

Sudden and sustained response of *Acacia koa* crop trees to crown release in stagnant stands

Patrick J. Baker, Andrew P. Robinson, and John J. Ewel

Abstract: We examined the growth response of *Acacia koa* Gray (koa) in dense (10 000 trees/ha), ~25-year-old, second-growth stands on Hawai'i to crown release (thinning) and grass control. Koa diameter increment increased within 2 months of thinning across the range of residual densities (200–900 trees/ha). After 3 years, diameter increment in the most intense thinning treatment was 180% greater than in the control treatment (1.4 vs. 0.5 cm/year); in the least intense thinning treatment diameter increment was 100% greater than the control (1.0 vs. 0.5 cm/year). Koa's growth response was independent of all measures of tree size (diameter at breast height, height, and leaf area) across the range of tree sizes sampled. A grass control treatment to determine if reduced competition for soil water would improve koa growth showed no improvement in growth response. Koa phyllode $\delta^{13}\text{C}$ values, which represent an integrated measure of tree water status, showed no evidence of tree water stress (mean $\delta^{13}\text{C} = -28.3\text{‰}$) and were not significantly different between the grass removal and control treatments. These results demonstrate that koa is capable of responding quickly and positively to crown release despite years of suppressed growth and suggest that landowners interested in managing koa forests may have considerable flexibility in the timing and application of thinning treatments to koa stands.

Résumé : Nous avons étudié la réaction en croissance d'*Acacia koa* Gray (koa) à la suite d'un dégagement de la cime (éclaircie) et de la maîtrise de la végétation herbacée dans des peuplements denses (plus de 10 000 tiges/ha) de seconde venue, âgés d'environ 25 ans et établis dans l'État d'Hawai'i, aux États-Unis. L'accroissement en diamètre du koa a augmenté moins de 2 mois après l'éclaircie pour toute l'étendue des densités résiduelles étudiées (200 à 900 tiges/ha). Pendant la période d'étude, d'une durée de 3 ans, l'accroissement en diamètre des arbres du traitement de dégagement de la cime le plus intense était 180 % plus élevé que celui du traitement témoin (1,4 vs. 0,5 cm/an). Dans le cas de l'éclaircie la moins intense, l'accroissement en diamètre des arbres était 100% plus élevé que celui du témoin (1,0 vs. 0,5 cm/an). La densité des arbres voisins avant l'éclaircie a eu un petit effet positif sur la réaction en croissance. Cependant, la réaction en croissance du koa était indépendante de toutes les mesures de la taille des arbres (diamètre à la hauteur de poitrine, hauteur et surface foliaire) pour toute l'étendue de taille des arbres échantillonnés. Un traitement de maîtrise de la végétation herbacée, qui a été appliqué pour déterminer si une diminution de la compétition pour l'eau dans les horizons supérieurs du sol pouvait améliorer la croissance du koa, n'a pas produit de réaction en croissance. Les valeurs de $\delta^{13}\text{C}$ des phylloides de koa, qui représentent une mesure intégrée du statut hydrique des arbres, n'ont pas démontré que les arbres subissaient un stress hydrique (valeur moyenne de $\delta^{13}\text{C} = -28,3\text{‰}$) et ne différaient pas significativement chez les traitements de maîtrise de la végétation herbacée et témoin. Ces résultats démontrent que le koa est capable de réagir rapidement et positivement à un dégagement de sa cime malgré des années de croissance opprimée et indiquent que les propriétaires intéressés à aménager des forêts de koa peuvent avoir une flexibilité considérable en ce qui a trait au moment et au mode d'application de l'éclaircie dans les peuplements de koa.

[Traduit par la Rédaction]

Introduction

One of the fundamental conundrums in forest management is that it is not possible to maximize stand growth and individual tree growth simultaneously (Assmann 1970; Smith et al. 1996). To maintain maximum stand-level growth, foresters must ensure that all of the growing space within the stand is always occupied. However, if all of the growing space is occupied, growth of individual trees will

decrease as they grow and experience competition for resources, particularly light, from their neighbors (Oliver and Larson 1996). This inherent trade-off in forest growth has required foresters to develop compromise solutions, in which stand growth and individual tree growth are alternately increased through a silvicultural regime of thinnings. The development of thinning regimes that provide the best compromise between stand- and tree-level growth has been the focus of forest science for over a century. However,

Received 5 February 2007. Accepted 22 June 2007. Published on the NRC Research Press Web site at cjfr.nrc.ca on 11 March 2008.

P.J. Baker^{1,2} and J.J. Ewel. USDA Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, 23 East Kawili Street, Hilo, HI 96720, USA.

A.P. Robinson.³ Department of Mathematics and Statistics, University of Melbourne, Parkville, Victoria 3010, Australia.

¹Corresponding author (e-mail: patrick.baker@sci.monash.edu.au).

²Present address: School of Biological Sciences, Monash University, Victoria 3800, Australia.

³Present address: Department of Botany, University of Florida, Gainesville, FL 32611, USA.

most of that research has focused on stand-level prescriptions for stand-level production of commodity tree species. Relatively little research has focused on individual-tree prescriptions, such as crop-tree release, that maximize the value of individual trees.

For high-value hardwoods, such as black cherry (*Prunus serotina* Ehrh.), teak (*Tectona grandis* L.), and mahogany (*Swietenia* spp.), that are shade intolerant and regenerate vigorously after intense disturbances, individual trees may be worth thousands of dollars. Early decisions during the management cycle for such species will determine their long-term value, making individual-tree thinning regimes such as crop-tree release a potentially valuable silvicultural tool (Ellis 1979; Lamson et al. 1990; Singer and Lorimer 1997). If landowners are able to focus their silvicultural energies on maximizing the value of individual trees, they may be able to maintain continuous forest cover for longer periods, which may be of conservation and aesthetic value, particularly to small-scale, nonindustrial landowners.

However, crop-tree release presents certain challenges. The primary challenge is to identify the level of thinning required to generate a significant and sustained growth response (e.g., Erdmann et al. 1981). In dense stands of regenerating trees, growth release may be slow because of stagnation or thinning shock. If the thinning is too light, it may have little effect on the future crop tree. If the thinning is too heavy, it might lead to thinning shock and little or no growth response, the formation of epicormic sprouts, or a reduction in wood quality due to the development of large branch knots. Also, where stands have experienced prolonged growth stagnation, it is important to assess whether individual trees are even capable of responding to thinning. In many cases, empirical guidelines for crop-tree release do not exist, thereby limiting its potential application.

Acacia koa Gray (koa) is one of two dominant tree species in the native submontane forests of Hawai'i. During the past century, widespread logging and cattle grazing have led to the degradation of koa forests across their historical range. The increasing scarcity of intact and productive stands of koa and the inherent beauty of the wood have led to sharp increases in the value of koa timber in the past 15 years. As a consequence, high-quality koa boards are among the most valuable timbers in the world, often reaching prices in excess of US\$50/board ft (US\$21 200/m³). Koa forests also have significant conservation values, because they provide habitat for many of Hawai'i's endemic, and often threatened, birds, insects, and plants (Gon 2006). As profits from cattle ranching decline and the value of koa rises, there is increasing interest in reestablishing koa forests for both conservation values and wood production. However, despite the ecological and economic importance of koa, many basic questions regarding its autecology and silviculture remain unanswered (Baker et al. 2008).

Currently, the standard method of regenerating koa is mechanical soil scarification by bulldozer during or immediately after logging operations. The hard-coated koa seeds germinate readily when exposed to direct sunlight and in contact with mineral soil (Whitesell 1990). As long as a viable koa seed bank exists and herbivory by ungulates is controlled, regeneration is often profuse. Indeed, koa sapling densities of 50 000–300 000 stems/ha have been reported

following natural and mechanical disturbances (Scowcroft and Nelson 1976; Scowcroft and Wood 1976). In such densely regenerating stands, the fast growth of koa quickly leads to intense intraspecific competition and considerable mortality from self-thinning (Pearson and Vitousek 2001; P.G. Scowcroft and D. Fujii, USDA Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, Hilo, Hawai'i, unpublished data). However, the self-thinning mortality does not reduce stand density sufficiently to maintain the early high growth rates of koa, and individual and stand-level basal area growth quickly stagnate (Pearson and Vitousek 2001). To avoid losing valuable years of growth to stagnation, forest managers must actively control stocking densities of koa (Baker and Scowcroft 2005). For most established second-growth koa stands, stocking control will involve thinning. However, because koa forests have historically been treated as extractive rather than renewable resources, forest managers in Hawai'i have little experience with silvicultural treatments, such as thinning.

The high value of koa and the premium value associated with good stem form mean that thinning prescriptions that target individual, high-quality trees may provide increased economic revenues to the landowner. However, evaluating growth response of koa to individual-tree crown release is not straightforward. Past logging practices that focused on extracting individual trees left networks of skid trails and logging decks on which koa seeds germinated. These ribbons and patches of dense koa vary in local density as a function of site conditions and scarification intensity. As a consequence, individual tree size, the density and size of neighboring trees, and the local abundance of grass cover are highly variable. Grass cover is of particular concern, because koa productivity is closely related to water availability (Ares and Fownes 1999). The thick mats of alien pasture grasses may limit koa growth by intercepting and absorbing much of the water reaching the soil surface before it can penetrate to the deeper koa roots. To determine the effects of thinning, it is important to account for the influence of these potential covariates. Most thinning studies have focused on replicated split-block designs in which a large area of uniform second-growth forest or plantation is divided into subunits, which are assigned to different stand-level thinning treatments (e.g., Bevilacqua et al. 2005; Brockley 2005). Because of the patchy nature of koa regeneration in the forest, this approach is not feasible for many koa stands. As such, to evaluate the response of koa to thinning, we have had to take a different approach to sampling and statistical analysis than previous studies of thinning response.

The broad goal of this study was to assess how koa in pure, dense patches scattered throughout an upland Hawaiian forest respond to a range of thinning treatments. To do so, we have addressed several specific questions. (i) Are koa in stagnant, overstocked stands capable of responding to release? (ii) If so, is growth response related to the intensity of thinning? (iii) Is there a threshold thinning intensity below which koa will not respond? (iv) Does removing the grass cover, which competes for available water and nutrients in the upper portion of the soil profile, lead to increases in growth? (v) Do other factors such as prethinning stand density and tree size influence koa growth response to thinning?

Table 1. Summary statistics for the initial conditions of the trees by treatment.

Treatment and target density (trees/ha)	Diameter (cm)		Pretreatment density (trees/ha)		Post-treatment density (trees/ha)	
	Mean	SD	Mean	SD	Mean	SD
No herbicide						
200	15.1	2.42	11 530	8 754	178	24.5
300	17.8	5.66	5 031	3 158	283	36.0
400	13.5	2.97	8 692	6 002	394	40.3
500	13.1	2.88	18 507	7 272	439	67.0
700	14.7	3.79	7 180	4 095	568	66.5
900	15.8	5.29	9 046	7 425	712	184.6
Unthinned	16.1	4.28	12 235	9 272	12 235	9271.9
Herbicide						
200	14.7	1.25	8 823	5 781	190	27.5
300	15.4	2.96	9 044	8 773	246	36.3
400	16.2	3.40	12 335	9 002	338	40.7
500	13.7	1.80	14 129	13 052	404	61.2
700	16.5	3.75	10 584	8 140	543	79.9
900	13.4	3.24	8 916	5 922	708	104.3
Unthinned	14.3	2.67	9 635	7 284	9 635	7283.8

Methods

Study area

The study was conducted in the Honomalino tract of The Nature Conservancy of Hawai'i's Kona-Hema Preserve located in south Kona on the leeward side of the island of Hawai'i (19°12'N, 155°47'W). Elevation at the study site ranges from 1450 to 1550 m above sea level. The soils are thin and overlay volcanic substrate ('a'ā lava) that formed ca. 1200–3000 year ago. Local topography is variable with a gentle slope to the east overlain by series of ridges and gulleys running perpendicular to the contour that were created by collapsing lava tubes. Mean annual precipitation is ca. 1200 mm and is relatively uniformly distributed throughout the year.

The study was conducted in dense ribbons and patches of even-aged, second-growth koa that developed after logging in the late 1970s. Unlike many other areas on Hawai'i, cattle were excluded from the Honomalino site for several years following logging, leading to the establishment of dense re-growth stands of koa. In the subsequent two decades, the landowners made no efforts to reduce the high stocking levels of koa in these stands. As a consequence, for at least the past 5 years, diameter increment has slowed because of overcrowding and poor differentiation of the koa canopy (The Nature Conservancy Hawai'i, unpublished forest inventory data (1998–2002)). The stands are largely dominated by koa, but other native canopy tree species, such as *Metrosideros polymorpha* Gaud. ('ō'hia), *Myoporum sandwicense* Gray (naio), and *Myrsine sandwicensis* A. DC. (kōlea), are also common.

Sampling and measurements

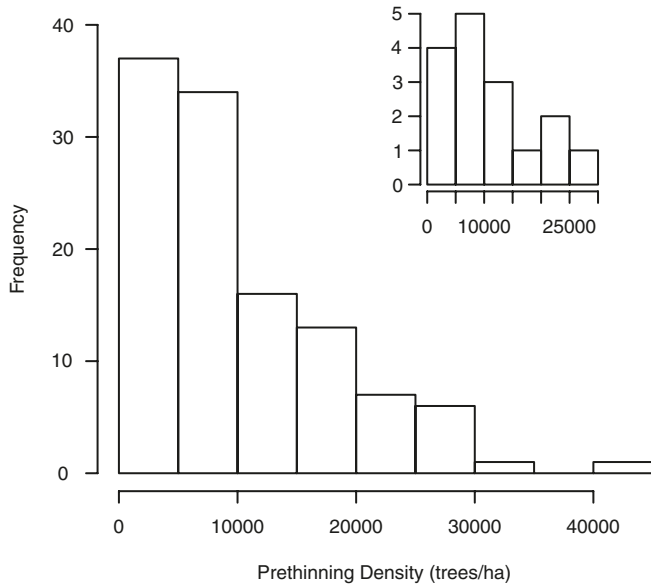
Randomly spaced transects extending away from former skid trails were established in an area of approximately 500 ha. At 25 m intervals along each transect, the nearest koa tree meeting the following criteria was selected for the study. Each koa tree in the study had to (i) be in the main

canopy of the forest (in general, this meant trees were >15 cm diameter at breast height (DBH, 1.4 m) and >12 m tall), (ii) have a healthy crown (i.e., no evidence of dieback or disease), and (iii) be free of obvious deformities or wounds along the main bole. These criteria focused tree selection on potential future koa crop trees. If no koa meeting these criteria could be found within 5 m of the selection point, the point was abandoned, and the next point along the transect was selected. One hundred and fifteen koa trees were selected for the thinning trial and randomly assigned to a thinning treatment.

Thinning treatments were designed to create a range of crown release conditions for individual koa trees. This was achieved by varying the distance from the focal study tree to within which all neighboring trees were cut and left on the forest floor. Six distances, ranging from 3.76 to 7.98 m, were used, representing approximate residual densities of 200, 300, 400, 500, 700, and 900 trees/ha. Focal tree height was 13.5 ± 1.8 m (mean \pm SD), meaning that the least and most intense thinning treatments were roughly equivalent to 30% and 60% of the mean canopy height of the stand. In addition, we included a control, in which no trees were cut, as the seventh treatment. Table 1 shows the summary statistics for each of the thinning treatments. Mean density around the control trees was 10 326 trees/ha (range 640–44 915 trees/ha) (Fig. 1). Individual study trees were randomly assigned one of the seven treatments, such that there were approximately equal numbers (16 or 17 trees) in each treatment. All koa trees within the selected radius of the study tree were mechanically harvested and left on the ground. In the few instances in which other native tree species were present, they were left uncut; however, none were larger than the study tree (most were 'ō'hia saplings <2 m tall).

To determine the influence of the thick grass cover on growth response of koa to thinning, we applied a grass control treatment around one-half of the study trees in each thinning treatment. From each thinning treatment, we ran-

Fig. 1. Frequency distribution of prethinning densities of all 115 study trees. The inset figure is the prethinning densities of the control trees showing the wide range of conditions included in the control “treatment.”



domly assigned a grass control treatment to eight trees. Grass control included application of a general herbicide (RoundUp™) 3–4 weeks prior to thinning and subsequent application of a grass-specific herbicide (Fusilade™) approximately 1 year later. The herbicide was applied to all grass cover within 7.98 m of the study trees (i.e., equivalent to the radius of the most intense thinning treatment).

Detecting early growth responses to thinning and grass control requires a sensitive measurement of tree size. The analyses presented here focus on DBH. To measure short-term changes in DBH, we attached band dendrometers (Series 5 manual band dendrometer; Agricultural Electronics Corporation, Tuscon, Ariz.) capable of measuring changes as small as 0.1 mm in circumferential growth (0.03 mm DBH growth). Measurements were taken approximately every 2 months from November 2002 until March 2006.

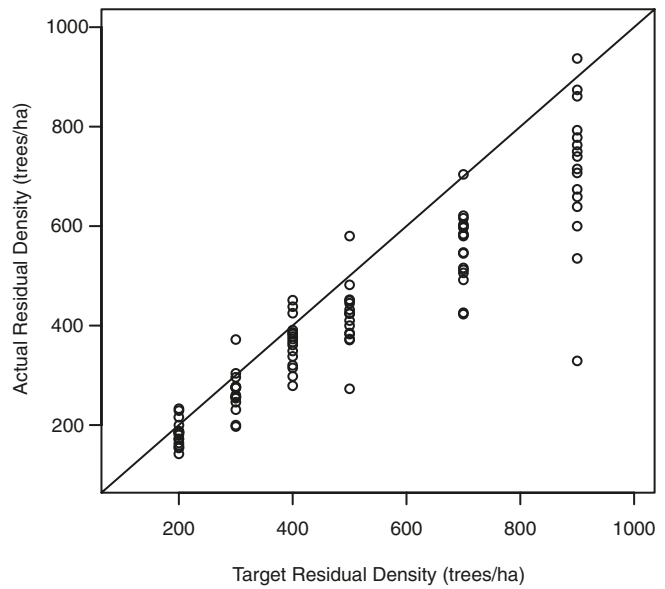
Several other measurements were taken for each study tree to identify covariates that might influence growth response to thinning intensity. These included initial DBH, tree height, and crown length. In addition, because prethinning stocking levels around individual study trees varied, we quantified pre- and post-thinning stocking levels using a point-centered quarter method (Fig. 2). The distance to the closest tree in each quadrant (D_i , defined by the cardinal directions, was measured before and after the thinning treatment. For each tree, the four measurements were averaged and used to calculate local density using an unbiased estimator (Pollard 1971):

$$D_i = \frac{3}{\pi \bar{r}_i^2}$$

where \bar{r}_i is the mean of r_{ij} , which is the distance from the center tree i to the nearest tree in quadrat j .

To assess whether the thinning and grass control treatments influenced the water status of the study trees, we ob-

Fig. 2. A comparison of target residual densities and actual residual densities for the thinning treatments used in the study. The line shows the expected 1:1 relationship and demonstrates that the actual treatments were more intense than expected. Actual residual densities were used in analyzing growth responses.



tained $\delta^{13}\text{C}$ values for phyllodes from each tree. The $\delta^{13}\text{C}$ value is commonly used as an index of plant water status as the $^{13}\text{C}/^{12}\text{C}$ ratio depends on the ratio of partial pressure of intercellular CO_2 (P_i) to ambient CO_2 (P_a). The P_i/P_a ratio reflects intrinsic water-use efficiency (= assimilation/stomatal conductance) (Farquhar et al. 1982) such that higher $\delta^{13}\text{C}$ values are associated with drier growing conditions. To measure $\delta^{13}\text{C}$ values for koa, we removed three or four small branches from the upper crown of each study tree. From each branch, we haphazardly selected and removed several phyllodes, which were then placed together in a labelled bag, stored in a cooler, and sent to the University of Hawai‘i’s Isotope Biogeochemistry Laboratory in Honolulu for determinations of $\delta^{13}\text{C}$. Ratios of $^{13}\text{C}/^{12}\text{C}$ were measured on a Thermoquest/CE Instruments (Waltham, Massachusetts) automated elemental analyzer (model 1110 NC 2500) interfaced to a Finnigan (Waltham, Massachusetts) MAT Delta-S stable isotope ratio mass spectrometer via a Finnigan MAT ConFlo II (continuous flow) interface. The $\delta^{13}\text{C}$ values were compared across thinning intensities and the grass control treatments with a linear model.

Analyses

We used a variety of graphical and statistical techniques to determine how thinning and grass control affected DBH increment of koa and how the growth response was influenced by several covariates related to stand and tree structure. Studies in which a subject is measured repeatedly to assess the impact of a treatment upon it can violate a basic assumption of many statistical models, which is that the residuals from individual observations must be independent of each other. When a tree’s DBH is remeasured several times, the observations are more likely to resemble one another than they are to resemble DBH measurements from a different randomly selected tree. Therefore, if inappropriately

modelled, the residuals within the tree will not be independent of one another—they will be correlated—making parameter estimates less efficient and biasing measures of variation and the results of tests that depend on them.

To account for this lack of independence, many studies that assess the growth response or physiological response of trees to silvicultural treatments use repeated-measures ANOVA (e.g., Aranda et al. 2001; Cañellas et al. 2004; Brockley 2005). However, although repeated-measures ANOVA is useful for certain repeated-measures experimental designs, it is not always the most appropriate statistical approach, because it assumes that the correlations among residuals and the variance of the residuals remain constant over time. When many repeat measurements are taken over a relatively short period, when they are relatively close to each other in time, or when the amount of time between measurement periods varies (all of which apply to our study), these assumptions may not hold (Kristensen and Hansen 2004).

Mixed-effects ANOVA and ANCOVA models provide an attractive alternative because of their greater flexibility and well-developed infrastructure (Pinheiro and Bates 2000) and have several distinct advantages over repeated-measures ANOVA. Firstly, by incorporating random effects that reflect the experimental design, the problems of nonconstant correlations and homogeneity of residuals may be avoided. Secondly, incorporation of the random effects of each experimental unit allows us to use each measurement to estimate the model parameters, as opposed to repeated-measures ANOVA, which treats each measurement period independently. Thirdly, because we made 16 measurements in 3.5 years, the temporal autocorrelation of the growth measurements is relatively complex. The mixed-effects modeling framework allowed us to explicitly incorporate the temporal autocorrelation structure of our data into the analysis, thereby eliminating a potentially important source of inefficiency in model estimation and bias in parametric testing. All analyses were conducted with the open-source statistical package R (version 2.4.1, R Development Core Team 2006). Mixed-effects models were implemented using the nlme package of R (Pinheiro and Bates 2000).

We were interested in the impact of five general factors on the growth response of koa. These were (i) time since treatment, (ii) tree size, (iii) stand conditions prior to treatment, (iv) stand conditions following treatment, and (v) the influence of grass control by herbicide. To assess the relative influence of these variables required a multistep modeling process. The first step involved addressing an important artefact of thinning studies with “control” treatments. Local stand density, the main thinning treatment effect, varies much more for the unthinned control trees than for crop trees receiving the release thinning. Because the control “treatment” is not a uniform treatment (Fig. 1), a single, straightforward statistical model will either result in an oversimplified picture of the underlying process or return a set of estimates that are not easily interpreted in the context of forest management. To accommodate this problem, we first tested the impacts of thinning on koa growth response by comparing the control treatments with all of the thinning treatments pooled together. Effectively, we treated thinning as a binary predictor variable (thinning vs. no thinning) to determine if thinning influenced the growth response of koa

(model 1). The second modeling step was then to exclude the control treatment and test for an effect of thinning intensity on growth response on only those trees that had received crown release (i.e., independent of the control trees) (model 2). In each case, as we describe in more detail below, these first two modeling steps included all of the potential covariates describing the influence of time since treatment, tree size, and stand conditions before and after treatment, as well as the interactions among them. We refer to these as the complete models. The third and final modeling step was to remove statistically insignificant terms from the complete models to identify which predictor variables influence koa growth response and to what degree. It is known that parameter estimation following variable selection procedures is prone to bias (e.g., see Chatfield 1995). We decided to trade off a modest risk of bias in our parameter estimates for a substantial increase in interpretability and utility of the end model. All of the models include a detailed random-effects structure to account for both the inherent hierarchy of the data set and the temporal autocorrelation of the residuals within the trees that results from the repeated-measures design of the experiment. Each of the models is now described in greater detail.

Model 1

The first model predicts growth as a function of time and a set of other predictor variables, incorporating thinning as a binary treatment variable. The response variable is the change in diameter from the first measurement. Therefore, the first measurement is not included in the fitting data, because it is automatically zero. The main effects included in the model are (i) the time that has passed since the first measurement, in years, up to cubic power; (ii) the stem density (trees/ha) prior to treatment; (iii) measures of tree size, including the initial DBH of the tree and a proxy measure of leaf area; (iv) herbicide treatment (yes or no); and (v) thinning of neighboring trees (yes or no).

The terms of interest are interactions involving the treatments and time, as these represent the effect of the treatments on the growth rates. We included quadratic and cubic terms for time since treatment to assess the linearity of the growth response. Many of the terms are included in the model to preserve heredity; that is, that the main effects included in interactions must all be present in the model. Our model incorporates up to five-way interactions, for example, we test whether the effect upon growth of the interaction of time, herbicide, thinning, and initial stocking varies depending on initial tree size (it does not, happily). Our proxy measure of leaf area (LA_p) was defined as the product of basal area and length of the live crown. We transformed two variables, pre- and post-thinning density around each study tree, prior to modeling to reduce collinearity between these terms and their quadratic powers. Both were centered and scaled by subtracting the mean density from the observed density and dividing the result by 1000.

Model 2

The second model also predicts growth as a function of time and a set of other predictor variables but only for the thinned trees. Again, the response variable is the change in diameter from the first measurement, which is not included

in fitting the data. The main effects included in the model are the same as in model 1 except that the binary thinning variable (the fifth main effect above) is removed, and thinning treatment now enters as a continuous variable: the number of stems per hectare after thinning. For the analyses, we used the actual post-thinning density and not the target post-thinning density, because the former provided a more accurate description of the local density following thinning (Fig. 2). We also added a quadratic term for post-thinning density to determine if there was a nonlinear effect of post-thinning intensity on growth response. The terms of interest are, again, interactions involving treatments and time, because these represent the effect of the treatments on the growth rates. The data transformations used in model 1 were also used in model 2.

Reduced models

To ease interpretability and to develop a quantitative model that best describes the impact of various factors on koa growth response, we developed two reduced models (one each for models 1 and 2). The reduced models include only those predictor variables and interactions that were significant in the complete models and any terms necessary to preserve model heredity. In both cases, the reduced model was much simpler than the complete model. Models 1 and 2 began with 27 and 28 predictor variables, respectively; the reduced models each had 10 predictor variables.

Results

Are koa in stagnant, overstocked stands capable of responding to release?

The mean diameter growth rate of koa in the untreated stands during the first year of the study was 2.9 mm/year, demonstrating the degree to which the growth of these koa stands had stagnated. This is further supported by unpublished growth data (1999–2002) from 60 permanent forest inventory plots at Honomalino that showed a mean growth rate for koa of 3.4 mm/year. Comparison of diameter growth of koa between the control (no thinning) and released (thinning) crop trees (model 1) demonstrated a highly significant positive impact of thinning on koa growth (Table 2). The temporal response of growth varied with time as evidenced by significant parameter estimates for the year variables. However, among the 23 variables related to the treatment of the stand, potential covariates, and the interactions among these terms, only one, thinning treatment, was significant at $\alpha < 0.01$. Based on these results, we fitted the reduced model using only the 3 year variables, thinning, and the year \times thinning interaction (Table 3). Although the quadratic year term and thinning term were not significant in the complete model, they are included in the reduced model, because they are required for heredity in the higher order polynomial and interaction effect, respectively. The results of both the complete and reduced models demonstrate that thinning has a significant impact on growth of koa.

Is growth response related to the intensity of thinning?

Having demonstrated that thinning has a significant positive impact on growth with model 1, we then evaluated the impact of thinning intensity by excluding the unthinned con-

Table 2. Summary of results for the complete model 1, which tests the effect of the thinning and herbicide treatments upon growth.

Parameter	<i>F</i>	<i>p</i>
Intercept	53.6	<<0.001
Year (Y)	651.0	<<0.001
Y ²	1.21	0.271
Y ³	33.6	<<0.001
Prethinning density (D _{pre})	0.58	0.449
Proxy leaf area (LA _p)	3.62	0.059
Y \times D _{pre}	3.85	0.049
Initial DBH (DBH _i)	0.23	0.635
Herbicide (H)	4.69	0.033
Thinned (T)	3.30	0.072
Y \times DBH _i	0.39	0.535
Y \times H	0.63	0.429
Y \times T	38.5	<<0.001
Y \times H \times T	0.06	0.800
LA _p \times T	1.23	0.270
Y \times LA _p	2.82	0.093
Y \times LA _p \times T	0.15	0.700
Y \times D _{pre} \times H	0.09	0.762
Y \times DBH _i \times H	0.04	0.849
Y \times D _{pre} \times T	1.03	0.310
Y \times DBH _i \times T	0.78	0.377
Y \times D _{pre} \times DBH _i	5.13	0.024
Y \times D _{pre} \times H \times T	0.003	0.953
Y \times D _{pre} \times DBH _i \times T	0.07	0.791
Y \times D _{pre} \times DBH _i \times H	2.41	0.121
Y \times DBH _i \times H \times T	0.35	0.553
Y \times D _{pre} \times DBH _i \times H \times T	0.16	0.688

Note: Our inference used sequential *F* tests as summarized by the *F*-value and *p*-value columns. Proxy leaf area is the product of basal area (m) and the length of the live crown (m). See text for details. DBH, diameter at breast height (cm).

Table 3. Summary of results for the reduced form of model 1.

Parameter	Estimate	SE	<i>F</i>	<i>p</i>
Intercept	-0.0217	0.0461	26.8	<<0.001
Year (Y)	0.0897	0.1301	604.0	<<0.001
Y ²	0.3488	0.0569	0.011	0.916
Y ³	-0.0633	0.0100	40.0	<<0.001
Thinned (T)	-0.0799	0.0457	4.15	0.044
Y \times T	0.6779	0.1186	32.7	<<0.001

Note: Our inference used sequential *F* tests as summarized by the *F*-value and *p*-value columns.

trol trees from our analyses in model 2. As with model 1, there was significant variation in the temporal response of growth release as evidenced by significant parameter estimates for the 3 year terms. Among the 24 variables related to treatment effects and pre- and post-thinning stand structure, only two were significant (Table 4). The most significant variable was the year \times thinning intensity interaction ($p = 0.00017$). The other significant variable was the year \times prethinning density interaction ($p = 0.011$). The reduced model included the 3 year terms and the pre- and post-thinning treatment densities and their interactions with the year term (Table 5). The year \times post-thinning treatment

Table 4. Summary of results for the complete model 2, which tests the effect of herbicide and the different thinning treatments upon growth.

Parameter	<i>F</i>	<i>p</i>
Intercept	54.5	<<0.001
Year (Y)	756.0	<<0.001
Year ²	0.00178	0.966
Year ³	31.3	<<0.001
Initial DBH (DBH _i)	2.05	0.156
LA _p	1.07	0.304
Prethinning density (D _{pre})	0.914	0.342
Y × D _{pre}	6.42	0.011
Y × DBH _i	0.394	0.531
Herbicide (H)	3.62	0.060
Y × H	1.12	0.289
Post-thinning density (D _{post})	0.290	0.591
Y × D _{post}	14.3	0.0002
Y × D _{post} ²	0.891	0.345
LA _p × D _{post}	0.988	0.323
Y × LA _p	2.65	0.104
Y × LA _p × D _{post}	4.06	0.044
Y × H × D _{post}	2.65	0.104
Y × D _{pre} × H	0.0001	0.991
Y × DBH _i × H	0.019	0.892
Y × D _{pre} × D _{post}	1.03	0.310
Y × DBH _i × D _{post}	0.0003	0.987
Y × DBH _i × D _{pre}	3.59	0.582
Y × D _{pre} × H × D _{post}	0.244	0.621
Y × DBH _i × D _{pre} × D _{post}	1.93	0.165
Y × DBH _i × D _{pre} × H	2.20	0.139
Y × DBH _i × H × D _{post}	0.0004	0.985
Y × DBH _i × D _{pre} × H × D _{post}	0.392	0.531

Note: Our inference used sequential *F* tests as summarized by the *F*-value and *p*-value columns. See Table 2 for abbreviations.

interaction, which represents the effect of thinning intensity on growth response, was highly significant and had a negative parameter estimate, reflecting the negative correlation between thinning intensity and residual density (i.e., 200 trees/ha treatment was the most intense thinning treatment, and 900 trees/ha was the least intense). This means that more intense thinning leads to a greater thinning response, as expected. For the prethinning density, the positive parameter estimate means that koa trees with more available space prior to thinning had lower growth responses following thinning. Thinning also did not significantly alter the water status of the study trees based on the phyllode $\delta^{13}\text{C}$ values (Table 6). We checked for a compensatory increase in phyllode N that might account for the lack of change in the $\delta^{13}\text{C}$ values but found no correlation between phyllode N and thinning intensity (data not shown). The lack of significant differences in phyllode $\delta^{13}\text{C}$ held for both the binary analysis of thinning versus no thinning and comparison across the levels of thinning intensity (excluding the control trees) (data not shown).

Is there a threshold thinning intensity below which koa will not respond?

Based on the range of thinning intensities that we examined, there was no apparent threshold thinning intensity for

koa growth response (Fig. 3). The least intense thinning treatment, which left an effective residual density of 900 trees/ha, involved removing all trees within 3.76 m of the focal study tree. Mean crown radii in these stands are 1.5 m, meaning that in practice only those trees that were in direct contact with the study tree were removed—that is, the minimum number of competing neighbors possible. Nonetheless, the trees in this treatment still showed a positive growth response to thinning.

Does removing the grass cover lead to increases in growth?

The herbicide treatment term alone was close to $\alpha = 0.05$ in both complete models, suggesting that the trees that received the herbicide treatment were marginally better growing trees at the time the experiment was initiated. However, the year × herbicide interaction was not significant, indicating that grass control alone had no effect on koa growth over the study period. Also, the interaction of grass control and thinning (year × herbicide × thinning) was not significant in either model, suggesting that grass control by herbicide treatment does not enhance the growth response of thinned koa. Grass control had no significant effect on phyllode $\delta^{13}\text{C}$ of koa (Table 6) suggesting that the water status of the tree was not influenced by the herbicide treatments.

Do other factors such as prethinning stand density and tree size influence growth response to thinning?

Although other factors influence growth response, the only other covariate that was sufficiently significant in the complete models to be included in a reduced model was prethinning density in model 2. The parameter estimate, as described above, was positive suggesting that trees growing in high-density stands prior to thinning had a greater growth response than those growing in low-density stands. No other covariates describing individual tree dimensions (DBH and proxy leaf area) or stand characteristics (prethinning density in model 1) influenced the growth response of koa, either independently or through interactions with the thinning treatment.

Discussion

Landowners in Hawai'i commonly use mechanical scarification (i.e., bulldozing) to regenerate koa from its long-lived soil seed bank (Baker et al. 2008), a practice that typically results in koa stands that are overstocked with slow-growing trees of small diameter. Such stands are of limited conservation (Pejchar et al. 2005) or economic value. Effective silviculture in these stands requires identifying and releasing potential high-value crop trees. This study addressed five questions regarding the application of crop-tree release thinning to dense, second-growth areas of koa. In short, our results demonstrate that individual koa trees for which growth had stagnated are capable of significant, rapid, and sustained growth responses to crown release. This is an important and encouraging result for landowners who currently manage koa stands as well as those interested in establishing new koa stands, because it shows that the timing of thinning operations can be relatively flexible (sensu Wilson and Baker 2001) without compromising the ability of koa to respond.

Table 5. Summary of results for the reduced form of model 2.

Parameter	Estimate	SE	<i>F</i>	<i>p</i>
Intercept	0.26284	0.1503	39.5	<<0.001
Year (Y)	-0.55121	0.3448	697.0	<<0.001
Y ²	0.38821	0.065	0.01	0.957
Y ³	-0.07268	0.0119	37.1	<<0.001
Prethinning density (D _{pre})	-0.00191	0.0024	0.52	0.471
Post-thinning density (D _{post})	0.24401	0.1003	0.10	0.755
Y × D _{pre}	0.01356	0.0054	6.39	0.012
Y × D _{post}	-0.88216	0.2253	15.3	<<0.001

Note: Our inference used sequential *F* tests as summarized by the *F*-value and *p*-value columns.

Table 6. Analysis of the influence of grass control and thinning on carbon isotope discrimination in koa phyllodes.

Parameter	Estimate	SE	<i>t</i>	<i>p</i>
Intercept	-28.25	0.131	-215.35	<<0.001
Post-thinning density (D _{post})	0.000061	0.000024	0.257	0.798
Herbicide (H)	-0.169	0.192	-0.881	0.380
D _{post} × H	0.00006	0.00005	1.232	0.221

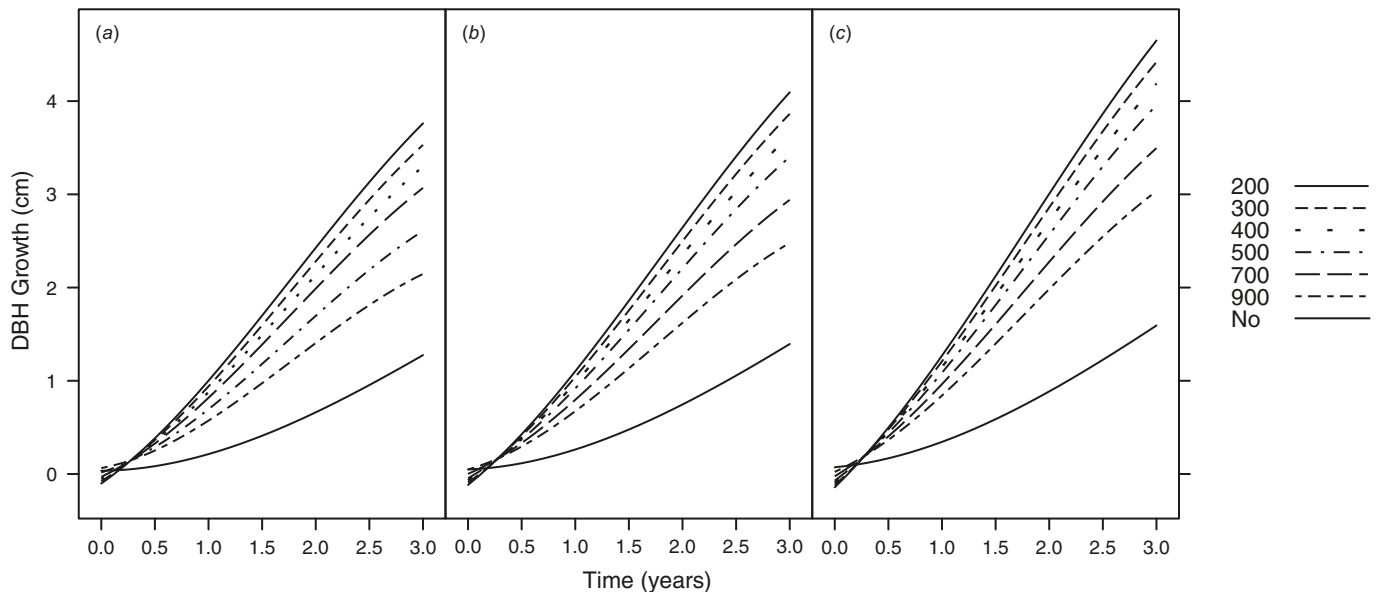
Crown release led to substantial gains in growth. Consider, for example, a released tree in a stand that had a prethinning density of 10 000 trees/ha (which is close to the mean prethinning local density of the 115 study trees) and received no application of herbicides. Over the 3 year period, such a tree would be expected to grow 4.1 cm in diameter compared with only 1.5 cm for a tree that had not been released. If this high growth rate could be maintained by repeated thinnings, it might be possible to grow trees of merchantable size in 25–30 years. Scowcroft and Stein (1986) conducted a thinning study in a stagnated stand of 12-year-old koa on Haleakala, Maui. The initial stand density, which averaged 2460 trees/ha (mean BA 26.4 m²/ha), was reduced to 750 trees/ha (mean BA 16.5 m²/ha) by thinning. The results showed a significant increase of ~30% in koa growth as a result of thinning. We also found no noticeable delay in the growth response of koa to thinning. Pearson and Vitousek's (2001) study of thinned 9-year-old koa also showed an immediate growth response. The amount of time required to detect a growth response varies among other crop-tree release studies. Phares and Williams (1971) showed that black walnut (*Juglans nigra* L.) trees subjected to crown release doubled their growth rate almost immediately after thinning. In contrast, Erdmann et al. (1981) found that yellow birch (*Betula alleghaniensis* Britt.) showed little evidence of increased growth until 2 years after crown release.

The intensity of thinning also has important implications for growth response of koa. As expected, the more intense the thinning treatment, the greater the subsequent growth response. For a tree in a stand that had a prethinning density of 10 000 trees/ha, the mean 3 year growth response to the most intense thinning treatment (200 trees/ha residual density) was ~65% greater than for the least intense (900 trees/ha residual density) thinning treatment (4.1 vs. 2.5 cm). Because there was no significant evidence of a curvilinear interaction of thinning intensity and time since thinning, the growth response of koa to thinning is roughly proportional to the intensity of thinning. This has two important management implications. Firstly, more intense thin-

ning will lead to greater growth response. Within the range of thinning intensities that we considered, there was no evidence of a threshold density below which koa growth reached a maximum, although there will certainly be a point at which excessive culling will lead to understocked stands and a decrease in stand-level growth. However, there is the risk that wood quality may be lowered as a consequence of persistent lower branches or the development of epicormic sprouts. Although we did not measure this response, we saw no evidence of it in our study trees. Secondly, less intense thinning, in which the fixed radius used to identify cull trees decreases, means that the crop tree will experience crown closure sooner and likely require subsequent thinning to reduce local competition and maintain relatively high growth rates.

Results from other crop-tree release studies have had mixed results in terms of DBH growth response. This may be, in part, due to the variation in defining the amount of thinning to do in the area immediately surrounding the study trees. Many studies of crop-tree release have applied thinning treatments in which all trees whose crowns are in contact with the focal tree are removed (e.g., Smith et al. 1994; Schuler 2006; Scowcroft et al. 2007). The intensity of the thinning treatment will then depend on the size of the focal tree's crown. Often, the resultant thinning treatment is relatively low intensity, and growth response may be muted. For example, Trimble (1974) found that dense thickets of advance regeneration of the relatively intolerant northern red oak (*Quercus rubra* L.) did not respond to crop-tree release; however, the thinning treatment only removed competing trees within 1.5 m of the crop trees and may not have sufficiently reduced local competition. Recently, Schuler (2006) found that a crop-tree release that removed only those trees touching the crown of the study tree only led to a ~25% increase in DBH growth of black cherry but an ~89% increase for northern red oak. In contrast, Erdmann et al. (1981) and Wood et al. (1996) showed that yellow birch saplings in northern Michigan responded to crown release across a range of thinning intensities. Their most intense

Fig. 3. The influence of thinning intensity on growth response of *Acacia koa* at prethinning stocking levels of (a) 1000 trees/ha, (b) 10 000 trees/ha, and (c) 25 000 trees/ha. The treatments are plotted in order from top to bottom of decreasing thinning intensity (i.e., 200 trees/ha is the most intense treatment, and 900 trees/ha is the least intense treatment). No thinning is the control treatment.



crown release treatments, in which all trees within 4.9 m (Erdmann et al. 1981) and 4.0 m (Wood et al. 1996) were removed, led to a doubling of annual DBH increment in yellow birch. In a recent koa thinning study, Scowcroft et al. (2007) found no significant effect of thinning on koa because of the large variation in DBH growth response within both thinning and control treatments. Because a crown-touching rule was used to determine cull trees in their study, the local residual density around the study trees varied substantially. In addition, their cull trees were girdled not felled, and in some cases the cull trees only died in the last year of the study, so the crop trees may not have experienced a growth release despite receiving a crown release treatment. Overall, it seems that interpreting the growth response to crop-tree release, where a crown-touching rule is applied, may be complicated and difficult to extrapolate to other silvicultural situations. In this study, we explicitly minimized this problem by applying a range of thinning intensities that were based on removing all trees within a range of fixed radii from the focal tree, allowing us to isolate more clearly the effects of thinning intensity on growth response.

The only significant covariate in this study was prethinning stem density and only on its effect on growth response to different thinning intensities (model 2). For prethinning density, the growth response was greater for trees that had higher initial local stocking. This result was unexpected; we had anticipated that trees with less dense local neighborhoods would have larger crowns and be more able to respond to thinning. One potential explanation is that in the denser areas the koa had begun to differentiate in terms of tree height and crown dimensions. Because our study tree selection criteria focused on individuals that could be future crop trees, our selection in the densest stands may have been biased towards individuals that had begun to exert their dominance and, therefore, were better able to respond to crown release. However, while the potential bias is small, it

is a realistic one. Our selection criteria were designed to mimic decision-making by foresters and landowners, who are unlikely to choose as crop trees individuals that are suppressed, have poor form, or possess obvious stem deformities. That said, the mean growth response after 3 years across the range of prethinning densities that we modeled (5000–30 000 trees/ha) differs by only ~20% for the most intense thinning treatment (4.0 vs. 4.8 mm) and by ~45% in the least intense thinning treatment (2.3 vs. 3.3 mm). It is not clear whether these relatively small differences in growth response associated with initial stand density are sufficient to warrant maintaining high stem densities during early stand development. Although growth response to thinning is greater in stands that had higher initial densities, individual tree growth is typically higher in stands of lower density. Thus, it may be more realistic to maintain lower stocking levels and higher growth rates, while foregoing a marginally better future thinning response, than to maintain high stocking and low growth in anticipation of a better thinning response in the future.

The lack of any other significant covariates, which described the size of the tree prior to thinning and herbicide treatment for grass control, is of particular interest. The lack of a relationship between our two measures of tree size, DBH, and a proxy measure of leaf area suggests that growth response to thinning is independent of absolute tree size across the range of sizes sampled. Thus, in second-growth stands of koa, foresters have considerable leeway in choosing future crop trees. Ellis (1979) reported similar results for the shade-tolerant sugar maple (*Acer saccharum* Marsh.) but found that growth responses to thinning of the intolerant black cherry and white ash (*Fraxinus americana* L.) were significantly and positively related to initial tree size.

Our other treatment, grass control by repeated herbicide application, did not influence the growth response of koa to

thinning. Although koa growth has been shown to be sensitive to moisture availability across soil moisture gradients on Hawai'i (Ares and Fownes 1999) and Kaua'i (Harrington et al. 1995), we found no evidence that killing grass reduced root competition for moisture and nutrients leading to an increase in the growth of koa, whether alone or in combination with thinning. Scowcroft et al. (2007) also found no evidence of an increased growth response of koa trees to grass control when accompanied by thinning. In our study, phyllode $\delta^{13}\text{C}$ values, which provide an index of integrated water status for trees, were similar for both the herbicide and control treatments. The koa phyllode $\delta^{13}\text{C}$ values at Honomalino (mean -28.3‰) were similar to values obtained for koa stands at approximately the same elevation on Hawai'i by Ares and Fownes (1999). These values are at the lower end of the range of reported $\delta^{13}\text{C}$ values for other studies on koa (e.g., Harrington et al. 1995; Ares and Fownes 1999) implying that the water status of our study trees was relatively good. Consequently, the effect of grass control on water availability may be of little importance to the water status of the koa at Honomalino. However, it should be noted that, at drier sites (such as at lower elevations on Hawai'i or higher elevations on Kaua'i) where water availability may limit koa growth (Harrington et al. 1995; Ares and Fownes 1999), grass control may have a more beneficial effect.

Conclusions

This study provides encouraging results for landowners interested in managing koa forests by demonstrating that koa responds well to crown release and that the ability to respond to this silvicultural treatment is seemingly immune to intense growth suppression. Because Hawaiian landowners encompass a wide range of ownership patterns (federal, state, private companies, and private individuals) and differ in their long-term availability of resources for forest management, narrowly defined silvicultural prescriptions that are highly dependent on timing and proper application would be of value to a small segment of the potential forest managers. The results from our study suggest that koa provides considerable flexibility, in terms of growth response to thinning treatments, allowing landowners considerable leeway in the timing and intensity of their treatments. This should, in turn, make koa silviculture more attractive to a wider range of landowners in Hawai'i.

Acknowledgements

This research was conducted as a collaborative effort between the USDA Forest Service and The Nature Conservancy of Hawai'i, which provided the site, logistical support, and personnel. In particular, we thank Mel Johannsen who helped identify study sites and provide logistical support at Honomalino and Derek Goo and Happy Fautanu who conducted the thinning operations with skill and efficiency.

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