# EFFECTS OF LIGHT, ALIEN GRASS, AND NATIVE SPECIES ADDITIONS ON HAWAIIAN DRY FOREST RESTORATION

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*Abstract.* Alien species invasions have already caused substantial ecological and economic damage and will likely have even greater negative consequences in the future. Thus, it is imperative to improve our basic ecological understanding of these invasions and enhance our ability to reverse or mitigate their often devastating effects. Invasions by fire-promoting alien grasses have played a particularly important role in the destruction of tropical dry forests and are a major reason why these ecosystems are now among the most endangered in the world. We investigated how light availability (full sun and 50% shade), alien grass control (bulldoze, herbicide, plastic mulch, and trim treatments), and native species additions (outplanting and direct-seeding) affected the establishment of native plants and the suppression of a dominant invasive bunchgrass (fountain grass, *Pennisetum setaceum*) within a highly degraded fenced dry forest remnant on the island of Hawaii. The percent cover of native species increased in all light, grass control, and species addition treatments throughout the 20 mo of the experiment, and was greatest in the shade, bulldoze, and outplant treatments. Although fountain grass cover also increased over time in all grass control treatments, the three more aggressive techniques all significantly reduced grass cover relative to the more moderate trim treatment. In addition, there was a significant overall negative correlation between the final cover of fountain grass and native species, suggesting that these native species may successfully compete with fountain grass for water and/or nutrients. Outplant survival and the number of individuals established from direct-seeding differed significantly among the grass control treatments, and in each case, the response was highly species specific. Photosynthetic rates of established outplanted individuals and fountain grass did not differ significantly across most experimental environments, indicating that the local dominance of fountain grass may not be due to superior physiological attributes. The results of this experiment highlight the importance of investigating species- and treatment-specific responses before attempting larger-scale restoration projects, particularly when using rare and endangered species. This study also suggests that relatively simple techniques may be used to simultaneously establish populations of vigorous understory native species and suppress alien grasses at relatively large spatial scales, and that remnant or newly created favorable microsites may be exploited to facilitate the establishment of rarer native overstory species.

*Key words: alien grass control; alien species invasions; endangered species; favorable microsites; fire-promoting alien species; Hawaiian dry forests; Kaupulehu Preserve, Hawaii; light availability; native biodiversity; native species reintroductions, restoration;* Pennisetum setaceum; *tropical dry forest.*

## INTRODUCTION

Alien species invasions may cause substantial ecological and economic damage (see recent reviews in Luken and Thieret 1997, Mack et al. 2000, Mooney and Hobbs 2000, Sakai et al. 2001). The severe negative impacts of invasive species are expected to eventually affect virtually all ecosystems as habitat distur-

bance and transport of alien species around the world increase (Drake et al. 1989, U.S. Congress 1993, Sakai et al. 2001). Since alien species will likely be an increasingly important component of future ecosystem disturbance and degradation, loss of biodiversity, and even global climate change (Vitousek et al. 1997, Dukes and Mooney 1999, Mack et al. 2000), it is imperative to improve our basic ecological understanding of these invasions and enhance our ability to reverse or mitigate their devastating effects.

For example, invasions by fire-promoting alien grasses have proven catastrophic to native arid and

semiarid forested ecosystems around the world. These grass invasions often catalyze a positive feedback loop in which the grasses increase the frequency and intensity of the fire regime, which leads to further reductions of woody vegetation and corresponding increases in the spatial distribution and biomass of fire-adapted grasses, which in turn lead to ever more frequent and widespread fires (Hughes et al. 1991, D'Antonio and Vitousek 1992). The dense root systems of many invasive grasses may also inhibit nutrient and water acquisition by native species, while the often extensive aboveground grass biomass may thwart their ability to germinate and establish (Soriana and Sala 1983, Gordon et al. 1989, D'Antonio and Vitousek 1992, Cabin et al. 2000). The end result of this grass/fire cycle is often virtual or complete conversion from a formerly diverse native ecosystem to near monocultures of alien grass species.

Alien grass invasions into tropical dry forest ecosystems have proven particularly devastating and have played a major role in their degradation and outright destruction. Although these dry forests (sensu Holdridge et al. 1971) were once the most common of all tropical forest types, today <0.1% of the original Pacific Mesoamerican, Australian, Southeast Asian, African, and South American dry forests are protected, and tropical dry forests are among the most endangered and degraded of all ecosystems in the world (Janzen 1986, Murphy and Lugo 1986, 1988a, Lerdau et al. 1991, Bullock et al. 1995, Maass 1995). Since these ecosystems also contain highly diverse and unique species assemblages, failure to preserve and restore dry forests will also clearly result in significant biodiversity losses. For example, >25% of the endangered plant taxa in the Hawaiian flora (which, as of 1995, had 38% of all federally listed plants in the United States [Loope 1998]) are from dry-forest or dry-scrub ecosystems (A. K. Sakai and W. L. Wagner, *unpublished data*).

Because most remaining tropical dry forests exist only as small remnants within a highly degraded landscape dominated by alien fire-promoting grasses, there is an urgent need to find effective methods to control these grasses and re-establish native populations, yet few studies have investigated these problems simultaneously. This study addresses both of these issues within the Kaupulehu Preserve in the North Kona region of the island of Hawaii. Although dry forests once covered most of this region (~128 000 ha), and this area still contains some of the largest and highest quality native dry forest remnants in the archipelago (Cuddihy and Stone 1990, Tunison 1992, Cabin et al. 2000), today, most remaining dry forest in North Kona consists of fragmented, degraded, and senescent patches. The understory of this region is dominated by dense stands of fountain grass (*Pennisetum setaceum*), a globally distributed, phenotypically plastic, $C_4$ African bunchgrass that suppresses native vegetation and greatly increases the risk of devastating fires (Jacobi and Scott 1985, Cuddihy and Stone 1990, Tunison 1992, Williams et al. 1995, Blackmore and Vitousek 2000). In addition, continued grazing and trampling by non-native ungulates often destroys remnant stands of native vegetation and increases vulnerability to further alien species invasions (Cabin et al. 2000).

Here we used an experimental approach to investigate if and under what conditions native dry forest species may effectively compete with fountain grass. Our previous research (Cabin et al. 2000, 2002; S. Cordell, R. J. Cabin, and L. J. Hadway, *unpublished manuscript*) has identified five factors that appear critical for effective restoration in this study system: (1) ungulate exclusion, (2) supplemental water, (3) light availability, (4) fountain grass control, and (5) native species additions. Due to the overwhelming importance of the first two factors, we conducted this study under ungulate-free conditions and provided supplemental water to all experimental plots. To investigate the relative importance and interaction of the latter three factors, we employed two light, four fountain grass control, and three native species addition treatments to examine how these variables affect both the suppression of fountain grass and the establishment of native plant populations.

METHODS

*Study site*

The Kaupulehu Preserve contains two adjacent dry forest remnants located ~17 km northeast of Kailua-Kona on the west side of the island of Hawaii between 500 and 600 m elevation. The substrate of this region is an a'a lava flow between 1500 and 3000 yr old (Moore et al. 1987). Average annual rainfall has been estimated at ~50 cm (Giambelluca et al. 1986), although precipitation in this region is extremely patchy and unpredictable over space and time. The upper, smaller (2.3 ha) preserve was fenced in 1956 to protect its rich diversity of native species from non-native ungulate and human disturbances, and still contains a rich diversity of native overstory and understory species. The present study occurred at the bottom of the lower, larger (25 ha) preserve. Although there are still some relatively diverse stands of native canopy trees within some of the higher elevation sections, tree density steadily declines with decreasing elevation to only sparsely distributed bands of scattered individual trees. Fountain grass dominates the entire lower preserve, and native understory species are almost completely absent, probably due in part to previous ungulate activity (the lower preserve was not fenced until 1997). At the beginning of this experiment, the study site consisted of a continuous, highly degraded, treeless fountain grass population with virtually no other native or alien species, except occasional clumps of the invasive shrub *Lantana camara* (for more details of this study system, see Cabin et al. 2000, 2002).
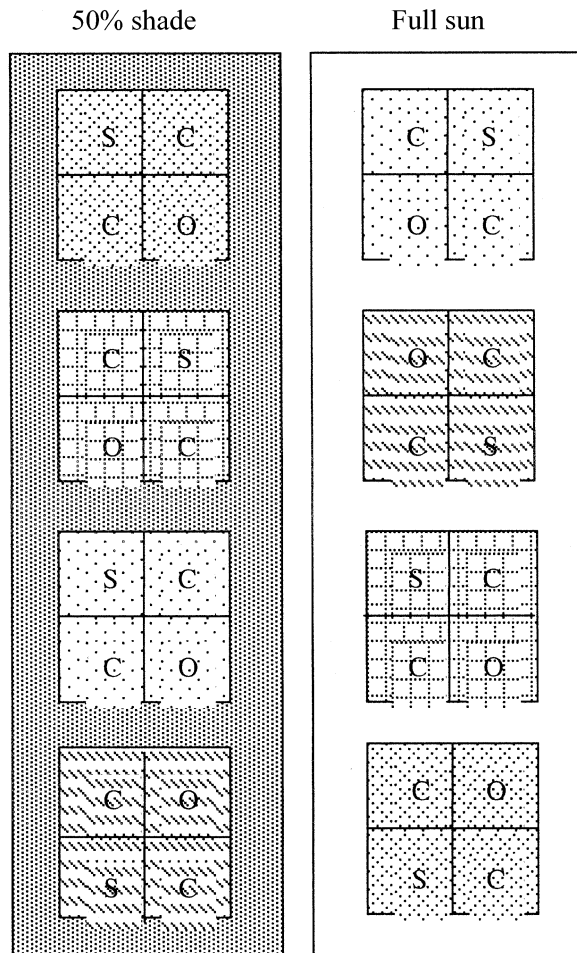
50% shade          Full sun



FIG. 1. Schematic of experimental design to test the establishment of native plants in a tropical dry forest in Hawaii. The diagram shows two adjacent strips that together comprise one of the four randomized blocks used in this experiment (drawing not to scale). The fill patterns in the plots inside each strip represent one of four fountain grass control treatments (bulldoze, herbicide, plastic mulch, and trim). Each plot was subdivided into four quadrats to receive one of three species addition treatments: outplanting (O), seeding (S), or control (C). See *Methods: Experimental design* for further details.

*Experimental design*

In December 1998, we established four randomized experimental blocks at the study site (Fig. 1). Each block consisted of two parallel 34 m long × 10 m wide strips, with 2.3-m spacing between the strips within a block, and 3-m spacing between adjacent strips in different blocks. To investigate the effect of available light, we erected 50% shade cloth structures over one randomly selected strip within each block, and allowed the remaining strip to receive ambient full sunlight. This treatment approximated the amount of shading produced by mature forest canopies in this study system (~1000 μmol quanta·m$^{-2}$·s$^{-1}$ photosynthetic photon flux density [PPFD]; S. Cordell, R. J. Cabin, and L. J.

Hadway, *unpublished manuscript*). Each strip contained four 6 × 6 m plots spaced 2 m apart from each other and the edge of the strip, for a total of 32 plots within this experiment (4 blocks × 2 strips/block × 4 plots/strip).

We randomly distributed four fountain grass control treatments (bulldoze, herbicide, plastic mulch, and trim) among the four plots within each strip so that each plot received a different grass treatment (Fig. 1). For the bulldoze treatment, we removed the top 15–25 cm of lava substrate and fountain grass by scraping the blade of a D-8 Caterpillar tractor backwards across the surface of each plot. For the herbicide treatment, we first weed-whacked the grass to ground level, then sprayed a 1% Roundup solution onto the cut grass in January and April 1999 as the grass began flushing back. For the plastic mulch treatment, we first weed-whacked the grass to ground level, then covered the entire plot with a heavy, 100% light-blocking black plastic mesh in an attempt to smother and "cook" the underlying fountain grass clumps and soil seed bank until the plastic was removed 1 d before the experiment began (120 d later). For the trim treatment, we weed-whacked the grass down to ~60 cm in height 1 wk before the experiment began. In the latter three treatments, we left the weed-whacked fountain grass stems and associated litter in place, and did not remove them from the plots. We did not use unmanipulated, intact fountain grass stands as a control treatment because previous research and observations (Cabin et al. 2000) have shown that few native species can germinate and/or establish within this environment. However, this trim treatment was a relatively moderate form of grass control that resulted in, on average, more than five times more initial fountain grass cover than any of the other treatments (see *Results*).

In May 1999, we subdivided each plot into four 3 × 3 m quadrats and randomly selected one quadrat within each plot to receive native outplants (Fig. 1). We then designated the quadrat located diagonally across from the outplant quadrat to receive native seeds, while the remaining two quadrats within each plot served as controls for these treatments (no native species added). We used this design so that quadrats with added native species would always be adjacent to and bordered by quadrats without added native species (and vice versa; see Fig. 1). Since each individual quadrat was equally likely to receive the outplant, seeding, or control treatment in a random and nonbiased manner, this restricted randomization design was unlikely to affect the statistical analysis of this experiment (J. Baldwin, *personal communication*). All outplants and seeds used in this experiment originated from seeds collected from plants growing within or close to the upper Kaupulehu Preserve. We chose species for the outplanting and/or direct-seeding treatments based on their seed abundance and ability to establish and grow in the field. To produce the outplants, seeds were sown

TABLE 1. List of species outplanted and/or direct-seeded in this experiment at the Kaupulehu Preserve, Hawaii, and sample size, outplant length, seed viability, and survival data (means ± 1 SE).

| Life form | Family | Species | Outplant treatment per quadrat | | |
|---|---|---|---|---|---|
| | | | No. outplanted | Initial length (cm) | Final length (cm) |
| Tree | Ebenaceae | *Diospyros sandwicensis* | 5 | 4.7 ± 0.2 | 6.3 ± 0.5 |
| | Malvaceae | *Kokia drynarioides*† | ... | ... | ... |
| | Rhamnaceae | *Colubrina oppositifolia*† | ... | ... | ... |
| Shrub | Amaranthaceae | *Nototrichium sandwicense* | 2 | 14.1 ± 0.8 | 36.2 ± 2.4 |
| | Chenopodiaceae | *Chenopodium oahuense* | 5 | 13.6 ± 0.4 | 129.8 ± 5.0 |
| | Fabaceae | *Sophora chrysophylla* | ... | ... | ... |
| | Malvaceae | *Sida fallax* | ... | ... | ... |
| | Rosaceae | *Osteomeles anthyllidifolia* | 4 | 5.9 ± 0.2 | 18.9 ± 1.6 |
| | Sapindaceae | *Dodonaea viscosa* | 12 | 9.0 ± 0.2 | 66.9 ± 1.7 |
| Herb | Cyperaceae | *Cyperus hillebrandii* | ... | ... | ... |
| Vine | Convolvulaceae | *Ipomoea indica* | 4 | 38.9 ± 1.6 | 20.2 ± 2.0% |
| | Fabaceae | *Canavalia hawaiiensis* | 12 | 37.1 ± 0.6 | 22.8 ± 3.4% |

*Notes:* Initial length data were measured at the time of outplanting, and final length data were recorded for all live outplants at the end of the experiment. Seed masses were calculated from five bulk samples of 100 individuals per species, and seed viability from greenhouse germination of $n = 100$ individuals per species. Because it was not possible to measure the final length or count the number of surviving individuals of the two vine species, percent cover data are shown instead.

† Federally endangered species.

in a greenhouse between December 1998 and January 1999 in flats containing Pro-Mix BX potting soil (Premier Horticulture, Rivière-du-Loup, Quebec, Canada), transplanted into conetainers as the seedlings developed, then transported from the greenhouse to the field site ~1 mo prior to outplanting to harden off. For each outplant quadrat, we transplanted ~44 individuals comprised of seven native species (Table 1) into a 1.8 × 1.8 m planting area centered within the quadrat, with ~32-cm spacing between each plant. Prior to transplantation, we mixed the outplants together so that the different species were haphazardly interspersed with each other.

The outplanting and direct-seeding treatments were performed on 17 May 1999. Outplanting was accomplished by creating or exploiting cracks in the lava with metal digging bars and mixing premoistened Pro-Mix soil into the planting hole as needed to support the transplanted seedlings. For the direct-seeding treatment, we sowed a mixture of 12 native species (Table 1) evenly across a 1.8 × 1.8 m area centered within each seeded quadrat. Prior to sowing, we soaked the seeds of some species for 24–48 hr in cold or hot water as necessary to scarify the seeds and facilitate germination as determined by preliminary trials (D. Goo and A. Urakami, *unpublished data*). We fertilized each outplant quadrat with Vita-Start B-12 (Lilly Miller Brands, Clackamas, Oregon, USA) and Peters 20:20:20 (Peters Chemical Company, Hawthorne, New Jersey, USA) following the manufacturer's recommendations in May, June, and October 1999. To help the establishing plants survive the extreme heat and drought during the summer of 2000 (see Fig. 2), in July 2000 we also fertilized all outplanted and seeded quadrats using Osmocote 14:14:14 (The Scotts Company, Marysville, Ohio, USA). We did not fertilize the control quadrats at this time, because they did not contain any establishing plants.

Because our previous research (Cabin et al. 2000, 2002) has demonstrated that few native species can establish without supplemental water during the extended drought periods that frequently occur within this study system, in this experiment we watered all quadrats (outplant, seeded, and the two controls within each plot) with an automated gravity-fed irrigation system using the following regime: every day for the first three weeks of the experiment, every other day for the next 3.5 mo, every third day for the following three months, once a week for the next five months, once every four days during the heat and drought of July–August 2000 (see Fig. 1), then back to once a week until the end of the experiment in December 2000. Water was administered in the early morning for 5 min using sprinkler heads positioned at the corners of each plot (four heads per plot) that delivered 3.8 L per head per min. The total amount of water delivered to each plot over the 20-mo experiment was ~2900 L.

*Data collection and analysis*

Approximately every month throughout the experiment, we estimated the percent cover of native species and fountain grass within the 1.8 × 1.8 m outplant, seeded, or control area centered within each quadrat. Although we also measured fountain grass height and percent in flower during these censuses, we only include these data in the correlation analysis because they yielded results very similar to the percent cover data in all other analyses. We also recorded the survival of each outplanted individual, measured the length of all live non-vine outplant species, and counted the number of live individuals of each species within each seeded quadrat.

To investigate how the light and grass control treatments affected the physiological performance of established native species and fountain grass, we mea-

TABLE 1. Extended.

| Direct-seeding treatment per quadrat | | | |
|---|---|---|---|
| No. sown | Mass (mg) | Seed viability (%) | No. surviving |
| 3 | 332.29 | 30 | 0.00 ± 0.00 |
| 132 | 51.61 | 55 | 0.25 ± 0.17 |
| 64 | 4.41 | 25 | 0.03 ± 0.03 |
| 1500 | 0.10 | 1 | 0.00 ± 0.00 |
| 9708 | 0.06 | 5 | 21.94 ± 6.62 |
| 1165 | 4.57 | 19 | 3.75 ± 1.15 |
| 55 | 0.33 | 29 | 0.06 ± 0.06 |
| 352 | 4.02 | 4 | 0.00 ± 0.00 |
| 1817 | 0.41 | 21 | 5.44 ± 1.21 |
| 1373 | 0.11 | 0 | 0.00 ± 0.00 |
| 32 | 5.94 | 24 | 5.06 ± 1.24 |
| 65 | 106.78 | 80 | 10.25 ± 2.49 |

sured maximum photosynthetic rates and leaf conductance values for outplanted individuals of *Canavalia hawaiiensis*, *Chenopodium oahuense*, *Dodonaea viscosa*, and naturally established fountain grass across the two light environments and in the bulldoze and trim treatments. We chose these two grass control treatments because they provided the greatest contrast in the percent cover of native species and fountain grass, and we selected these three native species because they were the only ones with sufficient numbers of healthy individuals in all treatment combinations. We measured two leaves per plant for each species in each replicate of the above treatment combinations (64 total plants) with a LI-6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA) equipped with an artificial light source that delivered 1500 $\mu$mol quanta·m$^{-2}$·s$^{-1}$ to the leaf surface. We calculated leaf mass per area for bulked samples of entire leaves of each species for each treatment combination, and used these data to calculate mass-based maximum photosynthetic rates of each species.

For illustrative purposes, we graphically present the temporal patterns of the percent cover of native species and fountain grass, outplant survival, and the number of native individuals in the seeded quadrats as a function of the experimental light and grass control treatments. We analyzed the final percent cover data at the end of the experiment with three-way ANOVA models using Proc GLM of SAS (SAS Institute 1990). In these models we specified the light, grass control, and native species addition treatments as fixed main effects (with interactions) and the experimental block, strip nested within block, and plot nested within block × strip as random effects. We analyzed the final survival data within the outplant quadrats using analogous two-way ANOVA models (light, grass control, and interaction as fixed main effects). We analyzed these survival data using ANOVA because the residuals within this analysis were approximately normally distributed, and because this model allowed us to test for significant main effects and interactions while accounting for the var-

iation generated by the above random effects. However, since none of these random effects were significant, we subsequently used chi-square tests to compare the survival proportions of individual species for the light and grass control treatments. We also used two-way ANOVA to analyze the final total number of surviving individuals in the seeded quadrats (the abundance of the individual seeded species was too sparse and patchy to permit analysis on a species-by-species basis). All data were transformed as necessary to meet the assumptions of ANOVA. All statistical tests other than ANOVA were performed using JMP Statistical Software (SAS Institute 1995).

## RESULTS

Throughout the experiment, rain was generally modest and patchy, with 11 of the 20 mo having <20 mm of total precipitation and only four months with >50 mm (Fig. 2). Total precipitation during the three summer months was only 5.3 and 43.2 mm in 1999 and 2000, respectively, while November was the wettest month in both years with 67.6 and 186.2 mm, respectively.

The percent cover of native species increased in all light and grass control treatments throughout the experiment (Fig. 3A). The percent cover of native species in the shaded quadrats was nearly twice that of the full-sun quadrats during most of the study. The relative percent cover of native species among the grass control treatments also remained fairly consistent over time, with the greatest cover in the bulldozed quadrats, intermediate cover in the plastic mulch and herbicide quadrats, and the least cover in the trim quadrats. The percent cover of fountain grass also increased in all treatments throughout the experiment (Fig. 3B). There was little difference in fountain grass cover between the shaded and full-sun quadrats, and between the bulldoze, plastic mulch, and herbicide quadrats, but the
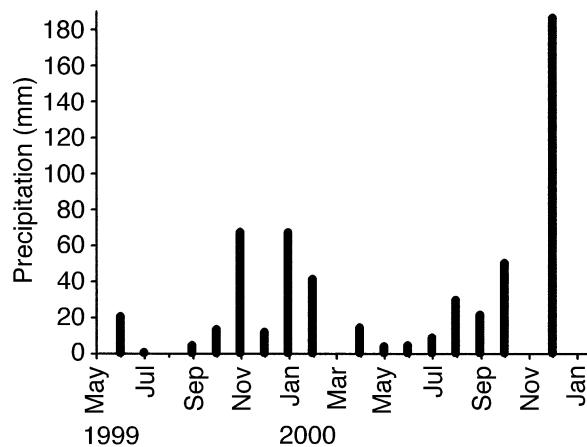


FIG. 2. Total monthly precipitation over the course of the experiment, recorded from a rain gauge ~1 km from the study site at the Kaupulehu Preserve, Hawaii.
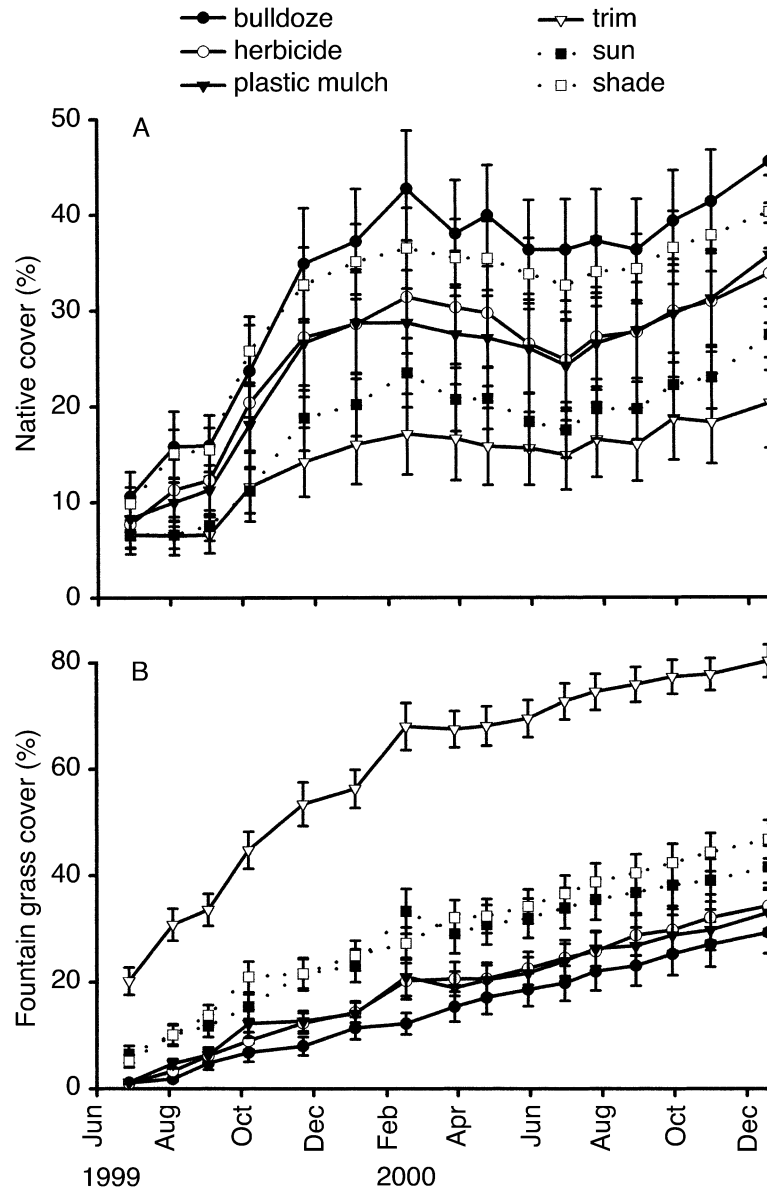
FIG. 3. Percent cover of (A) native species and (B) fountain grass for the four fountain grass control treatments (solid lines) and two light environments (dotted lines) over the course of the experiment. Data are means ± 1 SE.

percent cover of fountain grass in the trim quadrats was consistently about twice that of any other treatment.

The final percent cover of native species differed significantly among the light, grass control, and species addition quadrats, but there were no significant interactions among these three treatments (Table 2, Fig. 4). For the light treatments, there was significantly more native cover in the shaded vs. full-sun quadrats (40.2 ± 3.8% vs. 27.4 ± 3.7%, respectively [mean ± 1 SE]). Native cover among the grass control treatments was significantly greater in the bulldoze quadrats (45.5 ± 5.3%) than the herbicide (33.8 ± 5.2%) or trim quadrats (20.3 ± 4.7%), and marginally greater ($P = 0.096$, Tukey multiple comparisons) than in the plastic mulch

quadrats (35.7 ± 5.4%). The percent cover of natives did not differ significantly between the herbicide and plastic mulch quadrats, but both of these were significantly greater than the trim treatment. Among the species addition treatments, native percent cover in the outplanted quadrats (69.1 ± 3.5%) was significantly greater than the seeded (35.3 ± 5.6%) quadrats, and both of these treatments were significantly greater than the control (15.5 ± 1.7%, Tukey).

The final percent cover of fountain grass differed significantly among the grass control and species addition treatments, but not between the two light treatments (Table 2). Final fountain grass cover in the outplanted quadrats (36.3 ± 5.2%) was significantly less

TABLE 2. ANOVA results for the effects of the experimental treatments on final native species and fountain grass percent cover, outplant survival, and total seeded individuals.

| Source of variation | df | $F$ | $P$ |
|---|---|---|---|
| **Whole experiment, percent native cover** | | | |
| Light environment (L) | 1, 3 | 32.70 | 0.011 |
| Grass control (G) | 3, 18 | 20.46 | <0.001 |
| Species addition (S) | 2, 80 | 94.89 | <0.001 |
| L × G | 3, 18 | 0.53 | 0.669 |
| L × S | 2, 80 | 1.83 | 0.167 |
| G × S | 6, 80 | 1.60 | 0.158 |
| L × G × S | 6, 80 | 1.33 | 0.252 |
| **Whole experiment, percent grass cover** | | | |
| Light environment | 1, 3 | 0.74 | 0.453 |
| Grass control | 3, 18 | 21.08 | <0.001 |
| Species addition | 2, 80 | 4.91 | 0.010 |
| L × G | 3, 18 | 0.86 | 0.482 |
| L × S | 2, 80 | 0.80 | 0.452 |
| G × S | 6, 80 | 0.93 | 0.478 |
| L × G × S | 6, 80 | 0.67 | 0.671 |
| **Outplant quadrats, outplant survival** | | | |
| Light environment | 1, 3 | 0.21 | 0.679 |
| Grass control | 3, 18 | 3.81 | 0.028 |
| L × G | 3, 18 | 1.39 | 0.279 |
| **Seeded quadrats, total individuals** | | | |
| Light environment | 1, 3 | 4.06 | 0.137 |
| Grass control | 3, 18 | 4.98 | 0.011 |
| L × G | 3, 18 | 1.20 | 0.337 |

*Notes:* The whole experiment ANOVAs test the effects of the light environment, grass control, and species addition treatments on the percent cover of native species and fountain grass in all (outplant, seeded, and control) quadrats. The outplant quadrat ANOVA tests the effect of the light and grass control treatments on final outplant survival (pooled across all outplanted species). The seeded quadrat ANOVA tests the effect of the light and grass control treatments on the final total number of individuals (pooled across all seeded species).

than the control (47.7 ± 3.7%), and marginally less ($P$ = 0.094, Tukey) than the seeded quadrats (45.2 ± 5.8%), while the latter two treatments did not differ significantly from each other. Among the grass control treatments, the final percent cover of fountain grass was significantly greater in the trim (80.3 ± 3.1%) than in the herbicide (34.3 ± 4.3%), plastic mulch (33.0 ± 4.3%), or bulldoze quadrats (29.3 ± 3.9%), but there were no significant differences in fountain grass cover among the latter three treatments. The initial percent cover of native species and fountain grass at the beginning of the experiment were significantly, positively correlated with the final percent cover of native species and fountain grass at the end of the experiment, respectively (Table 3). The initial and final percent cover of fountain grass, as well as the initial and final grass height and percent grass in flower were all also significantly, negatively correlated with the final percent cover of native species.

Native cover was dominated by three shrub (*Chenopodium oahuense*, *Dodonaea viscosa*, and *Sophora chrysophylla*) and two vine species (*Canavalia hawaiiensis* and *Ipomoea indica*), while the percent cover of the remaining outplanted and seeded species (as well

as all alien species other than fountain grass) was generally negligible (also see Table 1 for mean initial and final outplant length and mean number of surviving seeded individuals for all species used in this experiment). Outplant survival in all light and grass control treatments declined fairly consistently over the course of the experiment (Fig. 5). Analysis of the temporal pattern of outplant survival between the light treatments showed that these two curves differed significantly (Kaplan-Meier product-limit $x^2$ for right-censored data = 17.44, df = 1, $P$ < 0.001), with generally higher survival in the shaded quadrats, although by the end of the experiment, survival was similar in both light environments. Outplant survival in the grass control treatments was highest in the herbicide and plastic mulch quadrats and lowest in the bulldoze and trim quadrats; analysis of these survival curves also found significant differences among these four treatments (Kaplan-Meier $x^2$ = 22.15, df = 3, $P$ < 0.001).

The proportion of outplants surviving to the end of the experiment differed significantly among the grass control treatments and among the different species outplanted, but it did not differ significantly between the light treatments and there was not a significant light by grass control interaction (Table 2). Although for most individual species, outplant survival was lowest in the trim quadrats, the grass control treatment with the greatest outplant survival varied considerably among the different species (Table 4). For example, for the three species with significantly different survival proportions across the grass control treatments (*Canavalia*, *Dodonaea*, and *Ipomoea*), survival was greatest in the plastic mulch, herbicide, and bulldoze treatments, respectively. In the light treatment, outplant survival was significantly greater in the shaded quadrats for *Diospyros sandwicensis*, *Ipomoea indica*, and *Os-*
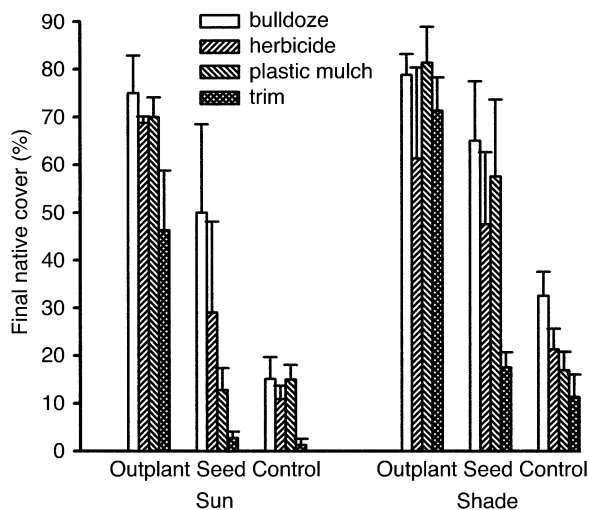


FIG. 4. Final percent cover of native species at the end of the experiment by light, native species addition, and fountain grass control treatments. Data are means ± 1 SE.

TABLE 3. Pearson product-moment correlation coefficients for the relationship between initial and final fountain grass and native species performance.

| | Initial | | | Final | | | |
|---|---|---|---|---|---|---|---|
| | Grass height | Grass percent flowering | Native cover | Grass cover | Grass height | Grass percent flowering | Native cover |
| **Initial** | | | | | | | |
| Grass cover | 0.28** | 0.09 | −0.03 | 0.61** | 0.29** | 0.12 | −0.22* |
| Grass height | | 0.68** | −0.19* | 0.56** | 0.70** | 0.53** | −0.20* |
| Grass flowering | | | −0.25** | 0.36** | 0.58** | 0.49** | −0.25** |
| Native cover | | | | −0.23** | −0.29** | −0.43** | 0.69** |
| **Final** | | | | | | | |
| Grass cover | | | | | 0.70** | 0.43** | −0.34** |
| Grass height | | | | | | 0.76** | −0.40** |
| Grass percent flowering | | | | | | | −0.47** |

*Notes:* Initial native species and fountain grass data were measured one month after the experiment began, and final data were measured during the last census at the end of the experiment. $N = 128$ quadrats.

&ast; $P < 0.05$; &ast;&ast; $P < 0.01$.

*teomeles anthyllidifolia*, and significantly greater in the full-sun quadrats for *Dodonaea viscosa* (Table 4).

Initial outplant length at the beginning of the experiment was significantly, positively correlated with final outplant length at the end of the experiment ($r = 0.45$, $P < 0.001$). Outplants that were initially relatively long (i.e., greater than the median species length at the time of outplanting) also survived at a significantly greater rate than outplants that were initially relatively short (58.3% vs. 52.9% survival, $\chi^2 = 4.09$, df = 1, $P < 0.05$). Final outplant length did not differ significantly between either the light or grass control treatments ($P < 0.05$ in each case), but the final length of the individual species varied considerably across the light and grass control treatments. For example, mean length was 143.2 ± 7.9 cm and 117.8 ± 6.0 cm for *Chenopodium*, but 63.7 ± 2.1 cm and 69.2 ± 2.5 cm for *Dodonaea* in the shade and full-sun quadrats, respectively. For the grass control treatments, mean *Chenopodium* length was greatest in the bulldoze quadrats (147.0 ± 9.8 cm) and similar in the other three treatments (range = 121.1–126.0 cm), whereas *Dodonaea* mean length was greatest in the herbicide quadrats (78.5 ± 2.8 cm) and 67.5 ± 3.4, 60.1 ± 3.1, and 56.5 ± 3.7 cm for the plastic mulch, bulldoze, and trim treatments, respectively.

The mean number of native individuals in the seeded quadrats peaked for all light and grass control treatments in late 1999/early 2000 and then declined sharply during the heat and drought of the summer of 2000 (Fig. 6). In the light treatments, there were consistently more individuals in the shaded vs. full-sun quadrats throughout the experiment. Among the grass control treatments, the bulldoze quadrats had the most seeded natives, the plastic mulch and herbicide treatments had an intermediate number, and the trim quadrats had the fewest. At the end of the experiment, the final total number of seeded individuals differed significantly among the grass control treatments, but not in the light

treatment or grass control by light interaction (Table 2).

Considerable numbers of both endangered canopy tree species sown into this experiment also germinated and survived at least until the hot and dry summer of 2000, but the response of these two species to the experimental treatments was distinct. At its peak, the trim quadrats contained the most *Kokia drynarioides* individuals and the plastic mulch quadrats had the fewest, while there was little difference between the shade and full-sun treatments (Fig. 7A). In contrast, at its peak, *Colubrina oppositifolia* abundance was greatest in the plastic mulch quadrats, and its abundance was more than three times as great in the shade vs. full-sun treatments (Fig. 7B).

At the end of the experiment, outplanted individuals of the three native species and naturally established fountain grass differed in maximum rates of photosynthesis across the light and grass control treatments ($F_{3, 103} = 10.52$, $P < 0.001$; Fig. 8). Overall area-based photosynthetic rates of fountain grass (11.92 ± 1.65 μmol $CO_2 \cdot m^{-2}$ leaf·$s^{-1}$) and *Chenopodium* (10.95 ± 0.90) were significantly higher than *Canavalia* (5.98 ± 0.45) and *Dodonaea* (6.29 ± 0.65, Tukey). A significant grass control treatment by light interaction ($F_{1, 103} = 8.96$, $P = 0.003$) was driven by *Chenopodium* and fountain grass (three-way interaction: $F_{3, 103} = 3.29$, $P = 0.02$). Pairwise comparisons showed that only photosynthetic rates of fountain grass growing in shade/trimmed-grass quadrats were significantly higher than photosynthetic rates of the native species ($P < 0.01$, Tukey). Mass-based photosynthetic rates showed similar, but weaker responses to the light and grass control treatments, although due to the relatively low leaf mass per area of *Canavalia* (data not shown), this species had a significantly higher photosynthetic rate (5.10 ± 0.38 μg $CO_2 \cdot g^{-1}$ leaf·$s^{-1}$) than fountain grass (3.63 ± 0.53), *Chenopodium* (4.43 ± 0.46), and *Dodonaea* (3.07 ± 0.31). Leaf conductance values were not sig-
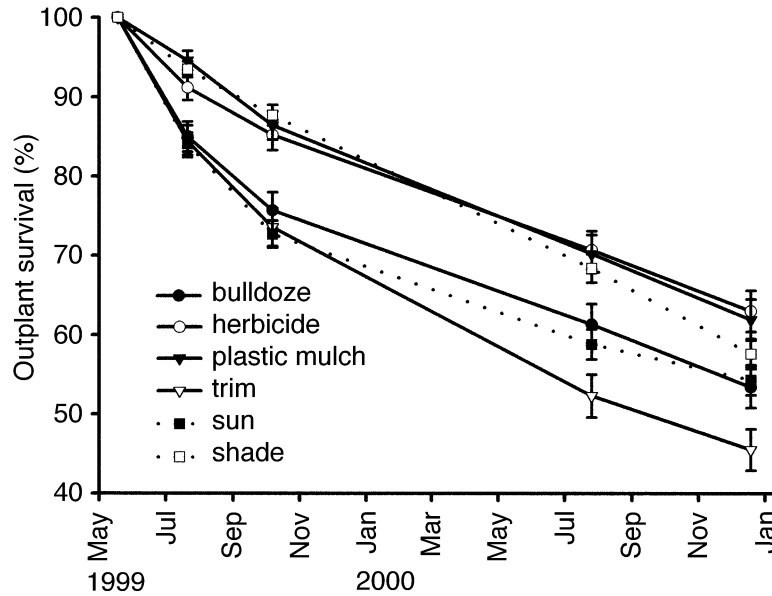
FIG. 5. Percent survival of all species in the outplanted quadrats shown by the four fountain grass control treatments (solid lines) and two light environments (dotted lines) over the course of the experiment. Data are means ± 1 SE.

nificantly affected by the light and grass control treatments, but there was a significant species effect ($F_{3, 103}$ = 9.27, $P < 0.001$) in which fountain grass (0.13 ± 0.015 μmol $H_2O·m^{-2}·s^{-1}$) and *Chenopodium* (0.12 ± 0.015) had significantly higher conductance than *Canavalia* (0.06 ± 0.009) and *Dodonaea* (0.07 ± 0.008).

## DISCUSSION

The results from this study and our previous research within this ecosystem suggest that even highly degraded tropical dry forests may be at least partially restored. This experiment began in a treeless section of a small Hawaiian dry forest preserve dominated by dense African fountain grass stands containing virtually no other alien or native species. Yet, by the end of the 20-mo study, some experimental quadrats had >80% cover of native species and <15% cover of fountain grass. Even in some control (nonplanted or seeded)

quadrats, the vegetative spread of native vines and establishment of native shrubs from newly produced seeds in adjacent quadrats resulted in >30% native cover and <25% cover of fountain grass.

Oceanic island communities in general, and Hawaiian ecosystems in particular, have proven notoriously susceptible to the devastating effects of alien species invasions (Loope 1998, Lonsdale 1999). The inability of island floras to successfully compete with alien plants is often attributed in part to their evolution in a relatively noncompetitive and unique environment (e.g., Loope and Mueller-Dombois 1989). However, the results of this study and other research within and outside of Hawaii suggest that in some cases, island plant species may successfully compete or at least co-exist with aggressive alien species. For example, in another experiment within this study system that occurred under essentially fountain grass-free conditions (Cabin et

TABLE 4. Outplant sample size and survival data, shown by percent surviving to the end of the experiment shown separately for the light and grass control treatments.

| Species | Total out-planted (N) | Overall survival (%) | Light treatment | | | Grass control treatments | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | Sun (%) | Shade (%) | P | Bull-doze (%) | Herb-icide (%) | Plastic mulch (%) | Trim (%) | P |
| All species | 1409 | 55.9 | 54.3 | 57.6 | 0.19 | 53.4 | 63.0 | 61.9 | 45.5 | <0.001 |
| *Canavalia* | 383 | 36.0 | 32.8 | 39.3 | 0.18 | 30.9 | 44.8 | 47.4 | 21.1 | <0.001 |
| *Chenopodium* | 161 | 91.3 | 92.6 | 90.0 | 0.52 | 94.9 | 87.5 | 92.7 | 90.2 | 0.67 |
| *Diospyros* | 160 | 23.1 | 10.1 | 35.8 | <0.001 | 22.5 | 30.8 | 20.0 | 19.5 | 0.62 |
| *Dodonaea* | 387 | 66.9 | 76.7 | 57.2 | <0.001 | 60.2 | 79.4 | 74.0 | 54.2 | <0.001 |
| *Ipomoea* | 126 | 73.8 | 59.4 | 88.7 | <0.001 | 84.4 | 80.6 | 75.0 | 54.8 | 0.04 |
| *Nototrichium* | 64 | 70.3 | 67.7 | 72.7 | 0.69 | 62.5 | 56.3 | 81.3 | 81.3 | 0.28 |
| *Osteomeles* | 128 | 53.9 | 45.3 | 62.5 | 0.05 | 53.1 | 62.5 | 59.4 | 40.6 | 0.31 |

*Note:* Values of P are from chi-square tests comparing the proportion of individuals surviving in each light and grass control treatment.
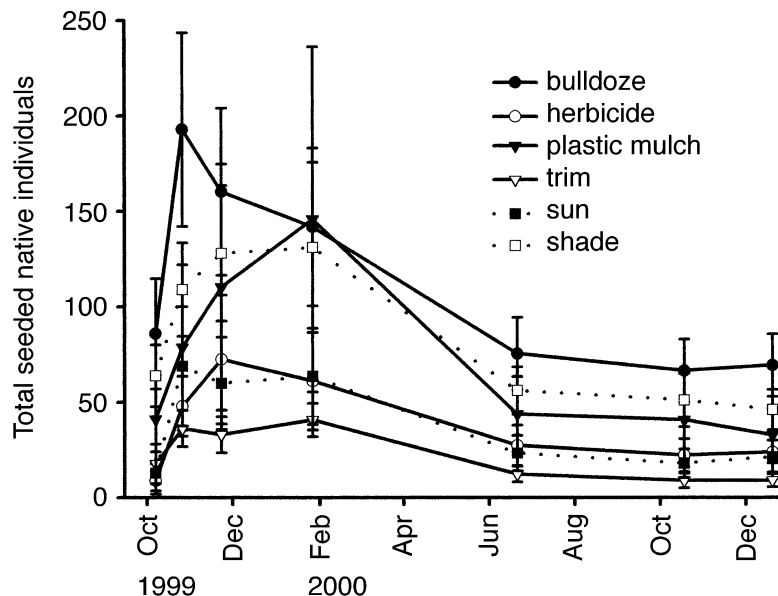
FIG. 6. Total number of alive native individuals in the seeded quadrats shown by the four fountain grass control treatments (solid lines) and two light environments (dotted lines) over the course of the experiment. Data are means ± 1 SE.

al. 2002), we found that subsequent weeding did not significantly improve the performance of native species, even though by the end of that experiment many non-weeded plots were completely covered by two notoriously noxious alien species (*Asclepias physocarpa* and *Lantana camara*). On a larger scale, some relatively intact native Hawaiian plant communities that have historically been inaccessible to ungulates have successfully resisted alien plant species invasions and/or have shown dramatic recovery following ungulate removal (Loope and Scowcroft 1985). A comparison of Pacific islands with and without introduced ungulates (Merlin and Juvik 1992) also indicated that many island plants can effectively resist alien plant invasions in the absence of ungulates and led the authors to speculate that the general vulnerability of island floras may be more the result of susceptibility to grazing than to inherently poor competitive abilities.

This study has also shown that some relatively simple and inexpensive techniques can greatly facilitate the establishment of native species in grass-invaded ecosystems. For example, the shading treatment by itself yielded nearly twice the percent cover of native species throughout the experiment relative to full-sun conditions. This result corroborates the results of other dry forest studies (e.g., Lieberman and Li 1992, Ray and Brown 1995, Teketay 1997), but is in contrast with tropical rain forest studies, where the establishment and subsequent growth of many species occurs primarily in or near treefall gaps (Hartshorn 1980, Denslow 1987). Since the generally more austere abiotic environment of dry forests typically leads to tree canopies that allow 20 times more light penetration than those found in wet forests (Coomes and Grubb 2000), these

results indicate that the regeneration and growth of dry forest species may be limited more by water than light availability (also see Lugo et al. 1978, Ray and Brown 1995, Gerhardt 1996, Teketay 1997).

Although in many studies the importance of light availability per se is often confounded by other variables that may also differ between forested and open microsites (e.g., differential nutrient concentrations and underlying root densities; see discussion in Cabin et al. 2002), the use of shade cloth rather than tree canopies in this study suggests that the positive response of native species to shading was most likely due to the more benign microenvironment associated with reduced light levels in this study system (e.g., lower air and soil temperatures and higher relative humidity; S. Cordell, R. J. Cabin, and L. J. Hadway, *unpublished manuscript*). However, shading did not significantly affect the performance of fountain grass in this study, nor have we observed any reduction in fountain grass cover or vigor beneath the canopies of native or alien trees elsewhere on the island of Hawaii (Cabin et al. 2000; R. J. Cabin, *personal observation*). Thus, in contrast to wetter tropical environments, where woody vegetation may quickly shade out dominant alien grasses (e.g., Vieira-Guimãres et al. 1994, Lamb et al. 1997, Holl 1999, Aide et al. 2000), the relatively sparse canopies produced by even mature dry forests may never be capable of effectively shading out invasive grasses.

Dominant invasive grasses may also severely inhibit the germination, establishment, and growth of forest species in tropical environments. For example, in a study of the factors limiting montane forest recovery in abandoned pastures in Costa Rica, Holl et al. (2000)
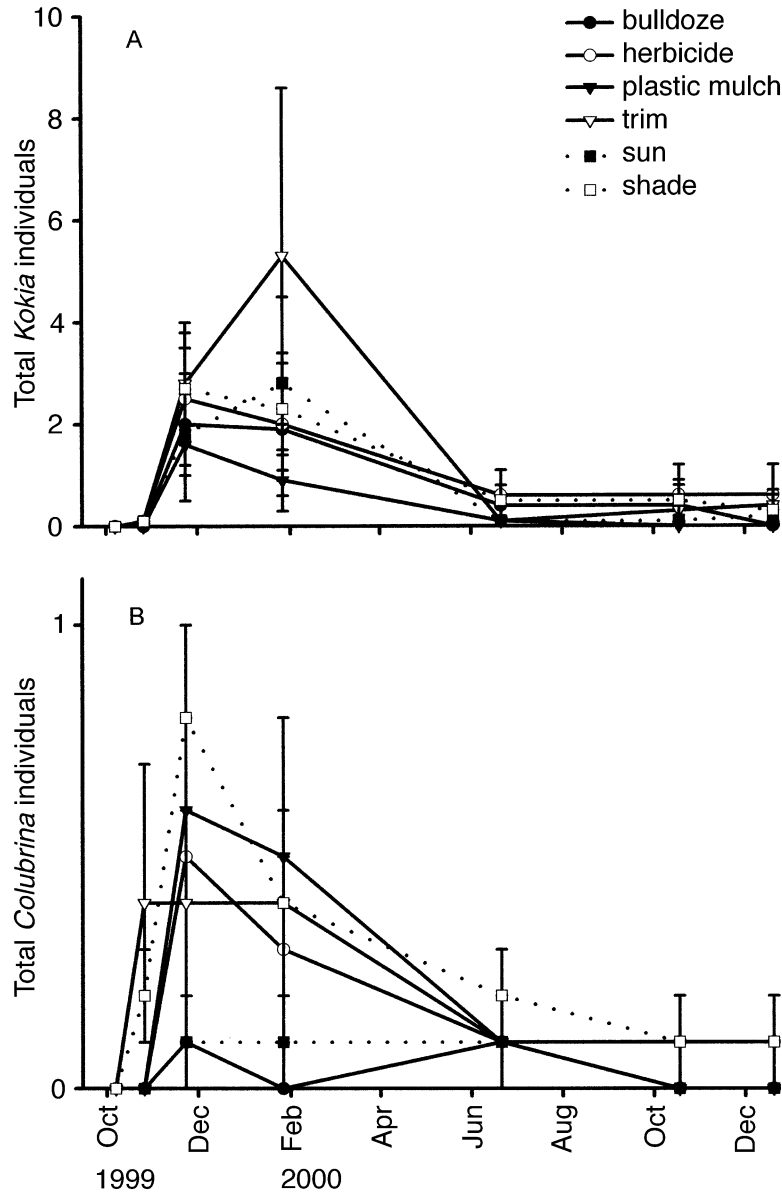
FIG. 7. Total number of alive individuals of the two endangered native canopy tree species, (A) *Kokia drynarioides* and (B) *Colubrina oppositifolia*, seeded into the experiment, shown by the four fountain grass control treatments (solid lines) and two light environments (dotted lines) over the course of the experiment. Data are means ± 1 SE.

found that, among many factors (e.g., herbivory, high light intensity, and stressful microclimates), competition with alien grasses was the single most important factor limiting the survival of forest seedlings. Our previous research in Hawaiian dry forests (Cabin et al. 2000) also showed that few native species can germinate or establish in unmanipulated fountain grass populations. In the present study we found that, even relative to trimmed fountain grass stands, all three more aggressive grass control treatments had significantly more native cover throughout the experiment. The most radical technique, bulldozing, produced the greatest native cover, even though its fountain grass cover was

not significantly less than the herbicide and plastic mulch treatments. This result may have been caused by decreased fountain grass root biomass and/or increased soil water availability (via crushing the lava substrate into smaller and more uniform pieces with the bulldozer tines) in the bulldozed quadrats, although we did not measure either of these variables in this experiment.

The results of this experiment clearly demonstrate the importance of native species additions to the restoration of degraded ecosystems such as Hawaiian dry forests. Despite creating numerous seemingly favorable microsites of supplemental water, shade, and aggres-
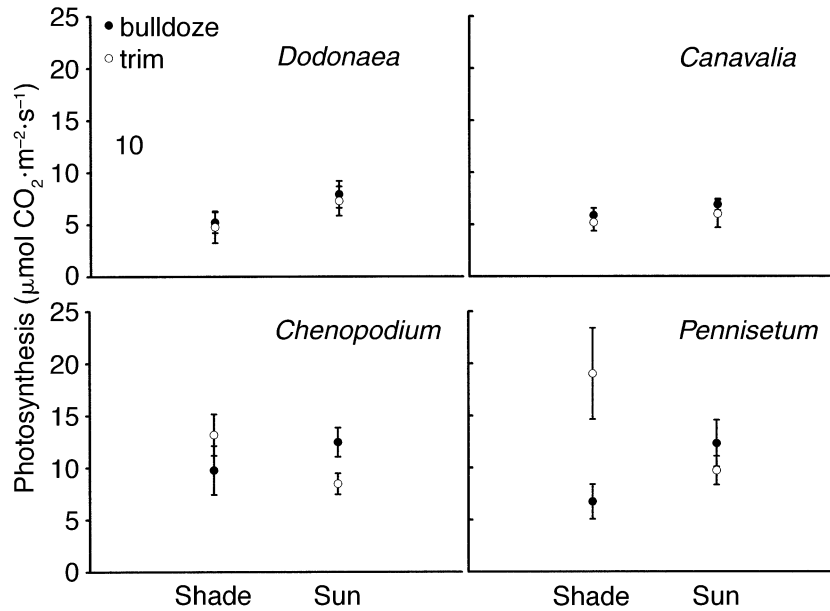
FIG. 8. Maximum photosynthetic rates measured at the end of the experiment for outplanted individuals of the native vine *Canavalia hawaiiensis*, native shrubs *Chenopodium oahuense* and *Dodonaea viscosa*, and naturally established *Pennisetum setaceum* across the two light environments and the bulldoze and trim grass control treatments. Data are means ± 1 SE.

sive initial grass control, there was virtually no "natural" (i.e., unplanted) recruitment of native species into these or any other experimental quadrats over the 20 mo of this study. In contrast, both the outplanting and direct-seeding treatments resulted in the establishment of relatively diverse populations of native vine and shrub species that continued to expand right up to the end of the experiment. We also found a significant overall negative relationship between the percent cover of native species and fountain grass cover, height, and percent in flower. This result may imply that in contrast to mature native canopy trees, these native understory species effectively compete with fountain grass for water and/or nutrients, and thus establishing vigorous populations of native vines and shrubs could be an effective technique for at least partially suppressing alien grass populations.

Plant performance in the outplanting and direct-seeding treatments showed considerable variation both among the different species and among the light and grass control treatments. For example, outplant survival ranged from 23% for the canopy tree *Diospyros sandwicensis* to 91% for the shrub *Chenopodium oahuense*, and while the survival of *Diospyros* outplants was more than three times greater in the shade, *Chenopodium* survival was virtually identical in the full-sun and shade environments. Similarly, four of the 12 species seeded into the experiment produced no surviving individuals, three species yielded an average of <0.3 individuals/quadrat, and the remaining five species produced between 3.8–21.9 individuals. We also did not find a consistent relationship between the performance of individual species in the outplant and seed-

ing treatments, or between the natural abundance of species and their performance in the experiment. For instance, seeds of the most common native shrub in this study system, *Nototrichium sandwicense* (Cabin et al. 2000), essentially failed to germinate in any experimental quadrat, but had 70% outplant survival. Conversely, *Chenopodium* produced nearly half of the total number of surviving seeded individuals, its outplants had the highest survival, and were on average twice as long as the next largest species, but its natural abundance and dominance is far less than three of the four other shrub species used in this experiment (Cabin et al. 2000).

We also found an inverse relationship between the performance of the two endangered canopy trees seeded into this experiment, *Colubrina oppositifolia* and *Kokia drynarioides*, and their natural abundance. Although the final survival of both species in this experiment was poor, at their peak before the heat and drought of the summer of 2000, there were a total of 13 *Colubrina* and 80 *Kokia* seedlings. Yet, while there are still bands of *Colubrina* trees scattered across the study site and ~280 individuals left in the state, the Hawaiian-island endemic *Kokia* has only three wild individuals remaining (Allen 2000). The response of these species to the experimental treatments was also distinct: whereas at its peak there were nearly three times more *Kokia* individuals in the trimmed-grass quadrats relative to the next most abundant grass treatment, and there was little difference in abundance between the two light environments, *Colubrina* abundance was more than three times greater in the shade

relative to full sun conditions, but did not differ dramatically among the grass control treatments.

These results highlight the importance of investigating species- and treatment-specific responses before attempting larger scale restoration projects, particularly when using rare species with limited seed availability. For example, this experiment suggests that direct-seeding vigorous sun-tolerant shrubs and vines might be a cost-effective technique for both suppressing fountain grass and creating microenvironments to facilitate the establishment of slower growing, rarer species like *Colubrina*, while carefully managed fountain grass stands might serve as a better nurse environment for *Kokia*.

Comparisons of the photosynthetic rates of native species and fountain grass suggest that the wide-spread success of fountain grass in this study system may not be due to superior leaf-level physiological attributes. In contrast to Hawaiian rain forests, where invasive species tend to have higher photosynthetic rates than natives (e.g., Pattison et al. 1998, Baruch and Goldstein 1999), photosynthetic rates of fountain grass were significantly greater than native species only for the shade/trimmed-grass treatment combination, and when the cost of leaf construction was included (mass-based photosynthesis), the native vine *Canavalia hawaiiensis* had significantly higher overall photosynthetic rates than fountain grass. This result was not surprising since vines require less investment in support tissues, and even under stressful conditions they can maintain high mass-based photosynthetic rates relative to woody species (Gentry 1983, Castellanos et al. 1989). In addition, whereas fountain grass photosynthesis was more than three times greater in the shade/trimmed-grass treatment than the shade/bulldoze environment, photosynthetic rates of the native species did not differ substantially across these two treatment combinations. These results generally corroborate the demographic responses of native species and fountain grass to these treatments, and suggest that it may be possible to create microenvironments within this ecosystem where native species can outcompete or at least co-exist with fountain grass.

### Synthesis and management implications

We may now have sufficient knowledge to attempt tropical dry forest restoration projects at ever larger spatial scales. Based on our research and the work of others, we believe that dry forest restoration in Hawaii and other regions with similar ecological dynamics should focus on three major objectives: (1) reduction or complete removal of non-native ungulates, (2) control of dominant invasive grasses, and (3) exploitation of existing or creation of new favorable microsites combined with reintroduction of carefully selected native species to these areas.

Although the ecological effects of ungulate grazing on ecosystems throughout the world continue to inspire passionate debate (e.g., Brussard et al. 1994, Fleischner 1994, Noss 1994, Brown and McDonald 1995), ungulate control in ecosystems such as oceanic islands that evolved in the absence of ungulates has proven to be an ecologically and economically cost-effective restoration strategy across large spatial scales and diverse ecological communities. In heavily degraded ecosystems such as Hawaii's dry forests, however, the results of the present experiment and our previous research in this study system (Cabin et al. 2000, 2002) have shown that ungulate exclusion is a necessary, but by no means sufficient restoration strategy, and that there appears to be little hope these areas can ever recover without additional management. Indeed, in the four years since we fenced the 25-ha area in which the present experiment occurred, there has been virtually no successful colonization of new or regeneration of existing native species within the entire preserve.

In addition to ungulate control, management of dominant alien grasses is critical to both facilitate the restoration process and reduce the risk of fire. Although there are many potentially effective techniques for controlling invasive grasses over relatively large spatial scales, most treatments also have significant risks that must be evaluated on a site-by-site basis. For example, in this experiment, bulldozing was the cheapest and most effective technique for both controlling fountain grass and establishing native plant populations, yet due to obvious aesthetic concerns, uncertainty over its long-term ecological consequences, and the destruction that bulldozers have wrought in other ecosystems, larger scale application of this technique may be problematic in Hawaii or elsewhere. Similarly, although managing invasive grasses with controlled burns followed by grass-specific herbicide applications may be an extremely effective technique (R. J. Cabin, S. Cordell, and L. J. Hadway, *personal observations*), there is always a risk that these fires can burn out of control and destroy remnant native forests and/or human property. Ironically, cattle grazing has also proven to be a highly effective tool for reducing grass fuel loads and the risk of catastrophic fires in Hawaiian and other dry forest ecosystems, yet continued grazing inevitably leads to a reduction in forest cover and native species diversity (Janzen 1988*b*, Blackmore and Vitousek 2000).

Numerous studies have shown that poor seed dispersal (particularly of animal-dispersed species) into open disturbed areas is often a major limiting factor in the recovery of degraded tropical forests (e.g., Janzen 1988*b*, Aide and Cavelier 1994, Nepstad et al. 1996, Holl et al. 2000, Zimmerman et al. 2000). Our research in Hawaiian dry forests has similarly found very short effective dispersal distances of wind-dispersed species and virtually no dispersal of animal-dispersed species (Cabin et al. 2000, 2002) due to the extinction or rarity of native birds (Giffin 1993) that presumably once functioned as seed dispersers. Because the seeds of most tropical forest species also rapidly lose viability

and do not form persistent seed banks (Garwood 1989, Vazquez-Yanes and Orozco-Segovia 1993), effective dry forest restoration in Hawaii and in other highly disturbed ecosystems must therefore include intensive species reintroductions. The success of these reintroductions may be dramatically improved if individual species are matched to particular microsites that favor their establishment. For example, the results of this experiment and other studies in grass-invaded tropical ecosystems (e.g., Vieira-Guimãres et al. 1994, Aide et al. 1995, D'Antonio et al. 1998, Holl 1999, Holl et al. 2000, Posada et al. 2000) suggest that remnant or reintroduced trees and shrubs may serve as important foci for the establishment of species that are less tolerant of the high light or high stress conditions typical of disturbed open areas.

The present lack of ''natural'' native Hawaiian dry forest regeneration and the difficulty of experimentally establishing some even locally abundant species raises many intriguing questions about the prehistoric regeneration ecology and structure of this ecosystem. For example, was there a regular pattern of dry forest succession as lava flows destroyed old patches of forest and created new openings? Was there a denser overstory and/or understory that created a more benevolent and stable environment for regeneration, or was regeneration highly episodic, perhaps depending on particular microsites with favorable combinations of precipitation and temperature that may only have occurred once or twice a century? Has extensive deforestation created a hotter and drier climate (see Cabin et al. 2002 for related discussion)?

Despite our limited knowledge, in order to preserve and restore Hawaiian and other tropical dry forest ecosystems, we believe it is now imperative to establish new populations of key native species at relatively large spatial scales. We have found that the greatest economic and logistic challenges for effective large-scale dry forest restoration are providing supplemental shade and water. While the specific methods used in this experiment (shade cloth structures with sprinkler irrigation) are probably not feasible for larger projects, the results of this and previous research suggest several more practical techniques might prove effective. First, despite the urgent need to create new populations of the native canopy tree species that are presently on the brink of extinction, we believe that larger scale restoration projects should start with direct-seeding the more common, vigorous, and stress-tolerant native vine and shrub species. Timing these initial seedings with relatively wet and cooler periods could also reduce or eliminate the need for supplemental water during the critical plant establishment period (Cabin et al. 2000). Favorable microsites within this newly created understory layer (e.g., beneath vine-covered shrubs) could be exploited to facilitate the establishment of the rarer and less vigorous species, which could then, if needed, be provided with modest amounts of supplemental wa-

ter using drip irrigation. Once established, most native Hawaiian dry forest species appear able to survive even extended drought periods without supplemental water (Cabin 1999).

Regardless of the specific techniques employed, the costs per unit area should decrease, and the effectiveness of the treatments increase as economies of scale are realized (Cordell et al. 2002). For example, in this experiment we found that the time and money required to get people, equipment, and supplies to the field site were often considerably more than the cost of performing the treatments themselves. Our small experimental plots also resulted in the presence of intact, unmanipulated fountain grass stands within a few meters of the center of all grass control treatments. Yet, if any of these treatments were applied on the scale of even a few hectares, the resulting increased distance to the nearest untreated fountain grass population and decreased supply of incoming grass seed would almost certainly reduce the rate of subsequent fountain grass colonization and establishment to a fraction of that observed in this study.

Given the highly fragmented and degraded condition of native dry forests in Hawaii and throughout the tropics, successful restoration projects of even a few hectares could create urgently needed new habitat for subsequent rare species reintroductions and serve as a much-needed propagule source and catalyst for future larger scale projects. While it may be impossible to ever understand, let alone recreate, the ecological and evolutionary interactions of prehistoric dry forest ecosystems, these efforts may ultimately create new highly diverse dry forest communities in which native and alien species co-exist in a dynamic but sustainable equilibrium.

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