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RESEARCH ARTICLE

Nutrient-use strategy and not competition determines native and invasive species response to changes in soil nutrient availability

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Non-native invasive plants often outcompete native species under high resource availability. Restoration techniques that lower resources may, therefore, create favorable conditions for resource conservative native species over resource exploitative invasive species. Research on this topic has focused on temperate grass and forb-dominated ecosystems and has rarely been tested for woody species or tropical vegetation. We evaluated growth, resource-use efficiency (RUE), ecophysiology, and competition (i.e. a relative interaction index based on biomass) of four woody native and two dominant invasive species from Hawaiian wet and dry tropical ecosystems in a greenhouse experiment. Density of plants was constant and species were grown with either a conspecific or the invasive species from that ecosystem type across a gradient of soil nutrient availability. Instantaneous photosynthetic rates varied minimally across nutrient availability. However, both invasive and one native species increased leaf area as nutrients increased, providing more photosynthetic area and increasing total biomass. Nitrogen RUE decreased with increasing nutrient availability for all but one native species, while phosphorus RUE remained constant for all but one native species. Competitive interactions were weak, variable, and not significantly impacted by soil nutrients. Overall, plants categorized as invasive or resource exploitative had larger changes in response variables with increasing soil nutrients compared to those categorized as native or resource conservative. These results suggest that manipulating soil nutrient availability is a potentially viable restoration tool for at least some woody species in tropical ecosystems. However, predicting restoration success requires understanding species-specific ecophysiological traits determining response to altered environmental conditions.

Key words: carbon amendments, resource conservative, resource exploitative, resource-use efficiency, restoration, soil nutrient availability, tropical ecosystems

Implications for Practice

- Restoration of invaded tropical ecosystems with high resource availability may be facilitated by soil nutrient manipulation (e.g. carbon amendments to lower soil nutrients) when native species are resource conservative and invasive species are resource exploitative.
- Decreasing soil nutrient availability is less likely to be successful for restoration when dominant native and invasive species have similar ecophysiological traits.
- Understanding differences in individual species resource-use strategies is critical for successful utilization of soil nutrient manipulation. It is too simplistic within a given site to categorize native and invasive species broadly as high and low resource-use efficiency.
- Field studies are needed to determine if soil nutrient manipulation will be useful with mature plant communities under variable field environmental conditions.

Introduction

Invasion by non-native species is a global threat to biodiversity and ecosystem function (Millennium Ecosystem Assessment 2005). Non-native invasive species (hereafter invasive species)

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often invade areas of high resource availability, owing their success in these environments to traits of rapid resource uptake and efficient utilization (Davis et al. 2000). However, the success of invasive species, in general, is often context and species dependent and can vary with resource availability (Daehler 2003; Funk & Vitousek 2007). Disentangling how resource availability, specifically soil nutrient availability, affects interactions between native and invasive species may provide useful insights into how resource strategies shape interactions in invaded plant communities.

In ecosystems where native plants are adapted to low resource supply, decreasing soil nutrient availability may reduce growth and reproduction, and/or increase mortality, of invasive species relative to that of native species (Blumenthal et al. 2003; Burke et al. 2013). One method for decreasing soil nutrient supply is to promote the uptake of available inorganic nutrients by soil microbes through the application of a metabolic substrate that is high in carbon and low in nutrients, such as sucrose, cellulose, or sawdust (Alpert 2010). While multiple studies have shown that carbon amendments can be effective in immobilizing nitrogen and thereby reducing soil nitrogen availability (Gallardo & Schlesinger 1995; Alpert 2010; Perry et al. 2010; Burke et al. 2013), the effects of a reduction in soil nutrient availability on native versus invasive species success have been mixed. Some studies have shown that carbon amendments successfully increase native biomass while decreasing invasive biomass (Allen & Zink 1998; Blumenthal et al. 2003; Perry et al. 2004; Prober et al. 2005; Eschen et al. 2007). However, other studies have shown that carbon amendments can reduce native species growth as much or more than invasive species (Morghan & Seastedt 1999; Monaco et al. 2003; Suding et al. 2004; Gendron & Wilson 2007). The mechanisms responsible for these contrasting outcomes are often not tested, but likely involve both the ecophysiological traits of the plants and the initial resource conditions of the ecosystem (Steers et al. 2011).

In general, nutrient manipulation should be the most successful where native species are resource conservative and invasive species are resource exploitative (Burke & Grime 1996; Daehler 2003). Resource exploitative species are typically characterized by rapid growth and low resource-use efficiency (RUE), whereas resource conservative species are typically characterized by slow growth and high RUE. Based on differences in resource-use strategy, increased nutrient availability often facilitates the establishment and growth of invasive species that are more plastic in response to changes in resource availability, whereas native species are often less able to take advantage of increased resources (Vitousek et al. 1987b; Hobbs & Huenneke 1996; Davis et al. 2000). Moreover, where nutrient supply is already low, native species have been found to be relatively unresponsive to decreased resource availability (Davidson et al. 2011). These resource-use strategy generalizations are often used to hypothesize how native and invasive species will respond to changes in resource availability.

Grouping species into native and invasive species with the assumption that native species are generally resource conservative and invasive species are resource exploitative does not, however, always hold true. This is evident in carbon amendment studies where invasive species growth under low nutrient availability is equal to or more than native growth (Morghan & Seastedt 1999; Monaco et al. 2003; Suding et al. 2004; Gendron & Wilson 2007). Further, some invasive species have been found to be as efficient with resource use as native species when resources are limiting, displaying traits typically associated with resource conservative species (Funk & Vitousek 2007). An understanding of a species ecophysiological response to soil nutrient availability may, therefore, help explain the response of individual species to soil nutrient manipulation experiments more than a simple dichotomy between native versus invasive.

Most research examining soil nutrient manipulation for restoration purposes has not linked growth responses of species to their ecophysiological traits. Surprisingly, the effect of nutrient-based restoration strategies on native versus invasive competition has received no attention in tropical systems or with woody species (Alpert 2010). To address these information gaps, we tested the effects of soil nutrient availability on a suite of common and primarily woody native and invasive species from two distinct ecosystem types (Hawaiian dry montane shrubland and Hawaiian wet montane forest) to determine the impacts of soil nutrient manipulation on invasive versus native species in a greenhouse study. This study had two major objectives: (1) to examine plasticity of native and invasive species in regards to growth, photosynthesis, and RUE across varying soil nutrient availabilities and (2) to determine if soil nutrient manipulation alters competitive interactions (i.e. growth, reproductive output, survival, and competition indices) of native and invasive species. We hypothesized that growth, photosynthesis, and RUE of native species, assumed a priori to be resource conservative, would respond minimally to changes in soil nutrient availability, while invasive species, assumed a priori to be resource exploitative, would show a more plastic response (H1). In addition, we hypothesized that soil nutrient manipulation would alter competitive interactions between native and invasive species through a reduction in soil nutrient availability, where native species would have a competitive advantage over invasive species under low soil nutrient availability (H2).

Methods

The study was conducted at the Institute of Pacific Islands Forestry (IPIF) greenhouse facility in Hilo, HI (19°41′55.6″N 155°05′43.5″W; 109 m asl). Two parallel experiments were run from June 2014 to June 2015 using common native and invasive species that are dominant in wet and dry montane ecosystems in Hawai‘i. *Dodonaea viscosa* Jacq. (a‘ali‘i), *Metrosideros polymorpha* Gaud. (‘ōhi‘a), and *Sophora chrysophylla* (Salisb.) Seem. (māmane) were utilized as the native woody species for the dry ecosystem, and *Acacia koa* A. Gray (koa) and *M. polymorpha* as the native woody species for the wet ecosystem. *Cenchrus setaceus* (Forssk.) Chiov. (fountain grass), the only non-woody plant in the study, and the shrub/tree

Psidium cattleyanum Sabine (strawberry guava) were utilized as the invasive species for the dry and wet ecosystems, respectively. Species selection was based on dominance in each ecosystem type, the availability of seedlings, and ease of propagation. The invasive species used are understory invaders in Hawai'i and elsewhere in the tropics, and often become canopy dominant through alterations in competition, regeneration, and disturbance regimes. Seedlings were sourced from local nurseries except for *P. cattleyanum* and *C. setaceus* (Knauf 2016). *Psidium cattleyanum* cuttings were propagated from stem sections and seedlings were collected from local stands surrounding the greenhouse. Live clumps of *C. setaceus* were collected from Saddle Road between Hilo and Kona, and cleaned and separated into small individuals of similar size. Both species were planted in the greenhouse 5 weeks prior to the start of the study to promote establishment and root development comparable to the seedlings used for the native species.

Four hundred and eighty (i.e. 280 for the dry ecosystem, 200 for the wet ecosystem; the dry ecosystem had an additional native species and therefore more total pots) 8-L pots were planted at a constant density of two plants per pot, and each species was planted with either a conspecific or the common invasive species from that ecosystem type. In June 2014, all plants were transplanted into pots representing one of five soil nutrient availability treatments: nutrient reduction high, nutrient reduction low, control, nutrient addition low, and nutrient addition high. Each species combination was replicated eight times across all five nutrient treatments.

The nutrient treatments were applied to a base standard soil mixture of ~3.14 kg of a 50:50 soil:cinder mixture containing topsoil of the Hilo Soil Series (Medial over hydrous, ferrihydritic, isohyperthermic Acrudoxic Hydrudands [NRCS 2010]) from the Hamakua Coast of the island of Hawai'i (Table S1, Supporting Information). The Hilo Soil Series was utilized for both the wet and dry experiments as a way to isolate soil nutrient availability treatments and to allow for comparisons across ecosystems. Soil from both the wet and dry ecosystems where these plants are commonly found form from volcanic ash and lava deposits and are similar to the Andisols of the Hilo Soil Series.

Nutrient reductions were implemented using high carbon, low nutrient content substrate amendments. Based on prior work, we used a combination of sucrose, which produces a rapid but short-term reduction, and sawdust, which produces a slower but longer-term reduction in nutrient supply (Burke et al. 2013). Sucrose was obtained in the form of table sugar from local grocery stores and the sawdust was sourced from a local mill as a mixture of *Eucalyptus robusta* and *A. koa*. Target C:Ns were determined from an initial soil C:N of 13.5 (SD = 1.07, $n = 6$) to represent high (C:N ~ 35) and low (C:N ~ 20) levels of nutrient immobilization (i.e. nutrient reduction high, and nutrient reduction low treatments). The quantity of sucrose and sawdust added to each treatment was determined from the initial and target C:N values (Table S2). The two nutrient addition treatments were implemented using Apex 16–6-12 NPK slow-release fertilizer following the manufacturer's recommendations for low and high fertilizer applications (Table S1). All soil nutrient availability treatments were mixed into the soil and thoroughly homogenized prior to planting.

Pots were arranged randomly in the greenhouse and rotated every 3 months to minimize any effects of shading or other environmental gradients. Plants were checked every other day and watered as needed to field capacity such that water was not a limiting resource. Because the dry ecosystem plants grew much more quickly than the wet ecosystem plants under greenhouse conditions, the dry ecosystem experiment was harvested after 6 months while the wet ecosystem experiment was harvested after 1 year. During the harvest, root distribution was observed and noted to be consistent throughout the pots, and no plants were root-bound at the time of harvest.

Growth Measurements

Initial plant measurements (height or basal diameter, and for *C. setaceus*, biomass) were conducted at the time of planting to quantify initial differences within random assignment of plants to nutrient treatments (see Statistical Analysis section). Plant mortality was quantified weekly throughout the experiment, and reproductive output (i.e. flowers and/or fruits on each individual plant) was recorded bi-monthly. At the end of the experiment, all plants were destructively harvested after 6 (dry ecosystem) or 12 (wet ecosystem) months and dried to a constant mass in a forced-air oven at 60°C to obtain belowground, aboveground, and total biomass. Relative growth rate (RGR) was calculated along with total biomass, but because these results did not differ from total biomass and carbon gain results they are not provided here.

Photosynthetic Capacity

Maximum instantaneous photosynthetic rate (A_{max}) was measured on one leaf from the most recently expanded cohort 6 months after experiment initiation in December 2014. Measurements were made with a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE) on three randomly chosen pots in each treatment for each species combination. The following conditions were maintained during measurements: constant light of 1,000 μmol m^{-2} s^{-1}, reference cell CO_2 concentration of 420 ppm, relative humidity between 55 and 65%, and temperature reflective of ambient greenhouse conditions. To scale individual leaf A_{max} to whole plant carbon gain, the six most recent fully expanded leaves were collected, analyzed on a leaf area meter, dried at 60°C to a constant mass, and weighed. The weight to area ratio for these six leaves was then used to scale photosynthesis to whole plant carbon gain based on the total weight of individual plant foliage determined from the destructive harvests.

Resource-Use Efficiency

Foliar samples collected for leaf area measurements (see Photosynthetic Capacity section, above) were analyzed for nutrient content to determine RUE, and as an index of the efficacy

of the soil nutrient availability treatments. Additional foliage was collected for nutrient analyses in the same manner as described above when the dry mass of the first six leaves was below the minimum sample size (0.25 g) for nutrient analyses. Leaf samples were dried at 60°C to a constant mass, weighed, grounded to a fine powder on a ball mill, and analyzed at the University of Hawai'i at Hilo Analytical Lab for %P, and the Cornell Stable Isotope Lab for %C and %N. During ecosystem development, P has been shown to limit plant production on older sites, whereas younger sites tend to be limited by N and intermediate-aged sites co-limited by both N and P (Crews et al. 1995; Vitousek 2004). As such, photosynthetic nitrogen (PNUE) and phosphorus-use efficiencies (PPUE) were calculated as the ratio of photosynthesis rates to leaf N or P content.

Competitive Interactions

A relative interaction index (*Rii*) was modified from Armas et al. (2004) to determine the effect of interactions between each species growing with a conspecific versus an invasive neighbor across varying soil nutrient availability:

$$Rii = (B_W - B_o) \div (B_W + B_o) \quad (1)$$

where B_w is plant biomass when grown with a non-conspecific neighbor and B_o is the mean biomass of two conspecifics grown in the same pot. In some cases, there were unequal pairs due to mortality (any pot with mortality was excluded from analyses). In these cases, the average biomass of the species grown in intraspecific competition across all replicates for that treatment and species combination were used (Tabassum & Leishman 2016). *Rii* quantifies the relative change in biomass of a target species as a result of growing with a neighbor and indicates the magnitude and direction (i.e. positive, negative, or neutral) that plants are affected by interactions with neighbors. *Rii* has defined limits [−1, 1], is symmetrical around zero, and negative values indicate suppressive effects (i.e. decreased biomass) while positive values indicate facilitative effects (i.e. increased biomass; Armas et al. 2004). There are a variety of methods available to quantify competition, and we used biomass as an indicator of plant competition as it provides a long-term proxy and captures both past and recent influences on species growth (Trinder et al. 2020).

Species Type Comparisons

For overall comparisons, species were first grouped by origin as native versus invasive. In addition, based on individual species responses to soil nutrient availability (i.e. their resource-use strategy) species were then grouped as resource conservative versus resource exploitative.

Species with statistically significant relative biomass responses to nutrient manipulations were classified as resource exploitative, while species without were classified as resource conservative.

Statistical Analysis

For each species (four native and two non-natives), we established the relationship between the response variables at the end of the experiment and soil target C:N (as a continuous variable) via linear regression models for all response variables except PNUE and PPUE. For PNUE and PPUE, quadratic models were utilized based on data fit. Rather than use the C:N themselves, we inverted them to $\frac{1}{\text{C:N}}$ so that (1) larger values are associated with higher soil nutrient availability and (2) relationships could be discussed in terms of relative change in soil nutrient availability. Linear and quadratic models on a log-transformed scale capture relativity and result in regression assumptions (i.e. goodness of fit, homoscedasticity, acceptable degree of Normality in the residuals) being met. Relativity in our regressions occurred as we logtransformed both the response variables (except *Rii*) and C:N (i.e. our predictor variable was $\log\left(\frac{1}{\text{C:N}}\right)$).

Initial height for woody species and weight for *C. setaceus* were analyzed with a one-way analysis of variance (ANOVA) to check for homogeneity in replicates across treatments at the start of the study. Despite being randomly assigned to treatments, initial plant size differed with soil nutrient treatment at the start of the study for all species except *C. setaceus* (Knauf 2016). As a result, models for the relationship of species response variables to C:N include initial height or weight, thus controlling for initial differences in plant size. Pots with mortality were excluded from data analyses outside of survival (n = 123). Reproductive output and mortality were analyzed using a binary logistic regression.

To assess differences in response variables between the species comparison groups (i.e. native vs. invasive; and resource exploitative vs. conservative), we compared the effects of nutrient changes measured by the slopes against $\log\left(\frac{1}{\text{C:N}}\right)$ between species from each group (i.e. native or invasive; exploitative or conservative) with a t test. Due to the small sample size, the use of a t test is not ideal because we cannot argue that the distribution of the statistic of interest (i.e. difference in slopes for linear models) is approximately normal. Therefore, interpreting p values from the t tests should be done conservatively, and conclusions drawn from these analyses considered with this in mind. For the resource-use strategy comparison, the native *D. viscosa* was classified as resource exploitative in addition to both invasive species based on individual species responses to soil nutrient availability. For four response variables (i.e. biomass, leaf area, $A_{\max}$, and carbon gain), invasive and resource exploitative species were expected to have a stronger response to nutrient availability and, therefore, we used one-tailed t tests. There was no clear argument for directionality of PNUE and PPUE and, therefore, we used two-tailed t tests. Additionally, for PNUE and PPUE, we used the simpler linear regression model, instead of the quadratic model, for ease of comparisons. IBM SPSS 25 was used for all statistical analyses, and significance was determined at $\alpha = 0.05$.

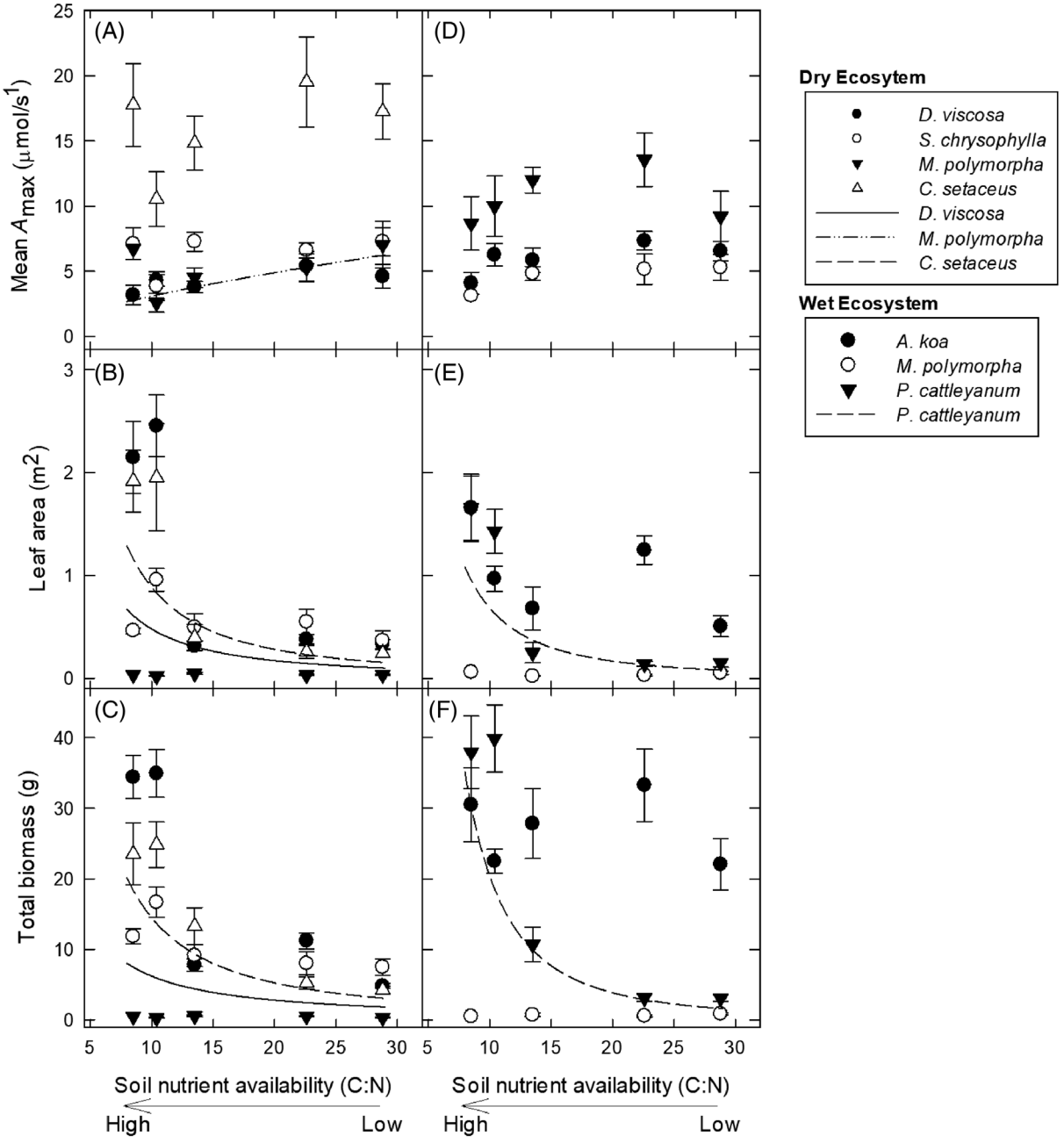

Figure 1. Instantaneous A_{max}, leaf area, total biomass (mean ±1 SD), and regression lines (for significant species) for species from the dry (A–C) and wet (D–F) ecosystems. Generally, mean A_{max} did not vary with soil nutrient availability (i.e. C:N; $p > 0.05$; A and D). Significant increases in leaf area (B and E) and biomass (C and F) with increases in soil nutrient availability were evident for both invasive species (*C. setaceus* and *P. cattleyanum)* and a single native species (*D. viscosa*) ($p < 0.05$). No significant changes in biomass were observed with varying soil nutrients for the other three native species (*M. polymorpha*, *S. chrysophylla*, and *A. koa*; $p > 0.05$). Note: Data are presented in an untransformed state for ease of interpretation.

Results

Growth and Photosynthetic Response

Instantaneous photosynthetic rates were generally not impacted by nutrient treatments for individual native or invasive species (Fig. 1A & 1C, Table S3). However, invasive species had higher A_{max} when compared to native species (Fig. 1A & 1D). While photosynthetic rates did not differ with soil nutrients, both invasive species ($p < 0.01$ for *C. setaceus* and *P. cattleyanum*) and one native (*D. viscosa*, $p < 0.01$) had more surface area for photosynthesis (i.e. higher leaf area; Fig. 1B & 1E, Table S3) with increasing soil nutrient availability, such that increased soil nutrient availability resulted in increased total biomass and carbon gain ($p < 0.01$ for all significant species; Fig. 1C & 1F, &

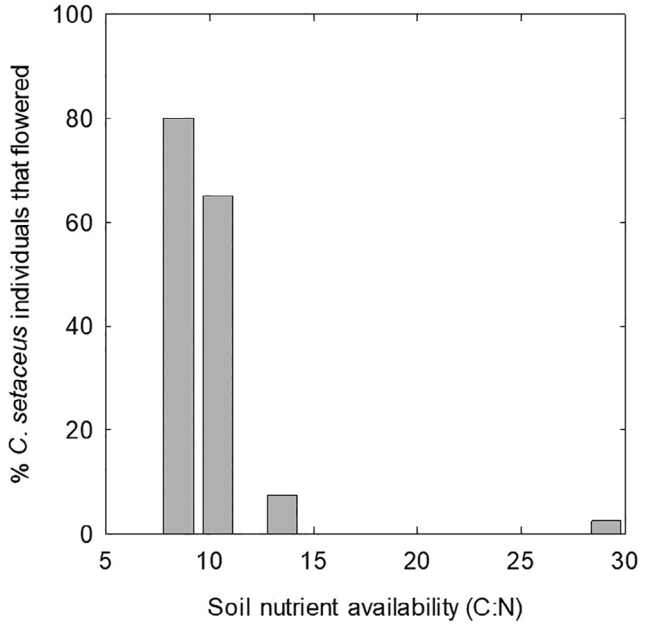

Figure 2. Percentage of *C. setaceus* individuals producing inflorescences during the study across a range of soil nutrient availabilities (note that no inflorescences were present when C:N = 22.6). Reproductive output of the invasive grass species increased significantly as soil nutrient availability increased ($p < 0.01$).

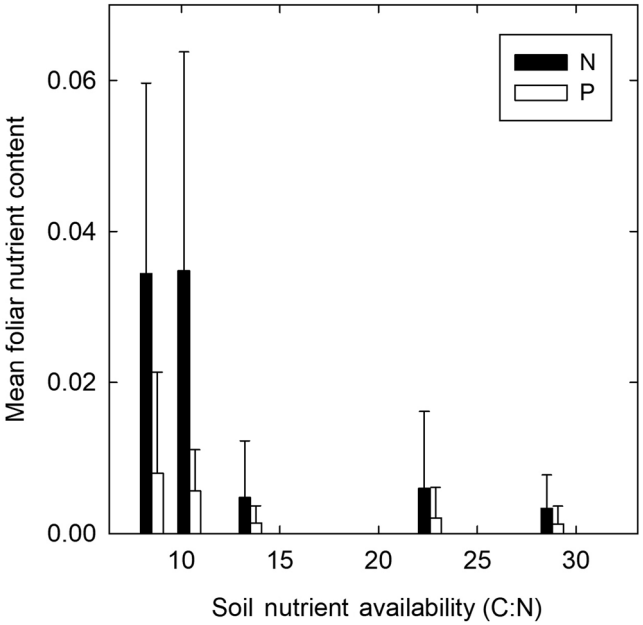

Figure 3. Foliar nitrogen and phosphorus content (mean +1 SD) for all species across soil nutrient availability. Both nitrogen and phosphorus content increased significantly with increasing soil nutrients when grouped across all species ($p < 0.01$).

S1, Table S3). The remaining three native species all had relatively constant biomass and carbon gain with changes in soil nutrients ($p > 0.05$; Fig. 1C & 1F, & Fig. S1, Table S3).

Soil nutrient availability strongly affected the survival of the native *M. polymorpha*. Mortality of *M. polymorpha* was, overall, higher than other species tested and increased with increasing soil nutrient availability ($p < 0.01$, $\chi^2 = 98.28$, $r^2 = 0.45$), with up to 100% mortality in nutrient addition treatments (Fig. S2, Table S5). In the control and nutrient reduction treatments, mortality of *M. polymorpha* was much lower, ranging from 0 to 38% across both ecosystem types. Average mortality of all other species was 8% (SD = 10%, $n = 25$) across all soil nutrient availabilities (Table S5).

Total biomass of invasive *P. cattleyanum* increased by 24% for every 10% decrease in C:N (i.e. increase in soil nutrient availability; $F = 124.04$, $p < 0.01$, $r^2 = 0.60$, $n = 88$). Invasive *C. setaceus* total biomass increased by 15% in response to each 10% decrease in C:N ($F = 68.06$, $p = 0.00$, $r^2 = 0.36$, $n = 122$). *C. setaceus* was the only species with reproductive output during the study, and reproduction increased strongly with soil nutrients to as high as 80% of individuals in the increased soil nutrient availability treatments ($p < 0.01$, $\chi^2 = 73.87$, $r^2 = 0.37$; Fig. 2). For one native species (*D. viscosa*), total biomass response to nutrient availability was similar to invasive species, increasing approximately 12% as C:N decreased ($F = 110.27$, $p = 0.00$, $r^2 = 0.77$, $n = 68$; Fig. 1). The other native species, *S. chrysophylla* ($F = 5.66$, $p = 0.11$, $r^2 = 0.22$, $n = 50$), *A. koa* ($F = 0.37$, $p = 0.55$, $r^2 = 0.01$, $n = 52$), and *M. polymorpha* ($F = 1.43$, 0.68, $p = 0.24$, 0.42, $r^2 = 0.03$, 0.02, $n = 47$, 43 for the dry and wet ecosystem), showed a much more neutral growth response to soil nutrient availability, with change in total biomass for all species <4% (Fig. 1).

Resource-Use Efficiency

Using plants as phytometers, foliar N and P was an indicator of treatment efficiency and generally increased with increasing soil nutrient availability (Fig. 3). PNUE did not vary with soil nutrient availability for the native species *S. chrysophylla* and *M. polymorpha* in the wet ecosystem (Table 1, Fig. S3). PNUE generally decreased as C:N decreased (i.e. nutrients increased) for the natives *M. polymorpha*, *A. koa*, and *D. viscosa* (Table 1). For the invasive species *C. setaceus and P. cattelyanum*, PNUE also decreased as C:N decreased. PPUE was not impacted by changes in C:N for any species except *A. koa*, where decreases in C:N generally decreased PPUE (Table 1, Fig. S3).

Competitive Interactions

The relative interaction index (*Rii*) showed that neither native nor invasive species consistently facilitated or suppressed neighbor species despite large differences in leaf area, total biomass, and whole plant carbon gain with varying soil nutrient availability (Figs. S4 & S5). Native species impact on *C. setaceus* and *P. cattleyanum* generally did not change with varying soil nutrient availability ($p > 0.05$; Table S3, Figs. S4 & S5). Two exceptions were that the suppressive effects of the native shrub *D. viscosa* on *C. setaceus* generally increased with increasing soil nutrient availability ($F = 6.54$, $p = 0.02$, $r^2 = 0.20$, $n = 36$; Table S3, Fig. S4). In addition, *M. polymorpha*'s facilitative effects on

Table 1. Results of quadratic regression models for PNUE and PPUE by species. Regression models were run between the log- transformed response variable and the C:N, specifically $\log\left(\frac{1}{C:N}\right)$ (i.e. as a continuous variable). Italicized *p* values indicate significant relationships. Quadratic regression model $Y = \beta_0 + \beta_1 X + \beta_2 X^2$, where Y is the dependent variable (e.g. PNUE or PPUE), β_1 is the linear coefficient, β_2 is the quadratic coefficient, X is the independent variable (i.e. C:N), and β_0 is the intercept. *indicates invasive species.

Species	*Response Variable*	*Intercept*	*Linear Coefficient (SE)*	*Quadratic Coefficient (SE)*	F *Value*	n	r^2	p *Value*
Dry ecosystem								
D. viscosa	PNUE	-10.20	-17.14 (3.32)	-6.69 (1.39)	31.66	30	0.66	*0.00*
S. chrysophylla	PNUE	-0.03	-0.46 (3.82)	-0.12 (1.60)	0.35	25	0.03	0.71
M. polymorpha	PNUE	-4.02	-6.36 (5.65)	-2.16 (2.29)	6.54	26	0.36	*0.01*
*C. setaceus**	PNUE	-7.93	-14.36 (3.99)	-5.52 (1.66)	18.98	56	0.41	*0.00*
Wet ecosystem								
A. koa	PNUE	-7.02	-12.78 (4.76)	-5.20 (2.00)	4.46	23	0.29	*0.02*
M. polymorpha	PNUE	-4.63	-8.26 (5.09)	-3.16 (2.04)	2.09	19	0.21	0.16
*P. cattleyanum**	PNUE	-5.55	-10.33 (3.56)	-4.15 (1.48)	5.57	38	0.24	*0.01*
Dry ecosystem								
D. viscosa	PPUE	0.96	-0.78 (3.63)	-0.34 (1.51)	0.05	35	0.00	0.95
S. chrysophylla	PPUE	3.44	3.42 (4.16)	1.51 (1.74)	0.68	27	0.05	0.52
M. polymorpha	PPUE	-1.19	-4.26 (7.59)	-1.61 (3.02)	0.36	24	0.03	0.71
*C. setaceus**	PPUE	6.58	8.18 (4.80)	3.39 (2.00)	1.46	57	0.05	0.24
Wet ecosystem								
A. koa	PPUE	-8.57	-17.07 (4.17)	-6.71 (1.74)	16.57	27	0.58	*0.00*
M. polymorpha	PPUE	1.63	-0.90 (13.59)	-0.68 (5.28)	3.17	18	0.30	0.07
*P. cattleyanum**	PPUE	-3.40	-8.58 (5.17)	-3.70 (2.15)	2.02	38	0.10	0.15

P. cattleyanum increased with increasing soil nutrient availability ($F = 12.25$, $p < 0.01$, $r^2 = 0.36$, $n = 24$; Table S3, Fig. S5). Dry ecosystem invasive species had no significant suppressive or facilitative effects on *S. chrysophylla* or *M. polymorpha* across treatments ($p > 0.05$), and wet ecosystem invasive species impact did not change with varying soil nutrients for *A. koa* or *M. polymorpha* (Table S3). The impact of *C. setaceus* on *D. viscosa* switched from suppressive in nutrient reduction treatments to facilitative in nutrient addition treatments ($F = 19.56$, $p < 0.01$, $r^2 = 0.37$, $n = 36$; Table S3, Fig. S4).

Species Type Comparisons

In general, plants categorized as invasive ($n = 2$; origin) or exploitative ($n = 3$; resource-use strategy) had larger changes in response variables with increasing soil nutrient availability than species categorized as native ($n = 4$) or conservative ($n = 3$; Table 2). For biomass and leaf area, invasive species showed a stronger response to nutrient availability than native species. Resource exploitative species (i.e. both invasive species and one native species, *D. viscosa*) showed a similar, but stronger, response for biomass and leaf area than the comparison based on origin (Table 2). Differences between groups for A_{max} also suggest that invasive and/or exploitative species were more responsive to changes in soil nutrient availability. Carbon gain, PNUE, and PPUE showed minimal differences when species were grouped by origin or resource-use strategy (Table 2).

Discussion

The results of this study suggest that invasive and resource exploitative species are more productive under increased nutrient availability not because they become more efficient in photosynthesis with increasing soil nutrients, but rather because they use increased nutrient availability to increase total leaf area, thereby providing more surface area for photosynthesis and higher whole plant carbon gain and total biomass. Modeling total plant carbon gain from photosynthetic parameters and anatomy can help to provide mechanistic interpretation of observed changes in biomass in response to soil nutrient availability. Moreover, our results emphasize that most native species, especially those which evolved on remote islands, tend to use resources efficiently relative to invasive species, perhaps as an adaptation to low nutrient environments (Vitousek 1982; Daehler 2003).

Results supported our hypothesis that native species would show a more neutral growth and photosynthetic response to changes in soil nutrient availability, while invasive species were more responsive. The exception to this case for the native *D. viscosa* indicates adaptation for rapid resource uptake and utilization (i.e. exploitative resource-use strategy) in this species, much like the invasive species studied, which potentially explains why it is a commonly used species for ecological restoration in Hawai‘i (Medeiros et al. 2003; Ammondt et al. 2013). These traits also likely explain why *D. viscosa* is commonly found in disturbed habitats in Hawai‘i and elsewhere that are otherwise dominated by invasive species (D’Antonio et al. 2000; Ainsworth & Kauffman 2009). The response of *D. viscosa* and the species type comparisons (i.e. origin, and resource-use strategy) emphasize the importance of understanding that generalizations based on origin do not always hold true, and grouping species by resource-use strategy may be more useful when predicting species-specific responses to soil nutrient availability.

Knowing species-specific responses to varying nutrient availability in regards to resource-use strategy can aid in success of

Table 2. Mean response (i.e., average of slopes for linear regressions) and standard deviation (+1 SD) to varying soil C:N, and overall comparison result for species grouped as (1) native versus invasive and (2) resource conservative versus resource exploitative. Bold values indicate significant differences with C:N in the tested response variables. The *p* values from the *t* test should be interpreted conservatively due to small sample sizes. For ease of comparison, the linear regression slopes were used for all response variables to calculate the values presented above. [a]Directional tests with the expectation that invasive and resource exploitative species would show larger responses. [b]Two-tailed tests.

	Mean of Slopes (SD)				*Mean of Slopes (SD)*			
Response variable	*Invasive*	*Native*	p *value*	t *value*	*Exploitative*	*Conservative*	p *value*	t *value*
Biomass[a]	1.94 (0.67)	0.41 (0.53)	**0.01**	2.81	1.67 (0.66)	0.17 (0.27)	**<0.01**	3.64
Leaf area[a]	1.67 (0.32)	0.39 (0.74)	**0.01**	2.95	1.61 (0.25)	0.02 (0.12)	**<0.01**	10.08
A_{max}[a]	-6.48 (3.34)	-0.36 (3.88)	**0.03**	-2.00	-5.25 (3.18)	0.45 (4.32)	**0.04**	-1.84
Carbon gain[a]	0.81 (1.24)	0.29 (0.80)	0.31	0.53	1.00 (0.94)	-0.07 (0.41)	0.07	1.81
PNUE[b]	-0.74 (0.54)	-0.49 (0.62)	0.64	-0.50	-0.89 (0.46)	-0.26 (0.52)	0.19	-1.56
PPUE[b]	0.18 (0.16)	-0.29 (0.49)	0.08	1.73	0.07 (0.22)	-0.34 (0.58)	0.16	1.12

ecological restoration treatments. In a restoration scenario, the desired response to carbon amendments is to favor native species by reducing the growth of invasive but not native species, or reducing growth of invasive species more than native species (Horn & Redente 1998; Alpert & Maron 2000; Paschke et al. 2000). The scenario of reducing the growth of invasive species but not the natives is in line with responses for five of the six species tested in this study. The neutral or minimal growth and photosynthetic response observed for three of the four native species illustrates adaptive fitness responses and the use of resource conservative traits and supports previous literature documenting that native species RUE can be unresponsive to changes in nutrient availability (Davidson et al. 2011; Heberling & Fridley 2016). The trade-off, however, is that native species adapted to low resource availability are not able to take advantage of increased resources to the degree that the invasive species were in this study (Vitousek et al. 1987a; Hobbs & Huenneke 1996).

High growth rates of invasive species under increased resource availability are often suggested to be indicative of resource exploitative strategies, contributing to their success on disturbed sites (Burns 2004; Burns 2006; Gurevitch et al. 2008). This is congruent with the observation that invasive species commonly invade areas of high resource availability (Burke & Grime 1996; Daehler 2003). Both invasive species tested in this study displayed large increases in biomass with increasing soil nutrients, in line with prior studies (Ostertag & Verville 2002; Blumenthal et al. 2003), and large decreases in biomass when soil nutrients were reduced, also in line with prior studies (Alpert & Maron 2000; Blumenthal et al. 2003). Further, reproduction of the invasive grass *C. setaceus* was greatly reduced with reduced soil nutrient availability. Reduced reproductive output with carbon amendments makes this technique promising for this aggressive invader, as the ability of a species to reproduce is critical to its continued success as an invader (Bryson & Carter 2004), and identifying methods to limit reproduction and recruitment are often a primary goal for managers (DiTomaso et al. 2010).

Our results further suggest that increased soil nutrient availability can negatively impact survival of at least some dominant native species, such as the early successional and canopy dominant *M. polymorpha*, which occurs across a wide range of environments including those with very limited resource availability. A prior field study similarly found that growth and density of *M. polymorpha* seedlings were reduced with the addition of nutrients (Ostertag & Verville 2002). Atmospheric N deposition and invasive N-fixing species, and associated increases in N availability, are global threats to biodiversity (Vitousek & Walker 1989; Maron & Connors 1996; Wedin & Tilman 1996), and our results indicate that elevated nutrient levels can negatively affect population dynamics of a keystone native species adapted to low resource environments.

To fully interpret growth and photosynthesis responses, it is necessary to examine them in the context of nutrient availability (i.e. RUE). RUE, mainly PNUE, was plastic for all resource exploitative and two resource conservative species, but this plasticity only conferred an advantage to resource exploitative species when resource availability was high. Even with increased RUE under lower nutrient availability, resource exploitative species experienced significant decreases in biomass. These results are similar to studies that have found invasive species to generally be more plastic than native species in RUE, even if this plasticity does not always result in improved fitness (Davidson et al. 2011). Our findings did not align, however, with prior studies showing that high or plastic RUE provides invasive species with a competitive advantage over native species in resource poor environments (Funk & Vitousek 2007; Funk 2008; Davidson et al. 2011; Heberling & Fridley 2016; Sardans et al. 2016). The general consistency in the response of two of the native species (*S. chrysophylla* and *A. koa*) may also be a result of their being leguminous species with capacity for N fixation, allowing them to maintain relatively constant growth rates across a broad range of soil nutrient conditions. These and other N-fixing species play an important role in tropical restoration efforts, and the results of our study suggest that N-fixing species may not respond strongly to soil nutrient manipulations. However, pretreatment soil nutrient levels may impact N-fixing species response to nutrient manipulations in the field.

Understanding how competition and varying soil nutrient availability, individually and collectively, affect species growth, photosynthesis, and resource use strategies could be beneficial in informing restoration strategies. This is one of only a limited

number of studies that directly tested competition between native and invasive plants on islands (Barton & Wong 2019). The competition index (*Rii*) results of this study do not support our hypothesis that lowering soil nutrient availability provides native species with a direct competitive advantage over invasive species. Further, we did not find evidence that invasive species consistently suppress native species under high soil nutrient availability. Rather we show that competition between native and invasive species is unaffected by nutrient availability, which is in line with prior studies (James et al. 2011; Vallano et al. 2012; Tabassum & Leishman 2016). Moreover, our competition index results emphasize that the impact of competition on growth and photosynthesis of native and invasive species is minimal and inconsistent when compared to individual species responses to soil nutrient availability. As such, species-specific differences in survival, reproduction, and growth appear to shape community composition more so than direct competition (Tabassum & Leishman 2016).

Field Implementation

The results of this study highlight species-specific responses and plasticity to varying soil nutrient availability. Additionally, these findings suggest that lowering resource availability may aid in the restoration of native species when native and invasive species resource-use efficiencies differ (Funk 2013), as they did for three of four native species tested here. However, simple native versus invasive designations are unlikely to capture responses across varied species and resource availabilities.

Dominant species common in Hawaiian tropical wet and dry ecosystems responded similarly to soil nutrient manipulation. For soil nutrient manipulation to be successful, understanding what resources are limiting and the expected response of target plant species based on their ecophysiology is critical. Field tests should be established before application of this method to increase understanding of possible unknown field conditions that may impact species responses and competitive outcomes. For example, in drier ecosystems, the response to soil nutrient manipulation may be at least partially, if not largely, overridden by water availability under field conditions (Steers et al. 2011). There was little to no light competition in this experiment; however, light competition strongly impacts growth and survival of tropical species (McDaniel & Ostertag 2010) and is likely to interact with nutrient competition to determine the success of native and invasive species. As a result, those species better adapted to current environmental conditions may be less affected by soil nutrient manipulations in ecosystems where nutrients are not the dominant limiting factor, regardless of their nutrient resource-use strategy. In addition, the application of carbon amendments to soil in mature plant communities may not affect established species as much as the recruitment and regeneration of new individuals. Higher plant competition and more diverse communities may also affect the outcome of soil nutrient manipulation in the field (Matzek 2011; Steers et al. 2011). However, using carbon amendments to target invasive species regeneration should help increase the success of this technique, at least in N limited ecosystems.

In summary, we show that soil nutrient manipulation may be a viable restoration method for tropical ecosystems and for woody species when resource-use strategies of native and invasive plants differ, but field tests are needed. Furthermore, simply grouping native and invasive species based on assumed resource-use strategies would have been misleading for at least one important restoration species in this study. As a result, it is important to understand the ecophysiological traits of the native species being considered for restoration, as well as the invasive species present on site, before implementing nutrient manipulations in the field in a restoration context.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Amount of substrate added to eat pot for each nutrient manipulation treatment.

Table S2. Initial carbon and nitrogen content in the different substrates used.

Table S3. Results of the linear regression models for each response variable by species.

Table S4. Mean biomass (SD) for each species across the five nutrient manipulation treatments.

Table S5. Percent mortality for each species across the five nutrient manipulation treatments.

Figure S1. Carbon gain across the five soil nutrient manipulation treatments.
Figure S2. Total percent mortality of *M. polymorpha* across all nutrient availabilities.
Figure S3. Mean PNUE and PPUE (SD) for each species across the five nutrient manipulation treatments.
Figure S4. *Rii* for dry ecosystem species combinations across treatments.
Figure S5. *Rii* for wet ecosystem species combinations across treatments.

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