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Estimating aboveground biomass of broadleaved woody plants in the understory of Florida Keys pine forests

J.P. Sah[a,*], M.S. Ross[a], S. Koptur[b], J.R. Snyder[c]

[a]*Southeast Environmental Research Center, Florida International University, Miami, FL 33199, USA*
[b]*Department of Biological Sciences, Florida International University, Miami, FL 33199, USA*
[c]*US Geological Survey, Florida Integrated Science Center, Ochopee, FL 34141, USA*

Abstract

Species-specific allometric equations that provide estimates of biomass from measured plant attributes are currently unavailable for shrubs common to South Florida pine rocklands, where fire plays an important part in shaping the structure and function of ecosystems. We developed equations to estimate total aboveground biomass and fine fuel of 10 common hardwood species in the shrub layer of pine forests of the lower Florida Keys. Many equations that related biomass categories to crown area and height were significant ($p < 0.05$), but the form and variables comprising the best model varied among species. We applied the best-fit regression models to structural information from the shrub stratum in 18 plots on Big Pine Key, the most extensive pine forest in the Keys. Estimates based on species-specific equations indicated clearly that total aboveground shrub biomass and shrub fine fuel increased with time since last fire, but the relationships were non-linear. The relative proportion of biomass constituted by the major species also varied with stand age. Estimates based on mixed-species regressions differed slightly from estimates based on species-specific models, but the former could provide useful approximations in similar forests where species-specific regressions are not yet available.
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1. Introduction

Direct harvesting techniques for estimating biomass are labor intensive and time consuming. The application of allometric equations is a commonly used, non-destructive alternative in which biomass is estimated on the basis of easily measured attributes of trees (e.g., Crow, 1978; Tritton and Hombeck, 1982; Dudley and Fownes, 1992; Ter-Mikaelian and Korzukhin, 1997) or shrubs (e.g., Whittakcr and Woodwell, 1968; Peek, 1970; Ludwig et al., 1975; Brown, 1976; Harrington, 1979; Smith and Brand, 1983; Vora, 1988; Buech and Rugg, 1989; Tietema, 1993; Pereira et al., 1995). However, species-specific equations are not currently available for the rich suite of shrubs common to South Florida pine rocklands, where fire plays an important

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* Corresponding author. Tel.: +1 305 348 6066;
fax: +1 305 348 4096.
 E-mail address: sahj@fiu.edu (J.P. Sah).

part in shaping the structure and function of ecosystems (Alexander and Dickson, 1972; Wade et al., 1980).

Biomass and its distribution within forest ecosystems vary with field conditions, e.g., with time since the fire or with fire intensity. At the same time, accumulation of fuel loadings in forest stands is an important determinant of fire frequency and severity (Paatalo, 1998; Cochrane et al., 1999). Therefore, information regarding the nature and distribution of fuels in relation to time elapsed since last fire has been used to project how rapidly fires will spread, their intensity, and ultimately their ecological effects (Rothermel, 1972; Kauffman et al., 1994; Paatalo, 1998). Unlike some southeastern pine forests, where flammable fuels are concentrated on the forest floor and/or in a continuous graminoid layer (Snyder, 1991), most burnable fuels in Florida Keys stands of *Pinus elliottii* var. *densa* appear to be associated with the crowns of live shrubs. Alexander and Dickson (1972) pointed out that the rate of development of this shrub layer after fire in South Florida exhibited considerable regional variation. In order to associate shrub fuel loads with different stages in post-fire stand development, we developed species-specific equations for estimating aboveground biomass at two levels: (1) total shrub biomass, which included plant parts of all sizes; and (2) shrub fine fuels, which included the biomass of leaves, reproductive parts, and stems <6.3 mm diameter.

Our primary intent was to establish dimensional relationships between two easily measured plant properties, crown area and height, and the total and fine fuel biomass for the major understory shrubs, which included a wide range of morphological types. We also wished to develop general allometric equations for all species together, and to assess the variability of stand-level estimates arrived at via generalized, mixed-species equations relative to species-specific regressions. Finally, we examined the dynamics of shrub biomass accumulation after fire.

2. Materials and methods

2.1. Study area

The study area is located in pine rocklands in the National Key Deer Wildlife Refuge (NKDWR) in the lower Florida Keys. Pine rocklands are characterized by a canopy of South Florida slash pine (*Pinus elliottii* var. *densa*), a very diverse shrub layer dominated by West Indian tropical hardwoods and a few species of palms, and a diversity of endemic herbs. Pine rocklands within the NKDWR are small but biologically important ecosystems that include habitat critical to the survival of the endangered Key Deer (*Odocoileus virginianus clavium*). Less than 1000 ha of lower Keys pinelands remain today, scattered over seven islands, among which the largest is Big Pine Key. In the NKDWR, prescribed burning has been applied sporadically since its creation in 1957 (Bergh and Wisby, 1996), resulting in a forest mosaic of varied structure developed since last fire.

On the basis of aerial photography and ground reconnaissance, six blocks of homogeneous pine forest of at least 4 ha were identified on Big Pine Key. Within each block, we established three plots of 1 ha each, separated by buffer strips of ≥20 m width. Altogether, 18 plots were distributed among six blocks, i.e., Buttonwood, Dogwood, Iris, Locustberry, Orchid and Poisonwood, named for plant species that characterized each area. Five of the blocks were last burned between 1985 and 1991, and a sixth had not burned in more than 30 years. Though it appeared structurally homogeneous, the Iris block was comprised of two sections whose most recent burn differed by 6 years (Table 1).

2.2. Sampling procedure

We developed allometric equations for biomass estimation of 10 species, representing nine families (Table 2). As a group, these taxa comprised more than

Table 1
Study sites with sampling years and time since last fire

Site	Site-code	Number of 1 ha plots	Year of sampling	Time since last fire (years)
Buttonwood	Bw	3	2000	>30
Dogwood	Dw	3	1999	11
Iris	Ir	2	1999	8
		1	1999	14
Locustberry	Lb	3	2000	14
Orchid	Or	3	1998	8
Poisonwood	Pw	3	1998	12

Table 2
Species, number of individuals, and range of plant dimensions in regression data sets

Species	Family	N	DBH (cm)	Crown area (m^2)	Height (m)
B. lucida	Malpighiaceae	8		0.52–5.72	1.1–1.6
C. erectus	Combretaceae	12		0.44–2.69	1.0–3.5
C. linearis	Euphorbiaceae	10		0.06–2.69	1.0–1.7
G. scabra	Rubiaceae	13		0.02–4.33	1.1–4.9
M. cerifera	Myricaceae	15		0.16–3.77	1.1–3.4
P. rotundata	Nyctaginaceae	12		0.27–2.83	1.1–2.4
P. guadalupense	Fabaceae	12		0.13–10.45	1.1–3.7
P. longipes	Myrtaceae	12		0.92–5.94	0.7–5.5
R. aculeata	Rubiaceae	12		0.02–3.11	1.1–2.5
M. floridana	Myrsinaceae	19	0.40–2.61	–	1.0–3.4

70% of the total vegetative cover in the shrub layer in pine forests on Big Pine Key (Ross et al. unpublished data), and a wide range of morphological forms. In the shrub layer of Florida Keys pine forests, two other important groups of plants are palms and pine saplings, which will be described in subsequent papers. Eight to nineteen individuals of each species were collected to represent the range of sizes common in the pine forest understory on Big Pine Key (Table 2). For nine species characterized by a shrub-like (multi-stemmed or low-branching) growth form, we measured the height of each individual, as well as the extent of the canopy along its widest dimension and perpendicular to it before harvesting. For *Myrsine floridana*, which had a tree-like (single-trunked) form, we measured diameter at breast height (DBH) instead of crown dimensions. After clipping each stem at the ground surface, the harvested material was separated, and weighed after oven drying at 65 °C to constant weight. Three biomass categories were recognized: necromass (dead plant materials – standing and attached), small live biomass (leaves, reproductive parts, and twigs <6.3 mm in diameter), and large live biomass (twigs ≥6.3 mm in diameter). From these data, equations were developed for total aboveground shrub biomass (sum of all three components) and shrub fine fuels (sum of dead and small live material).

The regression equations were subsequently applied to structural information collected in 1998–2000 from the shrub stratum (plants >1 m height and <5 cm dbh) of the 18 pine forest plots described above (Table 1). Within each plot, plant dimensions of each shrub/tree sapling rooted within 20 circular, 4 m radius sub-plots were measured. We measured height and two crown widths (the longest, and its perpendicular) for shrub-like plants, and height and DBH for tree-like plants.

2.3. Statistical analysis

Raw data were initially graphed to provide a visual assessment of the relationships between biomass and the independent variables. Least-square regression models were then developed for individual variables using several curve forms, including simple linear, second-order polynomial, and logarithmic models. The independent variables used were crown area in square meters (CA) and plant height in meters (HT). Assuming an elliptical crown shape (Peek, 1970), crown area was calculated as $CA = \pi(C_L/2)(C_W/2)$, where C_L is the crown length at its widest point and C_W the perpendicular crown extent at the same height.

To analyze relationships of biomass with multiple independent variables (i.e., CA or DBH and HT), a forward stepwise function was used and regression models were tested for significance on the basis of a "t" statistic ($p < 0.05$). The log transformation of the variables was chosen according to criteria described by Neter et al. (1983). Logarithmic models developed as $\ln(y) = \ln(a) + b \ln(x)$ were back-transformed to a power function ($y = ax^b$) form for estimation of biomass, and the anti-log of the intercept was multiplied by a correction factor in order to account for bias inherent in fitting the model to the geometric mean rather than the arithmetic mean (Baskerville, 1972; Sprugel, 1983). The correction factor (CF) was calculated as follows (Sprugel, 1983):

$$CF = exp(S_{y,x}^2/2),$$

where $S_{y,x}$ is the standard error of the estimate (S.E.E) of the regression.

For each model tested, normal probability plots of residuals, and plots of standard residuals versus predicted values were examined to test compliance with the assumptions of least-squares regression. In addition, plots of standardized residuals against fitted values of independent variables were used to test assumptions related to homogeneity of variance. The least squares solution to a regression problem is sensitive to outliers (Draper and Smith, 1998). If outliers were detected in any species in the present study, analysis was done after deleting those observations to test if there was a significant change of the coefficients.

In choosing among the various regression models, we generally selected the one with the highest R^2 and the lowest standard error of estimate (S.E.E) with significant fit ($p < 0.05$). However, R^2 statistics may not be directly compared among equations with untransformed and log-transformed independent variables (Draper and Smith, 1998; Crow and Schlaegel, 1988). To compare such equations, we calculated a Fit Index (FI), which like R^2 has a value of unity for an optimum fit (Schlaegel, 1981). FI is based on residuals in measured units (Brand and Smith, 1985; Crow and Schlaegel, 1988), according to the following equation:

$$FI = 1 - \frac{(S(Y_i - \hat{Y}_i)^2}{\Sigma(Y_i - \bar{Y})^2},$$

where Y_i is the ith observed value, $\hat{Y}_i$ is the ith predicted value for Y_i, and $\bar{Y}$ is the mean observed value of Y_i. If the Fit Index calculated for a logarithmic model was close to the R^2 for a linear model, the former was preferred, as the logarithmic transformation increases the statistical validity of the analysis by homogenizing the variance over the range of the sample data, and is suitable for data in which variance increases with an increase in the magnitude of the observation.

Best-fit species-specific and mixed-species equations were applied to the dimensional data. Mixed-species equations were developed separately for prediction of total and fine fuel biomass in shrub- and tree-like plants. The models for the former were based on individuals of the nine species for which specific models were developed using crown area and/or height as predictors. Mixed-species models for tree-like plants were based on the *M. floridana* data, augmented by a few individuals of *Eugenia axillaris*, another sapling found in pine rocklands. We used one-way ANOVA to assess differences among the six blocks in total and fine fuel biomass calculated on a species-specific basis. In deriving species-specific estimates of plot biomass, mixed-species equations were used for uncommon species for which individual regressions were not developed. Plot estimates derived from species-specific and mixed-species equations were compared by applying a paired '*t*'-test to data from all 18 plots.

3. Results and discussion

3.1. Model development

Most of the species-specific regression equations relating biomass with measured plant dimensions were statistically significant ($p < 0.05$). The best-fit model forms, however, were not the same for all species (Table 3). Among species-specific best-fit models, R^2-values varied from 0.680 for fine fuel biomass in *Psidium longipes* to 0.996 for total shrub biomass in *Pithecellobium guadalupense*, R^2-values for mixed-species best-fit models varied from 0.574 to 0.868 (Table 3). R^2-values produced by the best-fit models in this study were within the range reported by others for shrub biomass-structural relationships (Brown, 1976; Ohmann et al., 1981; Smith and Brand, 1983; Vora, 1988; Halpern et al., 1996; Uso et al., 1997). However, Fit index (FI) equation statistics, which are calculated based on predictions in measured units, were not always lower than R^2, as is normally observed for logarithmic models.

In three species, *Byrsonima lucida*, *Croton linearis* and *P. guadalupense*, a second order polynomial equation with crown area as the sole independent variable yielded the highest R^2-values ($R^2 > 0.96$) for both total aboveground shrub biomass and fine fuel (Table 3). In these species, the positive coefficients of the quadratic term indicate that the rate of increase of aboveground biomass with canopy area increases with canopy size over the range of sizes present in the study area (Table 3). Ludwig et al. (1975) also concluded

Table 3
Species-specific and mixed-species best-fit regression equations

Species	Regression equations	Fuel type	ln a	a or a'	b	c	CF	P-value	R^2	FI	S.E.E
B. lucida	$B = a + b(CA) + c(CA^2)$	T		0.310	0.672	0.035		<0.001	0.97	0.97	0.297
		F		0.280	0.272	0.036		<0.001	0.97	0.97	0.175
C. erectus	$B = a'CA^b HT^c$	T	−1.20	0.323	0.360	1.824	1.07	<0.001	0.86	0.77	0.816
		F	−1.83	0.169	0.246	1.512	1.06	<0.001	0.82	0.79	0.195
C. linearis	$B = a + b(CA) + c(CA^2)$	T		0.077	−0.086	0.175		<0.001	0.99	0.99	0.045
		F		0.057	−0.049	0.111		<0.001	0.99	0.99	0.034
G. scabra	$B = a'CA^b HT^c$	T	−2.20	0.119	0.419	2.159	1.08	<0.001	0.96	0.94	0.417
		F	−3.30	0.041	0.332	1.788	1.12	<0.001	0.90	0.92	0.089
M. cerifera	$B = a'CA^b HT^c$	T	−1.16	0.341	0.977	1.363	1.09	<0.001	0.93	0.80	0.701
		F	−1.29	0.306	1.028	0.649	1.12	<0.001	0.89	0.74	0.354
M. floridana	$B = a + b(DBH)^2 + c(HT)$	T		−0.258	0.124	0.003		<0.001	0.86	0.86	0.167
	$B = a + b(DBH) + c(HT)$	F		−0.043	0.179	0.000		<0.001	0.84	0.84	0.062
P. rotundata	$B = a'CA^b HT^c$	T	−1.03	0.379	0.510	0.983	1.06	0.001	0.79	0.90	0.127
		F	−1.86	0.159	0.616	0.813	1.03	<0.001	0.90	0.88	0.061
P. guadalupense	$B = a + b(CA) + c(CA^2)$	T		0.373	0.258	0.182		<0.001	0.99	0.99	0.446
		F		0.148	0.142	0.043		<0.001	0.99	0.99	0.158
P. longipes	$B = a'CA^b HT^c$	T	−0.54	0.672	0.956	0.872	1.16	0.002	0.76	0.67	1.591
		F	−1.46	0.270	0.995	0.503	1.16	0.006	0.68	0.64	0.505
R. aculeata	$B = a'CA^b HT^c$	T	−4.32	0.017	0.121	3.222	1.25	0.004	0.79	0.70	0.117
		F	−3.95	0.022	0.138	1.980	1.12	0.005	0.78	0.79	0.032
Mixed-species (shrub-like)	$B = a'CA^b HT^c$	T	−0.95	0.446	0.869	1.112	1.15	<0.001	0.87	0.72	0.911
		F	−1.48	0.269	0.855	0.609	1.18	<0.001	0.82	0.58	0.387
Mixed-species (tree-like)	$B = a + b(DBH)^2 + c(HT)$	T		−0.060	0.227	0.002		<0.001	0.57	0.57	0.437
	$B = a + b(DBH) + c(HT)$	F		−0.184	0.067	0.002		<0.001	0.58	0.58	0.136

that relationships for canopy area usually tended to be curvilinear and were best represented by quadratic models.

In six species, *Conocarpus erectus*, *Guettarda scabra*, *Myrica cerifera*, *Pisonia rotundata*, *P. longipes* and *Randia aculeata*, logarithmic models that included crown area and height as the predictors provided the best fit for both total biomass and fine fuel, based on high values of R^2 and low standard error. The good fit of the logarithmic model in these species is not surprising, as this model has previously been shown to predict aboveground biomass accurately in a variety of woody plant species (Brown, 1976; Smith and Brand, 1983; Freedman, 1984; Buech and Rugg, 1989; Paton et al., 1998). However, the logarithmic model generally gives under-predictions, and thus a correction factor (Sprugel, 1983) to be applied in the back-transformation is given for each of the models (a' in Table 3).

A linear model with dbh and height as predictors provided the best fit for the biomass of *M. floridana*. However, the best-fit models for *M. floridana* were not the same for total biomass and fine fuel. For total

biomass, a linear model with dbh-squared and height yielded the highest FI, whereas for fine fuel, the linear combination of dbh and height yielded highest FI (Table 3).

In general, species-specific models provide more accurate estimates of biomass than mixed-species models, especially for biomass components such as leaves and twigs, which turn over rapidly (Buech and Rugg, 1989). However, in order to estimate biomass for a species for which no regression model has been developed, one may select a model developed for a species of similar physical characteristics, or a mixed-species regression from an appropriate group (Brown, 1976; Crow, 1978; Tietema, 1993; Overman et al., 1994; Nelson et al., 1999). In this study, mixed-species regression models were developed for two different groups of plants, shrub- and tree-like species. For shrub-like plants, log-transformed models including as predictors both crown area and height were selected, because the logarithmic model had proven best for six species out of nine, and its R^2-values were also the highest ($R^2 > 0.8$) among all models. For tree-like plants, linear mixed-species models with dbh and

height as predictors were the best, and they had the lowest standard error of estimate.

Stem basal diameter, crown area, and/or height are typically used as independent variables in shrub biomass regressions. For some shrub species, stem diameter is the best predictor of biomass (Whittakcr and Woodwell, 1968; Martin et al., 1981; Alaback, 1986; Haase and Haase, 1995; Paton et al., 1998), but plot-based estimates of percentage cover or individual crown area have been used in several studies (Peek, 1970; Ludwig et al., 1975; Martin et al., 1981; Ohmann et al., 1981; Halpern et al., 1996), especially in low-growing shrubs whose multiple-stemmed growth form is not amenable to the measurement of individual shoot diameters. In multi-stemmed shrubs of small stature, Harrington (1979) found that the weakest relationships and highest errors of the estimate were obtained when basal diameter was used as the independent variable. In the Rocky Mountains, Brown (1976) used basal diameter class to develop equations for estimating shrub biomass, but he suggested that for species with numerous stems, percentage cover and height should be used as independent variables. In this study, we found that crown area could be used alone to predict total biomass and fine fuel in multi-stemmed shrub species with an acceptable level of accuracy and precision. However, the addition of height increased the level of precision in about 2/3 of the shrub species considered in our study.

The inclusion of height in biomass regression is less common for shrubs (Peek, 1970; Harrington, 1979; Murray and Jacobson, 1982; Halpern et al., 1996) than for trees (Overman et al., 1994; Nelson et al., 1999), probably because stem tissue usually constitutes a greater proportion of total biomass in the latter. The addition of height in the models developed for shrubs was reasonable because crown area-only models explain variation associated with lateral branching effectively, but not variation associated with extension growth (Halpern et al., 1996). Furthermore, height takes on added significance in accounting for variation in aboveground biomass in sites where shrub stems often respond by elongating rapidly after disturbances, such as cutting or fire (Martin et al., 1981). In Florida Keys pine forests, understories are chronically recovering from fire, and therefore height proved to be an important variable in

the predictive models developed for the majority of species in this study. Regression equations with multiple variables are also less sensitive to variations in plant form associated with site age (Alaback, 1987; Halpern et al., 1996). Study sites in our study also differed in time since last fire (Table 1), and thus models with crown area and height as predictors were reliable for most species. However, in species that are prostrate and stoloniferous, with little variation in height, biomass is usually well predicted by cover (Halpern et al., 1996). In shrub dimensional surveys, of the three species in which crown area-only models had the highest R^2-values, *B. lucida* and *C. linearis* exhibited the least variation in height among the 10 study species (Ross et al. unpublished data).

3.2. Application of the models

Significant among-block differences were detected in total aboveground shrub biomass ($p < 0.001$) and fine fuels ($p < 0.001$), estimated by applying species-specific models to the shrub dimensional data sets from the 18 plots. Total aboveground shrub biomass varied from 0.83 to 6.98 Mg/ha, and shrub fine fuel from 0.34 to 2.60 Mg/ha (Fig. 1A and B). In a fire-adapted community, biomass may vary among stands due to stage of succession (Brown, 1976), stand age and time since last fire (Van Wilgen, 1982; Saldarriaga et al., 1988; Wirth et al., 1999). In general, plant biomass increases with time after burning to some extent, and then becomes constant (McCaw et al., 2002). In this study, the average total shrub biomass leveled off at about 5.5 Mg/ha 12 years after burning, beyond which little increase was observed. However, our data also make clear that time since fire is not the sole determinant of shrub biomass accumulation. For instance, shrub biomass was similar in two sections of the Iris block burned 6 years apart. Shrub biomass in three plots in the Locustberry block, burned 14 years prior to our sample, was also much lower than in the more recently burned plots in Dogwood and Poisonwood blocks. Besides time since fire, factors such as soil and drainage characteristics, stage of succession, stand history, etc. also may have contributed to among-plot differences in shrub biomass. For instance, the Locustberry block is characterized by sparse vegetation associated with a large area of exposed ground, low density of pine seedlings and
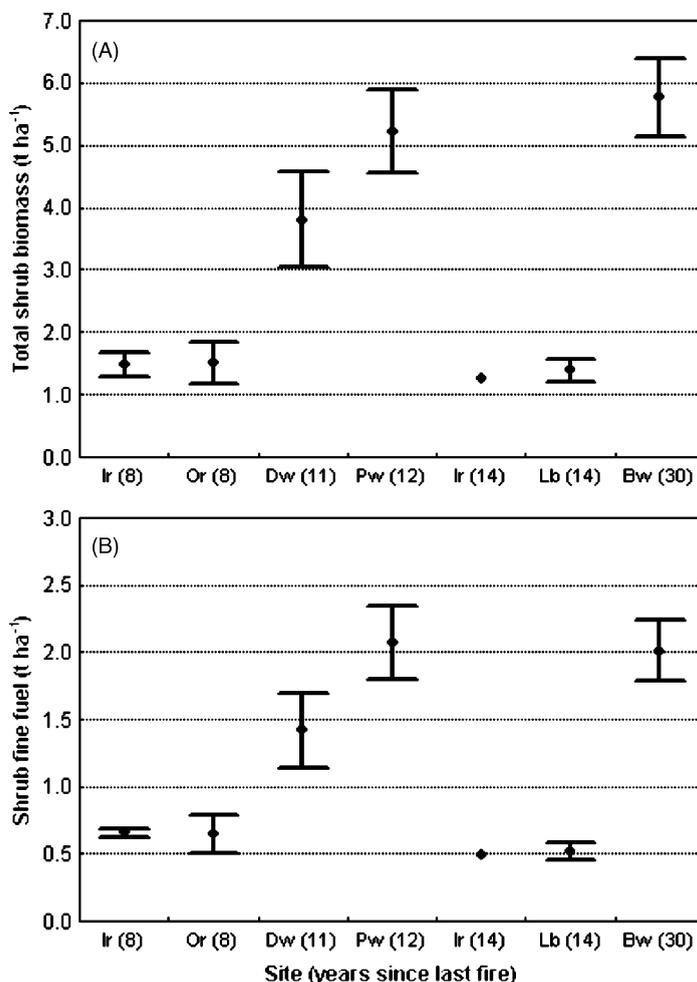
Fig. 1. Mean (±S.E.) of: (A) total biomass, and (B) fine fuel, calculated by applying best-fit regression equations to shrub dimensional data from 18 pine forest plots distributed in six blocks that differed in time since last fire. Block codes are as in Table 1.

saplings, and absence of hammock species in the sub-canopy even after 14 years of fire (Rocca, 1997). These indications of low productivity resulted in a low rate of biomass accumulation after fire, probably due to poor soil development (Ross et al., 2003). In contrast, the most recently burned plot in the Iris block is relatively wet, which may lead to faster vegetation recovery in the moisture-limited environment of these pine forests.

The relative proportion of biomass constituted by the major species varied with stand age. In particular, the biomass of *B. lucida*, one of the dominant woody plants in Florida Keys' understories, decreased with

time since fire, probably in response to changes in canopy structure (Fig. 2A and B). The abundance of species like *B. lucida*, which grow luxuriantly under open canopy conditions characteristic of recently burned plots, may decline in dense plots not burned for many years (Alexander and Dickson, 1970, 1972; Carlson et al., 1993; McCaw et al., 2002). Furthermore, variability in *B. lucida*'s growth form may also have contributed to its decrease in biomass with time since fire. Plants growing under dense canopy in an area that has not been cut or burned for a long period of time are often taller, with smaller crowns and fewer twigs than in recently burned open areas (Vora, 1988).
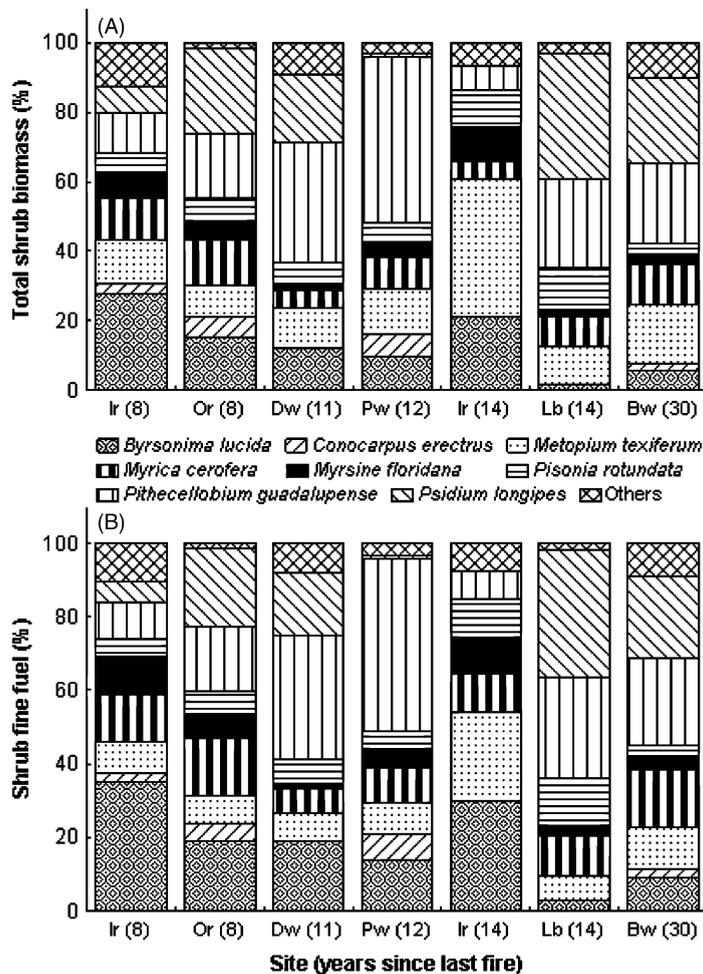
Fig. 2. Proportion of: (A) total shrub biomass, and (B) shrub fine fuel, constituted by nine major species and others in six blocks in Big Pine Key pine forests. Blocks differed in time since last fire. The Iris block comprised of two sections burned 6 years apart. Block codes are as in Table 1.

Mixed-species regression models yielded mean stand estimates 10.9% lower than estimates based on species-specific models for both total shrub biomass and shrub fine fuel (pair wise *t*-test; $p = 0.0002$ and 0.0003, respectively; Fig. 3A and B). The reason for this underestimate is unknown, but could involve the heterogeneity in the ages of plants used to calculate the generalized plant dimension-biomass equation. However, the difference in estimated biomass from the two sets of equations is not very high, and is in the lower end of the range (10–30%) obtained in other studies that compared species-specific and mixed-species regressions (Pastor et al., 1984). Therefore,

use of mixed-species models may be valuable, especially when the resources needed to develop species-specific equations are not available.

This work resulted in the development of species-specific and mixed-species allometric equations to estimate biomass for broadleaved woody plants in the shrub stratum of Florida Keys pine forests. One should be cautious in the use of these allometric equations, especially in extrapolating beyond the range of the regression data, and in their application in environments greatly different from those found in at the Florida Keys. We believe, however, that the equations developed in this study will be useful in estimating
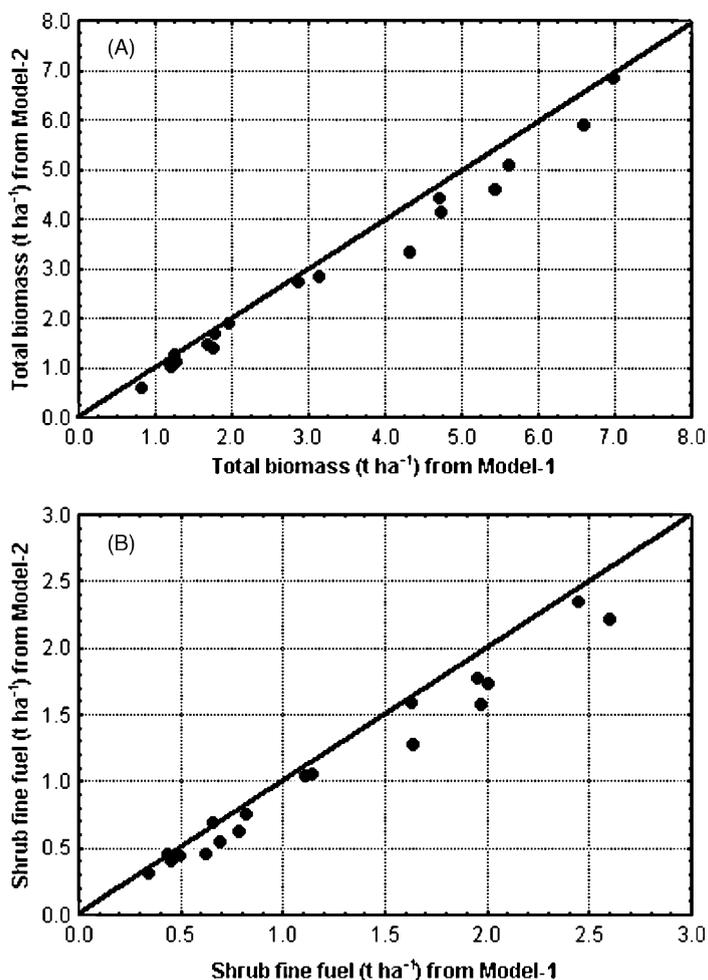
Fig. 3. (A) Total shrub biomass, and (B) shrub fine fuel, predicted from species-specific (Model-1) and mixed-species (Model-2) regression models developed for 10 shrub species and applied to shrub dimensional data from 18 plots in the Florida Keys pine forest. The line in the graph represents the 1:1 relation between the two regression models.

shrub biomass in pine forests elsewhere in the Caribbean basin, and in other dry tropical environments.

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