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Koa (*Acacia koa*) Ecology and Silviculture

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Cover:
A massive *Acacia koa* at the The Nature Conservancy’s Honomalino property in South Kona on the Big Island, Hawaii. Photograph by J.B. Friday.

Abstract

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Koa (*Acacia koa*) is a tree species endemic to Hawaii that is of immense ecological and economic importance. This species has been mined from local forests for its wood for more than 100 years, and extensive areas of koa-dominated forests have been converted to grazing lands. Today, in recognition of the great importance and value of koa and the forests in which it is found, there is substantial interest in restoration and management of koa forests. This report brings together knowledge on the biogeography, physiology, ecology, and silviculture of koa in an effort to assist landowners and resource stewards in making sound decisions about restoring and managing koa forests.

Keywords: Native forest silviculture, conservation, tree physiology, disturbance ecology, growth and yield, forest ecology.

Preface

Human-free for millions of years, the Hawaiian Islands were colonized by humans only within the past two millenia—a mere blink in geologic time. Yet human activities—particularly in the past 250 years—have changed the landscape forever. Hawaii's native forests have been reduced to a fraction of the area they once occupied as they have been transformed from seashore inland for plantation agriculture, from mountaintop downwards for sheep and cattle, and from dry lands to moist for production of charcoal and goats. The human-mediated introduction and subsequent naturalization of more than 1,000 plant species, an alien flora that now outnumbers the richness of native plants, has led to further, perhaps irreversible, changes in most remaining forests. Despite these pressures, native forests remain in many places in the Hawaiian Islands, and efforts to reestablish native forests are underway.

Like those of many remote oceanic islands, Hawaii's forests are species-poor. Most Hawaiian forests are dominated by either of two tree species, *Metrosideros polymorpha* (ʻōʻhia) or *Acacia koa* (koa). The distributions of both species have been greatly reduced as a consequence of forest conversion and logging, but koa, owing to its greater value as a timber species and its more restricted distribution, has been more severely affected. The reduction in the amount of koa-dominated forest in Hawaii is a major concern for several reasons. First, koa-dominated forests provide important habitat for native plants and animals, including many of Hawaii's endangered honeycreepers. Second, koa forests provide important economic benefits either directly through ecotourism and forestry or indirectly through watershed protection. Third, koa wood is an important part of Hawaiian culture—it was long associated with Hawaiian royalty and has long been used to build the traditional Hawaiian outrigger canoes for fishing, racing, and voyaging. Efforts to reverse the long-term trend of deforestation are beginning to focus on koa for these reasons.

In many ways, koa forest management is the ideal solution to balancing conservation and economic goals for Hawaii's modern landscapes. Both the economic value of koa timber and the conservation value of koa forests for birds, plants, and other organisms provide incentives to establish, restore, and manage koa forests. In addition, koa plays an important role in ecosystem functioning by fixing nitrogen, cycling nutrients, and sequestering carbon. Although different landowners will have different management priorities, it may be possible to manage koa forests for economic, ecological, and conservation values. However, to do so requires a sound science-based understanding of how koa trees grow as individual trees and as part of a forest community. This report is an attempt to synthesize the available literature on the biology, ecology, and management of koa to provide land managers, conservationists, foresters, ecologists, and other people interested in Hawaii's forests with the information required to make informed decisions about establishing, restoring, or managing koa forests.

We have organized the report into five chapters. The first chapter provides information on the biogeography, physiology, and reproductive biology of koa. Although these topics have not been exhaustively researched, we do have a relatively good understanding of these issues.

The second chapter focuses on how koa forests and their associated biota grow, and how koa-dominated ecosystems function. The availability of research findings on these topics is more variable. Considerable research effort has been put into describing the flora and fauna of the Hawaiian Islands. As such, the plants, animals, and even diseases associated with koa forests are well known. In contrast, studies of nutrient cycles and productivity in koa forests are scarce, and there are apparently no studies of koa forest hydrology.

In the third chapter we address the dynamics of koa forests, including stand development patterns, growth and yield, and responses to disturbance. Again, data are scarce for these topics. Few permanent study plots exist in koa forests, and those that do are small, irregularly measured, and represent a small subset of the potential development pathways.

In the fourth chapter we bring together information on the physiological ecology of koa trees and the biotic and abiotic environment in which they live to address questions of how to manage koa forests. Because there is scant history of koa forest management, most of which is anecdotal, this chapter is the most speculative of the report. Nonetheless, because koa is a shade-intolerant tree species, it is relatively uncomplicated from the point of view of silviculture. Other shade-intolerant tree species may therefore serve as guides to managing koa, thus allowing us to consider potential silvicultural pathways for koa based on experiences with tree species of similar ecology from other parts of the world. However, it must be recognized that the silvicultural pathways that we describe for koa are working hypotheses and will require careful monitoring and continuous reevaluation as they are applied. We have intentionally considered the full range of silvicultural alternatives, from individual tree selection to clearcut systems. We do this in the belief that there is no "best" silvicultural system for forest management; rather silvicultural systems should be chosen by landowners based on their management objectives, current land conditions, and the best available knowledge on the tradeoffs among future benefits associated with competing management options. By examining the broadest range of potential management tools, we hope to encourage reestablishment of koa forests across a wide range of ownerships in Hawaii.

We close the report with a short chapter on future research directions and strategies to improve our understanding of koa forests and their management. As with any attempt to synthesize the state of knowledge of a subject such as koa, many research questions remain unanswered. We have highlighted those that emerged repeatedly and that we believe need to be answered to advance significantly our understanding and management of koa forests. However, it is inevitable that these questions reflect our interests and biases and so should not be taken as exhaustive.

Each major subsection of the report begins with a box containing statements summarizing the main points that follow. Those key points are intended to provide a quick overview of important findings, and they are intended to be useful to the nontechnical reader. Accordingly, the boxed statements employ English units of measure, which are the ones most commonly used throughout Hawaii, as well as internationally standard metric units. Throughout this report we refer to the islands by their names (e.g., Kauai, Maui). As such, when we refer to Hawaii, unless otherwise stated or when clear from context, we are referring to the Island of Hawaii, not the State of Hawaii or the Hawaiian archipelago. For the sake of expediency and to avoid confusion regarding place names, we include in appendix A the names, locations, and environmental details of the study sites where most koa research has occurred. For plants and animals, we typically use the common names, although the appendixes contain the scientific names (and in some cases common names) of the native and introduced flora and fauna associated with koa forests.

Contents

Chapter 1: The Koa Tree

We begin by focusing on koa as a species and as an organism. We describe the distribution and taxonomy of koa and the workings of the koa tree—how individuals respond to the availability of light, nutrients, and water—that underpin the patterns in forest productivity and stand growth. We then describe the reproductive patterns of koa, which together with its physiological ecology provide the foundation for understanding the response of koa to different silvicultural strategies.

Biogeography

Taxonomy

Acacia koa A. Gray (koa) is a member of the family Leguminoseae, subfamily Mimosoideae, genus *Acacia,* subgenus *Phyllodineae*. *Acacia* is the largest genus in the Leguminoseae with 1,200 species; subgenus *Phyllodineae* is the largest of the three *Acacia* subgenera with 950 species (Mabberley 1997). The center of diversity for the subgenus is in Australia, where most of the species are found. Recent analyses of *Acacia* have suggested that the genus is not monophyletic and consists of three or more distinct monophyletic groups (Maslin et al. 2003, Pedley 1986). Recognition of the paraphyletic nature of the group has led to several proposed taxonomic revisions, some of which would have led to the renaming of *Acacia koa*. However, in 2005, the genus *Acacia* was retypified and the generic name *Acacia* was conserved with an Australian type in the subgenus *Phyllodineae*. As such, future taxonomic revisions of the current genus *Acacia* will not alter the naming of *Acacia koa*.

Within *Acacia koa* (sensu lato) there are three groups that earlier botanists considered as separate species, but which Wagner et al. (1990), the most authoritative reference on the flowering plants of Hawaii, indicated would be more appropriately treated as subspecies: *Acacia koa* sensu stricto, *A. kauaiensis* Hillebr., and *A. koaia* Hillebr. Koa populations on Oahu, Kauai, and Maui are more closely related than koa sampled from Hawaii (Conkle 1997). Phyllode morphology appears to be highly heritable and definitive of both clonal and population differences (Brewbaker 1974). Islands in the Hawaiian archipelago increase in geologic age from southeast to northwest, and koa on the older islands, such as Kauai, are characterized by narrow, highly curved phyllodes, whereas

Key Points

- Koa (*Acacia koa*) occurs naturally only in the Hawaiian Islands. It is one of about 1,200 members of the genus *Acacia* within the legume family.
- Koa is found at elevations ranging from sea level to more than 6,000 feet (1830 meters), across a broad range of climates, from dry to wet. It is not found in Hawaii's wettest forests. Today the greatest concentrations of koa are found at elevations between 3,000 and 6,000 feet (915 and 1830 meters).
- Koa growth form and habits are quite variable from island to island. Plants from Hawaii have phyllodes (the sickle-shaped, leaf-like structures) that are broader and less curved than those from trees native to the older islands in the Hawaiian chain. On Kauai, two local forms can be found: one that produces round seeds and another that produces oblong seeds.
- Koa's closest relatives may be other species of *Acacia* found on the islands of Reunion and Mauritius in the Indian Ocean, or Australian species of the genus, one of which, *Acacia melanoxylon* (blackwood acacia), is widely planted in Hawaii and is invasive in some places.

those on Hawaii have broad, less curved phyllodes (St. John 1979). Using phyllode width, curvature, and pubescence, among other morphological features, Daehler et al. (1999) concluded that accessions from Hawaii were both genetically distinct and more genetically diverse than those from Oahu and Kauai. Several authors have proposed that round-seeded and oblong-seeded koa from Kauai be treated as separate species (Lamoureux 1971, St. John 1979, Sun et al. 1997). Based on their morphological analyses of common garden trials from across the Hawaiian Islands, Daehler et al. (1999) recommended recognizing *A. koa* from Oahu and Kauai as a distinct variety, *A. koa* var. *latifolia*. On Hawaii *A. koa* subsp. *koaia* is found on drier sites and has phyllodes that are shorter and straighter than those typical of *A. koa*. In addition, the two subspecies have very different wood anatomy and wood properties, the wood of *A. koa* subsp. *koaia* being much harder than that of *A. koa* sensu stricto. However, for the purposes of this review, we follow Wagner et al. (1990) and consider *A. koa* in its broadest sense.

Morphological analyses of floral characters and seedlings suggest that *A. koa* is closely related to *A. heterophylla* (Lam.) Willd. of Reunion Island and Mauritius in the Indian Ocean (Vassal 1969). Recent molecular analyses of the genus *Acacia* suggest that *A. koa* is also closely related to *A. melanoxylon* R. Br. ex Ait. f., an important Australian timber species, and *A. paradoxa* DC, a prickly shrub of eastern Australia (Robinson and Harris 2000). However, because the molecular analysis did not include the majority of the 950 species in *Acacia* subg. *Phyllodineae* (including *A. heterophylla*), phylogenetic relationships within the subgenus and the position of *A. koa* therein are not well understood.

Distribution

Koa is endemic to the Hawaiian archipelago and although it occurs naturally on all of the main islands except Niihau and Kahoolawe, only on Hawaii, Maui, Oahu, and Kauai are densities and contiguous forest areas sufficiently great enough for vegetation to be classified and mapped as koa forests (table 1, fig. 1). It can grow from near sea level to over 2000 m elevation (Gagné and Cuddihy 1990). Koa is currently found or formerly occurred in 10 of the 26 subtropical Holdridge life zones represented on Hawaii (Tosi et al. 2002); these include lowland to montane areas and dry to semisaturated rain forests. Most koa-rich forests are in four life zones: Subtropical Moist Forest, Subtropical Lower Montane Moist Forest, Subtropical Wet Forest, and Subtropical Lower Montane Wet Forest. The largest populations of koa are found at 1000 to 2000 m on Hawaii, where they are a dominant element of the native lower montane forests. Mueller-Dombois (1992) listed 10 ecological zones for the Hawaiian Islands, and koa was a

Table 1—Total forested area and koa-associated forest across the Hawaiian Islands

Island	Total land area	Total forested area	Koa forested area
		Hectares	
Hawaii	1 011 301	314 087	78 929
Maui	189 499	79 555	3 638
Oahu	155 535	67 176	2 875
Kauai	144 076	70 936	2 394
Molokai	67 361	24 102	0
Kahoolawe	11 569	5 602	0
Lanai	36 628	14 752	0
Niihau	18 836	13 306	0

Source: Gon 2006.

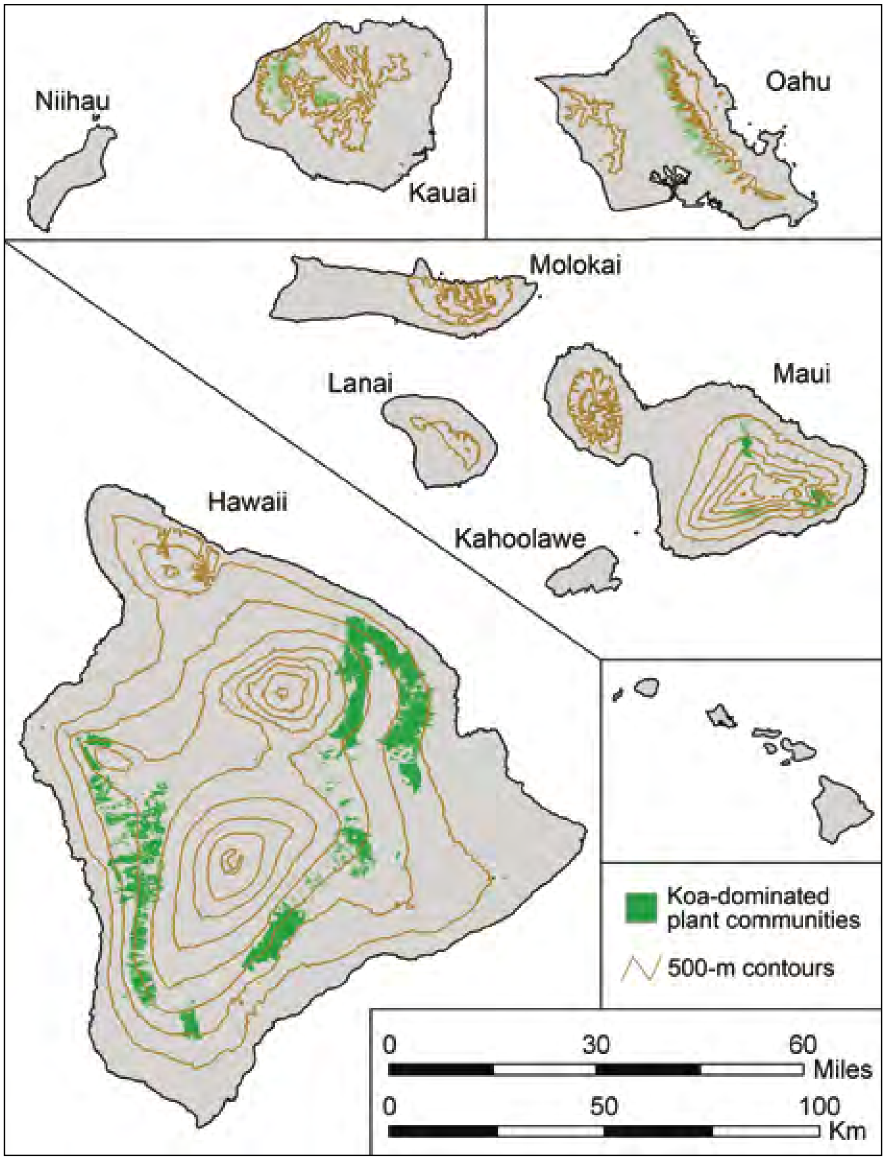

Figure 1—Distribution of *Acacia koa* across the Hawaiian Islands. (Map compiled from Gon 2006 and Jacobi 1990 and provided courtesy of James Jacobi)

dominant component of 3 of them: (1) xerotropical, mixed mesophytic forest; (2) pluviotropical upper montane rain forest; and (3) cool tropical mountain parkland (cf. Ripperton and Hosaka 1942). The current distribution of koa reflects the interactions of koa's environmental requirements and human land-use history.

On Hawaii, koa was originally a canopy dominant on more than 10 percent (about 1000 km^2) of forested land that included four vegetation types across a gradient of wet, mesic, and dry climates (fig. 2) (Jacobi and Scott 1985). A large number of endangered native birds and plants were found in three of the four vegetation types in the early 1980s. However, although most of the endangered forest bird populations were above 1500 m elevation, only 20 percent of the wet mixed forests of koa and ʻōʻhia (*Metrosideros polymorpha*) was above that elevation, and only 13 percent of the mesic koa-ʻōʻhia forest community was still dominated by native species in all vegetation layers (fig. 3). On Maui, koa and koa-ʻōʻhia forests are found from 670 to 1280 m elevation in Kapahulu Valley, Haleakala National Park (NP) (Anderson et al. 1992). Scott et al. (1986) found koa-ʻōʻhia forest northwest of Koʻolau Gap, in Kaupō Gap on the south flank of Haleakalā, and as scattered remnants in the Kahikinui Forest Reserve. On the northern (windward) flank of Haleakalā and outside the area examined by Scott et al. (1986), koa occurs in two relatively narrow zones, the first between approximately 600 and 1200 m elevation (Conrad et al. 1996, Kitayama and Mueller-Dombois 1995, Scowcroft and Stein 1986) and the second between 1750 and 1950 m elevation (Kitayama and Mueller-Dombois 1994b). Koa is absent from the intervening wet montane cloud zone (Kitayama and Mueller-Dombois 1994a). Scott et al. (1986) reported no koa in the forest bird survey area on west Maui, which covered an area of 44 km^2 and extended from 250 to 1760 m elevation. They also noted that the dry western slopes of Haleakalā formerly had extensive koa forest, but logging and grazing by cattle and feral ungulates had destroyed all but isolated remnant stands.

The other islands on which koa is found do not rise above 1200 m, and the highest regions are typically cloud forests that are too wet for koa. On these islands, koa is mainly confined to dry-to-mesic ridges and side slopes. On Lanai, Scott et al. (1986) found widely scattered koa between 300 and 500 m elevation on leeward slopes of Lānaʻihale. On Molokai, which has approximately 23 300 ha of forest (Buck et al. 1986), koa is restricted to dry forest remnants on leeward slopes of the eastern half of the island between approximately 500 and 900 m elevation (Scott et al. 1986). On Oahu, koa are found in mesic forests between 300 and 1000 m elevation on the windward and leeward sides of the Koʻolau Mountains and in small pockets of native forest on the windward slopes of the Waiʻanae Mountains (Buck

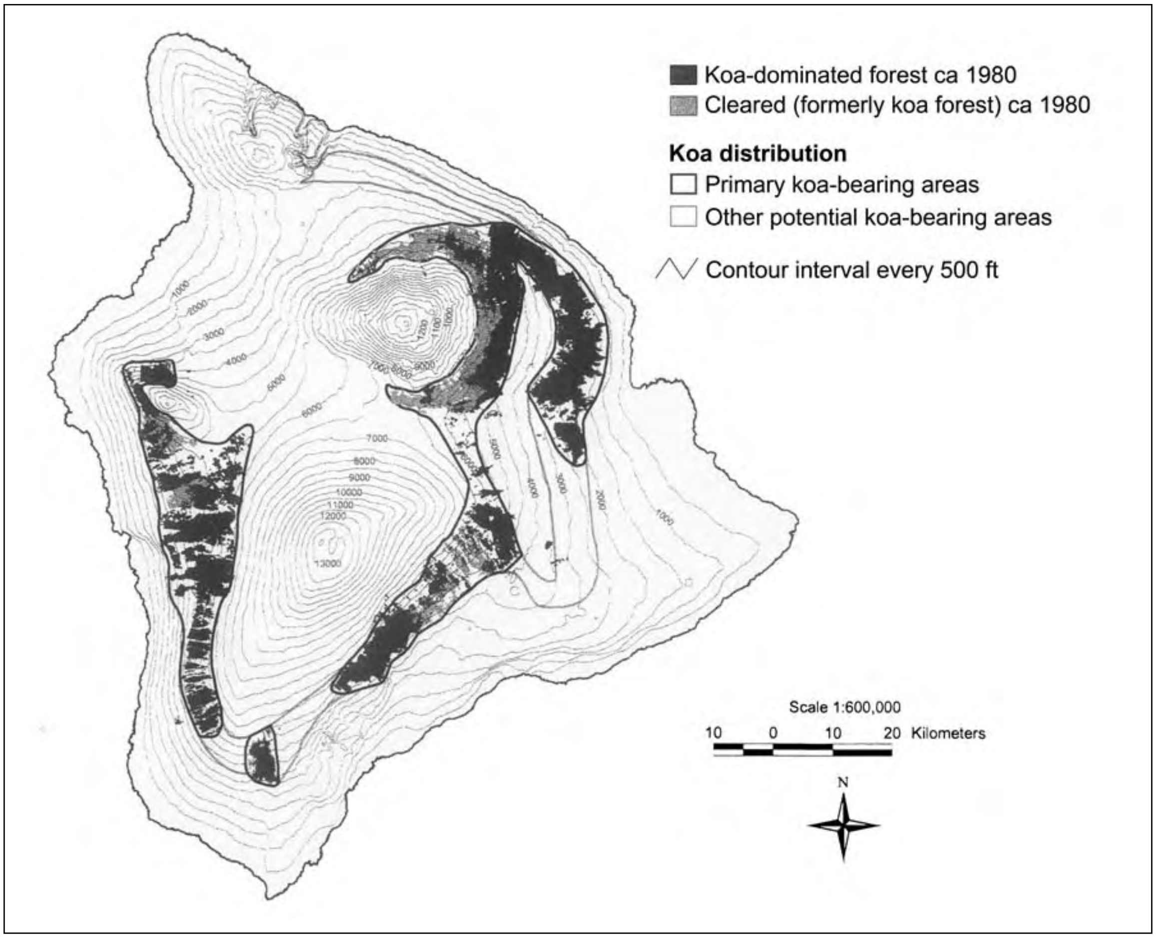

Figure 2—Current, former, and potential distribution of *Acacia koa* on Hawaii. (Map courtesy of Dwight Matsuwaki)

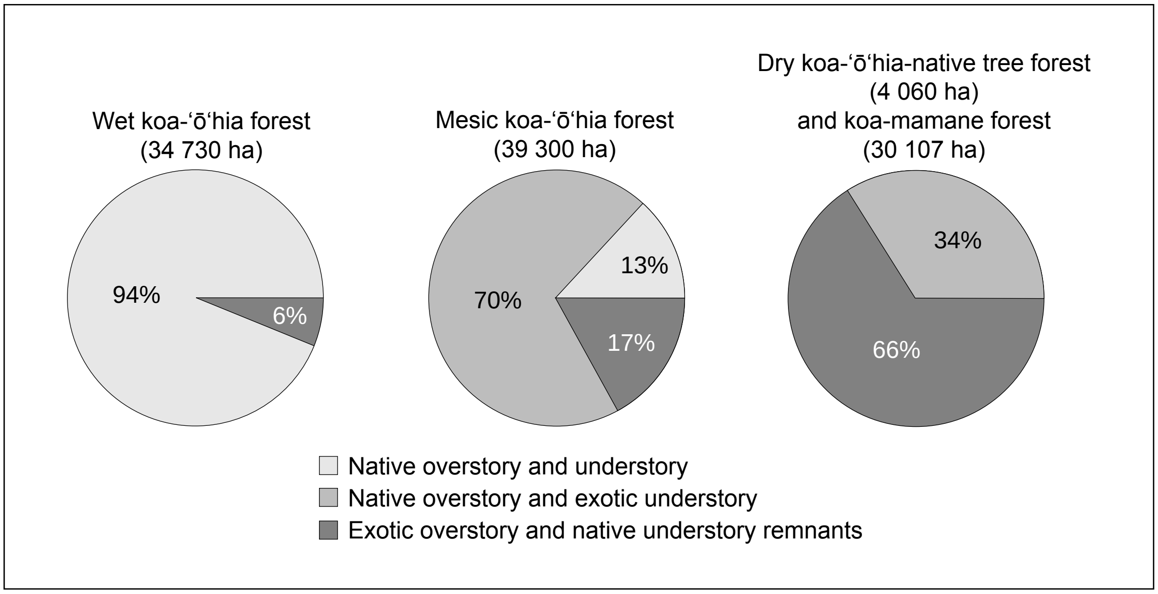

Figure 3—Size of wet, mesic, and dry koa forest types in which koa occurs, and the proportions of each that fall into three broad categories of overstory/understory composition on Hawaii. (Data from Jacobi and Scott 1985)

et al. 1988b, Mueller-Dombois and Wirawan 2005, Whitesell 1990). Koa are found on the west side of Kauai in the Pu‘u Ka Pele and Nā Pali Kona Forest Reserves and Kōke‘e State Park (Buck et al. 1988a, Whitesell 1990), and extend from dry forest ridges at 500 m elevation to wet forest areas at 1100 m elevation (Harrington et al. 1997). Koa is not found in the Alaka‘i Swamp (Scott et al. 1986).

Key Points

- Koa is intolerant of shade, growing best in large clearings. In the open, it is capable of using about 60 percent of the available sunlight on a cloud-free day, which is typical of shade-intolerant plants.
- As a juvenile, koa has compound leaves composed of many tiny leaflets, like many other members of the genus *Acacia*. As the tree matures, it produces phyllodes instead of true leaves. Phyllodes are flattened, sickle-shaped, leaf-like structures derived from the central stem (rachis) of the compound leaves; they are the things we commonly think of as koa “leaves.” Many members of the genus *Acacia*, particularly the dry-climate Australian species, also produce phyllodes.
- Phyllodes use water more efficiently than normal leaves, and they have chlorophyll near both surfaces, giving them an advantage over leaves in light absorption when they are oriented parallel to incoming light energy. Vertical orientation reduces heat loading and helps conserve water.
- The roots of koa form symbiotic relationships with nitrogen-fixing bacteria, which are housed in nodule-like protrusions on small-diameter roots. Those bacteria are capable of providing koa with nitrogen and are essential for the tree’s survival, especially on geologically young or degraded soils, where nitrogen supplies are limited.
- A number of species of nitrogen-fixing bacteria inhabit the roots of koa, and some are more effective at providing nitrogen than others. Nursery inoculation of seedlings with the most effective bacteria may result in more vigorous planting stock.
- Acid soil conditions reduce nitrogen fixation by koa and may lead to aluminum and manganese toxicity. Thus, growth of koa is slowed on extremely acidic soils, a problem that can be alleviated by liming.
- Like roots of most plants, those of koa support a root-fungus combination called a mycorrhiza (plural = mycorrhizae). The tree feeds the fungus, and the fungus assists the tree by taking up phosphorus and other nutrients. Early formation of mycorrhizae can be assured by inoculating seedlings in the nursery, although naturally occurring koa invariably have mycorrhizae.

Physiological Ecology

Photosynthesis

Acacia koa is shade intolerant (Whitesell 1990). As such, it should exhibit pronounced physiological and morphological changes when grown under low light. Walters and Bartholomew (1990) compared seedlings grown under full and partial (27 percent photosynthetic photon flux, PPF) sunlight. The most obvious morphological difference was that seedlings grown in shade did not develop phyllodes (fig. 4). Gleason and Ares (2004) reported similar morphological responses when seedlings were grown at full (100-percent PPF) and reduced (18-percent and 2-percent PPF) light levels. After 5 months, 80 percent of koa seedlings in the full light treatment and 30 percent in the 18-precent PPF treatment had produced phyllodes, while none of the seedlings grown in the 2-percent PPF treatment had. Koa seedlings are also able to switch between leaf and phyllode production in response to changes in the light environment (Walters and Bartholomew 1990). Seedlings that had produced only leaves under 27 percent of full sunlight began producing phyllodes within a few weeks of being switched to full sun. Similarly, seedlings that had produced


Paul G. Scowcroft

Figure 4—True bipinnate leaves and phyllodes of *Acacia koa*.

only phyllodes in full sun reverted to leaf production within 6 to 8 weeks of being switched to 27 percent full sunlight. In both cases, existing fully developed foliage of both types persisted and retained the shade-or sun-leaf characteristic under which it developed. Leaves and phyllodes that were developing when the light regime was switched developed foliage morphologically characteristic of the new regime.

The ability of koa seedlings to adapt physiologically to prevailing light conditions is unclear. Gleason and Ares (2004) showed that seedlings grown in full sunlight reached light saturation at a photosynthetic photon flux (PPF) of 900 μmol • m^{-2} • s^{-1} (about 60 percent of full sunlight) and had maximum photosynthetic rates (A_{max} at full light) of 12.6 μmol CO_2 • m^{-2} • s^{-1}, while seedlings grown under lower PPF levels (37 and 286 μmol • m^{-2} • s^{-1}) had lower light saturation points (122 and 198 μmol • m^{-2} • s^{-1}) and lower A_{max} (4.8 and 6.6 μmol CO_2 • m^{-2} • s^{-1}). In contrast, Walters and Bartholomew (1990) found that photosynthetic light response curves for leaves and phyllodes were the same regardless of the light regime under which plants developed. They also detected little effect of changing the light regime on photosynthesis—leaves and phyllodes that developed after a switch in light level showed nearly the same photosynthetic light response as leaves and phyllodes measured before the switch. Walters and Bartholomew (1990) attributed their results to the large adaptive potential of the light-harvesting and CO_2-fixing systems of koa foliage. In particular, they found that koa leaves and phyllodes were able to adjust concentrations of chlorophyll and the carboxylating enzyme ribulose 1,5-bisphosphate carboxylase (RuBPcase) to maintain a uniform photosynthetic light response regardless of light regime. The reason for the disparity between these two studies is unclear. Also note that in studies of photosynthetic rates conducted in the field, koa has exhibited a much wider range of A_{max} values (6.6 to 14.2 μmol CO_2 • m^{-2} • s^{-1} (Gleason and Ares 2004, Hansen 1996, Hansen and Steig 1993) than in greenhouse studies (12.6 to 15.3 μmol CO_2 • m^{-2} • s^{-1} (Ares et al. 2000; Gleason and Ares 2004; Walters and Bartholomew 1984, 1990). However, this may just reflect the inherently higher variability of samples from a tree canopy as compared to samples from greenhouse seedlings.

Photosynthetic characteristics such as A_{max} and light compensation point do not differ significantly between leaves and phyllodes of koa when both are displayed horizontally, which is the typical orientation of leaves but not of phyllodes (Hansen and Steig 1993, Walters and Bartholomew 1984). Phyllode orientation, which influences photosynthetic rate, may range from perpendicular to parallel to the incoming sunlight. Vertically displayed phyllodes receive about half of the overhead photosynthetically active radiation that horizontally displayed phyllodes receive (Walters and Bartholomew 1984). Owing to vertical orientation and layers of chlorophyll on both sides of the phyllode, maximum light interception occurs twice daily (midmorning and midafternoon), whereas horizontal orientation and a single chlorophyll-containing layer of the leaf allows maximum interception only at midday (Walters and Bartholomew 1984). Phyllodes are thicker than leaves because (1) phyllodes have a thick central parenchymatous mesophyll layer that is absent in leaves and (2) phyllodes have two palisade layers, one on either side of the central mesophyll layer, whereas leaves have a single palisade layer on the adaxial surface. Consequently, photosynthetic rates per unit leaf mass are less in phyllodes than in leaves (Walters and Bartholomew 1984). The photosynthesis system of koa leaves also responds more rapidly to sun flecks than does the system of phyllodes (Gleason and Ares 2004).

Water Relations

Water can be a major limiting factor for the growth of koa, especially toward the drier end of its broad climatic range. Intrinsic water-use efficiency (WUE: carbon assimilated per unit water lost) in koa is influenced by a number of factors. Ares et al. (2000) demonstrated a significant genetic component to WUE among koa genotypes chosen from an elevation gradient on Hawaii and grown in a common garden experiment in Oahu. They also found that leaf δ^{13}C signatures (a time-integrated measure of WUE) and instantaneous WUE were positively correlated with elevation and thus water availability. Across an elevation-precipitation gradient on Kauai, leaf δ^{13}C was highly correlated with leaf area, growth, and conversion efficiency (wood production per unit leaf area) (Harrington et al. 1995). As water availability decreased, the amount of wood produced per unit leaf area decreased, leading to substantial reductions in wood production. In support of those findings, Ares and Fownes (1999) showed that on leeward Hawaii, where the elevation-precipitation gradient is the reverse of that on Kauai, koa WUE and productivity were also positively correlated with precipitation.

Phyllodinous *Acacia* are commonly found in arid zones, particularly Australia, where isobilateral phyllodes are an important adaptation to low water availability. Hansen (1986, 1996) showed that koa phyllodes had greater WUE but lower rates of photosynthesis (mass basis) than juvenile leaves, suggesting that phyllodes are more drought-adapted than juvenile leaves. If this were the case, then koa seedlings growing across a moisture gradient should shift from juvenile leaves with greater carbon assimilation rates to phyllodes with better drought adaptations more quickly on drier sites. This hypothesis has not been tested either with common garden or reciprocal transplantation experiments.

Mineral Nutrition

Koa forms symbiotic relationships with two kinds of micro-organisms that facilitate nutrient acquisition: nitrogen-fixing bacteria and arbuscular mycorrhizal fungi (AMF). In low phosphorus (P) soils, AMF improve the P status of koa, which improves nodulation and nitrogenase activity, both of which require large amounts of P. Nodulation and nitrogenase activity improve the nitrogen (N) status of plants, thus allowing them to be more productive and supply both fungus and bacterium with photosynthate. Availability of soil N and P determine in part the extent of AMF and rhizobial colonization—low concentrations of P typically favor substantial mycorrhizal development, and low concentrations of N are associated with increased nodulation and high rates of N_2 fixation (Brundrett 1991, Sprent 1987). However, too low a nutrient status of the host plant can inhibit formation of root symbioses (e.g., Habte and Osorio 2001, Stamford et al. 1997).

Nitrogen fixation—

Irregularly shaped nodules, similar to those found in the soil on roots of beans, alfalfa, and other nodulating plant species, are a conspicuous feature of koa roots (fig. 5). The nodules house slow-growing bacteria of the genus *Bradyrhizobium* (Allen and Allen 1936), which convert atmospheric N_2 into ammonium that is readily assimilated by koa. Nodules can also occur on roots that grow into the decomposing, soil-like organic material that accumulates in forks of koa trees and on the upper surfaces of branches and under bryophyte mats that form around the base of tree trunks (Leary et al. 2004). The aboveground bacteria are probably different species than those found belowground because the former appear to infect only koa whereas the latter infect other legume species. Furthermore, isolates of *Bradyrhizobium* from aboveground nodules show less tolerance to aluminum (Al^{3+}) than isolates from belowground (Leary 2007).

James Leary

Figure 5—*Bradyrhizobium* nodules on the roots of *Acacia koa*.

Bradyrhizobium species from a broad range of plant hosts nodulate koa roots (Bohlool and Nakao 1991). The lack of specificity does not mean that all strains are equally effective at fixing N, and indeed, some isolates from species other than koa produce greater koa shoot and nodule biomasses than koa isolates. High density of indigenous *Bradyrhizobium* at a given planting site does not guarantee that koa will benefit from the symbiosis. Turk et al. (1993) recommended that species such as koa that are relatively nonspecific for nodulation be subjected to effectiveness tests. An effective strain could be used to inoculate nursery seedlings, and thereby increase their initial growth and probability of successful establishment after transplanting. Turk et al. (1993) also showed that inoculation should increase shoot N content and growth where indigenous soil rhizobial densities are low and mineral N availability limits growth.

In young, even-aged stands of koa, acetylene reduction (AR) assays indicated that potential nitrogenase activity (a surrogate for N-fixation) was the same (about 15 $\mu\text{mol} \bullet \text{g}^{-1} \bullet \text{ha}^{-1}$) for nodules in all stands sampled, regardless of age (Pearson and Vitousek 2001). However, because there were fewer nodules in older stands, effective nodule biomass was an order of magnitude greater in 6-year-old stands than in 20-year-old stands (Pearson 1997). Therefore, N-fixation rates were estimated to be about 23 $\text{kg N} \bullet \text{ha}^{-1} \bullet \text{yr}^{-1}$ in 6-year-old stands, but <2 $\text{kg N} \bullet \text{ha}^{-1} \bullet \text{yr}^{-1}$ in 20-year-old stands. Pearson and Vitousek (2001) hypothesized that the decline in N-fixation with age was due to a corresponding decline in soil P availability.

Although nodule biomass decreases and nitrogenase activity stays constant with stand age, the pattern changes with substrate age. Nodulation and nodule biomass are not correlated with substrate age, but potential nitrogenase activity of the nodules is (Pearson and Vitousek 2002). Comparisons of young and old lava flows showed AR rates were 16 $\mu\text{mol} \bullet \text{g}^{-1} \bullet \text{hr}^{-1}$ at the youngest site and 2 to 5 $\mu\text{mol} \bullet \text{g}^{-1} \bullet \text{hr}^{-1}$ at the older sites. Estimates of N-fixation were 8 $\text{kg N} \bullet \text{ha}^{-1} \bullet \text{yr}^{-1}$ at the youngest site and no more than 2 $\text{kg N} \bullet \text{ha}^{-1} \bullet \text{yr}^{-1}$ at the older sites. The decline in AR was associated with a marked decline in concentrations of labile soil P.

Other factors influencing the symbiotic relationship between koa and *Bradyrhizobium* are soil moisture and concentrations of toxic metal ions. Excess soil moisture is hypothesized to account for the absence of both in wet, mid-elevation sites on Haleakalā, Maui (Kitayama and Mueller-Dombois 1994a, Nakao and Kitayama 1996). High Al^{3+} or manganese (Mn^{2+}) concentrations, which characterize many of Hawaii's acid soils, are known to adversely affect some strains of *Bradyrhizobium* (Graham 1992).

Mycorrhizae—

Low plant-available P in highly weathered soils in the tropics can limit plant growth. Arbuscular mycorrhizal fungi, which form symbiotic associations with plants by hyphal penetration of host root cells, improve the P status and growth of plants in P-deficient soils. The benefit is mainly due to a greatly expanded mineral-absorbing surface area provided by hyphae extending farther out into the soil than root hairs. Koa roots are typically strongly colonized by mycorrhizae. For example, the incidence of functional AMF on old koa trees growing in montane forests on Kauai was consistently high, with more than 75 percent of root lengths infected (Koske et al. 1992).

There is good evidence that establishment of mycorrhizae while seedlings are in the nursery leads to better growth after out-planting. For example, Miyasaka et al. (1993) reported that initial growth of koa seedlings in P-deficient volcanic-ash soil was moderately increased by colonization with the AMF *Glomus aggregatum* Schenk & Smith in the nursery, and Habte et al. (2001) found that, after being transplanted into abandoned pasture, inoculated koa seedlings grew significantly faster than uninoculated seedlings, even though uninoculated plants were colonized by native mycorrhizae soon after planting.

Colonization of out-planted seedlings with mycorrhizae-forming fungi is not inevitable. Habte (1989) compared colonization rates in intact soil and soil from which the surface 7.5 cm had been removed. As expected, removal of the surface soil depleted the supply of fungal propagules, and root colonization was significantly greater in areas where surface soil was left intact. He recommended inoculation of koa seedlings before planting in eroded soils. In addition, other studies have shown that colonization of koa seedlings may be delayed after planting, but the factors impeding colonization are unknown (Habte 1989, Ikawa and Habte 1997).

Reproduction

Flowering and Fruiting

Koa flowers between December and June, although some flowering can occur throughout the year. Fruits ripen 3 to 4 months after pollination (Allen 2002, Whitesell 1974). Lanner (1965) described the reproductive phenology of koa along an elevation gradient on Mauna Loa over a 12-month period beginning in mid-1963. He found that koa growing at elevations below 1500 m flowered throughout the year, but that a heavy flush of flowering began in early December and lasted for approximately 2 months. The timing of the onset of heavy flowering was correlated with elevation, such that koa at the highest elevation flushed last. In Lanner's study, koa at about 2000 m initiated heavy flowering in early March, several weeks after the low-elevation koa had stopped flowering. The length of the flowering period was relatively uniform across the elevation gradient. In contrast to the low-elevation sites, high-elevation koa rarely flowered outside the 2-month period of intense flowering. Koa flowers appear to be fully self-fertile. However, self-pollination of any individual floret or flowering head (fig. 6), which consists of about 50 florets, is unlikely because the flowers are highly dichogamous—the anthers release their pollen about 5 days before the style and stigma are fully uncoiled and ready to be fertilized (Brewbaker 1977). Dichogamy in koa does not prevent cross-pollination among flower heads on the same tree. The 16-cell pollen grain is large, with a diameter of about 80 µm, and because of its weight, dispersal distance may be limited beyond 50 m from the source (Brewbaker 1972).


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Figure 6—Flowers of *Acacia koa* with each inflorescence containing about 50 florets.

Like other *Acacia*, koa requires insect pollinators for effective cross-fertilization (Brewbaker 1974). Although bees and flies are frequent visitors to koa flowers, the identity of the suite of potential insect pollinators and their relative importance are unknown (Scowcroft et al. 1991). Lanner (1965) demonstrated the importance of large insect pollinators in an exclusion experiment that compared seed-set in open-pollinated inflorescences and in inflorescences enclosed in fine mesh bags. Seed-set occurred in 15 percent of the open flowers and about 3 percent of the enclosed flowers. Despite considerable

Key Points

- The 2-month season of heaviest flowering of koa starts around December below about 4,800 feet (1460 meters) elevation, although some flowers may be produced year-round at these low elevations. At high elevation, flowering is delayed until March.
- Koa is pollinated by insects. Pollination success is not known, but one study reported that about 15 percent of the flowers produced seeds. After pollination, seeds take about 7 months to mature.
- Seed pods and the seeds they contain are vulnerable to a number of organisms (primarily insects) that attack them before they are dispersed. Thus, even with good pollination, a tree can fail to produce many seeds.
- Seeds of koa can remain viable for a long time in the soil—25 years or more.
- The roots and stumps of koa produce shoots that can develop into trees. The production of root sprouts is a common response upon suspension of grazing, and such sprouts are long-lived.

seed-set in several of his study plots, Lanner noted that within 2 months, nearly every seedpod was lost to an unknown agent that caused necrosis, curling, and subsequent death. The few surviving seedpods were attacked by the koa seed moth (*Cryptophlebia illepida*). Because of the catastrophic mortality of the seedpods, few data were available regarding pod and seed ripening. Indeed, Lanner reported that only one koa seedpod in his study reached maturity, having reached full length in about 10 weeks, but not fully ripening for nearly 7 months. Nonetheless, koa is known to be a prolific seed producer. Although Lanner's (1965) study provides a useful glimpse of the reproductive patterns of koa, the degree and causes of interannual variation in reproductive phenology and the factors that determine seed-production success are not known.

Seeds

Koa produces flattened pods that are generally 7 to 15 cm long and 1.5 to 2.5 cm wide (Allen 2002, Little and Skolmen 1989, Whitesell 1974). Pods may dehisce and release seeds while still attached to the tree (fig. 7) or they may fall to the ground unopened. In both cases, dispersal distance is limited, and wind is the main mechanism of dispersal. Each pod contains several ellipsoid, laterally flattened seeds that are 6 to 12 mm long and 4 to 7 mm wide, dark brown to black, and slightly shiny (Wagner et al. 1990). Koa seeds are subject to insect predation within the pod,

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Figure 7—Seedpods of *Acacia koa*.

and losses of 85 percent of the annual koa seed production have been recorded on Maui (Stein 1983a). Variation in seed size is partially dependent on source, with seeds from Hawaii tending to be larger than those from other islands (Allen 2002). The number of cleaned seeds ranges from 5,300 to 16,300 per kilogram (Whitesell 1974). Like most *Acacia* species, koa seeds have hard seedcoats that are impervious to water. Scarification is needed to break the seedcoat dormancy; common techniques include nicking an edge with nail clippers, or immersion in a sulfuric acid or hot water bath (Wilkinson and Elevitch 2003). The seedcoat of seeds deposited in the soil breaks down naturally, but the process is slow and seeds may remain viable for 25 years or more (Whitesell 1990). The longevity of buried koa seeds has important consequences for forest management and will be discussed at greater length in chapter 4 (Koa Silviculture).

Vegetative Reproduction

Koa sprouts vigorously from roots, but those sprouts quickly disappear if browsing animals are present. Baldwin and Fagerlund (1943) established fenced exclosures in Hawaii Volcanoes National Park (NP) to demonstrate the impacts of ungulates on establishment of koa regeneration. They showed that when ungulates were removed from the area, thousands of root sprouts per hectare emerged. Indeed, of all the koa reproduction that they examined, not a single individual originated from seed (Baldwin and Fagerlund 1943). Tunison et al. (1995) relocated Baldwin and Fagerlund's original plots 50+ years after their establishment and found that the sprout-origin stands had survived and grown substantially in the intervening decades. As a result of Baldwin and Fagerlund's (1943) research, Hawaii Volcanoes NP suspended grazing. By the 1970s, following a major effort to reduce feral cattle and goat populations, large areas of the park were blanketed by koa root sprouts


Laura Nelson

Figure 8—Sprouts on the stump of a recently cut *Acacia koa*.

(Tunison et al. 1995). Koa can also sprout from cut stumps and trunks below the points of girdling (fig. 8). Scowcroft and Wood (1976) reported sprouting from the root crowns of fire-killed koa that were ≤15 cm diameter at breast height, but none from larger individuals. Stump sprouts have been documented on koa stumps up to 1 m in diameter. On smaller stumps, the number and longevity of sprouts are highly variable. No data on the long-term survival or growth of koa stump sprouts are available.

Chapter 2: The Ecology of Koa Forests

In this chapter we consider the ecology of the koa forest as a whole. The focus is on patterns and processes occurring at the stand, forest, or landscape level that affect the forest community. We discuss the physical structure of koa forests across its range, the flora and fauna associated with koa forests, and productivity and nutrient cycling in koa forests and the factors that control them.

Forest Structure

Like many native trees on species-poor, remote islands, koa (*Acacia koa* A. Gray) is a conspicuous component of forests that occupy a wide range of environments. Koa's physiognomy is quite plastic, ranging from tall, straight-boled trees in diverse forests of wet and moist climates to short, contorted, multibranched trees whose crown widths can easily exceed their heights in dry climates on nutrient-poor soils. The form and stature of koa is reflected in the structure of the forests in which it is an important component. For example, on wet montane sites on Hawaii, koa forests achieve considerable structural complexity. These forests are stratified into five layers: herbaceous (0 to 0.5 m), tree ferns (*Cibotium* spp.) (>0.5 to 5 m), low-stature trees (>5 to 10 m), intermediate-stature trees (>10 to 15 m), and emergent trees (>15 m) (Mueller-Dombois et al. 1981). Koa and ʻōʻhia alone compose the intermediate-stature and emergent tree layers of these forests, where mature koa, which can account for 70 percent of crown cover, reach heights of 25 m, crown widths of >20 m, and diameter at breast height (DBH) >1 m (e.g., fig. 9). On drier mesic montane sites on Hawaii and Maui, where koa attains its greatest heights (35 m), vegetation composition and stratification are similar to those on wet sites but tree ferns are sparse, a shrub layer substitutes for the tree fern layer, and the canopy, which can be open to closed, is uneven (Gagné and Cuddihy 1990, Jacobi 1990). On still drier montane sites, koa occurs as scattered individuals or clonal colonies in mountain parkland and savannah vegetation (Mueller-Dombois and Krajina 1968). Maximum height of koa in these open stands is <20 m. In savanna, old koa trees have broad, spreading crowns, and many limbs are prostrate.

Key Points

- Forests in which koa is found differ widely in structure. Some forests are dominated by tall trees with straight stems, whereas others are composed of short, crooked koa trees. Koa also occurs as isolated individuals with large, spreading crowns in areas that have been converted to rangeland.
- Climatic conditions and site quality influence the physiognomy of individual koa trees and the overall structure of koa forests.
- Koa may be found in mixed-species stands as scattered individual emergent trees or in dense stands with few other species.
- Invasive plant species that successfully establish in koa forests may create forest structures that are new to these ecosystems. In some cases, such as with strawberry guava thickets, koa may be limited to the overstory and be unable to regenerate.

J.B. Friday

Figure 9—Large *Acacia koa* in mixed koa-ʻōʻhia forest on leeward Hawaii.

On the older islands (Oahu and Kauai), where soil fertility is relatively poor and elevations are lower, the stature of koa forests tends to be influenced most heavily by rainfall. Wet koa-ʻōʻhia forests on these islands have a canopy that is 15 to 20 m high with a well-developed understory in which tree ferns, though present, do not form a distinct layer (Gagné and Cuddihy 1990). In mesic forests, the koa and ʻōʻhia canopy is <15 m high, and the ground cover is often dominated by 1- to 2-m-thick mats of uluhe fern (*Dicranopteris linearis*) (see app. B for species names). Elsewhere, the invasive shrub, strawberry guava (*Psidium cattleianum*), forms dense thickets engulfing the scattered large koa that emerge above them. Koa regeneration is virtually absent in these *Psidium* thickets, and without intervention the remnant koa will eventually die out without replacement. At their xeric extreme, as for example on leeward Kauai, koa forests have an open canopy that is <10 m high (fig. 10). The koa trees are heavily branched, and stem form is typically convoluted and prostrate (Harrington et al. 1995). Only herbaceous, shrub/low-stature tree, and canopy tree layers are found in these dry forests.

Robin A. Harrington

Figure 10—Low-stature *Acacia koa* forest on a dry site on leeward Kauai.

Key Points

- The open canopy of koa forests, coupled with nitrogen-rich soils, leads to development of a rich understory of plants, sometimes natives and sometimes exotics.
- Widely used pasture grasses, such as kikuyu grass (*Pennisetum clandestinum*) and meadow ricegrass (*Ehrharta stipoides*), survive in the understory of koa forests where they provide forage for cattle but impede regeneration of native plants.
- About 30 percent of the threatened and endangered plant species in Hawaii can be found in koa forests. Loss of koa forests, primarily through conversion to rangeland, has been a major cause of plant extinction and endangerment in Hawaii.
- Of Hawaii's 35 remaining native forest bird species, 30 species, 17 of which are endangered, can be found in koa forests.
- Native birds known to nest in cavities in large, old koa trees include the ʻākepa (*Loxops coccineus coccineus*) and the ʻōmaō (*Myadestes obscurus*).
- At least seven of Hawaii's native forest bird species forage in koa trees. The most specialized of these is the ʻakiapōlāʻau (*Hemignathus munroi*), which uses its curved bill to extract insect larvae that bore into koa wood. Restoration of koa forests is a key to habitat provision for this endangered bird.
- Conversion of high-elevation koa forests to rangeland has removed the uppermost refugium of forest birds. As climate warms, reestablishment of those high-elevation forests, particularly on Hawaii and Maui, is essential if native forest birds are to have habitat in which to escape from avian malaria.

Associated Biota

Plants

Most plants associated with koa—whether trees, shrubs, vines, or ferns (but not grasses)—are native species (table 8 in app. B) (cf. Mueller-Dombois and Fosberg 1998). Of the 289 endangered plant species in Hawaii, 87 occur in forests where koa is present (table 2).

Whereas koa has a broad climatic range, the species that are associated with it change across climatic zones. The wet montane old-growth forests (fig. 11) contain a rich assemblage of herbs, ferns (dominated by the treefern, *Cibotium glaucum*), shrubs, and trees of lesser stature than the koa (Cooray 1974, Mueller-Dombois et al.1981).

In drier or cooler climates, the physiognomy of koa forests is less complex, but the associated flora is still quite diverse, if different from that of koa forests in wetter, warmer climates. In tree-islands (kīpukas) surrounded by younger lava in Hawaii Volcanoes National Park (NP), koa shares canopy dominance with *Sapindus saponaria* (mānele). In still drier montane areas on Hawaii (Hualālai and windward Mauna Loa and Mauna Kea), koa and *Sophora chrysophylla* (māmane) form the canopy of a short-stature (<10 m), open forest (Gagné and Cuddihy 1990). The understory vegetation of these forests has been degraded by feral animal and livestock grazing, but before the introduction of ungulates to Hawaii the biota of the drier koa-containing forests was much richer. Rock (1913), for example, regarded the moist-to-dry forests on the northern flank of Hualālai, Hawaii, as the most diverse communities in the islands, a situation that has changed dramatically in the past century as ungulates have all but eliminated regeneration of native plant species.

Table 2—Number of endangered plant species associated with koa forests

Island	Species		Reference
	Number	*Percent*	
Hawaii	19	32	U.S. Fish and Wildlife Service 1978, 2002, 2003e
Maui	15	21	U.S. Fish and Wildlife Service 2003b
Lanai[a]	1	3	U.S. Fish and Wildlife Service 2003c
Molokai	0	0	U.S. Fish and Wildlife Service 2003d
Oahu	21	21	U.S. Fish and Wildlife Service 2003g
Kauai	35	37	U.S. Fish and Wildlife Service 2003f
Statewide	87	30	

[a] Although remnant koa trees on Lanai are too sparse for forests to be classified as koa forests (see table 1), they are recognized as being part of the critical habitat for one endangered plant species.

The understory of lowland forests near agricultural and urban areas is usually dominated by alien plants and contains few, if any, native species (Jacobi and Scott 1985). Below 975 m elevation on the southeastern flank of Haleakalā, Maui, alien plant cover (primarily grasses and sedges) ranged from 43 to 77 percent, but was <10 percent at higher elevations (Anderson et al. 1992). In many places today, the dominant species in koa forests are aliens. The dense growth of *Psidium cattleianum* in parts of Haleakalā NP, Maui (Stone and Holt 1990) is a prime example.

Stands that develop after disturbance in moist and wet montane habitats often have closed canopies of pure koa for 20 to 30 years (Scowcroft and Fujii 2002, Scowcroft and Stein 1986). Nevertheless, light levels beneath koa canopies are not so attenuated that they preclude development of native or alien understory vegetation (Harrington et al. 1997, Mueller-Dombois and Howarth 1981, Skolmen 1990). The understory of grazed koa forests is commonly dominated by one of two introduced forage grasses: kikuyu grass (*Pennisetum clandestinum*) or meadow ricegrass (*Ehrharta stipoides*). Where those two grasses have equal opportunity to colonize, their relative

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Figure 11—Understory of *Acacia koa* forest dominated by hāpuʻu, the endemic tree-fern *Cibotium glaucum*.

proportions vary as a function of light transmitted: higher light levels favor kikuyu grass, whereas lower light levels favor meadow ricegrass (Grace 1995).

Coarse woody debris, which typically covers 9 to 25 percent of the ground in old-growth koa-ʻōʻhia forest (Cooray 1974), provides seedbeds for many species. Cooray (1974) classified nine tree species as either log-established or soil-established and found that eight of them (*Acacia koa, Cheirodendron trigynum, Coprosma rhynchocarpa* A. Gray, *Ilex anomala, Metrosideros polymorpha* [syn. *collina*], *Myrsine lessertiana*, *Pelea clusiifolia*, and *P. volcanica* A. Gray) preferentially established on decaying logs. At Laupāhoehoe, Hawaii, ʻōʻhia (*M. polymorpha*), ʻōlapa (*C. trigynum*), and kāwaʻu (*Ilex anomala*) had more than 95 percent of their regeneration rooted on decaying logs or other organic seedbeds (Scowcroft 2003), and among the ferns examined, *Asplenium* spp. were almost wholly dependent on organic substrates.

Lack of decaying logs and fallen tree fern trunks do not limit regeneration of koa, but they are crucial for some native species. Scowcroft (1992), working in abandoned grazing land, found that decaying logs covered <2 percent of the ground but supported 50 to 70 percent of the regeneration owing to their provision of a seedbed that raises them above the intense competition of alien pasture grasses.

Birds

Thirty of Hawaii's 35 extant species of endemic forest birds are found in forests where koa is a dominant or an associated species (see app. C for the list and scientific names) (Scott et al. 1986). Seventeen of these 30 species are listed as federally endangered (U.S. Fish and Wildlife Service 1984, 2003a, 2006). Although most of these species forage in koa, the ʻakiapōlāʻau is the only one that is narrowly specialized to use koa and depends on koa forests for its survival.

The ʻakiapōlāʻau (fig. 12), which is found only on Hawaii and numbered only 1,000 to 1,200 birds in 1995 (Fancy et al. 1996), is the signature bird of koa forests and a specialist on the koa tree. Scott et al. (1986: 133) described it as a "bizarre honeycreeper with a stout, woodpecker-like lower bill, and a slender, decurved, sickle-like upper bill." Ralph and Fancy (1996) considered the ʻakiapōlāʻau to be a habitat specialist requiring large, old-growth koa. However, Pejchar et al. (2005) showed that ʻakiapōlāʻau commonly use young koa stands as well. At Keauhou Ranch, Hawaii, ʻakiapōlāʻau were absent from very young stands of koa (Sakai 1988), but by the time the stands were 14 years old, several individuals had been sighted (Ralph and Fancy 1996). Subsequent surveys have shown that the 10- to 30-year-old stands of closed-canopy koa supported greater densities of ʻakiapōlāʻau than did mature koa-ʻōʻhia forests and that they were breeding in the young stands

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Figure 12—The native Hawaiian bird species, ‘akiapōlā‘au, foraging in an *Acacia koa* tree.

(Pejchar et al. 2005). The high density of ‘akiapōlā‘au in the young stands has been attributed to the density of koa and, by inference, the abundance of lepidoptera and wood-boring cerambycid larvae that make up a high proportion of the bird’s diet (Ralph and Fancy 1996).

‘Ākepa, which is found on Hawaii, Kauai, and Maui (Scott et al. 1986), also uses koa for foraging and nesting.The Hawaii subspecies is a cavity nester (Scott et al. 1986) and often uses very large (>70 cm DBH), multistemmed koa trees for nesting (Freed 2001). In a survey of potential ‘ākepa nesting sites, Freed (2001) found that 15 percent of koa trees with cavities appropriate for nesting contained ‘ākepa nests. However, because mortality rates for large koa trees were relatively high and little to no koa regeneration was found, Freed (2001) expressed concern about the long-term viability of the ‘ākepa population at his study site. ‘Amakihi, which is common and widespread throughout the Hawaiian Islands, also makes substantial use of koa trees and forests. In the old-growth Kilauea Forest, Hawaii, it spent more than 20 percent of its foraging time in koa (fig. 13).

Several other native birds including the endangered Hawaii creeper, ‘ōma‘o, ‘āpapane, and ‘i‘iwi are known to occur in koa forests, but are not necessarily dependent on them. For example, the Hawaii creeper is found in koa forests, but it is unclear if its abundance is linked to koa abundance and forest disturbance.

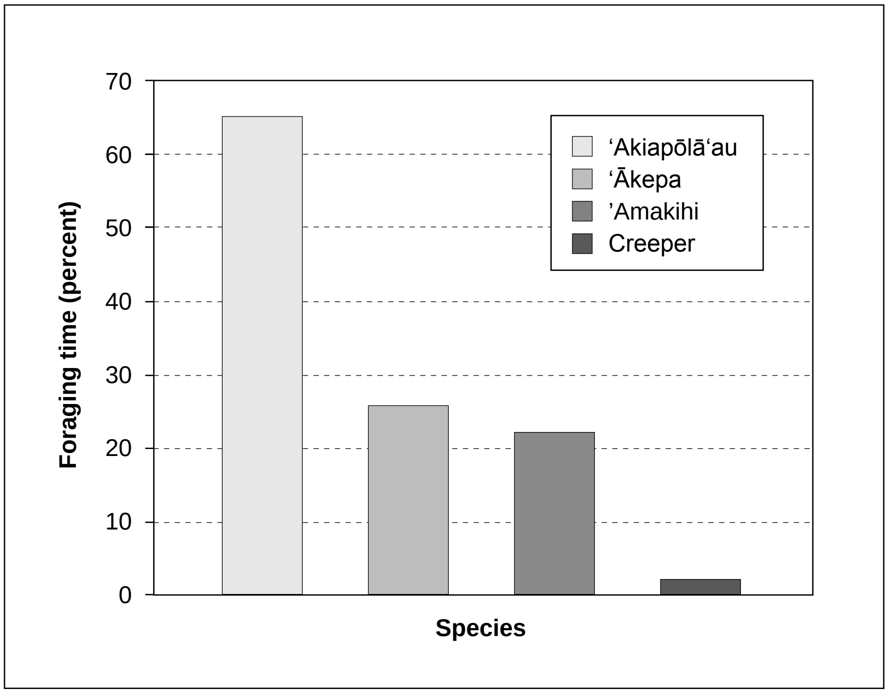


Figure 13—Percentage of time that four native Hawaiian bird species spend foraging in *Acacia koa* trees. Source: Conant 1981.

Although surveys have shown the Hawaii creeper to be common in relatively undisturbed koa-‘ō‘hia forest (Sakai and Johanos 1983), very little foraging time was spent in koa trees (fig. 13). The Hawaii creeper also inhabits disturbed koa-‘ō‘hia forests. Bird density was negatively correlated with koa density in one study (Ralph and Fancy 1994a) and positively correlated with koa density in another (Scott et al. 1986).

The ‘ōma‘o, like the ‘ākepa, also nests in koa tree cavities, but it spends most of its foraging time on ‘ōlapa and naio, common associates of koa (Ralph and Fancy 1994b). ‘Āpapane and ‘i‘iwi are two of the most common endemic species in koa-‘ō‘hia forests (Scott et al. 1986). Although these species spend up to 10 percent of their time foraging in koa trees (Ralph 1995), they are mainly nectarivorous and travel long distances in response to ‘ō‘hia and māmane flower availability (Hess et al. 2001, Scott et al. 1986). Despite their preference for nectar, ‘i‘iwi have been observed foraging extensively in 10- to 20-year-old koa corridors established in deforested areas of Hakalau Forest National Wildlife Refuge (NWR) (Jeffrey 2007) (fig. 14). On the eastern slopes of Mauna Kea, ‘āpapane and ‘i‘iwi roost in mid-elevation koa-‘ō‘hia forests (ca. 1600 to 1800 m). This behavior may be to avoid

Andrew Kikuta

Figure 14—Hakalau Forest National Wildlife Refuge, with *Acacia koa* planted in strips running up Mauna Kea to 2000 m elevation. The bands of koa are the foundation for a habitat restoration effort, crucial for the survival of some of Hawaii's most endangered forest birds.

the fog that forms at lower elevation, to obtain thermal protection afforded by dense forest, or to reduce exposure to night-flying, malaria-transmitting mosquitoes (*Culex quinquefasciatus*), which are common at lower elevations (MacMillen and Carpenter 1980, Ralph and Fancy 1995).

Conant (1981) also recorded observations of two alien bird species, the Japanese white-eye (*Zosterops japonicus*) and the red-billed leiothrix (*Leiothrix lutea*), at the Kilauea Forest. However, neither species used koa trees, although they did use species associated with koa, especially ‘ō‘hia (Japanese white-eye) and ‘ākala (red-billed leiothrix). At another time and in the same forest, Japanese white-eye were observed foraging on koa flowers (Ralph 1995).

Key Points

- The mammal fauna of koa forests includes all the most notorious alien species, from rats to feral cattle, none of which is a healthy addition to these ecosystems. Even a species such as the pig, whose rooting might stimulate germination of buried koa seeds, does more harm than good by uprooting plants of many species, by dispersing seeds of potentially harmful alien plants, and by creating wallows in which mosquitoes breed.
- More than 100 species of plant-eating insects have been collected from koa, but relatively few of these cause measurable damage. Among the most damaging ones are two native species—the koa moth (which defoliates koa) and the koa seedworm (which destroys most koa seeds in years when the seedworm population is large). An alien insect, the black twig borer, also causes substantial damage, but there is some indication that borer resistance might be achieved through plant breeding. Another alien, the acacia psyllid, kills terminal twigs of young koa resulting in loss of apical dominance and bushy crowns.
- Although nearly 100 fungal pathogens are known to attack koa, most of these are of little economic or ecological significance. Vascular wilt fungus is the most problematic disease to which koa is susceptible, particularly at low elevation.

Pests

Mammals

Most vertebrates found in koa forests are alien species (the single exception being the native Hawaiian hoary bat (*Lasiurus cinereus semotus*). These include pigs, goats, cattle, deer, rats, and others (Whitesell 1990). The adverse effects that these aliens have on native ecosystems and management options for mitigating the damage they inflict have been reviewed by a number of authors (Cuddihy and Stone 1990, Stone 1985, Stone and Loope 1987, Stone et al. 1992, Tomich 1986, Tummons and Dawson 2002) and remain a primary focus of conservation and land rehabilitation efforts in Hawaii.

Feral pigs (*Sus scrofa*) are nearly ubiquitous and are generally considered to be the most destructive of the large herbivores found in koa forests (Stone 1985, Warshauer and Jacobi 1982). Rooting by feral pigs destroys koa and other native tree seedlings (Cooray and Mueller-Dombois 1981) and may promote the spread of some alien plant species (e.g., *Passiflora tarminiana* and *Erharta stipoides*) but not others (e.g., *Psidium cattleianum, Rubus argutus*, and *Holcus lanatus*) (Anderson et al. 1992; Aplet et al. 1991; LaRosa 1984, 1992; Stone et al. 1992).

Cattle, goats, sheep, and deer browse koa seedlings and root suckers and, together with the black rat (*Rattus rattus*), strip bark from sapling- and pole-size trees (Baldwin and Fagerlund 1943, Scowcroft and Hobdy 1987, Scowcroft and Sakai 1984, Spatz and Mueller-Dombois 1973, Telfer 1988). Cattle are particularly destructive of understory vegetation. Their trampling exposes the soil, degrading the watershed value of native forest and fostering conditions favorable for invasion by alien plants (Cuddihy and Stone 1990).

Plants

Hundreds of invasive plants species have become established in the Hawaiian Islands. Many of these have had substantial adverse effects on Hawaiian forests. Many of these invasive species are found in koa forests, but we focus on three particularly pernicious species, banana poka, clidemia, and blackberry, whose impacts on koa forests are well-documented.

The first, banana poka, is a perennial liana from the Andes that has naturalized in koa-ʻōʻhia forests on Hawaii, Maui, and Kauai (LaRosa 1984, 1992). Although banana poka tolerates both high and low light levels, its growth increases in proportion to the amount of light it receives, allowing it to thrive in disturbed areas. Koa seedlings that regenerate naturally in treefall gaps or artificially in scarified planting areas are especially vulnerable to suppression and deformation by overtopping banana poka vines (Scowcroft and Adee 1991). The fungal pathogen *Septoria passiflorae* Syd., which was successfully introduced in 1996 to banana-poka-infested sites on Hawaii, Maui, and Kauai, has proven to be an effective biological control agent (Trujillo et al. 2001).

Disturbance also favors *Clidemia hirta*, another invader of koa forests. This evergreen shrub can form monospecific stands more than 3 m tall, with such low light levels in the understory that even mosses and liverworts, which are normally able to survive in dense shade, die out (Smith 1992). A *Clidemia*-specific fungal pathogen, *Colletotrichum gloeosporioides* (Penz.) Sacc., caused a striking decline of the weed. Nevertheless, the fungus failed to spread beyond the areas of inoculation because the extended period of wet, windy weather required for its airborne dispersal did not occur (Trujillo 2005). Where *Clidemia* decline did occur, seedlings of native plants, including koa, became established.

Finally, blackberry (*Rubus argutus*) is an aggressive weed found sparsely in the understory of many koa forests; it can survive beneath koa and responds vigorously if the canopy is opened by severe wind, thinning, or defoliation (Scowcroft and Stein 1986). The resulting dense stands are nearly impenetrable and compete with native species for light, nutrients, and water. No effective biological control has been developed for blackberry.

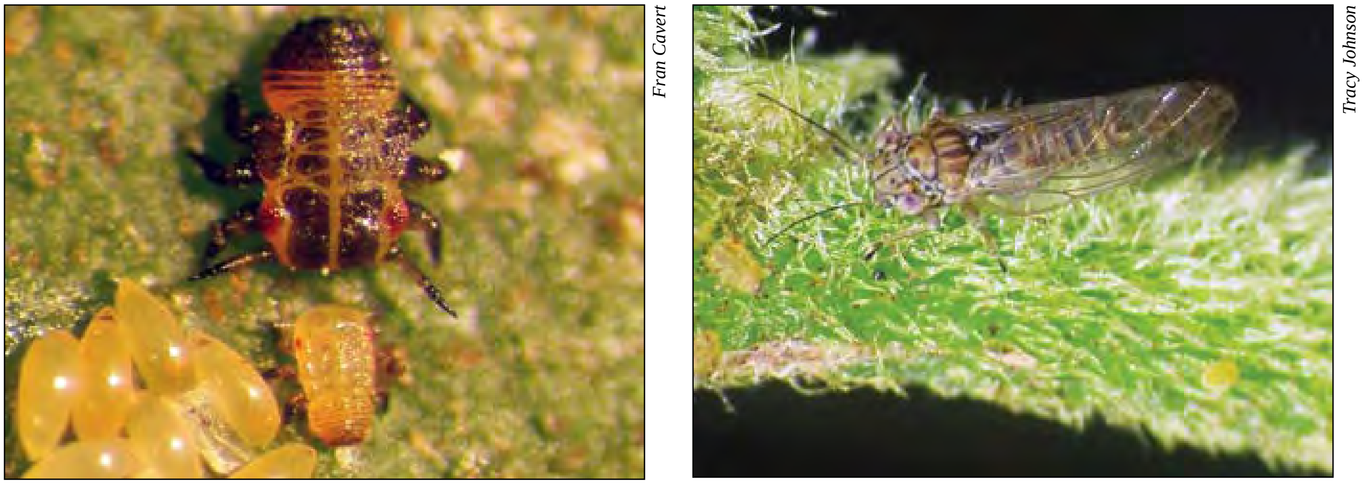
Insects

Stein (1983c) listed 101 species of phytophagous insects associated with koa: 64 were endemic, 30 introduced, and 7 of unknown origin. Gagné (1979) recovered 113 native and introduced taxa of canopy arthropods from koa along an altitudinal transect on the southeast flank of Mauna Loa and Kilauea volcanoes. Spiders and lepidopteran caterpillars (mainly koa moth larvae, *Scotorythra paludicola* Butler) composed most of the arthropod biomass found in koa canopies in Hawaii Volcanoes NP (Gagné 1979, Gagné and Howarth 1981). The koa moth is the most serious of the lepidopteran defoliators affecting koa and is capable of defoliating entire stands (Davis 1955). Since 1900, five major outbreaks have been recorded on Maui and one on Hawaii. The 1977 outbreak on Maui affected 7564 ha, of which 1841 ha (24 percent) was totally defoliated (Stein and Scowcroft 1984). The affected forest was a dense even-aged stand that had regenerated following a fire in 1962. Both height and diameter growth had slowed to low levels as a result of the high density of the stand. In the 20 months following the koa moth outbreak, mortality of koa trees was about 33 percent, and the relative diameter growth rate of survivors fell to just 2.2 percent per year compared to a relative growth rate of 6.7 percent per year before defoliation (Stein and Scowcroft 1984). The most recent outbreak was in 2003 on Maui. All size classes of koa were affected, and more than 50 percent of the trees above 670 m elevation lost at least 75 percent of their phyllodes (fig. 15) (Welton et al. 2004). Observations indicated that the vascular wilt fungus, *Fusarium oxysporum* (see next section), might have been a precursor to the insect outbreak.

Patti Welton

Figure 15—Landscape-scale impacts of the 2003 koa moth (*Scotorythra paludicola*) outbreak on Maui.

Other insects posing significant threats to koa include the endemic koa seedworm (*Cryptophlebia illepida* Butler), which can destroy most seeds in any given year (Stein 1983a, 1983b) and the alien black twig borer (*Xylosandrus compactus* Eichoff 1875), which contributes to mortality of koa seedlings and small saplings by weakening the stem, thus increasing susceptibility to breakage (Daehler and Dudley 2002) and damaging tree form. Resistance to attack by black twig borer seems to exist for some maternal koa families grown from seed sources on Hawaii, Maui, Oahu, and Kauai and planted in a common garden at 180 m elevation on Oahu. However, the differences were not related to the island of origin. The black twig borer is a vector for the spread of *Fusarium solani,* a nonpathogenic fungus, but it is not a vector for the spread of the pathogenic vascular wilt fungus, *Fusarium oxysporum* (Daehler and Dudley 2002). Another significant threat to koa, especially in moist to dry areas is the acacia psyllid, *Acizzia uncatoides* Ferris & Klyver (fig. 16), which was accidentally introduced to Hawaii in 1966 (Leeper and Beardsley 1973). The acacia psyllid was first described from introduced *Acacia* in New Zealand and is believed to be endemic to Australia (Ferris and Klyver 1932). It breeds and feeds on the new terminal growth of koa, and population levels closely track host flushing phenology (Leeper et al. 1981). Infestations cause dieback of new terminal growth and over time may have a cumulative debilitating effect on host plants (Leeper and Beardsley 1973). The acacia psyllid may contribute to the bushy growth form typical of planted koa in grasslands at high elevation.



Fran Cavert

Tracy Johnson

Figure 16—The exotic acacia psyllid, *Acizzia uncatoides,* on an *Acacia koa* leaf. The left panel shows the eggs (0.4 mm long) and nymphs; the right panel shows an adult (4 mm long).

Pathogens

Koa is vulnerable to at least 94 fungal pathogens (e.g., Bega 1979, Hodges 1984, Raabe et al. 1981), and the available information on 22 taxa was summarized by Gardner (1997). It is unknown how many of these pathogens are native and how many are exotic. Fortunately, relatively few organisms cause diseases of significance to koa populations. Some outbreaks, such as the seedling blight caused by *Calonectria crotalariae* (Loos) Bell & Sobers (fig. 17), can be locally damaging, but are rare, occurring only when particularly favorable conditions develop. Other pathogens, such as *Phytophthora cinnamomi* Rands, a root-infecting fungus, although ubiquitous, usually do not cause mortal disease in koa.

Paul G. Scowcroft

Figure 17—White mycelia and red fruiting structures are symptomatic of collar root disease on *Acacia koa* seedlings caused by *Calonectria crotalariae*.

Perhaps the most serious threat to koa is the virulent vascular wilt fungus, *Fusarium oxysporum* Sclecht. (Gardner 1980). In Hawaii Volcanoes NP, koa dieback generated by koa wilt spread radially from localized infection centers and affected all size classes of trees (Anderson et al. 2001). Typical symptoms include yellowing of the phyllodes and thinning of the upper crown, followed by wilting of the entire crown and death, although some trees produce numerous epicormic shoots along their main stem before they too die. In other trees, only a portion of the upper crown is affected. Symptomatic trees had lower leaf area, leaf mass, specific leaf mass (i.e., leaf mass per unit leaf area), and rate of photosynthesis compared to healthy trees. These symptoms are consistent with infection by a vascular wilt fungus. Soils in dieback stands were significantly wetter and more acid than adjacent healthy stands, but whether the differences reflect cause or effect could not be determined (Anderson et al. 2001). In a lowland common garden at Maunawili, Oahu, *F. oxysporum* was responsible for most of the mortality among the koa provenances that were planted (Daehler and Dudley 2002). *Fusarium oxysporum* was recovered from branches of diseased trees in plantations of koa undergoing dieback on the windward slopes of Mauna Kea, north of Hilo (Anderson 2003), but has not been isolated from seeds or seedpods (James 2004). Other *Fusarium* species may also play a role in koa wilt disease, including *F. solani* (Mart.) Appel. & Wollenw., *F. subglutinans* (Wollenw. & Reinking) Nelson, Toussoun & Marasas, and *F. semitectum* Berk. & Rav. (Dudley et al. 2007). One isolate of *F. solani* was particularly virulent. Unlike *F. oxysporum, F. subglutinans* has been recovered frequently from insect-predated seeds and seedpods, and one of two isolates tested was moderately virulent (James et al. 2006, Dudley et al. 2007).

Gardner (1997) noted that the only practical method of dealing with vascular wilt diseases, such as *F. oxysporum*, is development of resistant varieties. He speculated that genetic resistance is probably present in koa populations. The significant genetic variation among koa maternal families in rates of black twig borer attack (Daehler and Dudley 2002) suggests that genetic variation might be sufficiently large to allow selection for disease as well as insect resistance. Shi and Brewbaker (2004) reported that some koa families have shown exceptional tolerance to koa wilt. They identified 30 wilt-resistant families for further examination. Recently, Nelson (2006) suggested that grafting koa scions to root stocks of other *Acacia* species that are resistant to *F. oxysporum,* such as *A. confusa* Merr. and *A. mangium* Willd., can greatly reduce the impact of koa wilt. Grafting, however, would add greatly to the price of planting stock, probably making it cost prohibitive except for very small-scale operations.

The long-term impacts of animal, plant, and microbial pests on stand development are unknown, but given the number of highly competitive alien plant species that have become naturalized in Hawaii, koa regeneration following dieback or defoliation is likely to become ever more problematic. Reduced leaf area increases light at ground level, inviting competition. Where grasses are abundant, they grow vigorously in response to increased light and prevent koa seedlings from establishing. In drier climates, those grasses also fuel devastating wildfires. In sites where grasses are less abundant, relatively shade-tolerant alien shrubs may be favored by the increase in light availability associated with dieback or defoliation and similarly impede koa regeneration.

Nutrient Cycling

Many of the relationships between trees and their environment are reciprocal: rain, temperature, humidity, and soil fertility influence tree growth, while trees affect microclimate, and soil water, structure, acidity, and fertility. Among the most important and well studied tree-soil relationships are nutrient cycles, whereby plants take up the mineral elements essential for growth from the soil solution and return those elements to the soil via litterfall and root decay.

Koa is no exception to these processes. As an N-fixing canopy tree species in many Hawaiian forests, koa can have a substantial impact on soils. For example, Scowcroft et al. (2004) found that koa trees planted into high-elevation grasslands (former pastures) increased soil N availability. The concentration of soil ammonium-N increased above levels found even in intact forest, and the concentration of nitrate-N was intermediate between forest and grassland. Thus the N limitation to plant growth in grassland soil was alleviated. Changes in the physical and chemical properties of surface soil were also detected within 10 years. Soil below the planted koa had significantly lower soil bulk density and pH than soils in adjacent grassland, and had concentrations of total C and N, and extractable magnesium (Mg), plus C/N ratios, that were intermediate between grassland and mature forest.

Key Points

- Koa establishment on rangelands can lead to improvement of soil physical and chemical characteristics within 10 years. Among other changes, koa leads to increased soil nitrogen (N) and carbon (C), both of which are general indicators of fertility.
- Annual leaf fall in a 15-year-old koa stand at low elevation returned more than 110 kg/ha of N and 9 kg/ha of phosphorus (P) to the soil surface. These rates of nutrient return are high compared with most other Hawaiian forests.
- Koa litter, like that of many species that fix N, decays quickly: it takes about a year and a half for koa “leaf” (i.e., phyllode) litter to almost disappear, compared with about 2 years for ‘ō‘hia leaf litter. Leaves of some species (such as the exotic vine, banana poka) decay even more quickly, taking just over 4 months to almost disappear.

Litterfall, in the form of leaves, branches, and reproductive parts, is the major pathway by which nutrients are transferred from plants to the soil and can be a substantial fraction of a tree’s net productivity. Although some data are available on litterfall in koa forests (table 3), most measurements have not included contributions of the low-lying (0 to 50 cm) herbaceous layer of vegetation, nor have they accounted for death of roots.

In koa-dominated forests at Laupāhoehoe, Hawaii, Scowcroft (1986) found that leaf litter accounted for 50 to 70 percent of total litterfall. Of the leaf litter produced, koa foliage made up as little as 10 percent of the total in mature forest

Table 3—Productivity of koa-rich forests

Site ID[a]	Elevation	Annual rainfall	Stand age	ΔB	Litterfall	ANPP	Reference
	m	*mm*	*Years*	$Mg \cdot ha^{-1} \cdot yr^{-1}$			
O-03	260	1400	3	0.7–13.2	n.a.	n.a.	Scowcroft and Silva 2005[b]
	260	1400	3	0.3–7.2	n.a.	n.a.	
H-05	1680	2600	6	3.6	n.a.	n.a.	Scowcroft and Fujii 2002[b]
	1660	2800	8	5.6	n.a.	n.a.	
K-04	1100	1750	10	5.7	n.a.	n.a.	Harrington et al. 1995[b]
	1130	1800	10	7.1	n.a.	n.a.	
H-05	1690	2800	10	8.2	n.a.	n.a.	Scowcroft and Fujii 2002[b]
	1720	2800	11	6.0	n.a.	n.a.	
H-10	1500	3200	14	n.a.	6.3	n.a.	Scowcroft 1986
	1100	5000	15	n.a.	12.2	n.a.	
H-07	770	5700	28	2.5–3.1	2.3–3.1	4.8–6.2	Ares 1998, Ares and Fownes 1999
	1180	3660	28	2.8	3.7	6.5	
	1360	2700	36	0.9	0.9	1.8	
	1420	2380	36	0.3–2.7	1.6–2.9	2.0–5.6	
	1060	4300	37	4.3	2.7	7	
K-03	500	850	Old	0.7	n.a.	n.a.	Harrington et al. 1995[b]
	640	1000	Old	3.7	n.a.	n.a.	
	900	1270	Old	1.2	n.a.	n.a.	
H-01	760	6000	Old	4.7	6.1	10.8	Raich 1998
H-10	1500	3200	Old	n.a.	6.7	n.a.	Scowcroft 1986

ΔB = aboveground biomass increment; ANPP = aboveground net primary production.

[a] Site locations and descriptions are shown in appendix A (table 7 and fig. 46).

[b] Only koa wood is included in ΔB values.

and as much as 75 percent in secondary forest. Green leaf litter, which accounted for 1 to 3 percent of the annual foliar litterfall, occurred only from January through May and was probably due to blow-down by high winds. Not surprisingly, when the islands are struck by hurricane-force winds, the input of green leaves, and the nutrients they contain, to the forest floor can be immense; as much as 80 percent or more of the foliage can be blown down (Harrington et al. 1997).

The input of nutrients to the soil surface via leaf litter can be large. Scowcroft (1986), for example, reported that >132 $kg \cdot ha^{-1} \cdot yr^{-1}$ of N and >9 $kg \cdot ha^{-1} \cdot yr^{-1}$ of P were returned to the forest floor this way in a 15-year-old stand at low elevation. In similar pole-sized koa stands at high elevation, the amounts of nutrients transferred were less than one-half those at low elevation and were in the ranges reported for montane forests elsewhere in the tropics.

The nutrients contained in litterfall do not become available again for plant uptake until the plant material decomposes and its nutrients are released into the soil solution. Information on decomposition rates of koa litter are limited to a single study done in a montane ‘ō‘hia-koa rain forest at 1400 m on Mauna Kea (Scowcroft

1997). Although koa phyllodes are thick and fibrous, they decompose rapidly, losing 95 percent of their mass in about 1.6 years. In comparison, the sclerophyllous, C-rich leaves of ‘ō‘hia decay more slowly (95 percent loss in 2.1 years) and the thin, N-rich leaves of *Passiflora tarminiana* decay more rapidly (95 percent loss in 0.4 years). Koa twigs and bark decay more slowly than phyllodes, losing 95 percent of their initial mass in 4.5 years and 23.1 years, respectively.

The rate of litter decay is typically correlated with litter quality, defined in terms of concentrations of N, P, total ash, lignin, and polyphenols, and chemical ratios such as C/N and lignin/N (Aber and Melillo 1991, Swift et al. 1979). Litter that has a low C/N ratio (<20) decomposes rapidly, as lack of N does not limit microbial growth. Thus, N and other macronutrients are lost throughout the course of decay of nutrient-rich koa phyllode and twig litters (Scowcroft 1997). In contrast, nutrient-poor litter such as bark decomposes slowly and tends to accumulate nutrients during decomposition as micro-organisms transfer soil nutrients to litter to support their carbon metabolism.

Although environmental factors are well known to affect rates of litter decomposition, there is no information specific to koa. Studies of sclerophyllous Hawaiian plant species other than koa have shown that moisture and temperature influence decomposition rates. Dry conditions retard decomposition (7 to 9 times as long at the driest site), and increasing moisture tends to increase decay rates up to a point (Austin and Vitousek 2000). However, very wet conditions (beyond the natural range of koa) slow decomposition because of lower soil oxygen levels (two and one-half times as long at the wettest site) and poorer quality litter (three times as long for the poorest quality litter) (Schuur 2001). Decomposition is more rapid at warmer sites than at cooler sites (Scowcroft et al. 2000a). Greater soil nutrient availability has been associated with more rapid decomposition of litter (Ostertag 2001, Thompson and Vitousek 1997), and low soil P availability seems to limit decomposition more strongly than low N availability (Hobbie and Vitousek 2000).

Productivity

Measurement of stand structure and productivity requires estimates of aboveground biomass and leaf area. Allometric regression equations use easily obtained tree dimensions, such as stem diameter, to estimate leaf area and tree biomass. In its simplest form, the equation has the form ($Y = aX^b$) where Y is the biomass or leaf area to be estimated, X is the independent variable (often stem diameter or sapwood cross-sectional area), and a and b are coefficients. Equation development requires destructive harvest of trees representing the full range of sizes present in the population of interest. Several such harvests have been done at different locations in Hawaii; the results of these studies are summarized in appendix D.

The productivity of any forest is a function of the environment and the vegetation. Water, temperature, and soil fertility are among the principal environmental controls on productivity; physiological traits and light-capturing ability of the tree species as determined by amount and display of foliage, combine with the environment to dictate growth. At the ecosystem level, the abundance and traits of all species collectively influence the level of productivity. Vitousek and his co-workers have exploited the richness and steepness of environmental gradients and the

Key Points

- Over the moist, mid-elevation range where koa is abundant, its productivity generally increases with increasing rainfall and temperature. It is absent or very unproductive in environments that are extremely dry, wet, hot, or cold.
- In wet environments, koa is most productive on sites underlain by soils derived from ʻaʻā lava, which tend to be very well drained. In dry environments, there is less difference in productivity because of the tendency of pāhoehoe lava to retain moisture and, in some cases, koa can be more productive on soils derived from the latter.
- Koa maintains a sparse canopy of foliage, and because its leaves (phyllodes) are typically oriented parallel to incoming sunlight (a heat-reducing and water-conserving trait), substantial light penetrates to the understory. Koa forests on moist sites capture more sunlight than forests on dry sites.
- The amount of foliage supported by koa forests increases rapidly in young stands, remains more or less level for a number of years, then declines as the trees age and eventually senesce.
- The efficiency of sunlight use by koa tends to be lower than that of a number of alien tree species. Koa also intercepts less incoming solar radiation than do many exotics whose crowns are more compact and whose foliage is typically oriented perpendicular to sunlight. The combination of lower light-use efficiency and light interception results in lower productivity of koa relative to some exotic competitors.
- The aboveground productivity of koa forests is in the range of about 1 to 4 tons per acre (2 to 9 Mg/ha) per year, about half or more of which becomes litter in the form of fallen phyllodes, twigs, seeds, and branches. The remainder is growth, most of which is bole wood. The range of koa's productivity values would likely double if root production were added into the total.
- Koa productivity is typical of that of forests at mid-elevation and having similar sizes of trees elsewhere in the tropics and subtropics, but far less than that of a number of alien tree species commonly found in Hawaii. The productivity of many of those exotic species is at least double that of koa.

relatively modest biological richness of dominant species of the Hawaiian Islands to understand plant-environment relationships of broad, general importance (Vitousek 2004). Three environmental factors are the dominant controls on site productivity across the Hawaiian Islands: rainfall, temperature, and soil fertility (Aplet et al. 1998). Each is generally positively correlated with productivity, but at extreme levels each may limit productivity. For example, higher rainfall generally favors greater productivity and biomass accumulation (Aplet et al. 1998, Ares and Fownes 1999, Harrington et al. 1995). However, if rainfall is excessive, productivity may decrease as N availability decreases (Schuur and Matson 2001). Warmer temperatures at lower elevations generally promote greater productivity. Where water is not a limiting factor, such as on windward sites, temperature can exert primary control on productivity through its influence on photosynthetic rates and nutrient availability (Raich et al. 1997). The relationship between substrate quality and productivity is more complex. Soil fertility is influenced by the age of the underlying substrate, the type of substrate (e.g., pāhoehoe, ‘a‘ā), and the rate of substrate weathering (Vitousek 2004). For example, ‘a‘ā lava sites generally have greater biomass accumulation on wet sites owing to drainage of excess water, whereas pāhoehoe lava sites favor greater accumulation on dry sites owing to greater water retention (Aplet et al. 1998); however, these differences may be modest in some areas (Ares 1998, Ares and Fownes 1999).

The most important biotic factors controlling productivity include light capture and light-use efficiency. The amount of leaf area per unit ground area, leaf area index (LAI), is a common measure of light-capturing ability, and it varies with tree species, stand age, tree density, basal area, and site quality (table 4). The LAI values reported here refer to the surface area of foliage, one side, regardless of leaf or phyllode vertical angle of orientation. Koa forms a canopy of comparatively low LAI, typically in the range of 1.5 to 4, which is characteristic of many N-fixing leguminous tree species. Very young koa stands whose canopies have not yet closed have low LAI even if plant density is high (Ares 1996, Meinzer et al. 1996). The LAI tends to increase to a maximum within 5 to 25 years of stand initiation (Grace 1995), and koa stands can attain LAI values as high as 5.4 (table 4) (Harrington et al. 1995). The cross-sectional area of the tree trunks in a stand (i.e., their basal area) is related to the amount of conducting tissue in the trees, which is in turn linked to foliage. Thus, LAI is positively correlated with tree cross-sectional area, attaining a maximum at a basal area of about 20 m^2/ha (Grace 1995). After reaching a maximum, koa LAI stabilizes for a time, then declines as the stand ages (Grace 1995, Pearson and Vitousek 2001). In stands of koa, leaf area is positively correlated with moisture availability. Where water availability does not limit tree

Table 4—Leaf area index (LAI) values reported for koa stands in Hawaii

Site ID[a]	Elevation	Annual rainfall	Stand age	Density	LAI	Method	Reference
	m	*mm*	*Years*	*Stems/ha*	m^2/m^2		
H-10	1450	3800	2	4,640	1.0	Allometric	Fownes and Grace 1995
			8	3,360	2.2		
			13	1,460	2.4		
			22	770	2.3		
H-04	1500	2500	5	3,860	1.1	Allometric	Fownes and Grace 1995
			10	3,430	2.4		
			14	2,670	2.9		
			22	1,610	3.4		
			31	880	3.4		
H-02[b]	1250	3800	12	990	0.9	Allometric	Fownes and Grace 1995
			17	890	1.5		
			23	570	1.6		
			28	400	1.4		
			36	345	1.5		
			45	270	1.6		
	550	5000	5	4,100	1.8	Allometric	Fownes and Grace 1995
			10	1,600	1.7		
			17	770	1.8		
			22	580	1.7		
			31	240	1.2		
H-05	1700–1850	1800	6	12,940	3.6	Light interception	Pearson and Vitousek 2001
			9	16,470	4.6		
			13	5,310	2.4		
			20	3,150	2.6		
H-07 (pāhoehoe lava)	760	1940	28	290	2.2	Allometric	Ares and Fownes 1999
	780	1920	28	575	2.3		
	1065	1635	31	70	1.9		
H-07 (‘a‘ā lava)	1060	1640	37	685	3.7	Allometric	Ares and Fownes 1999
	1180	1520	28	860	3.2		
	1350	1350	36	320	2.6		
	1420	1280	36	375	2.6		
O-02[b]	260	1400	2	1,600	1.2	Allometric	Meinzer et al. 1996
			2	1,600	0.3		
	260	1400	4	1,600	0.3	Allometric	Ares 1996
K-02	500	850	Old	4,690	1.4	Light interception	Harrington et al. 1995
	640	1000	Old	1,210	3.5		
	900	1270	Old	1,880	2.5		
K-03	800	1165	Old	6,010	1.7	Light interception	Harrington et al. 1995
K-04	1100	1750	10	2,990	5.4	Light interception	Harrington et al. 1995
	1130	1800	10	8,240	4.1		
H-07	2000	700	Old	60	1.5	Allometric	Ares and Fownes 1999

[a] Site locations and descriptions are shown in appendix A (table 7 and fig. 46).

[b] Planted stands; all others are from natural regeneration.

growth, as on moist organic soils formed in pāhoehoe lava, stand-level leaf area can be relatively high. On drier soils formed on excessively drained ʻaʻā lava, koa LAI is substantially lower (Ares and Fownes 1999). Understory vegetation is affected by the forest canopy, which determines the fraction of transmitted light. Light transmission has important implications for retention and conservation of the rich native understory flora of koa forests, for invasions by alien species, and for growth of pasture grasses favored by ranchers. For example, a koa canopy with an LAI of about 3 transmits only about 20 percent of the incident sunlight (Grace 1995), the point at which kikuyu grass tends to be displaced by meadow ricegrass.

Productivity (P) is a function of the amount of light absorbed by foliage (R_a in MJ • m^{-2} • y^{-1}) and the efficiency (ε) with which it is used:

$$P = \varepsilon R_a$$

Radiation-use efficiency represents all photosynthetic and respiratory processes and is a simple measure of growth (Medlyn 1998). Ares (1998) reported that aboveground radiation-use efficiency ($\varepsilon_{\mathrm{ANPP}}$) (ANPP = aboveground net primary productivity) was 0.33 g/MJ, and efficiency of wood production (ε_B) was 0.15 to 0.18 g/MJ for 15-to-38-year-old koa stands. He found that these values were generally lower than those for stands of introduced tree species growing in the same area (fig. 18). Maximum $\varepsilon_{\mathrm{ANPP}}$ was 0.85 g/MJ for 1- to 2-year-old *Acacia auriculiformis* A. Cunn. ex Benth., a nonnative relative of koa, planted on Maui (Harrington and Fownes 1995). Koa crowns intercept less radiation (45 to 80 percent) than those of others, such as the introduced species *Eucalyptus saligna* Sm. (65 to 90 percent) and *Toona australis* (syn. *Toona ciliata* F. Roem.) (75 to 85 percent) (Ares 1998). Although LAI for these introduced species is similar to that of koa, differences in leaf or phyllode orientation and crown characteristics, such as shape and depth, as well as differences in albedo, probably account for differences in R_a. This is evident in a comparison of light extinction coefficients (k) as well: for koa, k is about 0.50, whereas for *T. australis* it is 0.64, and for *E. saligna* and *Fraxinus uhdei* it is about 0.75 (Ares 1998, Grace 1995). The combination of lower light-use efficiency and light interception results in lower P of koa relative to some exotic species.

The aboveground net primary productivity (ANPP) of koa-rich forests ranges from 2 to 10 or more Mg • ha^{-1} • yr^{-1} (table 3). Total productivity, incorporating both roots and aboveground plant biomass, is seldom measured, although Raich (1998) reported that about 15 percent more C was invested in belowground processes than in aboveground growth in a mixed species forest that included a substantial amount

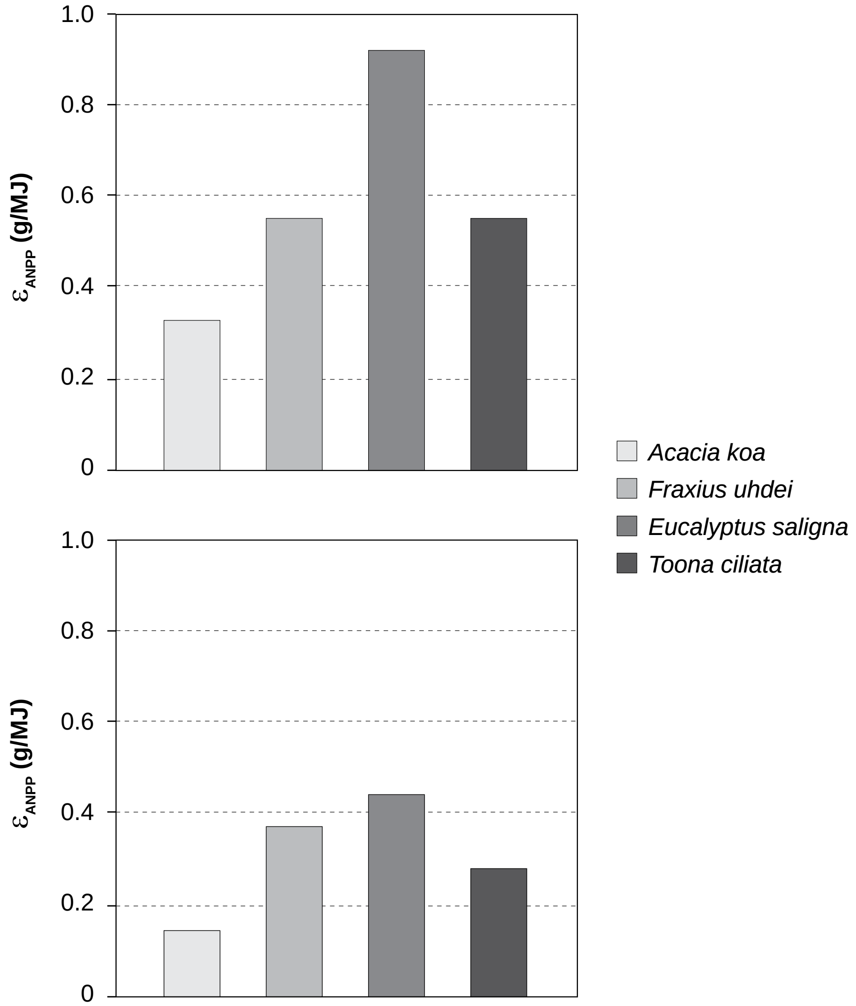


Figure 18—Average solar radiation-use efficiencies (ε) for *Acacia koa* and three introduced tree species growing in close proximity in the Hōnaunau area of North Kona, Hawaii. Radiation-use efficiency is shown in terms of aboveground net primary productivity (upper panel) and wood production (lower panel). (Data from Ares 1998)

of koa. The productivity values reported for koa forests are typical of similar-stature natural forests in the tropics and subtropics, although less than half those observed in plantations of fast-growing nonnative genera such as *Eucalyptus* and *Falcataria*, which routinely attain ANPP values higher than 20 Mg • ha^{-1} • yr^{-1} in Hawaii (Binkley and Ryan 1998).

Chapter 3: Koa Stand Dynamics

In the preceding chapters we described how koa (*Acacia koa* A. Gray) grows as an individual and how koa forests function as ecosystems. In this chapter we discuss how stands of koa change with time, where a stand is defined as a contiguous area of forest with similar forest structure, composition, and development history. We first review the range of abiotic disturbances that are known to influence koa forests, then consider how koa stands, both pure and mixed with ‘ō‘hia (*Metrosideros polymorpha*) (see app. B for species names), develop after disturbances of varying intensity. Finally, we review the limited data on stand-level growth and timber yield in koa forests.

Key Points

- Koa is wind resistant, but it is vulnerable to snapping off and uprooting in extremely high winds.
- The vast quantities of koa litter that fall on the ground during storms increase risk of fire, kill seedlings, impede regeneration, and may bind nutrients, making them temporarily unavailable to surviving trees.
- Recovery, even after a hurricane, can be fast, with productivity returning to pre-storm levels within 2 years.
- Hawaiian forests that are most vulnerable to fire (largely because of the presence of exotic grasses) also tend to be the forests that contain a large component of koa.
- In addition to the damage caused by browsing animals, postfire regeneration of koa is also impaired by exotic plants, especially grasses, which compete with koa seedlings for water, light, and nutrients, and serve as fuel sources for subsequent fires.
- Although fire kills koa trees, its seeds are stimulated to germinate by heat. Thus, stand destruction by fire can lead to a burst of regeneration. If the land is grazed after a fire, however, the new seedlings are browsed, almost inevitably leading to a complete loss of koa.
- Volcanic activity devastates koa forests, just as it does any other ecosystem. The destruction is caused by lava flows, fires, ash deposits, and acidic fumes. Unlike a number of other Hawaiian plants, koa does not effectively colonize new or young lava.
- Landslides, sometimes triggered by earthquakes, are unlikely to be recolonized quickly by koa because the seed bank slides away with the surface soil.

Disturbance and Recovery

Wind

The greatest wind damage to koa results from the hurricanes that infrequently strike the islands. Damage differs greatly, ranging from minor foliage loss to breakage of structural branches to toppling of trees. Hurricane Iniki, which passed over Kauai in September 1992, toppled 36 percent of the koa trees in sample plots. Of these, 55 percent were uprooted and 45 percent were snapped off; in addition, more than one-third of the standing trees appeared to be dead (Asner and Goldstein 1997). Those trees that survived the hurricane lost 30 to 80 percent of their foliage, leading to substantial (4 to 19 Mg/ha) local inputs of leaves and woody debris (Harrington et al. 1997). The hurricane-induced litterfall added 26 to 169 kg/ha of nitrogen (N), 0.4 to 4.6 kg/ha of phosphorus (P), and 4.6 to 24.2 kg/ha of potassium (K) to the forest floor but also led to increased seedling mortality and lower recruitment. In heavily affected stands, seedling mortality was twice as great as recruitment, whereas the reverse was true in stands that suffered minor foliage and branch loss. In the year following Iniki, basal area growth and rates of foliage recovery were higher in less severely defoliated stands than in severely defoliated stands. Within 2 years of the hurricane, however, stand leaf area and productivity had largely recovered to prehurricane conditions (Harrington et al. 1997).

Winds associated with winter storms can also damage koa. Koa is resistant to winds from the northeast, which is the direction of the prevailing tradewinds. However, winter windstorms typically blow from the opposite direction, and koa is vulnerable to damage from those counter-normal winds, which sometimes snap saplings and pole-size koa (fig. 19) (Judd 1920, Mueller-Dombois 1981b).


Jack Jeffrey

Figure 19—Damage to *Acacia koa* on Hawaii from a local windstorm in 1993. Note the prevalence of kikuyu grass (*Pennisetum clandestinum*), an introduced pasture grass.

Fire

Koa, like other *Acacia* species, has many traits of a fire-adapted species, such as seeds that persist for years or decades in the soil and require scarification for germination. Several species associated with koa are fire-tolerant, including mamane (*Sophora chrysophylla*), naio (*Myoporum sandwicense*), and ‘ō‘hia, which resprout after low-and moderate-intensity fires; tree ferns (*Cibotium* sp. and *Sadleria cyatheoides*), which grow new fronds; and the native grasses, *Deschampsia nubigena*, *Panicum tenuifolium*, and *Eragrostis* spp., which regenerate vegetatively (Mueller-Dombois 1981a, Mueller-Dombois and Fosberg 1998, Smith and Tunison 1992). Charcoal is found in many sediment cores at depths that pre-date human colonization (e.g., Burney and Burney 2003, Hotchkiss 1998; but cf. Athens 1997), and given koa's apparent reproductive adaptation to fire, it is possible that fire has played a role in shaping koa forests. Nevertheless, extensive fire is thought by many ecologists to have been a minor environmental force in Hawaii prior to colonization by people 1,300 to 1,500 years ago, especially in moist and wet forests (see review by Smith and Tunison 1992). In addition, it is believed that prior to human colonization, fuel was probably sparse and inflammable in most communities, and that the only ignition sources were volcanism (on the younger islands) and lightning, which is not as common on oceanic islands at Hawaii's latitude as it is on larger tropical and subtropical landmasses. However, as Mueller-Dombois (1981a) noted, there are other natural stressing factors that might account for koa's tolerance of fire. Indeed, given that many *Acacia* species, particulary in Australia, are well-adapted to fire and drought, koa's fire tolerance may be an inherited genetic trait that conferred a survival advantage on its progenitors (Smith and Tunison 1992).

Following colonization by humans, the occurrence of fire across the Hawaiian landscape increased substantially (Athens 1997, Burney and Burney 2003). Polynesians used fire to prepare land for agriculture (Kirch 1982), and westerners have introduced hundreds of flammable plant species. Alien grasses, many of which were intentionally introduced as forage crops (Ripperton et al. 1933, Whitney et al. 1939), are particularly well-adapted to fires and can form a dense layer of highly flammable fine fuels. Introduced species that have greatly increased wildfire frequency, size, and severity include fountain grass (*Pennisetum setaceum*), bush beardgrass (*Schizachyrium condensatum*), and molasses grass (*Melinis minutiflora*) (Cuddihy and Stone 1990). The result is a fire regime that leads to alien-dominated, fire-adapted ecosystems and ecosystem processes (Asner and Beatty 1996, D'Antonio 1998, D'Antonio and Vitousek 1992, D'Antonio et al. 2000, Freifelder et al. 1998, Hughes and Vitousek 1993, Hughes et al. 1991, Mack et al. 2001, Parman and Wampler 1977, Smith and Tunison 1992, Sorenson 1977).

Today fire is an important ecological factor during the dry season in the mesic forests of Hawaii and Maui where most koa are found (Smith and Tunison 1992). Such forests support fine fuel loads, including endemic grasses that are large enough and frequently dry enough to carry fire. The indigenous fern uluhe (*Dicranopteris linearis*) has fueled many fires in mesic and wet native forests (Cuddihy and Stone 1990, Scowcroft and Wood 1976, Wood et al. 1969). Many nongrass alien plant species also flourish after fire, to the detriment of regenerating koa and other native species. For example, 2 months after a fire on Oahu, there was only a sparse cover of *Clidemia hirta* seedlings, but within 2 years the entire study area was covered in mature individuals (Wister and Wood 1977). After about 7 years, many koa were taller than *C. hirta* (mean heights: koa = 3.5 m and *Clidemia* = 2.3 m); however, koa that were shorter than the *Clidemia* experienced high mortality and slow growth, and were unlikely to outgrow the overtopping *Clidemia*.

Although koa trees are killed by high-intensity fires (Scowcroft and Wood 1976, Wood et al. 1969), fire stimulates germination of buried koa seeds (fig. 20). Postfire seedling densities can be extraordinarily high, ranging from 95,000 to 350,000 per ha (Judd 1935, Scowcroft and Wood 1976, Wood et al. 1969). Such high densities inevitably lead to rapid self-thinning, such as the 60 to 80 percent mortality observed by Scowcroft and Wood (1976) during the first 28 months after a fire. If grazing follows fire, the nitrogen-rich koa seedlings are inevitably consumed, and if the process is repeated, the result is depletion of the soil seedbank, which limits future regeneration options to planting or direct seeding.

Paul G. Scowcroft

Figure 20—Fire stimulates germination of buried *Acacia koa* seeds.

Koa is also capable of sprouting after fire. Koa saplings and pole-sized trees produce sprouts from the root crown (fig. 21) (Scowcroft and Wood 1976), and those sprouts can eventually become large trees. The size threshold for postfire sprouting of koa trees is not known, but large koa trees do not produce root sprouts and are more likely to be killed by fire.

Volcanism

Burial under lava flows and cinders is the most obvious and long-lasting effect of volcanic eruptions on koa forests. Today active volcanism is confined to Hawaii, although the potential for activity still exists on Maui. On Hawaii, the greatest threat for volcanic activity is around Mauna Loa where more than 60 percent of the koa forests on Hawaii occur. Unlike ʻōʻhia, koa is not a pioneer on new lava flows (Mueller-Dombois and Fosberg 1998). For koa to grow on lava flows, favorable soil conditions must first be created through weathering and the action of lichens, mosses, and vascular plants that are adapted to grow on rock (Kitayama et al. 1995). Therefore, koa forests destroyed by lava may not reestablish for hundreds or thousands of years, despite seed inputs from forests adjacent to the lava flows and islands of vegetation (kīpukas) within the lava flows. The youngest flows supporting koa forests at Keauhou Ranch are estimated to be at least 2,000 years old (Pearson and Vitousek 2001). At The Nature Conservancy's Kona-Hema Preserve, koa are found on lava flows estimated to be 750 to 3,000 years old (Wolfe and Morris 1996).

Paul G. Scowcroft

Figure 21—*Acacia koa* sprouts from a tree whose top was killed by an intense grass fire.

In addition to the direct impact of lava flows from volcanic eruptions, Hawaii's forests are exposed to volcanic fumes, which are high in sulfur dioxide and react with sunlight, oxygen, dust particles, and water to form a mixture of sulfate aerosols, sulfuric acid, and other oxidized forms of sulfur. The resulting gas and aerosol mixture produces an atmospheric haze known as volcanic smog or "vog" (Sutton et al. 1997). Forests along the Kona (west) side of Hawaii are frequently exposed to vog as prevailing winds carry the pollutants from the active vents to the southwest where local wind patterns push it upslope. During periods of low windspeeds, pollutant concentrations rise to very high levels in the stagnant air over Hawaii Volcanoes National Park and surrounding areas. During one unusually severe vog event, koa growing northwest of the eruption suffered damage (fig. 22) (Skolmen 1990). Interestingly, Skolmen suggested that koa may possess a genetic adaptation to vog, as trees that originated from a seed source that received high exposure to vog were less severely affected (3 percent defoliation) than those from a distant seed source (15 percent defoliation) that experienced substantially less exposure to vog.

As in other regions with active volcanism, earthquakes are also a factor in Hawaii's forest disturbance regime, although they are far less common than the agents discussed above. In 1973, for example, a magnitude 6.2 earthquake toppled 2 to 3 large, old koa per hectare in the upper portion of the Hilo Forest Reserve. In addition to causing tree falls, earthquakes are likely to trigger landslides, particularly on the older islands where erosion has created steep valley walls that are inherently unstable. Landslides are unlikely to be recolonized quickly by koa because the soil seedbank is typically stripped away with the surface soil.

Paul G. Scowcroft

Figure 22—Leaf necrosis on *Acacia koa* from exposure to high levels of volcanic smog (vog).

Volcanic activity may also have a beneficial effect on vegetation. Heath and Huebert (1999) estimated that cloud-water deposition contributed 8 to 22 kg of inorganic N • ha^{-1} • yr^{-1} at their study site in Hawaii Volcanoes National Park. They found that 60 percent of this N deposition was associated with volcanic haze and that cloud-water nitrate (NO_3) concentrations were very high during those events. Huebert et al. (1999) showed that the source of this N, which is potentially available to plants, was thermal fixation of atmospheric N_2 at the surface of molten lava. The nitric oxide (NO) produced was oxidized to nitrite (NO_2) and NO_3, dissolved in cloud water, and then intercepted by vegetation.

Stand Development

Single- and Multiple-Cohort Stands

Understanding stand development patterns is a prerequisite to effective and efficient silviculture (Oliver and Larson 1996, Smith et al. 1997). Because most Hawaiian trees lack annual growth rings, stand development studies must depend on long-term observations or chronosequence studies. In perhaps the longest ongoing study of koa stand development, Scowcroft and Fujii (2002) have studied 17 years of development of unmanaged, single-cohort (i.e., even-aged) stands that regenerated following mechanical scarification at Keauhou Ranch, Hawaii. Initial koa density was high (6,000 to 21,000 trees/ha), but subsequent self-thinning reduced densities to about 1,500 trees/ha after 14 to 17 years. Accumulation of aboveground tree biomass was most rapid in the least dense stand, and diameter increment was negatively correlated with the total basal area of trees in larger size classes. Pearson and Vitousek (2001) found similar patterns in other study sites at Keauhou Ranch. Permanent plots established by the Hawaii Division of Forestry and Wildlife (DFW) during 1949–1972 show the same general trend (fig. 23): high initial stand densities, rapid growth to canopy closure, followed by declining growth and self-thinning (Constantinides 2004, Grace 1995). This pattern of stand development in koa forests follows closely the general model of postdisturbance stand dynamics proposed by Oliver (1981) for single-species, even-aged stands.

The development patterns of multiple-cohort koa stands are less understood than those of even-aged stands. Reconstruction of historical stand development patterns is impeded by the absence of annual growth rings in koa and the lack of historical inventories for koa forests. Without an effective means to age koa, tree size has been widely used as a surrogate measure of age. Stands that exhibit pronounced size disparities among

Key Points

- Even-aged stands of koa follow a predictable growth pattern during stand development typical of fast-growing, light-demanding species. Initially, high-density stands exhibit rapid growth to canopy closure, followed by declining growth and self-thinning.
- Stands containing koa of multiple ages are difficult to analyze because koa does not produce annual growth rings. Tree size is often used as a surrogate for age, but this can be misleading, as even-aged stands can have trees of very different sizes, just as multiple-aged stands can have trees of fairly uniform size. The most common multiage pattern with koa, a light-demanding species, is scattered older individuals in a matrix of younger trees.
- Although even-aged koa stands start out as pure koa, they are quickly colonized by other tree species. In one case, there were about 800 trees per acre of species other than koa after 24 years.
- Where the nearest neighbors of koa are other species, such as the slower growing ‘ō’hia, competition for resources is less intense, and koa’s growth is faster.
- It is increasingly common to encounter stands in which koa is grown together with other species (typically nonnatives, such as *Toona ciliata*, tropical ash (*Fraxinus uhdei*), and *Falcataria moluccana*). Overall, koa does not compete well with these faster growing exotic species, but proper management, including lower initial densities followed by thinning, could likely remedy this, resulting in productive mixed-species stands.

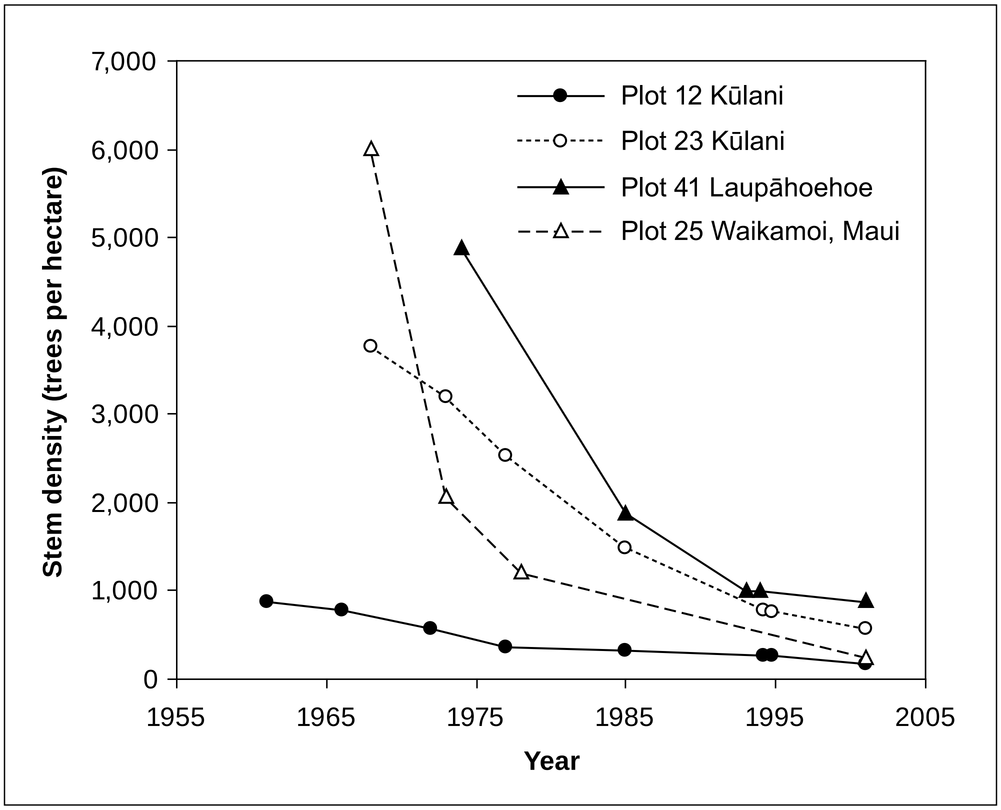


Figure 23—Changes in stem density over time of pure *Acacia koa* stands in permanent sample plots established by Hawaii Division of Forestry and Wildlife.

individuals are assumed to be multiple-cohort stands, whereas those that have a narrow range of stem diameters are assumed to be single-cohort stands. Perhaps the most common type of multiple-age-cohort stand is that in which a few scattered, extremely large koa are surrounded by a dense assemblage of smaller trees. The smaller trees may be koa or other native tree species such as ‘ō‘hia, ‘ōlapa (*Cheirodendron trigynum*), or kōlea (*Myrsine lessertiana*). Some caution is required in making such judgments, as single-cohort stands may exhibit a wide range of tree diameters owing to within-stand heterogeneity in resource availability. In contrast, it is also possible that for certain species, stands with multiple age cohorts may exhibit little variation in tree size. However, because koa is shade intolerant, few individuals are likely to establish in the understory or in small gaps and survive to grow into the canopy. Rather, younger trees will be most likely to occur in small groups where large gaps have formed in the canopy some time in the past. These small aggregations of koa should develop in a manner similar to a single-age-cohort stand of koa, although the effect of the gap edge will decrease growth and increase mortality of koa closer to the edge of the undisturbed forest.

Pure- and Mixed-Species Stands

Koa grows in both pure and mixed stands. Today, pure stands of koa are almost exclusively the result of human activity, particularly land clearing. Stands that establish after mechanical soil scarification and fire typically have an overstory dominated by koa for many years. Where scarification is confined to discrete areas, such as zones around individual seed and harvest trees and skid trails, other species often regenerate with koa. Pure stands of koa do not remain so until maturity. ‘Ō‘hia, understory tree species, tree ferns, shrubs, and other plants establish over time. On the windward flank of Mauna Loa, understory tree and tree fern species were observed within 5 years of scarification. Twenty-four years after scarification, density of trees other than koa was 1,960 stems/ha and accounted for 14 percent of the stand basal area (Scowcroft et al., 2008). Although most of the other tree species were in the understory, a few, such as naio (*Myoporum sandwicense*) and kōlea, were nearly as tall as the koa. Mixed stands are more prevalent at the lower elevational limits of koa’s distribution. In these stands, koa often shares canopy dominance with ‘ō‘hia. It is unknown whether the koa and ‘ō‘hia in these stands are similar in age or whether individuals of one species established before the other.

Even at high elevation, ‘ō‘hia can account for a large proportion of forest canopy and stand basal area. The abilities of koa and ‘ō‘hia to coexist in an old-growth montane rain forest that lacked both human disturbance and invasive alien plant species were examined by Hatfield et al. (1996). Their premise was that the coexistence of two shade-intolerant species in a space-limited community is a function of temporal variation in recruitment and death rates. Because they found no difference in death rates for koa and ‘ō‘hia, they concluded that the superior seed dispersal ability of ‘ō‘hia gives it a competitive advantage over koa when colonizing large gaps created by natural disturbances. Smaller gaps such as those created when a single koa tree topples were hypothesized to favor establishment of the faster growing koa and allow it to coexist with ‘ō‘hia. However, this analysis did not account for two important differences in the ecology of koa and ‘ō‘hia: seed longevity in the soil and early height growth rate. Although ‘ō‘hia seeds are better dispersed, koa seed may remain in the soil seed bank for many years until a large disturbance occurs. In addition, because koa seedlings grow much more rapidly in height during establishment, and quickly develop spreading crowns, the successful establishment of a small number of koa seedlings would allow koa to remain a significant component of the tree community following a large disturbance.

In mixed-species stands, differences in growth patterns among species may lead to greater structural heterogeneity and spatial variation in availability of resources such as light. Growth of koa might be influenced by neighboring trees.

At Honomalino, Hawaii, basal area increment of individual koa was not related to total tree basal area of neighbors within a radius of 10 m. However, koa basal area increment was negatively correlated with basal area of koa trees within 10 m and positively correlated to basal area of ‘ō‘hia within 10 m (Baker et al., n.d.) (fig. 24). The positive effect of ‘ō‘hia on growth of individual koa trees may be the consequence of neighboring ‘ō‘hia preventing or displacing other koa from establishing or competing near the focal koa tree. Because ‘ō‘hia grows slowly in height and diameter, it has little effect on the growth of an individual koa tree as long as the koa is not directly overtopped. In contrast, neighboring koa will compete intensely with each other owing to their similar growth patterns and resource requirements.

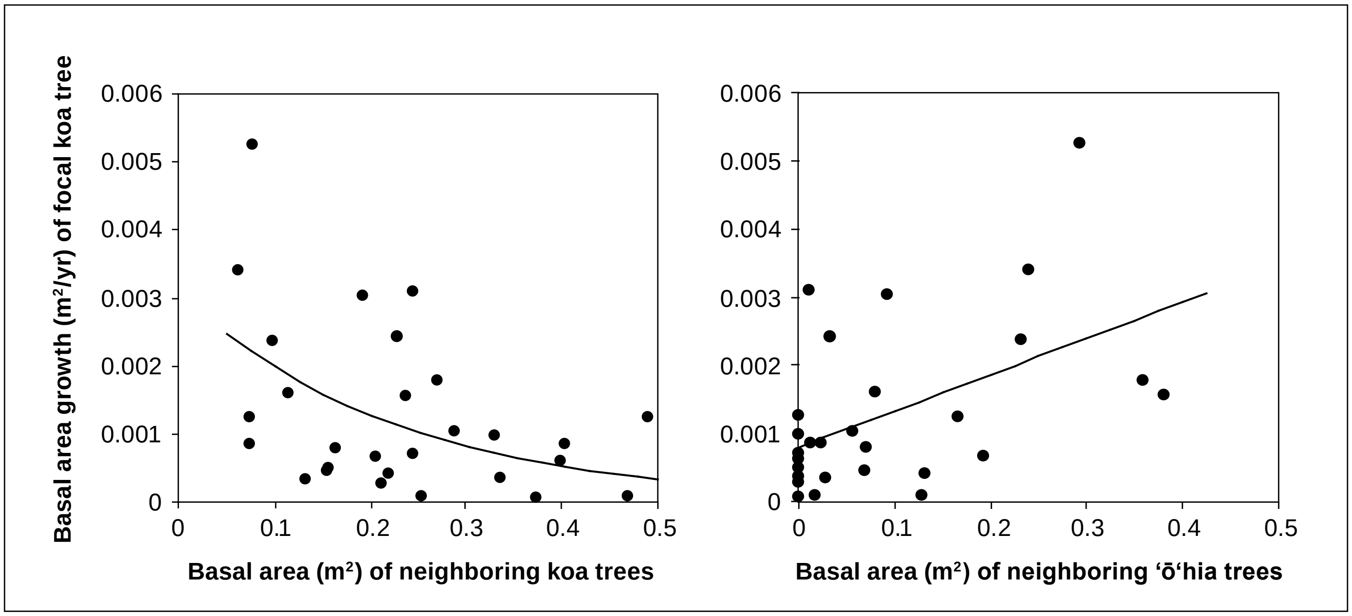


Figure 24—Influence of *Acacia koa* and *Metrosideros polymorpha* (‘ō‘hia) neighbors on basal area growth of koa trees.

Increasingly, mixed stands in Hawaii include nonnative tree species such as *Toona ciliata, Fraxinus uhdei* (tropical ash), and *Falcataria moluccana*. The different growth patterns among the species in these stands complicate management practices, particularly where each species’ growth pattern varies as a function of site. There are only two data sets describing the stand development patterns of mixed-species stands that include koa. The first, a study of mixed stands of koa and tropical ash at Hōnaunau on Hawaii, showed that the presence of tropical ash decreased koa’s contribution to stand basal area, leaf area index, and aboveground net primary production (Ares and Fownes 1999). In addition, competition for soil water with tropical ash increased water stress and reduced water-use efficiency

(WUE) for the koa. Conversely, the productivity of the tropical ash on N-limited Histosols was significantly enhanced in the presence of the N-fixing koa (Ares and Fownes 2001). On volcanic ash-derived soils (Andisols), which are fertile, and on low-elevation Histosols, tropical ash is highly productive. With increasing elevation, however, growth rates and productivity of tropical ash decrease substantially (Ares and Fownes 2001). Thus, at low-elevation sites, tropical ash would quickly outcompete koa in mixed stands, unless the density of tropical ash were kept extremely low. At higher elevation sites, the competitive ability of tropical ash and its ability to outcompete koa decreases, allowing for a greater density of tropical ash in mixed stands with koa. Ares and Fownes (2001) noted that despite the dominance of koa in the 36-year-old mixed stands at Hōnaunau, growth rates were low. They attributed this to the tropical ash that was beginning to overtop and suppress the koa and predicted that the tropical ash would eventually eliminate the koa from the stands.

The other data set on koa growth in mixed-species stands is from the DFW permanent forest inventory plot network and describes a koa-*Toona ciliata* stand at the Waiākea Forest Reserve, Hawaii. The site was planted with an even mix of *Toona* and koa. Initial spacing is unknown, but 5 years after planting, total density was about 2,000 stems per ha, which is equivalent to about 2.3-m (7.5-foot) spacing on a square grid. After 38 years, only two koa trees remained alive: the stand was effectively a monoculture of *Toona*, which had grown faster in height and diameter than the koa during the first decade after establishment. As the *Toona* overtopped and suppressed the koa, koa density declined dramatically. In contrast, *Toona* density remained nearly unchanged over the 38 years. It should be noted that the two koa that survived are among the largest trees in the stand and dominated neighboring *Toona* during the course of stand development. It is important to understand that the poor success of the koa in this planting trial should not be taken to mean that *Toona* and koa cannot be grown together. Rather it raises questions about the optimum spacing arrangements of the two species when grown together. Greater planting distances between koa and neighboring *Toona* or early release thinning of neighboring *Toona* would provide more growing space for individuals of koa and improve their long-term growth rates and survival in mixed stands with *Toona*.

Growth and Yield

Key Points

- Some data are available on koa growth, but no data are available on yield, as koa stands have not been managed through a full rotation.
- Diameter growth of koa is approximately linear throughout its early decades, slowing only as the trees approach 40 to 70 years of age. On a good site, koa can attain a diameter of almost 20 inches (50 cm) before age 40, although the average diameter in a stand is typically much less than that.
- Koa is highly sensitive to competition. When its crown is fully exposed, growth can be rapid—more than half an inch in diameter each year. When overtopped, however, the growth of koa slows or may even stop.
- Height growth of koa is usually fastest during the first 5 years and slows to about 20 inches (50 cm) per year thereafter, until approximately age 30 to 40, when height growth ceases. At that age, the tallest koa in a stand are typically 50 to 90 feet (15 to 30 meters) tall, depending upon the quality of the site.
- The sum of the cross-sectional areas of the tree trunks in a stand (i.e., the stand's basal area) is a good indicator of the mass of wood present. The basal area of koa stands spans a considerable range, 60 to 175 square feet per acre (14 to 40 m^2/ha) in stands 30 to 50 years old, even on good sites.
- Currently, three approaches are available for estimating koa volumes. One, seldom used, involves the measurement of a number of tree dimensions, some of which are difficult to obtain. Another approach is to use volume relationships developed for another species; this approach is used by Hawaii's DFW, but it remains unvalidated. The third approach uses a growth model requiring few field measurements; the single test of this model produced volume estimates that were much lower than actual measurements, indicating that it needs further refinement.
- Volume is seldom estimated in transactions involving koa trees or stands because trees currently being harvested are large, eccentrically shaped, and old enough to contain concealed rot. Furthermore, the economic value of a koa tree is due more to wood quality than wood quantity. Our ability to estimate koa wood volumes is likely to improve considerably as second-growth forests become more intensively managed.
- As with most tree species, small, slow-growing koa trees are more likely to die than are larger, fast-growing individuals. Mortality rates are as high as 20 percent per year for the slowest growing trees, compared with rates as low as 1 percent per year for trees growing about a half-inch in diameter yearly.

Forest management plans that incorporate timber harvesting require estimates of growth and yield at the stand scale. Here we present the available information on koa growth and yield. Inventory plots and growth modeling studies have provided empirical relationships for basal area and volume growth of koa stands. No data are available for koa yield however, because koa forests have not been managed through a full cycle of regeneration and harvesting. Consequently, yield estimates are based on estimated growth and assumptions regarding merchantable volume and anticipated losses to defects.

Long-term, stand-scale growth data for koa come primarily from the Hawaii DFW permanent inventory plots established during 1949–1972, which have been remeasured at irregular intervals (table 5). We have included data from two other DFW permanent plots for which measurements were taken for more than 20 years but discontinued when the sites were cleared in the late 1960s. As noted earlier, these plots are almost all located in dense stands that regenerated from the soil seed bank after mechanical scarification and have received no subsequent silvicultural treatments (such as thinning). The single exception is plot 12 at Kūlani, which was planted at about 3 m (10 foot) spacing, but also did not receive postestablishment silvicultural treatments. Consequently, the DFW plots do not represent the full range of growth patterns of koa stands.

Table 5–Permanent inventory plots established by the Hawaii Department of Forestry and Wildlife (DFW) that contain *Acacia koa*

Site ID[a]	Plot number	Elevation	Established	Last measured	Number of measurements
		Meters			
H-02	11	570	1942	1966	3
H-01	12[b]	1235	1946	2001	8
H-02	14	580	1942	1966	3
H-01	23	1495	1963	2001	7
H-02	24	580	1963	2001	8
M-01	25	1190	1962	2001	5
H-10	41	1540	1972	2001	7
H-01	42	1495	1971	1974	2

[a] Site locations and descriptions are shown in appendix A (table 7 and fig. 46).

[b] Planted stand.

Source: Constantinides 2004.

Height Growth

Height growth patterns for individual trees differ and may be sigmoidal, linear, or asymptotic within the range of tree sizes that have been measured. Height increment is usually greatest at an early age and declines thereafter. Height increments of 1 to 2 m/yr are common during a koa tree's first 5 years, but after that, growth rates are more likely to average about 0.5 m/yr (e.g., Pearson and Vitousek 2001). Despite differences in mean heights of the four tallest trees ranging from 15.3 m (36 years) to 28.5 m (38 years), height growth patterns among the plots were similar during the first 30 years of stand development (fig. 25). Height growth on all plots was fastest during the years immediately following stand establishment, but height growth slowed at different times among the plots. In plot 12, little height growth occurred after age 30. In contrast, mean height growth of the koa in plot 23 was just as rapid after age 30 as it was during the first 10 years following establishment. In some of the DFW plots, mean height growth of koa on the permanent plots was negative (data not shown) because of wind damage to tree tops, which reduces the mean height of individual trees. In other DFW plots, mean height growth has been positive, owing to either overall growth or, as in plot 23, mortality of suppressed trees, which are typically shorter, raising the mean tree height in the plot, irrespective of growth rates.

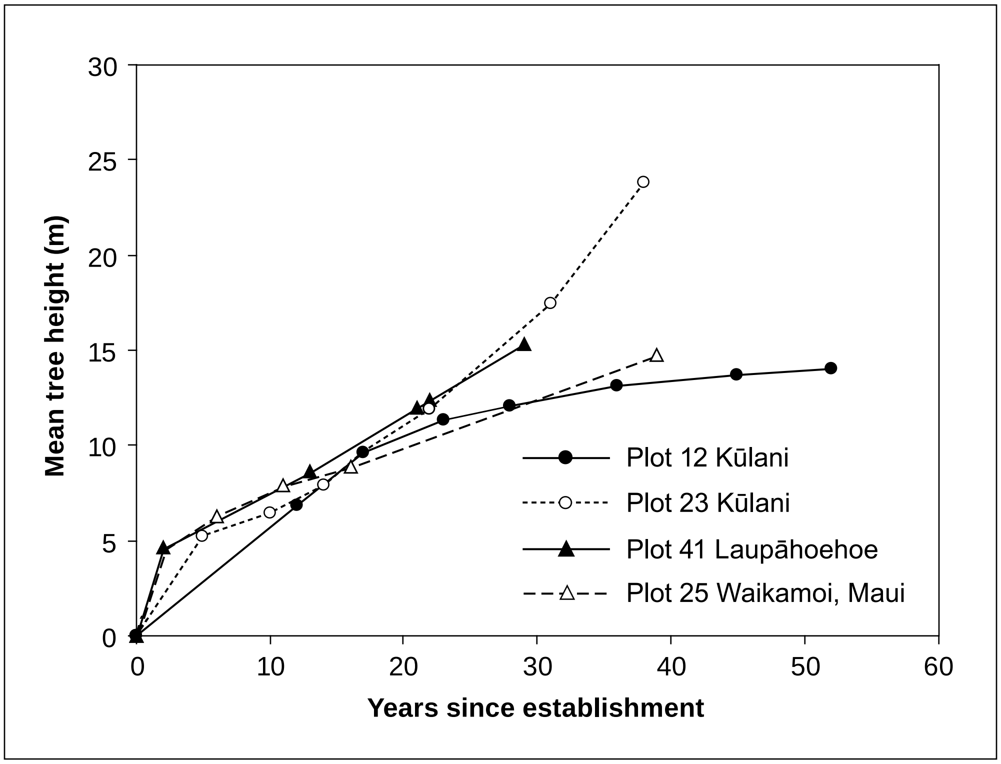


Figure 25—Height growth patterns of *Acacia koa* from the Hawaii Division of Forestry and Wildlife (DFW) long-term forest inventory plots.

Diameter Growth

Despite differences in the location and initial density of the DFW plots, long-term trends for mean diameter at breast height (DBH) are remarkably similar among the plots (fig. 26). In all plots, mean DBH growth was approximately linear for most of stand development. At the best site (plot 23 at Kūlani, Hawaii), mean DBH of koa after 38 years was 29.1 cm (7.6 mm/yr; SD = 9.2 cm; range = 17.5 to 49.3). However, the mean DBH of the four largest trees in the study plot (equivalent to the largest 40 trees per acre or about 100 trees per hectare) was 44.1 cm. On the poorest site (plot 12, also at Kūlani, but at a lower elevation) the mean DBH of koa after 39 years was 24.2 cm (6.2 mm/yr; SD = 7.6 cm; range = 13.7 to 35.6 cm); mean DBH of the four largest trees in the plot was 33.0 cm. Despite the poorer site quality at the lower Kūlani site, the trees had large diameters, which may be due to the low initial density of this site as compared to the higher elevation site at Kūlani.

Because koa is shade intolerant, its growth is strongly influenced by the amount of light available for photosynthesis and the amount of photosynthetic tissue available to harvest the light. Suppressed 25- to 27-year-old koa growing in an even-aged koa stand at 1700 m elevation on Hawaii showed no DBH growth and did not respond to increased light levels created by thinning (Scowcroft, et al. 2008). In contrast,

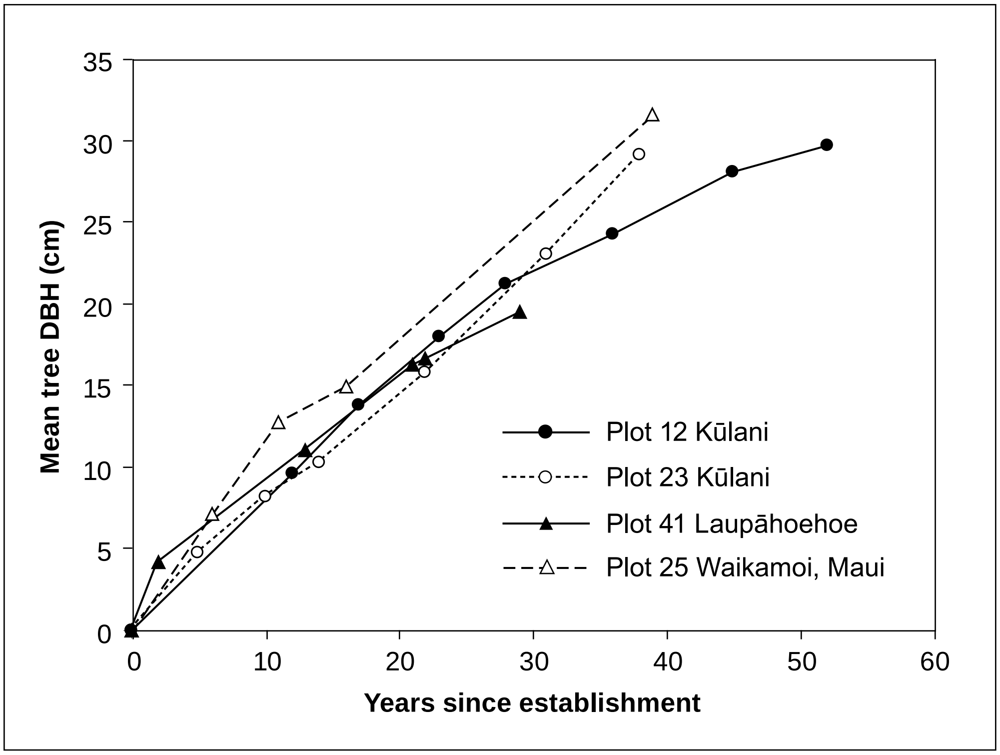


Figure 26—Diameter growth patterns of *Acacia koa* from the Hawaii Division of Forestry and Wildlife (DFW) long-term forest inventory plots. DBH = diameter at breast height.

dominant koa trees, in which the crown is exposed to direct sunlight, may have diameter growth rates of 10 to 15 mm/yr. Stand density directly affects the amount of photosynthetic tissue each tree can support, and therefore is an important factor in koa growth. Measures of local neighborhood density around koa trees in pure koa stands at Honomalino, Hawaii, showed a significant negative relationship between local density and growth of individual trees (fig. 27). Grace (1995) showed that annual diameter increment of koa was negatively correlated with the basal area of all larger neighbor trees. These results are further supported by thinning trials, described in the "Koa Silviculture" section, in which reduction of local tree density led to substantial increases in diameter growth of the remaining koa trees.

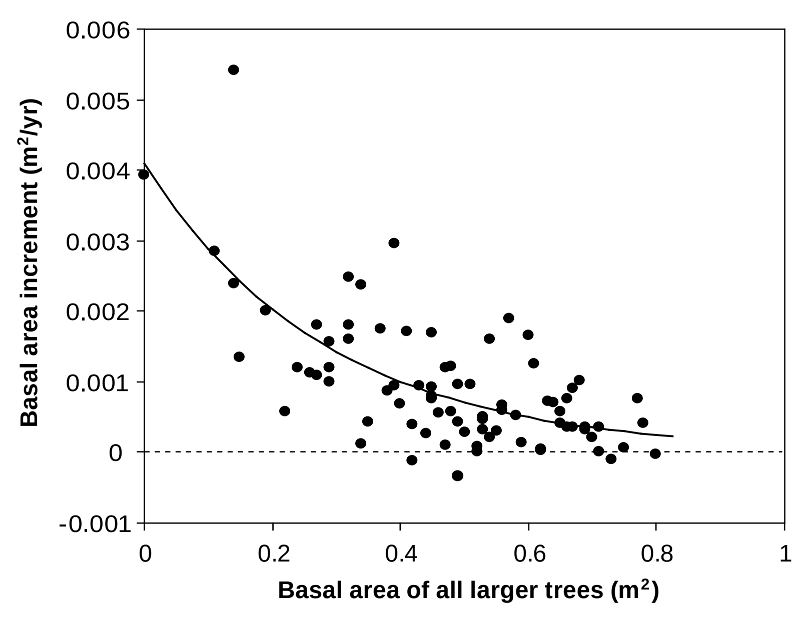


Figure 27—Relationship between basal area increment of *Acacia koa* and the basal area of larger trees within the same stand. The model is $G_{BA} = 0.0041e^{-3.52BA_{GT}}$ where G_{BA} is basal area increment and BA_{GT} is the basal area of neighboring trees larger than the focal tree ($r^2 = 0.49$).

Most koa trees grow quickly enough to have a DBH large enough to measure within 2 years of establishment. Like many tree species, diameter growth for koa trees follows a sigmoidal pattern. Initial growth rates are slow, but once the tree has established its root and crown systems, growth is rapid. As trees become larger and the stand reaches canopy closure, growth is at a maximum. Following canopy closure, average stem-diameter growth declines even as the growth of individual dominant trees may continue at high rates. Diameter increment is expressed as either mean annual increment (MAI = DBH/age at measurement) or periodic annual increment (PAI = $[DBH_2 - DBH_1]/[age_2 - age_1]$) where subscripts denote the beginning (1) and end (2) of the measurement interval. The sigmoidal nature of diameter growth results in PAI exceeding MAI early in the development of a stand of trees and then falling below MAI. In dense, unmanaged stands of koa, MAI and PAI both peaked within 6 years of establishment (Pearson and Vitousek 2001). At a drier site in South Kona, 25-year-old koa stands had MAI of 3.6 mm/yr; however, the fastest 5 percent of the koa trees grew 11.6 mm/yr, whereas the slowest 5 percent did not grow at all (Baker et al., n.d.). Although diameter increment declines early, basal area MAI continues to increase. Most 30-year-old trees were accumulating 12 to 15 cm^2/yr of basal area; the greatest basal area MAI observed was for trees at low elevation in the high rainfall Waiākea area of east Mauna Loa.

Basal Area and Volume Growth

The available data on stand-level growth of koa, whether as basal area or volume increment, are sparse. The Hawaii DFW plots provide the longest time series of data (38 to 55 years), but are limited in number (five plots). Inventory plots at The Nature Conservancy's South Kona Reserve are much more numerous (>150 plots), but provide only a brief (3-year) record of growth. Nonetheless, these plots do offer valuable insights into growth of koa stands, particularly in terms of basal area increment.

Long-term basal area dynamics of koa stands in the DFW plots have varied within and among sites (fig. 28). At plot 12 in Kūlani, basal area reached 16.2 m^2/ha after 23 years, but over the subsequent 30 years remained constant. Plot 25 at Waikamoi, Maui, showed the most rapid gain in basal area, reaching 28 m^2/ha within 11 years of establishment. Subsequent mortality has led to an overall decline in basal area in recent decades; by 2001 the stand basal area was about 30 percent lower than its 1972 maximum. The basal area growth patterns of plots 12 and 25 differ from those of plots 23 (Kūlani) and 41 (Laupāhoehoe) where basal area increased approximately linearly for the first 30 years of stand development but has begun to slow in the last decade. The most obvious difference among these plots is the total basal area that they support. At the most recent remeasurement in 2001, plot 23 had about 41 m^2/ha and plot 41 had 36.5 m^2/ha, whereas plot 12 had 15 m^2/ha and plot 25 had 19.5 m^2/ha. This dissimilarity is largely due to differences in tree density among the plots, with plot 12 (planted at 3- by 3-m spacing) and plot 25 (natural regeneration after logging) having substantially lower tree densities than plots 23 and 41, which were both regenerated by scarifying the soil with a bulldozer. Basal area dynamics for the Laupāhoehoe and Kūlani plots can be modelled using an asymptotic function that constrains basal area increment as a function of time since establishment and the maximum basal area that the site can support (fig. 29).

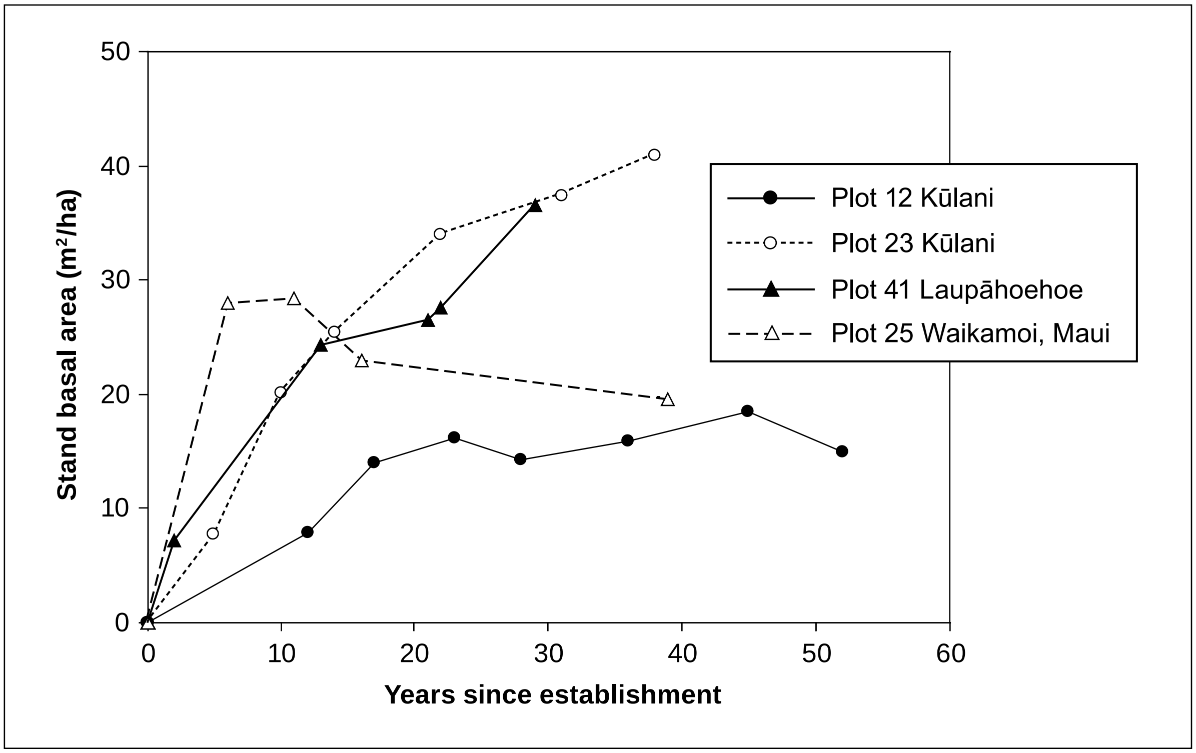


Figure 28—Basal area growth trajectories of *Acacia koa* stands in permanent sample plots established by the Hawaii Division of Forestry and Wildlife.

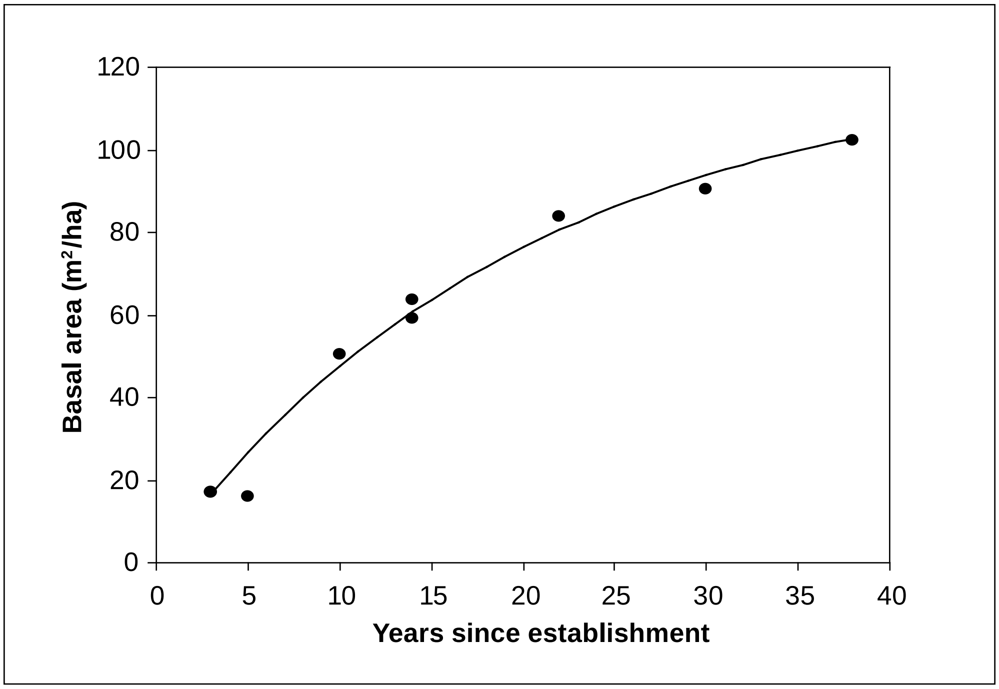


Figure 29—*Acacia koa* basal area growth modelled as a function of time since establishment for the Kūlani (plot 23) and Laupāhoehoe (plot 41) permanent forest inventory plots established by the Hawaii Division of Forestry and Wildlife. The model is BA = 120.81(1 - $e^{-0.05t}$) where t = years since establishment ($r^2 = 0.98$).

Knowledge of wood volume growth of koa trees is essential to developing economically viable forest management plans. However, little is known of volume growth patterns of koa because wood volume estimates are rarely made for koa trees. Several factors account for this. First, harvested koa are primarily large, old trees that often have eccentric bole shapes or defects owing to rot that are not well characterized by simple volumetric equations. Second, the substantial variation of wood grain and figure within a tree has a much greater influence on the value of a log than the volume of the log taken as a whole. Third, variation in koa height-diameter allometries and wood quality within and among islands requires developing site-specific volume equations. However, as the value of koa timber increases and landowner interest in establishing koa forests expands, there will be greater need for quantitative estimates of timber volume production and potential timber revenues. With second-growth koa stands becoming more common, estimating tree and stand wood volume will likely become easier as these stands tend to be more uniform in size, shape, and wood quality and less likely to have stem defects and rot that warrant volume deductions.

The only published volume equations for koa are from Sharpnack (1966), but they have not been widely applied because they require determination of five variables, several of which are time-consuming to obtain—DBH, total merchantable length, number of half-length logs contained in that total merchantable length, diameter inside bark (DIB) at the top of the merchantable length, and form class (FC) for the first full 5-m log (FC = (DIB at the top of the first log)/DBH). With these data, the multivariate equations estimate volumes for half-log segments, which when summed over all segments yield an estimate of total merchantable volume. The equations use English rather than metric data and resulting volumes are in units of board feet based on the International ¼-inch (0.64-cm) saw-kerf rule. The difficulty of obtaining DIB at the top of the merchantable length and FC for the first log is somewhat offset by the strong allometric relationship between (1) stem diameter outside bark (DOB) and bark thickness and (2) DBH and DOB at the top of a merchantable length of trunk, which allows estimation of those variables from measurements of DBH and merchantable length.

It should be noted, however, that the validity of these volume equations for second-growth koa is untested. In second-growth koa stands at The Nature Conservancy's South Kona Reserve, koa trees harvested as part of a thinning study were used to examine the relationship between DBH and stem volume. Within the limited size range of study trees, the relationship was very strong (fig. 30). This suggests that simple local volume tables could be made for areas as second-growth forest developed across a range of sites.

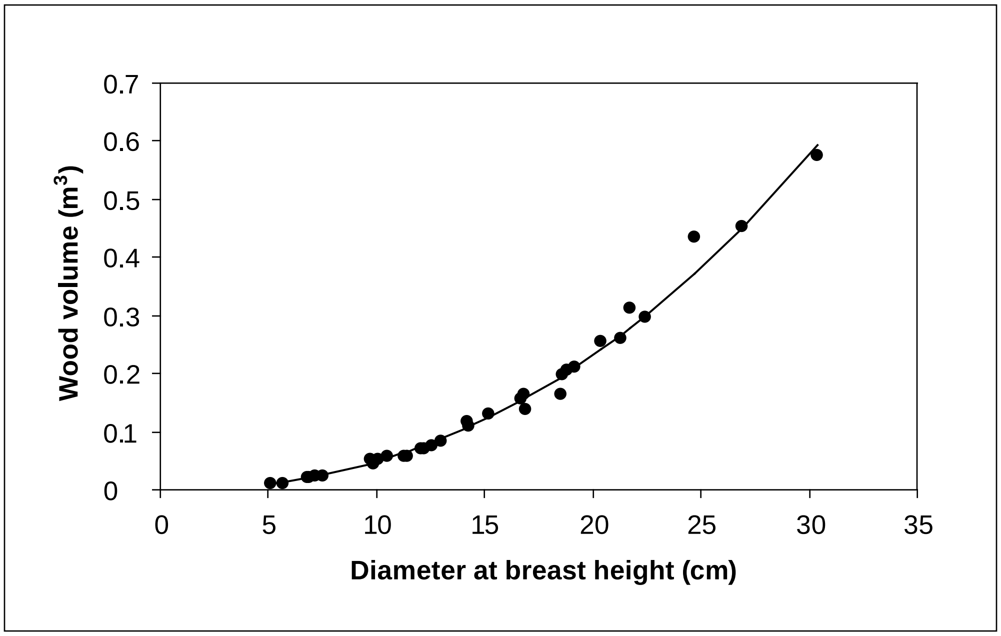


Figure 30—Log volume of second-growth *Acacia koa* from The Nature Conservancy's South Kona Reserve. The model describing the relationship between diameter at breast height (DBH) and stem volume is $V = 0.000273\ DBH^{2.25}$ ($r^2 = 0.99$).

Koa volume growth on the DFW permanent inventory plots was estimated using the volume equation shown in fig. 30. This equation is easier to apply than Sharpnack's as it only requires DBH. Koa volume growth patterns for the DFW plots show a range of patterns (fig. 31). Plot 23 at Kūlani had the greatest estimated volume (143 m^3/ha after 38 years) among the inventory plots, although plot 41 at Laupāhoehoe closely tracked the Kūlani curve and had 123 m^3/ha after 29 years. In contrast to these relatively high levels of wood volume production, other inventory plots had substantially less. Plot 12 at Kūlani had reached a maximum stand volume of 64m^3/ha after 45 years, but subsequently lost about 16 m^3/ha between 1994 and 2001. The sole Maui plot (plot 25 at Waikamoi) reached near-maximum volume quickly (80 m^3/ha in 11 years). However, 5 years later it had declined to 67 m^3/ha, where it remained for the next 23 years.

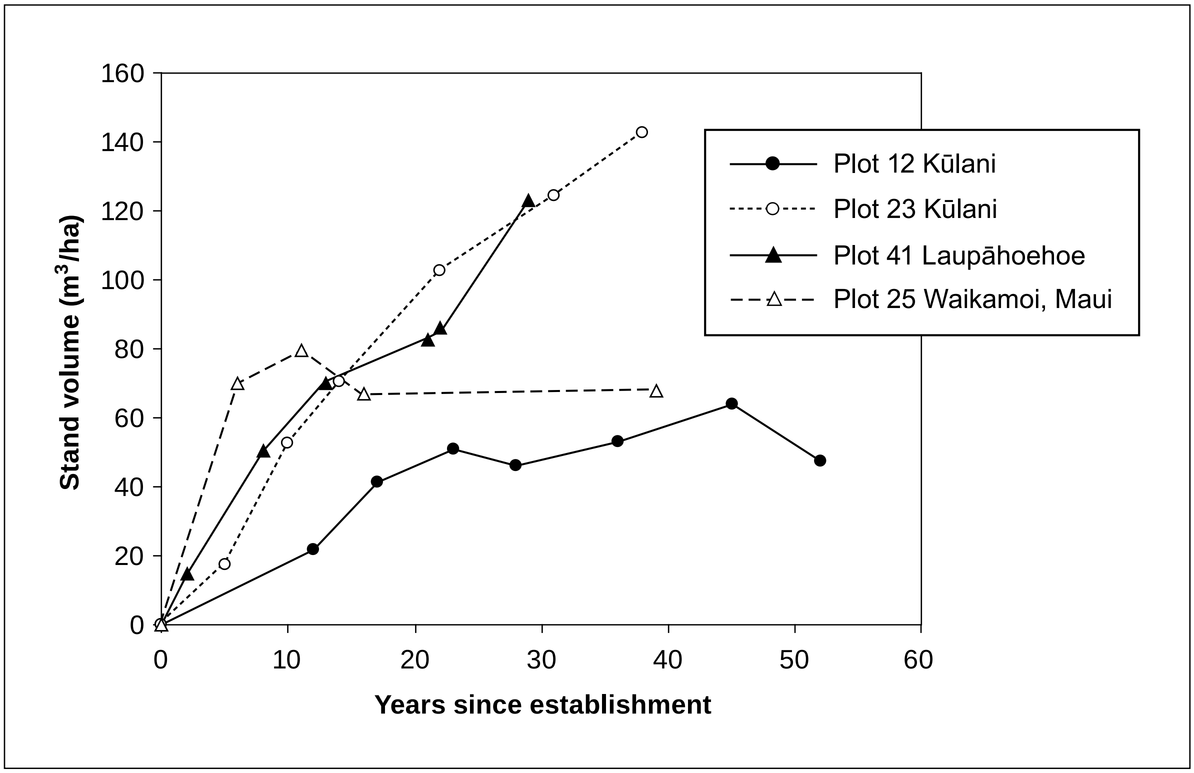


Figure 31—Estimated wood volume growth of A*cacia koa* on the Hawaii Division of Forestry and Wildlife permanent forest inventory plots. Wood volumes were estimated using volume equations for *Acacia koa* described in fig. 30.

Grace (1995) developed a growth model to simulate the dynamics of koa forests and compare various silvopastural management scenarios on productivity of koa for timber and grass for cattle grazing. The model was parameterized using three of the DFW permanent inventory plots in the Kilauea Forest Reserve near Hilo, Hawaii. Merchantable stem volume was calculated as a function of DBH, merchantable height, and diameter at the top of the merchantable log, although both merchantable height and top diameter were estimated as allometric functions of DBH. Using the initial inventory data as the starting conditions for the model runs, Grace (1995) grew the forest to the present and compared stand metrics obtained in each inventory with model outputs for the same time. To test whether his growth model provided reasonable estimates of koa volume production, Grace (1995) compared the observed total stand merchantable volume from the study plots with the volume estimates provided by the model. For the three plots used to parameterize the growth model, the estimated volumes were similar to the observed values. The fourth plot, which was not used for parameterization, showed the correct volume growth pattern, but the rate of early volume growth was slower, leading to a 10-year lag in volume accumulation when compared to the field data.

Mortality

Mortality of koa is greatly influenced by the growth rate and relative size of individuals within the stand (Grace 1995, Fownes 1997). Small, slow-growing trees die sooner than large, fast-growing individuals. Data from the DFW plots showed that mortality was negatively correlated with DBH growth rate (fig. 32). Mortality at Kūlani plot 23 was about 55 percent per year for trees growing 1 mm/yr in diameter. In contrast, trees growing >10 mm/yr had mortality rates of about 3 percent per year. Crown position relative to the general forest canopy is an indicator of likelihood of dying. In the koa reforestation area of Keauhou Ranch, Hawaii, mortality rates were much lower for dominant trees (3 percent per year) than suppressed and intermediate trees (14 percent per year) over the same period (Scowcroft, n.d.b). Koa at DFW's Kūlani plot 23 showed a similar pattern, with mortality being substantially lower for dominant trees than for suppressed trees (fig. 33).

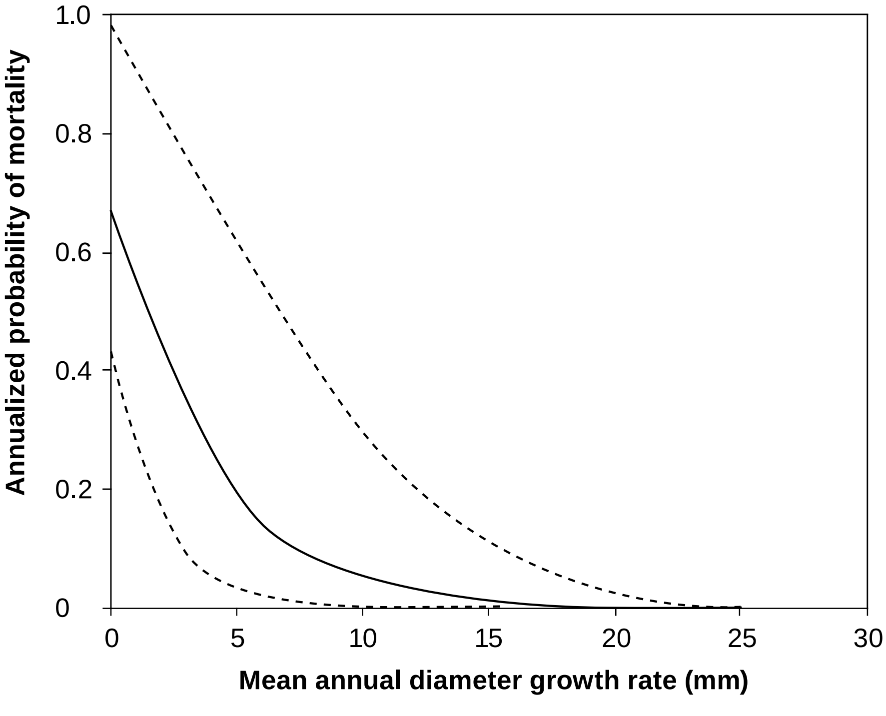


Figure 32—Growth-rate dependent mortality of *Acacia koa* from the Hawaii Division of Forestry and Wildlife (DFW) Kūlani plot 23, Hawaii. The model uses the 1968–1973 growth data to estimate the annualized probability of mortality during 1973–1977. Dotted lines represent 95-percent confidence intervals for the estimates of mean mortality.

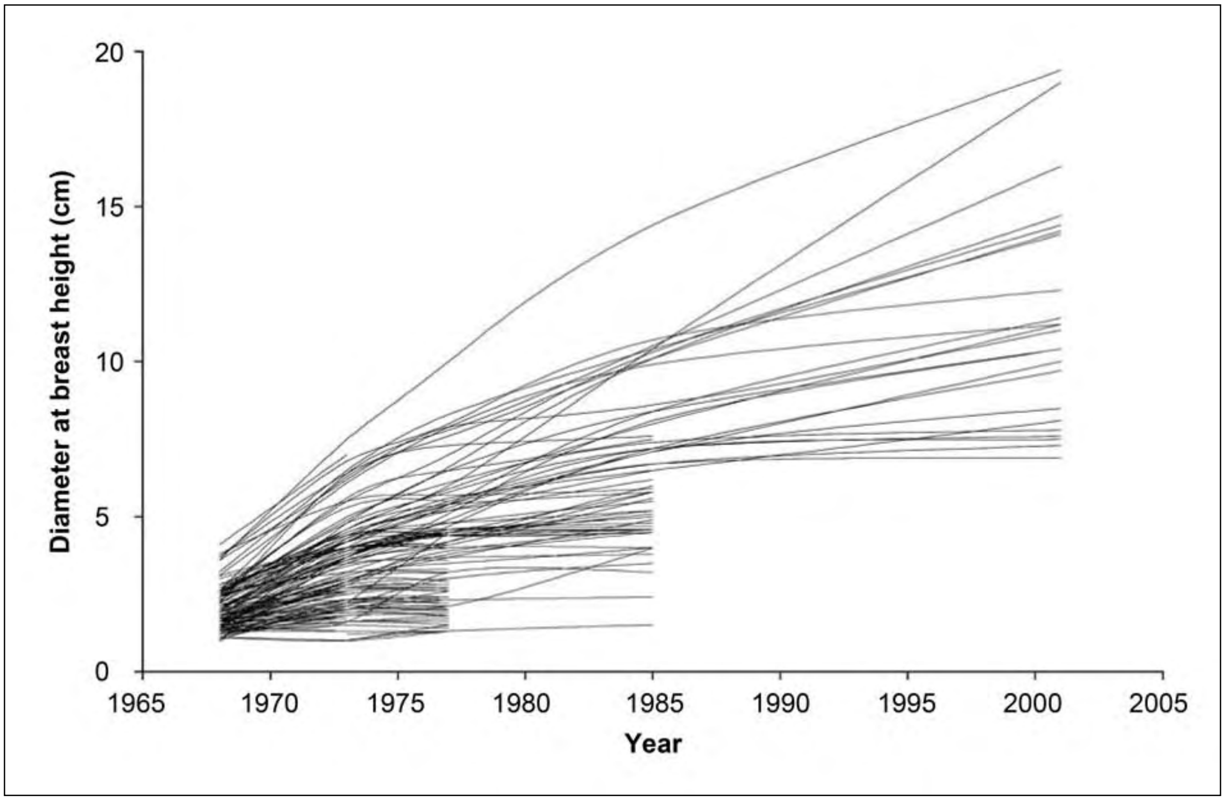


Figure 33—Diameter growth trajectories for all trees present on the Hawaii Division of Forestry and Wildlife (DFW) Kūlani plot 23, Hawaii. Each line represents an individual tree. Where a line terminates, the tree had died. Note that in each recensus (1977 and 1985) it is typically the smallest trees that died.

Chapter 4: Koa Silviculture

Despite the economic, ecological, and cultural value of koa, not a single stand of koa (*Acacia koa* A. Gray) in Hawaii has been through a full silvicultural rotation (i.e., establishment, stand improvement, harvest, and reestablishment). Historically, large, old koa were mined from forests with little provision made for renewing the resource and sustaining a wood supply. Now, early in the 21st century, the consequences of that approach are painfully obvious. Many areas of the Hawaiian Islands that formerly supported koa forests are grasslands with only the occasional relict koa tree. Those trees that do remain typically have crown dieback, poor form, and large pockets of rot or hollows in the stem (which is why they were not harvested). Because there is no history of long-term forest management of koa in Hawaii, our discussion of silvicultural systems is necessarily based not on direct experience, but on an understanding of the biology of koa trees and forests, consideration of short-term responses to silvicultural experiments, and evaluation of silvicultural systems for closely related *Acacia* species for which there is a longer history of silvicultural research and management. In this section, we bring together a range of studies that have been conducted on various operational aspects of koa silviculture. These include establishment, fertilization, pruning, and thinning. We then synthesize the patchwork of research on the ecology and silviculture of koa in a discussion of a range of silvicultural systems and their potential application to koa forests in Hawaii. We stress, however, that the silvicultural systems are presented as working hypotheses (Smith 1986)—that is, the best estimates possible given all available information. We conclude with a discussion of koa timber utilization and the potential for genetic improvement of koa for timber quality and disease resistance.

Establishment

Natural Regeneration

One of the silviculturally useful traits of koa is its propensity to form a long-lived soil seed bank, enabling resource managers to regenerate koa long after the last koa tree is gone from a site (fig. 34). Were it not for this, natural regeneration of koa would be inhibited by the inability of the heavy seeds to disperse into areas lacking live koa trees. Most land that formerly supported koa forests has gone through a protracted stage of use as rangeland. During that stage two things occur that impede later regeneration of koa from the soil seed bank. First, any seedlings that sprouted when livestock were present were inevitably browsed; successive episodes of germination followed by browsing predictably depleted the soil seed bank. Second, and perhaps even more important, successful establishment of the kind of dense sward of pasture grasses desired by ranchers greatly impedes germination of the koa seeds remaining in the soil.

Key Points

- The long-lived seeds of koa greatly facilitate its regeneration. Seed germination and seedling establishment are impeded by dense grass, and those seedlings that do appear are quickly browsed if the site is grazed. Exposure of koa seeds to sun and rain by disturbing the soil, coupled with removal of competing plants and browsing animals, typically leads to establishment of thousands to tens of thousands of koa seedlings per acre, unless the soil seed bank has been almost completely depleted.
- Even though forests containing koa have substantial numbers of viable seed in the soil, those seeds seldom produce seedlings that reach the canopy. This is because koa is so light-demanding. Gaps in the forest canopy are essential if koa is to be regenerated successfully, and large gaps are more likely to result in successful regeneration than are small gaps.
- On sites where there are no koa seeds in the soil, koa can be reestablished by planting nursery-grown seedlings. Those seedlings are typically grown in individual plastic tubes and are a foot tall or more at the time of planting. At the higher elevations of koa’s range, protection of seedlings from frost may be essential during the first year or two.
- Direct sowing of koa seeds is less widely used than planting seedlings, but it is a promising approach where seeds are readily available. Approximately two seeds have to be sown for every seedling established.
- Whether using seedlings or seeds, planters are well advised to pay close attention to seed source. Local seed sources often produce koa trees better adapted to local conditions than do seeds gathered at locations remote from the planting site.
- Where regeneration of a koa forest is primarily a restoration effort, reestablishing native understory plant species typically proves a more difficult task than regeneration of the koa itself. In general, the longer and more heavily used the site, the more difficult it is to regain the full complement of understory species. Among the factors that commonly impede establishment of native plants are competition from nonnative grasses, lack of seed sources or their dispersal agents, and absence of appropriate sites for seed germination.
- The mixture of native species that sometimes results when a koa-dominated stand is regenerated can work to good advantage in producing fast-growing koa of good form. This occurs because slower growing species with denser crowns act as trainers, inducing early shedding of koa’s lower branches and dominance by a single main stem.

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Figure 34—*Acacia koa* seedling emerging from the soil seed bank after mechanical scarification of a former pasture in South Kona, Hawaii.

Numerous anecdotal observations suggest that mechanical removal of the grass cover, whether with the intent of regenerating koa or not, often leads to the establishment of koa seedlings. Recently Denslow et al. (2006) provided experimental support for these observations by examining the factors limiting natural regeneration of a suite of native plant species in koa stands at Honomalino in South Kona, Hawaii. Grass cover, canopy density, and seed availability were experimentally manipulated to determine their relative influence on regeneration. The major factors limiting establishment of koa from the soil seed bank were the thick grass cover (predominantly meadow ricegrass) and forest canopy cover (fig. 35) (see app. B for species names). Removal of the grass led to a 20-fold increase in koa seedling establishment in study plots in which the overstory koa trees had been removed, but only a 3-fold increase when the grass was removed but the overstory was left intact. Removal of the overstory had no significant impact on koa regeneration where the grass cover was not eliminated. In sparsely wooded portions of Hakalau Forest National Wildlife Refuge (NWR), disk plowing was used to temporarily suppress competition from pasture grasses and to stimulate germination of buried koa seeds around live and dead koa trees and logs and in open areas at least 30 m from the nearest live or dead koa tree or log (Conrad et al. 1988). Within 2 months

Figure 35—Thick ground cover of an exotic pasture grass, *Ehrharta stipoides* (meadow ricegrass), under a young *Acacia koa* stand that regenerated naturally following logging in the late 1970s.

of scarification, koa seedling densities averaged more than 1,100 stems per hectare around both live and dead trees or logs. Even in the open, density ranged from 20 to 290 stems per hectare (Scowcroft, n.d.a). Survival after 3 years averaged 80 percent and heights averaged 2.0 to 2.5 m for koa regeneration around live and dead trees; in open areas, survival averaged 95 percent and heights averaged 3 m.

If koa seed trees are scarce or absent, which is typical of some high-elevation grasslands on Hawaii and Maui, and the seed bank has been depleted, dispersal limitation owing to the heavy seeds and pods of koa may substantially reduce or eliminate its natural regeneration. No studies have examined the dispersal profiles of koa to determine the minimum density of adult trees required to maintain a significant level of seed rain across a site.

In established forests, the success or failure of natural regeneration of koa depends on forest floor light levels, which can be as little as 1 percent of full sunlight. Under greenhouse conditions height growth and total seedling biomass were reduced significantly when light levels fell to one-third of full sunlight (fig. 36) (Walters 1981). At 19 percent of full sun, 23-week-old seedlings were only half as tall and had only one-sixth the biomass of plants growing at 70 percent of full sun. Relative allocation of carbon to stem, leaves, and roots was not greatly affected by light level. The implication of these findings is that forest canopy gaps are needed for successful establishment of koa (Mueller-Dombois 1981b); the larger the gap, the more likely koa is to occupy it in the long term.

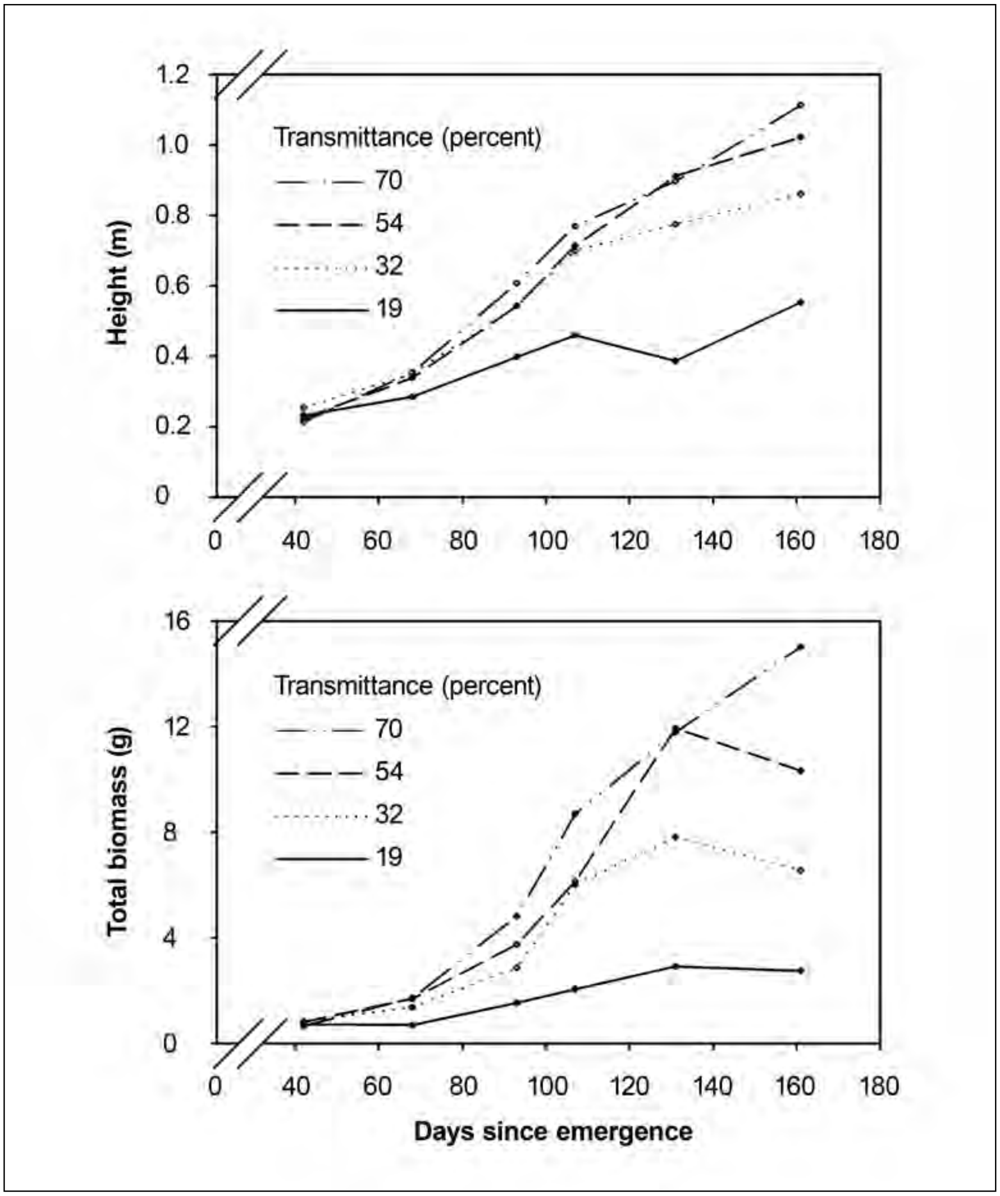

Figure 36—Seedling growth of *Acacia koa* as a function of available sunlight (transmittance). (Based on Walters 1981).

Artificial Regeneration

Planting—

Koa planting is primarily done in attempts to reforest areas that have been severely degraded or deforested owing to historical land-use practices. As such, most seedlings are planted in high light environments. Considerable work has been done on developing efficient and economical methods for regenerating koa stands by planting. In particular, the managers and scientists of the Hakalau Forest NWR have had remarkable success in revegetating large areas of grassland formerly dominated by koa (fig. 14). They use 30- to 45-cm-tall koa seedlings that have been grown in dibble tubes. Individual 1 m^2 planting spots are prepared by peeling back pieces of sod using a rake-like attachment mounted on the back of a bulldozer. One seedling is planted in the center of each spot and about 110 g of 10-30-10 fertilizer is placed in two holes located just uphill from the seedling (Horiuchi 2005). Seedlings do not receive postplanting care. Survival varies as a function of the frequency, duration, and timing of subfreezing temperatures, which are influenced by elevation (survival decreases with increasing elevation), topographic position (survival is poorest in drainage bottoms), and occurrence of dry, clear winter nights (survival decreases during El Niño years) (Scowcroft and Jeffrey 1999, Scowcroft et al. 2000b). Hakalau Forest NWR personnel deploy simple frost protection devices during El Niño events to reduce mortality the first winter after planting (Scowcroft and Jeffrey 1999). By blocking a large part of the night sky, shade cloth reduces radiant heat loss. As a result, leaf temperatures remain several degrees warmer than without the shade cloth. With a single layer of shade cloth placed vertically on the east side of seedlings at Hakalau Forest NWR, which is on an east-facing slope, survival improved from 15 to >95 percent.

Where natural regeneration is patchy, koa seedlings can be planted to create a more uniform stocking pattern. However, early experiences have shown that the planting stock must be well adapted to the site. For example, seedlings grown from koa seeds collected on the leeward flank of Hualālai, Hawaii, that were out-planted on the windward flank of Mauna Loa grew in height and diameter at breast height (DBH) more slowly than seedlings originating on site from buried seeds. Although survival and vigor were similar for naturally regenerated and planted seedlings, after 10 years, planted koa were 2 m shorter and 2 cm DBH smaller than natural regeneration (Scowcroft, n.d.b).

Direct seeding—

Sowing seeds directly is a viable alternative to planting nursery-grown seedlings in some situations. For example, germination rates of 60 to 70 percent followed direct seeding in a scarified Ultisol in central Oahu (table 6). On the nutrient-poor soils of the study site, postgermination survival was better for germinants derived from local seed sources than those derived from a nonlocal source, but application of fertilizer eliminated this difference. Overall, height growth of direct-seeded trees was equal to or better than that of planted trees. In another direct-seeding trial, in the Hōnaunau forest of North Kona, Hawaii, germination averaged 57 percent despite cutworms having killed some germinants before the first measurement (Fujii, n.d.). Twelve years after sowing, survival was nearly 40 percent and average tree height was 6 m. Survival of direct-seeded trees compared favorably to that of 12-year-old

Table 6—Average germination, survival, height, and annual height growth for seeded and planted *Acacia koa* at the Waiawa Community Correctional Center, Oahu, by fertilizer treatment[a] and seed source[b]

Treatment	Germination	Seedling survival		Height	Height growth
	Percent	*Percent*	*Number*	*cm*	*cm/yr*
Local seed source:					
Direct seeded[c]					
-F	66.7	62	10	44.7	31.9
+F	48.6	47	5	129.3	84.2
Planted[d]					
-F	n.a.	17	4	68.0	36.2
+F	n.a.	24	6	109.0	74.0
Off-site seed source:					
Direct seeded[c]					
-F	61.3	15	2	7.1	8.8
+F	25	41	2	23.8	22.6
Planted[d]					
-F	n.a.	14	3	19.6	-4.8
+F	n.a.	21	5	52.9	23.5

Each seeded experimental unit consisted of 24 seed spots on a spacing of 1 by 1.5 m; each planted experimental unit consisted of 24 nursery-grown seedlings (approximately 5 months old) on a spacing of 1 by 1.5 m.

n.a. = not applicable.

[a] Treatments were no fertilizer (-F) and 57 g 14-14-14 osmocote fertilizer (+F) applied to a shallow hole approximately 5 cm from the seed spot or seedling.

[b] The local Oahu seed source was Koa Ridge Ranch, a low-elevation site on the leeward slope of the Koolau Mountains; the offsite, Hawaii seed source was Keanakolu, a mid-elevation site on windward Mauna Kea.

[c] Survival denotes the percentage and number of germinants per experimental unit that were alive 1.6 years after sowing.

[d] Survival denotes the percentage and number of planted trees per experimental unit that were alive 1.8 years after planting.

naturally regenerated koa located near the direct-seeding trial (Scowcroft, n.d.b). Whitesell (1990) noted that other direct seeding efforts have had moderate to good success.

Only one study has examined the success of direct seeding in established forest. Whitesell (1976) spot-seeded koa seeds in two narrow strips (1.8 m and 3.7 m wide) that were bulldozed or hand-cleared into koa-ʻōʻhia forest at the Waiakea Forest Reserve on Hawaii. In both strips, survival after 8 years was about 40 percent, and most of the survivors had low vigor and poor form. In the 1.8-m strip, mean height of the koa trees was 8.8 m and mean DBH was 5 cm. In the 3.8-m strip, mean koa height was 9.8 m and mean DBH was 9.4 cm. Although tree form was very poor and all trees were scored as cull trees of no merchantable value, this was likely due to the low light levels in the planting sites and not the method of regeneration.

Overall, the few direct seeding studies that have been conducted suggest that direct seeding is at least as effective as planting in getting koa trees established, provided the seed source is adapted to local growing conditions. However, despite these successes, operational reforestation projects continue to rely on planting of nursery-grown seedlings. Comparative cost-benefit analyses of the two regeneration methods have not been undertaken.

Establishment of Mixed-Species Stands

Although most economically motivated koa reforestation efforts target that singularly valuable species, today it is increasingly common to encounter reforestation as part of an ecosystem restoration effort. In restoration, the issue involves not only regeneration of koa, but also the many other species that make up the koa forest community. Most of those species do not form soil seed banks, and their regeneration is a less tractable problem than regeneration of the koa itself.

Successful natural or artificial establishment of plant species associated with koa depends in part on the degree of site degradation. Since the mid-1800s, the land that is presently the Hakalau Forest NWR was converted from forest to grassland through logging, burning, pasture development, and cattle grazing. The grassland vegetation is dominated by perennial introduced forage species such as kikuyu grass (*Pennisetum clandestinum*), sweet vernalgrass (*Anthoxanthum odoratum*), velvet grass (*Holcus lanatus*), and narrow-leaved carpetgrass (*Axonopus fissifolius*) (Walker 1996). Only isolated trees and small patches of native plants in steep-sided ravines remained from the former koa-‘ō‘hia forest when Hakalau Forest NWR was created in 1985. Cattle grazing ended shortly after that, and intensive efforts were made in succeeding years to reforest the grassland with koa and associated understory species, such as ‘ō‘hia (*Metrosideros polymorpha*), ‘ōlapa (*Cheirodendron trigynum*), kōlea (*Myrsine lessertiana*), and māmane (*Sophora chrysophylla*). Although koa plantings have been successful, except at the highest elevations, establishment of understory species generally failed when seedlings were planted in the open, primarily owing to frost-induced mortality (Conrad et al. 1988, Horiuchi 2005, Scowcroft and Jeffrey 1999). Scowcroft et al. (2000b) found that unprotected ‘ō‘hia seedlings suffered severe frost damage and 100-percent mortality, whereas those planted under a canopy of koa rarely experienced subzero temperatures, suffered little damage, and had 100-percent survival. Koa trees reduced nighttime radiative cooling of underplanted species and buffered against the negative effects of topographic position on the intensity and duration of subzero temperatures in exposed grassland (Scowcroft and Jeffrey 1999).

In addition to protection from frost, natural regeneration of understory plant species is also a function of seed rain and suitable safe sites for germination and establishment (such as the decaying logs discussed earlier; e.g., Scowcroft 1992). Wildfire and decomposition have made such seedbeds scarce in areas that were long ago converted from forest to grassland. Although reestablishing koa in grasslands will not affect the amount of large woody debris in the short term, it might increase the abundance of safe sites by reducing grass competition. Scowcroft and Jeffrey (1999) found that an overstory of koa reduced aboveground grass biomass to about 30 percent of that in the open. The presence of koa trees in grassland might also increase seed rain by increasing the likelihood that frugivorous birds, such as the endemic ‘ōm‘ao (*Myadestes obscura*) (see app. C for bird common and scientific names), will use them as perch sites and disperse native seeds to the ground below (Pejchar et al. 2005).

In landscapes where koa forest has not undergone complete conversion to grassland, regeneration of associated plant species may be less problematic. The extensive areas of open-canopy, cattle-grazed koa-‘ō‘hia forest that were bulldozed and scarified at Keauhou Ranch, Hawaii, are instructive in this regard (fig. 37).


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Figure 37—Aerial view of *Acacia koa* growing in pure and mixed stands at Kamehameha School’s Keauhou Ranch, Hawaii. The area to the left of the road is a pure stand of koa established by scarification in the late 1970s. To the right of the road is secondary koa interspersed among remnant old-growth trees.

Scarification and fencing resulted in the successful regeneration (from buried seed) of pure stands of koa (Skolmen and Fujii 1981). The treatments began in 1977, and 24 years later, 56 native plant species had colonized the understory (Scowcroft, n.d.b). Native trees other than koa with DBH >1 cm accounted for 14 percent of the basal area, and although koa accounted for most of the basal area, naio (*Myoporum sandwicense*) was slightly more abundant than koa (945 and 919 trees per hectare, respectively). Density of all understory trees with DBH >1 cm was 1,822 stems per hectare. Average DBH ranged from 2.3 cm (±0.2 cm SE) for alani (*Pelea clusiifolia* Gray) to 5.1 cm (±0.4 cm SE) for ‘ōlapa. The tallest understory trees reached 9 to 14 m, which made them as tall as some of the shorter koa trees. ‘Ōlapa was sparse (55 stems per hectare) in the 24-year-old stand. Its scarcity might have been due to slow development of the requisite organic seedbeds (Scowcroft 1992) or a paucity of either a seed source or the frugivorous birds that disperse ‘ōlapa seeds (Ralph and Fancy 1994b).

In addition to their conservation and restoration value, tree species that grow together with koa may influence koa growth, form, and ultimately economic value. This is likely to be especially true in the early stages of koa stand development. For instance, as mentioned earlier, growth rates of 25-year-old koa at Honomalino, Hawaii, were negatively correlated to the basal area of neighboring koa, but positively correlated to the basal area of neighboring ‘ō‘hia. When koa grow in pure stands, they compete with other koa, which have similar growth rates, shade tolerance, and architecture. Consequently, little differentiation of tree height occurs, and without silvicultural interventions to reduce stand density, and therefore intertree competition, growth of individual trees and the stand as a whole slows considerably. Mixed stands, in which koa is one component, have species with a range of growth rates, shade tolerances, and tree architectures, enabling temporal and spatial competition for light, water, and nutrients. No studies have examined the impacts of local species composition on establishment success and subsequent stand development of koa.

Stocking

Forest managers try to control the stocking level of a stand to make the most efficient use of the available growing space for individual trees. Typically, the objective is to maintain high levels of growth while minimizing tree mortality. Quantitative models of the relationship between stand density and mean tree size provide foresters with an objective method for evaluating stocking levels and guiding decisions to alter these levels at different periods of stand development. Such stocking guidelines can be used to determine initial spacing of trees, as well as to develop sound precommercial and commercial thinning regimes. Stocking guidelines are typically developed from long-term spacing and thinning trials, from inventories of undisturbed, fully stocked, even-aged stands, or from growth and yield models. Unfortunately, these types of data are not available for koa.

Another approach, proposed by European foresters in the early 20th century and described in detail by Dawkins (1963), employs the allometric relationship between stem and crown diameters to predict basal area and stand density for a given mean stand diameter. Baker and Scowcroft (2005) used the crown-stem diameter relationship to develop stocking guidelines for secondary koa stands at three sites (two windward, one leeward) on Hawaii (fig. 38). They found that the windward sites were able to support denser stands of equivalently sized trees than the leeward sites. At Keauhou Ranch, a fully stocked koa stand with mean DBH of 50 cm would have twice as many trees per hectare as the drier Honomalino site (162 and 79 trees per hectare, respectively). Perhaps more importantly, the stocking guidelines show that fully stocked stands of merchantable size (>30 cm DBH) should be much less dense than commonly believed or practiced. For a stand of 50-cm-DBH trees growing on a square grid at the densities described above, spacing should be approximately 7 m for the moister sites and 10 m for the drier sites.

Key Points

- Dry sites can support fewer trees per unit area than moist sites. For trees 20 inches (50 cm) in diameter, the estimates range from just over 30 trees per acre (75 trees per hectare) on dry sites to about 65 trees per acre (160 trees per hectare) on moist sites.
- Optimum spacing for koa is wider than is commonly perceived, ranging from about 20 to 30 ft (6 to 9 m) between trees for trees 20 in (50 cm) in diameter on moist and dry sites, respectively.

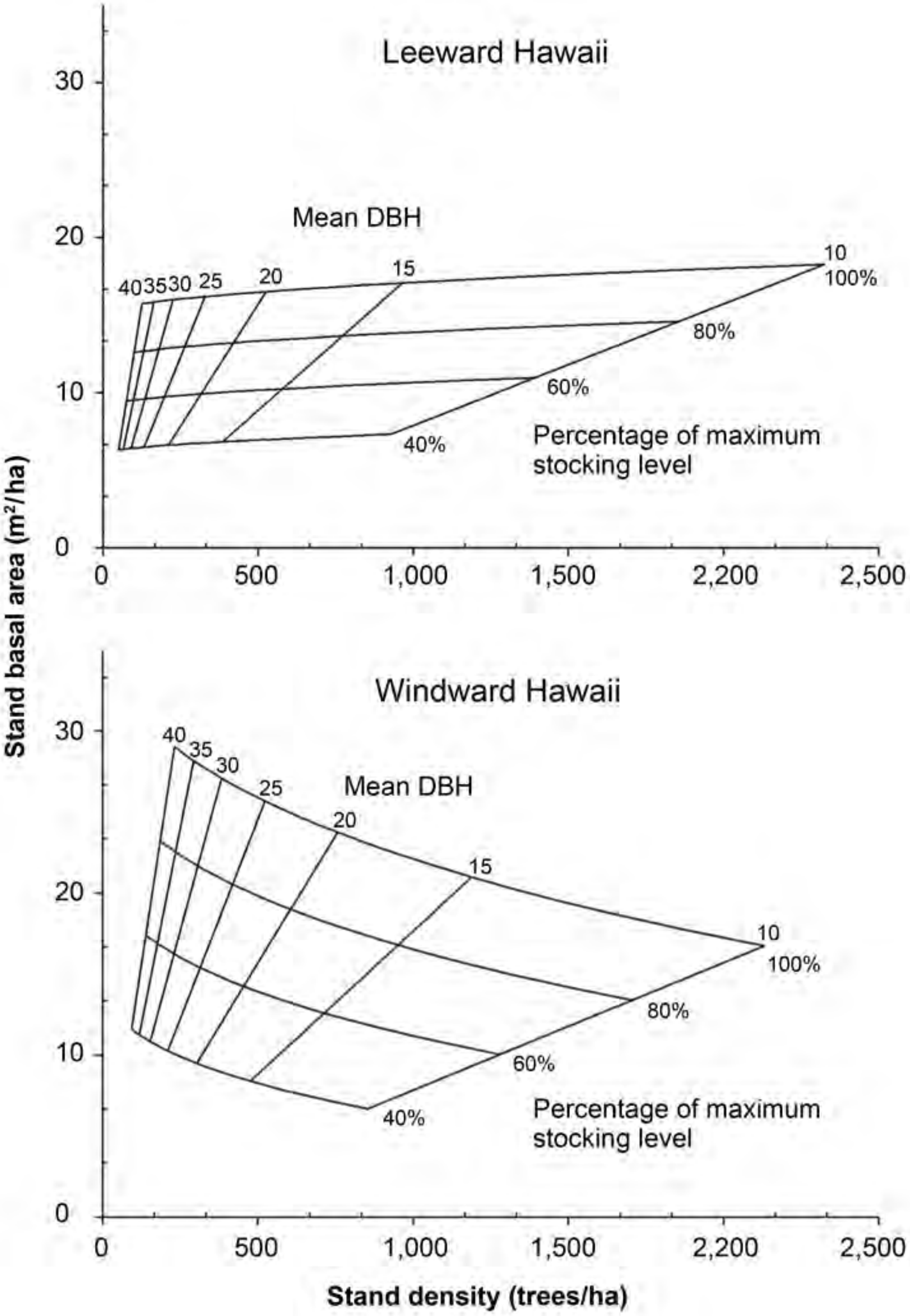

Figure 38—Stocking guidelines for *Acacia koa* stands on leeward and windward Hawaii based on allometric relationships between stem diameter and crown diameter. DBH = diameter at breast height. (See Baker and Scowcroft 2005 for details.)

Thinning

Historically, koa management practices have focused on extraction with little interest or perceived need for stand improvement. In recent decades, reforestation efforts have led to the establishment of dense stands of nearly pure koa in which thinning is often required to maintain high growth rates for individual trees. Repeat measurements of inventory plots in such stands demonstrate that DBH growth rates of individual koa trees are very low (<2 mm/yr) (Baker et al., n.d.) and that such low growth rates are correlated with high mortality rates (Constantinides 2004). These observations indicate that early, precommercial thinning is probably critical to maintaining high growth rates and tree vigor in dense young koa stands. Few koa stands presently have trees of sufficient size to make thinning operations commercially feasible. Consequently, no data are available on the costs or benefits of commercial thinning of koa stands.

Key Points

- Trees in dense, young stands of koa experience high rates of mortality and grow very slowly. Experience with even-aged stands ranging from 9 to 25 years, on both moist and dry sites, indicates that thinning leads to substantially increased growth of the remaining trees.
- Sometimes there is an added growth benefit to controlling grass in connection with thinning.
- Growth response to thinning can be very fast—within a couple of months. The larger trees in even-aged stands tend to respond more positively to thinning than do smaller individuals.
- Stands thinned to lower densities of trees (120 trees per acre [300 trees per hectare] at age 25) result in much faster growth of the remaining trees than do stands thinned more lightly.

Several studies have examined the response of koa to thinning. For example, Scowcroft and Stein (1986) conducted a thinning study in a stand of 12-year-old koa on Haleakalā, Maui, in which tree growth had slowed because of overcrowding. Stand density at time of thinning averaged 2,460 trees per hectare, and DBH ranged from 6 to 24 cm (mean BA = 26.4 m^2/ha). Thinning reduced stand density to 750 trees per hectare (mean BA = 16.5 m^2/ha). The results, expressed as relative basal area growth rate, showed a significant increase of about 30 percent in koa growth as a result of thinning. More recently, Pearson and Vitousek (2001) conducted a small-scale thinning experiment in dense 9-year-old koa stands at Keauhou Ranch, Hawaii. Study plots were thinned to a target of 50 percent of initial basal area. The thinning resulted in appoximately an 80-percent reduction in tree density (mean initial density of trees >1.5 cm DBH: 1630 trees per hectare; mean postthinning density: 340 trees per hectare) and 75 percent reduction in leaf area index (LAI) (mean initial LAI: 4.6; mean postthinning LAI: 1.2). After 1 year, LAI had nearly doubled in the thinned plots, and after 2 years it was similar to that of the control plots. Thinning increased the growth of the remaining trees by nearly 200 percent and the dominant trees in each plot by nearly 100 percent. Thinning also led to significant increases in soil nitrogen (N) pools and nitrification rates in the study plots, but did not have a significant impact on nodule biomass.

Another thinning study was installed in a 23-year-old koa stand located at Keauhou Ranch at 1700 m elevation on the windward slopes of Mauna Loa. Initial density of trees >1 cm DBH averaged 955 trees per hectare. Thinning was confined to removal of neighboring koa that were in direct crown competition with individuals with the greatest potential as future crop trees. Competing trees were eliminated by girdling. Herbicide control of introduced grasses and herbicide grass control plus phosphorus (P) fertilization were also used singly and in combination with thinning. Thinning alone or in combination with grass control increased stem diameter increment only 1.8 and 3.5 mm/yr above the 5.0 mm/yr level in control plots 2 to 3 years after treatment (Scowcroft et al. 2007). These treatments did not significantly affect koa leaf nutrient concentrations or soil N or P availability. Thinning in combination with grass control and P fertilization significantly increased annual DBH increment of crop trees to 10.9 mm/yr. Leaf P concentrations and soil P availability were also elevated. Although crown vigor and ratio of live crown to total tree height were correlated with tree growth rate, neither were affected by thinning or fertilization treatments. Likewise, leaf area and crown size were unaffected by thinning or fertilization. These findings suggest that the limited early growth response of 25- to 26-year-old koa to thinning alone was most likely due to the inability of the small crowns to expand rapidly into the crown growing space created by thinning. Improved P status and light conversion efficiency of koa foliage probably account for faster growth of thinned and fertilized trees. If treatment differences in growth rate over the first 3 years posttreatment are maintained, then thinning would reduce the rotation age for trees with a mean DBH of 30 cm by as much as 10 years and for trees with a mean DBH of 40 cm by as much as 25 years. Even shorter rotation ages might be realized by undertaking thinning earlier in the development of the stand, when potential crop trees still have large crowns.

Although these studies have demonstrated that koa responds well to thinning, they do not provide an indication of how koa will respond to different thinning intensities. Baker et al. (2008) examined the effect of different thinning intensities on tree growth in dense, stagnated stands of 25-year-old koa stands at Honomalino, Hawaii. Initial density of trees >5 cm DBH averaged approximately 1800 trees per hectare. Thinning treatments around individual trees reduced local tree density to the equivalent of 200, 300, 400, 500, 700, and 900 trees per hectare. Despite the obvious growth stagnation of trees within the stands (mean diameter growth of trees prior to thinning was <3 mm/yr), thinning led to almost immediate growth responses (fig. 39). Significant differences in diameter increment were observed 2 months after thinning between the control (unthinned) plots and the most intensively thinned plots. By the second measurement period (4 months postthinning),

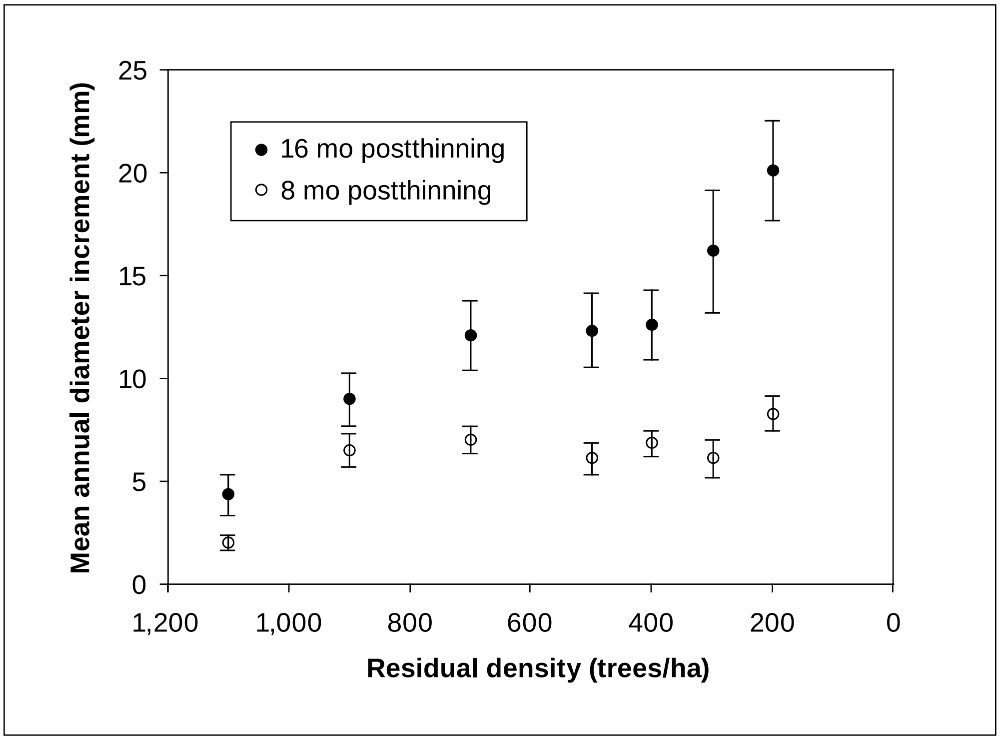

Figure 39—Diameter growth response of *Acacia koa* trees to a range of thinning intensities at The Nature Conservancy's Honomalino Reserve, South Kona, Hawaii. Thinning intensity increases from left to right; the leftmost data points are unthinned controls.

all thinning treatments had significantly higher growth rates than the unthinned controls. After 14 months, mean diameter increment in the most intensive thinning treatment (residual density of 200 trees per hectare) was 15.1 mm/yr compared with 2.9 mm/yr in the control plots. Mean diameter increments of the less intensive thinning treatments (residual densities of 300, 400, 500, 700, and 900 trees per hectare) were similar to one another (11.2 to 12.9 mm/yr) and were significantly higher than the controls as well. Analyses of covariance showed that the initial size (DBH) of a tree was a significant and positive covariate, implying that larger trees responded better than smaller trees to the same level of thinning release. The thinning study at Honomalino also included a grass control treatment to determine whether removal of grass, which may compete for water and soil nutrients with the roots of overstory trees, would improve the thinning response of koa. Half of the plots at each thinning intensity were randomly selected to receive a grass-specific herbicide treatment at the beginning of the experiment and then repeated every 18 months, while the other half received no herbicide. Although early measurements suggested that grass control had no effect on koa's growth response to thinning, after about 1 year, a significantly positive response to grass control was detected in most of the thinning treatments.

Each of these thinning studies involved dense young stands of koa established rapidly after disturbance: fire (Scowcroft and Stein 1986), intentional scarification (Pearson and Vitousek 2001, Scowcroft et al. 2007), or logging (Baker et al. 2008). The initial rapid growth of the young koa was followed by canopy closure and a subsequent sharp decrease in growth rates at the stand and tree levels. Thinning the dense koa stands led to significant increases in individual tree growth in all sites and studies. Land managers who use disturbance, particularly mechanical soil scarification, to stimulate dense regeneration of koa must be aware of the implications regarding future silvicultural operations. The dense regeneration that often follows such operations will require one or more thinnings to maintain sufficient growing space for individual trees if slow growth and stagnation are to be avoided.

Fertilization

Key Points

- Fertilizing koa does not lead to increased growth in all situations. Results depend on soil fertility, the vigor of the trees in the stand, and the presence of competing vegetation. Trees whose parents were native to infertile soils seem more responsive to fertilization than trees from fertile sites.
- Liming, coupled with phosphorus fertilization, can lead to better koa nutrition and reduced chance of toxicity by aluminum and manganese.
- Application of fertilizer to dense stands in which tree growth has stagnated is ineffective in increasing growth rates of individual koa unless fertilization is accompanied by thinning, and even then a positive growth response is not guaranteed. In most cases, however, fertilizer additions to thinned stands further augment the positive effects of thinning.

Research indicates that the response of koa to fertilization is dependent upon provenance, soil type, and stand condition at the time of fertization. Fertilizer is commonly applied at the time of planting, a practice that may stem, in part at least, from the findings of Skolmen (1990). He reported that application of 50 g of 10-30-10 fertilizer to the soil surface around individual seedlings stimulated growth of both nursery-grown and naturally regenerated koa. The response was so marked that he suggested that fertilization could be used to control stand density and selection of future crop trees.

The highly weathered, acidic Oxisols and Ultisols typical of older Hawaiian landscapes are often deficient in available P and have a large capacity to fix applied P into insoluble forms. Scowcroft and Silva (2005), working on such soils on Oahu, found that P applications increased growth of seedlings produced from a local Oahu seed source, but not those from a more fertile site on Hawaii. As little as 150 kg P/ha was sufficient to significantly increase basal stem diameter and aboveground woody biomass, and at 600 kg P/ha, height, basal stem diameter, DBH, crown volume, branchiness, and wood biomass of koa were all significantly greater for fertilized trees.

Acidic tropical soils typically contain low concentrations of cations and high concentrations of manganese (Mn^{2+}) and aluminium (Al^{3+}) ions, which can be toxic to plants. Liming such soils can reduce metal toxicities and improve cation and P availability. Cole et al. (1996) planted koa from Hawaii in an Ultisol on Oahu and applied several treatments to mitigate growth-limiting soil factors: 8 Mg/ha lime, 143 kg/ha 14-14-14 plus micronutrients, 200 kg P/ha, and 77 kg potassium (K)/ha. Treatments raised soil pH from 4.3 to 5.6, increased availability of P and calcium (Ca), and reduced the concentration of extractable Al^{3+} and Al saturation. As a result, mean annual height increments of treated koa were more than double (2.2 m/yr vs. 0.9 m/yr) those of koa that received a single application of 143 kg/ha 14-14-14 plus micronutrients.

Fertilization does not inevitably result in a koa growth response. Scowcroft and Stein (1986) reported that relative basal area growth of stagnated 13-year-old koa on Maui was not significantly increased by application of 460 kg/ha of 10-30-10 fertilizer and 170 kg/ha of magnesium sulfate ($MgSO_4$). Contrary to expectations, there was no response even when fertilization was combined with thinning, probably owing to competitive uptake of applied nutrients by blackberry (*Rubus argutus*), an invasive species that increased in abundance and biomass following thinning and fertilizing. Furthermore, neither fertilization nor fertilization plus thinning increased tree resistance to defoliation by the koa looper (*Scotorythra paludicola*). Likewise, there was no evidence that fertilization improved growth of trees that survived defoliation. They concluded that the cost of fertilization was not justified at their study site.

Young, less-weathered soils on Hawaii do not have toxic concentrations of metal cations, but they may be deficient in nutrients needed to sustain tree growth beyond the establishment phase. Although koa fixes N, evidence suggests that N-fixation can decline to negligible levels within 20 years after stand establishment, possibly owing to a decline in P availability (Pearson and Vitousek 2001). To determine whether N availability was limiting growth of koa saplings, Pearson and Vitousek (2001) applied ammonium nitrate (NH_4NO_3) twice a year for 2 years at an annual rate of 70 kg N/ha to a 9-year-old stand at Keauhou Ranch, Hawaii. They found that fertilization did not affect DBH increment even though N-fixation had declined to low levels. Apparently, high soil inorganic N pools were sufficient to supply the N needs of koa trees, and adding more N did not enhance growth. This lack of response to fertilizer may have been because the stands were overstocked and growing slowly owing to intense competition for light, and therefore the trees had little capacity to use additional N. Declining P concentrations in foliage and roots of koa trees with increasing stand age also suggested that P fertilization might enhance growth, but P fertilization was not included in the study.

Pruning

Neither published studies nor anecdotal information are available on the effects of pruning on individual tree growth, form improvement, knot closure, wood quality, or economic costs and benefits. The sole research citation regarding pruning is from Skolmen et al. (1991), who described the results of a thinning experiment and noted that pruning of thinned trees was unnecessary to achieve branch-free boles.

Several studies have examined the influence of pruning on the closely related Australian congener, *Acacia melanoxylon* R. Br. ex Ait. f. (blackwood). Medhurst et al. (2003) examined the joint influences of thinning and pruning on growth and stem form of blackwood grown in mixed plantations with a *Pinus radiata* D. Don. nurse-crop. Pruning treatments included removal of 25 or 50 percent of the leaf area of individual trees, with branches selected for pruning to create the greatest improvement in stem form. Although the light pruning (25-percent removal) did not significantly reduce diameter increment of individual trees, the heavy pruning (50-percent removal) did. Nonetheless, pruned trees recovered to prepruning levels of leaf area within 2 months (25-percent removal) to 10 months (50-percent removal). In addition, although pruning reduced the number of apical leaders per tree and the number of branches >30 mm in diameter immediately following pruning, after 2 years there was little difference in form between the control and pruned trees. It should be noted that blackwood is more shade tolerant and appears to exert less apical dominance than koa. As a consequence, tree form in koa may be easier to maintain through mixed-species plantings and pruning.

Key Points

- There is little experience with pruning koa, but research with a related species was unsuccessful in producing long, branch-free boles.
- By taking advantage of koa’s high demand for light, judicious pruning, coupled with growing it in mixed-species stands, might be used to good advantage in influencing bole form.

Silvicultural Systems

Single-Cohort (Even-Age) System

Widespread conversion of koa forest to pasture in the past requires that most current landowners interested in growing koa focus their initial silvicultural efforts on reestablishing tree cover (fig. 40). Where a seed source is present, either in the soil seed bank or from surviving trees, soil scarification is the most widely applied

Key Points

- Lack of experience with full-rotation management of koa forests leaves us with little knowledge about the pros and cons of various silvicultural systems that might be applied to koa forests. Recommendations are based instead on knowledge of koa's biology and ecological requirements. There is no ”best” silvicultural system for koa: the choice depends upon a site's history and its quality, and especially upon the management objectives of the land steward.
- Management of even-aged koa stands will be the likely starting point for most koa forest management, primarily because of past deforestation. A key to successful management of such stands is maintenance of the proper number of trees per unit area, a factor that can be adjusted through planting density and thinning.
- As trees in even-aged stands approach maturity, the manager can plan for either a second even-aged rotation or through selective harvesting can convert a stand to two or more age classes depending on the number of harvests. The latter may be tempting for many reasons, but because koa is shade-intolerant and gap dynamics are poorly quantified, managers have little information on which to base decisions regarding harvesting intensity, the spatial distribution of harvests within a stand, and anticipated growth rates in different sized gaps.
- Where conservation objectives are a high priority, managers might strive for the structural complexity resulting from two age classes—an overstory of unharvested trees and an understory of regeneration. The difficulty is in identifying the right number of overstory trees to leave that will enable the younger koa beneath them to grow vigorously. Subsequent harvest of the older trees can damage the next-generation trees in the understory.
- Koa stands containing many age classes of trees produce a diversity of conditions, habitats, and products, but they are likely to be very difficult to establish and even harder to sustain. Individual-tree-selection harvests are unlikely to be successful because koa will not regenerate in the small gaps created, resulting in a forest that is eventually depleted of koa. A better approach might be to harvest clusters of trees and achieve koa regeneration in the patches created.

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Figure 40—A typical forest structure on many upland sites on Hawaii—isolated *Acacia koa* of poor form and health surrounded by open rangeland and scattered small ‘ō‘hia.

regeneration method. Scarification reduces competition from alien pasture grasses and exposes buried koa seeds to conditions that stimulate their germination. Where a seed source no longer exists, planting or seeding is required. In both cases, the result is a stand of koa trees that are all approximately the same age (i.e., single-age cohort). Because postscarification regeneration is typically very dense and the koa are directly competing for the same set of resources, the primary silvicultural concern for such stands is controlling stand stocking levels. Koa in overstocked stands grow slowly, which not only increases the time required to reach merchantable size, but also increases susceptibility to insects and pathogens and leads to higher mortality rates.

Several approaches, each with associated tradeoffs, can be used to control stocking levels over the course of stand development in single-cohort stands. In sites where koa is planted, initial planting density will have important consequences for intertree competition for resources and thus individual tree growth. For example, if competing vegetation is controlled, wide spacing results in faster growth of koa for longer periods than narrow spacing. Nevertheless, wide initial spacing can lead to poor bole form, such as multiple trunks or large lateral branches, which may require costly prunings if timber production is the objective. Interplanting koa with other tree species that have similar initial growth rates but whose growth rates slow later in development (e.g., naio, māmaki (*Pipturus albidus*), ʻōlapa, ʻaʻaliʻi (*Dodonaea viscosa*) is another potential method, albeit untested, of controlling initial koa stocking levels. Although overall planting densities may be relatively high, koa density within the mixed-species stand may be relatively low. The non-koa species would provide side-shade for the koa to help maintain good form without directly competing for growing space in the main canopy. A current barrier to this approach is the difficulty and expense of obtaining sufficient planting stock of non-koa species and the lack of experience in applying the mixed-species planting system.

Using mechanical scarification to regenerate stands of koa has the benefit of producing a substantial germination response, but often leads to overstocked stands or a patchy distribution of regeneration, or both. Where postscarification density is high, individual trees will grow rapidly until crown closure, after which tree growth will decline and self-thinning will increase mortality of the smallest trees. To ensure that growth does not slow appreciably, managers will almost certainly have to thin, both precommercially and commercially. Where postscarification regeneration occurs in a mosaic of dense and sparse patches, managers may choose to maintain this variability as a source of future heterogeneity in stand structure or they may prefer to thin the dense patches to achieve a more uniform distribution of stem density across the stand.

Because upland Hawaiian landscapes have been largely deforested over the past century, most silvicultural systems incorporating koa will initially follow the single-cohort stand development pattern. As trees in the stand reach maturity, different harvesting patterns can be applied either to maintain the single-cohort stand or to shift the stand to a multiple-age-cohort stand. Maintaining a single-cohort silvicultural system requires harvesting all of the trees in a stand, either all at once (i.e., a clearcut) or in two or three stages (i.e., a shelterwood). The timing of the final harvest for a koa stand will be determined by the growth rate of the trees, the potential value of the harvested wood, the condition of other stands in the forest, and the landowner's management objectives. There is considerable interest, particulary within the conservation community, in creating multiple-age-cohort stands in native forest. This is due in part to a recognition that structurally complex native forests are rare across the Hawaiian landscape and in part to a desire for alternatives to even-age forest management systems. Although uneven-age management may be possible for koa forests, it is important to emphasize that the ecology of koa is not readily conducive to such stands except in specific circumstances. Mueller-Dombois et al. (1981) described the structure of the Kilauea Forest, Hawaii, which had a wide range of tree sizes (5 to 180 cm DBH), but little regeneration (100 seedlings per hectare and only 1 sapling [1 to 2 m tall] per hectare). Because koa is extremely shade-intolerant, silvicultural operations that retain a proportion of the forest canopy either as individuals or groups of koa trees will reduce the amount of light available to the koa regeneration. This will have several negative impacts on koa seedling and sapling development. It will reduce growth rates, increase mortality rates, and lead to poorer stem form, which reduces the merchantable value of the koa wood. If only a few scattered overstory trees are retained, these negative impacts may be limited to small-scale variation in size and growth rates of the subsequent age cohort of koa trees. Although this will diminish future economic returns from the stand, it may augment its conservation value by increasing structural diversity within the stand. However, as more of the canopy is retained, its detrimental influence on the koa regeneration and future economic returns will increase substantially. We discuss these issues in greater detail below in the multiple-age-cohort silviculture section, but, in general, attempts to convert single-age cohort stands to multiple-age-cohort stands should be approached with extreme caution.

Seed Tree and Shelterwood Systems

The seed tree and shelterwood silvicultural systems are single-age-cohort systems that retain some or all of the trees in the stand for a period at the end of the rotation to ensure sufficient regeneration success of the next age cohort. The difference between the seed-tree system and shelterwood system is one of degree (Smith 1986). Seed-tree systems retain fewer residual trees than shelterwood trees. In the seed-tree system, the number of trees retained is small enough that the microclimatic conditions at the soil surface are not different from a clearcut site (Smith 1986). For koa, the seed-tree system is probably unnecessary in terms of providing a seed source for the subsequent age cohort. Because koa reproduces prolifically from a young age and has seeds that are poorly dispersed but that can survive for many years in the soil seed bank, seed trees are unlikely to contribute much more to the regenerative capacity of the stand. Nonetheless, the seed-tree system may provide a measure of structural heterogeneity in the subsequent stand as the seed trees continue to grow, providing valuable high-quality wood and large trees for foraging and nesting habitat of native bird species.

Shelterwood systems are conceptually similar to the seed-tree system. At the end of the rotation, a certain number of trees are retained to provide an adequate seed source, but, more importantly, to provide a degree of shading for the subsequent regeneration (fig. 41). The advantages and disadvantages are similar. Retaining some of the large trees in a stand provides structural heterogeneity within the stand, which may have important conservation values for native plants and animals.

Roger Skolmen

Figure 41—Abundant *Acacia koa* regeneration below a shelterwood treatment in which a portion of the canopy trees were retained during an early 1980s harvest at Kamehameha School's Hōnaunau tract.

In addition, higher levels of shade at the forest floor may be conducive to establishment of native understory plant species. If the residual trees have healthy crowns and good form, the increased growth created by removal of most neighbors may add significant economic value to the trees over the following years or decades. Depending on the effects of the residual canopy trees on growth and survival of the koa regeneration, removal of the shelterwood could proceed in one or more steps over a few years or decades. One challenge in applying shelterwood systems to koa stands is deciding the appropriate residual density to ensure sufficient growth and survival of the shade-intolerant koa regeneration. If too many trees are retained, the shelterwood will reduce growth and increase mortality of the koa regeneration. A second challenge is proper planning of the subsequent extraction of residual trees to minimize damage to the younger age cohort. And whereas a dense shelterwood is unlikely to lead to successful recruitment of a new age cohort of koa trees, it might be a useful silvicultural system for reestablishing other native tree species that are more shade-tolerant than koa.

Because silvicultural systems that retain a portion of the overstory have not been applied through a complete harvest cycle to koa stands, the number and distribution of koa trees to be retained is not well known. Mortality rates of large koa trees and the likelihood of seeds producing successful seedlings are also poorly known. More than 15 percent of the large, single-stemmed, cavity-bearing ‘ō‘hia and koa that were used for nesting by the endangered ākepa fell over in a 7-year period in the Pua ‘Ākala section of Hakalau Forest NWR (Freed 2001). The damage was attributed to high winds that can exceed 145 km/hr during winter storms. The presence of relict trees in pastures suggests that koa trees are capable of surviving as single trees in exposed areas for many decades.

Multiple-Cohort (Uneven-Age) Systems

Silvicultural systems that create multiple age cohorts can produce diverse stand conditions, habitat features, and wood products, but are complex to apply, maintain, and manage. Multiple-cohort systems are commonly used when management objectives require that a stand always include some large trees (Smith 1986). Selection systems are commonly used to create or maintain multiple-cohort stands. In selection systems, individual trees or groups of trees are selected for harvest at short intervals. Typically, individual tree selection is used for shade-tolerant species that can establish and grow in small forest gaps. Although Pejchar et al. (2005) recommend individual tree selection be applied to koa stands, the outcome would likely be a population of slow-growing seedlings and saplings, few, if any, large trees, and a stand of little economic value.

Group-selection systems, which create larger canopy openings, would allow higher growth rates among koa seedlings and saplings. There are no data on the minimum gap size required for a koa seedling to establish and grow to canopy height without sacrificing growth rate. Small group harvests might be applied where good tree form is a primary management objective: for example, if koa trees were being grown for canoe logs. If group-selection harvests are large enough, the microclimatic conditions at the center of the canopy opening will eventually approach those of a clearcut. At some point a group selection harvest can justifiably be called a patch clearcut. Land managers interested in creating structural diversity within stands while maintaining reasonable growth rates of individual koa trees may find that a group-selection system that harvests large groups of trees may provide a reasonable balance of conservation values and economic returns. However, because most koa stands are currently single-cohort stands, lost opportunity costs associated with conversion to multiple-cohort stands may be significant and need to be considered.

Group-selection harvests typically create a small patch opening in the forest canopy; they may also be applied as linear strips through the forest. Whitesell’s

(1976) study of koa directly seeded into two narrow strips (1.8 m and 3.7 m wide) created in koa-ʻōʻhia forest at the Waiakea Forest Reserve demonstrate the challenges of group selection. The wider strip was bulldozed, which would have an effect on the amount of forest canopy removed similar to that of a very light group-selection harvest. Survival, growth, and tree form were all poor for koa in the strip and illustrate the difficulty of establishing koa in small canopy openings. Strips that are oriented along an east-west axis to maximize solar irradiance within the strip and strips that are much wider than 3.7 m would likely produce better results. Research on the minimum size, orientation, and shape of group-selection harvests required to regenerate koa successfully are needed.

Utilization

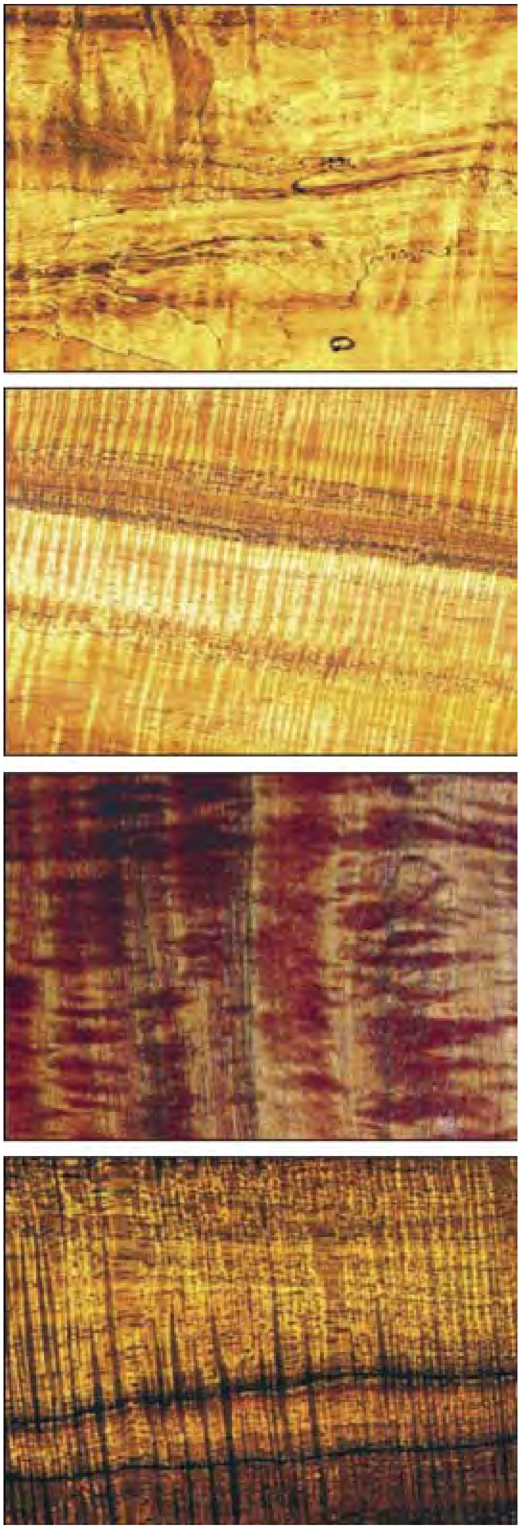
Koa is one of the most valuable hardwoods in the world. In 2006, most koa sold for $5 to $15 per board foot, and high-quality slabs were sold for as much as $125 per board foot. The price of individual pieces is determined by the color and figure (or grain) of the heartwood. The color and grain of koa vary considerably within and among individual trees (fig. 42).

Color ranges from blond to dark red, and the grain varies from plain to highly figured (“curly”). The most highly prized (and valued) koa is a rich dark red and has a dramatic curly grain. Environment, physical stress, and genetics likely influence the presence of curl in koa trees, although the relative contribution of each is unknown.

Historically, koa wood was used for ocean-going canoes, surfboards, spear handles, and ukuleles. It also served as the wood of Hawaiian royalty, being used for everything that the royal family came into contact with, such as steps and floors. Currently, koa wood is used for a wide variety of decorative woodworking (fig. 43), cabinetry, furniture (fig. 44), and musical instruments. Gerry (1955) reported on the working qualities of koa, noting that the wood is moderately heavy (specific gravity 0.55 to 0.87) and that it dries well, without splitting or cupping. However, koa is moderately brittle, and internal variations in wood density and hardness can make it difficult to work. It is difficult to plane, although it carves well and polishes to a high finish (Gerry 1955). Koa heartwood is resistant to insects and fungi, but its sapwood is susceptible to boring beetles.

Key Points

- A wood of extremely high value, koa is priced primarily by its color and figure (grain). Both environment and genetics apparently influence those traits, but to unknown degrees.
- Koa has a great variety of historical uses. Today most koa is converted into products of high added value, such as furniture, cabinetry, and musical instruments, although even smaller dimension material is widely used for picture frames and novelties.
- A factor that complicates koa forest management is the well-established tradition of using wood from large-diameter trees. This practice provides few markets for the smaller material that would be produced during thinnings.



Niklos Dudley

Figure 42—Variation in wood color and grain of *Acacia koa* wood.

Tai Lake

Figure 43—A bowl made from *Acacia koa*. The color and figure of the koa wood contribute to the high value of such decorative pieces.

Tai Lake

Figure 44—A trestle table made from a large slab of *Acacia koa*.

Most loggers and millworkers currently require a minimum merchantable tree size of 30 cm DBH (fig. 45). The rationale for that size limit is that the sapwood has little value because it is subject to attack by boring beetles and fungal stains and that the center cant of the log (15 by 15 cm) has little value because it is structurally unsound and cannot bear weight (Gomes 2002). Anecdotal information suggests that smaller material could be used, particularly for detailed decorative work such as framing, bowl turning, and souvenirs, although economic analyses on the profitability of such schemes are lacking.

Mel Johannson

Figure 45—A board cut from a 25-year-old second-growth *Acacia koa* about 30 cm DBH that was harvested in a thinning operation. Note the distinct sapwood-heartwood boundary and the fungal staining of the sapwood.

Tree Improvement

Key Points

- Genetic selection of koa might lead to improvements in tree form, wood color and figure, reduced susceptibility to insects and disease, enhanced water-use efficiency, and greater tolerance to poor soils.
- Koa can be cloned through tissue culture and reproduced vegetatively by air layering and rooting cuttings, but success has been mixed, and the procedures are costly.
- At least 500 accessions of koa seed have been made. Common garden trials, containing seedlings from individual trees representative of particular zones, are underway at three locations and should provide insight on the degree to which genetics and environment influence the growth of koa.

Brewbaker (1997) stated that tree improvement by genetic selection is indispensable to the future of koa forestry. He listed a number of wild traits that might be amenable to genetic improvement, including poor form (limbiness and fluting), pale wood color and absence of figured grain, susceptibility to insects and diseases, low water-use efficiency, and intolerance of low soil P. Previous studies indicate a high degree of genetic diversity in koa, which is a necessary requirement for successful breeding efforts. Conkle (1997) determined that heterozygosity (a measure of genetic diversity with larger numbers denoting greater diversity) was 0.41 for koa. In comparison, expected heterozygosity ranged from 0.11 to 0.37 for tropical angiosperms, 0 to 0.50 for conifers, and 0.12 to 0.27 for Australian *Eucalyptus* spp. (Ledig 1986). Brewbaker (1997) also noted that genetic variation is much greater within each island than among islands but that there is a high degree of self-fertilization, and hence greater genetic uniformity, within local koa populations (families). Thus, breeding efforts focused on within-island populations might generate the greatest benefits initially.

The ability to produce genetically identical plants is useful for tree improvement work, especially where propagation of superior growth form, disease and insect resistance, and wood color and grain are desired (Glover et al. 1991). Various vegetative techniques, including grafting, air layering, rooting of cuttings and root suckers, and tissue culture, have been tried with koa with varying degrees of success. Skolmen (1978) reported moderate success using air layering and rooting of cuttings to produce plants for outplanting, but grafting failed.

Recently, however, koa seedlings at the second true leaf stage of development have been successfully grafted to *A. confusa* Merr. and *A. mangium* Willd. root stocks (Nelson 2006). Tissue culture techniques have been used successfully to produce plantable koa trees (Skolmen 1977, 1986; Skolmen and Mapes 1976, 1978), but the techniques were labor-intensive and not suitable for mass propagation. Nagai and Ibrahim (1997) attempted to build on this earlier work but had limited success in getting shoot multiplication and rooting in culture medium from shoot and young phyllode tissue.

Glover et al. (1991) outlined a five-step strategy for genetic improvement of koa. The first task was delineation of seed zones for all islands. Specific koa genotypes would be identified for use throughout each zone. This has not been done. The next task was seed collection from at least 25 trees per zone. Sun et al. (1997) reported that approximately 400 koa accessions had been collected and documented from Hawaii, Maui, Oahu, and Kauai. Another 100 accessions had been added by 2004. Evaluation of genetic variability within and between koa populations was considered an important step, with isozyme analyses proposed as the primary tool. Clonal trials across a range of habitats were identified as essential for evaluating heritability and genotype/environment interactions, but no such work has been done, perhaps owing to the difficulty of producing clonal planting stock. Additional common-garden studies using seed from single trees within a seed zone (provenance and family) were recommended to further examine genetic/environment interactions. Such studies have been installed at the Hāmākua Agriculture Experiment Station on windward Mauna Kea (Sun 1996, Sun et al. 1997), at the Waiawa Community Correctional Center in central Oahu (Conrad et al. 1996), and at the Hawaii Agriculture Research Center's Maunawili station located on windward Oahu (Daehler et al. 1999). Initial results indicate that the genetic variances account for 32 to 70 percent of total phenotypic variance in DBH at age 4 years (Shi and Brewbaker 2004). Although 90 percent of families were assessed as ”genetic junk” (Brewbaker 1997), superior families were identified from all islands. Additional work at the experimental sites is being hampered by high mortality caused by koa wilt disease.

Chapter 5: Future Research Directions

Koa has long been an important part of Hawaii's environment, culture, and more recently its economy. As such, there is a substantial body of anecdotal information pertaining to its ecology, management, and utilization. In some cases anecdotal evidence is supported by research; in some cases it is not. In writing this report we have attempted to synthesize the available data on the ecology and silviculture of *Acacia koa* to disentangle fact and myth. In so doing, we have examined a wide range of data including research papers published in peer-reviewed journals, unpublished reports, and data sets that have been languishing unanalyzed for decades. In some cases, such as the physiological ecology of koa, multiple independent studies provide a clear consensus on most attributes. In other cases, such as silvicultural systems for koa, there has been almost no research. In this final section, we highlight what we believe to be the major gaps in our current knowledge of the ecology and silviculture of *Acacia koa*. As we mentioned in the preface, this is a necessarily subjective list. The authors each have their own research interests and experiences. However, we have tried to make the list as complete as possible, although we make no assertion that it is a full accounting of the knowledge gaps that exist. We have, however, organized this list as a set of priorities beginning with what we believe are the most important to address for koa silviculture to become a viable and widely used option for land managers.

Research Priority 1: Develop a Better Understanding of Koa Growth, Yield, and Form

Landowners interested in koa silviculture will need to invest substantial funds in site preparation, purchase and planting of seedlings if necessary, and tending operations such as thinning and pruning before the trees can be harvested. However, without reliable information on growth and yield, there is considerable uncertainty about the future returns from koa silviculture. This uncertainty is a substantial deterrent to investment in and adoption of koa silviculture (Goldstein et al. 2006, Pejchar and Press 2006). It also limits landowners' abilities to make informed decisions about which silvicultural strategy to pursue. There are three major sources of uncertainty regarding future koa yield. The first is growth form. There are many planted koa forests, and to our knowledge, most koa trees growing in plantations have poor form; that is, the trees have multistemmed trunks or sinuous boles, or both. This greatly reduces the future merchantability and value by lowering the log grade and utilization capability. For koa silviculture to be viable it will be critical to identify the causes of poor form. Is it herbivory from feral ungulates or insects, site quality, genetics, stand composition, or some combination of these factors? The second source of uncertainty is the yield of merchantable timber from a koa tree in terms of both volume and wood quality. How much wood is likely to be high-value, curly koa, and how much low-value, pale koa. Is wood quality primarily an intrinsic genetic trait and therefore heritable or is it influenced by environment conditions or growth rates? Because the answers to these questions may amount to many thousands of dollars difference in the value of individual stems, it will be of great practical value to have better data on koa growth and yield, as well as wood quality. The third source of uncertainty is the growth rate of koa. In particular, how much koa wood can be grown on a given site? Only a few permanent forest inventory plots in koa forest have been monitored for more than a couple of years (Constantinides 2004). Koa stocking guidelines developed by Baker and Scowcroft (2005) indicate that windward sites can support nearly twice as many trees of a given DBH as can leeward sites. Rainfall, soil type, and elevation are all known to influence the productive capacity of koa stands (Ares and Fownes 1999, Harrington et al. 1995, Idol et al. 2007). Developing a model to predict the potential growth and yield as a function of site variables such as mean annual rainfall, substrate age, soil fertility, and elevation would substantially reduce the uncertainty associated with initiating koa silviculture.

Research Priority 2: Develop a Better Understanding of the Growth Dynamics of Mixed-Species Stands

Mixed-species forests offer a range of potential benefits for landowners from increased conservation value to better tree form. There are also potential costs, in particular the reduced koa harvest. There is almost no research on koa performance when grown with other tree species whether native or nonnative (although see Ares and Fownes 2001 for koa/tropical ash mixtures) (see app. B for scientific and common plant names). For landowners interested in including an element of conservation in their forest management plans, a mixture of koa and other native tree species, particularly ‘ō‘hia , may provide valuable habitat for endemic forest birds while still allowing some financial gains from the koa. For landowners interested in financial returns, growing koa in mixtures with other valuable tropical hardwoods such as *Toona ciliata* would provide a more diversified range of future timber and buffer against potential market fluctuations for any one timber species. There are many questions that need to be answered before landowners can begin to explore mixed-species koa silviculture with confidence. For example, which species can be grown with koa? What spacings are required to avoid suppression of the koa? Can interplanting with other species reduce the incidence of poor stem form in koa? How do different plant and bird species respond to different species mixtures? How does establishing a koa canopy in deforested landscapes affect resource availability for growth of understory vegetation, and can management action accelerate establishment of native plant species? In the case of tropical ash (*Fraxinus uhdei*), there are also risks associated with its potential as an invasive weed species. Research to explore the range of potential species mixtures, the productive capacity of those mixtures, and the effects of tree-species mixtures on associated biodiversity is sorely needed.

Research Priority 3: Develop a Better Understanding of the Effects of a Range of Silvicultural Practices

We have little experience of sustainable management of koa forests and few examples of the long-term effects of different silvicultural systems on koa forests. Although koa regenerates prolifically from buried seed banks after fire or logging clears large areas (Grace 1995, Scowcroft and Wood 1976), little is known about regeneration of koa in natural treefall gaps. How large a gap or strip in the forest canopy is required for koa to regenerate successfully? The lack of knowledge and experience with koa silviculture limits the ability of landowners to plan silvicultural operations in the present to meet silvicultural goals in the future, be they financial, aesthetic, or conservation-oriented. Several studies on thinning in regrowth koa stands were recently established, and the results from these will help guide intermediate silvicultural operations; however, long-term planning for regeneration harvests is still difficult. The use of livestock to thin dense stands of koa has been tried with some success (Lake 2003), but controlled experiments are needed to further evaluate grazing as a silvicultural tool to control stand density. Silvicultural practices affect growth and yield, the biota associated with the forest, the ecology of the forest, and financial returns from the forest. Long-term studies that examine the full range of silvicultural operations, from establishment to thinning to harvesting, are critical to promoting koa silviculture across the Hawaiian Islands.

Research Priority 4: Develop a Better Understanding of Ecological Processes

Although some aspects of the ecology of koa forests are moderately well-documented there are still questions relevant to forest management that remain unanswered. Better knowledge of root growth during stand development would improve understanding of the mechanisms of intra- and interspecific belowground competition and vegetation responses to silvicultural treatments. The role of coarse woody debris, which hosts ecologically important invertebrates and micro-organisms and is known to play important roles in plant regeneration, nutrition, and fire diversion in other forests, is poorly known in koa forests. The impact of insects and pathogens on koa forests is poorly understood. Recently, koa wilt, which is associated with the vascular wilt fungus *Fusarium* (Anderson et al. 2001, Gardner 1980), has caused significant mortality in some koa plantations. It is still unknown which pathogen or combination of pathogens causes the disease and whether these are native or alien to Hawaii. The severity and future course of the disease is also unknown. Mapping the extent of the disease and discovering environmental limits, if any, would help foresters asses the risk the disease poses to the health of the native forest. Finally, the influence of stand structure, composition, restoration, and silvicultural practices on the hydrology of koa forests is unknown, despite the fact that fresh water for human use is perhaps the koa forest product of most direct relevance to society.

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English Equivalents

When you know:	Multiply by:	To find:
Millimeters (mm)	0.0394	Inches (in)
Centimeters (cm)	0.394	Inches
Square centimeters (cm^2)	0.155	Square inches (in^2)
Meters (m)	3.28	Feet (ft)
Kilometers (km)	0.621	Miles
Square kilometers (km^2)	0.386	Square miles
Hectares (ha)	2.47	Acres (ac)
Grams (g)	0.0022	Pounds (lb)
Kilograms (kg)	2.205	Pounds
Megagrams (Mg)	1.102	Tons (t)
Kilograms per hectare (kg/ha)	0.893	Pounds per acre
Megagrams per hectare (Mg/ha)	0.446	Tons per acre
Square meters per hectare (m^2/ha)	4.37	Square feet per acre
Megajoules (Mj)	948,000	BTU
Trees per hectare	0.405	Trees per acre
Cubic meters (m^3)	416.7	Board feet (bf)

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Appendix A: Descriptions of Primary Koa Research Sites

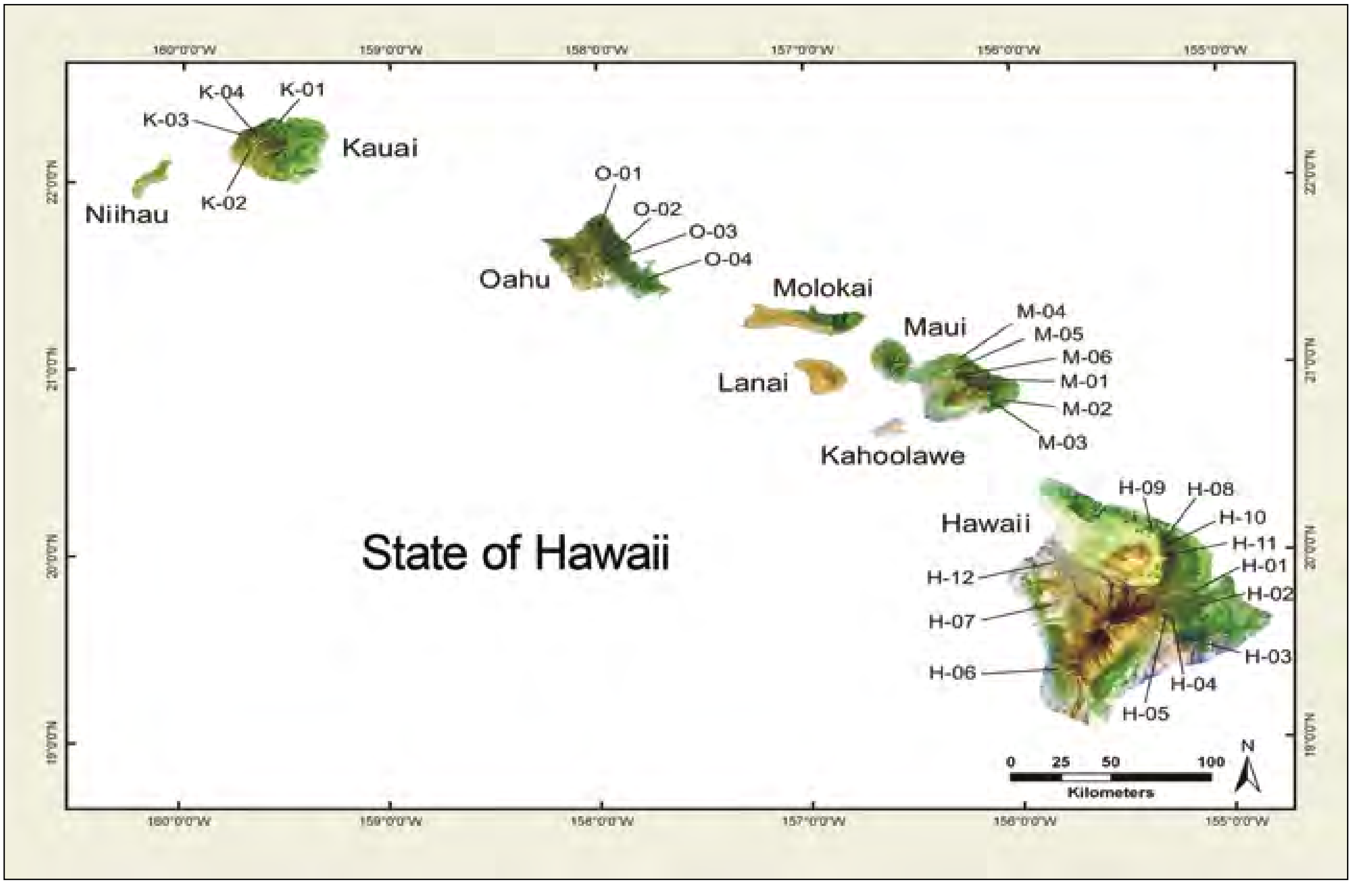

Figure 46—Primary locations of *Acacia koa*-related research across the Hawaiian Islands. Details of each site are found in table 7. (Map courtesy of Greg Asner.)

Table 7—Description of areas where field research in koa forests has taken place

Site ID[a]	Approximate latitude, longitude	Locale[b]	Ownership[c]	Soil order	Type of forest
H-01	19°45′N, 155°15′W	Kulani	DLNR	Andisol	Wet lowland ‘ō‘hia-koa, natural, primary
H-02	19°35′N, 155°12′W	Waiākea FR	DLNR	Histosol	Wet montane koa-‘ō‘hia, natural, secondary
H-03	19°27′N, 155°19′W	Hawaii Volcanoes NP	NPS	Histosol/Andisols	Mesic montane koa/koa-‘ō‘hia, natural/planted, primary/secondary
H-04	19°31′N, 155°18′W	Kilauea Forest	KS	Andisol	Wet montane koa-‘ō‘hia, natural, primary
H-05	19°31′N, 155°19′W	Keauhou Ranch	KS	Andisol	Wet montane koa-‘ō‘hia, natural, secondary
H-06	19°12′N, 155°48′W	Honomalino	TNC	Histosol	Mesic montane koa/koa-‘ō‘hia, natural, primary/secondary
H-07	19°27′N, 155°49′W	Hōnaunau Forest	KS	Histosol/Andisols	Wet montane koa-‘ō‘hia, natural, secondary
H-08	19°56′N, 155°20′W	Humu‘ula FR	DLNR	Andisol	Mesic montane koa/koa-‘ō‘hia, natural, primary/secondary
H-09	20°00′N, 155°23′W	Hamakua Experiment Station	UH	Andisol	Wet lowland koa-‘ō‘hia, planted, secondary
H-10	19°55′W, 155°18′W	Laupāhoehoe FR	DLNR	Andisol	Mesic montane koa-‘ō‘hia/wet ‘ō‘hia-koa, natural, primary/secondary
H-11	19°49′N, 155°19′W	Hakalau Forest NWR	FWS	Andisol	Mesic montane koa/wet koa-‘ ō‘hia, natural/planted, primary/secondary
H-12	19°44′N, 155°52′W	Pu‘uWa‘awa‘a	DLNR	Histosol	Mesic montane koa-‘ō‘hia forest, natural, primary/secondary
M-01	20°49′N, 155°16′W	Makawao FR	DLNR	Andisol	Mesic lowland koa-‘ō‘hia, natural, secondary
M-02	20°41′N, 155°5′W	Kīpahulu Valley	NPS	Andisol	Wet lowland/montane koa-‘ō‘hia, natural, primary
M-03	20°41′N, 155°8′W	Kīpahulu FR	DLNR	Andisol	Mesic montane koa/koa-‘ō‘hia, natural, primary/secondary
M-04	20°54′N, 156°18′W	Kuiaha	Private	Ultisol	Mesic lowland diverse forest, planted, secondary
M-05	20°50′N, 156°17′W	Makawao	UH	Ultisol	Mesic lowland koa-‘ō‘hia forest, planted, secondary
M-06	20°48′N, 156°17′W	Olinda	DLNR	Andisol	Mesic lowland koa-‘ō‘hia forest, planted, secondary
O-01	21°36′N, 155°50′W	Kawailoa FR, Training Area	US Army	Oxisol	Mesic lowland koa-‘ō‘hia, natural, primary/secondary
O-02	21°29′N, 155°56′W	‘Ewa FR	US Army	Oxisol	Mesic lowland koa-‘ō‘hia, natural, primary/secondary
O-03	21°30′N, 155°50′W	Waiawa Correctional Facility	DPS	Oxisol/Ultisols	Mesic lowland koa, planted, secondary
O-04	21°21′W, 155°46′W	Maunawili Experiment Station	HARC	Oxisols/Ultisol	Mesic lowland mixed species, natural/planted, primary/secondary
K-01	22°11′W, 155°29′W	Hanalei	DLNR	Inceptisol	Wet lowland mixed species, natural, primary/secondary
K-02	22°4′N, 155°41′W	Pu‘u Ka Pele FR	DLNR	Oxisol	Dry to mesic lowland koa, natural, primary
K-03	22°7′N, 155°43′W	Nā Pali Kona FR	DLNR	Oxisol	Dry lowland koa, natural, primary
K-04	22°7′N, 159°39′W	Kōke‘e State Park	DLNR	Andisol	Mesic lowland diverse, natural, primary/secondary

Map locations for each of these sites are shown in fig. 46 by Site ID.

[a] The letter in the site ID denotes the island name: H, Hawaii; M, Maui; O, Oahu; and K, Kauai.

[b] FR, Forest Reserve; NP, National Park; NWR, National Wildlife Refuge.

[c] DLNR, Hawaii Department of Land and Natural Resources; DPS, Hawaii Department of Public Safety; FWS, U.S. Fish and Wildlife Service; NPS, National Park Service; HARC, Hawaii Agriculture Research Center; KS, Kamehameha Schools; UH, University of Hawaii.

Appendix B: Common Native and Introduced Plants Associated With Koa

Table 8—Common native and introduced plants growing in forest types where *Acacia koa* is the dominant or codominant canopy tree species

		Lowland[a]			**Montane[a]**			
Species	**Common name**	**DK**	**MK**	**WK/O**	**DK/M**	**MK/O**	**MK/O/A**	**WK/O**
Native								
Trees:								
Charpentiera obovata Gaud.	pāpala		*				*	
Cheirodendron trigynum (Gaud.) A. Heller	ʻōlapa			*		*		*
Cheirodendron spp. Nutt. ex Seem.	ʻōlapa		*	*				
Coprosma spp. J.R. Forster & G. Forster	pilo		*	*		*	*	*
Diospyros spp. L.	lama		*					
Hedyotis hillebrandii W.L. Wagner & Herbst	manono			*		*		*
Hedyotis terminalis W.L. Wagner & Herbst	manono					*		
Ilex anomala Hook. & Arnott	kāwaʻu			*		*		*
Metrosideros polymorpha Gaud.	ʻōʻhia	*	*	*		*	*	*
Metrosideros spp. Banks ex Gaertn.			*	*		*		
Myoporum sandwicense A. Gray	naio					*	*	*
Myrsine lessertiana DC	kōlea		*			*	*	*
Myrsine spp. L.			*					
Pelea clusiifolia A. Gray	alani	*	*	*		*	*	*
Pipturus albida (Hook. & Arnott) A. Gray	mamaki			*			*	*
Pittosporum spp. Banks ex. Gaertn.	hōʻawa					*	*	
Platydesma spp. H. Mann	pilo kea			*				
Psychotria spp. L.	kōpiko		*	*		*	*	*
Santalum freycinetianum Gaud.	ʻiliahi	*	*			*		
Sapindus saponaria L.	mānele		*				*	
Sophora chrysophylla (Salisb.) Seem.	māmane				*	*	*	
Shrubs:								
Broussaisia arguta Gaud.	kanawao		*	*				*
Clermontia spp. Gaud.	ʻoha		*	*				*
Dodonaea viscosa Jacq.	ʻaʻaliʻi	*	*		*	*	*	
Dubautia plantaginea Gaud.	naʻenaʻe			*				
Embelia pacifica Hillebr.	kilioe							*
Osteomeles anthyllidiflolia (Sm.) Lindl.	ʻūlei	*						
Rubus hawaiiensis A. Gray	ʻākala, Hawaiian raspberry			*		*		*
Rumex giganteus W.T. Aiton	pawale, uhauhako							*
Scaevola spp. L.	naupaka	*	*	*				
Styphelia tameiameiae (Cham. & Schlectend.) F. v. Muell.	pūkiawe	*	*		*	*		
Vaccinium spp. L.	ʻohelo			*	*			*
Lianas:								
Alyxia olivaeformis Gaud.	maile		*	*		*		*
Freycinetia arborea Gaud.	ʻieʻie		*			*		
Smilax melastomifolia Sm.	hoi kuahiwi							*
Stenogyne spp. Benth.				*		*		*
Herbs:								
Peperomia spp. Ruiz & Pav.	ʻalaʻala wai nui		*	*		*	*	*
Ranunculus hawaiiensis A. Gray						*		

Table 8—Common native and introduced plants growing in forest types where *Acacia koa* is the dominant or codominant canopy tree species (continued)

		Lowland[a]			Montane[a]			
Species	**Common name**	**DK**	**MK**	**WK/O**	**DK/M**	**MK/O**	**MK/O/A**	**WK/O**
Ferns:								
Cibotium chamissoi Kaulf.	hāpuʻu pulu		*	*		*		*
Cibotium glaucum Hook. & Arnott	hāpuʻu		*	*		*		*
Cibotium menziesii Hook.	hāpuʻu ʻiʻi		*					*
Dicranopteris linearis (N.L. Burm.) Underw.	uluhe		*	*		*		*
Diplazium sandwichianum (K. Presl) Diels	pohole, hoio		*	*		*		*
Dryopteris wallichiana (Spreng.) Hyl.	laukahi		*	*		*		*
Pteridium aquilinum (L.) Kuhn	kīlau, bracken fern		*	*	*	*	*	*
Sadleria cyatheoides Kaufl.	ʻamaʻu					*	*	
Grasses:								
Deschampsia nubigena Hillebr.	hairgrass				*			
Eragrostis sp. von Wolf	lovegrass				*	*		
Panicum tenuifolium Hook. & Arn.	mountain pili				*	*		
Introduced								
Trees:								
Falcataria moluccana (Miquel) Barneby &Grimes	albizzia			*				
Fraxinus uhdei (Wenzig) Lingelsh.	tropical ash		*	*		*		
Leucaena leucocephala	koa haole	*	*					
Psidium cattleianum Sabine	strawberry guava	*	*			*		
Schinus terebinthifolius Raddi	Christmas berry	*	*					
Toona ciliata F. Roehm.	toon			*		*		
Shrubs:								
Ageratina adenophora (Spreng.) King & H.E. Robins.	Maui pamakani		*			*		
Ageratina riparia (Regel) King & H.E. Robins	Hamakua pamakani		*			*		*
Clidemia hirta (L.) D. Don	Koster's curse		*			*		*
Lantana camara L.	lanakana	*	*					
Rubus argutus Link	blackberry		*			*	*	*
Lianas:								
Passiflora tarminiana Coppens & V.E. Barney	banana poka	*	*			*		*
Grasses:								
Andropogon virginicus L.	broomsedge		*			*		*
Anthoxanthum odoratum L.	sweet vernalgrass					*		*
Axonopus fissifolius (Raddi) Kuhlm.	narrow-leaved carpetgrass			*		*		*
Ehrharta stipoides Labill.	meadow ricegrass				*	*		*
Holcus lanatus L.	velvet grass				*	*	*	
Melinis minutiflora P. Beauv.	molasses grass	*	*			*		
Paspalum conjugatum Bergius	hilo grass		*			*		
Pennisetum clandestinum Hochst. ex Chiov.	kikuyu grass				*	*	*	*
Pennisetum setaceum (Forsk.) Chiov.	fountain grass				*	*	*	*
Schizachyrium condensatum (Kunth) Nees	bush beardgrass	*	*			*		

Source: Vegetation types and species found within them are based on Gagné and Cuddihy (1990). Lowland, 15 to 2000 m elevation; montane, 500 to 2700 m elevation; dry, <1200 mm annual rainfall; mesic, 1200 to 2500 mm; wet >2500 mm.

[a] DK = dry koa forest; MK = mesic koa forest; WK/O = wet koa/ʻōʻhia forest; DK/M = dry koa/māmane forest; MK/O = mesic koa/ʻōʻhia forest; MK/O/A = mesic koa/ ʻōʻhia/aʻe forest.

Appendix C: Birds Associated With Koa Forests

Table 9—Endemic forest and woodland birds that are found in forests where *Acacia koa* is a canopy dominant or in mixed and diverse forests where it is an associate, except for the islands of Kaho‘olawe and Ni‘ihau

Island	Scientific name	Common name	Classification	Status[a]	Vegetation type[b]
Hawaii	*Asio flammeus sandwichensis*	Short-eared owl (Pueo)	Raptor		Mesic mountain parkland
	Buteo solitarius	Hawaiian hawk (I‘o)	Raptor	E	Dry to wet ‘ō‘hia-koa, mesic koa-‘ō‘hia, mesic koa forests/ woodlands
	Chasiempis sandwichensis sandwichensis	Hawai‘i ‘elepaio	Monarch flycatcher		Dry koa-māmane, mesic koa-‘ō‘hia, wet ‘ō‘hia-koa forests/woodlands
	Corvus hawaiiensis	‘Alalā	Hawaiian crow	E	Dry koa-māmane, mesic koa-‘ō‘hia, wet ‘ō‘hia-koa forests/woodlands
	Hemignathus munroi	‘Akiapōlā‘au	Honeycreeper	E	Dry koa-māmane, mesic koa-‘ō‘hia, wet ‘ō‘hia-koa forests/woodlands
	Hemignathus virens virens	‘Amakihi	Honeycreeper		All types of forests/woodlands with koa
	Himatione sanguinea sanguinea	‘Āpapane	Honeycreeper		All types of forests/woodlands with koa
	Loxops coccineus coccineus	Hawai‘i ‘ākepa	Honeycreeper	E	Mesic koa-‘ō‘hia and wet ‘ō‘hia-koa forests/woodlands
	Myadestes obscurus	‘Ōma‘o	Thrush		All types of forests/woodlands with koa
	Oreomystis mana	Hawai‘i creeper	Honeycreeper	E	All types of forests/woodlands with koa
	Vestiaria coccinea	‘I‘iwi	Honeycreeper		All types of forests/woodlands with koa
Maui	*Asio flammeus sandwichensis*	Short-eared owl	Raptor		Mesic koa-‘ō‘hia forests/woodlands
	Hemignathus lucidus affinis	Maui nuku pu‘u	Honeycreeper	E	Wet koa-‘ō‘hia forest
	Hemignathus virens wilsoni	‘Amakihi	Honeycreeper		Mesic koa-‘ō‘hia and ‘ō‘hia-koa forests
	Himatione sanguinea sanguinea	‘Āpapane	Honeycreeper		Mesic koa-‘ō‘hia and ‘ō‘hia-koa forests/woodlands
	Loxops coccineus ochraceus	Maui ‘ākepa	Honeycreeper	E	Mesic koa-‘ō‘hia forests/woodlands and ‘ō‘hia-koa forests
	Palmeria dolei	‘Ākohokohe	Honeycreeper	E	Mesic ‘o‘hia-koa forests/woodlands and koa-‘ō‘hia forests
	Paroreomyza montana newtoni	Maui creeper	Honeycreeper		Mesic ‘ō‘hia-koa and koa-‘ō‘hia forests/woodlands
	Pseudonestor xanthophrys	Maui parrotbill	Honeycreeper	E	Mesic ‘ō‘hia-koa and koa-‘ō‘hia forests/woodlands
	Vestiaria coccinea	‘I‘iwi	Honeycreeper		Mesic ‘ō‘hia-koa and koa-‘ō‘hia forests/woodlands
Molokai	*Hemignathus virens wilsoni*	‘Amakihi	Honeycreeper		Mesic to wet mixed forest with koa
	Himatione sanguinea sanguinea	‘Āpapane	Honeycreeper		Mesic to wet mixed forest with koa
	Vestiaria coccinea	‘I‘iwi	Honeycreeper		Mesic to wet mixed forest with koa
Lanai	*Himatione sanguinea sanguinea*	‘Āpapane	Honeycreeper		Mesic mixed forest with koa

Table 9—Endemic forest and woodland birds that are found in forests where *Acacia koa* is a canopy dominant or in mixed and diverse forests where it is an associate, except for the islands of Kaho‘olawe and Ni‘ihau (continued)

Island	Scientific name	Common name	Classification	Status[a]	Vegetation type[b]
Oahu	*Asio flammeus sandwichensis*	Short-eared owl	Raptor		Mesic open mixed forests with koa
	Chasiempis sandwichensis gayi	O‘ahu ‘elepaio	Monarch flycatcher	E	Diverse mesic ‘ō‘hia-koa forests
	Hemignathus virens chloris	‘Amakihi	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests
	Himatione sanguinea sanguinea	‘Āpapane	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests
	Paroreomyza maculata	O‘ahu creeper	Honeycreeper	E	Mesic to wet ‘ō‘hia-koa forests
	Vestiaria coccinea	‘I‘iwi	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests
Kauai	*Asio flammeus sandwichensis*	Short-eared owl	Raptor		Dry to mesic open forests with koa
	Chasiempis sandwichensis sclateri	Kaua‘i ‘elepaio	Monarch flycatcher		Dry to mesic koa and koa-‘ō‘hia forests
	Hemignathus parvus	‘Anianiau	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests
	Hemignathus procerus	Kaua‘i ‘akialoa	Honeycreeper	E	Mesic koa and koa-‘ō‘hia forests
	Hemignathus virens stejnegeri	‘Amakihi	Honeycreeper		Mesic koa and ‘ō‘hia-koa forests
	Himatione sanguinea sanguinea	‘Āpapane	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests
	Loxops coccineus caeruleirostris	Kaua‘i ‘akepa	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests
	Myadestes palmeri	Puaiohi	Thrush	E	Mesic koa-‘ō‘hia forests
	Oreomystis bairdi	Kaua‘i creeper	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests
	Vestiaria coccinea	‘I‘iwi	Honeycreeper		Mesic to wet ‘ō‘hia-koa forests

Sources: Compiled from Scott et al. (1986, 1988) and Jacobi and Atkinson (1995).

[a] E = Endangered.

[b] Only vegetation types containing koa are listed; most species also occur in varying densities in other vegetation types.

Appendix D: Allometric Equations for Koa

Table 10—Allometric equations for young *Acacia koa* trees from various sites in Hawaii

Tree component and site ID	Elevation	Age	DBH range	Equation form[a]	a[b]	b	R^2	Reference
	Meters	*Years*	*Centimeters*					
Whole tree biomass:								
H-05	1650–1850	4–8	1–8	$BA = aDBH^b$	0.106	2.286	0.97	Pearson and Vitousek 2001[c]
		15–17	8–30	$BA = aDBH^b$	0.144	2.221	0.94	
H-05/H-12	1400–1700	8–17	2–30	$BA = aDBH^b$	0.102	2.33	?	Grace and Fownes 1995
M-04[d]	300	6–8	5–16	$BA = aDBH^b$	0.0817	2.371	0.99	Conrad 2005
M-04[e]			1–19	$BA = aDBH^b$	0.2	1.991	0.95	
M-05[d]	640	6–8	1–27	$BA = aDBH^b$	0.125	2.264	0.99	
M-05[e]			2–26	$BA = aDBH^b$	0.094	2.338	0.99	
M-06[d]	1070	6–8	5–26	$BA = aDBH^b$	0.057	2.578	0.99	
O-03	260	2	?	$BA = aBD^b$	0.023	2.632	0.98	Ikawa 1995
Wood biomass:								
H-05/H-12	1400–1700	8–17	2–30	$BW = aBD^b$	0.067	2.418	?	Fownes and Grace 1995
Stem biomass:								
H-05	1650–1850	4–8	1–8	$BS = aDBH^b$	0.072	1.953	0.87	Pearson and Vitousek 2001[c]
		15–17	8–30	$BS = aDBH^b$	0.356	1.625	0.68	
Branch biomass: (>1 cm diameter):								
H-05	1650–1850	4–8	1–8	$BB = aDBH^b$	0.004	3.343	0.95	Pearson and Vitousek 2001[c]
		15–17	8–30	$BB = aDBH^b$	0.006	2.996	0.88	
Twig biomass (≤1 cm):								
H-05	1650–1850	4–8	1–8	$BT = aDBH^b$	0.022	1.909	0.85	Pearson and Vitousek 2001[c]
		15–17	8–30	$BT = aDBH^b$	0.023	1.75	0.62	
Foliage biomass:								
H-05	1650–1850	4–8	1–8	$BF = aDBH^b$	0.028	2.168	0.88	Pearson and Vitousek 2001[b]
		15–17	8–30	$BF = aDBH^b$	0.038	1.746	0.59	
Dead wood biomass:								
H-05	1650–1850	4–8	1–8	$BDW = aDBH^b$	0.003	2.789	0.87	Pearson and Vitousek 2001[b]
		15–17	8–30	$BDW = aDBH^b$	0.015	1.808	0.21	
Leaf area:								
H-05	1650–1850	4–17	1–30	$LA = aDBH^b$	0.605	1.314	0.74	Scowcroft n.d.a
H-05/H-12	1400–1700	8–17	2–30	$LA = aDBH^b$	0.161	1.75	?	Fownes and Grace 1995
H-12	1400	8	2–16	$LA = aDBH^b$	0.23	1.97	0.91	Grace and Fownes 1998
				$LA = aSA^b$	0.26	1.02	0.92	
H-05/H-12	1400–1700	8–17	2–30	$LA = aSA^b$	0.061	1.17	?	Grace and Fownes 1995
O-03	260	2	?	$LA = aBD^b$	0.046	2.912	0.87	Ikawa 1995

Note: see appendix A (table 7) for site information.

[a] BW = aboveground wood biomass (kg); BA = aboveground whole tree biomass (kg); BS = stem biomass (kg); BB = branch biomass (kg); BT = twig biomass (kg); BDW = dead wood biomass (kg); BF = foliage biomass (kg); LA = leaf area (m^2); DBH = stem diameter at breast height (cm); BD = basal stem diameter (cm); SA = sapwood cross-sectional area at breast height (cm^2).

[b] The a coefficients generated by linear regression analyses of log-log transformed data were corrected during back-transformation using the Baskerville correction.

[c] The a coefficients presented in Pearson and Vitousek (2001) were not corrected using the Baskerville correction, but corrected values are presented here.

[d] Seedlings were grown from seed collected from Kukaiau Ranch located on the eastern flank of Mauna Kea, Island of Hawaii.

[e] Seedlings were grown from seed collected from the Kaumana area along Saddle Road on the eastern flank of Mauna Loa, Island of Hawaii.

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