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Limitations to seedling establishment in a mesic Hawaiian forest

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Abstract While invasive species may be visible indicators of plant community degradation, they may not constitute the only, or even the primary, limitation to stand regeneration. We used seed-augmentation and grass-removal experiments under different canopy conditions to assess the relative importance of dispersal limitation, resource availability, and competition on seedling establishment in the understory shrubs *Sophora chrysophilla*, *Dodonea viscosa*, and *Pipturus albidus* in a montane mesic forest in Hawaii. The study location was an *Acacia koa-Metrosideros polymorpha* forest at 1000–1500 m elevation on the leeward side of Hawaii Island; it is a closed-canopy forest historically subject to logging and grazing by cattle and sheep and currently dominated by the exotic grass, *Ehrharta stipoides*, in the herb layer. Seedling establishment after 1 and 2 years was strongly dispersal limited in *Sophora* and *Dodonea*, but not in *Acacia*, a non-augmented species in which abundant seedlings established, nor in *Pipterus*, in which only one seedling established in 2 years. Grass cover reduced seedling establishment in *Acacia*, *Sophora*, and *Dodonea* and, for the latter two species, seedling establishment was substantially greater in the warmer, more moist forest at the lowest elevation. Light, moisture, and resin-captured N and P were more strongly affected by elevation and canopy composition than by grass cover, but in most cases seedling establishment was not positively correlated with resource availability. Limitations to the establishment of woody seedlings in this forest-grassland mixture vary among species; however, both dispersal limitation and competition from a shade-tolerant grass are important deterrents to regeneration in these forests.

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Introduction

Competition from invasive species is an important source of degradation to native plant communities and often a major impediment to their restoration (D'Antonio and Vitousek 1992; Mack et al. 2002). Nevertheless, while invasive species may be highly visible indicators of ecosystem decline, they may not constitute the only, or even the primary, limitation to stand regeneration. Site conditions, altered through a history of inappropriate management, may include changes in soil structure, moisture availability, nutrient supply, stand structure, light conditions, and disturbance regimes (Ewel and Putz 2004; Gurevitch and Padilla 2004). Loss of co-occurring and/or symbiotic species, including pollinators, dispersal agents, herbivores, and pathogens, may alter the competitive capacity of native species (Loope and Mueller-Dombois 1989; Denslow 2003). Further, the regeneration of native species may be limited naturally by dependence on rare or episodic weather conditions, dispersal limitation, competition, and population bottlenecks caused by periodic disturbances, such as fire and drought (Hughes and Vitousek 1993; Goergen and Daehler 2001, 2002; Hubbell 2001). In addition, the relative importance of these factors, including the impacts of invasive species, may vary under different environmental conditions, thereby challenging our understanding of the role of invasive species in limiting community development processes.

In Hawaii, as in much of the tropics, the conversion of tropical forest to pastures dominated by exotic grasses has been a major source of forest loss (for example, Tummons 2002). A common trajectory of decline begins with opening of the forest canopy by timber extraction and proceeds with the establishment of pasture grasses and ferns, increased grazing pressure, and soil compaction. The steady loss of remnant canopy

trees coupled with a failure of regeneration completes the transition from forest to grassland.

The extent of mid-elevation mesic forests in Hawaii has been reduced severely under this scenario, and the remaining forest has been altered substantially. Selective logging of a dominant overstory tree, *Acacia koa* A. Gray, has led to the replacement of a forest of large old trees by thickets of small-diameter, slow-growing saplings (Scowcroft and Nelson 1976). Chronic ungulate browsing has reduced seedling densities and lowered the diversity and abundance of understory shrubs (Scowcroft 1983; Scowcroft and Giffin 1983; Scowcroft and Conrad 1992). The combination of canopy opening, substrate disturbance, and ungulate grazing has encouraged the spread of a suite of alien grasses, some of which are shade-tolerant (Scowcroft and Giffin 1983). In this study, we investigated limitations to stand restoration, specifically addressing the relative importance of dispersal limitation, resource availability, and competition on seedling establishment.

An extensive literature documents the complexity of tree-grass interactions in tropical pasture and savannah ecosystems, suggesting that barriers to forest restoration in Hawaii are likely to be diverse. Lack of seed availability is a significant constraint on the establishment of woody shrubs and trees under many circumstances (Posada et al. 2000; Wijdeven and Kuzee 2000), but not all (Chapman and Chapman 1999; Zimmerman et al. 2000). Rain forest trees often have poor dormancy capacities, and seedbanks are depleted rapidly following grazing and fire (Holl et al. 2000). In addition, dispersal agents often do not frequent open grasslands (Aide and Cavelier 1994; Slocum and Horvitz 2000). Moreover, competition with grasses can reduce woody seedling establishment and growth to the degree that seed augmentation experiments may not alter establishment success. In heavily degraded sites, however, grass cover may facilitate seedling establishment (Aide and Cavelier 1994). Poor soil nutrient and moisture supply (Aide and Cavelier 1994) and seed predation (Holl et al. 2000) also may slow regrowth. The establishment of tree or shrub cover is often a high priority in pasture reforestation programs because it suppresses the grasses and facilitates establishment of other woody species (Kellman 1979, 1985; Guevara et al. 1986; Archer et al. 1988; Holl et al. 2000).

The Honomalino tract of the Kona-Hema Nature Reserve reflects the history of logging and grazing and the spread of invasive pasture grasses typical of many mesic montane forests in Hawaii. The forest is a mosaic of *Metrosideros polymorpha* Gaud. woodland and young *A. koa* forest, all undergrown by the shade-tolerant exotic grass, *Ehrharta stipoides* Labill. Our study assessed limitations to seedling establishment by comparing the impact of different site conditions on seedling establishment. We began the investigation with a number of expectations: (1) that dispersal limitation would be strong in all sites because of the loss of the disperser community and, in some circumstances, a reduction in the abundance of seed sources; (2) that dispersal limitation would be least pronounced where the forest was the most diverse and structurally intact; (3) that competition from grasses would reduce seedling establishment in all sites; (4) that the presence of grasses would reduce the supply of soil resources (moisture, N and P) at all sites, but most strongly at high-elevation sites where supply rates are expected to be lower because of lower rainfall and cooler temperatures; (5) that seedling establishment would be high under *A. koa*, an N-fixing canopy-dominant tree, and highest under an open canopy where light availability is highest. We examined these factors by establishing experimental treatments of seed augmentation and grass removal under canopy conditions selected to contrast conditions of light availability, canopy composition, and elevation.

Materials and methods

Site

The experiment was established at the 1627-ha Honomalino tract of The Nature Conservancy's Kona-Hema Preserve (155°48′W, 19°12′N) on the western (leeward) slope of Mauna Loa Volcano, Hawaii Island, Hawaii, USA. Experimental plots were established at two elevations – 1400–1500 masl and approximately 1000 masl – in montane mesic forest. Estimated annual rainfall from long-term gauge data (1916–1983; Giambelluca et al. 1986) was 1000–1500 mm at the high-elevation plots and 1500–2000 mm at the low-elevation plots. Gauge data taken at similar elevations on the adjacent Kapua tract of the Kona-Hema Preserve for the last 9 years show considerably less rainfall (median annual rainfall of 708 and 749 mm, at high- and low-elevation sites, respectively), reflecting recent low-rainfall years (S. Rice, unpublished data). Rainfall does not exhibit substantial seasonal variation (Juvik and Juvik 1998). Plots at both elevations occurred on the same, relatively young, lava flow formed 1500–3000 year BP (Wolfe and Morris 1996). High-elevation stands occurred on shallow excessively drained soils (Lithic Ustifolists, USDA-NRCS, unpublished data) over a lava bedrock. Soils under the lower-elevation stands were somewhat better developed (Typic Udifolists, USDA-NRCS, unpublished data). Projected mean annual temperatures based on adiabatic lapse rates were 15.5°C at the high-elevation plots and 17.5°C at the low-elevation plots (Juvik and Juvik 1998).

The high-elevation stands of the Honomalino forest are characterized as koa/ohia montane mesic forest type (Gagné and Cuddihy 1999) dominated by koa [*Acacia koa* A. Gray (Fabaceae)] and ohia [*Metrosideros polymorpha* (Myrtaceae)]. Following selective logging of the old-growth koa approximately 25 years ago, prolific koa regeneration from seed and sprouts produced dense patches of small-diameter trees at old

extraction sites and along skid trails. The forest is now a mosaic of young, high-density koa and older, unlogged ohia forest. At this elevation, ohia trees are generally <15–20 cm dbh (diameter at breast height). Other common woody species include *Coprosma rhynchocarpa* A. Gray (Rubiaceae), *Myoporum sandwicense* A. Gray (Myoporaceae), and *Myrsine lessertiana* A. DC (Myrsinaceae). The field layer is dominated by meadow-rice grass, *Ehrharta stipoides*, a relatively shade-tolerant species from Australia, New Zealand, and the Philippines (Wagner et al. 1999), and several species of ferns including *Dryopteris wallichiana* (Spreng.) Hyl. and *Pteris cretica* L. In addition to logging, the forest was open to grazing and browsing by cattle, goats, pigs, and mufflon sheep until TNC-Hawaii acquired the property in 1999, at which point Honomalino was fenced and ungulate removal initiated (M. Johansen, personal communication). With the exception of *Ehrharta*, other non-indigenous species, while common along trails, roadsides, and other disturbed areas, are scarce in this forest. Fire is uncommon in these mesic ecosystems.

The forest at the 1000-m elevation site (ohia montane mesic forest; Gagné and Cuddihy 1999) reflects somewhat higher productivity where moisture availability is greater and temperatures higher than in the high-elevation forest. The forest is dominated by large (>65 cm dbh) ohia trees, and tree ferns (*Cibotium glaucum* (Sm.) Hook & Arnott (Cyatheaceae) are common; koa was uncommon at this elevation. This stand was neither logged nor opened to cattle grazing, but feral pigs, mufflon sheep, and goats were present until recently (M. Johansen, personal communication). Minor canopy species include *Ilex anomala* Hook & Arnott (Aquifoliaceae), *Myrsine lessertiana* A. DC (Myrsinaceae), *Pittosporum hawaiiense* Hillebr. (Pittosporaceae), and *Cheirodendron trigynum* (Gaud.) A. Heller. *Ehrharta* is also the predominant grass in the understory at this elevation. The native grass, *Deschampsia nubigena* Hillebr., is common in gaps as are the ferns *Nephrolepis exaltata* (L.) Schott and *Dryopteris wallichiana* (Spreng.) Hyl.

Experimental design

The sampling protocol was designed to assess the relative importance of seed availability, grass cover, canopy openness, canopy composition, and elevation on seedling establishment, and resource availability in the Honomalino forest. We employed an unbalanced split-split plot design with two levels of seed augmentation nested within each of two levels of grass removal treatment nested in turn within each of the four canopy types. Each treatment combination was replicated five times for a total of 40 plots and 80 seedling subplots.

We established ten 5×5-m study plots (Fig. 1) under each of the following four forest canopy types: high-elevation koa forest thinned to create a 16-m diameter gap, high-elevation koa forest with closed canopy, high-elevation ohia forest with closed canopy, and low-elevation ohia forest with closed canopy. On one-half of the plots within each canopy type, we reduced grass cover by clipping and removing living grass and all dead litter mass while minimizing soil disturbance. Grass-clearing treatments were established in August 2002. After 30 days, the grass removal plots were treated once with a 5% solution of Round-up herbicide (glyphosate) to kill grass sprouts; no woody seedlings were observed at the time of herbicide treatment. Plots were re-treated periodically (four times) over the course of the study with Fusilade (fluzifop-*p*-butyl), a grass-specific herbicide at a rate of 0.75 fl oz/gal. water to maintain low grass cover on the treated plots.

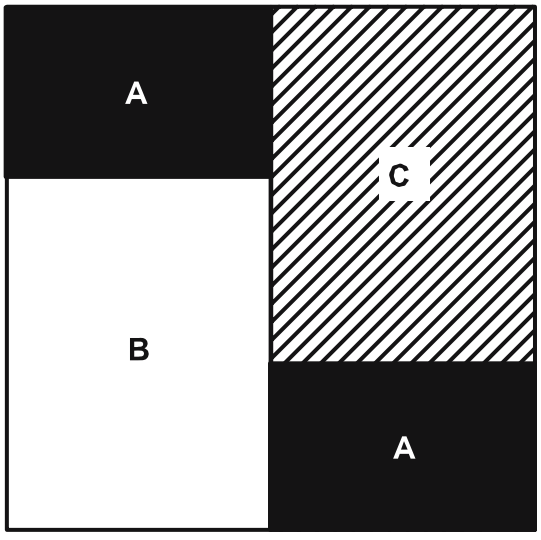

Fig. 1 Plot design. Entire plots (5×5 m) were either clipped to remove grass or left with the grass cover intact. Within each plot a 3×3-m core area was subdivided to sample soils (*A*) or record seedlings established from naturally dispersed seed (*B*) or from naturally dispersed seeds augmented with seeds from each of the three focal species (*C*)

Vegetation

The above-ground litter and grass biomass were sampled at the beginning of the study in all plots before establishment of the grass-removal treatment. All above-ground grass and litter were collected in 0.25-m^2 subplots within each of the sample plots and outside of the 3×3-m core area. Collections were sorted into grass, wood (<2 mm diameter), and other fine litter, oven dried at 70°C to a constant mass, and then weighed. Above-ground litter mass and grass biomass were re-sampled from both open- and closed-canopy koa plots after 18 months to determine whether grass biomass had increased following canopy opening. Vegetation on each 5×5-m plot was described from dbh measurements of all trees >2.5 cm dbh and counts of all smaller stems <2.5 cm dbh and >1 m tall.

Light

Percentage transmittance of photosynthetically active radiation (PAR) was estimated using LiCor (Lincoln, Neb.) quantum sensors (LiCor 190SA) attached to data loggers on LiCor Plant Canopy Analyzers (LiCor LAI2000) operated in the two-instrument mode. Two measurements were taken 1 m above ground in each 5×5-m plot for the below-canopy readings. Above-canopy incident radiation was estimated from simultaneous readings of instruments established in adjacent areas where there was no vegetation to obscure the sky within 52° of zenith. Percentage transmittance was calculated as the ratio of below-canopy to above-canopy PAR.

Soils

Soils were sampled within a portion of the 3×3-m core of each plot (Fig. 1). We characterized nutrient availability as measured by resin-captured NO_3-N, NH_4-N, and PO_4-P every 3 months for 1 year beginning 6 months following grass removal to avoid a potential pulse in nutrient availability due to the grass-clearing treatment. N and P availability were assessed following the method of Binkley and Matson (1983). Pairs of mixed-bed resin bags were inserted 4–6 cm under the soil surface in mineral soil in each field plot (five pairs per canopy-grass-removal combination) and left in the ground for 6 weeks. Retrieved bags were washed with deionized water to remove soil particles and extracted with 2 *M* KCl (NH_4-N, NO_3-N) or 0.5 *M* HCl (PO_4-P). Extracts were analyzed by the University of Hawaii, Manoa Agricultural Service Center (PO_4-P) using an automated molybdenum-blue method on a Scientific AS140 Auto Analyzer or by the Oregon State University Central Analytical Laboratory using the phenol method (NH_4-N) or cadmium reduction method (NO_3-N) on an Alpkem Flow Analyzer 550 (Alpkem, Clackamas, Ore.) (Kuo 1996; Mulvaney 1996). Results are reported as μg nutrient g resin^{-1} day^{-1}. The proportion of soil moisture was determined gravimetrically.

Seedling recruitment

Seedling recruitment was monitored in two 1.5×2-m subplots in the 3×3-m core area of the plot (Fig. 1). In one subplot we monitored seedling establishment originating from the natural seed bank and seed rain. In the other subplot, we augmented seed input with the addition of seeds from each of the three species: *Sophora chrysophylla* Seem. (Fabaceae), *Pipterus albidus* (Hook & Arnott) A. Gray (Urticaceae), and *Dodonea viscosa* Jacq. (Sapindaceae), all species of shrubs or small trees commonly found in *A. koa-M. polymorpha* forest at these elevations. Seeds were collected in the vicinity of the Honomalino Preserve prior to sowing and were sown in September 2002 at a rate of approximately 400 unscarified seeds of each species in each subplot. Laboratory germination trials indicated that seed viability was approximately 40% for *Sophora*, 59% for *Pipterus*, and 20% for *Dodonea*. Seedlings of both seeded and naturally recruiting species were counted twice, 1 and 2 years after sowing on all plots.

Statistics

This unbalanced split-split plot design allowed us to use pairwise comparisons between canopy types to assess the effects of stand composition, elevation, and light availability on seedling establishment and resource availability. Thus, among the high-elevation stands we tested the effects of light availability by comparing open- and closed-canopy koa stands, and we tested the effects of stand composition by comparing closed-canopy koa with closed-canopy ohia. We tested the effects of elevation by comparing closed-canopy ohia stands at high elevation with closed-canopy ohia at low elevation. Grass-removal and seed-augmentation treatments were applied to plots and subplots, respectively, within each of these canopy types.

Percentage soil moisture and nutrients were analyzed using a repeated-measure analysis of variance in PROC MIXED in the SAS System for Windows, ver. 8.02 (SAS Institute 1999–2001). We used a Satterthwaite approximation to calculate denominator degrees of freedom (*df*) for an unbalanced design and autoregressive covariance structure [AR(1)] for the repeated measure in recognition of a potential residual effect of the grass clearing on soil processes. Soil-nutrient data were log-transformed prior to analysis to correct heteroscedacity. The quantity 1 was added to all values prior to transformation to eliminate negative logs. The SLICE option on the SAS LSMEANS statement was used to perform tests of differences on subsets of data and to explore causes of significant interactions among main effects. Specifically, we tested the effects of canopy composition (ohia vs. koa) in unthinned high-elevation stands, the effects of canopy openness in high-elevation koa stands, the effects of elevation in unthinned ohia stands at high and low elevations, and the effects of grass removal under each canopy type. Differences in percentage light transmittance and in grass and litter dry mass at the plot level were tested using a one-way analysis of variance in SAS PROC GLM (SAS Institute 1999–2001).

Differences in numbers of seedlings establishing under different canopy types and treatments were tested using a Type-3 analysis with a Poisson distribution and a log link function in SAS PROC GENMOD (SAS Institute 1999–2001). In addition to the full model, pairwise comparisons were used as above to perform tests of differences on subsets of data and to examine sources of significant interactions among main effects. A Bonferroni correction was applied to adjust the α value for multiple comparisons.

Results

Vegetation

At the upper-elevation sites dominated by *A. koa*, few other species were encountered in the canopy or understory. Open-canopy plots contained occasional shrubs or saplings of *Myrsine*, *Metrosideros*, or *Coprosma*, but no trees, although high densities of koa trees surrounded these plots. Average total basal area of stems >2.5 cm dbh was 0.2 m^2 ha^{-1} in the open-canopy koa plots. Total basal area of koa trees on closed-canopy plots was estimated at 33.6 m^2 ha^{-1}, and stem densities averaged 4400 trees ha^{-1}. Similarly, high-elevation *Metrosideros* plots contained little more than ohia with occasional stems of *Myrsine* and *Coprosma*. Mean total stand basal area was 21.7 m^2 ha^{-1}, and stem densities were 4720 trees ha^{-1}. Low-elevation ohia plots were more heterogeneous and species-rich. Mean stand basal area was 33.9 m^2 ha^{-1} distributed among fewer, larger trees (stem density = 1200 trees ha^{-1}). In addition to ohia, common lower-elevation species included the tree fern, *Cibotium glaucum*, as well as *Ilex anomala*, *Myrsine lesertiana*, and *Clermontia clermontioides* (Gaud.) A. Heller (Campanulaceae). Ferns, similarly, were more abundant on the low-elevation plots.

Grass dry mass was higher on the high-elevation than on the low-elevation plots (Fig. 1a; $F = 6.40$; $p < 0.01$; $df = 3,36$), but not different among high-elevation stand types. Total above-ground, forest floor mass was highest on the koa plots (open and closed canopy) and lowest on the low-elevation ohia plots ($F = 15.86$; $p < 0.0001$; $df = 3,36$). Eighteen months after establishment of the experiment and creation of the openings in the koa canopy, grass dry mass under the open-canopy koa was significantly greater than under the closed-canopy koa (344 vs. 173 g m^{-2}, respectively; $F = 15.12$; $df = 1,8$; $p < 0.005$). However, total litter mass (grass dry mass + other litter mass) was similar (1,069 vs. 1196 g m^{-2}, respectively).

Light

Percentage light transmittance through the open-canopy koa was about threefold that through the other canopy types (Fig. 1b; $F = 54.54$; $p < 0.0001$, $df = 3,75$). The lowest light levels were under closed-canopy koa and under low-elevation ohia canopies.

Soils

Both soil moisture and soil nutrient levels varied as a function of canopy structure and composition (Table 1). Soil moisture levels were higher under open than closed koa canopy ($F = 28.5$; $p < 0.001$, $df = 1,60$) and higher in low elevation than in high elevation ohia stands ($F = 53.83$; $p < 0.001$; $df = 1,60$). Soil moisture levels did not differ between closed ohia and closed koa forests. Total resin-captured N (NO_3 -N + NH_4-N), an index of N availability in surface soils, was higher in high-elevation koa stands than in high-elevation ohia stands ($F = 15.31$; $p < 0.001$; $df = 1,45.8$), but resin-captured PO_4-P levels did not differ. (Note that the Satterthwaite approximation may yield fractional denominator degrees of freedom.) Canopy openness in the high-elevation koa stands did not affect N or P availability. Low-elevation ohia stands had significantly lower levels of both N and P than high-elevation ohia stands (Total N: $F = 41.73$, $p < 0.001$, $df = 1,45.8$; PO_4-P: $F = 5.63$; $p < 0.05$; $df = 1,33.4$). While month-to-month variation in both soil moisture and in nutrient availability were high, there was no consistent trend in resin-captured N or P with time of measurement (data not shown). Six months after treatment application, we were unable to detect a pulse in nutrient availability following removal of above-ground grass biomass.

Reduction in grass cover only weakly affected nutrient supply and did not affect moisture availability (Table 1). Experiment-wise, grass removal produced a significant increase in both resin-captured N ($F = 4.21$; $P < 0.05$; $df = 1,45.8$) and P ($F = 4.40$; $p < 0.05$, $df = 1,33.4$). However, grass removal effects on N and P availability were not strong and no within-canopy-type effects of grass removal were significant.

Seedling recruitment

In the high-elevation sites, *Acacia* germinated prolifically (673 seedlings in year 1 and 474 present after year 2). In the first year, only 13 other non-koa seedlings of at least six woody species established in plots. This increased to 86 seedlings of eight species in the second year, including 77 seedlings of *Metrosideros* in the low-elevation plot. Of the study species, only two *Sophora* seedlings and no *Dodonea* or *Pipturus* seedlings were found on non-seed-augmented plots in the first year, and none of these were found in the second year.

Among the three species for which we augmented seed input, we counted 441 seedlings of *Sophora*, 135 seedlings of *Dodonea*, and no seedlings of *Pipturus* after 1 year. Two years after setup, we counted 568 seedlings of *Sophora* (28% increase), 154 seedlings of *Dodonea* (14% increase), and one seedling of *Pipterus*. We report analyses for *Acacia*, *Sophora*, and *Dodonea* seedlings only from the seed augmentation plots. Because adult *Acacia* trees are naturally scarce at low elevations, we report analyses only from high-elevation sites for this species. Canopy cover had significant effects on the establishment of *Acacia* and *Sophora* but not of *Dodonea* seedlings (Table 2, Figs. 2, 3). Effects were similar 1 and 2 years after establishing the experiment. Significantly more koa seedlings established under open-canopy than under closed-canopy koa stands (Plot means: year 1: 16.5 vs. 2.8 seedlings; year 2: 12.5 vs. 2.2 seedlings), and

Table 1 Effects of grass and canopy conditions on soil moisture, total resin-extractable N (NH_4-N + NO_3-N), and resin-extractable phosphorus (PO_4-P)

	Soil moisture (g g^{-1} dry mass soil)	Nitrogen (μg g $resin^{-1}$ day^{-1})	Phosphorus (μg g $resin^{-1}$ day^{-1})
High elevation stands			
Koa (open canopy)	0.866 (0.798/0.935)[a]	28.98 (21.52/38.92)	0.167 (0.074/0.268)
+Grass	0.842 (0.746/0.940)	24.64 (16.12/37.42)	0.050 (−0.067/0.180)
−Grass	0.870 (0.793/0.987)	34.04 (22.39/51.50)	0.298 (0.154/0.459)
Koa (closed canopy)	0.608 (0.510/0.677)	30.80 (22.88/41.34)	0.176 (0.082/0.277)
+Grass	0.620 (0.523/0.717)	32.17 (21.14/48.72)	0.142 (0.016/0.284)
−Grass	0.597 (0.500/0.694)	29.47 (19.34/44.66)	0.210 (0.076/0.361)
Ohia (closed canopy)	0.660 (0.592/0.729)	13.47 (9.87/18.27)	0.306 (0.202/0.420)
+Grass	0.647 (0.550/0.744)	10.87 (6.93/16.79)	0.185 (0.054/0.333)
−Grass	0.674 (0.577/0.771)	16.64 (10.77/25.43)	0.440 (0.281/0.620)
Low elevation stands			
Ohia (closed canopy)	1.016 (0.948/1.085)	2.95 (1.96/4.26)	0.139 (0.048/0.238)
+Grass	1.006 (0.909/1.103)	2.01 (1.01/3.51)	0.212 (0.077/0.362)
−Grass	1.027 (0.930/1.124)	4.18 (2.46/6.76)	0.071 (−0.047/0.205)

[a]Values are back-transformed least-squares means; lower/upper 95% confidence intervals are given in parerenthesis

Table 2 Likelihood ratio test statistics for the effects of canopy characteristics and grass removal on seedling establishment 1 and 2 years after seed augmentation

Effect	*Acacia*		*Sophora*		*Dodonea*	
	2003	2004	2003	2004	2003	2004
Canopy	**38.8**[a]	**30.7**	**164.2**	**77.2**	4.0	1.5
Grass	**241.1**	**169.1**	**92.1**	**220.6**	**89.7**	**120.8**
Canopy × grass	**18.2**	4.7	**20.5**	**15.4**	5.1	3.1
Koa high open vs. Koa high closed	**15.8**	**965.6**	0.8	0.4	0.3	0.2
Koa high closed vs. ohia high closed	**2161.1**	**2,570.1**	**9.0**	1.9	0.0	0.0
Ohia high closed vs. ohia low closed			**35.0**	**49.2**	2.3	1.3
Koa high open, ±grass	**72.1**	**54.6**	1.2	**10.2**	**7.7**	**21.2**
Koa high closed, ±grass	**10.5**	**1,705.0**	**25.2**	**53.0**	**13.2**	**16.0**
Ohia high closed, ±grass	**666.1**	**37.1**	**9.1**	**29.8**	**12.6**	**11.1**
Ohia low closed, ±grass			**130.7**	**129.8**	**35.5**	**31.7**

The likelihood ratio is distributed as a Chi-square
[a]Values in bold are significant at $p < 0.01$ or less

more koa seedlings established under closed-canopy ohia (year 1: 18.1 seedlings; year 2: 10.9 seedlings) than closed-canopy koa stands (Table 2, Fig. 3). Canopy openness did not affect *Sophora* or *Dodonea* seedling establishment in high-elevation koa stands. However, after 1 year there were significantly more *Sophora* seedlings in closed-canopy koa than in closed-canopy ohia stands (Plot means: 4.1 vs. 1.3 seedlings); this difference had disappeared by the end of the second year. Within ohia-dominated stands, the establishment of *Sophora*, but not *Dodonea*, was significantly influenced by elevation (Table 2, Fig. 3), with more *Sophora* seedlings establishing by the end of year 1 in low-elevation forests by a factor of 13. *M. polymorpha* seedlings showed a similar response to elevation. In year 2, 77 ohia seedlings established in the low-elevation plot and no ohia seedlings established in the high-elevation plots.

Seedling establishment was reduced significantly by the presence of grass in all three species, at all sites and, in most cases, for both years (Table 2, Fig. 3). Koa seedling establishment was significantly higher following grass removal in high-elevation open-canopy koa (Plot means: 20.0 vs. 0.8 seedlings) and closed-canopy ohia stands (11.2 vs. 0.2 seedlings), but only marginally in closed-canopy koa stands (3.3 vs. 0.01 seedlings). Grass removal increased seedling establishment under almost all circumstances in *Sophora* and *Dodonea* (overall plot means: 18.8 vs. 3.2 seedlings for *Sophora* and 6.8 vs. 0 seedlings for *Dodonea* in year 1; Table 2, Fig. 3). Only in high-elevation open-canopy koa stands did grass removal not affect *Sophora* seedling establishment significantly in year 1, although it did by the end of year 2.

Discussion

Studies of forest ecosystems, including those from tropical forests, suggest that the distributions and abundances of many species are limited by their failure to recruit seedlings to sites otherwise suitable to their establishment and growth (Clark et al. 1998, 1999a; Turnbull et al. 2000; Beckage and Clark 2003; Makana and Thomas 2004; Svenning and Wright 2005; except see Webb and Peart 2001). A number of factors influence the probability of recruitment, including those affecting the size of the seed crop (fecundity and the density and

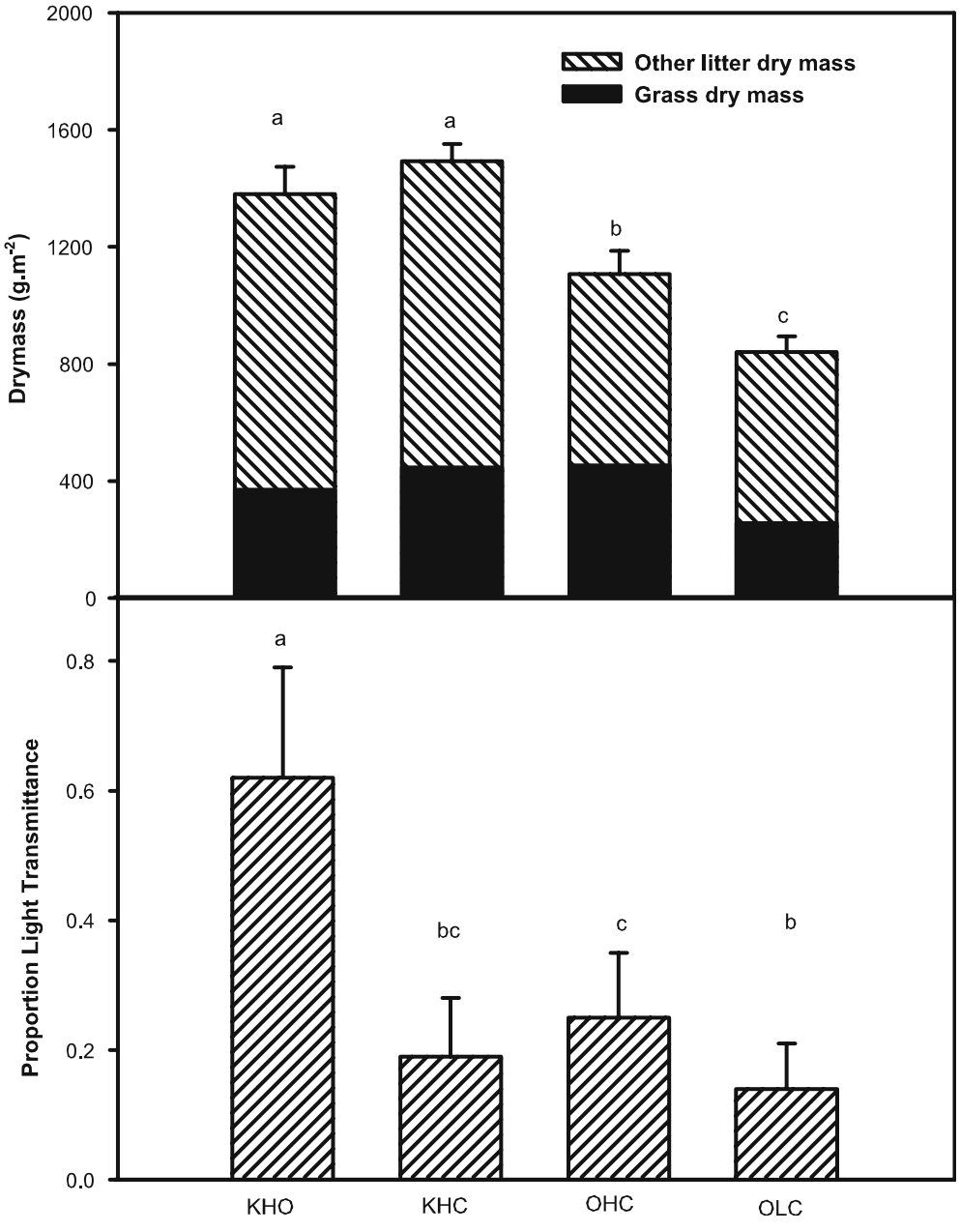

Fig. 2 Grass and litter dry mass (**a**) and percentage light transmittance (**b**) in four stand types (means + SE). *Bars with the same letters* indicate that differences between canopy types were not significant at $\alpha = 0.05$. Stand designations: *KHO* koa, high-elevation open-canopy, *KHC* koa, high-elevation closed-canopy, *OHC* ohia, high-elevation closed-canopy, *OLC* ohia, low-elevation closed-canopy

distribution of adult trees), close and distant dispersal (Clark et al. 1999b), and post-dispersal factors such as pests and pathogens which affect germination and seedling establishment (Clark et al. 1998; Turnbull et al. 2000; Nathan and Muller-Landau 2000; Zimmerman et al. 2000). Where previous models have assumed that competitive interactions determined dominance and distribution patterns in many plant communities, the important impacts of recruitment limitation on composition, relative abundances of species, and species diversity are now widely appreciated (Harms et al. 2000; Nathan and Muller-Landau 2000; Hubbell 2001; Clark et al. 1999b). Dispersal limitation is less often demonstrated in mesic grasslands (Turnbull et al. 2000), where competition strongly affects plant growth, seed production, and seedling establishment (for example, MacDougall and Turkington 2005). Nevertheless, recent long-term, comprehensive studies emphasize that in both forest and grassland ecosystems, some species are able to saturate the available space with seeds whereas others are strongly dispersal limited (Clark et al. 1998; Beckage and Clark 2003; MacDougall and Turkington 2005; Svenning and Wright 2005).

Where woody plants and grasses interact in successions on abandoned tropical pastureland, both dispersal limitation (Guevara et al 1986; Posada et al. 2000; Slocum and Horvitz 2000) and competition (Aide et al. 2000) can be important constraints on the establishment of trees and shrubs. The presence of grasses may deter (Holl 1998; Holl et al. 2000) or facilitate (Aide and Cavelier 1994; Chapman and Chapman 1999) the establishment of trees in abandoned pastures. As in

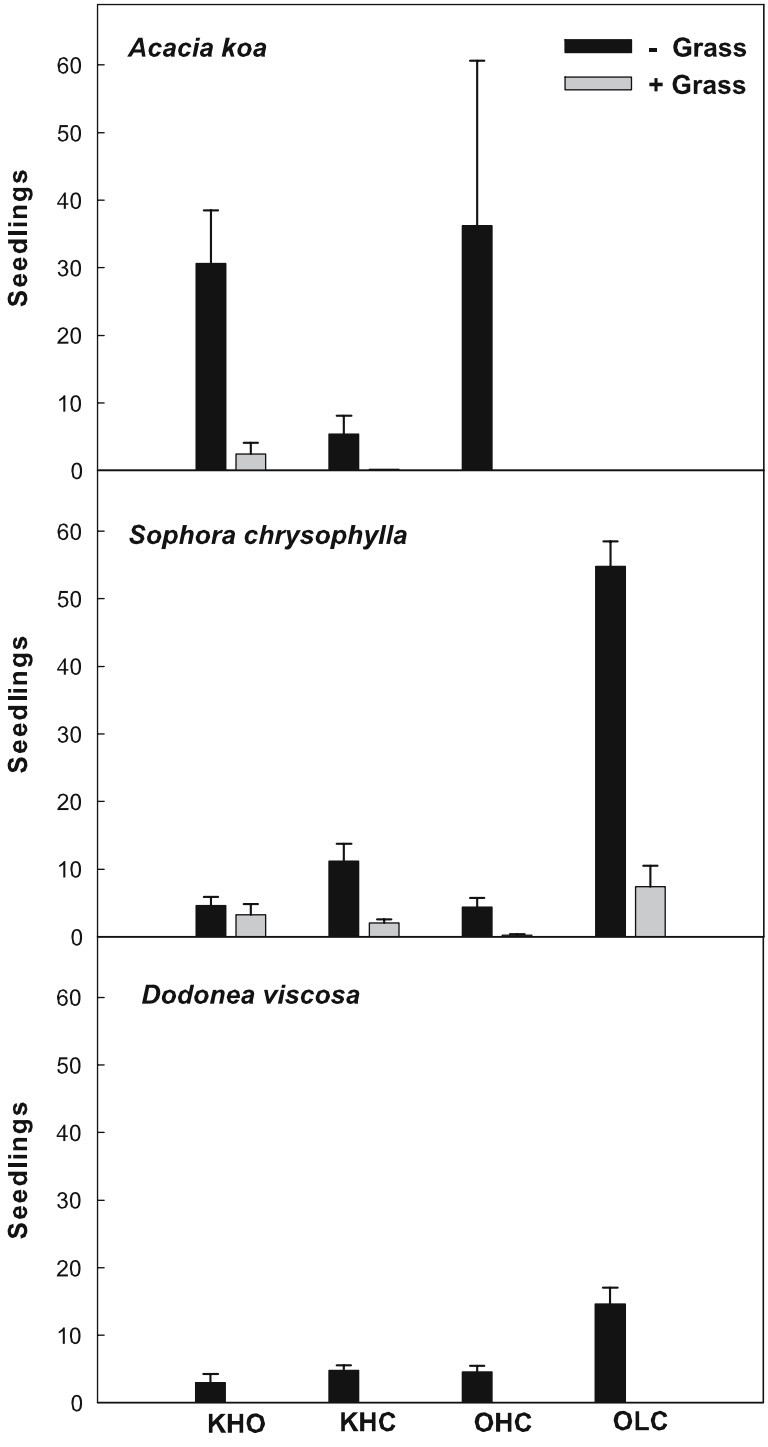

Fig. 3 Year 1 seedling establishment (mean ± SE) in four different stand types and two levels of grass clearing. Stand designations as in Fig. 2

temperate grassland ecosystems, woody plant encroachment on grassland is also influenced by the environmental context of the interaction, including factors such as disturbance regime (grazing pressure, habitat fragmentation, and fire frequencies), rainfall abundance and seasonality, and moisture and nutrient conditions (Kellman 1979; Corbin and D'Antonio 2004; House et al. 2003; MacDougall and Turkington 2005). In addition, the species dominating successions in abandoned pastures differ from those following other disturbances to tropical forests, such as swidden agriculture, logging, or hurricanes, suggesting that grassland environments provide a strong filter on seedling establishment as well (Aide et al. 1995, 1996, 2000; Chazdon 2003).

Our data from the Honomalino tract provide a further example of the complexity of woody plant-grass interactions and sources of variation in those interactions among species and across landscapes. Recruitment limitation was clearly present in two of the focal species

(*Sophora*, *Dodonea*). The lack of other native woody species in the seedling pools after 2 years suggests that dispersal limitation is a major constraint on community development in these forest. For many of these species, low densities of adult plants undoubtedly contributed to low seed abundances. In very common species, such as *Metrosideros*, factors contributing to the low seedling densities are less apparent. Interestingly, our data suggest that recruitment limitation was strongest (i.e., more seedling established from sown seed) at low elevations where the forest had been least heavily affected by prior disturbances. Loss of the seed bank due to years of ungulate browsing (Scowcroft and Giffin 1983), missing pollinators and dispersal agents (Loope and Mueller-Dombois 1989), low fecundity (Goergen and Daehler 2001), and seed loss to rodents, insects, and pathogens (Cabin et al. 2000) all may contribute to low recruitment rates in these forests. Low or episodic rainfall likely contributes to variation in seedling establishment that is characteristic of many seasonally dry tropical forests (e.g., Cabin et al. 2002; Goergen and Daehler 2002) and, in our study, may account for the higher recruitment in some species in 2004 than in 2003, which was a drought year. Hughes et al. (1991) and Cabin et al. (2002) also observed low-recruitment rates of many native species in other Hawaiian woodlands, and other authors have documented low recruitment rates in temperate forests (Harcombe and Marks 1978; Clark et al. 1998; Beckage and Clark 2003).

Not all species were dispersal-limited. We found only one seedling of *Pipterus alba* in either year despite almost 60% germination rates in the laboratory. Recruitment limitation in this species may be affected by other, unmeasured post-dispersal establishment conditions. Where *A. koa* is a canopy dominant or co-dominant plant species, it is able to saturate available space with seeds and seedlings. While we did not conduct seed augmentation experiments for koa, seedling densities in the second year (50,420 seedlings/ha) were substantially lower than in the first year (80,200 seedlings/ha), and stem densities of adult trees even in relatively young secondary forests (4,400 trees/ha) were much lower than first-year seedling establishment. These factors suggest that substantial post-recruitment thinning occurs in koa and that seed dispersal is not the principle limitation to adult density in these forests.

Grass cover clearly limits woody seedling establishment at Honomalino. Grass removal produced strong effects on seedling establishment for the three species examined under almost all canopy conditions. Koa regeneration was strongly suppressed by grass; where grass cover remained intact, 2900 seedlings ha^{-1} recruited in the first year versus 80,200 seedlings ha^{-1} in the grass removal plots. Although the suppressive effect is strong, koa recruitment through grass may nevertheless be substantial. Grass effects were strongest for *Sophora* and *Dodonea* at the low-elevation sites where total recruitment was also highest and grass and litter biomass the least. Both *Sophora* and *Dodonea* have relatively large seeds (4–8 mm and 3 mm, respectively; Wagner et al. 1999). We expect the impact of grasses on smaller-seeded species to be at least as strong.

The mechanisms behind these patterns of seedling establishment are not clear. While grasses may compete with trees and shrubs for soil resources (D'Antonio et al. 1998; Ehrenfeld 2003), our data provide no evidence that seedlings were N or P limited at Honomalino. Grass removal effects on soil N, P and moisture were not strong. MacDougall and Turkington (2005) reached a similar conclusion in a grass removal experiment in British Columbia. Soil N and P availability was higher in the high-elevation plots than in the low-elevation plots and, not surprisingly, N was higher under a canopy of *A. koa*, an N-fixing legume (Scowcroft and Jeffrey 1999), than under a *Metrosideros* canopy. Austin and Vitousek (1998) also observed decreasing N and P levels with increasing rainfall in a gradient of ohia forests near the 700 m elevation contour on Hawaii Island forests. Nevertheless, seedling establishment rates did not reflect the higher nutrient supply rates at the high-elevation sites nor, with one exception, the high N levels under koa canopies. Light availability increased seedling establishment in *Acacia* but not in *Sophora* or *Dodonea*, a reflection in part of the relatively high light levels under ohia and koa canopies. Other studies have attributed the suppressive effect of grasses on woody seedlings to a reduction in light availability due to both the grass canopy and the thatch accumulation (Scowcroft 1981; Hughes and Vitousek 1993; Hess et al. 1999; Mazia et al. 2001; MacDougall and Turkington 2005). Seedling establishment in montane Hawaiian rainforests is greatest on nurse logs and tree fern trunks in part because of strong grass thatch accumulation on soil surfaces (Santiago 2000).

Conclusion

A prerequisite of effective restoration and management of degraded plant communities is accurate assessment of the limitations to the establishment and growth of native species. While high densities of exotic species often are thought to be the cause of the low diversity or poor reproduction of native species, several recent studies emphasize that relative abundances of exotic and native species may also reflect other factors, including reduced seed supply, habitat fragmentation, and altered disturbance regimes and climate patterns (Seabloom et al. 2003; Gurevitch and Padilla 2004; MacDougall and Turkington 2005). In some cases, the supposed competitive advantage of exotic species could not be confirmed (Seabloom et al. 2003; Corbin and D'Antonio 2004; MacDougall and Turkington 2005). Moreover, the causes of rarity and abundance in intact native ecosystems are poorly understood, but likely to reflect variation in dispersal limitation and seedling establishment at small and large scales (Clark et al. 1998). Honomalino exemplifies landscapes subject to a variety of factors

contributing to ecosystem degradation and species loss. The natural openness and the disturbance history of the koa-ohia forest have facilitated the spread of pasture grasses. Competition from grasses contributes to the slow establishment rates of woody species, impeding the development of a native understory that might reduce the impact of grasses. Lack of seed availability, perhaps in part due to competitive effects of grasses, is implicated in low-establishment rates in some species although the degree of dispersal limitation within species varies among different stand types. While the removal of ungulates has undoubtedly increased the survival of palatable seedlings and saplings, it is clear that understory development will depend on the active intervention of managers through seeding and planting. Our study suggests that, for some species, improvement in the seedbed will be necessary, through grass cover reduction or the addition of nurse logs. However, some species may be able to establish through the grass thatch, and their abundance may be improved through increased seed availability.

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