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Taxonomic Revision of the Endangered Hawaiian Red-flowered Sandalwoods (*Santalum*) and Discovery of an Ancient Hybrid Species

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Abstract—The Hawaiian Islands are home to a quarter of the named diversity of sandalwoods in the genus *Santalum*. There has been considerable confusion on how to best interpret the variation patterns of the red-flowered Hawaiian sandalwoods, *S. freycinetianum* and *S. haleakalae*, and particularly of the endangered *S. freycinetianum* var. *lanaiense* in an appropriate taxonomy. In this study, nrDNA (ITS, ETS) and cpDNA (3' *trnK* intron) sequence, microsatellite, and morphological data are integrated to appropriately revise the taxonomy of this group by better understanding the genetic and morphological diversity within and between populations. Results reveal that populations of *S. freycinetianum* from O`ahu are genetically distinct from populations on Moloka`i, Lana`i, and Maui. *Santalum freycinetianum* is now considered only to occur on O`ahu. The East Maui endemic *S. haleakalae* intergrades morphologically and is not genetically distinct from populations of *S. freycinetianum* var. *lanaiense* based on the sequence and microsatellite data gathered thus far. We combine them here into a single species, *S. haleakalae*, with two varieties (var. *haleakalae* and var. *lanaiense*, comb nov.). Lastly, examination of populations of *S. freycinetianum* var. *pyrularium* suggest it is best treated at specific rank as *S. pyrularium*. Some populations that are sympatric with *S. pyrularium* and *S. ellipticum* in the coastal cliffs and valleys of northern Kaua`i, are morphologically similar to *S. pyrularium* but are more closely related to the white-flowered *S. ellipticum* clade according to both nrDNA and cpDNA data. However, at least three synapomorphic sites in the nrDNA data indicate that its origin may have been the result of an ancient hybridization event with the red-flowered clade. The morphological characteristics of this inferred ancient hybrid lineage appear to concord with the species *S. involutum* described by H. St. John.

Keywords—endangered species, Hawaiian Islands, microsatellites, molecular phylogeny, morphology, taxonomic revision.

Few plants are as medicinally, culturally, and economically important as the sandalwoods, commonly known for their aromatic heartwood oil. The sandalwoods comprise the small genus of shrubs and trees, *Santalum* L. (Santalaceae), which is widely distributed throughout India, Australia, and the Pacific Islands (Harbaugh 2007; Harbaugh and Baldwin 2007). More than a quarter of the currently recognized sandalwood species occur in the Hawaiian Islands, where it is known locally by its Hawaiian name `iliahii. Hawaiian sandalwoods have a long history of traditional ethnobotanical uses, and have a prominent contribution to the cultural and economic history of the islands. The grated wood and oil has been used to scent and waterproof kapa (barkcloth) (St. John 1947; Merlin and VanRavenswaay 1990), the wood used as firewood and to treat sores (Merlin and VanRavenswaay 1990) and urogenital diseases (Brennan and Merlin 1991), as well as carved into the musical instrument `ukeke (Buck 1964). Demand for their valuable products has led to drastic over-harvesting of sandalwoods, and now they are among the most heavily exploited groups of plants across their range (Merlin and VanRavenswaay 1990). The early 19th century in the Hawaiian Islands is known as the "Sandalwood Era," where it is estimated that as many as 90% of Hawaiian sandalwood trees were felled and exchanged for ships and supplies (Shineberg 1967; Kepler 1998). As a result, most Hawaiian sandalwood taxa are now rare or threatened, and one variety, *Santalum freycinetianum* Gaudich. var. *lanaiense* Rock is currently listed as endangered (Herbst 1986; Merlin and VanRavenswaay 1990). A single known species, *S. fernandezianum* F. Phil. from the Juan Fernandez Islands, has gone extinct due to human exploitation in the last century (Stuessy et al. 1992), and a number of other *Santalum* taxa, including several in the Hawaiian Islands described in this paper may warrant listing before they have a similar fate.

There have been a number of taxonomic treatments of the Hawaiian sandalwoods, starting with the description by Gaudichaud-Beaupré in 1829 of two species, the red-flowered *S. freycinetianum* Gaudich. and white-flowered *S. ellipticum* Gaudich. Reconstruction of the *Santalum* phylogeny has demonstrated that the Hawaiian sandalwoods are the result of two independent colonization events from Australia (Harbaugh and Baldwin 2007; Harbaugh 2008), which correspond to the red-flowered (section *Solenantha* Tuyama) and white-flowered (section *Hawaiiensia* Skottsberg) species. Tuyama (1939) separated the Hawaiian members of section *Santalum* into the endemic section *Solenantha* based on their longer perianth tubes, smaller ovaries, and absence of hairs proximal to the filaments. Section *Hawaiiensia* is characterized as having white, green, brown, or orange corollas that are as wide as long, and inferior ovaries (Skottsberg 1930; Stemmermann 1980a; Wagner et al. 1999b).

Subsequent treatments, including those by Gray (1860), Hillebrand (1888), Rock (1916), Skottsberg (1927), Stemmermann (1980a), and St. John (1984), have revealed a number of additional species within these two lineages. Wagner et al. (1999b) based their treatment on the revision by Stemmermann (1980a), which recognizes four named species, two in the white-flowered group (*S. ellipticum* and *S. paniculatum* Hook. & Arn.) and two in the red-flowered group (*S. freycinetianum* and *S. haleakalae* Hillebr.), with an additional three varieties (*S. freycinetianum* vars. *lanaiense* and *pyrularium* (A. Gray) Stemmerm., and *S. paniculatum* var. *pilgeri* (Rock) Stemmerm.). Several taxa described by St. John in his 1984 revision, including *S. majus* H. St. John and *S. involutum* H. St. John, were not recognized as distinct from *S. freycinetianum* var. *pyrularium* by Wagner et al. (1999b).

Despite the number of taxonomic treatments that have focused on Hawaiian sandalwood there remains considerable

confusion on how to apply the names to certain populations, especially for the red-flowered taxa, *S. haleakalae* and *S. freycinetianum*. This is because the “distinction between taxa is often not clear-cut” (Stemmermann 1980a), and there is considerable morphological diversity within their ranges, and even within populations. Another potential issue is whether to treat weakly distinct populations on different islands as separate species. This issue is common for many morphologically-based Hawaiian classifications and recent studies involving morphological data in conjunction with molecular data have shown that not only are morphologically similar populations on different islands sometimes distinct species (e.g. *Schiedea*), but there may be more cryptic species than could be distinguished using morphology alone (e.g. *Dubautia* see Baldwin and Friar 2010). An example of this taxonomic confusion in regard to *Santalum* is how to assign variable populations of *S. freycinetianum* var. *lanaiense*, which has implications for its conservation. It is unclear whether the populations of *S. freycinetianum* on West Maui should be assigned to the endangered var. *lanaiense*, also found on Lanaʻi, or to var. *freycinetianum*, which occurs on Oʻahu and Molokai. The lower elevation plants of Haleakala on East Maui have also been assigned to var. *lanaiense* (Wagner et al. 1999b); Stemmermann (1980a) circumscribed these plants as a new and restricted variety, *S. freycinetianum* Gaudich. var. *auwahiense* Stemmerm. Albeit, according to Stemmermann (1980a, 1980b), these plants may form a continuum in a number of morphological characters from the upper elevation plants from Haleakala, which have been considered a distinct species, *S. haleakalae*.

In this study we employ several new lines of evidence to investigate the morphological and genetic variation within and between populations of *S. freycinetianum* and *S. haleakalae* to answer the following questions: 1) Should the red-flowered *S. freycinetianum* be split into multiple varieties, or regarded as one variable species? 2) If the varieties are supported as distinct, are there characters or evidence to help delimit the endangered *S. freycinetianum* var. *lanaiense*? 3) Should *S. haleakalae* be considered as a separate species, or a variety of *S. freycinetianum*? 4) Should *S. freycinetianum* var. *pyrularium* on Kauai be considered as a separate species? 5) What were the patterns of colonization of the red-flowered sandalwoods in the Hawaiian Islands?

In past research, DNA sequence data were insufficient to completely resolve the relationships within *S. freycinetianum* and *S. haleakalae* (Harbaugh and Baldwin 2007; Harbaugh 2008). Therefore in this study, in addition to an expanded phylogenetic analysis based on nrDNA (ITS, ETS) and cpDNA (3' *trnK* intron) sequences, evidence is integrated from two novel sources including a Bayesian STRUCTURE analysis using microsatellites, as well as a morphological analysis of 28 quantitative and qualitative characters. Microsatellite data have been chosen for the present study because they have high mutation rates and polymorphism, and are good to determine population genetic diversity and structure in taxa that have recently diverged, such as in island archipelagos (Zhang and Hewitt 2003; Butaud et al. 2005; Lhuillier et al. 2006a).

MATERIALS AND METHODS

Phylogenetic Analysis—We sequenced a total of 42 specimens in this study, 17 of which were outgroup specimens including one of *Colpoön* Berg. and the remaining were *Santalum* specimens based on previous analyses (Harbaugh and Baldwin 2007; Harbaugh 2008). Twenty-five

accessions of *S. freycinetianum* and *S. haleakalae* were selected as the ingroup from across the morphological diversity of these taxa from across their natural ranges in the Hawaiian Islands. For each specimen, the internal transcribed spacer (ITS) and external transcribed spacer (ETS) regions of 18S-26S nrDNA, as well as the cpDNA 3' *trnK* intron were sequenced from genomic DNA extracted from silica-dried leaf material and herbarium specimens using the same primers and methods described in Harbaugh and Baldwin (2007). See Appendix 1 for locality and herbarium voucher information, as well as GenBank accession numbers for ITS, ETS, and 3' *trnK* intron sequences for all specimens used in this study.

Nuclear ribosomal and cpDNA matrices were aligned by eye and were not combined, based on the evidence for several instances of hybridization within the genus. A maximum likelihood (ML) analysis was performed using the web-based program RAXML (Stamatakis et al. 2005) with the GTR model of base substitution and gamma model of rate heterogeneity with 1,000 bootstrap replicates (Stamatakis et al. 2008). All identical sequences were removed prior to performing the analyses, leaving a total of 28 sequences in the final aligned nrDNA matrix. The ML analyses were each performed two times (with identical results) to ensure the stability of the topology. Additionally, a maximum parsimony (MP) analysis was performed on each dataset. Insertions and deletions (indels) were not coded as characters as they were in Harbaugh and Baldwin (2007) due to the lack of parsimony informative indels within the ingroup. For the nrDNA data set, which has 150 out of 1,101 bp parsimony informative, a heuristic search was performed in PAUP* 4.0b10 (Swofford 2002) with 10,000 random-addition sequences, TBR branch swapping, and MulTrees on. For the smaller cpDNA dataset, with only five out of 413 bp parsimony informative, an exhaustive search was performed in PAUP*. Parsimony bootstrap values were calculated for the nrDNA data sets using PAUP* using a full heuristic search, with 1,000 bootstrap replicates, 10,000 random-addition sequences, TBR branch swapping, and MulTrees on. Lastly, decay index values were estimated on the nrDNA data set by reiterating the MP analyses holding trees one step longer in successive runs, and comparing the consensus phylogenies.

Microsatellite Analysis—A total of 175 individuals were genotyped in this study using microsatellites (see Appendix 2 for locality and herbarium voucher information). This sampling encompasses representatives of *S. freycinetianum* and *S. haleakalae* from multiple populations across the ranges of each taxon. For all samples, total DNA was extracted from silica-dried leaf material using either a DNeasy plant mini kit (Qiagen) by hand or using the BioSprint 96 (Qiagen) robotic workstation.

Four polymorphic microsatellite loci were amplified for all 175 specimens using previously published primers, which included three nuclear microsatellites (mSiCIR33, mSiCIR139, and mSiCIR153) that were developed for *S. insulare* Bert. ex. A. DC. (Lhuillier et al. 2006b), as well as one cpDNA microsatellite (NTCP9; Bryan et al. 1999; Butaud et al. 2005). Amplifications were performed in a 10 µL volume [1 µL 10 × buffer (Applied Biosystems), 1 µL 10 µM dNTPs, 0.6 µL MgCl₂, 0.1 µL *Taq* DNA polymerase (Applied Biosystems), 0.5 µL of each primer (forward and reverse), and 1 µL DNA template] using a PT-100 thermal cycler (MJ Research, Waltham Massachusetts) under the following polymerase chain reaction (PCR) parameters: 94°C for 5 min followed by 30 cycles of 92°C for 45 sec, annealing temperature (Lhuillier et al. 2006b) for 45 sec, and 72°C for 1 min. The cycling ended with 72°C for 8 min, and then held at 6°C. Forward primers were fluorescently labeled on their 5' end with either Hex or Fam dyes (Sigma-Aldrich). Labeled PCR products were analyzed in an ABI capillary sequencing machine (Applied Biosystems) using Rox standard (Applied Biosystems). Electropherograms were analyzed using GENESCAN version 2.1 software (Applied Biosystems) and allele sizes were scored using GENOTYPER version 2.5 software (Applied Biosystems).

We used the Bayesian algorithm as implemented by the computer program STRUCTURE version 2.2 (Pritchard et al. 2007) to define genetic groups within *S. freycinetianum* and *S. haleakalae* from across their ranges in the Hawaiian Islands. A similar method was used to determine the genetic structure of North American sunflowers (Harter et al. 2004) and Hawaiian *Metrosideros* (Harbaugh et al. 2009). This algorithm infers genetic discontinuities from individual multilocus genotypes without any a priori knowledge of geographic location or taxonomy. The default settings of the program were used, including an admixture model. To determine the most likely number of groups (K) in the data, a series of analyses were performed from K = 1–20, using 40,000 burn-in and 100,000 repetitions, with ten iterations per K. These results were examined using the ΔK method (Evanno et al. 2005) to identify the most likely number of groups in the data, which in this study was determined unequivocally to be K = 2. At K = 2, a more thorough analysis was performed, using 100,000 burn-in and 1,000,000 repetitions, with only one iteration.

Morphological Analysis—A total of 28 qualitative and quantitative vegetative, floral, and fruit morphological characters were scored on representative herbarium specimens, including type material; many of the specimens that were examined were also used in the molecular analyses. For quantitative characters, measurements were taken from up to three randomly selected parts of interest. The characters that were scored are listed in Table 1, and the specimens examined are indicated with an asterisk in the species descriptions in the Taxonomic Treatment section of this paper. For populations with multiple specimens available, up to five specimens from each population were examined. This was performed to identify potential taxonomic characters that delimit taxa, as well as document the morphological variation within and between taxa, as well as within populations.

RESULTS

Phylogenetic Analysis—The results of the ML and MP analyses are consistent, with the nrDNA tree (Fig. 1; ML: $-\ln L = 4,171.30$, $L = 0.1630$; MP: No. trees = 24, $L = 556$, $CI = 0.0.840$, $RI = 0.792$; TreeBASE study number S10609) and better resolved than the cpDNA tree (not shown). In the nrDNA phylogeny (Fig. 1), there is little resolution within *S. freycinetianum* and *S. haleakalae* from O`ahu, Lana`i, Maui, and Moloka`i, due to a lack of variable characters; *S. haleakalae* var. *haleakalae* and most specimens of var. *lanaiense* group together in a very weakly supported clade, while *S. freycinetianum* and the remaining specimens of *S. haleakalae* var. *lanaiense* are in a polytomy that includes the *S. insulare*, *S. boninense*, and *S. pyrularium* clade. *Santalum freycinetianum* var. *pyrularium* is distinct and supported as nested within a clade including *S. insulare* (French Polynesia; sect. *Polynesica* Skotts.)

TABLE 1. The morphological characters of *Santalum* specimens examined in this study. Characters are identified as being either qualitative or quantitative.

	Character	Qualitative	Quantitative
	<i>Vegetative</i>		
1	Leaf thickness	X	
2	Leaf shape	X	
3	Leaf apex shape	X	
4	Leaf base shape	X	
5	Leaf margin	X	
6	Leaf surface	X	
7	Leaf venation	X	
8	Leaf color	X	
9	Leaf length		X
10	Leaf width		X
11	Petiole length		X
	<i>Floral</i>		
12	Inflorescence placement	X	
13	Pedicle length		X
14	Floral tube shape	X	
15	Floral tube length		X
16	Floral tube width		X
17	Corolla lobe length		X
18	Corolla lobe width		X
19	Flower color	X	
20	Disk lobe shape	X	
21	Floral hair position	X	
22	Stigma lobes		X
23	Ovary placement	X	
	<i>Fruit</i>		
24	Drupe shape	X	
25	Drupe length		X
26	Seed shape	X	
27	Endocarp texture	X	
28	Ring placement	X	

and *S. boninense* (Bonin Island; sect. *Santalum* Skotts.); morphological characteristics, namely of the floral color (cream, greenish to purple) also differentiate it from the other red-flowered taxa in sect. *Solenantha*. Additionally, several specimens from in and around Kalalau Valley, Kaua`i, which have been recognized within *S. pyrularium*, constitute a distinct lineage placed in a clade with white-flowered *S. ellipticum* and *S. paniculatum* (sect. *Hawaiiensia*) in cpDNA and nrDNA trees and shares at least three nrDNA mutations with the red-flowered clade, which predate the split of *S. pyrularium*. Although this genetically distinct lineage has most recently been treated as *S. pyrularium*, cryptic morphological characteristics namely of the leaves (see taxonomic treatment below) correspond to the previously recognized taxon described by St. John (1984), *S. involutum* H. St. John, although characteristics of the floral color and ovary position align it with section *Hawaiiensia*.

The cpDNA tree (not shown; MP: $-\ln L = 685.07$ and length = 0.0197; MP: No. trees = 6, $L = 29$, $CI = 0.931$, $RI = 0.724$) is mostly consistent with the nrDNA tree, but not well-supported. All accessions of *S. freycinetianum* and *S. haleakalae* from O`ahu, W. Maui, E. Maui, Moloka`i, and Lana`i, as well as *S. insulare* var. *raiateense* (J. W. Moore) Fosberg & Sacht have identical sequences. In another group of identical sequences are all accessions of *S. paniculatum*, *S. ellipticum*, and *S. boninense*. In the cpDNA tree, individuals of *S. pyrularium* from Kaua`i are identical to the *S. freycinetianum* and *S. haleakalae* sequences from O`ahu and Maui Nui, however the individuals from the Na Pali coast and valleys of northern Kaua`i, which are now considered *S. involutum*, are identical to *S. paniculatum* and *S. ellipticum*, consistent with the results of the nrDNA tree. There is also evidence for more recent hybridization between these two clades; one individual from Kaua`i (Wood and Perlman 3023 [PTBG]) which is considered morphologically to be *S. pyrularium* and sympatric with *S. ellipticum*, has polymorphic nrDNA sequences indicating a hybridization event between *S. pyrularium* and *S. ellipticum*, was identical to *S. paniculatum* and *S. ellipticum* in its cpDNA sequence.

Microsatellite Analysis—The four polymorphic microsatellite loci that were genotyped in this study have a range of allele numbers, including: three (mSiCIR139; 204–320 bp), five (NTCP9; 287–292 bp), six (mSiCIR153; 283–301), and 17 (mSiCIR33; 204–320). All four loci were successfully genotyped from all 175 specimens included in this study.

The results from the STRUCTURE analysis (see Supplementary Appendix online for data), which identified two distinct genetic groups in Hawaiian *Santalum*, are shown in Fig. 2. Although there is limited resolution in the microsatellite data, there are several important results that are elucidated. The first is that all specimens from from Moloka`i, W. Maui, E. Maui, and Lana`i occur in the same group, and are separate from all specimens from O`ahu. The other important result of the microsatellite data is that specimens of *S. pyrularium* are treated in a separate group from *S. involutum*. These data also place *S. pyrularium* in a group with *S. haleakalae*. Lastly, *S. involutum* is placed in the same group as *S. freycinetianum*, and not with *S. pyrularium*.

Morphological Analysis—Results from the morphological analysis reveal that a number of characters scored in this study (Table 1) are not taxonomically useful. Some of these

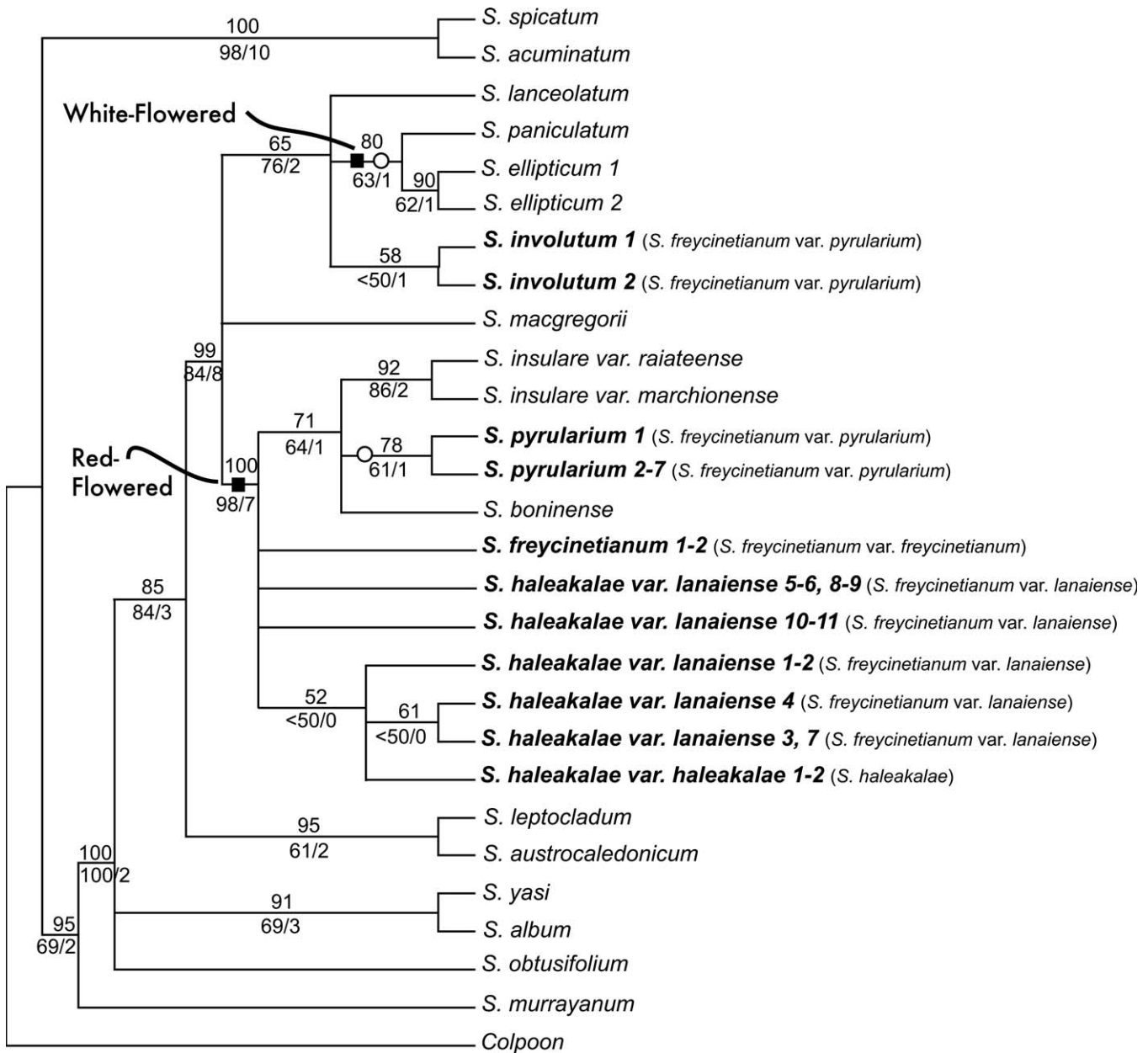


FIG. 1. The nrDNA (ITS + ETS) *Santalum* phylogeny. The ML and MP strict consensus phylogeny are congruent and shown here, with ML bootstrap values (> 50%) above and MP bootstrap values (> 50%) and decay index below the branches. Specific taxon, locality, and voucher information for all specimens are listed in Appendix 1, with corresponding sample numbers after taxon names. The revised classification of *Santalum* taxa featured in this study are in bold, while the old names are beside them in parentheses. The red- and white-flowered groups, as referred to in the text, are indicated on the phylogeny. Additionally, black boxes or white circles on the branches indicate the hypothesized branches on which the progenitors of the hybrid species *S. involutum* and *S. boninense* occurred.

characters are consistent among all taxa, such as floral tube shape, pedicel length, number of stigma lobes, seed surface texture, and drupe shape. Other characters, such as the disk lobe shape, are not useful as they vary widely within each taxon, and often within a single specimen.

DISCUSSION

The goals of this study were to elucidate the genetic structure within and between populations of the Hawaiian red-flowered sandalwoods to guide a new classification that reflects evolutionary history and gene flow. Based on the molecular data gathered here, and confirmed by the morpho-

logical analyses presented below, there are four important revisions that are warranted: 1) *S. freycinetianum* is restricted to O`ahu; 2) *S. haleakalae* now includes var. *haleakalae* on East Maui, as well as var. *lanaiense*, the latter includes populations on East Maui, West Maui, Moloka`i, and Lana`i; 3) *S. freycinetianum* var. *pyrularium* from Kaua`i should be considered *S. pyrularium*; and finally, 4) a set of small populations in and around Kalalau Valley, Kaua`i, should be regarded as a distinct species, *S. involutum*, an ancient hybrid between the white and red-flowered Hawaiian *Santalum* clades. Photos of each taxon are shown in Fig. 3.

Biogeography—The results from the current study suggest that the initial colonization event of *Santalum* from

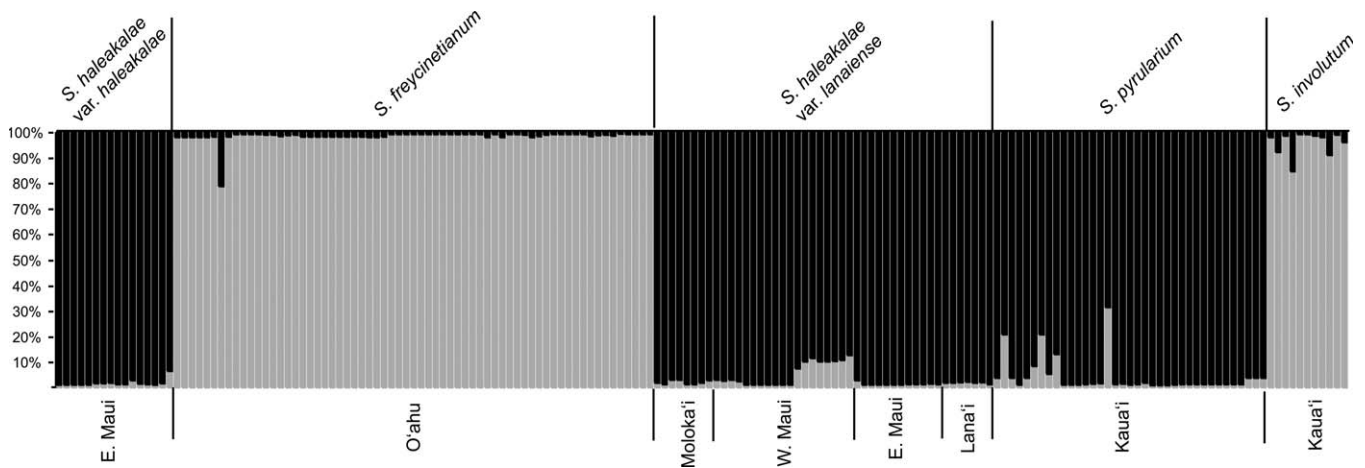


FIG. 2. Genetic STRUCTURE bar graph of *Santalum* microsatellite data. Each of the 175 individuals genotyped in this study is represented by a single vertical bar partitioned into two colored segments which represents the individuals probability of belonging to one of two ($K = 2$) groups. "Group 1" is represented in black, while "Group 2" is represented in grey. Along the top of the bar graph, the five taxa are indicated, while general localities are given below the graph. The order of individuals follows specimens listed in Appendix 2, which also includes detailed voucher and locality information.

Australia to the Hawaiian Islands occurred in the island of Kaua'i, approximately 1.0–1.5 million years ago (Ma; Harbaugh and Baldwin 2007). This first colonizer likely soon dispersed to the neighboring island of O'ahu sometime after and resulted in a single species, *S. freycinetianum*. Subsequently, a colonization from O'ahu to the Maui Nui complex occurred prior to the separation of the Maui Nui complex, in which the islands of Maui, Lana'i, Moloka'i, and Kaho'olawe were connected as a single landmass, which began to break apart approximately 0.6 Ma, but after the island of Moloka'i was separated from O'ahu, which was briefly connected via the Penguin Bank shoal until about 2 Ma (Price and Elliott-Fisk 2004); this colonization resulted in *S. haleakalae* including varieties *haleakalae* and *lanaiense*, which occurs throughout all island once included in the Maui Nui complex.

The second *Santalum* colonist arrived to the islands approximately 0.4–0.6 Ma (Harbaugh and Baldwin 2007) and led to the white-flowered *S. ellipticum*/*S. paniculatum* clade. This colonization likely also occurred on Kaua'i, as there was an ancient hybridization event forming the restricted Kaua'i endemic *S. involutum* between the ancestor of each Hawaiian *Santalum* clade, as indicated by the black squares in Fig. 1. Likely within less than 0.4–0.6 Ma (Harbaugh and Baldwin 2007), *S. pyrularium* diverged in Kauai from the original colonizing lineage. After this time, the endemic Bonin Island species *S. boninense* (Bonin Islands) also formed on Kaua'i as a hybrid event between *S. pyrularium* and the *S. ellipticum*/*S. paniculatum* clade (Harbaugh 2008), indicated by the white circles on Fig. 1. Lastly, the ancestor of *S. pyrularium* also dispersed out of Kaua'i southwards to French Polynesia, leading to the variable species *S. insulare* (Harbaugh and Baldwin 2007).

KEY TO *SANTALUM* TAXA

1. Leaves yellowish-green to grayish-green, thinly chartaceous and often translucent, linear elliptic (rarely conduplicate-falcate), margins involute (rarely flat), often appearing droopy; flowers cream to purple throughout, or greenish with purple interior; ovary inferior; ring on drupe apical (Kaua'i) *S. involutum*
1. Leaves light, medium, olive to dark green, chartaceous to coriaceous, narrowly to broadly ovate, elliptic, oblong, or conduplicate-falcate, margins flat to slightly recurved; ovary partly inferior (approx. 2/3); ring on drupe subapical (O'ahu, Lana'i, Maui, Moloka'i, Kaua'i) 2
2. Leaves medium to dark green, chartaceous to coriaceous, narrowly to broadly elliptic, ovate, to oblong (rarely conduplicate-falcate), margins flat (rarely wavy); flowers cream to purple Throughout, greenish with purple interior, or greenish white turning red with age (Kaua'i) *S. pyrularium*
2. Leaves light, medium, olive to dark green, chartaceous to coriaceous, conduplicate falcate, elliptic, oblong, ovate, or orbicular; margins flat (rarely slightly recurved) flowers light pink, or deep red throughout, or with white interiors 3
3. Leaves chartaceous, surface not paler abaxially, conduplicate-falcate, narrowly elliptic, oblong, to narrowly ovate, often appearing wilted; flowers light pink turning deep pink with maturity (rarely with white interiors); floral tubes 3.3–5.9 mm long (O'ahu) *S. freycinetianum*
3. Leaves chartaceous to coriaceous, surface paler and more glaucous abaxially, elliptic (rarely conduplicate-falcate); flowers deep pink to red throughout, or with white to pink interiors; floral tubes 3.9–8.5 mm long 4
4. Inflorescences dense, terminal (rarely axillary); bracts 5 mm long, persistent; leaves medium, olive to dark green, thickly coriaceous, broadly ovate, elliptic, to orbicular, 2.9–5.1 cm long × 1.8–3.1 cm wide; leaf lateral veins apparent on abaxial surface (to not apparent in thick leaves), yellowish to green; petioles 2.0–7.4 mm long (E. Maui) *S. haleakalae* var. *haleakalae*
4. Inflorescences fairly dense, terminal or axillary; bracts 1–4 mm long, not persistent; leaves light, olive, to dark green, chartaceous to coriaceous, narrowly to broadly ovate, to elliptic (rarely conduplicate-falcate), 4.4–6.8 cm long × 1.6–3.1 cm wide; leaf lateral veins apparent on both surfaces, yellowish to dark purple; petioles 7.4–15.4 mm long (Lana'i, Maui, Moloka'i) *S. haleakalae* var. *lanaiense*

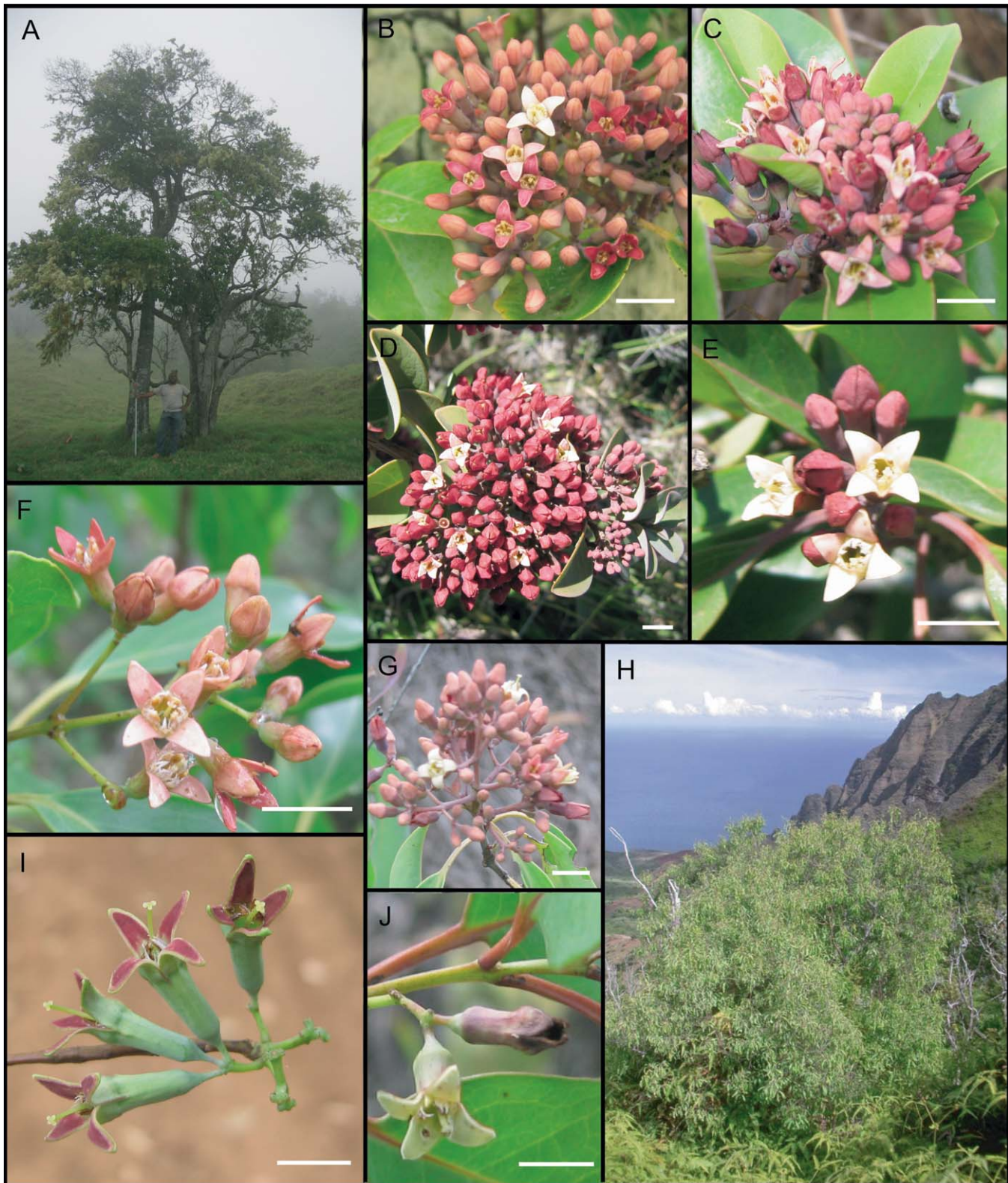


FIG. 3. A-B. *Santalum haleakalae* var. *lanaiense*, Auwahi Preserve, E. Maui. C. *S. haleakalae* var. *lanaiense*, Kanepu`u Preserve, Lana`i. D. *S. haleakalae* var. *haleakalae*, Haleakala National Park, E. Maui. E. *S. haleakalae* var. *lanaiense*, Kamakou Preserve, Moloka`i. F. *S. freycinetianum* Ko`olau Mts., O`ahu. G. *S. freycinetianum*, Wai`nae Mts., O`ahu. H. *S. involutum*, above Kalalau Valley, Kaua`i. I. *S. pyrularium*, Na Pali Kona Forest Reserve, Kaua`i. J. *S. pyrularium*, Waimea Canyon State Park. White scale bars (photos B-G and I-J) = 7 mm. All photos taken by D. T. Harbaugh except photo H by K. Wood.

TAXONOMIC TREATMENT

The specimens observed and characterized in this taxonomic treatment were carefully chosen to represent the extent of the natural ranges and morphological diversity of each taxon. The specimens indicated with an asterisk were those specimens for which a more extensive quantitative and qualitative morphological analysis was performed using the characters listed in Table 1. Photos of each taxon are shown in Fig. 3.

SANTALUM FREYCINETIANUM Gaudich. Voy. Uranie, part 11: 442. 1829.—TYPE: U. S. A. Hawaiian Islands: *Insulis Sandwichensibus* (Wahou), alt. 350–400 hex. 1817, C. Gaudichaud-Beaupré s. n. (holotype: P!; isotypes: B-photo! K-fragment!).

Santalum longifolium Meurisse, Bull. Mens. Soc. Linn. Paris 2: 1026. 1892. *Santalum freycinetianum* Gaudich. var. *longifolium* (Meurisse) O. Deg., Flora Hawaiiensis: 100. 1937.—TYPE: U. S. A. Hawaiian Islands: O`ahu, 1854–55, J. Remy 510 (holotype: P!).

Tree, or shrubby tree, evergreen, usually 4–10 m (rarely up to 20 m) in height, with a single or multiple stems; leaves opposite, more glaucous abaxially, light to dark green, chartaceous, surface not much paler on abaxial side, conduplicate-falcate, narrowly elliptic, oblong, to narrowly ovate, often appearing wilted, (4.1–)5.5–7.9(–10.1) cm long × (1.2–)1.6–3.3(–4.4) cm wide, margins flat (rarely wavy), apices acute, bases cuneate (rarely rounded), lateral veins barely apparent on both surfaces, yellowish to pink; petioles (7.7–)11.3–17.5(–20.7) mm long; inflorescences cymes, sparse, terminal or axillary; flowers light pink turning deep pink with maturity (rarely with white interiors); floral-tube campanulate to cylindrical (2.6–)3.3–5.9(–7.0) mm long × (2.2–)2.4–3.4(–4.3) mm wide, with vertical keel below each corolla lobe; pedicels (0.5–)1.0–2.0 mm long; corolla lobes 4 (rarely 5), concave with thickened margins, papillate, (2.8–)2.6–4.2(–5.8) mm long × (1.6–)2.2–2.9(–3.0) mm wide; disk lobes lingulate, apices acute or round; stigma lobes 3; stamens 4, hairs proximal to the filaments (rarely hairs distal); ovary partly inferior (approx. 2/3); drupe elliptic, with subapical ring, 9–14 mm long; seed muricate, with pointed beak on one end.

Representative Specimens Examined—U. S. A. Hawaiian Islands: O`ahu, Koolau Mts, Honolulu Watershed Forest Reserve, *Lammers and Imada* 5537 (MAK); Manana Ridge Trail, *Harbaugh* 318*, 322*, 323*, 324* (US); Aiea Loop Trail, *Lee* s. n. (BISH); Honolulu, Mauumae Ridge, Lanipo Trail, *Lennstrom* 1994–92 (BISH); Wai`anae Mts., Honouliuli Preserve, Palehua Rd., *Harbaugh* 24*, 25*, 30* (UC); Wai`anae Mts., West Makaleha Valley, along Ka`ala Rd., *Harbaugh* 208*, 209*, 212*, 215*, 216* (US); Wai`anae Mts., Honouliuli Preserve, *Harbaugh* 228*, 232*, 261*, 266*, 281* (US);

Common Names—*Santalum freycinetianum* is known as sandalwood, forest sandalwood, or Freycinet sandalwood (Pratt 1998), and by its Hawaiian name `iliahi (Kepler 1998).

Range and Environment—*Santalum freycinetianum* occurs scattered throughout the Wai`anae and Ko`olau Mountains on the island of O`ahu from approximately 300–800 m in elevation. It grows in partial shade to full sun, and is often associated with native taxa such as *Acacia koa* and *Metrosideros polymorpha*, and nonnative *Eucalyptus* spp., *Psidium cattleianum*, and *Schinus terebinthifolius* (Oppenheimer, pers. obs.).

Conservation Status—With Moloka`i populations now considered *S. haleakalae* var. *lanaiense*, this species is restricted to O`ahu in both the Wai`anae and Ko`olau Mts. There are likely fewer than 1,000 plants (Oppenheimer, unpubl. data), so listing as a threatened species may be warranted.

Notes—Stemmermann (1980a) was the first to treat certain populations from the island of Moloka`i as *S. freycinetianum* based on a few specimens. However, she said that “with further collections of plants from Moloka`i it may be possible to recognize the Moloka`i plants as distinct from *S. freycinetianum* at the varietal level, but that should only be done when the range of variation is better understood.” Wagner et al. (1999b) agreed with Stemmermann (1980a) that the plants on Moloka`i should be considered *S. freycinetianum*, but that they are intermediate in morphology towards var. *lanaiense* (on Maui). The new evidence gathered in this study reveal that the Moloka`i plants do not interbreed with plants of *S. freycinetianum* from O`ahu (consistent with the geological history of the islands at the time of colonization to the islands) and are in fact genetically and morphologically indistinguishable from populations of *S. haleakalae* var. *lanaiense* from West and East Maui, and Lana`i. Although the extremes of morphological variation are not present in Moloka`i plants (namely plants with flat, wide leaves), the morphological characteristics fall within the great morphological diversity present within populations of *S. haleakalae* var. *lanaiense* on West and East Maui, and Lana`i, and not within those from O`ahu.

SANTALUM HALEAKALAE Hillebr., Fl. Hawaiian Isl.: 390. 1888.—TYPE: U. S. A. Hawaiian Islands: Maui, Haleakala, 2440–3050 m, May 1872, W. Hillebrand & J. M. Lydgate s. n.* (holotype: B, presumably destroyed; lectotype, here designated: BISH-581851!; isolectotype: K!).

Tree, or shrubby tree, evergreen, single or multiple stems; leaves opposite, more glaucous abaxially, surface paler abaxially, apices acute or obtuse (rarely acuminate), bases cuneate, margins flat to slightly recurved; inflorescences cymes; flowers deep pink to red throughout, or with white to pink interiors; floral-tubes campanulate to cylindrical, without vertical keel below each corolla lobe; disk lobes lingulate, apices acute or round; corolla lobes 4 (rarely 5), concave with thickened margins, papillate; stigma lobes 3; stamens 4, hairs proximal to the filaments (rarely hairs distal); ovary partly inferior (approx. 2/3); drupe elliptic, with subapical ring; seed muricate, with pointed beak on one end.

var. *HALEAKALAE*

Usually 1–8 m in height; leaves medium, olive to dark green, thickly coriaceous, broadly ovate, elliptic, to orbicular, (2.2–)2.9–5.1(–6.5) cm long × (1.2–)1.8–3.1(–4.0) cm wide; leaf lateral veins apparent on abaxial surface (to not apparent in thick leaves), yellowish to green; petioles (1.2–)2.0–7.4(–11.6) mm long; inflorescences dense to dense, terminal (rarely axillary); bracts 5 mm long, persistent; floral-tubes (2.0–)3.9–8.5(–10.0) mm long × (2.0–)2.2–3.4(–3.5) mm wide, pedicels (0.7–)1.0–3.2(–4.4) mm long; corolla lobes (2.7–)3.1–5.7(–7.1) mm long × (1.9–)2.1–3.3(–4.0) mm wide; drupe 9–14 mm long.

Representative Specimens Examined—U. S. A. Hawaiian Islands, Maui, *Mann and Brighnam* 396 (G); Koolau Gap, *Degener* 2277 (G); Haleakala Crater, Namanaokeakua, *Stemmermann* 749 (BISH); Haleakala National Park, *Harbaugh* 42*, 43* (UC); Haleakala, *Alexander and Kellogg* 5290* (BISH); Haleakala National Park, Hosmer’s Grove Campground, *Harbaugh* 334*, 340*, 341*, 352*, 353* (US); Haleakala Ranch, *Harbaugh* 356*, 358* (US); Poli Poli/Kula Forest Reserve, Waiohuli Gulch, *Harbaugh* 359 (US); Kula Forest Reserve, Waiohuli, *Oppenheimer* H70709* (US, BISH); Kahikinui Forest Reserve between Pu`ukeokeo and Kanahau, *Oppenheimer and Perlman* H110731* (US, BISH); Kahikinui Forest Reserve, SE of Pu`ukeokeo, *Oppenheimer and Perlman* H110734* (US, BISH).

Common Names—*Santalum haleakalae* var. *haleakalae* is known as sandalwood or Haleakala sandalwood, and by its Hawaiian name `iliahi (Kepler 1998).

Range and Environment—*Santalum haleakalae* var. *haleakalae* is rare and is restricted to a single volcano, Haleakala on East Maui, and occurs at higher elevations (1,800–2,700 m) in subalpine and montane mesic forest plant communities.

Conservation Status—A large portion of the habitat of *Santalum haleakalae* var. *haleakalae* on the western slope has been converted to pasture and other agricultural uses. Seedlings are rarely, if ever, observed (Oppenheimer, pers. obs). Older trees readily spread vegetatively via root sprouts when surface roots are exposed or damaged, sometimes forming small stands. Threats include fire; browsing and/or trampling by introduced ungulates such as cattle (*Bos taurus*), goats (*Capra hircus*), deer (*Axis axis*), and pigs (*Sus scrofa*), and possibly black twig borer (*Xylosandrus compactus*). Seeds are commonly predated by rats (*Rattus rattus*, *R. exulans*), and mice (*Mus domesticus*). Competition for space, light, water, and nutrients with alien plant species such as *Rubus argutus*, *R. niveus*, *Pinus* spp., and *Fraxinus uhdei* are significant threats. Mat forming grasses such as *Melinis minutiflora* and *Pennisetum clandestinum* prevent seedling establishment (Oppenheimer, pers. obs.). Pollinators are mostly unknown but are probably depleted across the range. Dispersal is presumed by frugivorous passerines, many of which are also rare, endangered, or extinct. Additionally, there is at least one unconfirmed report of illegal harvesting of an unknown number of individuals in the past ten years. It is estimated that approximately 700 plants occur throughout its range, which is far more restricted than *S. haleakalae* var. *lanaiense*, which is currently listed on the USFWS Endangered Species List (as *S. freycinetianum* var. *lanaiense*). We suggest that further action should be taken to list *S. haleakalae* var. *haleakalae* as endangered.

Notes—We are transferring the formerly recognized *S. freycinetianum* var. *lanaiense* to a variety of *S. haleakalae* because there is no genetic evidence to separate it, and it is likely an ecological variant of the lower-elevation plants, which were considered a distinct species based on a variety of characters including its thick coriaceous leaves and bottle-shaped adaxial epidermal cells, congested cymes, deep red flowers, and persistent bracts. However, according to Wagner et al. (1999b) the “assignment to specific rank is tentative.” Additionally, Stemmermann (1980b) demonstrated that the development of the bottle-shaped adaxial epidermal cells characteristic of the highest elevation plants is correlated with environmental factors because there is a linear relationships between height of the cells and elevation. Leaf thickness and the density of the inflorescences appear also to be environmentally controlled, as there is a gradient with elevation and they intergrade with *S. haleakalae* var. *lanaiense* found at lower elevations on Haleakala.

var. **lanaiense** (Rock) Harbaugh, comb. nov. *Santalum freycinetianum* Gaudich. var. *lanaiense* Rock. Indig. trees Haw. Isl. 129 1913. Indig. Trees Haw. Isl.: 129. 1913. *Santalum lanaiense* (Rock) Rock, Hawai'i Board Agric. and For., Bot. Bull. 3: 21. 1916.—TYPE: U. S. A. Hawaiian Islands: Lana'i, on the highest ridge, Jul 1910, J. F. Rock 10061* (holotype: BISH-579847!).

Santalum freycinetianum Gaudich. var. *auwahiense* Stemmerm. Pacific Sci., 34(1): 47. 1980.—TYPE: U. S. A. Hawaiian Islands: Maui, Auwahi Forest Reserve, 1 Jun 1977,

R. L. Stemmermann & J. Kjargaard 2149* (holotype: BISH-430709!; isotypes: BISH-2 sheets!).

Usually 1–6 m in height; leaves light, olive, to dark green, chartaceous to coriaceous, narrowly to broadly ovate, to elliptic (rarely conduplicate-falcate), (3.4–)4.4–6.8(–8.4) cm long × (1.0–)1.6–3.1(–4.9) cm wide; leaf lateral veins apparent on both surfaces of the leaf, yellowish to dark purple; petioles (3.9–)7.4–15.4(–21.7) mm long; inflorescences fairly dense to dense, terminal or axillary; bracts 1–4 mm in length, not persistent; floral tubes (3.4–)4.2–8.0(–11.2) mm long × (1.9–)2.3–3.5(–4.0) mm wide; pedicels (1.0–)1.5–2.9(–4.0) mm long; corolla lobes (2.0–)3.0–4.4(–4.8) mm long × (1.8–)1.9–2.7(–3.8) mm wide; drupe 10–16 mm long.

Additional Specimens Examined—U. S. A. Hawaiian Islands, Lana'i, Kanepu'u, St. John and Cowan 22625* (BISH); Kanepu'u Forest, Munro 679* (BISH); Munro s. n.* (BISH); Kanepu'u, Montgomery and Ruffin s. n. (BISH); Mt. near Koele, Forbes 114L (BISH); Forbes 327L (BISH); Mts. on east end, Forbes 229L (BISH); Head of Lopa Gulch, the short ridge just N of Puhielelu ridge, Lau 2868 (BISH); NW extremity of island, Stone 883 (BISH); W of divide, O. Degener 35806 (BISH); Munro Trail, open shrubby rainforest at the top, O. Degener 24257 (BISH); NW part of Munro Trail, O. Degener and Hobdy 24255 (BISH); Kanepu'u, Desha et al. s. n. (BISH); Kaa, Kanepu'u, Herbst and Spence 5789 (BISH); Kanepu'u, Little 31251 (BISH); Kanepu'u, Stemmermann 811, 812, 813 (BISH); Lanaihale peak in *Metrosideros* forest, Little 31233 (BISH); Munro 211, 951 (BISH); Gulches between Kehewai and Kahinahina, Perlman and Montgomery 6375 (BISH); Pu'u A`ali'i, Kealia Aupu-Kaunolu divide, St. John and Eames 18712 (BISH); Kanepu'u Preserve, Harbaugh 374*, 375*, 376* (US); headwaters of Wai'opa Gulch, NE of Ha'alelepa`akai, Oppenheimer and Perlman H90704* (US, BISH); Puhielelu Ridge, near enclosure fence, Oppenheimer and Perlman H100732* (US, BISH). West Maui, Lahaina District, on a ridge dividing Kahoma Valley and Kealii Gulch, Oppenheimer et al. H20011 (BISH); Mts. above Napili and pineapple plantations, watershed land, Smith 2900* (UC); lowland ohia mixed forest, Welton and Haus 1507 (BISH); Hanaula, Ukumehame District, head of Papalaua Gulch, Medeiros 540 (BISH); Pu'u Kukui Watershed Preserve, Transect 4, Harbaugh 360*, 364*, 366*, 367*, 369* (US); South of Ukumehame, gulch of Hana'ula Iki, Oppenheimer H60722*, H60723* (US, BISH); Ridge NE of Kaua'ula Valley, Kaua'ula/Manowaiopae Divide, Oppenheimer et al. H100707*, H100708* (US, BISH); Wailuku District, Pohakea Gulch, Oppenheimer and Baldwin H110730* (US, BISH); Oppenheimer and Perlman H100701* (US, BISH). East Maui, Auwahi 8 mi E of Ulupalakua, S slope of Haleakala Crater, Little 31131* (BISH); Auwahi District, S slope of E Maui, Medeiros 196 (BISH); Auwahi, St. John 26863 (BISH); Auwahi SE Puu Ouli, S slope of Haleakala, Fosberg 41515a (BISH); Auwahi land beyond Ulupalakua, Sohmer 6603 (BISH); Haleakala S slope, just above the pipeline Rd. on W side of Auahi-Kanaia border, Medeiros 182 (BISH); Auwahi Forest Reserve, Stemmermann and Hobdy 755 (BISH); E. Funk's *Geranium arboreum* study site at Polipoli, Takeuchi and Funk East Maui 7a (BISH); Koolau Gap on N. slope of Haleakala, Stemmermann 734 (BISH); Auwahi Preserve, in Ulupalakua Ranch, along 4WD road, Harbaugh 394*, 395*, 396*, 406*, 413* (US). Moloka'i, Russell s. n.* (BISH); Kikiakala on steep gulch slope N of Kamiloloa, Hobdy 1163* (BISH); Lands of Makakupaia, Makakupaia Ridge jeep trail, Wagner et al. 4933 (BISH); Kawela AHU, Pu'u Hoi Ridge; upper part of Pelekunu Valley on narrow ridge, Warshauer and McEldowney 3003 (BISH); Wawa'ia AHU, Tr 9 (15); ridge E of Kua Gulch, Stemmermann and Montgomery 3896 (BISH); Kawela AHU, Tr 5 (19); Along W form of Kawela Gulch, Warshauer and McEldowney 2332 (BISH); ridge between east forks of Kawela Gulch, Davis 790 (BISH); upper Kaunakakai Pl along Makakupaia Rd., Hobdy 2619 (BISH); Kamakou reserve E. side of Kawela ridge, due SW of Puu O Kaeha, Lorence et al. 5612 (BISH); Puu Hoi ridge, Pelekunu valley, Kepler s. n. (BISH); upper Kaunakakai along Makakupaia, Hobdy 2620 (BISH); Kamakou Preserve, Harbaugh 384*, 386*, 388*, 389*, 393* (US); Kikiakala, Headwaters of Waihanau Stream, Oppenheimer H10811* (US, BISH); Central west fork of Kawela Gulch, Oppenheimer and Perlman H40815* (US, BISH); W side of Waiakuilani Gulch, east of Pu'u Kolekole, Oppenheimer and Perlman H80706* (US, BISH).

Common Names—*Santalum haleakalae* var. *lanaiense* is known as sandalwood, or Lana'i sandalwood, and by its Hawaiian name `iliahi (Kepler 1998).

Range and Environment—Scattered and rare in exposed or semishaded scrublands in the West Maui mountains (from

800–1,300 m), scattered on the southern slope of Haleakala Crater on East Maui (1,200–1,350 m), rare within the Kanepu`u Preserve on western Lana`i (550 m), scattered in the mountains of eastern Lana`i (750–950 m), and scattered in upper elevations of eastern Moloka`i (950–1,250 m). It is often associated with the following plant groups: *Metrosideros*, *Sadleria*, *Nephrolepis*, *Canavalia*, *Vaccinium*, *Alyxia*, *Myrsine*, *Clermontia*, *Dubautia*, *Doodia*, *Liparis*, *Dodonaea*, *Wikstroemia*, *Leptecophylla*, *Coprosma*, *Myoporum*, *Diospyros*, *Pisonia*, *Melicope*, *Pittosporum*, *Dryopteris*, and *Bidens*.

Conservation Status—Listed as Endangered by the US Fish & Wildlife Service (Herbst 1986), *Santalum haleakalae* var. *lanaiense* is now considered to occur on three islands. Despite this distribution, seedlings are rarely, if ever, observed. It spreads locally via vegetative means by root sprouts when surface roots are damaged or exposed. Threats include fire; and browsing and/or trampling by introduced ungulates such as goats (*Capra hircus*), deer (*Axis axis*), mouflon sheep (*Ovis musimon*), and pigs (*Sus scrofa*). Seeds are commonly predated by rats (*Rattus rattus*, *R. exulans*), and mice (*Mus domesticus*). Competition for space, light, water, and nutrients with alien plant species such as *Clidemia hirta*, *Grevillea robusta*, *Leptospermum scoparium*, *Morella faya*, *Psidium cattleianum*, *Acacia melanoxylon*, *Fraxinus uhdei*, *Tibouchina herbacea*, *Rubus argutus*, *R. discolor*, and *Schinus terebinthifolius* also degrades habitat. Mat forming grasses such as *Melinis minutiflora* prevent seedling establishment. The black twig borer (*Xylosandrus compactus*) potentially attacks these trees, and herbivory by several introduced slugs commonly found across its range likely prevents reproduction. Pollinators are mostly unknown but are probably depleted across the range. Dispersal is presumed by frugivorous passerines, many of which are also rare, endangered, or extinct. Fewer than 2000 plants are believed to occur (Oppenheimer, unpubl. data).

Notes—No genetic evidence was gathered to support separating populations of *S. haleakalae* var. *lanaiense* from Maui, Moloka`i, and Lana`i into separate varieties. This is a morphologically variable taxon, with leaf shapes, textures, and sizes ranging greatly, even within a population. However, several morphological characters unite these populations, including a paler abaxial side of the leaves, often dark purplish lateral veins in younger leaves, and deep red flowers at maturity, often with white interiors in younger flowers. With limited data, Stemmermann (1980a) observed that the Moloka`i plants were intermediate between those found on O`ahu and Lana`i, but assigned them to *S. freycinetianum*; with no new data to say otherwise, Wagner et al. (1999b) chose to retain the circumscription of Stemmermann (1980a). However, upon the inspection of a wide range of specimens, it is clear that these plants fall within the ranges of morphological diversity of populations of *S. haleakalae* var. *lanaiense* from Lana`i and Maui, which is consistent with results of the genetic analyses.

SANTALUM INVOLUTUM H. St. John, *Phytologia*, 55(4): 220. 1984.—TYPE: U. S. A. Hawaiian Islands: Kaua`i, between Ke`e and Hanakapiai, ridge top on NE side of last stream NE of Hanakapiai, 25 Jul 1976, C. Christensen 38* (holotype: BISH-498267!; isotypes: BISH-3 sheets!).

Small tree, evergreen, usually 2–7 m in height; leaves opposite, yellowish-green to grayish-green, chartaceous (often translucent), often drooping, more glaucous and slightly lighter on abaxial surface, linear elliptic (rarely conduplicate-

falcate), sides involute (rarely flat), (4.6–)5.7–8.1(–8.2) cm long × (1.4–)1.5–1.7(–1.8) cm wide, margins flat, apices acute, bases cuneate, lateral veins slightly apparent on adaxial surface; midvein yellowish, petioles yellowish to pinkish, (7.0–)8.1–16.3(–17.0) mm long; inflorescences cymes, sparse terminal or axillary; flowers greenish-white throughout (sometimes turning red with age); floral tubes campanulate to cylindrical, (5–)6–9(–11) mm long × 2–3 mm wide, without vertical keel below each corolla lobe; corolla lobes 4, concave with thickened margins, 3–4(–5) mm long × 1.5–3 mm wide; disk lobes lingulate, apices acute or round; stigma lobes 3; stamens 4; ovary inferior; drupe elliptic, with apical ring, 13–20 mm long; seed muricate, with pointed beak on one end.

Representative Specimens Examined—U. S. A. Hawaiian Islands, Kaua`i, Kalalau Valley, N side and E of Keanapuka Falls, (2,450 ft.), *Wood and Holmes 12482** (PTBG); Hanalei District, Pohakua, hanging valley between Kalalau and Hanakoa (600 m), *Wood et al. 1770** (PTBG); Wainiha Valley, Wainiha (400 ft), *Fosberg and Sachet 13946** (BISH); west of Waioli-Waipu Ridge in Koa forest (1,100 ft), *Christensen 69** (BISH); Lumahai-Wainiha Ridge, sides of ridge (1,000 ft), *Christensen 182** (BISH); Wahiawa, edge of Kanaele Bog (2,100 ft), *St. John 26766** (BISH); Wainiha Valley 1 1/8 mile in from last house (650 ft), *Christensen 121** (BISH); Na Pali Coast, Hanakapiai Ridge E. of stream (800–1,200 ft), *Christensen 57** (BISH).

Common Names—*Santalum involutum* has not been commonly recognized, though it would be considered by its Hawaiian name `iliahi. However, based on its Latin name and characteristic leaf margins, we suggest that this species be known as involute sandalwood.

Range and Environment—*Santalum involutum* is restricted to Kaua`i and occurs in the northwestern Na Pali coast valleys of Hanakapiai, Pohakua, and Kalalau, in addition to the northern valley of Wainiha and the southern region of Wahiawa (120–750 m). Although observed in *Metrosideros* wet forest, this species seems to prefer *Diospyros* mixed mesic forest which is extremely rare and known for its floristic diversity. Some of the associated genera, many of which are represented by numerous species, include *Acacia*, *Alphitonia*, *Bobea*, *Euphorbia*, *Charpentiera*, *Coprosma*, *Cyanea*, *Cyrtandra*, *Diospyros*, *Dodonaea*, *Dubautia*, *Elaeocarpus*, *Eugenia*, *Exocarpos*, *Flueggea*, *Hibiscus*, *Ilex*, *Isodendron*, *Kadua*, *Kokia*, *Labordia*, *Lysimachia*, *Melicope*, *Metrosideros*, *Myrsine*, *Neraudia*, *Nesoluma*, *Nestegis*, *Nototrichium*, *Pipturus*, *Pisonia*, *Pittosporum*, *Platydesma*, *Pleomele*, *Pouteria*, *Psychotria*, *Pteralyxia*, *Rauwolfia*, *Schiedea*, *Tetraplasandra*, *Wilkesia*, *Xylosma*, and *Zanthoxylum*.

Conservation Status—*Santalum involutum* is in need of further field research to better understand its distribution and abundance. Plants have not been observed around the holotype locality for more than 30 yr, and at this time it is only known from isolated forest pockets in Pohakua and Kalalau valleys. Currently *S. involutum* should be considered endangered considering its small range and area of occupancy, in addition to its low numbers (ca. 50–100 trees; Wood unpubl. data). This taxon is threatened by fire, loss of habitat, limited gene pool, and invasive nonnative species similar to those that threaten *S. pyrularium*.

Notes—The results from this study indicate that *S. involutum* is an ancient hybrid based on molecular data and this is consistent with morphological characters: the leaf-shape, floral tube shape, and overall habit have aligned it with the red-flowered taxa, although morphological characters first observed by St. John (1984) as distinguishing it from *S. pyrularium*, namely its shorter campanulate, white to greenish flowers, as well as inferior ovary and apical drupe ring unite *S. involutum* with the *S. ellipticum* clade (Harbaugh 2007). The exclusion of these plants from *S. pyrularium* helps

to more clearly define *S. pyrularium* as a unique species. Stemmermann (1980a) had dropped *S. freycinetianum* var. *pyrularium* from specific rank in part because of the significant variation in floral tube length, and in the rugosity of the endocarp (Skottsberg 1944); however this may be explained by the consideration of plants now separated into two distinct species, *S. pyrularium* and *S. involutum*.

The discovery of a distinct lineage of ancient hybrid origin between the two Hawaiian *Santalum* clades, in the rugged coastal valleys on northwestern Kaua'i is not surprising given that it is home to a great diversity of other restricted endemics, including species of *Schiedea* (Wagner et al. 1994), *Dubautia* (Baldwin and Carr 2005), *Remya* (Wagner and Herbst 1987), *Hibiscadelphus* (Lorence and Wagner 1995), *Chamaesyce* (Lorence and Wagner 1996), *Stenogyne* (Wagner and Weller 1991), *Nototrichium* (Lorence 1996), *Tetraplasandra* (Lowry and Wood 2000), and *Kadua* (Wagner and Lorence 1998), many of which are rare and endangered (Wood and Perlman 1993; Wagner et al. 1999a).

SANTALUM PYRULARIUM A. Gray, Proc. Amer. Acad. Arts 4: 327. 1860. *Santalum freycinetianum* Gaudich. var. *pyrularium* (A. Gray) Stemmerm., Pacific Sci., 34(1): 48. 1980.—TYPE: U. S. A. HAWAIIAN ISLANDS: Kaua'i, 1838–42, US Exploring Expedition s. n. (holotype: US-00055059!; isotype: P!).

Santalum majus H. St. John, Phytologia, 55(4): 223. 1984.—TYPE: U. S. A. HAWAIIAN ISLANDS: Kaua'i, Kumuela Ditch Trail, along border between Koke'e State Park and Na Pali-Kona Forest Reserve, 13 Aug 1964, M. R. Crosby & S. Anderson 2024* (holotype: BISH-68301!).

Santalum pyrularium A. Gray var. *sphaerolithos* Skottsberg., Vascular plants from the Hawaiian Islands. 4: 359. 1944.—TYPE: U. S. A. HAWAIIAN ISLANDS: Kaua'i, Alakai, 16 Aug 1938, L. M. Cranwell & C. Skottsberg 2979* (holotype: BISH-579831!).

Small tree, or shrubby tree, evergreen, usually 1–5 m in height, with a single or multiple stems; leaves opposite, medium to dark green, chartaceous to coriaceous, more glaucous abaxially, surface not much paler on abaxial surface, narrowly to broadly elliptic, ovate, to oblong (rarely conduplicate-falcate), (3.6–)5.4–7.8(–9.4) cm long × (1.2–)2.1–3.2(–3.8) cm wide, margins flat (rarely wavy), apices acute to obtuse (rarely acuminate), bases cuneate or rounded, lateral veins apparent on both surfaces of the leaf, yellowish to bright purple; petioles (5.9–)7.8–12.6(–15.7) mm long; inflorescences cymes, sparse, axillary (rarely terminal); bracts 1–4 mm, not persistent; flowers cream to purple throughout, or greenish with purple interior; floral-tubes campanulate to cylindrical, 3.6–8.5(–13.0) mm long × (2.6–)2.9–4.3(–4.4) mm wide, with vertical keel below each corolla lobe; pedicels (1.0–)1.1–2.7(–3.1) mm long; corolla lobes 4, concave with thickened margins, papillate, (3.4–)4.2–5.6(–5.8) mm long × (2.0–)2.4–3.3(–3.7) mm wide; disk lobes lingulate, apices acute or round; stigma lobes 3; stamens 4, hairs proximal to the filaments (rarely hairs distal); ovary partly inferior (approx. 2/3); drupe elliptic, with subapical ring, 15–22 mm long; seed muricate, with pointed beak on one end.

Representative Specimens Examined—U. S. A. HAWAIIAN ISLANDS, Kaua'i, Koloa District, Lihue-Koloa Forest Reserve, Wahiawa Bog, Lammers et al. 5863 (BISH); Wahiawa Bog, Herbst 2230 (PTBG); Waimea District, Na Pali-Kona Forest Reserve, Lorence 5218* (BISH); Waimea Canyon State Park, Hwy 550 near mi 11.5, Lorence and Jamieson s. n. (BISH);

Waimea Canyon/Koke'e State Park, on Hwy 550, Harbaugh 02*, 05* (UC); Waimea Canyon State Park, Hwy 550 near mile 11.5, Flynn 2744* (BISH); Koke'e State Park, along the Awaawapuhi trail, Harbaugh 415*, 425*, 426*, 430*, 431* (US); Alakai Picnic area, Harbaugh 438*, 441*, 447*, 451* (US); Na Pali-Kona Forest Reserve, Harbaugh 456*, 459*, 460*, 461*, 463*, 471* (US); Waimea Canyon, along Hale ele ele Ridge Road, Regalado 671 (PTBG); Hwy. 55 near entrance to Kokee State Park, Spence 191 (PTBG); Poomau Canyon Lookout Trail, Flynn 139 (PTBG); upper Kawaiiki, Kaluahaulu Ridge (Mohihi-Waialae Trail), Wood 764 (PTBG); Honapu Trail, Darwin 1127 (PTBG); Waimea district, Na-Pali Kona Forest Reserve, Makaha Valley, Lorence et al. 5218 (PTBG); Near Kalahu, Kalalau Valley, Degener and Hathaway 21369* (BISH); Kalalau Valley, slopes of Kalahu, 300 m east of navy plane crash (2,500 ft), Wood and Perlman 3393* (PTBG); upper Honopu drainage (north side), (3,550–3,700 ft) Wood 4923* (PTBG); Kalalau, lower Kalahu side w / rope, Wood 3647* (2,000 ft) (PTBG); Kalalau Rim, Kalahu side between and west of first lookout, 300 m east of plane crash (700–800 m), Wood 1414* (PTBG); Haena-Kalalau Trail, in Hoolulu Valley, Na Pali Kona Coast, Carlquist 1645 (BISH); ridge between Kalahu and Nianiau, between Kalalau and Honapu Valleys, Fosberg 12129 (BISH); Kalahu Trail, below Kalalau Lookout (3,700 ft), Stone 1618 (BISH); N. side of Awaawapuhi Stream, Christensen 183 (BISH).

Common Names—*Santalum pyrularium* is known commonly as sandalwood, or by its Hawaiian name `iliahi (Kepler 1998).

Range and Environment—*Santalum pyrularium* is restricted to Kaua'i (270–1,400 m) and can be common around Waimea Canyon and Koke'e State Parks where it consistently prefers partial to full shade. It is most often associated with mesic (summer dry) forest communities growing with genera such as *Acacia*, *Alphitonia*, *Coprosma*, *Diospyros*, *Ilex*, *Kadua*, *Melicope*, *Metrosideros*, *Myrsine*, *Nestegis*, *Pittosporum*, *Pleomele*, *Pouteria*, *Psychotria*, *Tetraplasandra*, and *Xylosma*. It occasionally penetrates wet forest communities and bog margins where it is associated with genera such as *Metrosideros*, *Cheirodendron*, and *Dicranopteris*.

Conservation Status—*Santalum pyrularium* can occasionally be a codominant in mesic forest communities and is not considered rare (ca. 10,000 + trees; Wood, unpubl. data). Never the less, this taxon is threatened by fire, loss of habitat, and invasive nonnative species. Nonnative animals include goats (*Capra hircus*), black-tailed deer (*Odocoileus hemionus*), pigs (*Sus scrofa*), rats (*Rattus* spp.), and mice (*Mus domesticus*). Some of the more threatening nonnative plant taxa include *Psidium guajava*, *P. cattleianum*, *Lantana camara*, *Rubus argutus*, *Hedychium gardnerianum*, *Clidemia hirta*, and *Melinis minutiflora*.

Notes—In 1927 Skottsberg recognized *S. pyrularium* as distinct from *S. freycinetianum* based on its long and narrow disc lobes and large fruit: the receptacle is wider in *S. pyrularium* and of nearly the same width across the rim as the base, and the drupe is much larger and rugose in *S. pyrularium*. Stemmermann (1980a) reduced *S. pyrularium* to a variety of *S. freycinetianum* because some collections had flowers 7 mm long (including pedicel), which is shorter than the recorded measurements for the flowers of this taxon and falls into the range of flower length for *S. freycinetianum*. The variability in these characters may be accounted for by the inclusion of individuals in Stemmermann's analysis from both *S. pyrularium* and *S. involutum*, as *S. involutum* tends to have flowers that are much shorter than *S. pyrularium*. Interestingly, a specimen annotated by H. St. John himself as *S. involutum* (Degener and Hathaway 21369) fits well within the morphological variability of *S. pyrularium*, as it has long dark-colored flowered, coriaceous elliptical leaves, and short petioles.

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LITERATURE CITED

- Baldwin, B. G. and G. D. Carr. 2005. *Dubautia kalalauensis*, a new species of the Hawaiian silversword alliance (Compositae, Madiinae) from Northwestern Kaua'i, U.S.A. *Novon* 15: 259–263.
- Baldwin, B. G. and E. A. Friar. 2010. *Dubautia carrii* and *D. hanaulaensis*, new species of the Hawaiian silversword alliance (Compositae, Madiinae) from Moloka'i and Maui. *Novon* 20: 1–8.
- Brennan, P. and M. Merlin. 1991. Biogeography and traditional use of Santalum in the Pacific region. Pp. 30–39 *Santalum in the Pacific region: proceedings of a symposium, 2 June 1991, at the XVII Pacific Science Congress, Honolulu, Hawaii*, ed. F. H. McKinnell. Canberra: Australian Center for International Agriculture Research Proceedings 49.
- Bryan, G. J., J. McNicoll, G. Ramsay, R. C. Meyer, and W. S. De Jong. 1999. Polymorphic simple sequence repeat markers in chloroplast genomes of solanaceous plants. *Theoretical and Applied Genetics* 99: 859–867.
- Buck, P. 1964. *Arts and crafts of Hawaii, section 9: musical instruments*. Honolulu: Bishop Museum Publication 45.
- Butaud, J.-F., F. Rives, D. Verhaegen, and J.-M. Bouvet. 2005. Phylogeography of eastern Polynesian sandalwood (*Santalum insulare*), an endangered tree species from the Pacific: a study based on chloroplast microsatellites. *Journal of Biogeography* 32: 1763–1774.
- Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software structure: a simulation study. *Molecular Ecology* 14: 2611–2620.
- Gray, A. 1860. Diagnosis of the species of sandalwood (*Santalum*) of the Sandwich Islands. *Proceedings of the American Academy of Arts and Sciences* 4: 326–327.
- Harbaugh, D. T. 2007. A taxonomic revision of Australian northern sandalwood (*Santalum lanceolatum*, Santalaceae). *Australian Systematic Botany* 20: 409–416.
- Harbaugh, D. T. 2008. Polyploid and hybrid origins of Pacific Island sandalwoods (*Santalum*, Santalaceae). *International Journal of Plant Sciences* 169: 677–685.
- Harbaugh, D. T. and B. G. Baldwin. 2007. Phylogeny and biogeography of the sandalwoods (*Santalum*, Santalaceae): repeated dispersals throughout the Pacific. *American Journal of Botany* 94: 1028–1040.
- Harbaugh, D. T., W. L. Wagner, D. M. Percy, H. F. James, and R. C. Fleischer. 2009. Genetic structure of the polymorphic *Metrosideros* complex in the Hawaiian Islands using nuclear microsatellite data. *PLoS ONE* 4: e4698.
- Harter, A. V., K. A. Gardner, D. Falush, D. L. Lentz, R. A. Bye, and L. H. Rieseberg. 2004. Origin of extant domesticated sunflowers in eastern North America. *Nature* 430: 201–205.
- Herbst, D. R. 1986. Endangered and threatened wildlife and plants; determination of endangered status for *Santalum freycinetianum* var. *lanaiense* (Lanai sandalwood or `iliahii). *Federal Register* 51: 3182–3185.
- Hillebrand, W. 1888. *Flora of the Hawaiian Islands*. New York: B. Westermann and Co.
- Kepler, A. K. 1998. *Hawaiian heritage plants*. Honolulu: University of Hawaii Press.
- Lhuillier, E., J.-F. Butaud, and J.-M. Bouvet. 2006a. Extensive clonality and strong differentiation in the insular Pacific tree *Santalum insulare*: Implications for its conservation. *Annals of Botany* 98: 1061–1072.
- Lhuillier, E., A. Vaillant, J.-F. Butaud, and J.-M. Bouvet. 2006b. Isolation and characterization of microsatellite loci in *Santalum insulare*, Santalaceae. *Molecular Ecology Notes* 6: 653–655.
- Lorence, D. H. 1996. A new species of *Nototrichium* (Amaranthaceae) from Kaua'i, Hawaiian Islands. *Novon* 6: 64–67.
- Lorence, D. H. and W. L. Wagner. 1995. Another new, nearly extinct species of *Hibiscadelphus* (Malvaceae) from the Hawaiian Islands. *Novon* 5: 183–187.
- Lorence, D. H. and W. L. Wagner. 1996. A new species of *Chamaesyce* section *Sclerophyllae* (Euphorbiaceae) from Kaua'i. *Novon* 6: 68–71.
- Lowry, P. P. and K. R. Wood. 2000. A new, threatened species of *Tetraplasandra* (Araliaceae) from Kaua'i, Hawaiian Islands, and notes on its conservation status. *Novon* 10: 40–44.
- Merlin, M. and D. Van Ravenswaay. 1990. *The history of human impact on the genus Santalum in Hawaii*. Pp. 46–60. in Proceedings of the symposium on sandalwood in the Pacific April 9–11, 1990, eds. L. Hamilton and C. E. Conrad. Honolulu: United States Department of Agriculture Forest Service.
- Pratt, H. D. 1998. *A pocket guide to Hawaii's trees and shrubs*. Honolulu: Mutual Publishing.
- Price, J. P. and D. Elliott-Fisk. 2004. Topographic history of the Maui Nui Complex, Hawaii, and its implications for biogeography. *Pacific Science* 58: 27–45.
- Pritchard, J. K., X. Wen, and D. Falush. 2007. Documentation for structure software version 2.2. Available: <http://pritch.bsd.uchicago.edu/software> via the internet. Accessed 14 Jul 2008.
- Rock, J. F. 1916. The sandalwoods of Hawaii: a revision of the Hawaiian species of the genus *Santalum*. *Hawaii Board of Agriculture and Forestry Bulletin* 3: 1–43.
- Shineberg, D. 1967. They came for sandalwood: a study of the sandalwood trade in the South West Pacific 1830–1865. Victoria: Melbourne University Press.
- Skottsberg, C. 1927. *Artemesia, Scaevola, Santalum* and *Vaccinium* of Hawaii. *Bulletin of the Bernice P. Bishop Museum* 43: 39–64.
- Skottsberg, C. 1930. The geographical distribution of the sandalwoods and its significance. Pp. 435–440 in Proceedings of the Fourth Pacific Science Congress, 1929, Java, Indonesia.
- Skottsberg, C. 1944. Vascular plants from the Hawaiian Islands. IV. Phaenogams collected during the Hawaiian Bog Survey 1938. *Meddelanden fran Göteborgs Botaniska Trädgård* 15: 275–531.
- Stamatakis, A., M. Ott, and T. Ludwig. 2005. RAxML-OMP: An efficient program for phylogenetic inference on SMPs. Pp. 288–302 in *Proceedings of 8th International Conference on Parallel Computing Technologies (PaCT2005), Lecture Notes in Computer Science, 3506*. Berlin: Springer-Verlag.
- Stamatakis, A., P. Hoover, and J. Rougemont. 2008. A fast bootstrapping algorithm for the RAxML web-servers. *Systematic Biology* 57: 758–771.
- Stemmermann, L. 1980a. Observations on the genus *Santalum* (Santalaceae) in Hawaii. *Pacific Science* 34: 41–53.
- Stemmermann, L. 1980b. Vegetative anatomy of the Hawaiian species of *Santalum* (Santalaceae). *Pacific Science* 34: 55–75.
- St. John, H. 1947. The history, present distribution, and abundance of sandalwood on Oahu, Hawaiian Islands: Hawaiian plant studies 14. *Pacific Science* 1: 5–20.
- St. John, H. 1984. Revision of the Hawaiian species of *Santalum* (Santalaceae): Hawaiian plant studies 109. *Phytologia* 55: 217–226.
- Stuessy, T. F., C. Marticorena, R. Rodriguez, D. Crawford, and M. Silva. 1992. Endemism in the vascular flora of the Juan Fernandez Islands. *Aliso* 13: 297–307.
- Swofford, D. L. 2002. PAUP*: phylogenetic analysis using parsimony (*and other methods) version 4.0 beta 10. Sunderland: Sinauer.
- Tuyama, T. 1939. On *Santalum boninense*, and the distribution of the species of *Santalum*. *The Journal of Japanese Botany* 15: 697–712.
- Wagner, W. L. and D. R. Herbst. 1987. A new species of *Remya* (Asteraceae: Astereae) on Kaua'i and a review of the genus. *Systematic Botany* 12: 601–608.

- Wagner, W. L. and S. G. Weller. 1991. Resurrection of a Kaua'i *Stenogyne*: *S. kealiae*. *Pacific Science* 45: 50–54.
- Wagner, W. L., S. G. Weller, and A. K. Sakai. 1994. Description of a rare new cliff-dwelling species from Kaua'i, *Schiedea attenuata* (Caryophyllaceae). *Novon* 4: 187–190.
- Wagner, W. L. and D. H. Lorence. 1998. A new, dioecious species of *Hedyotis* (Rubiaceae) from Kaua'i, Hawaiian Islands, and the taxonomy of Kaua'i *Hedyotis schlechtendahlia* resolved. *Novon* 8: 311–317.
- Wagner, W. L., M. Brueggemann, D. R. Herbst, and J. Q. Lau. 1999a. Hawaiian Vascular Plants at Risk: 1999. *Bishop Museum Occasional Papers* 60: 1–64.
- Wagner, W. L., D. R. Herbst, and S. H. Sohmer. 1999b. *Santalum*. Pp. 1218–1223 in *Manual of the flowering plants of Hawaii, vol 2, revised edition*. Honolulu: University of Hawaii Press.
- Wood, K. and S. Perlman. 1993. Rare and endangered flora of the Kalalau and Pohakuo valleys. *The Bulletin (National Tropical Botanical Garden)* 23: 41–50.
- Zhang, D.-X. and G. M. Hewitt. 2003. Nuclear DNA analyses in genetic studies of populations: practice, problems and prospects. *Molecular Ecology* 12: 563–584.

APPENDIX 1. List of specimens that were sequenced and used in the phylogenetic analyses, including taxon name, sample number (if multiple specimens), locality, collector and collection number, herbarium, and GenBank accession numbers (ITS, ETS, 3' *trnK* intron). Sample numbers follow numbering in Fig. 1. Herbarium abbreviations follow standard herbarium acronyms from Index Herbariorum. Dashes represent missing data. (HI = Hawaiian Islands.)

Santalum acuminatum (R. Br.) A. DC.—Western Australia, Australia; *Harbaugh* 142 (UC); EF569292, EF569378, EF569238. *Santalum album* L.—Northern Territory, Australia; *Harbaugh* 65 (UC); EF569318, EF569395, EF569253. *Santalum austrocaledonicum* Viell. — Erromango, Vanuatu; *Page SnEr16* (JCT); EF569327, EF569401, EF569258. *Santalum boninense* (Nakai) Tuyama—Hahajima, Bonin Islands, Japan; *Tuyama s. n.* (UC); EF569350, EF569419, EF569273. *Santalum ellipticum* Gaudich.—1: O'ahu, HI; *Harbaugh* 07 (UC); EF569361, EF569429, EF569282. 2: O'ahu, HI; *Harbaugh* 21 (UC); EF569368, EF569432.—. *Santalum freycinetianum* Gaudich.—1: O'ahu, HI, Ko'olau Mts., Aiea Loop Trail; *Lee s. n.* (BISH); EF569360, EF569428, EF569248. 2: O'ahu, HI, Waianae Mts., Honouliuli Preserve; *Harbaugh* 24 (UC); EF569359, EF569427, EF569280. *Santalum haleakalae* Hillebr. var. *haleakalae* — 1: E. Maui, HI, Haleakala National Park; *Harbaugh* 42 (UC); EF569358, EF569426, EF569279. 2: E. Maui, HI, Kula Forest Reserve; *Oppenheimer H70709* (US); FJ948182, GQ262757, GQ259429. *Santalum haleakalae* Hillebr. var. *lanaiense* (Rock) *Harbaugh*, comb. nov.—1: Lana'i, HI, Lanaihale; *Oppenheimer Lana'i_2* (US); FJ948181, GQ262754, GQ259426. 2: Lana'i, HI, Kanepu'u Preserve; *Harbaugh et al.* 374 (US); FJ948186, GQ262748, GQ259420. 3: Lana'i, HI, Puhielulu Ridge; *Oppenheimer H100732* (US) FJ948177, GQ262756, GQ259430. 4: E. Maui, HI, Ulupalakua Ranch, Auwahi Preserve; *Harbaugh et al.* 394 (US); FJ948180, GQ262750, GQ259422. 5: W. Maui, Lahaina District on a ridge dividing Kahoma Valley and Kealii Gulch; *Oppenheimer H20011* (BISH); EF569355,—. 6: W. Maui, HI, Mts. above Napili and pineapple plantations; *Smith 2900* (UC); EF569356, EF569424, EF569277. 7: Wailuku District, Pohakea Gulch; *Oppenheimer and Perlman 100701* (US); FJ948176, GQ262758, GQ259428. 8: Pu'u Kukui Watershed Preserve; *Harbaugh et al.* 360 (US); FJ948178, GQ262747, GQ259419. 9: Moloka'i, Kamakou Preserve, Hawaiian Islands; *Harbaugh* 384 (US); FJ948185, GQ262749, GQ259421. 10: Moloka'i, Pu'u Kolekole, Hawaiian Islands; *Oppenheimer H80706* (US); FJ948183, GQ262755, GQ259427. 11: Moloka'i, *Russell s. n.* (BISH); EF569357, EF569425, EF569278. *Santalum insulare* Bertero ex A. DC. var. *marchionense* Skottsblom—Hiva Oa, Marquesas Islands, French Polynesia; *Butaud HO24* (ALF); EF569337, EF569410, EF569266. *Santalum insulare* Bertero ex A. DC. var. *raiateense* (J. W. Moore)—Raiatea, Society Islands, French Polynesia; *Butaud R4* (ALF); EF569345, EF569417, EF569270. *Santalum involutum* H. St. John — 1: Kalalau Valley, N side and E of Keanapuka Falls, Kaua'i, Hawaiian Islands; *Wood and Holmes 12482* (1) (PTBG); FJ948187, GQ262752, GQ259424. 2: Pohakuo, hanging valley between Kalalau and Hanakoa (600 m), Kaua'i, Hawaiian Islands, *Wood et al.* 1770 (PTBG); FJ948187, GQ262752, GQ259424. *Santalum lanceolatum* R. Br.—Northern Territory, Australia; *Harbaugh* 77 (UC); EF569303, EF569384, EF569244. *Santalum leptocladum* Gand.—New South Wales, Australia; *Lally and Landsberg 298* (CANB); EF569301,—. *Santalum macgregorii* F. Muell.—Ishea Village, Papua New Guinea; *Unknown AA643* (UC); EF569323, EF569397, EF569255. *Santalum murrayanum* (T. Mitch.) C. A. Gardner—Victoria, Australia; *Harbaugh* 121 (UC); EF569310, EF569388,—. *Santalum obtusifolium* R. Br.—New South Wales, Australia; *Stauffer et al.* 5692 (UC); EF569313, EF569390,—. *Santalum panic-*

ulatum Hook. & Arn.—Hawai'i, Hawaiian Islands, *Harbaugh* 47 (UC), EF569369, EF569433, EF569286. *Santalum pyrularium* A. Gray—1: Na Pali Kona Forest Reserve, near boundary of Koke'e State Park, Kaua'i, Hawaiian Islands; *Harbaugh and Wood* 456 (US); FJ948184, GQ262751, GQ259423. 2: Waimea Canyon State Park, Kaua'i, Hawaiian Islands; *Harbaugh* 05 (UC); EF569354, EF569423, EF569276. 4: Kalalau Valley, slopes of Kalahu, Kaua'i, Hawaiian Islands, 300 m east of navy plane crash, *Wood and Perlman* 3393 (PTBG); EF569354, EF569423, EF569276. 5: upper Honopu drainage (north side), Kaua'i, Hawaiian Islands, *Wood* 4923 (PTBG); EF569354, EF569423, EF569276. 6: Kalalau, lower Kalahu side w/rope, Kaua'i, Hawaiian Islands, *Wood* 3647 (PTBG); EF569354, EF569423, EF569276. 7: Kalalau Rim, Kalahu side between and west of first lookout, 300 m east of plane crash, Kaua'i, Hawaiian Islands, *Wood* 1414 (PTBG); EF569354, EF569423, EF569276. *Santalum pyrularium* X *S. ellipticum*—Kalalau Valley, helicopter drop on isolated ridge between and W of first lookout, Kaua'i, Hawaiian Islands, *Wood and Perlman* 3023 (PTBG); GU189296, GU189297, GQ259424. *Santalum spicatum* (R. Br.) A. DC.—Western Australia, Australia; *Harbaugh* 144 (UC); EF569316, EF569393, EF569251. *Santalum yasi* Seem.—Eua, Tonga; *Whistler* 7360 (BISH); EF569333, EF569407, EF569263. *Colpoon compressum* Berg.—South Africa (cult. UC Berkeley Botanical Garden), *Harbaugh* 63 (UC); EF569288, EF569374, EF569233.

APPENDIX 2. List of specimens used in the microsatellite analysis, including taxon name, sample number (which corresponds to order of bars in graph shown in Fig. 2), locality within the Hawaiian Islands, collector and collection numbers, as well as the herbarium where voucher is housed. Herbarium abbreviations follow standard herbarium acronyms from Index Herbariorum.

Santalum haleakalae Hillebr. var. *haleakalae*—1-7: Maui, Haleakala National Park, Halemau'u Trail; *Harbaugh* 35-41 (UC) 8: Maui, Haleakala National Park, along main park road; *Harbaugh* 42 (UC). 9: Maui, Haleakala National Park, trail above Hosmer's Grove Campground; *Harbaugh* 334 (US). 10-13: Maui, Haleakala National Park, along main park road; *Harbaugh* 351, 353-354, 335 (US). 14: Maui, Haleakala Ranch, along highway to National Park; *Harbaugh* 336 (US). 15: Maui, Poli Poli/Kula Forest Reserve, Waiohuli Gulch; *Harbaugh and Bily* 359 (US). 16: Maui, Kula Forest Reserve, Waiohuli; *Oppenheimer H70709* (US). *Santalum freycinetianum* Gaudich.—17-23: O'ahu, Honouliuli Preserve, on trail above Hokuloa House, off Palehua Road; *Harbaugh* 24-28, 30-31 (UC). 24: O'ahu, Ko'olau Mts., Aiea Loop Trail; *Harbaugh* 153 (US). 25-28: O'ahu, Waianae Mts., West Makaleha Valley, along Kaala Rd; *Harbaugh et al.* 209-211, 215 (US). 29-33: O'ahu, Waianae Mts., Kahanai Gulch off of Makua Valley, in Army land; *Harbaugh et al.* 217-219, 223-224 (US). 34-45: O'ahu, Waianae Mts., Honouliuli Preserve, Kalua'a, along south pig fenceline; *Harbaugh et al.* 228-236, 238, 240-241 (US). 46-65: O'ahu, Waianae Mts., Honouliuli Preserve, Kalua'a, along Contour Trail; *Harbaugh et al.* 246-248, 250, 252, 254-258, 260, 262, 265, 273-278, 280 (US). 66-74: O'ahu, Waianae Mts., Honouliuli Preserve, Maunauna Gulch, along Contour Trail; *Harbaugh et al.* 285-286, 288, 291, 298, 303, 306, 310, 313 (US). 75-77: O'ahu, Waianae Mts., Honouliuli Preserve, on trail between Huliwai Gulch and Manuiwalelele Gulch; *Harbaugh et al.* 314, 316, 317 (US). 78-81: O'ahu, Ko'olau Mts., Manana Ridge Trail; *Harbaugh* 318, 323, 327, 332 (US). *Santalum haleakalae* Hillebr. var. *lanaiense* (Rock) *Harbaugh*—82-87: Moloka'i, Kamakou Preserve; *Harbaugh* 383-385, 388, 391-392 (US). 88-100: Moloka'i, Pu'u Kolekole; *Oppenheimer H80706* (US). 101-105: W. Maui, Lahaina District on a ridge dividing Kahoma Valley and Kealii Gulch; *Oppenheimer H20011.1-5* (BISH). 106: W. Maui; *Oppenheimer Iliahi04* (unknown). 107-108: W. Maui, Wailuku District, Pohakea Gulch; *Oppenheimer and Perlman 100701.1-2* (US). 109-120: E. Maui, Auwahi Preserve, in Ulupalakua Ranch, along 4WD road; *Harbaugh et al.* 396, 401-409, 411, 413 (US). 121-122: Lana'i, Kanepu'u Preserve; *Harbaugh et al.* 374, 376 (US). 123-124: Lana'i, Lanaihale, Wai'opa headwaters NE of Ha'alelepa'akai; *Oppenheimer Lanai_1*, 3 (unknown). 125-126: Lana'i, Puhielulu Ridge; *Oppenheimer H100732.1*, 4 (US). 127: Lana'i, E. Kunoa; *Oppenheimer H20080108* (US). *Santalum pyrularium* A. Gray—128-129: Kaua'i, Waimea Canyon State Park, at the Waimea Canyon lookout along Hwy 550; *Harbaugh* 05, 06 (UC). 130-142: Kaua'i, Koke'e State Park, along the Awaawapuhi Trail; *Harbaugh and Baldwin* 415-420, 422, 424-426, 428-429, 433 (US). 143-148: Kaua'i, Alakai Picnic area, near trailhead to Alakai Swamp Trail, at boundary of Koke'e State Park and Napali Kona Forest Reserve; *Harbaugh and Wood* 441, 443, 445, 447-449 (US). 149-164: Kaua'i, Na Pali Kona Forest Reserve, near boundary of Koke'e State Park, along Miloli'i Ridge Road; *Harbaugh and Wood* 456-460, 464-468, 470-475 (US). *Santalum involutum* H. St. John—165-175: Kaua'i, Kalalau Valley, north side and east of Keanapuka Falls; *Wood and Holmes* 1248.1-4, 7, 8, 10-14 (PTBG).