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Strategic light manipulation as a restoration strategy to reduce alien grasses and encourage native regeneration in Hawaiian mesic forests

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Abstract

Question: Is there a light level at which alien grass biomass is reduced while still supporting growth and survival of native woody species, allowing for native species regeneration in abandoned pastures?

Location: Island of Hawaii, USA.

Methods: In a two-part study we examined the effect of light availability on common native woody and alien grass species found in secondary forests in Hawaii. A field survey was conducted to examine the relationship between light availability and canopy type (open pasture, planted canopy and secondary forest) on understory grass biomass and litter accumulation. We then experimentally manipulated light levels to determine the effect of light availability on growth and survival of six native woody species and three alien grasses. Low-light (5%), medium-light (10%) and high-light (20-30%) treatments were created using shade structures erected beneath the existing secondary koa canopy.

Results: In the field survey, alien grass biomass was greatest under the open pasture and lowest in the secondary forest. There was a positive correlation between understory light availability and alien grass biomass. In the experimental study, large reductions in relative growth rates were documented for all of the grass species and four of the six woody species under the lowest light level. Although growth at 5% light is substantially reduced, survival is still high (84-100%), indicating that these species may persist under closed canopy.

Conclusion: Low-light conditions result in the greatest reduction in alien grass biomass while creating an environment in which native woody species can grow and survive.

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Keywords: Arrested succession; Invasive species; Secondary forest; Understory vegetation.

Nomenclature: (Wagner et al. 1990) for vascular plant species and plant communities.

Abbreviations: LAR = leaf area ratio; RGR = relative growth rate; SLA = specific leaf area.

Introduction

Conversion of large tracts of forest to pasture for cattle production is a common practice throughout the tropics across a wide range of climatic zones. This practice has significant negative biotic and abiotic consequences, including alteration of nutrient cycling and loss of biodiversity (Janzen 1988; Silver et al. 2004). After abandonment some of these areas are able to recover naturally (Aide et al. 2000); however, many are transformed into a grassland devoid of native trees and associated fauna (Janzen 1988). Landscape-level restoration of pastures after abandonment will require innovative solutions to mitigate serious barriers to natural forest succession.

One of the main mechanisms by which herbaceous vegetation, primarily grasses, limits forest recovery in abandoned pastures is through inhibition of the germination of native species (Pons 1992; Denslow et al. 2006) and competing with the seedlings for nutrients, water and light (D'Antonio et al. 1998). This situation is evident in Hawaii, where over 50% of the land is currently or was previously used for cattle grazing (Schmitt 1977). Logging and extensive grazing by cattle (feral and domestic) and goats have severely degraded native vegetation communities (Scowcroft 1983; Medeiros et al. 1986; Cuddihy & Stone 1990; Blackmore & Vitousek 2000). Included in these communities are large areas of former koa (*Acacia koa*)–'ōhi'a (*Metrosideros polymorpha*) forest that were actively logged to clear for ranchlands. After grazing pressures are released, koa has the ability to quickly reproduce by root suckers (Spatz & Mueller-Dombois 1973; Tunison et al. 1995). However, there is very little subsequent koa recruitment following the initial release from ungulate pressure, indicated by few young individuals in the understory and domination by alien grasses such as meadow ricegrass (*Ehrharta stipoides*), dallis grass (*Paspalum dilatatum*) and kikuyu (*Pennisetum clandestinum*) (Baldwin & Fagerlund 1943; Tunison et al. 1995). Without relictual mature forest species, recovery of other native forest species is poor. Therefore, succession in these areas becomes arrested and limited to a mono-dominant koa overstory and an understory of alien grasses.

To restore and maintain the biological diversity of these over-simplified koa forests, conservation managers are developing strategies to restore native subcanopy and understory species. The establishment of native plants, through direct seeding and outplanting, can be facilitated by temporarily removing grasses with herbicides (Denslow et al. 2006) or soil turnover (Cabin et al. 2002). It has been demonstrated that the development of a closed canopy cover, through plantation-style planting, can favor the establishment of woody trees over pasture grasses because of a reduction in the available light resources (Parrotta 1992; Zhung 1997; Uhl 1998; Holl 1999; Aide et al. 2000). A side-effect is that the increased canopy cover can decrease growth for some woody species (Kobe 1999; Alverez-Aquino et al. 2004; Maundrell & Hawkins 2004). For these rehabilitated forests to be sustainable, the closed forest canopy must limit alien grass establishment but still ensure subsequent native recruitment. A concern is that the grass species that dominate the understory in secondary koa forest in Hawaii have shown a high degree of shade tolerance (Grace 1995; Scowcroft & Jeffrey 1999), and the light reduction needed to suppress these grass species may also effectively suppress native woody recruitment.

In order to evaluate this restoration strategy, we directly examined the effect of light availability on the growth and survival of native woody and alien grass species in an observational and manipulative study on the island of Hawaii. In the first part of the study, we aimed to determine the natural light level, which is correlated to lower grass biomass in three different habitats. In a separate experiment, we manipulated understory light levels with shade cloth to mimic two levels of closed canopy forest, in addition to natural secondary forest canopy, to determine if light reduction would significantly inhibit alien grasses while still supporting growth and survival of native woody species. We hypothesized that low enough light levels existed that would hamper survival of grasses yet still allow woody species recruitment. In addition, we investigated morphological changes in biomass allocation and leaf structure for the woody species. Together these approaches will further our understanding of light requirements of native Hawaiian woody species and alien grasses and improve forest restoration practices in abandoned pastures.

Methods

Study sites

The observational field survey was conducted within Hakalau Forest National Wildlife Refuge (19°50′15″ N, 155°18′44″ W) on the northeast slope of Mauna Kea between 1600 m and 1800 m elevation to determine the effect of canopy cover on understory biomass and light availability. Annual rainfall in this region ranges from 2000 to 3000 mm (Giambelluca et al. 1986). The soils are uniform throughout and are classified as Typic Hydrudands derived from volcanic ash. Prior to extensive logging and subsequent cattle ranching, the forest was dominated by an open to closed canopy of 35 m tall koa (*Acacia*) and 25 m tall ‘ōhi’a (*Metrosideros*) with an understory composed of a diverse array of native ferns, shrubs and small trees (for a complete description see Wagner et al. 1990). Previous land use has degraded the upper sections of the Refuge to open pasture composed of alien grasses approximately 30-75 cm high. Cattle were removed incrementally beginning in 1987 and continuing through 1998. After removal, natural regeneration (secondary forest) was observed in the boundary between the intact forest and the pasture; however, succession in the upper section appears arrested (J. Jeffrey, pers. comm.). Active restoration began in 1989, creating a monoculture of koa trees in wide bands in the open pasture area stretching from the lower intact forest to the upper sections of the Refuge (J. Jeffrey, pers. comm.).

The light manipulation experiment was conducted in the Mauna Loa strip section of Hawaii Volcanoes National Park, located on the southeast flank of Mauna Loa extending from 1200 m elevation to the summit. The portion between 1200 m and 1700 m elevation has been severely affected by logging, cattle grazing, feral goats and pigs. Cattle grazing was discontinued in 1948, with the remaining ungulates and stray cattle removed by the mid-1970s. The resulting vegetation community is characterized by an open to closed forest of regenerated koa (10-15 m tall) with the understory dominated by alien grasses approximately 30-50 cm deep (Baldwin & Fagerlund 1943; Tunison et al. 1995). The substrate is a mosaic of Mauna Loa lava flows dating from the Pleistocene to historic times with the majority of flows dated between 750 and 10 000 yr old (Trusdell et al. 2006). Three study sites were randomly established within this vegetation community spatially separated by 100-200 m elevation. The plots were established on substrate 3000-10 000 yr old (Trusdell et al. 2006) with a mean annual rainfall of approximately 1500 mm (Giambelluca et al. 1986).

Field survey of light environments

In spring 2006, quadrats were established to compare understory leaf litter and above-ground grass biomass in three different light environments: open pasture, the understory of planted stands of *Acacia*, and the understory of a mixed species secondary forest at Hakalau Forest National Wildlife Refuge. Under two planted stands and one secondary forest stand, quadrats were located along three transects randomly placed within each canopy type. Six 50-m transects were established under two planted *A. koa* stands (1989 and 1994 were analysed together) with similar light environments. Three 30-m transects were established under secondary forest canopy. Along each transect five 0.25-m^2 quadrats were established at 10-m intervals under the planted koa canopy and at 6-m intervals under the secondary forest canopy. One-third of the quadrats in each canopy type were paired with quadrats in the adjacent open pasture. The open pasture quadrats were located along a 30-m transect perpendicular to the understory transect. In each of the 60 quadrats, all grass species were identified and recorded. All above-ground grass biomass and tree leaf litter within the quadrat was collected. Biomass samples were oven-dried (70°C) for 72 h and weighed.

Mid-day percent light transmittance was measured directly above the grass layer of each quadrat using a silicon photodiode LI-COR LI-191SA line quantum sensor and LI-COR LI-190SA point sensor (LI-COR, Lincoln, NE, USA). All readings were taken in overcast conditions between 10:00 h and 14:00 k. The line sensor was positioned directly above the grass layer under the forest canopy and the point sensor was positioned in the open environment (no canopy within 45° of the zenith) directly above the grass layer. Percent light transmittance was calculated by dividing the forest reading by the open reading and multiplying by 100.

A Kruskal–Wallis test was used to evaluate differences in grass biomass and leaf litter separately between the three environments (planted canopy, secondary forest and pasture) followed by nonparametric multiple comparison analysis (Gibbons 1993). Pearson's correlation test was used to evaluate the relationship between understory light availability (percent transmittance) and above-ground alien grass biomass. Both proportion of light available (arcsine of the square root) and grass biomass (natural log) were transformed prior to analysis. All statistical tests were performed in SAS System for Windows, ver. 9.1 (SAS Institute Inc., Cary, NC, USA) and Minitab ver. 15 (Minitab Inc., State College, PA, USA).

Experimental light manipulation

Shade structures were used to test the effect of light availability on the growth and survival of native woody and alien grass species (Table 1). Each of the woody species selected are commonly found in

Table 1. Native woody and alien grass species used for experimental shade trials ($n = 15$). Ten replicates of 100 seeds for each species were used to determine seed mass ($n = 10$).

Species	Code	Common Name	Family	Origin	Initial seedling height		Seed mass	
					Mean (cm)	SE	Mean (mg)	SE
Native woody species								
Acacia koa	AK	Koa	Fabaceae	Hawaiian endemic	17.5	0.41	104.90	0.017
Pipturus albidus	PA	Māmaki	Urticaceae	Hawaiian endemic	7	0.23	0.74	0.000
Metrosideros polymorpha	MP	ʻŌhiʻa	Myrtaceae	Hawaiian endemic	11	0.22	0.06	0.002
Coprosma rhynchocarpa	CR	Pilo	Rubiaceae	Hawaiian endemic	7.2	0.22	30.19	0.001
Dodonaea viscosa	DV	ʻAʻaliʻi	Sapindaceae	Pantropical, indigenous to Hawaii	8	0.37	5.14	0.000
Sophora chrysophylla	SC	Māmane	Fabaceae	Hawaiian endemic	17.4	0.36	63.91	0.003
Alien grass species								
Paspalum dilatatum	PD	Dallis grass	Poaceae	Central and South America	9.6	0.59	1.15	0.000
Pennisetum clandestinum	PC	Kikuyu grass	Poaceae	Tropical Africa	13.8	0.4	2.41	0.000
Ehrharta stipoides	ES	Meadow ricegrass	Poaceae	Australia, New Zealand, Philippines	10.2	0.28	4.77	0.000

secondary koa forest when seed sources exist and play a significant role in the recovery of forest structure and diversity (Cuddihy & Stone 1990; Wagner et al. 1990). The selected grass species dominate the vegetation community in abandoned pastures many decades after grazing has ceased (Cuddihy & Stone 1990). Seeds of each species were collected from at least 30 parent plants in the Mauna Loa Strip section of Hawaii Volcanoes National Park. Although inflorescences were observed in *Pennisetum*, seeds could not be located in natural conditions and had to be purchased from a local distributor. All seedlings were propagated at the Hawaii Volcanoes National Park plant propagation facility (approximately 1219 m elevation). In each of the three sites, three different light treatments were created using shade structures erected beneath the existing koa canopy. Unlike natural leaf canopy that produces an environment high in far-red light because of greater absorption of light in the photosynthetically active spectrum (400-700 nm), shade cloth alters the quantity of light without altering the quality. Effects of light quality are not addressed in this study although it may have a significant effect on growth and germination of some species (Pons 1992; Tinoco-Ojanguern & Pearcy 1995).

In Hawaii, a wide range of light levels in different types of forests have been documented. Values range from 1.9 to 10% for montane rainforest (Burton 1980; Burton & Mueller-Dombois 1984; Pattison et al. 1998), 5% for recovered mesic forest (McDaniel 2007, Kipuka Puaulu, HAVO), 10-20% in planted *A. koa* stands (Scowcroft & Jeffrey 1999), 20-30% in disturbed montane mesic closed canopy dominated by *Metrosideros* or *Acacia* (Denslow et al. 2006) and higher values in closed dry forest, 20-40% (Cordell pers. comm.). For the light manipulation study, we chose light levels representative of low light in closed canopy forest (5%) with limited grass presence (S. McDaniel unpubl. data), an intermediate level (10%) that has some restrictive effect on grass growth (Scowcroft & Jeffrey 1999) and high light (30%) known to support vigorous alien grass growth (Grace 1995; Denslow et al. 2006).

The structures were constructed using a PVC frame (5 m×5 m×1 m) covered with shade cloth of varying densities to create the desired light environment. Bird netting (5/8th inch in diameter) was used on the high-light treatment to simulate the use of shade cloth with minimal alteration of the light environment. Little variation in relative humidity (5-10%) and air temperature (< 5°C) was documented between treatments at the same site measured with HOBO H8 Pro RH/Temperature loggers (Onset Computer Corp., Pocasset, MA, USA). Greater variation was documented between sites than within sites, although variability was not consistent across time. Soil moisture (top 10 cm) was gravimetrically measured twice during the experiment. It did not substantially vary between treatments or sites. Established understory grasses were treated with a 10% solution of Roundup herbicide approximately 3 months prior to experimentation.

Within each site there were three replicate structures for each light treatment (nine structures per site). To ensure that similarly sized individuals were equally distributed between structures and sites, seedlings were first grouped by height into five size classes, and one seedling was taken from each size class to form a set of five seedlings that were randomly assigned to one of the treatment structures. One set of each of the nine species was planted in a randomized grid within each structure for a total of 45 seedlings per structure. Three sets (15 individuals) were not planted, but were used to obtain initial biomass estimates for the seedlings that were planted by correlating the strongest metric (height, cumulative stem length, stem basal diameter, volume or crown area) with total dry biomass for each species. Crown area was estimated for the grass species by multiplying the widest diameter of the crown and the perpendicular diameter measurement. In addition, volume was estimated by multiplying the crown diameter by the height.

After 6 months of growth, above-ground biomass of the surviving seedlings was harvested. At the seedling stage above-ground biomass can be a good indicator of response to changes in the light environment and has been used in similar studies (Pearcy et al. 1991). Although recent research has shown there may be a bias when comparing relative growth rate (RGR) of small- and large-seeded species (Turnbull et al. 2008), this experiment selected species with a range of seed sizes of which only two were < 2 mg (Table 1). In addition, variation of leaf traits and biomass allocation may provide insight into species-specific competitive advantages under different light environments. The total leaf area of each woody seedling was measured using a LI-3100 leaf area meter (Li-Cor). All leaves, stems, and leaf buds were separated and oven dried at 70°C for 72 h and then weighed. RGR of total biomass accumulation was calculated per plant as the difference between the natural logarithms of the actual final biomass weight and estimated initial biomass weight divided by the number of days between planting and harvest. Specific leaf area (SLA) was calculated by dividing total leaf area by total leaf biomass. Leaf area ratio (LAR) was calculated by dividing total leaf area by total above-ground plant biomass. Petioles were included in leaf area and leaf biomass. Data on photosynthetic rate, quantum yield, leaf chlorophyll and leaf mass per area on six of the species, grouped together by life forms, are presented in Funk & McDaniel (2009).

For each species, we first used a nested ANOVA (light treatment nested within site, proc nested in SAS) to evaluate the effect of light availability and site on RGR. The mean RGR for each species was calculated by averaging the RGR of the surviving seedlings in each light treatment ($n = 3$). Because there was no site effect, treatment data were combined by site ($n = 9$) and analysed with a one-way ANOVA to determine the effect of light availability on SLA and LAR. The coefficient of variation was calculated for survivorship by dividing the standard deviation by the mean survival of each species ($n = 9$) and multiplying by 100. All statistical tests were performed in SAS System for Windows, ver. 9.1 (SAS Institute Inc.).

Results

Field survey of light environments: Understory differences in biomass

Both grass ($\chi^2_{(2)} = 46.65$, $P \leq 0.0001$) and leaf litter biomass ($\chi^2_{(2)} = 37.12$, $P \leq 0.0001$) differed among the three canopy types (Fig. 1). The open pasture contained the greatest amount of grass biomass – almost three times greater than under the planted canopy. Grass biomass was nearly absent under the secondary canopy (2.17 g/0.25 m^2). In addition, the grass species composition was different in each environment (Table 2). The open pasture plots contained the highest number of grass species: *Pennisetum*, *Anthoxanthum odoratum*, *Ehrharta*, *Axonopus fissifolius* and *Holcus lanatus*. Only three grass species were found under the planted canopy: *Pennisetum*, *Anthroxanthum* and *Ehrharta*. The understory of the secondary forest primarily contained *E. stipoides*, with only three quadrats containing *A. odoratum*. The greatest amount of leaf litter was found under the planted (144.61 g/0.25 m^2) and secondary canopy (87.87 g/0.25 m^2) with very little found in the open pasture (0.61 g/0.25 m^2). In addition, under the planted canopy the litter was dominated by koa leaves, whereas the litter was composed of a mix of several different tree species under the secondary canopy.

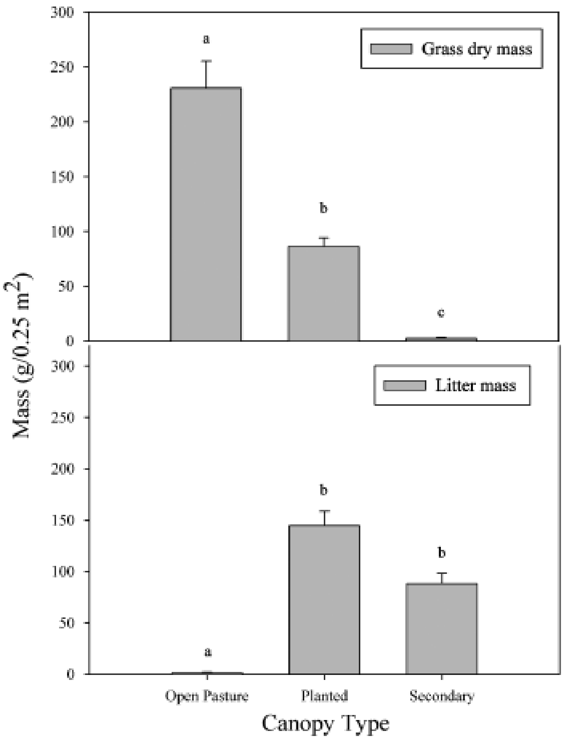

Fig. 1. Above-ground grass biomass (top) and leaf litter (bottom) under three canopy types (means+SE) was analysed with a Kruskall–Wallis test followed by a non-parametric multiple comparison. Bars with the same letter (a, b) indicate differences in mass between canopy types are not significantly different at $P \leq 0.05$.

Table 2. Prevalence of species in quadrats by canopy types.

Species	Canopy type (%)		
	Open $n = 15$	Planted $n = 30$	Secondary $n = 15$
Ehrharta stipoides	40	87	67
Pennisetum clandestinum	67	97	0
Anthroxanthum odpratum	60	17	20
Axonopus fisifolius	13	0	0
Holcus lanatus	13	0	0

Field survey of light environment: relationship between understory light availability and alien grass biomass

Lower levels of available light resources in the understory were accompanied by lower quantities of alien grass biomass (Fig. 1). Light availability was reduced under the planted canopy and the secondary forest canopy by 83-99% compared with open pasture. There was a positive relationship between understory light availability and alien grass biomass ($r = 0.854$, $P \leq 0.000$, $n = 45$; Fig. 2). However, results vary when the canopy types are analysed separately. Within the planted canopy there was a significant positive relationship ($P = 0.001$, $n = 30$), but the relationship was not as strong ($r = 0.615$). There was no significant relationship between light

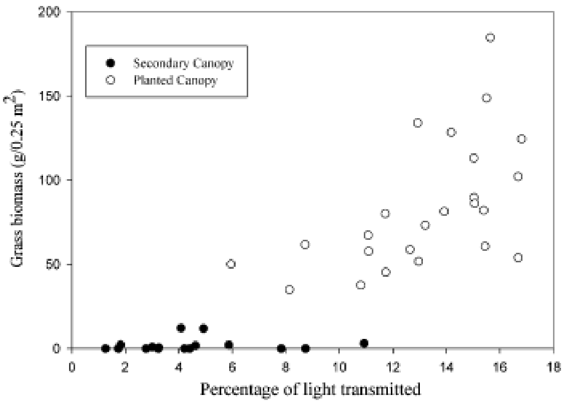

Fig. 2. Grass biomass as a function of percentage of light transmitted under planted and naturally regenerated canopy at Hakalau ($r = 0.854$, $P \leq 0.000$). When analysed separately the relationship is significant under the planted canopy ($r = 0.615$, $P < 0.001$), but not under the secondary forest canopy ($r = 0.182$, ns)

availability and grass biomass in the secondary forest understory. Light conditions ranged from 1% to 11%, but a sparse amount of grass biomass was encountered in any of the secondary forest quadrats.

Experimental light manipulation: RGR

There were no effects of site treatment for any of the grass species and five of the six woody species. The experimental light treatments affected RGR across sites and consistently decreased as light availability decreased for all of the grass species and four of the six woody species (Fig. 3). In the high-light treatment, all grass species were similar in their RGR values; grasses in the high-light treatment also had greater RGR than any of the woody species. In the medium-light treatment, the RGR of the grasses was greater than four woody species and nearly equal to two of the understory woody species, *Coprosma rhynchocarpa* and *Pipturus albidus*. In the low-light treatment, the highest growth rates were found for the grass *Ehrharta*, and two native species, *Coprosma* and *Pipturus*. *Acacia* was the only species that did not have a significant growth response to changes in the light environment (Fig. 3). The observed low growth rate relative to other woody species may indicate that *Acacia* is suppressed by all three light environments. In addition, the significantly lower RGR of *Sophora chrysophylla*

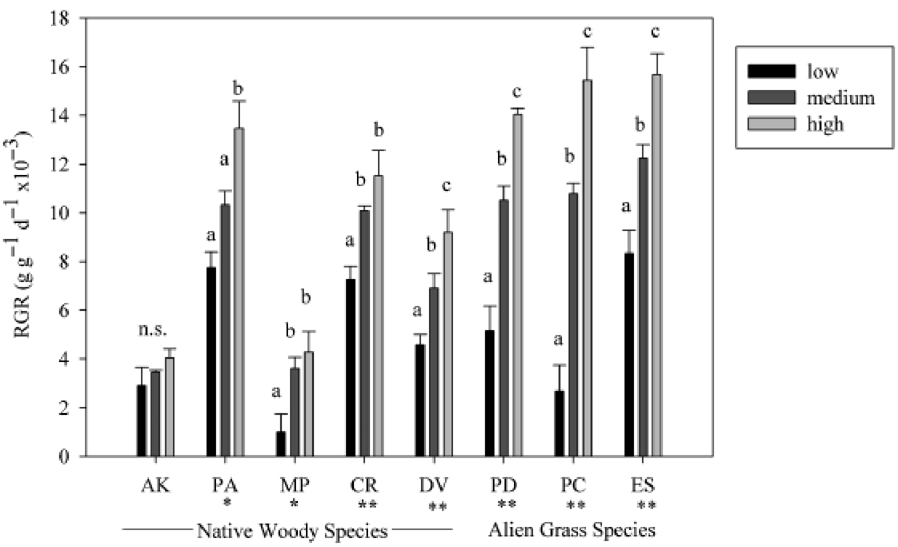

Fig. 3. Effect of light treatment (low 5%, medium 10%, high 25%) on the relative growth rate (RGR) of alien grasses and native woody species (AK = *Acacia koa*, PA = *Pipturus albidus*, MP = *Metrosideros polymorpha*, CR = *Coprosma rhynchocarpa*, DV = *Dodonaea viscosa*, PD = *Paspalum dilatatum*, PC = *Pennisetum clandestinum*, ES = *Ehrharta stipoides*). Significance level is indicated by *($P < 0.01$) and **($P < 0.001$). Results of the light treatments are displayed with all sites combined. *S. chrysophylla* is omitted because of significant site differences and no effect of light treatment. Significant differences between each light level are shown with different letters (a, b, c) for each species.

measured at the two lower elevation sites was possibly caused by intense insect herbivory. Insect damage was observed less frequently at the highest elevation site for this species. There was no insect damage observed on any of the other species.

Another way to examine the data is to consider the magnitude of the growth response (i.e. percent change). Going from high- to medium-light treatment, overall RGR reduction ranged from 12% to 30% for both the grasses and the woody species. More dramatic reductions in RGR were observed going from a high-light environment to low-light environment for some species. The largest reductions were found for *Pennisetum* (83%) and *Metrosideros* (77%). The smallest reduction in RGR from high light availability to low light availability was found for *Coprosma* (37%), *Pipturus* (42%) and *Ehrharta* (47%).

Experimental light manipulation: changes in leaf characteristics of woody species

Morphological changes in leaf structure, biomass allocation and stem architecture were evident for most of the woody species in response to light availability (Table 3). In general, leaves became thinner and a higher proportion of total biomass was allocated to leaves in low-light conditions. However, there were no significant morphological changes for *Sophora*. As light availability increased, LAR significantly decreased for five of the six species. The SLA also significantly decreased as light availability increased for four species. *Pipturus* and *Coprosma* had the highest SLA and LAR compared with the other species in each of the three light levels. The response to changes in the light environment was most pronounced for *Pipturus*, with a nearly 50% decrease in SLA and LAR in low light compared with high light.

Experimental light manipulation: survival

Survival was high (84-100%) across all species and treatments (Table 4). However, survival was more variable in the low-light environment than the medium-light and high-light treatments across species. The coefficient of variation (CV) was 5.0% for low light compared with 1.6% for medium light and high light.

Table 4. Survival of woody and grass seedlings under three different light treatments ($n = 9$). Standard error is displayed in parentheses.

	Light treatment		
	Low	Medium	High
Native woody species			
Metrosideros polymorpha	100% (na)	100% (na)	98% (2.22)
Pipturus albidus	96% (2.94)	98% (2.22)	96% (2.94)
Dodonaea viscosa	93% (3.33)	98% (2.22)	100% (na)
Coprosma rhynchocarpa	96% (2.94)	98% (2.22)	100% (na)
Sophora chrysophylla	93% (4.71)	100% (na)	100% (na)
Acacia koa	100% (na)	100% (na)	100% (na)
Alien grass species			
Paspalum dilatatum	98% (2.22)	100% (na)	100% (na)
Pennisetum clandestinum	84% (4.44)	96% (2.93)	100% (na)
Ehrharta stipoides	93% (3.33)	98% (2.22)	100% (na)

Table 3. Effect of light availability on leaf area ratio (LAR), specific leaf area (SLA). Standard error displayed in parentheses. Significant results are shown in bold type ($P \leq 0.05$). Differences between light treatments are shown with different letters (a, b, c).

Native woody species	Light treatment	LAR (cm^2/g) $n = 9$	SLA (cm^2/g) $n = 9$
Acacia koa	Low	**62.37 (4.22)^a**	**104.69 (5.56)^a**
	Medium	**45.99 (4.6)^b**	**83.51 (6.51)^b**
	High	**46.65 (4.5)^b**	**82.42 (7.26)^b**
Coprosma rhyncocarpa	Low	**178.89 (4.82)^a**	**281.48 (5.36)^a**
	Medium	**134.5 (2.39)^a**	**224.5 (4.82)^b**
	High	**120.94 (11.42)^b**	**207.12 (15.37)^b**
Dodonaea viscosa	Low	**135.27 (23.13)^a**	185.6 (2.60)
	Medium	**131.65 (16.30)^a**	189.44 (29.16)
	High	**92.38 (4.80)^b**	170.85 (43.23)
Metrosideros polymorpha	Low	**65.89 (2.28)^a**	**83.45 (2.99)^a**
	Medium	**66.83 (1.86)^a**	**85.98 (2.56)^a**
	High	**54.73 (2.01)^b**	**72.98 (2.88)^b**
Pipturus albidus	Low	**250.19 (12.28)^a**	**348.07 (21.91)^a**
	Medium	**191.04 (13.29)^b**	**270.31 (21.39)^b**
	High	**139.28 (8.06)^c**	**186.64 (9.15)^c**
Sophora chrysophylla	Low	57.94 (7.38)	137.33 (12.09)
	Medium	66.36 (5.55)	133.97 (8.52)
	High	52.46 (5.89)	111.12 (6.75)

Discussion

While many factors may contribute to the slow to absent rate of woody plant succession in abandoned pasture lands, our study demonstrates that light reduction is an important mechanism for overcoming the barrier of grass competition. The biomass of persistent grasses in abandoned pastures can be reduced by strategically lowering light availability without inhibiting the survival of common native Hawaiian woody species. The reduction of understory grass biomass through canopy development and subsequent light limitation has been demonstrated to facilitate the establishment of woody species in other regions (Zhung 1997; Uhl 1998; Holl 1999; Aide et al. 2000; Maundrell & Hawkins 2004) and may represent a sustainable strategy that can be applied on a landscape scale in Hawaii.

The lowest light conditions in both the field survey and the light manipulation experiment supported the lowest amount of alien grass biomass. This finding is supported by studies conducted in Hawaii (Grace 1995; Pattison et al. 1998; Scowcroft & Jeffrey 1999; Baruch et al. 2000) and elsewhere (Sanford et al. 2003; Maundrell & Hawkins 2004; Cavagnaro & Trione 2007) on herbaceous and woody species. Although the increased canopy cover can decrease growth for some woody species, as found in this and other studies (Kobe 1999; Alverez-Aquino et al. 2004; Maundrell & Hawkins 2004), the reduction in competition with herbaceous plants provides an overall positive effect (Levine 1999; Maundrell & Hawkins 2004).

Although growth rates in the light manipulation experiment were reduced, survival remained high across species and light treatments, which is encouraging for native species recovery. The degree of reduction in RGR was dependent on both species and treatment. Under intermediate light conditions the reduction in RGR was fairly moderate (12-30% reduction from high to medium light) across all species. In low light *Pennisetum*, *Paspalum* and *Metrosideros* demonstrated a higher proportional reduction in RGR (63-83% from high to low light) than other species (36-50%). The use of shade cloth may have minimized the effect of ‘sunflecks’ that provide short, intense bursts of full sunlight, which would be present under natural canopy conditions. Variation in duration and frequency of sunflecks has been demonstrated to affect plant growth (Pearcy 1983; Vierling & Wessman 2000). In addition, germination for these species was not suppressed by low-light conditions alone (McDaniel 2007); however, other factors present in the field may play a large role in species establishment, including low seed dispersal and depleted seed banks (Wunderle 1997; Holl 1999), microsite conditions (Guariguata et al. 1995; Zimmerman et al. 2000) and pathogens (Augspurger & Kelly 1984). Planted stands also had high amounts of leaf litter which can influence seedling germination and survival through the changes in light and water availability in addition to soil temperature and chemical alterations (Facelli & Pickett 1991; Molosky & Augspurger 1992; Xiong & Nilsson 1999).

While it is encouraging that grass biomass was suppressed, the differential growth responses observed for each of the grass species suggest that light effects are species-specific. Two of the grass species, *Pennisetum* and *Paspalum*, were severely affected by low-light conditions with RGR reduced by 83% and 62%, respectively. These two species appear to be more shade intolerant and may be eliminated under low-light conditions (Table 2). Campbell et al. (1999) found natural populations of *Pennisetum* in New Zealand least tolerant to low-light environments and *Paspalum* to be intermediate in solar radiation requirements when compared with other pasture species. In Hawaii, Grace (1995) determined that *Ehrharta* has a competitive advantage over *Pennisetum* in low light typical of the understory environment, whereas the relationship is reversed in high light. In addition, Grace (1995) found that the biomass of *Pennisetum* to be negatively correlated with the fraction of light transmitted, over a range of 20-100%. In contrast, he found no correlation with the biomass of *Ehrharta*; however, he did not evaluate light environments less than 20%. In this study we also found that *Ehrharta* is less affected by low-light conditions than *Pennisetum*. Given that *Ehrharta* has also been documented with low biomass in low-light conditions (2%) (Scowcroft et al. 2008), we feel that *Ehrharta* may be a species that will always persist in understory.

Examination of leaf traits and changes under different light environments may provide insight into species-specific competitive advantages, providing managers with a tool to select successful native species in particular light environments (Martinez-Garza et al. 2005). Similar to results from other studies on woody species (Pattison et al. 1998; Baruch et al. 2000; Sanford et al. 2003; Valladares et al. 2005; Portsmuth & Niinemets 2006), LAR and SLA decreased as light increased for the species we investigated (Table 2). However, we did not address how allocation changes with size might influence LAR (Reich 2002). Concurrent research suggests that differences in light use among native Hawaiian and invasive species can help to determine the utility of resource manipulation as a restoration tool and, more specifically, predict which native species will be optimal for restoration efforts that manipulate light availability (Funk & McDaniel 2010). Under closed canopy conditions species with higher investment in leaf construction (lower SLA) would have higher survival, whereas in high-light conditions faster growing species (higher SLA) would have a greater competitive advantage (Poorter & Bongers 2006). Using these generalizations regarding SLA we would predict *Coprosma*, *Dodonaea* and *Pipturus* to have higher growth rates, which was confirmed by this study (Fig. 3, Table 4), and lower survival in low light than *Metrosideros*. However in this study, all of the species investigated had high survival across light treatments indicating that these species would be able to persist under canopy conditions.

Conclusion

Effective landscape-scale strategies are needed to restore native Hawaiian vegetation communities that have been degraded by extensive logging and cattle ranching during the past 200 yr. The use of plantation-style plantings has been a successful technique elsewhere and here we show that the reduction of understory light levels can effectively reduce grass biomass and diminish this key barrier to secondary succession. Although growth is substantially reduced for native woody species in low light, survival is still high indicating that these species may persist under closed canopy (5% light availability). The grass species may also persist under low light, but reduced biomass may translate to reduced competition with woody species. Elimination of alien grasses can promote native seedling recruitment; however, given the high level of shade tolerance of the grass *Ehrharta* complete elimination is not realistic. Further investigation is needed to determine the amount of grass biomass that can be present without impeding recruitment of native species. Other factors present in the field, including litter and microsite conditions, may interact with light availability to determine the success of native woody and alien grass species in shaping the future composition of the forest. Active management of the light environment is a promising approach to create native self-sustaining communities through restoration of native structure and diversity.

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