

# Testing a theoretical framework on the linear segment of the biomass-density trajectory of forests with data from a mangrove forest

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## ABSTRACT

The linearity and slope of biomass-density trajectories of forests became a classical topic of discussion in the ecological literature since the 1930s. In 2003, a theoretical framework partially based on empirical evidence from mangrove forests articulated disparate available knowledge. The present article is the first empirical test of the framework for which data from Cuban mangroves were used. Nine plots were surveyed in 2005 in a predominantly *Avicennia germinans* monospecific forest on the south coast of La Habana province. For one of the plots data from 1980s were available and quoted. Instead of calculating mean biomass per individual, the present article addressed basal area per individual in order to allow a more direct use of the surveyed data (DBH) and avoid introducing further uncertainties in the discussion. The two empirical linear trends detected in the trajectory of individual mean basal area vs density of individuals (self-thinning) were explained by the theoretical framework. The qualitative validity of the framework stands. The observation of two linear self-thinning trends can be empirical evidence that the slope is specific to site conditions and can also change if site conditions change. Potential for further theoretical and modeling work can exist in revisiting available data in historical records of Cuban research organizations.

**Key words:** Self-thinning, stem diameter, skewness, model, mangroves

## RESUMEN

La linealidad y pendiente de trayectorias biomasa-densidad de bosques devino un tema clásico de discusión en la literatura ecológica desde los años 1930. En 2003, un marco teórico parcialmente basado en evidencias empíricas de bosques de manglar armonizó antecedentes contradictorios. El presente artículo es la primera evaluación empírica de dicho marco teórico, para lo que se emplearon datos de manglares cubanos. Se muestrearon nueve parcelas en el 2005 en un bosque predominantemente monoespecífico de *Avicennia germinans* en la costa sur de provincia La Habana. Para una de las parcelas, estaban disponibles datos de 1980 y fueron citados. En lugar de calcular biomasa media por individuo el presente artículo se enfoca en área basal por individuo para usar más directamente los datos colectados (DBH) y evitar la introducción de mayores incertidumbres en la discusión. Las dos tendencias lineales empíricas detectadas en la trayectoria de área basal individual media vs densidad de individuos (auto-raleo) fueron explicados por el marco teórico. La validez cualitativa del marco teórico se mantiene. La observación de dos tendencias lineales de auto-raleo puede ser evidencia empírica de que la pendiente es específica de cada sitio y puede cambiar si las condiciones en el sitio cambian. Los datos disponibles en registros históricos de organizaciones de investigación en Cuba pueden tener potencial para más trabajo teórico y de modelación.

**Palabras clave:** Auto-raleo, diámetro del tronco, asimetría, modelo, manglares

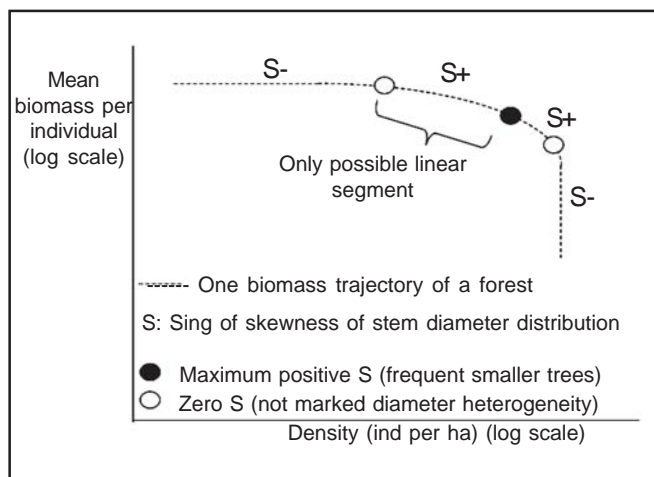
## INTRODUCTION

Biomass-density trajectories address the progressive decline in density in a population of growing plants (Begon & al. 2006). Self-thinning refers to linear segments in the trajectories. Self-thinning, and thus the linearity and slope of the trajectories, have experienced long debate in forest ecology and management (Reynolds & Ford 2005).

Debate originated when the works of Reineke (1933) and Yoda & al. (1963) led to the establishment of the so-called self-thinning rule, which proposes that a linear relationship between average plant biomass and plant density (logarithmic scale) was of general validity. The slope of the linear relationship was indicated at -1.5. Empirical findings and theoretical explanations in support of or against the rule followed without consensus (Chen & al. 2008, Li & al. 2000,

Reynolds & Ford 2005, Sackville Hamilton & al. 1995, Shaw 2006, Sun & al. 2011, Vanclay & Sands 2009, Weller 1987, Westoby 1984).

Berger & Hildenbrandt (2003) proposed a theoretical framework on biomass-density trajectories that articulates examples and counterexamples of the self-thinning rule. The framework is partially based on empirical evidence from mangrove forests and is expected to explain findings on the emergence of the different segments of biomass-density trajectories, the nature (*i.e.* linear or not) of each segment, and the slope of the linear segment. The modeling approach of the framework use growth parameters of the mangrove species *Rhizophora mangle* L., and defined the segments in a biomass trajectory by targeting reference points where the skewness of the stem diameter distribution of the forest changes.



**Fig. 1.** Theoretical framework on biomass-density trajectories of cohort of trees (after Berger & Hildenbrandt 2003).

The theoretical framework proposes that a biomass trajectory of the trees of a cohort in a forest can have a linear segment only after the skewness of stem diameter distribution has had a maximum positive value (Figure 1).

The linear segment would end once the trajectory reaches its second zero in the skewness of stem diameter distribution. The framework also explains that the value of the slope of a linear segment is not always -1.5, and allows explaining that different trajectories can occur in a cohort (Berger & Hildenbrandt 2003).

The theoretical framework proposed by Berger & Hildenbrandt (2003) has not yet been tested with empirical data. The aim of this article is to test that framework with data surveyed in Cuban mangroves.

## MATERIALS AND METHODS

### Study site

Field surveys were conducted in a predominantly *Avicennia germinans* (L.) L. monospecific mangrove forest in wetlands on the south coast of La Habana province, Cuba. Those wetlands occupy a coastal west-east oriented belt of 129 km length and 2-10 km width. Mangroves were surveyed in the western part of the wetlands, and are reported as the natural coastal vegetation (Capote Fuentes 2007, Menéndez 2000). The *A. germinans* monospecific mangrove forest had 80-100% vegetation cover and trees 7-11 m high.

Local wetlands develop on a very low and softly undulated (0-1m) littoral swampy plain of marine-palustrine origin. The dry (November-April) and rainy seasons (May-October) account for 21% and 79% of the annual average rainfall (800-1200 mm), respectively. The annual mean temperature reaches 24-26°C. The tides have low amplitude (25-50 cm).

## METHODS

In this mangrove, nine 10 m x 10 m plots were surveyed in 2005. For one of the plots (L2005), data from 1980s were available (Menéndez 2000) and the corresponding 2005 plot was placed inside the 20 m x 50 m plot of 1980s. Hereafter, data of that plot will be referred as L1980s and L2005. Coordinates of L1980s are 22.68° latitude N and 82.78° longitude W (ellipsoid WGS-84). Since self-thinning refers to a temporal process, the surveyed data can be considered a pseudo-time series (Mueller-Dombois & Ellenberg 1974, Snedaker & Snedaker 1984).

Density of mangrove stems (stems per 100 m<sup>2</sup>) and DBH of stems were recorded. The basal area of each tree was calculated as  $BA = 3.14 \times (DBH)^2 / 4$  (Cintrón & Schaeffer-Novelli 1983). Vegetation was surveyed in the dry season of 2005 (March-April). Soil salinity was surveyed in both dry (March-April) and rainy season (September-October), at about 20 cm depth with a hand-held refractometer (per mill, Atago ATC-S/Mill-E) from a soil sample extracted with a soil driller (Snedaker & Snedaker 1984).

The data obtained in the plots were graphed in order to discuss the theoretical framework of Berger & Hildenbrandt (2003). The mean basal area per individual was used instead of indirectly calculating mean biomass per individual. This avoided uncertainties in the discussion. When basal area is discussed instead of biomass, the theoretical framework of Berger & Hildenbrandt (2003) should be re-read as -0.5 is not always the value of slope in trajectories of mean basal area per individual versus density of individuals (Begon & al. 2006).

The analysis of the data was exploratory and focused on the biological processes and not on statistical tests. Empirical data on self-thinning has frequently not satisfied statistical tests (Begon & al. 2006, Weller 1987) because available data mix effects from different levels like population, site and species, which in the present study could have been negatively emphasized by the low number of surveyed plots. Skewness of stem diameter distribution was calculated and further explored by means of histograms, and the relative position of minimum, mean and maximum values of stem diameters and basal areas (Moore & McCabe 1998).

In the modeling approach of Berger & Hildenbrandt (2003) each stem counts as an individual. In the plots surveyed for this study, multi-stem trees (with more than one stem) were detected in 7 out of the 9 plots. Therefore, stems of trees were accounted in three ways: each stem accounted as an individual, only main stem accounted as an individual, and the equivalent stem of a multi-stem tree accounted as an individual.

For each multi-stem tree an equivalent stem was calculated. In summary, for the equivalent stem of a multi-stem tree: diameter is higher than each single stem diameter of the tree and basal area equals the sum of basal areas of the stems. First, basal area of the equivalent stem was calculated by summing up the basal areas of the main and secondary stems of the tree. Second, DBH of the equivalent stem was calculated from the basal area equation,  $BA=3.14 \times (DBH)^2/4$ . This analysis was not possible for plot L1980s, since 1980s data of each tree were not available.

## RESULTS

Mean basal area versus density of stems displayed a similar pattern in the three ways that the stems were accounted (Figure 2A, B, C). Plot b tended to have lower skewness and aligned more with the lower basal area linear trend when only main stems were accounted (Figure 2B) or an equivalent stem was accounted (Figure 2C). Plot g tended to have more negative skewness of stem diameter distribution when accounting stems proceeded from all stems accounted ( $S=0$ , Figure 2A) into only main stems accounted ( $S=-0.4$ , Figure 2B) and equivalent stems accounted ( $S=-0.5$ , Figure 2C). Annex 1 complements Figure 2 with details of plot values.

Two linear trends could be distinguished along plots with higher or lower values of basal area (Figure 2A, B, C). The linear trend with higher values of basal area included plots L1980s, a, b, c, d, L2005 and e. The trend with lower values of basal area included plots L1980s, a, b, h and g. In these last two plots (h and g) soil salinity had extreme values above 60 per mill in both, dry and rainy seasons (Figure 3). No trend achieved the segment in which mean basal area would become constant (Figure 2A, B, C).

Plot f and d can be considered outliers. Plot f was characterized by dead trees, which indicate the influence of particular plot conditions (e.g. tree diseases). Plot d would be expected to have lower positive skewness, or appear earlier on the linear trend (e.g., between a and b, c) with lower basal area and higher density of individuals.

The skewness of stem diameter distribution tends to diminish along plots in both, higher and lower basal area linear trend. Each linear trend starts with the plot that was surveyed in the 1980s (L1980s) (Figure 2A, B, C). This is the plot where skewness of basal area distribution tends to be more positive, as indicated by the relative position of minimum, mean and maximum basal area (Figure 2D). Although the corresponding data on skewness of stem diameter distribution was not available for L1980s, this plot can also be considered as the plot where skewness of stem diameter distribution

tends to be more positive. This is so because in plots surveyed in 2005, skewness of basal area and stem diameter distributions tended to be positively correlated in plots with positive skewness of stem diameter distribution (Figure 2E). At the same time the relative position of minimum, mean and maximum diameter (Figure 2D) tended to have a pattern similar to the corresponding basal area values (Figure 2F). Figure 4 shows the histograms of stem diameter distribution of plots surveyed in 2005.

## DISCUSSION

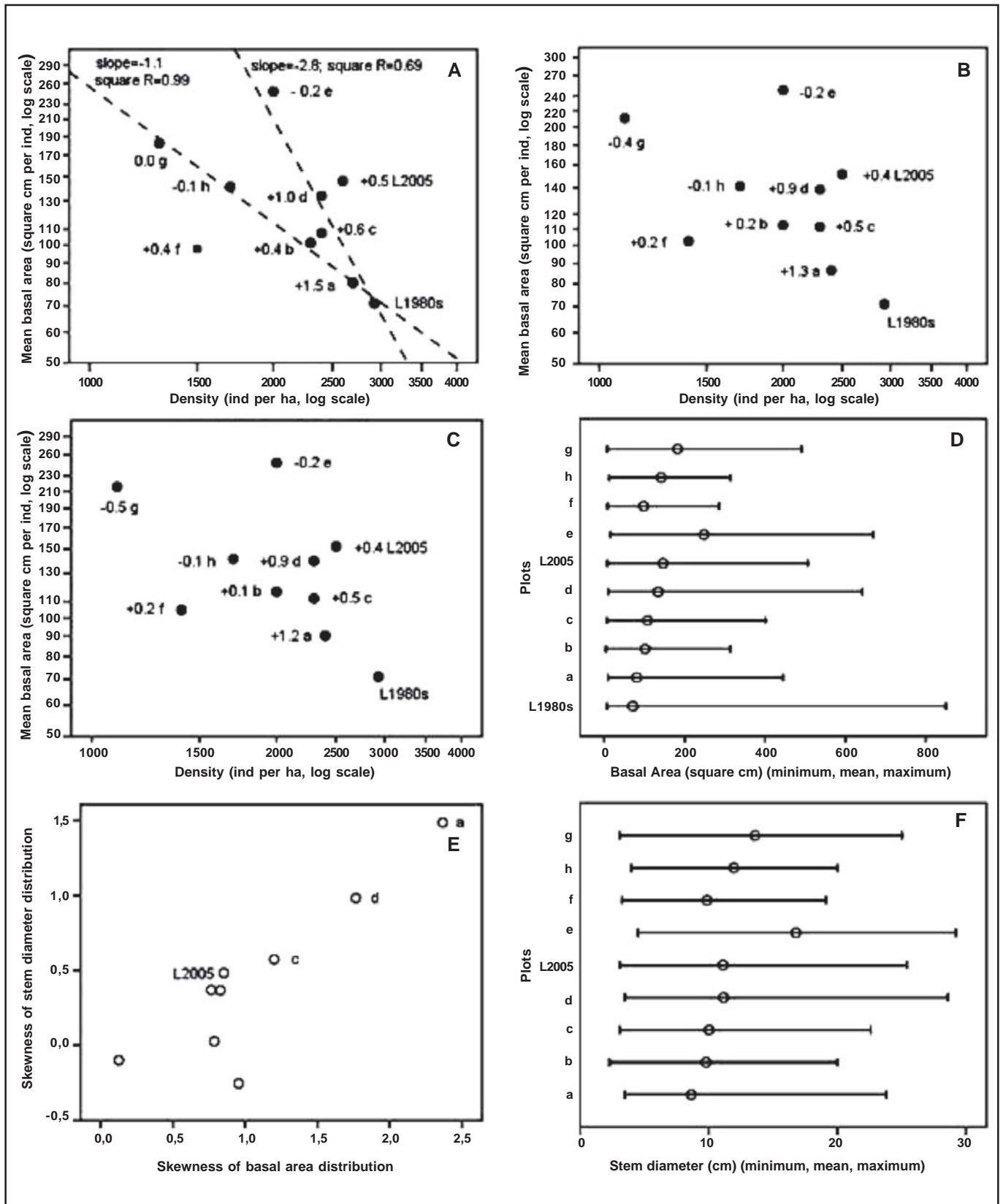
Since the modeling approach of the theoretical framework of Berger & Hildenbrandt (2003) accounts each stem as an individual, discussion of results will focus on all stems accounted as individuals (Figure 2A, D-F, Figure 4).

The two linear self-thinning trends can be explained by the theoretical framework proposed by Berger & Hildenbrandt (2003). As theoretically expected, the linear segment on each trajectory was observed between a plot having the highest positive skewness in the stem diameter distribution, and a plot having skewness close to zero. Also, the linear segments evidenced that different empirical values of slope can occur.

The fact that no trend achieved the segment in which mean basal area would become constant emphasizes that the assumptions for its existence (constant environmental conditions, no recruitment, loss through mortality balanced through growth of survivors) can be theoretically valid, but at the same time difficult to observe in nature (Berger & Hildenbrandt 2003, Begon & *al.* 2006). The outlier plot f could have been in that segment, but recruitment, together with the presence of stressed trees, may have led to the observed lower basal area and positive skewness of stem diameter distribution in plot f. Similarly, Fromard & *al.* (1998) reported one out of eight plots below the self-thinning line of mangroves in French Guiana.

Pseudo-time series allow discussing field data and thus going beyond controlled experiments and modeling. However, the data does not come from a single cohort of plants that has been studied through time. The outlier plot d may have occurred due to the mixed effects of all co-existing cohorts (Begon & *al.* 2006, Weller 1987).

The observation of two linear self-thinning trends in the present study can be empirical evidence that the slope is specific to site conditions and can also change if site conditions change. Such evidence has been theoretically proposed but not empirically documented (Berger & Hildenbrandt 2003). Starting from plot L1980s, mangroves could have evolved along the self-thinning trajectory of



**Fig. 2. A-C:** Basal area versus density as per the three ways in which stems were accounted (value of skewness of stem diameter distribution appears next to the plot label). **A:** each stem accounted as an individual. **B:** Only main stem accounted as an individual. **C:** Trees with more than one stem were accounted as only one equivalent stem. **D to F** corresponds to **A** (each stem accounted as an individual). **D:** Relative position of minimum, mean and maximum values of basal areas. **E:** Skewness of stem diameter distribution versus skewness of basal area distribution. **F:** Relative position of minimum, mean and maximum values of stem diameters. Data of plot L1980s were quoted from Menéndez (2000).

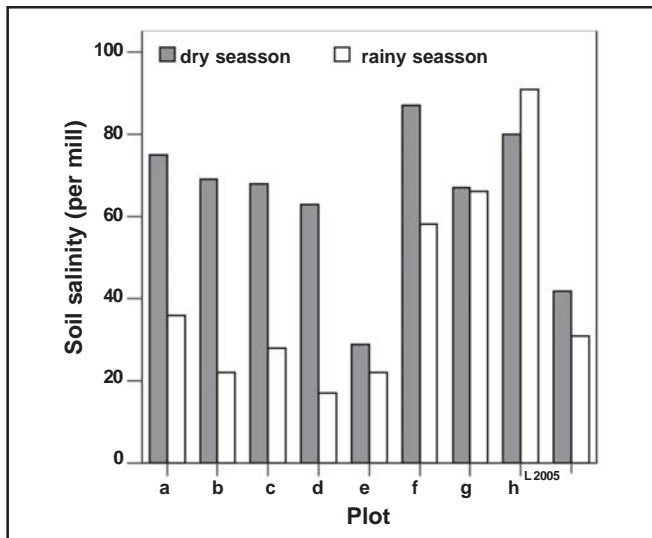


Fig. 3. Soil salinity in plots surveyed in 2005.

higher values of mean basal area and lower salinity. Changes in hydrological site conditions in mangroves can frequently occur (Tomlinson 1986), for instance due to changes in micro-topography after transportation of sediments by storms and sea surges. Such changes in hydrological conditions would cause salinity to increase and make mangroves evolve from plot L1980s into the self-thinning trajectory of lower values of mean basal area and higher salinity.

**CONCLUDING REMARKS**

Two empirical linear segments in the biomass-density trajectory (self-thinning) of an *Aicennia germinans* mangrove area were explained by the theoretical framework of Berger & Hildenbrandt (2003). This indicates the qualitative validity of the framework, which used a modeling approach with growth parameters of the mangrove species *Rhizophora mangle*.

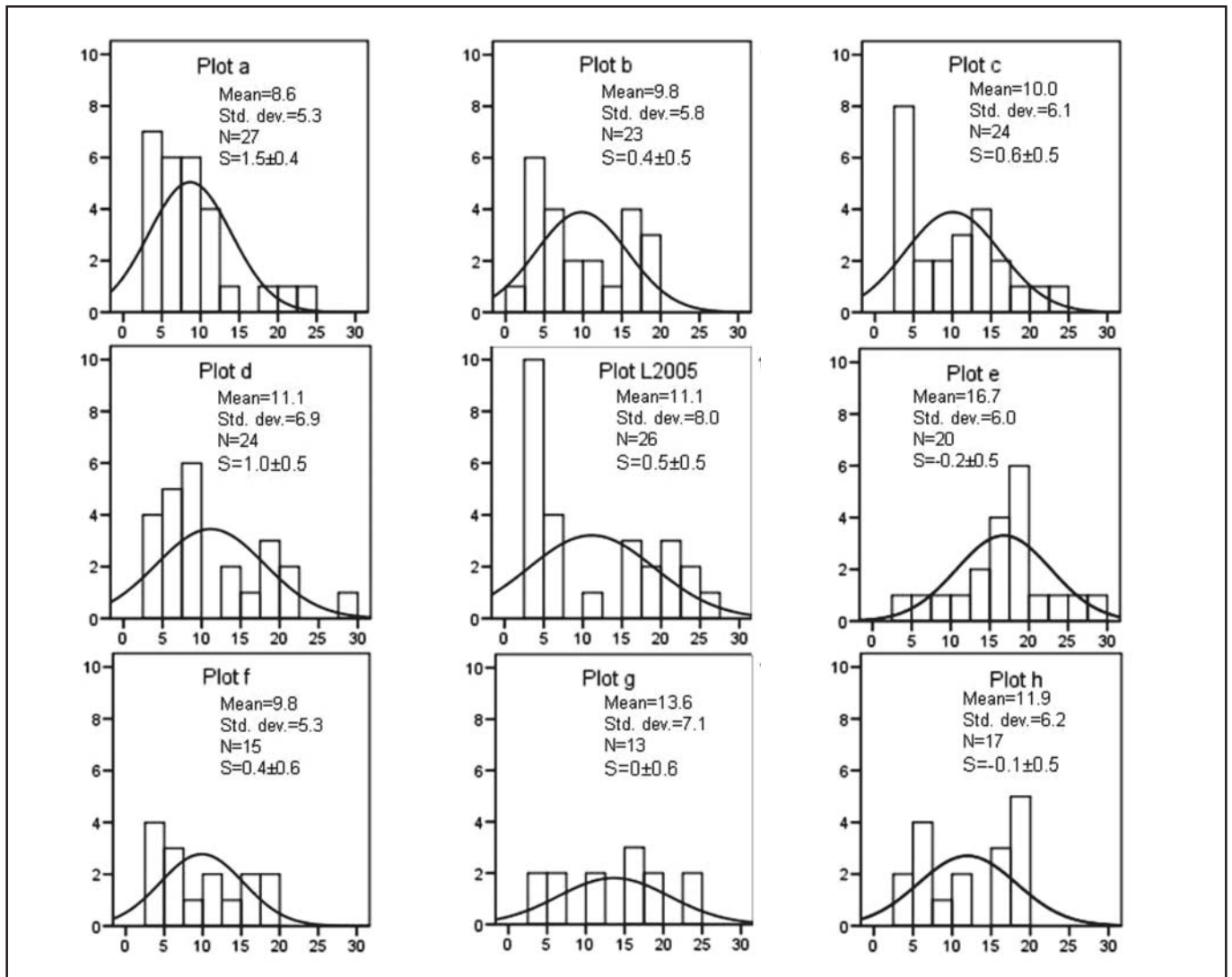


Fig. 4. Histograms of stem diameter distribution in plots surveyed in 2005. Each stem accounted as an individual, thus this Figure corresponds to Figures 2A, 2D-F. Order of histograms approximately follows order in which plots appear on trajectories in Figure 2A. x-axis = classes of stem diameter (cm); y-axis = frequency; s = skewness of distribution ± standard error of skewness. Normal distribution curve included.

Discussion has been possible by complementing recent surveys (2005) with few of the available historical data (1980s). Potential for further theoretical and modeling work exists in revisiting available data in historical records of Cuban research organizations.

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**ANNEX 1.** Sections A, B and C correspond to Figure 2A, 2B and 2C respectively.

**A:** each stem accounted as an individual. **B:** only main stem accounted as an individual. **C:** trees with more than one stem were accounted as one equivalent stem. Density: individuals per ha. Mean basal area: square cm per ind. Stem diameter distribution: skewness  $\pm$  standard error of skewness.

Plot	A			B			C		
	Density	Mean basal area	Stem diameter distribution	Density	Mean basal area	Stem diameter distribution	Density	Mean basal area	Stem diameter distribution
g	1300	182	0.0 $\pm$ 0.6	1100	210	-0.4 $\pm$ 0.7	1100	216	-0.5 $\pm$ 0.7
h	1700	141	-0.1 $\pm$ 0.5	1700	141	-0.1 $\pm$ 0.5	1700	141	-0.1 $\pm$ 0.5
f	1500	98	0.4 $\pm$ 0.6	1400	103	0.2 $\pm$ 0.6	1400	105	0.2 $\pm$ 0.6
e	2000	248	-0.2 $\pm$ 0.5	2000	248	-0.2 $\pm$ 0.5	2000	248	-0.2 $\pm$ 0.5
L2005	2600	146	0.5 $\pm$ 0.5	2500	152	0.4 $\pm$ 0.5	2500	152	0.4 $\pm$ 0.5
d	2400	134	1.0 $\pm$ 0.5	2300	139	0.9 $\pm$ 0.5	2300	140	0.9 $\pm$ 0.5
c	2400	107	0.6 $\pm$ 0.5	2300	112	0.5 $\pm$ 0.5	2300	112	0.5 $\pm$ 0.5
b	2300	101	0.4 $\pm$ 0.5	2000	113	0.2 $\pm$ 0.5	2000	117	0.1 $\pm$ 0.5
a	2700	80	1.5 $\pm$ 0.4	2400	86	1.3 $\pm$ 0.5	2400	90	1.2 $\pm$ 0.5
L1980s	2930	71	No data	2930	71	No data	2930	71	No data