Genetic Variation in Morphology and Growth Characters of Acacia koa in the Hawaiian Islands

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Substantial phenotypic variation in *Acacia koa* has been reported in the Hawaiian Islands. We grew 72 *A. koa* families from the islands of O‘ahu, Kaua‘i, and Hawai‘i in two common gardens to determine whether phenotypic differences in phyllode morphology, extrafloral nectary morphology, and other characters have a genetic basis. Significant differences among islands and families were observed for phyllode width, curvature, and pubescence, as well as extrafloral nectary size and pigmentation, retention of juvenile leaves, and branch bark color. Seed shape also differed significantly among islands. Discriminant analysis revealed that families from the island of Hawai‘i are distinct from O‘ahu and Kaua‘i families. The O‘ahu and Kaua‘i families, however, could not be reliably distinguished based on sapling morphology or growth characters.

**Keywords:** ecology, *Acacia koa*, forestry, genetic variation, Hawaiian Islands, morphology, phyllodes, seeds.

**Introduction**

In forests of the Hawaiian Islands, endemic *Acacia koa* A. Gray is a dominant canopy tree that can grow to 35 m in height. *Acacia koa* (commonly called koa) is present on all six of the main Hawaiian Islands, growing in moist habitats at elevations from 90 to 2100 m (Whitesell 1990). Large koa trees were traditionally used by Hawaiians to construct seafaring canoes (Cuddihy and Stone 1990). Today, koa wood is used in high-quality furniture and other woodcrafts, making koa one of the most economically important native species in the Hawaiian Islands.

The evolutionary relationship of *A. koa* to other *Acacia* species is uncertain, but it has been placed in the subgenus *Heterophyllum* and may share a common ancestor with an Australian species, such as *Acacia melanoxylon* (Wagner et al. 1990). Both species are phyllodinous, initially bearing primary leaves that are replaced by phyllodes in the sapling stage. Curiously, phyllodes of *koa* have been reported to have functional extrafloral nectaries on the adaxial surface, despite the fact that no ant species are native to the Hawaiian Islands (Keeler 1985). Phenotypic variation among trees in extrafloral nectaries is substantial (C. Daehler, personal observation). In addition to extrafloral nectary variation, early taxonomists noted other phenotypic differences among *koa* populations on different islands and across altitudinal gradients (Hillebrand 1888). Some of the most striking differences are in phyllode width and shape (St. John 1979). Rock (1919) and Judd (1920) suggested that phyllode shape was environmentally determined, with broad phyllodes developing in response to high altitude, fog, and mist. Based on casual field observations, Lamoureux (1971) postulated that both genetic and environmental factors may determine phyllode shape.

While much effort has been directed toward developing commercial koa wood plantations in the Hawaiian Islands (Whitesell 1990; Brewbaker et al. 1991; Loudat and Kanter 1996), surprisingly little has been published about the extent of genetic variation in this phenotypically variable species. Two recent studies have indicated that *koa* populations are genetically diverse. An isozyme survey showed substantial polymorphism within *koa* populations (Conkle 1996). Populations from O‘ahu, Maui, and Kaua‘i shared similar allele frequencies, while plants screened from the island of Hawai‘i had some unique alleles and substantially different allele frequencies (Conkle 1996). In the interest of identifying superior koa stock for silviculture, Sun (1996) reported variation in seed characters, seedling growth and color, phyllode development, sapling size, and survival among *koa* maternal families growing under greenhouse and common garden conditions on the islands of O‘ahu and Hawai‘i. Based on this variation, Sun et al. (1996) suggested a strong potential for genetic improvement of *koa* through selection.

The purpose of this study was to determine whether phenotypic differences in phyllode shape, extrafloral nectary development, and other distinctive morphological and growth characters in *koa* have a genetic basis. To address this question, we grew *koa* maternal families from the islands of O‘ahu, Kaua‘i and Hawai‘i in two common gardens and tested for significant variation among islands and among families within islands. Finally, we employed discriminant analysis to determine whether *koa* from O‘ahu, Kaua‘i and Hawai‘i can be reliably distinguished based on seed characters and genetically based differences in sapling morphology and growth. This study addresses the long-standing controversy over whether *koa* phyllode shape has a large genetic component (Lamoureux 1971) while also identifying additional genetically variable
characters of potential ecological, taxonomic, and silvicultural importance.

**Material and Methods**

*Seed Collections and Measurements*

Seeds of *Acacia koa* used for this study were collected from the islands of O‘ahu, Kaua‘i, and Hawai‘i as part of a larger effort to collect and store koa germplasm (Sun 1996). Each collection used in this study was made from a single tree. Trees were usually at least 100 m apart and from widely scattered sites on each island. In our study, 72 families from a range of elevations were represented (O‘ahu, 100–600 m; Kaua‘i, 800–1200 m; and Hawai‘i, 500–1600 m). In a recent taxonomic treatment, two highly localized Hawaiian species, *Acacia kauaiensis* Hillebr. and *Acacia koa* Hillebr., were lumped with *A. koa stricto* and considered as a single species, *Acacia koa sensu lato* (Wagner et al. 1990). However, for this study, we used only seeds collected from *A. koa stricto* (Wagner et al. 1990). Based on protandry and low seed set following pollinator exclusion (Lanner 1965), as well as failure of seeds to develop following controlled self-pollinations (W. Sun and N. Dudley, unpublished data), the mating system of koa has been considered as primarily outcrossing. Despite these experimental results, lone, isolated trees have sometimes produced seeds, suggesting that self-fertility is possible under some circumstances.

Seed size, shape, and mass were measured for 42 single tree collections (families). Three sets of 10 randomly chosen seeds were weighed for each family. Seed length, width, and lateral surface area (one side) were measured from computer-scanned images of 25–35 seeds per family with the assistance of Sigma Scan Pro 4.01 software (Jandel Scientific, San Rafael, Calif.).

**Common Garden Plots**

Two separate common garden plots were established on the island of O‘ahu. The main plot was at the Hawai‘i Agriculture Research Center’s Maunawili breeding station on the windward side of O‘ahu. This site is at an elevation of 180 m and receives ca. 100–350 cm of rainfall annually. The average temperature at Maunawili is 23°C, while the soil order is ultisol (Lokekea series), with a pH of ca. 5.0. The second plot was located at Opaeula on the north shore of O‘ahu at an altitude of 400 m. This site was a former sugarcane field and has ultisol soils (Leilehua series) with a pH of ca. 5.0. Rainfall at the Opaeula site ranges from 180 to 230 cm/yr and is distributed more seasonally than at the Maunawili site. Most rainfall occurs from October to April. Temperatures at the Opaeula site are slightly cooler than at Maunawili, averaging 21°C.

Before planting, seeds were nicked at the distal end with nail clippers to break dormancy. Nicked seeds were planted into 5-in dibble tubes containing a mixture of Perlite (Black Magic Products, Elk Grove, Calif.) and peat moss (sphagnum) (1:3), supplemented with 100 g/m² Osmocote 14-14-14 fertilizer (Scotts-Sierra, Marysville, Ohio). This mixture was inoculated with *Rhizobia* (group C) isolated from wild *A. koa* (Niftal, 1000 Holomua Road, Paia, Maui, Hawai‘i). After 8 wk in a greenhouse at Waimanalo, O‘ahu, seedlings were transferred to outdoor benches in full sun and maintained for 6 wk before transplanting into the field plots. During this time, plants were saturated once per week with a solution (1.25 g/L) of Peters Professional Foliar Feed 20-20-20 (Scotts-Sierra, Marysville, Ohio). At the time of field planting, seedlings were 20–50 cm tall.

Before planting, both field sites were disked and sprayed with Roundup (Monsanto, St. Louis) to control weeds. A randomized block design was employed at both sites. The Maunawili site consisted of two blocks, while the Opaeula site consisted of three blocks. At both sites, each block consisted of subplots containing 16 saplings of the same family in a 4 × 4 arrangement. Spacing between saplings was 1 × 1.5 m. The Opaeula plot was planted in April 1997 with 11 families per block, while the Maunawili plot was planted in May 1997 with 50 replicated families and 22 unreplicated families. For this study, the only families analyzed from the Opaeula plot were those that had also been planted at the Maunawili plot (six families). During the first 3 mo, drip irrigation was used at both sites to increase transplant survival. Weed control was performed ca. every 3 mo using the herbicide Fusillade (Zeneca Agro, Wilmington, Del.).

**Common Garden Field Measurements**

Plants at both sites were surveyed after 1 yr of growth in the field plots (April and May 1998 for Opaeula and Maunawili, respectively). An average of five trees (with a range of two to eight) per family per block were scored for color of bark on young branches, presence or absence of forking of the main trunk, and proportion of branches maintaining juvenile leaves. In addition, at the Maunawili plot, plant height (to the nearest centimeter) was recorded after 8 mo of growth (in January 1998).

**Phyllode and Nectary Morphology**

At both sites, three phyllodes were collected from each of three haphazardly chosen trees per family per block (1059 total phyllodes). Each phyllode was collected from a different haphazardly chosen branch on sampled trees. The fifth or sixth phyllode from the end of the branch was sampled in all cases to ensure that sampled phyllodes were fully developed and approximately the same age. Phyllodes were transferred to plastic bags for measurement in the laboratory.

In the laboratory, phyllodes were measured to the nearest millimeter for width at the widest point, length from end to end following the midvein (curved length), and length from end to end using a straight ruler (straight length). Phyllode area was measured using a Li-Cor 3000A leaf area meter (Li-Cor, Lincoln, Nebr.). Pubescence was scored as present or absent (plainly visible without a hand lens). Length of the structure attaching the phyllode to the branch (hereafter referred to as the petiole) was measured to the nearest millimeter. Diameter of the extrafloral nectary on the adaxial surface of phyllodes was measured to the nearest 0.1 mm under a dissecting microscope at ×24 magnification. Extrafloral nectaries were scored for presence or absence of red pigmentation and the presence or absence of a well-defined external pore (Bough-ton 1981).
Table 1
Mean Measurements of *Acacia koa* Seeds, by Island

<table>
<thead>
<tr>
<th>Island</th>
<th>Length (mm)</th>
<th>Width (mm)</th>
<th>Length/width</th>
<th>Area (mm²)</th>
<th>Mass of 10 seeds (g)</th>
<th>Families scored</th>
</tr>
</thead>
<tbody>
<tr>
<td>Oʻahu</td>
<td>8.7**</td>
<td>4.8</td>
<td>1.8</td>
<td>33</td>
<td>0.46</td>
<td>12</td>
</tr>
<tr>
<td>Kauaʻi</td>
<td>10.1</td>
<td>4.8</td>
<td>2.1**</td>
<td>39</td>
<td>0.6</td>
<td>4</td>
</tr>
<tr>
<td>Hawaiʻi</td>
<td>10.8</td>
<td>6.2**</td>
<td>1.8</td>
<td>52**</td>
<td>0.88*</td>
<td>21</td>
</tr>
</tbody>
</table>

* Significant difference from Oʻahu; Tukey test for multiple comparisons, *P* < 0.01.
** Significant difference from other islands; Tukey test for multiple comparisons, *P* < 0.01.

Statistical Analysis

All analyses were conducted using Systat 8.0 software (Jandel Scientific, San Rafael, Calif.). Seed size and shape differences among islands were assessed using ANOVA and post hoc contrasts between island means, using Tukey tests for multiple comparisons (Wilkinson 1998). Differences in phyllode, nectary, and growth measurements among islands were analyzed for the Maunawili site, using a blocked ANOVA with island as a fixed factor and family nested within island as a random factor. A second ANOVA using only the six families shared between the Maunawili and Opaekula sites was used to test for growth character differences between sites. Discriminant analyses using stepwise addition of variables (Engelman 1998) were performed on family means for seed measurements and family means of phyllode, nectary, and growth characters at the Maunawili site to determine whether linear combinations of characters could be used to discriminate families from different islands. Approximately 25% of the data were reserved for cross validation of the discriminant functions (Engelman 1998). Separate discriminant analyses were necessary for seed characters and sapling characters because different sets of families were used for these measurements.

Results

Seed Size and Shape

In comparing *Acacia koa* seeds from Oʻahu, Kauaʻi and Hawaiʻi, seeds from Hawaiʻi were significantly larger in terms of width, area, and mass when compared with seeds from Oʻahu and Kauaʻi (table 1). Oʻahu seeds were significantly smaller in terms of length than seeds from Hawaiʻi and Kauaʻi, while seeds from Kauaʻi had a significantly larger length : width ratio (table 1). Although there were significant differences in mean measurements among islands, there was also overlap in measurements of individual seeds from the different islands. For example, the lightest Hawaiʻi seeds were similar in mass to the heaviest seeds from Oʻahu. A discriminant analysis using a combination of characters proved better than individual characters for distinguishing seeds from different islands. The variables seed length, seed diameter, and seed mass were highly significant in the discriminant analysis. The first canonical discriminant function discriminated seeds from Hawaiʻi from those of Oʻahu and Kauaʻi (X-axis of fig. 1). Standardized coefficients for the first canonical discriminant function were 0.95 (length), 1.7 (diameter), and −1.7 (weight), where the distance of the coefficient from zero gives an indication of the relative contribution of each variable to the function (Engelman 1998). The second function discriminated Kauaʻi from Oʻahu and Hawaiʻi (Y-axis of fig. 1). Standardized coefficients for the second canonical discriminant function were 0.66 (length), −1.8 (diameter), and 1.4 (weight). The classification functions derived for each island (table 2) can be used to classify koa seed of unknown origin based on seed measurements. The discriminant function analysis correctly classified all families in the reserve data, but in the data used to build the model, one Oʻahu family was misclassified as a Hawaiʻi family (table 3).

Common Garden Measurements of Morphology and Growth at Maunawili

Phyllodes from Hawaiʻi families were significantly larger in terms of surface area than those from Oʻahu and Kauaʻi (table 4; fig. 2). This difference was caused by greater width of phyllodes of the Hawaiʻi families (averaging more than twice as broad), rather than greater length (table 4). When only families collected from comparable altitudes (ca. 500 m) were compared, families from the island of Hawaiʻi still had broader phyllodes than families from Oʻahu (2.7 cm vs. 1.5 cm, re-
respectively). The ratio of the phyllode straight length relative to curved length gives an indication of the degree of phyllode curvature. The significantly greater straight length:curved length ratio of the phyllodes of Hawai'i families (table 4) indicates that they were less curved, on average, than phyllodes from O'ahu and Kaua'i families. Families from the island of Hawai'i also had a larger percentage of phyllodes exhibiting obvious pubescence.

Phyllode differences were accompanied by significant differences in extrafloral nectary morphology. Mean nectary diameter was smaller for families from Hawai'i when compared with families from O'ahu and Kaua'i (table 4). Furthermore, families from Hawai'i had nectaries with significantly less red pigmentation than families from O'ahu and Kaua'i (table 4). On average, ca. 20% of nectaries lacked an external pore leading to the internal nectary cavity, but there were no significant differences among islands in frequency of porelessness (table 4). Cross sections made through ca. 20 poreless nectaries using a razor blade revealed that poreless nectaries had internal cavities, but these cavities were sealed by a layer of tissue over the top of the nectary.

Saplings of families from Hawai'i were significantly shorter than those from O'ahu and Kaua'i after 8 mo of growth on O'ahu (table 5). After 1 yr of growth, Kaua'i families averaged significantly greater retention of juvenile leaves (table 5). Families from Hawai'i averaged less forking of the main trunk, but this difference was not statistically significant (table 5). Families from Kaua'i often had dark red or purple branch bark, while the young branches of families from Hawai'i were usually green (table 5).

Significant variation among families within islands was observed for several characters (tables 4, 5). One of the most obvious differences among families was in the degree of juvenile leaf retention (table 5). After a year of growth, some families consistently retained juvenile leaves on most branches, while other families had developed phyllodes on all branches. Juvenile leaf retention rate was not significantly correlated with sapling height differences among families ($r = 0.05$, $P = 0.62$).

### Table 3

**Success Rates for Classification of *Acacia koa* Seeds from Different Islands Based on Discriminant Analysis**

<table>
<thead>
<tr>
<th>Island</th>
<th>Model-building data</th>
<th>Reserve data</th>
</tr>
</thead>
<tbody>
<tr>
<td>O'ahu</td>
<td>9/10 (90%)</td>
<td>3/3 (100%)</td>
</tr>
<tr>
<td>Kaua'i</td>
<td>3/3 (100%)</td>
<td>1/1 (100%)</td>
</tr>
<tr>
<td>Hawai'i</td>
<td>15/15 (100%)</td>
<td>5/5 (100%)</td>
</tr>
</tbody>
</table>

### Discussion

**Seed Morphology**

Clear differences were observed among koa seeds from different islands; however, because seeds were not collected from mothers grown in a common environment, we cannot definitively determine the degree to which maternal environment, as opposed to genetic effects, influenced seed characters. Larger seed size on the island of Hawai'i was not because of a thicker seed coat but was because of larger cotyledons (C. Daehler, personal observation). The larger seed size of Hawai'i families did not result in larger saplings in the O'ahu common garden. The conclusion that Kaua'i seeds are more elongate than

### Table 4

**Comparison of Phyllode and Nectary Characters of *Acacia koa* from Different Islands When Grown Together in a Common Field Plot**

<table>
<thead>
<tr>
<th>Phyllodes:</th>
<th>Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Curved length (cm)</td>
<td>O'ahu 17.8</td>
</tr>
<tr>
<td>Straight length (cm)</td>
<td>14.9</td>
</tr>
<tr>
<td>Width (cm)</td>
<td>1.4</td>
</tr>
<tr>
<td>Curved length/width</td>
<td>13.0</td>
</tr>
<tr>
<td>Area ($cm^2$)</td>
<td>17.8</td>
</tr>
<tr>
<td>Pubescent</td>
<td>6</td>
</tr>
<tr>
<td>Petiole (mm)</td>
<td>6</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Nectaries:</th>
<th>Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nectary diameter</td>
<td>1.4</td>
</tr>
<tr>
<td>Definite pore</td>
<td>83</td>
</tr>
<tr>
<td>Red pigmentation</td>
<td>58</td>
</tr>
</tbody>
</table>

Total families scored: 8 7 35 ns

* Variation among families within islands.

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Significant differences were observed between the two planting sites. Among the six families planted at both sites, phyllodes from 1-yr-old saplings averaged larger at the Opaeula site in terms of width but not length (table 6). In addition, nectaries at the Opaeula site were significantly larger, and nectary pigmentation was significantly less. There were no significant family-by-site interactions.

Discriminant analysis based on morphology and growth characters successfully distinguished most families from the island of Hawai'i, but many O'ahu families were misclassified as Kaua'i families (table 7; fig. 3). The first canonical discrimination function separated Hawai'i families from O'ahu and Kaua'i families. Variables involved in the first function and their standardized coefficients were curved length:width ratio (1.00), straight length (-0.49), branch color (0.16), and juvenile leaf retention (0.03) (X-axis of fig. 3). The second canonical discrimination function was of little value in separating families from different islands (Y-axis of fig. 3). On the canonical score plot, Kaua'i families appear to be nested within the more loosely clustered O'ahu families (fig. 3).

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Comparison of Morphology between Maunawili and Opaeula Common Gardens

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### Table 5

Comparison of Growth Characters in *Acacia koa* from Different Islands When Grown Together in a Common Field Plot

<table>
<thead>
<tr>
<th>Island</th>
<th>O'ahu</th>
<th>Kaua'i</th>
<th>Hawai'i</th>
<th>Family</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height after 8 mo (m)</td>
<td>1.38</td>
<td>1.51</td>
<td>1.10**</td>
<td>++</td>
</tr>
<tr>
<td>Juvenile leavesb</td>
<td>35</td>
<td>51*</td>
<td>38</td>
<td>++</td>
</tr>
<tr>
<td>Forked trunkc</td>
<td>69</td>
<td>71</td>
<td>55</td>
<td>ns</td>
</tr>
<tr>
<td>Branch colorationd</td>
<td>1.9**</td>
<td>2.3**</td>
<td>1.5**</td>
<td>++</td>
</tr>
<tr>
<td>Families surveyed</td>
<td>9</td>
<td>8</td>
<td>49</td>
<td>ns</td>
</tr>
</tbody>
</table>

* Variation among families within islands.

b Average percentage of plant branches exhibiting juvenile leaves in 1-yr-old saplings. Branches containing a mixture of phyllodes and juvenile leaves were classified as exhibiting juvenile leaves.

c Average percentage of trees per family exhibiting a major fork in the trunk at least 50% as wide as the main trunk, within 1 ft of the ground.

d Color of young branch bark, on a scale of 1 to 3 (light to dark), where 1 = no coloration (green), 2 = light brown/red, and 3 = dark red/purple.

* Significant difference from other islands; Tukey test for multiple comparisons, \( P < 0.05 \).

** Significant difference from other islands; Tukey test for multiple comparisons, \( P < 0.01 \).

### Table 6

Comparison of Phyllode and Nectary Morphology between Maunawili and Opaeula Field Plots

<table>
<thead>
<tr>
<th>Character</th>
<th>Site difference</th>
<th>Family-by-site interaction</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phyllodes:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Curved length (cm)</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Straight length (cm)</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Width (cm)</td>
<td>**</td>
<td>ns</td>
</tr>
<tr>
<td>Curved length/width</td>
<td>**</td>
<td>ns</td>
</tr>
<tr>
<td>Area (cm²)</td>
<td>**</td>
<td>ns</td>
</tr>
<tr>
<td>Pubescence¹</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Petiole (mm)</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Nectaries:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nectary diameter</td>
<td>*</td>
<td>ns</td>
</tr>
<tr>
<td>Definite poreb</td>
<td>ns</td>
<td>ns</td>
</tr>
<tr>
<td>Red pigmentationc</td>
<td>*</td>
<td>ns</td>
</tr>
</tbody>
</table>

* Percentage of phyllodes exhibiting pubescence visible without magnification.

b Percentage of nectaries having a definite external pore leading the central cavity.

c Percentage of nectaries with red pigmentation.

* Significant difference, Opaeula > Maunawili, \( P < 0.05 \), \( P > 0.01 \).

** Significant difference, Opaeula > Maunawili, \( P < 0.01 \).

+ Significant difference, Maunawili > Opaeula, \( P < 0.05 \).

O'ahu seeds is based on only a few seed samples from Kaua'i trees. However, this difference between O'ahu and Kaua'i seeds appears to be robust, based on independent measurements by Sun (1996). Average seed length for 15 families from Kaua'i was 10.0 mm (compared with 10.1 in this study), while O'ahu seeds averaged only 8.9 mm (Sun 1996).

** Sapling Morphology and Growth Characters**

Measurements of phyllodes and other characters were made more than a year after germination. In this study, we assume that maternal effects, which may have have affected the growth of young plants (Roach and Wulff 1987), did not strongly influence morphology and growth characters of the year-old saplings. Competition, which can prolong maternal effects (Stratton 1989), was minimized in our field plots by sapling spacing and weed suppression. Families used in this study were probably only half-sibs (some families might have been full sib), and only two replicates per family were available for study at Maunawili. Because of the low statistical power of this design, only characters with large genetic components are likely be statistically significant. If all full-sib families and

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**Fig. 2** Genetic differences in phyllode shape between *Acacia koa* populations from (A) O'ahu and (B) Hawai'i as revealed by growth in a common garden.
more replicates per family had been used, additional significant differences among families may have been observed.

*Acacia koa* from the island of Hawai’i had previously been noted to have broader phyllodes than *koa* from other islands (Hillebrand 1888; St. John 1979). The maintenance of the broad phyllode phenotype in our common garden on O’ahu indicates a genetic basis for this trait. Genetic variation in phyllode width has been reported in other *Acacia* species (Cody 1989; Morrison and Rupp 1995). In *Acacia suaveolens*, wider phyllodes were associated with larger seeds, as in *koa* (Morrison and Rupp 1995). Phyllode width also differed between common garden sites, averaging 3 mm wider at Opaekua, but this site difference is much smaller than between island differences within sites (table 1). Morphological differences in phyllodes may be adaptations for specific environments (Cody 1989); however, further studies are needed to confirm this speculation. Differences among families in retention of juvenile leaves are probably also adaptations to specific environments. Juvenile leaves have higher photosynthetic capacity than phyllodes, allowing more rapid growth; however, phyllodes confer superior drought tolerance (Walters and Bartholomew 1984; Hansen 1996).

*Acacia koa* from the island of Hawai’i had smaller extrafloral nectaries that were less pigmented and often obscured by pubescence. The red pigment associated with nectaries of *phyllodinous* *Acacia* spp. is probably anthocyanin (Knox et al. 1985), and these red nectaries attract bird pollinators in other *Acacia* species (Knox et al. 1985; Vanstone and Paton 1988). The reduced size and apparency of extrafloral nectaries in *koa* from Hawai’i, the youngest of the Hawaiian Islands, suggests that the nectaries have had little or no adaptive value. It is possible that red nectaries observed on the older islands were maintained to attract native bird pollinators. Alternatively, the red nectaries may simply be an ancestral condition, present in the original *Acacia* spp. that colonized the Hawaiian Islands, with no adaptive value on any of the Hawaiian Islands. We never observed birds feeding at the extrafloral nectaries of *koa* from any island; however, we did observe introduced ants feeding at nectaries on many occasions. Nectar feeding ants may be beneficial to *Acacia* species via several mechanisms, including defense against herbivores and local soil modification (e.g., Wagner 1997). Further studies are needed to determine whether the genetic variation that we have documented in nectary development can affect growth and survival among *koa* families as a result of differing degrees of ant colonization.

The Kaua’i and O’ahu populations could not be reliably distinguished based on phyllode, extrafloral nectary, or growth characters, suggesting that the two populations are closely related. Isozyme analyses by Conkle (1996) also suggest that Kaua’i and O’ahu populations are closely related. *Acacia koa sensu stricto* on Kaua’i occurs primarily in the northwest quarter of the island (on ridges in and around Waimea Canyon State Park). Sun (1996) noted that it is usually found along roadsides or trail sides and suggested that the population of *A. koa sensu stricto* on Kaua’i may have been planted using imported seeds from O’ahu or another island. Seeds from other islands were imported to Kaua’i during reforestation efforts in the 1930s (St. John 1979) or even earlier (Judd 1916). If *A. koa sensu stricto* on Kaua’i was imported from O’ahu, then differences in mean seed length, branch color, and juvenile leaf retention between O’ahu and Kaua’i populations might be explained by founder effects on Kaua’i. Classification functions like those we have presented here could help confirm the origin of other populations that are suspected of being planted with imported seeds.

We did not find statistically significant differences in rates of trunk forking among islands, but there was a trend toward lower average forking rates among families from Hawai’i. Forking will decrease the future value of *koa* trees for timber. Our measure of forking (presence or absence) was rather crude, and more detailed measures of the degree of forking might have resulted in detection of significant genetic differences in forking. Nevertheless, individuals within families exhibited substantial variation in trunk forking. Further experiments are needed to determine whether growing conditions within a plantation can be manipulated to promote the growth of trees with single, straight trunks. Such trees have been observed in some natural forests. Pruning of saplings might be one means of discouraging forking.

**Table 7**

<table>
<thead>
<tr>
<th>Island</th>
<th>Families correctly classified</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Model-building data</td>
</tr>
<tr>
<td>O’ahu</td>
<td>3/5 (60%)</td>
</tr>
<tr>
<td>Kaua’i</td>
<td>4/4 (100%)</td>
</tr>
<tr>
<td>Hawai’i</td>
<td>28/28 (100%)</td>
</tr>
</tbody>
</table>

**Fig. 3** Canonical scores plot showing separation of *Acacia koa* families from different islands based on sapling morphology and growth characters.

**Conclusions**

Over the past century, *koa* forests have declined in many places because of habitat destruction (including logging), invasive plants (Jacobi and Warshauer 1992), herbivore
outbreaks (Stein and Scowcroft 1984), and pathogens (Gardner 1996). There is now considerable interest in planting and managing koa forests both for conservation and to ensure sustainable yields for the growing koa wood industry. Our results indicate that koa in the Hawaiian Islands is genetically diverse. Any comprehensive plan to preserve koa should recognize this diversity. Acacia koa from the island of Hawai‘i is genetically distinct in terms of morphology and growth characters from that from O‘ahu and Kaua‘i and seems to deserve recognition as A. koa var. latifolia (Benth.) St. John, as proposed by St. John (1979) but not recognized by Wagner et al. (1990). Many of the genetic differences that we observed among families and populations likely have ecological significance, affecting growth rates and success in different environments. Although we could not immediately single out one family that was ideally suited for silviculture, the high degree of genetic variation in koa should permit selection for superior silvicultural lines that will grow well in forest plantations (Sun et al. 1996).

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