

Effects of Phosphorus Fertilization, Seed Source, and Soil Type on Growth of *Acacia koa*

P. G. Scowcroft¹ and J. A. Silva²

¹Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, Honolulu, HI, USA

²Department of Tropical Plant and Soil Sciences, University of Hawaii at Manoa, Honolulu, HI, USA

ABSTRACT

The endemic tree *Acacia koa* is used to reforest abandoned agricultural lands in Hawaii. Growth may be constrained by soil infertility and toxic concentrations of aluminum (Al) and manganese (Mn) in acidic Oxisols and Ultisols. The effects of phosphorus (P) fertilization at time of planting, soil type, and seed source on koa growth were studied for three years. Phosphorus, applied as triple superphosphate and at rates of at least 300 kg P ha⁻¹, significantly increased height, basal stem diameter, crown volume, and aboveground wood biomass of trees from the local (Oahu) seed source, but not those from off island (Hawaii). Manganese toxicity in the Oxisol probably slowed growth of the off-site trees. The local seed source grew similarly in both soil types, but the survival rate was lower in the Ultisol, possibly due to its lower water-holding capacity. Increased growth due to fertilization suggested improved P status, but such improvement was not detected by foliar analysis.

Keywords: *Acacia koa*, acid soils, Oxisol, plantation establishment, tree seedling nutrition, tropical reforestation, Ultisol, Hawaii

INTRODUCTION

Sugarcane and pineapple production in Hawaii declined markedly during the last quarter of the 20th century, leading to abandonment of extensive tracts of low-elevation agricultural land. Production forestry then became a potentially viable alternative land use. Considerable interest developed in reforestation

Received 7 November 2003; accepted 28 October 2004.

Address correspondence to P. G. Scowcroft, Institute of Pacific Islands Forestry, Pacific Southwest Research Station, USDA Forest Service, 1151 Punchbowl Street, Suite 323, Honolulu, HI 96813, USA. E-mail: pscowcroft@fs.fed.us

with the commercially valuable endemic legume *Acacia koa* A. Gray (koa), especially in areas where native forest had been cleared for agriculture and pasture. Symbiotic associations with *Bradyrhizobium* spp. (Allen and Allen, 1936) give koa the ability to biologically fix dinitrogen. Pearson and Vitousek (2001) estimated that a six-year-old stand of koa at 1750 m elevation on Mauna Loa, Island of Hawaii, fixed ~ 23 kg nitrogen (N) $\text{ha}^{-1} \text{yr}^{-1}$ and a 20-year-old stand fixed ~ 1.5 kg N $\text{ha}^{-1} \text{yr}^{-1}$. Koa also forms symbioses with arbuscular mycorrhizal fungi (AMF) and is moderately dependent on the association for maximum growth (Miyasaka et al., 1993). Infection of koa seedling roots with AMF, such as *Glomus aggregatum*, enhanced phosphorus (P) uptake and plant growth (Habte et al., 2001).

Areas being considered for lowland reforestation in Hawaii have high rainfall and many of the soils are highly weathered Oxisols and Ultisols, similar to those on more than 40% of land in the tropics (Sanchez and Salinas, 1981). These highly acidic soils can contain toxic amounts of aluminum (Al) and manganese (Mn); are low in available P and major plant nutrients, especially calcium (Ca); and can readily fix applied P into insoluble iron- and aluminum-phosphates, thus making it unavailable to plants (Nambiar and Brown, 1997; Stewart et al., 1991). High concentrations of hydrogen ions (H^+), Al^{3+} , and/or Mn^{2+} typically reduce nodulation (Foy et al., 1978; Fisher and Juo, 1995). Phosphorus deficiency commonly stimulates formation of mycorrhizal association (Graham et al., 1981), but Habte and Osorio (2001) suggested that a host-plant P status that is too low might inhibit infection by AMF, especially if the plant is highly dependent on AMF for P uptake and growth. Stamford et al. (1997) found that mycorrhizal infection of *Mimosa caesalpiniaefolia* growing in an acid soil was significantly increased by P fertilization.

Phosphorus is generally believed to be the key regulator of biological activity in older tropical soils (Chadwick et al., 1999). Crews et al. (1995) examined soil P fractions across a soil/ecosystem-development gradient in Hawaii and found that P was present mainly in primary minerals in early stages of pedogenesis and gradually became tied up in recalcitrant forms as weathering progressed. Nitrogen was least available in young soils. Long-term fertilization experiments showed that forest productivity on highly weathered soils, such as those Oxisols and Ultisols, was generally limited by low availability of P, whereas on relatively unweathered and moderately weathered soils, such as those found on the island of Hawaii, productivity was limited by low availability of N or a combination of N and P (Vitousek et al., 1993; Herbert and Fownes, 1995; Raich et al., 1996; Vitousek and Farrington, 1997; Herbert et al., 1999). Results of fertilizer experiments in Jamaican (Tanner et al., 1990) and Venezuelan (Tanner et al., 1992) forests led to the hypothesis that P might limit productivity in tropical lowland rainforests and that N might limit productivity in tropical montane rain forest (Tanner et al., 1998).

Constraints to plant growth in acid soil can be relieved by liming or fertilizing or both (Nambiar and Brown, 1997). Phosphorus fertilization has improved

tree growth in P-deficient Oxisols and Ultisols (Wan Rasidah et al., 1988; Netera et al., 1992; Fernandez et al., 2000; Xu et al., 2001), although no improvement has also been observed (e.g., Burslem et al., 1995).

In addition to constraints imposed by acid soils, the source of planting stock might influence the success of koa reforestation. Evidence suggests that koa from the island of Hawaii are genetically different from koa located on the other Hawaiian islands (Conkel, 1997; Daehler et al., 1999). Phyllode polymorphisms appear to be highly heritable and definitive of both clonal and population differences (J. Brewbaker, unpublished data). Common garden trials revealed that growth of koa from the island of Hawaii was slower than growth of koa from the islands of Kauai and Oahu when all three were planted together in a highly weathered acid soil on Oahu (Conrad et al., 1996). Similarly, total aboveground biomass of 3.5-year-old plantations established in an Oahu Oxisol was nearly 3 Mg/ha for koa from an Oahu seed source compared with 1.7 Mg/ha for koa from a Maui seed source (A. Ares, unpublished data). The difference was attributed to a greater leaf-area index for the local seed source.

The objectives of this study were to determine the effects of P fertilization, seed source, and soil type on growth of koa planted at low elevation on the Island of Oahu, Hawaii. The hypotheses were as follows:

- 1) Growth of planted koa will increase in proportion to the amount of P fertilizer applied.
- 2) The response of koa to P fertilization will be greater for the local than for the off-site seed stock.
- 3) Growth of local seed stock will be similar in high-Mn and high-Al soils.

Results of this study should be applicable to lowland koa reforestation efforts elsewhere on Oahu, Kauai, and Maui where Oxisols and Ultisols commonly occur, and should provide insights into limitations on growth of tree legumes elsewhere in the tropics where acid soils occur.

MATERIALS AND METHODS

Site Description

The study site lay within the 80 ha minimum-security Waiawa Correctional Facility, which is situated in the Waipio-Ewa area of Oahu on the southwest (leeward) slope of the Koolau Mountain Range (lat 21°30 N, long 157°50 W). The elevation was 260 m above sea level and the land was flat to very gently sloping. Mean annual rainfall at the site for the period 1991–1994 was approximately 1400 mm; the driest months were April through July. Mean annual air temperature was 21.9°C, with mean daily maximum and minimum temperatures

of 26.4°C and 18.7°C, respectively. Total solar radiation averaged 17.7 MJ m² day⁻¹.

The site had been used for military training from 1943–1985, after which the State of Hawaii took possession and established the Waiawa Correctional Facility. When this study began, the land lay idle and was dominated by weedy introduced species of grasses and herbs, including *Brachiaria mutica* (Forssk.) Stapf (Para grass), *Melinis minutiflora* P. Beauv. (molasses grass), *Crotalaria incana* L. (fuzzy rattlepod), *Stachytarpheta jamaicensis* (L.) Vahl (Jamaica vervain), and *Mimosa pudica* L. (sensitive plant).

Design

Two experiments were conducted simultaneously: In one, the effects of seed source and rate of P fertilization on planted koa were examined; in the other, the effects of soil type and rate of P fertilization were assessed. Treatments consisted of five rates of P (applied as triple superphosphate), two koa seed sources (one local and the other distant), and two soils (an Oxisol and an Ultisol). The seed source experiment was performed in the Oxisol, and the soil type experiment was performed using the local seed source. Both experiments were installed in a randomized complete block design with four blocks. A 4 m wide buffer strip separated blocks. Due to the small size of the experimental fields, plots within blocks were not separated by buffer strips. Tree spacing was 2 × 2 m, with 16 trees per plot. Seedlings were graded by size. The tallest seedlings were planted in block 1, with successively shorter seedlings planted in each succeeding block, so that block 4 contained the shortest seedlings. Data for the mid-range P fertilization treatment (300 kg P ha⁻¹) were discarded from the test of soil types because the growth data indicated that seedlings used for that treatment inadvertently came from the wrong seed source.

Site Preparation

Site preparation consisted of scraping away grass and shrub vegetation with a bulldozer blade. Surface soil was displaced by the clearing operation, so planting was actually done in subsurface material. A powered auger was used to excavate each planting hole to a depth of 18–21 cm, which was 5–8 cm deeper than the dibble tube containers (115 cm³) in which seedlings were grown (Walters, 1981). Planting was done during April 14–16, 1992. The outer edge of each planting spot was built up to retain irrigation water, which was supplied at a rate of 1 L per plant, twice weekly for eight weeks. Bark mulch was spread around the base of each seedling to retard evaporation from the soil surface, and competing vegetation was controlled by periodic cutting. Seedlings that died within three months of planting were replaced.

Phosphorus Fertilization Treatments

The five rates of phosphorus fertilization were 0, 150, 300, 600, and 1400 kg P ha⁻¹. These rates were based on the recommendation that an acceptable P concentration for forest trees would be about 0.02 μg P ml⁻¹ soil solution (R. Fox, personal communication). The P sorption curve (Fox and Kamprath, 1970) for the Ultisol indicated that 0.02 μg P ml⁻¹ was obtained with 300 kg P ha⁻¹. This rate was halved and doubled (150 and 600 kg P ha⁻¹, respectively) while the maximum rate was arbitrarily set at 1400 kg P ha⁻¹. The target soil solution P concentrations were 0.0128, 0.0155, 0.020, 0.031, and 0.100 μg P ml⁻¹. The corresponding rates of triple superphosphate were 0, 17.9, 35.7, 71.4, and 166.7 g seedling⁻¹, which assumed that fertilizer was applied to an area of 0.25 m² seedling⁻¹. Approximately one half of the fertilizer was placed in the bottom of the planting hole, mixed with soil, and then covered with a thin layer of unamended soil. A seedling was removed from its dibble tube, centered in the hole, and three quarters of the hole was then filled with unfertilized soil. The rest of the fertilizer was applied to the outer edge of the hole and the hole was then filled with soil. Localized placement of fertilizer was designed to minimize short-term P fixation by the mineral soil (Fernandez et al., 2000).

Seed Sources

Koa seeds were collected from two separate areas: Pacific Palisades on the island of Oahu (the local seed source) and Kukaiau Ranch on the island of Hawaii (the off-site seed source; at lat 19°57' N, long 155°23' W). The local collection area was at an elevation of 275 m, where rainfall averaged 1500 mm yr⁻¹ and air temperature averaged 22°C. The soil was an Oxisol of the Helemano series and was derived from basic igneous rock (very fine, kaolinitic, isohyperthermic, Rhodic Eustrustox). The off-site collection area on the island of Hawaii was at an elevation of 1100 m, where rainfall averaged 2000 mm yr⁻¹ and air temperature averaged 18°C. The soil was an Andisol of the Umikoa series and was derived from volcanic ash (medial, amorphous isomesic, Typic Hapludand).

Soils

Two acid soil types in the study area were selected. The Ultisol (Leilehua series) was a very fine, ferruginous, isothermic, Ustic Kanhaplohumult and the Oxisol (Wahiawa series) was a very fine, kaolinitic, isohyperthermic, Rhodic Haplustox. Selected chemical characteristics are listed in Table 1. Substantial amounts of extractable Al and high Al saturation indicated that Al toxicity might be a problem in the Ultisol. Hue et al. (1998) reported large amounts of total (17 g kg⁻¹) and extractable Mn (>500 mg kg⁻¹) in the Oxisol, which indicated that Mn toxicity might be a problem in that soil.

Table 1
Selected properties (0–30 cm depth) of the Oxisol (Wahiawa soil series), a Rhodic Haplustox, and the Ultisol (Leilehua soil series), an Ustic Kanhaplohumult

Property	Ultisol	Oxisol
Available water (%)*	8	16
pH (1:1 H ₂ O/1:2 0.01 M CaCl ₂)	4.8/4.3	5.0/4.8
Organic C (g kg ⁻¹)	26.1	20.3
Total N (g kg ⁻¹)	2.3	2.8
Ca (cmol kg ⁻¹)	0.4	1.8
Mg (cmol kg ⁻¹)	0.4	1.7
K (cmol kg ⁻¹)	0.2	1.2
Extractable Al (cmol kg ⁻¹)	3.10	0.45
Al saturation (%)	74.0	5.7
P-modified Truog (mg kg ⁻¹)	6.7	10.0

*Percent moisture held between 10 and 1500 kPa suction.

Response Variables

Response variables included plant height, basal diameter at approximately 10 cm aboveground, number of lateral branches, stem diameter at breast height (dbh), canopy diameter, and height to crown. Measurements were made monthly for the first year after planting, every four months during the second year, and once at the end of the third year. Lateral branches were counted only the first year after planting. Collection of crown diameter and height-to-base-of-crown data began with the 16-month measurement. All individuals were measured at 1, 12, 24, and 36 months after planting, while at other times only the four interior trees were measured. Percent survival was calculated for the 12-, 24-, and 36-month measurements using all 16 trees plot⁻¹ rather than only the four interior measure trees.

Crown diameter and height to base of crown were used to estimate crown volume for each measure tree assuming a cylindrical crown shape. Aboveground wood biomass (W) was estimated from basal stem diameter (BD) for each tree using the allometric relationship determined from biomass harvest of koa in a neighboring experiment (R. Harrington and J. Fownes, unpublished data). The allometric equation for estimating leaf area was also available, but was not used because fertilization probably affected coefficients (Harrington and Fownes, 1993). Woody biomass allometry, on the other hand, was assumed to be fairly constant across sites and treatments (R. Harrington, personal communication).

$$W = 0.0226 \times BD^{2.6323}$$

Foliar Analysis

Phyllode nutrient concentrations were determined one year after planting. Several phyllodes were collected from the upper crown of each surviving measure tree, and these were combined to make one composite sample per treatment block. Only the most recent, fully expanded phyllodes were sampled—usually the fifth phyllode back from the terminal bud. Analyses were done at the Agricultural Diagnostic Service Center, University of Hawaii at Manoa, and included concentrations (mass basis) of N, P, potassium (K), Ca, magnesium (Mg), Mn, iron (Fe), zinc (Zn), and boron (B) using methods described in Hue et al. (2000).

Data Analyses

Separate analyses were done for Experiment 1, which examined the effects of seed source and P level, and for Experiment 2, which examined the effects of soil type and P level. The repeated measures analysis option in SAS Proc Mixed was used with age as a covariate to determine the significance of treatment effects and their interactions on each of the koa response variables. Because differences in growth during the first 6–12 months after planting were small, to simplify analysis only the data for the 12–36 month measurements were used, except in the case of analyses of branchiness, in which only the data for 6–12 months after planting were used. The log transformation was used on height, basal diameter, dbh, branchiness, crown volume, and wood biomass data before analysis. The arcsine transformation was used on survival data before analysis. Type 3 tests for fixed effects were used for determining equality of slopes for seed source, soil type, and rate of P fertilization. Least-square means were back transformed for presentation of results. SAS Proc GLM was used to examine effects of treatments at 12 months after planting on foliar nutrient concentrations. Because the tallest plants were assigned to block 1 and the shortest ones to block 4, block was a fixed rather than a random effect. Pairwise comparisons of treatment means at 36 months (12 months for branchiness) after planting were performed using Tukey's HSD test and $\alpha = 0.05$.

RESULTS

Experiment I: Fertilizer Effects

Rate of P fertilization significantly affected height, basal stem diameter, dbh, and wood biomass trajectories during the 36-month period after planting (Figure 1, Table 2). Rate of P fertilization did not significantly affect branchiness, crown volume, or survival (Table 2). Fertilizer-seed source interactions were not significant, except for branchiness.

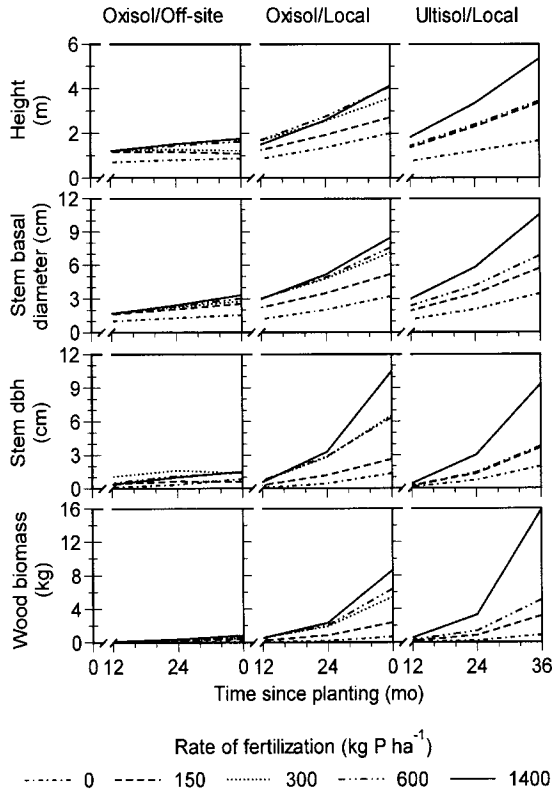


Figure 1. Effect of rate of P fertilization at time of planting on height, basal stem diameter (at 10 cm aboveground), stem diameter at breast height, and aboveground wood biomass of two seed sources of *Acacia koa* during the 36-month period after planting in an Oxisol (Wahiawa series) and an Ultisol (Leilehua series) on the island of Oahu, Hawaii. The off-site seed source was Kukaiau Ranch on the Island of Hawaii and the local seed source was Pacific Palisades on the Island of Oahu. Data are least squares means of four replicates at 12, 24, and 36 months after planting.

Fertilization had limited effects on trees from the off-site seed source, as shown by data collected 36 months after planting (Figure 2). Mean dbh and crown volume did not increase significantly in response to increasing rates of P fertilization (Table 3). Mean height and branchiness of fertilized trees were greater than those of unfertilized trees only at 1400 kg P ha⁻¹, and survival rate was greater than that of unfertilized trees only at 600 kg P ha⁻¹. Basal stem diameter and aboveground woody biomass of trees from the off-site seed source were increased significantly by fertilization at rates ≥ 300 kg P ha⁻¹ (Table 3).

In contrast to trees from the off-site seed source, trees grown from the local seed source responded strongly to P fertilization (Figure 2). As little as

Table 2
 Probability* (*P*) of a greater *F* value for Type 3 tests of slopes and intercepts of curves fitted to data in Experiment I, which examined seed source and P fertilization effects on growth of planted *Acacia koa*, and Experiment II, which examined soil type and P fertilization effects

Effect	Growth response variable						
	Height (m)	Basal diameter (cm)	Dbh (cm)	Branchiness (# m ⁻¹)	Crown volume (m ³)	Wood biomass (kg)	Survival (%)
Experiment I—Seed source effects							
Slope							
Seed source	< 0.001	< 0.001	< 0.001	0.050	< 0.001	< 0.001	0.090
P level	< 0.001	0.044	0.086	0.094	0.734	0.044	0.245
Seed source × P level	0.443	0.680	0.603	0.022	0.904	0.681	0.135
Intercept							
Seed source	0.841	0.001	0.046	0.196	0.896	0.001	0.142
P level	< 0.001	< 0.001	0.001	0.880	0.191	< 0.001	0.492
Seed source × P level	0.665	0.204	0.352	0.004	0.903	0.204	0.564
Experiment II—Soil type effects							
Slope							
Soil type	0.316	< 0.001	0.013	0.577	0.010	< 0.001	0.812
P level	0.004	0.011	0.296	0.938	0.054	0.011	0.390
Soil type × P level	0.498	0.652	0.954	0.312	0.458	0.652	0.624
Intercept							
Soil type	0.344	0.023	0.018	0.023	0.002	0.023	0.003
P level	< 0.001	< 0.001	0.026	0.102	0.135	< 0.001	0.422
Soil type × P level	0.651	0.718	0.386	0.591	0.820	0.718	0.856

* *P* ≤ 0.05 are in bold face.

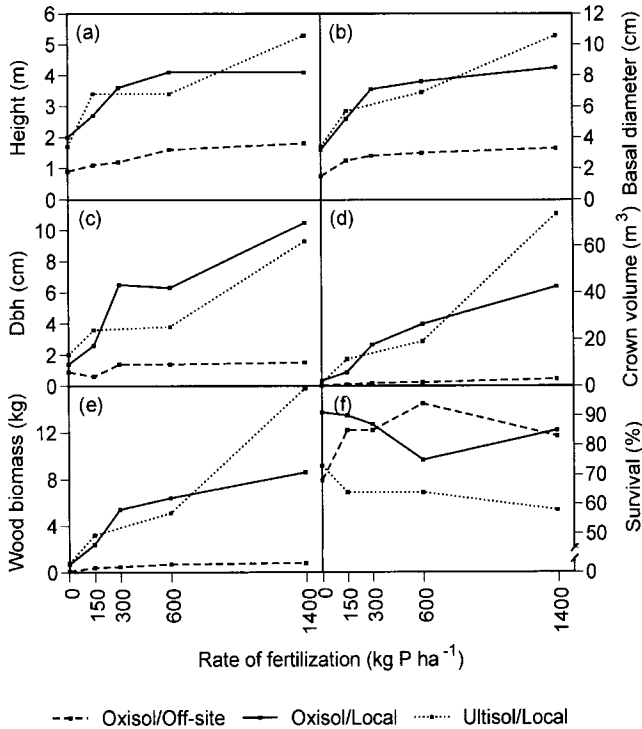


Figure 2. Effects of rate of P fertilization at time of planting, soil type, and seed source on growth and survival of *Acacia koa* trees at 36 months after planting. Each point is the least squares mean of four replicates.

150 kg P ha⁻¹ was sufficient to increase significantly basal stem diameter and aboveground woody biomass above controls (Table 3). At 300 kg P ha⁻¹, all response variables except branchiness and survival were significantly greater than those of the controls, and at 600 kg P ha⁻¹, even branchiness exceeded that of the controls. Only survival was unaffected by rate of fertilization (Table 3).

Experiment I: Seed Source Effects

Growth, but not survival, differed significantly between the two seed sources (Figure 1, Table 2). Effects were clearly evident 36 months after planting (Figure 2). Trees from the local seed source were significantly taller, had larger mean basal stem diameter, and more aboveground wood biomass than trees from the off-site seed source at all rates of P fertilization (Table 3). Sample means of branchiness were also greater for local-seed-source trees at all rates of P fertilization, but the only statistically significant difference was at 600 kg P ha⁻¹. Crown volume was significantly greater for local than for off-site trees

Table 3

Experiment I—Effect of seed source and rate of P fertilization on growth of *Acacia koa* trees planted in an Oxisol

Seed source*	Fertilization rate (kg P ha ⁻¹)				
	0	150	300	600	1400
	Height (m)				
Off-site	0.9f [†]	1.1ef	1.2ef	1.6def	1.8cde
Local	2.0cd	2.7bc	3.6ab	4.1a	4.1a
	Basal stem diameter (cm)				
Off-site	1.5e	2.5de	2.8d	3.0d	3.3cd
Local	3.2d	5.2bc	7.1ab	7.6ab	8.5a
	Branchiness (# m ⁻¹ tree height)				
Off-site	4.5d	8.7bcd	8.2cd	8.1cd	10.2abc
Local	7.5cd	12.2abc	13.4abc	15.3ab	18.0a
	Dbh (cm)				
Off-site	0.9c	0.6c	1.4c	1.4c	1.5c
Local	1.4c	2.6bc	6.5ab	6.3ab	10.5a
	Crown volume (m ³)				
Off-site	0.2d	0.6d	1.2d	1.5d	2.9cd
Local	2.2cd	5.9bc	17.5ab	26.5ab	42.5a
	Aboveground wood biomass (kg)				
Off-site	0.1d	0.4cd	0.5c	0.7c	0.8c
Local	0.7c	2.4b	5.4ab	6.4ab	8.6a
	Survival (%)				
Off-site	68b	85ab	85ab	94a	83ab
Local	91ab	90ab	87ab	75ab	85ab

*The off-site seed source was Kukaiau Ranch on the island of Hawaii and the local seed source was Pacific Palisades on the Island of Oahu.

[†]Multiple pairwise comparisons were done using Tukey's HSD test and $\alpha = 0.05$. Means for a given attribute followed by a common letter are not significantly different.

Data are least squares means calculated at 36 months, or in the case of branchiness at 12 months, using repeated measures analyses in SAS Proc Mixed.

at P rates ≥ 150 kg P ha⁻¹. At rates ≥ 300 kg P ha⁻¹, mean dbh of local trees was significantly larger than that of off-site trees. Survival was unaffected by P level (Table 3).

Experiment II: Fertilizer Effects

As found in Experiment I, height, basal stem diameter, dbh, and wood biomass growth during the 36-month period after planting were significantly affected by rate of P fertilization (Figure 1, Table 2). Changes in branchiness, crown

Table 4

Experiment I—Effect of soil type and rate of P fertilization on growth of *Acacia koa* trees from a local seed source (Pacific Palisades, Island of Oahu)

Soil type	Fertilization rate (kg P ha ⁻¹)			
	0	150	600	1400
	Height (m)			
Ultisol	1.7c*	3.4ab	3.4ab	5.3a
Oxisol	2.0bc	2.7abc	3.9a	4.1a
	Basal stem diameter (cm)			
Ultisol	3.4de	5.7bcd	6.9abc	10.6a
Oxisol	3.2e	5.0cd	7.3abc	8.3ab
	Branchiness (# m ⁻¹ tree height)			
Ultisol	6.0b	13.6ab	12.6ab	14.2ab
Oxisol	7.5b	12.1ab	15.2a	18.0a
	Dbh (cm)			
Ultisol	2.0bc	3.6abc	3.8abc	9.3a
Oxisol	1.4c	2.6ab	6.0ab	8.2a
	Crown volume (m ³)			
Ultisol	1.5c	11.4abc	19.1ab	74.0a
Oxisol	2.3c	5.6bc	28.4ab	45.4a
	Aboveground wood biomass (kg)			
Ultisol	0.8de	3.2bcd	5.1abc	15.8a
Oxisol	0.6e	2.2cd	5.7abc	7.9ab
	Survival (%)			
Ultisol	73a	64a	64a	58a
Oxisol	91a	90a	76a	85a

*Multiple pairwise comparisons were done using Tukey's HSD test and $\alpha = 0.05$. Means for a given attribute followed by a common letter are not significantly different.

Data are least squares means calculated at 36 months, or in the case of branchiness at 12 months, using repeated measures analyses in SAS Proc Mixed.

volume, and survival due to P fertilization were not significant. Fertilizer-soil type interactions were also not significant.

Phosphorus fertilization effects on the size of local trees in the two soil types were evident 36 months after application (Figure 2). Generally, at least 600 kg P ha⁻¹ was needed in the Ultisol to elicit a growth response (Table 4). Height was an exception in that it doubled with the addition of as little as 150 kg P ha⁻¹. Survival in the Ultisol soil was unaffected by P fertilization. In the Oxisol, 150 kg P ha⁻¹ was sufficient to increase significantly basal stem diameter, dbh, and aboveground woody biomass above those of the unfertilized controls (Table 4). Height, branchiness, and crown volume were not affected

until the rate of P fertilization reached 600 kg ha⁻¹. As in the Ultisol, survival was unaffected by fertilization (Table 4).

Experiment II: Soil Type Effects

Soil type significantly affected growth during the 36-month period after planting, except for height (Figure 1, Table 2). However, by 36 months after planting, none of the response variables for a given P level differed significantly between soil types (Table 4). This was true even in the cases of mean crown volume and aboveground woody biomass for the most heavily fertilized trees, which were 1.6 to 2 times greater in Ultisol than Oxisol (Figure 2d and 2e). High variability among blocks accounted for the lack of significance.

Foliar Nutrient Concentrations

Mean nutrient concentrations in fully expanded phyllodes one year after planting were consistently and significantly greater for trees from the off-site seed source than for those from the local seed source in the Oxisol (Table 5). Rate of fertilization did not affect nutrient concentrations, and none of the interactions with seed source were significant.

Soil type was associated with different mean foliar concentrations of N, Mg, and Mn only (Table 5). Concentrations of these nutrients were significantly greater in the Oxisol (14.1 g N kg⁻¹, 1.7 g Mg kg⁻¹, and 248 mg Mn kg⁻¹, respectively) than in the Ultisol (13.0 g N kg⁻¹, 1.3 g Mg kg⁻¹, and 146 mg Mn kg⁻¹, respectively). Rate of fertilization affected nutrient concentration of N and Mn only. Unfertilized trees had significantly greater concentrations of both nutrients than trees fertilized with 1400 kg P ha⁻¹ (14.2 and 12.6 g N kg⁻¹, respectively, and 248 and 156 mg Mn kg⁻¹, respectively).

DISCUSSION

Fertilizer Effects on Growth

The effect of P fertilization at time of planting lasted beyond the time when roots had access to readily available fertilizer P (Figure 1). Most likely, little of the highly soluble triple superphosphate remained by the end of the second year, and what was not taken up by roots was probably converted to insoluble iron and aluminum phosphates. Furthermore, although expanding koa root systems initially had a very good supply of added P, by the end of the second year they extended well beyond the small volume of fertilized soil. Despite these factors, increased growth rates were maintained during the second and third years (Figure 1).

Table 5
 Mean concentration of nutrients (mass basis) in fully expanded phyllodes of *Acacia koa* 12 months after planting, by soil type, seed source, and rate of P fertilization

Soil type/Seed source	Fertilization rate (kg P ha ⁻¹)					Mean
	0	150	300	600	1400	
	Phosphorus (g kg ⁻¹)					
Oxisol/Off-site	0.5	0.5	0.5	0.6	0.6	0.6a*
Oxisol/Local	0.4	0.4	0.4	0.4	0.4	0.4b/m
Ultisol/Local	0.4	0.4	n.a.	0.4	0.4	0.4m
	Nitrogen (g kg ⁻¹)					
Oxisol/Off-site	19.5	19.1	16.7	17.9	17.3	18.1a
Oxisol/Local	14.4	14.4	14.2	14.6	12.7	14.1b/m
Ultisol/Local	14.0	12.0	n.a.	13.7	12.6	13.0n
	Potassium (g kg ⁻¹)					
Oxisol/Off-site	6.3	5.1	4.7	4.6	4.9	5.1a
Oxisol/Local	4.7	4.8	4.4	4.1	3.4	4.3b/m
Ultisol/Local	5.0	4.1	4.1	4.5	3.6	4.2m
	Calcium (g kg ⁻¹)					
Oxisol/Off-site	5.7	6.0	6.2	5.7	6.0	5.9a
Oxisol/Local	4.4	4.3	3.5	3.7	3.0	3.8b/m
Ultisol/Local	4.1	3.2	n.a.	3.7	2.9	3.5m
	Magnesium (g kg ⁻¹)					
Oxisol/Off-site	2.4	2.8	2.6	2.5	2.9	2.6a
Oxisol/Local	1.8	1.8	1.6	1.8	1.5	1.7b/m
Ultisol/Local	1.4	1.3	n.a.	1.3	1.3	1.3n
	Manganese (mg kg ⁻¹)					
Oxisol/Off-site	384	513	411	378	371	411a
Oxisol/Local	312	260	238	245	184	248b/m
Ultisol/Local	185	140	n.a.	133	128	146/n
	Iron (mg kg ⁻¹)					
Oxisol/Off-site	81	74	63	58	60	67a
Oxisol/Local	59	52	50	56	49	53b/m
Ultisol/Local	59	66	n.a.	92	60	59m
	Boron (mg kg ⁻¹)					
Oxisol/Off-site	13	15	14	14	12	14a
Oxisol/Local	9	9	8	7	8	8b/m
Ultisol/Local	8	8	n.a.	9	9	9m
	Zinc (mg kg ⁻¹)					
Oxisol/Off-site	9	7	8	10	7	8a
Oxisol/Local	6	6	6	6	4	6b/m
Ultisol/Local	6	6	n.a.	5	6	6m

*Multiple pairwise comparisons were done using Tukey's HSD and $\alpha = 0.05$. Separate analyses were done to examine effects of seed source (*a* and *b* denote significant differences between off-site and local seed sources growing in the Oxisol) and soil type (*m* and *n* denote significant differences between the Oxisol and Ultisol planted with trees from the local seed source). For a given element, overall means followed by a common letter were not significantly different. Differences among P levels and interactions were generally not statistically significant.

The off-site seed source was from the Kukaiau area, island of Hawaii; the local seed source was from the Pacific Palisades area, island of Oahu. Data are least squares means based on four composite samples, one from each treatment block.

Several explanations might account for the prolonged effect of fertilizer P: (1) internal recycling of fertilizer P was efficient, (2) elaboration of root systems was proportional to the rate of fertilization, thus enabling koa to extract native P from increasing volumes of unfertilized soil sufficient to maintain growth rates, (3) nutrient return in litter and decomposition was proportional to rate of fertilization, thus allowing sufficient nutrient enrichment of surface soil directly under koa crowns to maintain growth rates, and (4) the increased crown volume (a surrogate for leaf area) that initially resulted from the P fertilization allowed more heavily fertilized trees to continue their more rapid growth. The first explanation seems unlikely because nutrient use efficiency reportedly decreases when nutrient-stressed trees are fertilized (Fisher and Juo, 1995). If more heavily fertilized trees had less-efficient internal recycling of P, they would return larger amounts of P to the soil in litter, which would strengthen the argument for external recycling. The second mechanism was probably involved, but differences in root elaboration among treatments were not evaluated. The significant fertilizer effect on crown volume of trees from the local seed source (Table 3) suggests that increased photosynthetic area was likely a factor in the prolonged growth response to P additions.

Seed Source Effects on Growth

Koa from the off-site seed source grew more slowly than koa from the local seed source at every level of P fertilization. Mean annual height increments ranged from 0.36 to 0.69 m yr⁻¹ for off-site koa and from 0.69 to 1.43 m yr⁻¹ for the local koa. Slow growth of the off-site koa was also observed in the Oxisol in a concurrent study (Conrad et al., 1996); three years after planting, off-site trees were only 0.7 m tall even after receiving two spot applications of 14-14-14 fertilizer. Not only did off-site trees do poorly in that study, but also koa from all seed sources from the island of Hawaii tested grew more slowly than did koa from the local seed source (0.2–0.5 m yr⁻¹ compared with 0.8 m yr⁻¹). Interestingly, koa produced from seed collected near the island of Hawaii seed source and planted in high-elevation acid soils of Rwanda grew in height at an average rate 1.5 m yr⁻¹ (Niang et al., 1995). These researchers also reported slower height growth of koa (1.0 m yr⁻¹) produced from seed collected on the drier, leeward slopes of Hualalai volcano, island of Hawaii. These data reinforce the importance of choosing a seed source adapted to the planting site.

Manganese toxicity might account for the limited response of off-site koa to P fertilization in the Oxisol (Table 1). Seedlings produced from seed collected from the Island of Hawaii might not have been as well adapted to cope with high concentrations of Mn as were the koa from the local seed source. Even varieties within a species might have different degrees of tolerance to Mn toxicity (Foy et al., 1988; El-Jaoual and Cox, 1998). As already noted, evidence suggests

that koa from the two seed-collection sites used in the present study were genetically different. Isozyme studies showed that trees on Oahu, Kauai, and Maui were closely related, while trees on Hawaii were substantially different from older island populations (Conkle, 1997). Using phyllode width, curvature, and pubescence, among other morphological features, Daehler et al. (1999) concluded that families from the island of Hawaii were genetically distinct from families on Oahu and Kauai. Koa from Oahu, including those from the local seed-collection area used in the present study, had narrow, highly curved phyllodes: those from the island of Hawaii had broad, less-curved phyllodes (St. John, 1979). Rock (1920) classified the latter as *A. koa* var. *hawaiiensis*. Sun et al. (1997) reported that family heritability estimates for early height and dbh averaged about 0.7, which is relatively high. Even the most recent authoritative manual of the flowering plants of Hawaii acknowledged that three subspecies probably exist (Wagner et al., 1990). If genetic differences account for the poor growth of the off-site provenance in the Oahu Oxisol, then that fact would have important implications for selection of koa seed sources/provenances for use in reforestation of acid soils (Conkle, 1997; Lesueur et al., 1993).

Hue et al. (2001) reported that the total Mn content of the Oxisol was 17 g kg⁻¹ and Mehlich-3 solution extractable Mn was 540 mg kg⁻¹. Such high levels are known to be phytotoxic for some species (Hue et al., 1998). If Mn toxicity inhibited growth of the off-site seed source, did it have a direct effect on internal physiological processes, or it was an indirect effect on rhizobial or mycorrhizal symbioses? Manganese concentrations in phyllodes, which did not increase in response to increased P availability (possibly because of the dilution effect of growth) were significantly elevated for the off-site koa (Table 5), so physiological processes might have been affected.

Although neither root nodulation nor N-fixation were examined in the present study, other work suggests that nodulation and number, size, and effectiveness of nodules of agricultural legumes are adversely affected by Mn toxicity (Foy et al., 1978; Graham, 1992). Ashwath et al. (1995) found that considerable specificity exists between species of *Acacia* and their *Rhizobium/Bradyrhizobium* symbionts, and that compatible and effective rhizobia were deficient for some plants in a Mn-toxic soil. They demonstrated that inoculation with compatible rhizobia alone or in combination with liming stimulated growth of some *Acacia*.

In the present study, phyllode N concentrations were significantly greater for the off-site seed source than for the local seed source (Table 5), but the higher concentrations did not translate into greater growth. Absence of a dilution effect of growth in the slow-growing, off-site trees might account for higher N concentrations even if nodulation was limited, ineffective, or non-existent. That neither foliar N concentrations nor estimated crown volumes of off-site trees were affected by P fertilization rate might indicate that N fixation was minimal and that trees were meeting their N requirement from mineralization of soil organic matter. For an N-fixing tree, foliar N concentrations seemed low

across all treatments. In a common garden experiment at 100 m elevation on the windward side of the island of Oahu, phyllode N concentrations averaged 25–30 g N kg⁻¹ for koa grown from off-site Island of Hawaii seed (Ares et al., 2000). Natural stands of koa at high elevation and in relatively young soils on the island of Hawaii typically average 23–32 g N kg⁻¹ (Pearson and Vitousek, 2001; Ares and Fownes, 1999), and on the much more weathered soils on the Island of Kauai phyllodes average 17–23 g N kg⁻¹ (Harrington et al., 1995).

Phosphorus concentrations in phyllodes of the off-site koa increased only slightly at higher levels of P fertilization (0.5 and 0.6 g kg⁻¹), while P concentrations in phyllodes of the local trees remained constant at all levels of fertilization and in both soils (Table 5). Assuming that increased growth at higher levels of P fertilization indicated better P status of koa, this finding suggests that foliar P concentration was not a good indicator of P status of sapling-size koa, although it can be a good indicator for seedlings (Habte et al., 1987) and is routinely used to assess P status of many crops.

Soil Type Effects on Growth

The relatively low survival of plants in the Ultisol was probably due in part to low water-holding capacity. Water availability was one-half that of the Oxisol, which was itself limited (Table 1). Rainfall during the initial months was low (22, 30, and 74 mm in April, May, and June 1992, respectively), and hand watering was used to keep seedlings alive. Despite those efforts, 20%–30% of the seedlings from the local seed source in the Ultisol died within three months of planting, and were replaced with new seedlings. In contrast, only 2%–8% of the local koa planted in the Oxisol died during the same period. Replants performed as well as the original koa in both soils (Figure 3), but because they were started later, they never grew as large as the original koa. Survival of replants was similar for both soils (data not shown), and did not vary consistently with increasing rates of P fertilization. In unfertilized plots, survival rate was about 50% in the Ultisol compared with 100% in the Oxisol. The difference, if real (data were too limited for statistical analysis), might be due to poor root development in the drier Ultisol. Nambiar and Brown (1997) noted that water stress could constrain plant growth, especially if soil acidity or Al toxicity, or both, restrict root elaboration into deeper, moister soil horizons.

Wang et al. (2001) found that cumulative desorbed P after 1000 pore volumes of 0.001 M CaCl₂ leachate was 275 mg P kg⁻¹ for the Oxisol compared with only 25 mg P kg⁻¹ for the Ultisol. If such differences existed in the field, then growth of koa should have been significantly greater in the unfertilized Oxisol than in the unfertilized Ultisol, but no differences existed (Table 4). Perhaps high concentrations of soil Mn prevented trees from the local seed source from responding to greater P availability in the unfertilized Oxisol. On the other hand, organic acids released from roots to chelate Al (Ma et al., 2001) can

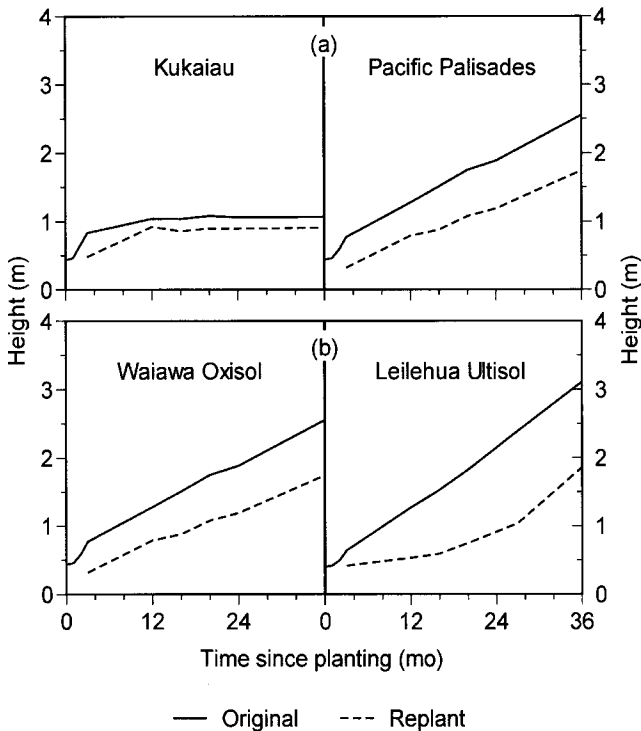


Figure 3. Height growth for replanted koa compared with that for originally planted koa between (a) seed sources and (b) soil types. Data are for the 150 kg P ha^{-1} fertilization treatment.

secondarily increase P availability in the rhizosphere (Fisher and Juo, 1995). Such action by koa could have stimulated growth in the unfertilized Ultisol, which contained substantial amounts of Al (Table 1).

High levels of Mn in the Oxisol might have influenced growth of the locally adapted koa. Foliar Mn concentrations were significantly greater for trees growing in the Oxisol than in the Ultisol (Table 5). This, finding coupled with a lack of difference in estimated crown volumes (Table 4), suggests that Mn uptake was significantly greater for the Oxisol. Loss of apical dominance is one symptom of Mn toxicity (El-Jaoual and Cox, 1998; Marschner, 1995), and although trees were slightly bushier (more branchy) in the Oxisol, differences were not significant (Table 4).

Although excess Mn probably suppressed growth of koa in the Oxisol (including the local adapted seed source), Al toxicity might have done the same in the Ultisol, with the net result being similar growth rates for koa in both soils (Figure 1). Greatest mean annual height increment (MAI) for koa in the Oxisol was 1.5 yr^{-1} (at $1400 \text{ kg P ha}^{-1}$). In a concurrent study, Cole

et al. (1996) found that koa from a maladapted seed source (630 m elevation, island of Hawaii) achieved a MAI of 2.2 m yr^{-1} in the same soil when liming and other treatments designed to mitigate growth-limiting soil factors were used. The effects of mitigations included significant reductions in surface soil (0–15 cm) acidity (pH 5.6), exchangeable Al, and Al saturation, which in turn enhanced growth of even an off-site provenance of koa. The relative contribution of reduced acidity and reduced Al toxicity to improved growth of koa could not be evaluated, nor was it possible to determine if improved growth was due to internal physiological plant processes or to external symbiotic processes, or both.

The results of Cole et al. (1996) indicated that growth of koa in acid soils of Hawaii could be enhanced beyond levels achieved in the present study with P fertilizer alone. Additional studies should be done to determine the biological basis of differential growth of genetically adapted and non-adapted provenances of this high-value tree legume. Physiological mechanisms that might be involved in tolerance of Mn- and Al-rich acid soils include restricted absorption of metal ions, restricted translocation to shoots, decreased ion concentrations in the rhizosphere due to increased pH by root action, and ability to sequester ions in large vacuoles of foliage (El-Jaoual and Cox, 1998). Particular attention should be directed at understanding the effects of Mn and Al on rhizobial and mycorrhizal symbioses, including evaluation of the efficacy of isolates of AMF and rhizobia for their ability to enhance tree legume productivity in acid soils. Such understanding would add greatly to the limited knowledge about the effects of acid soils on leguminous trees.

ACKNOWLEDGMENTS

This project was funded in part by the Hawaii Governor's Agricultural Coordinating Committee, Contract No. 91-04. We thank the administrators of the Waiawa Correctional Facility for providing land for the experiments and labor and equipment to prepare the study sites for planting. We gratefully acknowledge David Fujii, Janis Haraguchi, Don Goo, and Alan Urakami of the USDA Forest Service, and Stanley Oshita and Servillano Lamer of the Department of Agronomy and Soil Science, University of Hawaii, for their assistance in planting, fertilizing, tending, and measuring the trees, and we thank Jim Baldwin for his guidance on statistical analyses and Jack Ewel, Mitiku Habte, and two anonymous reviewers for critiquing earlier drafts of this manuscript.

REFERENCES

- Allen, O. N., and E. K. Allen. 1936. Root nodule bacteria of some tropical leguminous plants: I. Cross inoculation studies with *Vigna sinensis* L. *Soil Science* 42: 61–77.

- Ares, A., and J. H. Fownes. 1999. Water supply regulates structure, productivity, and water use efficiency of *Acacia koa* forest in Hawaii. *Oecologia* 121: 458–466.
- Ares, A., J. H. Fownes, and W. Sun. 2000. Genetic differentiation of intrinsic water-use efficiency in the Hawaiian native *Acacia koa*. *International Journal of Plant Science* 161: 909–915.
- Ashwath, N., P. J. Dart, D. G. Edwards, and P. K. Khanna. 1995. Tolerance of Australian tropical and subtropical *Acacias* to acid soil. *Plant and Soil* 171: 83–87.
- Burslem, D. F. R. P., P. J. Grubb, and I. M. Turner. 1995. Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rain forest in Singapore. *Journal of Ecology* 83: 113–122.
- Chadwick, O. A., L. A. Derry, P. M. Vitousek, B. J. Huebert, and L. O. Hedin. 1999. Changing sources of nutrients during four million years of ecosystem development. *Nature* 397: 491–497.
- Cole, T. G., R. S. Yost, R. Kablan, and T. Olsen. 1996. Growth potential of twelve *Acacia* species on acid soils in Hawaii. *Forest Ecology and Management* 80: 175–186.
- Conkle, M. T. 1997. Isozyme studies of genetic variability. In *Koa: A Decade of Growth: Proceedings of the Symposium*, eds. L. Ferentinos and D. O. Evans, 27–29. Honolulu, HI: Hawaii Forest Industry Association.
- Conrad, C. E., D. M. Fujii, and H. Ikawa. 1996. Seed source and performance in koa tree establishment. In *Proceedings, Hawaii Agriculture: Positioning for Growth*, 88–89. Honolulu, HI: College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa.
- Crews, T. E., K. Kitayama, J. H. Fownes, R. H. Riley, D. A. Herbert, D. Mueller-Dombois, and P. M. Vitousek. 1995. Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology* 75: 1407–1424.
- Daehler, C. C., M. Yorkston, W. Sun, and N. Dudley. 1999. Genetic variation in morphology and growth characters of *Acacia koa* in the Hawaiian Islands. *International Journal of Plant Science* 160: 767–773.
- El-Jaoual, T., and D. A. Cox. 1998. Manganese toxicity in plants. *Journal of Plant Nutrition* 21:353–386.
- Fernandez, J. Q. P., L. E. Dias, N. F. Barros, R. F. Novais, and E. J. Moraes. 2000. Productivity of *Eucalyptus camaldulensis* affected by rate and placement of two phosphorus fertilizers to a Brazilian Oxisol. *Forest Ecology and Management* 127: 93–102.
- Fisher, R. F., and A. S. R. Juo. 1995. Mechanisms of tree growth in acid soils. In *Nitrogen fixing trees for acid soils*, eds. D. O. Evans and L. T. Szott, 1–18. Morrilton, AR: Winrock International and Nitrogen Fixing Tree Association.
- Foy, C. D., R. L. Chaney, and M. C. White. 1978. The physiology of metal toxicity in plants. *Annual Review of Plant Physiology* 29:511–566.

- Foy, C. D., B. J. Scott, and J. A. Fisher. 1988. Genetic differences in plant tolerance to manganese toxicity. In *Manganese in soils and plants*, eds. R. D. Graham, R. J. Hannam, and N. C. Uren, 293-307. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Fox, R. L., and E. J. Kamprath. 1970. Phosphate sorption isotherms for evaluating the P requirement of soils. *Soil Science Society of America Proceedings* 34: 902-907.
- Graham, P. H. 1992. Stress tolerance in *Rhizobium* and *Bradyrhizobium*, and nodulation under adverse soil conditions. *Canadian Journal of Microbiology* 38: 475-484.
- Graham, R. D., R. T. Leonard, and J. A. Menge. 1981. Membrane-mediated decrease in root exudation responsible for phosphorus inhibition of vesicular-arbuscular mycorrhiza formation. *Plant Physiology* 68: 548-552.
- Habte, M., and N. W. Osorio. 2001. *Arbuscular mycorrhizas: Producing and applying arbuscular mycorrhizal inoculum*. Honolulu, HI: Department of Tropical Plant and Soil Sciences, College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa.
- Habte, M., R. L. Fox, and R. L. Huang. 1987. Determining vesicular-arbuscular effectiveness by monitoring P status of subleaves of an indicator plant. *Communications in Soil Science and Plant Analysis* 18: 1403-1420.
- Habte, M., S. C. Miyasaka, and D. T. Matsuyama. 2001. Arbuscular mycorrhizal fungi improve early forest-tree establishment. In *Plant nutrition—food security and sustainability of agro-ecosystems through basic and applied research*, eds. W. J. Horst, M. K. Schenk, A. Bürkert, N. Claassen, H. Flessa, W. B. Frommer, H. E. Goldbach, H.-W. Olf, V. Römheld, B. Sattelmacher, U. Schmidhalter, S. Schubert, N. von Wirén, and L. Wittenmayer, 644-645. Dordrecht, The Netherlands: Kluwer Academic Publishers.
- Harrington, R. A., and J. H. Fownes. 1993. Allometry and growth of planted and coppice stands of four fast-growing tropical tree species. *Forest Ecology and Management* 56:315-327.
- Harrington, R. A., J. H. Fownes, F. C. Meinzer, and P. G. Scowcroft. 1995. Forest growth along a rainfall gradient in Hawaii: *Acacia koa* stand structure, productivity, foliar nutrients, and water- and nutrient-use efficiencies. *Oecologia* 102: 277-284.
- Herbert, D. A., and J. H. Fownes. 1995. Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. *Biogeochemistry* 29: 223-235.
- Herbert, D. A., J. H. Fownes, and P. M. Vitousek. 1999. Hurricane damage to a Hawaiian forest: Nutrient supply rate affects resistance and resilience. *Ecology* 80: 908-920.
- Hue, N. V., J. A. Silva, G. Uehara, R. T. Hamasaki, R. Uchida, and P. Bunn. 1998. *Managing manganese toxicity in former sugarcane soils on Oahu*. Honolulu, HI: Cooperative Extension Service, College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa.

- Hue, N. V., R. Uchida, and M. C. Ho. 2000. Sampling and analysis of soils and plant tissues. In *Plant nutrient management in Hawaii soils: Approaches for tropical and subtropical agriculture*; eds. J. A. Silva, and R. Uchida, 23–30. Honolulu, HI: College of Tropical Agriculture and Human Resources, University of Hawaii at Manoa.
- Hue, N. V., S. Vega, and J. A. Silva. 2001. Manganese toxicity in a Hawaiian Oxisol affected by soil pH and organic amendments. *Soil Science Society of America Journal* 65: 153–160.
- Lesueur, D., H. G. Diem, M. Dianda, and C. LeRoux. 1993. Selection of *Bradyrhizobium* strains and provenances of *Acacia mangium* and *Faidherbia albida*: Relationship with their tolerance to acidity and aluminum. *Plant and Soil* 149: 159–166.
- Ma, J. F., P. R. Ryan, and E. Delhaize. 2001. Aluminum tolerance in plants and the complexing role of organic acids. *Trends in Plant Science* 6:273–278.
- Marschner, H. 1995. Adaptation of plants to adverse chemical soil conditions. In *Mineral Nutrition of Higher Plants*, 2nd edition, 596–679. London: Academic Press.
- Miyasaka, S. C., M. Habte, and D. T. Matsuyama. 1993. Mycorrhizal dependency of two Hawaiian endemic tree species: Koa and mamane. *Journal of Plant Nutrition* 16: 1339–1356.
- Nambiar, E. K. S., and A. G. Brown. 1997. *Management of soil, nutrients, and water in tropical plantation forests*. Canberra, Australia: Australian Centre for International Agricultural Research.
- Netera, S. N., B. Palmer, and R. A. Bray. 1992. Differential response to phosphorus and lime of two accessions of *Calliandra calothyrsus* on an acid soil. *Nitrogen Fixing Tree Research Reports* 10: 62–65.
- Niang, A. I., E. Styger, A. Gahmanyi, and J. Ugeziwe. 1995. Comparative growth of 15 exotic species and provenances in high-elevation acid soils of Rwanda. In *Nitrogen fixing trees for acid soils*, eds. D. O. Evans and L. T. Szott, 207–214. Morrilton, AR: Winrock International and Nitrogen Fixing Tree Association.
- Pearson, H. L., and P. M. Vitousek. 2001. Stand dynamics, nitrogen accumulation, and symbiotic nitrogen fixation in regenerating stands of *Acacia koa*. *Ecological Applications* 11: 1381–1394.
- Raich, J. W., A. E. Russell, T. E. Crews, H. Farrington, and P. M. Vitousek. 1996. Both nitrogen and phosphorus limit plant production on young Hawaiian lava flows. *Biogeochemistry* 32: 1–14.
- Rock, J. F. 1920. *The leguminous plants of Hawaii*. Honolulu, HI: Hawaii Sugar Planters' Association.
- St. John, H. 1979. Classification of *Acacia koa* and relatives (Leguminosae): Hawaiian plant studies 93. *Pacific Science* 33: 357–367.
- Sanchez, P. A., and J. G. Salinas. 1981. Low-input technology for managing Oxisols and Ultisols in tropical America. *Advances in Agronomy* 34: 279–406.

- Stamford, N. P., A. D. Ortega, F. Temprano, and D. R. Santos. 1997. Effects of phosphorus fertilization and inoculation of *Bradyrhizobium* and mycorrhizal fungi on growth of *Mimosa caesalpiniaefolia* in an acid soil. *Soil Biology and Biochemistry* 29: 959–964.
- Stewart, B. A., R. Lal, and S. A. El-Swaify. 1991. Sustaining the resource base of an expanding world agriculture. In *Soil management for sustainability*, eds. R. Lal and F. J. Pierce, 125–144. Ankeny, IA: Soil and Water Conservation Society.
- Sun, W., J. L. Brewbaker, and M. T. Austin. 1997. Genetic variations of *Acacia koa* seed, seedling, and early growth traits. In *Koa: A Decade of Growth: Proceedings of the Symposium*, eds. L. Ferentinos and D. O. Evans, 33–37. Honolulu, HI: Hawaii Forest Industry Association.
- Tanner, E. V. J., V. Kapos, and W. Franco. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology* 73: 78–86.
- Tanner, E. V. J., V. Kapos, S. Freskos, J. R. Healey, and A. M. Theobald. 1990. Nitrogen and phosphorus fertilization of Jamaican montane forest trees. *Journal of Tropical Ecology* 6: 231–238.
- Tanner, E. V. J., P. M. Vitousek, and E. Cuevas. 1998. Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* 79: 10–22.
- Vitousek, P. M., and H. Farrington. 1997. Nutrient limitation and soil development: Experimental test of a biogeochemical theory. *Biogeochemistry* 37: 63–75.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, and P. A. Matson. 1993. Nutrient limitations to plant growth during primary succession in Hawaii Volcanoes National Park. *Biogeochemistry* 23: 197–215.
- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1990. *Manual of the flowering plants of Hawai'i*, Vol. 1. Honolulu, HI: Bishop Museum and University of Hawaii Press.
- Walters, G. A. 1981. Why Hawaii is changing to the dibble-tube system of reforestation. *Journal of Forestry* 79: 743–745.
- Wan Rasidah, bt. A. K., A. bt. Hamsah, and P. Sundralingam. 1988. Effect of nitrogen and phosphorus on the early growth of three exotic plantation species in peninsular Malaysia. *Journal of Tropical Forest Science* 1: 178–186.
- Wang, X., R. S. Yost, and B. A. Linnquist. 2001. Soil aggregate size affects phosphorus desorption from highly weathered soils and plant growth. *Soil Science Society of America Journal* 65: 139–146.
- Xu, D., B. Dell, N. Malajczuk, and M. Gong. 2001. Effects of P fertilization and ectomycorrhizal fungal inoculation on early growth of eucalyptus plantations in southern China. *Plant and Soil* 233: 47–57.