Received: 14 May 2021 | Accepted: 9 August 2021

DOI: 10.1111/1365-2745.13767

Journal of Ecology

BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Above-ground net primary productivity in regenerating seasonally dry tropical forest: Contributions of rainfall, forest age and soil

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Funding information
NASA, Grant/Award Number: NS000107; U.S. Department of Energy, Grant/Award Number: DE-SC0014363; NSF Division of Environmental Biology, Grant/Award Number: DEB-1053237

Handling Editor: Han Chen

Abstract

1. Identifying factors controlling forest productivity is critical to understanding forest-climate change feedbacks, modelling vegetation dynamics and carbon finance schemes. However, little research has focused on productivity in regenerating tropical forests which are expanding in their fraction of global area have an order of magnitude larger carbon uptake rates relative to older forest.
2. We examined above-ground net primary productivity (ANPP) and its components (wood production and litterfall) over 10 years in forest plots that vary in successional age, soil characteristics and species composition using band dendrometers and litterfall traps in regenerating seasonally dry tropical forests in northwestern Costa Rica.
3. We show that the components of ANPP are differentially driven by age and annual rainfall and that local soil variation is important. Total ANPP was explained by a combination of age, annual rainfall and soil variation. Wood production comprised 35% of ANPP on average across sites and years, and was explained by annual rainfall but not forest age. Conversely, litterfall increased with forest age and soil fertility yet was not affected by annual rainfall. In this region, edaphic variability is highly correlated with plant community composition. Thus, variation in ecosystem processes explained by soil may also be partially explained by species composition.
4. These results suggest that future changes in annual rainfall can alter the secondary forest carbon sink, but this effect will be buffered by the litterfall flux which varies little among years. In determining the long-term strength of the secondary forest carbon sink, both rainfall and forest age will be critical variables to track. We also conclude that detailed understanding of local site variation in soils and plant community may be required to accurately predict the impact of changing rainfall on forest carbon uptake.
5. *Synthesis*. We show that in seasonally dry tropical forest, annual rainfall has a positive relationship with the growth of above-ground woody tissues of trees and that droughts lead to significant reductions in above-ground productivity. These

results provide evidence for climate change—carbon cycle feedbacks in the seasonal tropics and highlight the value of longitudinal data on forest regeneration.

KEYWORDS

Above-ground net primary productivity, biomass carbon, Costa Rica, forest regeneration, forest soils, litterfall, seasonally dry tropical forest, succession

1 | INTRODUCTION

Tropical forest regeneration has been frequently proposed as a strategy to reduce atmospheric CO_2 concentrations (Bastin et al., 2019). Rates of carbon uptake in regenerating tropical forest (~3 Mg C ha^{-1} $year^{-1}$; Chazdon et al., 2016; Poorter et al., 2016) are an order of magnitude greater than those of mature and old-growth tropical forests in general (~0.5 Mg C ha^{-1} $year^{-1}$; Mitchard, 2018). Furthermore, the fraction of global forests made up by regenerating tropical forests is expanding (FAO, 2015). However, there remains a lack of basic understanding of what controls the variation in tropical forest carbon uptake over space and time. Rising temperatures and altered annual precipitation patterns (Feng et al., 2013; Sullivan et al., 2020)will likely change the productivity of tropical forest ecosystems, thus affecting the land carbon sink and atmospheric CO_2 concentrations (Bonan, 2008; Hubau et al., 2020). Accurate climate predictions and land-use policy decisions require better understanding of the direct impacts of climate change on productivity and any potential feedbacks between the tropical forest carbon sink and the climate system (Mitchard, 2018).

Improving our understanding of climate–forest interactions requires long-term studies at landscape scales that quantify the interannual variation in primary productivity, the patterns of productivity across forest age in secondary forest and how productivity varies across space with abiotic factors. Net primary productivity, that is, the total amount of carbon taken up by photosynthesis minus the carbon lost through plant respiration, is a key flux of the forest carbon cycle, representing total carbon inputs over time and the energy base for heterotrophic organisms. While prior work has described the broadscale patterns of productivity in tropical forests (Clark, Deborah, et al., 2001; Schuur, 2003; Taylor et al., 2017), a detailed understanding of its fine-scale variation across space and the drivers of variation over time remains elusive (Šímová & Storch, 2017).

Three approaches are used to study forest productivity depending on scale and question: remote sensing (often enhanced with models informed by ground data), eddy covariance systems and forest inventories. Remote sensing methods relate measurements of reflectance or height profiles (in the case of lidar) to field measurements of forest biomass and/or productivity (Cao et al., 2016). These methods are used across large areas and can track changes over time but are limited by a number of factors including the limitations of reflectance data and the quality and availability of ground-based data. Eddy covariance systems are used to estimate gross primary productivity and net ecosystem exchange by measuring CO_2 concentrations and wind speed and direction (Baldocchi, 2014). These measurements are ideal for questions that require high temporal resolution at spatial extents from a few m^2 up to several km^2. Eddy covariance approaches are less optimal for questions where the knowledge is needed about the precise area contributing to the gas fluxes (i.e. understanding the effects of edaphic variation within a landscape). In addition, these systems require significant resources to install and maintain making their broad application in remote areas infeasible. Last, forest inventory studies measure ANPP by adding the change in woody biomass to the total foliar production over time (Clark, Brown, et al., 2001). Wood production is calculated as the change in above-ground biomass over time and foliar or canopy production is estimated as the total litterfall per unit area per year (Clark, Brown, et al., 2001). Forest inventory methods are ideal for long-term monitoring at the plot scale and can be used to contrast site characteristics like forest composition or environmental variables. Plot-scale methods are typically limited by the relatively coarse temporal scale (using litterfall to estimate foliar productivity allows for a single growing season to be the finest temporal scale possible). Further limitations exist around biomass allometry, errors associated with repeated measurements of trees (Chave et al., 2014) and sample sizes in secondary forest chronosequences (Becknell et al., 2018).

The environmental factors that control ANPP have been inferred from a variety of broad- and fine-scale studies. Most regional to continental studies of tropical forest ANPP invoke climatic controls to explain spatial or temporal variability in carbon stocks and fluxes. Productivity estimates from models, remote sensing or eddy covariance methods confirm that productivity increases with increasing mean annual rainfall (Castro et al., 2018; Ma et al., 2016; Mitchard, 2018). Other studies have documented increased ANPP with higher soil nutrient concentrations and with forest age in chronosequences (Alvarez-Clare et al., 2013; Herbert & Fownes, 1999; Wolf et al., 2011). However, few studies have examined interactions among the three coarse-scale drivers of variation in tropical forest ANPP, that is, climate, edaphic properties and successional age.

Rainfall is a key variable in tropical forest productivity (Taylor et al., 2017), and both rainfall patterns and drought frequency are likely to change as carbon dioxide emission-driven warming continues (Feng et al., 2013). Such changes may be especially consequential in seasonally dry tropical forest ecosystems where species composition and ecosystem function depend on how much rainfall occurs and when it occurs (Allen et al., 2017; Vasconcelos et al., 2012). Global patterns of tropical forest ANPP show increases with precipitation, but that relationship saturates at high precipitation values for locations with cool mean annual temperature (Taylor et al., 2017). At finer scales, tropical forest ANPP has been shown to vary with temperature and precipitation (Vasconcelos et al., 2012), but few long-term direct measurements of ANPP exist, especially in seasonally dry forests and secondary forest. Estimates of productivity using models, remote sensing or eddy covariance methods are more common and show evidence that tropical forest productivity is sensitive to rainfall variation and drought (Castro et al., 2018; Ma et al., 2016; Mitchard, 2018).

Net primary productivity in secondary tropical forests has been rarely studied, especially over long periods of time. The classic expectation for net primary productivity over the course of forest succession is an initial steep increase which levels off or declines over the course of forest succession (Kira & Shidei, 1967; Ryan et al., 2004). However, this model was developed from observations of plantations and temperate forests and has not been verified in tropical forest ecosystems (Pregitzer & Euskirchen, 2004; Šímová & Storch, 2017). Changes in ANPP can be inferred from observations of above-ground biomass stocks which reach 90% of mature forest levels in 66 years on average in neotropical secondary forest (Poorter et al., 2016). This suggests that, if the classic model applies to secondary tropical forest, ANPP would peak during this period of steep increase in biomass over time (between 20 and 40 years of forest regeneration). After that, ANPP is expected to decline towards values observed in mature forests.

Last, much attention has been given to the limitation of tropical forest productivity by nutrient availability over long time-scales, but the patterns observed are complex and elude generalization across tropical forests. A few studies have examined nutrient limitation in secondary forest finding some evidence for a shift from N to P limitation over the course of succession (Davidson et al., 2004). Other studies that examine the role of N-fixing legumes suggest that nutrient limitation varies both over the course of succession and across different climate regimes (Batterman et al., 2013; Gei et al., 2018). The role of soil nutrients may only be important at certain times and certain places when other dominant factors such as tree species community, land use, topography and landscape configuration do not mask nutrient limitation (Powers & Marín-Spiotta, 2017).

Here, we examine patterns of above-ground net primary productivity (ANPP) and its components (wood production and litterfall; Clark, Brown, et al., 2001) over 10 years in 18 forest plots that vary in successional age and soil characteristics using band dendrometers and litterfall traps. We asked how does ANPP and its components vary across forest age in secondary tropical dry forest? What are the patterns of interannual variation in ANPP and its components and are those related to variation in rainfall? To what degree does the variation in edaphic factors across the landscape influence productivity? Across forest age, we expected ANPP and its components to rise rapidly and then fall to a low and stable level. We expected higher levels of productivity in areas with soils on the high end of the fertility spectrum. We also expected higher ANPP, litterfall and wood production in years with greater rainfall. Our 10-year dataset allowed us to examine variability in ANPP as a function of forest recovery from disturbance, interannual variability in climate and edaphic variation.

2 | MATERIALS AND METHODS

2.1 | Study site

This study took place in two conservation areas separated by ~65 km in Guanacaste, Costa Rica: Palo Verde National Park (Area de Conservación Arenal-Tempisque) and the Area de Conservación Guanacaste (ACG; sectors Santa Rosa and Santa Elena). Based on data from the last 30 years, mean annual precipitation for Santa Rosa and Palo Verde are 1,575 and 1,445 mm respectively (www.acguanacaste.ac.cr; tropicalstudies.org). Precipitation in both conservation areas can vary strongly from year to year, and during our study ranged from 627 to 2,819 mm during our study years (2009–2018) in Santa Rosa and 953–2,129 mm in Palo Verde. The region experiences a strong 5- to 6-month dry season with little or no rainfall that typically begins in December and ends in May or June. Our data included the very strong drought in 2014 through 2015 driven by the 2015 El Niño event, where precipitation at Santa Rosa was ~40% of the long-term mean and 80% of the long-term mean in Palo Verde, the lowest annual rainfall in the ~65-year record (Cooley et al., 2019).

Both conservation areas have large areas of secondary tropical dry forest that are regenerating after being cleared for agriculture or pastures. These secondary forests include areas that have been growing back since the 1970s as well patches of younger forests (Becknell & Powers, 2014; Powers et al., 2009). Santa Rosa includes areas along a plateau with rocky pumice and ash soils that contrast with 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 (Powers et al., 2009). Mature patches of oak forests are 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, 1983). Species richness is higher in the lowlands and tree species range from being 100% deciduous to 75% evergreen (as a percent of individual trees). The soils of these areas are varied and heterogeneous in both chemistry and texture (Leiva et al., 2009; Powers 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 vary widely 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 colluvial deposits in the former and current flood plain lowlands (Janzen, 1983).

2.2 | Forest plots

This work was conducted in 18 plots (20 × 50 m each) located on relatively flat terrain that were the focus of previous studies of coarse woody debris (Kissing & Powers, 2010), fine roots and soils (Powers & Pérez-Aviles, 2013), nutrient dynamics (Waring et al., 2015), fungal communities (Waring et al., 2016) and litter decomposition (Schilling et al., 2016). The plots are stratified by age and forest subtype representative of the species composition, soil fertility and land-use history of plots from around this region (Becknell & Powers, 2014; Powers & Pérez-Aviles, 2013). Six of the plots occur on the oak *Q. oleoides*-dominated plateaus (identified in our study as SROAK), six occur in the lowland dry forests of Sector Santa Rosa ACG (SRTDF) and six occur in the lowland dry forests of Palo Verde (PVTDF). Previous measurements of soil chemical composition and nutrient dynamics show that the oak forests typically have the lowest soil nutrients and the highest are in Palo Verde (Waring et al., 2015, 2016). Approximate forest ages (ranging from 7 to 62 years of regeneration at the start of our study) were assigned to each plot based on satellite image analysis and interviews with local people (Becknell & Powers, 2014; Powers et al., 2009). Precipitation data for our analysis were taken from meteorological stations at Palo Verde and Santa Rosa within 1–4 km of most of our inventory plots. However, several of the SROAK plots are up to 8 km away from the Santa Rosa Meteorological station.

2.3 | Above-ground net primary productivity, litterfall and wood production

Above-ground net primary productivity (ANPP) is estimated as the sum of fine litterfall and wood production assuming relatively little losses to herbivory and volatile organic compounds (Clark, Brown, et al., 2001). To measure wood production, stainless steel dendrometer bands (Cattelino et al., 1986) were placed on trees ≥10 cm DBH. Dendrometers were placed at breast height or above buttresses and any other trunk irregularity. If trees were split into multiple trunks below 1.3 m, each stem was given a separate dendrometer. We waited 6 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. At the end of December or start of January each year, 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 & Tiffin, 2010) to calculate total above-ground biomass using general allometric equations and local climate information from each site (Chave et al., 2014). Wood production for each tree was calculated by subtracting the initial biomass from the final biomass for each measurement interval. Wood production from all trees in a plot was summed to yield total wood production expressed in units of megagrams of dry biomass per hectare per year (Mg ha^{-1} year^{-1}). During each annual census, we measured smaller trees and added dendrometers to those which had reached 10 cm DBH or above. Growth from these new recruits was not included in ANPP estimates until the following year. Dendrometers were removed from any trees found to be dead and their final diameter increment, if positive, was included in that year's estimate of new growth.

We measured litterfall to estimate canopy productivity. We placed four litter traps in each of our 18 plots. Each trap had a 0.5 × 0.5 m opening approximately 0.5 m from the ground. The litter traps were ~15 m apart along the centre 50 m transect of each plot but may be offset from this line if a tree or other obstacle was in the way. Litter was collected each month and dried at ~60°C. Then, the litter was sorted into leaves, flowers, fruit and seeds, twigs and frass, and weighed. Total litterfall was calculated by taking the average monthly total litterfall mass (including leaves, twigs <10 mm diameter, flowers, fruits and seeds) from the four litter traps in each plot and dividing it by the total measurement area of the traps, and is expressed as Mg ha^{-1} year^{-1}. Because frass is defined as material that has passed through the gut of a caterpillar and thus is considered secondary production, we omitted it from ANPP calculations.

2.4 | Forest type, soils and plant community variables

In addition to rainfall and forest age, our study was designed to investigate the variation in local ecological characteristics. We chose sites from the three distinct forest types (PVTDF, SRTDF and SROAK) that we knew were likely to vary in both plant community composition and soil characteristics. To represent soil variation across our sites, we used previously published data for these plots and extracted the first axis of a principal components analysis (PCA) of soil properties at each site which included bulk density, soil pH, available P (indexed by the Bray-1 method), cation exchange capacity and total element concentrations of C, Ca, K, Mg, Mn, Na, Zn and N (Powers & Pérez-Aviles, 2013). The PCA represents an integrated measure of soil variation in the surface 0–10 cm. The first axis (explains 62% of variation in soils data) is largely an index of soil fertility being correlated with cation exchange capacity, pH and total Ca (Table S1). We emphasize that these are large variations in soil properties among plots where there is a 45-fold range of in Bray P, a tenfold gradient in cation exchange capacity and threefold range in total nitrogen (Powers & Pérez-Aviles, 2013).

To represent tree species community variation, we used non-metric multidimensional scaling (NMDS) to quantify differences in tree species composition (for trees >10 cm DBH) among plots (Waring et al., 2016). However, we found a strong correlation between the NMDS index and the first axis of the soil PCA (Pearson correlation coefficient 0.84; Figure S1). In subsequent analyses, we used the first soil PCA axis as a quantitative metric that expressed the co-variation in soils and tree community composition among plots. While it is possible for plant communities to affect soils, in our study system, we believe that soil variation among our sites is largely a function of heterogeneous parent material (derived from volcanic pumice and lava flows in Santa Rosa vs. alluvial plains and eroding limestone hills in Palo Verde; Hartshorn, 1983), rather than successional processes, and thus edaphic variation is at least partly responsible for tree species distributions (Werden et al., 2018).

2.5 | Statistical analyses

Linear mixed models were used to assess the effects of stand age, forest type, soil properties and annual precipitation on ANPP and its components; litterfall and wood production using the R package lme4 (Bates et al., 2015). We conducted three analyses using the 'dredge' model selection approach in the R package MuMIn (Barton, 2020) for ANPP, litterfall and wood production. This approach assesses all possible variations of the model including possible interactions and ranks them by AIC. We selected the top model for each dependent variable. Our three full models had total ANPP and its components; litterfall and wood production as log-transformed response variables. Response variables were log transformed to meet the model assumption that residuals be normally distributed. The fixed effects were stand age, annual precipitation and the soil index (soil PCA axis 1). Stand age in our analysis represents estimated plot age at the start of the study and was not 'updated' each year. This allowed us to evaluate the long-term effect of the differences in forest age across our sites rather than the interannual differences represented by changes in annual precipitation. The variable 'plot number' was a random effect to account for autocorrelation due to repeated measures at each of our survey plots. The intercept was fixed and our full model included all possible interactions. Independent variables were standardized to units of standard deviations from the mean to allow for the comparison of model coefficients. We assessed covariation among independent variables using variation inflection factors (VIF) calculated with the R package car (Fox & Weisberg, 2019). VIF values were <5 for all variables. For each of the three analyses (ANPP, wood production and litterfall), we chose the top model as assessed by AIC using the dredge approach. The three final selected models are listed in Table 1 with standardized coefficients and *p*-values. Marginal and conditional R^2 values were calculated using the R package MuMIn (Barton, 2020. All statistical analyses were conducted using the statistical software R (R Development Core Team, 2021).

3 | RESULTS

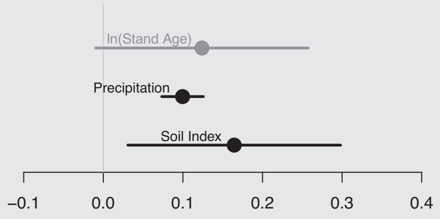
Averaged over 18 plots across all years, ANPP ranged from 7.9 (in 2015) to 12.5 (in 2011) Mg ha^{-1} year^{-1} and the 10-year grand mean was 10.3 Mg ha^{-1} year^{-1} (Figure 1; Table S1). Over the 10 years, mean ANPP in Santa Rosa oak-dominated forest (SROAK) was 7.8 Mg ha^{-1} year^{-1} compared to 11.7 and 11.5 Mg ha^{-1} year^{-1}, respectively, in diverse tropical dry forests in Santa Rosa (SRTDF) and Palo Verde (PVTDF). Averaged across plots, wood production accounted for 35% of total ANPP, but was as much as 49% and as little as 14% depending on the year and forest type (these

TABLE 1 The results of model selection and the effects of those models on above-ground net primary productivity (ANPP) and its components. ANPP is the sum of litterfall and wood production. Standardized coefficients are from models using variables which have been scaled in order to facilitate comparison among explanatory variables. The marginal R^2 (R^2_m) values represent the variance explained by the fixed effects and the conditional R^2 (R^2_c) values are the variance explained by both fixed and random effects respectively. Figures for each model represent standardized coefficients. Points represent coefficient values. Lines represent the 95% confidence intervals. Variables with *p*-values >0.5 are in grey

ANPP model: ln(ANPP) ~ ln(Stand Age) + Precipitation + Soil Index + Forest Type + 1|plot

$R^2_m = 0.43$
$R^2_c = 0.80$

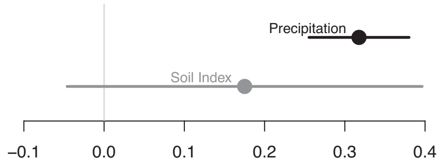
	Coefficient	*p*-value
ln(Stand Age)	0.124	0.071
Precipitation	**0.0996**	**3.8×10^{-12}**
Soil Index	**0.164**	**0.020**
Intercept	**2.26**	**$<2 \times 10^{-16}$**



Wood production model: ln(wood production) ~ Precipitation + Soil Index + 1|plot

$R^2_m = 0.26$
$R^2_c = 0.64$

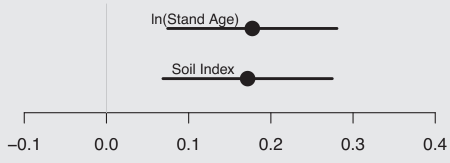
	Coefficient	*p*-value
Precipitation	**0.318**	**$<2 \times 10^{-16}$**
Soil Index	0.175	0.12
Intercept	**1.11**	**4.5×10^{-9}**



Litterfall model: ln(litterfall) ~ ln(Stand Age) + Soil Index + 1|plot

$R^2_m = 0.60$
$R^2_c = 0.84$

	Coefficient	*p*-value
ln(Stand Age)	**0.177**	**0.0022**
Soil Index	**0.172**	**0.0028**
Intercept	**1.81**	**$<2 \times 10^{-16}$**



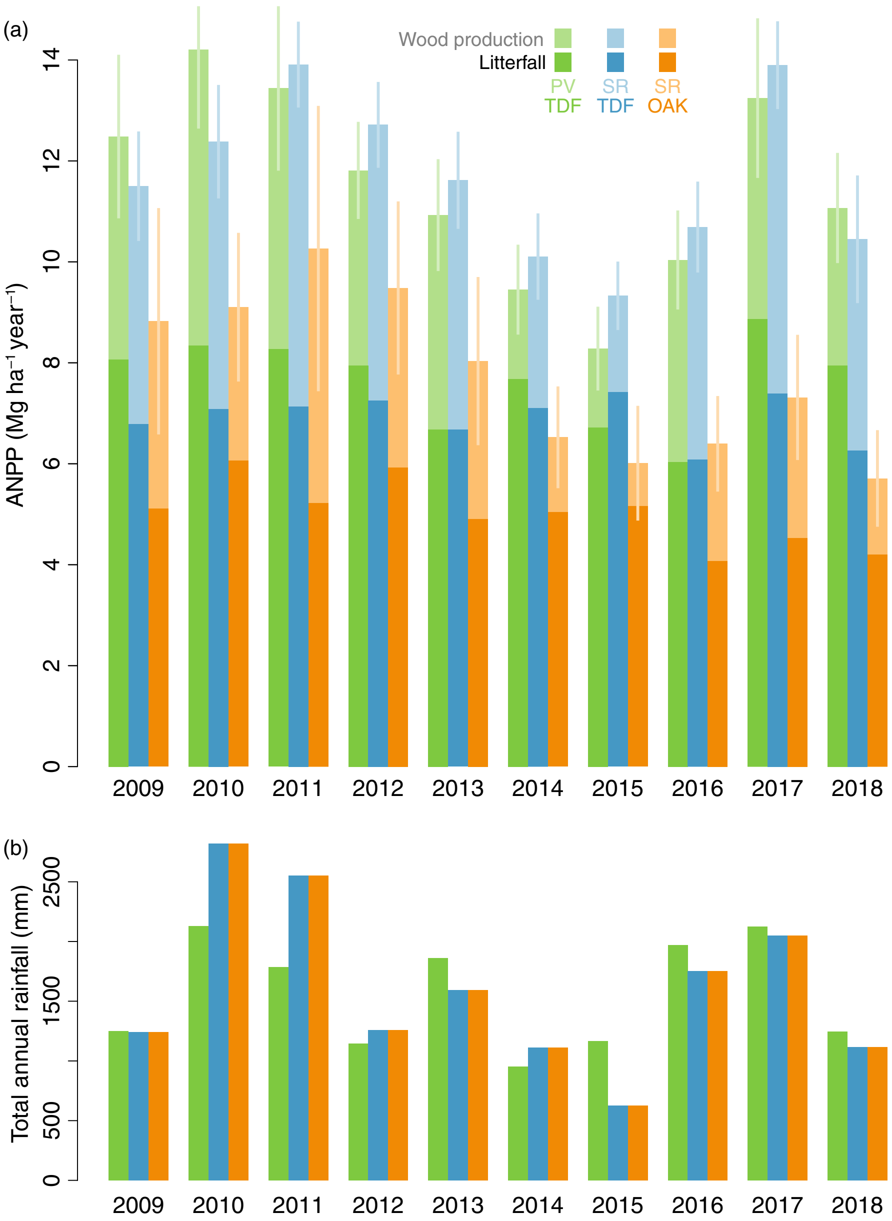


FIGURE 1 (a) Mean ANPP and its components wood production and litterfall by year forest type and forest type. The lower and darker coloured portion of each bar represents litterfall. The upper and lighter coloured portion of each bar represents wood production. Error bars represent standard error of total ANPP. (b). Annual precipitation by year for Santa Rosa and Palo Verde. The same precipitation values were used for both SROAK and SRTDF sites due to data availability and their relatively close proximity. Years 2014 and 2015 were drought years

proportions were lower during drought years but changed little with age). ANPP declined by 15% and 27%, respectively, during the drought years of 2014 and 2015 (Figure 1). These declines were largely a function of lower wood production while litterfall remained relatively stable.

ANPP appears to rise with forest age, then level off after ~40 years (Figure 2a). The highest ANPP values are at plots in the middle of our age range and the oldest sites have ANPP values that are above the overall mean. Wood production does not have a clear pattern with age (Figure 2b). The highest values (~10 Mg ha^{-1} year^{-1}) and the highest variance occur between 15 and 35 years of regeneration. The oldest sites have lower wood production levels, which are close to the overall grand mean of 3.8 Mg ha^{-1} year^{-1}. By contrast, litterfall appears to have a clear positive-saturating relationship with age which levels off around 10 Mg ha^{-1} year^{-1} (Figure 2c). The highest litterfall values are consistently at the older sites. There also appears to be a divergence in this pattern between the SROAK sites and the more diverse tropical forest sites of Santa Rosa and Palo Verde. With one exception, the oak-dominated forest appears to have lower litterfall, and in several plots, the litterfall declines over time. This decline may be related to drought-associated mortality of the dominate *Quercus oleoides*. Plots with the lowest ANPP, wood production and litterfall values have soils with low values of the soil index (Figure 1).

We used model selection to choose the lowest AIC linear mixed effects models for ANPP and its two components litterfall and wood production using the independent variables stand age, annual rainfall and soil PCA axis 1. The final model for ANPP included log-transformed stand age, annual rainfall and the soil index with no interactions (Table 1; Figure S2). Both annual rainfall and the soil index had significant positive effect effects on ANPP. Log-transformed stand age was marginally non-significant with a positive effect of

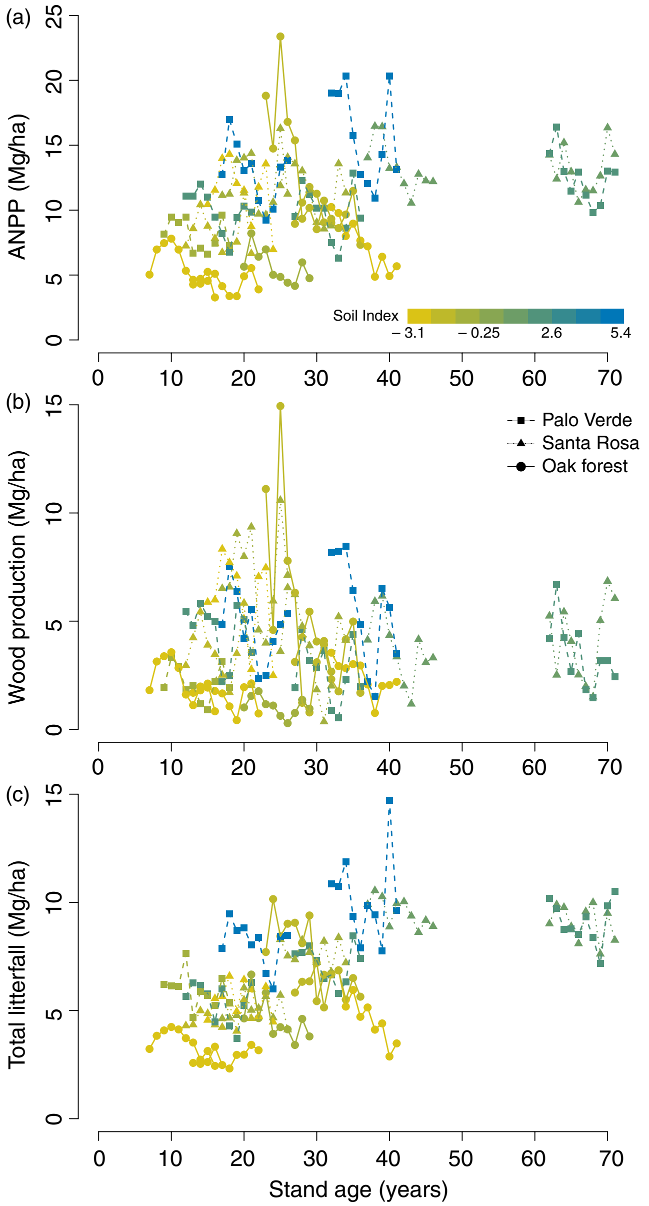


FIGURE 2 (a–c). ANPP, litterfall and wood production plotted against stand age. Each point represents one year in one site. Points from each site are connected by a line. Point and line symbology vary with forest type. Point and line colour are change from yellow to blue with the soil index. Lower values (yellow) are correlated with lower soil nutrient concentrations

similar magnitude to precipitation and the soil index, as assessed by the standardized coefficients. For the wood production component of ANPP, the final model included annual rainfall and the soil index. Annual rainfall had a significant positive effect on wood production and was clearly the primary driver. The soil index was not significant with a weaker effect than rainfall. In the litterfall component of ANPP, stand age and the soil index were included in the final model with no interactions. Both the soil index and log-transformed stand age had significant positive effects on litterfall with similar magnitude effect sizes.

4 | DISCUSSION

Our 10-year record of ANPP in 18 tropical dry forest plots allowed us to examine the relative influences of rainfall, succession and edaphic variability on the above-ground components of productivity. We found that ANPP increases with stand age and appears to plateau between 20 and 40 years of forest regeneration. This age-related increase appears to be driven primarily by the litterfall component of productivity. The interannual variation in ANPP is driven by rainfall-related fluctuations in wood production, but is buffered by the relatively low interannual variation in litterfall. Annual rainfall is the primary driver of variation in wood production with the potential for edaphic factors to play a role. Litterfall, the larger of the two ANPP components, is driven by the combination of stand age and edaphic factors (soil nutrient concentrations in particular). On more fertile soils, litterfall reached high levels and remained stable over time. On lower fertility soils, litterfall remained low and even declined over time at some sites. These results of the longest study of primary production in secondary forest of which we are aware have important implications for understanding the secondary forest carbon sink and modelling forest carbon flux.

The average ANPP we measured in secondary tropical forests (8.7–12.5 Mg/ha) was comparable to other lowland tropical forests with similar levels of mean annual precipitation (Clark, Deborah, et al., 2001; Schuur, 2003). Forests with similar annual precipitation and mean annual temperature typically have ANPP values between 5 and 15 Mg ha^{-1} year^{-1} (Taylor et al., 2017). Studies from seasonally dry forest with much lower mean annual precipitation in Mexico reported values of 6.8–9 Mg ha^{-1}year^{-1} (Jaramillo et al., 2011). A study, also from Santa Rosa, using similar methods (but a smaller sample size) found ANPP values similar to our study (6.4 Mg ha^{-1} year^{-1}) for 21-year-old secondary forest, similar to our study, but reported values 41%–66% higher than our study (17.8 and 15.2 Mg ha^{-1} year^{-1}) for forests aged 32 years or >50 years (Cao et al., 2016). Few studies have measured ANPP in secondary forests, but at least one study, from a considerably wetter location in the Amazon with higher ANPP, also found that rainfall affected wood production more than litterfall (Vasconcelos et al., 2012).

4.1 | Drivers of variation in litterfall and wood production

The effect of stand age on ANPP is marginally non-significant and lower than expected, as both biomass and leaf area increase with forest regrowth. Litterfall (63% of ANPP averaged across sites and years), which relates directly to leaf area, as expected, did have a stronger significant relationship with age. Litterfall has been measured at multiple secondary forest chronosequence sites throughout the tropics, and is reported to return to levels found in mature forest or even exceed those values after one to three decades (Ewel, 1976; Powers & Marín-Spiotta, 2017). There was no evidence of a relationship between forest age and wood production. However, we did find some patterns with age where the highest wood production values and highest variance occur in the first third of our ~60-year forest age range (Figure 2b). The expected early successional pulse in wood production seems to occur at some sites, but this pattern is clouded by interannual variation and sites with consistently low wood production. Our inability to see an age-wood-production effect may be in part due to our focus on trees 10 cm in diameter and above (see below).

The primary driver of wood production in our study is annual rainfall. We found a consistent pattern of higher wood production during wetter years and significant reductions during the drought years (2014 and 2015). That more rain leads to more growth is not surprising given the well-known geographic patterns of higher tree productivity rates and biomass at locations with more rainfall (Mondal & Sukumar, 2016; Schuur, 2003; Taylor et al., 2017). Furthermore, in seasonally dry tropical forests, our data underscore that rainfall is clearly a limiting factor to growth in a system where large interannual swings in rainfall are common. For example, in our 10-year study annual rainfall ranged from 600 mm to close to 3,000 mm.

Litterfall appears unaffected by precipitation. Across global and region rainfall gradients, litterfall quantity and seasonality vary to some degree with mean annual precipitation and more so with seasonal differences in rainfall (Chave et al., 2010; Read & Lawrence, 2003; Shen et al., 2019). However, within our region, the year-to-year differences in litterfall were not related to annual precipitation. In seasonal forests with many drought-deciduous trees such as our study sites, much of the rainfall in any given year occurs after the onset of the rainy season and the initial flushing of leaves. This might suggest a lagged effect of rainfall between years; however, we found no effect of previous year's rainfall on litterfall (analysis not shown), indicating that rainfall and litterfall fluxes are not connected in this system.

In our study region, soil variation was as important in explaining variation in litterfall as forest age, with sites on the fertile end of the soil index having higher litterfall (Figure 2c). Correlations between litterfall and soils have been observed in many tropical forest locations for decades (Vitousek, 1984), with studies investigating both the effects of soil nutrients on litter quantity and quality (Kaspari et al., 2008) and how variation in litterfall quantity or quality might alter nutrient cycling in soils (Sayer & Tanner, 2010). Fertilization experiments show mixed results with some studies showing no response of litterfall quantities to nutrient fertilization (Cusack et al., 2011) and others showing a positive response to fertilization (Mirmanto et al., 1999). Observational studies of litterfall across soil nutrient gradients also show mixed results with both positive nutrient–litterfall associations (Dent et al., 2006), and no detectable effect of soil on litterfall amounts (Chave et al., 2010). Together these results suggest that the impact of soil nutrients on litterfall (and ANPP) is likely context dependent and that other factors such as forest composition may be more important than soil at many sites.

In our study, age and soil both have positive effects on litterfall. The increase in litterfall as forests age is not surprising, as leaf area index increases with forest cover. The mechanisms behind increases in litterfall on higher fertility soil are less obvious. This soil-litterfall effect could be direct, due to increased canopy productivity on higher fertility soils. Or, this pattern could be indirect, and attributed to the distinct role that soils play as an environmental filter of tree diversity, favouring high productivity species on high fertility soils and vice versa. However, because of the tight co-variation between soil variation and tree species composition in our study region, we cannot further disentangle these cause–effect relationships from observational data alone. These results underscore the need for more fertilization studies which test the effects of different nutrients and combinations of nutrients on ecosystem processes. Our results do emphasize that, even in a successional context, where litterfall varies significantly with age, soil nutrients still play a detectable and important role explaining the variation in litterfall production. Importantly, these results imply that better understanding of soil nutrient variation across space and time is needed to properly quantify and model above-ground productivity and the secondary forest carbon sink (Fernández-Martínez et al., 2014).

There is significant variation in ANPP and its components among our 18 forest inventory plots that is not accounted for by the independent variables in our analyses. By comparing the marginal and conditional R^2 values (R^2_{m} and R^2_{c} respectively), we can see that in all three models, after the variance explained by the fixed effects, more than 20%–40% of additional variation is explained by the random effect *plot*. This suggests that there is important variation among our plots that is not captured by any variables that we have measured. For example, the wood production model has R^2_{m} and R^2_{c} values of 0.26 and 0.64 respectively. While rainfall is clearly a key factor in wood production, some of this additional variation explained by *plot* may be attributed to the moisture conditions that trees actually experience, which is likely mediated by microscale variation in hydrology, microtopography and soil texture. This additional variation in ANPP, wood production or litterfall that is explained by *plot* could represent functional differences in the plant community, differential impacts of land-use history, disturbance and stand dynamics during regeneration. Importantly, the existence of large plot-specific variability confirms that chronosequences with small sample sizes are likely insufficient for understanding the patterns and mechanisms that underlie successional change (Becknell et al., 2018; Johnson & Miyanishi, 2008), and underscores the value of longitudinal data such as ours.

4.2 | The potential contributions of unmeasured fluxes

Our productivity estimates do not include below-ground components or the contributions of small trees. This means that our estimates of ANPP are lower than the total ecosystem NPP. Furthermore, differences we observe in ANPP among our plots may reflect differences in allocation to roots versus shoots rather than differences in total NPP (Qi et al., 2019). Root productivity is difficult to measure and data on both coarse root biomass and productivity are scarce (Clark et al., 2017) and little of the existing data come from secondary forest or seasonally dry tropical forests, which likely have different patterns of root allocation than moist or wet tropical forest sites (Waring & Powers, 2017). A study of fine roots in the same plots where this study took place found that total fine roots biomass ranged from 0. 5 to 4.0 Mg/ha, about 1/100th of above-ground biomass (Powers & Pérez-Aviles, 2013). Total fine roots were correlated with soil chemistry but not with forest age, and the PVTDF plots, with some of the highest total nutrients, had the lowest fine root biomass (Powers & Pérez-Aviles, 2013). From what data on coarse roots or total below-ground biomass are available, root to shoot ratios appear to be dependent on both age and mean annual precipitation with drier and older forests having higher root to shoot ratios (Qi et al., 2019; Waring & Powers, 2017). Global meta-analyses suggest that the root to shoot ratios in this region would be close to 0.3, but whether below-ground productivity is proportional to ANPP is unknown.

The contribution to ANPP from lianas and trees <10 cm in diameter is not included in our estimates of above-ground net primary production. Because younger forests are likely to have larger numbers of small trees, this omission may underestimate the wood production of the younger sites more than in older sites, but it does not affect litterfall estimates. In our study area, data from a previous study show that the percentage of above-ground biomass from trees <10 cm DBH declines with age. The percentage of above-ground biomass from trees <10 cm was 24.8% and 8.4% at sites less with <30 and 30+ years of regeneration respectively (Becknell & Powers, 2014). If this pattern is the same in wood production, we might expect similar magnitude differences in this study; thus, an age-wood-production relationship may be clearer if growth in smaller trees were measured. Lianas vary in density across our plots and likely contribute relatively little to ANPP.

4.3 | Implications for modelling

There is a synergy between the mechanisms discussed above, the types of observations reported here and mechanistic ecosystem models: Models can be used to probe the mechanisms, and observations can be used to evaluate and inform models. The scale of the observations is critical. Being at annual time-scale, they can be used to respond to a recent call to improve model representations of the processes that control carbon cycle interannual variability (Piao et al., 2020). Furthermore, these plot-level observations of carbon fluxes can be especially useful for model analysis because they can complement the larger scale observations that are typically used to evaluate modelled interannual variability, such as the interannual variability in atmospheric CO_2 (Cox et al., 2013; Liu et al., 2017; Wang et al., 2013). Indeed, use of annual-scale measurements of biometric carbon fluxes at the plot scale has been relatively rare (Xu et al., 2016), in part because few such records exist for the tropics (Clark et al., 2003; Rifai et al., 2018). We therefore encourage the collection of such datasets, as well as their use to improve known model deficiencies that are especially apparent on interannual scales, such as drought response (Powell et al., 2013), the impacts of non-stationary carbon–nutrient interactions (Meyerholt et al., 2020), CO_2–climate interactions (Zuidema et al., 2020) or other time-lagged effects (Bloom et al., 2020). Finally, by improving the ability of models to simulate current-day interannual variation in the carbon cycle across a range of nutrient conditions, such datasets improve our foundation to make predictions of future carbon cycle interannual variability, especially across soil types.

5 | CONCLUSIONS

The secondary forest carbon sink is critical to many climate change mitigation strategies, yet we have a limited understanding of its dynamics over time and space. If, as our study shows, the magnitude of the secondary forest carbon sink is linked to variation in annual rainfall, expectations for the size of this sink going forward will need to be revised, especially in areas where strong changes in rainfall patterns are predicted. Furthermore, if rainfall sensitivity of the secondary forest carbon sink is modulated by soil variability directly and/or species composition indirectly, then the location of regenerating tropical forests becomes critically important. Despite the lower fraction of ANPP made up by wood production, it represents a key component with respect to carbon cycling, as carbon allocated to wood remains in the ecosystem longer than carbon allocated to leaves or reproductive tissues (Carvalhais et al., 2014). Regenerating tropical forest in areas with poorer soils may be less variable with rainfall but also less resilient to drought (Powers et al., 2020). These findings underscore the need for more long-term data from tropical forests that incorporate a spatial component and account for the variability in soils.

ACKNOWLEDGEMENTS

We thank Roger Blanco and the staff of the Area de Conservación Guanacaste, the staff of Palo Verde national Park and the Palo Verde OTS research station. We also thank those who have helped us in the field and in the lab including Damaris Pereira, David Pereira, Tomas Guttierez, Erik Schilling, Leland Werden, Maga Gei, Joey Reid, Stephanie Salute, Yana Sorokin, Alli Driessen. We thank Bonnie Waring for analytical advice. This work was conducted with funding from the Organization for Tropical Studies, the UMN Graduate School Thesis Research Grant and the UMN Department of Ecology, Evolution and Behavior to J.M.B. and funding to J.S.P. from a McKnight Land Grant Professorship from the University of Minnesota, a NASA New Investigator Award (NS000107) and National Science Foundation CAREER Award (DEB-1053237) and US Department of Energy, Office of Science, Terrestrial Ecosystem Science Program, Award DE-SC0014363.

CONFLICT OF INTEREST

None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS

J.M.B. and J.S.P. conceived of and designed the study; J.M.B., G.V.G. and D.P.-A. conducted the fieldwork and managed the data; J.M.B. analysed the data and wrote the manuscript; J.S.P., G.V.G. and D.M. contributed to and edited the manuscript.

DATA AVAILABILITY STATEMENT

Data used in this analysis are available at https://doi.org/10.5061/dryad.2jm63xsq4

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How to cite this article: Becknell, J. M., Vargas G., G., Pérez-Aviles, D., Medvigy, D., & Powers, J. S. (2021). Above-ground net primary productivity in regenerating seasonally dry tropical forest: Contributions of rainfall, forest age and soil. *Journal of Ecology*, 00, 1–13. https://doi.org/10.1111/1365-2745.13767