

RESEARCH ARTICLE

Competition between Native Hawaiian Plants and the Invasive Grass *Megathyrsus maximus*: Implications of Functional Diversity for Ecological Restoration

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Abstract

Biodiversity loss is a global crisis, due primarily to habitat destruction and widespread nonnative invasions. Invasive grasses are particularly problematic in many tropical ecosystems, where they possess traits that promote their persistence and can drastically alter native plant communities. We explored the ecophysiological basis for restoring native Hawaiian dryland ecosystems currently dominated by the nonnative invasive grass *Megathyrsus maximus* (guinea grass) in a garden experiment. Three native species—*Myoporum sandwicense* (naio; canopy tree), *Dodonaea viscosa* (aalii; shrub), and *Plumbago zeylanica* (ilice; groundcover)—were grown with *M. maximus* at three levels of native functional diversity (one, two, or three species) while holding overall plant density constant. We tested which individual and functional combinations of native species were more productive and best suppressed *M. maximus* growth and reproduction. *Megathyrsus maximus* had 39–94% higher maximum photosynthetic rates

(A_{\max}) than native species and increasing native functional diversity did not affect *M. maximus* A_{\max} . Aboveground, belowground, and total biomass of *M. maximus* varied with functional diversity, although intraspecific competition reduced growth as much as interspecific competition. Reproductive tiller production by *M. maximus* decreased significantly when planted with any of the native species and with increasing native functional diversity. These results indicate that high native functional diversity in an ecological restoration setting may aid in the control of a dominant invasive grass and the reintroduction of diverse native species. Recommendations for restoring degraded nonnative grasslands in Hawaii and throughout the tropics include selection of native species that are ecophysiological competitive and have high functional diversity.

Key words: ecophysiology, guinea grass, invasive species, landcover change, tropical dry forest.

Introduction

Nonnative invasive species can drastically alter native ecosystems, especially on oceanic islands (Vitousek et al. 1997). Invasive grasses are particularly problematic throughout the tropics, as they often possess ecophysiological traits that can inhibit natural regeneration (Thaxton et al. 2010), change competitive dynamics of native plant communities (Bryson & Carter 2004), and alter disturbance regimes (D'Antonio & Vitousek 1992). In Panama and Brazil, dense stands of nonnative invasive grasses prevent establishment and slow growth of native species (Hooper et al. 2002; Hoffmann & Haridasan 2008). In Hawaii, invasive grasses are numerous and highly competitive for light, water, and nutrients (Litton et al.

2006; Cordell & Sandquist 2008). Moreover, invasive grass-dominated tropical systems typically promote fire as a result of high fuel loads, low live:dead biomass, and high surface area:volume ratios (Brooks et al. 2004). In Australia, for example, nonnative grass invasion has increased the intensity of fires in the northern tropical savannas eightfold (Rossiter et al. 2003). Fire-promoting traits, coupled with rapid recovery following fire via seeding and resprouting, can create a positive feedback through which invasive grasses dominate tropical landscapes (D'Antonio & Vitousek 1992). Control of invasive grasses and restoration of native woody communities are critical for restoring ecosystem structure and function and native biodiversity, especially in dry lowland ecosystems in Hawaii where invasive grasses are a common component of most contemporary landscapes (Cabin et al. 2002).

Ecological restoration projects are often designed to alter the trajectory of degraded ecosystems dominated by invasive species via the introduction of native species and suppression of nonnative invaders. However, enrichment planting in dry

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landscapes where invasive grasses dominate can be exceptionally difficult, as dense stands of grass often outcompete native seedlings for light and water (Nepstad et al. 1990). Historically, the Hawaiian dry forests supported a high diversity of plants, with a relatively open canopy and sparse forest floor characteristic of a seasonally dry environment (Hatheway 1952). Invasive grasses, as a result, are believed to occupy a somewhat open niche in Hawaiian dry forests and competition from these grasses is frequently so intense that native species are unable to colonize without sustained grass removal efforts (Cabin et al. 2002; Litton et al. 2006). A better understanding of how ecological restoration with native species can be used to suppress aggressive grass invaders is critical.

One potential mechanism of increasing the success and sustainability of ecological restoration is to introduce native species assemblages that are highly competitive with extant invasive species and can provide future invasion resistance (Pywell et al. 2003). Restoring assemblages of native species instead of targeted individual species may further facilitate restoration, particularly if they are functionally diverse assemblages and thus preempt available niche space for invaders (Pokorny et al. 2005). Here, we follow Schleuter et al. (2010) in defining functional diversity as the diversity of species traits (e.g. resource use) in an ecosystem and use functional niche space in determining divergence in functional groups. Invasion resistance in functionally diverse restoration efforts can result from either positive species interactions or a sampling effect whereby an increase in the species pool increases the likelihood of the presence of a strong competitor (Fargione & Tilman 2005). Successful resistance to invasion may be further strengthened if restored native species are functionally similar to and competitive with invading species (Funk et al. 2008). An ecosystem with high functional diversity, therefore, may be more resistant to subsequent invasions compared to one with low functional diversity (Elton 1958; Kennedy et al. 2002; Brown & Rice 2010).

The objective of this study was to quantify competition and ecophysiological indices of the invasive grass *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs (guinea grass; formerly *Panicum maximum* Jacq.) and three native species, growing individually and in combinations of increasing functional diversity at a constant plant density. A native of Africa, *M. maximus* was naturalized in Hawaii by 1871 and is prevalent throughout the main Hawaiian islands (Motooka et al. 2003). The three native species differ in growth form (tree, shrub, and groundcover) and represent different functional groups in terms of light acquisition and use (Wagner et al. 1999). Specifically, we tested the theory that high functional diversity decreases success of a dominant nonnative invader (Tilman 1997) using a controlled garden experiment where all factors were held constant except native species functional diversity. We hypothesized that increased functional diversity would result in greater restoration success (i.e. suppression of *M. maximus* growth and reproduction, and increased native species growth), with the assumptions that *M. maximus* growth declines with declining light availability and that native species would occupy different canopy positions. We

further hypothesized that the native tree would result in greater suppression of *M. maximus* than the native shrub or groundcover as a result of high productivity (Stratton & Goldstein 2001). These hypotheses were tested within a randomized design of experimental plantings, where native species functional diversity was varied in the presence versus absence of *M. maximus*.

Methods

Site Description

The study was conducted at Magoon Research Facility at the University of Hawaii at Manoa (157°48'38"W, 21°18'21"N), located on leeward Oahu at 47 m.a.s.l. Mean annual precipitation is 792 mm, with a seasonal distribution of increased rainfall in winter months and mean annual temperature is 23.9°C (Giambelluca et al. 1986). The study spanned 6 months during winter, from 15 September 2009 to 2 March 2010. Total rainfall throughout the duration of the experiment was 388 mm and temperature averaged 24.2°C.

Experimental Design

Five gallon (18.9 L) nursery pots were planted at a constant density of four plants per pot, with functionally varying combinations of the native species *Myoporum sandwicense* (A. DC.) A. Gray (naio; canopy tree), *Dodonaea viscosa* (L.) Jacq. (aalii; shrub), and *Plumbago zeylanica* L. (iliee; groundcover) and the invasive grass *Megathyrsus maximus* (guinea grass) (Table 1). Pots were placed on outside benches and the entire design was replicated four times on adjacent benches (not all pots fit on one bench), for a total of 68 experimental planting pots. Native plants were purchased in 4 in. (10.2 cm) containers at a professional nursery (Hui Ku Maoli Ola, Hawaii), all grown from seed and approximately 3 months old when purchased. Native plants were initially planted without *M. maximus* on 15 September and the grass was introduced 1 month later. Soil for the pots was collected at Waianae Kai Forest Reserve on Oahu (158°9'181"W, 21°28'53"N), a

Table 1. Planting design diagram with invasive and native plant species.

<i>Megathyrsus maximus</i> Planted with and without Native Species				<i>Native Species</i> Planted Alone
NS0	NS1	NS2	NS3	
GGGG	GMMM	GMMD	GMDP	MMMM
	GDDD	GMMP		DDDD
	GPPP	GDDM		PPPP
		GDDP		MDPM
		GPPM		MDPD
		GPPD		MDPP

G, *Megathyrsus maximus*; *M*, *Myoporum sandwicense*; *D*, *Dodonaea viscosa*; *P*, *Plumbago zeylanica*.

Each letter corresponds to one plant and each grouping of letters refers to one five-gallon planting pot. The entire design was replicated four times (total of 68 planting pots). NS0, NS1, NS2, and NS3 refer to levels of native species functional diversity.

representative lowland dry ecosystem currently dominated by *M. maximus*. The soil is of the Ewa series, consisting of well-drained Aridic Haplustolls formed from alluvium weathered from upland basalt, found on slopes between 0 and 12%, and composed of reddish silty clay loam (Soil Survey Staff 2006). *Megathyrsus maximus* individuals were collected from the same location, separated into root aggregates weighing 20–25 g, and planted in four inch nursery containers for 1 month before introduction to the experimental pots.

Plant size at experiment initiation did not differ for individuals of *M. sandwicense* ($p = 0.817$, mean basal diameter = $5.5 \text{ mm} \pm 0.13 \text{ SE}$), *D. viscosa* ($p = 0.208$, mean basal diameter = $4.2 \text{ mm} \pm 0.11 \text{ SE}$), or *P. zeylanica* (a multi-stemmed groundcover, produced from the same seed source simultaneously). Aboveground shoots of *M. maximus* were trimmed back completely when introduced to experimental pots. All pots received ambient precipitation in addition to irrigation twice per week with approximately 1.5 L of water to provide adequate water supply and were rotated 45° biweekly.

Reproduction of *M. maximus* was assessed monthly by recording the presence of reproductive tillers. Native species reproduction was not assessed because most species did not reach reproductive maturity. Biomass and leaf-level gas exchange were used as indices of productivity to determine invasive and native species response to planting treatments and chlorophyll fluorescence was quantified as an index of plant stress. Leaf-level gas exchange was also quantified for all species to identify inherent physiological differences. All plants were destructively harvested at the conclusion of the experiment, separated into aboveground and belowground biomass components, dried at 70°C to a constant mass and weighed.

Leaf-level gas exchange (maximum photosynthetic rate, stomatal conductance, and water use efficiency [WUE]) was measured on two fully expanded leaves from the most recent leaf cohort on all plants approximately 5 months after experiment initiation between 9:30 and 14:00 hours on two consecutive cloud-free days with a LI-6400XT Portable Photosynthesis System (LI-COR Biosciences, Lincoln, NE, U.S.A.). Leaves were given saturating light ($1200 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and CO_2 ($400 \mu\text{mol/mol}$) to measure gas exchange under ideal, standardized conditions. Chlorophyll fluorescence, a measure of the efficiency of Photosystem II (PSII) reaction centers in energy harvesting of light-adapted leaves ($F'_m - F_s / F'_m$; ΦPSII) and an indicator of stress (Maxwell & Johnson 2000), was measured 1 week later using an LI-6400-40 Leaf Chamber Fluorometer.

Light response curves were generated from additional plants to examine how growth in two contrasting light regimes alters species photosynthetic capacity. Four plants of each species were grown in full sun and partial shade (23% of ambient photosynthetic photon flux density [PPFD]) for 2 months. Individual plant photosynthetic response to eight different photosynthetically active radiation (PAR) intensities was measured using the LI-6400XT on one fully expanded leaf from the newest leaf cohort of each plant, over two consecutive cloud-free days between 9:00 and 13:00 hours.

Statistical Analyses

Predictive Analytics Software (PASW) Statistics v.18 (IBM SPSS, Inc., Chicago, IL, U.S.A.) was used for all analyses, and all tests were performed on mean individual plant response variables by treatment. Most data passed initial tests of homogeneity of variance, but if not, a priori custom contrast output that does not assume equal variances is reported. One-way analysis of variance (ANOVA) was used to analyze reproduction, biomass, and leaf-level gas exchange across functional diversity treatments and a priori custom contrasts were used to test our specific hypotheses. One-way ANOVA with Tukey's Honestly Significant Difference (HSD) post hoc test was used to compare leaf-level gas exchange for all species across all treatments and to test for differences in light response curves across species. Two-sample Student's *t* tests were used to evaluate differences in native biomass when grown with and without *M. maximus* and to evaluate differences in light response curves of native and invasive plants grown in full sun versus partial shade.

Results

The percentage of *Megathyrsus maximus* plants that produced reproductive tillers decreased markedly with increasing native functional diversity (Fig. 1). *Megathyrsus maximus* plants produced more reproductive tillers when grown in monocultures than when the grass was grown with two ($t = 2.307$, degrees of freedom (df) = 28, $p = 0.015$) or three native species ($t = 4.392$, $df = 15$, $p < 0.001$), and when grown with one native versus three native species ($t = 2.803$, $df = 11$, $p = 0.009$). Aboveground biomass of *M. maximus* differed with native species functional diversity (Fig. 2a) and was higher when *M. maximus* was grown with one native species than when grown in monocultures ($t = 2.477$, $df = 10$, $p = 0.016$) or when planted with either two ($t = 4.583$, $df = 17$, $p < 0.001$) or three native species ($t = 3.051$, $df = 4$, $p = 0.017$). Belowground and total (aboveground + belowground) biomass of *M. maximus* also differed with functional diversity (Fig. 2b &

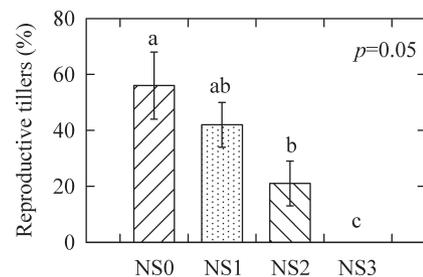


Figure 1. The percentage of *Megathyrsus maximus* plants that produced reproductive tillers in the varying native species functional diversity treatments. NS0 refers to *M. maximus* monocultures, and NS1, NS2, and NS3 refer to *M. maximus* grown with one, two, or three native species, respectively. Bars are mean values ± 1 SE. Different letters indicate statistically significant differences ($\alpha = 0.05$) between functional diversity levels tested with a priori custom contrasts and the *p* value refers to the overall effect of treatments on reproductive tiller production.

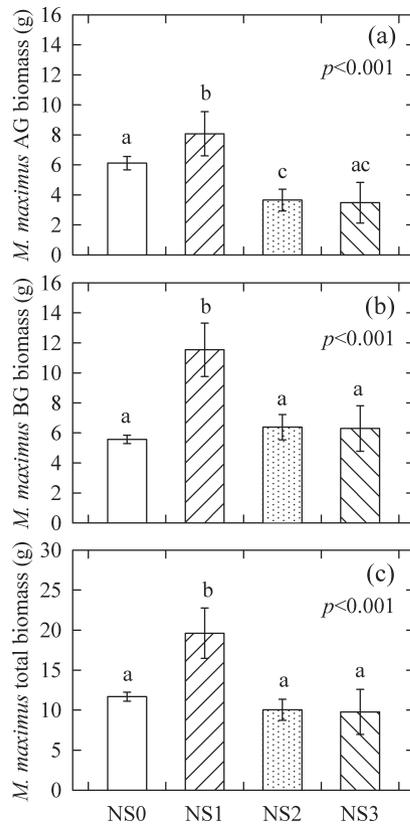


Figure 2. Mean individual plant (a) aboveground, (b) belowground, and (c) total biomass of *Megathyrsus maximus* grown in different native species functional diversity treatments (bars are mean values \pm 1 SE). NS0 refers to *M. maximus* monocultures, and NS1, NS2, and NS3 refer to *M. maximus* grown with one, two, or three native species, respectively. Different letters indicate statistically significant differences ($\alpha = 0.05$) between functional diversity levels tested with a priori custom contrasts and p values in each panel refer to the overall treatment effect on the response variables.

2c), with higher belowground and total biomass in plantings with one native species than in monocultures ($t = 4.445$, $df = 6$, $p = 0.002$ and $t = 4.407$, $df = 7$, $p < 0.001$) or plantings with two ($t = 3.542$, $df = 8$, $p = 0.004$ and $t = 4.453$, $df = 10$, $p < 0.001$) or three native species ($t = 2.613$, $df = 7$, $p = 0.017$ and $t = 2.909$, $df = 6$, $p = 0.014$).

Native species identity impacted *M. maximus* biomass when grown with a single native (Fig. 3). When grown with *Myoporum sandwicense*, aboveground biomass of *M. maximus* was lower than when it was grown with *Dodonaea viscosa* ($t = 4.670$, $df = 5$, $p = 0.003$), *Plumbago zeylanica* ($t = 7.984$, $df = 6$, $p < 0.001$), or in monocultures ($t = 4.283$, $df = 4$, $p = 0.005$). *Megathyrsus maximus* aboveground biomass was also lower when grown in monocultures than in plantings with *D. viscosa* ($t = 2.457$, $df = 4$, $p = 0.039$) or *P. zeylanica* ($t = 5.856$, $df = 4$, $p = 0.002$). Belowground and total biomass of *M. maximus* grown with *M. sandwicense* was lower than when it was grown with *D. viscosa* ($t = 2.305$, $df = 5$, $p = 0.036$ and $t = 3.177$, $df = 5$, $p = 0.013$) or *P. zeylanica* ($t = 4.452$, $df = 5$, $p = 0.003$ and $t = 5.925$,

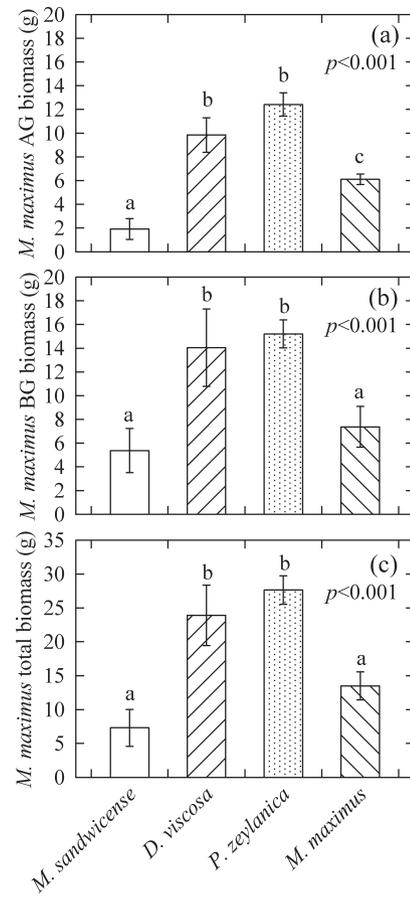


Figure 3. (a) Aboveground, (b) belowground, and (c) total biomass of *Megathyrsus maximus* individuals grown with different single native species plantings or in monocultures. Bars are mean individual plant biomass \pm 1 SE, p values correspond to overall ANOVA tests, and different letters indicate statistically significant differences ($\alpha = 0.05$) between treatments tested with a priori custom contrasts.

$df = 5$, $p < 0.001$), but did not vary from *M. maximus* monocultures ($t = 0.103$, $df = 3$, $p = 0.462$ and $t = 1.584$, $df = 3$, $p = 0.102$).

Native species biomass varied minimally across the functional diversity levels. *Dodonaea viscosa* aboveground ($t \geq 0.074$, $df = 4$, $p \geq 0.102$) and total biomass ($t \geq 0.087$, $df = 4$, $p \geq 0.073$) did not vary; however, belowground biomass was higher when grown with *M. maximus* and one other native species compared to when it was grown with just *M. maximus* ($t = 2.002$, $df = 18$, $p = 0.031$). Aboveground ($t \geq 0.426$, $df = 18$, $p \geq 0.061$), belowground ($t \geq 0.553$, $df = 18$, $p \geq 0.086$), and total biomass of *P. zeylanica* ($t \geq 0.043$, $df = 18$, $p \geq 0.099$) and aboveground ($t \geq 0.753$, $df \geq 4$, $p \geq 0.145$), belowground ($t \geq 0.048$, $df = 17$, $p \geq 0.116$), and total biomass of *M. sandwicense* ($t \geq 0.333$, $df \geq 4$, $p \geq 0.258$) did not vary with native functional diversity. In addition, both aboveground and total biomass of *M. sandwicense* increased when grown with one *M. maximus* plant versus when grown in monocultures (Fig. 4a, $t = 2.38$, $df = 26$, $p = 0.013$ and Fig. 4c, $t = 2.26$, $df = 26$, $p = 0.016$).

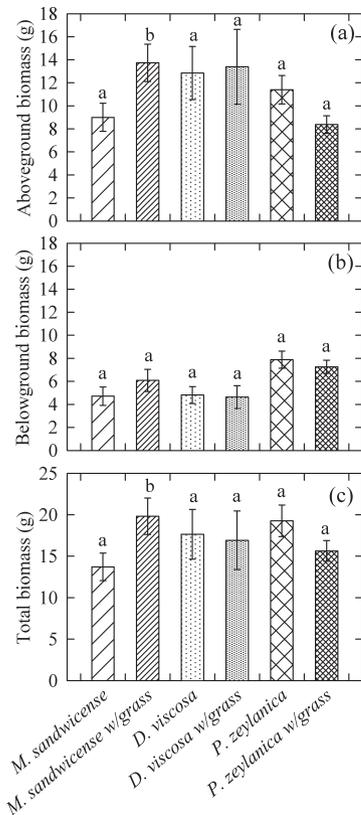


Figure 4. (a) Aboveground (b) belowground, and (c) total biomass of native species grown in monocultures (four individuals per container) versus native species grown with *Megathyrsus maximus* (three native individuals and one *M. maximus*). Bars are mean individual plant biomass ± 1 SE and different letters indicate statistically significant differences ($\alpha = 0.05$) between treatments analyzed with a two-sample Student's *t*-test.

Maximum photosynthetic rate (A_{\max} , $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) ($F = 180.254$, $df = 2$, $p < 0.001$), stomatal conductance (g_s , $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) ($F = 38.058$, $df = 2$, $p < 0.001$), WUE (defined as $A_{\max}/\text{Transpiration}$) ($F = 365.358$, $df = 2$, $p < 0.001$), and chlorophyll fluorescence (ΦPSII , defined as $F'_m - F_s/F'_m$) ($F = 8.317$, $df = 2$, $p < 0.001$) differed between *M. sandwicense*, *D. viscosa*, and *M. maximus* (*P. zeylanica* did not produce measurable leaves at the conclusion of the experiment) when individual plants were averaged across all treatments and replicates (Fig. 5). *Megathyrsus maximus* exhibited higher A_{\max} than *M. sandwicense* and *D. viscosa* and *M. sandwicense* was higher than *D. viscosa* (Fig. 5a; $p < 0.001$). *Myoporum sandwicense* had higher g_s than either *D. viscosa* or *M. maximus* (Fig. 5b; $p < 0.001$). *Megathyrsus maximus* exhibited approximately two times higher WUE than either *M. sandwicense* or *D. viscosa* ($p < 0.001$) and *D. viscosa* exhibited higher WUE than *M. sandwicense* (Fig. 5c; $p = 0.008$). Chlorophyll fluorescence was higher in *M. sandwicense* than *D. viscosa* ($p = 0.001$) or *M. maximus* (Fig. 5d; $p = 0.002$).

No differences were observed in *M. maximus* A_{\max} ($t \geq 0.104$, $df = 30$, $p \geq 0.175$), g_s ($t \geq 0.031$, $df = 30$, $p \geq$

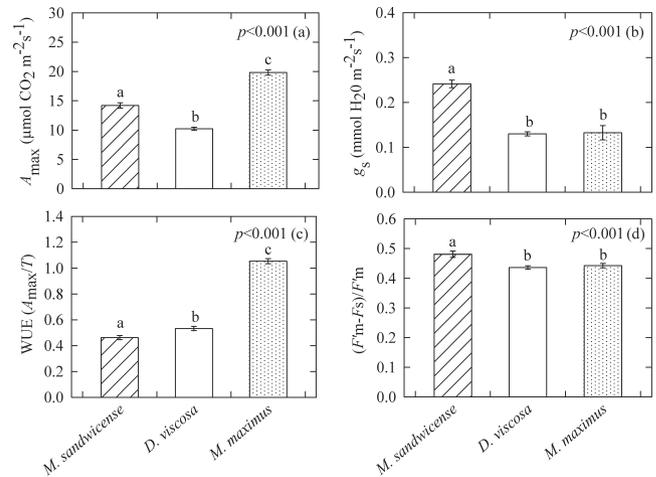


Figure 5. (a) Average maximum photosynthetic rate (A_{\max}), (b) stomatal conductance (g_s), (c) water use efficiency, and (d) chlorophyll fluorescence ($F'_m - F_s/F'_m$) of all plants across all treatments. Bars denote mean values ± 1 SE, p values correspond to overall ANOVA tests, and different letters indicate statistically significant differences ($\alpha = 0.05$) between treatments tested with Tukey's HSD post hoc test.

0.280), WUE ($t \geq 0.001$, $df = 30$, $p \geq 0.074$), or ΦPSII ($t \geq 0.282$, $df = 32$, $p \geq 0.095$) with increasing native functional diversity. Maximum photosynthetic rate ($t \geq 0.308$, $df = 17$, $p \geq 0.242$), WUE ($t \geq 0.287$, $df = 17$, $p \geq 0.163$), and ΦPSII of *M. sandwicense* ($t \geq 0.192$, $df = 17$, $p \geq 0.242$) also did not differ with functional diversity, but *M. sandwicense* g_s increased with native functional diversity ($t \geq 3.520$, $df = 17$, $p \leq 0.002$), as did both A_{\max} (Fig. 6a; $t \geq 2.723$, $df = 17$, $p \leq 0.005$) and g_s of *D. viscosa* (Fig. 6b; $t \geq 2.001$, $df = 17$, $p \leq 0.031$). In addition, ΦPSII of *D. viscosa* was higher in plants grown with *M. maximus* and one other native species than when *D. viscosa* was grown with only *M. maximus* (Fig. 6c; $t = 2.170$, $df = 18$, $p = 0.022$).

Photosynthetic light response curves varied across species grown under full sun and partial shade conditions (Fig. 7). When grown in full sun, the light compensation point [LCP; the point where CO_2 uptake matches CO_2 release (Taiz & Zeiger 2006)] differed across species ($F = 8.344$, $df = 3$, $p = 0.003$), and *M. sandwicense* LCP was 48 and 35% higher than *M. maximus* and *D. viscosa*, respectively ($p \leq 0.018$). When grown in partial shade, the LCP also differed ($F = 5.336$, $df = 3$, $p = 0.014$), but only *M. maximus* had a higher LCP than *D. viscosa* ($p = 0.014$). When grown in full sun, the light saturation point (LSP; the point at which increases in PAR no longer increase photosynthetic rates (Taiz & Zeiger 2006)) differed across species ($F = 16.277$, $df = 3$, $p < 0.001$) and was approximately 46% higher in *M. maximus* and *M. sandwicense* than in *D. viscosa* and *P. zeylanica* ($p \leq 0.002$). The LSP also differed when species were grown in partial shade ($F = 88.203$, $df = 3$, $p < 0.001$), and *M. maximus* LSP was 48, 68, and 64% higher than *M. sandwicense*, *D. viscosa*, and *P. zeylanica*, respectively ($p < 0.001$).

Species-specific differences between plants grown in full sun versus partial shade were also detected (Fig. 7). The

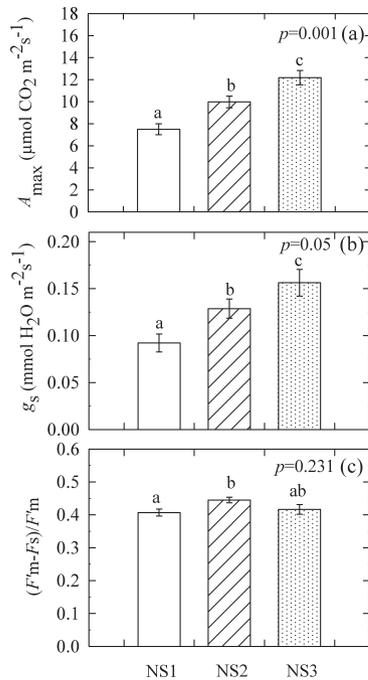


Figure 6. *Dodonaea viscosa* (a) maximum photosynthetic rates (A_{\max}), (b) stomatal conductance (g_s), and (c) chlorophyll fluorescence ($F'_m - F_s / F'_m$) across native species functional diversity treatments. NS1, NS2, and NS3 refer to *D. viscosa* grown with one, two, and three native species, respectively. Bars are mean individual plant biomass ± 1 SE, p values correspond to overall ANOVA tests, and different letters indicate statistically significant differences ($\alpha = 0.05$) between treatments tested with a priori custom contrasts.

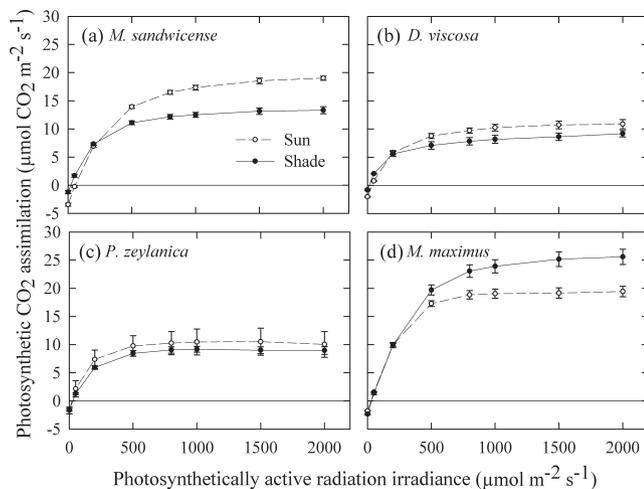


Figure 7. Light response curves of (a–c) native species and (d) invasive *Megathyrsus maximus* when grown in full sun (dashed lines and open circles) and shade (23% PPFD; solid lines and solid circles) environments. Points are mean individual values ± 1 SE.

LCP was 62% higher in *M. sandwicense* ($t = 14.088$, $df = 3$, $p = 0.001$), 61% higher in *D. viscosa* ($t = 44.091$, $df = 3$, $p < 0.001$) and 30% higher in *P. zeylanica* ($t = 3.573$, $df = 3$, $p = 0.037$) when grown in full sun versus partial shade.

However, LCP did not differ between *M. maximus* plants grown in full sun versus partial shade ($t = 1.732$, $df = 3$, $p = 0.182$). The LSP was 29% higher in *M. sandwicense* plants grown in full sun versus partial shade ($t = 9.627$, $df = 3$, $p = 0.002$), but did not differ in *D. viscosa* ($t = 1.948$, $df = 3$, $p = 0.147$) or *P. zeylanica* ($t = 0.446$, $df = 3$, $p = 0.686$). The LSP of *M. maximus*, in turn, was 24% lower when the invasive grass was grown in full sun versus partial shade ($t = 5.619$, $df = 3$, $p = 0.011$).

Discussion

Megathyrsus maximus responded to functional diversity with differences in biomass and fecundity. In general, increased native functional diversity may enhance restoration potential by negatively impacting *M. maximus* growth and reproduction, supporting our hypothesis and reflecting similar findings from other field studies (Tilman 1997; Kennedy et al. 2002; Pokorny et al. 2005). When functional diversity was increased from one to two or three native species, *M. maximus* biomass and reproductive output decreased, indicating that small increases in functional diversity in a restoration setting have the potential to positively enhance ecological restoration projects where invasive grasses like *M. maximus* are problematic. However, the highest *M. maximus* biomass occurred when grown with only one native species, indicating that restoration projects should incorporate a minimum level of diversity for effective suppression. Reproductive ability is a key contributing factor to invasion success (Bryson & Carter 2004), and this decreased reproductive output should provide greater potential for sustainable ecological restoration.

Myoporum sandwicense decreased *M. maximus* biomass more than *Dodonaea viscosa*, *Plumbago zeylanica*, or intraspecific competition, as hypothesized, and higher leaf-level productivity (indexed by A_{\max}) of *M. sandwicense* compared to *D. viscosa* may explain its competitiveness with *M. maximus*. However, other factors such as competition for belowground resources also likely contributed to this finding. Particular native species seem to have inherent physiological capacity to reduce invasion success more than others, a conclusion that supports a sampling effect (Fargione & Tilman 2005), although with only three species a sampling effect is difficult to quantify. Additionally, high intraspecific competition was evident in *M. maximus* monocultures, as has also been documented in other invasive grass species (Firn et al. 2010). Restoration practitioners should closely monitor initial grass control, as successive grass removal will likely be necessary due to a large seedbank and decreased intraspecific competition.

Ecological restoration may be constrained by physiological differences in invasive versus native species (McDowell 2002). In this study, *M. maximus* leaf-level gas exchange was not impacted by functional diversity treatments, but overall differences between invasive and native species were clear. *Megathyrsus maximus* chlorophyll fluorescence was lower than that of *M. sandwicense*, which may suggest a more stressed condition in the grass. However, *M. maximus* exhibited significantly

higher A_{\max} and WUE than the native species tested, similar to prior studies of native and invasive species across diverse environments (Pattison et al. 1998; Cavaleri & Sack 2010). Overall, the physiological differences between invasive grasses and native species may partly explain the widespread success of grass invaders across diverse tropical landscapes, where restoration may be facilitated by selecting native species with competitive physiological traits.

Both LCPs and LSPs decrease from the high canopy to understory (Ellsworth & Reich 1993). *Dodonaea viscosa* and *M. maximus* both exhibited lower LCPs than the upper canopy species *M. sandwicense* when grown in full sun, indicating that net photosynthesis of *D. viscosa* and *M. maximus* will occur at lower light levels (Craine & Reich 2005). *Myoporum sandwicense* and *M. maximus* both exhibited higher LSPs in the sun than did *D. viscosa* or *P. zeylanica*. *Megathyrus maximus* had a higher LSP than all the native species when grown in partial shade, demonstrating a higher photosynthetic capacity in the invasive grass when grown in the understory.

Native functional diversity had no effect on *M. maximus* leaf-level productivity or stress. Increasing native species functional diversity, therefore, decreased the quantity of *M. maximus* biomass but not leaf quality, a common response in plants exposed to altered resource availability (Toledo-Aceves & Swaine 2008). In addition, increased native functional diversity likely altered belowground resource availability and acquisition, and complementary belowground resource use in functionally diverse communities has been shown to increase resistance to invasion (Brown & Rice 2010). Overall, our results support the hypothesis that increased native functional diversity results in greater competition with and suppression of *M. maximus*, although the exact mechanism(s) remain to be identified.

The lack of differences in *M. maximus* biomass between functional diversity levels of two versus three native species may indicate that light availability was not a limiting factor to *M. maximus* growth or that *M. maximus* light acquisition was effectively preempted with only two native species. In addition, it is probable that *M. maximus* can grow in both sun and shade environments, unlike many invasive grasses in Hawaii (Funk & McDaniel 2010), as plants grown in shade had a higher LSP but a similar LCP compared to *M. maximus* grown in full sun. These results also suggest that shaded *M. maximus* has the ability to sustain high rates of photosynthesis if saturating light conditions occur, for example, through a forest canopy gap. However, shading decreased *M. maximus* photosynthetic rates to approximately 50% of rates in full sun, to rates similar to those of native species. As a result, a shading strategy in ecological restoration efforts may result in decreased *M. maximus* productivity, as seen with other invasive grasses in the tropics (Hooper et al. 2002).

The hypothesis that native species would respond positively to increased native functional diversity was unsupported for *M. sandwicense* and *P. zeylanica*. However, *D. viscosa* exhibited higher belowground biomass with increasing functional diversity, a finding that may explain its relatively high WUE as a positive correlation between root production and WUE has

been shown in other species (Gordon et al. 1999). *Dodonaea viscosa* also increased A_{\max} and g_s in response to functional diversity, a result that we have no clear explanation for. Additionally, *M. sandwicense* appeared to benefit from the presence of *M. maximus* when compared to *M. sandwicense* monocultures, an opposite pattern as seen in other restoration studies involving invasive grasses (Hooper et al. 2002), and possibly a result of low grass density in our treatments compared to field studies (Cabin et al. 2002).

This study presents evidence linking higher native functional diversity to decreased reproduction and growth of *M. maximus*, a problematic invader throughout much of the tropics (Parsons 1972). Our original assumption that increased native functional diversity would preclude light acquisition by *M. maximus* is supported by these data. However, it is also possible that factors such as competition for belowground resources (e.g. nutrients) with increasing functional diversity may have also negatively affected *M. maximus*. The results of this study are promising for ecological restoration efforts. Once invasive grasses are removed to allow establishment of other species, functionally diverse native species may provide resistance to future grass invasions. Additional benefits of this approach in invasive grass-dominated ecosystems across the tropics would be a reduction in fuel loads (Rossiter et al. 2003) and increased survival of native seedlings (Hoffman and Haridisan 2008), but it remains unclear whether these findings will hold in a field setting.

Increasing functional diversity may build resistance to species invasions (Kennedy et al. 2002; Fargione & Tilman 2005), especially in the absence of other extrinsic factors (Naeem et al. 2000). This study indicates that native species vary in terms of their competitiveness, and that an increase in native functional diversity provides the opportunity for greater suppression of a widespread and problematic tropical grass invader. Recommendations for restoration of degraded grasslands in Hawaii and throughout the tropics include selection of native species assemblages with high functional diversity that have competitive resource acquisition and use traits. However, trait-based information is largely lacking for the majority of native Hawaiian species (Sandquist & Cordell 2007), and future research is needed to fill this knowledge gap to assist in much needed restoration efforts throughout the Hawaiian Islands.

Implications for Practice

- Ecological restoration of tropical dryland systems dominated by nonnative invasive grasses may be facilitated by following invasive grass removal with the addition of functionally diverse native species assemblages.
- To increase restoration success, native species selection should include an understanding of the resource acquisition and use traits of both native and invasive species.
- Further studies in tropical ecosystems globally are needed on the ecophysiological and functional traits of both native and nonnative species to inform ecological restoration efforts.

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LITERATURE CITED

- Brooks, M. L., C. M. D'Antonio, D. M. Richardson, J. B. Grace, J. E. Keeley, J. M. Ditosmo, R. J. Hobbs, M. Pellant, and D. Pyke. 2004. Effects of invasive alien plants on fire regimes. *Bioscience* **54**:677–688.
- Brown, C. S., and K. J. Rice. 2010. Effects of belowground resource use complementarity on invasion of constructed grassland plant communities. *Biological Invasions* **12**:1319–1334.
- Bryson, C. T., and R. Carter. 2004. Biology of pathways for invasive weeds. *Weed Technology* **18**:1216–1220.
- Cabin, R. J., S. G. Weller, D. H. Lorence, S. Cordell, L. J. Hadway, R. Montgomery, D. Goo, and A. Urakami. 2002. Effects of light, alien grass, and native species additions on Hawaiian dry forest restoration. *Ecological Applications* **12**:1595–1610.
- Cavaleri, M. A., and L. Sack. 2010. Comparative water use of native and invasive plants at multiple scales: a global meta-analysis. *Ecology* **91**:2705–2715.
- Cordell, S., and D. R. Sandquist. 2008. The impact of an invasive African bunchgrass (*Pennisetum setaceum*) on water availability and productivity of canopy trees within a tropical dry forest in Hawaii. *Functional Ecology* **22**:1008–1017.
- Craine, J. M., and P. B. Reich. 2005. Leaf-level light compensation points in shade-tolerant woody seedlings. *New Phytologist* **166**:710–713.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* **23**:63–87.
- Ellsworth, D. S., and P. B. Reich. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**:169–178.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. The University of Chicago Press, Chicago, Illinois.
- Fargione, J. E., and D. Tilman. 2005. Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters* **8**:604–611.
- Firn, J., A. Macdougall, S. Schmidt, and Y. M. Buckley. 2010. Early emergence and resource availability can competitively favour natives over a functionally similar invader. *Oecologia* **163**:775–784.
- Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology & Evolution* **23**:695–703.
- Funk, J. L., and S. McDaniel. 2010. Altering light availability to restore invaded forest: the predictive role of plant traits. *Restoration Ecology* **18**:865–872.
- Giambelluca, T. W., M. A. Nullet, and T. A. Schroeder. 1986. *Rainfall atlas of Hawaii*. State of Hawaii, Department of Land and Natural Resources. Report R76, Honolulu, Hawaii.
- Gordon, C., S. J. Woodin, C. E. Mullins, and I. J. Alexander. 1999. Effects of environmental change, including drought, on water use by competing *Calluna vulgaris* (heather) and *Pteridium aquilinum* (bracken). *Functional Ecology* **13**:96–106.
- Hatheway, W. H. 1952. Composition of certain native dry forests: Mokuleia, Oahu, T.H. *Ecological Monographs* **22**:153–168.
- Hoffmann, W. A., and M. Haridasan. 2008. The invasive grass, *Melinis minutiflora*, inhibits tree regeneration in a Neotropical savanna. *Austral Ecology* **33**:29–36.
- Hooper, E., R. Condit, and P. Legendre. 2002. Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. *Ecological Applications* **12**:1626–1641.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. H. Knops, D. Tilman, and P. Reich. 2002. Biodiversity as a barrier to ecological invasion. *Nature* **417**:636–638.
- Litton, C. M., D. R. Sandquist, and S. Cordell. 2006. Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. *Forest Ecology and Management* **231**:105–113.
- Maxwell, K., and G. N. Johnson. 2000. Chlorophyll fluorescence—a practical guide. *Journal of Experimental Botany* **51**:659–668.
- McDowell, S. C. L. 2002. Photosynthetic characteristics of invasive and non-invasive species of *Rubus* (Rosaceae). *American Journal of Botany* **89**:1431–1438.
- Motooka, P., L. Castro, and N. Duane. 2003. *Weeds of Hawaii's pastures and natural areas: an identification and management guide*. University of Hawaii at Manoa, Honolulu.
- Naeem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**:97–108.
- Nepstad, D., C. Uhl, and A. E. Serrao. 1990. Surmounting barriers to forest regeneration in abandoned highly degraded pastures: a case study from Paragominas, Para, Brasil. Pages 15–229 in A. B. Anderson, editor. *Alternatives to deforestation steps toward sustainable use of the Amazonas*. Columbia University Press, New York.
- Parsons, J. J. 1972. Spread of African pasture grasses to the American tropics. *Journal of Range Management* **25**:12–17.
- Pattison, R. R., G. Goldstein, and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. *Oecologia* **117**:449–459.
- Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* **13**:448–459.
- Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* **40**:65–77.
- Rossiter, N. A., S. A. Setterfield, M. M. Douglas, and L. B. Hutley. 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. *Diversity and Distributions* **9**:169–176.
- Sandquist, D. R., and S. Cordell. 2007. Functional diversity of carbon-gain, water-use, and leaf-allocation traits in trees of a threatened lowland dry forest in Hawaii. *American Journal of Botany* **94**:1459–1469.
- Schleuter, D., M. Daufresne, F. Massol, and C. Argillier. 2010. A user's guide to functional diversity indices. *Ecological Monographs* **80**:469–484.
- Soil Survey Staff. 2006. *Soil Survey Geographic (SSURGO) Database for Oahu, Hawaii*, Natural Resources Conservation Service, United States Department of Agriculture. (available from: <http://soildatamart.nrcs.usda.gov>) [accessed 1 October 2010].
- Stratton, L. C., and G. Goldstein. 2001. Carbon uptake, growth and resource-use efficiency in one invasive and six native Hawaiian dry forest tree species. *Tree Physiology* **21**:1327–1334.
- Taiz, L., and E. Zeiger. 2006. *Plant physiology*. Sinauer Associates, Inc., Sunderland, United Kingdom.
- Thaxton, J., T. Cole, S. Cordell, R. Cabin, D. Sandquist, and C. Litton. 2010. Native species regeneration following ungulate exclusion and nonnative

- grass removal in a remnant Hawaiian dry forest. *Pacific Science* **64**:533–544.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**:81–92.
- Toledo-Aceves, T., and M. D. Swaine. 2008. Biomass allocation and photosynthetic responses of lianas and pioneer tree seedlings to light. *Acta Oecologica-International Journal of Ecology* **34**: 38–49.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* **277**:494–499.
- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999. *Manual of the flowering plants of Hawaii* (revised edition) Bishop Museum Special Publication 97. University of Hawaii and Bishop Museum Press, Honolulu.