A Species Monograph for *Metrosideros polymorpha* Gaud.

Scott P. Lacasse

Green Mountain College

BIO6073 Field Botany
July 16, 2018

A species monograph for *Metrosideros polymorpha* Gaud.

1. SPECIES DOCUMENTATION

Species: *Metrosideros polymorpha* Gaud.
Species Author: Gaudich.
Common Name: ʻŌhiʻa Lehua
Family: Myrtaceae
Plant Communities: *M. polymorpha* is the dominant species found in intact lowland and montane dry, mesic, and wet forests and is also considered a significant component of subalpine shrublands, and new lava flows (Friday & Herbert, 2006).
Species Range: *M. polymorpha* is endemic to the Hawaiian Islands, which range from 16º 55' N to 23º N latitude and 154º 40' W to 162º W longitude. Found on all of the eight main islands, (except Niʻihau and Kahoʻolawe), *M. polymorpha* ranges from 1 - 2,500 m in elevation with areas of annual precipitation from 400 – 10,000 mm and occurring on varied substrates from medium to heavy clay, rocky, and organic soils formed on recent lava flows (Friday & Herbert, 2006; Wagner et al., 1999).


Image 1 Leaf, flower, and floral bud of *Metrosideros polymorpha* Gaud. (image from Little & Skolmen, 1989).

2. VEGETATIVE MORPHOLOGY

Polymorpha, meaning "many forms" is an appropriate name for the ʻŌhiʻa; its growth habit can be tall and erect or shrubby and prostrate depending on the habitat it occupies. They are an evergreen species characterized as having multi-branched or compact crowns and mature trees can reach up to 20 – 25 m tall and diameters up to 90 cm (Gustafson et al., 2014). They are slow growing with an annual growth rate of 0.3 - 0.6 m in height and 1 – 3 mm in diameter (Friday & Herbert, 2006). "Larger, rounded trees with smooth oval-shaped leaves are found in wetter forests, whereas drier environments have produced smaller trees or shrubs with small, whitish hairy leaves to counteract the bright sun and dry conditions" (Lilleeng-Rosenberger, 2016, p. 268). Morphology also varies between pioneering and successional varieties with the former exhibiting pubescent leaves and the later glabrous (Adee & Conrad, n.d.).

The leaves are dorsiventral and vary from thick dark green with dense abaxial pubescence to thin, bright green, and glaborous. They are opposite, clustered, and range in shape from obovate to orbicular, elliptic or ovate, 1 – 8 cm long and 1 – 5.5 cm wide. Margins are flat to revolute, apex rounded or sometimes obtuse to acute, and the base cuneate to cordate. The petioles are 1 – 16 mm long by 1 – 3 mm wide (Wagner et al., 1999). Young bark is light gray and smooth on a cylindrical bole, and becomes twisted and deeply furrowed with age; the sapwood is very hard and strong, characterized as pale brown and grading gradually into reddish-brown heartwood (Friday & Herbert, 2006; Little & Skolmen, 1989). "Twigs slender, from hairless to covered with a dense coat of white hairs" (Little & Skolmen, 1989, p. 246).

'Ōhi'a varies greatly in its rooting habit and forms "shallow roots on pāhoehoe (sheet lava) or poorly drained areas but [is] deeply rooted in dry sites and on 'a'ā (rough) lava" (Friday & Herbert, 2006, p. 10). Adventious roots, developing from lower nodes, have been observed on specimens in a variety of habitats and serve as prop roots in wet soils and to support the 'ōhi'a as it reaches for light in closed-canopy environments. Some trees also form air roots that trap moisture, and plants of epiphytic origin develop stilt roots over the nurse logs and tree ferns they frequently germinate on (*Cibotium* spp.) (Little & Skolmen, 1989; *Metrosideros polymorpha*, 2013). The 'Ōhi'a's ability to adapt to a variety of environments is a major contributing factor to the species' success in Hawai'i.

3. A STUDY IN VARIATION

Influence of light on bract width in *Metrosideros polymorpha* Gaud.

Introduction

Through observation of six different populations of *Metrosideros polymorpha* (in roughly the same area), I noticed that the flower bracts of one population appeared to be smaller in diameter than the other five, which were relatively consistent in size. The one population with the smaller bracts was more open in its columnar form than the others and was in direct competition for light with a native palm of similar height. This short study will determine if the bracts in the shaded *M. polymorpha* Gaud. var. '*polymorpha*' were, in fact, smaller in diameter than the other populations.

Hypothesis

High available light is associated with large flowering bract diameter in *Metrosideros polymorpha* Gaud. var. '*polymorpha*.'

Methods

The populations chosen for the study were located along the north boundary of the Montessori School of Maui in Makawao, HI. The *Metrosideros polymorpha* Gaud. var. '*polymorpha*' were planted as part of a native buffer between the school and the adjacent property. Companion plantings include *Acacia koaia, Dodonea viscosa, Pritchardia* spp., and *Heteropogon contortus*. A drainage swale and property wall bound the buffer to the north and a reinforced gravel driveway and curb to the south. The property was in agricultural and ranch production prior to becoming a school in the 1980's.

To minimize differences in site conditions between populations, I chose the three individual populations of Metrosideros polymorpha closest to one another to take specimens from. I randomly chose forty different specimens from each population, with ovaries still inferior and no stamens present. I measured the interior diameter of each bract and entered the data into the chart table (see Table 1).

Results

The mean (3.63mm) bract diameter of the shaded population was less than population “b” (4.58mm) and population “c” (4.13mm) with standard deviations of 0.55, 0.43, and 0.43mm respectively (Table 1). This suggests that flowering bracts of Metrosideros polymorpha are affected by the plant’s ability to photosynthesize (Table 2).

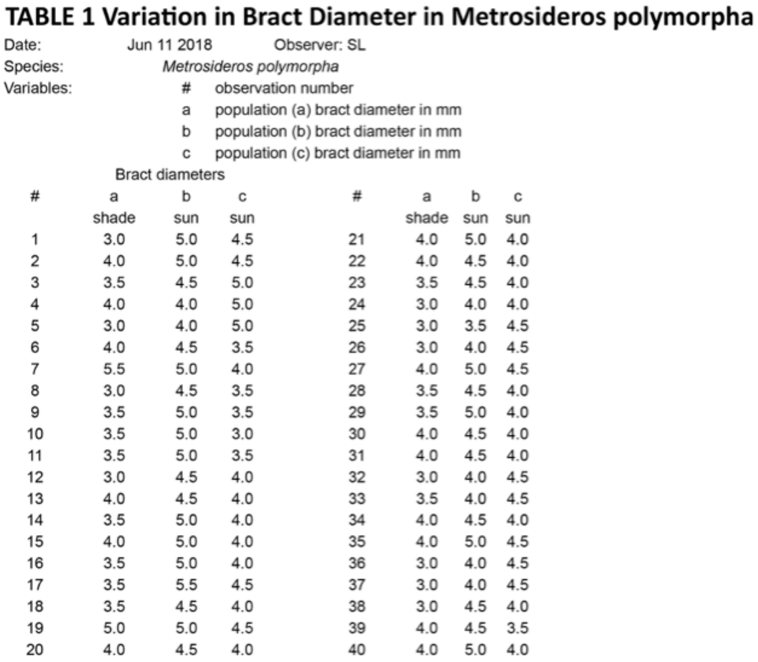


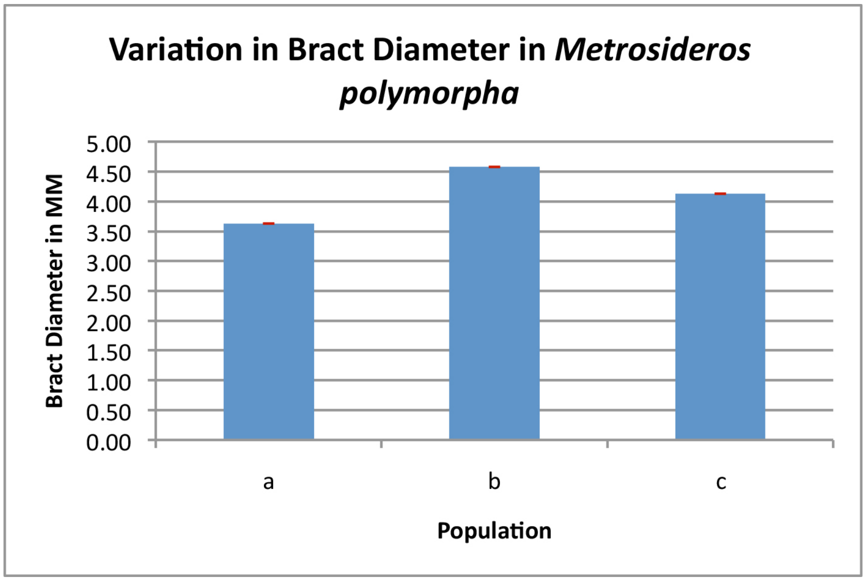
TABLE 1 Variation in Bract Diameter in Metrosideros polymorpha

Date: Jun 11 2018 Observer: SL
Species: *Metrosideros polymorpha*
Variables:
\# observation number
a population (a) bract diameter in mm
b population (b) bract diameter in mm
c population (c) bract diameter in mm

	Bract diameters						
#	a	b	c	#	a	b	c
	shade	sun	sun		shade	sun	sun
1	3.0	5.0	4.5	21	4.0	5.0	4.0
2	4.0	5.0	4.5	22	4.0	4.5	4.0
3	3.5	4.5	5.0	23	3.5	4.5	4.0
4	4.0	4.0	5.0	24	3.0	4.0	4.0
5	3.0	4.0	5.0	25	3.0	3.5	4.5
6	4.0	4.5	3.5	26	3.0	4.0	4.5
7	5.5	5.0	4.0	27	4.0	5.0	4.5
8	3.0	4.5	3.5	28	3.5	4.5	4.0
9	3.5	5.0	3.5	29	3.5	5.0	4.0
10	3.5	5.0	3.0	30	4.0	4.5	4.0
11	3.5	5.0	3.5	31	4.0	4.5	4.0
12	3.0	4.5	4.0	32	3.0	4.0	4.5
13	4.0	4.5	4.0	33	3.5	4.0	4.5
14	3.5	5.0	4.0	34	4.0	4.5	4.0
15	4.0	5.0	4.0	35	4.0	5.0	4.5
16	3.5	5.0	4.0	36	3.0	4.0	4.5
17	3.5	5.5	4.5	37	3.0	4.0	4.5
18	3.5	4.5	4.0	38	3.0	4.5	4.0
19	5.0	5.0	4.5	39	4.0	4.5	3.5
20	4.0	4.5	4.0	40	4.0	5.0	4.0

Discussion

The t-tests in Table 2 demonstrate that while sunlight has an affect on bract diameter in *M. polymorpha*, there is another contributing factor that is evidenced by the smaller bracts. Population “c” had smaller bract diameters than population “b,” therefore, there must be another variable affecting bract diameter that was not accounted for. The *M. polymorpha* represented by “c” was slightly uphill of “b,” thereby affecting drainage and potential water availability, which could play a role in the size of vegetative anatomy. Also, population “c” was windward of “b” and thereby exposed to greater environmental stress. Lastly, ants were present on “c” and could also have affected the diameter of the bracts. While these factors demonstrate the presence of additional environmental variables, they do not negate the fact that high available light plays a significant role in the size of plant anatomy. The effects of wind and insects on bract diameter represent an opportunity for further study.



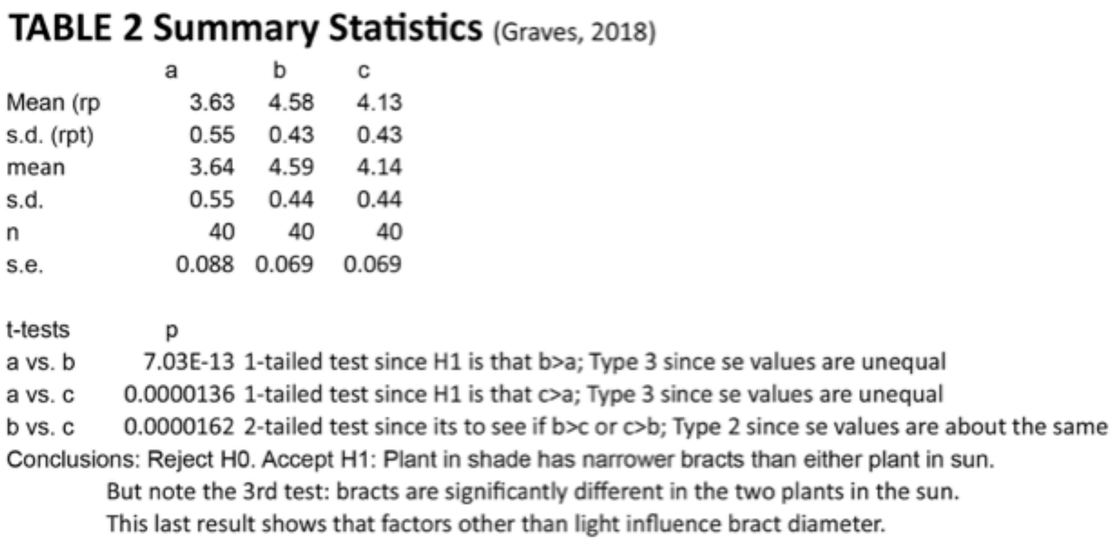


TABLE 2 Summary Statistics (Graves, 2018)

	a	b	c
Mean (rp	3.63	4.58	4.13
s.d. (rpt)	0.55	0.43	0.43
mean	3.64	4.59	4.14
s.d.	0.55	0.44	0.44
n	40	40	40
s.e.	0.088	0.069	0.069

t-tests	p	
a vs. b	7.03E-13	1-tailed test since H1 is that b>a; Type 3 since se values are unequal
a vs. c	0.0000136	1-tailed test since H1 is that c>a; Type 3 since se values are unequal
b vs. c	0.0000162	2-tailed test since its to see if b>c or c>b; Type 2 since se values are about the same

Conclusions: Reject H0. Accept H1: Plant in shade has narrower bracts than either plant in sun.
But note the 3rd test: bracts are significantly different in the two plants in the sun.
This last result shows that factors other than light influence bract diameter.

4. LIFE HISTORY AND REPRODUCTION

Metrosideros polymorpha Gaud. or ‘ōhi‘a lehua is part of the angiosperm taxon and exhibits those adaptive characteristics for life on land. These flowering plants have dominant diploid (2n) sporophytes that make them more genetically diverse. The ‘ōhi‘a exhibits that trait through the wide morphological and ecological variences found within the polymorphic species and its eight varieties. More generally, the vascular tissues, xylem and phloem, are responsible for the efficient transport of nutrients and water through the plant, and the cuticle and stomata control transpiration rates (Murrell, 2010).

The reproductive cycle begins with a dominant sporophyte stage exhibited by a flower with anthers (male) and ovules (female). Haploid microspores are a result of diploid meiosis in the anthers, and haploid megaspores are generated in the ovules. The microspores divide through successive mitosis to form two sperm and a pollen tube, the male gametophyte. The ovules house the female gametophyte, which is a result of the meiotic division into four megaspores. Three of these die and the remaining megaspore divides by mitosis to form the 8-nucleate female gametophyte, one of which functions as an egg. Fertilization of the egg to produce a zygote occurs through pollination, primarily by an animal vector as they deposit the male gamete onto the waiting flower stigma. One sperm fertilizes the egg through the pollen tube, and the remaining sperm fuses with two other nuclei in the female gametophyte to form a triploid (3n) endosperm that feeds the new young sporophyte embryo following seed germination. The seeds are formed in capsules at the ends of branches and the resulting dust-like seeds of the ‘ōhi‘a are dispersed by the wind as the capsules dry and split open (Lilleeng-Rosenberger, 2016).

Polymorpha literally means “many forms,” and the ‘ōhi‘a exhibits that characteristic throughout its morphology and phenology. Adee & Conrad (n.d.) stated “Individual trees or branches may produce flowers at any time of the year.” It is not uncommon to see specimens forming herbaceous new growth from terminal or axillary buds on one part of the tree, while determinate inflorescences simultaneously emerge on another part, and capsules release their seeds from yet another.

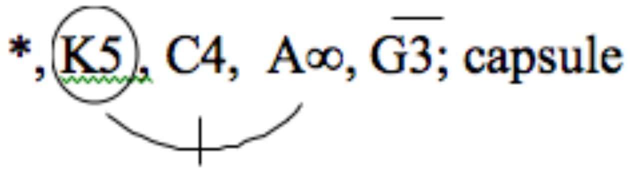
Wagner et al. (1999) describe the floral morphology of *M. polymorpha* Gaud. as:

> Flowers red, in inflorescences of 2-5 pairs of cymules, glabrous or appressed or wooly pubescent, peduncles 7-18 mm long, 1-3 mm wide, pedicels 2-8 mm long, 1-2 mm wide, bracts broadly ovate to suborbicular, 5-10 mm long, 3-5 mm wide; hypanthium 3-7 mm high, 3-8 mm wide; sepals rounded to triangular, 1.5-4 mm long. Fruiting hypanthium 3-8 mm long and wide, pubescent or glabrous, capsules slightly included to exserted. (p. 967)

Little & Skolmen (1989) described the floral morphology of *M. polymorpha* Gaud. as:

> Flower clusters (cymose corymbs) terminal, branched, of many short-stalked flowers in groups of 3 forming mass of threadlike stamens to 7.5 mm in diameter, varying in color from scarlet to pink, salmon, and yellow. Each flower is composed of a hypanthium to 6 mm long, which bears 5 blunt calyx lobes 3 mm long, 4 petals 3-6 mm long, and many spreading threadlike stamens 2.5-3 cm long with dot anthers; pistil with inferior 3-celled ovary and long threadlike style. Fruit (capsule) bell-shaped, 6-10 mm long and broad, brown, often hairy, slightly 3- lobed, 3-celled, with calyx remaining. Seeds many, minute. (p. 246)

The floral formula for *M. polymorpha* Gaud. can be diagrammed as follows:



5. PLANT IDENTIFICATION

SPECIES KEY FOR *M. POLYMORPHA* GAUD. (Wagner et al., 1999)

SYNOPTICAL KEY TO THE DIVISION OF MAGNOLIOPHYTA (Flowering Plants)
(Adapted from Cronquist, 1981) (p. 130)
1. Flower parts usually in fours or fives; leaf venation reticulate; primary vascular bundles in stem in a ring; often with vascular cambium and true secondary growth; cotyledons 2 or more (class Magnoliopsida) (2).
2. Plants more specialized in 1 or more respects than the Magnoliidae; stamens not laminar, usually with conspicuously differentiated anthers and filaments; pollen triaperturate or a type derived from the triaerturate condition; cotyledons (1)2; plants rarely producing benzyl-isoquinoline or aporphine alkaloids, but often accumulating other alkaloids, tannins, betalains, mustard oils, or iridoid compounds (3).
3. Flowers usually well-developed and with evident perianth, but if not so, then usually grouped into bi-sexual pseudanthia or else with numerous seeds on parietal placentas; pollen various, but rarely both porate and with a granular infratecal structure (4).

4. Petals distinct or sometimes connate or absent, if connate, then usually either with stamens more than corolla lobes or with 2 integuments or crassinucellate ovules; ovules rarely with integumentary tapetum; carpels 1 to numerous, distinct or connate into a compound pistil; plants often containing tannins, betalains, or mustard oils (5).
5. Stamens when numerous, usually initiated in centripetal sequence; placentation occasionally free-central, parietal, or basal, in 1-celled, compound ovaries, ovary usually 2 to several cells and 1-2 ovules per cell; petals usually distinct or sometimes absent, rarely connate; plants often with tannins, rarely with mustard oils and never with betalains – subclass V. Rosidae.

SYNOPTICAL KEY TO THE SUBCLASS OF V. ROSIDAE
(Adapted from Cronquist, 1981) (p. 133)
1. Flowers relatively specialized in one or more respects; usually with carpels connate into a compound ovary, usually with stamens less than twice as many sepals or petals (except numerous in Myrtaceae and then plants with internal phloem); plants sometimes parasitic or specialized aquatics (8).
8(1). Stems usually with internal phloem; flowers perigynous or epigynous, often 4-merous; stamens often numerous; ovules numerous (Myrtales) (9).
9. Ovary inferior or only partly so (11).
11(9). Stamens usually numerous, sometimes only as many or twice as many as sepals or petals; leaves glandular punctate……………………………………………73. Myrtaceae

OR

ARTIFICIAL KEY TO ARRIVE AT THE GENERA MYRTACEAE (p. 148)
1. Flowers usually 2-merous, 4-5-merous, or polymerous; cotyledons usually 2; leaves usually net-veined, ultimate veins with free endings; vascular bundles in a ring in stem; mature root systemusually with taproot persistent (2).
2. Petals connate at base, sometimes shortly so, and calyx present (131).
131. Ovary inferior or partly inferior (172).
172. Flowers usually not born in dense heads , but never on a common receptacle, the flowers not surrounded by an involucre; corollas all alike in an inflorescence; fruit various, but not an achene (173).
173. Flowers in various types of inflorescences, but not in umbellate or racemose-umbellate inflorescences; pubescence various, but not of stellate hairs (174).
174 (173). Stamens numerous; calyx and corolla connate to form an opercula ……..……………………………………………………………………..73. Myrtaceae

THEN

KEY TO THE GENERA OF MYRTACEAE – Myrtle Family (p. 947)
1. Fruit a capsule; leaves alternate, opposite (2).
2. Flowers in terminal or axillary cymes, racemes, umbels, panicles, or solitary (3).
3. Sepals and petals distinct; flowers in terminal or axillary cymes or racemes, or axillary and solitary (4).

4. Mature leaves alternate or opposite, those of branches not in pseudoverticels; staminal filaments distinct (5).
5. Leaves opposite……………………………………………………………6. *Metrosideros*

KEY TO THE SPECIES OF *METROSIDEROS* (p. 964)
1. Petioles ¼ as long as blades or less; expanding vegetative buds rounded at the tip (2).
2. Leaves not rugose, glaborous or lower surface wooly or appressed pubescent: HI exc. Ni &Ka………………………………………………………………2. *M. polymorpha*

DESCRIPTION OF *M. POLYMORPHA* GAUD. from Wagner et al. (p. 967)

Habit: small erect to prostrate shrubs to tall trees
Bark: usually rough and fissured, separating in thick flakes, sometimes smooth and separating in long thin strips
Vegetative Buds: obovoid
Leaves: obovate to orbicular or sometimes elliptic, broadly ovate or ovate, 1-8 cm long, 1-5.5 cm wide, several pairs of raised veins radiating from base, upper surface glaborous, lower surface glaborous or pubescent
Margins: revolute to flat, apex rounded or sometimes obtuse to acute
Base: cuneate to cordate
Petioles: usually short, usually much less than 1/3 as long as blades, 1-16 mm long, 1-3 mm wide
Flowers: red, in inflorescences of 2-5 pairs of cymules, glabrous or pubescent, peduncles 7-18 mm long, 1-3 mm wide, pedicels 2-8 mm long, 1-2 mm wide, bracts broadly ovate to suborbicular, 5-10 mm long, 3-5 mm wide
Hypanthium: 3-7 mm high, 3-8 mm wide;
Sepals: rounded to triangular, 1.5-4 mm long
Fruiting hypanthium: 3-8 mm long and wide, pubescent or glabrous
Capsules: slightly included to exserted

“Despite the wide morphological and ecological range exhibited, a broad view of *Metrosideros polymorpha* is maintained. There is still insufficient detailed knowledge to determine the basis for the observed variation and the extent to which the difficulties in delimiting entities within the complex are due to hybridism and/or genetic polymorphism. Eight varieties of *M. polymorpha* are recognized: Vars. dieteri, glaberrima, incana, macrophylla, newellii, polymorpha, pseudorugosa, and pumila.” (Wagner et al., p. 967)

6. PHYLOGENY

Table 4 - Common Plant Families in Vegetative Zones on Maui

Coastal Zone

Scophulariaceae	Aizoaceae	Portulaceae	Thymelaeaceae	Malvaceae
Cyperaceae	Fabaceae	Lamiaceae	Pandanaceae	

Dry Forest Zone

Sapindaceae	Chenopodiaceae	Convovulaceae	Malvaceae	Arecaceae
Solanaceae	Rhamnaceae	Asteraceae	Myrtaceae	Fabaceae

Fabaceae	Campanulaceae	Apocynaceae	Araliaceae	Cibotaceae
Myrtaceae	Lindsaeaceae	Liliaceae		

Subalpine Zone

Onagraceae	Caryophyllaceae	Asteraceae	Geraniaceae
Ericaceae	Fabaceae		

Polynesian Introduced

Piperaceae	Zingiberaceae	Araceae	Agavaceae	Moraceae
Muscaceae	Euphorbiaceae	Taccaceae	Convolvulaceae	

Table 5 - Common Plant Families in Six Taxonomic Groups on Maui

Monilophyta	**Gymnospermae**	**Monocots**	**Rosids**	**Asterids**
Cibotiaceae	Pinaceae	Liliaceae	Myrtaceae	Campanulaceae

Magnoliids
Lauraceae

Table 6 – Floristics for Plant Families in the Wet Forest Zone

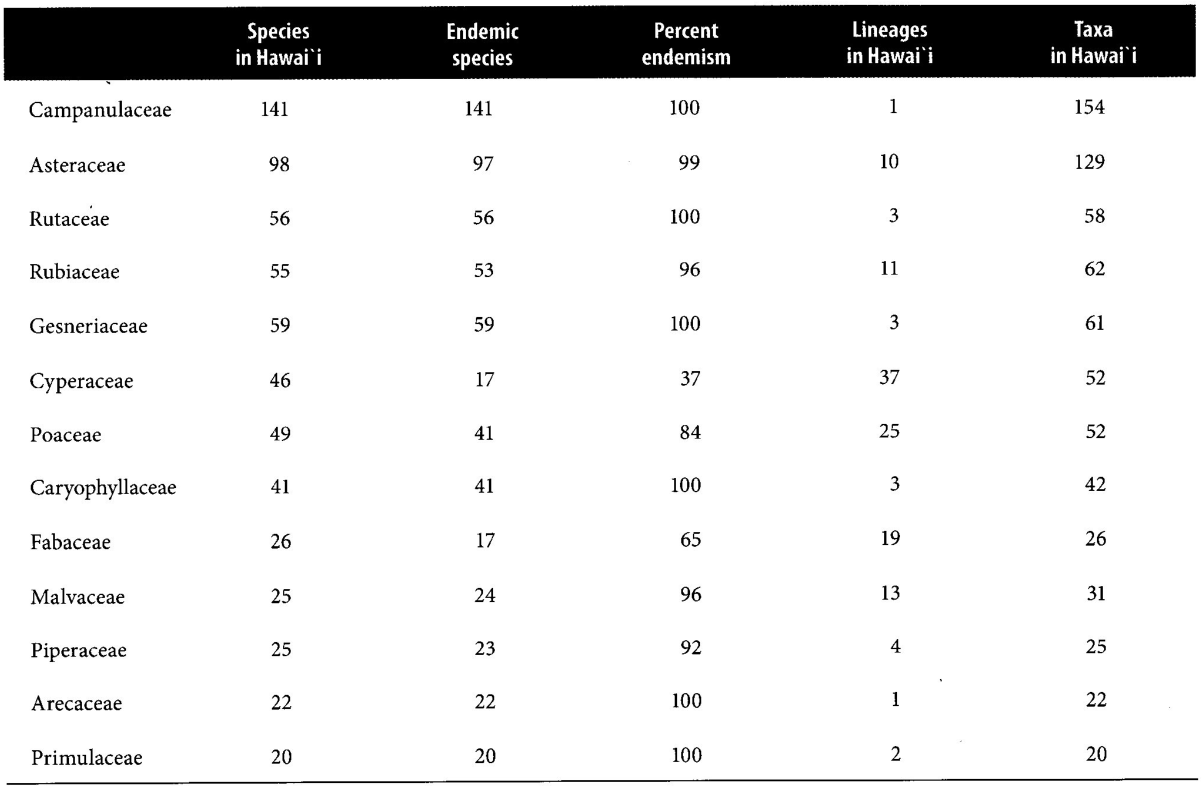
Family	Clade	Genera ~	Distribution	Distribution
Apocynaceae	Asterid	6 ~ 10	Tropical,	Northern 1/3
Araliaceae	Asterid	6 ~ 15	Tropical,	Northern
Campanulaceae	Asterid	8 ~ 124	Temperate,	Middle
Cibotaceae	Monilophyta	1 ~ 11	Tropical,	Northern 1/3
Fabaceae	Rosid	50 ~ 114	Worldwide	
Liliaceae	Monocot	3 ~ 5	Temperate,	Middle
Myrtaceae	Rosid	9 ~ 50	Temperate,	Middle
Lindsaeaceae	Monilophyta	2 ~ 2	Tropical,	Northern 1/3

7. GEOGRAPHY

The Hawaiian Islands are the oldest island chain and are one of the most geographically remote landmasses in the world (Grigg, 2012; Culliney, 2006). Their geographic isolation has resulted in only 375 colonizing lineages for the 1,207 species of native vascular plants, yet has created the highest level of endemism in the world at 88% (Gustafson et al., 2014). Of the native fern and fern ally lineages that arrived in Hawaiʻi, 52% originated in Asia, 12% in America, and 36% are unknown and the flowering plants show a similar trend with 56% from Asia, 19% from America, and 25% as yet unknown (Ziegler, 2002). “The source is undetermined for a large percentage of the native biota, primarily because the usual high degree of endemism in the more speciose groups largely prevents determination of the exact ancestral species of most island taxa” (Ziegler, p. 165).

The origination data points heavily to Asia as the primary source of colonization and with good reason. Most immigration pathways to Hawaiʻi come from the “richest source of biodiversity in the world,” the Indonesian West Pacific (IWP) in the regions of the Philippine and Indonesian archipelagos, Borneo, Celebs, and Papa New Guinea located to the south/southwest of Hawaiʻi (Grigg, 2012, p. 64). How they travel to Hawaiʻi varies between wind, wing, and water vectors. Ninety-five percent of ferns and their fern allies are distributed by wind, and five percent by birds, while twenty-three percent of flowering plants are distributed by sea, two percent by wind, and seventy-five percent by bird (Ziegler, 2002).

Of the lineages that successfully colonized Hawai‘i, some, such as Begoniaceae and Campanulaceae, predate the existence of the oldest modern island of Kaua’i, aged 4.7 Ma and suggest evidence of island hoping “down the chain” from Kure atoll, aged 30 Ma (Gustafson et al. 2014). The remaining native lineages in Hawai‘i have been proven to be younger than Kaua’i with the five largest families, (Campanulaceae, Asteraceae, Rutaceae, Rubiaceae, and Gesneriaceae) forming 40% of Hawaiian angiosperm species, which originated from twenty-nine founding lineages to evolve into 411 species (Fig. 1) (Gustafson et al. 2014).



	Species in Hawai`i	Endemic species	Percent endemism	Lineages in Hawai`i	Taxa in Hawai`i
Campanulaceae	141	141	100	1	154
Asteraceae	98	97	99	10	129
Rutaceae	56	56	100	3	58
Rubiaceae	55	53	96	11	62
Gesneriaceae	59	59	100	3	61
Cyperaceae	46	17	37	37	52
Poaceae	49	41	84	25	52
Caryophyllaceae	41	41	100	3	42
Fabaceae	26	17	65	19	26
Malvaceae	25	24	96	13	31
Piperaceae	25	23	92	4	25
Arecaceae	22	22	100	1	22
Primulaceae	20	20	100	2	20

Figure 1 - Species richness and endemism in Hawaiian angiosperm families with more than 20 species (Gustafson et al., 2014, p. 31)

The genus, *Metrosideros*, is made up of about 50 species that range from the Philippines through New Guinea and New Caledonia to New Zealand and out of the high volcanic islands of the Pacific with one outlying species occurring in South Africa (Wagner et al., 1999.) The Hawaiian lineage originated in New Zealand and spread via wind to colonize the high Pacific islands, while remaining absent from atolls and raised limestone islands, (Fig. 2) (Gustafson et al. 2014).

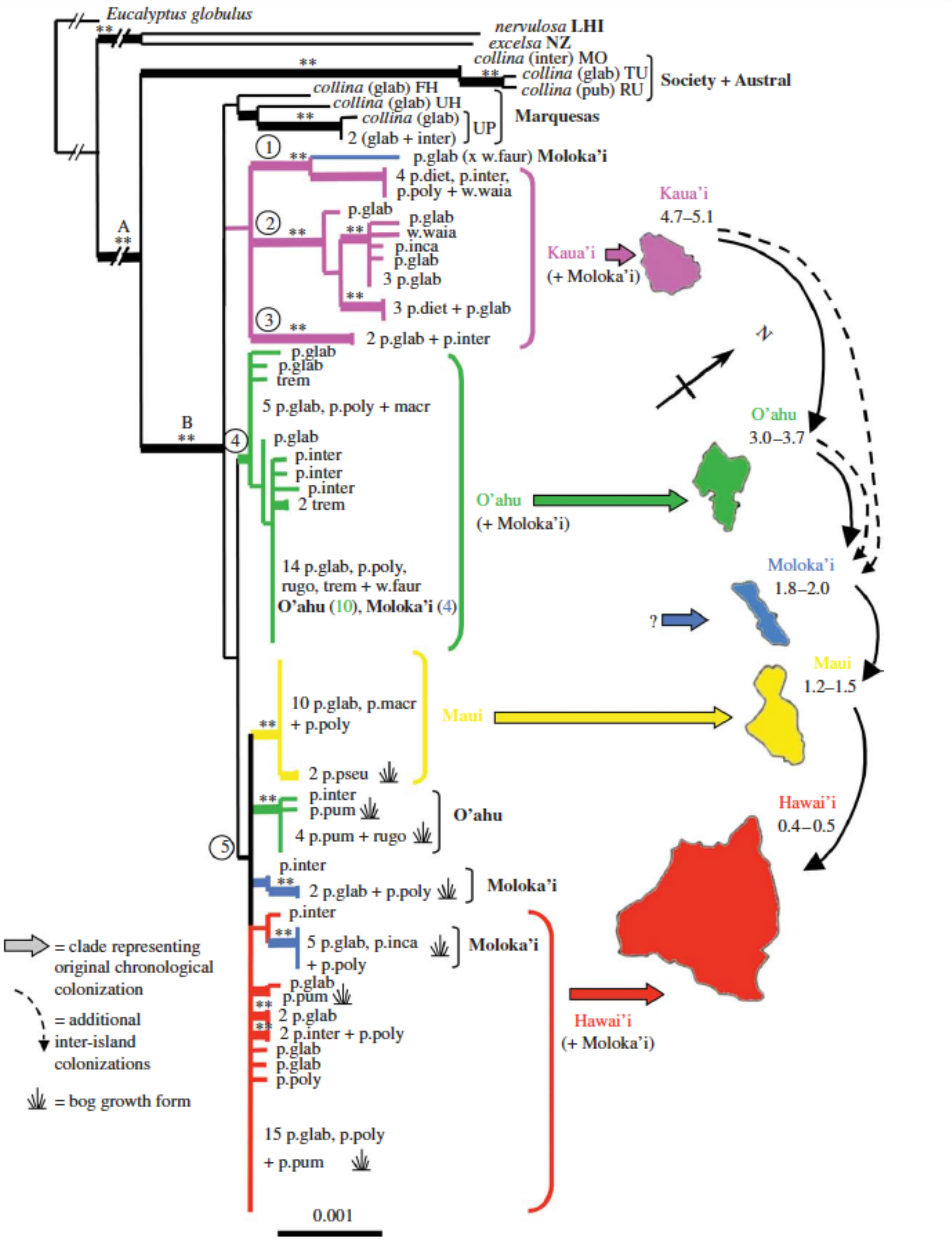


Figure 2 – "Maximum-likelihood tree showing the five main haplotype groups (circled numbers). Interrupted branches at the base of the tree are not to scale. Thick branches indicate ML bootstrap greater than 50; asterisk indicates greater than 75

and double asterisk indicates greater than 85 in at least one of ML or MP analyses (table 1). Hawaiian and French Polynesian taxa fall into two main phenotypic groups: glabrous and pubescent, which can be differentiated using a multivariate analysis of the 12 morphological characters (see electronic supplementary material, appendix B). Taxa shown here can be partitioned as follows: glabrous group—M. macropus (macr); M. polymorpha var. glaberrima (p.glab); M. polymorpha var. macrophylla (p.macr);M. tremuloides (trem); M. waialealae var. fauriei (w.faur); M. waialealae var. waialealae (w.waia); pubescent group—M. polymorpha var. dieteri (p.diet); M. polymorpha var. incana (p.inca); M. polymorpha var. polymorpha (p.poly); M. polymorpha var. pseudorugosa (p.pseu); M. polymorpha var. pumilla (p.pum); M. rugosa (rugo); p.inter designates a phenotype intermediate between glabrous and pubescent. Where a haplotype is shared by multiple individuals the number of individuals is given followed by the taxa/phenotypes; bog growth form is also indicated. LHI, Lord Howe Island and NZ, New Zealand. Society, Austral and Marquesas Islands are abbreviated as follows: MO, Moorea; TU, Tubuai; RU, Rurutu; FH, Fatu Hiva; UH, Ua Huka; UP, Ua Pou. Hawaiian Islands are shown with ages of emergence. (chart and text Percy et al., 2008).

8. ECOLOGY

The endemic ʻŌhiʻa lehua (*Metrosideros polymorpha* Gaud.) is the dominant tree species of the six main Hawaiian Islands. It accounts for 50% of the basal area within almost every habitat and moisture zone and is found from near sea level to the tree line at 2,800 m (as cited in Mortenson et al., 2016). The colonization of this multi-formed, slow-growing, and long-lived, generalist species began approximately 3.9 million years ago on Kauaʻi (Percy et al., 2008) and led to its present-day 350,000 ha establishment across the archipelago (Gon et al., 2006). The widespread distribution of this canopy tree across its ecological range provides critical habitat for Hawaiʻi's wildlife and protection for its invaluable watersheds (Loope & Uchida, 2012).

The jet stream, a strong high-altitude wind, is believed to be responsible for the initial transport of the tiny, wind-dispersed ʻŌhiʻa seeds that arrived in Hawaiʻi by way of the Marquesas (Ziegler, 2002; Gustafson et al., 2014). However, an argument has also been made that, because of the Marquesas' location 3,000 km to the south and east of Hawaiʻi, the high altitudinal airflow created by the ITCZ's summer location offers a more likely explanation (Part 31 Myrtaceae, 2016). Once established on the Islands, *Metrosideros* evolved into five different species, with the most prevalent, *M. polymorpha* Gaud., comprised of eight varieties that are "distinguished by vegetative characters" (Stacy et al., 2014). Through the process of evolution and hybridization, *M. polymorpha* "expanded its ecological range through increased intraspecific variation" (as cited in Drake, 1993, p. 67).

Energy Transfer

M. Polymorpha directly utilizes solar energy and transforms it into glucose through the process of photosynthesis. The chlorophyll in its leaves acts as a catalyst that metabolizes sunlight, water, and CO_2 into glucose and O_2 (Ricklefs & Miller, 2000). The O_2 is released into the atmosphere and the simple sugars produced are either stored in the plants or converted into starch and cellulose, which form the plant's structure (Ziegler, 2002). Because plants have the ability to manufacture their own food, they are labeled as autotrophs and are considered the primary producers in the trophic levels.

The transfer of available energy through the trophic system via consumption operates at a net loss primarily due to respired energy that is dissipated "through radiation into the surrounding air of the combined heat from metabolism of the organisms, abiotic chemical reactions, and solar heating of the system" (Ziegler, 2002, p. 100). This loss begins in the primary producers as they utilize some of the gross primary production from photosynthesis to build and maintain their systems; what remains, called net primary production, is the energy that accumulates in the plant and becomes bioavailable to the herbivorous primary consumers at the next higher trophic level (Ricklefs & Miller, 2000).

Ricklefs & Miller (2000) stated that the ecological efficiencies for a tropical forest average 5% with a net primary production of 8,000 kcal m^{-2} yr^{-1} (p. 200). Thus, if the montane wet forest community's plant biomass produces 8,000 kcal m^{-2} yr^{-1} of metabolic energy, only 400 kcal m^{-2} yr^{-1} is available in the bodies of the primary consumers that have eaten this plant material; only 20 kcal m^{-2} yr^{-1} is available in the secondary consumers and only 1 kcal m^{-2} yr^{-1} is available in the tertiary consumers.

Plant Competition

In order to gain a height advantage over other canopy trees to reach light, some specimens of *M. polymorpha* will develop adventitious roots, stimulated by the plant hormone auxin, from their lower branch nodes. This adaptation supports the increased vertical growth of the ʻŌhiʻa in wet tropical soils by expanding the tree's base with prop roots (Capon, 126).

Defense Against Herbivores

Prior to Polynesian colonization of the Hawaiian Islands just over 1,500 years ago, there were only two species of mammals in the Islands due to its geographical isolation; the Hawaiian hoary bat or ʻōpeʻapeʻa (*Lasiurus cinereus semotus*), an insectivore, and the Hawaiian monk seal, or llio holo I ka uaua, (*Neomonachus schauinsland*), a marine mammal that feeds on fish. As such, neither animal posed a threat to indigenous plant species; therefore, *M. polymorpha* had no need to adapt defenses against grazing herbivores. In fact, many Hawaiian indigenous plant species represent adaptive shifts demonstrated by a lack of spines, thorns, stinging hairs, and chemical defenses against grazing herbivores (Juvik et al. 1998). These defense losses placed indigenous plants at a distinct disadvantage over alien species when widespread distribution of feral ungulates in Hawaiʻi took place in the 19th century and continues to this day.

Life Cycle & Cohort Senescence

The success of the ʻŌhiʻa as an early colonizer is due to a high number of widely dispersed seeds, the result of pollination by insects and birds, that germinate under adverse conditions on a variety of substrates (Drake, 1993). Flowering occurs throughout the year and the random dispersion of prolific seeds results in the exponential growth of dense seedling populations that are established on newly disturbed lava substrates, and in canopy gaps found in old-growth forests (Friday & Herbert, 2006). As the shade-intolerant seedlings mature, they experience increased mortality due to the density-dependent limiting process of self-thinning that is "concentrated among the smallest individuals in the stand, preventing continuous regeneration and recruitment into the canopy" (Drake, 1993, p. 32). The resulting local population, or "cohort stand" consists of individual trees that are born within a limited time span of 50 years and grow up together with a uniform tree structure throughout their life cycle (Mueller-Dombois, Jacobi, Boehmer, & Price, 2013).

After 400 years, the first generation of an ʻŌhiʻa cohort, with a mean population density of 820 trees per hectare, experience a stand-level dieback that is triggered by large density-independent events at senescence due to "synchronized origin and site specific habitat constraints during stand demography," (Boehmer, et al. 2013). The local population is then reestablished in about

30-40 yr with the same canopy species through auto-succession (Mueller-Dombois, & Boehmer, 2013). The process recurs for two – three generations over a 1,000+ yr before enough nutrients exist in the soil substrate to support an "old growth forest" composed of "limited tree flora" due to its evolution in geographic isolation (Mueller-Dombois, et al., 2013).

M. polymorpha is under threat from an onslaught of introduced organisms, pathogens, and habitat loss. Kāhili ginger (*Hedychium gardnerianum*), strawberry guava (*Psidium cattleianum*) and feral ungulates disrupt and displace the ʻŌhiʻa canopy and lead to severe changes in the native trophic levels and nutrient cycles (Mueller-Dombois, et al. 2013). Pathogens such as *Ceratocystis fimbriata,* aka Rapid ʻŌhiʻa Death, threaten to extirpate local populations, potentially spread to other islands, and alter forest composition, structure, and function (Mortenson, et al., 2016). Changing land use patterns and human encroachment due to resource extractors, land developers, and special interest groups have steadily eroded these critical habitats.

9. ETHNOBOTANY

Culturally, the tree is "considered one of the *kinolau*, a physical manifestation of Kū, one of the four Hawaiian deities. Kū stands for strength and anchor [...] and can be translated into the ecological concept of keystone species" (Mueller-Dombois, et al., 2013, p. xiii). The ʻŌhi'a Lehua predominantly resides in the wet montane forest zone or in what was traditionally referred to as the *Wao Akua*, or the realm of the gods. The higher status of this elevation was representative of living things that were not there because of human activity; rather they existed there and flourished as a result of the gods, or forest spirits (Williams, 1997). The transition moving between the *Wao Kanaka*, or realm of the people, and the Wao Akua was not taken lightly and some sort of offering or protocol asking permission was required to enter the forest.

A Hawaiian legend is associated with the tree and blossom, which are culturally considered separate entities; the ʻōhiʻa is the tree and lehua are the blossoms. The legend is told that there once was a handsome, strapping young man named ʻŌhi'a who caught the eye of Pele, the goddess of fire. However, he was betrothed to his one love, Lehua, and denied the advances of the fiery goddess. In her rage at being rejected, she unleashed a fury of lava that surrounded the two young lovers. Trapped by the molten ring of fire, ʻŌhi'a lifted Lehua upon his great shoulders as the lava enveloped his powerful legs. Meanwhile, the forest spirits saw what was happening to the two lovers, but they were unable to stop the powerful Pele. In an effort to save them, the spirits transformed ʻŌhi'a into a tree of the hardest wood, and Lehua into a beautiful blossom, which was placed in his branches, the two never to be separated again. The legend claims that if you pick the Lehua blossom without asking permission, it will soon begin to rain tears from the separated lovers.

The ʻŌhi'a Lehua was an important resource and provided many uses for the Ancient Hawaiians. The hard wood from the tree was traditionally used in agricultural engineering, construction of house and temple walls, spears, mallets, and for the carving of sacred *tikis* (*Metrosideros polymorpha*, 2013; Friday & Herbert, 2006). The Lehua is also the official flower of Hawaiʻi Island and has been used in traditional lei making practices for centuries. However, because of the recent threat of *Ceratocystis fimbriata*, or Rapid ʻŌhi'a Death, hula practitioners on Hawaiʻi

Island have foregone their traditional harvesting practices of the Lehua blossom in an attempt to mitigate the spread of the pathogen, which threatens to wipe out this keystone species (Miner, 2016).

10. CONSERVATION

Hawai'i is the most geographically remote group of islands on Earth, and as such has evolved to become host to a high number of endemic species. In fact, 19% of the 2,176 marine organisms and 64% of the 11,511 terrestrial biotas found in the archipelago are considered endemic (Ziegler, 2002). Despite its unique diversity, Hawai'i is an ecological disaster. Due to habitat loss and degradation; noxious alien species; introduced predators; and exotic diseases, "three-quarters of all America's bird and plant extinctions have occurred within these islands [...] all four of its counties now rank in the top five US counties for federally endangered plants and animals, and forty-eight of the fifty-nine endangered species listed by the Obama administration [...] have been Hawaiian plants and birds." (Cabin, 2013, p.xxi).

Since 2012, large stands of healthy *M. polymorpha* on Hawaiʻi Island have been dying within days to weeks from *Ceratocystis fimbriata*, a fungal pathogen, and has "result[ed] in localized to extensive stands of predominantly dead ʻŌhiʻa trees" (Mortenson et al. 2016, p. 84). The otherwise healthy trees "exhibit rapid, synchronized death of leaves on individual branches that eventually spreads to the entire canopy" (Keith et al. 2015, p. 1276).

Mortenson et al. (2016) conducted a study entitled "Assessing spatial distribution, stand impacts and rate of *Ceratocystis fimbriata* induced ʻōhiʻa (*Metrosideros polymorpha*) mortality in a tropical wet forest, Hawaiʻi Island, USA" in order to obtain a clearer picture of the spread of *C. fimbriata.*

Goals of the Study

Mortenson et al. (2016) outlined the goals of the study as:

1. To date, how much area of ʻohiʻa-dominated forest has experienced *C. fimbriata*-induced mortality?
2. What is the rate of spread of this disease in areas that we have detected it in?
3. What are the forest dynamics in areas affected by the disease?
4. Do certain size classes of ʻohiʻa succumb to the disease more readily than others?
5. At what rate are ʻohiʻa trees dying and do mortality rates differ greatly among different stands? (p. 84)

Goals of Plant Sampling

"To estimate the distribution of C. fimbriata-induced mortality and the change in that distribution between 2012 and 2014" (Mortenson et al. 2016, p. 84). They also established a series of forest plots to measure stand composition, structure, and the degree of plant mortality and repeated the measurements a year later to note any changes.

Sampling Methods

Study Site: Included the Puna District and the southern portion of the South Hilo District of Hawai'i Island, USA. It was selected based on its being the "least altered" existing lowland wet tropical forest. The overall site was also selected based upon a preliminary inventory of recent ‘ohi’a death, which was conducted along roads and by helicopter.

Within the plot, nine monitoring plots were established “to capture variety with regard to abundance of non-native species, composition, stem density, proximity to anthropogenic activities, and prior recent ‘ohi‘a mortality levels” (Mortenson et al. 2016, p. 87). They were established in 2014 and re-inventoried in 2015.

Samples: Within the plots, “sampling and measurements were conducted on GPS fixed-radius 18 m, permanently monumented, circular plots, with 6 m radius co-located subplots to measure invasive species presence/ abundance and ‘ohi‘a regeneration (all seedlings 15 cm in height inventoried)” (Mortenson et al., p. 87) Samples targeted specimens exhibiting signs

Methods: After extensive areal visual training in recognizing the vegetative differences of the species in the region, aerial photographs from 2012 were used to map a 33,000 ha area exhibiting ‘ohi’a mortality. In 2014, satellite imagery of the same region was used to re-evaluate ‘ohi’a mortality.

Within the monitoring plots, a vegetation profile was conducted on a 6 m radius subplot within each plot to provide an ocular estimation of percent cover and mean height by species. Each tree 1.5 cm DBH encountered in the plot was tallied, and its species identity, DBH, crown position (i.e. open grown, dominant, co-dominant, suppressed, overtopped), and status (live or dead) were recorded” (Mortenson et al., p. 87)

Pathogen presence was confirmed via wood samples from all specimens exhibiting signs of mortality found within 200 m of all monitoring locations.

Statistical analysis was then used to account for variation in mortality among plots and to calculate annual mortality rates.

The methods seemed appropriate to me in that they allowed for an analysis at multiple scales.

Variables: Considered in the study were mean annual temperature (MAT), mean annual precipitation (MAP), soil types, and consideration that mortality in some instances may not have been caused by *C. fimbriata*.

Field Botany in the Study

Field botany played a key role in identifying the mechanism of increased mortality and ultimately led to the positive identification of the pathogen in the lab. Dark, radial staining within the xylem of the dead ‘Ōhi‘a trees shows evidence of *C. fimbriata*, with the darkest staining indicating the infection site, generally a wound ("Rapid ‘Ōhi‘a Death," 2018). As the fungus travels upwards, it interferes with the plant's ability to transport water and nutrients from the roots to the canopy through the xylem. The leaf stomata close in response to the stress, and transpirational pull is disrupted causing mortality in the tree.

The methods required an ability to identify the species in the community and ascertain the rapidly failing health of individual ‘ohi’a specimens in the field and from aerial photographs. The presence of field botanists on the ground provided verification of what the plant communities looked like through the remote sensing techniques employed. Additionally, an understanding of the community structure helped account for potential variables that may have affected the study. Furthermore, some varietals of *M. polymorpha* have shown resistance to *Ceratocystis fimbriata,* and it took the trained eye of a field botanist to ascertain the differences between the eight varieties and the ability to notice subtle variations that identified them as resistant.

Results of the Study and a Current Perspective of the Issue

Current aerial surveys from 2017 estimate the range of mortality at hundreds of thousands of trees spread over ~30,000 ha throughout Hawai‘i Island ("Rapid ‘Ōhi‘a Death," 2018) with mortality rates averaging around 24% but increasing to 47% in some test plots (Mortenson et al. 2016). Other sources have reported up to 90% mortality in certain stands ("Rapid ‘Ōhi‘a Death," 2018). Mortenson et al. (2016) claimed that this pattern was distinct from the well-documented cases of *M. polymorpha* cohort senescence as described earlier.

Humans are thought to be the primary vector via transport of contaminated soil, wood, tools, and vehicles; additionally, there is a theory that fungal spores are also disbursed by the wind through contaminated wood-boring beetle frass that becomes mixed with spores (Brewer, 2017). Possible wind dispersion is concerning due to "the potential spread of the disease to other islands, which have not yet had any detections of Rapid ‘Ōhi‘a Death" (Brewer, 2017). The ‘Ōhi‘a is Hawai‘i's most widespread tree and constitutes ~80% of all forest trees in Hawai‘i's native forests and occupies about 400,000 ha across the State (da Silva et al. 2014). "Mortality of ‘Ōhi‘a at this scale is of great concern as the understory in these forests is often occupied by invasive non-native plants capable of severely limiting ‘Ōhi‘a regeneration" (Mortenson et al. 2016, p. 83).

The transformation of ‘Ōhi‘a forest from native dominated to non-native dominated will result in lost plant-pollinator mutualisms, decreased carbon sequestration, and diminished hydrological services. The limiting factor of habitat loss, due to the eradication of large numbers of *M. polymorpha* and the subsequent encroachment of invasive species*,* will result in the extirpation and extinction of Hawai‘i's endemic birds (Reynolds et al. 2003). The mutualistic aspect of this relationship between the endemic Hawaiian honeycreepers [Drepanididae (Cabanis)] and bees [Hylaeus (Fabricius)] are "critical to the overall functioning of island ecosystems and are severely impacted by invasive species" (Hanna et al. 2013, p. 148). Although insects are capable of pollinating the weakly self-compatible hermaphroditic ‘Ōhi‘a flowers, their structure is adapted to bird pollination and thus endemic birds are adapted to them (Hanna et al. 2013). Neither species will prosper without the other.

The threat of Rapid ‘Ōhi‘a Death via the fungal pathogen *Ceratocystis fimbriata* is of such magnitude that it is beyond the scope of any single agency to address measures for the preservation of Hawai‘i’s most abundant native tree and its associated ecosystems. Rather, management strategies, based upon scientific research, must originate from the coordinated interdisciplinary effort of watershed partnerships, NGOs, government agencies, scientists, economists, political leaders, resource managers, and concerned citizens. Additionally, consensus building around common goals must be encouraged and facilitated through open lines of communication and group bonding conferences.

Currently, biosecurity measures prohibiting the export of soil, wood, and many plants from Hawai'i Island have been enacted and public educational campaigns on identifying infected trees and the current best management practices for the pathogen's containment have been well broadcasted. In addition, funding and awareness campaigns at the local, state, and federal levels must be organized to support the development of scientific modeling, experimentation, and data collection; the results of which can be used to develop a management plan and strategies to implement effective solutions; some of which might include fungicidal biocontrol measures, and plant hybridization resistant to *C. fimbriata.*

Unfortunately, all of these strategies need to have happened already. Every moment of every day is another step closer to the extinction of one of Hawai‘i’s most precious organisms and its associated ecosystem. In the meantime, land managers must continue their efforts at containing the damaging effects of invasive alien species on Hawai‘i’s insular biota in hopes that one day we find a steady state balance.

11. REFERENCES

Adee, K. & Conrad, E. (n.d.). *Metrosideros polymorpha* Gaud. Retrieved from https://www.srs.fs.usda.gov/pubs/misc/ag_654/volume_2/metrosideros/polymorpha.htm

Boehmer, H. J., Wagner, H. H., Jacobi, J. D., Gerrish, G. C., Mueller-Dombois, D., & Ward, D. (2013). Rebuilding after collapse: evidence for long-term cohort dynamics in the native Hawaiian rain forest. *Journal of Vegetation Science*, *24*(4), 639–650. https://doi.org/10.1111/jvs.12000

Brewer, F. (2017, September). *Press Release: ROD detected in North Kohala*. Big Island Invasive Species Committee. Retrieved from https://gms.ctahr.hawaii.edu/gs/handler/getmedia.ashx?moid=20753&dt=3&g=12

Cabin, R. J. (2013). *Restoring paradise: rethinking and rebuilding nature in Hawai'i*. Honolulu: University of Hawai'i Press.

Capon, B. (2010). *Botany for gardeners* (3rd ed). Portland, Or: Timber Press.

Cronquist, A. (1981). *An integrated system of classification of flowering plants*. Columbia Univ. Press, New York, 1262 pp.

Culliney, J. L. (2006). *Islands in a far sea: the fate of nature in Hawai'i* (Rev. ed). Honolulu: University of Hawai'i Press.

da Silva, A. C., de Andrade, P. M. T., Alfenas, A. C., Graça, R. N., Cannon, P., Hauff, R., … Mori, S. (2014). Virulence and Impact of Brazilian Strains of Puccinia psidii on Hawaiian 'Ōhi'a (*Metrosideros polymorpha*). *Pacific Science*, *68*(1), 47–56. https://doi.org/10.2984/68.1.4

Drake, D. "Population ecology of *Metrosideros polymorpha* and some associated plants of Hawaiian volcanoes." Doctoral dissertation, University of Hawaii, 1993. Retrieved from http://hl-128-171-57-22.library.manoa.hawaii.edu/bitstream/10125/9454/2/uhm_phd_9325021_r.pdf

Part 31 Myrtaceae. (2016). Flowering Plants of Hawaii (Beta). In *Floridata*. Retrieved from https://floridata.com/tracks/hawaii/Myrtaceae31.html

Friday, J.B., & Herbert, D., (2006). *Metrosideros polymorpha* ('ōhi'a). In: Elevitch, C.R. (Ed.), *Traditional Trees of Pacific Islands*. Permanent Agriculture Resources, Hōlualoa, HI, pp. 465–490. Retrieved from http://www.traditionaltree.org

Gon, S.M., Allison, A., Cannarella, R.J., Jacobi, J.D., Kaneshiro, K.Y., Kido, M.H. (2006). A GAP Analysis of Hawaii: Final Report. US Department of the Interior. US Geological Survey, Washington, DC.

Grigg, R. W. (2012). *In the beginning: archipelago : the origin and discovery of the Hawaiian Islands*. Waipahu, Hawai‘i: Island Heritage.

Gustafson, R., Herbst, D. R., & Rundel, P. W. (2014). *Hawaiian plant life: vegetation and flora*. Honolulu, Hawaii: University of Hawai‘i Press.

Hanna, C., Foote, D., & Kremen, C. (2013). Invasive species management restores a plant–pollinator mutualism in Hawaii. *Journal of Applied Ecology*, *50*(1), 147–155. https://doi.org/10.1111/1365-2664.12027

Juvik, S. P., Juvik, J. O., & Paradise, T. R. (1998). Atlas of Hawaiì. University of Hawaii at Hilo, Department of Geography. Honolulu: University of Hawaiì Press.

Keith, L. M., Hughes, R. F., Sugiyama, L. S., Heller, W. P., Bushe, B. C., & Friday, J. B. (2015). First Report of *Ceratocystis* Wilt on `Ōhi`a (*Metrosideros polymorpha*). *Plant Disease*, *99*(9), 1276. https://doi.org/10.1094/PDIS-12-14-1293-PDN

Lilleeng-Rosenberger, K. E. (2016). *Growing Hawai‘i's native plants: a simple step-by-step approach for every species*. Honolulu: Mutual Publishing.

Little, E. L., Jr., & Skolmen R.G. (1989). *Common forest trees of Hawaii (native and introduced)*. U.S. Department of Agriculture, Agric. Handb. 679.

Loope, L. L., & Uchida, J. Y. (2012). The Challenge of Retarding Erosion of Island Biodiversity through Phytosanitary Measures: An Update on the Case of Puccinia psidii in Hawai'i. *Pacific Science*, *66*(2), 127–139. https://doi.org/10.2984/66.2.3

Metrosideros Polymorpha. (2013). In CABI (Ed.), *The CABI encyclopedia of forest trees*. Oxford, UK: CABI. Retrieved from http://mccproxy.lib.hawaii.edu:2048/login?url=https://search.credoreference.com/content/entry/cabicabi/metrosideros_polymorpha/0?institutionId=4869

Miner, M. (2016, April 11). The cultural significance of ohia lehua. *Hawai‘i Magazine*. Retrieved from https://www.hawaiimagazine.com/content/cultural-hawaiian-significance-ohia-lehua

Mortenson, L., Hughes, R., Friday, J., Keith, L., Barbosa, J., Friday, N., Liu, Z., Sowards, T. Assessing spatial distribution, stand impacts and rate of *Ceratocystis fimbriata* induced ‘ōhi‘a (*Metrosideros polymorpha*) mortality in a tropical wet forest, Hawai‘i Island, USA. (2016). *Forest Ecology and Management*, *377*, 83–92. https://doi.org/10.1016/j.foreco.2016.06.026

Mueller-Dombois, D., & Boehmer, H. J. (2013). Origin of the Hawaiian rainforest and its transition states in long-term primary succession. *Biogeosciences*, *10*(7), 5171–5182.

Mueller-Dombois, D., Jacobi, J., Boehmer, H.J., & Price, J. (2013). *ʻŌhiʻa Lehua rainforest: born among Hawaiian volcanoes, evolved in isolation ; the story of a dynamic ecosystem with relevance to forests worldwide*. Hawaii: Friends of the Joseph Rock Herbarium

Murrell. 2010. *Vascular Plant Taxonomy*. 6th. Dubuque:Kendall/Hunt.

Percy, D. M., Garver, A. M., Wagner, W. L., James, H. F., Cunningham, C. W., Miller, S. E., & Fleischer, R. C. (2008). Progressive island colonization and ancient origin of Hawaiian Metrosideros (Myrtaceae). *Proceedings of the Royal Society B: Biological Sciences*, *275*(1642), 1479–1490. https://doi.org/10.1098/rspb.2008.0191

Rapid ʻŌhiʻa Death, (2018). College of Tropical Agricultural and Human Resources: University of Hawaiʻi. https://cms.ctahr.hawaii.edu/rod/HOME.aspx

Reynolds, M. H., Camp, R. J., Nielson, B. M. B., & Jacobi, J. D. (2003). Evidence of change in a low-elevation forest bird community of Hawai'i since 1979. *Bird Conservation International*, *13*(3), 175–187. https://doi.org/10.1017/S0959270903003149

Ricklefs, R. E., & Miller, G. L. (2000). *Ecology* (4th ed). New York: W.H. Freeman & Co.

Stacy, E. A., Johansen, J. B., Sakishima, T., Price, D. K., & Pillon, Y. (2014). Incipient radiation within the dominant Hawaiian tree Metrosideros polymorpha. *Heredity*, *113*(4), 334–342. https://doi.org/10.1038/hdy.2014.47

Wagner, W. L., Herbst, D. R., & Sohmer, S. H. (1999). *Manual of the flowering plants of Hawai'i* (Rev. ed). Honolulu, HI: University of Hawai'i Press : Bishop Museum Press.

Williams, J. S. (1997). *From the mountains to the sea: a Hawaiian lifestyle*. Honolulu: Kamehameha Schools Press.

Ziegler, A. C. (2002). *Hawaiian Natural History, Ecology, and Evolution*. Honolulu: University of Hawai'i Press.