

Contrasting Structure and Function of Pubescent and Glabrous Varieties of Hawaiian *Metrosideros polymorpha* (Myrtaceae) at High Elevation

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ABSTRACT

Hawaiian dominant tree species *Metrosideros polymorpha* varieties *glaberrima* and *polymorpha* have glabrous and pubescent leaves, respectively. Sympatric populations at 2040 m elevation showed major differentiation beyond the pubescence itself. The varieties differed substantially in stomatal traits and in leaf composition, leaf water status, and instantaneous gas exchange rates, despite similarity in leaf and wood cross-sectional anatomy. Functional differentiation among varieties represents a possible mechanism facilitating the occupation of an exceptional ecological range.

Key words: Hawaii; leaf mass per area; model species; population-level differences; specific leaf area; trichomes.

UNDERSTANDING POPULATION-LEVEL DIFFERENCES IN FUNCTIONAL TRAITS OF SPECIES across their natural ranges is increasing in importance in plant biogeography, evolution, and physiology (e.g., Sparks & Black 1999, Maherali *et al.* 2002, Cavender-Bares *et al.* 2004b). *Metrosideros polymorpha* Gaud. (Myrtaceae) has clear advantages as a model species. *Metrosideros polymorpha* is the most dominant tree in native Hawaiian forests, extending in range from sea level to tree line (ca 2500 m), from new lava flows to substrate aged millions of years, and across sites varying in annual precipitation from < 500 mm to > 6000 mm (Joel *et al.* 1994, Mueller-Dombois & Fosberg 1998, Vitousek 2004). *Metrosideros polymorpha* has been sorted into eight varieties based on morphological traits, which have a genetic basis (Stemmermann 1983, Kitayama *et al.* 1997, Cordell *et al.* 1998, Wagner *et al.* 1999). The varieties tend to have overlapping, but partially distinct ecological distributions. Glabrous-leaved *M. polymorpha* var. *glaberrima* is common at low-to-middle elevation sites with high precipitation and well-developed soils, whereas pubescent-leaved *M. polymorpha* var. *polymorpha* is common at higher elevations, zones of low rainfall, and on younger substrates (Kitayama & Mueller-Dombois 1992; Aplet & Vitousek 1994; Kitayama *et al.* 1995, 1997; Cordell *et al.* 1998; James *et al.* 2004). On the windward slope of Mauna Loa, due to the Trade Wind inversion, annual precipitation increases from ca 3200 mm at sea level to over 5000 mm at ca 650 m, and then decreases with elevation to ca 500 mm at the top of the mountain; mean daily minimum and maximum temperatures decline, respectively, from 18°C and 25°C at sea level to 4°C and 15°C at 2500 m (Giambelluca *et al.* 1986, Aplet & Vitousek 1994, Carbone *et al.* 1998; see plot in Aplet & Vitousek 1994). At 1000 m, *M. polymorpha* var. *glaberrima* can represent 30–70 percent of the vegetation biomass,

and var. *polymorpha* only 3–25 percent; at 2000 m var. *glaberrima* represents < 2 percent of vegetation biomass, and var. *polymorpha* up to over 80 percent (Aplet & Vitousek 1994). These varieties coexist most commonly at low and mid-elevations, where water is abundant. Leaf pubescence itself has been considered adaptive for plants occurring in stressful environments by potentially modifying energy balance, reducing transpiration rates, and contributing to freezing avoidance and to herbivore resistance, but would involve a cost in tissue investment (Ehleringer & Mooney 1978, Cordell *et al.* 2000, Schreuder *et al.* 2001, Gruner *et al.* 2005). In *M. polymorpha*, even the pubescent variety increases in pubescence at sites that are drier or at higher elevation (Joel *et al.* 1994).

Studies of the variation of *M. polymorpha* across environmental gradients have sometimes compared pubescent and glabrous varieties at given sites (e.g., Vitousek *et al.* 1990, Meinzer *et al.* 1992, Joel *et al.* 1994, Cordell *et al.* 1998, Martin *et al.* 2007), especially for leaf compositional traits directly related to pubescence. To our knowledge there have not been any detailed studies on whether sympatric populations of glabrous- and pubescent-leaved varieties differ more generally in structure and function beyond the pubescence itself. We compared sympatric populations of *M. polymorpha* var. *glaberrima* and var. *polymorpha* at the extreme edge of the overlap of the species' distribution, at high elevation. Major differences in phenotype between the varieties at the edge of the species' range would be most likely to indicate a role for contrasting ecological function among varieties as a mechanism contributing to the species' wide range (Cavender-Bares *et al.* 2004a, Bridle & Vines 2007). One hypothesis was that the varieties differ only in the degree of pubescence per se, and consequently in leaf mass per area and in mass-based nutrient concentrations (which would be, respectively, higher and lower due to the mass of the pubescence; Joel *et al.* 1994). Alternatively, varieties may differ in many aspects of functional morphology, associated with adaptation to their contrasting

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typical ranges. In that case, var. *polymorpha*, more common at high elevation and younger substrates, might be expected to show lower stomatal density, smaller stomata, and a higher water-use efficiency, as well as narrower wood xylem vessels and lower sapwood: leaf area ratio, putatively contributing to a lower hydraulic conductance to the leaves, and lower maximum rates of gas exchange. We hypothesized that the two varieties would converge in traits associated with drought tolerance, including small, thick leaves and pronounced cuticle.

The study site was located at approximately 2040 m elevation, on the upslope of Mauna Loa on Hawai'i Island (19°29'37.6" N, 155°23'6.1" W). The vegetation was dominated by *M. polymorpha* var. *polymorpha*, coexisting with var. *glaberrima*, which was much less common at this site. The trees ranged in height from < 0.5 m to 6 m, growing in soil-filled crevices in the lava rock. Data from the closest weather station indicate a mean annual temperature of 13°C and mean annual precipitation of 1020 mm with a pronounced dry season between May and December (Giambelluca *et al.* 1986, Juvik & Juvik 1998). Plants each of *M. polymorpha* var. *glaberrima* and var. *polymorpha* were paired according to their size and proximity ($N = 11$). All leaf anatomical and physiological traits were taken from the same sets of plants, using mature leaves of recent flushes at exposed areas of the canopy.

Measurements of leaf structure were made in July 2003. Leaf area, leaf dry mass per area (LMA), and carbon isotope composition ($\delta^{13}\text{C}$; methods of Cordell *et al.* 1998) were averaged for 2–3 leaves per plant. Leaves were treated for anatomical measurements by fixing with an antifreeze solution of 4 percent paraformaldehyde, 10 percent dimethyl sulfoxide, one percent Tween 80, and 0.1 M sodium cacodylate, pH 7.4, and placed in vacuum for at least 24 h. Thickness measurements (adaxial cuticle, hypodermis, mesophyll, trichome height) were made for cross-sections of the central portion of leaves with a freezing microtome (Cryocut 1800, Leica, Reicher-Jung, Deerfield, IL, U.S.A.), imaged with light microscope and analyzed digitally (SigmaScan Pro version 4.01 software, Jandel Scientific, Chicago, IL, U.S.A.), with values averaged for four leaves per plant. Scanning electron microscopy was used to visualize characters. Trichomes were removed from the abaxial side of pubescent leaves with a razor blade. One leaf per plant for six plants of each variety were postfixed in 1 percent OsO_4 in 0.1 M sodium cacodylate, pH 7.4, and dehydrated with ethanol, critical point dried (Samdri-795, Tousimis, Rockville, MD, U.S.A.) and sputter coated with gold/palladium. Photographs of 10 randomly chosen regions of abaxial surface were made for each sample with a field emission scanning electron microscope (Hitachi S-800, San Jose, CA, U.S.A.). Images were analyzed for stomatal density and cuticular pore area (using SigmaScan Pro).

Chlorophyll and nitrogen concentrations were measured for leaves sampled in February 2005. Total chlorophyll per leaf area was determined using a SPAD meter (Minolta Co., Osaka, Japan) for fully developed leaves from the most recent flush (two leaves per plant for 11 plants of each variety). For a given species SPAD measurements are correlated with total chlorophyll ($a + b$) per unit area regardless of pubescence (Manetas *et al.* 1998). Total chlorophyll per leaf mass was calculated by dividing by LMA (in

units $\text{SPAD}/\text{g}/\text{m}^2$). The same leaves were analyzed for nitrogen concentration, after drying at 70°C for 48 h. Dried samples were ground with a tissue-grinding mill (Mini Mill, Thomas Scientific, Swedesboro, NJ, U.S.A.) using #20 mesh, and nitrogen analysis was done on a 150-mg dried sample with a CNS analyzer (Vario MAX CNS Macro Elemental Analyzer, Elementar Analysensysteme GmbH, Hanau, Germany).

Measurements of wood xylem vessels were made from outer branches of at least 15-mm diam, to ensure the presence of several years of mature conducting xylem (one stem sample per plant for 10 plants of each variety). Samples were cross-sectioned using a sliding microtome, and digital micrographs were taken of secondary xylem. Maximum vessel diameters were determined for 10 typical vessels per stem (using SigmaScan Pro). Shoots were collected in February 2005 for determination of sapwood to leaf area ratio (six shoots per plant for five plants of each variety). The sapwood area was calculated by subtracting the heartwood area from the total wood cross-sectional area, with area estimated by multiplying the square of measured radius by π .

Measurements of stomatal conductance (g) were made on sunny days during the summer dry season on 18–19 July 2003, between 1000 and 1400 h; five measurements were made each day on one leaf per plant for six plants of each variety (LI-1600; LI-COR Biosciences, Lincoln, NE, U.S.A.). Photosynthetically active radiation (PAR) was over 1500 $\mu\text{mol}/\text{m}^2/\text{sec}$, and null point humidity was set at ambient. A second set of measurements was made on sunny days in the winter wet season on 20–21 February 2005; light-saturated net photosynthetic rate and g were measured for six plants of each variety, with measurements repeated on these two days (LI-6400; LI-COR Biosciences). For these measurements, cuvette temperature was set at 25°C; PAR at 1200 $\mu\text{mol}/\text{m}^2/\text{sec}$, which was above saturation irradiation; CO_2 at 400 $\mu\text{mol}/\text{mol}$; and relative humidity at ambient. As an index of water availability, pre-dawn water potential measurements were made on 20 February 2005 for two shoots per plant for five plants of each variety (Plant Moisture Systems Pressure Chamber Model 1000, Albany, OR, U.S.A.). Previous studies in other systems found that nocturnal transpiration can lead to disequilibria, such that pre-dawn water potentials underestimate the weighted average soil water potential (Donovan *et al.* 2003, Bucci *et al.* 2005). To reduce the impact of any nocturnal transpiration, shoots were bagged for 20 min before excision for measurement of pre-dawn water potential. Nocturnal transpiration for *M. polymorpha* at high elevation was expected to be extremely low, due to subzero pre-dawn temperatures (and thus very low vapor pressure deficit), and the very low epidermal conductance of *M. polymorpha* (ca 4 $\text{mmol}/\text{m}^2/\text{sec}$; L. Sack and W.K. Cornwell, pers. obs.).

Data were analyzed using Minitab Release 14 (Minitab, State College, PA, U.S.A.) and Genstat 5th edition (VSN International, Hemel Hempstead, Herts, UK). Paired t -tests were used when comparing trait values for matched plants (Zar 1999).

There was extreme difference in pubescence between the varieties. *Metrosideros polymorpha* var. *polymorpha* had dense pubescence (Fig. 1A and C; Table 1), while var. *glaberrima* was entirely glabrous (Fig. 1B and D). Leaves of var. *polymorpha* had on average a 62 percent higher LMA, as found in previous comparisons of pubescent

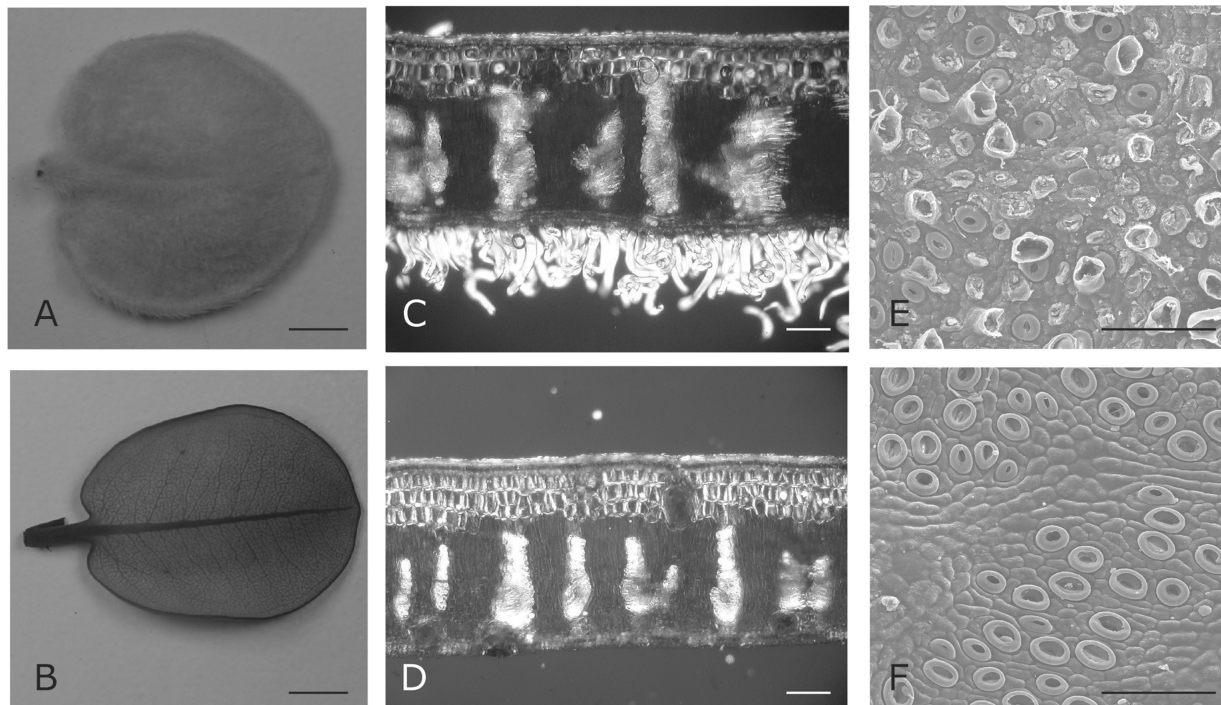


FIGURE 1. Leaves of *Metrosideros polymorpha* var. *polymorpha* (A, C, E) and var. *glaberrima* (B, D, F) were similar in size and shape (A, B; scale line = 5 mm), and in cross-sectional anatomy, apart from the abaxial pubescence *per se* (C, D; scale line = 100 μm), but differed strongly in density and area of stomatal pores on the abaxial side (E, F; scale line = 75 μm ; in [E], leaves were shaved, and trichome stumps are visible). Trees were sampled growing at a common site at 2040 m on Mauna Loa, Hawaii.

and glabrous leaves at lower elevations (e.g., Joel *et al.* 1994, Cordell *et al.* 1998), where the difference in LMA was accounted for by the mass of the pubescence itself (Table 1). Functional traits observed for *M. polymorpha* var. *glaberrima* were consistent with its typical zonation on moister, well-developed soils at lower elevations. *Metrosideros polymorpha* var. *polymorpha* had on average a 40 percent higher foliar chlorophyll per area than var. *glaberrima*, and similar nitrogen per area. Due to the differences in LMA, var. *glaberrima* had 16 percent higher foliar chlorophyll per mass and 27 percent higher nitrogen per mass than var. *polymorpha* (Table 1). The leaves of *Metrosideros polymorpha* var. *glaberrima* had 39 percent higher stomatal density than those of var. *polymorpha*, and the stomatal pores were 78 percent larger in area (Fig. 1E and F; Table 1), suggesting the capacity for higher stomatal conductance and photosynthetic rates per area for plants growing in high resource supply (Brodribb & Hill 1997, Sack *et al.* 2003).

These structural differences were consistent with the differences in water status and gas exchange observed during instantaneous measurements (Table 1). Despite the plants of var. *glaberrima* having lower chlorophyll and nitrogen concentrations per leaf area than var. *polymorpha*, and a similar g during the 'wet' season in February 2005, they had a $1.6 \times$ higher light-saturated photosynthetic rate per area (A_{area}) suggesting a higher mesophyll activity at this site, probably due to greater access to the available water (Kubiske & Abrams 1993). Despite the proximity of plants of both varieties, and their matched sizes, var. *glaberrima* was 1.3 MPa higher

in pre-dawn shoot water potential than var. *polymorpha* (Table 1), suggesting an equilibration with moister soil overnight than var. *polymorpha*. This hypothesis was supported by the fact that during the previous summer dry season, instantaneous g values were substantially lower for both varieties, but more strongly reduced for var. *polymorpha* than for var. *glaberrima*. Potentially, plants of var. *glaberrima* access soil in deeper or wider-ranging crevices than that on which var. *polymorpha* establishes; or, alternatively, the roots of var. *glaberrima* may store more water. To test these hypotheses directly would require excavation of lava rock, soil, and roots, potentially in tandem with determination of water isotope composition, but such approaches are precluded by the endangered status of the habitat. For var. *glaberrima*, the combination of higher A_{area} and lower LMA resulted in a $2.6 \times$ higher light-saturated photosynthetic rate per mass (A_{mass}) than var. *polymorpha*, which would correspond to higher mass-based relative growth rates for a given level of leaf allocation (Givnish *et al.* 2004, Wright *et al.* 2004).

By contrast, var. *polymorpha* possessed characteristics associated with adaptation to dry soil and high elevation, including dense pubescence, fewer stomata, and smaller stomatal pores, as well as higher LMA, lower chlorophyll and N concentrations per mass, and lower A_{mass} . These traits would contribute to the ability to persist with a slower metabolism and carbon assimilation rate in low resource supply (Grubb 1998), such as at this site at which pre-dawn water potentials reach -2 MPa even in the wet season. Plants of var. *polymorpha* also had a less negative $\delta^{13}\text{C}$, indicating

TABLE 1. Mean \pm SE for leaf traits of *Metrosideros polymorpha* var. *polymorpha* and var. *glaberrima* coexisting at high elevation on Mauna Loa, Hawaii.

Trait	<i>M. polymorpha</i> var. <i>glaberrima</i>	<i>M. polymorpha</i> var. <i>polymorpha</i>	Significance
Leaf structure			
Trichome density (/mm)	—	829 \pm 47	
Trichome canopy height (μ m)	—	232 \pm 7.4	
Leaf area (cm ²)	5.7 \pm 0.6	6.1 \pm 0.3	ns
Lamina thickness, not including pubescence (μ m)	523 \pm 5.8	516 \pm 11.0	ns
Hypodermal thickness (μ m)	129 \pm 3.1	133 \pm 4.1	ns
Mesophyll thickness (μ m)	352 \pm 6.0	334 \pm 7.9	*
Adaxial cuticle thickness (μ m)	29.1 \pm 1.0	29.9 \pm 1.0	ns
Leaf mass per area (g/m ²)	123 \pm 2.67	200 \pm 4.52	***
Leaf composition			
Total chlorophyll per area (SPAD)	46.6 \pm 1.43	65.4 \pm 1.93	***
Total chlorophyll per mass (SPAD m ² /g)	0.379 \pm 0.0179	0.327 \pm 0.0156	*
N concentration per area (g/m)	0.931 \pm 0.0444	1.19 \pm 0.252	ns
N concentration per mass (mg/g)	7.57 \pm 0.238	5.96 \pm 0.354	***
δ^{13} C (‰)	-27.26 \pm 0.262	-25.97 \pm 0.338	**
Stomatal traits			
Stomatal density (/mm ²)	368 \pm 33	264 \pm 16	*
Cuticular pore area (μ m ²)	80.8 \pm 11.1	45.5 \pm 5.5	*
Wood traits			
Stem vessel diameter (μ m)	43.9 \pm 3.0	44.0 \pm 1.2	ns
Sapwood: leaf area ratio (m ² /m ² \times 10 ⁻⁴)	1.65 \pm 0.731	1.84 \pm 0.83	ns
Physiological measurements			
July 2003, 'dry season'			
<i>g</i> (mmol/m ² /sec)	41.5 \pm 3.1	22.0 \pm 2.7	**
February 2005, 'wet season'			
Shoot water potential (MPa)	-0.64 \pm 0.18	-1.94 \pm 0.11	**
<i>g</i> (mmol/m ² /sec)	108 \pm 7.6	104 \pm 14	ns
<i>A</i> _{area} (μ mol/m ² /sec)	7.4 \pm 0.68	4.6 \pm 0.42	*
<i>A</i> _{mass} (nmol/g/sec)	60.4 \pm 5.6	23.0 \pm 2.1	**

*A*_{area} = light-saturated net rate of carbon assimilation, area based; *A*_{mass} = light-saturated net rate of carbon assimilation, mass based; *g* = stomatal conductance. ***Significant at $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns = not significant at $P < 0.05$. Paired *t*-tests used for all traits except total chlorophyll per mass and *N* concentration per area; for these traits, standard errors were calculated by propagation of error, and standard *t*-tests were used.

a higher ratio of intercellular to atmospheric partial pressure of CO₂ over the lifetime of the leaf, associated with greater water-use efficiency (Vitousek *et al.* 1990; Meinzer *et al.* 1992; Cordell *et al.* 1998, 1999). This study indicated that var. *polymorpha* had a lower *A*_{area} than var. *glaberrima*, despite a similar *g*, and thus may have had a lower instantaneous water-use efficiency during the measurement period. However, for leaves transpiring naturally (*i.e.*, outside of the measurement cuvette), the trichomes of var. *polymorpha* would probably maintain a thicker boundary layer with lower conductance, which would have raised the leaves' water-use efficiency. In addition, for *M. polymorpha* in droughted habitats, most growth is achieved immediately after rainfall events (Stratton *et al.* 2000). At those times, the lower stomatal density and smaller stomatal pores of var. *polymorpha* would probably correspond to a lower stomatal conductance (Sack *et al.* 2003), also linked with a higher water-use efficiency.

Despite their strong differences, the two varieties converged in several key traits, including leaf size; the thicknesses of mesophyll, hypodermis and adaxial cuticle; stem cross-sectional anatomy; and sapwood: leaf area ratio (Table 1; Fig. 1A–D). Convergence in lamina internal anatomy was also reported for glabrous- and pubescent-leaved *M. polymorpha* at 750 m on Mauna Loa (Joel *et al.* 1994), and the leaves in our study were much thicker in all components, as expected for higher elevation. The leaves of both varieties were thick, with cuticle-formed overarching ledges resulting in donut-shaped pores above the guard cells (Fig. 1E and F), protecting the stomata, as previously reported for *Populus* leaves (Pallardy & Kozlowski 1980); these characteristics are associated with the ability to survive prolonged drought (Grubb 1998). The xylem vessels of both varieties were similar in their relatively large diameter, suggesting high hydraulic conductivity, which may provide an advantage in dry soil and at higher elevation, by supplying leaves with relatively high

capacity (Santiago *et al.*, in press). However, stems with mean vessel diameters above 40 μm are typically highly sensitive to freeze-thaw-induced embolism (Davis *et al.* 1999, Pittermann & Sperry 2003), suggesting that freeze-thaw-induced embolism might contribute to the upper elevation limit for *M. polymorpha*.

This study demonstrates strong functional differentiation among sympatric varieties of *M. polymorpha*, highlighting a need for further work on this species. More work is needed to characterize the diversification in structure and function of all eight varieties of Hawaiian *M. polymorpha* (Wagner *et al.* 1999), and indeed, for the full range of *M. polymorpha* genotypes. This genetic and functional variation is thought to have radiated from a single colonizer, with pubescent leaves (Wright *et al.* 2001), but little is known of the mechanisms for the origin of this variation, or for the maintenance of this variation in the face of population mixing and potential hybridization (Porter 1973, Aradhya *et al.* 1993, Berlin *et al.* 2000, James *et al.* 2004). The phenotypic divergences between *M. polymorpha* var. *glaberrima* and var. *polymorpha* indicate genotypic differentiation that would in principle contribute to the competitiveness and resilience of *M. polymorpha* across its exceptional ecological range (Whitham *et al.* 2003, Cavender-Bares *et al.* 2004a, Vellend 2006). The convergences in traits related to drought tolerance would contribute to this species' apparent ability to persist under adverse conditions across its range. Further studies are needed to determine the degree to which differences in structure and function among varieties scale up to ecological differences along natural environmental gradients.

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