Distribution of biomass dynamics in relation to tree size in forests across the world


1Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panama City, Panama; 2Conservation Ecology Center, Smithsonian Conservation Biology Institute, Front Royal, VA 22630, USA; 3UR Forests and Societies, Ciriad, Université de Montpellier, Montpellier 34000, France; 4Forest Global Earth Observatory, Smithsonian Tropical Research Institute, Washington, DC 20560, USA; 5Department of Botany, National Museum of Natural History, Washington, DC 20560, USA; 6Department of Biology, Middlebury College, Middlebury, VT 05753, USA; 7School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 3UU, UK; 8Instituto Amazónico de Investigaciones Científicas Sinchi, Bogota, DC, Colombia; 9Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung City 80424, Taiwan; 10Department of Botany and Plant Physiology, University of Buea, Buea, Cameroon; 11Institute of Pacific Islands Forestry, USDA Forest Service, Hilo, HI 96720, USA; 12Centre for Ecological Sciences, Indian Institute of Science, Bangalore, Karnataka, India; 13Departamento de Ciencias Forestales, Universidad Nacional de Colombia Sede Medellín, Medellín, Colombia; 14Department of Science and Technology, Faculty of Applied Sciences, Uva Wellassa University, Badulla 90000, Sri Lanka; 15Faculty of Sciences, University of Kisangani, BP 2012, Kisangani, Democratic Republic of the Congo; 16Department of Plant & Microbial Biology, University of Minnesota, St Paul, MN 55108, USA; 17Binatang Research Centre, Madang, Papua New Guinea; 18Department of Natural and Applied Sciences, University of Wisconsin–Green Bay, Green Bay, WI 54311-7001, USA; 19Institute of Ecology and Evolutionary Biology, National Taiwan University, Taipei 10617; 20Department of Ecology and Evolutionary Biology, University of California, Los Angeles, Los Angeles, CA 90095, USA; 21Graduate School of Science, Osaka City University, Osaka 5588585, Japan; 22Department of Forest Ecology, Silva Tarouca Research Institute, Brno 602 00, Czech Republic; 23Wildland Resources Department, Utah State University, Logan, UT 84322, USA; 24Forest Global Earth Observatory, Smithsonian Environmental Research Center, Edgewater, MD 21037, USA; 25State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Xiangshan, Beijing 100093; 26Research Development and Innovation Division, Forest Department Sarawak, Bangunan Baitul Makmur 2, Medanraya, Petrajaya, Kuching 93050, Malaysia; 27Biological Centre, Academy of Sciences of the Czech Republic and Faculty of Science, University of South Bohemia, Ceske Budejovice 37005, Czech Republic; 28Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, Móstoles 28933, Spain; 29Department of Biology, University of Hawaii, Hilo, HI 96720, USA; 30Forest Ecology Group, Smithsonian Environmental Research Center, Edgewater, MD 21037, USA; 31The Royal Society SEARRP (UK/Malaysia), Danum Valley Field Centre, Lahad Datu, Sabah, Malaysia; 32Forestry and Environment Division, Forest Research Institute Malaysia, Kepong, Selangor 52109, Malaysia; 33Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY 10027, USA; 34Department of Ecology and Evolutionary Biology and Herbarium, University of Michigan, Ann Arbor, MI 48109, USA; 35College of Chemistry and Life Sciences, Zhejiang University, Hangzhou; 36CAS Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016; 37Department of Environmental Sciences, University of Puerto Rico, San Juan, PR, USA
Summary

- Tree size shapes forest carbon dynamics and determines how trees interact with their environment, including a changing climate. Here, we conduct the first global analysis of among-site differences in how aboveground biomass stocks and fluxes are distributed with tree size.
- We analyzed repeat tree censuses from 25 large-scale (4–52 ha) forest plots spanning a broad climatic range over five continents to characterize how aboveground biomass, woody productivity, and woody mortality vary with tree diameter. We examined how the median, dispersion, and skewness of these size-related distributions vary with mean annual temperature and precipitation.
- In warmer forests, aboveground biomass, woody productivity, and woody mortality were more broadly distributed with respect to tree size. In warmer and wetter forests, aboveground biomass and woody productivity were more right skewed, with a long tail towards large trees. Small trees (1–10 cm diameter) contributed more to productivity and mortality than to biomass, highlighting the importance of including these trees in analyses of forest dynamics.
- Our findings provide an improved characterization of climate-driven forest differences in the size structure of aboveground biomass and dynamics of that biomass, as well as refined benchmarks for capturing climate influences in vegetation demographic models.

Introduction

Forests are highly size-structured: tree size influences access to resources and impact of disturbances, and thereby growth and mortality rates (Muller-Landau et al., 2006a; Anderson-Teixeira et al., 2015b; Stark et al., 2015). Larger diameter trees generally have access to higher light environments, which in turn enables greater tree growth rates (Stark et al., 2012). However, larger trees also tend to be more vulnerable to drought (Bennett et al., 2015; McGregor et al., 2021) and to windthrow (Gardiner et al., 2005; Gora & Esquivel-Muelbert, 2021). By contrast, smaller trees are more likely to die from competition-induced carbon (C) starvation (McDowell et al., 2018), from neighboring trees and falling branches (Meer & Bongers, 1996), and may be more vulnerable to fire (Brando et al., 2012; Hood et al., 2018).

Among-site differences in climate, disturbance intensity, and other drivers lead to variation in the size dependence of tree growth and mortality rates, and thus in tree size distributions and the distribution of aboveground biomass (AGB), woody productivity, and woody mortality fluxes with tree size (Muller-Landau et al., 2006b; Meakem et al., 2018; Gora et al., 2020). Critically, as climate change and anthropogenic disturbances alter resource availability (e.g. light and water) and disturbance regimes (Lewis et al., 2015; Seidl et al., 2017), the size structure of forests will modulate forest C cycle responses. For example, climate change that increases stresses, and thus mortality rates, of large trees will have greater impact on forests with larger concentrations of biomass and productivity in large trees. Understanding the distribution of C stocks and fluxes with tree size is thus a foundation for accurately quantifying current and future forest C stocks and cycling, and for projecting climate change feedbacks to these measures (Zuidema et al., 2013). Consistent, comparative data on size-related C stocks and fluxes for multiple forests are also particularly valuable today as benchmarks for the size-dependent demographics of vegetation models, which are increasingly used to represent vegetation dynamics in Earth system models (Fisher et al., 2018).

Tree size distributions vary strongly with climate among sites, as do size-specific growth and mortality rates, and thus the distributions of C stocks and fluxes with tree size vary as well. Large trees are typically more abundant and contribute a greater proportion of AGB in warmer, lower latitude forests (Lutz et al., 2018). The proportion of large trees also increases with precipitation (Segura et al., 2002), likely due to the greater sensitivity of large trees to water stress (Bennett et al., 2015). Abundances of small trees also vary among sites; they are higher in wet or moist tropical forests than in temperate forests (King et al., 2006). This may be because these aseasonal environments enable longer (multipar year) leaf lifespans of broadleaved understory trees (Coley, 1988), which effectively reduce the cost of deploying leaves, and thereby enable survival even in low-light environments. Moreover, shade tolerance (i.e. the ability to survive and grow in low-light environments) increases in strength with the length of the growing season and is inversely related to tolerance to other environmental stresses, such as drought (Valladares & Niinemets, 2008). Given these patterns, we expect distributions of forest AGB with tree size to be more dispersed and right skewed – that is, a greater proportion of small trees and a longer tail to large trees – in warmer, wetter forests. We expect similar size distributions in annual AGB fluxes (i.e. aboveground woody productivity (AWP), the flux in AGB associated with tree growth and recruitment) and aboveground woody mortality (AWM, the flux from AGB to necromass due to mortality) when conditions are relatively stable.

Yet, we expect size distributions of AWP and AWM to be shifted towards smaller size classes relative to AGB. Studies across many different forest types and tree species have observed decreasing productivity per unit biomass with tree size (e.g. Mentuccini et al., 2005; Kohyama et al., 2020). This occurs even
though absolute productivity generally continues to increase with tree size (e.g. Stephenson et al., 2014), because productivity increases more slowly than biomass. Our focus here is on AWP/AGB, henceforth termed relative AWP (RAWP). Multiple mechanisms can contribute to reductions in RAWP with tree size, including lower ratios of leaf area to stem mass (H. Poorter et al., 2015), higher maintenance costs (Magnani et al., 2000), increasing hydraulic limitation (Drake et al., 2010), and allocation shifts towards reproduction and other nonwoody tissues (Ryan et al., 2004; Thomas, 2011). The contributions and strengths of these mechanisms, and thus the strength of the decline in RAWP with tree size, is likely to vary among sites and species. However, few studies have specifically quantified stand-level patterns of RAWP with tree size, much less compared them among sites — but see Meakem et al. (2018). In old-growth forests at steady state, in which size distributions are not changing directionally, productivity and mortality at a given size class are on average equal, and thus we expect patterns for relative aboveground woody mortality (RAWM = AWM/AGB) with tree size to follow those of RAWP.

To our knowledge, no study has investigated how stand-level stocks and fluxes of AGB (the largest and most easily estimated tree C pool) are distributed by tree size across a large variety of forest types and biomes. Previous studies have analyzed among-site variation in total stand-level AGB stocks and fluxes (Anderson-Teixeira et al., 2021; Banbury Morgan et al., 2021; Muller-Landau et al., 2021) and in tree size distributions (i.e. the densities of trees of different sizes; e.g. Muller-Landau et al., 2006b). Studies have also quantified total AGB stocks and fluxes in one particular size class – large trees – and have shown that they contain a large proportion of the AGB (Slik et al., 2013; Lutz et al., 2018; Mildrexler et al., 2020) and are good predictors of forest structure (Bastin et al., 2018). However, very few studies have examined the relative contribution of all tree sizes to both AGB stocks and fluxes, even though smaller trees can also have a role in shaping AGB dynamics (Newbery et al., 2013; Hubau et al., 2019; Mensah et al., 2020). Rare exceptions include a study quantifying size-related distributions of AGB, AWP, and AWM in three forest plots along a precipitation gradient in Panama (Meakem et al., 2018).

In this study, we quantified how AGB, AWP, and AWM are distributed with respect to tree diameter at breast height (DBH; diameter at 1.3 m height or above any stem irregularities) in large-scale (4–52 ha) forest plots across the world belonging to the ForestGEO network of large forest plots (https://forestgeo.si.edu; Anderson-Teixeira et al., 2015a; Davies et al., 2021) and tested associated hypotheses. We quantified the median, dispersion, and skewness of distributions of each variable with DBH and investigated how they vary among sites with climate. We examined how RAWP = AWP/AGB and relative AWM (RAWM = AWM/AGB) vary with DBH and among sites. We also specifically quantified the relative importance of the smallest (1 ≤ DBH < 10 cm) and largest (DBH ≥ 60 cm) trees for AGB stocks and fluxes. We expected size-related distributions of AGB, AWP, and AWM to be more dispersed and right skewed; that is, a greater proportion of small trees and a longer tail to large trees in warmer, wetter forests (Hypothesis 1). Thus, we specifically expected the skewness and dispersion of the size-related distributions to increase with mean annual temperature (MAT) and mean annual precipitation (MAP) (Hypothesis 1a), and to be higher in tropical forests than in temperate forests (Hypothesis 1b). We also expected RAWP and RAWM to decrease with tree diameter in all sites, such that, although large trees dominate biomass stocks and fluxes, small trees are proportionally more important to AWP and AWM than they are to AGB (Hypothesis 2a). Consistent with this, we expected the probability distributions of AWP and AWM to be shifted towards smaller size classes than those of AGB (lower medians; Hypothesis 2b), the contributions of the smallest trees (1 ≤ DBH < 10 cm) to AWP to be larger than their contributions to AGB (Hypothesis 2c), and the contributions of the largest trees (DBH ≥ 60 cm) to AWM to be smaller than their contributions to AGB (Hypothesis 2d).

Materials and Methods

Study sites and data

Repeated tree censuses were conducted in 25 forest plots (Table 1; Supporting Information Fig. S1; Table S1) distributed across five continents following a standardized protocol (Condit, 1998; Davies et al., 2021). Plots are located in old-growth or mature secondary forests, and several have been subjected to some level of natural and/or historical human disturbances (Anderson-Teixeira et al., 2015a; Table S2), although we lack consistent, quantitative data on the intensity, size-selectivity, and timing of those disturbances at each site. All stems with DBH ≥ 1 cm were mapped, tagged, identified to genus or species, and measured in DBH. For stems measured at a height > 1.3 m in tropical sites, we applied a taper correction to estimate the equivalent DBH at 1.3 m height following Cushman et al. (2021). We excluded lianas, tree ferns, and strangler figs from the analysis. We analyzed data for the most recent census interval at each site, or the next-to-last interval if the most recent census interval had been affected by a major disturbance (e.g. El Niño drought in Cocoli; Meakem et al., 2018). Climate variables were provided by each site (Table 1; Anderson-Teixeira et al., 2015a; Davies et al., 2021).

We estimated total AGB for each tree at each census from the measured DBH using the pantropical allometric equation from Chave et al. (2014) and Réjou-Méchain et al. (2017) for tropical sites, and the generalized allometric equations from Chojnacky et al. (2014) for other sites. For all tropical sites (except Fushan) we used eqn 7 from Chave et al. (2014), which does not include height as an input variable. For the Fushan site, where frequent typhoons result in lower tree height than the global prediction, we used a local height allometry (McEwan et al., 2011) in combination with eqn 4 from Chave et al. (2014). For temperate sites, we used the equations in table 5 of Chojnacky et al. (2014), which rely on information on wood density and taxonomic identity. Each tree was assigned a wood density, based on its taxonomic identity, from the Global Wood Density Database (Zanne et al., 2014).
et al., 2009) using the R package BIOMASS (Réjou-Méchain et al., 2017). Unidentified trees and trees that lacked a species or genus-level wood density value in the database were assigned a stand-level mean wood density over all individuals.

Size-related stand dynamics

We calculated total AGB stocks and fluxes by 20 m x 20 m quadrats and 1 cm diameter classes. Specifically, we examined the following variables: (1) AGB (Mg ha\(^{-1}\) cm\(^{-1}\)), (2) AWP (i.e. annual megagrams increment from stem growth of surviving trees and recruitment; Mg ha\(^{-1}\) yr\(^{-1}\) cm\(^{-1}\)); and (3) AWM (Mg ha\(^{-1}\) yr\(^{-1}\) cm\(^{-1}\)). We corrected for bias induced by different lengths of census interval using a method described in Kohyama et al. (2019), and we gap-filled unrealistically large changes in measured DBH with the expected DBH change for the corresponding size class and site (Figs S2, S3; Methods S1, S2). For graphical visualization (but not for analysis), we aggregated data into wider size classes, with size class boundaries defined separately for each site, based on the total number of stems and their distribution with size (Fig. S4; Table S3; Methods S3). Values were standardized per centimeter of diameter class width (i.e. dividing size class totals by the width of the diameter class size in centimeters).

To summarize size distribution patterns for each variable and site, we calculated the median, dispersion, and skewness of each distribution. The median is the DBH at which 50% of the total stock or flux is below and 50% above. We calculated the dispersion as the quartile coefficient of dispersion (dimensionless); that is, the difference between the third and first quartiles divided by the sum of the first and third quartiles. We calculated the skewness as Pearson’s first skewness coefficient (dimensionless); that is, the difference between the mean and median of the distribution divided by its SD. These summary statistics (median, dispersion, and skewness) were calculated based on 1 cm wide diameter classes. We analyzed the relationship of these summary statistics (median, dispersion, and skewness) with climate by performing multiple linear regressions with the MAT and AWM. We gap-filled unrealistically large changes in measured DBH with the expected DBH change for the corresponding size class and site (Figs S2, S3; Methods S1, S2). For graphical visualization (but not for analysis), we aggregated data into wider size classes, with size class boundaries defined separately for each site, based on the total number of stems and their distribution with size (Fig. S4; Table S3; Methods S3). Values were standardized per centimeter of diameter class width (i.e. dividing size class totals by the width of the diameter class size in centimeters).
(Karger et al., 2017). We tested for differences between tropical and temperate forests in the summary statistics (median, dispersion, and skewness) for AGB, AWP, and AWM by performing Wilcoxon signed-rank tests (Table S6). We tested whether the medians of AGB were larger than the medians of AWP and AWM by performing Wilcoxon signed-rank tests. To quantify the importance of small (DBH < 10 cm) and large (DBH ≥ 60 cm) trees, we calculated their contributions as proportions of total AGB, AWP, and AWM. We also explored two other definitions of large trees: the top 5% of trees with DBH ≥ 10 cm and the largest trees that account for 50% of the stand AGB (following Lutz et al., 2018; Figs S5, S6; Table S7).

Because of their relevance to understanding the distribution of AGB, AWP, and AWM with size, we also calculated the following variables by aggregated size classes (as defined in Methods S3): RAWP (% yr⁻¹), defined as the ratio of AWP to AGB; RAWM (% yr⁻¹), defined as the ratio of AWM to AGB; mean individual stem AGB (Mg); and mean stem diameter growth (cm yr⁻¹; Figs S7–S9; Notes S1).

We calculated 95% confidence intervals on all variables by bootstrapping over 20 m × 20 m quadrats with 1000 replicates. Static variables, such as AGB, were calculated based on the initial census of the focal census interval.

Results

Climate and size-related distributions of biomass stocks and fluxes

The distributions of AGB stocks and fluxes across size classes peaked at intermediate size classes in all sites, were very uneven, and varied strongly among sites (Fig. 1). In comparison with the temperate sites, tropical forests had a greater share of their total AGB and AWP in the small stems (DBH < 10 cm) and had more very large stems that store large amounts of AGB but made relatively smaller contributions to AWP (Fig. 4c). Most temperate sites (with the exception of Wind River) accumulated AGB between censuses, and their net change in AGB (calculated as AWP − AWM) was positive (Fig. S10).

As expected (Hypothesis 1a), dispersion and skewness of AGB and AWP distributions generally increased with MAT and MAP (Fig. 2). Multiple regression analyses found significant positive effects of both MAT and MAP on the dispersion of AGB distributions (Fig. 2a,b) and on the skewness of AWP distributions (Fig. 2g,h); that is, AGB was more broadly distributed between size classes, and AWP distributions were more right skewed at higher MAT and higher MAP. There was also a significant positive effect of MAT on the dispersion of AWP and AWM distributions (Fig. 2c; Table S4) and a significant positive effect of MAP on the skewness of AGB distributions (Fig. 2f). MAT and MAP had no significant effect on the skewness of AWM or the medians of AGB, AWP, or AWM (Fig. 2; Table S4). Consistent with these results and with Hypothesis 1b, the dispersion and skewness of AGB, AWP, and AWM were significantly higher in tropical vs temperate forests, but the medians were not significantly different (Table S6).

Relative aboveground biomass fluxes as a function of tree size

Across all sites, RAWP decreased with increasing tree size: small trees had, on average, higher AWP relative to their AGB than large trees did (Fig. 3a,b), consistent with Hypothesis 2a. RAWM also decreased with tree size in most sites (Fig. 3c,d), paralleling the patterns for the stem mortality rate (Fig. S9a; Notes S1). However, in some tropical sites (Pahoh, Korup, Wanang, Sinharaja) the curve was U-shaped, with RAWM being the highest for small and large trees and the lowest for intermediate tree sizes. In the Zofin temperate site (Czech Republic), RAWM was particularly low for small trees and increased with tree size (under 0.3% yr⁻¹ for all diameter classes with DBH < 25 cm; Fig. 3d).

The median of the AGB distribution was greater than (23/25) or equal to (2/25) the median of the AWP distribution in all 25 sites, and across sites the difference between the medians was significantly greater than zero (W-statistic 276; P = 2.85 × 10⁻⁵), consistent with Hypothesis 2b. The AGB median was larger than the AWM median in 14 of 25 sites, but overall the difference between the medians of AGB and AWM was not significantly greater than zero (W-statistic 195.5; P = 0.381).

The roles of large and small trees in biomass stocks and fluxes

As expected, large trees (DBH ≥ 60 cm) contributed a large fraction to all biomass stocks and fluxes, whereas small trees (DBH < 10 cm) typically contributed < 15% (Fig. 4). Across all sites, small trees contributed more to AWP than to AGB (Fig. 4a), with contributions to AWP being typically twice the AGB contributions, consistent with Hypothesis 2c. Conversely, large trees contributed less to AWP than to AGB (Fig. 4c), consistent with Hypothesis 2d. Small trees also contributed relatively more to AWM than to AGB in most sites (Fig. 4b), whereas large trees contributed similarly to AWM and AGB (Fig. 4d). Results were qualitatively similar for the two other definitions of large trees: the largest trees that comprise 50% of the total AGB, and the top 5% of stems ≥ 10 cm (Figs S5, S6; Table S7).

To provide a resource for model benchmarking and simple comparisons among sites, we calculate size class values of all variables (AGB, AWP, AWM, and mean stem diameter growth) and their 95% confidence intervals for standardized diameter classes of [1, 5], [5, 10], [10, 20], [20, 30], [30, 40], [40, 50], [50, 100], [100, 200], and [200, +∞) cm DBH (Dataset S2) in addition to the site-specific diameter classes presented in the main text (Dataset S1).

Discussion

Understanding among-site variation

Our results show that the size-related distributions of AGB stocks and fluxes associated with growth (AWP) and mortality (AWM) vary substantially among sites. Climate explained considerable...
among-site variation in the size-related distribution of AWP. In warmer, wetter climates, the size-related distributions of AGB and AWP had higher dispersion and were more right skewed (supporting Hypothesis 1), reflecting the presence of a dense understory and some very large trees. These results were consistent with results from previous studies (Segura et al., 2002; King et al., 2006; Lutz et al., 2018) and with expected patterns of increased growth and survival of small understory trees (Valdadares & Niinemets, 2008) as well as very large trees (Koch et al., 2004; Bennett et al., 2015) in forests with higher water availability and longer growing seasons. In addition, many temperate forests have high population densities of deer and other meso-herbivores (due to missing or reduced abundances of their predators; Côté et al., 2004; Estes et al., 2011), and browsing by these herbivores may also contribute to low understory tree densities in these sites (McGarvey et al., 2013). Another factor that may contribute to the observed patterns is that many of our temperate sites (which are colder and in many cases have lower precipitation...
Fig. 2 Relationships of the dispersion and skewness of aboveground biomass (AGB) and of aboveground woody productivity (AWP) with mean annual temperature (MAT) and mean annual precipitation (MAP). Colors represent the value of the other climate variable: (a, c, e, g) MAP and (b, d, f, h) MAT. Lines display estimated effects from the multiple linear regressions dispersion $\approx$ MAT + MAP and skewness $\approx$ MAT + MAP, and the associated P-values for these effects are shown; the regression lines are represented by solid lines when the P-value is < 5% (i.e. the slope is significantly different from zero) and by dashed lines when the P-value is > 5%. The full results (including results for the dispersion and skewness of AWM and the medians of all the variables, which have a P-value > 5%) are presented in Supporting Information Table S4.
than tropical sites; Table 1) are late-succession secondary forests that might lack very large trees, and thus have less dispersed distributions of AGB with tree size (Table S2).

Soil substrate, disturbance regime, species composition, and other factors also influence AGB dynamics and their distribution as a function of tree size, within and among sites. A more stable soil substrate (e.g. deeper soils and flatter topography) could decrease the probability of windthrows, thus allowing trees to grow larger and dominate biomass fluxes; this effect has been proposed as an explanation of basin-wide variations in Amazonian forests’ structure (Quesada et al., 2012), and may explain why small trees dominate biomass dynamics in the Wanang plot that experiences frequent and severe disturbances (Figs 1, S10; Table S2; Vincent et al., 2018). Forest composition and diversity are also expected to have an important role in shaping size-related distributions of biomass stocks and fluxes (L. Poorter et al., 2015). For example, Southeast Asian forests dominated by Dipterocarpaceae had some of the largest trees and highest AWP among our sites (Danum Valley, Lambir, Pasoh, Sinharaja; Fig. 1; Table 1), even though their environmental conditions were not distinctive, suggesting potential synergies with ectomycorrhizal dominance (Brearley, 2012). Compositional shifts can also act to reduce differences in size-related distributions of biomass stocks and fluxes; for example, shifts towards more drought-tolerant species in drier sites may limit increases in mortality among large trees (Meakem et al., 2018). These environmental factors should be evaluated in future studies encompassing more sites, ideally chosen along independent environmental and disturbance gradients to reduce confounding effects of multiple variables covarying across sites.

Fig. 3 Size-related variation in relative aboveground woody productivity (RAWP, the ratio of aboveground woody productivity to aboveground biomass) and relative aboveground woody mortality (RAWM, the ratio of aboveground woody mortality to aboveground biomass) in (a, c) tropical and (b, d) temperate sites. Sites are listed in order of absolute latitude in the legend, with warm colors for tropical sites, and in cold colors for temperate sites. BCI, Barro Colorado Island; MBW, Michigan Big Woods; SCBI, Smithsonian Conservation Biology Institute; SERC, Smithsonian Environmental Research Center.
Importance of small trees in aboveground biomass fluxes

Overall, RAWP decreases across tree size classes, consistent with our expectations (Hypothesis 2a), with previous findings in tropical and temperate forests (Mencuccini et al., 2005; Kohyama et al., 2020), and with the expected decrease in photosynthetic activity (per unit mass; Drake et al., 2010; H. Poorter et al., 2015) and increase in nonwoody tissue investment (Ryan et al., 2004; Thomas, 2011) as trees get larger. This pattern was surprisingly similar across all our sites. This decrease in RAWP with size means that, consistent with our Hypothesis 2d, larger trees contribute less to AWP than to AGB, although they still dominate AWP and show higher absolute growth rates per individual tree (Müller-Landau et al., 2006a; Stephenson et al., 2014). By contrast, stems between 1 and 10 cm DBH – which are often omitted from forest inventories (e.g. Malhi et al., 2002; Ploton et al., 2020) – contribute more to AWP than to AGB (consistent with our Hypothesis 2c), with wide variation in proportional contributions among sites. Though focusing on large trees has been suggested as an effective way of reducing sampling effort in forest inventories (Bastin et al., 2018) and is the default for many remote-sensing methods that can only measure canopy trees, it could result in biased estimation of forest biomass (and thus C) fluxes.

Synergies with vegetation demographic models

Dynamic global vegetation models integrated within Earth system models increasingly include explicit modeling of tree size

---

**Fig. 4** Proportion of biomass stocks and fluxes in (a, b) small (1 ≤ DBH < 10 cm) and (c, d) large trees (DBH ≥ 60 cm). AGB, aboveground biomass; AWP, aboveground woody productivity; AWM, aboveground woody mortality; DBH, diameter at breast height. Sites are listed in order of absolute latitude in the legend and are colored in warm colors (red to green) for tropical sites and in cool colors (green to blue) for temperate sites. Tropical sites are represented by triangles and temperate sites by circles. Error bars represent 95% confidence intervals after bootstrapping 20 m × 20 m quadrats with 1000 replicates. Dashed lines correspond to (starting from the top): $y = 2x$, $y = x$, and $y = x/2$. The upper limit of the x and y-axes on panels (a) and (b) has been set to 0.20 for readability reasons; the full graph (including the Palamanui site) is shown in Supporting Information Fig. S12. BCI, Barro Colorado Island; MBW, Michigan Big Woods; SCBI, Smithsonian Conservation Biology Institute; SERC, Smithsonian Environmental Research Center.
distributions and demographic processes (Fisher et al., 2018), presenting opportunities for synergies with empirical analyses of size-structured biomass dynamics. The results presented here provide valuable benchmarks to evaluate the performance of these models, especially with respect to size-structured biomass dynamics (Fisher et al., 2018; Martínez Cano et al., 2020). Vegetation demographic models can also be used to test mechanistic hypotheses for how potential drivers (climate, soil, stand age, disturbance regime) contribute to differences in observed tree-size-related distributions of biomass stocks and fluxes. Comparative performance of different vegetation demographic model formulations against observed tree size distribution can provide insights into the relative importance of different processes in shaping size-related biomass dynamics (Longo et al., 2019; Koven et al., 2020; Martínez Cano et al., 2020). For example, a study applying the vegetation demographic model FATES to Barro Colorado Island (Panama) found that FATES overpredicted the abundance of large trees and thus overestimated forest C stocks (Koven et al., 2020). By contrast, a study applying the vegetation demographic model Lm3Ppa-Tv, which incorporates branch turnover and hydraulic constraints on photosynthesis (unlike FATES) predicted a more realistic tree size distribution at Barro Colorado Island, as well as in eight other tropical forests (including 6 sites included in this study; Martínez Cano et al., 2020).

In particular, among-site variation in size-related distributions of AWP and AWM may be explained in part by variation in how crown canopy position (e.g., emergent vs canopy vs understory) varies with diameter. After all, light availability and microclimate (e.g., wind speed, temperature, vapor pressure deficit) depend more on a tree’s relative size, and thus canopy position, than on its absolute size (Stark et al., 2012; Bachofen et al., 2020; Zelleweger et al., 2020). Crown illumination or canopy position explains considerable variation in growth and survival among trees within sites, including on the Barro Colorado Island plot (Clark & Clark, 1992; Bohlman & Pacala, 2012). Among-site variation in how crown canopy position varies with tree size can itself be explained in large part by variation in tree size distributions, because the likelihood that a tree of a given size will be in the canopy depends on the abundance of larger trees. Vegetation demographic models seek to capture these patterns through algorithms that estimate light availability for trees as a function of local stand structure (Fisher et al., 2018). These models have taken a variety of approaches to capturing size-specific AWP and AWM, from no redistribution of light between trees of different sizes to perfect plasticity approximation approaches that fill successive tree crown layers from the top down and thus lead to much higher light availability for larger trees (Adams et al., 2007). Our results on tree abundance and productivity by size class could be used to refine algorithms used to translate imposed vertical light distribution into modeled vegetation dynamics, with the goal of comparing the potential of different algorithms to capture observed AGB, AWP, and AWM patterns.

**Sources of uncertainty**

Size-specific patterns of AWP and AWM are variable over time within sites. This is especially true for AWM, which has a much larger sampling error and temporal variation than for AWP and AGB (Muller-Landau et al., 2021), which may explain why there were fewer significant effects of climate on AWM in our analyses. Climate variation and periodic disturbances, such as El Niño events, can alter size-structured mortality and productivity patterns (Meakem et al., 2018). For example, the low mortality of small stems observed in Zofin can be largely attributed to the recovery from two winter windstorms in 2007 and 2008 that created large gaps in the canopy and, thus, increased productivity and decreased mortality of small stems (Janík et al., 2018). Analyses such as ours that rely on a single 5–10 yr time period may not adequately represent long-term averages, nor the shorter term responses to weather events such as wind storms or droughts. In addition to increasing the frequency and number of censuses, pairing census data with analyses of the differential climate sensitivities of large and small trees derived from tree-ring analyses (e.g., McGregor et al., 2021) or long-term dendrometer band records could reveal how forest productivity and its size structure vary in response to climatic differences. Furthermore, combining such analyses with mechanistic modeling could enable us to test the effects of multiple environmental drivers on the distribution of biomass stocks and fluxes with tree size.

One major source of uncertainty in the patterns shown here derives from biomass allometries. AGB, AWP, and AWM were all calculated from generalized AGB allometric equations that fail to fully capture among-site (and within-site) variation (Noguenda et al., 2014). Moreover, large trees are usually undersampled in biomass allometric equations, increasing errors in estimates of their contributions (Burt et al., 2020; Disney et al., 2020). A crucial step for future research is to improve the accuracy of allometric equations across tree size classes and forests, or to get beyond the use of allometric equations altogether by developing other direct forest biomass estimation methods. One promising approach involves recently developed methods to nondestructively estimate tree woody volume, a good proxy for biomass, from terrestrial LiDAR (Stovall et al., 2018; Disney, 2019).

**Future directions**

Future work should expand on the results presented here by assessing how other C stocks and fluxes are distributed with tree size. Our analysis focuses on estimated AGB, the largest and longest-lived tree C pool, but not the only one of interest. Leaves, reproductive organs, and roots are responsible for a large proportion of net primary productivity (Malhi et al., 2011; Anderson-Teixeira et al., 2021), and allocation of C to these organs varies with ontogeny and tree size. For example, large trees allocate a larger proportion of their resources to reproduction than small trees do (Thomas, 2011). By contrast, small trees allocate a greater proportion of their C to roots than large trees do (Ledo et al., 2018). Further, our analysis of woody productivity encompasses only net increases in biomass of trees as estimated from their diameter, missing the woody productivity associated with branch turnover. Branchfall contributes to a large proportion of woody turnover (Marvin & Asner, 2016; Ouimette et al., 2018), and branch loss is expected to be higher for large senescent trees.
(Jans et al., 1993), which may moderate the lower contribution of large trees to AWP than AGB. Correctly accounting for allocation to branch turnover is critical to obtaining accurate stand-level forest dynamics in vegetation models (Martínez Cano et al., 2020), but this is difficult, and no data are available for our forest plots.

Looking forward, a key question is how climate change will alter forest biomass stocks and fluxes and their distribution across tree size. The frequency and intensity of extreme climatic events, such as droughts, floods, lightning strikes, and cyclones, are expected to increase in the future (Diffenbaugh et al., 2017; Marsooli et al., 2019). These disturbances will likely increase the mortality of large-canopy trees (and of understory trees that large trees damage when they fall) because large trees are more vulnerable to water stress (Bennett et al., 2015), are more exposed to lightning (Gora et al., 2020), and have lower mechanical stability (James et al., 2006). Lower abundance of large trees after disturbance in turn increases understory light availability, and the number and woody productivity of smaller trees (Hogan et al., 2016). However, the effect of increased light availability on the productivity of small trees adapted to dense forest microclimates may be limited by more variable precipitation regimes, and by higher temperatures that increase evaporative demand (Elliott et al., 2015; Germain & Lutz, 2020; Konapala et al., 2020; Smith et al., 2020; Muller-Landau et al., 2021). More research is needed to understand how forest tree size structure and biomass dynamics are related to climate and, in turn, how forest dynamics will respond to global climate change. In providing the first global-scale analysis of tree size structuring of biomass dynamics in forests, our analyses set a foundation for building better climate models and understanding the interactions between forests and future climate change.

Acknowledgements

CP was supported by the ForestGEO network of the Smithsonian Tropical Research Institute. We thank all technicians, volunteers and students who participated in field data collection. Acknowledgments for the support that the 25 sites included in this study received are provided in the Notes S2.

Author contributions

CP, KJA-T and HCM-L designed the research. CP carried out the data analysis, under guidance of HCM-L and KJA-T, and with input from LS. CP, HCM-L and KJA-T interpreted the results. All coauthors (except CP) participated in data collection. CP wrote the manuscript, with the help of HCM-L and KJA-T. The manuscript was reviewed by all coauthors.

ORCID

David Allen https://orcid.org/0000-0002-7443-1992
Kristina J. Anderson-Teixeira https://orcid.org/0000-0001-8461-9713
Norman A. Bourg https://orcid.org/0000-0002-1752-0637
Mohizah Bt. Mohamad https://orcid.org/0000-0003-1645-2469
David F. R. P. Burslem https://orcid.org/0000-0001-6033-0990
Chia-Hao Chang-Yang https://orcid.org/0000-0003-3635-4946
Susan Cordell https://orcid.org/0000-0003-4840-8921
Stuart J. Davies https://orcid.org/0000-0002-8596-7522
Sisira Ediriweera https://orcid.org/0000-0002-2270-6085
Christian P. Giardina https://orcid.org/0000-0002-3431-5073
Robert Howe https://orcid.org/0000-0001-8393-4981
Chang-Fu Hsieh https://orcid.org/0000-0003-4165-8100
Akira Itoh https://orcid.org/0000-0002-2493-1681
David Janik https://orcid.org/0000-0002-8271-7456
David Kenfack https://orcid.org/0000-0001-8208-3388
Kamil Král https://orcid.org/0000-0002-3848-2119
James A. Lutz https://orcid.org/0000-0002-2560-0710
Jean-Remy Makana https://orcid.org/0000-0002-6006-2938
Sean M. McMahon https://orcid.org/0000-0001-8302-6908
William McShea https://orcid.org/0000-0002-8102-0200
Xiangcheng Mi https://orcid.org/0000-0002-2971-5881
Helene C. Muller-Landau https://orcid.org/0000-0002-3526-9021
Vojtěch Novotný https://orcid.org/0000-0001-7918-8023
Michael J. O’Brien https://orcid.org/0000-0003-0943-8423
Rebecca Ostertag https://orcid.org/0000-0002-5747-3285
Geoffrey Parker https://orcid.org/0000-0001-7055-6491
Camille Piponiot https://orcid.org/0000-0002-3473-1982
Lawren Sack https://orcid.org/0000-0002-7009-7202
Sheng-Hsin Su https://orcid.org/0000-0003-1337-3335
I-Fang Sun https://orcid.org/0000-0001-9749-8324
Duncan W. Thomas https://orcid.org/0000-0003-1818-0057
Jill Thompson https://orcid.org/0000-0002-4370-2593
Maria Uriarte https://orcid.org/0000-0002-0484-0758
Yunquan Wang https://orcid.org/0000-0001-6022-2340
Ian M. Ware https://orcid.org/0000-0002-2101-5653
George D. Weiblen https://orcid.org/0000-0002-8720-4887
Timothy J. S. Whitfeld https://orcid.org/0000-0003-1850-6432
Amy Wolf https://orcid.org/0000-0001-8983-8181
Mingjian Yu https://orcid.org/0000-0001-8060-8427
Zuoqiang Yuan https://orcid.org/0000-0001-9197-7076
Daniel Zuleta https://orcid.org/0000-0001-9832-6188

Data availability

Data for plots in the ForestGEO network are available through the online portal at: http://www.forestgeo.si.edu. Aggregated data used in this study are provided in the Datasets S1–S3.

References


Condit RS. 1998. Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Berlin, Germany: Springer-Verlag.


Germain SJ, Lutz JA. 2020. Climate extremes may be more important than climate means when predicting species range shifts. *Climatic Change* 163: 579–598.


Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Total AGB, AWP, and AWM for each site and site-specific diameter classes (in cm), as presented in the figures.

Dataset S2 Total AGB, AWP, and AWM for each site by standardized diameter classes of [1,5), [5,10), [10,20), [20,30), [30,40), [40,50), [50,100), [100,200), and [200, +∞) cm DBH.

Dataset S3 Median, dispersion, and skewness of AGB, AWP, and AWM distributions at each site.

Fig. S1 Location and environmental conditions of study sites.

Fig. S2 Distribution of modulus-transformed DBH growth values from individual trees in the BCI data as an example.

Fig. S3 Distribution of modulus-transformed DBH growth values from individual trees in five different sites.

Fig. S4 Definition of diameter classes per site.

Fig. S5 Proportions of AGB stocks and fluxes in large trees, when defined as the 5% largest stems in each site.

Fig. S6 Proportions of AGB stocks and fluxes in large trees, when defined as the largest trees comprising 50% of total AGB in each site.

Fig. S7 Size-related variation in stem density, mean individual stem aboveground biomass, and total aboveground live biomass.

Fig. S8 Size-related variation in mean stem diameter growth and total aboveground woody productivity.

Fig. S9 Size-related variation in stem mortality rate and total aboveground woody mortality.

Fig. S10 Size-related distribution of AGB stocks and fluxes per site.

Fig. S11 Untruncated Fig. 1.

Fig. S12 Untruncated Fig. 4.

Methods S1 Methods for calculating instantaneous biomass fluxes.

Methods S2 Methods for gap-filling DBH growth.

Methods S3 Methods for gap-filling DBH growth.

Notes S1 Description of additional variables.

Notes S2 Site-specific acknowledgments.

Table S1 Plot initiation papers.

Table S2 Disturbances at ForestGEO sites used in this study.

Table S3 Total number of diameter classes per site.

Table S4 Estimated effects of the multiple linear regressions of the median and skewness with mean annual temperature and precipitation.

Table S5 Estimated effects of the multiple linear regressions of the median, dispersion, and skewness with mean annual temperature and SHC (moisture index).

Table S6 Wilcoxon signed-rank tests results comparing the median, dispersion, and skewness of size-related distributions in tropical vs temperate forests.

Table S7 DBH threshold per site for the alternative definitions of large trees.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the authors. Any queries (other than missing material) should be directed to the New Phytologist Central Office.