Precommercial release thinning of potential *Acacia koa* crop trees increases stem and crown growth in dense, 8-year-old stands in Hawaii

Travis W. Idol^{1a}, Rodolfo Martinez Morales², James B. Friday¹, and Paul G. Scowcroft³

Affiliations

¹Department of Natural Resources and Environmental Management, University of Hawaii-Manoa, 1910 East West Rd, Honolulu, HI 96822, USA

²Current affiliation for Rodolfo[

³ Institute of Pacific Islands Forestry, Pacific Southwest Research Station, United States

Department of Agriculture, Forest Service, 60 Nowelo Street, Hilo, HI 96720, USA (retired)

a Corresponding author

Abstract

An 8-year-old dense monotypic stand of naturally regenerated koa (*Acacia koa* A. Gray) on the Island of Hawai'i was selected to determine the effects of precommercial release thinning, phosphorous (P) fertilization and herbaceous weed control on growth of potential crop trees over approximately 30 months. Thinning consisted of cutting down all stems within a 4.5-m radius of the crop tree. Phosphorus was added at a rate of 300 kg ha⁻¹ over two years. Herbaceous weeds were sprayed once with imazapyr, a broad-spectrum herbicide. Thinning alone or in combination with P fertilization significantly increased stem diameter increment and allometric estimates of the growth of leaf area and aboveground biomass. There was no significant increase in stem diameter, leaf area or biomass in the absence of thinning. Within the thinned treatment, P fertilization resulted in significant increases in tree height over time. Herbaceous weed control had no effect on tree growth. The atmospherically resistant vegetation index (ARVI), which was derived from spectral analyses of high-resolution satellite imagery (GeoEye1), was significantly

higher for thinned than unthinned trees 25 months after study initiation, suggesting greater light absorbance and a possible explanation for overall greater growth of thinned trees. When considered with results from previous studies, these findings indicated that crop tree selection and precommercial release thinning in dense, even-aged koa stands should be done early in stand development to prevent loss of crown vigor and growth potential. Additional interventions like P fertilization or herbaceous weed control may not be necessary until trees are older or site conditions suggest important soil resource limitations.

Keywords:

Acacia koa, silviculture, precommercial thinning, phosphorus fertilization, herbicide, crop tree release

1. Introduction

The endemic Hawaiian koa tree (*Acacia koa* A. Gray) is the most valuable native timber species from Hawaii's forests. Traditionally, koa was used for construction of voyaging canoes and surfboards. Today the wood is used for cabinetwork and fine furniture; koa products account for three-quarters of Hawai'i-grown wood products (Friday et al., 2006). Koa forests are critically important for watershed function and protection, habitat for threatened and endangered species, particularly forest birds (Pejchar et al., 2005), and native forest diversity (Baker et al., 2009). Koa is a fast-growing, shade intolerant, nitrogen-fixing tree that grows from near sea level to 2000 m elevation in mesic sites across a range of soil types on several of the main Hawaiian Islands. Mature trees can grow to over 25 m in height with stem diameter at breast height (DBH) greater than 1.5 m (Friday, 2011). The hard-coated seed can remain viable in the soil for many years, even after deforestation (Baker et al., 2009).

Conversion of forests to cattle pastures reduced koa forest coverage throughout the 19th

and 20th centuries (Cuddihy and Stone, 1990), but declining profitability of grazing, increasing koa wood prices, and increased emphasis on conservation of biodiversity and native ecosystems have resulted in increased interest in reforestation (Baker et al., 2009). Today, harvests are almost exclusively from old-growth forests, but private landowners have expressed interest in commercial reforestation with koa if silvicultural guidelines can be developed (Pejchar and Press, 2006). Natural regeneration of koa may be accomplished by soil scarification in degraded forests or open pastures where there is a remnant seed bank, and these monotypic, even-aged stands can reach initial densities of over 20,000 seedlings ha⁻¹ (Scowcroft et al., 2007). Where seed banks are lacking, koa seedlings are planted at densities of approx. 1000 trees ha⁻¹ (Friday, 2011). Both methods of stand establishment lead to early canopy closure and intense intraspecific competition. Self-thinning does occur, but stands often remain overstocked, which can result in a significant loss of crown vigor, reduced live crown depth, and branch dieback within the crown (Scowcroft and Yeh, 2013). This can greatly reduce average tree growth in stands as young as 10 years of age (Scowcroft and Stein, 1986).

Koa trees, being legumes, typically have poor apical dominance and branchy or even multiple-stemmed form. Open-grown trees or plantations planted at wide spacing may produce few potential crop trees with single, straight boles long enough to be commercially valuable (Scowcroft et al., 2010). Intra-specific competition among individuals in dense, naturally regenerated stands results in enough trees per hectare with good form to produce a reasonable crop if these trees are released from competition. Baker et al. (2009) summarized a number of silvicultural studies that provide useful guidelines for management, but they acknowledged that much work needs to be done to improve understanding and consequently management recommendations. Recommendations for established stands generally include thinning to a target

density to achieve desired stocking levels (Baker and Scowcroft, 2005). Stocking is based on crown space requirement of trees at different stem diameters (DBH), calculated as the growing space index (GSI), which is equal to the ratio of average crown diameter:stem DBH. While no one approach to thinning is generally accepted for koa, several studies of hardwood trees have used crop tree selection, which is a thinning method that targets future crop trees for release by removing at least competing canopy dominant or co-dominant trees if not all woody tree stems within a fixed radius of the crop tree main stem or crown (Perkey et al., 1993; Smith et al., 1997; Ward, 2013).

Selection of crop trees prior to thinning usually takes into account canopy dominance, crown vigor, stem diameter, stem form and length of clear bole. Koa displays poor apical dominance; thus both natural and planted stands often have a low frequency of commercially valuable trees. Crop tree selection, thus, may offer advantages in reducing overall thinning effort while ensuring desirable trees have sufficient space and resources to reach their growth potential. Although the criteria for acceptable crop trees may vary (e.g. Scowcroft and Stein, 1986), it requires trees to grow to a certain size for differentiation of these characteristics to become manifest and measurable. Waiting for trees to meet the acceptable criteria, however, may result in significant loss of crown vigor and tree growth due to high stem density. This can reduce their growth potential, even in response to silvicultural interventions (e.g. Scowcroft et al., 2007). Thus, deciding when to first conduct thinning operations depends on a balance between tree size and stand density in order to distinguish superior tree stems without compromising growth potential.

While intraspecific competition can be relieved by thinning, additional interventions have been deployed to maximize crop tree and overall stand growth response. Thinning typically re-

allocates growth to selected trees but decreases stand growth, overall. Fertilization and control of understory weedy species may be able to increase overall stand productivity (Smith et al., 1997). For koa, several studies have demonstrated significant increases in DBH increment in response to thinning at different stand ages, from approximately 10 to 30 years of age (Baker et al., 2008; Pearson and Vitousek, 2001; Scowcroft and Stein, 1986). In Baker et al. (2008), DBH growth increased with increasing thinning intensity, down to a residual stand density of 200 trees ha⁻¹ for a stand with crop trees that averaged 13-18 cm DBH. There was no additional response to control of understory grasses. Similarly, in Scowcroft and Stein (1986) addition of a multi-element fertilizer (N-P-K and MgSO₄) had no significant effect on basal area growth in either thinned or unthinned plots. However, in Scowcroft et al. (2007), crop tree thinning alone did not change DBH increment for trees that averaged 20-25 cm DBH. Only thinning combined with herbicide grass control and phosphorus (P) fertilization (at a rate of 750 kg ha⁻¹ of P added incrementally over two years) produced a significant response. The variable soils and climates over which koa naturally exists and pre-existing stand conditions likely influence crop tree response to these combinations of interventions, but there are no generalized guidelines at present other than stocking rates.

Measuring forest structure to select crop trees and soil or other conditions to determine the need for thinning and other interventions requires a tradeoff between sampling intensity and spatial coverage, which can be costly and admittedly imprecise. A complementary approach that has the potential to provide valuable information on crown vigor and thus relative response to silvicultural intervention is analysis of high resolution imagery. The analysis of spectral bands from fine pixel resolution satellites (2 to 4 m multispectral, 0.5 to 1 m panchromatic), such as Quickbird, IKONOS and GeoEye1, has provided reliable tools to analyze canopy conditions and

to extract biophysical information of forest stands and individual trees across entire regions quickly and reliably (Clark et al., 2004; Martinez Morales et al., 2008; Morales et al., 2012). Low forest canopy reflectance in the red region (~650 nm wavelength) is associated with chlorophyll absorption, and strong reflectance in the near infrared region (NIR, 750-1500 nm wavelengths) is related to internal leaf structure (Asner, 1998; Roberts et al., 1997). Therefore, these two bands have been commonly used to calculate vegetation indices (VIs) for biomass assessment (Baugh and Groeneveld, 2006), detection of phenological changes (Huete et al., 2002) and detailed identification of forest tree species (Soudani et al., 2006).

Similar analysis using VIs has been applied to accurately classify productivity of koa forests in Hawaii. Morales et al. (2012) compared several VIs calculated from IKONOS data to differentiate koa stands across an 850-m elevation gradient in Hawaii. Stands with higher VI values had greater average tree height and foliar nutrient concentration. A similar approach may allow for assessment of koa growth responses to silvicultural treatments, both as a selection criterion and as an evaluation of growth response after treatment application.

In this study, an 8-year-old koa stand growing on the Island of Hawai'i was chosen to apply a combination of silvicultural treatments that included precommercial release thinning, phosphorus fertilization, and herbaceous weed control via herbicide application. Based on previous research, phosphorus was chosen as the most likely limiting nutrient, and nitrogen was assumed to be non-limiting (Pearson and Vitousek, 2001; Scowcroft et al., 2007). To our knowledge, this was younger than any stand previously chosen for experimental thinning and other silvicultural interventions. Standard responses of forest growth and productivity from ground-based measurements were combined with analysis of a high-resolution satellite image in order to relate ground-based to canopy spectral measurements. The objectives of the study were:

1) to measure a broad range of individual-tree responses to thinning and other interventions in order to understand both drivers of tree growth response and ways in which crop trees respond to changing resource availability; and 2) to test whether canopy spectral information is related to growth responses or other tree characteristics. We hypothesized that the combination of thinning, P fertilization and herbaceous weed control would result in the greatest growth responses through alleviation of light, nutrient, and water limitations. We also hypothesized that the crowns of released trees would have distinct reflectance characteristics and VIs that positively correlate with indicators of productivity, such as larger crown area, leaf area, and depth of live crown.

2. Methods

2.1 Site location and description

During the summer of 2006, an 8-year-old koa stand located on the north slope of Mauna Kea on the Island of Hawai‘i (19° 55’ N, 155° 20’ W) was selected to test the growth response of koa trees to several silvicultural treatments. More than 100 years of grazing, intensive timber harvesting to promote conversion to pasture and establishment of exotic pasture grasses had left the area an open pasture with scattered, mature koa trees. Natural koa regeneration from the soil seed bank was inhibited by cattle browsing and competition with the dense mat of the exotic pasture grass *Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone. Reforestation began in 1998 with the fencing of a 30-ha area, livestock removal and soil scarification by bulldozers to suppress grass competition and stimulate germination of buried koa seeds. A patchwork of dense, even-aged koa stands naturally regenerated on approximately half of the area. *C. clandestinus* persisted in the understory in some locations, and almost no other native plants were present. Soils in this site are of 10,000-30,000-year-old tephra deposits from Mauna Kea, classified as medial, amorphic, isomesic Typic Hapludands (NRCS, 2013). Elevation and mean annual

temperature range from 1560-1620 m and 16-17° C, respectively. Winter months are cooler, with some nights approaching 0° C. Mean annual precipitation is estimated to be 2000-2500 mm, with monthly means ranging 100-300 mm and generally wetter winter than summer months (Giambelluca et al., 2013). The life zone classification is a lower montane subtropical mesic forest (Tosi et al., 2002). Growth occurs year-round but is noticeably slower in winter than spring and summer.

2.2 Experimental design and silvicultural treatments

The experiment was designed as a randomized complete block with three crossed silvicultural treatments: thinning (T), phosphorus fertilization (F), and herbaceous weed control (H) with two levels of each treatment (treated, + or untreated, -). In December 2006, 64 koa trees with superior stem form, crown vigor, and above-average stem diameter were selected as crop trees. Crop trees were separated equally (32 trees each) into upper and lower blocks that differed in elevation and topography. Individual crop trees were randomly assigned to treatment combinations within each block. Stem diameter at breast height (DBH) was measured for all crop trees in order to determine desirable spacing for the crop trees. Based on an average crop tree DBH of 8 cm, each tree was designated as the center of a 4.5-m radius circular plot. Thinning to this spacing represented a target crop tree density of approximately 500 stems ha⁻¹ based on calculations to obtain an average crop tree DBH of 30 cm before a second thinning would be required (Baker and Scowcroft, 2005). Crop trees of this size may be large enough and with sufficient heartwood development for a commercial harvest (HFI, 2012), so combining a partial crop tree harvest with a second round of thinning might partially offset costs.

Scheduling conflicts prevented simultaneous imposition of all three treatments. Thinning and fertilization were imposed in March and May 2007, respectively. Herbaceous weed control

was imposed in November 2008. To accommodate these differences in treatment imposition, we split the study into two overlapping experiments. The first experiment analyzed thinning and P fertilization effects from March 2007 until November 2009. This resulted in eight replications of four treatment combinations within each block. The second experiment analyzed all three treatments and began with imposition of the herbaceous weed control from November 2008 until September 2010; thus, there were four replications of eight treatment combinations within each block.

Stand density varied considerably within the blocks, so crop trees were selected from patches of regeneration that were measurably overstocked (> 2500 stems ha^{-1}). In March 2007, thinning was imposed by felling all neighbor koa trees rooted inside each T+ plot. Cut trees were moved to the borders of each plot to allow access to the crop tree. Granular triple super phosphate was manually broadcast to F+ plots at a rate of 300 kg P ha^{-1} on July 2007 and again in November 2008. The H+ plots were sprayed on November 2008 with a commercial formulation of the herbicide imazapyr (brand name "Polaris AC", NuFarm Ltd., Melbourne, Australia) with a single-nozzle Boomless FieldJet™ sprayer (TeeJet, IL) using a 3-m swath at a rate of 100 L ha^{-1} of solution containing 0.4 kg ha^{-1} active ingredient. This herbicide has shown good selective control of grasses, including *C. clandestinus*, without any apparent damage to koa (James Leary, person. comm.). The control consisted of unthinned plots that received neither herbicide nor fertilizer.

2.3 Field measurements and calculations

Data on crop tree stem DBH, height, crown characteristics, and gap size (for T+ plots) were collected at different times and intervals from May 2007 until November 2010 (Table 1). Leaf area (LA) and aboveground biomass (AGB) were estimated allometrically from DBH for

each measurement. The allometric equations to estimate LA and AGB were derived from measurements made of twenty-one co-dominant trees ranging from 3.1 cm to 23.2 cm DBH that were harvested outside the experimental plots. Trees were sectioned into samples of stem, branches, and fine twigs less than 1 cm diameter, and all components were weighed on a hanging scale in the field to the nearest 20 g. Subsamples were randomly chosen for determination of wet:dry ratios. Ten subsamples of twigs from each tree were randomly chosen for determination of leaf:twig weight ratios. Leaf samples were refrigerated and leaf areas were determined on a LI-COR 3100C leaf area meter (LI-COR Inc., Lincoln, NE). All subsamples were dried to a constant weight at 70°C and weighed. A simple power equation of the form $y = ax^b$ [Eq. 1] was used to estimate LA and AGB (y-variables) from DBH (x-variable) (Pearson and Vitousek, 2001). The Pearson product-moment correlation coefficient (R^2) was used to estimate goodness-of-fit. The resulting allometric for AGB was $0.1309 \times \text{DBH}^{2.2918}$ ($R^2 = 0.97$) and for LA was $0.0511 \times \text{DBH}^{2.3584}$ ($R^2 = 0.88$).

Crown measurements were made only for released crop trees due to the inability to distinguish individual tree crowns in unthinned plots. Height (HT) and depth of live crown (DLC) were measured using a height pole on May 2007 and March 2009. Live crown ratio (LCR) was calculated as the ratio of DLC to HT. The projected crown area of each crop tree (CA) and gap area of each thinned plot (GA) were estimated by measuring distances along eight radii centered on the crop tree and aligned along cardinal directions (N, NE, E, SE, S, SW, W, and NW). A vertically aligned height pole was used to locate the outer edge of the crop tree crown and the outer edge of the gap along each radius. The associated distances from the center of the crop tree stem to the height pole were recorded. CA and GA were calculated from the triangles constructed from the measured distances. Gap area was not adjusted by subtracting the

crown area of the crop tree; thus, GA does not represent the open space around each crop tree but rather the entire area between the crop tree stem and the crowns of neighboring trees outside the thinned area. Growing space index (GSI) was calculated as in Baker and Scowcroft (2005), i.e. the ratio crown diameter:DBH. Crown diameter was calculated as the average of the longest crown diameter along the eight cardinal directions and the diameter perpendicular to this direction. Crown and gap diameters were measured five times from August 2007 until November 2009 (Table 1). For consistency, GSI for each time period was calculated using crown diameters in the same directions as those used at the first measurement (August 2007).

Finally, complete plot inventories of DBH for the unthinned treatment were collected in September 2007 and September 2010 in order to monitor basic changes in stand development, including basal area ($BA = m^2 ha^{-1}$), stem density ($SD = stems plot^{-1}$), and quadratic mean diameter (QMD), where $QMD = (\sum DBH^2 / SD)^{0.5}$.

2.4 Image analysis

A set of cloud-free images with a near-nadir view from the GeoEye1 satellite (GeoEye, Inc, Dulles, VA) covering the whole scarified area at the site was obtained for July 2009. The images consist of 2-m pixel multi-spectral (MS) bands in the visible spectrum including the blue (450-510 nm), green (510-580 nm), red (655-690 nm) and near-infrared (NIR) (780-920 nm) regions, and a 0.5-m pixel panchromatic band that includes the visible and NIR spectral regions (450-829 nm). All bands were ortho-rectified to a horizontal accuracy of less than 5 m using a 10-m-pixel resolution digital elevation model and the nearest-neighbor resampling methods in ENVI image analysis software (ITT Visual Information Solutions, Boulder, CO, USA). Therefore, the quality of the remote sensing data used for this study ensures the highest pixel

resolution available on the market at the time with highly accurate geometric and topographic corrections important in sloped areas.

All 64 crop koa trees were geo-located using a Trimble GeoXT differential global positioning system (GPS) (Trimble, Sunnyvale, CA) with sub-meter accuracy. The GPS was mounted on a tripod, placed a few centimeters from each crop tree stem and left recording for 30 minutes at 1-second intervals. Geo-located points were overlaid on a natural color image composite in order to identify individual crop trees. Because the satellite imagery allowed for resolution of single crowns of thinned crop trees, drawing polygons around the crown area edge facilitated the extraction of spectral information. Because high tree density obscured the edges of single crop-tree crowns in unthinned plots, crop tree polygons in those plots were delineated by careful inspections of slight tone changes around GPS points. Both crown delineations and extraction of spectral information were made using ENVI. As the number of extracted pixel values per tree was highly variable, single-tree average reflectance was calculated from the visible and NIR bands. This information was used to calculate vegetation indices (VIs) previously used in studies of koa forest canopies (Morales et al., 2011, 2012) () () (). The atmospherically reflective vegetation index (ARVI) was chosen as the best VI for distinguishing koa tree crowns.

2.5 Data analysis

Statistical analyses appropriate for the randomized complete block experimental design were carried out using the software R, Ver. 3.1.2 (R Core Team, 2014). Potential differences by thinning treatment and/or block for initial crop tree size – DBH, LA, AGB, HT, DLC, LCR, CA, and GA – were tested using one-way ANOVA. The effects of thinning, fertilization and their interactions on all response variables were analyzed for the period 2007-2009. Because the

herbaceous weed control treatment (H) was imposed in 2008, more than 1 year after thinning and P fertilization, its effect on DBH, AGB and LA was analyzed only for the period 2008-2010.

Because most of the measurements were repeated on the same trees over the course of the study, we modeled the change in the dependent variables over time rather than using repeated measures analyses to test for the significance of time as a within-subjects effect (Ramsay and Silverman, 1997). In the simplest case, a response is constant over time and conforms to the linear model $y = ax + b$ [Eq. 2], where y is the response variable and x is time. Other common response types, such as $y = ax^b$ [Eq. 1] or $y = a \cdot \ln(x) + b$ [Eq. 3] can be made linear through a simple transformation of the repeated measure (x -variable). The parameter values then substitute for the raw data for comparison of treatments (between-subjects effects) via univariate ANOVA. To test for the significance of the effect of time, we constructed a baseline model in which the response variable, y , was modeled simply as the mean across time periods, $y = \sum y_{ij} / \sum n_j$, [Eq. 4], where i = individual crop trees, j = individual time period, and n = number of trees. We then constructed models based on Eq. 1-3. The baseline model was compared to the fitted models using ANOVA. We then selected a single model from among all those significantly better than the baseline model based on visual examination of fitted curves to a scatterplot of the response variable over time, the proportion of variation accounted for by the model (R^2), and its residual error. The selected model was then applied to the response of each tree to generate parameter values for comparison of treatment effects via ANOVA. Where there was a significant treatment interaction effect (e.g. thinning by fertilization), we used Tukey's honest significant difference test (TukeyHSD in R) for means comparisons.

Differences over time for DBH, LA, and AGB analyzed from 2007-2009 and 2008-2010 were well-approximated by a simple linear model and so were analyzed using Eq. 2. Similarly,

CA displayed a linear change over time and thus was modeled using Eq. 2. For GA, visual inspection suggested a curvilinear response, especially near the final time period, so the data were fitted to a linear [Eq. 2] and a quadratic model ($y = ax + bx^2 + c$ [Eq. 5]) as well as linearized forms of logarithmic equations (Eq. 1 and 3). The quadratic model provided the best fit but was only slightly better than the linear model, based on amount of variation accounted for (R^2) and residual error. Models based on Eqs. 1 and 3 were worse than the linear model. For ease of comparison, the simple linear model was chosen for analysis of treatments. For GSI, the quadratic but not the linear model was significant, so it was chosen for analysis of the effect of P fertilization. For all these responses, the alternate model was significantly better than the baseline model, meaning responses changed significantly over time. For HT, DLC, and LCR, measurements were taken once in 2007 and again in 2009 only on thinned trees; thus, the difference in these measurements was used for analysis of the effect of P fertilization. Similarly, BA, SD, and QMD were measured twice (2007 and 2010) for unthinned plots, so the difference was used to test for the effect of P fertilization. Except for LCR, the effect of time was significant, so the modeled time effect was used for analysis of treatments in all other cases. The effect of P fertilization on LCR was analyzed using the 2009 data only. For ARVI, values were based on a single satellite image taken in 2009; thus, treatment effects were analyzed based on these values.

The data used for ANOVA were checked for Normality using Shapiro-Wilks test (shapiro.test in R) and for homogeneity of variance using Bartlett's test (bartlett.test in R). Where data failed these tests, we employed the Box-Cox power transformation, using the "MASS" package in R (Venables and Ripley, 2002), to explore possible transformations. The selected transformation was then applied to the data, and it was rechecked for Normality and

homogeneity of variance. Normal probability plots were compared between transformed and untransformed data to confirm results of the Shapiro-Wilks tests.

For initial crop tree size, only CA and GA failed the Shapiro-Wilks and Bartlett's test and so were subjected to the Box-Cox procedure. Based on the log-likelihood plots, we chose a logarithmic (ln) transformation. The change over time in crop tree DBH, LA, and AGB all failed the Shapiro-Wilks and Bartlett's tests and so were subjected to the Box-Cox procedure. Based on the log-likelihood plots, we chose a logarithmic (ln) transformation. Crop tree CA failed the Shapiro-Wilks test but not the Bartlett test, so transformation was decided to be unnecessary. Initial DBH was found to be significantly correlated with the change in these variables so we used analysis of covariance (ANCOVA) to control for the effect of initial DBH. Likewise, the influence of initial size was significant for DLC, so the initial measurement was used as a covariate in an ANCOVA for this variable. The ARVI data failed the Shapiro-Wilks and Bartlett's tests, and the Box-Cox procedure suggested a square transformation (y^2).

3. Results

Initial crop tree size generally did not differ significantly by block or thinning treatment (Fig. 1). Means in these groups generally varied < 20% from the corresponding overall mean. The one exception was crown area (CA, Fig 1g); average initial CA in Block 2 (7.3 m²) was almost 70% greater than in Block 1 (4.3 m²). Comparison of the log-transformed means indicated this was significant. Tree size distributions also tended to skew toward a few large trees.

For both the 2007-2009 and 2008-2010 data, thinning significantly increased annual growth rates of diameter at breast height (DBH), leaf area (LA), and above ground biomass (AGB) (Table 2). For the 2007-2009 data, the ANCOVA indicated a significant thinning by

fertilization (TxF) interaction, but the Tukey's HSD test separated the treatments into the two groups: unthinned (T-) with or without P fertilization (1.03 cm y^{-1}) and thinned (T+) with or without fertilization (1.99 cm y^{-1}). The ANCOVA for the 2008-2010 data also showed a significant thinning effect (1.17 for the unthinned trees vs 1.89 cm y^{-1} for thinned trees) but no additional effect of P fertilization or TxF interaction. Adding the herbaceous weed control treatment had no effect on tree growth, and interactions with the other treatments were not significant. Growth rates showed no signs of slowing over the 40-month measurement period (Fig. 2).

For thinned trees, both height (HT) and depth of live crown (DLC) increased significantly over time, but there was no change in live crown ratio (LCR) (Table 3). P fertilization significantly increased HT but not DLC or LCR. The average crown area (CA) of thinned trees increased from 5.8 to 12.0 m^2 over the 30-month measurement period, an increase of $2.5 \text{ m}^2 \text{ yr}^{-1}$ (Fig. 3). The average area of the gaps created by thinning (GA) decreased from 49 to 28 m^2 over that same time period, a contraction of $8.5 \text{ m}^2 \text{ yr}^{-1}$. There was no significant effect of P fertilization (F) on either CA or GA. Growing space index (GSI) showed an initial increase for the first year after thinning but then declined towards the end of the 30-month measurement period (Fig. 4). There was no significant effect of P fertilization on change in GSI.

The ARVI vegetation index, calculated from imagery collected 26 months after thinning, was significantly higher for thinned than unthinned crop trees, 0.84 and 0.65 , respectively. There was no significant effect of P fertilization. There was no significant relationship of ARVI to crop tree crown response variables, including direct canopy measures such as the change in tree height, crown area, depth of live crown, live crown ratio or growing space index (Table 4). The significance of the correlation between ARVI or the square transformation (ARVI^2) with the

overall change in growing space index did not quite meet the $p < 0.05$ threshold ($p = 0.06$ and 0.05 , respectively).

The average basal area (BA) of unthinned plots increased significantly from 30 to $37 \text{ m}^2 \text{ ha}^{-1}$ from 2007-2010 (36 months), while stem density (SD) declined significantly from 6100 to $4500 \text{ stems ha}^{-1}$ (Fig. 5). The average quadratic tree diameter (QMD) increased significantly from 8.1 to 10.5 cm over that time. Phosphorus fertilization had no significant effect on these changes (data not shown).

4. Discussion

Results from this research confirm previous studies that demonstrate the importance of silvicultural management of high density stands to increase growth of potential timber trees, including temperate deciduous forests (Joudvalkis et al., 2005; Ward, 2013; Wood et al., 1996) and studies with koa in Hawaii (Baker et al., 2008; Pearson and Vitousek, 2001; Scowcroft and Stein, 1986; Scowcroft et al., 2007). Previous studies of koa stands, even as young as 11 years of age (Pearson and Vitousek, 2001; Scowcroft and Stein, 1986) have shown significant reduction in growth potential due to overstocked conditions. While self-thinning reduces density over time, stands can remain overstocked for decades, especially in drier sites (Baker et al., 2008; Idol et al., 2007; Scowcroft et al., 2007).

Taken together, these results indicate that the first precommercial thinning in dense koa stands should occur no later than 10 years of age, ideally 2-3 years earlier, provided that superior individuals can be identified at that time. Combined with the often patchy regeneration of seedlings and generally low frequency of desirable trees in overstocked koa stands, we recommend using crop tree release thinning rather than thinning to a target residual density or basal area. In these young stands, it is likely sufficient to choose crop trees based on DBH as

well as stem form and length of clear bole. Trying to measure depth of live crown or estimate crown dieback is difficult in crowded conditions, which is why we restricted crown measurements to thinned trees. For stands 20-30 years or older, crown condition is an important consideration for crop tree selection, as significant dieback may have already occurred (Scowcroft et al., 2007).

Even in the relatively young stands we measured, at the time of thinning some crop trees displayed misshapen crowns or crown dieback, showing the effects of the high initial stand density. The published stocking guidelines of Baker and Scowcroft (2005) are based on growing space index (GSI) for canopy dominant trees. Despite our observations of crown dieback at the beginning of the study, the initial GSI of thinned trees, based on measurements of crown area (CA), averaged 21.3, within the range of healthy trees of this age and size for this growing region (Baker and Scowcroft, 2005). The significant increase in GSI during the first year suggests that release thinning stimulated canopy area growth more than stem DBH. Modeled trends for trees in this area predict a decline in GSI with increasing stem DBH (Baker and Scowcroft, 2005). Our results suggest that tree crowns for crop trees at this age and size are likely limited by intraspecific competition, even if the GSI is within an expected range. However, tree crowns do appear capable of partially recovering from this suppression after thinning.

The effect of these silvicultural interventions on koa tree crowns is an important determinant not just of overall growth response but also the time during which gap closure may be expected to occur. Our goal was to create gaps sufficiently large to delay the need for a second thinning until the trees averaged 30 cm DBH, at which size a commercial thinning might be possible to help offset the cost of additional thinning of non-crop trees. Almost two and a half years after the first measurement, average crown area of crop trees had increased from 6 to 12

m², while canopy gap area had declined from 50 to 28 m². At these rates of change, gap closure would be expected in four to five years after thinning. For some of the largest crop trees, overlap with the crown of some neighboring trees had occurred by the final measurement (November 2009), although only in one or two of the eight measured directions. Assuming no reduction in the observed DBH growth rates, we estimate that average crop tree DBH would be approximately 21 cm at the time of gap closure, which is short of the target diameter. To achieve our target DBH of 30 cm before crown closure and subsequent decreases in diameter growth, an initial gap radius of approximately 5.5 m would have been needed. A subsequent round of thinning would normally be recommended at gap closure, but given the variation in crown growth and gap closure rates among crop trees, additional release thinning might better be done selectively or less intensively based on visual determination of needs.

It may also be possible to delay thinning by continuing to add P fertilizer to thinned crop trees. A common measure of forest site productivity is site index, which is the average dominant canopy tree height at a standard base age (Smith et al, 1997, p. 240). Fertilization with growth-limiting nutrients can increase realized site index (Fox et al., 2007), i.e. height growth of canopy dominant trees, as we found in our study. While the effect of P fertilizer on height growth in our study was relatively modest (0.42 m over 22 months), annual P additions may allow that effect to persist or even increase, allowing crop trees to increase their dominant canopy position and perhaps develop into canopy emergents, in which most of the live crown is above the height of competing trees, as the gaps close in. Adding P fertilization requires much less labor than selective thinning of competing trees and avoids the risk of damaging the crop tree during felling.

The lack of clear or consistent effects of P fertilization and herbaceous weed control may

be due to the large variation in initial stem density and grass cover. Although average stem density for unthinned plots did not differ much between the blocks (~15%), the coefficient of variation across all unthinned plots was 30%. We also observed much lower grass cover in plots in the lower block, which would limit any effect of herbicide control. Within thinned plots, we did observe differences in soil available P and foliar P concentrations (data not shown), but these differences were much lower than in Scowcroft et al. (2007), where thinning combined with P fertilization significantly improved DBH increment growth of crop trees over trees in control plots. Repeated applications of P fertilization and herbaceous weed control throughout the study may have improved the significance of these effects, but the tradeoff is repeated entry into the forest after thinning to achieve marginal improvements in crop tree growth over thinning alone.

The ARVI data distinguished thinned from unthinned crop trees, but it did not correlate strongly with any measures of crown vigor. Because reflectance provides an integrated measure of canopy function, and VIs provide an assessment of net light absorption for photosynthesis, it is possible there were biochemical or physiological improvements in leaf function in response to thinning and possibly the other silvicultural treatments that are not reflected in greater crown and leaf area, such as increased leaf nutrient or chlorophyll concentration or photosynthetic rate. Other studies with koa have demonstrated relationships of ARVI with crown dieback or overall koa productivity (Morales et al., 2011; Morales et al., 2012); thus, across diverse stands or landscapes, ARVI is capable of identifying healthier, more productive trees and stands. Post-treatment determination of VIs may indicate improved canopy function, but this requires verification with direct measurements.

High-resolution satellite images have been used successfully to estimate canopy cover overall (Sprintsin et al., 2009; Donmez et al., 2015) and to evaluate the presence and size of

canopy gaps (Espírito-Santo et al., 2014; Malahlela et al., 2014). This could be useful to identify areas in need of thinning, i.e. where stem density is higher, and for monitoring gap closure after thinning. The ability to identify canopy dieback on an individual tree basis (Dennison et al., 2010; Morales et al., 2011) also provides a rapid guide for discriminating potential crop trees based on canopy characteristics that may be difficult to assess on the ground due to high stem density and multiple canopy layers. In Scowcroft et al. (2007), the DBH growth response of koa crop trees to thinning, P fertilization, and herbicide grass control was strongly related to visual estimates of crown vigor or dieback.

Finally, although this study was not designed to evaluate various metrics of growth stagnation, given observations in earlier koa studies (e.g. Scowcroft and Stein, 1986), we did monitor stem density and basal area in the unthinned plots from 2007-2010 (36 months). The 25% increase in BA and 27% decrease in SD over 3 years suggested that stands were still undergoing self-thinning and addition of basal area. However, given the QMD of 8-10 cm for koa trees in unthinned plots, stem density was still well above 100% stocking levels (Baker and Scowcroft, 2005). Moreover, the periodic annual DBH increment of crop trees in unthinned plots during the study period, approximately 1 cm yr^{-1} , was less than the mean annual DBH increment at 8 years of age, approximately 1.5 cm yr^{-1} . Thus, intraspecific competition was clearly important at this relatively young age, but the stand did not appear to be stagnating with respect to self-thinning or basal area growth.

5. Conclusion

This research demonstrated the benefits of release thinning for improving individual tree growth and crown vigor in young *Acacia koa* stands, with an additional benefit of increased height growth in response to P fertilization. Since natural koa regeneration and stand

development result in persistently overstocked stands, we recommend the time of first thinning should be as early as 6-8 years of age, depending upon the ability to distinguish trees with good stem form and growth potential. While stand growth may not be stagnating at this young age, periodic DBH increment growth of crop trees is already slowing compared to the mean annual increment. The improvements in crown vigor with thinning and P fertilization should maintain increased DBH and height growth until gap closure occurs, which in this case is expected to be four to five years after thinning. Subsequent release thinnings can then be done selectively, based on natural variation in crown expansion and gap closure. Alternatively, periodic additions of P to the thinned crop trees may allow them to improve canopy dominance, reducing or delaying the need for thinning based on gap closure. The remotely sensed index of crown reflectance could provide a rapid and large-scale assessment of post-treatment analysis of canopy expansion and gap closure or a way to discriminate potential crop trees based on canopy vigor prior to thinning.

6. Acknowledgments

We thank Umikoa Ranch for hosting the research site. We thank Janis Haraguchi, Lorena Martinez, Cortney Midla, Spencer Nagata, Larz Stewart, and Adel Youkhana for their field assistance; Dr. Dean Meason for his field assistance and thoughtful discussions on project objectives, measurements, and analysis; Dr. James Leary for applying the herbicide; Ken Gerow for assistance with statistical analysis; and the Institute of Pacific Islands Forestry, US Forest Service for logistical support. This work was supported by the USDA National Institute of Food and Agriculture, Tropical and Subtropical Agricultural Research program, Hatch project 119H and McIntire Stennis project 196M, managed by the College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa.

7. References

- 506 Asner, G.P., 1998. Biophysical and biochemical sources of variability in canopy reflectance.
507 Remote Sensing of Environment 64, 234-253.
- 508 Baker, P.J., Robinson, A.P., Ewel, J.J., 2008. Sudden and sustained response of *Acacia koa* crop
509 trees to crown release in stagnant stands. Canadian Journal of Forest Research 38, 656-666.
- 510 Baker, P.J., Scowcroft, P.G., 2005. Stocking guidelines for the endemic Hawaiian hardwood,
511 *Acacia koa*. Journal of Tropical Forest Science 17, 610-624.
- 512 Baker, P.J., Scowcroft, P.G., Ewel, J.J., 2009. Koa (*Acacia koa*) ecology and silviculture. Gen.
513 Tech. Rep. PSF-GTR-211 US Department of Agriculture, Forest Services, Pacific Southwest
514 Research Station, Albany, CA, 132 pp.
- 515 Baugh, W.M., Groeneveld, D.P., 2006. Broadband vegetation index performance evaluated for a
516 low-cover environment. International Journal of Remote Sensing 27, 4715-4730.
- 517 Clark, D.B., Castro, C.S., Alvarado, L.D.A., Read, J.M., 2004. Quantifying mortality of tropical
518 rain forest trees using high-spatial-resolution satellite data. Ecology Letters 7, 52-59.
- 519 Cuddihy, L.W., Stone, C.P., 1990. Alteration of native Hawaiian vegetation: effects of humans,
520 their activities and introductions. Cooperative National Parks Studies Unit, University of
521 Hawaii ,Honolulu, HI, 146 pp.
- 522 Dennison, P.E., Brunelle, A.R., Carter, V.A., 2010. Assessing canopy mortality during a
523 mountain pine beetle outbreak using GeoEye-1 high spatial resolution satellite data. Remote
524 Sensing of Environment 114, 2431-2435.
- 525 Donmez, C., Berberoglu, S., Erdogan, M.A., Tanriover, A.A., Cilek, A., 2015. Response of the
526 regression tree model to high resolution remote sensing data for predicting percent tree cover
527 in a Mediterranean ecosystem. Environmental Monitoring and Assessment 187, 1-12.
- 528 Espírito-Santo, F.D., Keller, M.M., Linder, E., Oliveira Junior, R.C., Pereira, C., Oliveira, C.G.,

2014. Gap formation and carbon cycling in the Brazilian Amazon: measurement using high-resolution optical remote sensing and studies in large forest plots. *Plant Ecology & Diversity* 7, 305-318.

Friday, J.B., 2010. Farm and forestry production and marketing profile for koa (*Acacia koa*). In: Elevitch C (Ed.), *Specialty crops for Pacific Island agroforestry*. Permanent Agriculture Resources, Holualoa, HI, pp. 251-284.

Friday, J.B., Yanagida, J.F., Illukiptiya, R.J., Mamiit, R.J., Edwards, Q.A., 2006. Characteristics of Hawaii's retail forest industry 2001. *Economic Issues* 8. College of Tropical Agriculture and Human Resources, University of Hawai'i, Honolulu, HI, 3 pp.

Giambelluca, T.W., Chen, Q., Frazier, A.G., Price, J.P., Chen, Y.-L., Chu, P.-S., Eischeid, J.K., Delparte, D.M., 2013. Online rainfall atlas of Hawaii. *Bull. Amer. Meteor. Soc.* 94, 313-316.

HFI. 2012. Growing koa in Hawaii nei. 2012 Koa Symposium. Hawaii Forest Institute. 16-17 November, 2012, Volcano, HI. Available URL:

http://hawaiiiforest.org/index.php/article/2012_Koa_Symposium. Last accessed, 31 October 2016.

Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., Ferreira, L.G., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sensing of Environment* 83, 195-213.

Idol, T.W., Baker, P.J., Meason, D., 2007. Indicators of forest ecosystem productivity and nutrient status across precipitation and temperature gradients in Hawaii. *Journal of Tropical Ecology* 23, 693-704.

Juodvalkis, A., Kairiukstis, L., Vasiliauskas, R., 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. *European Journal of Forest Research* 124,

552 187-192.

553 Malahlela, O., Cho, M.A., Mutanga, O., 2014. Mapping canopy gaps in an indigenous
 554 subtropical coastal forest using high-resolution WorldView-2 data. *International Journal of*
 555 *Remote Sensing* 35, 6397-6417.

556 Martinez Morales, R., Miura, T., Idol, T., 2008. An assessment of Hawaiian dry forest condition
 557 with fine resolution remote sensing. *Forest Ecology and Management* 255, 2524-2532.

558 Morales, R.M., Idol, T., Friday, J.B., 2011. Assessment of *Acacia koa* forest health across
 559 environmental gradients in Hawai'i using fine resolution remote sensing and GIS. *Sensors*
 560 11, 5677-5694.

561 Morales, R.M., Idol, T., Chen, Q., 2012. Differentiation of *Acacia koa* forest stands across an
 562 elevation gradient in Hawai'i using fine-resolution remotely sensed imagery. *International*
 563 *Journal of Remote Sensing* 33, 3492-3511.

564 NRCS. Web soil survey., 2013. <http://websoilsurvey.nrcs.usda.gov/app/> (accessed 05 May, 2016).

565 Pearson, H.L., Vitousek, P.M., 2001. Stand dynamics, nitrogen accumulation, and symbiotic
 566 nitrogen fixation in regenerating stands of *Acacia koa*. *Ecological Applications* 11, 1381-
 567 1394.

568 Pejchar, L., Holl, K.D., Lockwood, J.L., 2005. Hawaiian honeycreeper home range size varies
 569 with habitat: implications for native *Acacia koa* forestry. *Ecological Applications* 15, 1053-
 570 1061.

571 Pejchar, L and D. M. Press. 2006. Achieving conservation objects through production forestry:
 572 The case of *Acacia koa* on Hawaii Island. *Environmental Science and Policy* 9, 439-447.

573 Perkey, A.A., Wilkins, B.L., Smith, H.C., 1994. Crop tree management in eastern hardwoods.
 574 NA-TP-19-93. USDA Forest Service, Northeastern Area State and Private Forestry,

575 Morgantown WV., 53 pp.

576 R Core Team. 2014. R: A language and environment for statistical computing. R Foundation for
577 Statistical Computing, Vienna.

578 Ramsay, J.O., Silverman, B.W., 2005. Functional data analysis. Springer-Verlag, New York, 428
579 pp.

580 Roberts, D.A., Green, R.O., Adams, J.B., 1997. Temporal and spatial patterns in vegetation and
581 atmospheric properties from AVIRIS. Remote Sensing of Environment 62, 223-240.

582 Scowcroft, P.G., Stein, J.D., 1986. Stimulating growth of stagnated *Acacia koa* by thinning and
583 fertilizing. Research Note - Pacific Southwest Forest and Range Experiment Station, USDA
584 Forest Service, 8 pp.

585 Scowcroft, P.G., Yeh, J., 2013. Passive restoration augments active restoration in deforested
586 landscapes: The role of root suckering adjacent to planted stands of *Acacia koa*. Forest
587 Ecology and Management 305, 138-145.

588 Scowcroft, P.G., Friday, J.B., Idol, T.W., Dudley, N., Haraguchi, J., Meason, D., 2007. Growth
589 response of *Acacia koa* trees to thinning, grass control, and phosphorus fertilization in a
590 secondary forest in Hawai'i. Forest Ecology and Management 239, 69-80.

591 Scowcroft, P.G., Friday, J.B., Haraguchi, J., Idol, T.W., and Dudley, N.S., 2010. Poor stem form
592 as a potential limitation to private investment in koa plantation forestry in Hawai'i. Small-
593 Scale Forestry 9: 243-262. doi: 10.1007/s11842-009-9107-1

594 Smith, D.M., Larson, B.C., Kelty, M.J., Ashton, P.M.S., 1997. The Practice of Silviculture:
595 Applied Forest Ecology. New York: Wiley. 537 pp.

596 Soudani, K., Francois, C., Maire, G.L., Dantec, V.L., Dufrêne, E., 2006. Comparative analysis of
597 IKONOS, Spot, and ETM data for leaf area index estimation in temperate coniferous and

- 598 deciduous forest stands. . Remote Sensing of Environment 102, 161-175.
- 599 Sprintsin, M., Karnieli, A., Sprintsin, S., Cohen, S., Berliner, P., 2009. Relationships between
600 stand density and canopy structure in a dryland forest as estimated by ground-based
601 measurements and multi-spectral spaceborne images. Journal of Arid Environments 73, 955-
602 962.
- 603 Tosi, J.A., Jr., Watson, V., Bolaños, R., 2002. Life zone maps Hawaii, Guam, American Samoa,
604 Northern Mariana Islands, Palau, and the Federated States of Micronesia. Joint Venture of the
605 Tropical Science Center, San Jose, Costa Rica and the Institute of Pacific Islands Forestry,
606 USDA Forest Service, Hilo, Hawaii.
- 607 Venables, W.N., Ripley, B.D., 2002. Modern applied statistics with S. Fourth edition. Springer,
608 New York, 428 pp.
- 609 Ward, J.S., 2013. Precommercial crop tree release increases upper canopy persistence and
610 diameter growth of oak saplings. . Northern Journal of Applied Forestry 30, 156-163.
- 611 Wood, J.E., Von Althen, F.W., Mitchell, E.G., 1996. Crown release improves growth of 20-year-
612 old *Betula alleghaniensis* in tolerant northern hardwood stands. New Forests 12, 87-99.

Table 1. Dates of measurement for crop tree and plot response variables. DBH, stem diameter at breast height; LA, leaf area; AGB, aboveground biomass; CA, canopy area; GA, gap area; HT, height; DLC, depth of live crown; LCR, live crown area; ARVI, atmospherically resistant vegetation index; BA, basal area; SD, stem density, QMD, quadratic mean diameter.

Table 2. Summary of statistical analyses for effects of thinning (T) and P fertilization (F) from 2007-2009 and the effects T, F, and herbicide grass control (H) from 2008-2010 on annual growth rates of crop tree stem diameter at breast height (DBH), leaf area (LA), aboveground biomass (AGB), height (HT), depth of live crown (DLC), live crown ratio (LCR), canopy area (CA), gap area (GA), growing space index (GSI) and on canopy reflectance measured in 2009 (ARVI). DBH, LA, and AGB data were log-transformed (natural logarithm) prior to analysis to improve normality and homogeneity of variance. Effects of location (Block) and initial tree size (INT) are included. *, significant at $p < 0.05$; ns, not significant.

Table 3. Effect of P fertilization (F) on the change in the height (HT), depth of live crown (DLC), and live crown ratio (LCR) of thinned crop trees from May 2007-March 2009.

Table 4. Correlation coefficients between ARVI index of canopy reflectance crop tree response variables in both raw format and as transformed to meet Normality and homogeneity of variance assumptions.

Figure 1. Initial crop tree size by block (number) and/or thinning treatment (unthinned, T- and thinned, T+). Measurements made in May 2007: a, stem diameter (DBH); b, leaf area (LA); c, aboveground biomass (AGB); d, tree height (HT); e, depth of live crown (DLC); f, live crown ratio (LCR). Measurements made in August 2007: g, crown area (m^2); h, gap area (m^2). Each box plot shows median (solid line), 25th and 75th percentiles (box ends), and extreme values (whiskers and open circles).

Figure 2. Effect of silvicultural treatments on mean stem diameter at breast height (DBH), leaf area (LA), and aboveground biomass (AGB) as a function of time since thinning (March 2007) for the periods (a) 2007-2009 and (b) 2008-2010. Solid lines are fitted to the thinned data points and dashed lines are fitted to the unthinned data points.

Figure 3. Effect of phosphorus fertilization (unfertilized, F– and fertilized, F+) on (a) expansion of crop tree crown area (CA) and (b) contraction of gap area (GA) for thinned plots as a function of time since thinning (March 2007) for the period 2007-2009.

Figure 4. Effect of phosphorus fertilization (unfertilized, F– and fertilized, F+) on growing space index (GSI) of thinned crop trees as a function of time since thinning (March 2007) for the period 2007-2009. Line represents the quadratic model of the effect of time on the change in GSI across both treatments.

Figure 5. Change in basal area (BA), stem density (SD), and quadratic mean diameter (QMD) for unthinned plots between September 2007 and September 2010. Each box plot shows median (solid line), 25th and 75th percentiles (box ends), and extreme values (whiskers and open circles).

Table 1.

[illegible]

Table 2.

Source		Response Variable								
of		<u>All Crop Trees</u>				<u>Thinned Crop Trees Only</u>				
Variation	df	DBH	LA	AGB	ARVI	HT	DLC	LCR	CA	GA
<i>2007-2009 data</i>										
Block	1	*	*	*	ns	ns	ns	ns	ns	ns
INT	1	*	*	*	ns	ns	ns	ns	*	*
T	1	*	*	*	*					
F	1	ns	ns	ns	ns	*	ns	ns	ns	ns
T*F	1	*	*	*	ns					
<i>2008-2010 data</i>										
Block	1	ns	ns	ns						
INT	1	*	*	*						
T	1	*	*	*						
F	1	ns	ns	ns						
H	1	ns	ns	ns						
T*F	1	*	*	*						
T*H	1	ns	ns	ns						
F*H	1	ns	ns	ns						
T*F*H	1	ns	ns	ns						

Table 3.

Date	HT	DLC	LCR
May 2007			
Unfertilized	8.53	2.78	0.33
Fertilized	8.63	2.82	0.33
March 2009			
Unfertilized	9.11	3.13	0.34
Fertilized	9.63	3.55	0.37

Table 4.

Variable	ARVI	(ARVI) ²
DB	-0.231	-0.249
LA	-0.134	-0.145
BM	-0.137	-0.148
ln(DBH)	-0.213	-0.230
ln(LA)	-0.106	-0.115
ln(AGB)	-0.110	-0.120
CA	0.248	0.252
GA	-0.090	-0.097
HT	0.121	0.102
DLR	0.136	0.120
LCR	0.132	0.120
GSI	0.364	0.374

Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.