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Demographic Drivers of Aboveground Biomass Dynamics During Secondary Succession in Neotropical Dry and Wet Forests

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ABSTRACT

The magnitude of the carbon sink in second-growth forests is expected to vary with successional biomass dynamics resulting from tree growth, recruitment, and mortality, and with the effects of climate on these dynamics. We compare aboveground biomass dynamics of dry and wet Neotropical forests, based on monitoring data gathered over 3–16 years in forests covering the first 25 years of succession. We estimated standing biomass, annual biomass change, and contributions of tree growth, recruitment, and mortality. We also evaluated tree species' contributions to biomass dynamics. Absolute rates of biomass change were lower in dry forests, 2.3 and 1.9 Mg ha^{-1} y^{-1}, after 5–15 and 15–25 years after

abandonment, respectively, than in wet forests, with 4.7 and 6.1 Mg ha^{-1} y^{-1}, in the same age classes. Biomass change was largely driven by tree growth, accounting for at least 48% of biomass change across forest types and age classes. Mortality also contributed strongly to biomass change in wet forests of 5–15 years, whereas its contribution became important later in succession in dry forests. Biomass dynamics tended to be dominated by fewer species in early-successional dry than wet forests, but dominance was strong in both forest types. Overall, our results indicate that biomass dynamics during succession are faster in Neotropical wet than dry forests, with high tree mortality earlier in succession in the wet forests. Long-term monitoring of second-growth tropical forest plots is crucial for improving estimates of annual biomass change, and for enhancing understanding of the underlying mechanisms and demographic drivers.

Key words: Biomass accumulation; carbon sink; forest dynamics; Neotropics; species' dominance; tree demography; second-growth tropical forest.

INTRODUCTION

Understanding the contribution of tree growth, recruitment, and mortality to aboveground biomass accumulation during forest succession is critically important for improving estimates of global carbon budgets and fluxes, and for assessing their response to global change. In the tropics, second-growth forests are rapidly becoming an important component of the current forest area (FAO 2010; Chazdon 2014; Chazdon and others 2016), and act as a larger carbon sink than old-growth forests (Pan and others 2011; Grace and others 2014). However, considerable uncertainty remains regarding the magnitude of the carbon sink represented by second-growth tropical forests on post-agricultural land (for example, Pan and others 2011; Anderson-Teixeira and others 2013; Bongers and others 2015; Poorter and others 2016). The magnitude of the carbon sink depends on the age of second-growth forests (that is, the post-agriculture recovery time, or fallow age), previous land use, seed availability in the landscape matrix, and environmental conditions (Brown and Lugo 1990; Guariguata and Ostertag 2001). In temperate forests, several studies have used long-term monitoring of forest plots to quantify changes in aboveground biomass over succession (for example, Caspersen and others 2000; Hudiburg and others 2009; McMahon and others 2010). In tropical forests, in contrast, estimates of biomass change during succession still rely largely on chronosequence studies, a ''space-for-time'' substitution, where rates of biomass accumulation are inferred from standing biomass in plots of contrasting ages (Silver and others 2000; Marín-Spiotta and others 2008; Poorter and others 2016; but see Feldpausch and others 2007; Rozendaal and Chazdon 2015).

In tropical regions, climatic factors drive an important part of the geographic variability in biomass recovery of second-growth forests (Poorter and others 2016), and rainfall is a major driver of the structure, species richness, and stand dynamics of old-growth forests (for example, Toledo and others 2011; Lewis and others 2013; Poorter and others 2015). Tropical wet forests generally have higher stature, a denser canopy, higher standing biomass, and higher tree species richness than tropical dry forests (Brown and Lugo 1982; Murphy and Lugo 1986). Wet forests are also more dynamic (Condit and others 2004), with higher absolute rates of tree growth, mortality, and recruitment. Chronosequence studies report higher rates of biomass accumulation during succession with increasing rainfall (Silver and others 2000; Marín-Spiotta and others 2008; Becknell and others 2012; Poorter and others 2016). However, longitudinal studies on successional biomass dynamics that evaluate contributions of tree growth, recruitment, and mortality to annual rates of biomass change (Feldpausch and others 2007; Rozendaal and Chazdon, 2015), have not previously been compared between tropical wet and dry forest systems.

Successional changes in tropical wet and dry forests are driven by the availability of different key resources (Lohbeck and others 2013). In wet forests, decreasing light availability is typically regarded as a major driver of shifts in tree species composition during succession (Bazzaz 1979). Short-lived pioneer species are dominant early in succession, but their fast growth in high light trades off against high mortality in low light (Kobe 1999; Wright and others 2010), leading to a gradual increase in the abundance and biomass of shade-tolerant species during succession (Gómez-Pompa and Vázquez-Yanes 1981; Finegan 1996; Guariguata and Ostertag 2001). In dry forests, in contrast, changes in water availability are a stronger driver of successional species turnover. Light availability decreases during succession, but less so

than in wet forests (Lebrija-Trejos and others 2011). Soil water availability and relative humidity increase with the development of vegetation cover during succession (Lebrija-Trejos and others 2011; Pineda-García and others 2013), which reduces the extremely dry conditions early in succession. In the first years of succession, drought-tolerant species with high wood density (Markesteijn and others 2011), or the ability to store water in stems or roots (Pineda-García and others 2013), dominate. Dry conditions reduce seedling survival rates (for example, McLaren and McDonald 2003), whereas resprouting is an important mode of regeneration, which leads to a high abundance of multi-stemmed trees (Ewel 1977; Busby and others 2010; Dupuy and others 2012; Maza-Villalobos and others 2013).

These contrasting environmental drivers of succession are likely to differentially influence tree growth, recruitment, and mortality rates, and thus rates of biomass accumulation, in tropical dry and wet forests. Lower growth rates in dry forests are expected to result in lower rates of biomass accumulation compared to wet forests, despite higher mortality rates in wet forests. In a tropical wet forest in Costa Rica, absolute rates of biomass accumulation resulting from tree growth decreased over succession, whereas biomass loss increased due to mortality of large pioneer trees (Rozendaal and Chazdon 2015). Such changes may be less pronounced in tropical dry forest. Rates of tree growth, and particularly mortality (Lebrija-Trejos and others 2010a), may not show dramatic changes in the first decades of succession due to slower canopy development, and changes in growth and mortality rates may occur later than in wet forests. Low mortality early in succession has also been observed in temperate forests with low initial tree density and recruitment rates (Peet and Christensen 1987).

Contrasting environmental drivers of species' replacement during succession will likely also influence species' dominance of standing biomass and biomass dynamics over succession. In both dry and wet forests, biomass dynamics early in succession are probably dominated by a few tree species that successfully cope with the harsh environmental conditions in open fields (for example, Brown and Lugo 1990; Martin and others 2013). Species' dominance may be particularly common in young second-growth dry forests where strong environmental filtering results in dominance of the few species that are able to cope with extreme drought.

Here, we compare biomass dynamics during the first 25 years of succession between three dry and three wet forests, monitoring trees in permanent sampling plots from six Neotropical forest landscapes over 3–16 years. This approach allows evaluating rates of biomass change and their underlying demographic drivers across successional stages. Specifically, we test the following hypotheses: (1) absolute rates of annual biomass change will be higher in wet than in dry forests due to limited water availability in dry forest; (2) biomass change resulting from growth, recruitment, and mortality, will be higher in wet than in dry forests, and tree mortality will occur earlier in succession in wet than in dry forests because of faster canopy development in wet forests; and (3) species' dominance of biomass dynamics early in succession will be stronger in tropical dry than wet forests due to stricter environmental filtering in dry forests.

MATERIALS AND METHODS

Study Sites

We studied biomass dynamics in six Neotropical second-growth forest sites that differ in annual rainfall and rainfall seasonality. The dry forest sites, Chamela (Mora and others 2015), Nizanda (Lebrija-Trejos and others 2008), and Kiuic (J.M. Dupuy and J.L. Hernández-Stefanoni unpublished data), are located in Mexico, and vary in annual rainfall from 788 to 1129 mm, and in dry season length (<100 mm rainfall per month) from 6 to 7 months (Figure 1A; Table 1). Moist and wet forest sites, hereafter referred to as wet forest, are located in Brazil (Manaus, *Cecropia* pathway; Mesquita and others 2001; Williamson and others 2014), Mexico (Chajul; van Breugel and others 2006; van Breugel and others 2007), and Costa Rica (Sarapiquí; Chazdon and others 2005), and ranged in average annual rainfall from 2200 to 3900 mm (Figure 1A; Table 1). Manaus and Chajul have a dry season of one month and three months, respectively, whereas Sarapiquí has no dry season according to the previous definition. Prior to abandonment, land use in our second-growth forest sites was either shifting cultivation, cattle ranching, or the forest was cleared, but the land was not subsequently used (Table 1). In each forest site, trees, palms, shrubs, and columnar cacti at least 5 cm diameter at breast height (dbh) were repeatedly measured over 3 to 16 years in permanent plots, varying in size from 0.03 to 1 ha, that represented a wide range of stand ages (Figure 1B; Table 1). For multi-stemmed trees, only stems at least 5 cm dbh were included. Census interval
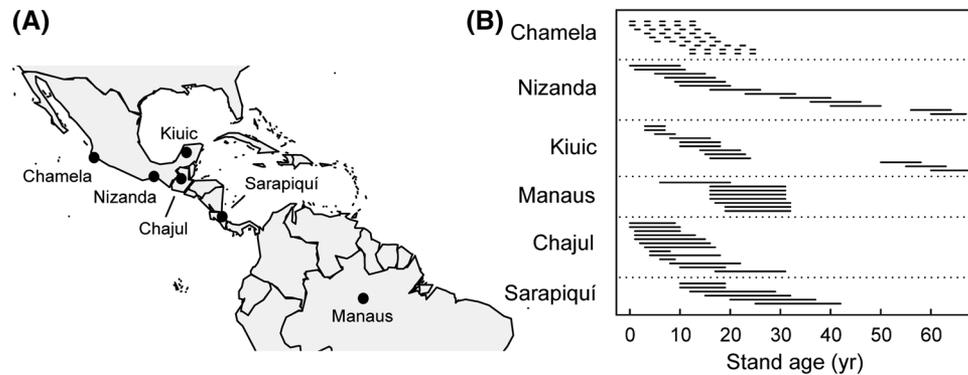
Figure 1. Geographic location and range of stand ages of the second-growth forests in each study site. **A** Map with the location of the six study sites. **B** Stand age range over which biomass dynamics were monitored for each site; each *horizontal line* represents the age range for a single plot. Plots in Chamela were monitored over 3-year intervals, plots in the other study areas were monitored at annual intervals.

length was three years for Chamela, whereas plots in the other five sites were censused annually.

Biomass Dynamics

A general allometric equation for tree biomass has yet to be developed for tropical second-growth forests. Instead, we used a global allometric equation for tropical trees based on dbh, wood density (WD), and climatic variables that was developed including trees from dry, moist, and wet second-growth forests (Chave and others 2014). We used local, or regional, species-specific WD measurements for Chamela (Barajas-Morales 1987; Martí-nez-Yrízar and others 1992), Nizanda (Lebrija-Trejos and others 2010b), Kiuic (Barajas-Morales 1987; Reyes-García and others 2012; Sanaphre unpublished data, Yam-Uicab unpublished data), Chajul (Lohbeck and others 2012), Sarapiquí (Plourde and others 2015; Rozendaal and Chazdon, 2015), and Manaus (Nogueira and others 2005; G.B. Williamson unpublished data). For species for which local WD values were not available, we used species-specific WD from a global database for all six forests (Chave and others 2009; Zanne and others 2009). If species-specific WD was not available in the global database, we used a genus-level WD average preferably based on local measurements, but otherwise from the global database. Genus-level WD is generally a good proxy for species-level WD (Chave and others 2006). If a genus-level estimate was unavailable in the global database, we applied the basal area-weighted mean WD (compare Garnier and others 2004), calculated for each plot and year.

Per plot, we calculated aboveground biomass (AGB), biomass change (ΔAGB), and biomass change resulting from tree diameter growth (ΔAGB$_{growth}$), tree recruitment (ΔAGB$_{recr}$), and tree mortality (ΔAGB$_{mort}$), per census interval. We calculated annual ΔAGB, ΔAGB$_{growth}$, ΔAGB$_{recr}$, and ΔAGB$_{mort}$ by dividing each of these variables by the length of the census interval. Biomass dynamics were calculated at the level of individual trees, not stems, as in Chamela, Nizanda, and Kiuic stems of multi-stemmed trees were not separately labeled. Thus, recruitment and loss of stems within a single tree were included in the overall biomass change fraction resulting from growth of that individual tree.

We compared biomass dynamics for two 10-year stand age classes, 5–15 years and 15–25 years after abandonment, which facilitates a comparison of biomass dynamics in two early-successional time periods. Age classes were chosen as such that all sites were represented in both age classes. For plots for which stand ages fell in both age classes, data were split to assign each resulting census interval to the corresponding age class. Although we focused on just the first 25 years of succession, estimated rates of biomass change are likely representative of second-growth forest dynamics in general, as most of these forests are cleared within 25 years after abandonment (for example, Etter and others 2005; Neff and others 2006; van Breugel and others 2013). The percent contribution of ΔAGB$_{growth}$, ΔAGB$_{recr}$, and ΔAGB$_{mort}$ to ΔAGB per site and age class was calculated by dividing average ΔAGB$_{growth}$, ΔAGB$_{recr}$, or ΔAGB$_{mort}$ (across all plots and years per age class) by the sum of average ΔAGB$_{growth}$, ΔAGB$_{recr}$, or the absolute value of average ΔAGB$_{mort}$. To compare the strength of species' dominance of biomass dynamics between dry and wet forests, we calculated the

Table 1. Characteristics of the Six Study Sites

Site	Forest type	Country	Rainfall (mm)	Temp. (°C)	Dry season	Soil type	No. of plots	Plot size (ha)	Land use history	Starting year	Last year
Chamela	DRY	Mexico	788	25	November–May	Regosols	9	0.1	Pasture	2004	2013
Nizanda	DRY	Mexico	878	27.7	November–May	Leptosols	13	0.04	Shifting agriculture	2003, 2005	2012
Kiuic	DRY	Mexico	1129	26	November–April	Lithosols, luvisols, cambisols	12	0.1	Shifting agriculture	2005, 2009	2012
Manaus	WET	Brazil	2400	26.7	August	Oxisols	8	0.03, 0.06	Clear-cut, not used	1999, 2000, 2002	2013
Chajul	WET	Mexico	3000	24	February–April	Humic acrisols	13	0.05	Shifting agriculture	2000	2013
Sarapiquí	WET	Costa Rica	3900	26	–	Oxisols, ultisols	6	1	Pasture	1997, 2005	2013

Chamela, Nizanda, and Kiuic are regarded as tropical dry forests, whereas Manaus, Chajul, and Sarapiquí are regarded as tropical wet forests. Average annual rainfall, average annual temperature, and the length of the dry season (<100 mm rainfall per month) are indicated for each site. Sarapiquí has a relatively weak dry season (>100 mm rainfall per month) from January to April. Monitoring in all sites is ongoing; the last year refers to the last monitoring year included in this study.

number of species that accounted for 80 % of standing biomass and biomass change variables per age class and site. Focusing on the dominant species only, instead of the total number of species, is unlikely to be influenced by the differences in area that was sampled across sites. We calculated the percent contribution of each species to AGB per stand age class, per site, based on the sum of AGB across all plots and years. Similarly, we calculated species' contributions to biomass change per age class as an average across all plots and years separately for biomass gain (sum of ΔAGB_{growth} and ΔAGB_{recr}) and biomass loss (ΔAGB_{mort}). In this analysis, we only included age classes for which data in at least two plots were available to provide a robust estimate of the number of species that dominate biomass dynamics for each forest site, as species composition may vary strongly from plot to plot.

Statistical Analysis

We compared AGB, annual ΔAGB, and annual contributions of growth, recruitment, and mortality to ΔAGB between tropical dry and wet forests, and between stand age classes (5–15 years and 15–25 years), using linear mixed-effects models. To assess effects of forest type and age class, we compared five models with varying fixed-effect structures: (1) forest type, age class, and their interaction; (2) forest type and age class; (3) forest type; (4) age class; and (5) a model with only an intercept. In each model, we included a random intercept per site and per plot. We applied a model selection approach based on Akaike's Information Criterion, adjusted for small sample size (AIC_c). We regarded models that differed less than two AIC_c units from each other as equally supported (Burnham and Anderson 2002). Biomass changes resulting from recruitment and from mortality were log-transformed (base 10) prior to analysis to enhance normality and homoscedasticity. We calculated the marginal (m) and the conditional (c) R^2 (Nakagawa and Schielzeth 2013). R^2 (c) indicates the variance explained by the fixed and random effects together, whereas R^2 (m) indicates the variance explained by fixed effects only. Mean predicted AGB, ΔAGB, and contributions of growth, recruitment, and mortality per age class and forest type, were calculated from the full model, based on the fixed effects only. Standard errors of the predictions were calculated using parametric bootstrapping. All analyses were conducted in R 3.1.2 (R Core Team 2014). Community-weighted mean WD was calculated using the 'FD' package (Laliberté and others 2014). Linear
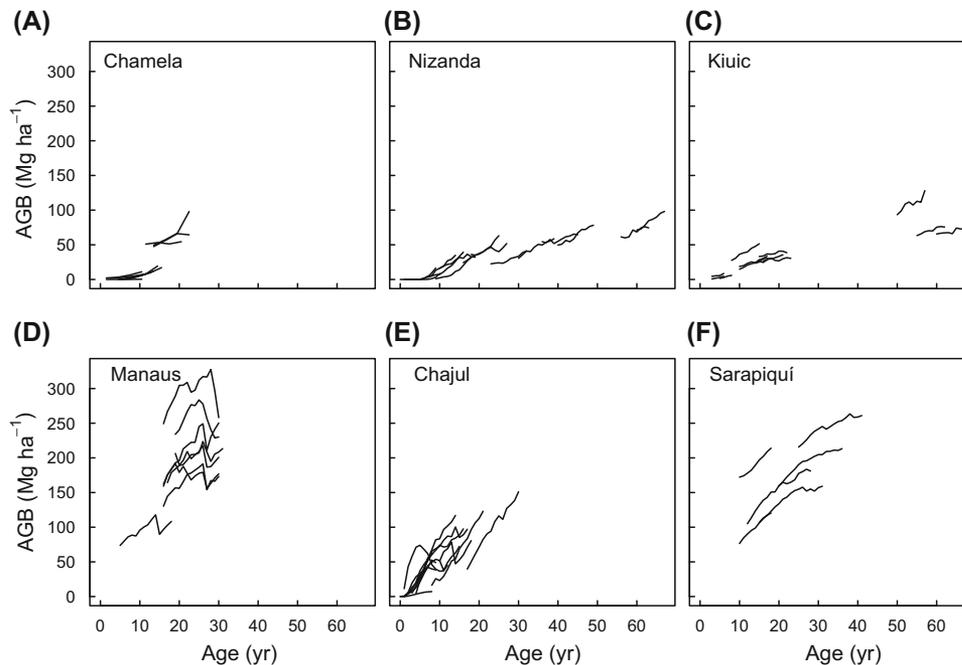
Figure 2. Aboveground biomass (AGB) against stand age in six Neotropical second-growth forests; each line represents the change in AGB over time in one plot. **A–C** Tropical dry forests. **D–F** Tropical wet forests.

mixed-effects models were performed using the 'lme4' package (Bates and others 2014).

RESULTS

Standing Biomass in Second-Growth Forests

Standing aboveground biomass (AGB) strongly varied across sites, and across plots within sites (Figures 2, 3A, B). The best model included effects of forest type and stand age class on AGB, and their interaction (Table 2). AGB was generally higher in wet than in dry forests, and increased from the 5–15 year to the 15–25 year age class (Figure 4A). For tropical dry forest, estimated AGB was 16.7 ± 25.0 (mean $\pm$ bootstrapped SE) and 31.0 ± 25.1 Mg ha^{-1} in the first and second age class, respectively, and for tropical wet forests 114.5 ± 25.0 and 143.4 ± 25.1 Mg ha^{-1}, respectively (Figure 4A).

The percentage of AGB contributed by multi-stemmed individuals varied across sites, with larger contributions in tropical dry forest sites. In dry forest, the average percentage of AGB accounted for by multi-stemmed trees across all plots and census intervals in stands 5–25 years old was $56.8 \pm 4.4\%$ (mean $\pm$ SE) for Chamela, $58.3 \pm 2.6\%$ for Nizanda, and $45.8 \pm 2.6\%$ for Kiuic. In wet forest, the average percentage of AGB in multi-stemmed trees was $19.4 \pm 2.0\%$ in Manaus, $17.4 \pm 1.5\%$ in Chajul, and $20.8 \pm 1.9\%$ in Sarapiquí.

Rates of Biomass Change in Second-Growth Forests

Annual rates of aboveground biomass change (ΔAGB) varied strongly among and within sites (Figures 3C, D, S1). On average, ΔAGB was positive in all sites (Figure 3C, D), indicating net AGB accumulation (Figure 2). In some census intervals, however, ΔAGB was negative, particularly in Manaus and Chajul (Figures 2, S1), due to large biomass losses from tree mortality. Variation in ΔAGB was largely explained by forest type, although a model with both forest type and age class, and the full model, were equally supported (Table 2). Estimated annual ΔAGB was lower in dry forest (2.3 ± 0.8 and 1.9 ± 0.9 Mg ha^{-1} y^{-1} for the first and second age class, respectively) than in wet forest (4.7 ± 0.8 and 6.1 ± 0.7 Mg ha^{-1} y^{-1}; Figure 4B).

Biomass Dynamics During Secondary Succession

Variation in annual biomass change resulting from tree growth (ΔAGB$_{growth}$) was largely explained by forest type (Table 2): ΔAGB$_{growth}$ was considerably lower in tropical dry forests than in tropical wet forests, but did not differ between age classes (Figure 4C). Surprisingly, biomass change resulting from recruitment (ΔAGB$_{recr}$) did not differ significantly between tropical dry and wet forests (Fig-
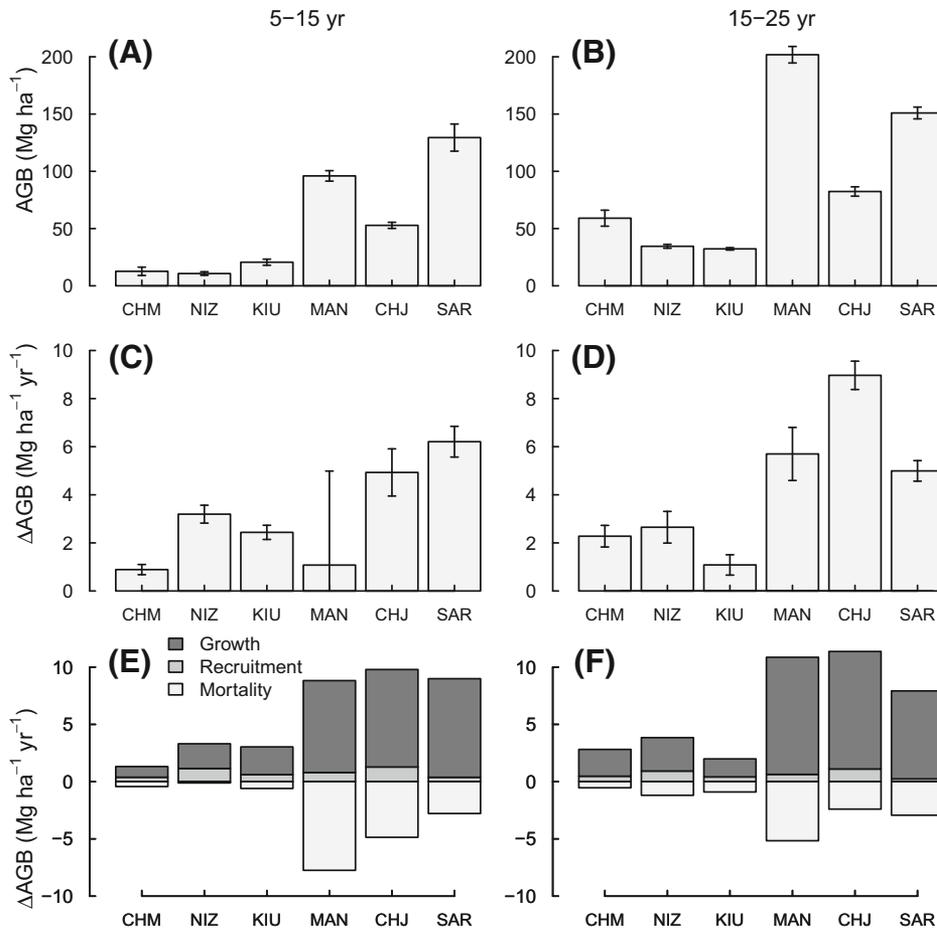
Figure 3. Standing aboveground biomass (AGB), annual biomass change (ΔAGB), and the contribution of tree growth, recruitment, and mortality to ΔAGB in two stand age classes (5–15 years and 15–25 years) for second-growth forests in six study sites in the Neotropics. For a given age class and forest site, bars indicate the mean (± SE) across all plots and years. **A**, **B** AGB; **C**, **D** ΔAGB; **E**, **F** Contribution of tree growth, recruitment, and mortality to ΔAGB. CHM = Chamela; NIZ = Nizanda; KIU = Kiuic; MAN = Manaus; CHJ = Chajul; SAR = Sarapiquí. CHM, NIZ, and KIU are dry forests; MAN, CHJ, and SAR are wet forests.

Table 2. Results from Mixed-effects Models for Standing Aboveground Biomass (AGB), Annual Biomass Change (ΔAGB), and Biomass Change Resulting from Tree Growth (ΔAGB_growth), Recruitment (ΔAGB_recr), and Mortality (ΔAGB_mort) as a Function of Forest Type (Dry vs. Wet) and Age Class

Model (fixed effects)	AGB			ΔAGB			ΔAGB_{growth}			ΔAGB_{recr}			ΔAGB_{mort}		
	ΔAIC_c	R^2(m)	R^2(c)	ΔAIC_c	R^2(m)	R^2(c)	ΔAIC_c	R^2(m)	R^2(c)	ΔAIC_c	R^2(m)	R^2(c)	ΔAIC_c	R^2(m)	R^2(c)
Forest type + age class + forest type × age class	**0.00**	**0.58**	**0.96**	1.81	**0.08**	**0.14**	3.17	0.56	0.69	3.19	0.03	0.20	**0.00**	**0.27**	**0.37**
Forest type + age class	8.22	0.57	0.96	**1.17**	**0.08**	**0.14**	**1.09**	**0.56**	**0.69**	**1.31**	**0.03**	**0.20**	17.53	0.21	0.41
Age class	12.72	0.02	0.96	9.53	0.01	0.14	20.07	0.00	0.69	**0.00**	**0.01**	**0.20**	20.20	0.02	0.40
Forest type	92.37	0.51	0.96	**0.00**	**0.07**	**0.14**	**0.00**	**0.55**	**0.69**	2.32	0.02	0.20	21.17	0.21	0.41
None (intercept only)	96.30	0.00	0.96	9.42	0.00	0.14	18.67	0.00	0.70	**0.84**	**0.00**	**0.20**	24.66	0.00	0.42

The deviation in Akaike's Information Criterion, adjusted for small sample size (ΔAIC_c), from the best model is indicated. Best models are indicated in bold. The marginal R²(m) indicates the variance explained by fixed effects only, the conditional R²(c) indicates the variance explained by both the fixed and random effects.

ure 4D), and did not change across age classes (Table 2). The best model for biomass change resulting from mortality (ΔAGB_mort) included forest type, age class, and their interaction (Table 2). Generally, ΔAGB_mort was higher in wet forests,

particularly in the 5–15 year age class (Figure 4E). In tropical dry forests, ΔAGB_mort increased from the first to the second age class, while in tropical wet forests, ΔAGB_mort decreased over succession (Figure 4E).
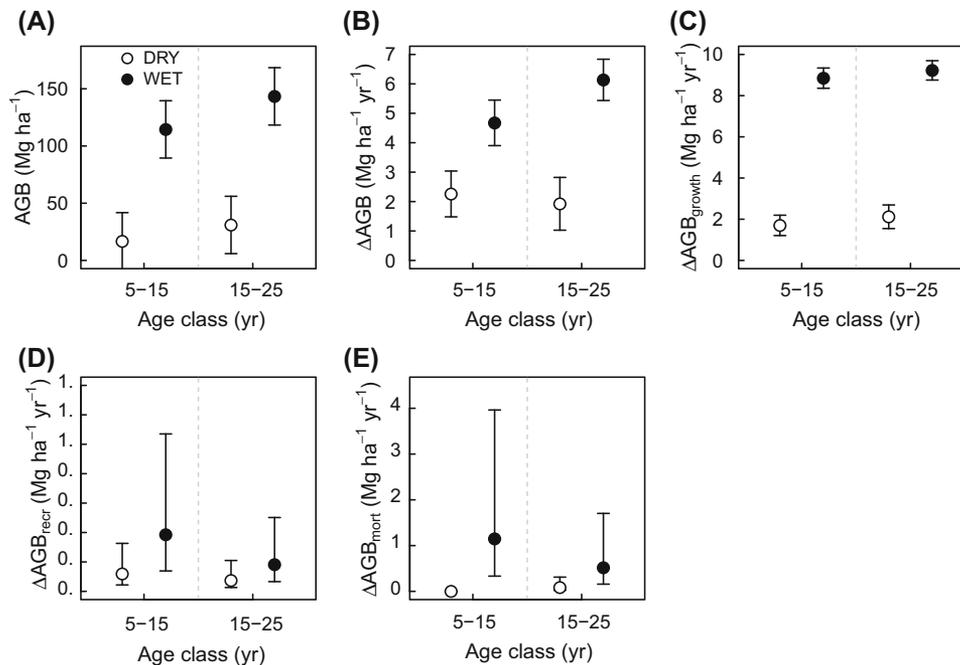
Figure 4. Predicted mean (±SE) standing aboveground biomass (AGB), annual biomass change (ΔAGB), and the contribution of tree growth, recruitment, and mortality to ΔAGB in two stand age classes, compared between dry and wet tropical forest sites, and across age classes (5–15 years and 15–25 years after abandonment). **A** Mean standing aboveground biomass (AGB), **B** annual biomass change (ΔAGB), **C** contribution of tree growth (ΔAGB$_{growth}$), **D** contribution of recruitment (ΔAGB$_{recr}$), and **E** contribution of mortality (ΔAGB$_{mort}$).

For both forest types, tree growth was the main driver of annual biomass change (ΔAGB) in the first age class, accounting for an average of 53.3–69.7% and 48.4–74.5% of ΔAGB in tropical dry and wet forests, respectively (Figure 3E, F). In the same age class, the contribution of mortality was much higher in tropical wet forests (23.6–46.7% of ΔAGB) than in dry forests (3.3–24.5% of ΔAGB). Although the absolute contribution of recruitment to ΔAGB (ΔAGB$_{recr}$) did not differ between forest types, its relative contribution was higher in tropical dry forests, 16.9–33.7% of ΔAGB, than in wet forests, (3.2–8.7%; Figure 3E, F). In 15- to 25-year-old forests, tree growth was still the main driver of ΔAGB in both forest types. Mortality became an equally important driver of ΔAGB in tropical dry forests (16.0–31.3%), as in tropical wet forests (17.4–32.2%), but recruitment remained more important in dry than in wet forests (Figure 3E, F).

Species Contributions to Standing Biomass and Biomass Dynamics

Standing aboveground biomass (AGB) tended to be dominated by fewer species in dry than in wet forests, but differences between age classes were small (Figure 5). In Nizanda, one of the dry forest sites, only two species (*Mimosa acantholoba* var. *eurycarpa* and *Mimosa tenuiflora*) accounted for 80% of AGB across age classes during the first 25 years of succession. In Kiuic, eight species comprised 80% of AGB across age classes. In Chamela, 18 and 16 species, in the first and second age class, respectively, accounted for 80% of AGB. In the wet forests, 16–23 species comprised 80% of AGB across all sites and age classes (Figure 5).

Across all sites and age classes, an average of 18 species comprised 80% of ΔAGB resulting from the sum of tree growth and recruitment. Fewer species dominated ΔAGB resulting from mortality (on average seven species; Figure 6). Both ΔAGB resulting from the sum of growth and recruitment, as well as ΔAGB resulting from mortality, tended to be driven by fewer species in tropical dry than wet forests, with the exception of one dry forest site, Chamela (Figure 6). Differences in species' dominance of biomass change between age classes were not consistent across sites, as dominance either increased or decreased from the first to the second age class (Figure 6).
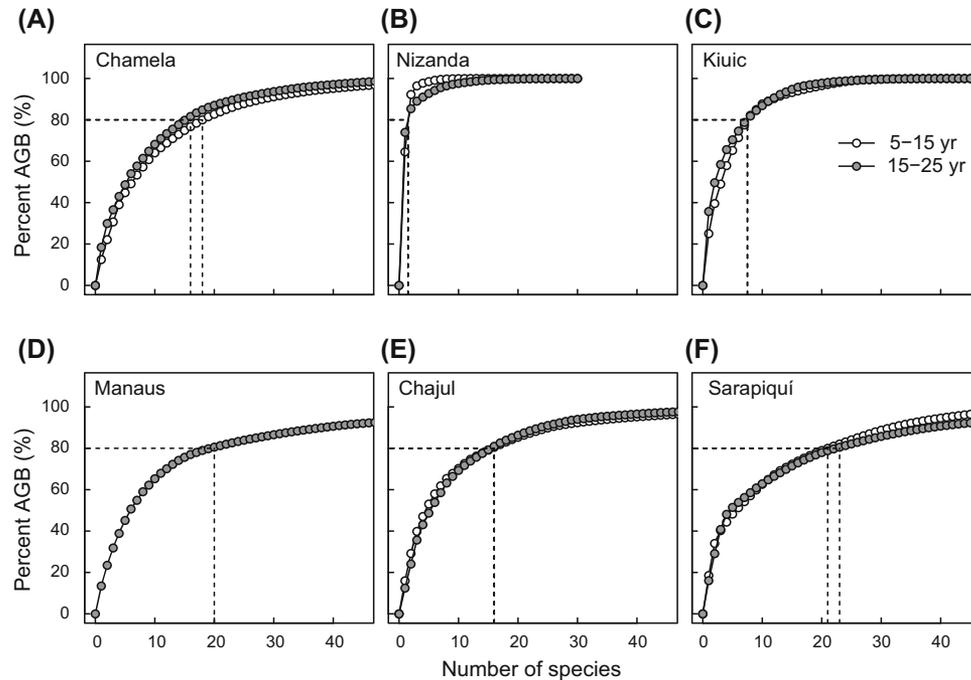
Figure 5. Cumulative contribution (in %) of individual species to standing aboveground biomass (AGB) in young (5–15 years) and intermediately aged (15–25 years) Neotropical second-growth dry and wet forests. Percentages are calculated based on the sum of AGB across all plots and years per age class for each of the sites. Only age classes with data from at least two plots for a site were included. *Dashed lines* indicate the number of species that account for 80% of AGB per age class.

DISCUSSION

Contrasting Biomass Dynamics in Second-Growth Tropical Dry and Wet Forests

Biomass dynamics contrasted strongly between early-successional tropical dry and wet forests. Absolute rates of biomass accumulation during early succession were faster in tropical wet than in tropical dry forests, supporting hypothesis 1. Differences in biomass dynamics in our study likely resulted from differences in total annual rainfall. Previous land use may also influence successional change (Longworth and others 2014; Jakovac and others 2015; Mesquita and others 2015), and thus biomass dynamics, but land use types were not consistently different between the dry and wet forests in our study (Table 1). Nevertheless, the relatively fast biomass dynamics in Manaus may have resulted from the fact that fallows were clearcut, but not subsequently used. Soil fertility may also be an important driver of tree growth early in succession (van Breugel and others 2011), and thus of successional change (Powers and others 2009).

In our sites, however, total annual rainfall is likely a stronger driver of biomass dynamics than soil fertility, as on average, our three dry forest sites have higher site-level soil fertility than the three wet forest sites (Poorter and others 2016), but slower biomass dynamics. Although previous land use and soil fertility likely also influence biomass dynamics during succession, we cannot quantify their effects with the currently available data on successional biomass dynamics in the Neotropics.

As expected, faster biomass change in wet forests resulted from high tree growth rates, despite high mortality rates. These results support the notion that successional changes proceed faster in wet than in dry forests (Ewel 1977). Tree mortality during stand-level thinning was lower, and occurred later in succession, in dry than in wet forests (Figures 3E, F, 4E), presumably because of weaker competition for light in dry forests and slower tree growth due to limited water availability. Recruitment did not differ among forest types, thus hypothesis 2 was just partly supported. Previous results for the Nizanda dry forest site also indicate that relative mortality rates increased with stand
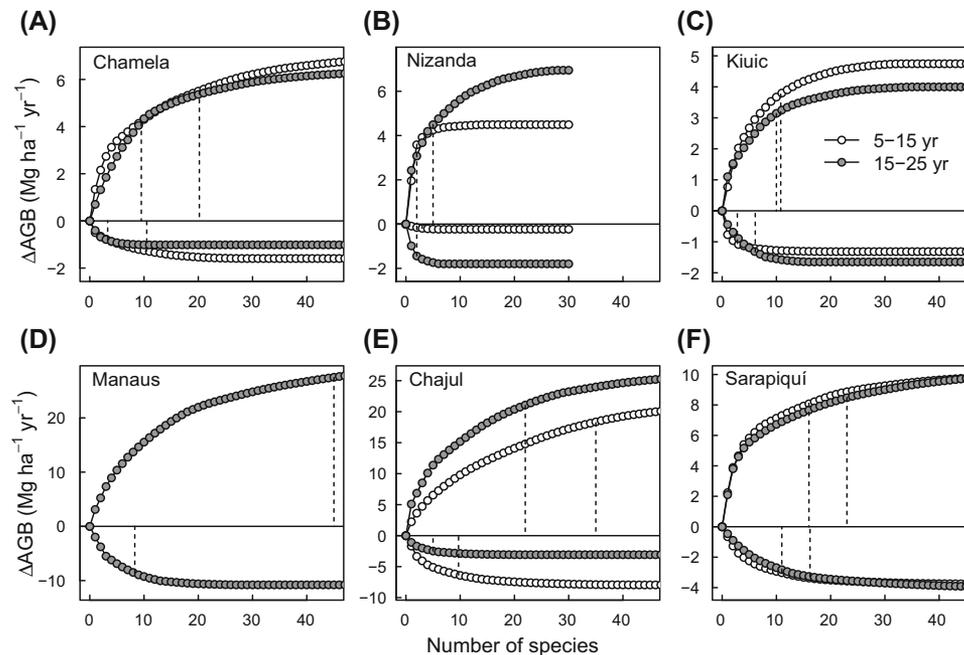
Figure 6. Cumulative contribution of individual species to annual aboveground biomass change (ΔAGB) in young (5–15 years) and intermediately aged (15–25 years) Neotropical second-growth dry and wet forests. *Positive values* are the sum of ΔAGB resulting from tree growth and recruitment, *negative values* indicate ΔAGB resulting from tree mortality. Cumulative values are calculated based on species' averages across plots and years per age class for each of the sites. *Dashed lines* indicate the number of species that account for 80% of ΔAGB resulting from either the sum of growth and recruitment, or from mortality, per age class. Note the different scales on the *y*-axis.

age during early succession, and that a maximum was attained around 20 years after abandonment (Lebrija-Trejos and others 2010a). The high mortality in the first age class in wet forests likely reflects mortality of small, suppressed pioneer trees (Chazdon and others 2005; van Breugel and others 2006; van Breugel and others 2013; Longworth and others 2014), and in some plots pathogen outbreaks may also have contributed to high mortality of pioneer trees (van Breugel and others 2007). The overall higher mortality in wet forests during the first 25 years of succession might also partly result from the short lifespan (a few decades) that characterizes pioneer species (Finegan 1996; Martínez-Ramos and Alvarez-Buylla 1998; Guariguata and Ostertag 2001). In Manaus, mortality in the second age class even decreased plot-level AGB in some plots (Figure 2D) due to massive mortality of the short-lived pioneer *Cecropia* (Figure 2D; Longworth and others 2014). Although short-lived pioneer species are also found in tropical dry forests (Brienen and others 2009), drought-tolerant species with a conservative strategy (Lohbeck and others 2013), and probably a longer lifespan, dominate the vegetation.

Species' Dominance of Biomass Dynamics During Dry and Wet Forest Succession

Species' dominance was strong in both dry and wet early-successional forests. In both forest types, few species accounted for 80% of standing biomass and biomass change. Species' dominance decreased over succession, in agreement with other studies (Finegan 1996; van Breugel and others 2007; van Breugel and others 2013), as biomass change resulting from mortality was driven by fewer species than biomass change resulting from growth and recruitment (Figure 6). Standing biomass and biomass dynamics tended to be driven by fewer species in tropical dry than wet forests, partly supporting hypothesis 3, which may indicate stronger environmental filtering in dry systems that prevents species establishment under harsh conditions (compare Lebrija-Trejos and others 2010b).

We hypothesize that dominance is driven by distinct ecological mechanisms in early-successional dry and wet forests, as different processes can lead to species' dominance during succession (Lohbeck and others 2014). In dry forests, only the few

species with functional traits to cope with severe drought may persist early in succession. In addition, dominance might partly result from the high abundance of multi-stemmed trees in our dry forests. Resprouting may promote dominance through enhanced persistence of individual trees of a few species early in succession, as multi-stemmed trees have a lower risk of mortality than single-stemmed trees (compare Bellingham and Sparrow 2009; Tanentzap and others 2012). Resprouting was more prominent in our dry forests, but similar processes could lead to dominance by multi-stemmed trees in second-growth wet forests after high-intensity land use (Jakovac and others 2015). In our wet forests, in contrast, dominance likely results from intense competition for light, where the first-established, fast-growing, short-lived pioneer species monopolize access to light (van Breugel and others 2012). Shade-tolerant species establish early in succession (Peña-Claros 2003; van Breugel and others 2007; van Breugel and others 2013), but their biomass remains low because of their low growth rates (Chazdon and others 2010; Rozendaal and Chazdon 2015). Future studies should unravel underlying mechanisms, and the nature of competitive interactions among individual trees, as well as other biotic interactions (for example, herbivory, diseases, mutualisms) during old-field succession in tropical dry and wet forest sites, to enhance understanding of processes leading to species' dominance of biomass change.

Implications of Contrasting Successional Biomass Dynamics in Dry and Wet Forests

To our knowledge, this is the first study that quantifies annual biomass change and its underlying demographic drivers in second-growth tropical dry and wet forests during the first 25 years of succession. We found higher standing biomass in second-growth wet than dry forests and calculated AGB values roughly agree with estimates from chronosequence studies in other tropical dry and wet forest landscapes (Hughes and others 1999; Silver and others 2000; Read and Lawrence 2003; Gehring and others 2005; Marín-Spiotta and others 2008; Becknell and others 2012; Poorter and others 2016). However, our estimates of annual biomass change in the first 25 years of succession, 1.9–2.3 Mg ha^{-1} y^{-1} in second-growth tropical dry forests, and 4.7–6.1 Mg ha^{-1} y^{-1} in wet forests, are lower than previously reported estimated rates from chronosequence data. A worldwide meta-analysis of chronosequence data found higher rates of bio-

mass accumulation for two age classes (<18 years and ≥18 years; Bonner and others 2013), but no second-growth forest sites with average annual rainfall below 1200 mm were included, thus their study likely overestimates rates of biomass accumulation for dry forests. Similarly, proposed rates of biomass change for country-level calculations of carbon fluxes for forests not more than 20-year old are higher than our estimates: 11 Mg ha^{-1} y^{-1} for tropical rain forest, 7 Mg ha^{-1} y^{-1} for tropical moist forest, and 4 Mg ha^{-1} y^{-1} for tropical dry forest (IPCC 2006). The rate of carbon accumulation of 3.8 Mg C ha^{-1} y^{-1} for tropical forest regrowth in the Americas calculated by Pan and others (2011) is also higher than our estimates.

Our estimates of annual rates of biomass change are likely to improve predictions of the extent of the carbon sink in regenerating tropical forests (for example, Grace and others 2014). Incorporating estimated rates of biomass change for dry and wet forests separately could have profound consequences for the estimated size of the carbon sink in second-growth Neotropical forests, depending on the area that they comprise. Estimates of rates of biomass accumulation during succession could be further improved by quantifying rates of biomass change in forests beyond 25 years after abandonment, and by including more sites along the rainfall gradient instead of two broad forest types. Within second-growth dry forests, for example, rates of biomass accumulation increase with annual rainfall (Becknell and others 2012). Also, estimated rates could be refined further by accounting for effects of previous land use and soil fertility. With the increasing area of second-growth forest in the Neotropics, our improved estimates of biomass dynamics are highly important for fueling realism into the debate on the role of tropical forests in climate change mitigation.

Overall, our results indicate that biomass dynamics during succession are faster in Neotropical wet than dry forests, with high tree mortality earlier in succession in the wet forests. Long-term monitoring of second-growth tropical forest plots is crucial for improving estimates of annual biomass change, and for enhancing understanding on the underlying mechanisms by quantifying demographic drivers.

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