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Growth response of *Acacia koa* trees to thinning, grass control, and phosphorus fertilization in a secondary forest in Hawai'i

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Abstract

Koa (*Acacia koa* A. Gray) is an endemic Hawaiian hardwood tree of high ecological, cultural and economic value. Despite its multiple values, research on the silviculture of koa has been minimal until recently because the preferred land-use was pasture for livestock, and logging was done mainly to facilitate and reduce the costs of conversion. This study examined growth response of selected potential crop trees to three treatments: (1) thinning of surrounding non-crop koa trees; (2) herbicide control of exotic grasses; and (3) herbicide grass control plus phosphorus (P) fertilization. These treatments were applied in a split-plot design to a 24-year-old stand of koa located at 1700-m elevation on the island of Hawai'i. Treatments had variable effects on stem diameter increment of crop trees, measured at breast height during the second and third years after treatments were imposed. Neither thinning alone nor grass control alone significantly increased stem diameter increment or leaf nutrient concentrations of crop trees, or soil nitrogen (N) or P availability. Grass control in combination with P fertilization in the unthinned plots increased stem increment by 50% compared with unthinned control subplots, but again not significantly so. In these unthinned plots, grass control plus P fertilization greatly increased soil P availability and foliar P, but not those of other nutrients. Thinning in combination with grass control and P fertilization significantly increased annual diameter increment at breast height by 118%. Crown vigor and live crown to total tree height ratio were correlated with crop tree growth rate, which emphasizes the need to select crop trees that have healthy, full crowns and maintain a high live crown ratio, in addition to straight, defect-free stems. Overall, our results suggest that the benefits of release thinning of intermediate age koa crop trees on similar sites can be enhanced when combined with weed control and fertilization. Although even greater benefits might be realized if treatments are imposed before crown vigor and live crown ratio decline, the timing will need to be balanced against higher cost of thinning denser stands and the ability of managers to identify potential crop trees.
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1. Introduction

Koa (*Acacia koa* A. Gray) is a fast growing, nitrogen-fixing tree endemic to Hawai'i, and one of two native canopy emergent tree species in mesic to wet Hawaiian forests. Koa's native range spans a wide range of soil types on all major Hawaiian Islands (Whitesell, 1990). As a result, koa is a keystone species for Hawai'i's ecosystems, particularly for many of Hawai'i's listed threatened and endangered endemic bird species. Koa is also Hawai'i's premier tropical hardwood (Jenkins, 1983) with high cultural and economic value. The highly figured, richly colored wood (Skolmen, 1968) is valued in traditional Hawaiian culture, is among the world's most highly valued tropical timbers (Jones, 1997), and is the lynchpin of the Hawaiian forest industry, which is valued at over $30 million (Yanagida et al., 2004; Friday et al., 2006).

Presently, the high demand for koa wood exceeds the sustainable supply and the result has been a large increase in price. Koa stumpage has increased from approximately $0.15 per board foot in 1986 to $3.00 per board foot in 2006, with

finished koa lumber currently selling for as much as $50 per board foot for veneer grade material. Because of historically low value, however, many koa forests were converted to higher valued agricultural and pastoral land-uses in the 19th and early 20th centuries (Cuddihy and Stone, 1990; Juvik and Juvik, 1998). In the past decade, declining supplies of koa, and associated higher prices, combined with declining profitability of alternative land-uses, particularly sugar cane, pineapple and cattle ranching, have focused the attention of landowners on restoration and management of koa forests as a commercially competitive and viable land-use (Newell and Buck, 1996).

Landowners today know how to successfully regenerate stands of koa. Research has shown that long-lived seeds buried in the soil readily germinate following disturbance (Scowcroft and Wood, 1976; Scowcroft and Nelson, 1976; Skolmen and Fujii, 1981). Where the seed bank has been exhausted, planting has proven to be a successful method of getting koa established, albeit at greater cost (Judd, 1916; Conrad et al., 1988). What is largely unknown is how best to overcome three critical factors limiting the growth of potential crop trees in young, even-aged stands: intraspecific competition with non-crop trees; inter-specific competition with competing understory vegetation, often exotic grasses; and low soil fertility.

Studies across a diverse range of tropical and temperate tree species have shown that the growth of identified crop trees can benefit significantly from pre-commercial liberation thinning (e.g., Mead and Miller, 1991; Guariguata, 1999; Wadsworth and Zweede, 2006). In Hawai'i, Scowcroft and Stein (1986) reported accelerated growth of koa following thinning and thinning plus fertilizing of dense 12-year-old stands on the island of Maui. Likewise, trees in thinned portions of a 9-year-old stand on the island of Hawai'i, grew significantly faster than trees in unthinned control plots (Pearson and Vitousek, 2001). In both cases, better growth of shade-intolerant koa (Whitesell, 1990) following thinning was most likely due to increased light availability. It is also possible that other resource limitations were alleviated by thinning (Kaufmann and Ryan, 1986; Meinzer et al., 1996; Waring, 1983).

Chemical control of competing weeds and nutrition management often form the basis of many commercial forestry operations in temperate regions and increasingly so in tropical regions (Smith et al., 1997; Nambiar and Brown, 1997; Fisher and Binkley, 2000). In Hawai'i, the understory of many young koa stands is dominated by meadow rice grass (*Erharta stipoides* Labill.) and pasture grasses, such as kikuyu grass (*Pennisetum clandestinum* Chiov). A persistent grass understory may lead to competition with the regenerating koa for water or nutrients, especially on drier sites or older soils. Although plant productivity might be typically limited by low availability of N in young soils in Hawai'i (Vitousek and Farrington, 1997; Herbert and Fownes, 1999; Harrington et al., 2001), recent studies showed no such limitation for koa (Ares and Fownes, 2001; Pearson and Vitousek, 2001). Instead, reduced P availability was hypothesized to limit both koa productivity and N fixation on young soils (Pearson and Vitousek, 2001). Where regenerating koa forest follows agriculture or pasture land-uses, the nutrient and organic

matter capital of site can be greatly reduced compared to native and intact forests (e.g., Scowcroft et al., 2004).

The objective of this study was to measure the short-term (3 years) growth response of potential koa crop trees to: (1) pre-commercial thinning of surrounding non-crop koa trees; (2) herbicide control of exotic understory grasses; and (3) herbicide grass control plus P fertilization. We hypothesized that (1) thinning alone or a combination of grass control with P fertilization would each increase stem diameter increment of crop trees and (2) grass control alone would not increase growth. We expected greatest growth response for crop trees exposed to the combination of thinning, grass control, and fertilization. We also hypothesized that crown attributes, such as live crown ratio and crown vigor, would be positively correlated with growth.

2. Methods

2.1. Study area

The study area is located between 1650 and 1740 m elevation on the eastern (windward) slope of Mauna Loa, one of two large volcanoes on the island of Hawai'i (19°31′12″ N, 155°19′14″ W). The life zone is classified as a subtropical lower montane wet forest (Holdridge, 1967). Long-term rainfall averages about 2800 mm year^{-1} with winter and spring months being on average wetter than other months (Giambelluca et al., 1986). Long-term 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.

The 20-ha study area comprises a matrix of relatively young lava flows of Ka'u basalt (Pearson and Vitousek, 2001). To eliminate potential confounding effects of substrate age, we confined our study to a single flow, dated between 1500 and 3000-year old, which covered 12 ha of the site (Wolfe and Morris, 1996). The preliminary soil taxonomy for the flow is medial-skeletal, amorphic, isomesic Typic Hapludands (NRCS, 2006). It belongs to the Ke'amoku series, which consists of deep, well drained medial silt loam soils that formed in basic volcanic ash, possibly Pahala ash (Stearns and Macdonald, 1946), deposited over basic 'a'ā lava (rough scoriaceous).

2.2. Stand history

The area had been heavily logged in the 1960s and subsequently grazed by cattle, which resulted in conversion of the closed-canopy to open-canopy koa-'ōhi'a forest (15–60% crown cover) (Jacobi, 1989; USFWS Vegetation Map Overlay, Kulani Quad). Understory trees and shrubs consisted of native species only (Pearson and Vitousek, 2001). However, logging and grazing fostered proliferation of exotic grasses including kikuyu grass, meadow rice grass and sweet vernalgrass (*Anthozanthum odoratum* L.).

The site was mechanically scarified in 1978 with a bulldozer, which was used to knock down and pile remnant vegetation. Small patches of intact vegetation were protected around

individuals of the endangered Hawaiian vetch (*Vicia menziesii* Spreng.). Koa regenerated from buried seed (Skolmen and Fujii, 1981), and 1 year after disturbance, regenerating koa averaged 20,000 seedlings ha^{-1}. Density declined to approximately 1000 trees ha^{-1} in 2002. Leaf area index (LAI, m^2 single sided foliage area m^{-2} ground area) peaked at 3.7 m^2 m^{-2} when the stand was about 10-year old (Scowcroft, unpub. data), and declined to 2.6 m^2 m^{-2} by age 24 years. At the time of this study, mean tree stem diameter was 17.9 cm (± 0.1 S.E.) and the forest overstory was composed entirely of koa with other native woody species common in the understory.

2.3. Experimental design

Our split-plot design consisted of eight 60 m × 60 m plots, which we split into four 25 m × 25 m subplots, only three of which were actually used. Each of the three nested subplots was surrounded by a 2.5-m wide buffer, creating a 5-m buffer between adjacent subplots. Four replicates of the main treatment resulted in a total of 8 main plots and 24 subplots.

The main treatment consisted of a pre-commercial thinning with two levels: "thinning" as described below and a "no thinning" control. The subplot treatments were applied to the forest floor and had three levels: grass control through application of a grass-specific herbicide, the same herbicide grass control but with P fertilizer, and a "no herbicide/no fertilization" control. Fertilization by itself was not applied as a subplot treatment.

Plot and subplot selection was done as follows. On a computer-generated map we overlaid as many 60 m × 60 m plots as could fit within the bounds of the selected lava flow (17 plots). We then laid out each plot in the field and discarded those that had large canopy gaps, that were dissected by roads or skid trails, or that fell on complex terrain (e.g., steep-sided ravine). The boundaries of four subplots per plot were laid out in the field. For each subplot we measured DBH of all koa trees ≥1 cm, identified potential crop trees, and noted neighboring trees whose crowns were touching the crowns of crop trees. Potential crop trees had to be single-stemmed trees with clear, defect-free, straight trunks that provided at least a 4-m butt log and preferably with crowns that were of average fullness and vigor. Trees in suppressed and intermediate crown classes were not considered even if they met the stem form criteria. The 195 crop trees thus identified in DBH from 12.5 to 34.7 cm with a median and mean of 20.9 and 21.2 cm, respectively; of these, 175 were classified as crown co-dominants and the rest crown dominants. Two plots were not used for the study because they contained fewer than three acceptable subplots, which we defined as having at least five crop trees. We used the ratio of crop tree basal area to neighbor tree basal area (arbitrarily set at $0.3 \leq BA_C/BA_N \leq 0.7$) to guide our selection of three subplots in each of the remaining eight plots. Main and sub-treatments were then assigned at random to plots and subplots. The resulting average number of crop and neighbor trees and the average ratio of BA_C/BA_N for main and sub-treatments are listed in Table 1.

We thinned only trees near crop-trees rather than an area-wide thinning to minimize cost of treatment and limit negative effects on non-target plant and animal species. Further, evidence from temperate forests indicates that competitive stress on individual trees is induced only by the trees surrounding the subject tree (Cole and Lorimer, 1994). Therefore, only non-crop neighbor koa trees that were in direct crown competition with koa crop trees were selected for removal (i.e. crown thinning). In practice this meant the removal of any neighbor of similar height to crop trees and whose crown had branches ≤1 m from the crown edge of a crop tree. Given operational and market considerations and the stem diameters of competitors, our thinning treatment would be classified as a pre-commercial thinning.

Based on an earlier girdling trial with koa, double ring chainsaw girdling without poison or removal was chosen to kill neighboring competitors. Tree felling was not considered because girdling is more cost-effective and limits damage to crop trees because by the time girdled snags fall, they are less dense and more brittle than felled live trees. Further, standing dead snags would provide habitat for insect prey of the endangered forest bird, 'akiapōlā'au (*Hemignathus munroi*), which was known to forage on standing trees in the 24-year-old stand (Pejchar et al., 2005). Girdling was done during 4 days in December 2001. A few missed trees were girdled with a machete within 3 months of the initial girdling.

Herbicide and fertilization treatments were first imposed 5 and 11 months, respectively, after the girdling treatment was imposed, at which point most girdled trees began to lose vigor and die (see Section 3.1). Grasses were controlled by application of the grass-specific herbicide, Fusilade DX [Syngenta Professional Products, Greensboro, NC] at the rate of 0.42 kg active ingredient (Fluazifop-P-butyl) ha^{-1}. It was first applied May 2002 and reapplied 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 same amount of fertilizer was applied to each designated subplot, but fertilizer distribution was not uniform throughout a subplot due to the uneven terrain and the application method.

Initial measurements of crop trees in thinned plots were collected from November 2001 to February 2002; initial measurements of crop trees in unthinned plots were collected March to June 2002. In July and August of 2003, 2004 and 2005, crop trees were re-measured for stem diameter at breast height (DBH), tree height, height to the base of the live crown, crown width at its widest point and 90° to the first axis and crown vigor. Four subjective crown vigor classes were recognized based on crown fullness and presence within the main crown of any bipinnately compound juvenile foliage.

Table 1

(a) Average number of crop trees and neighboring koa trees that touched a crop tree crown (stems ha^{-1}), and average ratio of crop tree basal area to neighbor tree basal area (BA$_C$/BA$_N$), by canopy and forest floor treatments; (b) diameter class distribution of crop trees, by 5 cm wide classes

Forest floor treatment	Canopy treatment					
	Thinned			Unthinned		
	Crop tree	Neighbor	BA$_C$/BA$_N$	Crop tree	Neighbor	BA$_C$/BA$_N$
(a) Average number of crop trees						
Control	108 (8)	328 (36)	0.34 (0.02)	100 (5)	256 (28)	0.49 (0.07)
Herbicide	112 (10)	348 (49)	0.35 (0.03)	100 (9)	264 (35)	0.42 (0.01)
Herbicide + P	96 (9)	304 (36)	0.48 (0.10)	100 (10)	248 (47)	0.56 (0.09)

(b) Diameter class distribution of crop trees	DBH class end point	Crop tree density (stems ha^{-1})	
		Thinned	Unthinned
Control	15	8 (7)	0 (0)
	20	48 (8)	36 (7)
	25	44 (10)	44 (5)
	30	8 (6)	16 (9)
	35	0 (0)	4 (5)
Herbicide	15	4 (5)	4 (5)
	20	36 (9)	32 (9)
	25	44 (7)	40 (8)
	30	24 (8)	24 (8)
	35	0 (0)	0 (0)
Herbicide + P	15	0 (0)	4 (5)
	20	36 (5)	20 (7)
	25	36 (7)	56 (8)
	30	24 (7)	16 (7)
	35	4 (5)	4 (5)

Values in parentheses are ±1 S.E. of the mean.

Adult foliage typical for saplings and larger trees consists of phyllodes, which are flattened and expanded petioles. The presence of juvenile foliage, usually on epicormic shoots, indicates a stress response (Whitesell, 1990). Class 1 was assigned to full, healthy crowns lacking juvenile foliage (V1); Class 2 was assigned to full crowns with juvenile foliage present (V2); Class 3 was assigned if a crown was less than full (a major fork or limb had died) but juvenile foliage was absent (V3); and Class 4 was assigned to trees with partial crowns with juvenile foliage present (V4). The DBH and crown diameters of competing koa trees were also measured initially. A clinometer was used to determine locations of edges of the projected crown. A laser range/height finder (Impulse 200, Laser Technologies, Inc., Centennial, CO) was used for tree height and height to base of crown measurements, except for 2005 when a 15-m telescoping height pole was used. Calculated tree variables included live crown ratio (crown depth divided by total tree height), projected crown area, crown volume, and leaf area (Table 2).

2.4. Soil N and P availability

To determine treatment effects on the relative availability of surface soil N and P, we used the buried ion-exchange resin bag method similar to that described by Pearson and Vitousek (2001). Sampling was done May–June 2003 using separate cation and anion resins and again in November–December 2003 using anion and mixed-bed resin. For the spring sampling, we weighed 3 g of cation-exchange resin (AG 50W-X8, 20–50 mesh [340–850 μm diameter], H$^+$ form [Bio-Rad Laboratories, Hercules, CA]) and 3 g of anion-exchange resin (Bio-Rad AG 1-X8, 20–50 mesh, Cl$^-$ form) into separate 30-cm^2

Table 2

Equations used to calculate projected crown area, crown volumes, and leaf area

Variable	Equation	Parameters	Units
Projected crown area (CA$_p$)	CA$_p$ = $W_1 \times W_2 \times \pi/4$	W_1 = largest crown width (m) W_2 = crown width (m) at 90° to largest width Assumes projected crown area is an ellipse	m^2
Gross crown volume (V$_c$)	V$_c$ = $W_1 \times W_2 \times C_d \times \pi/6$	W_1 and W_2 as above C_d = crown depth (m) = total height minus height to crown Assumes crown is an ellipsoid	m^3
Leaf area (LA)	LA = $0.6052 \times$ DBH$^{1.3135}$	Allometric equation derived from harvest of 76 trees DBH (cm) (r^2 = 0.74) (Scowcroft, unpubl. data)	m^2

bags of no. 86 monopolyester silkscreen material (David's Distributing, Inc., Glenshaw, PA). For the winter sampling, we used 52-cm^2 screen bags of mixed-bed resin to sample soil NO_3^- and NH_4^+ concentrations. Each bag contained 6 g of mixed-bed resin (Ionac NM-60, Type 1, 16–50 mesh [110–850 μm diameter], H^+/OH^- form [Mallinckrodt Baker, Inc., Phillipsburg, NJ]. Phosphate concentrations were sampled with the anion exchange resin bags as described for the spring sample. We used the resins as they came out of the container without additional charging. The open end of each bag was sewn shut and bags were sealed in plastic containers and refrigerated 5 days until use.

For the spring sample, three bags constituted a set and included one cation (for NH_4^+ analysis) and two anion bags (for NO_3^- and PO_4^- analyses); for the winter sample, a set included one mixed-bed bag (for NO_3^- and NH_4^+ analyses) and one anion bag (for PO_4^- analysis). Bags were installed 2 days before application of fertilizer. For each of the 4 thinned and 4 unthinned plots, we randomly selected 5 crop trees per subplot (120 sets of resin bags). Sample locations were chosen randomly within the drip line of selected crop trees. A trowel was used to make inclined slits into the soil to a depth of 4–6 cm, one bag was inserted in each slit, and the soil was pressed back into place. A tether line of polyester thread was attached to a flagged wire pin that was pushed into the soil. After 45 days (spring sampling) or 55 days (winter sampling), bags were retrieved, rinsed with deionized water, and extracted for 6 h on a rotary shaker in 80 ml (spring sampling) or 100 ml (winter sampling) of 2 mol KCl for NO_3^- and NH_4^+ analyses, and 80 ml of 0.5 mol HCl for PO_4^- analysis. Unincubated resin blanks were used to correct for contaminant N and P. Extracts were frozen until analysis at the University of Hawai'i Agriculture Diagnostic Service Center (ADSC). Nitrate and NH_4^+ concentrations were determined using an autoanalyzer (Technicon, Tarrytown, NY); PO_4^- concentrations were determined using autoanalyzer (WESTCO Scientific Instruments, Danbury, CT). For comparative purposes, data are reported as mass of N or P accumulated per bag per day.

2.5. Foliage sampling

Foliar nutrient analyses were conducted on phyllodes collected from 4 randomly selected crop trees for all subplots in 2 thinned and 2 unthinned plots. A telescoping pruning pole (12 m maximum reach) or for tall trees a slingshot were used to clip sun leaves from the south side of crowns, which were immediately sealed inside a plastic bag and placed in a cooler. Only fully expanded phyllodes were kept for analyses. Leaf area was determined for fresh samples within 1 day of sampling, after which samples were oven-dried, weighed, ground and analyzed at ADSC to determine concentrations of N, P, and major cations. Total N was determined by Kjeldahl digestion and analysis by colorimetric methods (Shuman et al., 1973; Issac and Johnson, 1976). Sub-samples of digests were dry ashed (Issac and Johnson, 1985). Potassium concentrations were determined by Technicon continuous-flow flame-emis-

sion spectrophotometry. Phosphorus, Ca and Mg were determined by inductively coupled plasma emission spectrometry (Perkin Elmer ICP model 6500).

2.6. Statistical analysis

We examined treatment effects on the following crop tree variables: DBH, crown diameter (C_D), projected crown area (C_A), crown volume (C_V), and allometric leaf area (LA). We used the 2003–2005 interval (approximately 1–3 years after thinning) because most girdled trees were still alive before 2003. Live crown ratio (LCR) in 2002 was used as a covariate in each analysis because tree growth and capacity to respond to increased availability of resources should be strongly influenced by the relative size of its crown (Dyer and Burkhart, 1987; Dolph, 1988). The effect of the plot and subplot treatments, and changes in these effects over time were examined using repeated measures ANOVA in SAS Proc Mixed (SAS Institute, 1996). Comparisons of factor-level least squares means were performed using Tukey's HSD test with α set at 0.05. The log transformation was used to equalize variances, and means reported in this paper were backtransformed and corrected for bias using the term, exp(MSE/2), where MSE was the sum of the covariance parameter estimates (Sprugel, 1983). Patchy distribution of P fertilizer within subplots resulted in highly variable P capture by anion exchange resins. Because mean P capture was a poor descriptor of the highly skewed sample population, we report medians as well as means for the various factors.

3. Results

3.1. Responses of girdled trees

One year after girdling 11% of trees had lost all foliage and 25% showed no noticeable loss of foliage. Neither DBH nor projected crown area influenced foliage loss (data not shown). Stem sprouts below the girdle characterized most trees, and these eventually died after defoliation was complete. Over 75% of trees were dead 2 years after girdling, with the remainder dead by 3 years.

3.2. Thinning effects on stand structure

Across plots, initial stand density averaged 955 koa trees ha^{-1} (±38 S.E.), while total stand basal area averaged 26 m^2 ha^{-1} (±0.6 S.E.). Identified crop tree density was 103 trees ha^{-1} (±11 S.E.). Crop trees comprised approximately 15% of initial stand basal area (4 m^2 ha^{-1} ± 0.2 S.E.) and 13% of initial stand leaf area (0.34 m^2 m^{-2} ± 0.02 S.E.). Initial density of competing neighbor koa averaged 291 trees ha^{-1} (±40 S.E.), with a total basal area of 9 m^2 ha^{-1} (±0.6 S.E.). Non-crop trees accounted for 34% of initial stand leaf area, which averaged 2.56 m^2 m^{-2} (±0.61 S.E.). Thinning decreased stand density to 655 trees ha^{-1} (±34 S.E.) and basal area to approximately 20 m^2 ha^{-1}. Most of the thinning reductions occurred in intermediate-size trees between 10 and 30 cm DBH.

3.3. Responses of crop trees

3.3.1. Tree height and related attributes

Between 2002 and 2005 mean height of crop trees increased from 11.9 to 13.7 m (Fig. 1a). Average crown depth ranged from 1.7 to 2.7 m and did not change between 2002 and 2005 (Fig. 1b). Average height to the base of the live crown increased from 9.6 to 11.5 m during that time (Fig. 1c). Live crown ratio for most trees was less than 20% and did not differ by canopy or forest floor treatments or over time (Fig. 1d). While all variables measured increased over the measurement period, the thinning, herbicide and herbicide plus P treatments did not significantly affect height growth or related crown attributes.

3.3.2. Stem increment

Significant treatment effects on stem growth were detected for the period 2003–2005 (Fig. 2). Thinning alone did not significantly increase stem increment of crop trees. While thinning plus grass control increased mean stem increment by 70%, this increase was not significant. However, thinning plus grass control in combination with P fertilization more than doubled diameter increment at breast height (0.5–1.1 cm year^{-1}; $P < 0.0001$). The effects of thinning were multiplicative when combined with forest floor treatments: the difference in ΔDBH between thinned and unthinned plots was 1.3 times greater with grass control and 1.9 times greater with grass control plus P fertilization than without forest floor treatment.

Over time, increment data showed that crop trees in thinned plots had an advantage over crop trees in unthinned plots across forest floor treatments (Fig. 3). Declining growth rates in unthinned plots resulted in significantly smaller diameter increments in 2004–2005 than at the start of the study (Fig. 3). In contrast, crop trees in thinned plots grew at the same rate during 2004–2005 as during the initial measurement interval, regardless of forest floor treatment.

3.3.3. Tree crown attributes and growth rates

Live crown ratio (LCR) in 2002 was a significant covariate in every ANCOVA performed (data not shown). As LCR increased, diameter increment increased (Fig. 4). In general, crop trees in thinned plots showed greater growth than those in unthinned plots for a given LCR. Forest floor treatments had limited effects on the relationship, although there was a hint of improved growth for trees with the smallest LCRs when fertilization was combined with grass control. Changes in LCR between 2003 and 2005 were not significantly affected by treatments.

Most crowns, even of crop trees, showed the effects of prolonged crowding. Crop trees spanned the range of crown vigor classes (V1 to V4). In 2002 before treatments were fully imposed, 45% of the crop trees had full, healthy crowns that were free of juvenile stress foliage (V1). Another 18% had full crowns but with juvenile foliage in the main crown (V2); 25% had partial crowns without juvenile foliage (V3); and the rest (12%) had partial crowns with juvenile foliage (V4). Crown vigor did not appear to be responsive to silvicultural treatments (data not shown) possibly because the time required for a tree to recover from competition-induced stress and regrow a full crown exceeded the time allotted to this study.

Crown vigor was correlated with diameter increment during the 2003–2005 interval. Crop trees with healthier, fuller crowns were more likely to grow faster (Fig. 5). For example, stem increment for 80–85% of trees that had full crowns in 2002 (i.e.,
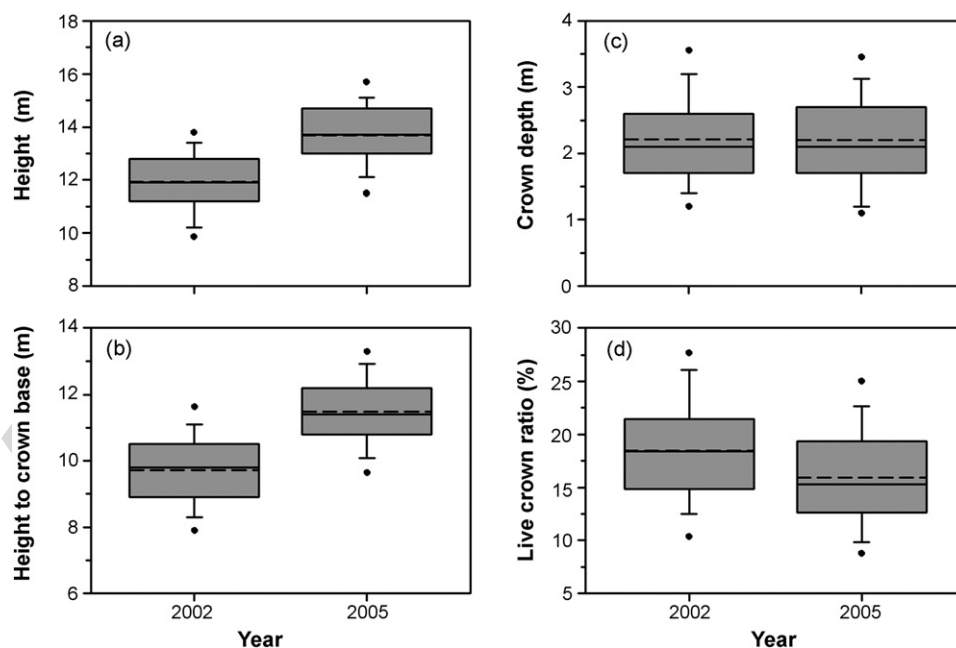

Fig. 1. Difference in (a) tree heights, (b) heights to the base of crowns, (c) crown depths and (d) live crown ratios of koa crop trees between 2002 and 2005 irrespective of canopy or forest floor treatments. Plots show means (dashed horizontal lines), medians (solid horizontal lines), 25th and 75th percentiles (box ends), 10th and 90th percentiles (whiskers), and 5th and 95th percentiles (closed circles).
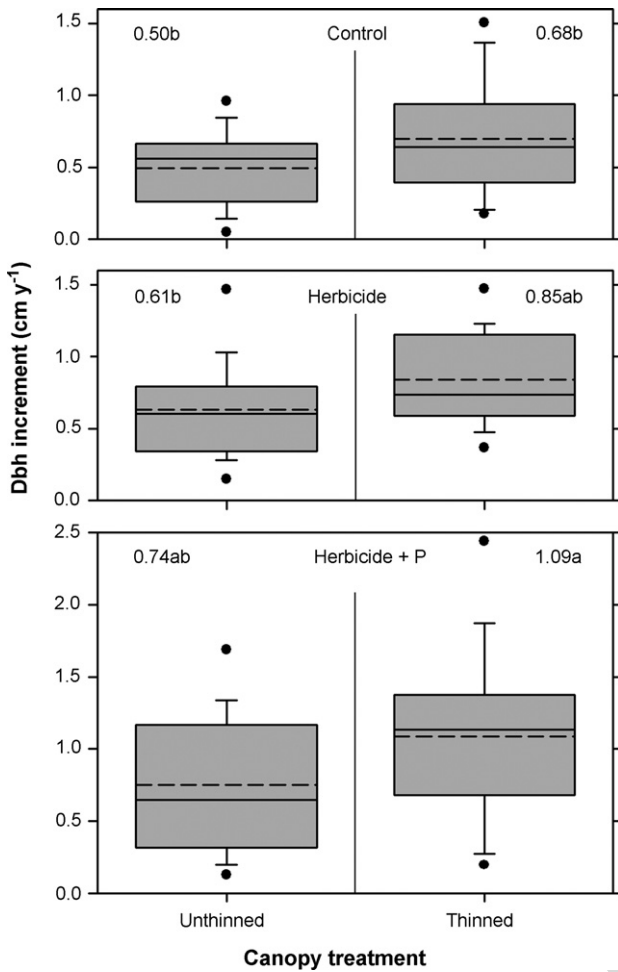
Fig. 2. Effects of canopy and forest floor treatments on stem diameter increments of koa crop trees during the 2003–2005 measurement interval (0.7–2.7 years after all treatments were in place). Plots show means (dashed horizontal lines), medians (solid horizontal lines), 25th and 75th percentiles (box ends), 10th and 90th percentiles (whiskers), and 5th and 95th percentiles (closed circles). Least squares means generated for the treatments during statistical analysis are shown in their respective panels. LS means followed by a common letter are not significantly different (Tukey's HSD test, $\alpha = 0.05$).

crown vigor classes V1 and V2) exceeded 0.5 cm year^{-1}, whereas only 35–45% of trees with partial crowns (i.e., crown vigor classes V3 and V4) exceeded that rate. Differences were more pronounced when 2005 vigor ratings were used: 95% of

V1 trees grew faster than 0.5 cm year^{-1} compared to only 28% of V4 trees. Notably, more than one-third of trees classified as V1 in 2002 grew faster than 1 cm year^{-1} during 2003–2005 compared to 12–15% of trees in lower vigor classes. Again, differences were greater when 2005 vigor ratings were used.

Analysis of allometrically derived estimates of leaf area (LA) indicated that the rate of increase in leaf area was significantly greater for crop trees in thinned than unthinned plots during 2003–2005 (1.9 and 1.3 m^2 year^{-1}). Likewise, grass control plus P fertilization resulted in faster LA accumulation than the control treatment (2.0 and 1.2 m^2 year^{-1}). Thinning also increased the rate of expansion of C_D during 2003–2005 (0.1 m year^{-1}), whereas no thinning resulted in an equally small decrease (-0.2 m year^{-1}). These changes, although statistically significant, were not reflected in changes in other crown attributes. Treatments had no effect on rates of change in projected crown area, or crown volume (data not shown).

3.4. Foliar nutrient concentrations

Specific leaf area and phyllode nutrient concentrations (leaf area basis) were unaffected by thinning or grass control in February 2004, approximately 1 year after all the treatments had been applied. P fertilization did lead to a significant increase in phyllode P concentration (Table 3). Phyllodes in thinned and unthinned plots had similar P concentrations (0.30 and 0.27 g m^{-2}, respectively).

3.5. Soil P and N availability

Phosphorus availability in surface soil was not significantly affected by thinning or by killing grasses (Table 4). However, application of triple super phosphate significantly increased soil inorganic P concentrations over levels in other sub-treatments. Where fertilizer was applied, median values for resin-captured PO$_4^-$-P were 4–86 μg bag^{-1} day^{-1} compared with <0.1 μg bag^{-1} day^{-1} where no fertilizer was applied. Availability was greater in the winter than in late spring, especially in unthinned fertilized plots.

Nitrate-N availability in surface soil was 15–40 times higher than NH$_4^+$-N availability for the spring sample and 4–10 times higher for the winter sample. Neither form of soil nitrogen was
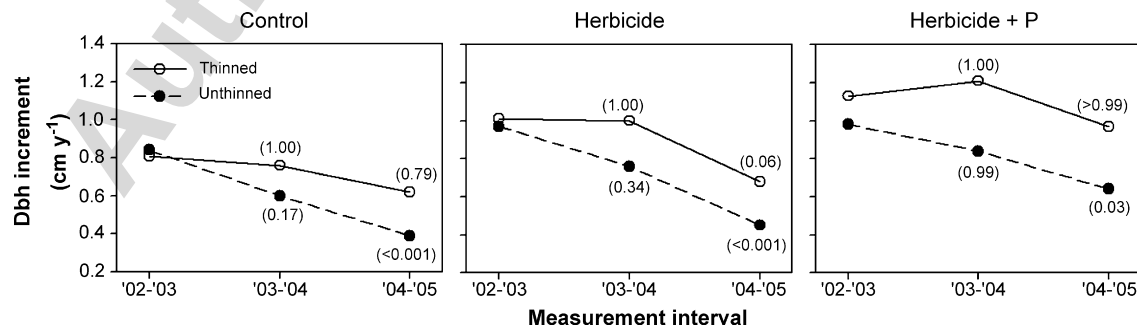

Fig. 3. Trajectories for average stem diameter increments of koa crop trees between 2002 and 2005, by canopy and forest floor treatments. Values in parentheses are adjusted P values for pairwise tests of differences in growth rates between initial and subsequent measurement intervals. Adjusted P values of ≤0.05 denote a growth rate that is significantly different from the rate during 2002–2003.
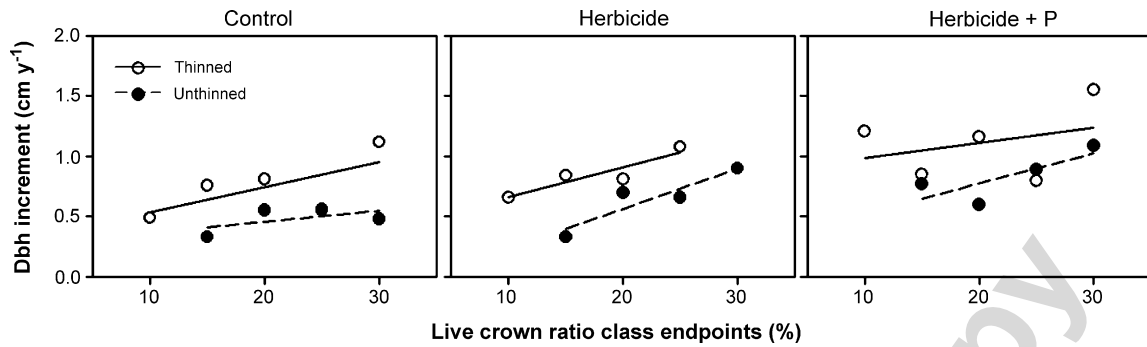
Fig. 4. Average stem diameter growth of koa crop trees during 2003–2005 as a function of live crown ratio class in 2002, by canopy and forest floor treatments. Width of each class is 5%. Plotting points based on a single observation were excluded.
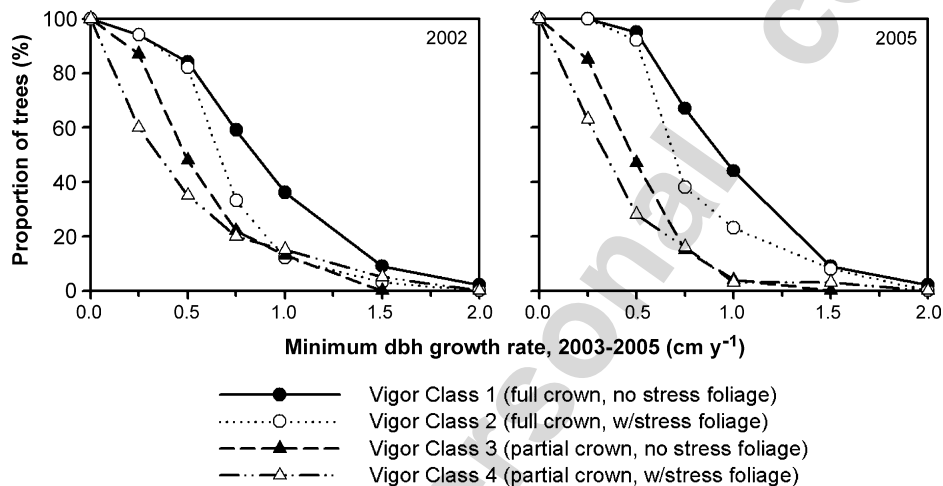

Fig. 5. The proportion of koa crop trees that were growing faster than a minimum rate during the 2003–2005 growing period as a function of crown vigor class in 2002 and 2005. Stress foliage refers to juvenile, true bipinnate leaves that are produced on epicormic sprouts along branches in the main crown and are symptomatic of stress.

affected by thinning or either forest floor treatment (Table 5). Time of year was the only factor that affected N availability. Ammonium-N availability was significantly higher during the winter sampling period than during the spring sampling period (median values were 13 and 6 μg N bag^{-1} day^{-1}, respectively). Nitrate-N availability was significantly lower during the winter than spring sampling period (median values were 100 and 141 μg N bag^{-1} day^{-1}, respectively).

4. Discussion

4.1. Responses of crop trees

One objective of our silvicultural treatments was to accelerate tree growth, thereby shortening time to harvest. Producing larger trees faster might be attractive where the goal is to accelerate restoration of large-tree wildlife habitat (Freed, 2001). Stem increment trajectories were shifted upward but were still parallel to the original trajectories (Fig. 3). In the case of thinning combined with grass control plus P fertilization, the slopes were also changed between the first and second growth intervals. Once the canopy closes again, further treatments may be necessary to maintain increased growth responses of selected crop trees. If

growth rate differentials in 2004–2005 can be maintained between crop trees in treated versus untreated plots, then it should take the thinned and herbicided/fertilized trees approximately 10 years less time than untreated trees to reach an average DBH of 30 cm and 25 years less to reach a DBH of 40 cm. Thinning alone would shorten these times by about 5 and 15 years, and thinning combined with grass control would shorten them by 7 and 17 years. This means that instead of rotation ages of 42 and 67 years for a completely unmanaged stand at our study site, it could be as short as 31 and 41 years with application of appropriate silvicultural treatments. Shorter rotation ages might be realized by earlier silvicultural interventions.

Land owners and forest managers are also interested in knowing whether to expect growth responses to silviculture if treatments are delayed until sometime after crown closure, which can occur within 5 years of establishment in high density stands of natural regeneration. Such delay improves the prospect of identifying potential crop trees. Older trees, however, might be less capable of responding to increasing resource availability (Chapin et al., 1986). Because live crown ratio is related to tree vigor and potential response to thinning (Smith et al., 1997), conventional wisdom has held that the thinning response of older trees might be limited, slow in

Table 3

Average specific leaf area ($m^2 \, kg^{-1}$) and concentrations of nutrients (leaf area basis, $g \, m^{-2}$) for phyllodes of koa crop trees sampled in February 2004, by canopy and forest floor treatments

Canopy treatment	Forest floor treatment			
	Control	Herbicide	Herbicide + P	All
Specific leaf area				
Thinned	4.30[a]	4.14	4.60	4.34
Unthinned	4.29	4.32	4.67	4.42
All	4.30	4.23	4.63	
Nitrogen				
Thinned	5.28	5.33	5.11	5.24
Unthinned	5.01	5.10	5.03	5.05
All	5.15	5.22	5.07	
Phosphorus				
Thinned	0.16a	0.19a	0.30b	0.21m
Unthinned	0.18a	0.17a	0.27b	0.20m
All	0.17r	0.18r	0.29s	
Potassium				
Thinned	1.01	1.00	0.93	0.98
Unthinned	1.12	1.09	0.91	1.03
All	1.06	1.04	0.92	
Calcium				
Thinned	3.43	4.41	3.20	3.65
Unthinned	3.52	3.90	3.61	3.67
All	3.47	4.15	3.40	
Magnesium				
Thinned	0.50	0.69	0.55	0.58
Unthinned	0.76	0.77	0.61	0.71
All	0.62	0.73	0.58	

[a] Among factor levels and among combinations of factor levels, least square means 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. Logarithmic means were transformed back to the original units and corrected for bias.

coming, or fail altogether. Our data suggest that this might be true for koa trees greater than 20 years of age.

Growing space index (GSI), the ratio of crown diameter to DBH, provides another criterion for determining not just how much but when to thin around crop trees. Larger GSI values

Table 4

Median (mean) PO_4^--P captured on anion exchange resins ($\mu g \, P \, bag^{-1} \, day^{-1}$) that were buried 4–6 cm below the soil surface and incubated for approximately 45 days (May–June 2003) or 55 days (November–December 2003), by canopy and forest floor treatments, and by sample period

Canopy treatment	Forest floor treatment			
	Control	Herbicide	Herbicide + P	All[a]
May–June				
Thinned	0.16 (0.01)	0.22 (0.02)	49.75 (4.60)	1.20 (0.11)m
Unthinned	0.49 (0.04)	0.32 (0.03)	40.95 (3.79)	1.85 (0.17)m
Both[a]	0.28 (0.03)r	0.27 (0.02)r	45.14 (4.17)s	1.49 (0.14)
November–December				
Thinned	0.97 (0.09)	0.78 (0.07)	324.69 (30.03)	6.25 (0.58)m
Unthinned	0.75 (0.07)	0.56 (0.05)	928.48 (85.88)	7.28 (0.67)m
Both[a]	0.85 (0.08)r	0.66 (0.06)r	549.06 (50.78)s	6.75 (0.62)

[a] Marginal LS medians and means connected by lines were not significantly different (Tukey's HSD test, $\alpha = 0.05$).

reflect a greater crown space requirement for trees of a given stem diameter, which can help guide thinning intensities. However, GSI can also change as trees get larger, reflecting different allocation patterns over time. Thinning should ideally be applied after canopy closure but when trees are at their maximum GSI. This allows for the greatest stem growth response. On wet sites, GSI of koa declines with stem diameter and reaches an asymptotic value at ~20 cm; on dry sites the opposite is true: GSI increases with stem diameter until ~20 cm DBH (Baker and Scowcroft, 2005). According to this criterion, thinning on wet sites should occur soon after canopy closure; whereas, on dry sites, it can be delayed until crop trees approach 20 cm DBH. Applying this criterion to the present study, thinning should have been done earlier for optimum growth response.

The most likely explanation for a lack of response to thinning alone is that insufficient time had elapsed for released trees to expand their crowns into the empty growing space created by thinning (e.g., Carlyle, 1998). Tree crowns did not increase in size the second and third years after treatment in response to thinning alone. It is possible that the relatively small crowns of released trees will increase in size over time and that

Table 5

Median (mean) NO_3^--N and NH_4^+-N captured on ion-exchange resins ($\mu g \, N \, bag^{-1} \, day^{-1}$) that were buried 4–6 cm below the soil surface and incubated for approximately 45 days (May–June 2003) or 55 days (November–December 2003), by canopy and forest floor treatments, and by sample period

Canopy treatment	Nitrate-N				Ammonium-N			
	Control	Herbicide	Herbicide + P	All[a]	Control	Herbicide	Herbicide + P	All[a]
May–June								
Thinned	173.79 (211.31)	119.54 (145.35)	124.73 (151.66)	137.35 (167.01)	4.38 (10.59)	8.46 (19.38)	9.58 (21.81)	7.13 (16.53)
Unthinned	134.62 (163.68)	161.05 (195.82)	141.90 (172.54)	145.44 (176.84)	6.23 (14.57)	4.65 (11.17)	7.13 (16.52)	5.92 (13.92)
Both[a]	152.96 (185.98)	138.75 (168.71)	133.04 (161.76)	141.34 (171.85)	5.23 (12.43)	6.31 (14.75)	8.28 (18.99)	6.50 (15.17)
November–December								
Thinned	132.94 (161.64)	100.10 (121.72)	80.04 (97.32)	102.13 (124.18)	14.17 (31.70)	9.59 (21.82)	7.89 (18.17)	10.26 (23.28)
Unthinned	104.77 (127.39)	89.31 (108.59)	102.71 (124.88)	98.68 (119.99)	17.05 (37.90)	11.72 (26.43)	22.94 (50.60)	16.65 (37.04)
Both[a]	118.02 (143.50)	94.55 (114.97)	90.67 (110.24)	100.39 (122.06)	15.55 (34.67)	10.61 (24.02)	13.59 (30.45)	13.10 (29.39)

[a] No significant differences were detected among factor level medians (means) for either ion for either incubation period (Tukey's HSD test, $\alpha = 0.05$).

tree growth will increase proportionately. If so, it would argue for thinning before age 20 years in wet forest sites, before severe reduction in crown size limits the potential for rapid growth responses. Growth responses within 2 years of thinning have been reported in young koa stands (Pearson and Vitousek, 2001; Scowcroft and Stein, 1986).

The lack of a statistically significant crop tree response to thinning alone might also be due in part to the fact that neighbor-tree competition for light was minimal. All of the crop trees in the present study were in dominant and co-dominant crown classes; tree crowns did not overlap or intermingle and shading appeared to be confined to the lowest edges of each crown (Perry, 1985). In dense young stands neighbor shading probably plays a bigger role in regulating growth, which would explain why residual 9- and 12-year-old koa grew significantly faster when thinned (Pearson and Vitousek, 2001; Scowcroft and Stein, 1986).

The 25–30-year-old koa trees in this study did respond significantly to thinning when combined with grass control and P fertilization. The response might have been caused by increased leaf area, increased light use efficiency due to increased P concentrations in foliage (Table 3), or increased allocation of photosynthate to stem wood rather than root production (Keith et al., 1997; Ryan et al., 1997). The most obvious reason for growth increases would be increased leaf area. Application of triple superphosphate at time of planting produced significant increases in crown volumes and, by implication, leaf area of 3-year-old koa that were grown in highly weathered, low elevation Oxisol and Ultisol soils on the island of Oʻahu (Scowcroft and Silva, 2005). Data from the present study are somewhat ambiguous, however. Analysis of leaf area increment, which was based on an allometric equation, indicated that thinning significantly increased leaf area of crop trees between 2003 and 2005. The increases were small, though: trees in thinned plots gained approximately 10% more leaf area during the period and trees in unthinned plots gained just 6% more leaf area. Furthermore, the use of allometric equations developed for unfertilized trees might be inappropriate for fertilized ones (Harrington and Fownes, 1993). Analysis of crown diameter growth, which was an independent index of leaf area increment, also showed that fertilization combined with thinning significantly increased crown diameter increment, but again the changes were all quite small (<0.25 m year^{-1}). Other measures of crown attributes, such as projected crown area, crown depth, live crown ratio and crown volume were unaffected by treatments. Based on these observations and lacking an independent measure of leaf area, such as hemispherical photos, we hesitate to credit increased DBH growth to stimulation of leaf production.

The lack of an independent measure of leaf area or photosynthetic rate also limits our ability to determine whether or not greater photosynthetic efficiency of existing foliage is responsible for increased growth rates. In general, leaf chlorophyll content and photosynthetic capacity are strongly related to N concentration, including koa (Ares et al., 2000). Our study showed no differences in leaf N concentration with any treatment. Although leaf P concentration can affect

photosynthetic capacity, trees appear to respond to increased soil P availability by greatly increasing soil P uptake and leaf concentration out of proportion to any corresponding growth response (Harrington et al., 2001). This response may be due to the large investment plants make in acquiring soil P, which is only sparingly soluble and highly immobile in most soils. Thus, when soil P availability increases, higher uptake may lower P use efficiency but increase biomass P.

Additionally, plant energy expenditure per unit of P acquired should be reduced under high soil P availability. Coupled with greater internal P concentrations, reduced energy expenditure per unit of P uptake might mean that trees and other perennial plants have greater energy available for allocation to above-ground growth under conditions of greater soil P availability. Thus, it is quite possible that alteration of energy and biomass allocation is in large part responsible for the growth response of koa in the P fertilization sub-treatment in our study. We have not made estimates of root growth or biomass allocation, so this hypothesis remains untested.

4.2. Soil nutrient limitations to growth

The prevailing view about the effect of soil development on nutrient limitations to plant productivity is that N is limiting on young, relatively unweathered substrates, P is limiting on old, highly weathered substrates, and both N and P are potentially limiting on intermediate age substrates (Crews et al., 1995; Vitousek and Farrington, 1997). In our study, soil N availability was relatively high on these relatively young soils. Pearson and Vitousek (2001) found similarly high soil N availability in a 9-year-old koa stand in the Keauhou area. Koa is an N-fixing tree, although estimated annual rates in young stands are generally less than 20 kg ha^{-1} and these rates decline with stand age (Pearson and Vitousek, 2001). The high soil N availability is perhaps a reflection of a slow accumulation of N from fixation coupled with rapid cycling among plant biomass, soil organic matter, and mineral N pools.

Pearson and Vitousek (2001) suggested rather that growth of koa may be increasingly P limited with stand age, a situation brought about when input of P by weathering lags P accumulation in biomass. Chapin et al. (1994) indicated that large N inputs to relatively unweathered parent material from an N-fixer could create a P limitation for plant growth that would not otherwise exist. Our data supports this hypothesis. Along with high soil N availability, we saw a significant increase in soil P availability, leaf P concentration, and crop tree growth response to P fertilization.

5. Conclusions

Girdling is an effective means of killing competing koa trees and is appropriate for use in secondary stands where the management objective is to minimize damage to animal life and advanced native understory vegetation. Where the understory is comprised of alien grasses and other introduced species, or where the koa stand is relatively young and in the early stage of self-thinning, felling might be preferable to girdling.

The limited 3-year growth response of 25–30-year-old koa crop trees to thinning alone was most likely due to the inability of the small, relatively unshaded crowns to take advantage of growing spaces created by thinning. Greater response might still occur given more time. Failing that, we believe that our results and those of other studies support the notion that thinning, as a sole treatment should be done early in stand development while crowns are large relative to stem diameters. Positive correlations between stem diameter growth rate and both crown vigor and live crown ratio argue for early thinning. However, the timing of such thinning will have to be balanced against the high cost of treating younger, denser stands and the manager's ability to differentiate potential crop trees from non-crop trees.

Our results indicate that thinning well after stand closure can elicit an immediate growth response on moist/wet sites if supplemented with grass control and fertilization. Improved P status and the light conversion efficiency of foliage might account for improved growth because leaf area and crown size changed very little 3 years after thinning. Increased biomass allocation aboveground might also contribute to increased growth rates. The failure of grass control alone or in combination with thinning to significantly improve crop tree growth indicates that grass competition for water and/or nutrients was minimal.

Acknowledgements

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