Review

Botany, Ecology and Diversity of *Acacia koa* in the Hawaiian Islands

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Abstract: *Acacia koa* (koa) is a valuable leguminous timber-wood tree endemic to the Hawaiian Islands. Over the past century, conversion of some native forests for agriculture and ranching, uncontrolled spread of invasive plant species and outbreak of a deadly fungal wilt disease severely reduced *A. koa* forests. However, recently there has been a growing interest in re-establishing *A. koa* as an agroforestry tree because the tree has significant importance in economy, ecology and culture of Hawai'i. This review presents the current knowledge on *A. koa,* including its ecological roles, various morphological forms, genetics, evolution and development of methods for seedling selection and propagation. A better understanding and awareness of the nature of *A. koa* will help successful development of wilt-resistant *A. koa* trees with high wood quality that can support Hawaii's ecology, economy and culture.

Keywords: *Acacia koa*, *Fusarium oxysporum*, *Acacia heterophylla,* Tree Legume, Timber-Wood Tree

Introduction

Acacia koa A. Gray (koa) is an important leguminous tree endemic to the Hawaiian Islands (Fig. 1). It is a member of the legume family (Fabaceae) and the mimosa subfamily (Mimosoideae). The native A. koa forests are broadly distributed across all five major Hawaiian Islands, Hawai'i, Moloka'i, Maui, Lāna'i, O'ahu and Kaua'i (Wagner *et al*., 1999). It is the largest native tree of the Hawaiian Islands and can grow up to 35 m (Elevitch *et al*., 2006). *Acacia koa* serves as a vital resource for the Hawaiian Islands, providing benefits ecologically, culturally and economically. First, as a nitrogen-fixing legume, it enhances soil fertilities of forests besides providing habitats for many native fauna and flora, including the endangered Hawaiian honeycreepers, such as 'akiapōlā'au (*Hemignathus munroi*) and 'ākepa (*Loxops coccinea;* Sakai, 1988; Whitesell, 1990; Elevitch *et al*., 2006; Baker *et al*., 2009). Also, epiphytes, such as *Korthalsella platyphylla* and lichens, can be often observed on *A. koa* (Fig. 2). Culturally, *A. koa*, with the word "koa" meaning bravery or warrior in Hawaiian, provides a valuable wood to native Hawaiians. It was traditionally associated with royalty and was used to make outrigger canoes for fishing, racing and voyaging, canoe paddles, spears, surfboards and ukuleles (Abbott, 1992; Krauss, 1993; Elevitch *et al*., 2006; Baker *et al*., 2009). In addition, due to

the beautiful texture, hardiness and carving quality of the wood, the *A. koa* timber, also referred to as Hawaiian mahogany, is a highly priced commodity with a current market value of up to $125 per board foot (Baker *et al*., 2009). The wood color, varying from blond to dark red and the grain figures, ranging from plain to curly (highly figured), are the most important determinants of the price; curly wood with a dark red color is the most highly valued (Baker *et al*., 2009). The wood is used for fine furniture, decorative items, musical instruments and jewelry. The gross value of *A. koa* timber and the wood products produced is estimated to be in the range of $20-$30 million annually (Yanagida *et al*., 2004; Baker *et al*., 2009).

General Characteristics

Acacia koa is found in a broad range of habitats; it grows at elevations from near sea level to 2000 m in mesic or wet forests with annual rainfall from 1850 to 5000 mm (Harrington *et al*., 1995; Anderson *et al*., 2002; Wilkinson and Elevitch, 2003; Baker *et al*., 2009). It is a fast-growing tree, growing at the rate of ~1.5 m in height per year for the first five years under favorable conditions (Elevitch *et al*., 2006). It typically reaches heights of 15-25 m with a canopy spread of 6-12 m, but some populations have a smaller and shrubbier form (Elevitch *et al*., 2006; Baker *et al*., 2009).

Fig. 1. *A. koa* tree with the ground covered by *Dicranopteris linearis* (uluhe), the Aiea Loop Trail, Aiea, Hawaiʻi

Fig. 2. Epiphytes on *A. koa* stems: (a) *Korthalsella platyphylla* (b) lichens

Acacia koa belongs to the *Acacia* subgenus *Phyllodinae,* recognized by their unique phyllode "leaves" in mature plants. It produces two types of leaves throughout its life cycle; young trees have bipinnately compound true leaves with 12 to 24 pairs of leaflets (Fig. 3a), whereas mature plants produce phyllodes, which are sickle-shaped pseudo-leaves derived from the flattened petioles (Fig. 3c). Phyllodes are 7 to 25 cm long and 0.5 to 5 cm wide (Rock, 1919; Elevitch *et al*., 2006). There is also a transitional form having both flattened petiole and bipinnate leaves (Fig. 3b). Multiple hypotheses have been made to explain the change from true leaves to phyllodes; true leaves may be more important in earlier developmental fast-growing stages, while phyllodes provide the plant higher tolerance to drought (Walters and Bartholomew, 1984; 1990; Hansen, 1986; 1996; Hansen and Steig, 1993).

Pasquet-kok *et al*. (2010) tested these hypotheses on *A. koa* and observed that true leaves showed higher mass-based gas exchange necessary for growth; on the other hand, phyllodes had characteristics for drought tolerance, which is due to greater capacitance of the water storage tissue and its ability to keep stomata closed under hot and dry conditions. Furthermore, the orientation of the leaf types may support these hypotheses; the true leaves, which spread horizontally, absorb more irradiance within small canopies under shadows, whereas the vertically arranged phyllodes protect the plant from intense sunlight (Walters and Bartholomew, 1984; Hansen, 1986; 1996). With lower sunlight, a tree with phyllodes can switch back to true leaf production (Walters and Bartholomew, 1984); such phenomena can be observed in a tree which has true leaves on lower branches while having phyllodes on higher branches.
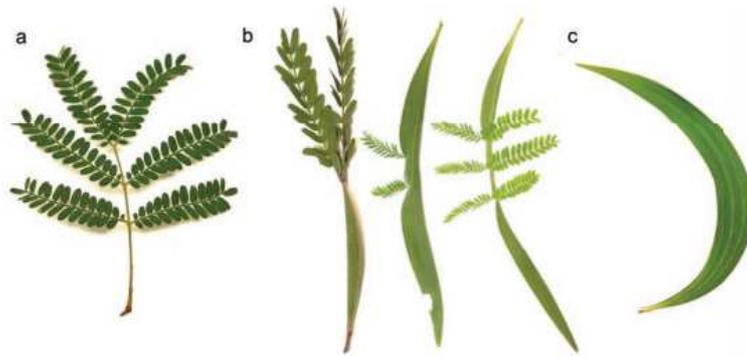
Fig. 3. Different leaf forms of *A. koa*: (a) bipinnate compound true leaf, (b) transitional leaf forms, (c) phyllode

Fig. 4. Flowers of *A. koa*: (a) flowers arranged in axillary racemes (b) flowers and flower buds
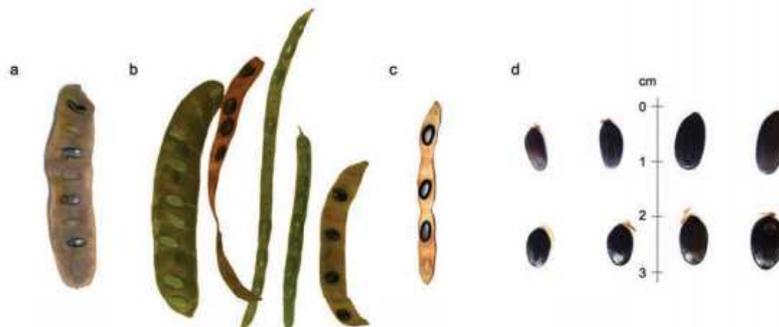

Fig. 5. Different morphological varieties of seed pods and seeds: Seed pods of (a) the 'koa' type, (b) 'koaia' type, (c) 'intermediate' type and (d) seeds from different populations of *A. koa*

The flowers of *A. koa* form spherical, pale-yellow heads of about 8-10 mm in diameter arranged in axillary racemes (Fig. 4). The flowers bloom year-round, with peaks in mid-to late-winter and early summer (Whitesell, 1990) starting from when the trees are 2-3 years old (Allen, 2002). The flowers are hermaphroditic (bisexual) and have numerous long, curled stamen filaments and corollas as well as a single style (Whitesell, 1990; Wagner *et al.*, 1999). They are dichogamous, with anthers releasing pollen 3 to 8 days before the stigma reaches maturity. This arrangement is favorable for cross-pollination among flower heads on different trees and also on the same trees (Elevitch *et al.*, 2006; Baker *et al.*, 2009). The pollens are large 16-cell grains with a diameter of about 80 µm, so dispersal distance by wind may be difficult beyond 50 m from the source (Elevitch *et al.*, 2006; Baker *et al.*, 2009). For longer-distance cross-pollination, insect pollinators are essential. With its flowers providing good quantities of nectar, *A. koa* is pollinated by various insects, such as honeybees (*Apis mellifera*), allowing long-distance dispersal of pollens (Lamoureux, 1971; Sakai *et al.*, 1995; Elevitch *et al.*, 2006).
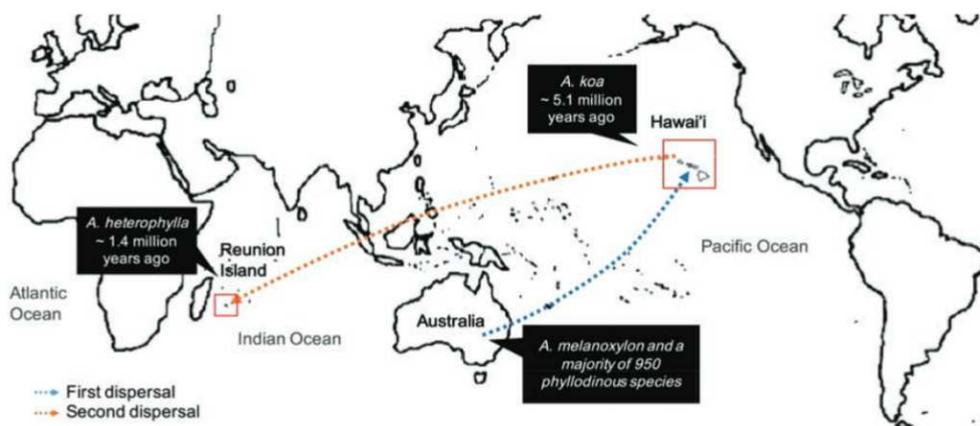
Fig. 6. Nodules in the root of *A. koa*

Fig. 7. Australian acacia, *A. melanoxylon*, traversed the globe. The spread of *A. melanoxylon* traveled to two insular landmasses separated by vast distances. It is suspected that the colonization of Hawaiʻi originated from Australia, followed by secondary dispersal to Réunion Island just east of Madagascar. Seabird is the suspected transfer agent of *A. melanoxylon* seeds to Hawaiʻi and *A. koa* seeds to Réunion Island

Three to four months following pollination, *A. koa* produces flattened, oblong pods with the length of 8 to 30 cm and the width of 0.8 to 2.5 cm (Wagner *et al*., 1999; Baker *et al*., 2009). Pods fall to the ground unopened or dehisce while on the tree; wind may carry pods or seeds to on some distance, but dispersal distance is limited (Whitesell, 1990). Each pod contains 6 to 12 seeds arranged in either transversely, longitudinally, or at an angle in the pods, depending on *A. koa* varieties (Fig. 5a-c). The seeds are laterally flattened ellipsoid, 6 to 13 mm long and 3 to 9 mm wide, dark brown to black in color and slightly shiny (Fig. 5d; Whitesell, 1990; Sun *et al*., 1997; Wagner *et al*., 1999). On Kauaʻi, populations have distinctly round-shaped seed (Sun *et al*., 1997). The seed weight varies among different populations (Whitesell, 1974; Sun *et al*., 1997; Allen, 2002); we observed that the seed weight of different *A. koa* families may range from 3 to 7 g per 100 seeds. *Acacia koa* seeds remain viable for many years under cool, dry conditions; they may stay viable for over two decades on the forest floor (Judd, 1920; Whitesell, 1990).

Fig. 8. Out-planting of the rooted shoot cuttings of Fusarium wilt resistant families of *A. koa* at the Maunawili Research Station of Hawaii Agriculture Research Center (HARC), Kailua, Hawaii. Courtesy of Nick Dudley

Acacia koa forms a strong lateral root system besides having a large taproot; some of its shallow lateral roots may be partially exposed at the soil surface (Elevitch *et al*., 2006). As a legume species, *A. koa* forms root nodules, which are occupied by the symbiotic nitrogen-fixing bradyrhizobia (Fig. 6). Interestingly, nodules are also found in the adventitious roots established within the canopy of *A. koa*. The bradyhizobia in canopy nodules reside in "pockets" within the canopy, which may contain soils consisting of decomposing heartwood and phyllode litter. These soils have significantly higher nitrogen content and lower aluminum levels than the terrestrial soil (Leary *et al*., 2004). The *Bradyrhizobium* isolates from the tap root, on the other hand, are more tolerant of aluminum than those collected from the canopy, so the canopy *Bradyrhizobium* isolates are likely to be different from terrestrial ones (Leary, 2007). No other *Acacia* species have been reported to develop canopy nodules (Leary *et al*., 2004).

Associated Plants

Many plants, including native species, are associated with *A. koa*. It is commonly associated with 'ōhi'a lehua (*Metrosideros polymorpha*), one of the most important trees in Hawaiian forests along with *A. koa*. There are many endemic understory trees in mesic *A. koa* forests, including naio (*Myoporums and wicense*), 'ōlapa (*Cheirodendrontrigynum*), kāwa'u (*Ilexanomala*), kōlea (*Myrsine lessertiana*), kōpiko (*Psychotria spp*.), 'iliahi (*Santalum* spp., sandalwood), olopua (*Nestegis sandwicensis*) and pilo

(*Coprosma* spp*.)*. In *A. koa* forests on wetter sites, ferns, such as palapalai (*Microlepia strigosa*), are common understory plants and in montane dry forests, *māmane* (*Sophora chrysophylla*) grows with *A. koa* (Mueller-Dombois and Fosberg, 1998; Wagner *et al*., 1999; Elevitch *et al*., 2006; Baker *et al*., 2009). The indigenous fern *uluhe* (*Dicranopteris linearis*) is also common plant species covering the ground of *A. koa* forests (Fig. 1).

Varieties of *A. koa*

The *A. koa* populations on the Hawaiian Islands are morphologically diverse and grouped into three distinguishable forms of the 'koa,' 'koaia,' and 'intermediate' types (Wagner *et al*., 1999; Adamski *et al*., 2012). Individuals of the 'koa' type are larger trees, whereas trees of the 'koaia' type grow only up to about 5 m in height and have a gnarled appearance. The 'koaia' type has harder wood and grows in drier open woodlands on the islands of Hawai'i, Kaua'i, Moloka'i, Lāna'i and Maui (Wagner *et al*., 1999; Elevitch *et al*., 2006; Adamski *et al*., 2012; Ishihara *et al*., 2016). Also, in the 'koa type," seeds are arranged transversely in wider pods while in the 'koaia' type, they are arranged longitudinally in narrower pods. Another distinct characteristic is the phyllode; the "koa type" has broader phyllodes (1-5 cm), while the "koaia type" has narrower phyllodes (< 1cm; Rock, 1919; Elevitch *et al*., 2006; Adamski *et al*., 2012). Because of their distinct features, the 'koa' and 'koaia' types have been suggested to be different subspecies or species (Adamski *et al*., 2012; Ishihara *et al*., 2016). The existence of the 'intermediate'

type suggests that the 'koa' and 'koaia' types may be subspecies rather than distinct species. The 'intermediate' type, which can grow up to 10 m with its mixed characteristics of phyllodes, pods and seeds, could be the result of the natural hybridization between the 'koa' and 'koaia' types (Adamski *et al*., 2012).

Genetics of *A. koa*

As a predominately outcrossing tree, *A. koa* populations show wide genetic diversity. Variations in tree form, phyllode development, tolerance of rust and other traits have been observed among various *A. koa* populations and these phenotypic differences appear to be highly heritable (Sun, 1996; Brewbaker, 1997; Sun *et al*., 1997; Daehler *et al*., 1999). According to Brewbaker (1997), variation was greater within each island than among islands, while uniformity was generally observed within each population, which implied high degree of self-fertilization within a population. Genetic differences among *A. koa* populations in the Hawaiian Islands were evaluated based on variation in isozymes (Conkle, 1996) and microsatellites (Fredua-Agyemann *et al*., 2008). The isozyme survey showed that the expected heterozygosity of *A. koa* was 0.41, a high value compared with many other organisms and that *A. koa* trees on the island of Hawai'i were distinct because they had unique alleles and different allele frequencies from those on O'ahu, Maui and Kaua'i (Conkle, 1996). Fredua-Agyemann *et al*. (2008) conducted a microsatellite analysis using a thorough sampling of *A. koa* trees from various populations on each island. The results showed that the populations on the islands of Hawai'i, Maui and O' ahu were more closely related to each other than any of them was to populations on Kaua' i (Fredua-Agyemann *et al*., 2008). Recently, genetic analysis on interrelationships among the three forms, the 'koa,' 'koaia,' and intermediate types, was also conducted by Adamski *et al*. (2012). Using 12 microsatellite loci, genetic variation among the three types was analyzed and the results suggested that they should be recognized as different subspecies rather than as different species, which is consistent with the morphological analysis in previous studies (Adamski *et al*., 2012).

Although *A. koa* has been studied for a long time, its genomic data is still limited. *Acacia koa* is a tetraploid ($2n = 4x = 52$; Atchison, 1948; Carr, 1978; Conkle, 1996; Hipkins, 2004) and it has been proposed to be an allotetraploid based on the observation that only one pair of the chromosomes contain secondary constrictions, which is one of the indications of allotetraploidy (Shi, 2003). Instead of

sequencing the complex genome of the tetraploid tree, the transcriptome of *A. koa* seedlings have been sequenced from *A. koa* seedlings through the Illumina platform (Ishihara *et al*., 2015). Sequencing and *de novo* assembly yielded over 85,000 unigenes and more than half of them were annotated. Among them were complete coding sequences of many proteins, including enzymes that may be involved in wood formation and development, such as monolignol biosynthesis enzymes (Ishihara *et al*., 2015). A substantial number of potential SSR markers were also predicted from the transcriptome data. All the assembled sequences are publicly available on the National Center for Biotechnology Information (NCBI) and it will be a useful genetic resource for further studies of *A. koa*.

Evolution

The genus *Acacia* is made up of over 950 species categorized (Mabberley, 1997; Robinson and Harris, 2000; Orchard and Maslin, 2003). The majority of these species are found in Australia and only 18 of the 950 species, like *A. koa*, reside outside of Australia (Brown *et al*., 2012). *Acacia koa* is a descendant of an Australian acacia, *A. melanoxylon,* another important timber tree (Le Roux *et al*., 2014). *Acacia koa* and *A. melanoxylon* have similar morphological characteristics, such as maximum height of ~35 m and long, wide pods and phyllodes (Table 1). Consistent with their morphologies, a plastid DNA analysis showed that *A. koa* has a close relationship with *A. melanoxylon* as well as *A. paradoxa*, an Australian prickly shrub (Robinson and Harris, 2000). Similarly, Adamski *et al*. (2013) determined genetic diversity in seven nonnative *Acacia* species in the Hawaiian Islands using 31 microsatellite markers developed from *A. koa* and observed that *A. melanoxylon* had the highest percentage of amplified loci. They thus concluded that *A. koa* of the Hawaiian Island is most likely a descendant of *A. melanoxylon* from Australia. In spite of their morphological similarities, their ploidy levels are different as *A. koa* is a tetraploid while *A. melanoxylon* is a diploid (Table 1); this polyploidy formation happened during the evolution of *A. koa* as it is a common phenomenon in many angiosperms (Masterson, 1994). In plants, polyploidy is considered to be an important mechanism for adaptation (Te Beest *et al*., 2012). A recent study showed that *A. koa* has significantly different ecological niches from *A. melanoxylon*, thriving in wider geographical ranges and environmental conditions. It may be due to the increase in ecological tolerance in the tetraploid *A. koa* (Le Roux *et al*., 2014).

Table 1. Variation in characteristics among three *Acacia* species in three geographical locations*

	A. koa	*A. heterophylla*	*A. melanoxylon*
Distribution	Hawaiian Islands	Réunion island	Eastern Australia
Habitat	Wet/mesic forest	Wet/mesic forest	Wet/mesic forest, open woodlands
Tree height	10-35 m	20-25 m	~ 35 m
Pods	Long, wide	Small, narrow with curvature or coil	Long, wide
Phyllodes	Commonly long and wide	narrow	Long and wide
Ploidy	Allotetraploid; 4n = 52	Autotetraploid; 4n = 52	Diploid; 2n = 26

*Descriptions of *A. koa* are based on Adamski *et al.* (2012); *A. heterophylla* are based on Wagner *et al.* (1999) and Louppe *et al.* (2008); *A. melanoxylon* are based on Wagner *et al.* (1999) and Searle (2000)

The closest relative of *A. koa* is *A. heterophylla* (highland tamarind), which is an endemic species of Réunion Island, east of Madagascar (St. John, 1979; Le Roux *et al.*, 2014). *Acacia heterophylla* has narrower pods and phyllodes than *A. koa* (Table 1), but they otherwise have strong morphological similarities (Le Roux *et al.*, 2014). An ecological-niche-overlap study showed significant similarities between habitats of *A. koa* and *A. heterophylla* (Le Roux *et al.*, 2014); both species inhabit wet to mesic forests (Table 1). Recently, phylogenetic dating analyses found that acacia seeds were dispersed, not from Australia, but from the Hawaiian Islands to the faraway Réunion Island ≤1.4 million years ago, with an assumption that the establishment of *A. koa* in Hawai'i was 5.1 million years ago (the age of Kaua'i, the oldest Hawaiian island; Fig. 7; Le Roux *et al.*, 2014). Furthermore, phylogenetic and genetic analyses indicate that *A. heterophylla* is derived from and nested within the variation of *A. koa* and as such, Le Roux *et al.* (2014) suggest that they should be considered the same species (Le Roux *et al.*, 2014). However, *A. heterophylla* is proposed to be an autotetraploid with two sets of chromosomes containing secondary constrictions (Coulaud *et al.*, 1995) whereas *A. koa* is proposed to be an allotetraploid. Since they should be the same species and one is derived from the other, they must both be auto- or allo-tetraploids. There is a possibility that the chromosomal analysis for determining polyploidy nature of the two species was inaccurate due to limitation of the technique as Shi (2003) mentions. Thus, further studies are needed to validate the polyploidy nature of the species.

The long-distance dispersal mechanism of acacia from Australia to the Hawaiian Islands and then to the Réunion Island, is another question (Fig. 7). Arrival by human assistance, birds and free-floating seeds are the most possible dispersal strategies. Brown *et al.* (2012) proposed geological history and human-mediated dispersal as the main strategy of phyllodinous species of acacias including *A. koa* to move outside Australia; yet, given the preponderance of other data to the contrary, this hypothesis is not acceptable. For instance, recent research by Le Roux *et al.* (2014), using phylogenetic dating analysis, suggested that natural long-distance dispersal is more likely rather than human-assisted dispersal since human colonization of the Hawaiian

Islands occurred only in 400-600 A.D. (Olson and James, 1982). Carlquist (1966) favored oceanic transfer suggesting that mature *A. koa* seed pods on tree branches may have drifted in ocean currents for prolonged periods of time. Others have suggested dispersal by seabirds (Cheke and Hume, 2008; Kull and Rangan, 2008). For the dispersal between the Hawaiian Islands and Réunion Island, Cheke and Hume (2008) speculated that the Hawaiian Petrel accidentally found a new similar habitat on Réunion Island. Barau's Petrel, a seabird of Réunion Island possibly came as a descendant from Hawaiian Petrels; both nest at high altitudes concurrent with distribution of *A. koa* and *A. heterophylla*, respectively (Cheke and Hume, 2008; VanZandt *et al.*, 2014). Migrating petrels with *A. koa* seeds in their guts might have allowed introduction of *A. koa* into new habitats separated by vast distances (Ryan and Jackson, 1987; Ryan, 1988). With a hard seed coat, *A. koa* seeds can withstand intense acidity, so they may have been able to remain viable in the gut of a petrel for long distances of travel.

Silviculture and Agroforestry

Propagation

Acacia koa is typically propagated from seeds, which are collected from pods. Pods are ready to be harvested when the color changes from green to brown or black. To extract seeds, pods are dried in the sun so that they can be opened easily (Elevitch *et al.*, 2006). Seeds have a hard, impermeable coat that requires scarification to allow water to contact the germ. Under natural conditions, friction between the seed and soil or rock substrate scarifies them. Artificial scarification can be accomplished chemically by soaking in concentrated sulfuric acid for ten minutes, mechanically by nicking the seed coat on the edge with nail clippers, or with a hot water treatment by soaking the seeds in near-boiling water for a few minutes. The scarified seeds are planted into containers filled with well-drained potting media, in a depth of about the width of the seeds. The medium should be kept moist and they will germinate in 2 to 7 days (Elevitch *et al.*, 2006). They can be grown outdoors and no special greenhouse area is needed, but some cover is helpful for the first two weeks after germination to protect seedlings from hard rains (Wilkinson and Elevitch, 2005). Seedlings should be inoculated with appropriate

Bradyrhyzobium strains after 1 to 2 weeks for enhancement of the growth (Leary *et al.*, 2004; Elevitch *et al.*, 2006). When seedlings reach 15-30 cm, they mature enough to be out-planted to their permanent planting site (Elevitch *et al.*, 2006).

Due to the outcrossing nature of *A. koa*, the plants are highly heterozygous and heterogeneous and it is difficult to grow a uniform population of *A. koa* trees with desired qualities. Therefore, many studies have been performed to develop a method for vegetative propagation of *A. koa*, which is useful to produce genetically identical plants with superior properties, such as certain wood colors and disease resistance. Skolmen (1978; 1986) developed tissue culture techniques for vegetative propagation by air layering or by rooting of cuttings under mist, as well as by callus cultures derived from shoot tips. The tissue-cultured trees have been successfully out-planted. However, these methods are labor-intensive, time consuming and currently unsuitable for large-scale propagation (Skolmen, 1986). Building upon these earlier works, Nagai and Ibrahim (1997) developed a method for micropropagation through multiplication and rooting of shoots and phyllodes of *A. koa*. Similarly, Dudley *et al.* (2015) used rooted cuttings as a method to propagate disease-resistant genotypes. They determined rooting efficiency of *A. koa* seedlings from disease-resistant varieties and successfully out-planted the rooted shoot cuttings (Fig. 8). However, rooting success was still limited and further work is necessary to optimize for higher efficiency so that it will be suitable for mass propagation. Although the tissue culture methods are currently suboptimal, Nelson (2006) reported successful grafts of young *A. koa* seedlings onto rootstocks of another *A. koa* and *A. confusa*. Grafts from *A. koa* to another *A. koa* and from *A. koa* to *A. confusa* had a success rate of about 70%. The graft method of cutting and clipping two plants together is simple, rapid and inexpensive (Nelson, 2006). The application of this method will be especially useful to manage soil-borne plant pests by joining koa to disease-resistant rootstocks.

Acacia koa Reforestation

Over the past century, cattle ranching, grazing by wild animals, agriculture, land developments and invasive plant species have severely reduced *A. koa* forests, which have been replaced by vegetation dominated by shallow-rooted herbaceous plants (Whitesell, 1990; Ewel and Bigelow, 1996). Consequently, ecosystem functions, such as nutrient cycling and water budgets, have been altered (Scowcroft and Jeffrey, 1999). As mentioned earlier, *A. koa* is one of the most important trees of the Hawaiian Islands and many efforts have been made for reforestation (Mitchell *et al.*, 2005; Perkins *et al.*, 2014). On the island of Hawai'i, numerous sites have been managed for protection of native species and habitats via

A. koa reforestation, such as the Big Island National Wildlife Refuge Complex (NWR) administered by U.S. Fish and Wildlife Service (USFWS; Mitchell *et al.*, 2005). In addition, the USFWS, the Nature Conservancy (TNC), the Division of Forestry and Wildlife (DOFAW), the National Park Service (NPS) and many other agencies manage mesic montane forests and parklands on the island of Hawai'i to protect forest birds, such as 'akiapōlā'au and 'ākepa, as well as to develop sustainable *A. koa* forestry that will help landowners maintain the economic value of their lands. On Maui, the Leeward Haleakala Watershed Restoration Partnership (LHWRP) has been fencing koa-'ōhi'a watershed forests and removing ungulates at the Department of Hawaiian Home Lands (DHHL) and the DOFAW, Kahikinui for watershed protection (DWS, 2014). Forest restoration of leeward Haleakala has improved hydrologic function by facilitating rapid underground water transfer and by increasing the amount of soil water for aquifer recharge (Perkins *et al.*, 2014). In recent years, there has been a growing interest in the re-establishment of *A. koa* as a commercial plantation species on abandoned sugarcane and pineapple lands (Newell and Buck, 1996). With these efforts, *A. koa* forests will be further restored in the future to enhance wildlife habitat and the economy.

Fusarium Wilt and Pests

In spite of the growing interest in *A. koa* forests, restoration attempts are hampered due to a devastating vascular wilt disease caused by a fungal pathogen *Fusarium oxysporum* f. sp. *koae*, the major cause of decline of *A. koa* in the native Hawaiian forests in recent years (Gardner, 1980; 1996; Anderson and Gardner, 1998; Anderson *et al.*, 2002; James, 2005; Pejchar and Press, 2006; Dudley *et al.*, 2007). *Fusarium oxysporum* is a soil-borne fungus, which typically infects the host plants through the root system (MacHardy and Beckmann, 1981). Upon entering the roots, mycelia penetrate intercellular to the plant's xylem vessels, where it is then able to spread upwards, leading to clogging of vessels due to the mycelium accumulation and formation of host plant defense, such as formation of tyloses and gum (Pietro *et al.*, 2003). Once too many xylem vessels are clogged, the host dies due to the disruption of water movement (MacHardy and Beckmann, 1981). *Fusarium oxysporum* can also survive an extended period of time in the soil without its hosts (Yadeta and Thomma, 2013), so it is difficult to control this ubiquitous and hardy pathogen.

Efforts have been made to breed koa for wilt resistance by selecting resistant families (half-sibling seeds from single mother trees) of koa in field trials. In the trials performed by Shi and Brewbaker (2004), the seedlings were exposed to naturally occurring levels of *F. oxysporum* infection and the survival rate was determined after several years. James (2005) and Dudley *et al.* (2007) isolated virulent *F. oxysporum* strains, which are useful

for screening of resistance in *A. koa*; the mixture of virulent isolates were used to artificially inoculate the seedlings for 100-day greenhouse trials to determine the survival rate and select resistant families (Dudley *et al.*, 2015). Currently, field trials are being conducted to confirm if this screening method can be used to select resistant *A. koa* families prior to out-planting (Dudley *et al.*, 2015). Also, Rushanaedy *et al.* (2012) observed that expression of chitinase genes *Akchit1a* and *Akchit1b* was higher in resistant koa families than in susceptible ones following inoculation by virulent strains of *F. oxysporum*. Chitinases are important defense enzymes that break down chitin in fungal cell walls (Punja and Zhang, 1993; Sharma *et al.*, 2011); thus they may be useful as markers for fungal resistance in *A. koa*.

Although they account for lower levels of mortality than *F. oxysporum*, many insect pests also infest *A. koa*. An alien black twig borer (*Xylosandrus compactus*) weakens the stem and increases its susceptibility to breakage and mortality (Daehler and Dudley, 2002). The endemic koa seed worm (*Cryptophlebia illepida*) is also a threat, destroying most seeds produced in any given year (Stein, 1983; Leeper and Beardsley, 1973). The acacia psyllid (*Psylla uncatoides*) is another serious pest that feeds on the terminal growth of *A. koa* and can eventually cause mortality (Whitesell, 1990). The endemic koa moth (*Scotorythra paludicola*) undergoes sporadic outbreaks in *A. koa* forests, especially on islands of Hawai'i and Maui and defoliates the trees. In 2003, there was a koa moth outbreak in the forests on East Maui in which approximately 16 km^2 was defoliated (Haines *et al.*, 2009); interestingly, the outbreak may have been associated with infection with *F. oxysporum* (Welton *et al.*, 2004).

Conclusion

Improvement of A. koa as an Agroforestry Tree

The future of *A. koa* as an agroforestry tree depends upon continuation of selection for disease resistance and wood quality and capability to provide a good source of seeds using selected trees. As mentioned above, efforts have been made to develop methods to select for disease resistant *A. koa*; however, there is currently no definitive selection strategy for wood qualities in *A. koa*. Important wood properties for selection include the grain figures and the color, which are influenced by environmental factors, such as geographic location, to a large extent (Loudat and Kanter, 1996; Dudley and Yamasaki, 2000). It appears that variations of the grain figure also have a genetic basis; some *A. koa* have the most valued curly grain figure systemically throughout the entire trees, while others do not (Dudley, 2007). Therefore, there is a potential for genetic improvement. The formation of the heartwood color is not well understood (Wilton *et al.*, 2015) and the evaluation of clonal *A. koa* trees from different sites may help to determine genetic and environmental factors affecting the wood color. Further research may lead to successful development of wilt-resistant *A. koa* trees with high wood quality that can support the ecology, economy and culture of Hawai'i.

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Authors' Contributions

Kazue Lee Ishihara and Maia Corpuz: Collected literature, created figures and wrote the manuscript.

Clifford Wayne Morden: Provided expertise in phylogenetics and Hawaiian botany, gave conceptual advice and revised the manuscript for intellectual content.

Dulal Borthakur: Contributed in conceptualization through a thorough discussion, assistance in writing and critically reviewing the final version. All authors read and approved the final manuscript.

Ethics

This article is original and contains unpublished material. The corresponding author confirms that all of the other authors have read and approved the manuscript and no ethical issues involved.

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