

Understory structure in a 23-year-old *Acacia koa* forest and 2-year growth responses to silvicultural treatments

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Received 19 July 2007; received in revised form 17 November 2007; accepted 21 November 2007

Abstract

Restoration of degraded *Acacia koa* forests in Hawaii often involves mechanical scarification to stimulate germination of seed buried in the soil and to suppress vegetation that competes with shade intolerant *A. koa*. Resulting even-age stands are gradually colonized by other plant species, but understory structure is poorly quantified, and the effects of management on understory vegetation are unknown. We examined the structure of the dominant understory species 23 years after stand initiation and determined their subsequent 2-year growth responses to silvicultural treatments prescribed to improve growth of koa. Release thinning, chemical control of introduced grasses, and phosphorus fertilization were applied in a split-plot experimental design. Results for DBH and height class distributions indicated that recruitment for most tree species began within a few years of stand initiation. By 23 years understory trees made up only 14% of total stand basal area, but they added greatly to native plant biodiversity. Alien grasses covered 92% of the forest floor and averaged 1.35 Mg ha⁻¹. Of the four most abundant native understory tree species, only shade intolerant *Myoporum sandwicense* grew faster in response to the treatments. P-fertilizer combined with grass control significantly increased production of the native shrub, *Rubus hawaiiensis*. Notably, alien grass biomass did not increase in response to thinning, and actually declined in P-fertilized plots. Only, where P-fertilizer was applied were P concentrations of understory leaves elevated. Foliar concentrations of other nutrients were generally unaffected by treatments. Our findings suggest that the conservative silvicultural treatments we used can be applied without adversely impacting the capacity of aggrading *A. koa* forests to support a diversity of native understory plants. Lack of an increase in alien grass biomass, and in the case of P fertilization, a reduction in grass biomass, indicates that treatments should not increase competition with native species.

Published by Elsevier B.V.

Keywords: Subtropical lower montane wet forest; Introduced-grass control; Release thinning; P fertilization; Leaf nutrient concentrations; Hawaii

1. Introduction

Hawaii is a microcosm of global deforestation and forest degradation. Conversion of forests to non-forest use began about 500 A.D. when the islands were first colonized by Polynesians, and accelerated greatly after 1798 with the arrival of Europeans (Cuddihy and Stone, 1990). Lowland forests were cleared for agriculture while the cooler drier uplands were converted to pastures (Tummons, 2002). Today most native forests occur in precipitation belts too wet or cool for agriculture or pasture. Little remains of native low or high elevation forests, and the loss of biodiversity has been significant, especially understory species that are of great ecological importance for native forest birds (Scott et al., 1986).

Acacia koa A. Gray, a high-value endemic timber species, dominated upland forests but was extensively logged to defray cost of conversion to pasture. The species is a fast growing, nitrogen-fixing tree, and one of two native canopy emergent tree species in mesic to wet Hawaiian forests. *A. koa* forest ecosystems harbor 30 of Hawaii's remaining 35 endemic bird species, 17 of which are endangered (U.S. Fish and Wildlife Service, 1984, 2003, 2006). Furthermore, approximately 20% of endangered plants in Hawaii are understory species that occur in forests containing *A. koa*.

The decline of ranching since 1980 has prompted land-owners to seek alternative land uses for Hawaii's uplands. Reforestation with *A. koa* is one such alternative, especially between 1200 and 1800 m elevation—the heart of the historical distribution of mesic *A. koa* forests (Mueller-Dombois and Krajina, 1968; Gagné and Cuddihy, 1990). Two recent studies suggest that growing *A. koa* commercially may be compatible with re-establishment of other forest ecosystem services

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including biodiversity, carbon sequestration, watershed protection, scenic beauty and recreational opportunities (Goldstein et al., 2006; Pejchar and Press, 2006). Both studies identified financial and silvicultural uncertainties as the major obstacles to private landowners embarking on commercial forestry with *A. koa*.

Lack of silvicultural knowledge for *A. koa* was explicitly identified as hampering private investment in commercial forestry (Pejchar and Press, 2006). To address this knowledge gap, we initiated an experiment in 2002 to determine the growth response of potential *A. koa* crop trees to pre-commercial thinning of competing non-crop *A. koa* trees, chemical control of exotic grasses and P fertilization (Scowcroft et al., 2007). We found that thinning combined with grass control plus P fertilization increased annual stem diameter increment at breast height by nearly 120%. But did the silvicultural treatments have any undesirable effects on understory vegetation and the services it provides?

A forest understory provides several ecosystem services. Whole ecosystem biodiversity is strongly influenced by understory vegetation (Croat, 1978; Gentry and Dodson, 1987; Halpern and Spies, 1995). The future forest community is formed in the understory. Intact, healthy understory vegetation provides wildlife habitat (e.g., Pearlman, 2002) and offers a degree of protection against invasion by alien plant species (Martin et al., 2004; Von Holle et al., 2003). The understory also helps regulate nutrient and water cycling, and supports activities such as harvesting of floral greens (Ballard et al., 2002) and other minor forest products. Thus, it is important to know how the understory responds to silvicultural practices.

The changes in light, water, nutrient and CO₂ regimes that result from thinning and fertilization extend throughout the forest profile and are known to affect non-target understory vegetation in temperate ecosystems. Thinning can accelerate growth and density of tree regeneration, especially shade intolerant species (Ward, 1992; Yanai et al., 1998), increase density and cover of herbaceous and shrub species (Harrington and Edwards, 1999), and enhance habitat conditions for some bird species (Artman, 2003). Fertilization alone or in combination with thinning can change understory species composition, diversity and cover (Thomas et al., 1999) and improve quality of wildlife habitat (VanderSchaaf et al., 2004).

Here, we examine the effects that conservative silvicultural treatments had on understory plant species in a secondary *A. koa* forest. Most of these species are endemic to Hawaii, most produce fruit or serve as habitat for arthropod prey taken by forest birds, and all are common to *A. koa* forests elsewhere in Hawaii. Our objectives were to (1) characterize the structure of key understory trees, tree fern and shrubs of a naturally regenerated, unmanaged 23-year-old *A. koa* forest; (2) determine if the structurally dominant native plant species responded to silvicultural treatments; and (3) determine if alien grasses that dominated the forest floor increased in biomass following treatments.

2. Methods

2.1. Study area

The study area was located between 1650 and 1740 m elevation on the eastern (windward) slope of Mauna Loa, one of five volcanic mountains that make up the island of Hawaii (19° 31' 12"N, 155° 19' 14"W). The climate is wet and cool. Rainfall averages about 2800 mm y⁻¹ with winter and spring months being the wettest seasons (Giambelluca et al., 1986). Average annual maximum and minimum air temperatures are about 18 °C and 8 °C, respectively. Temperatures near or below freezing occur occasionally in the open during clear winter nights, especially during El Niño events. Incident solar energy is mainly a function of cloud cover and can range from as little as 1 MJ m⁻² day⁻¹ during winter storm events to as much as 30 MJ m⁻² day⁻¹ during clear summer days.

The study area consists of a matrix of relatively young lava flows of Kau basalt (Pearson and Vitousek, 2001). Our study was confined to a single flow 1500–3000-year-old (Wolfe and Morris, 1996). The soil is a deep, well-drained medial silt loam that formed in basic volcanic ash, possibly Pahala ash (Stearns and Macdonald, 1946), deposited over basic aa lava (rough scoriaceous). The soil taxonomy is medial-skeletal, amorphic, isomesic Typic Hapludands (<http://www2.ftw.nrcs.usda.gov/osd/dat/K/KE@AMOKU.html>). Although relatively young soils in Hawaii have been characterized as nitrogen (N) not phosphorus (P) limited for plant growth (Vitousek et al., 1993; Crews et al., 1995), the reverse appears to be true for our study site (Pearson and Vitousek, 2001; Scowcroft et al., 2007).

The life zone (sensu Holdridge, 1967) is subtropical lower montane wet forest. The original vegetation likely resembled the native, relatively pristine forest in the adjacent Kilauea Forest Reserve. Cooray (1974) recognized four structural vegetation types: (1) closed *Cibotium glaucum* (Sm.) Hook. and Arnott with scattered low-stature trees punctuated with occasional gaps; (2) closed, low-stature tree group with emergent *A. koa* and a closed *C. glaucum* understory; (3) open forest with intermediate- and low-stature trees and tree groups and a closed-canopy *C. glaucum* understory; and (4) emergent tree groups with scattered low-stature trees and a closed-canopy *C. glaucum* understory. *A. koa* and *Metrosideros polymorpha* Gaud. were the only emergent tree species (15–25 m). At our site, the low-stature understory tree species (5–10 m) included *M. polymorpha*, *Coprosma rhynchocarpa* A. Gray, *Cheirodendron trigynum* (Gaud.) A. Heller, *Ilex anomala* Hook. and Arnott, *Myoporum sandwicense* A. Gray, and *Myrsine lessertiana* A. DC. The shrub-fern vegetation was predominantly native and included *Carex alligata* Boott, *Athyrium microphyllum* (Sm.) Alston, *Broussaisia arguta* Gaud., *Rubus hawaiiensis* A. Gray, and *Vaccinium calycinum* Sm.

2.2. Stand history

Heavy logging of koa in the 1960s and subsequent cattle grazing removed most emergent koa, greatly reduced native plant cover, and fostered proliferation of non-indigenous forage species, including *Pennisetum clandestinum* Chiov., *Ehrharta*

stipoides Labill. and *Anthozanthum odoratum* L. (Jacobi, 1989). The degraded forest typifies landscapes across wide belts on Hawaii and Maui where forest bird populations are high (Scott et al., 1986; Ralph and Fancy, 1996).

In an attempt to restore koa to the site, a bulldozer was driven across the site in 1978 to mechanically scarify the soil. Except for small patches of intact vegetation that were left around individuals of the endangered *Vicia menziesii* Spreng. (Warshauer and Jacobi, 1982), all vegetation was knocked down and debris was bulldozed into piles and left to decay. No additional management intervention occurred for 24 years.

A. koa regenerated from buried seed (Skolmen and Fujii, 1981) and 1 year after treatment, stand densities averaged 20,000 seedlings ha⁻¹. As a result of self-thinning density steadily declined during the next 23 years to approximately 1000 trees ha⁻¹ (Scowcroft et al., 2007). Average height, DBH and stand basal area of *A. koa* at 24 years of age were 11.9 m, 18.0 cm and 25.7 m² ha⁻¹, respectively. Leaf area index was 2.6 m² foliage m⁻² ground. Native tree species began colonizing the secondary *A. koa* stand within a few years of establishment, while *E. stipoides* became the dominant ground cover, except in small scattered openings where higher light levels allowed *P. clandestinum* to dominate the herbaceous layer (Grace, 1995).

2.3. Experimental design

A split-plot design was used in this study. It consisted of eight 60 m × 60 m main plots and four 25 m × 25 m subplots nested within each main plot. Only three of each set of four subplots were actually used. Each main plot received one of two canopy treatments—“thinned” as described below or “unthinned.” There were four thinned and four unthinned main plots. Each of the three subplots nested within a main plot received one of the following forest floor treatments: (1) “herbicided” with a grass-specific herbicide, (2) “herbicided (H) + P-fertilized,” or (3) “untreated” with neither herbicide nor fertilizer being applied. Fertilization by itself was not used as a forest floor treatment. Each of the three forest floor treatment was applied to a total of eight subplots. All treatments were randomly assigned. Additional details about plot and subplot selection are described in Scowcroft et al. (2007).

The thinned treatment consisted of girdling neighboring *A. koa* that were in direct crown competition with identified *A. koa* crop trees, i.e. crown or high thinning (e.g., Cole and Lorimer, 1994). In practice this meant the removal of any dominant or co-dominant neighbor whose crown was within 1 m of the crown edge of a crop tree. For reasons detailed in Scowcroft et al. (2007), double-ring chainsaw girdling without poison or removal was used to kill neighboring competitors. Girdling was done during 4 days in December 2001.

Herbicide and fertilizer treatments were first imposed 5 and 11 months, respectively, after the girdling treatment was imposed. Grasses were controlled using the grass-specific herbicide Fusilade DX (Syngenta Professional Products, Greensboro, NC) applied at the rate of 0.42 kg active ingredient (Fluazifop-P-butyl) ha⁻¹. The first application was made in

May 2002; a second one was made in June 2004 to control regrowth. The herbicide was confined to ground areas defined by the drip line of target crop trees to minimize expense and application time. Phosphorus was applied to subplots as triple super phosphate at 6-month intervals beginning November 2002 and ending November 2004. The first application of P was 300 kg ha⁻¹, and the three subsequent applications were 150 kg ha⁻¹ each for a total of 750 kg ha⁻¹. In contrast to the herbicide, fertilizer was broadcast by hand over entire subplots due to the anticipated imprecision of hand application at the individual tree level.

The initial measurement of understory trees was done in May–June 2001 when the stand was 23 years old. Stem diameter at breast height (1.4 m) was determined for all individuals with DBH ≥ 1 cm. All species other than *A. koa* were in the understory. Only suppressed and intermediate crown class *A. koa* were in the understory, but no such classification was done in 2001, so we were unable to determine mean DBH, density, or basal area for understory *A. koa*.

Evaluations of treatment effects on woody understory vegetation were done using only individuals that were located under *A. koa* crop trees. In the fall of 2002 and again in the fall of 2004, we measured the DBH, basal stem diameter (BD) at 0.3 m above ground and height of all understory trees rooted within the projected crown areas of crop trees. Aboveground tree biomass was estimated using allometric equations from Aplet and Vitousek (1994). We recorded the height to the top of tree fern fronds and tallied the number live fronds for each individual, including those that were only partially uncurled. Stem counts were made for the two most common shrubs, *R. hawaiiensis* and *V. calycinum*.

Total aboveground grass biomass was determined in August–October 2002 and April–May 2005 by harvesting grass from 0.5 m × 0.5 m square quadrats randomly located beneath the crowns of trees that had been marked for girdling in both thinned and unthinned plots. Overhanging grass was included in each harvest. Grass was cut at ground level and put into a labeled paper bag. Samples were oven dried at 70 °C for at least 48 h, weighed, and weights recorded. Although we occasionally found *P. clandestinum* and *Anthoxanthum odoratum* in the samples, their contributions were negligible. So for practical purposes, grass biomass hereafter refers of *E. stipoides* biomass.

In October 2002, the fraction of light transmitted to the forest floor was determined for 25 grass sample quadrats that represented a range of total grass biomass. A line quantum sensor was positioned at 30 cm above a quadrat and synchronized with a second sensor located in the center of a nearby large opening. Data were logged for one full daylight cycle and corrected to account for slight differences in sensor output. The fraction of light transmittance (T) to the forest floor was calculated as total incident radiation in the forest divided by total incident radiation in the open. These data were changed to optical density, a measure of light absorbance as it passes through a medium, using the transformation, $\log_{10}(1/T)$.

2.4. Foliage sampling

Leaves of understory *M. polymorpha*, *M. sandwicense*, *C. rhynchocharpa* and *I. anomala* trees were randomly sampled February 2004. Only understory trees rooted within the projected crown area of *A. koa* crop trees were sampled. The second and third fully expanded leaves were taken from twigs clipped from the upper one half of the southern hemisphere of tree crowns. For each understory species, two composite samples representing at least two different trees were collected from two of the four replicate subplots (i.e. the subplot is the experimental unit, so $n = 2$). Too few *C. trigynum* and *M. lessertiana* trees occurred for them to be included in the statistical analyses.

Random composite grass samples were also collected. Because two of the forest floor treatments involved application of a grass-specific herbicide, grass samples were collected from areas immediately adjacent to herbicided areas. In practice, this meant that (1) samples from the herbicide treatment were equivalent to those from the control treatment and (2) samples from the herbicide plus P-fertilizer represent a P effect only. Grass samples included both live and dead material. All foliage samples were placed in a separate labeled bag and placed on ice for transport to the lab where number of leaves, total leaf area (except grass), and total oven-dry weight were determined. Approximately, 2 g (oven-dry weight) sub-samples were sent to the UH Agricultural Diagnostic Service Center for determination of P and cation concentrations (see Scowcroft et al., 2007). Approximately, 1 g (oven-dry weight) sub-samples were sent to the UH Isotope Biogeochemistry Laboratory for determination of total N and ^{13}C and ^{15}N isotope ratios.

2.5. Statistical analyses

The structure of key components of the understory was examined as follows. We used the 2001 DBH data to: (1) construct DBH class distributions for each of the six most abundant understory tree species; and (2) calculate their mean DBH, stand density, basal area and stocking level. The 2002 data on height of trees, including suppressed koa and tree fern located within the projected crown area of koa crop trees, allowed us to construct pre-treatment height class distributions. Using the curve fitting function of SigmaPlot 10 software (Systat Software, Inc., Point Richmond, CA), we fitted the

Chapman 4-parameter model to the DBH/height (H) data to estimate the average maximum height attainable by each tree species in the understory: $H = y_0 + a*(1 - e^{(-b*DBH)})^c$, where y_0 is the y-intercept and a , b , and c are parameters. The sum of $y_0 + a$ yields the maximum height. We constructed a frequency distribution histogram that used 50-g m^{-2} wide biomass classes to examine pre-treatment distribution of grass biomass within the study area. Linear regression was used to describe the relationship between grass biomass and optical density of the vegetation above herbaceous layer (>30 cm).

SAS Proc Mixed (SAS Institute, 1996) was used to examine the species-specific effects of thinning and forest floor treatments on understory tree (a) DBH, height and aboveground biomass increments and (b) specific leaf area and leaf chemistry. Because *C. rhynchocharpa*, *M. polymorpha* and *M. sandwicense* were the only tree species found in all 24 plots, only they were analyzed for treatment effects on DBH, height, and aboveground biomass increment. Pre-treatment (2002) values of DBH, height, and tree biomass were used as covariates in their respective analyses. Proc Mixed was also used to test treatment effects on total aboveground grass biomass and changes in shrub stem density. Comparisons of factor-level least squares means were performed using Tukey's HSD test with α set at 0.05. A log transformation was used to equalize variances, and reported means were back transformed and corrected for bias using $\exp(\text{MSE}/2)$, where MSE was the sum of the covariance parameter estimates (Sprugel, 1983). As no significant interactions among treatments were detected in any of the analyses, results deal with comparisons of main effects, i.e. (1) thinned vs. unthinned and (2) untreated vs. herbicided vs. H + P-fertilized.

3. Results

3.1. Understory structure

3.1.1. Endemic species

Six endemic understory tree species with DBH >1 cm were commonly found in sample plots 23 years after scarification (Table 1). The natives, *Melicope clusiifolia* A. Gray T. Hartley and B. Stone (33 each) and *Pipturis albidus* (Hook. and Arnott) A. Gray (5 each) occurred infrequently, while suppressed koa occurred throughout. *M. sandwicense* was the most abundant tree species and occurred on all sample units; *C. trigynum* was

Table 1

Mean (S.E.) stand density, arithmetic and quadratic mean DBH, basal area, and stocking for the six most abundant understory tree species in a 23-year-old stand of *Acacia koa* before imposition of silvicultural treatments

Species	Density ^a (# ha ⁻¹)	Mean DBH (cm)		Basal area ^a (m ² ha ⁻¹)	Stocking ^a (%)
		Arithmetic	Quadratic		
<i>Myoporum sandwicense</i>	1049 (78)	4.9 (0.1)	5.6	2.54 (0.16)	100
<i>Metrosideros polymorpha</i>	470 (52)	3.2 (0.1)	3.7	0.51 (0.08)	100
<i>Coprosma rhynchocharpa</i>	324 (49)	3.6 (0.1)	3.9	0.40 (0.07)	100
<i>Ilex anomala</i>	115 (22)	4.9 (0.2)	5.6	0.28 (0.06)	92
<i>Myrsine lessertiana</i>	106 (20)	3.2 (0.1)	3.6	0.11 (0.02)	92
<i>Cheirodendron trigynum</i>	63 (13)	5.1 (0.3)	6.1	0.18 (0.04)	83

^a Based on 24, 25-m × 25-m subplots.

the least abundant and occurred on fewest sample units. *M. polymorpha*, which ultimately becomes co-emergent with *A. koa*, occurred on all sample units, but its density was less than one-half that of *M. sandwicense*. The density of *R. hawaiiensis* averaged 4550 stems ha^{-1} (335 S.E.); *V. calycinum* averaged 795 stems ha^{-1} (105 S.E.); and *Cibotium glaucum* averaged 485 individuals ha^{-1} (60 S.E.).

Mean DBHs for the six tree species were between 3 and 6 cm (Table 1). The DBH class distributions indicated that *M. sandwicense* had significantly fewer trees in the smallest <3 cm class than in the next smallest class, ≥ 3 and <5 cm (Fig. 1). *M. polymorpha*, *C. rhynchocarpa*, and *M. lessertiana* showed reverse-J distributions typical of populations with active, ongoing sapling recruitment. Distributions for *C. trigynum* and *I. anomala* were relatively flat across the first four DBH classes (i.e., DBH <9 cm). *M. sandwicense* was represented in 10 out of 12 DBH classes.

Stand basal areas (BA) for understory trees were only a small fraction of that for *A. koa*, which averaged 25.5 $\text{m}^2 \text{ha}^{-1}$

(0.5 S.E.), including all individuals ≥ 1 cm DBH. Of the six understory trees, *M. sandwicense* had the greatest BA (2.5 $\text{m}^2 \text{ha}^{-1}$). *M. polymorpha* had the next greatest BA, but it was only one-fifth that of *M. sandwicense* (Table 1). Although *C. trigynum* were least abundant, its BA was not the smallest due to a large mean DBH. *M. lessertiana* had the least basal area.

Height class distributions for trees that occurred under the crown of *A. koa* crop trees are shown in Fig. 2, including *C. glaucum* and *A. koa*. With the exception of *C. glaucum*, all species had some individuals that were 7.5–9.5-m tall, but none were taller than the tallest *M. sandwicense* trees (>13.5 m). Approximately, 70% of understory *A. koa* were unhealthy, suppressed trees with mostly true juvenile bipinnate leaves rather than adult phyllodes. The remaining 30% *A. koa* were larger, received sunlight from directly above and expressed mostly adult foliage. The Chapman 4-parameter model adequately described the relationship between DBH and height for all understory trees species (Fig. 3). Average maximum

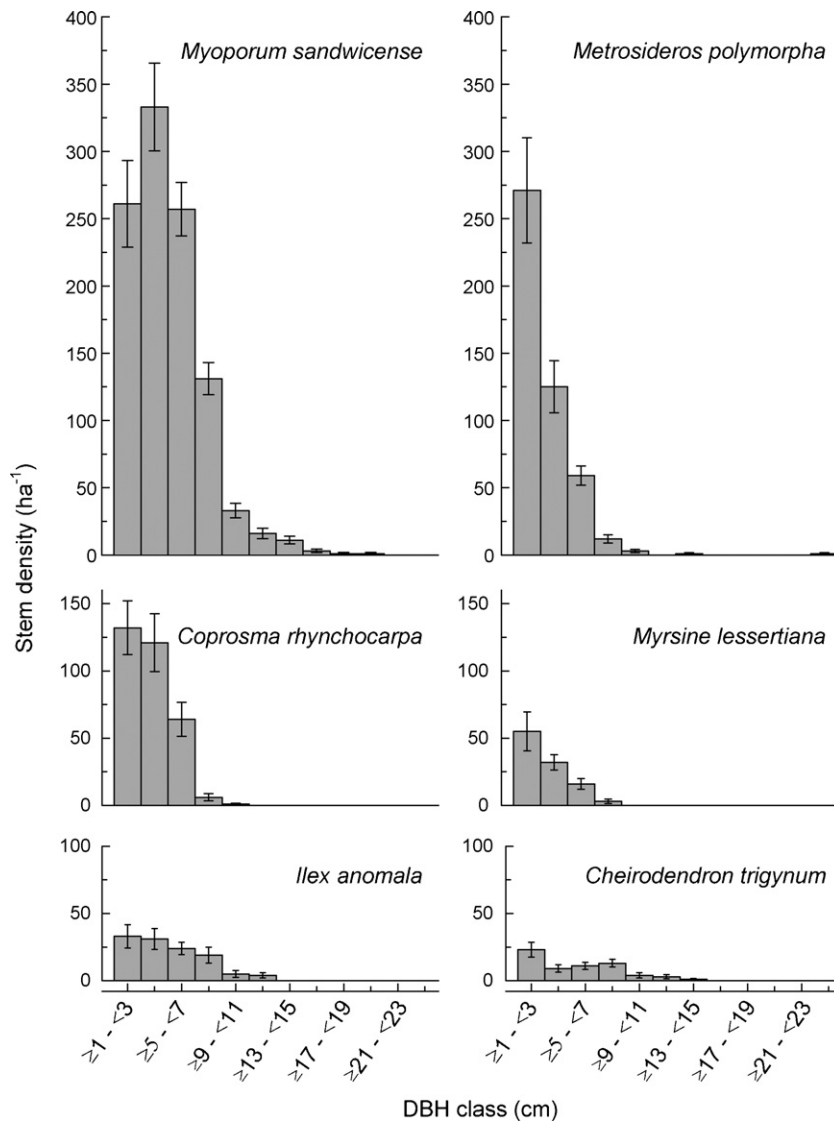


Fig. 1. Pre-treatment stem diameter class distributions for common tree species found in the understory of a 23-year-old *Acacia koa* forest. Values are based on a complete inventory of trees with DBHs ≥ 1 cm and located within each of 24, 25-m \times 25-m plots.

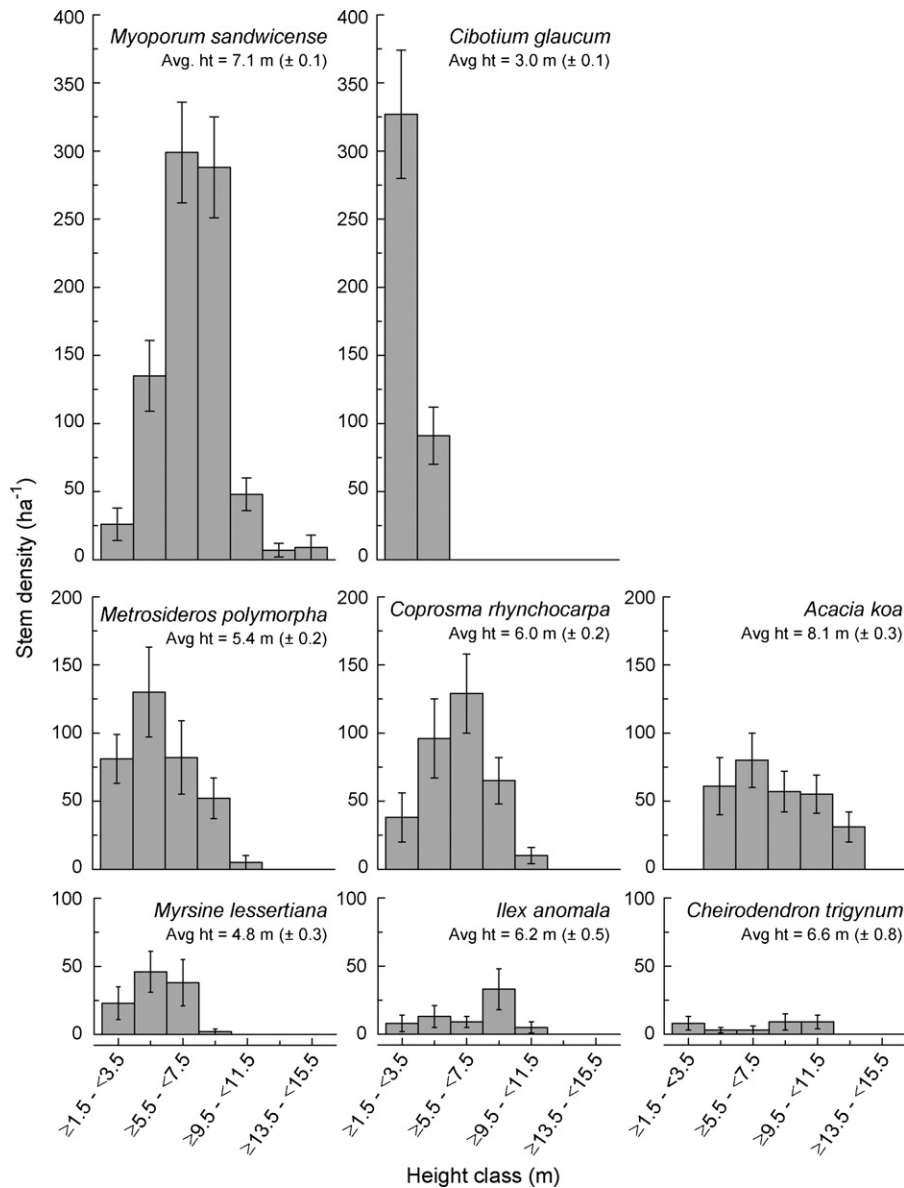


Fig. 2. Pre-treatment height class distributions for common tree species and tree fern found in the understory of a 23-year-old *Acacia koa* forest. Heights were estimated from DBH and height data collected for individuals with DBHs ≥ 1 cm that were located within the projected crown area of 195 koa crop trees, and fitted to the Chapman 4-parameter model: $H = y_0 + a*(1 - e^{(-b*DBH)^c})$.

heights predicted by the model ranged from 8.7 m for *M. lessertiana* to 13.2 m for *M. sandwicense*. Most *C. glaucum* were upright with trunk lengths averaging 0.55 m (± 0.02 m S.E.) and fronds adding an average of 2.40 m more (0.05 m S.E.) to total height.

3.1.2. Exotic grasses

Total aboveground grass biomass averaged 1.35 Mg ha⁻¹ (0.13 S.E.) across all plots. Introduced grasses covered 92% of the forest floor (Fig. 4). Nearly, 30% of ground that had grass cover had < 0.5 Mg ha⁻¹. Greater optical density, i.e. greater absorbance of light by overhead vegetation, was associated with lower grass biomass. The linear equation relating log₁₀ of grass biomass (G_b) to optical density (O_d) was $\log_{10}(G_b) = 3.85 - 1.41O_d$ ($r^2 = 0.53$). *E. stipoides* occurred

at light levels of $\sim 2\%$ of full sun but biomass was negligible (< 0.002 Mg ha⁻¹).

3.2. Response to silvicultural treatments

3.2.1. Endemic species

Of the four species analyzed statistically, *M. polymorpha*, *I. anomala* and *C. rhynchocarpa* showed no response to canopy or forest floor treatments (Table 2). Conversely, the DBH increment of *M. sandwicense* doubled in thinned plots, while average aboveground biomass increment increased from 0.6 to 0.9 kg tree⁻¹ yr⁻¹. Where the forest floor treatment was H + P-fertilized *M. sandwicense* showed significantly greater DBH increment (0.2–0.3 cm tree⁻¹ yr⁻¹) and biomass increment (0.6–0.9 kg tree⁻¹ yr⁻¹) than where the forest floor was left

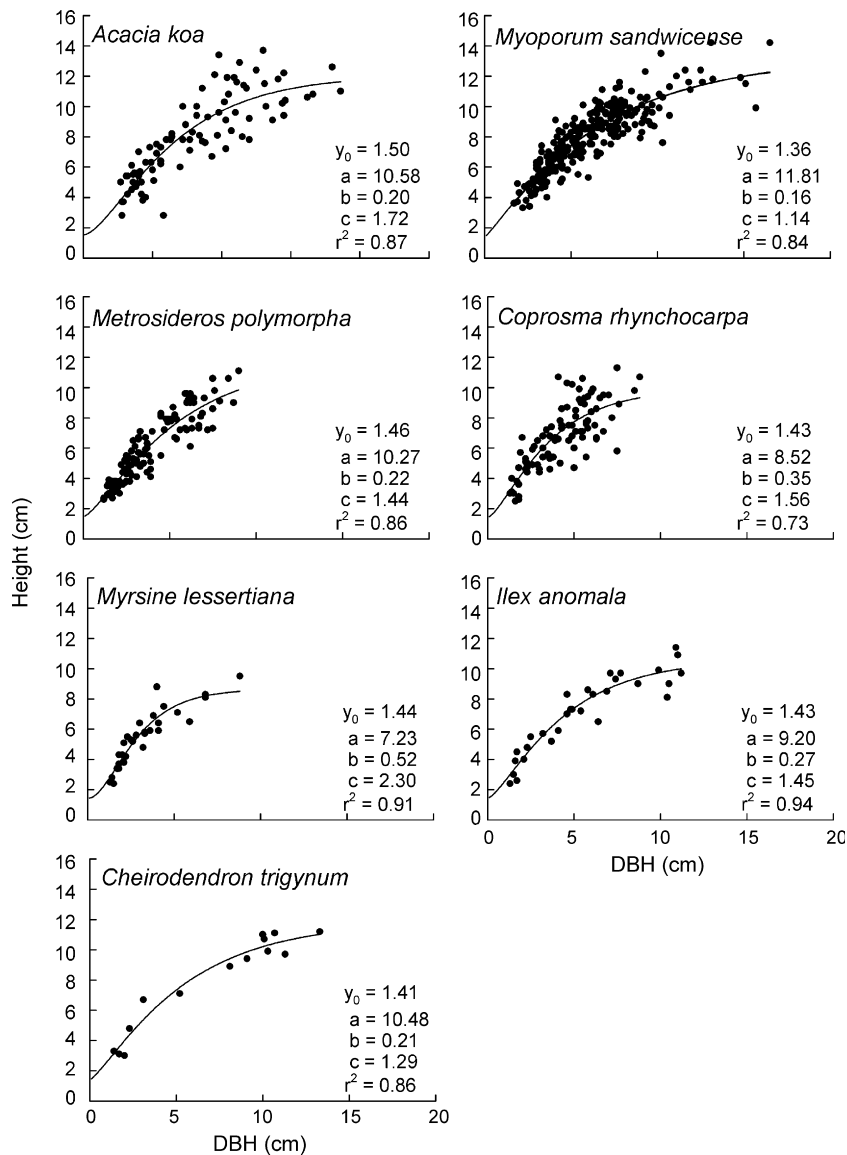


Fig. 3. Height–DBH relationships for seven common tree species found in the understory of a 24-year-old *Acacia koa* forest. Data are for individuals with DBHs ≥ 1 cm and located with the projected crown area of the 195 *koa* crop trees. Solid curves are least squares best fits of the Chapman 4-parameter model: $H = y_0 + a*(1 - e^{(-b*DBH)^c})$. The sum of y_0 and a estimates the average maximum height that each species can attain in the understory.

untreated. The herbicided treatment by itself had no effect on growth of *M. sandwicense*. Neither canopy nor forest floor treatments affected height increment for any of the species (Table 2).

Stem production by *R. hawaiiensis* and *V. calycinum* was not significantly different in thinned and unthinned plots. *R. hawaiiensis* but not *V. calycinum* responded positively to the H + P-fertilized treatment producing 1379 stems $ha^{-1} yr^{-1}$ compared to 216 stems $ha^{-1} yr^{-1}$ where the forest floor was left untreated (Table 3).

The number of fronds per *C. glaucum* trunk was greater in thinned than unthinned plots: the former had an average of 1.5 more fronds per trunk in 2004 than 2002 while the latter had only 0.8 more ($\alpha_{adj} = 0.05$). During the 2-year study period, 18% of the *C. glaucum* died across all plots. Mortality was greatest in thinned plots with 20 out of 77 individuals dying; in contrast, only 5 out of 62 individuals died in unthinned plots. In

terms of the forest floor treatments, mortality was least in the herbicided plots (7%) and similar in untreated and H + P-fertilized plots (26% and 20%, respectively).

Foliar P concentrations were unaffected by canopy treatments (data not shown). Likewise, foliar P concentrations in herbicided plots were not significantly different from those where the forest floor was left untreated (Table 4). In contrast, significantly greater P concentrations were detected for all species where the forest floor treatment was H + P-fertilized. *M. sandwicense* showed the greatest increase with a P concentration more than double that found in plots where the forest floor was left untreated. The herbicided treatment had no effect on P concentrations for any species. Canopy and forest floor treatments generally had no significant effect on other nutrients, including N (Table 4). Neither did they influence specific leaf mass, except for *M. sandwicense*, which had more leaf area per unit mass in H + P-fertilized than untreated plots.

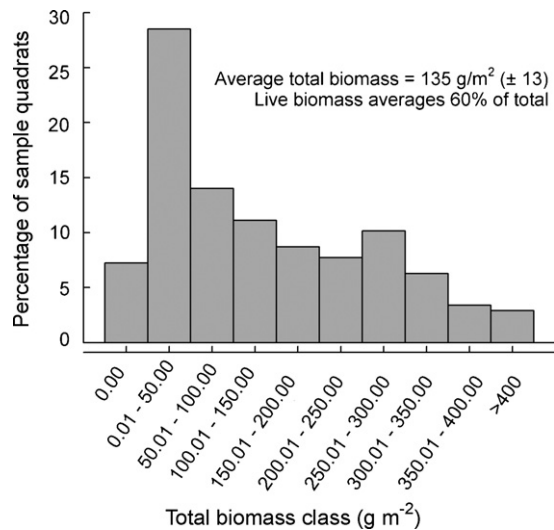


Fig. 4. Total aboveground grass biomass distribution in a 24-year-old *Acacia koa* forest. Biomass was adjusted to account for partial occlusion of 0.5-m × 0.5-m sample quadrats by rock and coarse organic detritus. Sample size = 207.

Nitrogen isotope ratios were positive for *M. sandwicense* and *C. rhynchosarpa* and negative for *M. polymorpha* and *I. anomala* (Table 4). Canopy treatments had no effect on $\delta^{15}\text{N}$ for any species. The only forest floor treatment that resulted in a significant change in foliar $\delta^{15}\text{N}$ was H + P-fertilized, and that only for *I. anomala*. Foliar $\delta^{13}\text{C}$ for trees were generally unaffected by silvicultural treatment (Table 4). The exception was that leaf $\delta^{13}\text{C}$ for *M. sandwicense* was significantly more negative in H + P-fertilized plots than in untreated plots.

Table 2

Effects^a of canopy and forest floor treatments on (a) DBH, (b) height and (c) aboveground biomass increments of individual trees between 2002 and 2004 for the four most abundant understory tree species in the Keauhou Ranch study area

Species	Canopy treatment		Forest floor treatment		
	Unthinned	Thinned	Untreated	Herbiced (H)	H + P-fertilized
(a) DBH increment (cm tree ⁻¹ yr ⁻¹)					
<i>Acacia koa</i> ^b	0.04 ^c	0.06	0.04	0.05	0.05
<i>Coprosma rhynchosarpa</i>	0.06	0.09	0.08	0.09	0.03
<i>Metrosideros polymorpha</i>	0.10	0.15	0.11	0.11	0.15
<i>Myoporum sandwicense</i>	0.14 ⁿ	0.32 ^m	0.19 ^b	0.19 ^b	0.30 ^a
(b) Height increment (m tree ⁻¹ yr ⁻¹)					
<i>Acacia koa</i> ^b	0.01	0.31	0.42	0.13	-0.06
<i>Coprosma rhynchosarpa</i>	0.36	0.34	0.36	0.30	0.41
<i>Metrosideros polymorpha</i>	0.27	0.27	0.21	0.30	0.29
<i>Myoporum sandwicense</i>	0.41	0.41	0.36	0.43	0.43
(c) Biomass increment (kg tree ⁻¹ yr ⁻¹)					
<i>Acacia koa</i> ^b	n.d. ^d	n.d.	n.d.	n.d.	n.d.
<i>Coprosma rhynchosarpa</i>	0.45	0.51	0.47	0.44	0.52
<i>Metrosideros polymorpha</i>	0.41	0.59	0.40	0.63	0.47
<i>Myoporum sandwicense</i>	0.59 ⁿ	0.91 ^m	0.64 ^b	0.72 ^{ab}	0.89 ^a

^a DBH, height, or tree biomass in 2002 was used as a covariate in the respective statistical analyses.

^b Understory *Acacia koa* trees were mostly unhealthy suppressed individuals.

^c Means for a given species and variable followed by common letters are not significantly different (Tukey's HSD test, $\alpha = 0.05$). No significant differences were detected among means where lowercase letters are absent. Each canopy treatment mean was based on $n = 4$; each forest floor treatment mean was based on $n = 8$.

^d Biomass increment was not done for koa because no allometric equation existed for suppressed trees.

3.2.2. Exotic grass

Initially (2002) aboveground grass biomass was the same in all treatment plots (Table 5). Two years after treatments were applied, H + P-fertilized plots had only about one-third the amount of grass found in untreated and herbiced plots; no statistical difference was found between the two latter forest floor treatments. Thinning had no effect on grass biomass.

Although grass nutrient concentrations were unaffected by canopy treatments (data not shown), there were several effects due to forest floor treatment. Grass P concentrations were significantly elevated in H + P-fertilized plots (Table 4). N and Mg concentrations were also greater in those plots. The tissue chemistry of grass in herbiced plots was no different from that in untreated plots. The $\delta^{15}\text{N}$ of grass was not significantly different from zero and was unaffected by any treatment (Table 4). The $\delta^{13}\text{C}$ were more negative for grass than trees. Neither thinning nor forest floor treatments affected $\delta^{13}\text{C}$.

4. Discussion

4.1. Understory structure

4.1.1. Endemic species

The native understory species that re-established beneath the pure *A. koa* canopy were components of the original forest, and they still occur commonly across Hawaii (Gagné and Cuddihy, 1990). Data from an earlier study in the same area (P.G. Scowcroft and D.M. Fujii, unpublished data) show that recolonization was rapid at our study site for species capable of regenerating on the forest floor, which included *M. sandwicense*, *C. glaucum*, *M. polymorpha* and *C. rhynchosarpa* (Scowcroft, 1992; Santiago, 2000). Eight years after stand

Table 3
Effects of canopy and forest floor treatments on rate of change in stem density (stems ha⁻¹ yr⁻¹) of two common native understory shrub species^a between 2002 and 2004

Species	Canopy treatment		Forest floor treatment		
	Unthinned	Thinned	Untreated	Herbicided (H)	H + P-fertilized
<i>Rubus hawaiiensis</i>	792 ^b	853	216b	873ab	1379a
<i>Vaccinium calycinum</i>	-100	21	58	-3	-175

^a Data were collected from within the project crown area of each of the 195 koa crop trees located in the study area.

^b Species means for a given type of treatment that are followed by common letters are not significantly different (Tukey's HSD test, $\alpha = 0.05$). No significant differences were detected among means where lowercase letters are absent. Each canopy treatment mean was based on $n = 4$; each forest floor treatment mean was based on $n = 8$.

initiation densities for these species averaged 1848, 692, 467 and 265 stems ha⁻¹, respectively. Those species that preferentially regenerate on moss-covered decaying logs, which included *I. anomala*, *M. lessertiana* and *C. trigynum*, had lower densities in the 8-year-old *A. koa* stand: 114, 74 and 19 stems ha⁻¹, respectively. These relatively low densities probably reflect lack of suitable seedbeds in the form of moss-covered decaying logs due to bulldozer disturbance during site preparation and insufficient time for decomposition of newly added coarse woody debris.

Tree density 15 years later (2001) still showed the influence of seedbed availability (Table 1). Survivors from the initial

wave of colonizing individuals were among those with a DBH ≥ 1 cm in 2001, and relative densities for all six species were remarkably similar to those 15 years earlier. *C. trigynum*, *I. anomala* and *M. lessertiana* still had low densities relative to their soil-establishing associates. The density of understory *M. sandwicense* exceeded that of all sizes of *A. koa* (1049 and 955 stems ha⁻¹, respectively), although stand basal area for *M. sandwicense* was only one-tenth that of *A. koa*'s 26 m² ha⁻¹ (Scowcroft et al., 2007). *C. glaucum*, which preferentially establishes on the forest floor, had densities of 692 and 485 individuals ha⁻¹ in 1986 and 2001, respectively. The lower density in 2001 is an artifact of sampling only *C. glaucum* with total height ≥ 1.5 m (cf. Fig. 2), whereas *C. glaucum* of all sizes were included in the previous estimate. Of the two shrubs that we examined, *R. hawaiiensis* established preferentially on the forest floor, and both earlier and later in stand development its densities were large—2054 and 4550 stems ha⁻¹ in 1986 and 2001, respectively.

The secondary *A. koa* forest that we examined is distinct with respect to composition and structure from old-growth Kilauea Forest adjacent to our study site. However, Table 6 shows that key structural components of the understory in the old-growth forest are already well represented in the 5–10 m low-stature tree layer of the 23-year-old forest. In terms of density, *M. sandwicense* and, to a lesser degree, *C. rhynchosarpha* are over-represented in the young forest, whereas *M. polymorpha* and *C. trigynum* are under-represented. The understory light environment of the young forest should become darker as *M. polymorpha* trees emerge from the understory and become part of the general forest canopy. That

Table 4
Average specific leaf mass, leaf nutrient concentrations, and nitrogen and carbon isotope ratios for foliage collected in February 2004, by species and forest floor treatment

Forest floor treatment	Specific leaf mass (m ² kg ⁻¹)	Concentration (g kg ⁻¹)					Isotope ratios (‰)	
		N	P	K	Ca	Mg	$\delta^{15}\text{N}$	$\delta^{13}\text{C}$
<i>Coprosma rhynchosarpha</i>								
Untreated	8.5 ^a	17.0	0.8a	2.9	27.2	3.8	0.46ab	-29.10
Herbicided (H)	8.5	16.8	0.8a	2.8	23.2	3.8	0.19b	-28.84
H + P-fertilized	10.1	19.1	1.3b	2.3	28.6	3.2	0.73a	-29.37
<i>Ilex anomala</i>								
Untreated	4.8	11.0	0.5a	4.9	11.6	5.7	-0.74b	-28.75
Herbicided (H)	4.7	10.8	0.5a	4.2	10.4	6.7	-0.97ab	-28.53
H + P-fertilized	4.7	13.3	0.6b	4.1	11.9	5.3	-1.73a	-27.82
<i>Metrosideros polymorpha</i>								
Untreated	6.7	10.5ab	0.6a	4.1	12.2	2.6	-1.82	-30.00
Herbicided (H)	6.8	10.3a	0.5a	3.4	11.6	2.4	-1.59	-29.80
H + P-fertilized	7.4	11.6b	0.9b	3.9	12.7	2.4	-1.79	-30.00
<i>Myoporum sandwicense</i>								
Untreated	8.6a	18.8	1.0a	8.2a	17.4ab	2.1	0.33	-27.14a
Herbicided (H)	9.0a	19.4	1.0a	10.8b	16.6a	2.2	0.35	-27.55ab
H + P-fertilized	10.6b	21.1	2.2b	8.8a	21.8b	2.3	0.72	-28.00b
<i>Ehrharta stipoides</i>								
Untreated	n.d.	29.4a	1.2a	18.9	3.5	2.0a	0.17	-32.12ab
Herbicided (H)	n.d.	27.9a	1.2a	16.5	3.6	2.0a	-0.03	-31.91a
H + P-fertilized	n.d.	33.7b	3.7b	17.5	3.5	3.2b	0.04	-32.87b

^a Means for a given species and within a given column followed by common letters are not significantly different (Tukey's HSD test, $\alpha = 0.05$). No significant differences were detected among means where lowercase letters are absent. Each forest floor treatment mean was based on a sample size of 4.

Table 5
Average total aboveground grass biomass (g m^{-2}) in August/September 2002 and in May/June 2005, by canopy and forest floor treatments

Forest floor treatment	Canopy treatment		
	Unthinned	Thinned	All
2002			
Untreated	126 ^a	113	120a
Herbicided (H)	150	157	154a
H + P-fertilized	130	133	132a
All	135a	134a	135
2005			
Untreated	162	173	168a
Herbicided (H)	189	234	212a
H + P-fertilized	58	62	60b
All	137a	156a	146

^a For a given year, marginal means followed by common letters are not significantly different (Tukey's HSD test, $\alpha = 0.05$). Each marginal canopy treatment mean was based on a sample size of 4; each marginal forest floor treatment mean was based on a sample size of 8.

should negatively impact shade intolerant *M. sandwicense* causing a decline in its density. Continued decomposition of existing and new logs should create additional seedbeds suitable for regeneration of *C. trigynum* and *M. polymorpha*, both of which showed a high rate of log establishment in old-growth forest (Cooray, 1974).

The height class structure of the species that comprise the *C. glaucum* and understory tree layers (0.5–5 and 5–10 m, respectively) indicates that these layers are already well formed (Fig. 2). Some of the tallest *M. polymorpha* trees are near the base of the *A. koa* forest canopy (10–11 m), and poised to begin the transition from the understory to canopy co-dominants, and ultimately to emergent trees (Mueller-Dombois et al., 1981). A few of the tallest *M. sandwicense* trees (≥ 13.5 – < 15.5 m height class) are into the general forest canopy, which suggests that they began life shortly after stand initiation. That only a small fraction of the *M. sandwicense* trees are in the ≥ 1.5 – < 3.5 m height class might indicate a decline in sapling recruitment. Unlike *M. polymorpha*, *M. sandwicense* is a mid-story species not a canopy co-dominant.

Individual *C. glaucum* at our study site were short compared with those in the adjacent Kilauea Forest, where fronds were up to 8 m above ground (J. Beachy, 2001, unpublished thesis, Harvard College). The difference reflects the species inherent slow growth and relative young age of the *C. glaucum* that we sampled. Using the height growth rate (2.5 cm yr^{-1}) reported by Wick and Hashimoto (1971) and the average trunk length of 0.55 m in our study area, we estimated that most *C. glaucum* were 22 years old, which was close to the stand age of 23 years. Trunk growth rates about 2.5 times greater than those of Wick and Hashimoto (1971) have been reported (Walker and Aplet, 1994), and when applied to the largest *C. glaucum* in our data set yielded an estimated age of 20 years. In either case, it is likely that some *C. glaucum* began re-colonizing the understory within a few years of stand initiation, but will take centuries to reach heights found in mature forests.

4.1.2. Exotic grass

E. stipoides dominated the herbaceous layer vegetation in all but a small fraction of the secondary forest. Although it reached heights of 1 m, the greatest percentage of ground cover occurred below 30 cm (J. Beachy, 2001, unpublished thesis). *E. stipoides* even occurred where light levels were below 5% of those in the open. Only in the densest shade (i.e. $< 2\%$) was biomass negligible. By itself, the closed canopy of 12–15 m tall *A. koa* only reduced light levels to about 20% of that in the open, which is typical of such stands elsewhere (Denslow et al., 2006). Multiple layers of vegetation reduced light further, with *C. glaucum* forming an effective sub-canopy barrier (Burton and Mueller-Dombois, 1984). We observed the lowest cover of grass under tree fern canopies.

In the present study, grass biomass averaged 1350 and 1470 kg ha^{-1} in 2002 and 2005, respectively. These values are greater than the approximately 500–1200 kg ha^{-1} reported by Grace (1995) for *E. stipoides* growing under light levels of 20–50% of full sun. In the old-growth Kilauea forest, grasses are virtually absent due to low light levels under multi-layered native vegetation (Cooray, 1974; Hatfield et al., 1996). So grass cover will continue to dominate the forest floor of the secondary stand until the leaf area index of native vegetation increases.

Table 6
Estimated stem densities and stand basal area of the six common understory tree species that were ≥ 5 m tall in Kilauea Forest and Keauhou Ranch^a

Species	Kilauea Forest 1971 ^b		Kilauea Forest 1990 ^c		Keauhou Forest 2001 ^d	
	Density ($\# \text{ ha}^{-1}$)	BA ($\text{m}^2 \text{ ha}^{-1}$)	Density ($\# \text{ ha}^{-1}$)	BA ($\text{m}^2 \text{ ha}^{-1}$)	Density ($\# \text{ ha}^{-1}$)	BA ($\text{m}^2 \text{ ha}^{-1}$)
<i>Cheirodendron trigynum</i>	101	1.3	144	0.9	40	0.2
<i>Coprosma rhynchocarpa</i>	10	0.1	159	0.7	234	0.4
<i>Ilex anomala</i>	30	0.4	173	1.6	87	0.3
<i>Metrosideros polymorpha</i>	321	13.5	770 ^e	24.0 ^e	199	0.4
<i>Myrsine lessertiana</i>	9	0.1	107	1.2	60	2.5
<i>Myoporum sandwicense</i>	18	0.7	54	0.9	830	0.1

^a At Keauhou Ranch all trees ≥ 5 m tall were in the understory of an *Acacia koa* forest canopy.

^b Cooray (1974); old-growth forest located at 1650 m elevation.

^c Hatfield et al. (1996); old-growth forest located between 1599 and 1850 m elevation.

^d This study; height of trees was estimated from DBH in 2001 using the Chapman 4-parameter equations developed from the 2002 sub-samples of trees in experimental plots (see Fig. 3).

^e Includes individuals in the forest canopy and canopy emergents as well as individuals in the understory.

The continued presence of grasses will likely negatively affect seedling establishment of native species (Denslow et al., 2006).

4.2. Responses to silvicultural treatments

4.2.1. Endemic species

Response to silvicultural treatments was probably a function of species adaptation to low light and soil P fertility. As is often the case for shade intolerant tree species (Oliver and Larson, 1990, p. 85, 87), *A. koa* that ended up in suppressed and sub-dominant crown classes did not respond to thinning. DBH increments for such individuals averaged 0.05 cm yr⁻¹, whereas increments for unthinned/untreated individuals averaged 0.50 cm yr⁻¹ (Scowcroft et al., 2007). The moderately shade intolerant, gap-phase *M. sandwicense* (Cooray and Mueller-Dombois, 1981a,b) grew faster in thinned plots and in H + P-fertilized plots. In contrast, growth of other native understory tree species, which are moderately shade tolerant (Cooray and Mueller-Dombois, 1981b; Burton and Mueller-Dombois, 1984), were unaffected by any of the treatments. Gerrish et al. (1988) reported that removal of competing *M. polymorpha* neighbors did not improve DBH growth of the remaining *Metrosideros* trees. However, they studied ~20-m-tall trees that were not light limited rather than ones found in the forest understory. *M. polymorpha* seems to be tolerant of low nutrient availability (Mueller-Dombois, 2000), although large sun-lit trees under chronic low nutrient stress have been shown to respond to multi-element fertilization (Gerrish et al., 1988). Our data suggest that smaller *M. polymorpha* in the understory are not P limited. Whether that is due to effective colonization of roots by vesicular–arbuscular mycorrhizae (Koske et al., 1992) or low requirement for P by trees growing at low light levels or both is unknown.

The lack of growth response by the understory shrub, *R. hawaiiensis*, to thinning was unexpected because it is often found in greater abundance in gaps than under closed forest canopy (Cooray and Mueller-Dombois, 1981a). *R. hawaiiensis* showed a six-fold increase in stem productivity where P fertilization and grass control were combined, which indicated that low soil P availability was limiting its growth. Although grass competition for soil P might also have contributed to suppressed growth of *R. hawaiiensis*, Scowcroft et al. (2007) detected no increase in resin extractable P following grass control alone.

Thinning increased the number of *C. glaucum* fronds per trunk. We suspect that this was because the species is moderately shade intolerant, a supposition based on the observation that it forms a continuous canopy in open but not closed-canopy forests (Cooray, 1974), although Durand and Goldstein (2001) suggested otherwise. Unfortunately, and for unknown reasons, any benefits from thinning seemed to be offset by greater mortality in thinned areas. The lack of response to P fertilization agrees with Walker and Aplet (1994) who found that neither N nor P fertilization affected frond production in forests >1000 years old. Inherent slow growth rate (Wick and Hashimoto, 1971) and mycorrhizal roots (Gemma et al., 1992) might explain the lack of fertilization response.

The only consistent treatment effect on foliage chemistry of understory trees was elevated P concentrations associated with P fertilization. The general lack of treatment effects on foliar N concentrations might indicate that the silvicultural treatments we used did not make leaves more susceptible to insect herbivory (Mattson, 1980). The modest but statistically significant increase in foliar N for *M. polymorpha* might favor larger populations of canopy arthropods, which would be advantageous for insectivorous forest birds. The N concentrations for understory *M. polymorpha* in this study (10.3–11.6 g kg⁻¹) were greater than those reported for open-grown trees on ~3000-year-old wet aa and pahoehoe flows at 1200-m elevation on Mauna Loa (8.5–8.9 g kg⁻¹) (Vitousek et al., 1988, 1992). Concentrations of cations were in the same range for all sites.

The $\delta^{15}\text{N}$ values for our understory tree species were generally close to zero indicating that they might all be shallow rooted. Because (a) substantial N fixation occurred during the first 10 years of stand development (Pearson and Vitousek, 2001), (b) koa leaf litter typically has $\delta^{15}\text{N}$ values of -0.3 to $+0.6\text{‰}$ (Vitousek et al., 1989), (c) N in near surface soil tends to be enriched in ^{15}N relative to plant litter (Nadelhoffer and Fry, 1988), and (d) N available for plant uptake is generally depleted in ^{15}N relative to total soil N (Nadelhoffer and Fry, 1988), it is possible that much of the N in circulation at our study site originated from N fixation by *A. koa*. The only treatment that significantly affected $\delta^{15}\text{N}$ of foliage was H + P fertilization and then only for *I. anomala*: leaves in H + P-fertilized plots were depleted in ^{15}N relative to control plots (Table 4). We have no explanation for that response.

The foliar carbon isotope ratios for understory trees conformed to the generalization that $\delta^{13}\text{C}$ values are more negative for intermediately shade intolerant (hemitolerant) species than shade tolerant species (Guehl et al., 2004). The $\delta^{13}\text{C}$ for *M. sandwicense*, a hemitolerant, averaged -27.6‰ while the $\delta^{13}\text{C}$ for shade tolerant tree species ranged from -29.9 to -28.4‰ . By way of comparison, the $\delta^{13}\text{C}$ for foliage of shade intolerant (heliophilic) overstory *A. koa* trees averaged -28.7‰ , which also fits the findings of Guehl et al. (2004) in that such species have carbon isotope ratios more similar to shade tolerant than hemitolerant species. Data for understory *A. koa* were not collected, but we suspect that they would have been less negative in the shaded environment (e.g., Jackson et al., 1993). The $\delta^{13}\text{C}$ for ohia in this study were more negative ($\sim -30\text{‰}$) than reported in earlier studies (-26.4‰ in Vitousek et al., 1990; -28‰ in Meinzer et al., 1992). The difference probably is due to our trees being in the understory while theirs were in the overstory and exposed to higher light levels and the less negative $\delta^{13}\text{C}$ of bulk atmospheric air ($\sim -8\text{‰}$).

4.2.2. Exotic grass

The decline in grass biomass in H + P-fertilized plots might be attributed to increased shading due to increased leaf area of overstory and understory vegetation. However, that seems unlikely because (1) no increase was detected in the projected crown area or crown depth of overstory crop trees even though their DBH increment was significantly greater than controls

(Scowcroft et al., 2007) and (2) except for *M. sandwicense*, none of the other understory trees showed greater DBH increment. Regardless, the 2.8–3.5-fold reduction in grass biomass in H + P-fertilized plots is probably too large to attribute to increased shading. Using a grass biomass datum of 60 g m⁻² and solving the regression equation presented earlier for fraction of light transmitted produces a value of 3%, which is the level typically found in the dense shade of *C. glaucum* fronds. Because harvest quadrats were not located in such dense shade, it is obvious that something else caused the decline in grass biomass in H + P-fertilized plots. One possibility is that the VA fungi associated with grass roots acted as facultative parasites once soil P supply was no longer limiting to plant growth (e.g., Buwalda and Goh, 1982; Peng et al., 1993). This mechanism deserves investigation.

4.3. Implications for forest birds

The above findings indicate that the conservative silvicultural treatments used in this study were either neutral or beneficial with regard to forest bird habitat: none were detrimental. All the woody species, except ohia and koa, bear fleshy fruits that are eaten by Hawaii's frugivorous forest birds, including the endemic Omao (*Myadestes obscurus*) (Ralph and Fancy, 1994). All the woody species provide habitat for canopy arthropods, which are eaten by Hawaii's insectivorous birds, such as the Hawaii Elepaio (*Chasiempis sandwichensis sandwichensis*), which forages almost entirely in the understory (Mountainspring and Scott, 1985). The Akiapolaau forages on each of the native understory species that we studied, although it prefers koa, naio and kolea (Ralph and Fancy, 1996; Pejchar et al., 2005). Ohia flowers are the principal source of nectar for nectarivorous birds such as the Iiwi (*Vestiaria coccinea*) and Apapane (*Hematione sanguinea sanguinea*) (Ralph and Fancy, 1995). We conclude that, barring delayed negative growth responses, active management of secondary koa forests can be done without degrading forest biodiversity, including the habitat of endemic forest birds.

5. Conclusions

The understory of the 23-year-old forest in this study was populated by the same structurally dominant species that make up the understory of the nearby old-growth *A. koa* forests. With time, the existing difference in structure should diminish as the understory canopy closes, shading out alien grasses and creating conditions favorable for the suite of native ferns found in old-growth forest. Understory species that preferentially establish on decayed-log and other organic seedbeds should eventually become as abundant as they are in the old-growth forest as such seedbeds become more common.

The conservative silvicultural treatments use in this study did not adversely affect growth of native understory species. Positive growth responses to thinning occurred only for shade intolerant species. Alien grass biomass did not increase in thinned plots. Grass control alone had no effect on any native species. *M. sandwicense* and *R. hawaiiensis* were the only native species that

responded positively to P fertilization. In contrast, alien-grass biomass was reduced by P fertilization to one-third the level found in unfertilized plots. Except for elevated foliar P concentration in herbicided + P-fertilized plots, treatments had no effects on leaf nutrient concentrations, and by implication on insect herbivory. Our findings coupled with those of Scowcroft et al. (2007) indicate that young stands of *A. koa* can be managed for wood production as well as the ecosystem service afforded by healthy, intact understory vegetation.

Acknowledgements

We thank the many persons that worked on this study including Lance DeSilva for writing the environmental assessment and, together with Ron Miyashiro, laying out the plots in the field and collecting pre-treatment data; J.B. Friday Nick Dudley, and Aileen Yeh for applying the silvicultural treatments; Jim Baldwin for invaluable statistical guidance; and Susan Cordell and Christian Giardina for constructive review comments. We thank Kamehameha Schools for their ongoing cooperation and access to the experimental sites. This research was supported in part by a grant from the Hawaii Forestry and Communities Initiative.

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