



Restoration of native plant communities in a Hawaiian dry lowland ecosystem dominated by the invasive grass *Megathyrsus maximus*

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Keywords

Ecological restoration; Ecophysiology; Guinea grass; Invasive species; Native vegetation; Randomized block design

Nomenclature

Wagner et al. (1999) for all native Hawaiian species USDA ARS-GRIN (www.ars-grin.gov/npgs/) for *M. maximus*

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Abstract

Questions: How does a highly degraded Hawaiian tropical dry lowland ecosystem dominated by the non-native invasive *Megathyrsus maximus* (guinea grass) respond to different restoration treatments (three native species outplanting treatments; four native broadcast seed treatments)? What effect do restoration treatments have on invasive and native species groundcover, biomass and physiological activity, and volumetric soil water content?

Location: Waianae Kai Forest Reserve, Island of Oahu, Hawaii, USA.

Methods: The invasive grass *M. maximus* was suppressed by initial mowing and pre- and post-planting herbicide applications. Native species were added in three outplant and four broadcast seed treatments in a complete randomized block design. Native species and *M. maximus* growth and ecophysiology, and volumetric soil water content were quantified for 8 mo following treatment establishment.

Results: Native species outplant survival ranged from 38% to 67%. Cover of *M. maximus* was significantly reduced in all outplant treatments compared with control and treated control (mowing and herbicide without native species additions), but did not differ across outplant treatments. Of the native species, *Dodonaea viscosa* biomass was higher than *Cordia subcordata*, while other native species did not differ. Maximum photosynthetic rates (A_{max}) did not differ across species in July. However, in August (drier period), *M. maximus* exhibited lower A_{max} than all native species except *T. populnea*, indicating adaptive dormancy during drought. Broadcast seeding with native species was not an effective restoration treatment, as field germination ranged from 0.5% to 2.3%.

Conclusions: Ecological restoration of highly invaded Hawaiian tropical dry lowland ecosystems can be mediated through aggressive invasive species suppression and native species outplanting. Recommendations for restoration include initial removal of invasive grasses, adaptive suppression of grasses post-outplanting, and utilization of diverse native species assemblages that are ecophysiologicaly adapted to local conditions and competitive with *M. maximus*.

Introduction

Ecological restoration is designed to initiate the recovery of ecosystems that have been damaged or destroyed and, ultimately, reverse degradation. Non-native species invasions, however, often challenge restoration efforts, particularly where invaders modify biotic interactions (Vitousek 1990; Mitchell et al. 2006), disturbance regimes (D'Antonio & Vitousek 1992; Veldman et al.

2009), ecosystem carbon and nutrient dynamics (Mack & D'Antonio 2003; Litton et al. 2006) or ecohydrology (Cavaleri & Sack 2010). Invasive grasses, in particular, are characterized by high growth rates and superior competition with native species for limiting resources that can ultimately displace native communities (D'Antonio & Vitousek 1992; Pivello et al. 1999). In addition, invasive grasses often have high seed production, efficient dispersal mechanisms and high tolerance to disturbances

such as ungulate grazing and fire (Bryson & Carter 2004). Isolated and small oceanic islands such as the Hawaiian Islands are especially vulnerable to species invasions (Paulay 1994; Gimeno et al. 2006). Non-native grass invasions have caused dramatic biodiversity and habitat loss in tropical dry forests in Hawaii and elsewhere (Janzen 1988; Veldman et al. 2009), and the reintroduction of native species to these invaded landscapes can facilitate ecological restoration (Cabin et al. 2002b).

Globally, tropical dry forests are one of the most threatened ecosystem types (Khurana & Singh 2001; Vieira & Scariot 2006), yet provide habitat for a unique biodiversity that is highly vulnerable to anthropogenic threats (Miles et al. 2006). Although the original extent of tropical dry forest in Hawaii is largely unknown due to widespread land-use change and species invasions (Hatheway 1952), it is estimated that over 90% of this ecosystem type has already been lost (Bruegmann 1996), and the majority of that which remains is highly degraded and exists as remnant patches surrounded, and typically invaded, by non-native grasses (Blackmore & Vitousek 2000; Cabin et al. 2002a). Of the main Hawaiian Islands, the densely populated island of Oahu has the least amount of forest cover remaining (Cuddihy & Stone 1990), and the invasive grass *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs (guinea grass; formerly *Urochloa maxima* and *Panicum maximum* Jacq.), a C₄ grass native to tropical Africa, dominates many lowland areas. Naturalized as a pasture grass by 1871, *M. maximus* is currently present on all of the main Hawaiian Islands (Motooka et al. 2003). Suppression of invasive grasses and establishment of native species communities through ecological restoration is crucial for both conserving the unique biodiversity of Hawaiian tropical dry ecosystems, and as a potential mechanism for controlling further invasions by non-native species (O'Dowd et al. 2003).

Without intervention, remaining Hawaiian dry forests will likely continue to shift towards dominance by invasive grasses, resulting in increased susceptibility to fire and further loss of native habitat (D'Antonio et al. 1998). The reintroduction of native woody species to invasive grass-dominated landscapes via ecological restoration can reduce fuel loads and fire spread associated with invasive grasses, as well as increase native biodiversity (Mack & D'Antonio 2003). However, ecological restoration in ecosystems where invasive grasses have naturalized can be exceptionally difficult, as native seedlings must compete with dense grass cover for above- and below-ground resources (Nepstad et al. 1990), as well as a typically pervasive invasive seed bank (Cordell et al. 2009).

Successful restoration of native plant communities in highly invaded, non-native grass-dominated ecosystems in

Hawaii has been accomplished to some degree through exclusion of non-native ungulates, control of invasive grasses and outplanting of native species (D'Antonio et al. 1998; Cabin et al. 2000). However, none of these prior studies were conducted in areas dominated by *M. maximus*, which is one of the more problematic grass invaders in Hawaii and throughout the tropics, largely because it grows taller and produces more biomass (up to 3-m tall and 50 t·ha⁻¹ dry matter) than other dominant invasive grasses in Hawaii (e.g. *Pennisetum setaceum* and *Pennisetum ciliare* rarely exceed 1 m in height and typically produce ~50% less biomass) (Duke, 1983, Handbook of Energy Crops, unpublished data).

To address this knowledge gap, we conducted a randomized complete block field experiment to restore a tropical dry lowland ecosystem on Oahu that is currently dominated by *M. maximus*. Building upon prior work in Hawaii, non-native ungulates (cattle, pigs) were excluded with a fence, *M. maximus* was suppressed via mowing and both pre- and post-planting herbicide application, and native Hawaiian species were added by outplanting five species in three treatment combinations, and broadcast seeding three species in four treatment combinations. We utilized both top-down (grass removal) and bottom-up [planting functionally diverse assemblages of species (Ammond et al. 2012)] approaches to explore restoration potential in this system (D'Antonio & Chambers 2006). The three outplanting treatments included a constant groundcover (*Plumbago zeylanica* L.) and a constant mid-canopy shrub species [*Dodonaea viscosa* (L.) Jacq.], with variation in the upper-canopy tree species [*Thespesia populnea* (L.) Sol. Ex Correa, *Myoporum sandwicense* (A. DC.) A. Gray and *Cordia subcordata* Lam.] Broadcast seeding was accomplished with three species (*D. viscosa*, *T. populnea* and *C. subcordata*), both individually and all three in combination.

We hypothesized that competition for above- and below-ground resources (light and water) between native species and *M. maximus* would vary as a result of differential resource use and growth rates of functionally diverse native species assemblages (Ammond et al. 2012). Specifically, we hypothesized that: (1) outplanting a combination of native species that included *M. sandwicense* would result in higher restoration success (i.e. higher native species survival, cover, above- and below-ground biomass, and leaf-level indices of productivity; and lower *M. maximus* cover) (Culliney & Koebele 1999; Stratton & Goldstein 2001) than other outplanting combinations due to high growth rates of *M. sandwicense*; (2) soil volumetric water content would be highest where *M. maximus* was successfully suppressed (Litton et al. 2008); and (3) broadcast seeding would be more effective when three species were broadcast in combination vs individually (Baskin & Baskin 2001).

Methods

Study site

The study was conducted in a Hawaiian dry lowland ecosystem on leeward Oahu, Hawaii, US, currently dominated by the invasive grass *M. maximus* (Waianae Kai Forest Reserve, 300 m a.s.l., 158°9'181" W, 21°28'53" N) (Fig. 1). Soils are well-drained, Ewa series reddish silty clay loams (Aridic Haplustolls) formed from alluvium weathered from upland basalt (Soil Survey Staff 2006). Mean annual precipitation is 1258 mm (Giambelluca et al. 2011), and mean annual temperature is 22 °C (T. Giambelluca, unpublished data). During the study period of 7 January to 24 August 2010, precipitation totalled 324 mm (drier than the 2003–2009 average of 547 mm for the same period) and temperature averaged 22.4 °C.

Experimental design and sampling

The study area was mowed in July 2009, and in October 2009 a 0.13-ha fence was constructed to exclude all ungulates. Twenty-four experimental 9-m² plots were established inside the fence in a randomized block design, grouped into four blocks down a ~10-m elevation gradient. Each block consisted of the following six treatments: Outplant-*Thespesia*, Outplant-*Myoporum*, Outplant-*Cordia* (refers to genus names of upper-canopy tree species; all outplant treatments also included *Dodonaea viscosa* and *Plumbago zeylanica*), Treated Control (grass removal with-

out native species additions), Control (neither grass removal nor native species additions), and Seed (broadcast seeded plots).

On 7 September 2009 (50–60 d after mowing), herbicide was applied to suppress *M. maximus* regrowth on all replicates except untreated Controls. The initial treatment was a combination of the active ingredients glyphosate (KleenUp[®], Loveland Products, Inc., Greeley, CO, US, EPA reg. no. 34704-890) and imazapyr (Habitat[®], BASF Corporation, Research Triangle Park, NC, US, EPA reg. no. 241-426) applied at 2.5 kg a.e.·ha⁻¹ and 1.7 kg a.e.·ha⁻¹, respectively, in a water carrier with non-ionic surfactant (0.5% v/v), with a uniform foliar broadcast application delivery technique at a rate of 280 L·ha⁻¹. On 17 November 2009, a cut stump maintenance application of triclopyr (Pathfinder[®] II, Dow AgroSciences, Indianapolis, IN, US, EPA reg. no. 62719-176) was made to a small number of *Leucaena leucocephala* (Lam.) de Wit., applied to the circumference and sides of cut stumps using a pre-mixed 13.6% triclopyr formulation. On 5 January 2010, 2 d prior to native species outplanting, glyphosate was reapplied to new *M. maximus* regrowth in all treatment plots (excluding untreated Control plots) as a broadcast foliar treatment at a rate of 5 kg a.e.·ha⁻¹. On 12 April 2010 (95 d post-planting), an application of the grass-selective herbicide fluazifop p-butyl (Fusilade[®] DX, Syngenta Crop Protection, Inc. Greensboro, NC, US, EPA reg. no. 100-1070) was applied for continued suppression of *M. maximus* regrowth. In addition, herbaceous weeds were hand-pulled monthly from May to August, 2010 (combined across treatments:

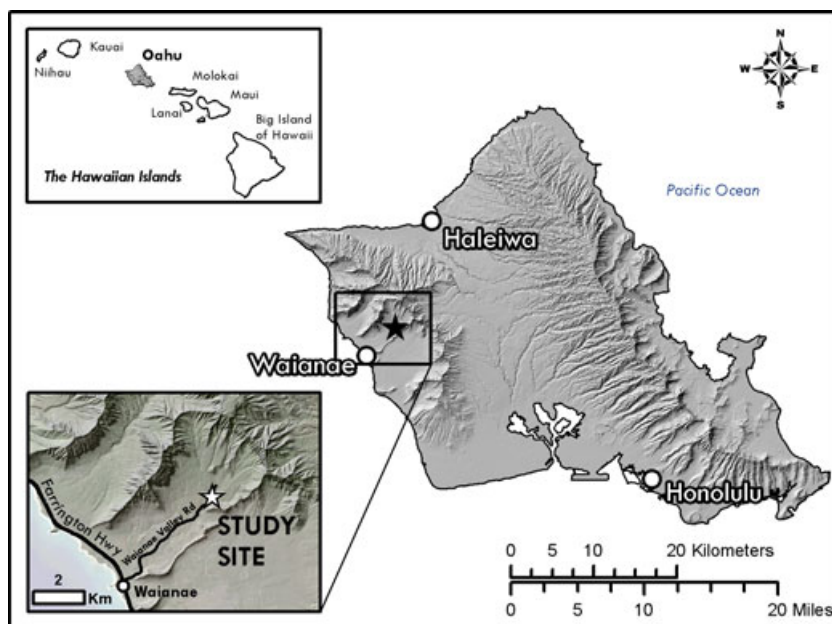


Fig. 1. Study site location on the Island of Oahu, Hawaii, US.

May: 22.5 g·m⁻²; June: 10.6 g·m⁻²; July: 1.3 g·m⁻²; August: 1.3 g·m⁻²; end of August: 0.9 g·m⁻²). Untreated Control treatments were completely dominated by *M. maximus*.

Native species additions (all species used are native to Hawaii) coincided with the winter rainy season and occurred via outplanting of nursery-grown seedlings on 7 January 2010, and broadcast seeding on 15 January 2010. Outplants were commercially produced and purchased from a local source (Hui Ku Maoli Ola, Kaneohe, Hawaii) in 10-cm containers, hand-planted in each treatment plot at a density of two plants m⁻² (25 plants·plot⁻¹: 12 groundcover (*P. zeylanica*), nine shrub (*D. viscosa*) and four canopy tree individuals plot⁻¹), and given 1 L of supplemental water (total of 25 L·plot⁻¹) immediately following planting and once per week for 3 wk. Mortality in the first month (21%) was offset by a replacement planting. In addition, 20 plants of each species, excluding the groundcover *P. zeylanica*, were planted outside of treatment plots for development of allometric models to estimate biomass. Harvest of these additional plants occurred monthly throughout the duration of the experiment. Above-ground biomass was cut at ground level, below-ground biomass was excavated (roots >2-mm diameter), and all biomass was cleaned, dried at 70 °C to a constant mass, and weighed.

Seeds of *D. viscosa*, *T. populnea* and *C. subcordata* from the Plant Material Center on Molokai, Hawaii, were broadcast following pretreatment to break dormancy. Physical dormancy of *D. viscosa* seeds was broken with a 10-s submergence in boiling water (Baskin et al. 2004). Seeds of *T. populnea* were abraded with 40 grit sandpaper, the capsule end of the woody fruit of *C. subcordata* was cut, and both were soaked in water for 24 h prior to broadcasting (Friday & Okano 2006). Seed treatments were split into four 1.5-m² quadrats, where 100 seeds of each species were broadcast individually in each of three quadrats, and 99 seeds of an equal mixture of the three were broadcast in the fourth quadrat. Rodent snap-traps were installed around the seed treatments and maintained for the first 2 mo following seed additions. To determine germination rates under ideal conditions, 100 seeds of each species were pretreated as above, sown in a greenhouse tray with sterilized growing media at the University of Hawaii at Manoa (157° 48'38" W, 21°18'21" N), and kept moist for 2 mo.

All data were collected during January–August 2010. Final native species outplant survival was recorded on 24 August 2010 (230 d post-outplanting). Percentage cover of *M. maximus* and native species was evaluated on 24 August 2010 with a point-intercept method (81-point frame encompassing each 9-m² treatment plot). Above- and below-ground biomass of *T. populnea*, *M. sandwicense* and *C. subcordata*, and below-ground biomass of *D. viscosa* were

estimated with species-specific allometric models developed in this study from destructive harvest to predict biomass from stem basal diameter measurements. Above-ground biomass of *D. viscosa* was estimated using an existing allometric model developed in Hawaii (Litton & Kauffman 2008). Seed germination and seedling survival was assessed monthly.

Leaf-level gas exchange was quantified for all species in all treatments as an index of productivity and relative competitive ability. Maximum photosynthetic rate (A_{\max}), stomatal conductance (g_s) and water use efficiency (WUE (A_{\max} /Transpiration)) were measured twice (29–30 July and 30–31 August 2010) on two fully expanded leaves of all plants with a LI-6400XT Portable Photosynthesis System (LI-COR Biosciences, Lincoln, Nebraska, USA). Leaf chamber light and CO₂ levels were standardized with saturating light (1200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and CO₂ concentration (400 $\mu\text{mol}\cdot\text{mol}^{-1}$). A separate study generated plant-specific photosynthetic light response curves in two distinct light environments [full sun and 23% photosynthetic photon flux density (PPFD)] for the majority of the species used in this study [see Ammond & Litton (2012) for details]. Here we present information for an additional two species used in this experiment (Fig. 6) using identical procedures. Finally, volumetric soil water content in the top 12 cm of mineral soil was quantified monthly from January to August 2010, with a CS620 HydroSense Water Content Sensor (Campbell Scientific, Logan, UT, USA), where six measurements were averaged across each treatment replicate.

Statistical analyses

All statistical analyses were based on mean values for each species and treatment. PASW Statistics v.18 (IBM SPSS, Inc., Chicago, IL, USA) and Minitab v. 15 (Minitab, Inc., State College, PA, USA) were used for analyses, and significance was assessed at the $\alpha = 0.05$ level. Following a significant ANOVA, Tukey's honestly significant difference (HSD) *post-hoc* analyses were used to analyse differences across all treatments, and *a priori* custom contrasts were used to test specific hypotheses.

Randomized block ANOVAs were used to analyse percentage survival of native species outplants by treatment and by species, percentage native species and *M. maximus* cover by treatment, native species above- and below-ground biomass by treatment and by species, and volumetric soil water content by treatment. Seed germination and seedling survival data are presented, however, too few seeds germinated in the field for statistical analysis. Above- and below-ground biomass data were log-transformed to meet assumptions of the ANOVA model. Non-linear regression was utilized to develop species-specific allomet-

ric equations for predicting above- and below-ground biomass from basal diameter. Power, quadratic and cubic models were explored, and final model selection was based on R^2 values and plots of residuals. Leaf-level gas exchange (A_{\max} , g_s , WUE) from two time periods was analysed for species and treatment effects with repeated measures ANOVA. One-way ANOVA was used to compare light response curve metrics across species, and two-sample Student's t -tests were used to evaluate differences between plants grown in full sun vs partial shade (23% ambient PPFD).

Results

Averaged across all treatments, outplant survival did not differ by species ($P = 0.217$), with 67% of *P. zeylanica*, 60% of *D. viscosa*, 56% of *T. populnea*, 44% of *C. subcordata* and 38% of *M. sandwicense* surviving for 8 mo. Outplant treatment also did not affect survival rates ($P > 0.10$). Eight mo after outplanting, cover of *M. maximus* was significantly lower in all outplant treatments than in Treated Control and Control ($P \leq 0.025$), but did not differ between the three outplant treatments ($P > 0.10$; Fig. 2). Mean cover of all native species did not significantly differ by outplant treatment ($P = 0.053$), but there was a trend of increasing native species cover from Outplant-*Thespesia* to Outplant-*Myoporum* to Outplant-*Cordia* (Fig. 2). Native species cover in Treated Control, Control and Seed treatments was 0%, as natural recruitment of native species did not occur and plants germinating from seed were too few and small to affect cover. Cover of *P. zeylanica* (native

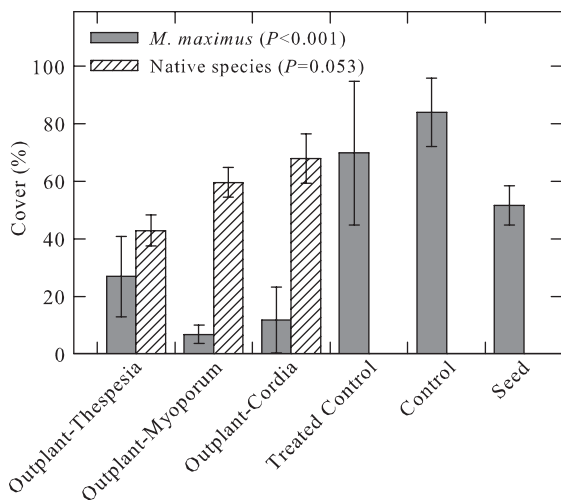


Fig. 2. Percentage cover by outplant treatment. Percentage cover of native species and the invasive grass *M. maximus* 8 mo after restoration experiment initiation. Bars are mean percentage cover by outplant treatment ± 1 SE, and P -values correspond to overall ANOVA tests.

groundcover species) also did not differ across treatments ($P = 0.088$).

Basal diameter was a relatively accurate estimator of total above-ground biomass for all native species ($R^2 \geq 0.71$), and to a lesser degree of below-ground biomass for all native species ($R^2 \geq 0.60$) (Table 1). All final models were highly significant ($P < 0.001$). Log transformation of dependent and/or independent variables and the inclusion of tree height did not significantly improve allometric models. When initially planted, only *M. sandwicense* had higher biomass than the other natives ($P \leq 0.019$). Mean individual plant above-ground biomass across all treatments after 8 mo of growth was 101, 21, 84 and 12 g ($P < 0.001$), and below-ground biomass was 18, 12, 13 and 5 g ($P = 0.003$) for *D. viscosa*, *T. populnea*, *M. sandwicense* and *C. subcordata*, respectively. *D. viscosa* above-ground biomass was higher than *C. subcordata* and *T. populnea* ($P < 0.001$) but did not differ from that of *M. sandwicense* ($P = 0.191$). *D. viscosa* below-ground biomass was also higher than that of *C. subcordata* ($P = 0.002$). Of the canopy trees, only *M. sandwicense* had higher above-ground biomass than *C. subcordata* ($P = 0.042$). When analysed by treatment, *D. viscosa* above-ground (Fig. 3a) and below-ground (Fig. 3b) biomass did not differ with outplant treatment ($P \geq 0.210$), nor did above- or below-ground biomass of canopy trees differ with outplant treatment (Fig. 3a,b; $P \geq 0.161$).

Some differences in leaf-level physiology were observed for all species across all treatments through time (Fig. 4). A species by time interaction was detected for maximum photosynthetic rates (A_{\max} , $\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$; Fig. 4a; $P = 0.001$). Native species and *M. maximus* A_{\max} did not differ in July ($P = 0.373$), however in August, *M. maximus* A_{\max} was lower than all native species ($P \leq 0.015$) except *T. populnea* ($P = 0.056$). Stomatal conductance (g_s , $\text{mmol H}_2\text{O}\text{m}^{-2}\text{s}^{-1}$) varied between species ($P = 0.001$) and by time ($P < 0.001$), and species showed similar patterns over time (Fig. 4b; $P = 0.839$). *P. zeylanica* had 26%, 36% and 53% greater g_s than *D. viscosa*, *T. populnea* and *M. maximus* ($P \leq 0.033$), respectively. Water use efficiency (WUE, defined as $A_{\max}/\text{Transpiration}$) did not differ by species or time, nor was there a significant species by time interaction (Fig. 4c; $P \geq 0.133$). In addition, *P. zeylanica* and *D. viscosa* exhibited 41% and 54% higher A_{\max} , and 54% and 67% higher g_s in July than in August, respectively ($P \leq 0.001$).

All native outplant treatments had significantly higher volumetric soil water content than untreated control treatment ($P < 0.001$). However, no differences were observed between different native outplanting treatments (Fig. 5b; $P \geq 0.965$). Mean volumetric soil water content was highest in March–April, and declined steadily through August, when all treatments had similarly low volumetric soil water content (Fig. 5a).

Table 1. Allometric models for predicting native species above-ground (leaf, wood and total) and below-ground (roots >2 mm) biomass in Hawaiian dry lowland ecosystems.

Dependent variable (Y)	N	a (SE)	b (SE)	b ₂ (SE)	b ₃ (SE)	R ²
<i>Dodonaea viscosa</i>						
Leaf biomass	20	0.08 (0.10)	2.25 (0.40)			0.78
Wood biomass	20	0.08 (0.06)	2.63 (0.26)			0.93
Total above-ground biomass	20	0.13 (0.09)	2.55 (0.21)			0.95
Below-ground biomass	20	0.06 (0.04)	2.21 (0.37)			0.69
<i>Thespesia populnea</i>						
Leaf biomass	17	0.04 (0.04)	2.204 (0.42)			0.83
Wood biomass	17	0.03 (0.01)	3.26 (1.01)			0.64
Total above-ground biomass	17	0.03 (0.04)	2.66 (0.56)			0.80
Below-ground biomass	17	0.05 (0.09)	2.14 (0.70)			0.60
<i>Myoporum sandwicense</i>						
Leaf biomass	20	-45.33 (54.38)	12.79 (12.89)	-1.02 (0.93)	0.04 (0.02)	0.99
Wood biomass	20	-35.68 (27.57)	9.20 (6.53)	-0.74 (0.47)	0.03 (0.01)	0.99
Total above-ground biomass	20	-89.92 (56.71)	24.16 (13.51)	-1.92 (0.98)	0.08 (0.02)	0.99
Below-ground biomass	20	-37.82 (16.35)	10.97 (3.89)	-0.89 (0.28)	0.03 (0.01)	0.99
<i>Cordia subcordata</i>						
Leaf biomass	15	0.13 (0.17)	1.56 (0.37)			0.61
Wood biomass	15	0.15 (0.18)	1.50 (0.46)			0.66
Total above-ground biomass	15	0.28 (0.27)	1.54 (0.38)			0.71
Below-ground biomass	15	0.05 (0.07)	1.85 (0.56)			0.61

*Models for *D. viscosa*, *T. populnea* and *C. subcordata* are power functions ($Y = aX^b$), and the model for *M. sandwicense* is a cubic function ($Y = b_3X^3 + b_2X^2 + b_1X + a$). Y is the dependent variable (g dry weight), X is the predictor variable [basal diameter (mm)], and a and b are constants. *D. viscosa* leaf, wood and total above-ground biomass equations are from Litton & Kauffman (2008).

Seed germination was moderate when viability was indexed under ideal conditions in the greenhouse (*D. viscosa*: 19%, *T. populnea*: 45% and *C. subcordata*: 75%). In the field, however, seed germination and seedling survival was exceedingly low. *D. viscosa* and *C. subcordata* each germinated at rates of 0.5% (two seeds of each species germinated across all treatments). Both seedlings of *D. viscosa* persisted for the duration of the study, and one *C. subcordata* seedling survived 8 mo. *Thespesia populnea* germination rate was 2.3%, and only one seedling survived to the end of the study. All four surviving seedlings were located in quadrats where species were broadcast individually.

When grown in greenhouse conditions in full sun and partial shade (23% of ambient PPFD), native species and *M. maximus* differed in their light response curves [Fig. 6, and Ammond & Litton (2012)]. Light compensation points (where CO₂ uptake matches CO₂ release) and light saturation points [when photosynthetic rates no longer increase in response to increased PAR (Taiz & Zeiger 2006)] did not differ for the canopy trees *T. populnea* and *C. subcordata* (Fig. 6), but varied between native species collectively and *M. maximus* [see Ammond & Litton (2012)]. When *M. maximus* was grown in full sun vs partial shade, the light compensation point did not differ ($P = 0.182$), however the light saturation point was 24% lower ($P = 0.011$) (Ammond & Litton in press).

Discussion

Invasive grasses have been shown to inhibit natural recruitment of native species in many dry environments, including neotropical savanna in Brazil (Hoffmann & Haridasan 2008) and abandoned pastures in Puerto Rico (Zimmerman et al. 2000), and have been attributed to ecosystem-level changes, including alterations in resource availability (D'Antonio & Vitousek 1992). Based on the initial results of this study, however, ecological restoration of native plant communities is possible in Hawaiian dry lowland ecosystems dominated by invasive grasses. Ungulate control, aggressive manual and chemical grass removal prior to native species additions, and follow-up herbicide application during native species development was critical for early outplant establishment at our study site, where a history of frequent fire and ungulate disturbance has exacerbated non-native grass invasion (D'Antonio & Vitousek 1992; Cabin et al. 2000). Some mortality was anticipated and offset by high-density outplanting in the experiment, and outplant survival after 8 mo was moderate. The native Hawaiian species used are well-adapted to dry lowland environments. Reduced competition with the invasive *M. maximus* provided by manual and chemical suppression in our study likely explains initial native species success (Cabin et al. 2002b). While there is limited evidence to suggest that *M. maximus* may

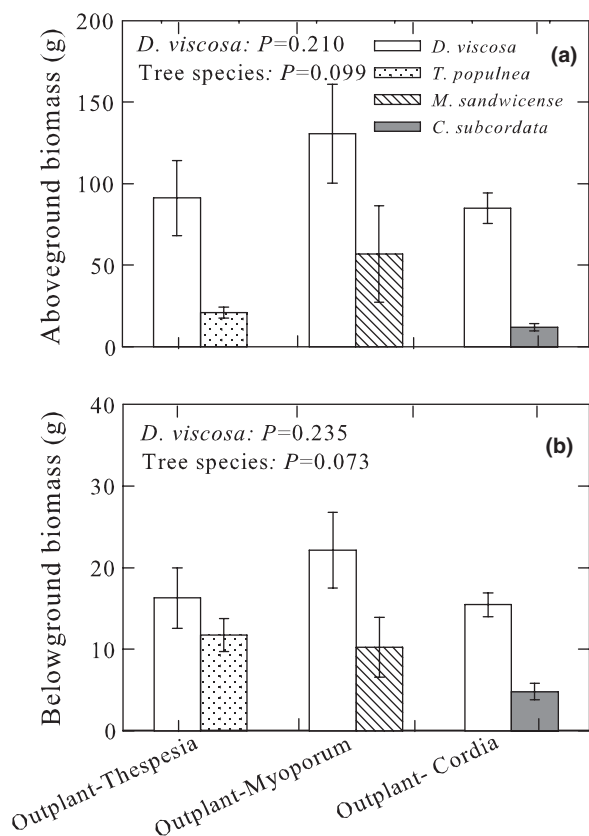


Fig. 3. Biomass by treatment. Total (a) above-ground and (b) below-ground biomass of native species in three outplanting treatments. Bars are mean biomass ($\text{g}\cdot\text{plant}^{-1}$) by plot ± 1 SE, and P -values correspond to overall ANOVA tests. Note the different scales in (a) and (b).

exhibit allelopathy (Chou & Young 1975), it is more likely at our study site that rapid germination and growth, abundant seed production and efficient dispersal, fire promotion and strong competition for above- and below-ground resources by *M. maximus* typically results in its dominance over native species in the absence of management (Bryson & Carter 2004).

Megathyrsus maximus suppression and native species restoration

Invasive grass removal alone was not an effective restoration method, as no native species recruited naturally when *M. maximus* was suppressed without native species outplantings. This finding is not surprising, given the complete absence of native species on the site prior to restoration and its isolation from native forest remnants, indicating low native seed bank and seed rain (Zimmerman et al. 2000). Furthermore, cover of *M. maximus* was substantially higher in treatments where the grass was controlled but no native species additions occurred (Treated Control) compared to any of the outplant treatments.

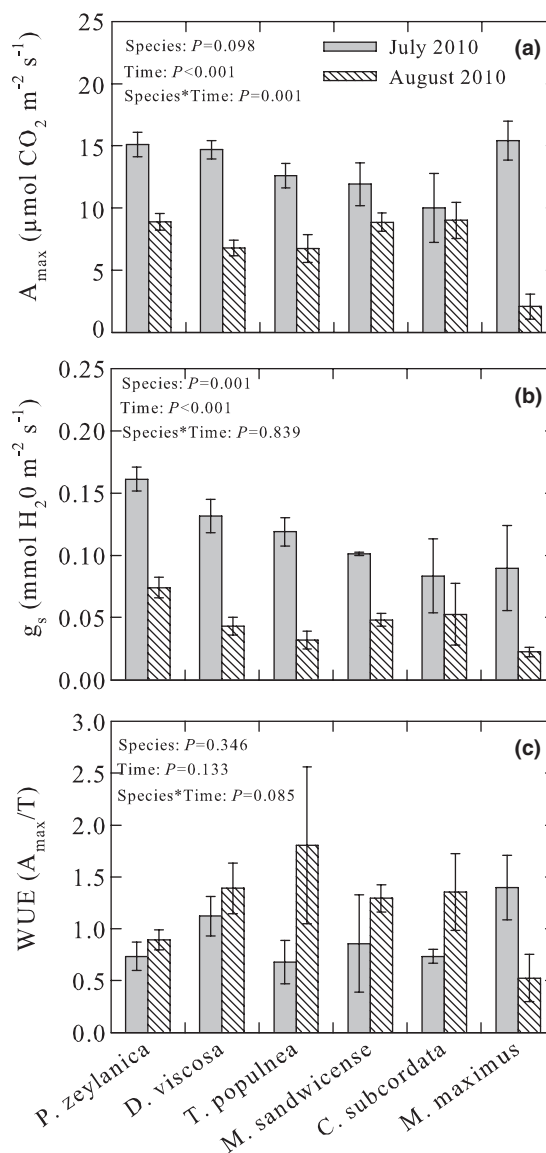


Fig. 4. Physiological measurements by species. (a) Maximum photosynthetic rates (A_{\max}), (b) stomatal conductance (g_s) and (c) water use efficiency (WUE) of species averaged across all treatments. Bars are mean individual plot values ± 1 SE, and P -values correspond to overall ANOVA tests.

Thus, competition with native species suppressed grass invasion more than grass control alone. All outplant treatments performed similarly 8 mo following planting, and longer-term results are likely needed to fully evaluate outplant treatment differences. In a similar dry forest in Puerto Rico, 5–7 yr of native species growth following restoration was necessary to effectively shade and suppress *M. maximus* (Francis & Parrotta 2006). While it may be unrealistic to design for complete eradication of *M. maximus* in these environments, we highlight that native species can provide grass suppression through competition,

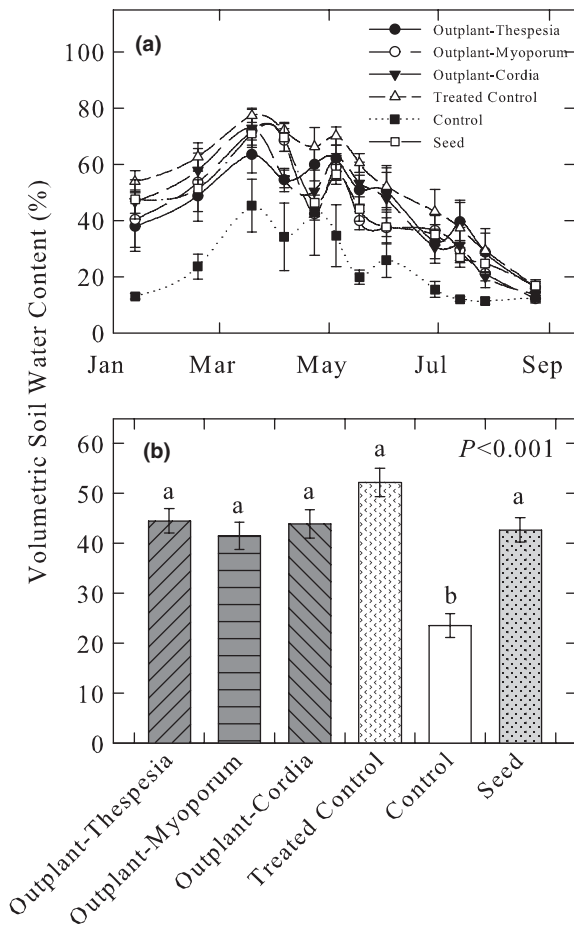


Fig. 5. Soil volumetric water content by treatment. Soil volumetric water content (%) in the top 12 cm of mineral soil (a) through time and (b) by treatment averaged across time. Points and bars are mean treatment values ± 1 SE, the P -value corresponds to the overall ANOVA test, and different letters above bars indicate significant differences ($\alpha = 0.05$) between species following a Tukey's HSD *post-hoc* test.

especially when outplanted in combinations that utilize available resources effectively.

While differences between outplant treatments were not observed in this study, individual native species demonstrated greater restoration potential than others. After 8 mo, *D. viscosa* plants were larger and exhibited higher growth rates than some canopy tree species planted. Since this species can provide shade with a sizeable canopy in < 1 yr, it has potential to be a useful pioneer species for initial ecological restoration efforts. Similarly, in a dry forest on Maui, *D. viscosa* has been shown to establish and grow quickly following restoration outplanting and to regenerate naturally from seed thereafter (Medeiros & Von Allmen 2006). *Dodonaea viscosa*, as a nurse tree, could provide a more suitable microclimate for seedling establishment of other native species than grass-dominated or open areas (Santiago-Garcia et al. 2008). *Dodonaea viscosa*

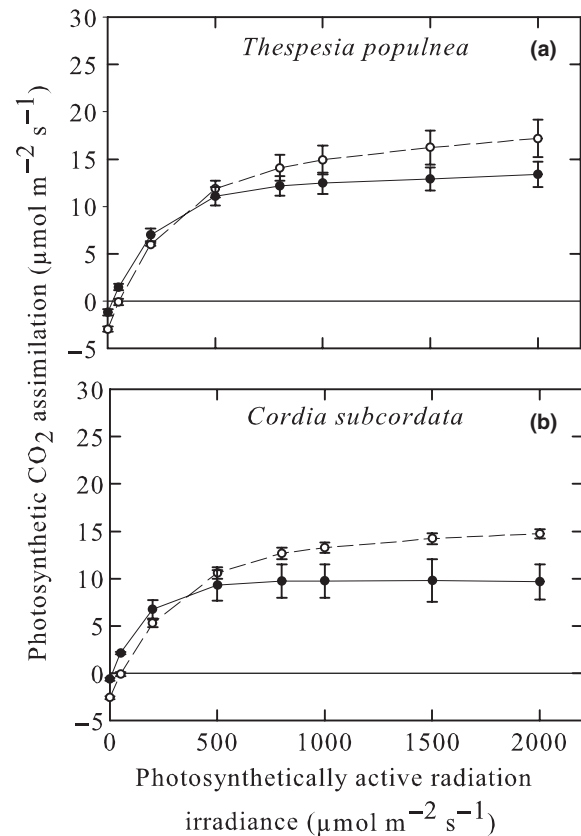


Fig. 6. Light response curves by species. Light response curves of the native canopy tree species (a) *T. populnea* and (b) *C. subcordata* when grown in full sun (dashed lines and open circles) and shade (23% PPFD; solid lines and solid circles). Points are mean individual plant values ($n = 4$) ± 1 SE. Light response curves for the other native species used in this experiment (*P. zeylanica*, *D. viscosa*, *M. sandwicense* and *M. maximus*) are presented in Ammond & Litton (2012).

also shows adaptations to fire (Ainsworth & Kauffman 2009), an important advantage in fire-prone ecosystems.

Ecophysiology

Leaf-level physiological activity (A_{max} and g_s) was lower for all species during August than July, 2010, most likely due to dry season stress in August (precipitation of 23.6 mm in July and 9.6 mm in August). The physiological differences between the two sampling dates were especially pronounced for the invasive *M. maximus*, which on average had an A_{max} of $15 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ in late July (not different from native species) compared to $2 \mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ in late August (lower than most native species), indicating dry-season dormancy for this invasive grass. Most native species restoration efforts occur during the rainy season, and must be coupled with invasive grass removal because of high competition from the grass. These results indicate that additional grass suppression is likely

not necessary during the dry season. In the wetter month of July, photosynthetic rates were comparable between native species and the invasive grass, similar to results found in another dry forest in Hawaii where invasive grass dominance was not attributed to superior physiological activity (Cabin et al. 2002b). We expect *M. maximus* to compete for and utilize water resources better when precipitation becomes less limiting.

Soil water availability

Soil volumetric water content was higher where the invasive grass was successfully suppressed, as hypothesized, with all outplant treatments exhibiting higher soil volumetric water content than the untreated control treatment. In addition, treatments where grass was suppressed but no outplanting occurred (Treated Control) had twice the soil volumetric water content than the Control. However, soil volumetric water content did not differ between the three outplanting treatments. Decreased water availability due to invasive grasses in dry landscapes in Hawaii is a strong limiting factor to native seedling success (Thaxton et al. 2012), and as seen in *Pennisetum setaceum* invasions in a tropical dry forest on the Island of Hawaii (Cordell & Sandquist 2008), *M. maximus* appears to actively use a large proportion of available surface water in the dry environment at our study site.

Native species broadcast seeding

Seed germination and seedling survival were exceedingly low in all broadcast seed treatments, and hypotheses were unsupported, reflecting other studies conducted in dry tropical environments (Ray & Brown 1995), including Hawaii (Brooks et al. 2009). In this study, seed dormancy was broken and seeds broadcast during the rainy season. Grass litter was removed to provide contact between the seeds and soil, and seed predators were few (only four rodents and one mongoose were trapped on-site). We observed that most germinated seeds either desiccated in full sunlight or were out-competed by newly established *M. maximus* within a few weeks of germination. In this study, we were unable to identify a viable seed dispersal method that would be conducive to restoration success. It could, however, be a valuable secondary approach following native species outplanting, when outplanted seedlings have established shade and more favourable microclimates for seed germination and survival (Francis & Parrotta 2006).

Light response curves

When grown in both full sun and partial shade in greenhouse conditions, *M. maximus* light saturation points were

higher than most of the native species, and higher when the grass was grown in partial shade vs full sun (Ammond & Litton in press). This indicates that the invasive grass can grow in both high and low light environments (Ostertag et al. 2008). However, shading of *M. maximus* does result in reduced photosynthetic rates that are more similar to those of the native species tested (Ammond & Litton 2012).

Conclusions

Restoration of degraded landscapes, as well as conservation of the few remnant native dry lowland forests, is integral to halting the continued decline of native Hawaiian dry lowland ecosystems (Goldman et al. 2008). Ecological restoration of non-native grasslands can increase native biodiversity, as well as buffer adjacent native ecosystems from non-native grass invasions. Restored native stands, in turn, can provide a valuable native seed source in areas where seed banks may be entirely invasive (Daehler & Goergen 2005), as well as increased landscape connectivity if many small nuclei of native species are restored in an otherwise invasive landscape (Reis et al. 2010).

Ecological restoration in highly invaded ecosystems will require active and adaptive management, as well as long-term monetary and personnel commitment (Norton 2009). Aggressive site preparation and continued post-planting grass removal is critical to allow a native species canopy to establish and suppress *M. maximus*. In this study, we used both bottom-up and top-down approaches to suppress *M. maximus* by planting diverse assemblages of species in addition to manual and chemical removal (D'Antonio & Chambers 2006; Ammond & Litton 2012). We also gained considerable insight from the science of restoration ecology to inform ecological restoration at this site (Giardina et al. 2007). This study highlights the viability of ecological restoration in re-establishing native species to invasive grass-dominated tropical dry lowland ecosystems in Hawaii, and elsewhere in the tropics. Although restoring historical pre-invasion ecosystem structure and function may be impractical, the restoration and maintenance of native plant communities offers a wide range of ecosystem functions and services that include watershed protection and hydrologic recharge, native biodiversity, habitat creation and fire mitigation.

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