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Growth and Refoliation of Koa Trees Infested by the Koa Moth, *Scotorythra paludicola* (Lepidoptera: Geometridae)[1]

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ABSTRACT: Since the early 1900s, four major infestations of the koa moth, *Scotorythra paludicola* (Butler), have defoliated koa (*Acacia koa* Gray) stands on the island of Maui. After trees on 7564 ha of the Makawao Forest Reserve were damaged in 1977, a study was begun to determine growth and refoliation response of completely defoliated trees in a stand previously subjected to three different silvicultural treatments. Relative growth rates before defoliation ranged from 5.7 percent to 14.2 percent per year. Trees on thinned-and-fertilized plots showed significantly greater relative growth rates than control trees. The relative growth rates of trees on plots that were thinned only or fertilized only were not significantly different from those of the control trees. After defoliation, relative growth rates ranged from 1.1 percent to 4.3 percent with differences between treatments not significant. The 71 percent reduction in growth after defoliation was statistically significant. About one-third of the sample trees died within 20 months of defoliation.

KOA (*Acacia koa* GRAY), AN ENDEMIC tropical hardwood, is the most valuable native timber species in Hawaii and ranks second only to ohia (*Metrosideros polymorpha* Gaud.) as the most abundant. The koa moth (*Scotorythra paludicola* Butler), endemic on the islands of Maui and Hawaii (Zimmerman 1958), is a koa defoliator. Since 1900, there have been five major outbreaks of the koa moth, four on Maui, and one on Hawaii (Swezey 1931, Fullaway 1946, Davis 1954). The most recent outbreak on Maui, in January 1977, affected 7564 ha, with total defoliation occurring on 1841 ha of koa in the Makawao Forest Reserve and the land of Halehaku (Figure 1) (Stein 1981). A less severe infestation (25 to 45 percent defoliation) was reported in 1973 (pers. comm., R. Hobdy, Hawaii Div. Forestry and Wildlife). This report evaluates the effect of complete defoliation of koa in a stand previously subjected to three silvicultural practices.

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MATERIALS AND METHODS

The study area is located at the upper end of the Makawao Forest Reserve on the northeast flank of Haleakala, on Maui, Hawaii. The site is known locally as Borge Ridge. The study area is 730 m long, 245 m wide, varies from 1050- to 1160-m elevation, and is located on a moderately shallow phase of the Olinda soil series. This reddish-brown loam is low in phosphorus, potassium, calcium, and magnesium, with a surface pH from 4.0 to 4.5. Annual rainfall averages 190 cm, with a mean annual soil temperature of 21° C (Foote et al. 1972).

The forest overstory is even-aged koa, the result of a fire in 1962 and subsequent regeneration. In 1968, the resulting koa stand contained an average of 6200 trees/ha. In 1973, the stand density was 2100 trees/ha.

Foresters familiar with the development of the koa stand reported that height growth had stagnated and none of the trees had expressed dominance (Wesley Wong, pers. comm.). Data from a growth plot established by the Hawaii Division of Forestry and Wildlife in 1968 confirmed this assessment. The average diameter growth was 16 mm/yr (±4 S.D.) for the period 1962 to 1968; 6 mm/yr (±3 S.D.)

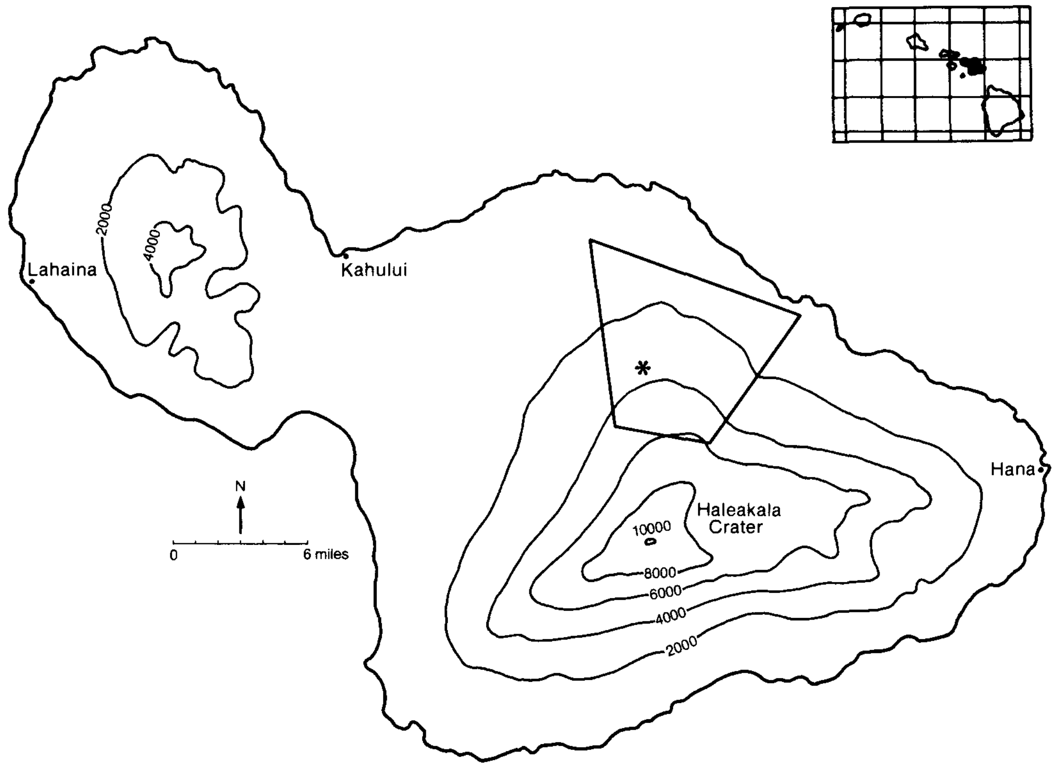

FIGURE 1. An infestation of koa moth (*Scotorythra paludicola*) occurred in 1977 on the northeast flank of Haleakala (asterisk indicates study site).

for the period 1968 to 1973; and only 3 mm/yr (± 3 S.D.) for the period 1973 to 1978, the years during which this study was conducted. The simultaneous decrease in growth rate and stand density strongly indicate stagnation.

In 1974, the stagnated young koa stand was subjected to three silvicultural treatments: (1) thinning to a maximum density of 490 trees/ha; (2) fertilizing with Mg at the rate of 140 kg/ha plus 460 kg/ha of N-P-K (10-30-10); and (3) a combination of (1) and (2). The koa stand was divided into four blocks for treatment replication, with treatments randomly assigned to the four sections of each block. Within each section, three 0.04-ha sample plots were randomly established. Diameter at 1.4 m was recorded in 1975 for all live koa in each plot. After the trees were completely defoliated in 1977 and again in 1978, we measured stem diameter and visually estimated percent refoliation of the crown and the percent of the trunk involved with epicormic sprouting for six randomly selected trees from each sample plot after each defoliation.

The basal area growth model for each tree was based upon the ratio between two periods of time calculated by using

$$A_{t_2} = A_{t_1}(1+R)^{t_2-t_1}$$

where A_{t_1} is the basal area at time t_1, A_{t_2} is the basal area at time t_2 and R is relative growth rate for each tree. Solving for R gives

$$R = (A_{t_2}/A_{t_1})^{1/(t_2-t_1)} - 1.$$

Relative growth rate is independent of initial tree size.

Mean relative growth rate ($\bar{R}_{ijk}$) was determined for the replicates in each treatment by the formula

$$\bar{R}_{ijk} = \left(\sum_{k=1}^{n_{ij}} R_{ijk}\right) / n_{ij}$$

TABLE 1

SOURCE AND DEGREE OF VARIATION UPON THE BASAL AREA RESPONSE OF KOA, 1975–1977 (BEFORE DEFOLIATION)

SOURCE OF VARIATION	DF	MEAN SQUARE	F
Subgroups			
Treatments	3	203.5	5.8*
Blocks	3	261.7	7.4*
Interaction	9	43.4	1.2
Error	272	35.2	

* Significant with $p < 0.01$.

where R_{ijk} is the relative growth rate for the kth tree in the jth replication of the ith treatment, and n_{ij} is the number of trees in each replicate. The mean relative growth rate ($\bar{R}_i$) for each treatment was determined by the formula

$$\bar{R}_i = \sum_{j=1}^{4} \bar{R}_{ij}/4.$$

Because we thought that the variance of $\bar{R}_i$ might depend upon the initial size of the tree, the following transformation was used to equalize the variance

$$\ln(1 + R) = (\ln A_{t_2} - \ln A_{t_1})/(t_2 - t_1).$$

(This equation is the same mean relative growth rate "R" as defined by Kvet et al. 1971). Our analysis indicated, however, that the transformed and untransformed growth ratios were nearly identical and the estimate of skewness and Kurtoises verified that both data fit the normal distribution equally well. Mean relative growth rates ($\bar{R}_i$), therefore, were computed with untransformed rather than transformed data.

Relative growth rate data were subjected to analysis of variance for randomized complete block design. Dunnett's procedure was used to examine differences between treatment means and the control for the predefoliation period (Halperin and Ware 1974). Because missing plots made Dunnett's t test inapplicable, a two-sample t test with the Bonferroni 't' statistic (Bailey 1977) was used to examine differences between treatment means during the postdefoliation period.

TABLE 2

MEAN RELATIVE GROWTH RATE OF KOA TREES FOR EACH BLOCK DURING PRE- AND POSTDEFOLIATION PERIODS, BY TREATMENT

TREATMENTS	BLOCK	MEAN RELATIVE GROWTH RATE (% per year)* 1975–1977	1977–1978
Control	1	6.0	2.1
	2	8.5	—†
	3	6.6	1.7
	4	5.7	2.9
	$\bar{x}$	6.7	2.2
Fertilize	1	6.3	1.1
	2	9.3	—†
	3	7.4	2.9
	4	8.0	3.9
	$\bar{x}$	7.8	2.6
Thin	1	8.1	4.3
	2	14.2	1.1
	3	9.3	3.2
	4	8.0	3.9
	$\bar{x}$	9.9	3.2
Thin and fertilize	1	5.6	2.0
	2	12.4	1.2
	3	12.1	1.6
	4	10.7	2.9
	$\bar{x}$	10.2	1.9

* Results of t tests for all paired comparisons between 1975–1977 and 1977–1978 differed significantly ($p < 0.05$).
† Not measured.

RESULTS AND DISCUSSION

Growth Response

Koa trees increased in basal area from an average of 258.9 cm²/tree (±1.90 S.E.) in 1975 to 297.3 cm²/tree (±1.4 S.E.) in 1977. The relative growth rate for individual plots during the period 1975–1977 ranged from 5.7 percent to 14.2 percent per year with an overall average of 8.7 percent per year.

Silvicultural treatment significantly influenced relative stem growth between 1975 and 1977 (Table 1). Pair-wise comparisons showed a greater basal area on thinned-and-fertilized plots ($p < 0.051$) than on untreated plots. Thinning only and fertilizing only did not significantly increase growth.

The relative growth rate ranged from 1.1 to 4.3 percent per year for the 1977–1978 postdefoliation period (Table 2) with an average of

FIGURE 2. Koa trees on Borge Ridge study area: (A) Typical defoliation with bark chewed on small branches; (B) 12 months after complete defoliation (about 25 percent of the stand canopy had refoliated).

2.5 percent per year. There were no significant differences between treatments and the control plots. Relative growth rates after defoliation were significantly smaller than before defoliation, however. When all sample trees were considered, the mean basal area growth rate decreased 71 percent after complete defoliation.

Refoliation Patterns

In late 1977, refoliation in the outbreak area was slow with bark damage still evident on small branches (Figure 2*A*). Three months elapsed before leaf buds began to expand and, at the end of 6 months we estimated that less than 1 percent of the stand canopy had refoliated. Most of this new foliage was true compound leaves rather than phyllodes that had predominated before defoliation. Regression to juvenile foliage appears to be a common response of koa to injury (Degener 1930). After 12 months, 25 percent of the original stand canopy had refoliated and many dead branches were exposed (Figure 2*B*). Also, after 12 months, most of the juvenile foliage had been replaced by phyllodes.

Extensive epicormic branching and basal sprouting within 2 m of the ground were observed. Four patterns of foliage developed based on the proportion of trunk and crown involved in foliage production: Type I— <25 percent involvement of crown and trunk; Type II— < 25 percent involvement on the trunk and >50 percent of the crown; Type III— >50 percent involvement of the trunk and <25 percent involvement of the crown; and Type IV— >25 percent involvement of both trunk and crown. Among all sample trees, 38 percent were Type I and 15 percent were Type III. We believe these patterns were indicative of a weak recovery. Thirty-four percent were Type II and only 13 percent were Type IV.

We assumed that trees growing in thinned and fertilized plots experienced the least environmental stress, an assumption partly supported by better growth of these trees before defoliation. Consequently, we expected most of these trees to be Type II with substantial crown refoliation. Support for this idea was provided by an analysis of thinned-and-fertilized plots showing that crown involvement in foliage production was positively correlated ($y = 0.354X + 8.701$, $r = 0.521$), and trunk involvement was negatively correlated ($y = -0.487X + 38.538$, $r = -0.623$), with basal area increment. Rapidly growing trees, therefore, met our expectations because their crowns produced more foliage than their trunks. Overall mortality was about 35 percent 20 months after defoliation.

Most populations of most forest insects in the tropics are considered relatively stable because of the diversity of tree species, and lack of distinct seasons. Gray (1972), however, cited several examples of insect outbreaks in natural tropical forests where a single tree species predominated. Rausher (1981) noted that plants growing in dense stands of native vegetation are often less susceptible to defoliation than isolated plants or plants growing in monocultures. The same general conditions prevail in the endemic koa stands of Hawaii. Koa can form pure stands after natural- or human-caused disturbances as was true in this study. Even in mixed stands, emergent koa can form a pure overstory. Because of the large number of phytophagous insect species recorded from koa (Stein 1983), it is not surprising that pure stands of koa are prone to insect outbreaks.

In temperate climates, defoliation has been known to reduce hardwood tree growth; however, most deciduous hardwoods can survive repeated and severe defoliations (Rose 1958). This does not appear to be true with tropical hardwoods. Plantations of *Gmelina arborea* in India were killed after 2 successive years of defoliation by *Calapepla leayana* Latreille (Lamb 1968). Another study reported 40 percent mortality of *Eucalyptus regnans* and significantly reduced diameter growth after a single complete defoliation by the phasmatid, *Didymuria violenscens* (Neuman, Harris, and Wood 1977).

Complete defoliation stops the transpiration stream, thereby preventing transport of nutrients to growth centers (Kramer and Kozlowski 1979). Furthermore, the loss of foliage removes an important source of growth regulating hormones that may direct transport of substrates. Defoliation can also stimulate increased root mortality (Kozlowski 1969), thereby restricting water and nutrient uptake.

The silvicultural treatments were originally applied because none of the trees in this dense stand had expressed dominance and height growth had decreased to one-fifth of what it was during the initial 6 years of stand development. Smith (1962) pointed out that these conditions "are most common on poor sites and in species that can regenerate prolifically there." Stress, the result of low fertility and competition for water, nutrients, and light, was presumably high. Stressed trees generally have reduced amounts of stored carbohydrate and elevated concentrations of sugars and amino-nitrogen. Stress also affects levels of phagostimulants and repellents (Hanover 1975). Furthermore, the effects of defoliation depend on the extent to which various processes are disturbed and on the physiological well-being of the plant at the time of attack (Kozlowski 1969). Stress in the koa stand, therefore, may have predisposed the trees to attack (Mattson and Addy 1975), affected factors that influence fecundity and, thereby, increased the level of koa moth abundance and inhibited recovery after defoliation.

The magnitude of crown and whole tree

mortality, pattern of refoliation, and growth loss in koa differed from temperate forest trees existing on good sites. After a single complete defoliation of *Populus* and *Quercus* species, growth reduction ranged from 7 to 40 percent in healthy stands and up to 80 percent in mature stands under stressful conditions. The loss of radial growth of koa the year after complete defoliation (71 percent) lies at the upper end of this range (Baker 1941, Rose 1958, Hildahl and Reeks 1960, Arru 1964). Koa mortality (at least 33 percent) was greater than the mortality associated with temperate hardwoods but similar to that of the evergreen hardwood *Eucalyptus regnans* (L.) in Australia (Ghent 1958, Duncan and Hodson 1958, Neuman, Harris, and Wood 1977).

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