Carbon cycling in secondary tropical dry forest from species to global scales

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Abstract

Tropical forests play an important role in the global carbon cycle but significant questions remain about the distribution of carbon stocks and the controls over carbon cycle processes in these forests. This is especially true with tropical dry forests which comprise as much as 43% of global tropical forests, but have been studied less and impacted more by human activities. In many areas, tropical dry forests are recovering from clearing by humans and few studies have investigated the regional and global carbon cycle implications of this increasing area of secondary tropical dry forests. This dissertation describes three projects that examined the global, regional, and stand-scale patterns of carbon uptake and storage in secondary tropical dry forests. In Chapter 1, I reviewed literature on carbon stocks in mature and secondary tropical dry forests around the world and analyzed the global contribution of these forests. I found that carbon stocks in mature tropical dry forests increased linearly with mean annual precipitation and I conclude that restoring tropical dry forest could make a significant global contribution to climate change mitigation. In Chapter 2, I studied landscape level controls of aboveground biomass and plant functional trait distributions in secondary tropical dry forests of northwestern Costa Rica. I found that edaphic factors, and plant functional traits explain little additional variation in biomass after accounting for stand age but that the dominant plant traits in a community are well correlated with succession and soil properties. I conclude that plant trait distributions indicate soil and succession driven changes in stand level function, but that these changes are not reflected in the landscape scale distribution of biomass. In Chapter 3, I measured aboveground net primary productivity in 18 secondary forest plots in northwestern Costa Rica over three years. I found that large inter-annual differences in precipitation do not significantly affect ANPP and that variation in litterfall and biomass among our plots is explained by different factors. I conclude tropical dry forest ANPP is well buffered against future climate change driven variation in precipitation and that community weighted means of plant functional traits explain significant portions of the variation in ANPP and its components among our plots. Overall, I conclude that the landscape-scale distribution of ecosystem processes like aboveground net primary productivity is easier to explain with stand age, soils, and plant functional traits compared to ecosystem properties like biomass stocks, which may be in part driven by stochastic stand level processes. Despite these difficulties in understanding variation, secondary tropical dry forests have a large potential to be significant carbon sinks and restoration of these forests should be promoted to mitigate climate change.

Table of Contents

List of Tables

List of Figures

Chapter 1

Introduction

It is well known that tropical forests play an important part in the global carbon cycle but significant questions remain about the distribution of carbon stocks and the controls over carbon cycle processes in these forests. More than half of the world's carbon stored in forests is located in the tropics (212-247 Gt C; (Dixon et al. 1994, Saatchi et al. 2011)) and tropical forests account for 32% of the world's terrestrial net primary productivity (Field 1998). Due to their significance for the global carbon cycle, preserving and restoring tropical forests has been promoted as an important climate change mitigation strategy (Pacala and Socolow 2004, Gibbs et al. 2007). Nevertheless, important questions remain about the amount of carbon of taken up by forests (Clark 2004), and the variation of carbon pools and fluxes at both landscape and regional scales (Clark and Clark 2000, Baraloto et al. 2011, Cleveland et al. 2011). A complete understanding of the size, geographic distribution, and controls on carbon pools and fluxes in tropical forests is thus necessary for both global biogeochemistry and policy formation, but the complexity and diversity of tropical forests makes achieving this goal difficult.

Tropical dry forests make up as much as 42% of all tropical forests (Murphy and Lugo 1986), but have historically been impacted more by human activities (Trejo and Dirzo 2000, Hoekstra et al. 2004), and studied less by researchers (Sanchez-Azofeifa et al. 2005), compared to tropical rain forests. Like other tropical forests, dry forests take up and store significant amounts of carbon (Jaramillo et al. 2011). Furthermore, tropical dry forests are recovering from disturbances in many areas due to conservation efforts and land use changes (Calvo-Alvarado et al. 2009, Redo et al. 2012) and these secondary forests have the potential to take up and store significant amounts of carbon (Silver et al. 2000). Currently our understanding of carbon cycling in tropical dry forests, and especially secondary dry forests, lags behind that of other ecosystems (Sanchez-Azofeifa et al. 2005).

Secondary forests across the tropics are receiving more attention due to their increasing area and potential for carbon storage and biodiversity conservation (Brown and Lugo 1990a, Finegan 1996, Silver et al. 2000, Wright 2005, Dent and Wright 2009). Carbon storage in aboveground biomass has been found to recover rapidly with forests gaining as much as 70% of their height and basal area after just 25 years (Silver et al. 2000, Marín-Spiotta et al. 2008). This potential carbon sink deserves more attention, especially in tropical dry forests where forest recovery is growing.

Understanding the spatial distribution of carbon pools and fluxes across large and small scales is important for determining the effects of tropical forests on regional and global carbon cycling. Tropical forests experience significant amounts of land cover change and their disproportionately high carbon density means that clearing or restoring a hectare of tropical forest is likely to have greater carbon cycle consequences than altering the same area of most other ecosystems (Foley et al. 2005, Houghton 2005). Furthermore, increased temperatures and altered precipitation patterns due to climate change are likely to affect tropical forests and feed back to the carbon cycle and the climate system (Miles et al. 2004, Cramer et al. 2004, Corlett 2011). Predicting these effects of both land-use change and climate change on tropical forest carbon cycling requires a detailed understanding of how tropical forest pools vary across regional and local scales with climate, environment, and biotic factors. While some progress has been made towards meeting this need, both biomass distributions and net primary productivity remain poorly understood (Houghton 2005, Cleveland et al. 2011).

The work reported in this dissertation addresses the important question of understanding the distribution of carbon cycle pools and fluxes and the factors that drive them at multiple scales. This work focused on tropical dry forests globally and locally in the Guanacaste Province of northwestern Costa Rica. I focused on secondary tropical dry forests and worked to understand how carbon storage in biomass and net primary productivity vary both spatially across the landscape and temporally with secondary succession. The three chapters of this dissertation address three goals, to: 1) describe the global distribution of biomass carbon stocks in mature and secondary tropical dry forest across climate and succession, 2) determine what factors drive the landscape scale distribution of aboveground biomass in a secondary tropical dry forest of northwestern Costa Rica, and 3) quantify aboveground net primary productivity in secondary tropical dry forests and study its variation across years, biotic and abiotic variables, and succession. Collectively, these three studies provide measurements of carbon pools and fluxes where few exist, contribute to the understanding of which factors drive carbon cycling, and synthesize current knowledge from around the globe.

In Chapter 2, I performed a literature review of the global patterns of tropical dry forest biomass with climate and succession. Patterns from other studies suggest that biomass increases with annual precipitation, and I investigated that pattern among tropical dry forest sites from around the world with the largest database of both published and unpublished studies that has been assembled to date. A large portion of biomass data from tropical dry forests is from secondary forests of various ages, and I also explored how the recovery of tropical dry forests varied from the dry to the wet end of the tropical dry forest range. I used newly developed spatial data on both the distribution of tropical dry forests and biomass to estimate how much biomass currently exists in tropical dry forests and how much more biomass could potentially exist if tropical dry forests were restored to a mature state. These results provide a global picture of aboveground biomass in tropical dry forests and how it varies across climate and succession. However, a major limitation of this dataset was a lack of ancillary data to evaluate the effect of other biotic or abiotic factors on the distribution of biomass. To address this question I examined biomass distribution at a much finer scale.

Chapter 3 presents results from a regional scale study of biomass and its drivers across succession and the landscape. I used stand age, soil physical and chemical properties, tree species richness, and the community weighted functional traits of species to explain the distribution of biomass. I used structural equation modeling, a technique that also allowed me to examine how succession and soils affect the distribution of functional traits across the secondary tropical dry forest. These results about the distribution of functional traits and the distribution of biomass can aid carbon cycle modelers and those that seek to understand the effects of changing species composition over space and time on ecosystem processes.

Chapter 4 explores net primary productivity, the total carbon gained by an ecosystem through photosynthesis minus the carbon lost to plant respiration. I measured leaf litterfall and biomass increment – the two largest component fluxes of aboveground net primary productivity, in plots arrayed along gradients of stand age, edaphic variation and species composition for three years. This study design allowed me to partition variation in ANPP into sources due to climate, succession, plant functional traits and soils. I further examined the inter and intra-annual variation in litterfall and its components, which determines in part how much carbon is moving from the forest canopy to the forest floor each year. Finally, I examined the relationships between relative growth of common tree species and the functional traits of these species.

Together these results represent a significant contribution to tropical dry forest ecology and carbon cycle research. My findings also inform efforts to use forest restoration as a climate change mitigation tool. The large area of tropical dry forest that has been converted to pasture or agricultural land represents a large potential carbon sink if some of this can be restored to forest. This work also contributes to efforts to understand how plant functional traits might be used to explain or predict ecosystem functions like carbon uptake and storage. As with much research, this work may open up as many questions as it answers, but it remains a solid set of results which push these areas of research forward.

Chapter 2

Aboveground biomass in mature and secondary seasonally dry tropical forests: a literature review and global synthesis

Introduction

Seasonally dry tropical forests (SDTFs) comprise a globally extensive but understudied biome. Estimates of the global extent of SDTF vary between 1 and 7 million km^2 depending on methods and the definition of seasonally dry tropical forest (Grainger 1996, Mayaux et al. 2005, Miles et al. 2006). SDTF, typically defined as tropical forests with 250-2000 mm of rain per year and a strong dry season of at least 3-4 months, may represent as much as 42% of all tropical forest ecosystems (Murphy and Lugo 1986). Despite their classification as “dry” forests, SDTF can receive large amounts of annual precipitation relative to most temperate forests and likely store significant amounts of carbon per unit land area due to both large stature and high wood density (Chave et al. 2006). However, large areas of SDTF have been cleared for agriculture because both the climate and soils that support SDTF are also suitable for many types of farming and ranching (Trejo and Dirzo 2000). The original extent of SDTF is unknown but estimates suggest that 48.5% of total SDTF area has been converted to other land use (Hoekstra et al. 2004). Due to social and economic changes large areas of SDTF are growing back in Central America (Calvo-Alvarado et al. 2009). These factors underscore the importance of understanding carbon stocks in SDTF, but to date relatively little research has been done in these ecosystems.

Protecting and restoring tropical forests is one strategy for mitigating climate change (Pacala and Socolow 2004) and estimating and monitoring carbon stocks is a necessary first step (Gibbs et al. 2007). Future carbon offset markets may mean that nations and land owners can receive payment for restoring and preserving forested lands

(Parker et al. 2008). To assess the carbon value of a particular forest stand, traders and landowners must be able to estimate the size of forest carbon stocks. Predicting forest carbon stocks requires an understanding of the factors that control the potential biomass at a site and the expected rate of carbon accumulation on sites recovering from disturbance.

Both the total amount of biomass in mature forest and the rate of biomass accumulation following forest clearing or disturbance may vary as a function of biophysical factors (Brown and Lugo 1990b). Published estimates of aboveground biomass for SDTF vary by an order of magnitude from 28 to 390 Mg ha^{-1} (Martínez-Yrízar 1995, Jaramillo et al. 2011). This large range includes estimates from early and late successional forests and from forests in flood plains as well as more typical upland areas. Moreover, these estimates are biased towards a few sites, especially those in Mexico, and give little understanding of how climatic and successional factors lead to different levels of carbon stored in SDTF.

Biomass in mature tropical forest is generally assumed to increase along precipitation gradients (Brown and Lugo 1982, Murphy and Lugo 1986, Malhi et al. 2006). Evidence from the Amazon basin shows that biomass is well correlated with annual rainfall across a gradient from 1000 mm to 2400 mm (Saatchi et al. 2007). Precipitation is likely the most important factor in setting an upper limit for SDTF (Brown and Lugo 1982). Deciduous trees are a conspicuous component of SDTF (Singh and Kushwaha 2005), and the length of the leafless period is correlated with the amount of precipitation. This suggests that more precipitation allows for greater biomass accumulation each year and, ultimately, larger overall biomass stocks. While there are other potential factors controlling biomass in SDTF including life history traits and the availability of light and nutrients (Baker et al. 2003), water may have the strongest effect as it varies dramatically between conditions of scarcity in the dry season to overabundance in the wet season. In wetter forests nutrients and light may be more important for limiting growth and carbon storage (Graham et al. 2003, Cleveland et al. 2011) whereas dry forests are thought to have less nutrient leaching and their strong and lengthy droughts mean that water availability often constrains growth (Eamus 1999).

Aboveground biomass increment (ABI) is the change in standing biomass from one measurement period to the next. Globally, ABI has been found to be related to stand age, growing season length, and mean growing season temperature, but soils and past land use are also important factors (Johnson et al. 2000, Zarin et al. 2001). Other studies explain ABI in tropical forests as a function of stand age and have shown that the relationship between ABI and stand age changes with MAP (Marín-Spiotta et al. 2008). The data used in these studies are largely based on chronosequences or repeated measurements of the same stands. Problems exist with both approaches as forest age can be difficult to estimate and the length of repeated measurement studies is rarely longer than a few years (Feldpausch et al. 2007). However, studies using either approach typically show that biomass increases with time, but at a decreasing rate until the forest reaches a near steady state (Brown and Lugo 1990a, Pregitzer and Euskirchen 2004).

Here we combine published and unpublished estimates of aboveground biomass from SDTF around the world and examine the variation in aboveground biomass across the range of successional stages and climates in which SDTF occur. Other efforts have reviewed estimates of SDTF biomass (Martínez-Yrízar 1995, Marín-Spiotta et al. 2008, Jaramillo et al. 2011). Our study differs from Jaramillo et al. (2011) and Martínez-Yrízar (1995) in that we include a larger number of sites and separately analyze the affects of both forest age and environmental factors on the distribution of biomass. We also use the results of these analyses to evaluate the significance of SDTF for the global carbon cycle. The goals of this study were to: 1) explain the patterns of aboveground biomass in mature SDTF across precipitation gradients, 2) explain the patterns of biomass accumulation in regenerating SDTF with different precipitation levels, and 3) use spatial data to calculate current and potential estimates of global SDTF carbon in biomass.

Methods

Database compilation

There are a number of different definitions of SDTF mostly based on a combination of MAP and dry season length (Portillo-Quintero and Sánchez-Azofeifa 2010). Annual precipitation ranges vary among studies. Sánchez-Azofeifa et al. (2005) define tropical dry forest as having 700 – 2000 mm yr^{-1} while Murphy and Lugo (1986) use 250 – 2000 mm yr^{-1}. Some definitions specify a dry season (Singh and Kushwaha 2005, Sanchez-Azofeifa et al. 2005, Pennington et al. 2009) while others do not. Our definition is a balance of large and small precipitation ranges, corresponds with the precipitation range of the Holdridge definition of tropical dry forest, and includes a specific dry season length. We included sites with MAP from 500 to 2000 mm yr^{-1} and a minimum of 4 months of dry season. We collected data from published studies found through searches of online databases and we also contacted researchers directly to obtain unpublished data. Where data were published in graphs rather than in tables, data were obtained from authors or by estimating the value from figures in the publications. Biomass data were converted to a common unit (Mg biomass ha^{-1}) but were not otherwise altered.

The methods used to quantify biomass varied among the studies we reviewed. Most studies measured the diameter at breast height (DBH) of trees and then estimated biomass with allometric equations, but some studies harvested sections of forests and measured the biomass directly. Studies also differed with respect to the minimum DBH cutoff and the allometric equation used. We excluded studies using a minimum DBH greater than 10 cm or where methods concerning the estimation of biomass were unclear. Treatment of seedling biomass varied between studies. Studies either measured seedling biomass and reported it separately, measured it but did not report it separately from total biomass, or did not measure seedlings. The inclusion and methods used to estimate other components of aboveground biomass such as coarse woody debris, litter, and understory biomass also differed among studies. Therefore we excluded these pools from our final biomass numbers. The final biomass estimates we analyzed include all reported live components of aboveground stem biomass. Some studies we included did not report details as to whether dead components were included and thus we cannot be certain that all biomass estimates excluded dead biomass components. What we refer to as aboveground biomass includes the live components of woody biomass in most cases but in some cases may include dead or understory components in the case where studies did not explain which components were included. Where available we collected a number of other site characteristics and methodological details from each study. These included plot sizes, minimum DBH measured, stand age estimates, soil physical and chemical characteristics, basal area, and stem density.

Statistical Analysis

To analyze the data, we divided all observations into two groups based on stand age (mature or secondary). This division allowed us to understand how climatic variables affect mature forest without being confounded by stand age. We considered mature sites to be those labeled “mature” or “undisturbed” in the original study or secondary sites with more than 100 years of recovery time. For sites with more than one aboveground biomass measurement in mature forest, we took the average of these multiple measurements. Linear regression was used to determine the relationship between aboveground biomass in mature sites and climatic variables of MAP and dry season length. We used analysis of covariance to test for regional differences beyond those explained by MAP. To investigate patterns of biomass increase in secondary forests over time and the extent to which these patterns depend on MAP, we separated data from secondary forests into three precipitation classes based on MAP (dry: 500-1000 mm, intermediate: 1000-1500, and moist: 1500-2000 mm yr^{-1}). We then regressed aboveground biomass against log-transformed stand age for each precipitation category. To validate these models we tested for the normality of residuals using QQ plots, histograms, and the Shapiro-Wilk test. We also plotted fitted values against residuals to test for non-constant variance. All statistical analyses were conducted using the R statistical software package (R Development Core Team 2012).

SDTF contributions to the global carbon cycle

To estimate current and potential contributions of SDTF biomass to the global carbon cycle we combined the derived climate-biomass relationship with geographic climate, biomass, and biome distribution datasets. Our goals were to 1) estimate how much carbon was currently stored in the aboveground biomass of SDTF and 2) estimate the amount of carbon that could potentially be stored in SDTF biomass if all SDTF were restored to mature forest. While we acknowledge that this scenario is unlikely, it provides an upper boundary to the amount of carbon that could be sequestered in SDTF.

We used the World Wildlife Fund (WWF) Ecoregions map to identify SDTF areas across the globe (Olson et al. 2001). We further reduced this SDTF area to only those areas that have MAP of 500 to 2000 mm using the Worldclim.org global climate data (Hijmans et al. 2005). Within this SDTF area we estimated the total current SDTF biomass C using global estimates of tropical C stocks data which account for variation due to current land use (Saatchi et al. 2011). These data are based on a model which used satellite imagery and both plot and LIDAR based estimates of biomass with a maximum entropy approach to estimate forest biomass (Saatchi et al. 2011).

We also estimated the potential biomass of mature SDTF within the WWF SDTF range reduced to areas with 500 to 2000 mm MAP. This estimates the potential global SDTF biomass if all the worlds SDTF were restored to a mature state. To make this estimate we used the statistical relationship between mature forest AGB and precipitation derived in this study with the Worldclim.org MAP data. This statistical relationship gave us biomass density of each 1 km^2 based on the MAP of that location and the MAP-mature-biomass relationship developed in this study. For both current and potential estimates, biomass was converted to carbon stocks by assuming that biomass is 50% carbon. We summed values across the globe to produce estimates of the total amount of current and potential SDTF carbon in biomass. The final results produced a raster dataset of biomass values with 1 km^2 resolution.

Results

Distribution of study sites

We found 229 estimates of aboveground biomass from 44 studies. Of these estimates, 135 were from SDTF of Central America, 53 from South America, 20 from Africa, and 21 from Asia (Table 2-1). There were 51 estimates out of 229 (22%) that were from mature or undisturbed forest and 178 from secondary forest at various stages of recovery. Of the secondary sites, 59 had been recovering from disturbance for less than 10 years, 40 sites were in forests with 10 to 20 years of recovery time, 54 sites had between 20 and 49 years of recovery time, and 25 sites had more than 50 years of recovery time.

Methodological variation in biomass estimates

There was no consistent minimum DBH cutoff among studies, though most studies measured all trees with a height above 1.3m. DBH cutoffs of 2cm, 4cm, and 10 cm were also common. Likewise, there was no single allometric equation that most studies used. While plot size ranged from 0.001 to 1.2 ha, the two most common plot sizes were relatively small: 0.01 ha (17% of observations) and 0.1 ha (30% of observations). The largest plot sizes were a hectare or more but only accounted for 3 studies in our database.

Aboveground biomass

Mean aboveground biomass (AGB) in mature forests ranged from 39 Mg ha^{-1} in Chamela, Mexico to 334 Mg ha^{-1} in Guanacaste, Costa Rica. Aboveground biomass in mature sites had a positive linear relationship with MAP where AGB (Mg ha^{-1}) = MAP (mm) * 0.1872 - 52.5608 (Figure 2-1; p-value = 1.564×10^{-06}, $R^2 = 0.55$). AGB had a negative linear relationship with dry season length (Figure 2-2; p-value = 0.0032, R^2 = 0.25). We found no significant differences in mature forest biomass among regions that were not explained by the covariation between region and MAP (Figure 2-3). In other words, Central America had lower biomass compared to other regions but this appeared to be driven by lower MAP at the sites where biomass measurements were made.

The variation in biomass among secondary SDTF was correlated with log-transformed stand age and the strength of this correlation increased with MAP (R^2 = 0.35, 0.46, and 0.58, p-values = 6.9×10^{-4}, 3.0×10^{-6}, and, 7.6×10^{-12} for dry, intermediate, and moist SDTF respectively; Figure 2-4). Analysis of covariance shows that the intercepts of these three models are not significantly different but that the slopes are significantly different (p-values all < 0.002 = 0.0016, 5.8×10^{-12}, and 1.1×10^{-5} for dry to intermediate, dry to moist, and intermediate to moist pairwise comparisons respectively). Sites with lower MAP had a lower maximum attainable biomass, but the number of years it takes to reach maximum biomass was similar across precipitation classes. Biomass accumulation appears to level off around 40 years for all precipitation ranges based on visual inspection. Biomass accumulation after 40 years reached 50-100, 100-150, and 200+ Mg ha^{-1} in dry, intermediate, and moist forests respectively.

Contributions to the Global Carbon Cycle

Our geographic analysis estimated that 8.7 Pg of carbon are currently being stored in aboveground biomass of SDTFs worldwide based on the carbon stocks data from

Saatchi et al. (2011). This can be regionally partitioned into 3.28, 5.05, and 0.34 Pg C for the Americas, Asia, and Africa respectively (Table 2-2), and includes area that could potentially be SDTF but may currently be in other land use. If all SDTF were restored to a mature state we estimate that they would contain 22 Pg of C in aboveground biomass (Figure 2-5). Potential biomass is partitioned regionally at 8 , 12, and 2Pg C for the Americas, Asia, and Africa respectively (Table 2-2).

The large amount of current and potential biomass in Asia relative to the Americas, is primarily due to larger areas of the SDTF biome in India and Southeast Asia. This difference is not due to Asian SDTF being skewed more towards wetter climates as both regions have similar precipitation distributions when examined on a area-weighted basis.

Discussion

We assembled a large database on aboveground biomass in SDTF to evaluate patterns among sites and successional stages. The biomass at maturity for SDTF was remarkably well correlated with precipitation but less so with dry season length. Our regression model implies that mature forest biomass increases linearly with MAP and that an increase of 500mm corresponds with an increase in maximum biomass of 94 Mg ha^{-1} in SDTFs. This AGB-MAP relationship is remarkably close to that reported by Marínez-Yrízar (1995) which used only 9 data points and found a linear relationship with the same slope (0.187). This evidence is consistent with the hypothesis that precipitation limits the maximum amount of biomass attained in SDTF. Mean annual precipitation explained 55% of the variation in biomass among mature sites. We cannot rule out the possibility that the strong correlation between biomass and mean annual rainfall is spurious, and driven by some other variable that co-varies with precipitation. We also acknowledge that there is an alternative interpretation of the aboveground biomass - MAP relationship where sites below MAP of 900 mm have lower biomass than sites above 900 mm but within those groups there is no correlation between the two, i.e. 900 mm is a threshold level. Despite these caveats, the ecology and climate of SDTF suggest that water availability, even expressed through a coarse index like MAP, is highly likely to play a role in SDTF biomass content.

It is likely that other factors such as nutrients, soil, land use history, and species composition are responsible for some of the remaining variation (Powers et al. 2009), but we cannot account for these factors in our dataset. While species composition varies widely among SDTF sites (Pennington et al. 2009), our data show that biomass is well predicted by simple climatic variables, implying that differences in species composition do not eclipse the climate signature in determining biomass across sites. However, we temper this conclusion by acknowledging that our database is limited in the number of testable explanatory variables. There was no way to extract data on other potential environmental and anthropogenic factors from the studies in the literature, either because they were omitted or measured using inconsistent methods that precluded comparison.

Aboveground biomass in secondary SDTF recovers at a rapid rate, appearing to close on its maximum attainable biomass after approximately 3 to 5 decades (Figure 2-4). The rapid rates of forest recovery following disturbance in SDTF have been noted previously and attributed to a combination of factors including their relatively simple structure compared to wetter tropical forests, the predominance of wind-dispersed seeds (Vieira and Scariot 2006), and the large number of trees that can resprout following disturbance (Ewel 1977).

In our global database, we found that biomass accumulation in secondary SDTF is primarily a function of stand age but that the accumulation pattern is also affected by MAP. The maximum biomass attained as sites age is higher in the wettest sites (1500-2000 mm MAP) than in the drier or intermediate sites. There were no detectable differences in the time needed to reach maximum biomass among dry, intermediate, and moist SDTF, implying that the rate of biomass accumulation, a major component of productivity, does increase as sites get wetter. This is consistent with studies showing that net primary productivity increases with precipitation in tropical forests receiving less than 2000mm MAP (Schuur 2003), and that soil fertility or disturbance are less important than climatic variables in determining tree and forest growth rates (Toledo et al. 2011). As with mature sites, we cannot assess the relative influence of other biophysical factors on biomass accumulation due to the limitations of our dataset. However, the patterns of biomass accumulation that we document in combination with evidence from studies on physiology of SDTF tree species (Segura et al. 2003, Singh and Kushwaha 2005, Balvanera et al. 2011), support the hypothesis that MAP limits the maximum attainable biomass and possibly the rate of biomass accumulation as well. Disturbance history, including the extent to which trees were removed, post-disturbance management, the introduction of exotic species, and the proximity of intact forest or regeneration sources all are factors likely to impact the regeneration rate and the amount of biomass attained by secondary forests (Griscom and Ashton 2011).

The common deciduous leaf habit of trees in SDTFs is likely an important mechanism behind the MAP–biomass relationship. Many tree species in SDTF are distributed according to water availability (Balvanera et al. 2011), and lower rainfall sites have a greater proportion of deciduous trees (Singh and Kushwaha 2005). By playing a role in bud break and leaf abscission, water availability limits the start and end of the growing period of deciduous trees (Reich and Borchert 1984, Borchert 1994). Unlike evergreen trees, deciduous trees cannot take advantage of intermittent dry season rain fall and are potentially damaged if dry season rains cause early bud break. These circumstances may lead to lower productivity and ultimately lower biomass stocks in mature forest. Deciduous trees in wetter areas can hold on to their leaves longer (have a longer growing season) with the potential for higher productivity and are likely to have lower mortality. After years of higher productivity and lower mortality, forests on the wet end of the SDTF spectrum attain a greater biomass than the driest forest. Experimental studies have shown that increasing water availability may or may not increase productivity but restricting water certainly decreases productivity (Cavelier et al. 1999, Yavitt and Wright 2001). Furthermore, tree mortality appears to increase with water scarcity (Segura et al. 2003). In India, tree mortality is negatively correlated with annual rainfall with a two or three year lag (Suresh et al. 2010). Together these findings suggest that the mechanism behind the relationship between MAP and maximum AGB is that water scarcity induces leaf abscission and dormancy in many SDTF species. As the dry periods lengthen, mortality increases while productivity, biomass accumulation, and maximum attainable biomass all decrease.

Our estimates of maximum biomass attained by secondary forests are slightly larger than those of a previous review of aboveground biomass in secondary forests (Marín-Spiotta et al. 2008). Our study contrasts Marín-Spiotta et al. (2008) in that it includes more data from the driest sites and from older secondary forests. However, in both studies, the abundance of data decreases with stand age and the variance among estimates of biomass increases with stand age. We also found a larger range in aboveground biomass than Jaramillo et al. (2011) and Martínez-Yrízar (1995), who reviewed biomass in sites on the driest end of the SDTF spectrum. Future studies should include seasonal forests on both ends of the precipitation spectrum and focus on secondary forests sites of greater maturity than most past studies have. Particularly scarce are data from sites with stands aged between 50 and 100 years since disturbance. However, we acknowledge that the extensive conversion of SDTF to other land-uses and relatively recent history of secondary forest regeneration likely limits the availability of sites in this age class, and this is reflected in the literature.

One of the most salient results from our study is the large explanatory power of a simple parameter, mean annual rainfall, in predicting aboveground biomass among SDTFs. Other studies have sought to predict biomass across coarser spatial scales by using more complicated variables. For example, Johnson et al. (2000) explain biomass accumulation in sites around the world using “growing-season degree years,” a statistic combining stand age, growing season length, and temperature. They included tropical forests but few if any from the dry end of the tropical forest spectrum. Zarin et al. (2001) showed that “growing-season degree years” were significantly correlated with biomass accumulation in Amazonian forest. Growing-season degree years did not explain more of the variance in our dry forest database than did stand age alone (results not shown). Because the growing-season degree years statistic includes temperature, this result supports the hypothesis that within SDTFs, precipitation controls biomass variation more than temperature.

Because of the nature of the studies reviewed, we lacked sufficient data on other likely explanatory variables leaving the commonly measured climate variables as the only testable hypothesis. This fact underscores the need for studies that measure biomass alongside other possible explanatory variables or long-term experimental work testing water or nutrient availability as the ultimate control over SDTF carbon stocks. The Tropi-Dry network serves as a current example of standardized data collection in SDTF (Sanchez-Azofeifa et al. 2005). Irrespective of the underlying mechanism, the large explanatory power of MAP allows us to predict carbon stocks in SDTFs across the globe.

Our geographic analysis used available spatial data on climate and biome distribution to estimate the current and potential carbon stocks in aboveground biomass of SDTF. We caution that these values combine the errors of the respective geographic datasets and additional inaccuracies due to the fact that the regression model used only explains 55% of the variation in SDTF aboveground biomass. Nevertheless these results suggest that significant amounts of carbon storage are lost with the well known conversion of SDTF to other land uses and that the restoration of formerly forested sites in the SDTF biome would result in the sequestration of globally significant quantities of carbon. To put our global estimates in context, Pan et al. (2011) estimates that above and below ground live biomass in tropical forest sum to 262 Pg C. We estimate that SDTF aboveground biomass alone currently make up 3% of this total and if restored SDTF would amount to 8% of the current total tropical live biomass stock.

Our analysis also highlights the geographic bias in the available data on SDTF carbon cycling as others have noted (Powers et al. 2011). While Asia holds 58% of current global SDTF biomass C, only 9% of the 229 estimates of biomass in our literature were from Asia. In contrast, Central and South America hold 38% of current SDTF biomass C and while making up 82% of existing biomass estimates. This bias suggests the need for more C cycling research in India and Southeast Asia which hold the bulk of Asia's SDTF.

Conclusions

Our results show strong support for the hypothesis that precipitation is the most important factor explaining the global variation in biomass among SDTF. That said, our ability to make inferences about the roles of other biophysical factors is limited by the lack of data on factors other than precipitation reported in the literature. Understanding the remaining variance in biomass that is not explained by precipitation is an important part of moving forward on initiatives to protect and restore SDTF for climate change mitigation. Further research on the distribution of aboveground biomass is needed to explain both local and global variation. We conclude with several recommendations. First, future studies should employ consistent protocols, as advocated by recent networks of SDTF researchers (Quesada et al. 2009). Second, biomass and accumulation studies in SDTF should investigate a larger number of factors that might account for variation among sites including species composition, functional composition, soil quality, and land-use history (Griscom and Ashton 2011). Last, future studies should include estimates of belowground carbon stocks and coarse woody debris (Kissing and Powers 2010). Our review excluded belowground biomass stocks due to the scarcity of comparable belowground data in the literature, as others have noted (Vargas et al. 2008). While studies of SDTF belowground biomass do exist (Martínez-Yrízar 1995, Mokany et al. 2006, Powers and Peréz-Aviles 2012), extrapolating these few studies that vary in methods to the global scale is problematic. Belowground carbon and biomass stocks may be a significant component of total biomass (Mokany et al. 2006), especially in water-limited dry forests where trees can invest substantial amounts of photosynthate in building fine and coarse roots. Standardized, comparable measurement of fine roots, coarse roots, and rooting depth may prove critical in explaining a complete picture of SDTF carbon cycling.

Tables and Figures

Table 2-1. Studies used in our analysis separated by the region in which the study was conducted.

Central America	South America	Africa	Asia
Alvarez-Yepiz et al. (2008)	Delaney et al. (1997)	Bartholomew et al. (1953)	Andriesse and Shelhaas (1987)
Balanavera and Aguirre (2006)	Kauffman et al. (1993)	Glenday (2008)	Drew et al. (1978)
Becknell and Powers (In Prep)	Kennard (2002)	Greenland and Kowal (1960)	Misra (1972)
Campo and Varquez-Yanes (2004)	Madiera et al. (2009)	Hall and Swaine (1976)	Ogawa et al. (1965)
Castellanos et al. (1991)	Malhi et al., (2006)	Jensen and Friis (2001)	Ogawa et al. (1961)
Ewel (1971)	Pyle et al. (2008)	Jung (1969)	Sabharasri (1978)
Jaramillo et al. (2003)	Rolim et al. (2005)	Muller and Nielsen (1965)	Singh and Singh (1981)
Kalacska (2008)	Sampaio et al. (1998)		Singh and Singh (1991)
Lambert et al. (1980)	Sampaio et al. (1990)		
Lugo et al. (1978)	Uhl et al. (1988)		
Martinez-Yrizar et al. (1992)			
Martinez-Yrizar et al. (1996)			
Murphy and Lugo (1986)			
Ray and Brown (1995)			
Read and Lawrence (2003)			
Rico Gray et al. (1992)			
Saynes et al. (2005)			
Urquiza-Haas et al. (1991)			
Vargas et al. (2008)			

Table 2-2. Geographic analysis of aboveground carbon stocks by region.

Global area and carbon stocks in tropical dry forests (SDTF) grouped by region. SDTF area was estimated using the WWF eco-region map. Current SDTF was calculated by summing C stocks estimates from Saatchi et al. (2011) within SDTF area delineated by the WWF biome map. Potential SDTF C stocks were estimated using the precipitation-biomass relationship developed from the literature review in this study.

Region	**SDTF area (million km^2)**	**Mean SDTF MAP by area (mm)**	**Current SDTF C (Pg) (Saatchi et al. 2011)**	**Potential SDTF C (Pg) (this study)**
Americas	1.0	1088	3.28	8.30
Asia	1.5	1119	5.05	11.86
Africa	0.2	1403	0.34	1.89
World	2.7	1187	8.67	22.06

Figure 2-1. Aboveground biomass and mean annual precipitation.

Aboveground biomass in mature tropical dry forest sites as a function of mean annual precipitation (p-value = 1.6×10^{-06} ,R^2 = 0.55).

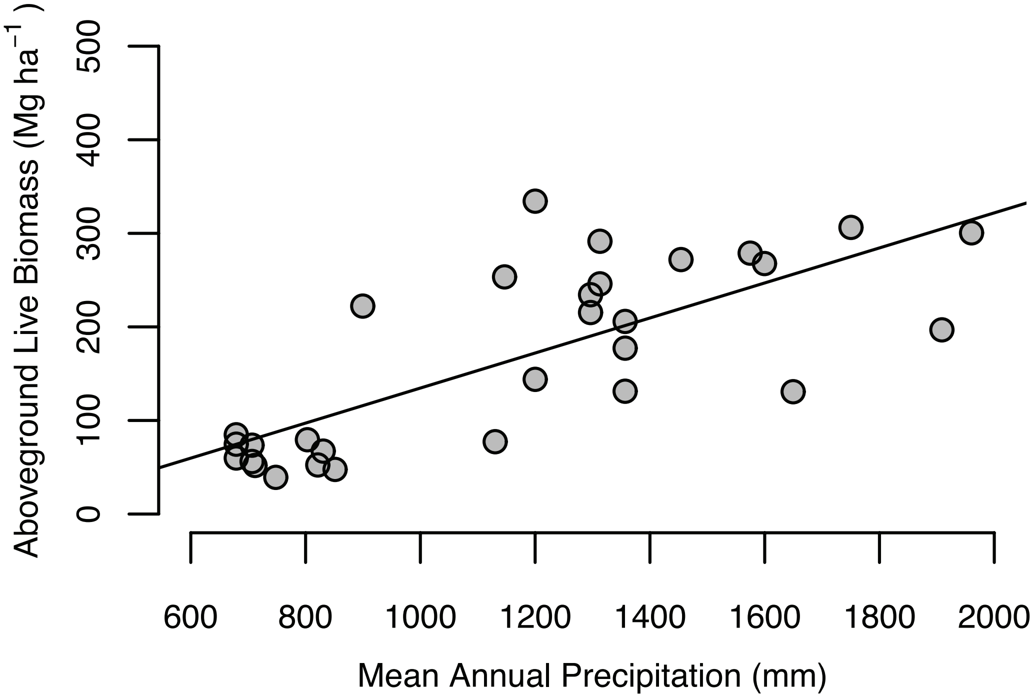


Figure 2-2. Aboveground biomass and dry season length.

Aboveground biomass in mature tropical dry forest sites as a function of dry season length (p-value = 0.003,R^2 = 0.25).

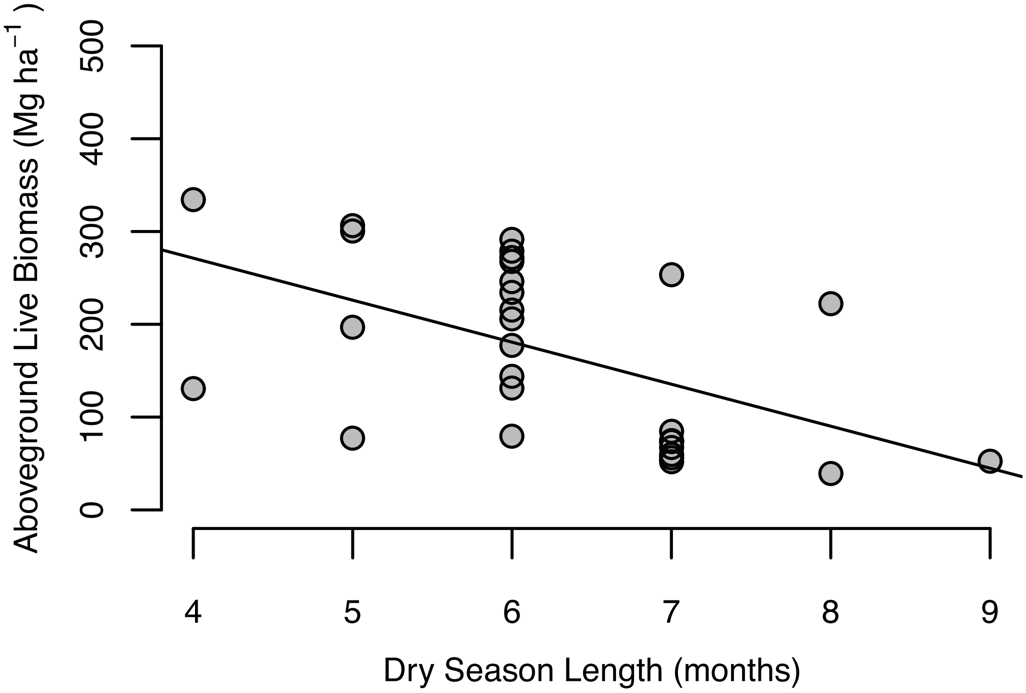


Figure 2-3. Aboveground biomass and annual precipitation by region.

Mean annual precipitation and aboveground biomass of mature sites separated by region. An analysis of covariance indicates that the explanatory power of region on biomass disappears when mean annual precipitation is included.

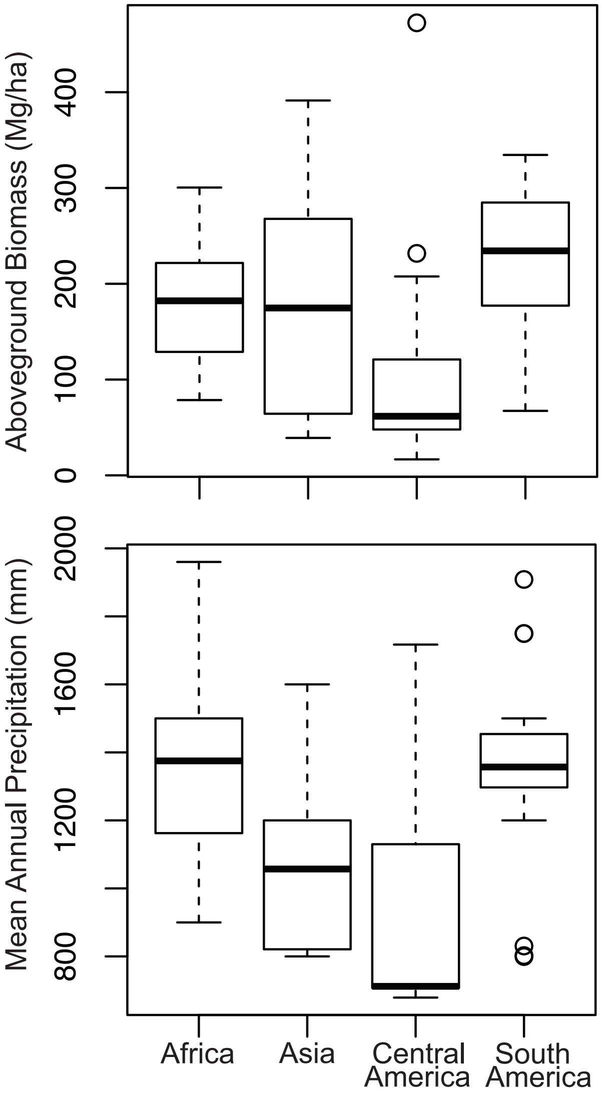


Figure 2-4. Aboveground biomass and stand age across three precipitation ranges. Aboveground biomass as a function of log-transformed stand age for sites with mean annual precipitation of 500-1000 mm yr-1 (A), 1000-1500 mm yr-1 (B), and 1500-2000 mm yr-1 (C). Both the correlation of biomass with stand age and the maximum attainable biomass increase with MAP. Recovery rates are modeled by the equation AGB = A*ln(stand age) + B. R^2 for A, B, and C are 0.35, 0.46, and 0.58 respectively. P-values for A, B, and C are 6.9×10^{-4}, 3.0×10^{-6}, and $7.6\times10^{-1}2$ respectively.

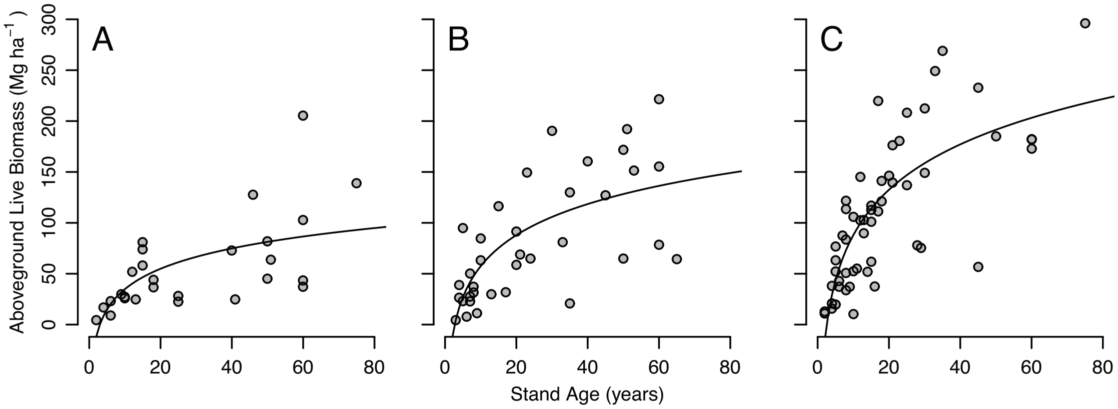
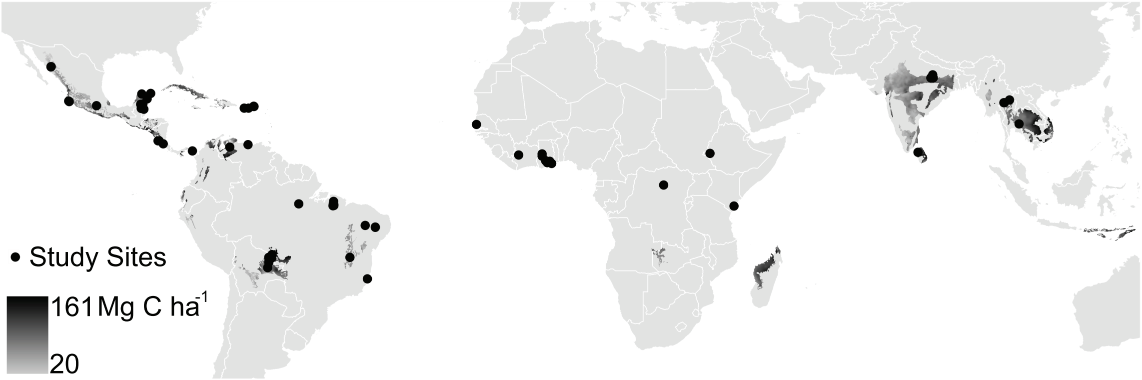


Figure 2-5. Map of study sites and dry forest aboveground biomass distribution. Study sites used in literature review and aboveground biomass predicted by biomass – precipitation relationship in mature sites in area defined by World Wildlife Foundation tropical dry forest extent.



Chapter 3

Aboveground biomass, functional traits, and edaphic variation in secondary tropical dry forests

Introduction

Forest biomass is one of the largest and most dynamic pools of carbon, yet in tropical forests we lack a complete understanding of how carbon stocks vary and what controls that variation (Clark and Clark 2000, Houghton 2005, Saatchi et al. 2007). Tropical forests have a large capacity to store carbon, and preserving and restoring tropical forests is an important climate change mitigation strategy (Pacala and Socolow 2004, Gibbs et al. 2007). Despite their importance, questions remain about the amount of biomass in tropical forests (Houghton 2005), the distribution of biomass across the landscape (Clark and Clark 2000, Saatchi et al. 2007), and the rate of biomass accumulation (Chazdon et al. 2007, Marín-Spiotta et al. 2008). This uncertainty exists in part because tropical forest biomass varies across the landscape with changes in time since disturbance, species composition, and abiotic factors like topography, soil fertility, light, and water availability (Clark and Clark 2000, Townsend et al. 2008, Baraloto et al. 2011). Understanding how these factors control variation in biomass at the plot and landscape scale has become a goal of several recent tropical rain forest biomass studies (Clark and Clark 2000, Asner et al. 2009, Baraloto et al. 2011), and here we ask this question in tropical dry forest.

Tropical dry forests are an important part of tropical forests worldwide and have been greatly impacted by human activities. Tropical dry forests (TDFs) include forested lands receiving between 500 and 2000 mm of annual precipitation and have a distinct dry season longer than 3 months (Becknell et al. 2012). While their exact area depends on the definition used, TDFs may comprise as much as 42% of all tropical forests (Murphy and

Lugo 1986). Aboveground biomass in mature tropical dry forests ranges from 34 to 334 Mg ha^{-1} and increases linearly with mean annual precipitation (Becknell et al. 2012). Tropical dry forest has been disproportionally impacted by humans compared to wetter forests because the climate is more hospitable and the soils are often more suited to agriculture (Trejo and Dirzo 2000, Stoner and Sanchez-Azofeifa 2009). In recent decades, due to conservation efforts and economic changes, TDF in some areas like northwestern Costa Rica is recovering from agricultural clearing (Calvo-Alvarado et al. 2009, Redo et al. 2012). This forest recovery represents the accumulation of a potentially significant carbon stock that has yet to be closely examined (Silver et al. 2000).

Our goal in this study was to quantify the landscape-scale distribution of aboveground biomass (AGB) in regenerating TDF and understand the degree to which this distribution is driven by various biotic and abiotic factors including soils, diversity of tree species and their functional traits. To do so, we constructed a conceptual framework of the factors that potentially influence forest biomass, which was informed by three areas of ecological research: 1) landscape-scale variation in ecosystem processes as ecosystems recover from disturbance (Chazdon 2003, Turner 2010), 2) the variation in plant diversity and physiology across successional gradients (Bazzaz and Picket 1980, Chazdon et al. 2009, Lebrija-Trejos et al. 2010a), and 3) the environmental filtering effects of soils on species composition (Clark et al. 1999, Valencia et al. 2004, Katabuchi et al. 2011). Below we discuss each of these areas and our conceptual model that integrates them.

While there is a theoretical understanding of how ecosystem properties like biomass stocks vary across successional time, applying this theory at the landscape scale is difficult. Each point in the landscape can have a different carbon storage trajectory across succession (Turner 2010), i.e., for any given successional stage there can be variation across the landscape attributable to factors other than ecosystem age. Carbon in biomass is generally expected to increase logistically as forests recover from disturbance (Chapin et al. 2011), but the maximum level of biomass reached and the time it takes to reach it can vary across the landscape (Turner 2010). This variation could be influenced by abiotic factors such as the physical and chemical properties of soil (Laurance et al. 1999, Clark and Clark 2000). Biotic factors such as seed sources and availability (Aide and Cavelier 1994), species diversity (Balvanera and Aguirre 2006), and the composition of plant functional traits in a forest may also affect the rate of biomass accumulation or the maximum biomass attained (Poorter and Bongers 2006, Baker et al. 2009).

The availability of light, nutrients, and water resources in tropical forests changes through succession and concurrent changes in species presence and abundance lead to ecosystem-scale variation in physiological processes like photosynthesis and growth (Bazzaz and Picket 1980, Alvarez-Anorve et al. 2012). These changes in diversity and physiology over successional time can affect the accumulation and storage of carbon in biomass (Hooper et al. 2005). Functional traits can represent these changes in plant physiology across succession and the community weighted means of traits could be a useful explanatory variable in studies of ecosystem properties and functions (McGill et al. 2006). The traits of the most dominant species are hypothesized to have the greatest effect on ecosystem function (Grime 1998), and empirical studies have confirmed this for certain processes and ecosystems (Mokany et al. 2008, Schumacher and Roscher 2009, Laughlin 2011). In landscapes made up of forest stands of diverse ages, the variation in these community-level functional traits across succession (Campetella et al. 2011, Lohbeck et al. 2012) and environmental variables (Markesteijn et al. 2007, Maharjan et al. 2011) may explain some of the variation in biomass or other ecosystem properties and processes.

Evidence from many studies suggests that soil properties influence the composition of tropical forests (Clark et al. 1999, Valencia et al. 2004, Powers et al. 2009, Katabuchi et al. 2011), providing strong support for a role of environmental filtering in explaining some of the variation in species distributions within and among tropical forests (Gourlet-Fleury et al. 2011). Seedling survival and growth rates can vary across gradients of soil nutrients and water availability (Lawrence 2003, Engelbrecht and Kursar 2003). This variation leads to disproportionate survival of species adapted to local soil conditions and loss of less adapted species, which may have differential potentials to grow and store carbon. This filtering of species represents one potential mechanism through which soil can indirectly affect ecosystem processes like aboveground carbon storage in addition to direct effects soils might have through effects on tree growth (Cleveland et al. 2011, Baribault et al. 2012).

Combined, these three frameworks inform our conceptual model of the controls over biomass variation in secondary tropical dry forests (Figure 3-1). This model combines multiple direct and indirect effects of biotic and abiotic factors, many of which can vary across successional gradients. In our model AGB is affected directly by stand age, soil properties, tree species diversity, and the functional traits of species aggregated at the community level. We predicted that stand age would be the primary determinant of AGB in secondary forests but that significant variation in AGB would remain after accounting for stand age. Soil chemical and physical properties directly affect biomass as chemical properties influence the degree to which growth is limited by nutrients and physical properties are related to water availability, a potentially significant factor in seasonal forests (Balvanera et al. 2011). Diversity and species traits also affect biomass directly as differences in the physiology of species add up to differences in growth and decomposition at the stand level. All of these factors may have direct effects on AGB but stand age and soil properties also have indirect effects through their effects on other variables. The succession-driven changes in diversity and the community-weighted distribution of functional traits may lead to changing AGB across the landscape. Soils, acting as environmental filters of species (Gourlet-Fleury et al. 2011), may alter diversity and trait distributions in ways that ultimately affect AGB. We hypothesized that together these multiple direct and indirect factors would explain the variation in AGB across the landscape.

In this study, we examined biomass, functional composition, and soil characteristics in a series of 84 plots stratified across gradients of stand age, tree species diversity and composition, and soil physical and chemical properties in northwestern Costa Rica. We examined the relationships among these factors to understand the controls over variation in aboveground biomass across the landscape. We used datasets of soil properties and plant functional traits to understand how these factors affect each other and biomass accumulation. Our goals were to 1) quantify the accumulation of aboveground biomass across successional gradients, 2) understand which factors beyond stand age affect the aboveground biomass of secondary tropical dry forest, and 3) quantify how community weighted mean values of functional traits change across succession and soil gradients.

The conceptual framework described above leads to several hypotheses: 1) as forests age, aboveground biomass increases but saturates after structural maturity with considerable variation across the landscape, 2) the dominant functional traits of trees at a site vary with stand age as species composition changes with succession, 3) after stand age is accounted for, edaphic factors affect the dominant traits at a given site, and 4) changes in diversity and the dominant functional traits due to both succession and edaphic factors explain the residual variation in aboveground biomass after accounting for stand age.

Our approach differs from many studies of succession and secondary forest regeneration that use chronosequences or “space-for-time” substitutions. Most studies select a series of plots that are presumably similar in every way except forest age or time since disturbance, and attribute any differences among plots to successional processes (Chazdon et al. 2007). In order to account for both variation across succession and across the landscape, we selected a large series of plots distributed among different forest ages and edaphic conditions, and used structural equation modeling to partition variation in aboveground biomass into the direct and indirect effects of forest age, soil variables, and plant community characteristics.

Methods

Site Description

We conducted this study in two national parks in the province of Guanacaste, Costa Rica: Parque Nacional Santa Rosa in the Área de Conservación Guanacaste and Parque Nacional Palo Verde in Área de Conservación Tempisque. Santa Rosa has a 30 year mean annual precipitation of 1765 mm (www.investigadoresACG.org) and Palo Verde has a 30 year mean annual precipitation of 1444 mm (www.ots.ac.cr). Both locations experience a five to six month dry season with little measurable precipitation. The soils of Santa Rosa have developed on an eroding plateau made up of volcanic lava flows and ash deposits transition into alluvial marine terraces at the lowest elevations (Hartshorn 1983). They are dominated by entisols and vertisols though there exists a high degree of heterogeneity in soil type and chemical composition (Leiva et al. 2009). The soils of Palo Verde developed from alluvial areas along the floodplain and wetlands of the Tempisque River and the eroding limestone hills (Hartshorn 1983). Both parks contain patches of older forest but are dominated by secondary forests that were previously used for agriculture or pasture land. After the parks were established in the 1970s, forest began to grow back (though anthropogenic fires may have slowed regeneration in some areas), and the current landscape is a heterogeneous mix of forests of different ages with different land use histories on different types of soils. Forests are made up of a mix of evergreen and deciduous tree species, the number and relative abundance of which varies across successional and soil gradients (Powers et al. 2009).

Young forests are thought to be dominated by wind dispersed deciduous trees and the frequency of animal dispersed and evergreen tree species is thought to increase with forest age (Janzen 1988a).

Data Collection

We measured biomass and sampled soils in a network of 84 20 x 50 m plots distributed across gradients of stand age, soil properties, and functional composition. The first 60 of these plots were established on level ground in 2008. Their diversity and structure were previously described by Powers et al. (2009). In 2010 we sampled an additional 24 plots arrayed along toposequences to explicitly characterize variation in biomass due to topographic position (topographic position was later determined to have no significant effects on biomass and was not included in further analyses). Stand age estimates were made using a combination of remote sensing observations for younger sites and expert local knowledge (Powers et al. 2009). Stand age represents the approximate number of years between the previous land use being abandoned and the year our measurements were made. Sites determined to be mature forests were assigned a stand age of 100 for our analysis.

Biomass estimation

Within each plot we identified to species and measured the diameter at breast height (DBH) of all live trees with trunks ≥10 cm diameter. When necessary, DBH was measured above buttresses or trunk irregularities. In 200 m^2 subplots we measured the DBH of all trees <10 cm in diameter that were >1.4 m in height but we did not identify the species of these trees. The biomass of each tree ≥10 cm was estimated using an allometric equation that incorporated both DBH and species-specific wood density (Chave et al. 2005). Biomass of multi-stemmed trees was calculated separately for each stem. Average wood density for each species came from a previous study conducted in the same area (Powers and Tiffin 2010). For trees <10 cm DBH and for species in which we had no wood density data we calculated biomass using the community weighted mean of wood density for that plot. Biomass for all trees in each plot was summed to yield plot biomass and converted to megagrams of biomass per hectare (Mg ha^{-1}).

Soil sampling and analysis

Soil physical and chemical characteristics for 60 of the 84 plots were measured in 2008 and described in a previous study (Powers et al. 2009). The 24 additional plots were sampled in 2010 and identical laboratory methods were used to analyze the physical and chemical properties. We measured soil physical properties that were likely to be related to soil water holding capacity and drainage (particle size distribution, bulk density, and stone content). Soil chemical properties were used to represent inherent soil fertility of a site. We measured total nutrient stocks because we expected them to be less likely to vary across successional gradients than more labile components (Powers et al. 2005, Powers and Peréz-Aviles 2012). In each plot 10 samples were taken from the mineral soil with a punch core sampler to a depth of 10 cm and bulked by site. Three separate samples were taken at each site using a turf sampler to measure bulk density and stone content. Soils were analyzed for elemental content after hot nitric acid digestion at the Research Analytical Lab of the University of Minnesota. Particle size distribution was measured with the hydrometer method. Total carbon and nitrogen were measured along with their stable isotopes ^{15}N and ^{13}C and the UC Davis Isotopes Lab. We measured the pH of air dried soils in distilled water at a 1:2.5 soil to solution ratio with an Oakton pH meter. We are confident that measuring soil characteristics in different years did not affect their values.

Soil Principal Components Analysis

To evaluate the effects of soil physical and chemical properties we conducted two principal components analyses (PCAs). The first PCA used five physical soil variables: bulk density, stone content, percent sand, percent silt, and percent clay. The second PCA used 15 soil chemical variables: pH, boron, calcium, carbon, chromium, copper, iron, manganese, magnesium, nitrogen, nickel, phosphorus, potassium, sodium, and zinc. Both PCAs used correlation matrices of the included variables because of different sampling units and ranges of variation among variables. Analyses were conducted using R 2.15.1 (R Development Core Team 2012).

Community weighted means of traits

To evaluate the distribution of functional traits in our forest plots we calculated community weighted mean values for a set of functional traits from a trait database developed by Powers and Tiffin (2010) that included 87 species from our study area. For each tree species in the trait data base we included wood density, specific leaf area (SLA), leaf N, leaf P, and leaf carbon isotope composition (δ^{13}C, an index of water use efficiency). Community weighted mean (CWM) values for each trait were calculated with the FD package for the R statistical software (Lavorel et al. 2008). This perspective assumes that the proportional abundance of functional traits corresponds to the effects of those traits and that intraspecific variation in trait values is low relative to interspecific variation. We first calculated the basal area of each tree and then used each species' relative basal area in each plot as a measure of proportional abundance in the CWM calculations. Of the 3959 trees ≥10 cm DBH 91% were represented in the traits database. Trees belonging to species which did not occur in our trait database were omitted from the CWM calculations. To study how CWMs of traits changed across succession we used linear regression with the natural log of stand age as the explanatory variable.

Structural Equation Modeling

Structural equation modeling (SEM) is a statistical method used to simultaneously evaluate multiple relationships between response and explanatory variables in multivariate datasets (Grace 2006). Using maximum likelihood estimation, parameter values defining the relationships between variables are found that best produce a covariance matrix that is as close as possible to the observed covariance matrix (Grace 2006). We chose SEM for our analysis because we wanted to analyze multiple direct and indirect relationships among variables in our multivariate data set where some variables are both explanatory and response variables. SEM has been shown to more effectively deal with such problems compared to using multiple univariate analyses (Grace and Bollen 2005). We used SEM to assess the relative direct and indirect influence of stand age, soil physical and chemical properties, species richness, and plant functional traits on the variation in aboveground biomass in our 84 forest inventory plots. We omitted wood density from the functional traits because it appears in the allometric equations used to estimate biomass. We evaluated several measures of diversity to choose which metric to include in our SEM model by calculating Pearson's correlation coefficients (PCCs) between various diversity indices and AGB. We evaluated species richness, Shannon's diversity index, functional dispersion, functional richness, and functional evenness (Villéger et al. 2008, Schleuter et al. 2010). Species richness had the highest PCC and thus was included in our SEM model.

We started with the initial full model (Figure 3-2) that included all theoretical casual connections between the included variables. To find the best fit model (Figure 3-3) we iteratively removed connections between variables and assessed the effect of the overall model fit (p-value and chi-square value), the Akaike Information Criteria (AIC) value, and the squared multiple correlation values for each variable. Each connection was removed and left out if the indicator statistics showed a better model fit and explanatory power of the model as measured by squared multiple correlation values. The final model had the best overall fit, the lowest AIC, and the best balance of squared multiple correlation values for the various dependent variables. Following convention, correlations between the errors of variables not otherwise connected were added to the complete model before we revised the model if a Pearson correlation score was higher than 0.5. The SEM analysis was conducted using the Software package (Arbuckle 2010).

Results

Soil Variation

As documented previously, edaphic characteristics varied widely across the landscape (Powers et al. 2009). Individual coefficients of variation (Table 3-1) show the relative variation of each soil physical and chemical property across the 84 plots. In general the physical properties showed less variation relative to the chemical properties, although stone content was a notable exception. The first axis of the soil physical property PCA explained 37% of the variation across the five variables and the second axis explained 32% of the variation. Loadings and Pearson's correlation coefficients revealed which soil properties were correlated with each PCA axis (Pearson's correlation coefficients followed by loadings are in parentheses after variables). Soil physical PCA axis 1 was correlated with sand (0.90, 0.669), and to a lesser degree bulk density (-.63, -0.463), silt (-0.47, -0.345), and clay (-0.55, -0.406). Soil physical PCA axis 2 was correlated with silt (0.85, 0.665), stone content (0.63, 0.497), and to some extent clay (-0.66, -0.520). With respect to the PCA of soil chemical properties, the first PCA axis represented 47% of the variation among plots in the fifteen variables and the second axis represented 15% of that variation. Soil chemical PCA axis 1 was correlated with calcium (-0.90, -0.34), magnesium (-0.85, -0.321), soil pH (-0.82, -0.309), nitrogen (-0.76, -0.287), phosphorus (-0.76, -0.286), potassium (-0.75, -0.284), chromium (-0.74, -0.280), and carbon (-0.73, -0.275). Soil chemical PCA axis 2 was correlated with iron (0.68, 0.459), manganese (0.49, 0.328), and chromium (0.46, -0.280).

Plant functional traits and species richness

Species richness and the community weighted mean values of foliar N, foliar P, and SLA increased with stand age while foliar $\delta^{13}C$ decreased with stand age (Table 3-2). Linear regression between trait values and the natural log of stand age were all significant (except for wood density). Stand age explained 15 to 31% of the variation in traits and 41% of the variation in species richness (Table 3-2; Figure 3-4). Coefficients of variation indicate that while the CWM of SLA, foliar N, and foliar P all display similar levels of variation, foliar $\delta^{13}C$ varies by an order of magnitude less. Community weighted means of leaf traits across plots were well correlated with each other. All between trait Pearson's correlation coefficients were higher than 0.5. Community weighted means of SLA, foliar N, and foliar P were positively correlated with each other and all three were negatively correlated with foliar $\delta^{13}C$ (results not shown). Pearson's correlation coefficients for relationships between wood density and leaf traits were significant but lower than those among leaf traits and negative for all but foliar $\delta^{13}C$.

Aboveground Biomass

Aboveground biomass ranged from 10 to 473 Mg ha^{-1} with an overall mean value of 167 Mg ha^{-1} and a coefficient of variation of 50.07%. Aboveground biomass was strongly correlated with the natural log of stand age (Figure 3-5; R^2 of linear regression = 0.46). The pattern of AGB accumulation appears to be a rapid increase in the first 20 years following by a slower increase in biomass between stand ages of 20 and 100. AGB in sites of 50 or greater years of recovery ranged from 132 to 473 Mg ha^{-1} with a mean of

241 Mg ha^{-1}. As expected, for any given stand age there was a relatively large range of variation in biomass.

SEM results

After removing 17 of the 39 connections from the original model (Figure 3-2) we found the best fit structural equation model with 22 connections (Figure 3-3). Model fit in SEM is determined by comparing the observed correlation matrix with the correlation matrix produced by the maximum likelihood derived model parameters. The correspondence between this modeled covariance matrix and the observed covariance matrix can be evaluated with multiple statistics, and overall model fit is measured with a Chi-square test. For our final model this test produced a Chi-square value of 6.51 and a p-value of 0.999 (the null hypothesis of this test being that modeled and observed covariance matrices are equivalent). This measure of overall fit indicates a high correspondence between the data and the model in that the correlation matrix produced by the model was not significantly different than the correlation matrix of the data.

Overall our model explained 50.8% of the variation in aboveground biomass which includes the effects of stand age, soil properties, species richness and traits. Soil properties and stand age together explained between 28.8 and 58.1% of the variation in CWM of leaf traits, and 43.4% of the variation in species richness (Table 3-3). As expected, relatively little of the variation in soil properties was explained by our model. Zero of the variation in the second PCA axis of soil physical properties was explained by the model but 14.5% of the variation in the first PCA axis of soil physical properties was explained by stand age. The first and second axes of the soil chemical property PCA had 3.7 and 4.7% of their variation explained by stand age respectively.

In the final SEM model (Figure 3-3), the variation in aboveground biomass was directly explained by a combination of stand age, species richness, CWM - foliar N, and CWM - foliar δ^{13}C. The soil PCAs of both physical and chemical soil properties were not directly related to aboveground biomass, but did have an indirect effect through their effect on species richness and plant traits. Stand age had both direct and indirect effects on aboveground biomass. The indirect effects of stand age occurred through its effects on traits and soil properties. The soil properties then affected traits and species richness, some of which were connected to biomass. The first axis of the soil physical property PCA only affected foliar P, indicating that sites with higher fertility also supported vegetation with higher foliar P concentrations. The second axis of the soil physical PCA was correlated with SLA, foliar P, and foliar N, again suggesting positive correlations between fertility and high values of foliar nutrients and SLA. The first axis of the soil chemical PCA was correlated with species richness and all traits but SLA. The second axis of the soil chemical PCA was correlated with foliar δ^{13}C and foliar P. Foliar P is the only trait that was correlated with all of the soil PCA physical and chemical axes. The standardized coefficients of each model relationship are printed in Figure 3-3 and represent the relative magnitude of each model relationship. These are in units of standard deviations to simplify comparison. If an explanatory variable were to increase by one standard deviation, the corresponding response variable would increase by the number of standard deviations represented by the numbers in Figure 3-3 (e.g. if stand age were to increase by one standard deviation, aboveground biomass would correspondingly increase by 0.60 standard deviations).

Discussion

We studied the variation in biomass, functional traits and soil properties in the secondary tropical dry forest landscape to find both the direct and indirect relationships among these factors. We hypothesized that biomass increase would follow a saturating pattern with stand age but that site-specific differences would lead to variation around that pattern. We further hypothesized that the dominant functional traits would vary in response to both stand age and soil properties, and that diversity, traits, and soil properties would explain some of the variation in biomass unaccounted for by stand age. Our findings indicate that 1) the landscape-scale variation in biomass accumulation does exist (Figure 3-5), 2) that both stand age and soil properties affect the distribution of functional traits, but 3) that only 5% of additional variation in AGB was explained by soils, traits, and species richness after accounting for stand age. Plant functional traits were found to vary with both stand age and soil properties, as we predicted. Stand age alone explained between 15 and 31 % of the variation in the CWM of the four leaf traits we studied (Figure 3-4). Our SEM model, which included stand age and soil physical and chemical properties, explained between 29 and 58% of the variation in CWMs of traits (Table 3-3). We also found that soil properties had an indirect effect on AGB through their effect on species richness and traits but soils did not directly affect AGB. We found some evidence to support our last hypothesis, that traits and soil properties would explain the residual variation in AGB after stand age. But only a small amount of additional variation in AGB was explained when soils and traits were included (51% compared to 46% with stand age alone).

The most striking result from our SEM model was the degree to which it explained the variation in the community weighted means of leaf traits. For example, soil properties and stand age explained 58% of the variation in foliar P. These completely independent data sets (forest age, soil properties, and plant functional traits) were strongly correlated. The correlations between foliar nutrients and soil properties have two possible explanations; that tree species with higher requirements for nitrogen and phosphorus are limited to areas with more nutrients or greater water holding capacity, or that soil nutrient concentrations are influenced by the composition of tree species at a site. While we cannot rule out either explanation (and both may be true to some extent), our results support the former because we measured total quantities of soil nutrients and we assume that these are a better reflection of parent material and weathering-induced differences among sites (at least for rock derived nutrients).

The sign and magnitude of the coefficients in the final SEM model provide some insight into the effects of soil variation on the CWMs of traits. Foliar P is related to all four soil PCA axes and 58% of its variation is explained by our model, which is more than any other trait. The first soil chemistry PCA axis, which is greatly influenced by soil P has the strongest relationship with leaf P, suggesting filtering of species with greater nutrient requirements from sites with low soil P. Leaf N is influenced by the same chemical PCA axis and by the second soil physical property PCA axis, which is driven in part by silt content. Given the relationship between silt content and soil water holding capacity (Rawls et al. 1982, Saxton et al. 1986), we interpret this as the CWM-leaf N being driven by both soil nutrients and water holding capacity. CWM-SLA was also correlated with water-related soil properties while CWM of leaf $\delta^{13}C$ was only connected to soil chemical properties. This is surprising given that $\delta^{13}C$ is related to water use efficiency and that SLA and $\delta^{13}C$ are negatively correlated when examined on a species basis (Powers and Tiffin 2010). Soil chemical properties were also found to be related to species richness though the effect of soils on richness was small relative to that of stand age.

CWMs of leaf N, $\delta^{13}C$, and species richness were all related to AGB, although the percentage of variation they explained was small. CWM of leaf N and $\delta^{13}C$ had negative relationships with AGB while the richness-AGB relationship was positive. The positive affect of richness is unsurprising given the documented relationship between richness and productivity (Waide et al. 1999) and the fact that both richness and AGB increase in a similar fashion across successional time (Powers et al. 2009). The negative correlation between CWM of leaf N and AGB is surprising as leaf N itself is positively correlated with stand age. This means that biomass and the CWM of leaf N both increase with stand age, but among sites of the same age, sites with higher leaf N have lower biomass. This may reflect potential physiological trade-offs among strategies requiring greater N and those leading to more biomass storage. For example, leaf N is negatively correlated to $\delta^{13}C$ among 87 species in our region, suggesting a possible tradeoff between carbon gain and water use efficiency (Powers and Tiffin 2010). The negative AGB – CWM-$\delta^{13}C$ relationship is similarly surprising as it indicates that lower water use efficiency is associated with higher biomass. Again, this may be evidence of physiological tradeoffs or indicate that the trait-biomass correlations found in this study result from factors not accounted for in our study design.

Stand age had only a small effect on soil physical and chemical properties and the model explains only 3.7 - 14.5% of the variation in the soil PCA axes. The small amount of variation in soil physical PCA 1 explained by stand age is corroborated by a separate study in this area which showed a typical decline in bulk density with stand age as soils recover from compaction by cattle with forest recovery from conversion to pasture (Powers et al. in press). Soil Physical PCA 2 had no relationship with stand age but also is not strongly influenced by the variation in bulk density. These results are unsurprising given that we selected soil variables that we expected to be little affected by short-term secondary succession like total nutrients and soil particle-size distribution. Our goal was not to explain the variation in soil properties through this model but to account for any indirect effect of stand age on traits and AGB through soil properties.

The AGB of older forests at our study site is comparable to that of other TDF that receive a similar amount of annual precipitation (Becknell et al. 2012) but this is not surprising as data from this study were included in that global analysis of secondary TDF biomass (Becknell et al. 2012). The range of AGB in our study is similar to global values of TDF where the rate of biomass accumulation appears to slow after about 40 years (Becknell et al. 2012). Other studies have examined the variation of AGB in tropical forests and its drivers, but few consistent patterns across sites have emerged. Studies of forest structure and biomass across successional gradients in seasonal forests of the Yucatan found that stand age explains much of the variation in biomass and basal area, and that landscape structure and soil properties explain much less of this variation relative to stand age (Hernández-Stefanoni et al. 2011, Dupuy et al. 2012). While Clark and Clark (2000) found that in mature forests, soil and topography affect forest structural characteristics like stem density but not biomass, other studies in tropical forests have found positive relationships between soil fertility and biomass (Gourlet-Fleury et al. 2011). Biomass in rain forests of southwestern Borneo was found to increase with soil percent sand (Paoli et al. 2007). In the Amazon, biomass has been found to be associated with several soil physical and chemical properties but the pattern and sign of these relationships varies among studies (Quesada et al. 2009, Laurance et al. 1999). By contrast, (Baraloto et al. 2011), also working in the Amazon, found little relationship between soil properties and AGB. These contrasting findings likely represent site-specific conditions where different combinations of abiotic and biotic factors control biomass at different sites. A pan-tropical pattern between forest biomass and soil properties is unlikely given the large differences in potential drivers including geology, climate, disturbance history, and species composition. A pan-tropical study of the factors that control variation in ANPP supports this in that it found only a weak relationship with soil P (Cleveland et al. 2011). Additionally, our study explicitly focused on recovering forest, where successional processes may subsume any edaphic driven effects on biomass.

Several studies have found relationships between traits like wood density or SLA and tree growth and/or mortality rates (Poorter and Bongers 2006, Poorter et al. 2008, Keeling et al. 2008) implying similar relationships may exist between traits and biomass. A study of tree growth and traits in our area found that foliar N was the only trait positively correlated with relative growth rates (Becknell and Powers in prep). However, a study of wood density and biomass across neo-tropical forests including our study area, found no consistent relationship between wood density and biomass (Stegen et al. 2009). Two studies in the Amazon have found little or no role of traits like wood density and maximum tree height on biomass and productivity (Baraloto et al. 2011, Baker et al. 2009). These contrasting results suggest that trait-biomass correlations may be site-specific, or where they are found, may be a result of spurious, indirect correlation.

In general, diversity is positively correlated to biomass in tropical dry forest sites, especially when disturbance is present (Alvarez-Yepiz et al. 2008, Balvanera and Aguirre 2006). The increase in diversity with stand age (Powers et al. 2009, Lebrija-Trejos et al. 2010b) that mirrors the increase in biomass may mean that the small diversity effect we find only exists in secondary forests with strong diversity gradients. We interpret this relationship in our model between diversity and biomass as causal, but do so with caution because the same environmental factors that allow for higher or lower biomass in secondary forests of the same age may allow for higher or lower numbers of species. However the potential for a causal link between diversity and biomass in tropical forest has been predicted by modeling work (Bunker et al. 2005) and has been observed in other forest types (Jonsson and Wardle 2010, Ruiz-Jaen and Potvin 2010).

Our finding that trait distributions are influenced by both soil and stand age is reinforced by studies in multiple forest ecosystems, but the sign and strength of these relationships was not always what we expected. Evidence from many tropical forests suggests non-random distribution of species across edaphic and other resource gradients

(Clark et al. 1999, Bohlman et al. 2009, Gourlet-Fleury et al. 2011). Evidence of edaphic determinants of plant traits has also been found in multiple ecosystems (Kraft and Ackerly 2010, Katabuchi et al. 2011) and these patterns appear to be widespread (Ordoñez et al. 2009). Succession has been found to play a role in trait distributions in temperate forest (Kutsch et al. 2009, Campetella et al. 2011) and wet and dry tropical forests (Chazdon et al. 2009, Lebrija-Trejos et al. 2010a). These findings of other studies combined with ours suggest that predicting dominant trait values at a site using environmental variables may be possible. However, the use of these community trait values to explain or predict variation in stand-level properties like biomass remains unproven, at least in this secondary tropical dry forest landscape.

The common paradigm of pioneer species being replaced by shade-tolerant species over succession yields the prediction that fast growing species with low wood density and high nutrient contents should be more abundant in young forests and decrease in abundance as forests age (Brown and Lugo 1990a, Guariguata and Ostertag 2001). By contrast, we found no relationship between stand age and wood density and further, foliar nutrients increase with stand age (Figure 4). Possible interpretations of this result are that young forests are not dominated by fast growing species or, more likely based on a recent study of tree growth at this site (Becknell and Powers in prep) that fast growing early successional species include species with both high and low wood density. For example, many young sites are dominated by species like *Rehdera trinervis* and the legume *Gliricidia sepium*, which have high wood densities of 0.74 and 0.78 g cm^{-3} respectively (Powers et al. 2009). This may be a finding specific to water limited dry forests where growth rate on an annual basis is a balance of both growth rate when resources are abundant and the ability to continue growth as water resources become scarce.

Our results show that stand age primarily drives AGB variation and that there is a small additional contribution from traits, diversity and edaphic properties. Our results explain 51% of the variation in AGB in the study landscape. The remaining variation in aboveground biomass may be due to soil or physiological variables that we did not measure, previous land use, unknown recent disturbances, and/or stochastic and non-measurable processes that affect stand dynamics (such as past dispersal limitation, herbivory, disease, or past climate patterns that younger stands have not experienced). Soils and functional composition may have a stronger effect than our data show, but the properties we measured do not show these effects. In terms of functional composition, we used easily measured leaf traits to quantify functional diversity and these particular traits may not have much bearing on growth and carbon storage properties of the trees. We also use community weighted means of traits based on measurements done in a subset of trees of each species. These traits were not measured in each plot to account for potential site-specific variation and plasticity, i.e. our community weighted mean values may not represent the actual mean trait values of each stand (Hulshof and Swenson 2010, Violle et al. 2012).

Forest dynamics are another potentially important source of variation among stands that may explain different amounts of biomass in stands of similar age. Our study quantified live biomass in trees, and omitted standing dead trees or fallen coarse woody debris. We know from the observed species turnover with stand age (Powers et al. 2009) that early successional trees regularly die and are replaced by mid and late successional species. As this turnover proceeds, total live biomass at the plot level fluctuates, adding potentially significant variation across the landscape. In a prior study, we found that coarse woody debris increases with stand age in these forests (Kissing and Powers 2010) but in young stands (< 15 yrs), dead trees are largely absent. Thus, it is possible that within-stand forest dynamics may explain large differences in biomass among plots of similar age. Processes that may influence these stand dynamics include herbivory and defoliation which is often species-specific (Janzen 1981) and may lead to significant mortality (Kissing and Powers 2010). We suggest that future landscape-scale studies of biomass of succession measure dead biomass components in order to capture these stand dynamics effects.

Conclusions

We found that the variation in leaf traits across the landscape is controlled by both edaphic properties and succession. Both soil physical properties, which are related to water availability, and soil chemical properties were important in explaining stand-level variation in functional traits. We found that the CWMs of two leaf traits, foliar N and foliar $\delta^{13}C$, explain a small amount of the variation in AGB of secondary forest. Species richness plays a small role in AGB, but the primary driver of the variation in AGB is stand age.

These results reinforce evidence that plant traits can be indicators of changes in function as forests regenerate and underscore the role of edaphic gradients in filtering species and traits. This study provides only marginal evidence that frequently used and easy to measure leaf traits can be used to explain the variation in ecosystem properties such as carbon storage in biomass in a successional context. However, the marginal evidence we found suggests that this link may be found using other plant functional traits or in ecosystems that are not dominated by disturbance related processes.

Tables and Figures

Table 3-1. Coefficients of variation for individual soil physical and chemical properties. Stone content, chromium, magnesium and nickel all have higher variation relative to other soil variables.

Soil physical properties	Coefficient of variation
Bulk density	16.52
Stone content	135.35
% sand	17.16
% silt	21.56
% clay	19.85
Soil Chemical Properties	
pH	6.67
Boron	33.07
Calcium	77.35
Carbon	38.59
Chromium	163.99
Copper	44.81
Iron	28.10
Manganese	42.70
Magnesium	162.20
Nitrogen	30.31
Nickel	136.56
Phosphorus	89.04
Potassium	72.00
Sodium	66.85
Zinc	32.61

Table 3-2. Variation of community weighted mean values of traits.

Average, minimum, maximum, coefficient of variation and Pearson's correlation coefficients (PCCs) for the correlation with stand age of CWM values of traits and species richness. Significant PCCs are noted with an asterisk.

Traits	SLA (cm^2g^{-1})	Foliar $\delta^{13}C$ (‰)	Foliar P (%)	Foliar N (%)	Wood density (g cm^{-3})	Species richness
Mean	95.1	-29.1	0.1	2.17	0.67	13.5
Min	63.8	-30.77	0.06	1.354	0.48	1
Max	129	-28.27	0.13	2.712	0.80	27
Coefficient of variation	15.0	1.5	16.2	15.7	10.4	44.1
PCC w/ stand age	0.52*	-0.35*	0.41*	0.37*	-0.07	0.50*
R^2 from regression with stand age	0.314	0.155	0.217	0.165	0.026	0.413
p-value from regression w/ stand age	$1.82x10^{-8}$	$1.28x10^{-4}$	$4.74x10^{-6}$	$7.35x10^{-5}$	0.0782	$0.26x10^{-11}$

Table 3-3. Squared multiple correlations from SEM analysis.

These numbers represent the percent of variation in each response variable explained by their associated explanatory variables.

Response variables	Percent variance explained
Aboveground Biomass	50.8%
Species Richness	43.4%
CWM Leaf N	37.9%
CWM Leaf P	58.1%
CWM Specific leaf area	41.2%
CWM $\delta^{13}C$	28.8%
Soil Chemical PCA axis 1	3.7%
Soil Chemical PCA axis 2	4.7%
Soil Physical PCA axis 1	14.5%
Soil Physical PCA axis 2	0%

Figure 3-1. Conceptual Model

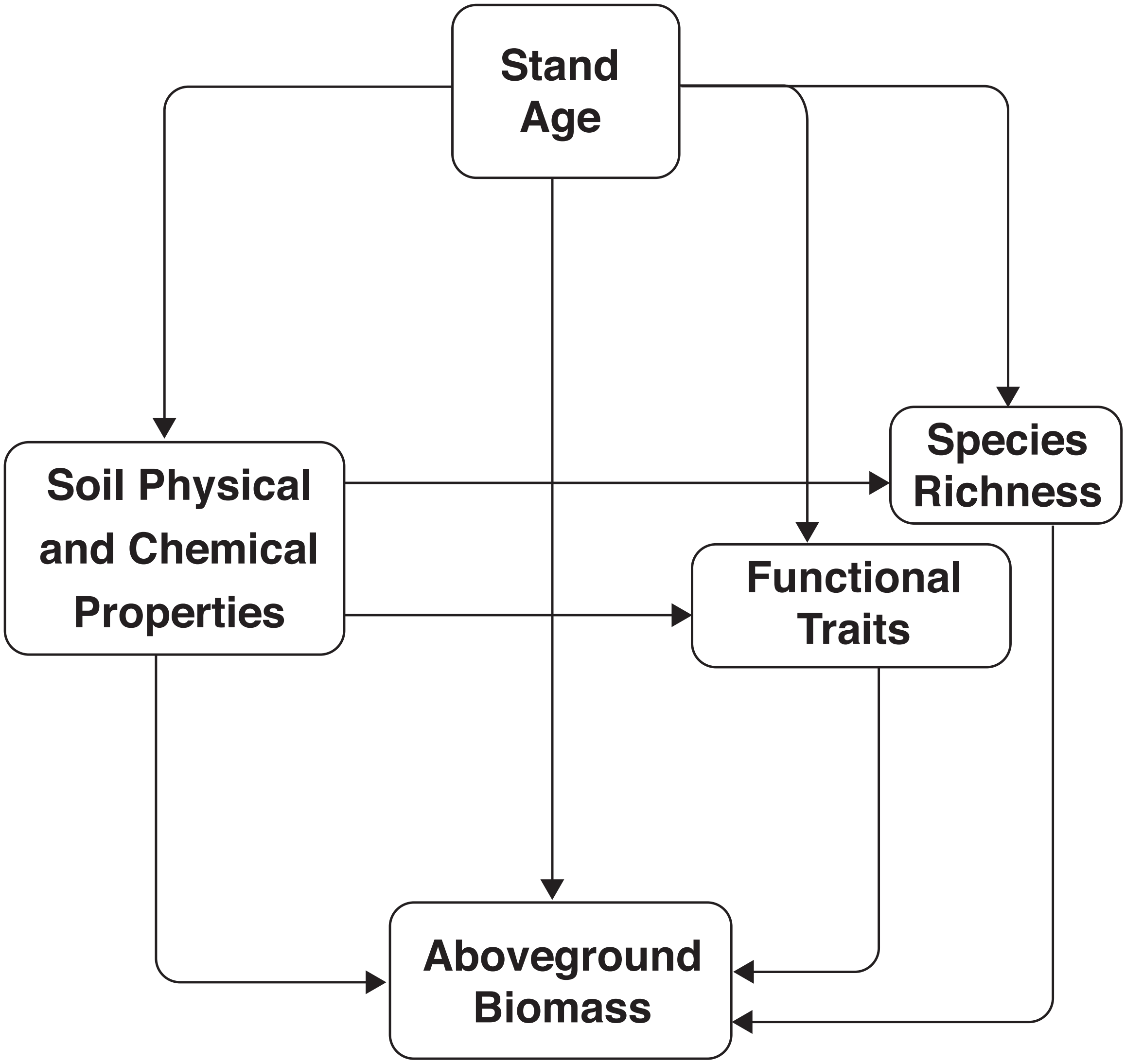


Figure 3-2. Initial SEM Model

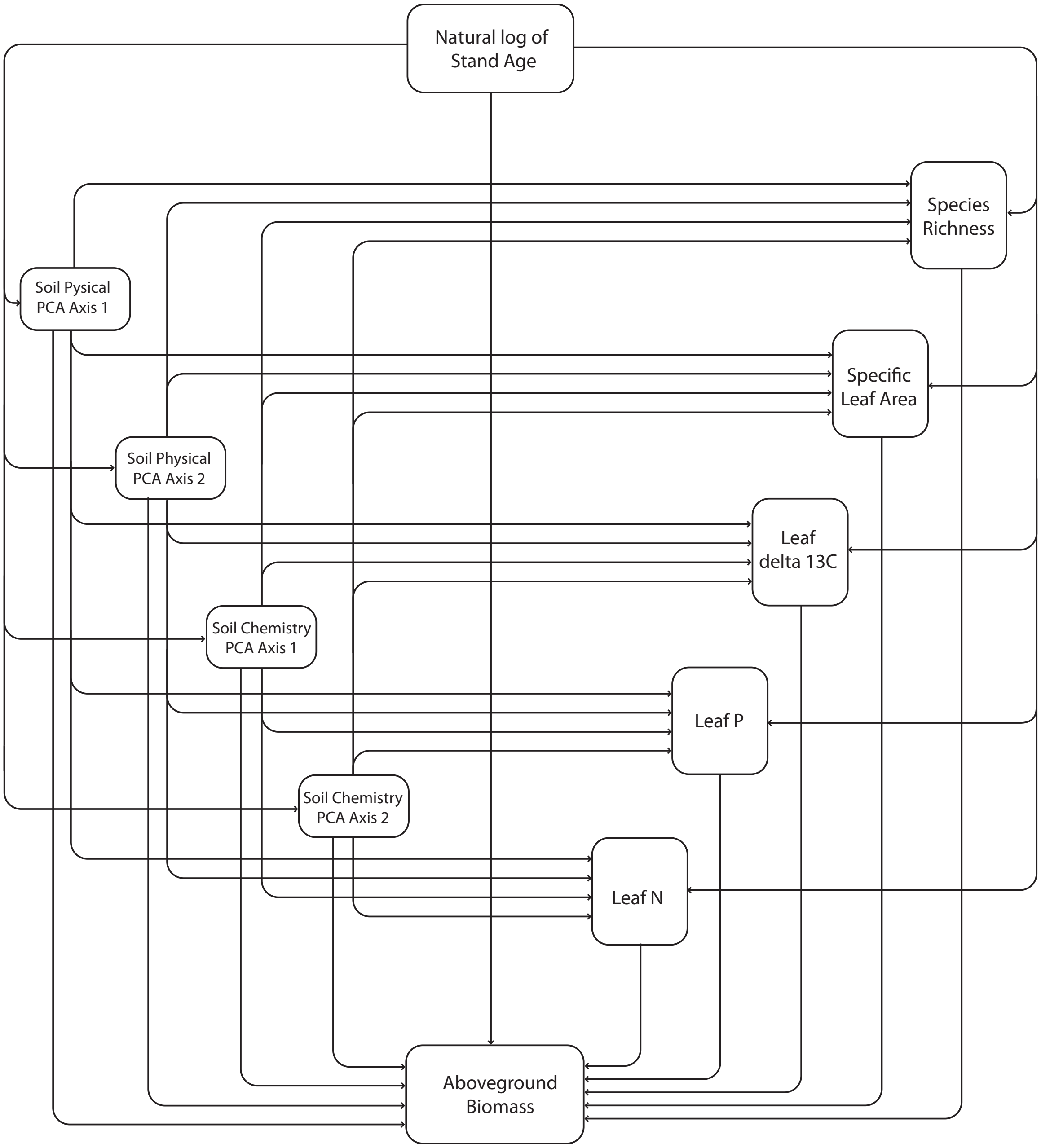


Figure 3-3. Final SEM Model with standardized coefficients.

The traits are represented by the community weighted mean of each trait in each plot where biomass was measured.

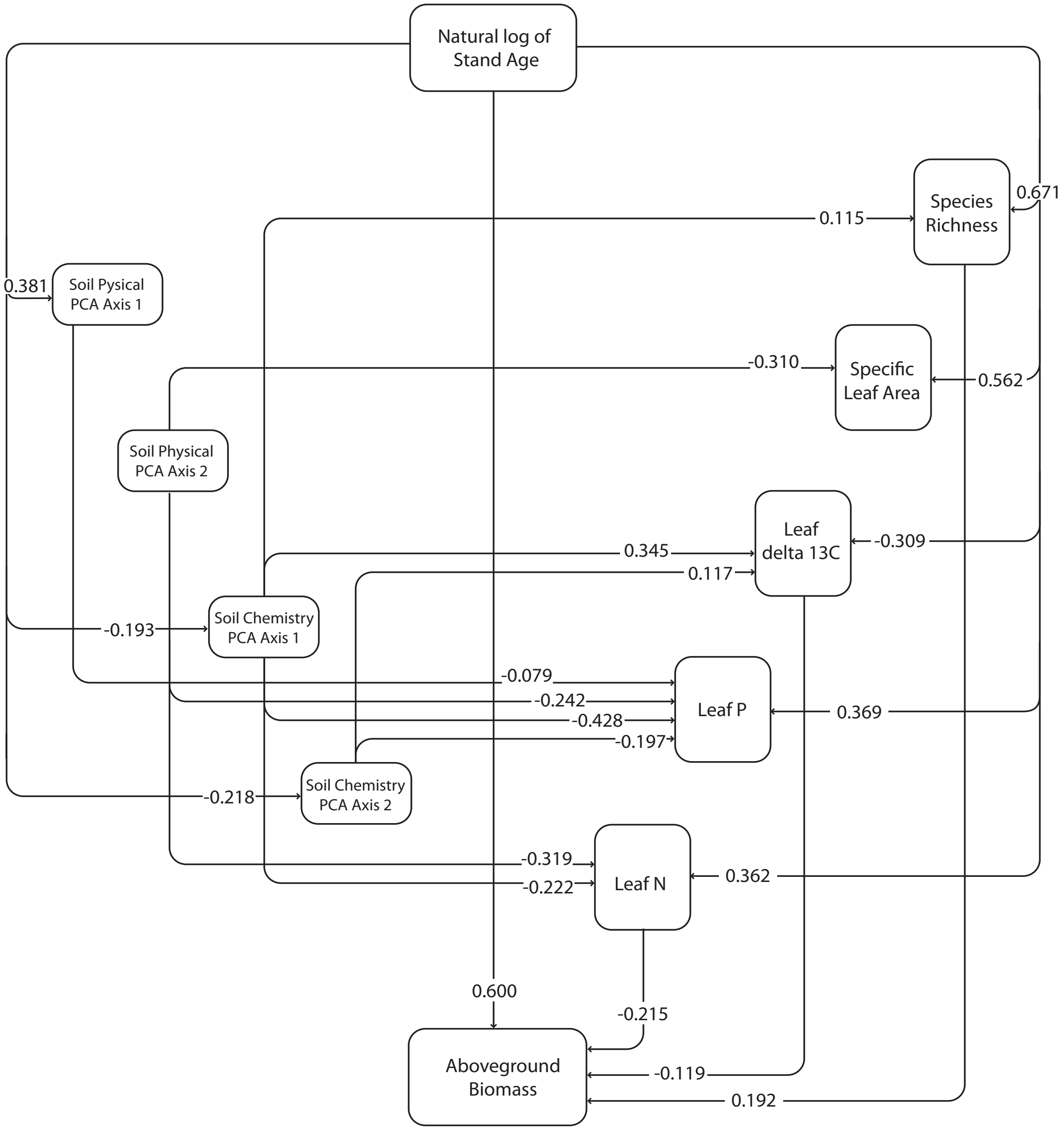


Figure 3-4. Community weighted means of plant traits across stand age.

Relationship between stand age and the community weighted means of plant functional traits. Linear regression between CWMs of traits and the natural log of stand age are shown. R^2 and p-values for regression in Table 3-2.

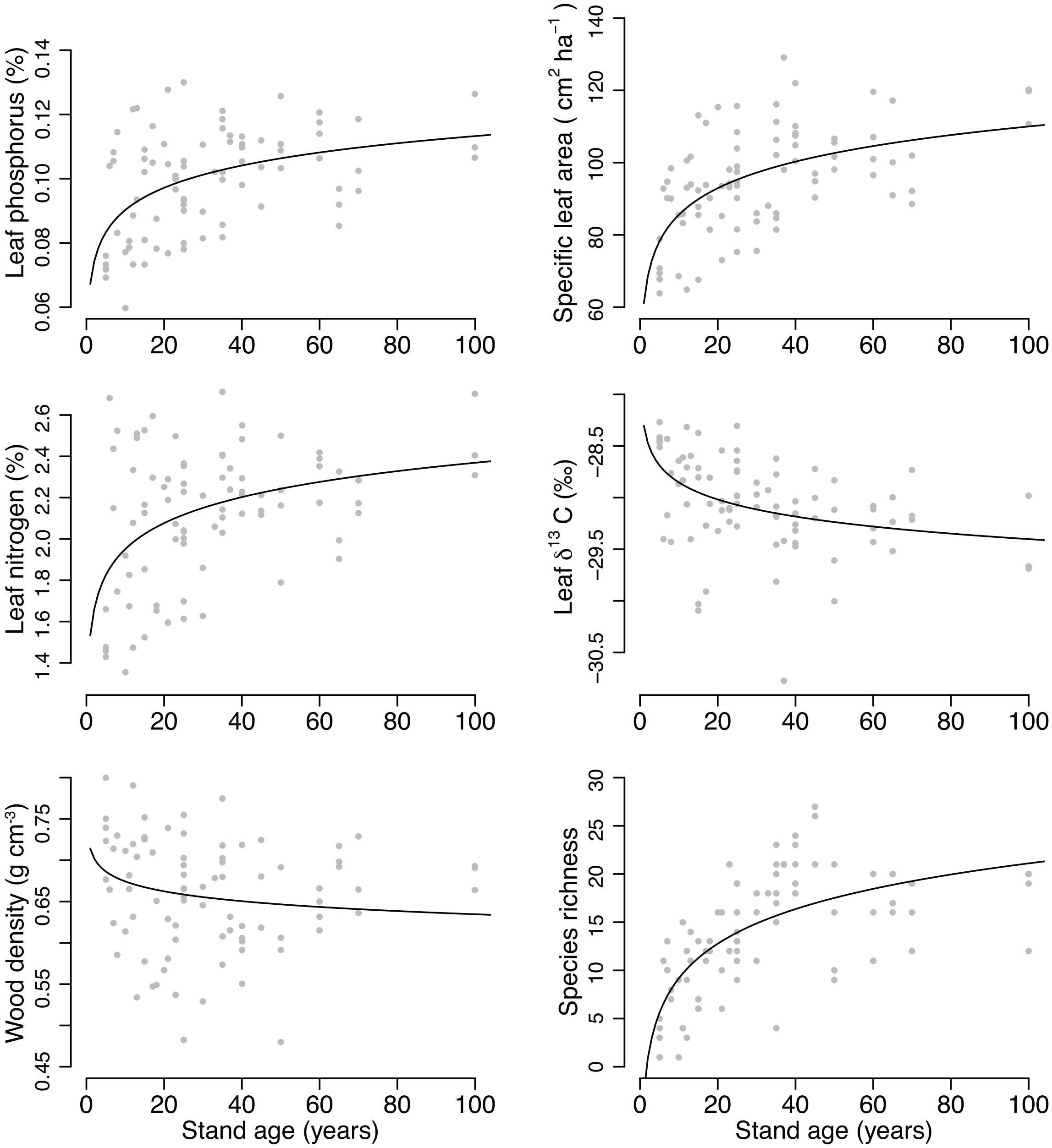
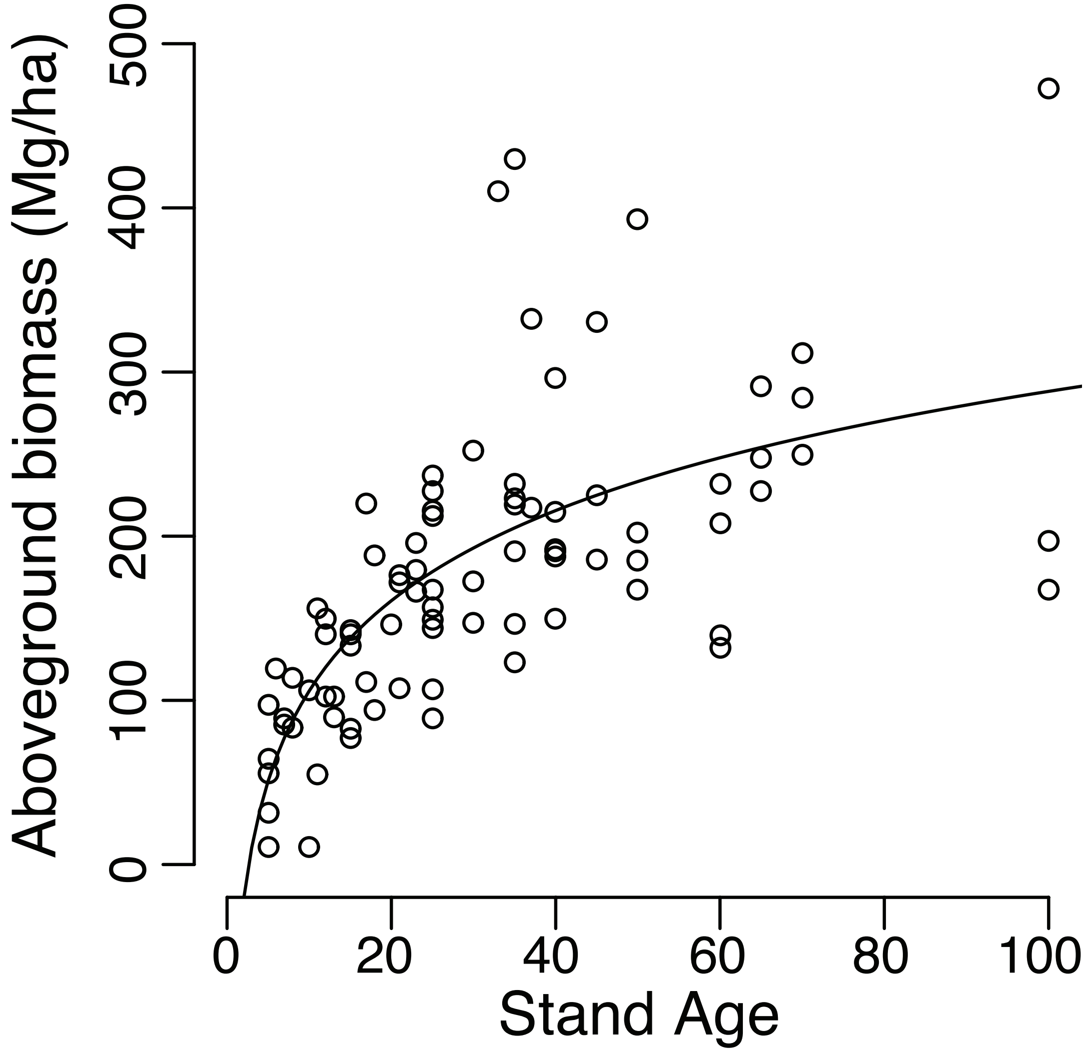


Figure 3-5. Aboveground biomass and stand age.

Relationship between stand age and aboveground biomass. Line shows the result of a linear regression between aboveground biomass and the natural log of stand age. P-value $= 7.7\times10^{-13}$ and R^2 value = 0.46.



Chapter 4

Inter-annual variation in aboveground net primary productivity in Costa Rican secondary tropical dry forest: environmental, successional, and species effects

Introduction

Net primary productivity represents the total amount of carbon taken up by photosynthesis minus the carbon lost in plant respiration and is operationally defined as the biomass accumulated during a time interval (Clark et al. 2001a). Understanding how NPP varies across space and time is important for global carbon cycle modeling and quantifying the effect of terrestrial productivity on climate. Tropical forests contain approximately 264 Pg of carbon in above and belowground biomass and overall hold about 55% of the world's forest carbon stocks (Pan et al. 2011). Despite their importance in global carbon cycling, tropical forest NPP is poorly characterized (Clark et al. 2001b), and little certainty exists about the extent to which variation in NPP is controlled by various environmental factors in tropical forest ecosystems (Lewis et al. 2009, Cleveland et al. 2011, Malhi 2011).

The factors potentially driving variation in tropical forest NPP include climate, nutrient availability, disturbance history, and the species composition of primary producers (Schuur 2003, Baker et al. 2003, Toledo et al. 2011). Literature reviews have bounded the range of tropical forest NPP from 1.7 to 21.7 Mg C ha^{-1} yr^{-1} (Clark et al. 2001b) and examined the relationships between NPP and climate and other environmental factors (Schuur 2003, Cleveland et al. 2011). Across the tropics, NPP is related to temperature and precipitation (Schuur 2003), but this relationship is less clear when upland sites are analyzed separately from lowland sites (Cleveland et al. 2011). Tropical dry forests (TDF), which receive <2000 mm of rainfall annually and experience a dry season lasting at least 4 months, are less studied than wet forests (Clark et al.

2001b, Jaramillo et al. 2011). The seasonality of TDF and strong relationship between mean annual precipitation and biomass (Chapter 2) suggests that controls on NPP might be different for TDF compared to wetter tropical forests where soil P is the best overall correlate of NPP (Cleveland et al. 2011).

Species diversity and composition may affect NPP via the well documented relationship between diversity and productivity (Waide et al. 1999, Tilman et al. 2001, Hooper et al. 2005). For forests or grasslands of the same age, productivity increases with diversity, due to niche complementarily (Tilman et al. 2001, Ewel 1980), reduced species-specific disease loads at higher diversity (Schnitzer et al. 2011), and/or sampling effects (Huston 1997). These diversity-productivity relationships can also be described in the context of plant function, where differences in the dominant traits in a community drive its stand-level function (Grime 1998). For example, species-specific differences in growth rates add up to ecosystem-level differences in NPP. In tropical dry forests in Costa Rica, the community weighted means (CWM) values of plant functional traits change along gradients of stand age and soil properties (Chapter 3), and this variation in traits has some effect on aboveground biomass and may also affect productivity.

Forest diversity and composition change with succession and these changes are likely to affect NPP. Across succession, species vary in both their response to changing resources and in their effect on ecosystem-level processes (Bazzaz and Picket 1980, Chazdon et al. 2007). Tree species show individualistic growth responses to variation in climate and/or resources like light, soil moisture, and nutrients (Enquist and Leffler 2001, Baker et al. 2003, Poorter et al. 2008). In general, as tropical forests age and undergo succession, species composition transitions from domination by short-lived, fast growing species to an increased abundance of longer-lived, slower growing and more shade tolerant species (Bazzaz and Picket 1980, Guariguata and Ostertag 2001). As the dominant growth rates and environmental tolerances of tree species change, concurrent changes in productivity may be expected as forest composition changes during secondary succession.

During forest regeneration, NPP is generally thought to increase rapidly with stand age, then level-off and decline as forests reach maturity (Kira and Shidei 1967, Gower et al. 1996, Ryan et al. 1997, 2004). Litter production, often the largest component of NPP, increases asymptotically as forests age (Lawrence 2005, Marín-Spiotta et al. 2008). Biomass increment, the other large component of NPP, is expected to increase during early succession and decrease as forests mature. This decline in woody growth is believed to be the source of the decline in ANPP in older forests (Gower et al. 1996, Ryan et al. 1997, He et al. 2012).

Despite this generally accepted relationship between forest age and NPP there are questions as to whether it always applies (Luyssaert et al. 2008). Significant divergences from this pattern have been found, and represent an important unresolved question in studies of global carbon cycling (Phillips 1998, Luyssaert et al. 2008, McMahon et al. 2010, He et al. 2012). There is ample evidence for this pattern in temperate forests (Gower et al. 1996, Pregitzer and Euskirchen 2004) and some in tropical forests (Brown and Lugo 1990a, Ryan et al. 2004) but long term studies of productivity in secondary tropical forests are rare (Pregitzer and Euskirchen 2004). Different forest types have been found to have different patterns of NPP change with forest regeneration (Wang 2007, Kutsch et al. 2009, He et al. 2012). While in most forest types NPP decreases after an initial peak, some forests have been found to level off and remain unchanged or to continue increasing at a slower rate (He et al. 2012). Whether similar differences exist among secondary tropical forests is unknown due to the scarcity of data.

What is known about NPP in TDF comes from a relatively small number of studies that often differ in methods and are biased towards the driest parts of the TDF range (Jaramillo et al. 2011). Methods differs in the components of ANPP that are measured (biomass increment and litterfall) and the length of the study. Estimates of ANPP from seven mature TDF sites range from 2.7 to 13.1 Mg C ha^{-1} yr^{-1} but few of these estimates include both biomass increment and litter components (Clark et al. 2001b), making it difficult to judge their accuracy or relate these patterns to potential drivers. In many studies, only litterfall is measured and used to estimate ANPP. Across sites, litterfall appears to increase linearly with mean annual precipitation and ranges from 2.9 to 8.5 Mg ha^{-1} yr^{-1} in dry forests (Martínez-Yrízar 1995, Jaramillo et al. 2011). Other studies measure biomass increment directly, or in secondary forests, divide aboveground biomass by the age of forests to estimate the annual biomass increment. These studies show a range of 0.4-5.6 Mg C ha^{-1} yr^{-1} across different sites, but are unable to detect inter-annual variation (Worbes and Raschke 2012). The majority of both litterfall and biomass increment studies have been conducted at sites on the drier end of the TDF precipitation spectrum (Jaramillo et al. 2011) and the considerable differences in carbon stocks across the precipitation gradient (Chapter 2) imply likely large differences in ANPP.

The most frequently measured component of NPP is litterfall which by itself is an ecologically important flux of carbon and nutrients from the canopy to the forest floor. At regional or continental scales, litterfall quantity does not vary consistently with precipitation or soil type but does increase with seasonality (Chave et al. 2010, Malhi et al. 2011). At local scales there is some evidence that soil nutrients affect the amount of reproductive components in litterfall, but not leaf litterfall (Kaspari et al. 2007). Tropical dry forests are marked by their seasonal patterns in litterfall with the majority of litterfall occurring after rains cease in the early dry season (Frankie et al. 1974, Martínez-Yrízar and Sarukhán 1990, Justiniano and Fredericksen 2000, Sanches et al. 2008). Beyond these patterns of litterfall phenology, little is known about the abiotic and biotic factors that affect site to site variation in total litterfall and the relative distribution of its components: leaves, flowers, fruit, seeds, twigs, and frass.

In this study we measured litterfall and biomass increment for 3 years in plots arrayed across gradients of succession, forest type, and edaphic properties in tropical dry forests in Costa Rica. We specifically address the questions: 1) How does ANPP vary with climate, forest type, stand age, tree species composition, and edaphic factors? 2) How does litterfall and the contribution of its components (leaves, twigs, fruits and seeds, flowers and frass) vary with climate, forest type, stand age, tree species composition, and edaphic factors? 3) Is inter-specific variation in the growth rates of trees correlated with functional traits? Our data allowed us to examine spatial patterns at the landscape scale and temporal patterns across chronosequences and among years. We predicted that ANPP would initially increase with forest age followed by a subsequent decrease in the oldest sites. Litterfall quantities were expected to increase logistically with increasing stand age, and be correlated with soils and tree functional composition. Finally, we expected that tree growth rates would be correlated with plant functional traits such as foliar nitrogen or phosphorus concentrations, wood density, and measures of water use efficiency.

Methods

Study site

This study took place in two conservation areas in Guanacaste, Costa Rica: Palo Verde National Park (Area de Conservación Arenal-Tempisque) and Santa Rosa National Park (Area de Conservación Guanacaste). Based on data from the last 30 years, mean annual precipitation for Santa Rosa and Palo Verde are 1575 and 1445 mm respectively (investigadoresacg.org; www.ots.ac.cr). Precipitation in both parks can vary strongly from year to year with as little as 700 mm in dry years and up to 3000 mm in wet years. The region experiences a strong 5-6 month dry season that begins in December and ends in May or June. Both parks have large areas of secondary tropical dry forest which are regenerating after being cleared for agriculture or pasture land. These secondary forests include areas that have been growing back since the 1970s as well as patches of younger forests (Powers et al. 2009). Santa Rosa includes areas along an upper plateau with rocky pumice and ash soils and fertile lowlands with deeper soils and taller stature forests. On the plateau, forests are often dominated by the evergreen oak species *Quercus oleoides* and subsequently are lower in species richness. Mature patches of oak forests appear to be rare and older oaks are likely to be open grown trees that remain from when these areas were pastures. Below the plateau, there is a heterogeneous mix of forest ages ranging from very young forests to patches that may never have been cleared (Janzen 1988b). Species richness is higher in the lowlands and sites range from being 100% deciduous to 75% evergreen. The soils of these areas are varied and heterogeneous in both chemistry and texture (Leiva et al. 2009). Palo Verde includes forested lowlands and hills along the banks of the Tempisque River. Forests are generally thought to be secondary but are wide ranging in the time they have been recovering. Species richness at Palo Verde is similar to the lowlands of Santa Rosa but forests are never more than 50% evergreen species. Soils are formed from limestone in the hills or clay and silt in the former and current flood plain lowlands (Hartshorn 1983).

ANPP plots

We worked in 18, 20 × 50 m plots that were the focus of previous studies of coarse woody debris (Kissing and Powers 2010) and fine roots and soils (Powers and Peréz-Aviles 2012). The plots are stratified by age and forest cover type, allowing us to evaluate the relative roles of these factors in carbon cycling (Kissing and Powers 2010). Six of the plots occur on the oak (*Quercus oleoides*) dominated plateaus in Santa Rosa (SROAK), six occur in the lowland dry forests of Santa Rosa (SRTDF), and six occur in the lowland dry forests of Palo Verde (PVTDF). These “forest-types” differ in both plant community and edaphic characteristics with the oak forests typically having the lowest soil nutrients contents and Palo Verde having the highest (Powers et al. 2009). All trees >10 cm diameter at breast height (DBH) were identified to species and growth and litterfall were measured using methods described below.

Aboveground net primary productivity

Aboveground net primary productivity (ANPP) is the most commonly measured component of NPP because of the difficulty of making belowground measurements.

Estimates of ANPP are typically made by measuring the incremental change in biomass and the amount of foliar production, i.e. litterfall (Clark et al. 2001a). The sum of these components approximates ANPP assuming relatively little losses to herbivory and volatile organic compounds (Clark et al. 2001a).

Litterfall

We placed 4 0.5 × 0.5 m litter traps along the center 50 m transect of each plot. Litter was collected monthly starting in December 2007 in twelve plots in Santa Rosa and since March 2008 in Palo Verde. This gave us four complete years of litterfall data from Santa Rosa and three from Palo Verde. The litter from each trap was dried at ~60 °C, sorted into leaves, flowers, fruit and seeds, twigs <10 mm, and frass and then weighed. Total litterfall was calculated by taking the average monthly total litterfall mass (including all components) from the 4 litter traps in each plot and dividing it by the total measurement area of the traps, and is expressed as megagrams of dry biomass per hectare (Mg ha^{-1}).

Biomass increment

Stainless steel dendrometer bands were used to measure biomass increment in all trees >10 cm DBH (Cattelino et al. 1986). Altogether, we followed the growth of 1009 trees, and saplings were added following recruitment into the 10 cm and greater DBH class. Dendrometers were placed at breast height or above buttresses and any other trunk irregularity. If trees were split into multiple trunks below breast height, each stem was given a separate dendrometer. We waited six months between dendrometer installation and the first data collection to minimize errors associated with bands adjusting to their position on trunk and slack in the band (Keeland and Sharitz 1993, O'Brien et al. 2007). At the approximate start and end of each rainy season, we measured the distance between the dendrometer sleeve and a mark etched into the band using a digital caliper. This increase in circumference was converted to increase in diameter and added to each tree’s diameter at the start of the interval to estimate the diameter at the end of the time interval. At the start and end of each measurement interval we used the DBH and species-specific wood density data from a previous study (Powers and Tiffin 2010) to calculate total aboveground biomass using a general tropical dry forest allometric equation (Chave et al. 2005). Trees with trunks split into multiple stems below 1.4 m were treated as separate trees for biomass calculations. The biomass increment for each tree was calculated by subtracting the initial biomass from the final biomass for each measurement interval. Biomass increment from each tree in a plot was summed to yield total plot biomass increment. Total ANPP was estimated by adding the annual biomass increment to the total annual litterfall over the same time interval. Here we analyze three complete years of dendrometer and litterfall data for all 18 plots, plus additional litterfall data from 2008 for twelve plots in Santa Rosa.

Soils

To study the effects of soil fertility on productivity, we used data on soils from the 18 plots that have been previously published (Powers and Peréz-Aviles 2012). We used 5 soil physical properties: bulk density, stone content, and particle size distribution (percent sand, silt, and clay) and 15 soil chemical properties: pH, boron, calcium, carbon, chromium, copper, iron, manganese, magnesium, nitrogen, nickel, phosphorus, potassium, sodium, and zinc. All elements were total concentrations, rather than extractable or labile, as we reasoned that land-use change is less likely to affect the total rather than labile element availability (Powers and Peréz-Aviles 2012). These were combined using two principal component analyses, one for physical and one for chemical properties of the soil (R Development Core Team 2012). The first and second of these principal component axes for physical and soil properties were used as potential explanatory variables.

Traits and functional diversity

The effect of species composition on ANPP and its components was evaluated using a functional diversity index and community weighted means of several leaf traits. Functional diversity describes the relative homogeneity or heterogeneity in trait values of the species present and is thought to be an important driver of ecosystem properties like NPP (Hooper et al. 2005). Many indices have been proposed to describe different aspects of functional diversity (Schleuter et al. 2010). In this study we use functional divergence as an index of functional diversity (Villéger et al. 2008). Functional divergence describes the degree to which the relative abundances of individuals in a community fill the potential “trait space” as defined by the range of functional traits available (Villéger et al. 2008). We used wood density, specific leaf area, foliar N, foliar P, and $\delta^{13}C$ content of leaves, measured in a separate study of functional traits (Powers and Tiffin 2010), to calculate functional divergence. To further evaluate the effect of various functional traits on ANPP and its components, we calculated the community weighted means of traits using the relative basal areas of trees of difference species in our plots. Tree species for which we did not have trait data were omitted from these calculations. We calculated the CWM of specific leaf area, foliar N, and foliar P. We did not use the CWM of wood density as an explanatory variable because the wood density of species were included in the allometric equations used to calculate biomass increment (Chave et al. 2005). We also calculated the CWM of the $\delta^{13}C$ of leaves but this was not found to be a useful explanatory variable in any of our regression models and is not discussed further. Both CWMs and functional divergence were calculated using the FD package of the R statistics software (Laliberte and Legendre 2010, R Development Core Team 2012).

Drivers of productivity and its components

We used repeated measures ANOVA to test for differences among years and forest types (SROAK, SRTDF, and PVTDF) in both ANPP and litterfall. We used linear regression to test the association of ANPP, biomass increment, litterfall, and the components of litterfall with potential biotic and abiotic drivers. First, using repeated measures ANOVA, we found that there was no significant difference in ANPP or its components among years. Based on this knowledge we used the plot average of ANPP and its components over three years to test for associations with stand age, soil physical and chemical properties, diversity, and functional traits. The Akaike's Information Criterion (AIC) was used to find the best possible model starting with a full model and eliminating non-significant variables, then later adding back variables until the lowest AIC value was found. The final models indicate which variables best explain the variation in ANPP and its components. All statistical analyses were conducted using the statistical software R (R Development Core Team 2012).

Species growth patterns

To examine patterns of growth among species we calculated the average annual and overall average relative diameter increment (RDI) for each species with 5 or more individuals in our study (29 species). RDI is the annual diameter increment of an individual tree divided by its DBH. We calculated log-transformed RDI values and removed zero values to meet parametric normality assumptions, and then used ANOVA to test for the effects of species and year. We also then plotted overall average RDI for each species against functional traits for those species measured in a separate study (Powers and Tiffin 2010). We used linear regression to test for relationships between functional traits and overall average RDI using average values per species as each data point.

Results

Soil principal component analyses

The first and second axes of the soil physical PCA explain 43 and 38% of the variation in these variables respectively. The soil physical PCA loadings show that the first axis is driven by stone content (0.61) and bulk density (-0.54), while the second axis in driven by particle size distribution (loadings for sand silt and clay are 0.72, -0.48, and -0.48 respectively). The first and second axis of the soil chemical property PCA explain 48 and 24% of the variation in the 15 variables. The loadings of these PCA axes are highest for pH (0.32), Ca (0.32), and Mg (0.33), however the loadings for B, C, N, K, P, Cr, and Zn are all between 0.23 and 0.29 indicating that the variation of all of these variables (many of which co-vary) is incorporated in this first chemical PCA axis. The loadings of the second PCA axis indicate its variation best represents that of Fe (0.41), Cu (0.36), and Cr (0.31). These data establish the fertility relationships among sites and confirm that a gradient in fertility exists among the oak forest sites (least fertile) to the plots at Palo Verde (most fertile), with Santa Rosa dry forest sites being intermediate.

Rainfall, ANPP, and its components

Precipitation over our study period differed between Palo Verde and Santa Rosa, varying between 1242 mm in 2009 and 3341 mm in 2008 (Table 4-1). The driest year at both sites was 2009 when they had nearly the same annual precipitation. The wettest year at both sites was 2008, followed by 2010 and 2011. At Santa Rosa 2008, 2010, and 2011 all had annual precipitation that was more than twice that of 2009. Palo Verde was both drier and slightly less variable than Santa Rosa (except in 2009 when rainfall was nearly equal).

Over three years and across 18 plots, ANPP ranged from 4.25 to 19.81 Mg ha^{-1} with an overall mean of 11.49 Mg ha^{-1}. Repeated measures ANOVA showed that there were no significant differences in ANPP among years or forest types (and no interactions), but the patterns of relative variation are notable in that they somewhat followed the large variation in precipitation. In Santa Rosa, a more than doubling of precipitation between 2009 and 2010 in was accompanied by a 14% and 7% increase in ANPP for the oak forest and lowland dry forest respectively. In Palo Verde precipitation increased by 71% and ANPP by 16% between 2009 and 2010. In general, ANPP was higher in the years with above average annual precipitation (2010 and 2011) compared to the year with below average precipitation (2009). The Santa Rosa Oak forests had lower ANPP than the other forest types (Figure 4-1). The specific response to precipitation differed between Palo Verde and the ACG. In Palo Verde, mean ANPP was higher than in the ACG, while precipitation tended to be lower. The relative level of ANPP among years in Palo Verde mirrored annual precipitation with 2009, the dry year having the lowest ANPP and 2010, the wettest year having the highest ANPP. The pattern was slightly different in the ACG. The driest year was again the lowest in ANPP, but the wettest year (2819 mm of precipitation) was not the highest in ANPP. We emphasize that these differences in ANPP among years and sites were not statistically significant.

ANPP increased significantly with stand age but appeared to level off after about 40 years of recovery (Figure 4-2). The highest ANPP occurred in sites with stand ages between 20 and 30 years. Individual components of ANPP differed in their variation with stand age and other drivers (Figure 4-3). Biomass increment had little discernible relationship with stand age while leaf litter quantities were higher in older forests, but did not appear to increase much after 40 years (Figure 4-3). Averaged over three years, various combinations of log-transformed stand age, soil physical and chemical properties, functional divergence, and community weighted means of traits explained between 43 and 77 % of the variation in ANPP and its components (Table 4-2). Log-transformed stand age appeared in the best fit models of ANPP, total litter, leaf litter and twigs (Table 4-2). The first axis of the soil chemistry PCA axis was in the best fit model for all categories except biomass increment. Community weighted mean of foliar P appeared in the best fit models for all litter, leaf litter, fruit and seeds, and twigs. Community weighted mean of specific leaf area was included in the best fit models for all dependent variables but frass. Only the two axes of the soil chemical PCA were needed to explain 57% of the variation in frass across plots.

Litterfall patterns

Across the three forest types, Palo Verde forests had the most litterfall in all three years (Table 4-3; data for Palo Verde were not complete in 2008) but this difference was non-significant. While litterfall was generally higher in wetter years than in drier years, repeated measures ANOVA revealed no significant differences between years or forest types. The 126% increase in precipitation between 2009 and 2010 in Santa Rosa was accompanied by nonsignificant increases in total litterfall of 19% and 18% in dry forest and oak forest plots respectively (an increase largely due to leaves and twigs). Over that same period, Palo Verde rainfall increased by 71% and total litterfall increased by 4.5%. The proportion of litterfall made up of leaves, flowers, fruits and seeds, twigs, and frass was relatively constant among years. Leaves comprised between 73 and 80% of total litterfall, followed by twigs (9-14%), fruit and seeds (4.5-5.9%), frass (2.0-5.1%), and flowers (3.2-3.5%). Leaves and twigs in litterfall varied seasonally following precipitation, with the largest pulse of litter in January after rainfall has dropped to near zero for several months (Figure 4-4). Flowers in litter peaked between March and July in the late dry season and early rainy season but there were large differences among sites. Fruit and seed-fall appeared variable and site-specific while frass increased in the rainy season and dropped to near zero during the dry season.

Species-specific Growth Rates

Relative diameter increment varied by an order of magnitude from 0.003-0.008 cm cm^{-1} yr^{-1} in the slowest growing species *Byrsonima crassifolia*, *Semialarium mexicanum*, and *Bursera tomentosa* to 0.033-0.040 cm cm^{-1} yr^{-1} in the fastest growing species, *Ateleia herbert-smithii*, *Cedrela odorata*, *Lysiloma divaricatum*, and *Swietenia macrophylla*. After removing zero values, analysis of variance showed that both year and species had significant effects on RDI values. RDIs were significantly lower in 2009 than 2010 and 2011, which were not significantly different from each other (p-values for year and species were $2x10^{-7}$, and $2x10^{-16}$ respectively).

Species-specific mean growth rates were compared to the functional traits of those species measured in another study (Powers and Tiffin 2010). Relative diameter increment was positively associated with the natural log of foliar N (Figure 4-6; p-value= 0.009, $R^2 = 0.24$). No other significant relationships were found between RDI and functional traits or plant functional type groupings based on leaf habit and status as a legume (results not shown).

Discussion

We measured biomass increment and litterfall to estimate ANPP in tropical dry forest plots across gradients of stand age, composition, and soil properties over three years. We expected that stand age, soils, and species composition would explain variation in ANPP and its major components, and that ANPP would change with annual precipitation. We also predicted that functional traits would explain some of the variation in the relative growth rates of species. We found that combinations of stand age, soil properties, and measures of functional diversity did explain much of the variation in ANPP and its components, but that each component was related to different biotic and abiotic factors. We also found that of several leaf traits and wood density, only foliar N was related to species average relative growth rates.

Our results support the hypothesis that ANPP and its components are driven by stand age, soils, and functional composition, however we found that inter-annual variation rainfall over three years had relatively small (and no significant) effects. Despite a more than doubling of precipitation, ANPP and litterfall changed very little. Among components of ANPP, the factors that best explained their variation were different. The variation in litterfall and its components was much better explained than the variation in biomass increment. The best fit model for biomass increment included FD and the CWMs of foliar N and SLA. Neither stand age nor soil properties explained variation in biomass increment. While it is not surprising that these traits and FD affect biomass increment, it is surprising that stand age and soil properties do not explain additional variation given the findings of other studies that soil properties contribute to tree growth (Baker et al. 2003, Toledo et al. 2011, Baribault et al. 2012) and known changes in growth and demographics across succession (Chazdon et al. 2007). This unexplained variation in biomass increment may be due to differences in resources we did not measure such as available nutrients, light, and water, or due to potentially stochastic factors such as herbivory, disease, and natural disturbances like wind. This result was surprising and suggests that the predicted patterns of biomass increment over succession may not apply to these sites.

Our models were much better at accounting for the variation in litterfall compared to biomass increment, however different factors explained variation in different components of litterfall. Soil chemistry was found to explain variation in every component of litterfall and soil physical properties were found to affect reproductive tissue. Total litterfall and individual components all increased with the abundance of total soil nutrients. Reproductive tissues increased with soil physical variables that are presumably associated with greater water holding capacity. These results reinforce findings from other studies that soils play an important role in determining litter quantity (Martínez-Yrízar and Sarukhán 1990, Kaspari et al. 2007, Chave et al. 2010). Leaves and twigs were the only litter components correlated with stand age, likely due to the increase in stand biomass in older stands (Chapter 3). Other studies have found evidence of increased litterfall with stand age (Chave et al. 2010) and with stand biomass (Lawrence 2005). Saturating increases in leaf area index over stand age have been documented in many forest types and are well correlated with litterfall (He et al. 2012). While the quantities of both flowers and fruit were higher in more fertile stands, the aspects of functional diversity that mattered differed between them. Flower biomass was best explained by functional divergence while fruit and seeds were best explained by the CWMs of foliar P and SLA.

Our study differed from many tropical litterfall studies in that we explicitly separated and weighed the frass component of litter. Measuring this component gives insight into herbivore activity and the rapid transfer of carbon and nutrients from the canopy to the forest floor. Spikes in frass found in our litter traps indicate periodic defoliation events, where more than half of the dry mass content of our litter traps were frass during certain months. In other words, during such events over half of the material falling to the forest floor had passed through the gut of a caterpillar. This has potentially significant consequences for carbon and nutrient transfer from the canopy to the litter layer. These defoliation events may also have subsequent consequences for ecosystem processes such as growth, reproduction, and mortality (Kissing and Powers 2010). The finding that soil chemical properties alone accounted for 57% of the variation in frass across our sites indicates a close relationship between soils and frass. This relationship is likely indirect: we know that species sort over soil gradients (Powers et al 2009), and that insect herbivores are highly host-specific (Janzen 1981). This evidence points to a soil chemistry-frass relationship mediated by tree species distributions.

As with other studies of litterfall in TDF, we found high intra-annual, seasonal variation in litterfall (Jaramillo et al. 2011). Litterfall peaked at the start of the dry season each year and was lowest during the rainy season. When separated by component, the seasonal patterns of flowers and fruit appear to be most variable across sites, though in general flowers peak during the end of the dry season and start of the rainy season. Similarly large variations in reproductive litter have been observed in other dry forests (Justiniano and Fredericksen 2000, Tang et al. 2010). Other studies have found increased litter seasonality with forest age (Lawrence 2005). While the amount of litter is higher in older forests of our study, there does not appear to be a marked change in seasonality between young and old sites (Figure 4-4). In our dataset, the proportion of litter comprised of leaves was similar to other studies reporting that leaves make up 65 to 90% of litterfall in neo-tropical dry forests (Jaramillo et al. 2011).

We did not find inter-annual variation in litterfall despite the more than doubling of precipitation between the wettest and driest years. While surprising, other studies in wet and dry tropical forests also have found little or no significant inter-annual variation in litterfall (Martínez-Yrízar and Sarukhán 1990, Tang et al. 2010, Anaya et al. 2012) and an experimental irrigation study showed little effect on total litter mass (Cavelier et al. 1999). Still other studies have shown differences (Whigham et al. 1990), implying that site-specific variation in soils or species may lead to differing sensitivities of litterfall to precipitation.

While across South America litterfall shows little relationship with rainfall (Chave et al. 2010), among TDF sites, litterfall has been found to increase linearly with precipitation (Martínez-Yrízar 1995, Lawrence 2005). Our results from two sites do not follow this pattern as we consistently found greater litter quantities at Palo Verde sites (though this difference was non-significant), which, on average received less precipitation during this study period (Table 4-3). The higher litterfall in Palo Verde was most evident among younger sites suggesting that species compositional differences in early successional sites may cause this pattern where *Rehdera trinervis*, *Cochlospermum vitifolium*, and *Gliricidia sepium* dominate younger forests at Santa Rosa, and at Palo Verde the dominant tree species in our young forest plots include *Guazuma ulmifolia* and *Luehea candida*.

Across stand age, ANPP and some of its components appeared to follow different trajectories with different forest types (which are represented by different symbols in Figures 4-2 and 4-3). For example ANPP was highest at Palo Verde (Figure 4-1). Palo Verde sites appeared to follow a logistic trajectory over time, which was higher than that of sites in Santa Rosa (Figure 4-2). The Santa Rosa lowland forests appear to have a similar pattern of ANPP increase across stand age but slightly lower ANPP than Palo Verde. The Oak forests (with one exception) had lower ANPP than the other two forest types but the pattern of increase is similar. Figure 4-2 separates the components of ANPP across stand age and this pattern of differing trajectories across forest types is again evident in leaf litterfall but few other components. These forest types are distinguished by both soil variables and species composition (Powers et al. 2009) and both of these factors could potentially explain these patterns.

The fact that our results show ANPP increasing with stand age and not declining is somewhat counter to expectations based on a classic model of ANPP variation across succession. In general, ANPP is expected to have a hump-shaped pattern with stand age where the intermediate ages are the highest, and older sites decline with age (Gower et al. 1996, Ryan et al. 1997). Figure 4-2 may be interpreted as following this pattern where our sites represent the early portion of this curve. However an examination of Figure 4-3 confuses this explanation. While litterfall increases in a saturating pattern with stand age, much the same as biomass (Chapter 3), biomass increment has little discernible relationship with stand age. Intermediate-aged sites have both higher and lower biomass than the youngest and oldest sites. Since biomass increment is the component of ANPP that drives the classic hump-shaped pattern, it is here where we most expect to see it. There are several possible interpretations of these results: The site-specific trajectories of biomass increment over stand age may be so different in these forests that a chronosequence approach fails to find patterns that would be found if the same site were monitored over 50 years. The hump-shaped pattern of biomass increment may not be present or very weak in these forests as has been found in other forests. Biomass increment could have little or no relationship with stand age in these forests. Many other studies do show declines in biomass increment over stand age, though the majority of these studies come from temperate forests and divergences from this pattern are found in some forest types (He et al. 2012). To our knowledge biomass increment has not been measured across stand age in secondary tropical dry forests in any previous studies.

We found no significant differences in ANPP between years or between forest types however the pattern of increasing ANPP in wetter years remains informative. For example sites in Palo Verde had the highest ANPP when precipitation was the highest (2010). In Santa Rosa, which received more precipitation than Palo Verde in both 2010 and 2011, ANPP was the highest in the year with slightly lower precipitation. While these patterns may simply be a result of random variation, we interpret them as some evidence for a weak link between annual precipitation and ANPP in TDF. Other precipitation-related variables may also affect ANPP such as dry season length or heavy cloud cover lowering light availability during the rainy season.

Our comparison of relative growth (as measured by RDI) to functional traits found a relationship between foliar N and RDI. No other traits were found to have a significant relationship with RDI. This analysis was based on 24 of the 69 species of trees in our study for which we had 5 or more individuals and that overlapped with our trait database (Powers and Tiffin 2010). The natural log of foliar N accounted for 24% of the variation in RDI. Correlations between wood density or SLA and relative growth of species have been reported in other studies in wetter forests (Poorter et al. 2008, Baker et al. 2009), but that pattern was not observed in our dataset. The lack of a relationship in our study may be due to differences in patterns between forest types as have been found in wood density- biomass relationships (Stegen et al. 2009). Tree species in TDF are subject to greater water stress and species with higher wood density may be more resistant to embolism associated with drought (Chave et al. 2006). This may give high wood density an advantage because even if their growth is slower incrementally, when measured over periods of time that include drought conditions, they may grow as much or more than fast growing but drought intolerant species with lower wood density.

We calculated an overall mean ANPP of 11.18 Mg ha^{-1} over 3 years across our 18 plots. The average of sites with stand ages over 30 is 13.45 Mg ha^{-1}. This is higher than ANPP values reported in other neo-tropical dry forests such as 9 Mg ha^{-1} at Guanica, Puerto Rico (Lugo and Murphy 1986, Clark et al. 2001b) or 6.8 Mg ha^{-1} at Chamela, Mexico (Martínez-Yrízar et al. 1996). However both of these sites are considerably drier than our study site and our ANPP estimate falls within the 6 – 16 Mg ha^{-1} reported by (Murphy and Lugo 1986) and is comparable to ANPP values for dry forests reported in other reviews of productivity (Clark et al. 2001b, Malhi et al. 2011). Our litterfall data, with an overall average of 7.14 Mg ha^{-1}, also falls within reported ranges for tropical dry forests of 2.9 – 8.5 Mg ha^{-1} (Martínez-Yrízar 1995, Jaramillo et al. 2011). We found an overall average biomass increment of 4.03 Mg ha^{-1} and for sites older than 30 years it is 3.75 Mg ha^{-1}. This again falls within the range of other TDF studies (0.4-5.6 Mg C ha^{-1}) (Worbes and Raschke 2012).

While one of the few multi-year studies of productivity in tropical dry forests, our study is still limited by its three years of data. Descriptions of inter-annual patterns and trends must be made with that caution. Our litter study took place from 2008-2011, and our measurements of ANPP begin in 2009. In Santa Rosa, three of these four years (2008, 2010, and 2011) are among the wettest years of the last 30 (www.investigadoresACG.org), and this may have influenced our findings. There are several methodological limitations that bear mentioning. Our monthly collection of litter did not account for decomposition that may have occurred in litter traps between the fall of litter and collection. While we believe this is negligible, we may have underestimated litterfall, particularly in the wettest months when litter rarely dries in our traps. Our estimates of ANPP are likely underestimates because our measurements of biomass increment only include trees above 10cm and do not include lianas or understory vegetation. While small trees and understory vegetation are likely negligible, it is possible that lianas are a significant contribution to productivity in some sites.

Conclusions

Overall we found that stand age, soil properties and functional diversity all contribute to ANPP but that the relative influence of these factors varied among the different components of ANPP. We found no significant inter-annual variation in ANPP despite a more than doubling of precipitation between years of our study. While we can explain 77% of the inter-plot variation in litterfall with these factors, we can only explain 44% of the variation in biomass increment. Biomass increment had no relationship with stand age and thus does not follow classic models of changes in growth over succession. Instead, we found that biomass increment remains relatively constant up to the oldest forests we measured. Seasonal patterns in litterfall mirror those found in other studies where litterfall peaks in TDF as the dry season begins and is likely triggered by a drop in soil moisture. The relative growth rates of the species for which we had sufficient data were correlated with foliar N but not wood density, SLA or foliar P.

With respect to using functional traits of tree species to predict and understand ecosystem processes like productivity, our study yielded mixed results. We found only one weak relationship between relative growth of species and foliar N. No other traits we measured were related to relative growth. However we did find that community weighted means of functional traits and functional divergence could explain some of the variation in ANPP, biomass increment, and litterfall (but not in frass). For example, community weighted means of SLA and foliar N along with functional divergence explained 44% of the variation in biomass increment. These results suggest that despite the lack of strong relationships between relative growth and traits on a species basis, functional traits can be used to explain ecosystem level processes.

The unexpected patterns in ANPP across succession and between years with varied precipitation highlight the need for more research on productivity in both tropical secondary forest and tropical dry forest. Productivity is rarely measured in secondary forests in the tropics and we know of no other studies in secondary dry forests. Our findings suggest that ANPP does not decrease appreciable with forest age (at least in forests of <60 years). This suggests that dry forests may continue to accumulate carbon after reaching structural maturity and may continue to be a carbon sink for decades after initial regeneration. This finding, if verified, would have important implications for the use of restored TDF to sequester carbon and mitigate climate change. Before such conclusions are made, more long-term measurements are needed, especially in older secondary forest.

Tables and Figures

Table 4-1. Total annual precipitation in Palo Verde and Santa Rosa 2008-2011. Data for Palo Verde are available through the Organization for Tropical Studies (ww.ots.ac.cr). Data for Santa Rosa are available through Investigadores del Área de Conservación Guanacaste (investigadoresACG.org).

	Palo Verde precipitation (mm)	Santa Rosa Precipitation (mm)
2008	2455	3341
2009	1247	1242
2010	2129	2819
2011	1785	2551

Table 4-2. Results of linear regression analysis with ANPP and components averaged over three years. The best model was chosen by comparing the AIC values for models that included different parameters. Flower biomass was log-transformed to meet the assumption of normality. Variables included in the best-fit model are indicated with an “X”.

Component	Mean ($Mg\ ha^{-1}$)	Coefficient of Variation	p-value	R2 value	Ln Stand age	Soil Chem PCA 1	Soil Chem PCA 2	Soil Phys PCA 1	Soil Phys PCA 2	Functional Divergence	CWM Leaf N	CWM Leaf P	CWM SLA
ANPP	11.18	0.317	0.0079	0.5167	X	X					X		X
Biomass inc	4.03	0.466	0.01095	0.4385						X	X		X
All litter	7.14	0.352	8.3×10^{-5}	0.768	X	X						X	X
Leaf litter	5.43	0.319	0.00038	0.7044	X	X						X	X
Twigs	0.38	0.413	0.00243	0.6017	X	X						X	X
Flowers	0.28	0.868	0.00037	0.7055		X	X		X	X			
Fruit/seeds	0.43	0.706	0.0031	0.6311		X	X	X				X	X
Frass	0.24	0.526	0.00064	0.5749		X	X						

Table 4-3. Average total litterfall across years and forest types.

Total litter includes leaves, fruit, flowers, twigs, and frass and are expressed in Mg ha^{-1}. Repeated measures ANOVA found no significant differences between years or forest types in litterfall.

	Litterfall (Mg ha^{-1} yr^{-1})		
	PVTDF	SROAK	SRTDF
2008	NA	5.92	8.31
2009	8.44	5.31	7.00
2010	8.82	6.26	7.41
2011	8.49	5.31	7.27

Figure 4-1. Aboveground net primary productivity and precipitation for each forest type over three years.

Each colored bar represents one year of data from each of the respective forest types. Black half bars represent the annual precipitation at each site. Dots represent individual plot measurements of ANPP and error bars are standard error.

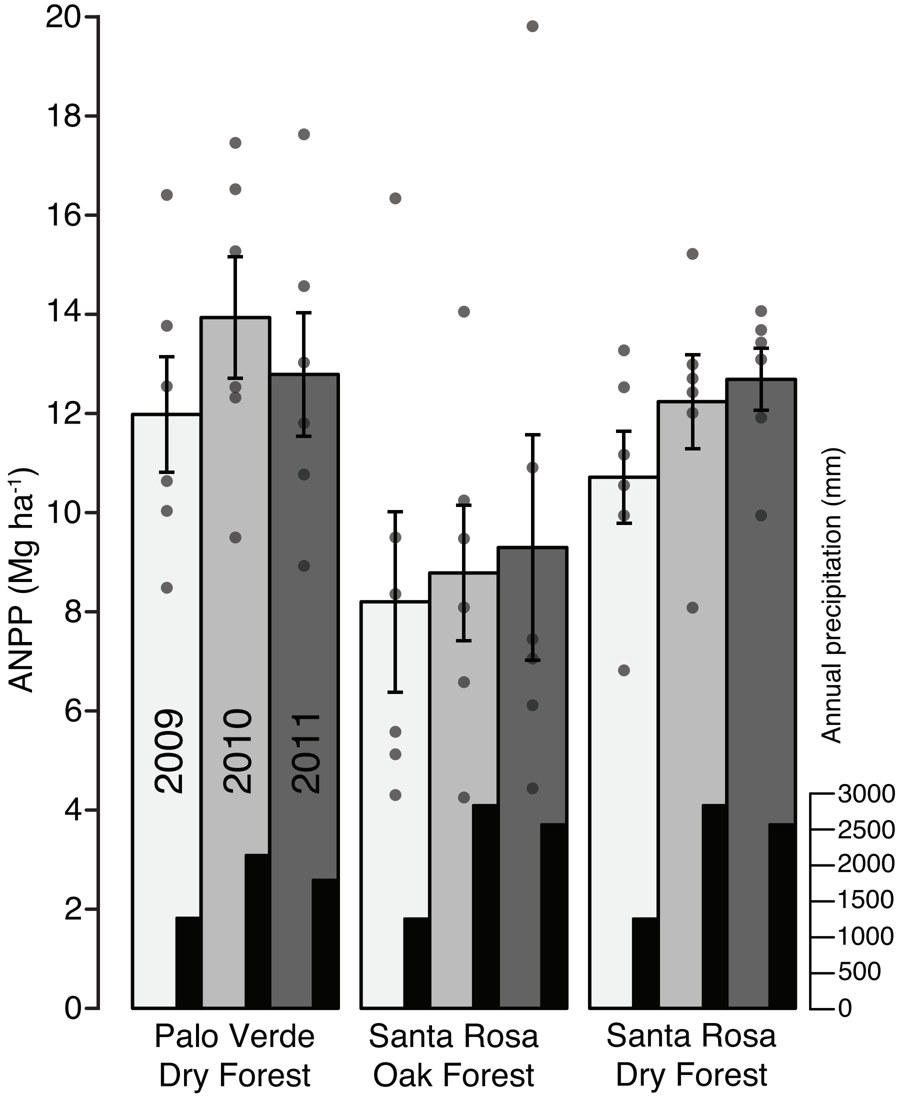


Figure 4-2. Aboveground net primary productivity across stand age.

The symbols represent different forests types and lines connect points from the same plot. ANPP appears to increase until stand age of 30. These increases appear to follow differing trajectories for each forest type.

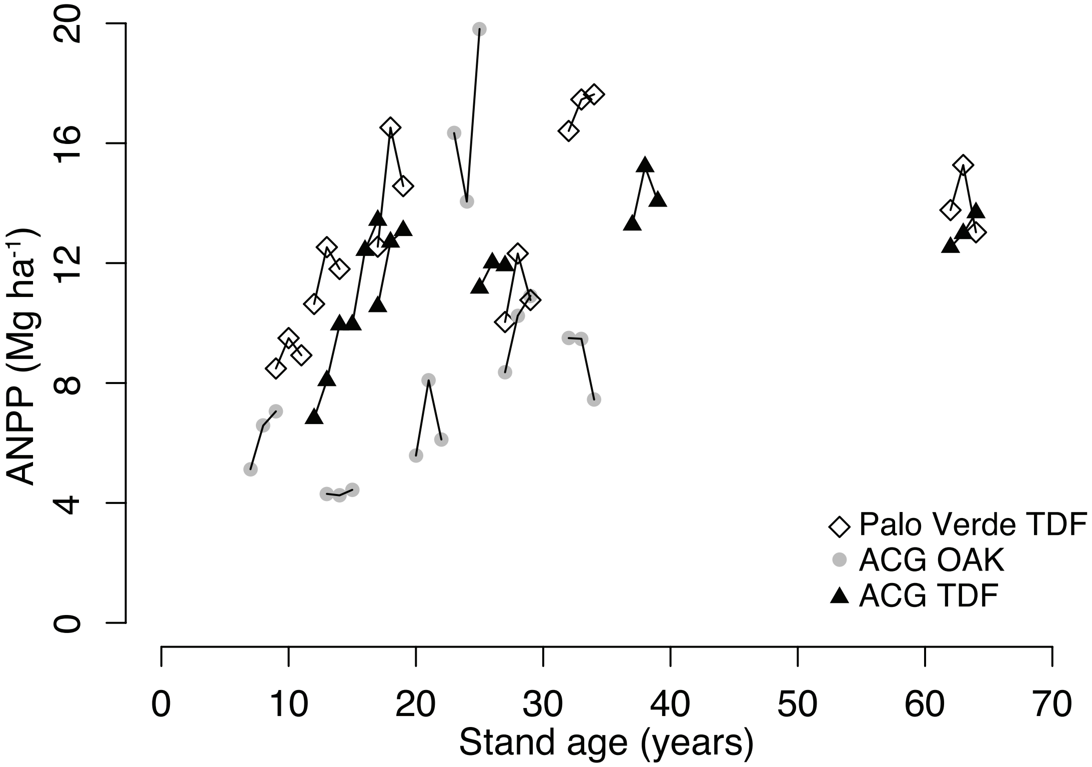


Figure 4-3. Components of ANPP over stand age.

Symbols represent forest types and lines connect measurements from each plot over the three years of our study.

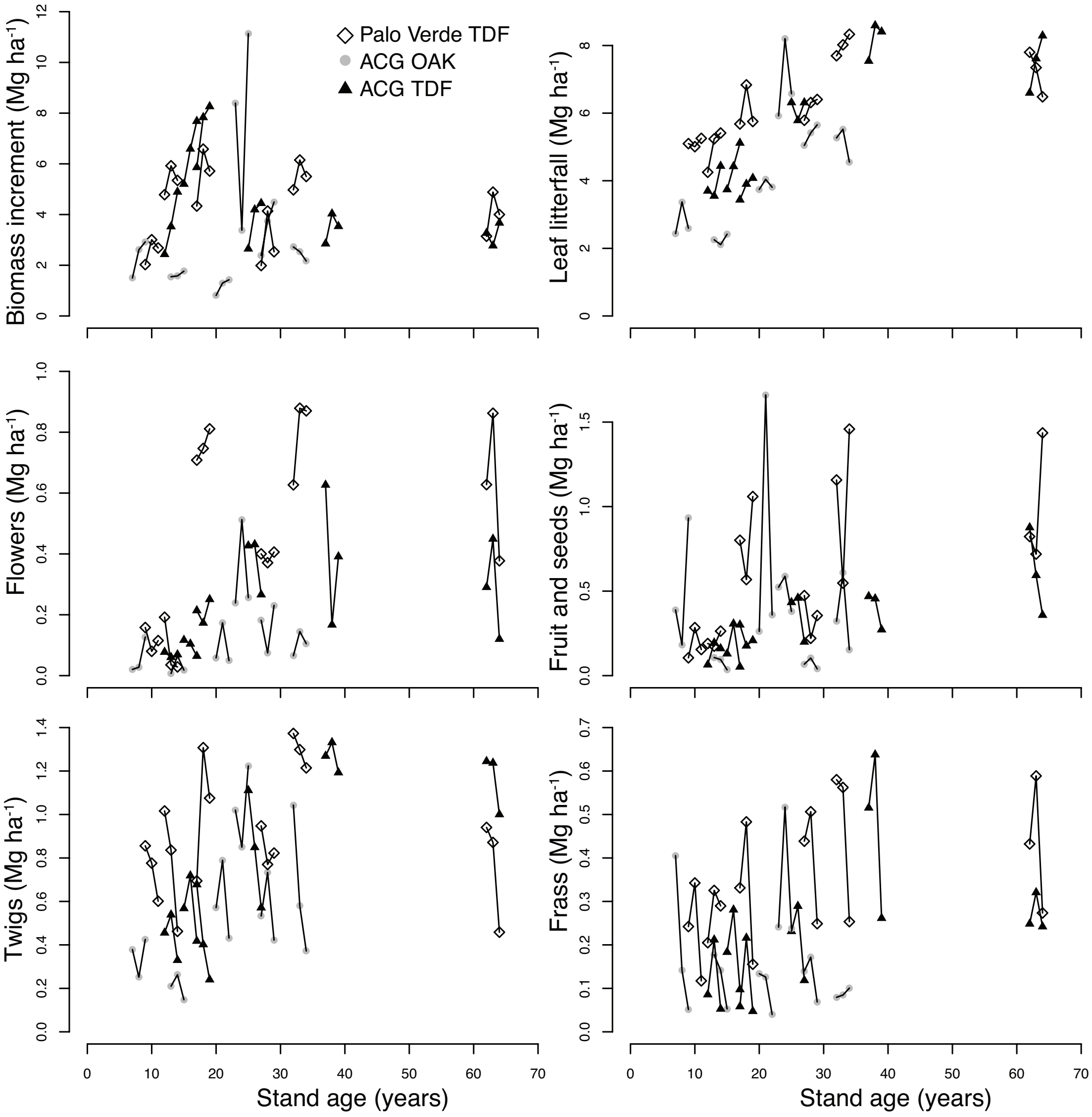


Figure 4-4. Litter components and precipitation over four years.

Dark green and brown lines show mean values for old and young plots (old plots have stand ages between 25 and 65 years, and young plots are between 7 and 24). Light green and brown lines are monthly litterfall from each plot.

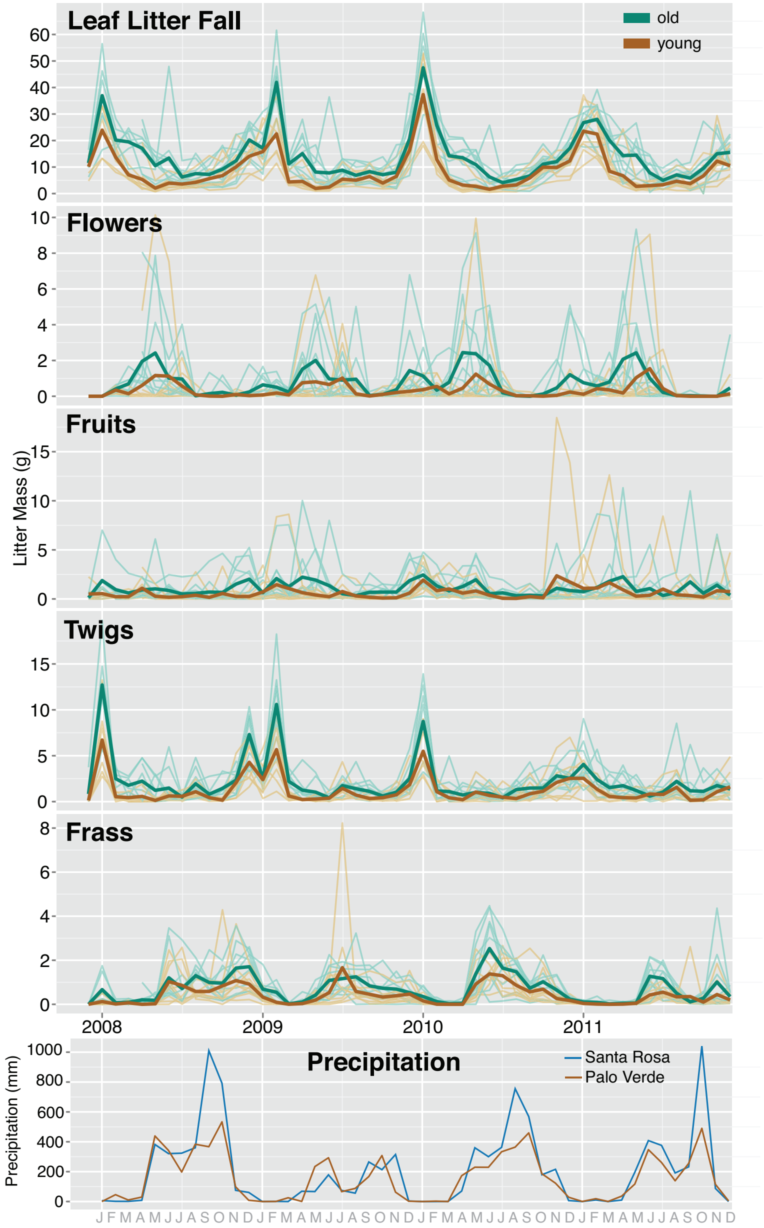


Figure 4-5. Specific diameter increment of common species by year.

Specific diameter increment (SDI = [DBH_2-DBH_1] / DBH_1) for species with more than 6 individuals in 2009, 2010, and 2011.

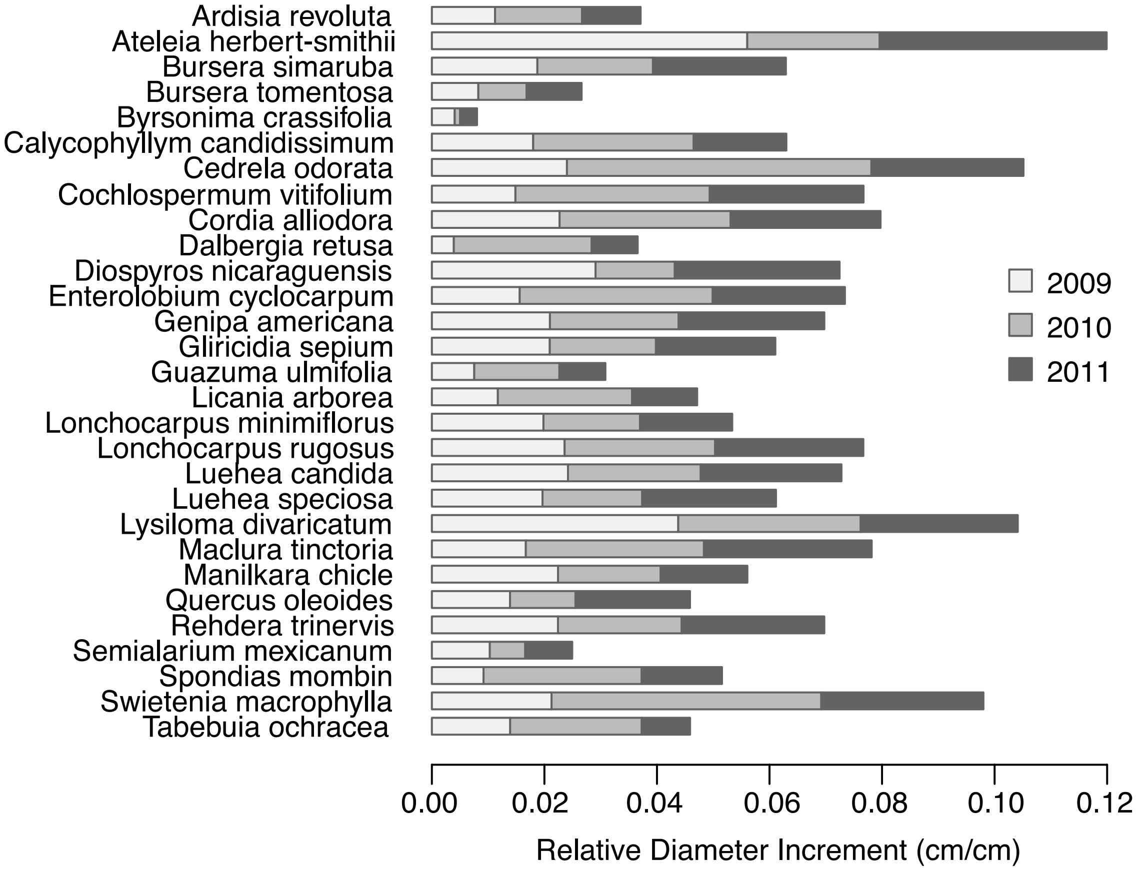
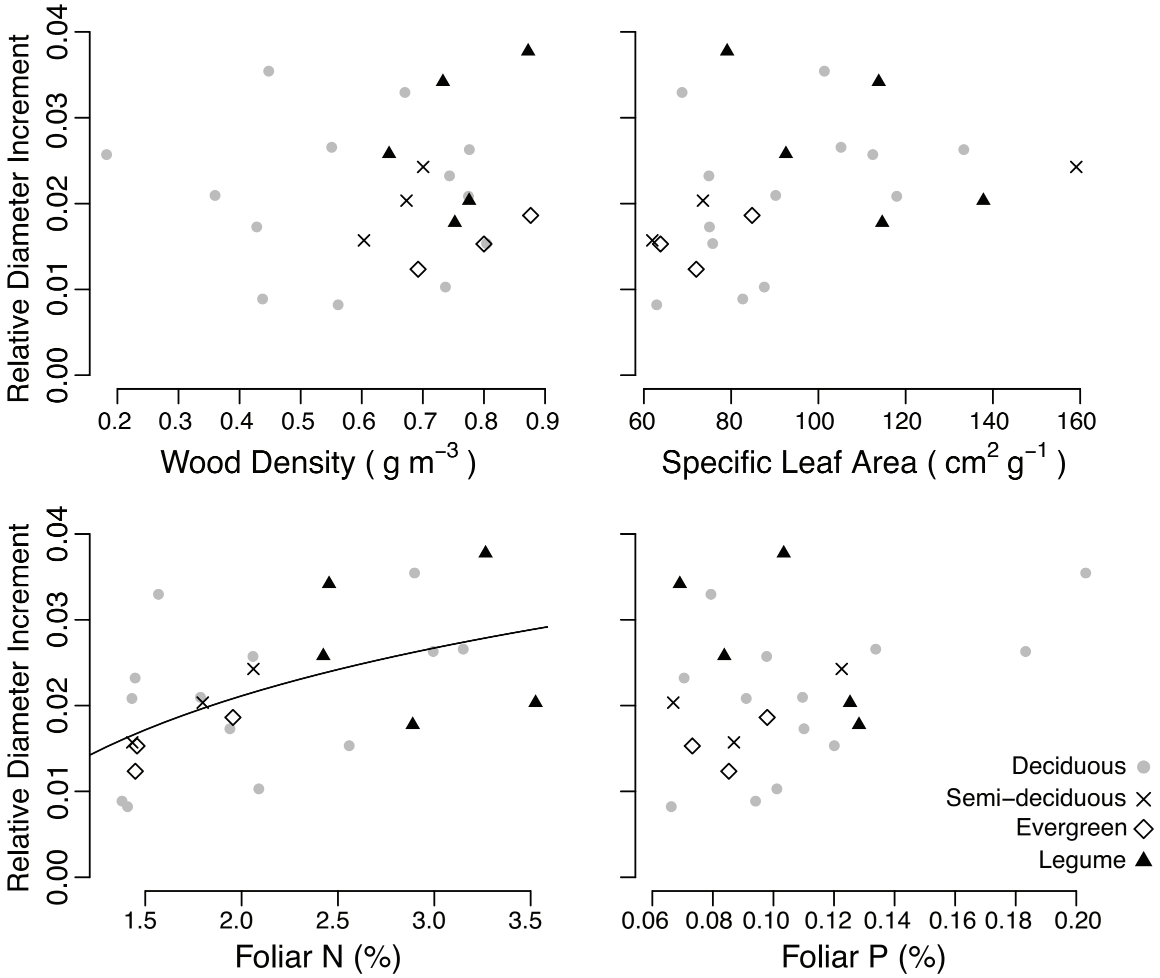


Figure 4-6. Relative diameter increment and plant traits.

Relative diameter increment (RDI) versus trait values for species with more than 6 individuals and match our traits database. Log transformed foliar N has a significant relationship with RDI (p-value = 0.009, $R^2 = 0.24$). All other relationships were not significant.



Chapter 5

Conclusions and Synthesis

The introductions of much of the tropical dry forest literature include statements about how dry forests are understudied compared to wet forests (Murphy and Lugo 1986, Bullock et al. 1995, Dirzo et al. 2011). While it certainly is true that there are fewer studies on dry forests relative to wet forests (Meli 2003, Sanchez-Azofeifa et al. 2005), in the 30 years since Daniel Janzen began advocating for dry forest research and conservation (Janzen 1988b, 1988c), significant progress has been made towards understanding the ecology of tropical dry forests (Pennington et al. 2009). What is clear is that the impact of human activities has destroyed a significant proportion of tropical dry forests (Mass 1995) and restoration and conservation has been slow (Miles et al. 2006). This implies that the future of tropical dry forests lays with restoration efforts and that secondary tropical dry forests will be increasingly important. These facts validate the importance of the research presented here on carbon cycling in secondary tropical dry forests. Below I describe the key findings of each chapter and explain how these findings together point to some interesting patterns and future research priorities.

Chapter 2 examined the global distribution of biomass in tropical dry forests. The most salient result is the large effect of precipitation on determining the coarse-scale distribution of aboveground biomass. The positive linear relationship appears to hold form the driest to the wettest end of the tropical dry forest precipitation spectrum. This is important for coarse scale modeling of tropical dry forest biomass and informs efforts to understand the potential consequences of climate change mediated alterations of precipitation patterns. Next is the finding that biomass recovers rapidly in both the driest and wettest tropical dry forests nearing their maximum potential biomass after 40 years.

The implications of these results are that restoring tropical dry forests could be a promising carbon sink, potentially taking up and storing 25 – 100 Mg C ha^{-1} after a few decades without management. Applying this idea at the global scale I estimated that restoring tropical forests world wide (while an admittedly unlikely scenario), could sequester more than 10 Pg of C over five or six decades. Together these results firmly establish the carbon value of tropical dry forest and the global distribution of their biomass.

Chapter 3 explored the distribution of aboveground live biomass and plant functional traits across the secondary tropical dry forest landscape. We found that both soil properties and successional time were important in explaining the distribution of leaf traits among sites. We also found that, contrary to our expectations, traits and soils explained no more than 5% of the variation in aboveground biomass after accounting for stand age. Stand age, soils, traits, and species richness combined explained 51% of the variation in aboveground biomass. Structural equation modeling allowed us to simultaneously explore the relationships among these variables, and yielded the result that soil properties strongly influence trait distributions but only affect biomass indirectly. These results indicate that, at least in the secondary forest landscape, the dominant driver of forest biomass is stand age. The large amount of residual variation in biomass may be due to factors we did not measure or could be due to the effects of processes that are difficult to account for such as stand dynamics over the course of forest regeneration and the impacts of herbivory, continued disturbance, or past land use.

Chapter 4 focused on aboveground net primary productivity (ANPP) in the same secondary tropical dry forests of northwestern Costa Rica. We measured ANPP over 3 years with highly varied rainfall and explored its variation across years, succession, soils, and plant communities. We found that a 127% increase in precipitation between 2009 and 2010 was associated with a 7 – 14% increase in ANPP. In fact these large differences in precipitation did not lead to any significant differences between years for ANPP or its components. Instead a multiple regression analysis found that the variation in different components of ANPP across sites was explained by different environmental variables. Stand age was important in explaining leaf litterfall but not in biomass increment or reproductive tissues. Frass was explained by soil chemistry alone. Community weighted means of plant functional traits and functional divergence explained the variation in biomass increment. Our models explained 77% of the variation in litterfall across sites but only 44% of the variation in biomass increment. These results suggest that ANPP has greater sensitivity to successional stage, species composition, and soils than to inter-annual variation in precipitation. This implies that model predictions of carbon uptake across the tropical dry forest landscape may require detailed knowledge of soils and species rather than using simple ecosystem wide parameters and precipitation.

These three chapters together point to several interesting conclusions. First, biomass accumulation over succession may not conform to generally accepted models that predict a rise in biomass accumulation followed by a decline as forests mature structurally (Kira and Shidei 1967, Ryan et al. 1997). There are at least two ways to estimate annual biomass accumulation: 1) measure it directly (Chapter 4), or 2) divide biomass stock by estimated stand age (Chapter 3). Biomass accumulation estimates obtained from the 84 biomass plots I sampled yield an average rate of biomass increase at 2.25 Mg C $ha^{-1}yr^{-1}$. This is remarkable close to the overall average rate of biomass increment at 2.0 Mg C $ha^{-1}yr^{-1}$ that I measured in a subset of these plots. This not only provides me with confidence in the data, but also suggests that, contrary to theory (Kira and Shidei 1967, Ryan et al. 2004), biomass increment may be relatively constant across succession.

The important role that precipitation plays in determining the biomass of mature sites across the globe found in chapter 2, seems to contradict the result that inter-annual variation in rainfall has little affect on productivity found in chapter 4. There are several possible explanations that may reconcile these findings. First, the fact that the variation biomass increment is explained by functional traits may mean that mean annual precipitation is an important filter of species. In other words, rainfall determines the species composition, which in turn determines biomass increment. Alternatively, mean annual rainfall is also (not surprisingly) well correlated with dry season length, which also was correlated with aboveground biomass in mature forests (Chapter 2). It is possible that dry season length is a better predictor of ANPP than total rainfall through a number of different mechanisms. Once soils reach some threshold soil moisture value, additional rainfall does not increase growth. Alternatively, months of high rainfall are also correlated with reduced sunlight, and it is possible that NPP is limited by light during years with very high rainfall.

The variation in biomass increment was poorly explained relative to other components of ANPP (44% of variation explained). This combined with the large amount of unexplained variation in the statistical model for aboveground biomass (Chapter 3) indicates potential gaps in our theories of biomass distribution. This may also mean that if measurable and if identified the same factors may explain this large amount of residual variation in both biomass stocks and biomass increment.

These results highlight numerous, unresolved questions. First and foremost is the identification of variables which may explain the residual variation in biomass and biomass increment. As suggested in chapter 3, this residual variation may be due to stand dynamics across succession. Combining measurements of biomass, standing dead, and coarse woody debris may increase our ability to predict biomass stock from stand age alone. Other factors may be less easy to measure such as the effects of herbivory, access to ground water during the dry season, and prior disturbance history.

The next logical steps are experimental studies that test the patterns suggested by these results. Watering (or water removal) manipulations may test the extent to which inter-annual variation in precipitation or precipitation patterns affects productivity. Particularly interesting is the hypothesis that dry season length and not precipitation total is the most important driver of tree growth and forest NPP. Other avenues of research include using tree rings to look for a relationship between precipitation and growth. A relationship, if it exists even in a small subset of species, could greatly increase our ability to assess the potential impacts of climate change on tropical dry forests. The data we currently have could be used to pin point which species are particularly sensitive to climate.

Other interesting directions this work points to include analysis of other traits, the effects of frass, and secondary forest ecology in other similar ecosystems. The traits we have used thus far include mostly so called “soft traits” which are easiest to measure and may or may not be the most informative in this ecological context. Other traits such as rooting depth and those related to resistance to water stress may be more informative in the tropical dry forest. Chapter 4 presents interesting results with respect to frass. Soil chemistry explains 57% of the variation in frass across sites, and spikes in frass indicate large defoliation events. These defoliation events move large amount of carbon and likely other nutrients from the canopy to the forest floor but the ecological effects of this are unknown. As previously noted, secondary forests are increasing in importance and may represent a substantial carbon sink. Secondary forests across the tropics may have interesting patterns of their own and investigating the similarities and differences among secondary forests across the tropics may yield interesting results.

This volume contributes several important results to the growing body of knowledge about the ecology and carbon cycling in tropical dry forest. My results highlight the potential for restoring dry forests to mitigate climate change. I have made significant progress towards understanding how various biotic and abiotic factors explain ecosystems processes across the landscape. These results combined with many other studies show tell an increasingly detailed and coherent story about the ecology of tropical dry forests. While they remain less studied compared to wet forests, significant research has been done the last few decades and during that time tropical dry forest attention and conservation efforts have both increased. Many questions remain but given the questions and complications that remain throughout the tropics, dry forests appear to be as well understood as any tropical forest.

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