Allometric Models for Predicting Aboveground Biomass in Two Widespread Woody Plants in Hawaii

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ABSTRACT

Allometric models are important for quantifying biomass and carbon storage in terrestrial ecosystems. Generalized allometry exists for tropical trees, but species- and site-specific models are more accurate. We developed species-specific models to predict aboveground biomass in two of the most ubiquitous natives in Hawaiian forests and shrublands, *Metrosideros polymorpha* and *Dodonaea viscosa*. The utility of the *M. polymorpha* allometry for predicting biomass across a range of sites was explored by comparing size structure (diameter at breast height vs. tree height) of the trees used to develop the models against trees from four *M. polymorpha*-dominated forests along a precipitation gradient (1630–2380 mm). We also compared individual tree biomass estimated with the *M. polymorpha* model against existing generalized equations, and the *D. viscosa* model with an existing species-specific model. Our models were highly significant and displayed minimal bias. *Metrosideros polymorpha* size structures from the three highest precipitation sites fell well within the 95% confidence intervals for the harvested trees, indicating that the models are applicable at these sites. However, size structure in the area with the lowest precipitation differed from those in the higher rainfall sites, emphasizing that care should be taken in applying the models too widely. Existing generalized allometry differed from the *M. polymorpha* model by up to 88 percent, particularly at the extremes of the data range examined, underestimating biomass in small trees and overestimating in large trees. The existing *D. viscosa* model underestimated biomass across all sizes by a mean of 43 percent compared to our model. The species-specific models presented here should enable more accurate estimates of biomass and carbon sequestration in Hawaiian forests and shrublands.

Key words: Allometry; *Dodonaea viscosa*; generalized allometric models; Hawaii Volcanoes National Park; *Metrosideros polymorpha*; nonlinear regression.

THE CYCLING OF CARBON IN FOREST ECOSYSTEMS IS A TOPIC OF CONSIDERABLE IMPORTANCE WITH rising atmospheric CO_2 concentrations, global climate change, and the poorly defined role that terrestrial ecosystems play in mitigating or exacerbating these phenomena. In addition, increasing value is being placed on ecosystem services in forests and carbon cycling is among the most important of these services. Aboveground biomass—the amount of organic matter in living and dead plant material—is a critical component of the carbon cycle in forest ecosystems, providing both short- and long-term carbon sequestration. Tropical forests, in particular, are major components of the terrestrial carbon cycle, accounting for 26 percent of global carbon storage in biomass and soils (Dixon *et al.* 1994, Geider *et al.* 2001, Grace 2004). Yet, accurate estimates of carbon sequestration in tropical forests are lacking for many areas, due in large part to a paucity of appropriate allometric models for predicting biomass in species-rich tropical ecosystems (Chave *et al.* 2005). Due to the high species diversity in tropical forests, much attention has been placed on developing generalized allometric models for tropical trees (Brown 1997, Zianis & Mencuccini 2004, Chave *et al.* 2005, Pilli *et al.* 2006). However, the use of generalized equations can lead to a bias in estimating biomass for a particular species (Clark *et al.* 2001, Cairns *et al.* 2003, Chave *et al.* 2004, Litton *et al.* 2006, Pilli *et al.* 2006), although recent

approaches incorporating data on wood density hold more promise (Chave *et al.* 2005).

In many Hawaiian forests, generalized allometric equations do not accurately predict aboveground biomass (Litton *et al.* 2006). However, because tree diversity is low in Hawaii compared to the continental tropics, species-specific allometry can be more easily developed and applied to estimate carbon sequestration in biomass. Two of the primary woody species in Hawaiian forests and shrublands are *Metrosideros polymorpha* Gaud. and *Dodonaea viscosa* Jacq., respectively. Both of these species have wide distributions across extreme climatic gradients, ranging from sea level to > 2000 m (Wagner *et al.* 1999), and they frequently account for most of the individuals and biomass in native-dominated areas (Aplet & Vitousek 1994, Crews *et al.* 1995, Vitousek 2004, Mueller-Dombois 2006).

Allometric equations exist for predicting aboveground biomass in *M. polymorpha* in Hawaii (Aplet & Vitousek 1994, Raich *et al.* 1997), and in the pantropical *D. viscosa* in Hawaii and elsewhere (Harrington 1979, Aplet *et al.* 1998). However, the provenance of the individuals used in the development of these earlier models is unclear and, therefore, the geographic locality to which the models are most applicable is largely unknown. Moreover, existing equations are limited in their utility because they require measurements of both individual plant basal diameter and total height to predict biomass. Most inventory studies, in turn, do not commonly measure these variables but instead measure diameter at breast height

(dbh) and, at times, commercial height for trees, and basal diameter for shrubs (Chave *et al.* 2005, Segura & Kanninen 2005). As with most tropical forests, it is difficult and time consuming to accurately measure individual tree heights in closed canopies dominated by *M. polymorpha*.

Our objectives here were to: (1) develop allometric models to predict *M. polymorpha* individual tree foliage, wood, and total aboveground biomass from measurements of dbh using an existing data set of harvested trees (Raich *et al.* 1997); (2) develop allometry from destructive harvest to predict foliage, wood, and total aboveground biomass for *D. viscosa* individuals from measurements of basal diameter; (3) determine if the allometry developed for *M. polymorpha* in this study is applicable across the range of climatic conditions where this species is found, by comparing size structure relationships (dbh vs. tree height) between trees from which the equations were developed and trees from each of four sites along a precipitation gradient (1630–2380 mm); (4) determine if our species-specific allometry for *M. polymorpha* differs from existing generalized equations for tropical trees (Brown 1997, Chave *et al.* 2005); and (5) determine if the allometry developed for *D. viscosa* in this study differs from an existing model developed in Hawaii, which relies on both basal diameter and plant height (Aplet *et al.* 1998).

METHODS

METROSIDEROS POLYMORPHA ALLOMETRY.—*Metrosideros polymorpha* is a Hawaiian endemic, the only native dominant canopy species present in wet forests, and one of only two found in mesic forests (Mueller-Dombois 2006). In mesic to wet forests, *M. polymorpha* is the most common pioneer species occupying early-successional sites and also maintains dominance in later seral communities (Wagner *et al.* 1999, Mueller-Dombois 2006), accounting for ≥ 75 percent of total canopy coverage across large gradients in climate and substrate age (Crews *et al.* 1995). In drier forests, *M. polymorpha* is the primary pioneer species, but can be replaced by other taxa at later seral stages (Stemmermann & Ihsle 1993).

A subset of an existing data set of harvested trees, originally analyzed in Raich *et al.* (1997), was used to develop allometric models for predicting *M. polymorpha* foliage, wood, and total aboveground biomass from dbh. Harvested trees represent a cumulated data set from the Island of Hawaii, U.S.A. The dbh range of trees comprising the data set was 0.3–33.3 cm (Table 1). Details on harvest locations are not available, but all trees were harvested from the windward side of the island. We used all trees >1.33 m height and > 0.3 cm dbh, reducing the original data set from 44 to 30 individuals for leaf and total biomass and to 36 individuals for wood biomass. For harvested trees, basal diameter was measured in lieu of dbh. For these trees, we estimated dbh from basal diameter using a taper equation ($r^2 = 0.96$) following Raich *et al.* (1997).

The same 36 harvested trees used to develop the allometric models were used to develop a dbh versus total tree height curve. We then randomly sampled dbh and height from a total of 170 trees

TABLE 1. *Allometric models for predicting aboveground live biomass in individuals of* Metrosideros polymorpha *and* Dodonaea viscosa *in Hawaii.*

Dependent variable	N	a (SE)	b (SE)	MSE	R^2
Metrosideros polymorpha					
Leaf biomass (kg)	30	0.09 (0.03)	1.45 (0.11)	0.85	0.94
Wood biomass (kg)	36	0.53 (0.21)	2.00 (0.12)	1166.2	0.96
Total tree biomass (kg)	30	0.88 (0.41)	1.86 (0.14)	1178.8	0.95
Dodonaea viscosa					
Leaf biomass (g)	20	0.08 (0.10)	2.25 (0.40)	596.0	0.78
Wood biomass (g)	20	0.08 (0.06)	2.63 (0.26)	2396.9	0.93
Total shrub biomass (g)	20	0.13 (0.09)	2.55 (0.21)	2673.1	0.95

Note: Models for all dependent variables are of the form $Y = aX^b$ where Y is the dependent variable (kg dry weight for *M. polymorpha* and g dry weight for *D. viscosa*), X is the predictor variable (dbh (cm) for *M. polymorpha* and basal diametes (mm) for *D. viscosa*), and a and b are constants in the equation. SE is the asymptotic standard error of the parameter estimate, MSE is the mean square of the error, and R^2 is the coefficient of determination. All models were highly significant ($P < 0.001$).

in four areas along a precipitation gradient in Hawaii Volcanoes National Park on the windward side of the Island of Hawaii (Table 2), and developed separate dbh-height curves for each area. Sites along the gradient were within 5 km of each other and ranged from a low of 1630 mm mean annual precipitation (MAP) at 440 m elevation, to 2380 mm MAP at 815 m. All sites were located on relatively young (400–750 yr) pahoehoe lava flows (Trusdell *et al.* 2005). To determine if the allometric models we developed could be used at these sites that represent variation in climate and growth form, we compared the dbh-height curves from each site to the 95% CIs for

TABLE 2. *Diameter at breast height versus total tree height models for* Metrosideros polymorpha *trees used to develop the allometric models in Table 1 (Harvest), four sites across a precipitation gradient in Hawaii Volcanoes National Park, and all sites combined.*

Site	dbh range	N	a (SE)	b (SE)	MSE	R^2
Harvest	0.3–33.3	36	21.89 (1.84)	0.071 (0.012)	3.69	0.92
2380 mm	4.7–83.5	25	23.80 (1.54)	0.039 (0.006)	4.62	0.91
1930 mm	4.0–44.0	75	22.82 (1.23)	0.053 (0.005)	3.27	0.84
1730 mm	2.7–60.0	38	15.58 (1.26)	0.045 (0.007)	2.14	0.85
1630 mm	2.5–70.0	32	9.39 (0.44)	0.074 (0.009)	0.81	0.84
All sites	0.3–83.5	206	17.70 (0.92)	0.062 (0.007)	12.45	0.60

Note: Models for all dependent variables are of the form $Y = a * (1 - exp(-b \times X))$ where Y is the dependent variable (total tree height (m)), X is the predictor variable (dbh (cm)) and a and b are constants in the equation. SE is the asymptotic standard error of the parameter estimate, MSE is the mean square of the error, and R^2 is the coefficient of determination. All models were highly significant ($P < 0.001$).

the curve developed from the harvested trees (*i.e.*, we determined if the curve for individual sites fell within the 95% CIs of the harvested tree curve across the entire data range).

Total biomass estimates for individual plants derived from the allometric model developed here for *M. polymorpha* were compared to existing generalized equations for tropical trees (Brown 1997, Chave *et al.* 2005) by plotting the models on a common axis, and by estimating biomass in each model across a range of dbhs and calculating percent difference. In all model comparisons we used a common range of dbhs (5–35 cm) that encompassed the entire range of the harvested *M. polymorpha* trees (0.3–33 cm). This is well within the range of dbhs used to construct the generalized allometric models—the Brown (1997) and Chave *et al.* (2005) models were constructed from trees ranging in dbh from 4–148 and 5–156 cm, respectively.

The Brown (1997) and Chave *et al.* (2005) models were developed separately for moist and wet climatic zones, defined as 1500–3500 mm and > 3500 mm MAP, respectively. The Brown (1997) models require only dbh (cm) to predict total aboveground biomass (kg dry weight). However, the Chave *et al.* (2005) models require species-specific information on wood specific gravity and provide a set of equations for each climatic zone that requires either dbh alone or both dbh and total tree height to predict total aboveground biomass. We used a wood specific gravity of 0.69 g/cm^3 for *M. polymorpha* (R.F. Hughes, pers. comm.) when estimating aboveground biomass with the Chave *et al.* (2005) generalized models.

The generalized allometric models used to predict total aboveground biomass (kg dry weight) in individual trees were:

$$\text{Brown Moist}: \exp(-2.134 + 2.530 \times \ln(D)) \tag{1}$$

$$\text{Brown Wet}: 21.297 - 6.953 \times D + 0.740 \times D^2 \tag{2}$$

$$\text{Chave Moist}: \rho \times \exp(-1.499 + 2.148 \times \ln(D) + 0.207 \\ \times (\ln(D))^2 - 0.0281 \times (\ln(D))^3) \tag{3}$$

$$\text{Chave Wet}: \rho \times \exp(-1.239 + 1.980 \times \ln(D) + 0.207 \\ \times (\ln(D))^2 - 0.0281 \times (\ln(D))^3) \tag{4}$$

$$\text{Chave Moist}: 0.0509 \times \rho D^2 H \tag{5}$$

$$\text{Chave Wet}: 0.0776 \times (\rho D^2 H)^{0.94} \tag{6}$$

where *D* is diameter at breast height (cm), *H* is total tree height (m), and ρ is wood specific gravity (g/cm^3).

DODONAEA VISCOSA ALLOMETRY.—*Dodonaea viscosa* is a pantropical species that typically occurs as a shrub in Hawaii, but can also be a small tree (Stemmermann & Ihsle 1993, Wagner *et al.* 1999). Much like *M. polymorpha*, this species occupies, and often dominates, a wide variety of sites ranging from pastures, coastal dunes, low elevation and subalpine shrublands, dry, mesic and wet forests, to open and recently disturbed areas, from sea level to 2350 m elevation in both early and late seral stages (Wagner *et al.* 1999).

Twenty individuals of *D. viscosa* ranging from 4.8 to 29.1 mm basal diameter were harvested from Hawaii Volcanoes National Park at elevations of 440–500 m to develop allometric models for predicting foliage, wood, and total aboveground biomass from basal diameter. Harvest sites were in open shrubland/grassland where *D. viscosa* is a dominant component of the landscape. We measured basal diameter (mm; measured at ground level) and total height (cm) for each individual, cut the shrubs at ground level, transported entire plants to the laboratory, dried all material to a constant weight in a forced air oven, separated biomass into foliage and wood, and weighed all dried samples to the nearest 0.01 g.

We compared total aboveground biomass estimates for individual plants from the allometric model developed here for *D. viscosa*, with an existing species-specific equation presented by Aplet *et al.* (1998) across the entire range of harvested basal diameters (5–29 mm) by plotting both models on a common axis. The Aplet *et al.* (1998) model requires both basal diameter and shrub height to predict total aboveground biomass, and was developed from an unknown number of individuals of unknown sizes harvested from unknown locations on the leeward side of the island of Hawaii (R.F. Hughes, pers. comm.). Thus, it is possible that our model comparison is somewhat arbitrary because it may extend the use of the Aplet *et al.* (1998) equation to individuals outside of its intended size range. In light of this, we emphasize the comparative nature of this exercise and aim to demonstrate differences and similarities between the two models that will allow future researchers to make informed decisions about appropriate model selection.

STATISTICAL ANALYSES.—Nonlinear regression techniques were used to develop allometric models to predict individual plant foliage, wood, and total aboveground biomass from dbh (cm) for *M. polymorpha* and basal diameter (mm) for *D. viscosa* in SPSS 10.0 for Windows (SPSS Inc., Chicago, IL, U.S.A.) using untransformed data and a power function of the form:

$$Y = aX^b \tag{7}$$

where *Y* = the dependent variable (*e.g.*, aboveground foliage biomass; kg dry weight for *M. polymorpha* and g dry weight for *D. viscosa*), *X* = the independent variable (dbh [cm] for *M. polymorpha* and basal diameter [mm] for *D. viscosa*), and *a* and *b* are, respectively, the scaling coefficient (or allometric constant) and scaling exponent derived from the regression fit to the empirical data.

We also explored the use of log transformed linear models for estimating biomass. While many authors note that the nonlinear power function in equation (7) is the most common mathematical model used in biomass studies (*e.g.*, Ter-Mikaelian & Korzukhin 1997, Zianis & Mencuccini 2004, Pilli *et al.* 2006), it has become conventional practice to linearize data by means of logarithmic transformation (Niklas 2006). However, Niklas (2006) argues that log transforming data does not necessarily provide a better fit of data to a regression model compared to nonlinear techniques, and that final model choice should be based on analyses of residuals. In all cases we used nonlinear models because: (1) all of the relationships we examined were nonlinear; (2) linear regression techniques using log transformed data introduce a systematic bias that must be corrected when back-transforming values (Sprugel 1983, Duan 1983); and

(3) for our data nonlinear models always resulted in better model fit than log transformed linear models based on the goodness-of-fit parameters outlined below, including analysis of residuals.

For the *M. polymorpha* dbh versus tree height curves, nonlinear regression techniques were also used with untransformed data and an exponential rise to a maximum function

$$Y = a(1 - \exp(-bX)) \qquad (8)$$

where Y = the dependent variable (tree height (m)), X = the independent variable (dbh [cm]), and a and b are, respectively, the scaling coefficient and scaling exponent derived from the regression fit to the empirical data. A variety of models are purported to provide superior fit for constructing dbh-height curves (*e.g.*, Huang *et al.* 1992, Fang & Bailey 1998), including the exponential model used here (Meyer 1940). Feng and Bailey (1998) compared 33 dbh-height models for 8352 tropical island trees and found the exponential model in equation (8) to be the best solution. Many dbh-height models are merely slight variations of equation (8) that add one or more parameters to the regression equation. We ultimately chose equation (8) for its simplicity and ease of use and because for our data it provided at least as good a fit as other commonly used models such as the Chapman-Richards and Weibull-type functions (see Huang *et al.* 1992).

Goodness of fit for all regression equations was determined by examining P-values, the mean square of the error (MSE), the coefficient of determination (R^2), the coefficient of variation (CV), and by plotting the residuals (observed minus predicted values) against dbh. R^2 was calculated as 1 minus the sum of squares of the residuals (SSR) divided by the total sum of squares of deviations from the overall mean (Corrected SST). The best-fit models were selected as having the highest R^2; the lowest P-value, MSE, and CV; and the least amount of bias for under or over prediction of biomass across the entire range of sizes.

RESULTS

Metrosideros polymorpha allometry.—Diameter at breast height was an effective predictor of all categories of aboveground live biomass in *M. polymorpha* (Fig. 1A–C), with R^2 values ranging from 0.94 to 0.96 ($P < 0.01$ for all models; Table 1). Larger diameter trees exhibited greater error variance than smaller trees (Fig. 1D–F), and such heteroscedasticity is common for biomass data (Parresol 1993). However, plots of the residuals demonstrated that there was no large or systematic bias toward over- or underestimation of biomass at any dbh within the range used to develop the models.

Size structure models (dbh vs. tree height) for the harvest trees and four sites along the precipitation gradient were all highly significant ($P < 0.01$), with R^2 values of 0.84–0.92 (Table 2). Maximum tree heights occurred at dbhs of ~30–40 cm, regardless of site. The a coefficient in each model specifies the maximum tree height for a given site (Table 2), and maximum heights were very similar for the harvest trees and the two high precipitation sites but
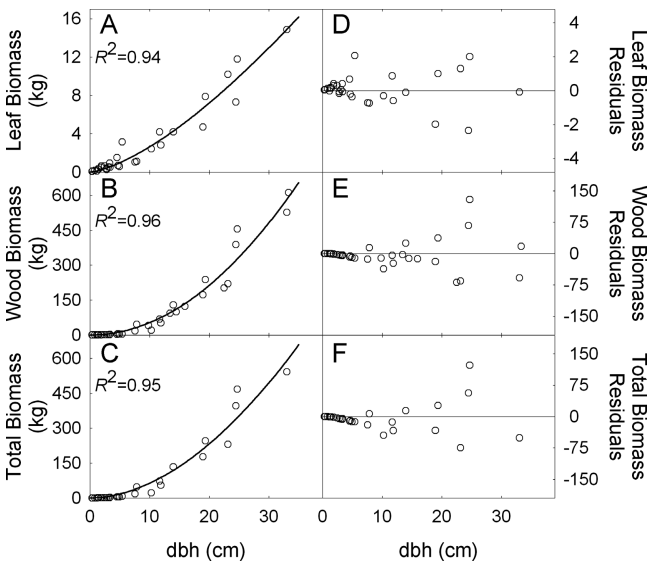

FIGURE 1. Allometric models for predicting (A) leaf, (B) wood, and (C) total aboveground tree biomass (kg) from dbh (cm) in individuals of *Metrosideros polymorpha*, and biomass residuals (D–F; observed minus predicted values). Equation parameters are given in Table 1.

were 29 and 57 percent lower at the 1730 and 1630 mm MAP sites, respectively. The dbh versus height curves revealed that there was little difference between size structures of the harvest trees and trees from the two highest precipitation sites, while size structures for the two lowest precipitation sites varied somewhat (Fig. 2). Size structure curves for all sites except the lowest precipitation area fell well within the 95% CIs for the model derived from the harvested trees.
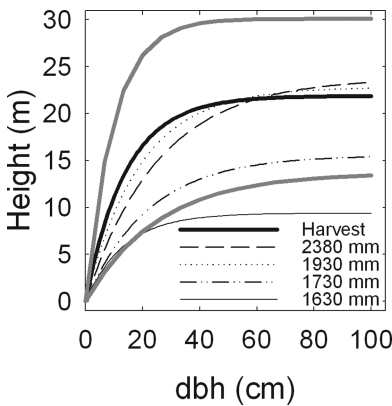

FIGURE 2. Diameter versus tree height relationships for *M. polymorpha* trees that were harvested to develop the allometric models for predicting biomass (Harvest, bold solid line), and *M. polymorpha* trees from four sites across a precipitation gradient in Hawaii Volcanoes National Park. The solid gray lines are the 95% CIs for the dbh versus height curve based on the harvested trees. Regression parameters are given in Table 2.

We found large differences in aboveground biomass estimates for individual trees when comparing the results of the allometric model developed in this study with generalized tropical tree models across a range of 5–35 cm dbh (Fig. 3A–C). All generalized models greatly underestimated biomass at smaller dbhs (< 15 cm) and tended to greatly overestimate biomass at larger dbhs (> 25 cm), with better agreement at intermediate dbhs (Table S1). No single generalized model performed well across the entire range of dbhs. The Brown (1997) model for wet climates displayed the least bias at dbhs > 25 cm (4–12%), but greatly underestimated biomass

FIGURE 4. Allometric models for predicting (A) leaf, (B) wood, and (C) total aboveground shrub biomass (g) from basal diameter (mm) in individuals of *Dodonaea viscosa*, and biomass residuals (D–F; observed minus predicted values). Equation parameters are given in Table 1.

at dbhs < 20 cm (23–71%). No generalized model was a good fit to small diameter individuals. The Chave *et al.* (2005) model for wet climates based on both dbh and tree height displayed the least amount of bias across the entire data range for estimating aboveground biomass in *M. polymorpha*.

DODONAEA VISCOSA ALLOMETRY.—Basal diameter alone was an effective predictor variable for estimating aboveground biomass in *D. viscosa* (Fig. 4A–C). Models were highly significant for all biomass categories ($P < 0.01$), with R^2 values of 0.78–0.95 (Table 1). Model fit was better for wood and total biomass than foliage biomass. However, all models showed minimal bias across the entire range of basal diameters (Fig. 4D–F).

The allometric model developed in this study for predicting total aboveground biomass in *D. viscosa* individuals differed from an existing model (Aplet *et al.* 1998) by an average of 43 percent across the entire data range (5–29 mm basal diameter). The Aplet *et al.* (1998) model consistently underestimated biomass, and underestimates were particularly large (up to 80%) at basal diameters < 18 mm (Fig. 5).
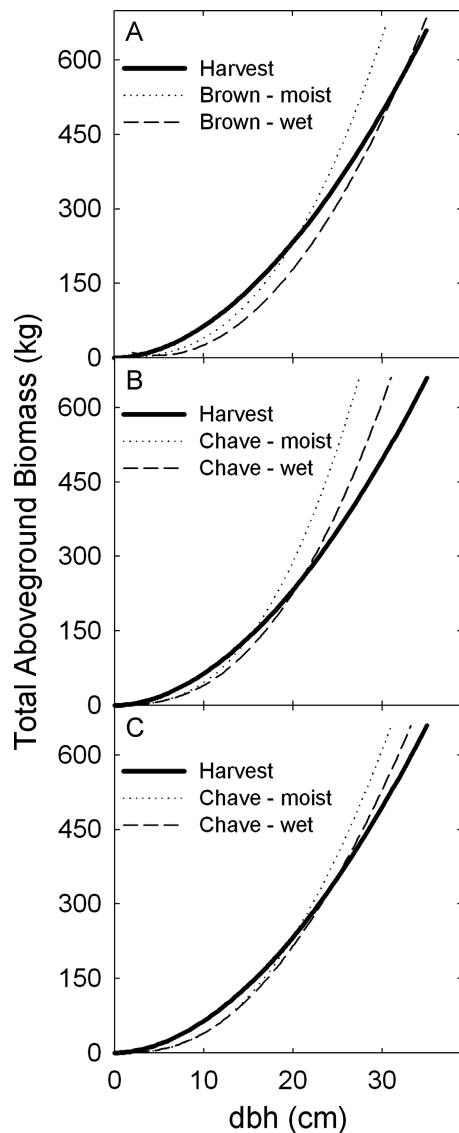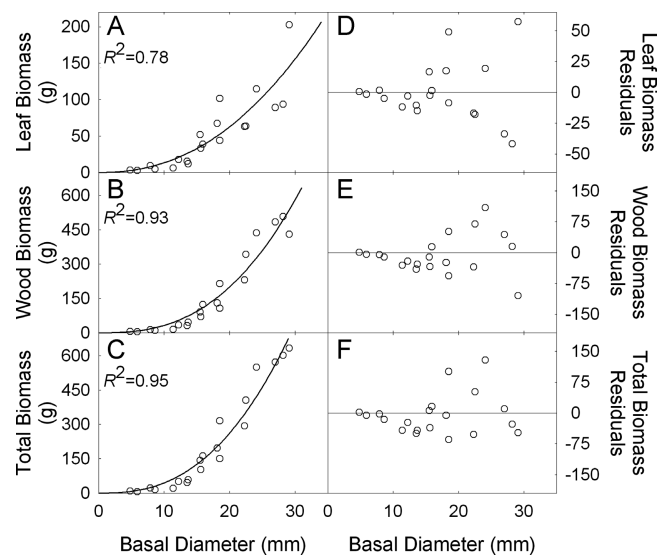

FIGURE 3. Comparison of allometric model fit for *M. polymorpha* total aboveground biomass in individual trees between that developed here (Harvest, bold line) and existing generalized equations for moist (Moist, dotted line) and wet (Wet, dashed line) tropical forests. Existing equations are from: (A) Brown (1997); (B) Chave *et al.* (2005) with dbh alone as the predictor variable; and (C) Chave *et al.* (2005) with both dbh and total tree height as predictor variables.

DISCUSSION

METROSIDEROS POLYMORPHA ALLOMETRY.—The allometric models presented here predict biomass accurately in *M. polymorpha* individuals across the range of dbhs used to develop the equations (0–33 cm; Fig. 1). Extrapolating beyond the data range used in model construction (*i.e.*, > 33 cm dbh) may cause bias in estimating biomass for larger trees, which is problematic because the largest trees at a
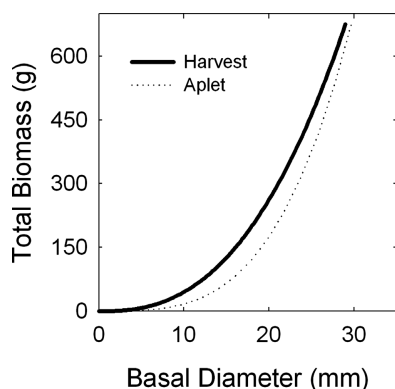
FIGURE 5. Comparison of allometric model fit for *Dodonaea viscosa* total aboveground biomass in individual shrubs between that developed here with basal diameter as the sole predictor variable (Harvest, bold line) and an existing allometric equation from Aplet *et al.* (1998), which uses both basal diameter and total shrub height (Aplet, dotted line).

given site can account for most of the biomass in the continental tropics (Brown & Lugo 1984). However, *M. polymorpha*-dominated forests in Hawaii do not contain many individuals > 33 cm dbh as is often the case in the continental tropics. In the same relatively pristine forests in Hawaii Volcanoes National Park where we quantified size structures, prior work demonstrated that *M. polymorpha* comprises 94 percent of the trees in these forests, and < 8 percent of *M. polymorpha* have dbhs exceeding 33 cm and < 1.5 percent have dbhs in excess of 50 cm (Ainsworth 2007).

The size structure analysis indicates that care should be taken in applying these models to estimate biomass across the entire climatic gradient in which this species is found (Fig. 3). In particular, the models we developed are likely to be less accurate in predicting biomass at the driest sites because of differences in size structure. The allometric models developed here appear to be adequate for predicting biomass in sites receiving > 1700 mm MAP, as size structure curves for all sites above this MAP fell well within the 95% CIs for the curve derived from the harvested trees. However, total yearly precipitation may not be useful at all sites for determining the applicability of the models, due to interactions between substrate age (*i.e.*, soil development) and precipitation in determining plant available water. We suggest that the most reliable way to determine if the models are appropriate at a given site is to sample a random set of trees to construct a size structure curve, and then compare the curve to that presented here for the harvested trees (Table 2).

Prior studies have demonstrated that a single allometric model based solely on dbh can accurately predict biomass in *Eucalyptus pilularis* across sites that vary in MAP and temperature by 55 and 35 percent, respectively, as well as tree size, wood density, and size structure (Montagu *et al.* 2005). This is particularly useful for estimating biomass and carbon sequestration across large spatial scales using forest inventory data. Thus, even though we found differences in size structure as a result of precipitation, the allometric models we developed here may be applicable at drier sites depending

on the desired accuracy or information needed. However, the degree of departure would be verifiable only by harvesting individuals from drier areas and comparing predicted versus actual biomass estimates.

The allometric models we present for predicting aboveground biomass in foliage and wood for *M. polymorpha* rely on dbh alone, while earlier models required estimates of both basal diameter and total tree height (Aplet & Vitousek 1994, Raich *et al.* 1997). The practicality of measuring only dbh makes the equations presented here more attractive and more likely to be used by both land managers and researchers. In addition, dbh measurements are typically more accurate, with measurement error for dbh at 3 percent while that for tree height is of the order of 10–15 percent (Montagu *et al.* 2005). Moreover, measuring tree height is a labor intensive and costly endeavor in closed canopy evergreen tropical forests where tree heights cannot be easily seen from within the sampled stand. Finally, most private, state, and federal forest inventories typically measure dbh for individual plots and trees, but do not commonly measure tree height.

The models presented here were based on harvested trees, precluding the need for estimates of specific wood gravity. Generalized equations for tropical trees have recently been improved by incorporating wood density information as a model parameter (Chave *et al.* 2005). These equations did not fit the *M. polymorpha* data well (Fig. 4), and earlier work has also shown that generalized allometric equations do not accurately predict biomass in Hawaiian dry forests (Litton *et al.* 2006). Our estimate of *M. polymorpha* wood density (0.69) is a mean value derived from multiple samples taken at one site (R.F. Hughes, pers. comm.), and wood density can vary across sites for a given species, as well as within a given site (Montagu *et al.* 2005). Better estimates of wood specific gravity for a particular site should, theoretically, improve the ability of generalized models to accurately predict aboveground biomass. However, wood specific gravity is a constant parameter in the equation for a given species at a given site. Therefore, unless wood density for each tree is measured, the pattern we observed (*i.e.*, generalized equations do not compare well with our species-specific model) would hold true even if more accurate wood density data were available (*i.e.*, the line would shift to the left or the right, but the shape of the line in Fig. 4C would not change).

DODONAEA VISCOSA ALLOMETRY.—Basal diameter accurately predicted aboveground biomass in the shrub *D. viscosa*. In contrast, height was not as good a predictor of biomass, either alone or in combination with basal diameter ($R^2 < 0.75$; data not shown). As before, simple measurements of diameter are not only easier to take in the field but are also more likely to exist in historical data.

Little information is available on the species-specific equations for *D. viscosa* presented in Aplet *et al.* (1998). In particular, it is unknown how many individuals were sampled, what the size distribution was for harvested individuals, or even where individuals were harvested. Despite this, their model has a very similar shape to that developed here. However, it underestimates biomass across the entire data range, and this may well be a result of differences in site characteristics and, therefore, growth form between the two areas where plants were harvested.

In conclusion, the species-specific allometric models we present for quantifying aboveground biomass in two of the most widespread woody plants in Hawaiian forests and shrublands should significantly improve capacity to accurately estimate biomass, fuel loads, and carbon sequestration in Hawaiian terrestrial ecosystems. In particular, the use of dbh as a sole predictor variable for *M. polymorpha* and basal diameter for *D. viscosa* will facilitate the use of inventory data to examine temporal and spatial variability in ecosystem structure and function. In addition, our models can be used to predict aboveground biomass in foliage and wood separately. The utility of estimating biomass by component is readily apparent for studies of carbon sequestration and fire dynamics, as foliage and wood have different residence times and fuel characteristics. However, care should be taken in applying the allometric models developed in this study to other sites within the archipelago without knowledge of size structures. We recommend that dbh versus tree height curves be constructed for the area of interest and compared to that presented in this study to determine how appropriate the allometric models are for a given site.

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SUPPLEMENTARY MATERIAL

The following supplementary material for this article is available online at: www.blackwell-synergy.com/loi/btp

Table S1. Percent difference in *Metrosideros polymorpha* predicted total aboveground biomass for individual trees between that estimated with the allometric model developed here versus that estimated with generalized models for tropical trees.

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