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Reproduction of *Acacia koa* after Fire[1]

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ABSTRACT: The abundance, distribution, growth, and mortality of koa (*Acacia koa* Gray) seedlings after fires were monitored periodically on two burned areas on Oahu for 2.5 years. On one area, seedling density peaked at 95,300/ha 6 months after the fire; 21 months later it had declined to 18,500/ha. On the other area, peak seedling density occurred at 2 months, with 20,400/ha; 26 months later, density had dropped to 7900/ha. Seedlings were not distributed uniformly over the burned areas but were concentrated near koa seed trees. Height growth for seedlings on one area averaged 2.6 cm/mo; on the other, 1.9 cm/mo. Several pathogens were identified, but only the root-crown fungus, *Calonectria crotalariae*, caused serious damage. More than 50 percent of the mortality on one burn was attributed to it. The regeneration in the burned areas studied indicates that koa will continue to be a component of the forest vegetation.

KOA (*Acacia koa* Gray) seedlings emerge prolifically soon after the forest floor has been disturbed. This characteristic of the species has been well documented (Judd 1920, Whitesell 1964, Vogl 1969, Lamoureux 1971). In Hawaii, the most common large-scale agent of such disturbance is wildfire. Judd (1935) and Wood, Merriam, and Schubert (1969) have reported on the abundance of emerging seedlings after fire. Little quantitative data exist on the subsequent fate of seedlings after emergence.

Because of the importance of koa to Hawaii's forest ecosystems, we studied the abundance, distribution, growth, and mortality of koa seedlings on two burned areas in Oahu. Results are reported here.

STUDY AREAS

The burned forest areas are on the leeward slopes of the Koolau Mountains (Figure 1). Both fires occurred in 1970: the Kipapa fire started on 21 February, and burned more than 1600 ha; the Waimea fire started on 25 March, and burned about 320 ha.

Both areas are similar in physiography and climate. Elevation ranges from 300 to 600 m. The topography is precipitous with sharp ridges, narrow canyons, and intermittent streams running east-west. Mean annual rainfall ranges from 1900 mm/yr at the lower elevations to more than 3800 mm/yr at the higher elevations (Taliaferro 1959).

Prefire vegetation on the Kipapa site consisted predominantly of scrub koa; ohia-lehua, *Metrosideros collina* (Forst.) Gray, subsp. *polymorpha* (Gaud.) Rock; false staghorn fern, *Dicranopteris linearis* (Burm.) Underw.; kukui, *Aleurites moluccana* (L.) Willd.; and broomsedge (*Andropogon virginicus* L. (Figure 2). Open woodland characterized the forest at lower elevations with large openings being occupied by broomsedge or false staghorn fern. Small stands of planted eucalyptus, *Eucalyptus* sp.; brushbox, *Tristania conferta* R. Br.; and Norfolk Island pine, *Araucaria heterophylla* (Salisb.) Franco occurred also. Ravines and stream bottoms were heavily wooded with guava, *Psidium guajava* L.; purple strawberry guava, *Psidium cattleianum* Sabine; and kukui.

The composition of prefire vegetation at the Waimea site was similar to that at Kipapa, but false staghorn fern was less abundant. Stands of planted eucalyptus and paperbark,

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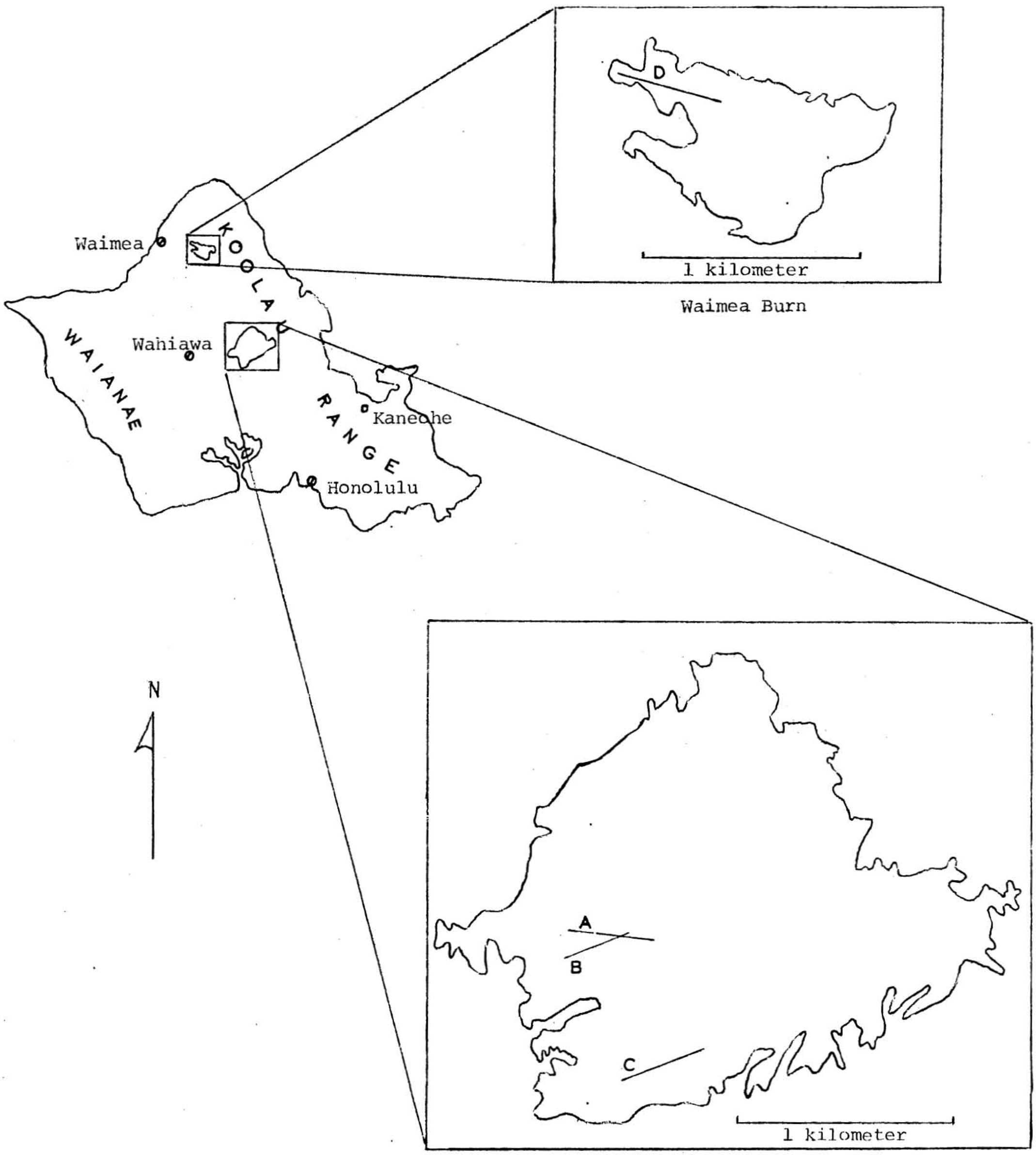

FIGURE 1. Koa reproduction was studied along four transects within the Kipapa and Waimea burns on Oahu, Hawaii.

Melaleuca quinquenervia (Cav.) S. T. Blake were more extensive.

Throughout both burns most of the prefire vegetation was consumed, leaving only scattered, charred tree remnants. Most koa and ohia trees were killed. Many of the introduced trees (eucalyptus, brushbox, etc.), even though severely burned, survived.

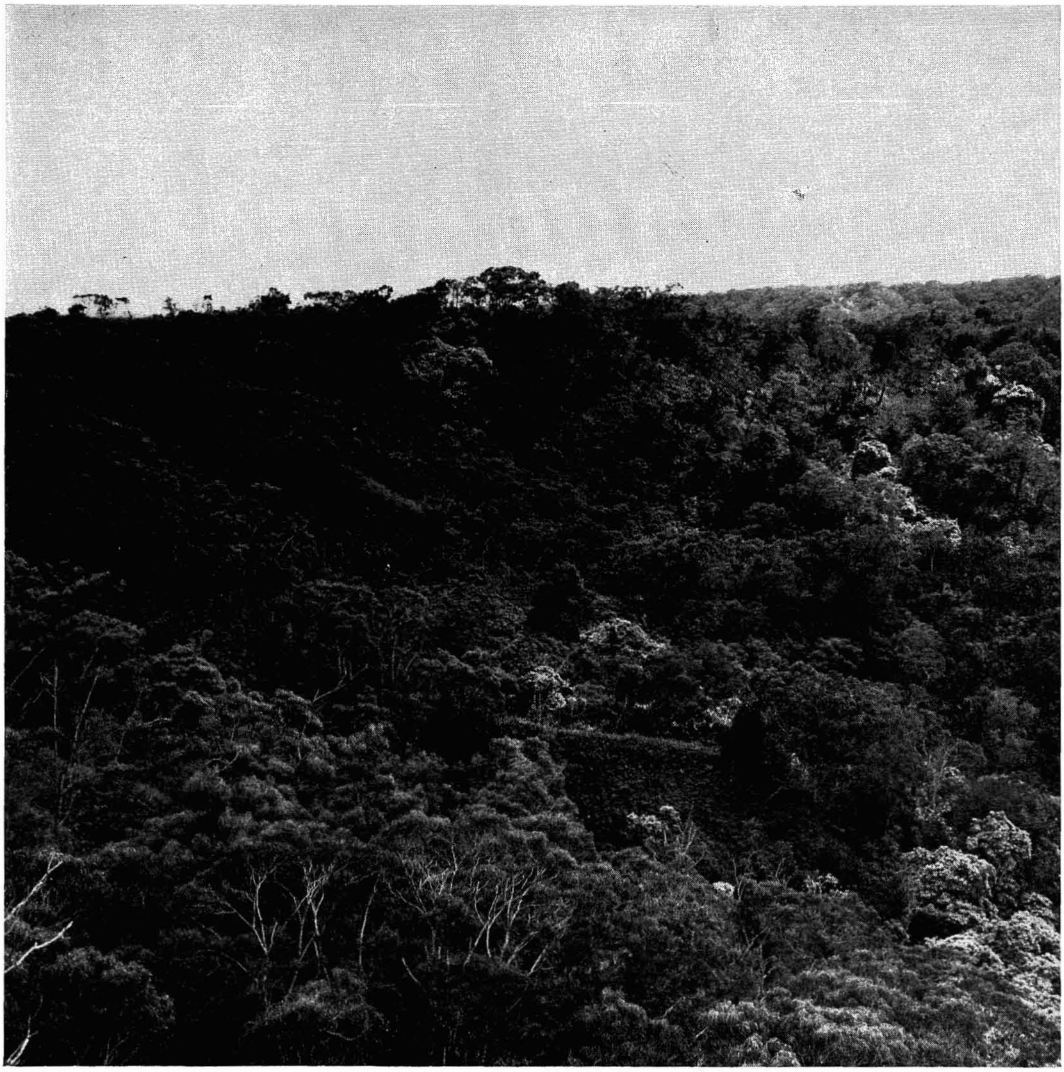

Figure 2. Predominant prefire forest vegetation consisted of koa (foreground), ohia (scattered individuals), kukui (lower right), false staghorn fern (open slopes), and broomsedge (open ridge tops).

METHODS

We examined sample quadrats located along four straight-line transects (Figure 1). Accessibility and topography were determining factors in the location and length of these transects. We believe they traversed typical portions of the burns. Three transects, totalling 2713 m, were established on the Kipapa burn. A 1128-m-long transect was laid out on the Waimea burn. Sampling points were spaced at 61-m intervals along transects. Five 0.3 m^2 quadrats were established randomly within 6.4 m of each sampling point. Unburned areas were not sampled. In all, 200 quadrats were set up at Kipapa and 95 at Waimea. We inventoried them periodically for 2.5 years.

As quadrats were established, the location, date, seedbed slope, surface condition, and position with respect to the nearest potential koa seed tree were recorded. Three surface conditions were recognized: (1) burned to

FIGURE 3. Koa seedlings that emerged in randomly placed 0.3 m² quadrats were marked and monitored periodically during the 2.5-year study period.

mineral soil; (2) burned with unburned litter remaining; and (3) burned with only stubble left. Depth of unconsumed litter and duff was recorded.

All koa seedlings growing within a quadrat were counted and marked (Figure 3). Heights were measured to the nearest 0.5 cm. Seedling condition was recorded as: (1) healthy with no stem or leaf injury; (2) foliage chlorotic; (3) terminal or lateral shoot dieback; (4) insect damage to foliage or stems; (5) dead, stem present; and (6) dead, stem missing. The probable cause of death or injury was recorded when possible.

RESULTS

Seedling Density

Seedling density 2 months after the Kipapa fire averaged about 83,000 seedlings/ha (Table 1). By the 6th month, density had increased 13 percent to more than 95,000 seedlings because

TABLE 1

Average Density, Quadrat Stocking, Mortality, and Height Growth of Koa Seedlings on the Kipapa and Waimea Burns, Oahu, Hawaii, by Months after the Fire

AREA	AVERAGE NUMBER MONTHS AFTER FIRE	DENSITY (number/ha)	QUADRAT STOCKING* (%)	MORTALITY† (%)	HEIGHT GROWTH (cm/mo)
Kipapa	1.9	83420	21.0	—	3.2
	5.8	95261	23.0	5.2	3.8
	8.3	86111	23.0	13.5	4.2
	14.6	53281	19.0	46.5	3.2
	19.0	41978	15.0	57.8	2.7
	27.4	18486	8.5	80.0	2.6
Waimea	2.3	20394	12.7	–	2.3
	6.3	19262	11.6	11.1	1.8
	14.3	13596	8.4	36.8	2.4
	18.8	7930	5.3	63.2	1.8
	28.0	7930	5.3	63.2	1.9

* Quadrats with at least one koa seedling.
† Based on the number of seedlings alive at one measurement time but dead the next.

of continued seedling emergence. About 80 percent of the seedlings tallied had died by the 27th month. By contrast, only one-fourth as many seedlings (20,400/ha) emerged on the Waimea site 2 months after the fire. By the 6th month, density had decreased 6 percent to about 19,300 seedlings/ha in spite of the emergence of new ones.

Koa root-sprouts were found throughout both burns, but none were found in the sample quadrats. Sprouting from the root-crown occurred only on small-diameter trees (< 15 cm) and only in one portion of the Kipapa burn. In some instances where root-crown sprouting occurred, the aerial portions of scorched trees were still alive. But in others, the entire aboveground portion of the tree had been killed. Many of the sprouts were still alive when we made our final measurements.

Seedling Distribution

To characterize koa seedling distribution, we examined quadrat stocking (a stocked quadrat is one which contains at least one live koa seedling) (Table 1). Maximum quadrat stocking was about 23 percent or 46 out of 200 quadrats at Kipapa 6 months after the fire. At Waimea, maximum stocking was reached 2 months after the fire with only 13 percent of the 95 quadrats stocked. Our final measurements indicated that stocking had dropped to 8.5 percent at the Kipapa burn, and to 5.3 percent at the Waimea burn.

Another measure of seedling distribution was whether at least one of the five quadrats around a sampling point was stocked. Twenty points (50 percent) at Kipapa were stocked 2 months after the fire, while 6 points (32 percent) were stocked at Waimea. The final measurements showed point stocking values of 22 percent for the Kipapa burn, and 26 percent for the Waimea burn.

Stocked quadrats tended to occur initially in groups. Two or more stocked quadrats were associated with 65 percent of the stocked sample points 2 months after the Kipapa burn. At 19 months, this figure had dropped to 53 percent. For the final measurement, only eight sample points were stocked, with 50 percent of these having two or more stocked quadrats around them. Two months after the Waimea burn, 67 percent of the stocked sample points contained two or more stocked quadrats. By the 19-month measurement, this figure had dropped to zero.

Of the 46 quadrats at Kipapa that were stocked 6 months after the fire, 50 percent were free of any surface litter and 47 percent had thin litter depths ranging from 0.5 to 5 cm.

Only 3 percent of the stocked quadrats had litter in excess of 5 cm. Also, 97 percent of the individual seedlings were stocked in quadrats with litter depths of 5 cm or less. Of the 154 nonstocked quadrats, 94 had no litter on them.

Two months after the fire at Waimea, 55 percent of the 11 stocked quadrats had no surface litter, whereas 36 percent had litter depths up to 4 cm. Only one stocked quadrat had litter in excess of 4 cm. About 89 percent of the individual seedlings were in quadrats with litter depths of 4 cm or less.

In the Kipapa burn, the distance to the nearest seed tree (living or fire-killed) averaged 4.4 m for quadrats that were stocked any time during the study, and 15.1 m for quadrats that were never stocked during the study. The difference is statistically significant (1-percent level). Stocked quadrats in the Waimea burn averaged 9.4 m from the nearest koa seed tree as compared to 13.8 m between nonstocked quadrats and the nearest seed tree. This difference is not statistically significant. We found no correlation between number of seedlings per quadrat and distance from the nearest seed tree on either burn.

The distribution of quadrats by number of seedlings/quadrat showed that during the 6 months after the Kipapa fire, more than two-thirds of the stocked quadrats had more than one koa seedling. The number of seedlings/stocked quadrat ranged from 1 to 24 at 6 months (Figure 4). Density averaged 3.8 seedlings/stocked quadrat (41/m^2). At 27 months, only 46 percent of the stocked quadrats had more than one seedling. The number of seedlings/stocked quadrat ranged from one to six at 27 months, with density averaging 2.2 seedlings (24/m^2).

On the Waimea burn, the maximum number of seedlings within a quadrat was three. Six months after the fire, five of the stocked quadrats had more than one seedling, with density averaging 1.6 seedlings (17/m^2). Average density at 28 months decreased slightly to 1.4 seedlings (15/m^2).

Height Growth

Height growth of koa seedlings at Kipapa increased relatively rapidly, peaking at an average of 4.2 cm/mo about 8 months after the fire (Table 1). Growth rates at Waimea tended to be uniform throughout the study period, the average never exceeding 2.4 cm/mo.

Average seedling height for transects A, B, and C in the Kipapa burn was greater at most measurement periods than it was for transect D, the Waimea burn. The exception was the last measurement period when the mean seedling height for transect C was less than that for transect D (Figure 1; Table 2). Variation in height was generally less at Waimea than at Kipapa. There was considerable variation in seedling heights along individual transects at each measurement time, as shown by the large standard deviations. Two seedlings along transect B ultimately exceeded the heights of all others, 258 and 238 cm.

We found that some seedlings had not grown at all between measurements and others had suffered dieback; that is, the terminal shoot or upper portion of the main stem had died as a result of insect or disease activity. Of the 37 live seedlings recorded during our final measurement at Kipapa, 18 had suffered dieback. Eight of these had shown positive height growth following dieback. Of the 148 seedlings that died before the final measurement, 44 had suffered dieback during their brief lifetime. Only eight of these had shown positive growth before they died. The situation at Waimea was similar.

Mortality

The root-crown fungus, *Calonectria crotalariae* (Loos) Bell & Sobers, was associated with the death of 80 koa seedlings or over 50 percent of the mortality on the Kipapa burn. We had first discovered this disease in the burned area in September 1970, 7 months after the fire. Aragaki, Laemmlen, and Nishijima (1972) verified the pathogenicity of the fungus. We did not find the fungus on seedlings within the Waimea burn.

Fusarium sp., *Rhizoctonia solani* Kuehn, and *Uromyces koae* Arthur were also identified on koa seedlings. The *Fusarium* fungus was found in association with the black twig borer in both living and dead seedlings. Beardsley (1964) reported that certain species of *Fusarium* may be at least partly responsible for the death of infested twigs and branches. *Rhizoctonia solani*,

FIGURE 4. As many as 258 koa seedlings/m² were found beneath koa seed trees 6 months after the fires, with seedling height averaging about 22 cm.

a primary root pathogen, was isolated from the roots of a single dead seedling at Kipapa. *Uromyces koae*, a rust, was found on many live seedlings at both burns from the 6th month on.

Three insects were found boring in or feeding on koa seedlings. The black twig borer, *Xylosandrus compactus* Eichhoff, was associated with the death of at least six seedlings. Nelson and Davis (1972) reported injury and mortality associated with the black twig borer on other tree species. Though present, the Fuller rose beetle, *Pantomorus cervinus* Boheman, a defoliator, and the false powder post beetle, *Xylopsocus castanoptera* Fairm., a borer, could not be linked directly to the death of any seedling.

As to the mortality of the other seedlings, six at the Kipapa burn were uprooted by feral pigs, *Sus scrofa* L.; two were trampled to death during our field inspection; and 23 had died but we were unable to identify the responsible agent. We could not find 42 other seedlings, and assumed that they had died and decomposed between measurements.

Seedling mortality on the Kipapa burn was

TABLE 2

AVERAGE, MAXIMUM, AND MINIMUM HEIGHTS, AND PERCENTAGE OF DIEBACK OF KOA SEEDLINGS ON THE KIPAPA AND WAIMEA BURNS, BY TRANSECT AND MONTHS AFTER FIRE

AREA AND TRANSECT	MONTHS AFTER FIRE	LIVE SEEDLINGS	SEEDLING HEIGHT MAXIMUM (cm)	MINIMUM (cm)	MEAN (cm)	STANDARD DEVIATION (cm)	SEEDLINGS WITH DIEBACK (%)
Kipapa A	2.5	27	12.7	2.0	7.9	3.0	0.0
	6.0	32	83.8	7.1	32.3	22.9	0.0
	8.8	31	142.2	7.1	54.6	38.6	6.4
	13.8	20	182.9	12.7	62.0	40.1	0.0
	19.2	14	99.1	12.7	49.3	30.2	57.1
	26.0	2	110.5	41.9	76.2	48.5	0.0
Kipapa B	1.8	100	12.7	1.3	6.6	7.4	0.0
	6.0	110	72.4	2.5	19.3	14.0	12.7
	7.9	94	119.4	5.1	30.0	23.1	16.0
	14.9	58	168.9	5.1	40.9	33.3	6.9
	19.0	48	224.0	3.0	53.3	45.7	18.8
	26.0	26	257.8	11.4	72.4	62.7	23.1
Kipapa C	1.8	28	12.7	2.0	5.8	2.5	0.0
	5.8	35	50.8	5.8	18.8	9.9	0.0
	9.0	35	59.7	7.1	23.9	10.9	11.4
	19.0	16	139.7	10.2	35.6	32.0	25.0
	31.5	9	154.9	5.6	38.9	48.5	66.7
Waimea D	2.3	18	10.2	2.5	5.3	2.3	0.0
	6.3	17	34.3	5.1	11.2	7.4	5.0
	14.3	12	132.1	2.5	33.5	34.5	8.3
	18.8	7	62.2	5.1	33.3	22.6	0.0
	28.0	7	91.4	16.6	53.3	31.2	0.0

not related to seedling height or rate of growth. We compared the periodic height and rate of growth of two groups of seedlings: (1) those which were alive at the final measurement, and (2) all others alive at the different measurement periods but dead before the last measurement. Differences between the two groups of seedlings in either height or rate of growth are not statistically significant.

DISCUSSION

Fire affected the koa component of the vegetation in numerous ways. Most koa trees were killed. Vegetation and heavy accumulation of litter and debris which might have interfered with the germination, survival, and growth of seedlings were eliminated in much of the area. Millions of seedlings emerged soon after the fires.

If fires repeatedly burn an area before koa seedlings are able to mature into seed-bearing trees, the seed reserves and seed sources will eventually be depleted. The continued existence of koa would, in the absence of seed, be a function of the sprouting capability of individual trees. This situation seems to be developing in portions of the southwest corner of the Kipapa burn, where the two most recent fires occurred within 8 years of each other. Sapling stands of koa, the obvious result of the earlier fire, suffered substantial losses with few seedlings replacing those killed. It was here, however, that koa root-crown sprouting occurred.

Koa seedling densities greater than those found in our study have been reported. Judd (1935) observed as many as 354,686 koa seedlings/ha in the vicinity of old koa trees in burned-over areas. Wood, Merrimam, and Schubert (1969) found an average of 25.8 seedlings/m^2—over 258,000/ha—on a burned area on Kauai 4 months after a fire.

Reduction in density of koa seedlings of the magnitude we observed is not ususual. Unpublished data on file with the U.S. Forest Service, Honolulu, Hawaii, shows that about 247,000 seedlings/ha emerged after land clearing in the Waiakea Forest Reserve, island of Hawaii. Seedling density 4.5 years later had dropped to 4000 stems/ha.

We expected greater mortality among the slower-growing, shorter koa seedlings than among the taller, faster-growing ones. We reasoned that rapidly growing plants such as broomsedge and Koster's curse, *Clidemia hirta* (L.) D. Don, would soon overtop short koa and shade them out. Koa is considered to be intolerant of shade (Whitesell 1964). However, we did not detect any difference in survival as related to seedling height or rate of growth.

Little is known about the distribution of the root-crown fungus, *Calonectria crotalariae*, in Hawaii's forests. Apart from those taken in the vicinity of the Kipapa burn, no records of infestation in koa or other forest species exist. The pathogenicity of the fungus with respect to koa has been established but its potential virulence is unknown.

Calonectria crotalariae seriously damaged koa seedlings at Kipapa. It infected all sizes of seedlings, both the rapid- and slow-growing ones. Diseased seedlings were found from ridge tops to drainage bottoms. *C. crotalariae* has also been found on a mature koa, 0.9 m in diameter, in the vicinity of the Kipapa burn (communication with A. Martinez, plant pathologist, University of Hawaii).

Unpublished data on file with the U.S. Forest Service, Honolulu, Hawaii, show that 95 percent of the koa seedlings recorded 7 weeks after land clearing in the Waiakea Forest Reserve, island of Hawaii, occurred within 12.2 m of the edge of a seed tree crown. In comparison, data from the Kipapa burn show that over 97 percent of all recorded seedlings grew within 12.2 m of a seed tree crown, whereas 72 percent of those at Waimea were within that distance. Judd (1920) and Whitesell (1964) also reported this phenomenon. Our analysis, however, shows no correlation between seedling density and quadrat distance to the crown of the most likely seed tree. We believe that such a correlation does exist but that our sample was inadequate to detect it.

We suspect that heat is an important mechanism in breaking koa seed dormancy. In a wildfire, the amount of heat reaching koa seeds will be determined, in part, by the depth to which they are buried in the soil or litter layer. Our data show that few seedlings were found where litter exceeded 5 cm. However, because we did not know if koa seeds were buried in the soil or litter of unstocked quadrats, we could not determine a critical litter depth above which seedlings would rarely be found. Besides, the absence of seedlings in litter-covered areas may be caused by factors other than lack of heating by the fire.

Deep compact layers of litter, i.e., mats of unburned false staghorn fern stems, not only insulate koa seed within or below them but also present physical barriers to stem elongation and penetration of light. Spatz (1973) reported that koa seedlings known to have developed beneath a 15-cm layer of dense grass-mulch were not able to grow through that mulch. On the other hand, he found that some seedlings originating under a 15-cm layer of loose koa litter were able to push through and survive.

Small stands of planted nonnative trees are in portions of the burned areas. These include brushbox; robusta eucalyptus, *E. robusta* Sm.; blackbutt eucalyptus, *E. pilularis* Sm.; and paperbark. Not only did the original stands survive the fires, but abundant regeneration of the parent species has grown up near the stand edges. In these mixed stands of regeneration, koa has been overtopped by the introduced species. We believe that the chances for survival of such overtopped koa are low.

Koster's curse, an aggressive, noxious weed, was widespread over the entire Kipapa burn when the final measurements were made and it appeared to be increasing in density. What impact this species had on koa seedling regeneration and what role it will play in the future development of the young stands are not known.

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