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INSIGHT

Radiocarbon estimates of age and growth for a dominant Amazon palm species

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Abstract

We used destructive sampling to assess ^{14}C-calibrated age and growth of five individuals of *Oenocarpus bataua* from 7.35 to 21.6 m of total height. The largest individual was 59-year-old. Age decreased from the collar to the top of the aboveground stem and was positively correlated with number of leaf-scars and height.

Abstract in Portuguese is available with online material.

KEYWORDS
^{14}C, age estimation and structure, ARECACEAE, biomass, forest dynamics and management, *Oenocarpus bataua*, patauá

Palms (monocotyledons) are visually distinct from other woody plants. They have relatively large leaves, split partly, or completely into leaflets or leaf segments and, when existing, an unbranched stem with leaf scars (Hallé et al., 1978; Tomlinson, 1979). There are >2300 registered palm species distributed in ca. 190 genera, with the higher diversity reported in tropical and subtropical forests (Eiserhardt et al., 2011; Govaerts & Dransfield, 2005). Although accounting for a smaller portion of the forest carbon balance, palms are an important floristic and ecological element that regulates light, competes for resources, supports fauna, and affects the demography of trees (Emilio et al., 2014; Harms et al., 2004; Muscarella et al., 2020).

As opposed to trees, palms have no secondary vascular cambium or meristem, that is, no heartwood or juxtaposed xylem and phloem (Tomlinson, 1979). Vascular bundles are dispersed throughout the stem and embedded in non-uniform parenchyma. Formation of new vascular bundles occurs by adding fronds to a central axis (Tomlinson & Zimmerman, 1969). This allows palm stems to be totally filled with vascular tissue, with oldest portions closer to the base of the

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individual (Tomlinson, 2006; Wiesberg & Linick, 1983). By lacking secondary growth, palms do not form annual rings, and increase in stem diameter results from sustained primary growth that can include cell division (Tomlinson & Huggett, 2012). Primary thickening of the stem may cease early or be continuous, which results in more cylindrical or conical shapes, respectively (Tomlinson, 2006).

Estimates of age and growth rates of palms are usually made from functions describing continuous measurements of individual height or the number of leaf-scars (Guarín & del Valle, 2014; Lieberman et al., 1988). In tall and dense tropical forests, however, height data may be inaccurate due to systematic and random errors (Larjavaara & Muller-Landau, 2013). Measurement of ^{14}C radiocarbon allows for the estimation of the time elapsed since C in structural tissues was originally fixed from the atmosphere, and is especially useful in plants that do not form reliably annual structures, including palms (del Valle et al., 2014; Herrera Ramírez et al., 2017).

Our focal species, *Oenocarpus bataua* Mart. (ARECACEAE) develops a thick and tall stem, and can reach up to the canopy of varying Amazon forest types. During the establishment stage, *Oenocarpus* spp. may already have long leaves but lack an aboveground stem (Kahn & Granville, 1992). Instead, it develops a belowground stem from which adventitious roots grow (Figure S1). Like other palm species, once the individual is established and light is not limiting, the belowground stem stops growing downward and the apical meristem starts developing the aboveground stem (de Granville, 1992; Tomlinson, 1979, 2006).

Although *Oenocarpus* spp. is an abundant and well distributed genus in Amazon forests, little is known about its age distribution and growth patterns. Studies carried in a premontane forest in the Central Cordillera of the Colombian Andes reported ^{14}C-calibrated ages for *O. bataua* varying from 14.8 to 53.6 years (del Valle et al., 2014; Guarín et al., 2014), and stem height-growth calculated from leaf-scar monitoring data varying from 0.07 to 0.8 m year^{-1} (Guarín & del Valle, 2014). Here, we aimed at assessing age, length of the establishment period, and growth patterns over the life of *O. bataua* individuals from a Central Amazon forest, with different climate, soil, and topography. To the best of our knowledge, this is the first research investigating the age of this species in Amazon forests.

We assessed the age and growth patterns of aboveground and belowground stems of *O. bataua* using ^{14}C radiocarbon from samples taken at several vertical and radial positions (Figure S1). Further, we combined ^{14}C-calibrated ages (hereafter referred as ages) with size attributes (Table S1). We studied palms growing in a valley area (sandy soil and shallow water table) of an old-growth *terra-firme* forest at the *Estação Experimental de Silvicultura Tropical* (EEST) from the *Instituto Nacional de Pesquisas da Amazônia* (INPA), Manaus, Brazil (2°38′ S, 60°09′ W). Palms were uprooted in closed-canopy areas using a tirfor winch-system (Ribeiro et al., 2016) as part of a complementary investigation (dos Santos, 2019). ^{14}C measurements were carried by accelerator mass spectrometry by the WM Keck Carbon Cycle AMS Facility at the University of California, Irvine, US (Xu et al., 2007). Further details on tissue sampling and ^{14}C measurements can be accessed in the Supplementary Information.

We reported radiocarbon data as Fraction Modern (FM) ^{14}C (Stuiver & Polach, 1977). In all cases, FM was >1.0, indicating that C in the samples was fixed after 1955 and contains "bomb" ^{14}C produced by atmospheric weapons testing. Calibrated ages were determined from FM using the OxCal Project platform and the Bomb 13 SH3 curve (Bronk-Ramsey, 2009a, 2009b). For samples containing C fixed after 2010, we used a complementary curve (Graven et al., 2017; Graven et al., 2020).

For radiocarbon data indicating the presence of bomb ^{14}C, two dates are usually possible. One when ^{14}C in the atmosphere rapidly increased from the late 1950s to 1964, and another during the time since 1964 when ^{14}C in the atmosphere has been decreasing. Our decisions of which date to choose were supported by assumptions based on field observations and existing literature: (i) taller palms are older than shorter palms; (ii) the oldest part of the aboveground stem is at the collar or base and (iii) the youngest part is at the top. We expected no clear patterns among radial positions and assumed these would have similar ages for a given stem height. For growth estimates, we assumed palms grew constantly over time.

We analyzed age patterns among individuals and at different vertical and radial positions using generalized linear mixed models. We considered that radial samples were nested at vertical positions and respective individuals, which were computed as random effects. We tested for correlations between size variables and age using Kendall ranking. Although our sample size did not allow for a robust estimation of the magnitude of associated errors, we used linear regressions to further investigate the strong correlations. Statistical analyses were carried in the R 4.1.2 software platform (R Core Team, 2020).

1 | WHAT IS THE AGE RANGE OF *O. bataua* OF VARYING SIZE?

While the belowground stem of older and larger individuals (Ind1 and Ind2) were relatively more obconical shaped, younger and smaller individuals were more cylindrical. This reinforces the idea that *O. bataua* may not develop the typical saxophone-shape (Guarín et al., 2014) reported for other tropical palms (Souza et al., 2017; Tomlinson & Huggett, 2012). In all individuals, the belowground stem was densely covered with adventitious roots (Figure S1).

The FM ^{14}C of samples ranged from 1.012 to 1.214, corresponding to plausible ages ranging from 0 to 59 years (Figure 1). The oldest palm was also the largest and heaviest (Ind1, total height, aboveground stem height and biomass of 21.6 m, 11.1 m, and 282.3 kg, respectively). It is important to realize that calibration programs are updated only every several years, so that sometimes young tissues with C fixed in years after the most recent used by the calibration program are ascribed only the older possible calendar age. For example, without having updated the atmospheric ^{14}C record with data from 2013 to 2018, we would have erroneously inferred for Ind1 that the age of the top of the aboveground stem (which should be the newest growth) was greater than that at the base. Without

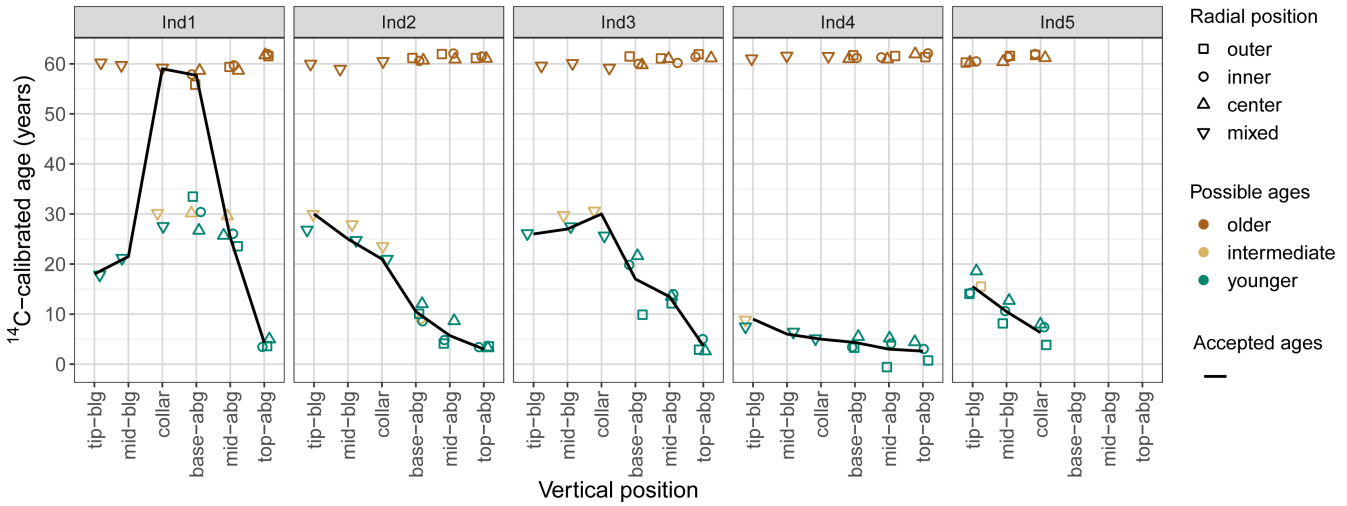


FIGURE 1 ^{14}C-calibrated ages at different vertical and radial positions of the stem from five individuals (Ind1-Ind5) of *Oenocarpus bataua* Mart. (Arecaceae) harvested in a Central Amazon forest. The 2-3 possible calendar ages for each radiocarbon measurement are identified as older, intermediate, and younger. Those we accepted as most plausible given the relative age of tissues from adjacent positions and estimated growth rates are connected by black lines. Vertical positions: tip-blg—tip of the belowground stem (deepest portion); mid-blg—mid portion of the belowground stem (50% of the stem depth); collar—stem collar (i.e., portion on the intersection of the belowground and aboveground stem); base-abg—base of the aboveground stem (~5 cm aboveground); mid-abg—mid portion of the aboveground stem (50% of the stem height); top-abg—top portion of the aboveground stem (below the crownshaft). Radial positions: outer—most outer tissue from the radial cut; inner—tissue from the inner part of the radial cut (at ½ radius of the cross section); center—tissue from the center of the radial cut (at the radius of the cross section); mixed—mixed tissue integrating the three positions of the radial cut (see Figure S1 for details).

several samples from the same individuals and understanding how the species grows, it could be impossible to choose between older and younger possible calendar ages.

2 | WHAT ARE GROWTH PATTERNS AND RATES?

Age decreased continuously from the collar to the top of the aboveground stem (i.e., below the crownshaft) in all individuals (Figure S2 and Table S2). While age also decreased from the tip of the belowground stem to the collar of Ind2 (0.57 m depth), Ind4 (0.4 m) and Ind5 (0.2 m), the opposite pattern was observed in Ind1 (1.25 m) and Ind3 (0.7 m).

An establishment period of 4.7 and 19.5 years for Ind2 and Ind4 (respectively) is supported by the age of the belowground tip being greater than the base of the aboveground stem. These estimates are considerably less than the 37.5 years reported for the same species in a premontane forest in the Colombian Andes (Guarín et al., 2014). Although growing on soils with presumably less nutrients, the overall faster establishment of *O. bataua* in our study region may reflect the more stable climate and flat terrain that exerts a relatively lower water stress, and a higher frequency of gaps that can increase light availability during the different grow stages.

Ind5, as yet with no aboveground stem, had an age of 15.5 years based on the oldest belowground tissue (average over radial positions, Figure S2). This result reinforces that during the establishment time, palms may develop deep roots and tall crown/leaves while still lacking an aboveground stem (de Granville, 1992; Tomlinson, 1979). In contrast, Ind1 and Ind3 had younger ages of the belowground tip compared with the collar and the base of the aboveground stem, indicating that the belowground stem can grow deeper once the establishment period is completed and light is not limiting (de Granville, 1992; Kahn, 1986; Tomlinson, 1979). This would allow palms to increase mechanical stability and root density to cope with demands for water and nutrients as required with achieving larger sizes. Larger variations among individuals in establishment and growth (as discussed below) support that the growth of *O. bataua* is influenced by life history, resource availability, and the frequency of disturbances promoting mechanical injuries/damage such as herbivory and wind.

As opposed to trees, we found no clear aging pattern related to the radial position (Table S2). However, as observed for all individuals, a reduction in diameter from the base to the top of the aboveground stem and the overall older samples at the center of the radial cuts (Figure 1) support that *O. bataua* sustains primary growth (Tomlinson & Huggett, 2012). In Central Amazon, *Oenocarpus* spp. occupies the lower canopy. By increasing stem thickness and thus vessel area, palms can reduce risk of embolism (Aparecido et al., 2015). Lower slenderness also allows for higher mechanical stability (Ribeiro et al., 2016), that reduces the vulnerability to extreme wind and rain, a major natural disturbance in our study region (Marra et al., 2014; Negrón-Juárez et al., 2017).

Stem growth of palms can vary with local conditions, competition and ontogeny (Svenning, 2001; Tomlinson, 1979), which is supported by our data. Vertical growth of the belowground and aboveground stems ranged from 0.01 to 0.35 m year^{-1} and 0.01–0.57 m year^{-1}, respectively (Figure 2a). Root: shoot ratio varied from 0.05 to 0.93 (mean of 0.383) (Table S1). Overall, our results

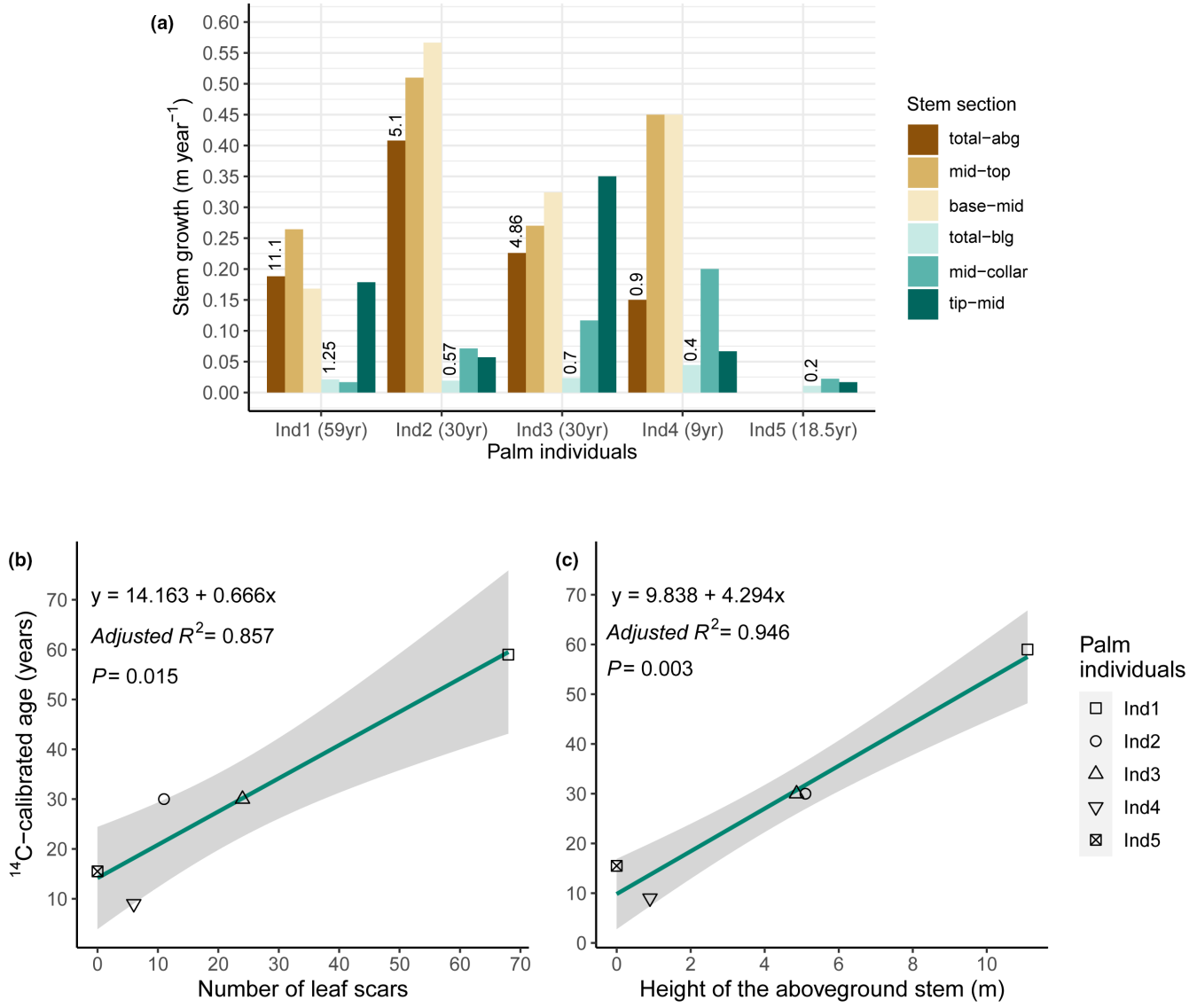


FIGURE 2 Radiocarbon estimates of stem growth and correlations between age and size attributes for five individuals of *Oenocarpus bataua* Mart. (Arecaceae) harvested in a Central Amazon forest. Growth rates for the belowground (blg) and the aboveground (abg) stem (a). ^{14}C-calibrated age as a function of the number of leaf scars (b) and height of the aboveground stem (c). For Ind1-Ind4, growth estimates for the belowground stem were calculated based on the age of mixed samples. For the aboveground stem, we used the oldest samples at respective vertical positions, which yielded more conservative numbers. In a, the total height (m) of stems is given on the top of respective bars. In b and c, lines designate positive correlation, as specified by the given equations and respective summary of fitting measures. Shaded areas designate the 90% confidence interval for respective fits.

indicated that the growth of the belowground is relatively slower and more irregular than that of the aboveground stem. This finding indicates that *O. bataua* may increase rates of aboveground growth during periods of lower competition for light, water, and nutrients (e.g., gap recovery).

Compared with trees that grow relatively slowly (Silva et al., 2002) and can live for centuries (Vieira et al., 2005), our results show that *O. bataua*, like other tropical palms (Lieberman et al., 1988), is a fast-growing species that can achieve relatively large sizes within decades. Fast-growing abilities combined with low predation/herbivory rates (Eiserhardt et al., 2011), differential vulnerability to extreme winds (Canham et al., 2010; Marra et al., 2014) and efficient fauna dispersal transporting seeds to recently disturbed areas (Kahn & Granville, 1992) corroborate the high demographic importance of this and other caulescent palm species across the Amazon (Emilio et al., 2014; Muscarella et al., 2020).

3 | HOW DOES AGE CORRELATE WITH SIZE ATTRIBUTES?

We considered the oldest sample as defining the overall age of each individual. Age was marginally positively correlated (Kendall $p < .1$, Table S3) with the height of the aboveground and depth of

the belowground stems, slenderness, number of leaf scars, and belowground biomass. Among variables describing individual size, the number of leaf-scars (Figure 2b) and the height of the aboveground stem (Figure 2c) captured a higher fraction of the variation in age among individuals.

Positive correlation between age and the number of leaf-scars was previously reported for *O. bataua* (Guarín et al., 2014; Guarín & del Valle, 2014). As indicated by our data, a lack of correlation between age and total biomass (Table S3) may be explained by the large variation in the relative contribution of the aboveground stem and crown (Table S1). Apart from locally calibrated allometries for reducing the uncertainty of biomass estimates (Magnabosco Marra et al., 2016), scaling up the contribution of palms to carbon balance requires assessments to better describe how environmental conditions influence establishment and growth patterns.

Our study reinforces the suitability of radiocarbon for dating tropical palms (del Valle et al., 2014). Since we found no clear aging patterns related to radial positioning (Figure 1 and Table S2), further assessments may focus on samples taken from the center of varying heights of the belowground and aboveground stem. If possible, samples should be collected from a larger number of individuals growing in forests with varying structure, different climate, and disturbance dynamics. In the region of Manaus, counting leaf scars and measuring stem height is an efficient method for estimating the age of *O. bataua*. Nonetheless, individuals lacking an aboveground stem can be at least 15-year-old due to the time required for belowground establishment.

AUTHOR CONTRIBUTIONS

DMM and ST designed research; DMM and BOS performed research; DMM and ST analyzed the data; and DMM wrote the paper with contribution of all other authors.

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DISCLOSURE STATEMENT

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study (DOI: 10.17871/atto.306.3.1240) are available on request at the ATTO data portal (https://attodata.org/).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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