

Allometric estimation of total leaf area in the neotropical palm *Euterpe oleracea* at La Selva, Costa Rica

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Abstract We estimated the magnitude of the total leaf area of the neotropical palm *Euterpe oleracea* and examined its allometry relative to the variation in stem height and diameter at La Selva Biological Station in Costa Rica. The allometric relationships between frond leaf area and frond length (from tip to base), and between frond leaf area and number of leaflets, were determined by natural logarithmic regressions to estimate the total area of each frond. Palm total leaf area was then estimated by adding the area of the composing fronds. We fit 14 separate regression models that related one or more of the morphological variables (number of fronds, diameter at breast height, stem height) to the total leaf area. Our results show that palm total leaf area is directly proportional to the number of fronds and palm size as reflected in stem height and diameter. Eight out of the 14 models had r^2 values of >0.90 and incorporated a diverse combination of predictor variables. Simple linear regression models were more congruent with the observed values of total leaf area, whereas natural logarithmic models overestimated the value of total leaf area for large palms. Both approaches show a high degree of association among morphological characters in *E. oleracea* supporting the hypothesis that palms behave like unitary organisms, and are morphologically constrained by the lack of secondary meristems. To afford

attaining canopy heights, woody palms need to show a high degree of phenotypic integration, shaping their growth and allometric relationships to match spatial and temporal changes in resources.

Keywords Total leaf area · Palm allometry · *Euterpe oleracea*

Introduction

The performance of an organism, and its growth and competitive ability, are reflected in the functional expression of its physical construction (Arnold 1983). Morphology influences the capacity to acquire resources due to the tight coupling between structure and function (Valladares and Niinemets 2007). Plants, for the most part, occupy a fixed point in space and their architecture and allometry reflect the effect of natural selection acting upon the optimality of changing form and function to benefit from current resource levels (Kohyama 1987; King 1990). Furthermore, architecture and allometry are subject to morphological plasticity in the face of temporal resource change (Kohyama 1987; King 1990). The study of the allometry of biomass allocation to specific modules, such as leaves, and leaf architectural display, is critical to understand current performance (i.e., light interception and its impact on photosynthetic capacity), and to determine how physical limits on morphology influence plant evolutionary diversification (West-Eberhard 2003).

Since leaf level characters integrate most selective pressures acting on plants across biomes (Meinzer 2003; Reich et al. 1997; Wright et al. 2004), the estimation of total leaf area in arborescent species has important implications on life history strategies, and would help to refine

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models that approximate carbon sequestration in tropical ecosystems. The analysis of allometric relationships that estimate the magnitude of total leaf area becomes especially important when attempting to estimate the carbon sequestration capacity of tropical species (i.e., Drake et al. 2002; Chapin 2003). Estimates of biomass and carbon sequestration in tropical forests are biased towards the most common life forms (usually trees) and the most abundant species (Chambers et al. 2004). Despite their overall abundance and importance in forest structure and function (palms represent 44.3% of stems ≥ 10 cm DBH at Los Tuxtlas in Mexico and 25.5% at La Selva Biological Station in Costa Rica; Lieberman et al. 1985, 1996; Martínez-Ramos 1997), palms are not usually considered in these efforts (i.e., Chave et al. 2003, 2005).

Total leaf area can be determined by direct or indirect methods. Direct methods impose significant logistical limitations for large woody plants, such as canopy trees and palms, which usually requires harvesting of all leaves. Consequently, there is a paucity of information using direct measurements of total leaf area in arborescent palms. Palms are bulky organisms that do not easily lend themselves to routine evaluation of their total leaf area. Indirect methods have been developed to estimate total leaf area for a few economically important palms, for example *Cocos nucifera* (De Sousa et al. 2005) and *Metroxylon sagu* (Nakamura et al. 2005). The efficiency of leaf area display has been determined for a few understory palms (i.e., Alvarez-Clare and Avalos 2007; Chazdon 1985), but little is known about total leaf area in rainforest canopy palms.

In this study, we estimated the total leaf area of the neotropical canopy palm *Euterpe oleracea* and examined its allometry relative to stem diameter and height. *E. oleracea* is harvested throughout its latitudinal range for its nutrient rich heart of palm and its *acai* fruit production. This species is one of the most important sources of heart of palm with a reputation as an exotic or gourmet product which is associated with a high market value (Muñiz-Merit et al. 1996; Pollak et al. 1995). Specifically, *E. oleracea* fruit has been substantially investigated due to findings reporting antioxidant capacity of palm seeds (Rodrigues et al. 2006) and pulp (Lichenthaler et al. 2005). This demonstrates the multiple human uses associated with this palm, and an additional need to improve our understanding of its growth within agroforestry systems.

Despite *E. oleracea*'s importance on the international palm heart market (Pollak et al. 1995) the allometric relationships of total leaf area and its scaling with other morphological variables have not been fully explored (but see Cole and Ewel 2006). Furthermore, little has been studied in terms of total leaf area of other palms in the *Euterpe* clade (*Euterpe*, *Hyospathe*, *Neonicholsonia*, *Oenocarpus*, and *Prestoea*, Henderson 2002). Variation in

growth and size of plants affects the expression of other traits such as reproductive allocation, and thus allometry can be useful in exploring these ecological and evolutionary relationships (Niklas and Spatz 2006; Preston and Ackerly 2004). The objective of this research is to present a suite of empirical models to estimate the total leaf area of *E. oleracea* across a wide range of size categories through the incorporation of variables that are easily measured in the field and that can be applied to other species within the *Euterpe* clade.

Methods

Study site

This study was conducted in 2006 at the La Selva Biological Station in the NE Caribbean lowlands of Costa Rica (1,600 Ha, 10°25'N, 84°00'W, 30–150 m). The area is weakly seasonal, with a mean annual precipitation of 3,962 mm and at least 100 mm of rain per month (Sanford et al. 1994). Our study area was located in 1 Ha experimental plot consisting of various cultivated tree species (*Cedrela odorata*, *Cordia alliodora*, and *Hyeronima alchorneoides*), including the introduced species *E. oleracea*.

Study species

The neotropical palm *E. oleracea* Mart. (Arecaceae) is found in lowland wet areas on the Pacific coastal regions of Colombia and Ecuador, and on coastal regions of Venezuela, Trinidad, the Guyanas and Brazil (Grayum 2003). *E. oleracea* is a monoecious palm capable of clonal reproduction. It is an important palm throughout its range for the production of heart of palm and fruits, and is the focus of studies on sustainable harvesting (Muñiz-Merit et al. 1996; Weinstein and Moegenburg 2004). La Selva introduced *E. oleracea* as part of the agroforestry trials started at this site in the early 1990s. *E. oleracea* palms in our study plot were destined to be removed because of growing concerns that this species would become invasive. Our study was carried out in 2006 before these palms were eliminated.

Leaf area calculation

Twelve stems in the experimental plot were selected to represent palms across a wide range of size classes, from juveniles to adults, and then subsequently harvested. The selected palms ranged in height from 0.48 to 16.81 m. The following variables were measured in all harvested stems: diameter at breast height (DBH), stem height from the top of the cone of stilt roots to the base of the fronds (H),

number of fronds (NF) and their respective lengths (FL, from the base to the tip of the frond), and number of leaflets (NL) within each frond. For palms smaller than 1.3 m, DBH was measured at 1/3 of the stem length. One or two fronds were randomly selected from each individual palm in order to obtain the frond leaf area (FA in m²). The fronds were cleaned with a dry cloth, and the area of all leaflets was subsequently determined using a Li-Cor LI-3100C leaf area meter (Li-Cor, Lincoln, Nebraska). The allometric relationships between FA and FL, and between FA and NL were determined by natural logarithmic regression to produce the following relationships [the value in parenthesis corresponds to the correction factor recommended by Sprugel (1983)]:

$$FA = 0.26 \times FL^{1.60} \times (1.09), (r^2 = 0.888, p < 0.0001, n = 18) \quad (1)$$

$$FA = 5.61 \times 10^{-6} \times NL^{2.7} \times (1.09), (r^2 = 0.944, p < 0.0001, n = 18) \quad (2)$$

$$FA = 4.1 \times 10^{-9} \times FL^{-1.13} \times NL^{4.51} \times (1.08), (r^2 = 0.954, p < 0.0001, n = 18) \quad (3)$$

We selected Eq. 2 to estimate FA since it was the most parsimonious model. Total leaf area per palm (TLA) was estimated by adding up the FA of every frond after applying the correction factor suggested by Sprugel (1983) and de-transforming the logarithmic regression equation

back into linear space. After determining TLA, we examined its scaling with respect to other morphological variables (NF, DBH, H). This was accomplished by fitting 14 separate regression models that related one or more of the morphological variables to TLA (both linear as well as natural log-transformed models). All data analyses were done using JMP 7.0 Statistical Software, and data were inspected for normality and equality of variances before running statistical analyses.

Results

Ordinary linear regression models gave in general higher r^2 values relative to those of natural logarithmic models (Table 1). Models that included NF approached r^2 values equal or higher than 0.94. A similar pattern was observed for the natural logarithmic models, for which models that only included DBH and H had r^2 values lower than models including NF (which were always higher than 0.90). The correction factor for natural logarithmic models containing only DBH and H were also higher relative to the correction factors of models including NF, indicating a stronger difference between observed and predicted TLA values. The root mean square error values tended to increase in models without the NF factor. It is clear that NF was the leading variable that best predicts TLA in this palm species,

Table 1 Summary of the regression models calculated to determine total leaf area per palm (TLA) in 12 *E. oleracea* palms at La Selva Biological Station, Costa Rica

Model	Variable		RMSE	r^2
Linear models				
1	DBH	0.058 + 1.44 DBH	3.109	0.844
2	H	2.938 + 1.176 H	3.134	0.842
3	NF	-6.142 + 2.199 NF	1.922	0.940
4	DBH × H	1.293 + 0.768 DBH + 0.566 H	3.157	0.856
5	DBH × NF	-5.476 + 0.229 DBH + 1.891 NF	1.973	0.944
6	H × NF	-4.350 + 1.689 H + 0.322 NF	1.798	0.953
7	DBH × H × NF	-4.149-0.586 DBH + 0.664 H + 1.933 NF	1.787	0.958
Natural Logarithmic models				
8	DBH	0.199 × DBH ^{1.861} × (2.28)	3.611	0.652
9	H	0.809 × H ^{1.393} × (1.51)	2.481	0.826
10	NF	0.006 × NF ^{3.492} × (1.26)	1.979	0.953
11	DBH × H	1.950 × DBH ^{-0.975} × H ^{2.005} × (1.50)	2.459	0.846
12	DBH × NF	0.003 × DBH ^{4.352} × NF ^{-0.60} × (1.25)	1.958	0.914
13	H × NF	0.003 × H ^{-0.144} × NF ^{3.827} × (1.29)	2.048	0.902
14	DBH × H × NF	0.009 × DBH ^{-0.85} × H ^{0.435} × NF ^{3.71} × (1.28)	2.011	0.917

TLA is in m², DBH is in cm, and Height (H) is in m

In parenthesis, the correction factor recommended by Sprugel (1983) for the natural logarithmic models

NF number of fronds, RMSE Root Mean Square Error of the regression model (detransformed back into linear space for the natural logarithmic models)

Fig. 1 Relationship between number total leaf area in m^2 (TLA), number of fronds (NF), height (H in m) and DBH in cm in *E. oleracea* at La Selva Biological Station, Costa Rica

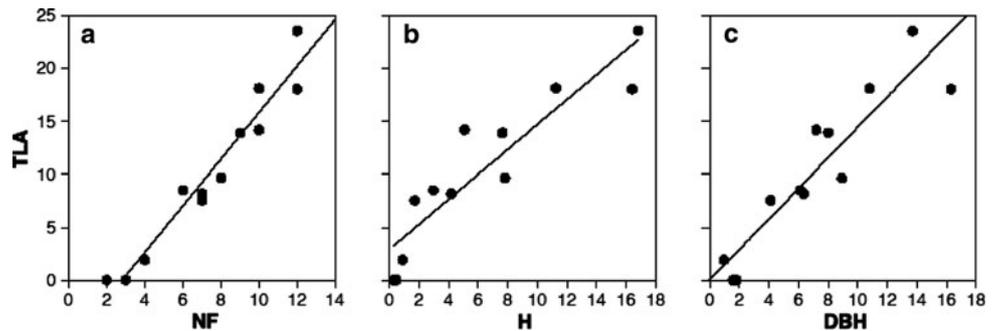
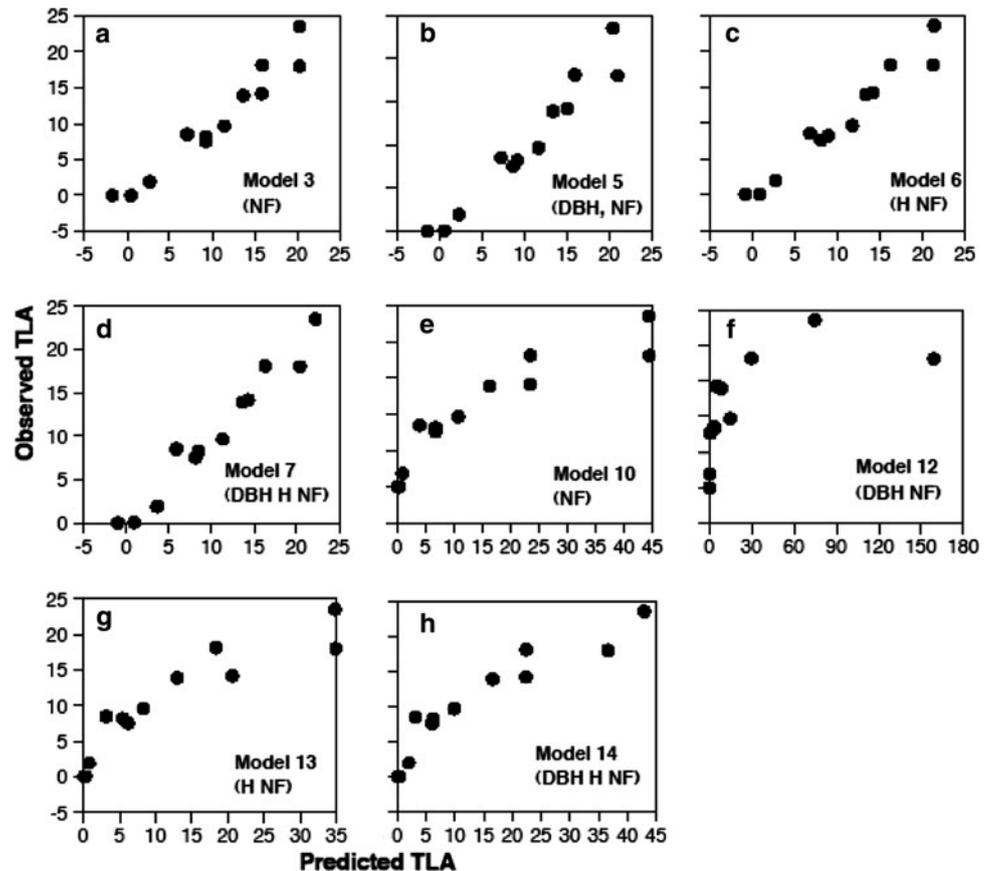


Fig. 2 Scatter plots of observed and expected values of total leaf area in m^2 (TLA) according to the models presented in Table 1 (predictor variables included in the model) with r^2 values above 0.90 in *E. oleracea* at La Selva Biological Station, Costa Rica



showing a direct, linear relationship with it (Fig. 1). DBH and H also scaled significantly with TLA , but not as strongly as NF (Fig. 1).

We selected linear and natural logarithmic models with r^2 values higher than 0.90 from Table 1, and examined the congruence between observed and expected values of TLA as predicted by these models. In all cases, natural logarithmic models overestimated the actual value of TLA as predicted by these models. In all cases, natural logarithmic models overestimated the actual value of TLA as predicted by these models. In all cases, natural logarithmic models overestimated the actual value of TLA as predicted by these models. In all cases, natural logarithmic models overestimated the actual value of TLA as predicted by these models. Simple linear regressions gave a better fit between the expected and the observed value of TLA .

Discussion

We provided 14 simple models to estimate the total leaf area of *E. oleracea*, which can be extended to include other morphologically similar species in the *Euterpe* clade. The results of this study show that TLA is directly proportional to NF as well as palm size as reflected in DBH and H . Although the leading variable explaining TLA was NF , the scaling between TLA , DBH and H was linear and highly associated (linear models for DBH and H gave an r^2 of 0.844 and 0.842, respectively). The high degree of association among morphological characters in *E. oleracea* supports the belief that palms behave like unitary

organisms (Tomlinson 2006). Although constrained by the lack of secondary meristems, palms show a high degree of morphological integration, diverging from the typical modular construction of woody plants. Morphological integration implies constraints on the ability to increase in height while continuing to provide adequate structural support for aerial parts and still satisfying respiratory demands by having sufficient TLA. TLA also influences the time and intensity of the reproductive effort, as was found for *Astrocaryum mexicanum* at Los Tuxtlas Research Station in Veracruz, Mexico (Piñero and Sharukhán 1982).

By compiling results of studies on other species from the genus *Euterpe*, Henderson (2002) showed that leaf dimensions, specifically petiole length, rachis length and pinnae length were significantly related to stem diameter. Our results support this further when examining the allometric relation of TLA relative to DBH in *E. oleracea* (linear model, $r^2 = 0.844$). In contrast to our results, Kimura and Simbolon (2002) predicted that adult palms of *Pinanga coronata* should have a constant crown mass irrespective of stem height once the stem diameter has been fixed. Contrary to palms in which the stem diameter is fixed at an early stage, species like *E. oleracea*, *E. precatória* and *E. edulis*, *Prestoea decurrens*, *P. acuminata*, *Iriartea deltoidea* and *Socratea exorrhiza* are able to exhibit a sustained increased in diameter with increasing stem height (Alves et al. 2004; Avalos et al. 2005; Avalos 2007; Avalos and Fernandez-Otarola 2010).

Our allometric models allow for non-destructive TLA estimates of this economically important and widespread species. In addition, the models presented here should help to increase the accuracy of the estimations of carbon sequestration in tropical forests by adding to the existing database on allometric equations for tropical species and life forms.

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