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RESEARCH ARTICLE

Non-Native Grass Removal and Shade Increase Soil Moisture and Seedling Performance during Hawaiian Dry Forest Restoration

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Abstract

Invasive non-native species can create especially problematic restoration barriers in subtropical and tropical dry forests. Native dry forests in Hawaii presently cover less than 10% of their original area. Many sites that historically supported dry forest are now completely dominated by non-native species, particularly grasses. Within a grass-dominated site in leeward Hawaii, we explored the mechanisms by which non-native *Pennisetum setaceum*, African fountain grass, limits seedlings of native species. We planted 1,800 seedlings of five native trees, three native shrubs, and two native vines into a factorial field experiment to examine the effects of grass removal (bulldozed vs. clipped plus herbicide vs. control), shade (60% shade vs. full sun), and water (supplemental vs. ambient) on seedling survival, growth, and physiology. Both grass removal and shade independently increased survival and growth, as well as soil moisture. Seedling survival and relative growth rate were also significantly dependent on soil moisture. These results suggest that altering soil moisture may be one of the primary mechanisms by which grasses limit native seedlings. Grass removal increased foliar nitrogen content of seedlings, which resulted in an increase in leaf-level photosynthesis and intrinsic water use efficiency. Thus in the absence of grasses, native species showed increased productivity and resource acquisition. We conclude that the combination of grass removal and shading may be an effective approach to the restoration of degraded tropical dry forests in Hawaii and other ecologically similar ecosystems.

Key words: bulldozing, invasive species, shade structures, supplemental watering, tropical dry forest, weeding.

Introduction

Invasive non-native species present a barrier to restoration within many ecosystems. These species can degrade communities both by direct interactions with natives (Walker & Vitousek 1991; MacDougall & Turkington 2005) and indirectly through effects on ecosystem processes (D'Antonio & Vitousek 1992; Gordon 1998). Non-native species may also contribute to feedback mechanisms that maintain degraded communities in persistent alternative states (Suding et al. 2004). As a result, restoration is often not a simple process of non-native species removal followed by native species recovery (Cabin et al. 2000) and may require both top-down (e.g. direct removal of the invaders) and bottom-up approaches (e.g. seeding and alteration of environmental characteristics to favor natives) (D'Antonio & Chambers 2006). Identifying the mechanisms by which non-native species limit natives and alter resource availability may thus increase the effectiveness of restoration strategies that incorporate both types of approaches.

Tropical dry forests (sensu Holdridge et al. 1971) make up 42% of all tropical forests worldwide (Van Bloem et al. 2004), and 97% of these forests are at risk from multiple threats (Miles et al. 2006). Non-native grasses are a major threat to dry forest conservation and restoration. In Hawaii, for example, non-native grass invasion has dramatically increased fire frequency, size, and intensity (Tunison et al. 2001). This has contributed to a greater than 90% reduction of native dry forest cover (Bruegmann 1996); consequently, the Hawaiian dry forest flora is among the most endangered in the world (Sakai et al. 2002). Even when Hawaii's remnant dry forests are protected from fire and grazing, non-native grasses generate an almost complete barrier to native plant regeneration by severely limiting resource availability to native plants (Hughes & Vitousek 1993; D'Antonio et al. 1998; Cabin et al. 2000; Cordell & Sandquist 2008). Effective restoration of this ecosystem thus requires knowledge of the mechanisms by which grasses limit native species regeneration and how these mechanisms might be overcome.

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Removing these invasive grasses during restoration is complicated because while they may strongly compete with native plants for water, they also can provide substantial shade which in turn creates both positive and negative effects. While seedling regeneration in tropical dry forests is often strongly limited by water (McLaren & McDonald 2003), shading can significantly increase seed germination and seedling survival probably as a result of decreased moisture stress (Ray & Brown 1995; McLaren & McDonald 2003). However, there appear to be trade-offs between seedling growth and survival in relation to shade. For example in Hawaii, Cabin et al. (2000) found increased native seedling survival but decreased growth in the presence of non-native grass. Thus, grass removal may both reduce water competition with native species and create unfavorable high light microsites. While the role of water and shade has been addressed in other studies, few have specifically aimed to identify how these factors may relate to the mechanisms by which invasive grasses affect dry forest restoration.

We investigated these mechanisms on sites dominated by *Pennisetum setaceum* (Forssk.) Chiov. (fountain grass) in Hawaii. This highly invasive C_4 grass was introduced from North Africa during the early 20th century and now dominates many sites in leeward Hawaii (Wagner et al. 1999). *Pennisetum setaceum* strongly limits regeneration of native woody species (Cabin et al. 2000) and grass removal concurrent with seeding or planting appears to be necessary to establish native seedlings on invaded sites (Cabin et al. 2002). However, the complete removal of fountain grass may not be possible or even desirable given the potential trade-offs between seedling growth and survival in the presence of grass. To generate information that can be used to develop more effective restoration strategies, we investigated the mechanism(s) by which fountain grass may limit native plant establishment. We hypothesized that it may be possible to establish some native species on sites where grass has not been completely removed by using bottom-up approaches that manipulate light and water.

Methods

Study Site

This study was conducted at the Kaupulehu dry forest preserve (approximately 600 m elevation) on the leeward (western) side of Hawaii Island (19°46′05″N, 155°56′19″W). Vegetation in the approximately 28 ha preserve ranges from diverse native forest dominated by *Diospyros sandwicensis* (A. DC) Fosb. to treeless areas completely covered by *Pennisetum setaceum*. The preserve has been protected from ungulates and fire for more than 10 years (Cabin et al. 2000). Substrate is a 1,500–3,000-year-old a'a lava (Moore et al. 1987). Long-term average annual rainfall is 500–750 mm (Giambelluca et al. 1986) with high annual variation. Since 1999, a maximum annual total of 1,249 mm (2004) and a minimum of 225 mm (1999) have been recorded (Thaxton et al. 2010). Rainfall is not distinctly seasonal, but summer months tend to be drier than winter (Cordell & Sandquist 2008).

Field Methods

We used a field experiment to test the effects of grass removal, shade, and watering on seedlings and soil moisture. In January 2004, we established three replicate randomized blocks within a treeless area (approximately 1 ha) that contained nearly 100% ground cover of *P. setaceum* (approximately 1–1.5 m height). The area was completely devoid of native species, but dead trunks of *D. sandwicensis* and adjacent patches of live *D. sandwicensis* on similar substrate suggested that the area supported native trees in the past.

Each block contained three whole plots (10 × 15 m) to which we applied one of three grass removal treatments: "bulldozed" (grass removal with soil disturbance), "clipped" (grass removal without soil disturbance), or "control" (grass present). Whole plots were separated from each other by at least 3 m. For the bulldozed treatment, we removed all grass along with the upper 15–30 cm of substrate by passing the blade of a D-6 Caterpillar bulldozer once over the plot in February 2004. For the clipped treatment, we initially used a weed-whacker to clip all grass clumps to ground level and then treated resprouting clumps with herbicide (2% Roundup solution). Weed-whacking was carried out in early January 2004 and herbicide was initially applied in late January and again to a few remaining clumps in late February 2004. These two grass removal methods are commonly used by restoration practitioners in dryland systems in Hawaii (Cabin et al. 2000, 2002; Cordell et al. 2002*a*). Both bulldozed and clipped plots were maintained free of grass for the duration of the experiment by hand-pulling.

We applied shade (60% shade or full sun) and water (supplemental or ambient) treatments in a factorial arrangement to subplots (3 × 6 m) within each grass treatment whole plot. We erected shade cloth structures that reduced ambient radiation by 60%, producing shade comparable to that of the native dry forest tree canopy (approximately 58%; Cordell et al. 2002*b*) and slightly lower than that produced by fountain grass (approximately 68%; Thaxton & Cordell unpublished data).

Because these structures were approximately 1.5 m tall, they shaded both planted seedlings and grasses in treatments where grasses were not removed. Supplemental water treatments were applied by hand directly to each transplanted seedling weekly to mimic a series of 15-mm rainfall events. Individually calibrated soil psychrometers (PST-55) were placed in a randomly chosen corner of each subplot and used to measure soil water potential at 10 cm depth during the first 6 months of the experiment (April–October). Data were collected biweekly within 1 hour of sunrise using a microvolt meter (HR-33 T) functioning in dewpoint mode (Wescor, Inc., Logan, UT, U.S.A.).

We planted 1,800 native seedlings (five tree species, three shrubs, and two vines) in April 2004. Fifty seedlings were planted within each replicate subplot. The number of seedlings per species differed but the proportion of each species was

held constant across all subplots. The species and number planted per subplot were trees (*Caesalpinia kavaiensis* = 5, *D. sandwicensis* = 6, *Kokia drynarioides* = 3, *Pleomele hawaiiensis* = 6, *Reynoldsia sandwicensis* = 5), shrubs (*Chenopodium oahuense* = 5, *Senna gaudichaudii* = 4, *Sida fallax* = 3) and vines (*Canavalia hawaiiensis* = 4, *Cocculus orbicularis* = 9). Species selected included the most common canopy tree species in adjacent forest (*D. sandwicensis*), species that had been successfully used in previous restoration activities at the site (e.g. *C. hawaiiensis, C. oahuense*), and species of particular conservation concern (e.g. *C. kavaiensis, K. drynarioides, P. hawaiiensis*). All seedlings were grown from seed either collected onsite or at a nearby dry forest preserve (<10 km away). To plant the seedlings within the lava substrate, we made cracks or holes among the rock and filled the holes with premoistened potting soil (Pro-Mix BX, Premier Horticulture, Quakertown, PA, U.S.A.) to support the seedlings. At the time of planting, all seedlings were watered (1 minute per plant) and fertilized with Vita-Start B-12 (Lilly Miller Brands, Clackamas, OR, U.S.A.) and Peters 20:20:20 (Peters Chemical Company, Hawthorne, NJ, U.S.A.). Seedlings were censused four times (July 2004, September 2004, January 2005, March 2005) for survival and growth.

We measured physiological variables on a subset of the plants in September 2004. We measured maximum photosynthetic rates and leaf conductance for one to two randomly selected individuals of *Reynoldsia, Chenopodium,* and *Canavalia* within each treatment combination using an LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, U.S.A.). We collected fresh leaves from the seven most abundant species (*Canavalia, Chenopodium, Cocculus*, *Diospyros, Reynoldsia, Senna, Sida)* for foliar nitrogen (%N) and carbon (δ^{13}C) isotope analysis. For each species, three to five fresh leaves were collected from three individuals within each treatment combination for a total of 252 plant samples.

Statistical Analyses

We used generalized linear models in PROC MIXED in SAS (Vers. 9.1; SAS Institute, Cary, NC, U.S.A.) to analyze treatment effects within a split-plot design. Models were constructed with grass removal (whole plot) and shade and water (split-plot) as fixed effects, blocks as random effects, and seedling survival, stem length, photosynthetic output, %N, δ^{13}C ratio, and soil water potential as separate dependent variables. For measures taken on plants, lifeform (shrub, tree, or vine) was introduced as another fixed effect and split-plot factor. Similarly, when measures were repeated, time was introduced as another fixed effect and modeled using a spatial power covariance structure. Seedling height at planting was used as a covariate in analysis of final stem length. For seedling survival, we invoked PROC MIXED within the GLIMMIX macro allowing us to incorporate a binomial error structure with logit link. In each analysis, a priori linear contrasts were used to explore differences among grass removal treatments. The first contrast compared plots with grass removed (bulldozed + clipped) to plots without grass removal (control). The second contrast compared bulldozed removal (removal with soil disturbance) to clipping removal (removal without soil disturbance). Sources of significant interactions and other differences among treatments were explored using the SLICES statement in SAS which provides estimates of simple main effects.

We used simple linear regression to analyze the relationships between seedling performance and soil water potential. For each lifeform (shrub, tree, or vine) separately, we used PROC REG in SAS to regress plot-level survival or relative growth rate on plot-level soil water potential averaged over time.

Results

Treatment Effects on Seedling Survival and Growth

Grass removal, shade, and supplemental water increased survival, but the magnitude of these effects varied over time (Fig. 1a). Final percent survival in bulldozed (70 ± 5.9%) was more than 1.5 times that of clipped (43 ± 8.5%) and more than twice that of control (34 ± 8.4%). The overall effect of grass removal was significant ($p = 0.018$, Table 1), as were linear contrasts for differences between grass removal

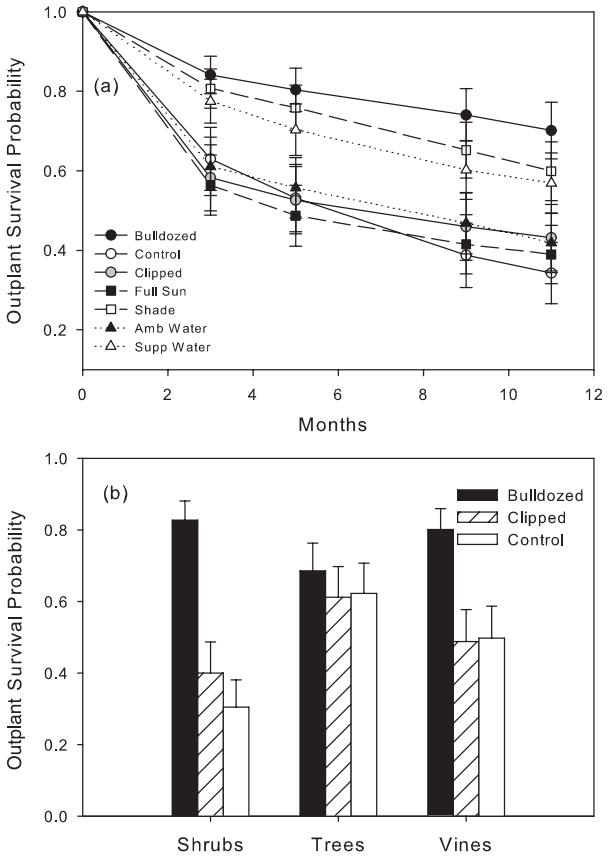

Figure 1. (a) Probability of outplant survival over time (April 2004–March 2005) within grass removal, shade, and watering treatments. (b) Seedling survival probability among grass removal treatments for shrubs, trees, and vines. Data are least squares means (± 1 SE) back-transformed from logits.

Table 1. Results from generalized linear mixed model ANOVA for seedling survival.

Source of Variation	*NDF*	*DDF*	*F*	*p*
Fixed effects:				
Grass Removal	2	4.16	12.2	**0.018**
Shade	1	18.7	28.8	**<0.001**
Water	1	18.7	10.81	**0.004**
Grass Removal*Shade	2	18.7	0.25	0.78
Grass Removal*Water	2	18.7	1.05	0.369
Shade*Water	1	18.7	0.37	0.548
Grass Removal*Shade*Water	2	18.7	0.35	0.712
Lifeform	2	50.7	6.62	**0.003**
Grass Removal*Lifeform	4	50.9	12.34	**<0.001**
Shade*Lifeform	2	50.7	1.03	0.363
Water*Lifeform	2	50.7	0.12	0.884
Grass Removal*Shade*Lifeform	4	51	1.03	0.401
Shade*Water*Lifeform	2	50.7	0.11	0.9
Grass Removal*Shade*Water*Lifeform	8	50.7	1.56	0.16
Time	3	254	84.43	**<0.001**
Grass Removal*Time	6	254	4.15	**0.001**
Shade*Time	3	255	4.67	**0.003**
Water*Time	3	255	2.99	**0.031**
Lifeform*Time	6	253	8.66	**<0.001**
Grass Removal*Shade*Time	6	254	0.77	0.598
Shade*Water*Time	3	254	0.45	0.717
Water*Lifeform*Time	6	253	0.17	0.985
Grass Removal*Shade*Water*Time	12	252	1.2	0.286
Shade*Water*Lifeform*Time	12	252	1.16	0.311
Linear contrasts (grass removal)				
(Bulldozed + clipped) versus control	1	4.07	8	**0.047**
Bulldozed versus clipped	1	4.26	16.87	**0.013**

ANOVA, analysis of variance; DDF, denominator degrees of freedom; NDF, numerator degrees of freedom.
Model was fit using the GLIMMIX macro in SAS and incorporates binomial error structure, logit link, and spatial power covariance structure. Error term for Grass Removal = Block*Grass Removal. Error term for Shade and Water = Block*Grass Removal*Shade*Water. Error term for Lifeform = Block*Grass Removal*Shade*Water*Lifeform. Error term for Time = Residual.
Bold indicates significance at $p < 0.05$.

treatments and controls ($p = 0.047$), and between bulldozed and clipped plots ($p = 0.013$). Final survival in shaded plots was 54% higher than that of full sun, and final survival with supplemental water was 27% higher than with ambient water. The main effects of shade and supplemental water were both significant (Table 1). Survival decreased significantly over time ($p < 0.001$). Grass removal, shade, and supplemental water effects were significant at each census period (all effect slices $p < 0.05$), but changes in relative differences among treatment means resulted in significant time-by-treatment interactions for all main effects (Table 1).

Lifeforms differed in their response to grass removal resulting in a significant interaction ($p < 0.001$, Table 1). Shrub and vine survival (83 and 80%, respectively) in bulldozed plots was approximately two times greater than that of clipped or control plots (Fig. 1b). Treatment differences within shrub and vine lifeforms were significant (effect slices $p < 0.001$ and $p = 0.01$, respectively), but tree survival was unaffected by grass removal (effects slice $p = 0.62$).

After adjusting for differences in initial stem length ($p < 0.001$), both grass removal and shade (but not supplemental water) positively affected final seedling size, but the magnitude of effects depended on lifeform (Table 2). Similar to the pattern for survival, grass removal effects were more pronounced for shrubs and vines than for trees resulting in a significant interaction ($p = 0.002$). Shrub seedlings in grass removal plots were more than three times larger than shrubs in control plots (Fig. 2a). In contrast, shade nearly doubled the final size of vine seedlings and produced a significant 15% size increase for tree seedlings, but did not significantly affect shrubs (Fig. 2b). The interaction of shade with lifeform was significant ($p < 0.001$).

Table 2. Results from ANCOVA for final outplant size (length).

Source of Variation	*NDF*	*DDF*	*F*	*p*
Fixed effects:				
Initial Height (Covariate)	1	887	211.48	**<0.001**
Grass Removal	2	4.76	32.59	**0.002**
Shade	1	113	12.31	**0.001**
Grass Removal*Shade	2	95.6	0.81	0.448
Water	1	112	3.23	0.075
Grass Removal*Water	2	95	1.13	0.329
Shade*Water	1	114	0.78	0.378
Grass Removal*Shade*Water	2	96.4	0.71	0.496
Lifeform	2	91.5	183.11	**<0.001**
Grass Removal*Lifeform	4	77.3	4.64	**0.002**
Shade*Lifeform	2	86.1	10.4	**<0.001**
Grass Removal*Shade*Lifeform	4	76.9	0.96	0.432
Water*Lifeform	2	87	0.29	0.748
Grass Removal*Water*Lifeform	4	77.3	2.53	0.055
Shade*Water*Lifeform	2	86	0.48	0.619
Grass Removal*Shade*Water*Lifeform	4	76.9	1.13	0.347
Linear contrasts (grass removal):				
(Bulldozed + clipped) versus control	1	6.02	61.61	**<0.001**
Bulldozed versus clipped	1	3.87	2.47	0.194

ANCOVA, analysis of covariance; DDF, denominator degrees of freedom; NDF, numerator degrees of freedom.
Model was fit using PROC MIXED in SAS. Heights were natural-log transformed to meet model assumptions. Models include initial seedling height at planting as a covariate. Error term for Grass = Block*Grass. Error term for Shade and Water = Block*Grass*Shade*Water. Error term for Lifeform = Block*Grass*Shade*Water*Lifeform. Bold indicates significance at $p < 0.05$.

Soil Moisture and Seedling Performance

Soil moisture fluctuated over time in response to rainfall, but treatment effects persisted across both wet and dry periods. Total rainfall for the 12-month period beginning April 2004 (1,183 mm) was more than twice the long-term average (537 mm), but monthly rainfall totals varied substantially (Fig. 3a), from less than 15 mm (December 2004) to greater than 243 mm (January 2005). Soil water potential tracked changes in rainfall and varied across months by greater than 6 MPa ($p < 0.001$, Table 3).

Shade, grass removal, and supplemental water all produced significant increases in soil moisture relative to other treatments. Soil water potential in shaded plots averaged more than twice that of full sun plots (Fig. 3b, $p < 0.001$). Grass removal by either method produced a significant increase in soil water potential ($p = 0.046$), and this effect tended to

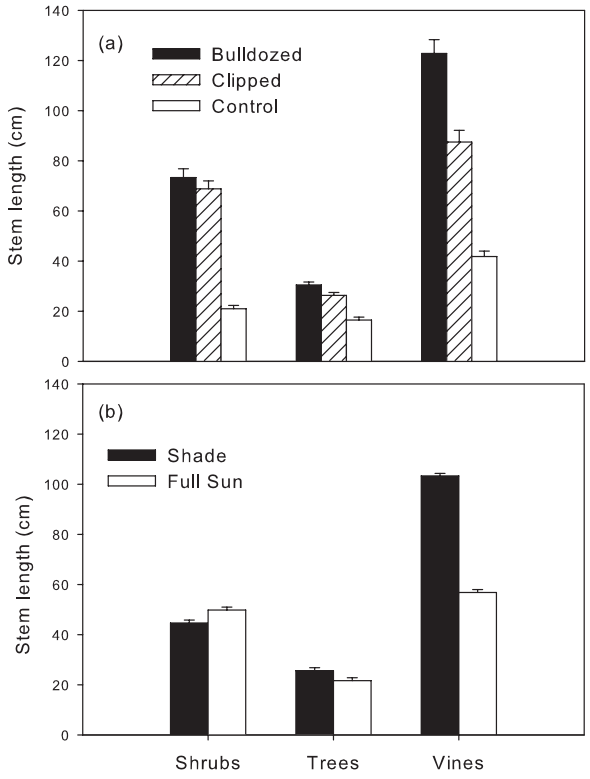

Figure 2. Final stem length (± 1 SE) for shrubs, trees, and vines within (a) grass removal treatments and (b) shade treatments.

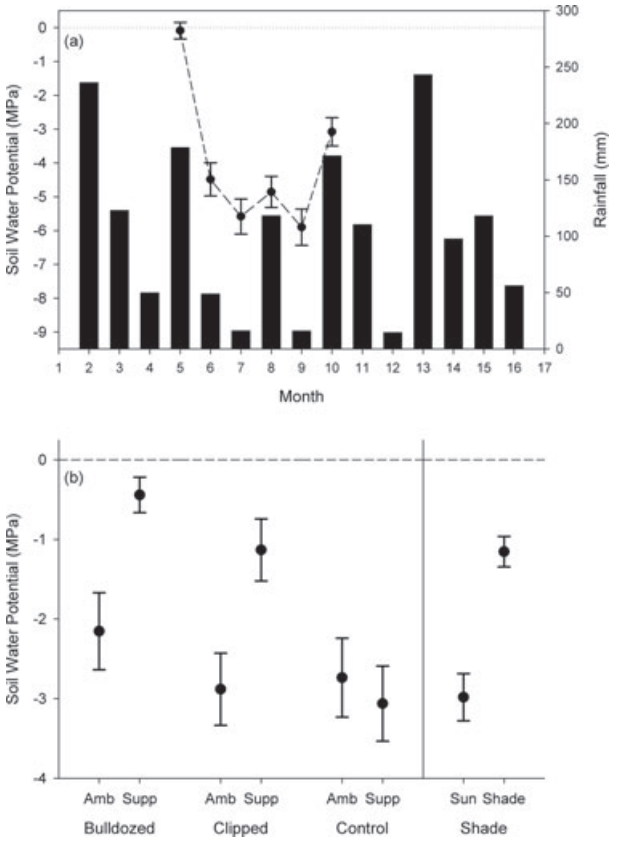

Figure 3. Soil moisture: (a) monthly total rainfall (bars) and mean (± 1 SE) soil water potential (points and dashed line) of control plots during the study. (b) Average (± 1 SE) soil water potential over the entire study among grass removal by water treatments, and separately for shade treatments.

be greater for bulldozed (-1.8 ± 0.35 MPa) than for clipped plots (-1.1 ± 0.37 MPa), although the difference was not significant. Supplemental watering increased soil water potential ($p = 0.004$) but only where grass had been removed (Fig. 3b), resulting in a significant grass removal-by-water interaction ($p = 0.024$).

Seedling performance showed significant linear dependence on plot-level soil water potential averaged over time. For seedling survival probability, linear regressions were highly significant ($p < 0.001$) for shrubs ($r^2 = 0.38$), trees ($r^2 = 0.39$), and vines ($r^2 = 0.34$). The pattern was similar for linear relationships between relative growth rate (natural-log transformed) and soil water potential. The linear regressions were significant at the $p < 0.01$ level for trees ($r^2 = 0.26$) and vines ($r^2 = 0.25$), while for shrubs $p = 0.02$ with $r^2 = 0.15$.

Physiological and Foliar Responses to Treatments

Maximum photosynthetic rates were greatest in plots where grass was removed (Fig. 4). Rates in clipped plots averaged 7.6 times that of controls, while values in bulldozed plots were 5 times greater than controls. The overall effect of grass removal was significant ($p = 0.008$) as was an a priori linear contrast comparing grass removal plots to controls ($p = 0.004$). A linear contrast comparing clipped plots and bulldozed plots approached significance ($p = 0.054$). A three-way interaction among grass removal, shade, and water was also significant ($p = 0.043$). This appeared to be driven by a greater than 3-fold difference in photosynthetic rate between plants in full sun and ambient water in bulldozed plots versus full sun and ambient water in clipped plots (Fig. 4). The overall effect of species was not significant; however, the interaction of species with shade treatment approached significance ($p = 0.053$). The vine, *Canavalia hawaiiensis*, tended to have a higher photosynthetic rate in full sun than in shade plots, while trees and shrubs tended to have higher rates in the shade.

Stomatal conductance differed among grass removal treatments ($p = 0.024$) and in a pattern similar to that of maximum photosynthetic rate. Conductance in clipped plots was 1.8 times that of bulldozed plots, and control plots were significantly lower than both grass removal treatments. Instantaneous water use efficiency (photosynthetic rate/conductance) did not differ significantly among any treatment combinations.

Carbon isotope ($\delta^{13}C$) values were significantly affected by grass removal, shade, supplemental water, and the interaction of shade and lifeform (Table 4). $\delta^{13}C$ values were lower in control plots ($-27.99 \pm 0.2‰$) than in either bulldozed ($-26.82 \pm 0.2‰$) or clipped ($-27.27 \pm 0.26‰$) plots The overall effect of grass removal on $\delta^{13}C$ was highly significant ($p < 0.001$) as was an a priori linear contrast comparing

Table 3. Results from mixed model repeated-measures ANOVA for soil water potential.

Source of Variation	*NDF*	*DDF*	*F*	*p*
Fixed effects:				
Grass Removal	2	4.02	5.24	**0.046**
Shade	1	48.7	28.55	**<0.001**
Grass*Shade	2	48.7	1.33	0.275
Water	1	48.7	9.33	**0.004**
Grass Removal*Water	2	48.7	4.04	**0.024**
Shade*Water	1	48.7	1.33	0.255
Grass Removal*Shade*Water	2	48.7	0.36	0.7
Time	6	97.1	11.16	**<0.001**
Grass Removal*Time	12	97.1	1.71	0.076
Shade*Time	6	97.1	2.17	0.06
Grass Removal*Shade*Time	12	97.1	1.1	0.365
Water*Time	6	97.1	0.52	0.795
Grass Removal*Water*Time	12	97.1	0.65	0.79
Shade*Water*Time	6	97.1	0.89	0.51
Grass Removal*Shade*Water*Time	12	97.1	0.35	0.977
Linear contrasts (grass removal):				
(Bulldozed + clipped) versus control	1	3.98	8.47	**0.044**
Bulldozed versus clipped	1	4.06	2.04	0.23

ANOVA, analysis of variance; DDF, denominator degrees of freedom; NDF, numerator degrees of freedom.
Model was fit using PROC MIXED in SAS with a spatial power covariance structure. Error term for Grass = Block*Grass. Error term for Shade and Water and Repeated subject effect = Block*Grass*Shade*Water. Bold indicates significance at $p < 0.05$.

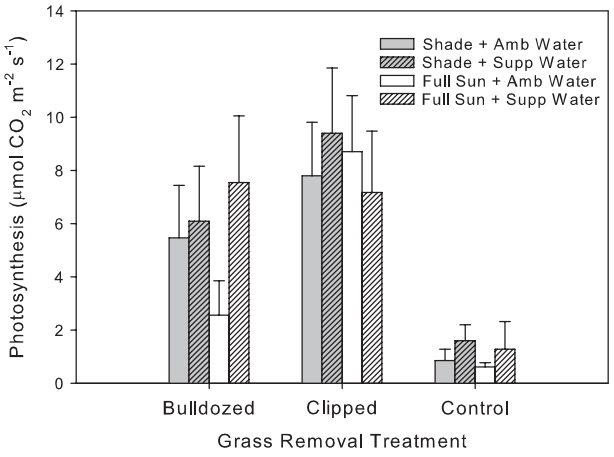

Figure 4. Mean (± 1 SE) maximum photosynthetic rates for plants within grass removal, shade, and watering treatments 6 months after planting.

grass removal plots with controls ($p < 0.001$). The difference between bulldozed plots and clipped plots approached significance ($p = 0.07$). δ^{13}C tended to be lower in shade plots than in full sun ($p < 0.001$); however, this pattern was only significant for shrubs and vines. The interaction of shade with lifeform was significant ($p = 0.004$) with significant p-values ($p < 0.001$ and $p = 0.03$) for shrubs and vines, but not trees. Plants which received ambient water had significantly lower δ^{13}C values than those that received supplemental water (-27.64 ± 0.18 vs. $-27.08 + 0.18$‰), respectively; ($p = 0.006$), and this difference appeared to be driven primarily by the response of vines (Table 4).

Foliar nitrogen (%N) differed among shrubs, trees, and vines and was strongly affected by grass removal (Table 4). Overall, foliar N was significantly higher in grass removal treatments than in controls ($p = 0.008$). Foliar N also differed among lifeforms, with vines having higher values than shrubs, which were in turn greater than trees ($p < 0.001$). However, the interaction of grass removal-by-lifeform was highly significant ($p < 0.001$). This appeared to result from shrubs and vines being more affected by grass removal than trees. For both shrubs and vines, foliar N nearly doubled in bulldozed plots relative to controls, while there were no significant differences in foliar N across treatments for trees.

Discussion

Restoration success at our site was greatly enhanced by invasive grass removal through bulldozing and the construction of artificial shade structures. Bulldozing had large positive effects on seedling performance and soil moisture and consistently outperformed grass removal by clipping. Shade similarly had strong positive effects on seedling survival and soil moisture even in the presence of grass, but positive effects on growth were more limited unless grass was removed. Positive effects of grass removal or shade during dry forest restoration have been noted previously (Cabin et al. 2002; Hooper et al. 2002; Griscom et al. 2005; Thaxton et al. 2010). Our results indicate that the top-down approach of grass removal is an important first step to enhancing the establishment, survival, and growth of restoration plantings in our sites. However, bottom-up approaches such as shading can also be used either in conjunction with or independent of grass removal to enhance seedling performance. A combination of these two approaches is likely to be the most successful at overcoming initial restoration barriers in grass-invaded tropical dry forests.

Pennisetum setaceum appears to be limiting seedling survival and growth primarily by decreasing soil moisture rather than by limiting light availability. Seedling performance was positively associated with soil moisture and grass removal significantly increased soil moisture. In abandoned pastures in eastern Amazonia, Nepstad et al. (1996) also found a link between grasses and increased moisture stress on woody seedlings. Furthermore, we found no evidence of negative effects of shade, suggesting that light limitation alone at the level produced by *P. setaceum* is not the primary barrier to native seedlings.

Grass removal by bulldozing produced significant increases in soil moisture, but our results contrast with some previous studies that removed invasive grasses without altering substrate conditions. In Hawaii, grass removal in dry (Litton et al. 2008) or mesic (Denslow et al. 2006) forest did not alter soil moisture, while removal in submontane woodland (D'Antonio et al. 1998) decreased soil moisture. Similarly, grass control in dry pastures in Panama (Griscom et al. 2005) caused either a decrease or no change in soil moisture. This suggests that removal method and substrate type may contribute to how grass alters soil moisture. Because we conducted our study on a very rocky lava substrate, bulldozing broke up coarse rocks

Table 4. Foliar carbon isotope ratios and foliar nitrogen values (mean ± SE) for plants within grass removal, shade, and supplemental water treatments.

	Grass Removal			*Shade*		*Water*	
	Bulldozed	*Clipping*	*Control*	*60% Shade*	*Full Sun*	*Supplemental*	*Ambient*
δ^{13}C (‰)							
Shrubs	**−27.99 ± 0.37**	**−28.18 ± 0.49**	**−29.32 ± 0.28**	**−29.35 ± 0.28**	**−27.64 ± 0.3**	−28.71 ± 0.29	−28.28 ± 0.33
Trees	**−26.67 ± 0.24**	**−27.38 ± 0.38**	**−28.02 ± 0.25**	−27.4 ± 0.22	−27.32 ± 0.26	−27.64 ± 0.27	−27.07 ± 0.22
Vines	−25.8 ± 0.19	−26.26 ± 0.27	−26.62 ± 0.31	**−26.63 ± 0.22**	**−25.83 ± 0.21**	**−26.58 ± 0.25**	**−25.88 ± 0.2**
All species	**−26.82 ± 0.2**	**−27.27 ± 0.26**	**−27.99 ± 0.2**	**−27.79 ± 0.18**	**−26.93 ± 0.17**	**−27.08 ± 0.18**	**−27.64 ± 0.18**
Foliar N (%)							
Shrubs	**3.24 ± 0.16**	**2.84 ± 0.13**	**1.61 ± 0.07**	2.69 ± 0.16	2.44 ± 0.14	2.46 ± 0.17	2.66 ± 0.14
Trees	1.88 ± 0.11	2.14 ± 0.13	1.71 ± 0.11	2.01 ± 0.13	1.81 ± 0.08	1.81 ± 0.12	2.01 ± 0.09
Vines	**3.74 ± 0.12**	**3.69 ± 0.24**	**2.17 ± 0.14**	3.28 ± 0.19	3.12 ± 0.17	3.13 + 0.19	3.28 ± 0.17
All species	**2.96 ± 0.11**	**2.87 ± 0.13**	**1.83 ± 0.07**	2.66 ± 0.18	2.46 ± 0.17	2.47 ± 0.1	2.65 ± 0.18

Bold text indicates significant differences among treatments.

(decreasing particle size) and brought significant quantities of organic soil to the surface. Our study was also conducted in a year with above average rainfall. Thus, it is possible that under different conditions, the increased incidence of solar radiation following grass removal may counteract the positive effects of grass removal on soil moisture.

The increased seedling survival with grass removal is concordant with changes in physiological responses. Plants in grass removal plots had higher photosynthetic rates, higher foliar nitrogen concentrations, and higher δ^{13}C values than plants in control plots. These patterns suggest that improved seedling survival and growth in these plots may relate to increased productivity associated with changes in soil resource availability. Higher δ^{13}C values indicate greater water-use efficiency (carbon gain relative to transpirational water loss) (Farquhar et al. 1989), which likely results from the greater foliar nitrogen concentrations causing an increase in photosynthetic demand relative to conductance of water from leaves. Increases in photosynthesis and water-use efficiency coupled with greater soil moisture availability may help explain why many plants had such large responses to grass removal. This contrast in leaf-level physiological function contradicts the findings of Cordell and Sandquist (2008), who found no differences in leaf-level gas exchange among adult trees in plots with or without fountain grass in Hawaii. However, they did find that grass removal increased allocation to leaf canopy suggesting this may be the primary mechanism by which trees increased growth with grass removal. Our results suggest that seedling responses are different, being primarily a physiological change leading to increased performance when competition is reduced and resource availability increases. These findings further underscore the importance of grass removal to promote the initial stages of dry forest restoration.

Non-native grass invasion has contributed to the development and persistence of degraded community states in forests and woodlands worldwide (Cabin et al. 2002; Standish et al. 2009; Flory & Clay 2010). These degraded communities often show characteristics of alternative stable states, and their restoration is complicated by interactions that develop within the degraded community (Suding et al. 2004). Although our study site has been protected from fire and ungulate grazing for many years, the presence of non-native grass continues to limit native species regeneration, largely through competition for water. To restore these sites means manipulating soil moisture so that planted native seedlings can establish and persist. Grass removal by bulldozing accomplishes this, at least in a year with above average rainfall, and is a treatment that can be implemented over relatively large areas. In drier years, it may be most effective to use shading to complement grass removal. Furthermore, as shade alone significantly increases soil moisture and seedling performance, it may be possible to use this approach even without grass removal on sites where bulldozing is not practical. For example, shading could be used to promote seedling survival where bulldozing would damage native species already present on the site or would enhance the risk of invasion by other non-natives.

Implications for Practice

- Grass removal by bulldozing was particularly effective for increasing seedling performance and soil water availability. Grass removal by clipping also had positive but less substantial effects.
- On sites without remnant native species, it may be possible to implement bulldozing treatments in a relatively quick and cost-effective manner. In contrast, clipping plus herbicide application would be more difficult to implement over large areas but could be used where the presence of native species makes bulldozing impossible.
- During very dry years, it may be necessary to use other treatments (particularly shade) to increase soil moisture and complement grass removal.
- Shade can also be used alone to increase soil moisture and seedling survival in areas where bulldozing would not be possible, such as where some native species are already established.
- Because fast-growing native shrubs and vines responded particularly well to grass removal, these species may be the most effective during the early stages of restoration.

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