**Title:** Characteristics of tall trees in Bornean tropical forests

**Authors:** Elsa M. Ordway1\*, Lucie Gallegos2, Roberta E. Martin3, Gregory P. Asner3, David Burslem4, Michael O’Brien5, Stuart Davies6, Simon Lewis7, Reuben Nilus8, Oliver Phillips7, Lan Qie9, Paul R. Moorcroft1

1. Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, MA 02138, USA
2. Lucie affiliation
3. Center for Global Discovery and Conservation Science, Arizona State University, 1001 McAllister Ave., Tempe, AZ 85281, USA
4. School of Biological Sciences, University of Aberdeen
5. Universidad Rey Juan Carlos
6. Smithsonian Tropical Research Institute
7. School of Geography, University of Leeds
8. Sabah Forestry Department
9. School of Life Sciences, University of Lincoln[eo3]

\*Corresponding Author: Elsa M. Ordway, [elsa\_ordway@fas.harvard.edu](mailto:elsa_ordway@fas.harvard.edu)

**Abstract.**

**Keywords:** emergent trees, demographic rates, Southeast Asia, traits, diversity

**Introduction.**

* Motivating the study? Why it matters? Problem statements
* Questions/hypotheses
  + Are there certain traits associated with the biggest size classes of trees?
    - Traits per unit area and/or per unit mass
    - Normalize by LMA – look at differences/variation in residuals
      * Mention traits that we don’t have data on (e.g. terpenoids)
  + Look at tannins and other traits ~ height for sunlight portion of crown
* Introduce 3 different definitions (in methods, stem level and species level analysis)
* Make this an ideas paper
  + Positing: what would make a good emergent / mega tall tree?
* Risk giving them a name 🡪 say they’re the largest
  + Not only “emergents” extending their crown above the canopy
  + What should we call these things?
  + “foundation trees”
* READ: Tree flora of Sabah and Sarawak
  + Classify species as “mega/large trees” or other based on my species from my notes and this book
* Largest trees not necessarily older, probably younger than other large canopy trees
* Use Sabrina’s data to look at ontogenetic plasticity
  + Sapling vs adult and sun vs. shade – look at plasticity this way
* Compare traits and demography for tall vs. not tall
  + Dipterocarp species (mega dipterocarps vs not-mega dipterocarps)
  + Legumes (mega Fabaceae vs. not-mega Fabaceae; Bombacaceae?)

**Why might trees get so big**

* Fast growing?
  + Optimal growth conditions / high growth rates
    - No limitations (nutrients, water, light)
    - Defense mechanisms (XX terpenes? – see Sabrina’s comments; tannins, phenols, other)
* Long lived?
  + Low mortality (based on plant traits)
  + Low disturbance rates (based on environmental conditions)
* Both?
* high disturbance scenario
  + e.g. Alluvial
* low disturbance scenario
  + e.g. Sandstone
* nutrient poor conditions
* nutrient rich conditions
* hydraulic constraints or lack thereof
  + annual precipitation
  + seasonality
* EM/AM associations

Emergent trees are typically defined as trees with crowns that extend above the mean canopy level (Clark and Clark 1992) Emergent trees are also referred to as large trees, very large trees, or tall trees in the literature, and have been defined in various ways, often using different DBH and height cut-offs, depending on whether the research was based on field measurements or remotely sensed data as well as the location of the study. For example, the following thresholds have been used in previous studies: 60 cm DBH (Clark *et al* 2019) Losos and Leigh 2004), 70 cm DBH (Brown and Lugo 1992, Clark and Clark 1992, 1996), and 30-50 m height (da Costa *et al* 2019). While these thresholds are often arbitrary, King *et al* (2006) chose a criterion based on the distribution of their data, defining emergent as larger than the 95th percentile of trunk diameter of all diameters greater than 10 cm. However, a more general definition of emergent based on height is needed given the widely varying height-diameter relationships across continents (Banin *et al* 2012). Here, we use forest inventory plot data and airborne LiDAR data to classify a tree as emergent based on three different criteria: 1) the site-level diameter at breast height (DBH) distribution, 2) the site-level LiDAR derived height distribution, and 3) the LiDAR derived crown-level height relative to surrounding neighbors. We then analyzed diversity, demography, and trait characteristics to examine whether the emergent characteristics differ from non-emergent trees and whether emergent characteristics vary with environmental conditions across sites. We also compare results using the different definitions to evaluate their generalizability.

**Methods.**

***Study Area***

We analyzed data from two locations in Sabah, Malaysian Borneo: Danum Valley Conservation Area (4°54′ N, 117°48′ E) and Sepilok Forest Reserve (5°10’ N 117°56’ E). Danum is equatorial, with a mean annual temperature of 26.9 °C, ranging between 19.8-34.8°C. Mean relative humidity at 14:00 h averages between 78%, and 95% at 08:00 h. Mean annual rainfall (1985–2006) is 2,825 mm (Llusia *et al* 2014). Similarly, Sepilok experiences average annual rainfall (1976-1995) of 2,975 mm and a mean monthly temperature of 26°C (Malaysian Meteorological Department, unpublished data, Frank 1996). This study focused on the diversity, abundance, demography, and leaf traits of emergent trees at ten plots spanning seven forest communities within these two locations. Forest inventory data were curated in the ForestPlots.net database (Lopez-Gonzalez *et al* 2011) and the ForestGEO.si.edu database.

In this study, we use data from six 4-ha forest plots in Sepilok, and three 1-ha plots and 1 50-ha plot in Danum. Three forest types spanning an edaphic gradient are present within Sepilok: alluvial forest in the valleys (n = 2 plots); sandstone forests on hillsides and crests (n = 1 plot); and heath forests (*kerangas*) dominating more acidic podzolic soils (n = 3 plots) (XX). Previous studies have underscored how these distinct forest types differ not only in their species composition and diversity, but also in terms of nutrient cycling, forest structure, and aboveground carbon (Austin & GreigSmith 1968; Dent et al. 2006; Coomes et al. 2017).

The three 1-ha Danum plots differ topographically and in terms of soil characteristics (Table X). We thus analyzed them separately as three distinct sites (referred to as DNM1, DNM2, and DNM3). The DNM1 plot is located on a relatively low lying, flat area, close to a stream. The DNM2 plot is on a SW facing slope, also near a stream, while the DNM3 plot is located on a small ridge. Although much larger, the Danum 50-ha plot (referred to as DNM50) incorporates an area with relatively homogeneous soil topography, dominated by a single mudstone/sandstone soil association.

***Inventory plot and airborne remote sensing data***

Each plot, except the 50-ha plot, was censused three times, between 2006 and 2016 for the Danum plots, and between 2001 and 2014 for the Sepilok plots. The 50-ha plot in Danum was censused twice between 2011 and 2019. For the purposes of this analysis, each 4-ha and 50-ha plot was subdivided into 1-ha subplots.

***Three definitions of emergent / Three tall tree definitions***

* Species vs. tree-level classification as emergent

The first definition used for classifying emergent stems was based on the distribution of DBH, defined as the 99th percentile of all canopy trees (stems ≥ 10 cm DBH; Fig. 2). Species were classified as emergent if any individual within the entire sample of trees across all plots was ≥ X cm DBH (the DBH 99th percentile), based on their observed potential to become emergent. The second definition was similarly based on a percentile of a distribution, although the definition was determined based on tree height rather than diameter measurements. We used LiDAR top-of-canopy height data for the Danum 50-ha plot to quantify height percentiles for the second definition, and estimated height from DBH measurements across all sites for comparison using the Southeast Asia regional height-diameter allometry described in Feldpausch et al. (2011). Using the LiDAR data, we hand delineated all visible tree crowns in DNM50. The mean height was then estimated, and the 90th percentile of the distribution of the crown-level mean height (57 m high) was used to identify the threshold for defining crowns as emergent or non-emergent. The cut-off of 57 m was identified and then applied across all sites using the estimated height of the forest inventory plot data. Thus, for definitions one and two, a species was classified as emergent if at least one stem for a given species was ≥100 cm DBH or ≥57 m height respectively.

The third definition was based on the relative height of a tree compared to its neighbors. Definition three leveraged the LiDAR data and was thus only possible to derive at DNM50. We first masked the LiDAR TCH data to only include the tallest pixels, equivalent to the mean canopy height plus 1.5 standard deviation (> 56.96 m; Davies et al. 2017). To select crowns that were taller than their neighbors, we calculated the local maxima across DNM50, defined as the tallest pixel within a circular neighborhood of 25 m (Alexander et al. 2018). All hand-delineated crowns that contained a local maximum were defined as emergent crowns.

**Diversity, demography, and trait variation**

***Diversity analysis***

For all stems ≥10 cm, we calculated stem density, basal area, species richness (number of species) and the Shannon Wiener index per hectare by dividing each plot into several 1-ha plots (e.g., 50 1 hectare plots for the large Danum 50-ha plot). To examine XXX, we conducted these calculations for all non-emergent and emergent stems. We use bootstrapping method to determine confidence intervals of the Shannon Wiener Index. (SM?) We report the mean and standard error for each site (Table 2).

***Demographic rates***

To analyze demography rates, we compared emergent species and non-emergent species. We removed stems where family, genus or species was unknown. For all stems ? 10 cm, we calculated growth rates in terms of annual increment (cm yr-1) and mortality rates (% yr-1). Annual increment was calculated as the difference of DBH between two measurements, divided by the time: days between measurements divided by 365 and mortality rate was calculated at the plot-level as log(S) – log(N)/ Time where N is the number of trees in the population in the first census, S is the number of those trees which survived till the subsequent census and time is the mean census interval for the population. (King, Davies, and Noor 2006). Growth rates and mortality rates were calculated using the fgeo package in R (citation for fgeo package).

To identify whether the relationship between annual increment and DBH varied according to the type of species i.e. emergent or non-emergent species, we conducted a breakpoint analysis. Breakpoint analysis, also known as structural change or breakpoint analysis is an algorithmic approach using maximum-likelihood estimation to quantify the point at which the statistical properties of a sequence of observations change (Killick and Eckley 2014). A linear segmented regression of the annual increment as a function of DBH was performed. Then, we conducted two linear regression before and after the breakpoint for each type of species to determine whether the relationship between growth rate and size changed in different ways for emergent and non-emergent species OR stems.

***Traits analysis***

***Airborne Remote-Sensing Data.***

Foliar characteristics were derived from XXX data …, we used coaligned LiDAR and hyperspectral data collected by the GAO in … using the Airborne… Reference the papers that describe the methods (Martin et al. 2018) and just summarize relevant information here.

Hyperspectral data were collected at 4-m ground-level resolution using a visible to shortwave imaging spectrometer.

Leaf mass per area, foliar nitrogen content, foliar phosphorus content, chlorophyll, phenols, tannins and lignin content were estimated/calculated.

We applied a shade mask and then we remove pixels of low leaf area and non-foliated canopy thanks to a threshold for Normalized Difference Vegetation Index (NDVI). In tropical forests NDVI thresholds of 0.75-0.80 have been used to ensure inclusion of highly foliated canopies

**Results.**

***Diversity***

Do the presence/abundance/diversity of emergent stems vary across sites with differing topographic conditions and soil characteristics?

***General emergent vs non emergent species differences***

***Demographic rates***

***Traits analysis***

**Discussion.**

Motivation: ecosystem services and ecosystem functions

DIVERSITY Are emergent stems/emergent species preferentially in certain sites ?

Are some sites more suitable for the establishment of emergent stems/species?

- (Environmental factors) 🡪 discussion

- Diversity in each sites

EMERGENT VS NON EMERGENT: What are the main characteristics/traits of an emergent tree? In what way are they different?

- Small paragraph on recruitment/ seed dispersal

- Talk about the resilience and/or the resistance of emergent stems

- Major climatic events : ENSO, El Nino (discussion!!!!!)

(Hiromi et al. 2012) (Delissio and Primack 2003) : El Nino southeast Asia

(Condit, Hubbell, and Foster 1995) (Nepstad et al. 2007) (Meakem et al. 2018), (Condit et al. 2004) (Clark et al. 2017): El Nino – Amazon

DNM1: most trees infested with lianas, many killed by liana, creating gaps.

***Demography***

Emergent species exhibit lower mortality rates than non-emergent species, except in DNM02. The three Danum plots exhibit higher mortality rates than the Sepilok plots, indeed most trees were infested and killed by lianas, creating gaps.

There was evidence found of an extreme precipitation and storm event at Sepilok, Sabah in July 2006 have caused much higher short stem mortality among dipterocarp trees (> 30cm) on alluvial site, explaining the higher mortality rates in Sepilok Alluvial sites. (Ghazoul 2016)

**Acknowledgements.**

**Literature Cited**

Banin L, Feldpausch T R, Phillips O L, Baker T R, Lloyd J, Affum-Baffoe K, Arets E J M M, Berry N J, Bradford M, Brienen R J W, Davies S, Drescher M, Higuchi N, Hilbert D W, Hladik A, Iida Y, Salim K A, Kassim A R, King D A, Lopez-Gonzalez G, Metcalfe D, Nilus R, Peh K S H, Reitsma J M, Sonké B, Taedoumg H, Tan S, White L, Wöll H and Lewis S L 2012 What controls tropical forest architecture? Testing environmental, structural and floristic drivers *Glob. Ecol. Biogeogr.* **21** 1179–90

Brown S and Lugo A E 1992 for Tropical Moist Forests of the Brazilian Amazon *Interciencia* **17** 818

Clark D A and Clark D B 1992 Life History Diversity of Canopy and Emergent Trees in a Neotropical Rain Forest Author ( s ): Deborah A . Clark and David B . Clark Published by : Ecological Society of America LIFE HISTORY DIVERSITY OF CANOPY AND EMERGENT TREES IN A NEOTROPICAL RAIN FOR *Ecol. Monogr.* **62** 315–44

Clark D B and Clark D A 1996 Abundance, growth and mortality of very large trees in neotropical lowland rain forest *For. Ecol. Manage.* **80** 235–44

Clark D B, Ferraz A, Clark D A, Kellner J R, Letcher S G and Saatchi S 2019 Diversity, distribution and dynamics of large trees across an old-growth lowland tropical rain forest landscape *PLoS One* **14** 1–23 Online: http://dx.doi.org/10.1371/journal.pone.0224896

da Costa G S, Dalmolin Â C, Schilling A C, Sanches M C, dos Santos M S and Mielke M S 2019 Physiological and growth strategies of two Cariniana species in response to contrasting light availability *Flora Morphol. Distrib. Funct. Ecol. Plants* **258** 151427 Online: https://doi.org/10.1016/j.flora.2019.151427

King D A, Davies S J and Noor N S M 2006 Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest *For. Ecol. Manage.* **223** 152–8

Llusia J, Sardans J, Niinemets Ü, Owen S M and Peñuelas J 2014 A screening study of leaf terpene emissions of 43 rainforest species in Danum Valley Conservation Area (Borneo) and their relationships with chemical and morphological leaf traits *Plant Biosyst.* **148** 307–17

Lopez-Gonzalez G, Lewis S L, Burkitt M and Phillips O L 2011 ForestPlots.net: A web application and research tool to manage and analyse tropical forest plot data *J. Veg. Sci.* **22** 610–3

**Tables**

**Table 1.** Table title

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| **Site** | **pH** | **Elevation (m)** | **Sand fraction**  **(%)** | **Clay fraction (%)** | **Soil N (%)** | **Soil Total P**  **(mg kg-1)** |
| **Danum 1 a**  **(DNM1)** | 4.70 | 184 | 26.6 | 23.7 | 0.33 | 415.25 |
| **Danum 2 a**  **(DNM2)** | 3.90 | 296 | 62.0 | 2.7 | 0.30 | 285.85 |
| **Danum 3 a**  **(DNM3)** | 4.30 | 329 | 49.6 | 8.4 | 0.29 | 275.19 |
| **Danum 50 b, c**  **(DNM50)** | 5.30  (0.03) | 277  (0.05) | 26.8  (3.7) | 31.1  (1.9) | 0.20  (0.01) | 258.0  (7.4) |
| **Sepilok Alluvial d**  **(SPKA)** | 4.65  (0.03) | 74.39  (15.16) | 40.4  (14.7) | 34.7  (9.6) | 0.16  (0.06) | 343.7  (70.5) |
| **Sepilok Heath d**  **(SPKH)** | 4.10  (0.03) | 127.48  (7.12) | 75.4  (6.2) | 14.5  (4.7) | 0.1  (0.04) | NA |
| **Sepilok Sandstone d**  **(SPKS)** | 4.54  (0.03) | 110.24  (13.08) | 67.8  (7.7) | 19.8  (5.6) | 0.09  (0.02) | 74.85  (14.11) |
| a ForestPlots.net data  b Unpublished data (from Ben Turner and David Burslem)  c Elevation values calculated from Global Airborne Observatory DEM data  b Dent et al 2006 | | | | | | |

**Table 2.** Table title (Diversity & Abundance table)

**Figures**

**Une image contenant texte, carte

Description générée automatiquement**

**Figure 1.**

**Une image contenant capture d’écran

Description générée automatiquement**

**Figure 2.**

Une image contenant capture d’écran

Description générée automatiquement

**Figure 3.** Basal area (a) and stem density (b) across sites for emergent and non-emergent stems. Grey bars represent emergent stem and white bars represent non emergent stems. (all stems ≥10 cm) To facilitate visual comparison of the relative differences in stem density, emergent stem density was increased by one order of magnitude. Error bars are the standard deviation of the mean calculated for each 1 ha plot. Standard deviations could not be calculated for DNM01, DNM02, and DNM03 because they are 1 ha plots.

Une image contenant carte, texte

Description générée automatiquement

**Figure 4.** Comparison of demography rates between emergent and non-emergent species. (a) Annual increment across the different sites for all stems ≥10 cm DBH. The grey dots represent each observation, one or two observations per stem, depending on the number of censuses (n = 39,872 observations). (b) Mortality rates across the different sites. The grey points with error bars represent the mortality rates calculated for each consecutive census period for each plot. The Danum 50-ha plot has only been censused twice, hence there is only one mortality rate per type of species. Error bars are the 95% confidence interval. An asterisk indicates that emergent species are significantly different from non-emergent species (median outside of the confidence interval). (c) Segmented linear regression of annual increment as a function of DBH (cm). Observations are aggregated by 4 cm bins between 0 and 116 cm and the point is centered for each class (2 cm for 0-4cm bins). After 116 cm, bins are grouped so there are at least 30 observations in each bin (the bins are 124-134, 134-156 cm and 156-196 cm with 44, 40, 30 observations respectively).

**Une image contenant texte, carte

Description générée automatiquement**

**Figure 5.** XXX

**Figure 6.** (possible 2nd trait figure – relationships)