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Effects of microsite, water, weeding, and direct seeding on the regeneration of native and alien species within a Hawaiian dry forest preserve

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Abstract

Tropical dry forests are among the most endangered ecosystems in the world in general and in Hawaii in particular. To investigate the regeneration ecology of native and alien dry forest species on the island of Hawaii, we used a factorial experiment with microsite (sub-canopy vs. inter-canopy), water (supplemental vs. ambient), and weeding (alien species removed vs. not removed) treatments, and also seeded six native woody species into each plot at the start of the experiment. At the end of the 21-month study, the biomass of the volunteer native and alien species (i.e. unplanted species consisting mainly of relatively fast-growing shrubs) was nearly three and 13 times that of the seeded species, respectively. The biomass of the native volunteers was greater in the inter-canopy plots, greater for the seeded species in the sub-canopy plots, and did not differ significantly within this treatment for the alien species. Few species survived in the ambient water plots, resulting in greater biomass in the watered plots for all species. There were no significant differences in the biomass of the native species within the weeded vs. non-weeded plots; on the contrary, we found consistently positive correlations between the abundance of the seeded species and the volunteer native and alien species. Thus it may be possible to restore Hawaii's degraded dry forests by manipulating these naturally recruiting species to create microsites favorable for the eventual re-establishment of the endangered native canopy tree flora. © 2002 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Tropical dry forests are among the most endangered and exploited ecosystems in the world (Murphy and Lugo, 1986; Janzen, 1988; Lerdau et al., 1991; Bullock et al., 1995). Dry forests (sensu Holdridge et al., 1971) were once the most common of all tropical forest types, but today less than 0.1% of the original Pacific Mesoamerican dry forest ecosystem is protected, and the situation is as bad or worse in Australia, Southeast Asia, Africa, and much of South America (Murphy and Lugo, 1986; Janzen, 1986, 1988; Maass, 1995). In the Hawaiian islands, over 90% of the original dry forests have been destroyed (Mehrhoff, 1993; Bruegmann, 1996), and over 25% of the officially listed 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).

As in other parts of the tropical world, Hawaii's once extensive and diverse dry forests have been severely fragmented and degraded by deforestation, non-native ungulate grazing, fire, alien species invasions, and conversion to agricultural uses such as ranching (Cuddihy

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and Stone, 1990; Stemmermann and Ihsle, 1993; Brueg-mann, 1996; Blackmore and Vitousek, 2000). These direct impacts have also been exacerbated by less quantifiable, indirect effects such as the actual or functional loss of species that once performed critical ecological services such as pollination and seed dispersal and scarification (e.g. Olson and James, 1982; Giffin, 1993). At present, there appears to be little hope that Hawaii's dry forest ecosystems can survive without intensive, aggressive management and reintroduction of native species.

In Hawaii, protecting degraded native ecosystems from ungulates is often considered a key first step toward promoting their restoration and eventual recovery. In a previous study (Cabin et al., 2000) we examined the effects of ungulate exclusion from the Kaupulehu dry forest preserve on the island of Hawaii by comparing its flora to the flora of an adjacent area subjected to continuous grazing since the preserve was fenced over 40 years ago. We found that although the fenced preserve contained a more diverse flora with substantially greater coverage of native species, their regeneration appeared to have been largely thwarted by a dominant herbaceous cover of an introduced African grass (fountain grass, *Pennisetum setaceum*) and predation by three alien rodent species. Our subsequent efforts to control these alien species facilitated the recruitment of several native and alien understory species, but not the highly endangered and senescent native canopy tree flora.

Successful establishment of later successional forest species in degraded, formerly forested areas has proven difficult throughout the tropical world. Because many tropical forest seeds are short-lived and do not form viable seed banks (Garwood, 1989), the recovery of forest species in areas such as abandoned neotropical pastures is generally dependent on the dispersal of new seeds from nearby forest remnants (Holl et al., 2000). However, perhaps because the majority of tropical trees are animal dispersed by species that tend to avoid non-forested areas (Howe and Smallwood, 1982), relatively few forest seeds appear able to disperse into open, disturbed habitats, and thus seed availability is often a major factor limiting forest recovery in these areas (e.g. Aide and Cavelier, 1994; Holl, 1999; Nepstad et al., 1996; Zimmerman et al., 2000).

In this study we investigated the regeneration ecology of native and alien dry forest species in experimental plots established within the Kaupulehu preserve. We used a factorial design to assess the relative importance of three factors: microsite, water, and presence of alien plants. Previous studies (Cabin et al., 2000) suggested that these factors most directly affect regeneration in this system. To examine the importance of seed availability for the recruitment of native trees and shrubs, we also seeded six native woody species into each plot at the start of the experiment.

2. Methods

2.1. Study site

The Kaupulehu preserve is a 2.3 ha exclosure 17 km northeast of Kailua-Kona on the west side of the island of Hawaii at 600 m elevation. In recognition of its rich diversity of native species, this area was fenced in 1956 to exclude cattle and feral goats. Despite its small size this preserve remains one of the best native dry forest remnants left in Hawaii (Cabin et al., 2000). The substrate of the preserve and surrounding area is an a'a lava flow between 1500 and 3000 years old (Moore and Claque, 1987). Rainfall has been estimated at approximately 50 cm per year (Giambelluca et al., 1986), although precipitation in this region is extremely patchy and unpredictable over space and time (RJC, personal observations; also see Fig. 1).

Most of the understory of the entire North Kona region of the island of Hawaii is dominated by fountain grass, an alien perennial bunch grass first seen in the Hawaiian islands in 1914 (Jacobi and Warshauer, 1992). This highly invasive species suppresses native vegetation (Cabin et al., 2000) and greatly increases the risk of devastating fires in areas that historically did not support frequent burns (Blackmore and Vitousek, 2000). To control fountain grass and facilitate native plant regeneration at Kaupulehu, in 1995 we weed-whacked the entire preserve and followed up with five complete applications of a grass-specific herbicide over the next year. By the winter of 1996 we had achieved a 90% reduction in fountain grass cover within the preserve (Cabin et al., 2000). Despite the success of these past and on-going periodic weed control efforts, vigorous fountain grass clumps remain in scattered patches throughout the enclosure today. Large quantities of fountain grass seed also continues to disperse into the preserve from the surrounding unmanaged area.

2.2. Experimental design

In May 1998 we established 64, 1-m^2 plots distributed throughout the preserve in a randomized factorial block design of three treatments: (1) microsite (sub-canopy vs. inter-canopy); (2) water (supplemental vs. ambient); and (3) weeding (all emerging alien species removed vs. weeds not removed). We blocked the plots into groups of four, and haphazardly located eight blocks beneath eight different canopy trees (sub-canopy microsites), and the remaining eight blocks in nearby open, full-sun areas (inter-canopy microsites). Mean maximum photosynthetic photon flux density over the course of this experiment was ca. 750 and 2000 µmol m^{-2} s^{-1} in the sub and inter-canopy microsites, respectively (Cordell et al., unpublished data). Within each block, we randomly assigned two plots to receive supplemental water, and two plots to

receive the weeding treatment in a fully crossed design (i.e. each block contained a supplemental water/weeded, supplemental water/not weeded, ambient water/weeded, and ambient water/not weeded plot). For the supplemental water treatment, we manually delivered 20 l of water per plot three times a week for the first 6 months of the experiment, and once a week thereafter. Throughout the experiment, we removed all alien species in the weeded plots within a few days of their emergence to minimize any potential disturbance to the adjacent native plants.

To investigate the importance of seed availability for the recruitment of trees and shrubs, we selected six native species: two relatively common shrubs, two locally abundant trees, and two federally endangered trees (Table 1). We chose these particular species because they represented an ecologically diverse subset of the woody North Kona native flora, and although their seeds were relatively abundant, previous studies (Cabin et al., 2000) found that natural regeneration of these species (with the exception of the common shrub *Sophora chrysophylla*) was rare and unlikely to occur within this experiment. We performed all seed collections between 1996 and 1998 from mature individuals growing within or close to the preserve, and stored and treated these seeds prior to sowing using the best available horticultural practices derived from preliminary germination trials (Table 1). On May 27, 1998, we haphazardly marked 10 areas within each plot with plastic stakes. At each stake we sowed three seeds for each of the two shrub species, two seeds from each of the locally abundant tree species, and one seed from each of the endangered tree species ($n = 30$, 20, and 10 total seeds per plot for each shrub, locally abundant tree, and endangered tree species, respectively). These sample sizes were necessarily uneven due to differences in the number of seeds we were able to collect from the six species.

2.3. Data collection and analysis

We performed monthly censuses of all 64 plots over the 21 month course of this experiment. During each census, we recorded the number of live individuals within each plot, including both the six seeded native species and any naturally recruiting native and alien species (see Table 1 for a list of the most common of these unplanted species). Approximately every 5 months, we also measured the stem length of all live individuals of the seeded species to the nearest millimeter. At the conclusion of the experiment on 15 February, 2000, we harvested, dried, and weighed all surviving plants within each plot (including as much of the root system as possible) to obtain final biomass data.

For analysis, we divided the plants that emerged within this experiment into native and alien species
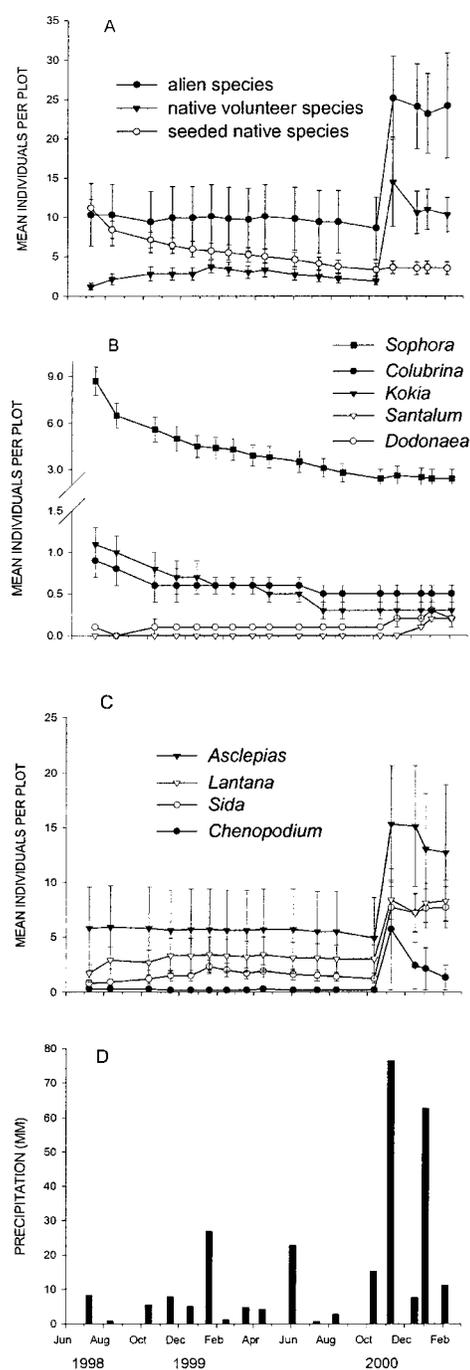

Fig. 1. (A–C) Number of individuals of plants emerging within the 64, 1-m^2 experimental plots in the Kaupulehu preserve on the island of Hawaii: (A) major native and alien species categories; (B) individual seeded native species; and (C) most common native and alien volunteers (i.e. unplanted species). (D) Monthly precipitation at the study site over the course of the experiment.

categories, and further sub-divided the natives into see-ded (the six native woody species sown into each experimental plot) and volunteer (any non-seeded native species) categories. Since half of the 64 plots were wee-ded, we only analyzed the alien species data from the 32 non-weeded plots. Because the number of individuals per plot for most species was extremely patchy in space and time, we generally could not analyze these data using parametric statistics. Consequently, for illustrative purposes we present the mean monthly number of indi-viduals per plot for the native and alien species cate-gories, and for the most common individual species within each of these categories (Fig. 1). We used 2×2 chi-square contingency tables to test the effect of the three experimental treatments (microsite, water, and weeding) on the total number of individuals surviving to the end of the experiment within (Table 2) and between (Fig. 3) each of the different native and alien species categories. To test for the effect of the experimental treatments on final plant biomass, we used non-para-metric Kruskal–Wallis ANOVA on $\log + 1$ transformed total plot biomass data within (Table 2) and between (Table 3) the native and alien species categories. We used Spearman rank correlations to test for significant associations between the initial abundance of the most common native and alien species (during the first census in July 1998) and the native and alien species biomass at the end of the experiment (Table 4). All statistical tests were performed with JMP Statistical Software (SAS Institute, 1995).

3. Results

The first 16 months of this experiment were char-acterized by prolonged drought conditions (92 mm total precipitation), while the final 5 months were relatively wet (173 mm total precipitation; Fig. 1D). During the drought, the number of individuals from the six native seeded species declined from an initial mean of 11.2 to 3.7 per plot, the number of naturally recruiting, volun-teer native individuals fluctuated between one and four, and the number of alien individuals remained near 10 (Fig. 1A). Following the rains at the end of the experi-ment, the mean number of seeded individuals per plot was 3.5, while the number of volunteer native and alien individuals increased to 10.3 and 24.2, respectively.

Within the seeded species category, the locally com-mon shrub *Sophora chrysophylla* was by far the most abundant, followed by the two endangered canopy trees *Colubrina oppositifolia* and *Kokia drynarioides* (Fig. 1B). The abundance of these three species similarly declined during the drought but remained fairly constant during the final wetter period. In contrast, there were virtually no individuals of the locally common tree *Santalum paniculatum* and shrub *Dodonaea viscosa* during the drought, but some modest recruitment of these species during the final wetter months. Throughout the experi-ment, there was only one seedling of the locally domi-nant canopy tree *Diospyros sandwicensis*, and this seedling died 3 months later. The number of individuals of the two most common alien (*Asclepias physocarpa* and *Lantana camara*) and volunteer native species (*Sida fallax* and *Chenopodium oahuense*) also remained fairly constant during the drought but increased sharply dur-ing the final wetter months (Fig. 1C).

In addition to being the most abundant seeded spe-cies, *Sophora* also grew faster than the other seeded species during both the drought and relatively wet periods (Fig. 2). The combination of *Sophora*'s greater abundance and higher growth rate resulted in this species producing almost 90% of the total biomass of all the seeded spe-cies (Table 2). However, the mean plot biomass of the volunteer native and alien species was nearly three and thirteen times greater, respectively, than that produced by all the seeded species combined (Table 2).

Microsite location differentially affected the total number of individuals and mean plot biomass of the

Table 1

List of the six native species sown into 64, 1-m^2 experimental plots within the Kaupulehu preserve on the island of Hawaii, and seed storage and treatment procedures of these species prior to sowing (also shown are the two most common volunteer (unplanted) native and alien species that emerged within the experimental plots)

Category	Family	Genus	Species	Life form	Seed storage	Seed treatment	Seeds per plot
Seeded Species	Ebenaceae	*Diospyros*	*sandwicensis*	tree	refrigerator	untreated	20
	Fabaceae	*Sophora*	*chrysophylla*	shrub	desiccator	4 hour cold water soak/manual scarification	30
	Malvaceae	*Kokia*	*drynarioides*[a]	tree	desiccator	manual scarification	10
	Rhamnaceae	*Colubrina*	*oppositifolia*[a]	tree	desiccator	24 hour cold water soak	10
	Santalaceae	*Santalum*	*paniculatum*	tree	refrigerator	48 hour cold water soak	20
	Sapindaceae	*Dodonaea*	*viscosa*	shrub	ambient	untreated	30
Volunteer Natives	Chenopodiaceae	*Chenopodium*	*oahuense*	shrub			
	Malvaceae	*Sida*	*fallax*	shrub			
Alien Species	Asclepiadaceae	*Asclepias*	*physocarpa*	herb			
	Verbenaceae	*Lantana*	*camara*	shrub			

[a] Federally listed endangered species.

Table 2
Comparisons of the number of individuals and biomass for plants within the 64, 1-m² experimental plots in the Kaupulehu preserve on the island of Hawaii[a]

Category	Overall		Microsite				Water				Weeding			
	Total individuals	Mean biomass	Total individuals		Mean biomass		Total individuals		Mean biomass		Total individuals		Mean biomass	
			Inter-canopy	Sub-canopy	Inter-canopy	Sub-canopy	Extra	Ambient	Extra	Ambient	Weeded	Not weeded	Weeded	Not weeded
All species	1657	191.4	773	884*	269.5*	113.4	909***	748	355.0***+	27.9	493**	391	94.7	41.5
Native species	884	68.1	348	536***+	96.4**	39.8	515***+	369	128.8***+	7.5				
Seeded species	227	17.8	51	176***+	12.5	23.0**	217***+	10	34.2***+	1.4	98	129	20.6	14.9
Colubrina	30	0.5	5	25***	0.1	0.8*	30***+	0	1.0***	0.0	12	18	0.6	0.3
Dodonaea	15	1.1	10	5	1.5	0.7	9	6	2.2*	0.0	7	8	1.5	0.7
Kokia	18	0.4	1	17***	0.0	0.7**	17***	1	0.7**	0.1	7	11	0.4	0.4
Santalum	11	0.0	5	6	0.0	0.1	9	2	0.1***	0.0	3	8	0.0	0.1*
Sophora	153	15.8	30	123***+	10.8	20.7	152***+	1	30.3***+	1.2	69	84	18.2	13.3
Volunteer species	657	50.4	297	360*	83.9**	16.8	298	359*	94.6***+	6.1	395***+	262	74.1	26.6
Chenopodium	86	12.5	10	76***+	24.8*	0.2	12	74***+	24.8*	0.2	81***+	5	14.6	10.4
Sida	492	36.6	257	235	58.4*	14.7	235	257	68.4***+	4.8	283***	209	57.3	15.9
Alien species	773	222.5	425**	348	313.0	132.0	394	379	419.9***+	25.1				
Asclepias	406	141.5	351***+	55	260.6**	22.4	203	203	260.2***+	22.8				
Lantana	267	62.1	19	248***+	36.2	87.9	120	147	122.6***+	1.6				
Pennisetum	50	15.5	12	38***	14.2	16.7*	28	22	30.4**	0.6				

*P < 0.1. **P < 0.05. ***P < 0.01; + Sequential Bonferroni adjustment: P < 0.05 (adjusted).

[a] Data are shown by experimental treatments and native (total, seeded, and unplanted volunteer) and alien species categories. Individual data are final totals summed across all plots, and biomass data are means of total final plot biomass in grams. P-values for the individual comparisons represent chi-square values testing the deviation from an equal distribution of individuals within categories, and P-values for biomass comparisons are from Kruskal–Wallis ANOVA tests. n = 64 plots for native species and 32 plots for alien species (non-weeded plots only). See Table 1 for specific epithets. To correct for multiple tests of the same null hypothesis within treatments a sequential Bonferroni adjustment (i.e. 0.05/30; Rice, 1989) is shown for illustrative purposes.

seeded, volunteer native, and alien species (Table 2). For the seeded species category as a whole, and for most of the individual species within this category, there were more individuals and greater mean biomass in the sub-canopy vs. inter-canopy plots. The volunteer native species also had marginally more individuals in the sub-canopy, but their mean plot biomass was significantly greater in the inter-canopy plots. Within the alien species category, there were significantly more individuals in the inter-canopy, but due to substantial variation among plots and individual species, the mean plot biomass was not statistically greater in the inter-canopy even though it was almost 2.5 times that produced in the sub-canopy plots.

Despite initially promising germination and survival of many of the seeded species in the ambient water plots, virtually none of these individuals survived the prolonged drought, and thus by the end of the experiment there were significantly more individuals of most seeded species in the supplemental water plots (Table 2). In contrast, due to the widespread recruitment of new volunteer native and alien individuals during the final wetter months in both the supplemental and ambient water plots, with the exception of *Chenopodium*, there

were no significant water treatment differences in the number of individuals within these species categories. However, because virtually all native and alien individuals within the ambient water plots were still very small at the end of the experiment, the mean biomass in the supplemental water plots was marginally or significantly
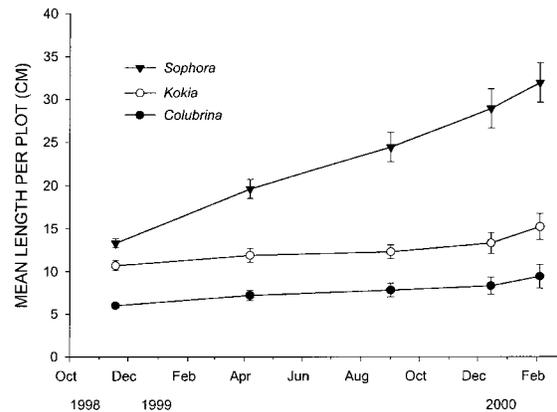

Fig. 2. Stem length measurements for the three most abundant native seeded species within the 64, 1-m^2 experimental plots in the Kaupulehu preserve on the island of Hawaii.

Table 3
Results of Kruskal–Wallis ANOVAs testing the effects of the experimental treatments on final plot biomass between each native (total, seeded, and unplanted volunteer) and alien species category at Kaupulehu on the island of Hawaii[a]

	D.F.	Aliens vs. all natives		Aliens vs. seeded natives		Aliens vs. volunteer natives		Seeded natives vs. volunteer natives	
		F	P	F	P	F	P	F	P
Block[canopy]	14	1.6	0.086	1.2	0.302	1.6	0.101	1.6	0.088
Species comparison	1	15.3	<0.000	34.4	<0.000	19.4	<0.000	4.6	0.035
Microsite	1	5.7	0.029	5.1	0.037	6.7	0.020	2.2	0.164
Water	1	42.6	<0.000	37.5	<0.000	38.6	<0.000	15.7	0.000
S×M	1	2.5	0.120	7.5	0.008	2.1	0.151	6.5	0.012
S×W	1	12.0	0.001	26.9	<0.000	15.4	0.000	3.4	0.070
M×W	1	6.0	0.016	3.6	0.061	6.8	0.011	3.1	0.081
S×M×W	1	1.2	0.273	4.5	0.037	1.0	0.315	5.2	0.025

[a] Because the effect of weeding was not significant in all cases, it was removed from the seeded native vs. volunteer native model. The block nested within canopy was tested as a random effect.

Table 4
Spearman rank correlations of the number of individuals per plot of the most common species during the first census in July 1998, and final plot biomass at the end of the experiment in February 2000 at the Kaupulehu preserve on the island of Hawaii

	Number of individuals in July 1998						Biomass in February 2000	
	All natives	Colubrina	Sophora	Kokia	Lantana	Asclepias	All aliens	All natives
All aliens	0.46***	0.30*	0.46***	0.65***+			0.70***+	0.38**
All natives					0.67***+	0.32*	0.57***+	0.54***+
Colubrina			0.69***+	0.64***+	0.59***+	0.23	0.41**	0.34***
Sophora				0.76***+	0.62***+	0.27	0.54***+	0.46***
Kokia					0.65***+	0.52***+	0.59***+	0.47***
Lantana						0.41**	0.47***	0.27
Asclepias							0.71***+	0.34**

See Table 1 for specific epithets. *P<0.1. **P<0.05. ***P<0.01. +Sequential Bonfern adjustment: P<0.05 (adjusted).

greater within all native and alien species categories and individual species within each category.

There were no significant differences in the total number of seeded individuals in the weeded vs. non-weeded plots, and there were more individuals of each seeded species in the non-weeded plots (Table 2). In contrast, there were more volunteer native individuals in the weeded plots, both overall and for the two most common individual volunteer species. In most cases the mean biomass of the seeded and volunteer native species was also greater in the weeded plots, although these differences were not in any instance statistically significant.

The microsite, water, and weeding treatments differentially affected the total number of surviving individuals in the native and alien species categories (Fig. 3). There were proportionally more alien individuals within the inter-canopy vs. sub-canopy plots than there were within the total, seeded, and volunteer native categories, and proportionally more volunteer than seeded native individuals in the inter-canopy plots. Within the supplemental vs. ambient water plots, there were proportionally more total and seeded native individuals, but proportionally fewer volunteer native individuals, than there were alien individuals. There were also proportionally more volunteer native than seeded species in the weeded vs. non-weeded plots.

The final mean plot biomass of alien species was significantly greater than that of the total, seeded, and volunteer native species categories (Table 3). Within each of these species comparison categories, there were also significant microsite, water, and species by water effects, as well as a significant species by microsite by water interaction within the alien vs. seeded native comparison. Within the seeded vs. volunteer native comparison, final mean plot biomass was also significantly

Fig. 3. Comparisons of the effect of the experimental treatments on the number of individuals within each species category surviving to the end of the experiment in the Kaupulehu preserve on the island of Hawaii (see Table 2 for actual numbers of surviving individuals within each treatment/species category combination). Within each treatment, the proportion of individuals surviving differed significantly among each species category (Chi-square tests, $P < 0.01$).

affected by the species, water, species by microsite, and species by microsite by water interaction.

In general, there were significant, positive correlations between the number of alien and native individuals per plot during the first census in July 1998 (Table 4). There were positive associations between the alien and native species categories as a whole, and within and between most of the individual alien and native species. These 1998 plot abundance data were also significantly, positively correlated with the final total alien and native plot biomass at the end of the experiment in February 2000. In addition, the initial abundance of both the native and alien species categories as a whole, and the individual species within these categories, were more strongly correlated with final alien biomass than they were with the final native biomass data.

4. Discussion

4.1. Species response

We did not find a single naturally recruiting native tree seedling within our experimental plots despite regularly watering and/or weeding a subset of these plots for almost 2 years. In contrast, the initial germination and establishment of the six native woody species seeded into the experimental plots was relatively encouraging. However, only one-third of these plants survived the prolonged drought conditions that characterized the first 16 months of the experiment. Yet during the final 5 months of the experiment, in which conditions were relatively wet, the density of these seeded species remained fairly constant.

We did not find any consistent pattern between the performance of the individual seeded species and their natural abundance or growth form. For example, *Sophora chrysophylla*, a relatively common shrub within this preserve and throughout most of the Hawaiian islands, had more than twice as many surviving individuals and produced nearly eight times the biomass of all the other seeded species combined. However, only one of the locally dominant canopy tree *Diospyros sandwicensis* seeds germinated, and there were no naturally recruiting seedlings of this species even though several plots were located directly beneath mature fruiting trees. These results highlight the urgent need for more basic research on how best to propagate dry forest species that have low or unreliable germination patterns.

We found very different temporal patterns of volunteer (unplanted) native and alien species recruitment over the course of this experiment. The density of these species remained fairly constant during the drought, but then increased sharply during the final wetter months, so that by the end of the experiment the volunteer native and alien species each outnumbered the seeded species
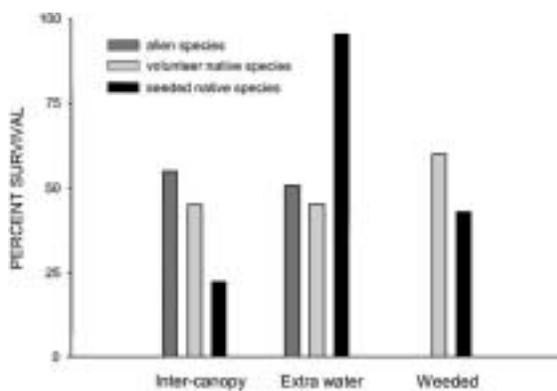
by a roughly 3:1 margin. Other studies of regeneration in disturbed tropical areas suggest that this differential response may be due in part to the contrasting life-histories of the majority of seeded (relatively slow-growing, shade-tolerant species producing fewer, larger, presumably animal-dispersed seeds) versus naturally recruiting (relatively fast-growing, shade-intolerant species producing many smaller, wind-dispersed seeds) species. For instance, weedy, wind-dispersed small trees and shrubs also tend to dominate the initial colonization of abandoned neotropical pastures, whereas the establishment of later successional tree species is often severely limited by the absence of viable seed banks within and poor seed dispersal into these disturbed areas (e.g. Holl et al., 2000; Posada et al., 2000).

4.2. Effects of experimental treatments

Microsite placement (sub-canopy vs. inter-canopy) also differentially affected the performance of the seeded and unplanted native and alien species. Whereas the seeded species had significantly more surviving individuals and produced more biomass in the sub-canopy plots, both the native and alien unplanted species produced more biomass in the inter-canopy plots. These results again suggest that unlike the slower-growing seeded species, these naturally regenerating, relatively fast-growing species are able to exploit the exposed, high light areas, particularly when sufficient water is available. Other dry forest studies (Lieberman and Li, 1992; Ray and Brown, 1995; Teketay, 1997) have also shown that the establishment and/or growth of later successional species tends to be higher beneath existing tree canopies or shaded areas than in adjacent, more open regions.

In tropical rain forests, light availability is generally believed to be a major causal factor affecting seedling performance so that the establishment and subsequent growth of most understory seedlings occurs primarily in or near treefall gaps (Hartshorn, 1980; Denslow, 1987). Unfortunately the seedling ecology of tropical dry forests has received far less attention. Nevertheless, there appears to be a general trade-off in seasonal dry forests of increased seedling growth and survival with increasing light during the rainy season (Rincón and Huante, 1993; Gerhardt, 1996), but greater seedling mortality with increasing light during the dry season (Lieberman and Li, 1992; Gerhardt, 1996; Teketay, 1997). This pattern may be a result of the more severe microclimate of high light, forest gap patches (Bazzaz and Pickett, 1980; Hubbell and Foster, 1986; Denslow, 1987). Since dry forests in general typically allow 20 times more light penetration than wet forests (Coomes and Grubb, 2000), and rains are often seasonal, sparse, and/or unpredictable (Murphy and Lugo, 1986), the regeneration and growth of many dry forest trees may be limited more by soil moisture than by the availability of suitable high light patches (Lugo, 1978; Ray and Brown, 1995; Gerhardt, 1996; Teketay, 1997).

The results of this experiment show that at least during drought periods, water is a major limiting factor for both native and alien dry forest species. This result was not surprising because virtually no native or alien species survived the initial drought period without supplemental water, so that almost all of the plants in the ambient water plots at the end of the experiment had emerged during the preceding few months and were still very small. Our results also showed that natives as a whole, and the slower growing woody species in particular, may be more vulnerable than alien species to water stress.

Our most unexpected result was that weeding did not significantly affect the performance of the native species. This was especially surprising because by the end of the experiment, many non-weeded plots were completely dominated by notoriously noxious weeds. However, we did find that there were nearly a third more seeded individuals in the non-weeded plots but over a third more volunteer native individuals in the weeded plots. This differential response may be due in part to the volunteer species more effectively exploiting the higher light levels and tolerating the likely lower soil moisture conditions in the weeded plots.

5. Implications and conclusions

The results of this experiment raise many intriguing questions about the prehistoric regeneration ecology and structure of this ecosystem. For example, before humans first reached the Hawaiian islands some 1500 years ago, what was the spatial and temporal pattern of canopy tree regeneration? 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? Was there a denser overstory and/or understory that created a more benevolent and stable environment for regeneration? Was there a regular pattern of dry forest succession as lava flows destroyed old patches of forest and created new openings, perhaps resulting in a diverse mosaic of different aged stands with largely unique species assemblages?

Even though we probably will never know the answer to these and many other related questions, we may now have sufficient knowledge to begin effective dry forest restoration programs in Hawaii. First, our own research and recent studies in abandoned neotropical pastures (e.g. Holl et al., 2000; Posada et al., 2000) indicate that alien grasses play a major role in limiting the regeneration and establishment of native tree species. Yet we found that fountain grass was a very minor component

of the flora within our cleared experimental plots even though there were still vigorous fountain grass clumps adjacent to these plots and an abundant supply of viable incoming seeds. Thus once fountain grass is controlled on even a small local scale, there appears to be a window of at least a few years in which it is not a major deterrent to subsequent restoration efforts.

This experiment also demonstrated that in-situ direct seeding appears to be a biologically promising and potentially cost-effective technique for establishing at least some Hawaiian dry forest species that apparently are no longer able to regenerate on their own. In addition, we found that several unplanted, relatively fast-growing species were able to vigorously colonize and establish within a subset of the experimental plots. Rather than inhibiting the seeded species, we found consistently positive correlations between the abundance of virtually all of the seeded and naturally recruiting species. Moreover, in contrast to the seeded species, these unplanted species tended to grow best in the more severe inter-canopy areas, and were not as dependent on supplemental water. These results thus suggest that it may be possible to restore Hawaii's degraded dry forests by manipulating these relatively fast-growing understory species in order to create microsites more favorable for the establishment of the native canopy tree flora.

Acknowledgements

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