the native and non-native species at our sites may differ in terms of the importance of seedling establishment as a regeneration mechanism; the non-native ginger *Hedychium gardnerianum* is well known for its vegetative spread through rhizomes (Stone and Pratt 1994) and *Rubus argutus* resprouts from basal and subterranean shoots (Cronk and Fuller 1995).

We hypothesize that continued long-term fertilization will lead to even greater dominance of these non-native species through two mechanisms: stimulation of the growth and abundance of the non-native species and reduced recruitment of native species due to the decreased area of organic substrates for native seedling establishment. In other areas of Hawaii, non-native species have been demonstrated to have a variety of traits that are correlated with more efficient carbon capture, such as higher specific leaf area, lower cost of construction, higher photosynthetic rates, and greater foliar N and P concentrations (on a mass basis) than native species (Baruch and Goldstein 1999). While we did not test the effects of the non-native species on ecosystem properties, we suspect that they may have significant consequences on the ecosystem in several ways. Both *Hedychium gardnerianum* and *Rubus argutus* form dense thickets in these forests, potentially shading out native species as well as altering microclimatic variables such as soil moisture. Leaves of both of these species are also less sclerophyllous than many of the common native flora (e.g., *Vaccinium*, *Ilex*, *Coprosma*, *Alyxia*), and may have faster decomposition rates or higher rates of herbivory, altering rates of nutrient cycling. Faster rates of decomposition were demonstrated with another introduced species (*Passiflora mollissima*) in these forest types (Scowcroft 1997). Finally, we note that understory community responses vary depending on the nutrient that limits overstory growth. Although N-fertilization is effectively increasing in tropical regions due to deposition from human activities (Matson et al. 1999), this increased N may not affect species invasions as dramatically in tropical forests in which productivity is often P-limited, relative to N-limited temperate systems.

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