Title

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Potential ecosystem-level effects of genetic variation among populations of *Metrosideros polymorpha* from a soil fertility gradient in Hawaii

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Abstract This study assessed intrinsic differences in tissue quality and growth rate among populations of *Metrosideros polymorpha* native to sites with a range of soil fertilities. We collected seedlings from three Hawaiian mesic forests that were either phosphorus-limited, nitrogen-limited, or relatively fertile. These individuals were grown in a common garden under a factorial high/low, N/P fertilization regime for 1.5 years and then harvested to determine genetic divergence; aboveground growth rate; and lignin, N, and P concentrations in leaves and roots. Allozyme analyses indicated that the three groups had genetically diverged to some degree (genetic distance=0.036–0.053 among populations). Relative growth rate did not differ significantly among the populations. Senescent leaves from the fertile-site population had the highest N concentrations (due to low N resorption) and had lower lignin concentrations than plants from the N-limited site. Across treatments, P concentrations in senescent leaves were highest in plants from the fertile and P-limited site. Root tissue quality did not generally differ significantly among populations. Since decomposition rate of senescent leaves in this system is related positively to N concentration and negatively to lignin concentration, senescent leaves from the fertile-site population may have a genetic tendency toward faster decay than the others. The intrinsic qualities of the three populations may provide positive feedbacks on nutrient cycling at each site–nutrient availability may be raised to some degree at the fertile site, and reduced at the N- or P-limited sites. Our results suggest that even a small degree of genetic differentiation among groups can influence traits related to nutrient cycling.

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Introduction

In ecosystem science, the composition (i.e. genotypes) of plant communities has long been recognized as an important factor in nutrient dynamics (Jenny 1941, 1980), and much recent attention has been focused on the roles of different species or functional groups (e.g. Wedin and Tilman 1990; Hobbie 1992; Binkley 1995; Chapin et al. 1997; Steltzer and Bowman 1998). However, intrinsic differences in plant traits that could affect ecosystem processes (such as morphology, physiology, and allocation) also occur among populations within species (e.g. Clausen et al. 1940; Gauhl 1976; Chapin and Chapin 1981; Eriksen and Nordal 1989; Norton et al. 1995; Mansfield et al. 1999). Few studies have assessed the consequences of this intraspecific variation on ecosystem function; one notable exception is the finding by Holland and colleagues (1992) that populations of grasses with different intrinsic grazing tolerances have distinct effects on productivity and nitrogen mineralization.

We examined intrinsic differences in plant populations from sites that varied in soil nutrient availability, and focused on traits that should feed back to affect nutrient cycling. Plant traits that vary among species and could potentially vary among populations include nitrogen (N), phosphorus (P), and lignin concentrations of plant tissue; nutrient resorption upon tissue senescence; relative growth rates; and allocation strategies (e.g. Grime 1977, 1979; Chapin 1980; Coley et al. 1985; Chapin et al. 1986, 1990, 1993; Chapin 1991). Each of these characteristics is known to affect nutrient dynamics through influences on tissue decomposition and/or ecosystem productivity.

We focus on *Metrosideros polymorpha* (Myrtaceae), an evergreen tree that dominates most rain forests in Hawaii (Kitayama and Mueller-Dombois 1995). Like many Hawaiian plants, *Metrosideros* occupies a wide range of

habitats within the archipelago, some with very different selection pressures (Carlquist 1980). In addition, gene flow among the islands is sufficiently restricted to allow differentiation to occur, and many plants and animals, including *Metrosideros*, have evolved island-endemic varieties, subspecies, or species (Carlquist 1980; Kitayama and Mueller-Dombois 1995).

To examine intrinsic differences among *M. polymorpha* populations from areas with a range of soil fertilities, we established a common garden with individuals from three mesic forests in Hawaii that represent gradients in soil N and P availability. Large differences in nutrient availability among these sites could have created distinct selection pressures on the plants, particularly for traits related to nutrient use. We tested the populations occupying the different sites for intrinsic differences in tissue quality and growth rate. Finally, to assess the influence of genetic variation on any phenotypic variation observed in field-grown plants, we compared the common garden results with in situ data obtained in earlier experiments.

Materials and methods

Sites

Our study areas are located near Thurston lava tube in Hawaii Volcanoes National Park (Island of Hawaii), in Laupahoehoe Forest Reserve (Island of Hawaii), and in the Napali-Kona Forest Reserve (Kauai) (Fig. 1). These sites have soil substrates of different ages (300-, 20,000-, and 4.1 million years old, respectively), but are relatively uniform in parent material (volcanic tephra), elevation (~1,200 m), precipitation (2,500 mm/year), average temperature (16°C), plant species composition, and topography [described in detail by Crews et al. (1995) and Kitayama and Mueller-Dombois (1995)]. Phosphorus availability (as resin P) varies six-fold among the sites and is highest at Laupahoehoe, while N availability (as resin NH_4–N and NO_3–N) varies four-fold and is highest in Kauai (Table 1, Crews et al. 1995). Long-term fertilization experiments at these sites demonstrate that plant productivity is limited by N at Thurston (Vitousek et al. 1993), P at Kauai (Herbert and Fownes 1995), and by neither N nor P alone in Laupahoehoe (Vitousek and Farrington 1997). We will therefore refer to Thurston, Laupahoehoe, and Kauai as N-limited, fertile, and P-limited sites, respectively.

Genetic analyses

To determine whether the populations of *M. polymorpha* had differentiated from one another genetically, we analyzed allozymes on individuals from each population and calculated genetic distance among populations. Eight to ten individuals from each population were scored for genotypes at ten loci encoding eight functional groups of enzymes (Table 2). We followed protocols developed for allozyme analysis of *M. polymorpha* (Aradhya et al. 1991, 1993). Briefly, about 25 mg of fresh leaf tissue was ground in 0.1 ml extraction buffer (Aradhya 1992) and absorbed onto filter paper wicks. Wicks were loaded into 12% starch gels, and electrophoresis was conducted at 4°C at 300 V and 40 mA for 6 h. The gels and running buffer were prepared with a histidine-citrate pH 6.5 solution. Gels were stained for eight enzyme systems (Table 2). Genotypes were inferred from allozyme phenotypes.

Genetic differentiation among populations was assessed by determining the genetic distance between pairs of populations. Allele frequencies were calculated for each population, then the genetic distance of pairs of populations was derived following Wright (1978). A genetic distance greater than zero indicates some degree of genetic differentiation among populations, and a distance of one indicates complete divergence.

Common garden setup

In July 1996, 10–40 cm tall seedlings of *M. polymorpha* were collected from fallen tree trunks, transplanted to 2-gallon pots, and placed in an open area at the University of Hawaii Volcano Experimental Farm in the Olaa Forest Reserve, Hawaii. A mixture of sand, vermiculite, and cinder was used as potting soil. Pots were rearranged at random every 3 months to reduce effects of environmental heterogeneity within the garden site. Collection from nurse logs ensured that seedlings experienced a relatively common rooting substrate across sites before transplant. Maternal effects on seedling phenotypes are likely to be a minimal source of variation, as seed sizes of *M. polymorpha* are small (about 0.1 mg; Corn 1972).

Response to nutrient availability was examined through N and P fertilization treatments in the common garden. Seedlings received either high or low levels of N and P in a factorial design. Plants in high N and P treatments received 6 mg P $month^{-1}$ (as triple superphosphate) and 22.5 mg N $month^{-1}$ (as ammonium nitrate), respectively. Low levels of N and P were 10% of high fertilization levels. Overall, at least ten individuals from the three sites were assigned each of four possible treatments: high N/high P, high N/low P, low N/high P, or low N/low P. All plants received

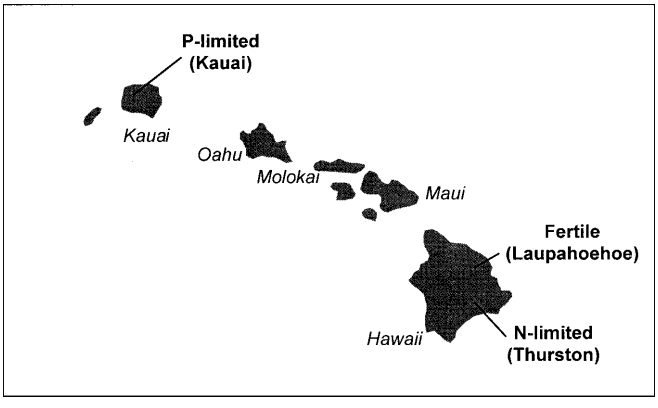

Fig. 1 Locations of chronosequence sites across the Hawaiian Island chain

Table 1 In situ phosphorus and nitrogen availability. Resin N is the sum of resin ammonium-N and resin nitrate-N. Data are from Crews et al. (1995), and numbers are means ± 1 SE

Site	Nutrient status	Site age (year)	Resin P (μg bag^{-1} day^{-1})	Resin N (μg bag^{-1} day^{-1})
Thurston	N-limited	300	0.20±0.08	3.31±1.56
Laupahoehoe	Fertile	20,000	1.21±0.28	12.37±3.32
Kauai	P-limited	4,100,000	0.41±0.17	14.41±7.20

Table 2 Enzymes resolved in *Metrosideros polymorpha*

Enzyme	EC number	Locus
Cytosol aminopeptidase	EC 3.4.11.1	*Cap*
Fructose-bisphosphate aldolase	EC 4.1.2.13	*Fba*
Glucose-6-phosphate isomerase	EC 5.3.1.9	*Gpi*
Isocitrate dehydrogenase	EC 1.1.1.42	*Idh*
Malate dehydrogenase	EC 1.1.1.37	*Mdh-1* *Mdh-2*
Peroxidase	EC 1.11.1.7	*Per*
Phosphogluconate dehydrogenase	EC 1.1.1.44	*Pgdh-1* *Pgdh-2*
Shikimate dehydrogenase	EC 1.1.1.25	*Skdh*

identical amounts of potassium (as potassium sulfate) and calcium and magnesium (as dolomite) at sufficient levels to ensure that these nutrients were not limiting to growth.

At the onset of the experiment, an additional set of seedlings was used to estimate allometric relationships between seedling height and dry biomass. A separate equation was developed for plants from each site. Only aboveground biomass was included, as root systems could not be collected intact from the nurse logs. Seedling heights were measured in September 1996 to calculate initial biomass.

Leaf and root characteristics

To identify and avoid leaves produced on seedlings prior to transplant, all leaves present immediately after transplant were marked with wire twist ties. By January 1998, nearly all tagged leaves had dropped, indicating that most leaves on the plants had grown since transplant. In February 1998, we collected active, fully expanded leaves from each plant for nutrient analyses and leaf mass per unit area (LMA) measurements. For senescent leaves, we placed 1-cm-mesh plastic netting around the base of each seedling stem in June 1998, and returned 3 weeks later to collect leaves that had senesced and dropped into the netting. To calculate LMA of active and senescent leaves, leaf areas were measured within 2 h of collection on a digital area meter (Delta T). Leaves were then dried for 3 days at 70°C and weighed.

In January 1998, a bulb corer was used to collect a 5-cm diameter by 10-cm deep soil core from each of the potted seedlings. Roots were washed four times in deionized water. Fine roots (<2 mm diameter) that were neither clearly active nor clearly dead (based on color and texture) were classified as senescent and used for measurements of tissue quality. Since seedlings had few fine roots upon transplant, the majority of collected roots had grown after transplanting.

To determine lignin concentrations of senescent leaves and roots, dried tissue was ground to at least 20 mesh. Lignin concentrations were measured by extraction in acetyl bromide following the procedure of Iiyama and Wallis (1990) and using a U-2000 spectrophotometer (Hitachi) with a pine standard from the United States National Bureau of Standards. For total N and P of active and senescent leaves, and senescent roots, dried tissue was digested at 380°C in sulfuric acid with a mercuric oxide catalyst. Concentrations of N and P were assessed using an Alpkem RFA/2 continuous flow autoanalyzer (Alpkem Corporation, Wilsonville, Oregon) and were compared to a pine standard. We calculated resorption of N and P on an area basis as

$$1-\left(\frac{\mathrm{LMA}*(\%\mathrm{Nor}\%\mathrm{P})_{\mathrm{senescent}}}{\mathrm{LMA}*(\%\mathrm{Nor}\%\mathrm{P})_{\mathrm{active}}}\right) \quad (1)$$

where $(\%\mathrm{N}\text{ or }\%\mathrm{P})_{\mathrm{senescent}}$ is the percentage of N or P in senescent tissue, and $(\%\mathrm{N}\text{ or }\%\mathrm{P})_{\mathrm{active}}$ is that of active tissue.

Prediction of leaf decomposition

The expected decomposition rate of senescent leaves was calculated for each common garden plant based on its lignin and N levels by using the following linear regression derived by Vitousek and Hobbie (2000): Portion of mass loss after 1 year =1.23+(-0.051)(%lignin)+(0.63)(%N).

This equation is the best fit (r^2=0.43) for a dataset derived by decomposing *M. polymorpha* litter in a common site and measuring mass loss after 1 year. In the dataset, lignin concentrations ranged between 10.8% and 28.0%, and N concentrations varied from 0.28% to 0.85%.

Relative growth rate

Relative growth rate (RGR) was calculated following Chiariello et al. (1989). In September 1996, initial biomass was estimated using allometric equations (height versus weight, described above). In July 1998, seedlings were harvested and dried to determine final aboveground biomass. Belowground biomass was excluded from RGR calculations because initial root weight was difficult to estimate.

Statistics

Statistical analyses were performed with Systat version 8.0 for Windows (SPSS 1998). Data were log-, square root-, or arcsine-transformed. Three-way ANOVAs (including all possible two-way interactions) were conducted with site, N treatment, and P treatment as independent variables. Tukey-Kramer tests on least-square means were conducted for pairwise comparisons (Sokal and Rohlf 1995). We tested for normal distribution of data by calculating standard deviates for each sample, pooling all deviates, then applying a Kolmogorov-Smirnov test for goodness of fit (Sokal and Rohlf 1995). We used an F_{max}-test to confirm homogeneity of variances (Sokal and Rohlf 1995). The latter two tests indicated that normality and homogeneity of variances were achieved for each ANOVA.

Comparison of common garden and in situ results

To evaluate the role of genetic variation in any phenotypic variation observed in situ, we compared our common garden results with published data obtained from *M. polymorpha* individuals growing in the sites. In every case, these in situ data were collected on adult trees, so our ability to directly compare values was somewhat limited. For this reason, the field data were excluded from any statistical analyses.

Results

Genetic analyses

Some genetic differentiation had occurred among the three populations. The population from the N-limited site was most distinct, with a genetic distance of 0.053 between that population and the others (Fig. 2). The populations from the fertile and P-limited site were most closely related, with a genetic distance of 0.036. Two of the ten loci resolved, *Gpi* and *Skdh*, had no variation among populations in allele frequency (Table 3).

Tissue quality of leaves

In this and the following sections, interactions between population, P treatment, or N treatment were not signifi-

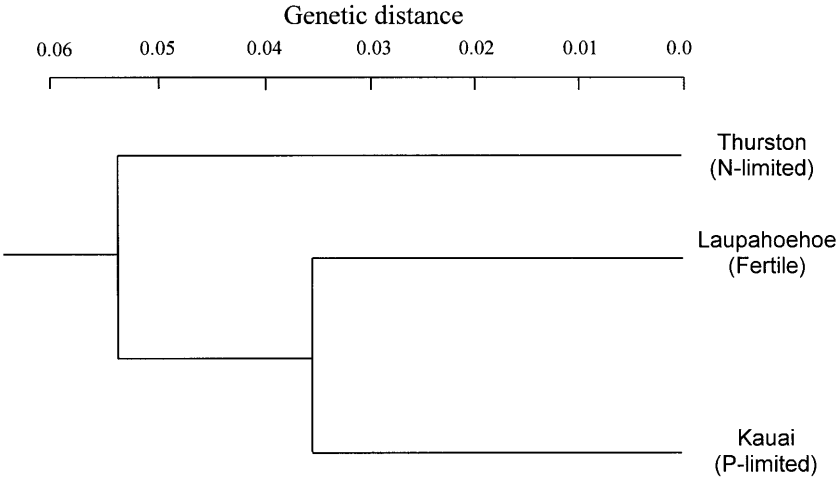

Fig. 2 Genetic distance between pairs of populations of *Metrosideros polymorpha*. Distances were calculated from allele frequencies at 10 loci (see Table 3)

Table 3 Allele frequencies at each locus for each population, as assessed through allozyme analyses

Locus	Allele	Allele frequencies		
		N-limited (Thurston)	Fertile (Laupahoehoe)	P-limited (Kauai)
Cap	A	0.444	0.357	0.450
	B	0.389	0.286	0.450
	C	0.167	0.357	0.100
Fba	A	0.722	0.875	0.900
	B	0.278	0.125	0.100
Gpi	A	1.000	1.000	1.000
	B	0	0	0
Idh	A	1.000	0.917	1.000
	B	0	0.083	0
Mdh-1	A	0.889	1.000	0.950
	B	0.111	0	0.050
Mdh-2	A	0.444	0.938	0.900
	B	0.556	0.063	0.100
Per	A	0.938	1.000	1.000
	B	0.063	0	0
Pgdh-1	A	0.917	0.938	1.0
	B	0.083	0.063	0
Pgdh-2	A	1.000	1.000	0.944
	B	0	0	0.056
Skdh	A	1.000	1.000	1.000
	B	0	0	0

cant unless explicitly stated. Lignin concentrations of senescent leaves, which have a strong negative influence on decomposition rates of tissues (e.g. Aber and Melillo 1982; Aber et al. 1990), differed significantly among populations (Fig. 3; ANOVA: $F_{2,42}$=3.839, P<0.030). Plants from the fertile site had lower lignin contents than did those from the N-limited site (fertile: 16.3%, N-limited: 20.1%; Tukey-Kramer: P<0.025). The variability of lignin concentrations from common garden seedlings approached that observed in plants growing in situ (Fig. 3; Vitousek 1998). In contrast to the common garden, in situ lignin concentrations are highest in the fertile site. Lignin concentrations in common garden plants were not affected significantly by fertilization treatment.

Nitrogen concentrations, which are positively related to decomposition rate in this system (Vitousek and Hobbie 2000), were lower than those observed in the field, and did not vary significantly among populations or fertilization treatments in active leaves (Fig. 4 a). However, percent N in senescent leaves differed significantly among populations (Fig. 4b; ANOVA: $F_{2,97}$= 32.642, P<0.001), because the populations varied in the proportion of N resorbed from leaves upon senescence (Fig. 4c; ANOVA: $F_{2,81}$=20.832, P<0.001). Nitrogen resorption was higher in plants from the N-limited site (53%) versus both the fertile site (23%; Tukey-Kramer: P<0.001) and P-limited site (40%; Tukey-Kramer: P<0.006). Resorption was also significantly greater in the P-limited population than in the fertile site population (Tukey-Kramer: P<0.002). Due to the pattern of resorption, plants from the fertile site had greater N concentrations in senescent leaves (0.47%) than did those from the N-limited (0.29%; Tukey-Kramer: P<0.001) or P-limited (0.33%; Tukey-Kramer: P<0.001) sites (Fig. 4b). This same pattern in senescent leaf N was found in situ, with a greater degree of variation (Vitousek 1998). Neither senescent leaf %N nor N resorption responded significantly to fertilization treatment.

Phosphorus concentrations in leaves varied substantially among populations and, unlike N, were affected by fertilization treatment. Specifically, percent P in active leaves differed significantly among sites (Fig. 5a; ANOVA: $F_{2,120}$=12.688, P<0.001) and was higher in plants from the P-limited (0.154%) versus N-limited (0.103%; Tukey-Kramer: P<0.001) or fertile (0.101%; Tukey-Kramer: P<0.001) sites. Likewise, P concentrations in senescent leaves varied significantly among populations (Fig. 5b; ANOVA: $F_{2,97}$=24.898, P<0.001), but was lower in the N-limited population (0.032%) than in the fertile (0.057%; Tukey-Kramer: P <0.001) or P-limited (0.063%; Tukey-Kramer: P<0.001) groups. High N fertilization reduced P concentrations in active leaves (low N: 0.152%, high N: 0.084%; ANOVA: $F_{1,97}$=43.343, P<0.001) and in senescent leaves (low N: 0.067%, high N: 0.038%; ANOVA: $F_{1,120}$=72.624, P<0.001). In senescent leaves only, high P fertilization

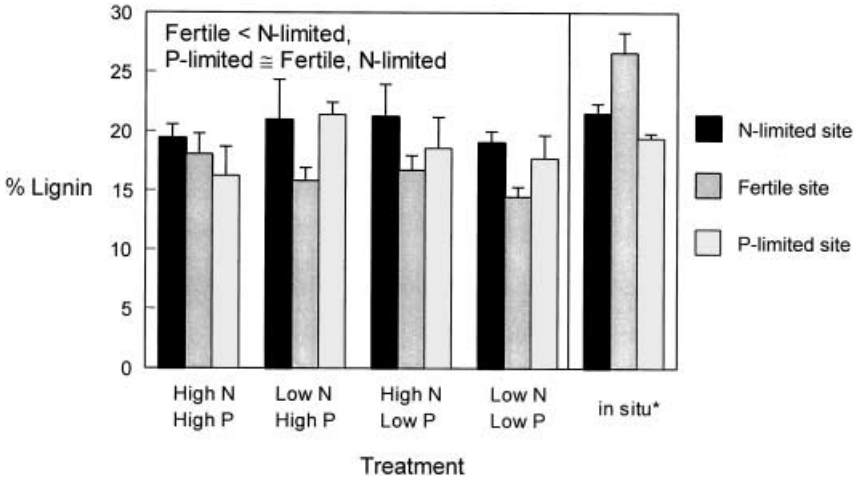

Fig. 3 Lignin concentrations of senescent leaves from common garden plants. Plants were grown from seedlings collected at each field site. Significant pairwise differences are noted in graph. *Bars* represent means of 2–5 samples. *Error bars* are +1 SE. *In situ data from Vitousek (1998)

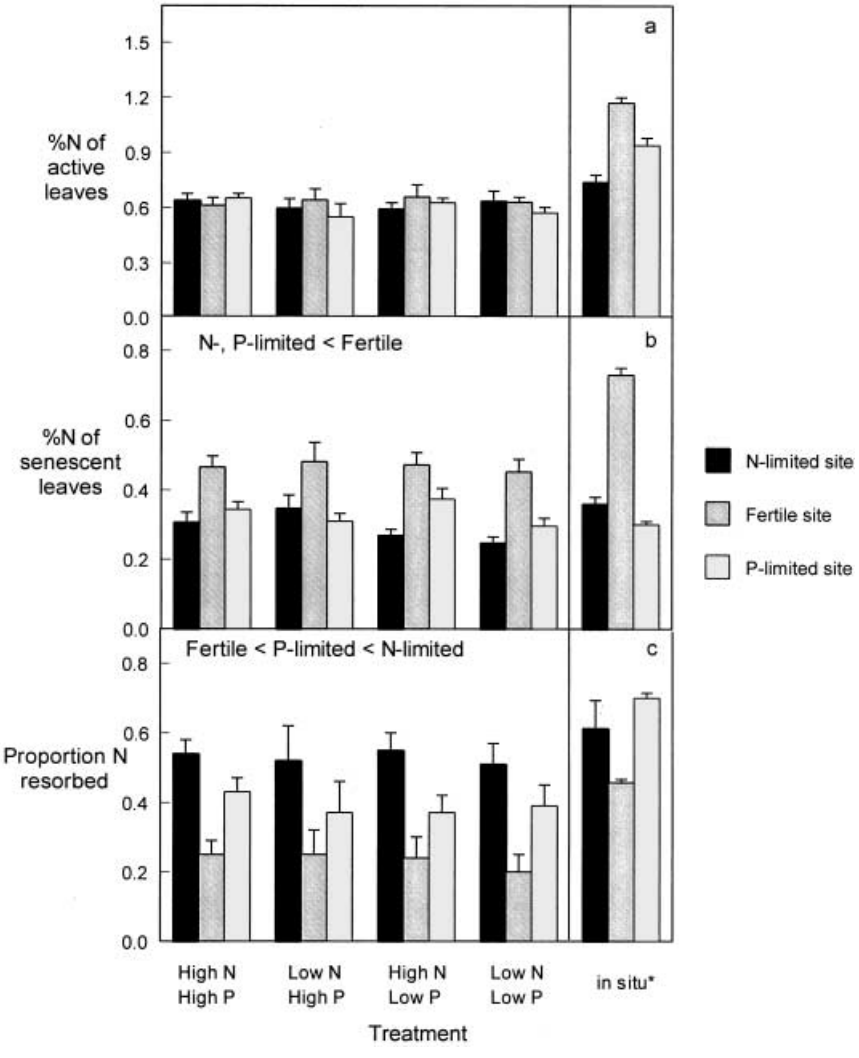

Fig. 4 Tissue N of leaves from common garden plants: percentage nitrogen in **a** active and **b** senescent leaves, and N resorption upon leaf senescence (**c**). Plants were grown from seedlings collected at each field site. Significant pairwise differences among garden-grown leaves are noted in the graph. *Bars* represent means of 4–11 samples. *Error bars* are +1 SE. *In situ data from Vitousek (1998)

increased percentage P (low P: 0.046%, high P: 0.056%; ANOVA: $F_{1,97}$=5.177, P<0.026). In addition, in senescent leaves, plants receiving the low N/high P treatment had higher P concentrations (0.083%) than did those receiving all other treatments, and those receiving the low N/low P treatment (0.054%) had higher concentrations than did the high N/high P (0.037%) and high N/low P (0.039%) plants (Tukey-Kramer: P <0.05 for all comparisons). These differences drove a significant N- by P-treatment interaction (ANOVA: $F_{1,97}$=7.687, P<0.008).

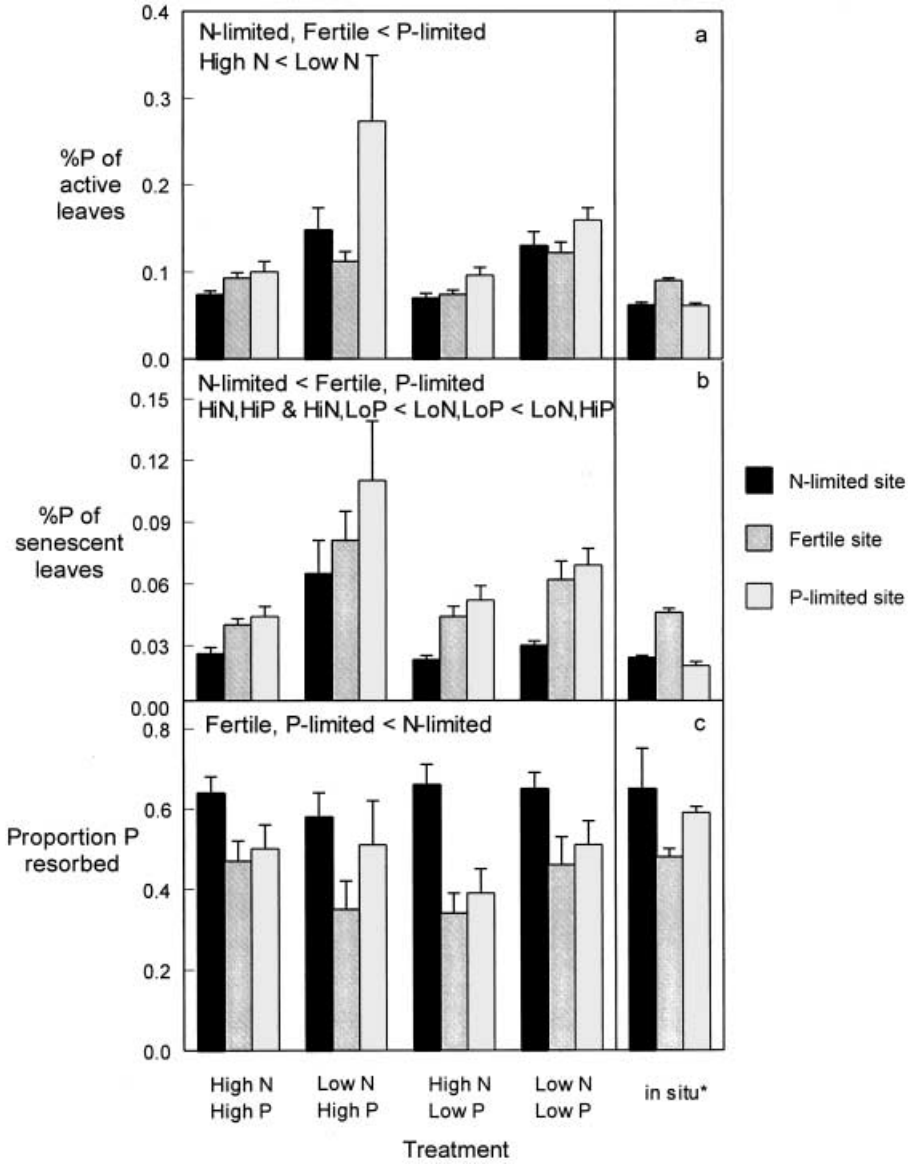

Fig. 5 Tissue P of leaves from common garden plants: percentage phosphorus in **a** active and **b** senescent leaves, and P resorption upon leaf senescence (**c**). Plants were grown from seedlings collected at each field site. Significant pairwise differences among garden-grown leaves are noted in graph. *Bars* represent means of 4–11 samples. *Error bars* are +1 SE. *In situ data from Vitousek (1998)

Phosphorus resorption varied significantly among populations (Fig. 5c; ANOVA: $F_{2,87}$=14.986, P<0.001), and was significantly higher in those from the N-limited site (64.1%) than from the fertile (40.2%, Tukey-Kramer: P<0.001) or P-limited (47.1%, Tukey-Kramer: P<0.002) site. Phosphorus resorption was not affected significantly by N or P fertilization level.

Phosphorus concentrations in active and senescent leaves did not mirror the patterns seen in situ, where percentage P was highest in the fertile site (Fig. 5a, b; Vitousek 1998). Ranges and levels of percentage P among populations in the garden were close to that observed in situ, although active leaf percentage P in seedlings from the P-limited site were near those seen in P-fertilized, field-grown plants in that site (0.212%; Vitousek 1998; in situ fertilization data not shown).

Predicted decomposition rate of senescent leaves varied significantly among populations (Fig. 6; $F_{2,41}$=7.737, P<0.002). Because plants from the fertile site had senescent leaves with the lowest percent lignin and highest percent N, their leaves had significantly higher predicted decomposition rates (67.8% loss in 1 year) than did the N-limited (38.1%; Tukey-Kramer: P<0.003) or P-limited sites (51.1%; Tukey-Kramer: P<0.028), based on the linear regression developed by Vitousek and Hobbie (2000). Fertilization treatments did not significantly affect predicted rates. Variation among sites was more pronounced in the common garden versus the field (Fig. 6; Vitousek 1998).

Tissue quality of senescent roots

Nitrogen concentrations in common garden roots were much lower than those in the field, while P concentrations were much higher (Fig. 7 b, c). Tissue quality of senescent roots did not generally vary among populations, although there were significant responses to nutri-

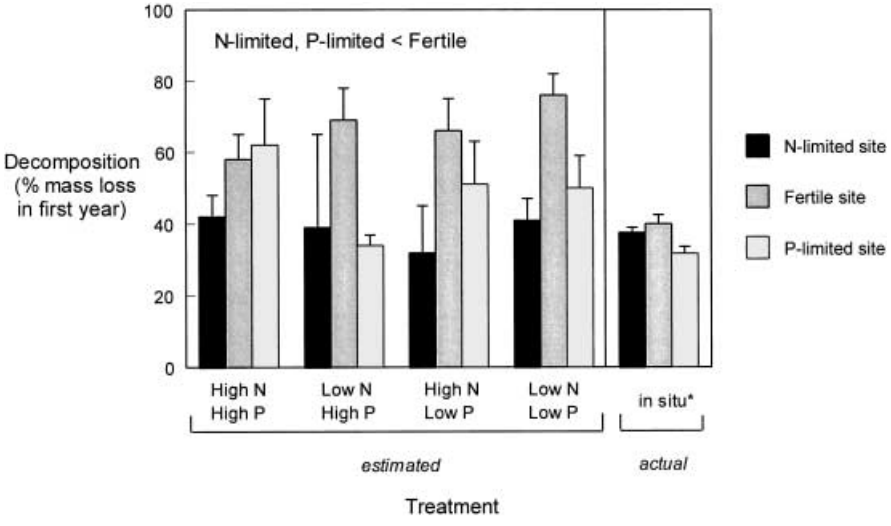

Fig. 6 Estimated decomposition rate of leaf litter from common garden, and actual decomposition rates in situ. Estimations are based on tissue concentrations of lignin and N. Plants were grown from seedlings collected at each field site. Significant pairwise differences among garden-grown leaves are noted in graph. *Bars* represent means of 2–5 samples. *Error bars* are +1 SE. *In situ data are actual decomposition rates as reported in Vitousek (1998)

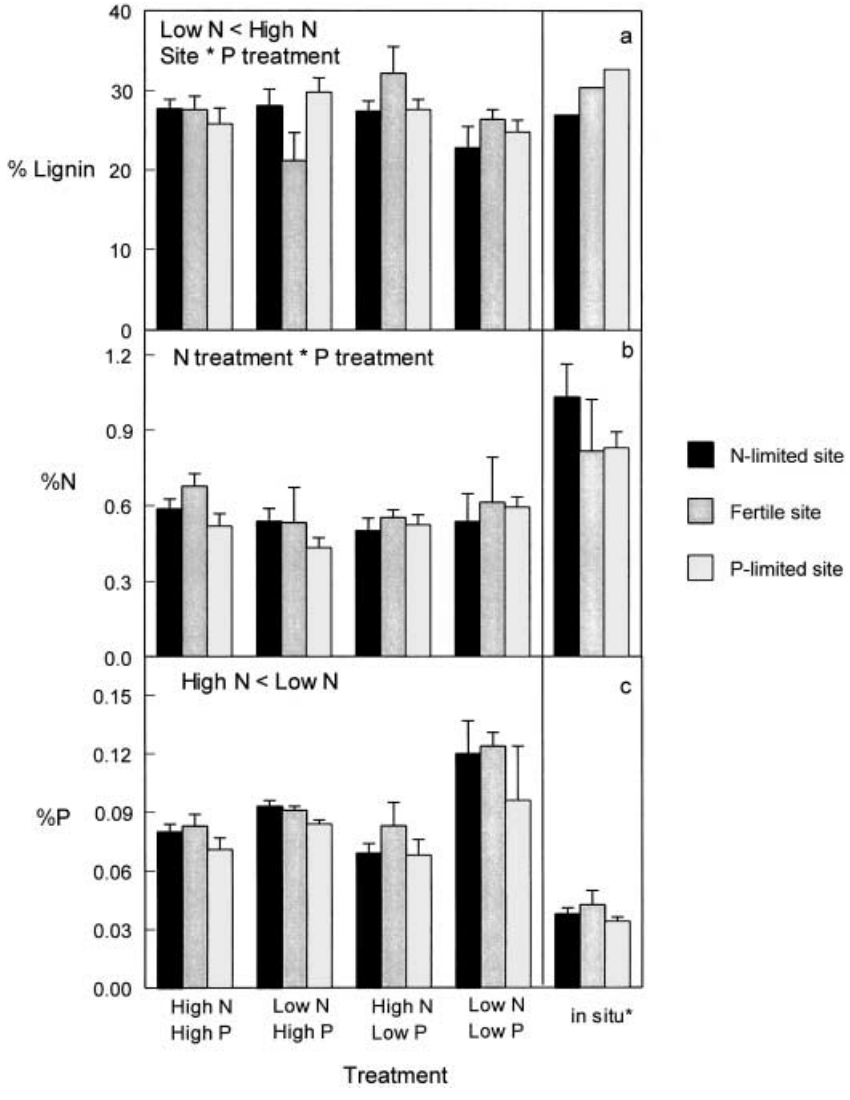

Fig. 7 Tissue quality of senescent roots from common garden and of live roots in situ: **a** percentage lignin, **b** percentage N, **c** percentage P. Plants were grown from seedlings collected at each field site. Significant pairwise differences among garden-grown roots are noted in graph. *Bars* represent means of 2–10 samples. *Error bars* are +1 SE. *In situ data are from Ostertag and Hobbie (1999) and Ostertag (2000)

ent treatments. These patterns are consistent with in situ observations (Fig. 7; Ostertag and Hobbie 1999; Ostertag 2000). The only significant population effect occurred with lignin concentrations (Fig. 7a), in which there was a significant interaction between population and P treatment (ANOVA: $F_{2,75}$=3.685, P<0.031). Specifically, plants from the fertile site tended to have higher lignin concentrations with lower P additions (although this

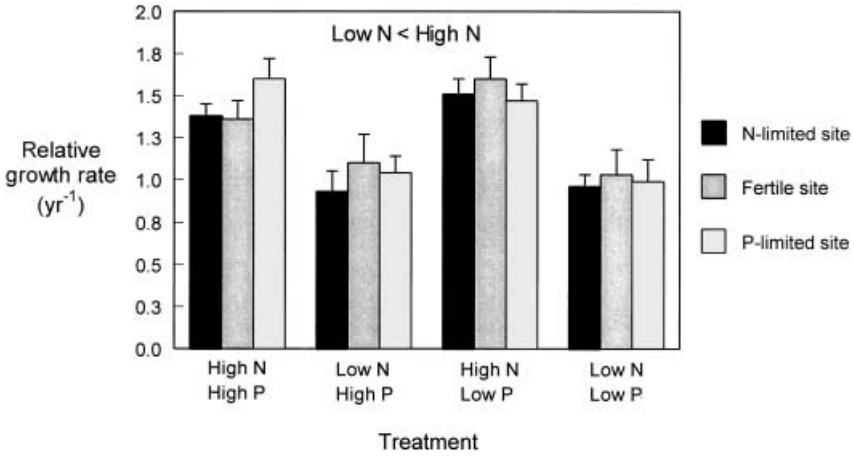

Fig. 8 Relative growth rate of aboveground biomass in seedlings from common garden. Plants were grown from seedlings collected at each field site. Significant pairwise differences are noted in graph. *Bars* represent means of 9–13 samples. *Error bars* are means +1 SE

response was non-significant in a Tukey-Kramer test), while other populations had a weaker response to P availability. Lignin concentrations were greater under high versus low N fertilization (27.7% and 26.1%, respectively; ANOVA: $F_{1,75}$=5.349, P<0.025), while P fertilization had no significant effect. The degree of variation among populations in this trait was similar in the common garden and in the field (Fig. 7; Ostertag and Hobbie 1999).

Nitrogen and P concentrations in senescent roots did not vary significantly among populations (Fig. 7b, c), a pattern also found in field-grown plants (Ostertag 2000). High N treatments produced roots with significantly lower percentage P (Fig. 7c; high N: 0.075%, low N: 0.103%; ANOVA: $F_{1,57}$=13.294, P<0.002). In addition, there was a significant interaction between N treatment and P treatment for percentage N of roots (Fig. 7b; ANOVA: $F_{1,58}$=4.102, P<0.048) – the high N/high P (0.58%) and low N/low P (0.57%) treatments produced the higher N concentrations than the high N/low P (0.53%) and low N/high P (0.50%) treatments, although pairwise differences were not significant in Tukey-Kramer tests. There were no other fertilization effects on N or P concentrations of roots.

Relative growth rate

To determine RGR, we used allometric equations to estimate initial aboveground biomass of seedlings upon transfer to the common garden. Separate equations (height versus weight) were derived for each population, with r^2 values of 0.85, 0.93, and 0.95 for the N-limited, fertile, and P-limited sites, respectively. RGRs did not vary significantly among populations, although growth was significantly faster in the high N treatments (Fig. 8; low N: 1.010 year^{-1}, high N: 1.481 year^{-1}; ANOVA: $F_{1,124}$=49.136, P<0.001). Phosphorus fertilization did not affect growth rate.

Discussion

The populations of *M. polymorpha* from the fertility gradient had diverged from one another, although genetic differences were small (Fig. 2). The genetic distance of 0.053 between the two Hawaii Island populations (N-limited and fertile sites) was comparable to the distance among populations of *M. polymorpha* collected from an elevation gradient on Haleakala crater on the island of Maui (0.024–0.071; Aradhya et al 1993). A similar degree of differentiation had occurred among populations collected from two mountain ranges in the island of Oahu (Aradhya 1991).

Even though the populations were closely related, their senescent leaves differed intrinsically and significantly in several traits related to decomposition, including lignin, N, and P concentrations. For example, senescent leaves from the fertile-site population had significantly lower lignin concentrations than did those from the N-limited site (Fig. 3). This pattern follows the resource availability hypothesis by Coley et al. (1985) that slow-growing species from relatively infertile environments tend to invest extra resources in anti-herbivore defenses like lignin and tannins.

Garden-grown leaves also varied significantly among populations in P content. However, P availability in the common garden appears to be higher than that of even the fertile site, as percentage P in active leaves and senescent roots was greater in the common garden than in situ (Figs. 5a, 7c). In these high nutrient conditions, P concentrations in active leaves were greatest in plants from the P-limited site (Fig. 5a). The same response to fertilization was observed in the field; *M. polymorpha* in P-limited sites accumulated much more foliar P following P fertilization than did those in the N-limited or fertile sites (Vitousek 1998). This result is consistent with Chapin's (1980) hypothesis that plants from infertile sites respond to high nutrient concentrations differently than do those from fertile sites. Given the same amount of nutrients, slow growing plants from N- or P-limited sites will store the nutrients for future growth. In contrast, plants from fertile sites tend to grow faster and essentially dilute tissue N or P with extra photosynthate. Unfortu-

nately, we can draw no conclusions about possible intraspecific variation in leaf P content under low P status, because the common garden seedlings may not have been P-limited in the low P treatment.

In contrast to P availability, N availability seems to have been reduced in the garden compared to the field, since N concentrations in active leaves and senescent roots of garden plants were lower than those of trees growing in all sites (Figs. 4a, 7b). In these relatively low N conditions, common garden plants did not differ from one another in the percentage N of active leaves, nor were there any significant differences among fertilization treatments (Fig. 4a). This fertilization response is consistent with the significant increase in growth rate under higher N applications (Fig. 8) – additional tissue N may be diluted with additional biomass. Nevertheless, higher N resorption in the N- and P-limited populations produced senescent leaves with significantly lower N concentrations compared to plants from the fertile site (Fig. 4). Nitrogen resorption may contribute to N use efficiency (productivity per unit uptake) in plants from the N-limited site.

Recent reviews have suggested that nutrient resorption is not generally related to nutrient availability among plants growing in different sites, and is not necessarily reduced after fertilization (Aerts 1996; Killingbeck 1996). Nonetheless, intrinsic differences among genetic varieties of the same species were not addressed. Populations of *M. polymorpha* have a similar origin (i.e. the founder group which initially colonized the islands) and may have diverged in nutrient-related traits across the fertility gradient. Variation among the populations therefore may be more directly related to nutrient availability (versus other environmental factors or developmental constraints) than is typical of variation among species.

Intrinsic differences in tissue quality among these populations may produce differences in decomposition rates of senescent leaves. Across most treatments, plants from the fertile site had lower lignin concentrations and higher N concentrations in garden-grown senescent leaves. For field populations of *M. polymorpha*, decomposition was correlated positively to percent N, and negatively to percent lignin in senescent leaves (Vitousek and Hobbie 2000). Based on a linear regression derived from this relationship, predicted rates in the fertile-site population were up to twice as fast as those in plants from the N-limited sites (Fig. 6). Since faster decomposition rates increase rates of nutrient cycling in ecosystems (Flanagan and Van Cleve 1983; Hobbie 1992), variation in tissue quality among *M. polymorpha* populations could feed back to affect soil characteristics. Plants from the fertile site may augment the relatively high N or P availability there (Crews et al. 1995), while those from the N- or P-limited sites may reduce soil fertility to some extent by producing slowly decomposing litter that will then immobilize a larger portion of N and P in the system.

Growth rate also affects nutrient cycling as a component of productivity, but this factor did not vary significantly among populations (Fig. 8). This result is not consistent with the nutrient use scenario suggested by Chapin (1980), which suggests that plants from fertile sites should have faster growth rates and should respond more strongly to increases in nutrient availability than should populations from relatively infertile areas.

These findings complement other common garden experiments that have examined the role of genetic or ecotypic variation in ecosystem function. Pearson (1998) found that in three populations of Hawaiian *Acacia koa*, capacity for N fixation was positively related to the P availability of the populations' native sites. Growth rates were also slowest in those from the site with lowest P availability, a drier site near our P-limited site. Furthermore, in a study by Miranda and Boddey (1987), isotopic evidence indicated that ecotypes of *Panicum maximum* vary in N fixation rates. Bazzaz et al. (1995) reported that genotypes of *Abutilon theophrasti* and *Betula alleghaniensis* differed in growth response to elevated CO_2, although accompanying changes in productivity of intact communities were not necessarily indicated. In addition, Holland et al. (1992) found that grasses native to heavily grazed sites maintained higher productivity with grazing than did those from areas exposed to less herbivory. Nitrogen mineralization levels were also estimated to be higher in systems dominated by the grazing-tolerant population. As a whole, our studies indicate that even small degrees of genetic differentiation among plant groups can influence aspects of nutrient cycling. Finally, we suggest that genetic variation within species may be an important consideration in conservation policy.

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