

Article

Dynamics of Carbon Accumulation in Tropical Dry Forests under Climate Change Extremes

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Abstract: We analyze here how much carbon is being accumulated annually by secondary tropical dry forests (TDFs) and how structure, composition, time since abandonment, and climate can influence the dynamics of forest carbon accumulation. The study was carried out in Santa Rosa National Park in Guanacaste province, Costa Rica and Mata Seca State Park in Minas Gerais, Brazil. Total carbon storage and carbon accumulation were obtained for both sites from the sum of the aboveground carbon and belowground carbon gain plus the annual litterfall. Carbon accumulation of these TDFs varied from 2.6 Mg C ha⁻¹ y⁻¹ to 6.3 Mg C ha⁻¹ y⁻¹, depending on the age of the forest stands. Time since abandonment and number of stems per plot were the best predictors for carbon storage, annual carbon gains, and losses. Mortality rates and carbon losses were also associated with seasonal climate variability. We found significant correlations between tree mortality, carbon losses and mean seasonal temperature, mean seasonal precipitation, potential evapotranspiration, and the Oceanic Niño Index. Carbon dynamics in tropical dry forests are driven by time since abandonment and forest structure; however, rising temperature and El Niño Southern Oscillation (ENSO) events can have a significant impact on tree mortality and carbon losses. Depending on their location and land-use history, some dry forests are more impacted by climatic extremes than others, and differences between secondary stages are expected.

Keywords: tree mortality; biomass; carbon sequestration; tropical dry forest; successional stages; ENSO



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1. Introduction

The current extent of tropical dry forests (TDFs) has been reduced globally by 48.5% and 66% in the Neotropics [1]. The few remnants of TDFs that used to be large continuous tracts of forest cover in lowlands and submontane areas are now highly fragmented patches under high anthropogenic pressure [1]. Secondary TDFs are increasingly dominant in tropical regions, and they currently occupy more area than old-growth forests [2,3]; however, it remains unclear how these secondary TDFs cope with current and predicted climate change. In the case of TDFs, changes in climate, forest structure, and diversity loss would add even more stress to these highly fragmented, threatened, disturbed, and understudied ecosystems [1,4–6].

Tropical secondary dry forests are important aboveground and belowground carbon reservoirs [7–9]. The aboveground live biomass for deciduous TDFs in the Americas is estimated to range from 39 to 334 Mg ha⁻¹ [10]. The belowground biomass ranged from 17 Mg ha⁻¹ in Chamela-Cuixmala TDF in Mexico to 66.8 Mg ha⁻¹ in Venezuela [11]. Due to their large extension in the Neotropics, TDFs play an important role in the terrestrial C balance [12]. It has been estimated that if all the world's TDFs were restored, this ecosystem

could contain 22 Pg of carbon in aboveground biomass, of which 8 Pg of carbon could be from restored TDFs in the Americas [10]. Secondary TDFs can also regain aboveground biomass rapidly after disturbance; they can reach maximum potential biomass after approximately 3–6 decades, because of the predominance of sprouting species and wind-dispersed seeds [3,10]. However, dynamics of C accumulation during forest recovery in the TDF Neotropics and the impact of climatic events are still poorly understood.

Even though TDFs are ecosystems adapted to dry climatic conditions and seasonal rainfall [13–15], carbon dynamics might change under periodic extreme drought events. Increases in temperature and intense droughts can be significant threats to the persistence of TDFs [16–18]. The frequency of extreme El Niño Southern Oscillation (ENSO) is predicted to increase [19–22], which will bring more extreme droughts to areas where TDFs are found in the neotropics. Increases in the frequency and intensity of extreme climatic events will affect plant demography (tree mortality and recruitment) of TDFs [17,23]. Persistent changes in mortality rates can dramatically modify the structure and composition, as well as compromise forest diversity and productivity [24]. Nonetheless, it is still unclear how extreme climate changes (e.g., increased drought and hurricane events) will affect forest carbon dynamics in TDFs. Although biomass and carbon accumulation are likely to be affected negatively by increasing droughts, there is limited information available of long-term studies in TDF that evaluate biomass and carbon accumulation for continuous periods across successional gradients, and there are even less data that evaluate the impact of climate variability on carbon accumulation.

Carbon accumulation is influenced also by time since abandonment or stand age, disturbance history, land-use intensity, and species composition [25,26]. Studies in TDF have found that stand age can be even more influential than rainfall variability for carbon accumulation in biomass [27] and litterfall [28], with differences across stands of different ages explained by the changes in species composition during secondary successional changes. To understand and to predict how TDFs respond to changes in climate, it is important to assess the synergistic effect of rising temperature and drought on carbon dynamics and how TDF structure and composition mediate forest responses. Here, we quantified biomass and carbon dynamics in two TDFs over a 12-year period along a successional gradient to address the following questions: (i) How much carbon is being accumulated annually by secondary TDFs of different ages?; (ii) How do structure, composition, and time since abandonment influence the dynamics of forest carbon accumulation?; (iii) How does climate affect mortality, and carbon accumulation across stand ages? We addressed these questions in two TDFs, representing two extremes in the spectrum of TDFs along a precipitation gradient. One was a high-rainfall, semi-deciduous TDF (30–75% of deciduous species), with 5 months of dry season located in Costa Rica. The other TDF was a low-rainfall deciduous TDF (90–95% of deciduous species), with a marked dry season (6 months) located in Brazil.

2. Materials and Methods

2.1. Study Site

The study was conducted in Santa Rosa National Park Environmental Monitoring Super Site (SRNP) in Costa Rica and the Mata Seca State Park (MSSP) in Brazil (Figure 1). The study sites are classified as seasonal TDFs (<2000 mm annual precipitation), according to the Holdridge life zones [29]. SRNP is located in the Guanacaste Conservation Area in northwestern Costa Rica. SRNP's historical mean annual temperature is 27 °C, and mean annual precipitation is 1700 mm. The dry season at SRNP extends over five months from December to April [30]. The MSSP is situated in Minas Gerais in Brazil. Historical mean annual temperature of the site is 24.4 °C, and the mean annual precipitation is 651 mm, which is concentrated during the rainy season (November to April). These two TDFs contain a mosaic of different successional stages, defined in [31,32] as early (~20 in MSSP and ~30 years old in SRNP), intermediate (~50 years old), and old growth forest

(>100 years) according to the stage of succession based on the years of abandonment since last disturbance and forest composition and structure.

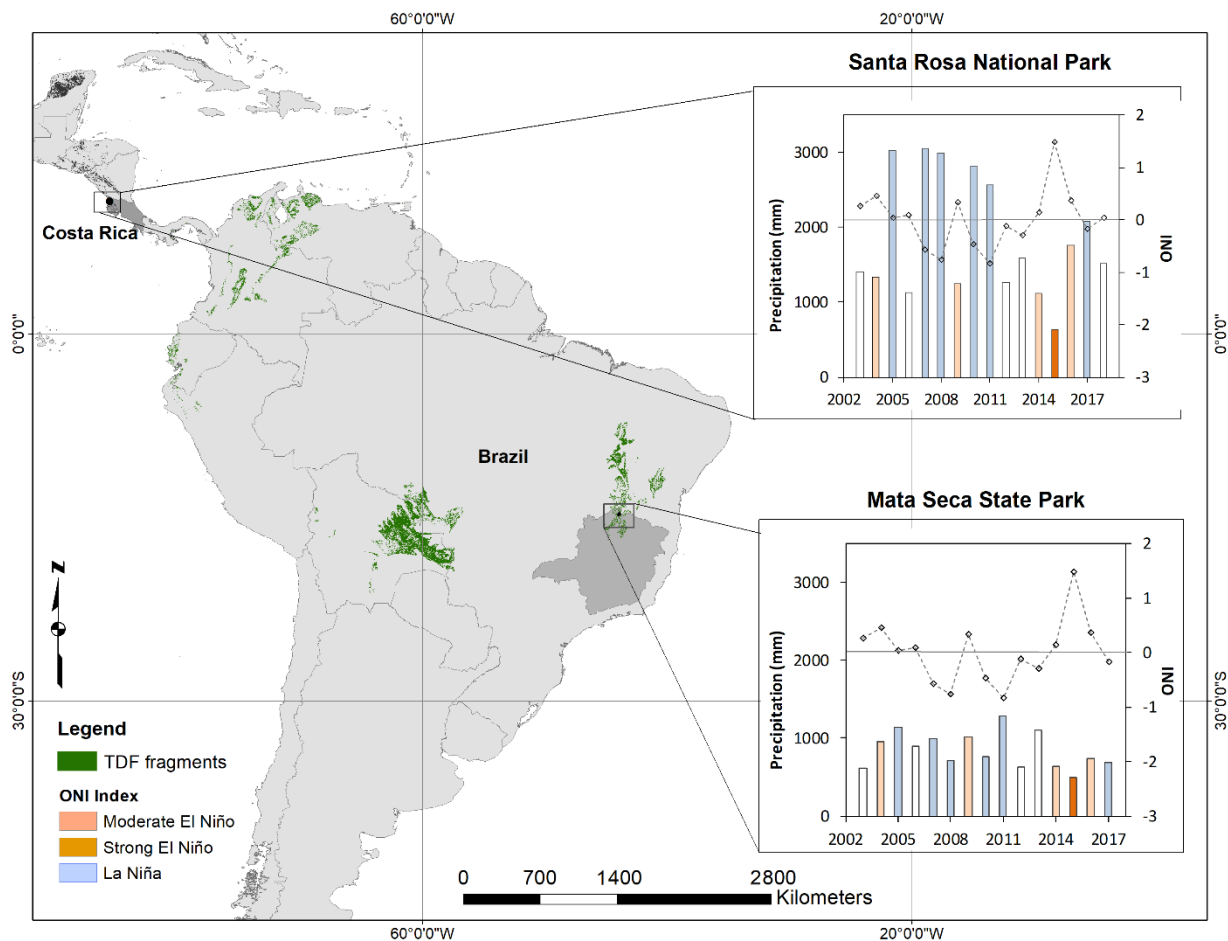


Figure 1. Location of tropical dry forests (TDFs) used in this study with insets of temporal variability of precipitation in bars and the Oceanic Nino Index (ONI) for 2003–2018 for Santa Rosa National Park Environmental Monitoring Super Site (SRNP) and 2003–2017 for Mata Seca State Park (MSSP). Orange bars represent years for “El Niño” occurrence ((ONI > 0.5), less precipitation) and blue bars for “La Niña” occurrence ((ONI < −0.5), increased precipitation), according to the National Oceanic and Atmospheric Administration (NOAA).

2.2. Climatic Variables

Climate data for 2007–2017 in SRNP were obtained from the SRNP park administration, where data have been collected and recorded daily for the last 30 y. MSSP’s monthly climate data for 2007–2017 were obtained from a local meteorological station that was managed by the Brazilian National Institute of Meteorology (INMET). In order to explore the relationship between mortality, recruitment, carbon losses with climatic variables, we calculated mean seasonal temperature (MST), mean seasonal precipitation (MSP), seasonal potential evapotranspiration (PET) and seasonal number of rainy days (RD). Seasonal climatic variables were calculated for each site for MAM (March to May), JJA (June to August), SON (September to November), and DJF (December to February) The seasonal occurrence and intensity of “El Niño” or “La Niña” events and the Oceanic Nino Index (ONI) at both sites were obtained from NOAA (ERSST.v5), where “El Niño” and “La Niña” are defined as periods with five consecutive 3-month running mean of sea surface temperature anomalies in the Pacific Ocean above or below the threshold of ± 0.5 °C (https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php).

2.3. Forest Inventory Plots

At the SRNP, nine permanent plots were established (three per forest stand). Each plot has an area of 0.1 ha. The young forest stands (30-year-old) grew after several pasture fires that occurred in the late 1980s, and the intermediate forest stands (50-year-old forest) regenerated after logging activities and less intense fires in the early 1970s. The old-growth (OG) forests were located in areas where the last reported selected timber harvesting took place >100 years ago [32]. At MSSP, 18 permanent plots were established (six plots per forest stand) with an area of 0.1 ha each. The young forest stands (20-year-old) were used as pastureland for 20 years, and cattle were not removed until 2000. The intermediate forest stands (50-year-old forest) were also used for pastureland for an unknown period and were abandoned in the early 1970s. The old-growth (OG) forests have no record of logging over the last 100 years [31,33].

At each plot, all tree stems with diameters at breast height (DBH ~1.3 m) >0.05 m were tagged and measured yearly to record tree mortality, recruitment, and increase in diameter. Data were collected in the rainy season between February and April in MSSP from 2007 to 2017 and between September and November in SRNP from 2007 to 2019. A total of 1131 individuals were tagged and measured in SRNP plots (360 in 30-year-old stands, 330 in 50-year-old stands, 441 in old-growth forests), and 2431 individuals in MSSP plots (845 in 20-year-old stands, 785 in 50-year-old stands, 801 in old-growth forests).

2.4. Forest Dynamics and Carbon Accumulation

Tree recruitment and mortality were determined for all individuals (>5 cm DBH) for all plots at each site. Tree mortality (m) and recruitment (r) were calculated using a logarithmic model [34,35]. Tree mortality and recruitment in each successional stage were calculated using the following formulas:

$$m = \frac{\ln N_i - \ln N_s}{T} \quad (1)$$

$$r = \frac{\ln N_f - \ln N_s}{T} \quad (2)$$

where N_i is the initial number of individuals, N_s is the number of individuals that survived at time T . For recruitment (r), N_f is the final number of individuals that survived plus the number of individuals recruited during the period T . For each tree >0.05 m in DBH, we calculated the aboveground biomass at each year of the census using the equation for tropical tree species from [36]:

$$AGB = 0.0673 \times (\rho \times DBH^2 \times H)^{0.976} \quad (3)$$

where AGB is aboveground biomass, ρ is wood density (g cm^{-3}), DBH is the diameter at breast height (cm), and H is tree height (m). Wood density values specific for the species at SRNP and MSSP were obtained from published and unpublished data [37]. When site data were not available, species values or mean genus values were used from other locations [38]. For individual trees with multiple stems, we calculated the AGB of each stem and summed them. Biomass was then converted to carbon by using the average wood carbon fraction for tropical forests and TDFs of 47% [7,39,40]. We then estimated the annual total carbon storage gain (AGCgain) in $\text{Mg C ha}^{-1} \text{ year}^{-1}$ as the gain due to increases in growth plus tree recruitment (new trees entering the census >5 cm of DBH each year). The annual total carbon storage loss in $\text{Mg C ha}^{-1} \text{ year}^{-1}$ was estimated as the loss due to tree mortality (AGCloss).

Belowground biomass at each year of the census was calculated for each individual using the root to shoot ratio (0.275) estimated for TDF by [41]. We then estimated the belowground annual gain in total carbon stored in $\text{Mg C ha}^{-1} \text{ year}^{-1}$ (BGCgain) due to tree recruitment and tree growth, and then the annual loss in total carbon stored in

Mg C ha⁻¹ year⁻¹ (BGC_{loss}). The total carbon accumulation in Mg C ha⁻¹ year⁻¹ was calculated as the aboveground and belowground annual carbon gains from tree growth and recruitment plus the annual litterfall.

2.5. Litterfall Data

Leaf litterfall was collected from May 2007 to March 2010 in SRNP and from May 2008 to April 2011 in MSSP. At each plot in all successional stages at both study sites, eight litter traps were established with an area of 0.5 m² following research protocols found in [33]. Bulk leaf litter (leaves, twigs and reproductive parts) was collected manually from the traps every 4 w and oven-dried (<70 °C) to obtain dry matter mass at each collection.

2.6. Analysis

To evaluate biomass and carbon dynamics over time, we compared all results at each site between years and forest stands using analysis of variance (repeated-measures ANOVA) and subsequent post-hoc Tukey honest significant differences ($p < 0.05$ or $p < 0.001$). To test how different predictors drive carbon losses and carbon gains, we used linear models in the packages MASS and JTOOLS available in R-software (R Development Core Team 2012). We related biomass dynamics (carbon losses, carbon gains, and carbon storage) to the time since abandonment (TSA), litterfall, number of species, and stems per plot.

Pearson's correlation matrix was used to evaluate site specific relationships between mortality, recruitment, carbon losses and the essential climatic variables obtained at each site for all the years of the study. This analysis allowed us to identify statistically significant relationships, and the direction and strength of the relationships between mortality, carbon losses and essential climatic variables. Furthermore, using simple linear regression we analyze the relationship of carbon losses, mean annual temperature and mean annual precipitation separating data by site and successional stage.

3. Results

3.1. Biomass and Carbon Dynamics

At both sites, aboveground and belowground biomass increased from the first census to the final census (Figure 2). Average annual increment in total biomass ranged from 3.98 Mg ha⁻¹ y⁻¹ in the younger forests to 0.72 and 0.29 Mg ha⁻¹ y⁻¹ in mature forest in the Brazilian TDF and from 0.5 Mg ha⁻¹ y⁻¹ in the younger forest to 2.87 and 2.0 Mg ha⁻¹ y⁻¹ in the 50-year-old stands and old growth forest in the Costa Rican TDF. The forest stands that grew fastest were the 20-year-old forest in Brazil, where biomass increased significantly ($p < 0.001$) compared with the initial biomass. Moreover, biomass storage in the young forest in Brazil was significantly different ($p < 0.001$) from the 50-year-old and the old-growth forest. In the TDF of Costa Rica, there was no significant increase in AGB or BGB in any of the forest stands; however, biomass storage in the younger forest was significantly different ($p < 0.001$) to the 50-year-old and the old-growth forest.

The annual average of litterfall at both sites varied with the succession (Table 1), but only in the SRNP the younger stands had significantly lower values of litterfall than more advanced stages. As we only had 3 years of data from litterfall, we calculated annual average of litterfall production for each successional stage and annual average of AGC and BGC gains for each stage derived from all the years of the inventory (2007 to 2017 for MSSP and 2007 to 2019 for SRNP). Total carbon accumulation was then calculated using the gains in AGC, BGC and litterfall production for each plot. At the SRNP site, higher values of annual average carbon accumulation were observed in the 50-year-old forest stands and the old-growth forest stands (with no significant difference $p < 0.001$) and significantly lower carbon accumulation was observed at the younger forest stands (Table 1). However, for the Brazilian site, there was no significant difference between the young stands and the older forest stands for carbon accumulation.

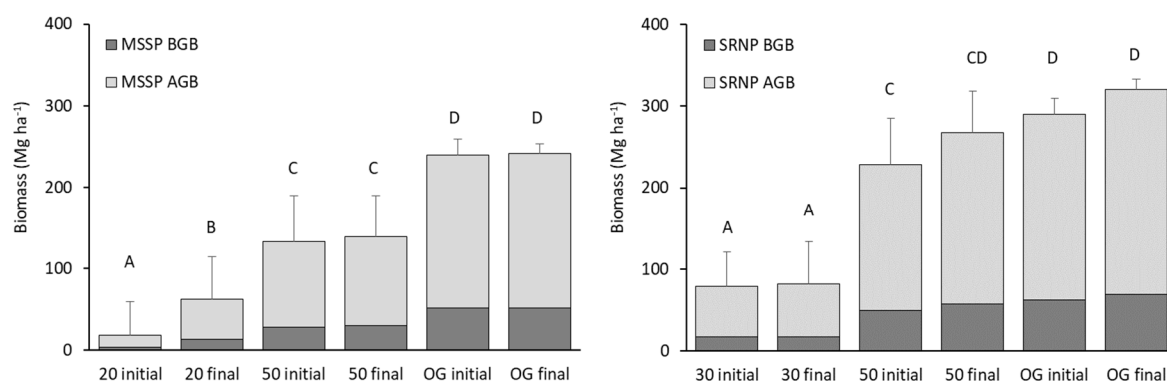


Figure 2. Initial and final aboveground biomass (AGB) and belowground biomass (BGB) at each forest stand (20, 30 and 50-year-old and old-growth = OG) in Mata Seca State Park (MSSP) and Scheme 0. According to one-way ANOVA and a Tukey test.

Table 1. Changes in aboveground carbon (AGC) and belowground carbon (BGC), litterfall production, and carbon accumulation averaged per forest stand (20, 30 and 50-year-old and old-growth = OG) for Mata Seca State Park (MSSP) and Santa Rosa National Park (SRNP).

Site	AGC Gain (Mg C ha ⁻¹ y ⁻¹)	BGC Gain (Mg C ha ⁻¹ y ⁻¹)	Litterfall (Mg C ha ⁻¹ y ⁻¹)	Carbon Accumulation (Mg C ha ⁻¹ y ⁻¹)
MSSP				
20	1.7 ± 0.9 ^a	0.4 ± 0.2 ^a	1.9 ± 0.1 ^a	4.0 ± 1.2 ^a
50	2.1 ± 1.2 ^a	0.6 ± 0.3 ^{ab}	1.8 ± 0.1 ^a	4.5 ± 1.6 ^a
OG	2.2 ± 0.6 ^a	0.6 ± 0.2 ^b	2.2 ± 0.2 ^a	4.9 ± 0.7 ^a
SRNP				
30	1.6 ± 0.5 ^a	0.4 ± 0.1 ^a	0.6 ± 0.5 ^a	2.6 ± 1.1 ^a
50	3.0 ± 1.1 ^b	1.3 ± 1.0 ^b	2.0 ± 0.5 ^b	6.3 ± 2.4 ^b
OG	2.6 ± 0.8 ^b	0.7 ± 0.2 ^b	1.9 ± 0.3 ^b	5.2 ± 0.8 ^b

Different letters in the same column indicate significant differences between forest stands in a post-hoc Tukey test ($p < 0.001$).

3.2. Relationship of Forest Structure and Composition on Carbon Dynamics

Linear models were built to test how carbon storage, carbon gains (recruitment and diameter growth) and carbon losses (mortality) were driven by different predictors, such as time since abandonment (TSA), litterfall, number of species, and stems per plot. From the models built, we found that the time since abandonment had a significant positive effect (Figure 3; Appendix A) on carbon storage ($p < 0.05$) and also on carbon loss ($p < 0.001$). The number of stems had a significant positive effect on carbon storage ($p < 0.05$) and also on carbon gain ($p < 0.001$). Litterfall was not a significant predictor ($p > 0.05$), although it influenced positively the carbon gains and negatively the carbon losses. The number of species only had a significant positive effect on carbon losses ($p < 0.05$).

3.3. Relationship of Climate Variability on Carbon Dynamics

From the correlations between the annual percentage of mortality, annual percentage of recruitment and annual carbon losses grouped per site and the seasonal climatic variables (MSP, MST, PET, RD, and ONI), we found significant correlations ($p < 0.05$) varied between seasons (Figure 4). For the site in MSSP, we found significant correlations between mortality and climatic variables only for March to May with MSP and June to August with RD. Recruitment was only correlated with MST from June to August. For carbon losses, we found significant correlations with MST, PET, and ONI in the months from December to February, also with PET and ONI in March to May, and with RD in June to August.

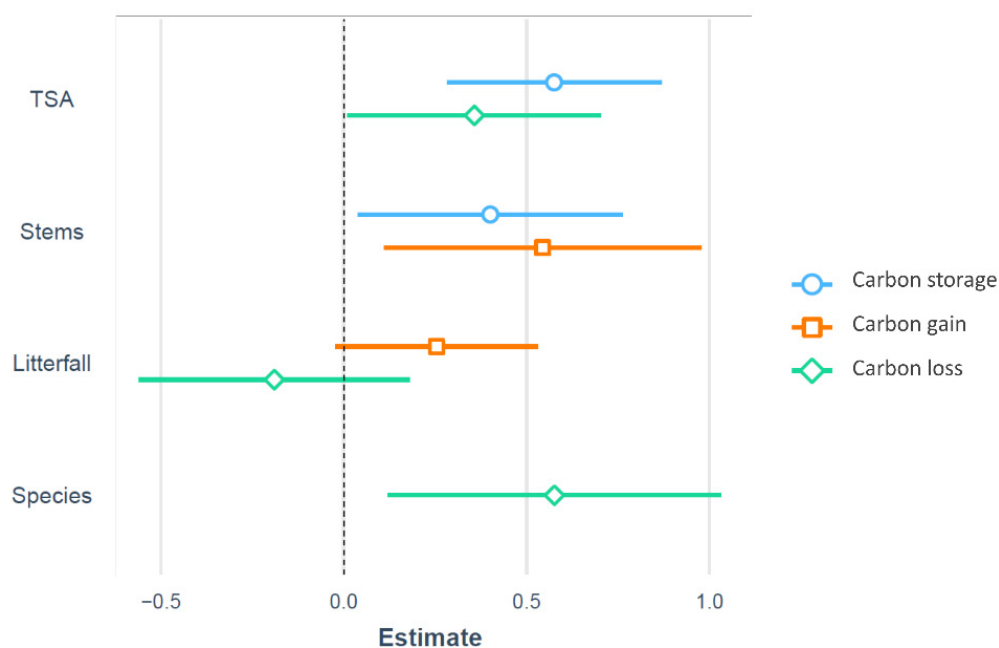


Figure 3. Comparison of the effect of time since abandonment (TSA), averaged annual litterfall per plot, number of species, and stems per plot on carbon storage, carbon gain and carbon loss at both TDF (Mata Seca State Park and Santa Rosa National Park). Standardized regression coefficients can directly be compared among each other; the higher the value, the stronger the relationship observed. If the line crossed the zero, then there was no statistical significance found ($p > 0.001$).

For the site in SRNP, we found significant correlations between mortality, MST, and PET in the months from December to February, which is the dry season. In addition, mortality was correlated with MSP and ONI in the months from March to May, including dry season months and the beginning to wet season at the end of May. From September to November, we only found a significant correlation between mortality and MAT. For recruitment rates, we only found significant correlations in the wet season months of September to November with MSP, MAP, MAT, PET and ONI. For carbon losses, we found significant correlations with all climatic variables in the months from March to May and June to August.

From the linear relationship between the annual carbon losses at each site separated by successional stage and the seasonal climatic variables (MSP, MST), we found significant relationships ($p < 0.05$) for the MSSP only with increasing MST (Figure 5). However, the strength in the relationship between carbon losses and MST varies between seasons and between the successional stages. For the young forest stand, the relationship was only significant in the wet season from December to February. For the old growth forest, the relationship was only significant from September to November. The 50-year-old forest had significant relationships with MST from December to February, June to August, and September to November.

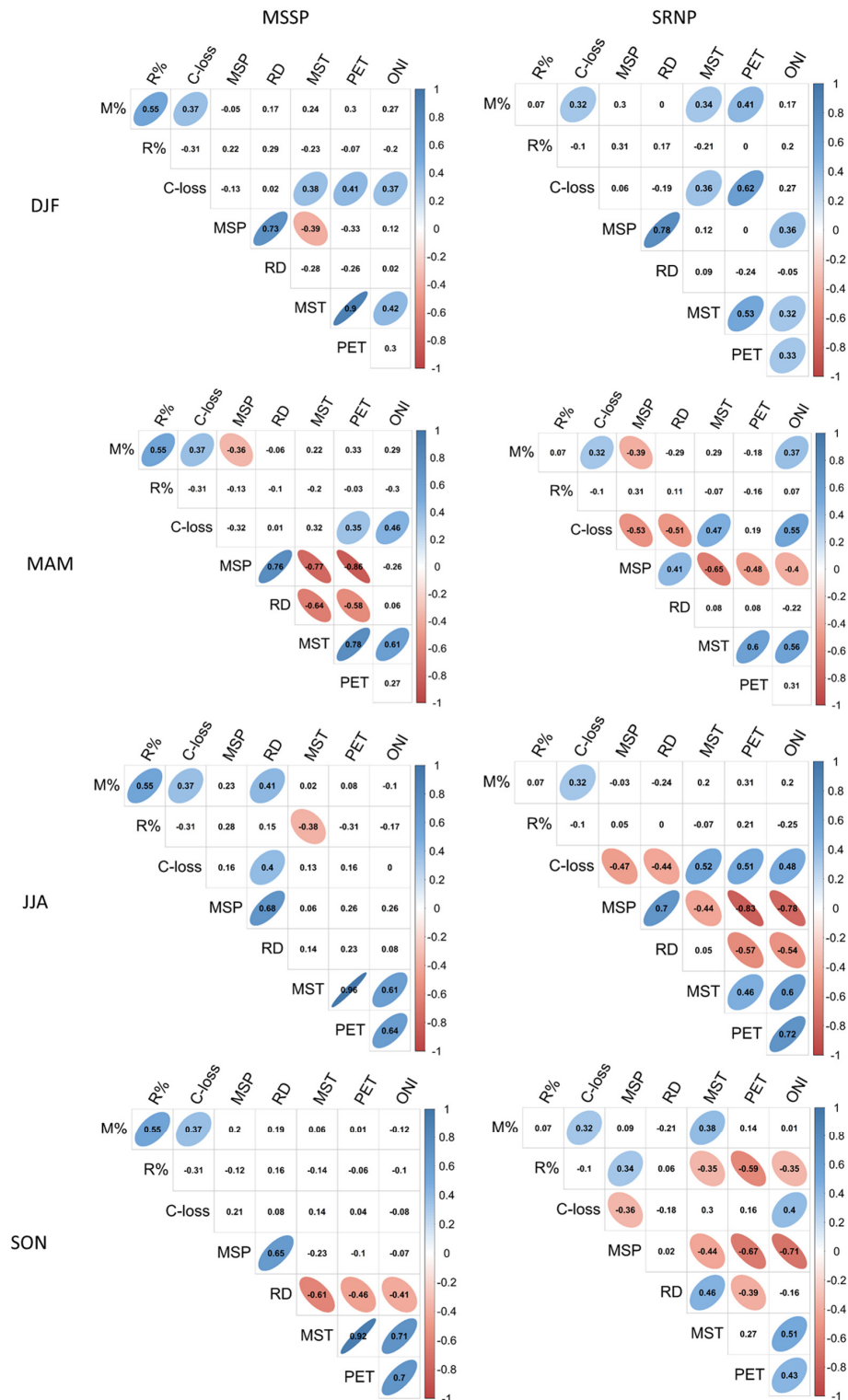


Figure 4. Pearson’s correlation coefficients for annual percentage of mortality (M%), annual percentage of recruitment (R%), annual carbon losses caused by mortality (C-loss), mean seasonal precipitation (MSP), mean seasonal temperature (MST), seasonal rainy days (RD), seasonal potential evapotranspiration (PET) and Oceanic El Nino Index (ONI) in Mata Seca State Park MSSP, and Santa Rosa National Park (SRNP). Only significant correlations ($p < 0.05$) are shown in red or blue circles in the graph. DJF (December to February), MAM (March to May), JJA (June to August), SON (September to November), and DJF (December to February).

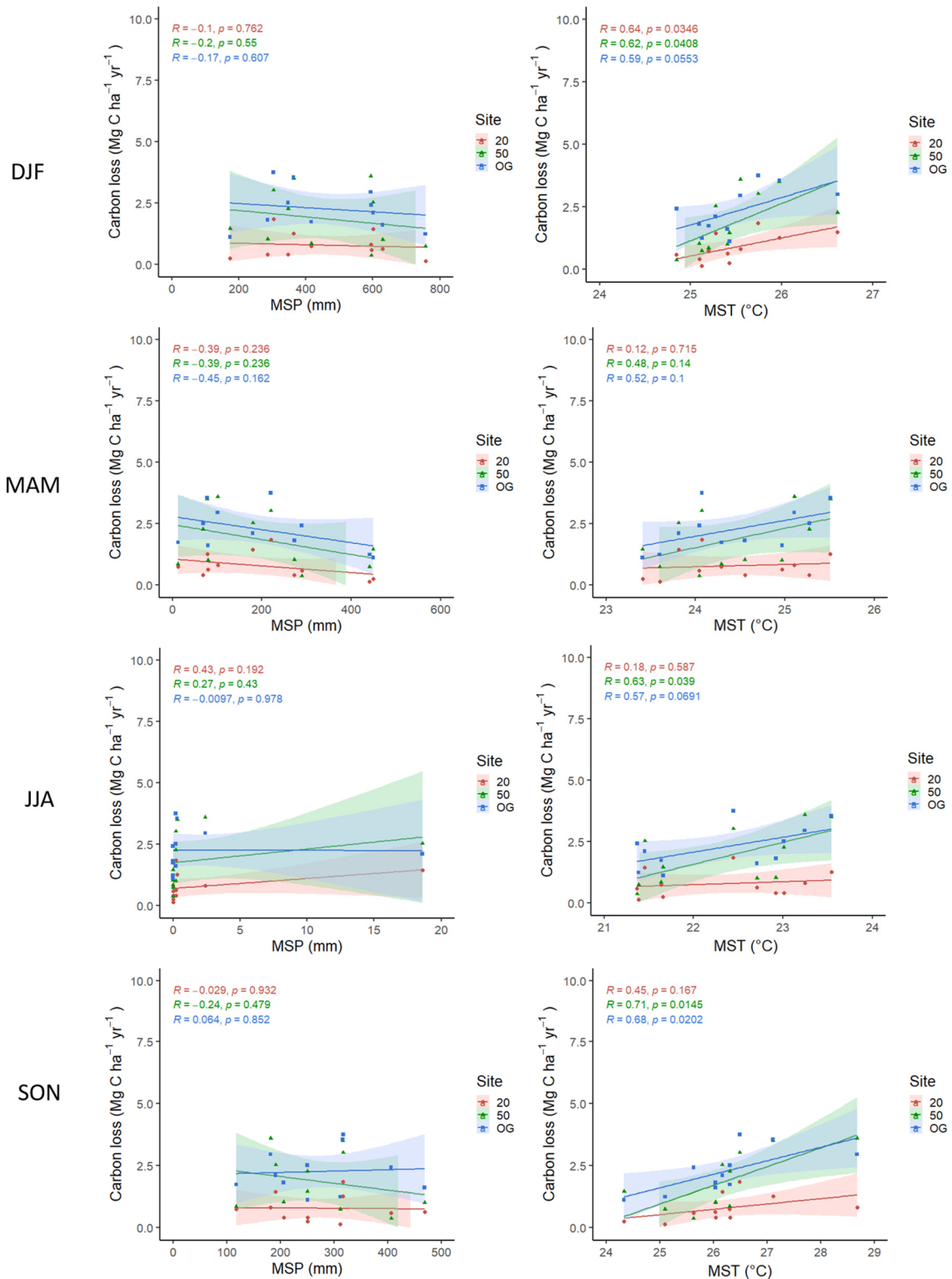


Figure 5. Linear relationship between carbon losses, mean seasonal temperature (MAT), and mean seasonal precipitation (mm) in Mata Seca State Park MSSP. DJF (December to February), MAM (March to May), JJA (June to August), SON (September to November), and DJF (December to February).

For the SRNP, we found significant relationships ($p < 0.05$) with MSP from March to May (except in the 50-year-old forest) and from June to August (except in the 30-year-old forest), and from June to August (except in the 30-year-old forest). For MST, the carbon losses also related significantly from March to May and June to August (except in the 50-year-old forest).

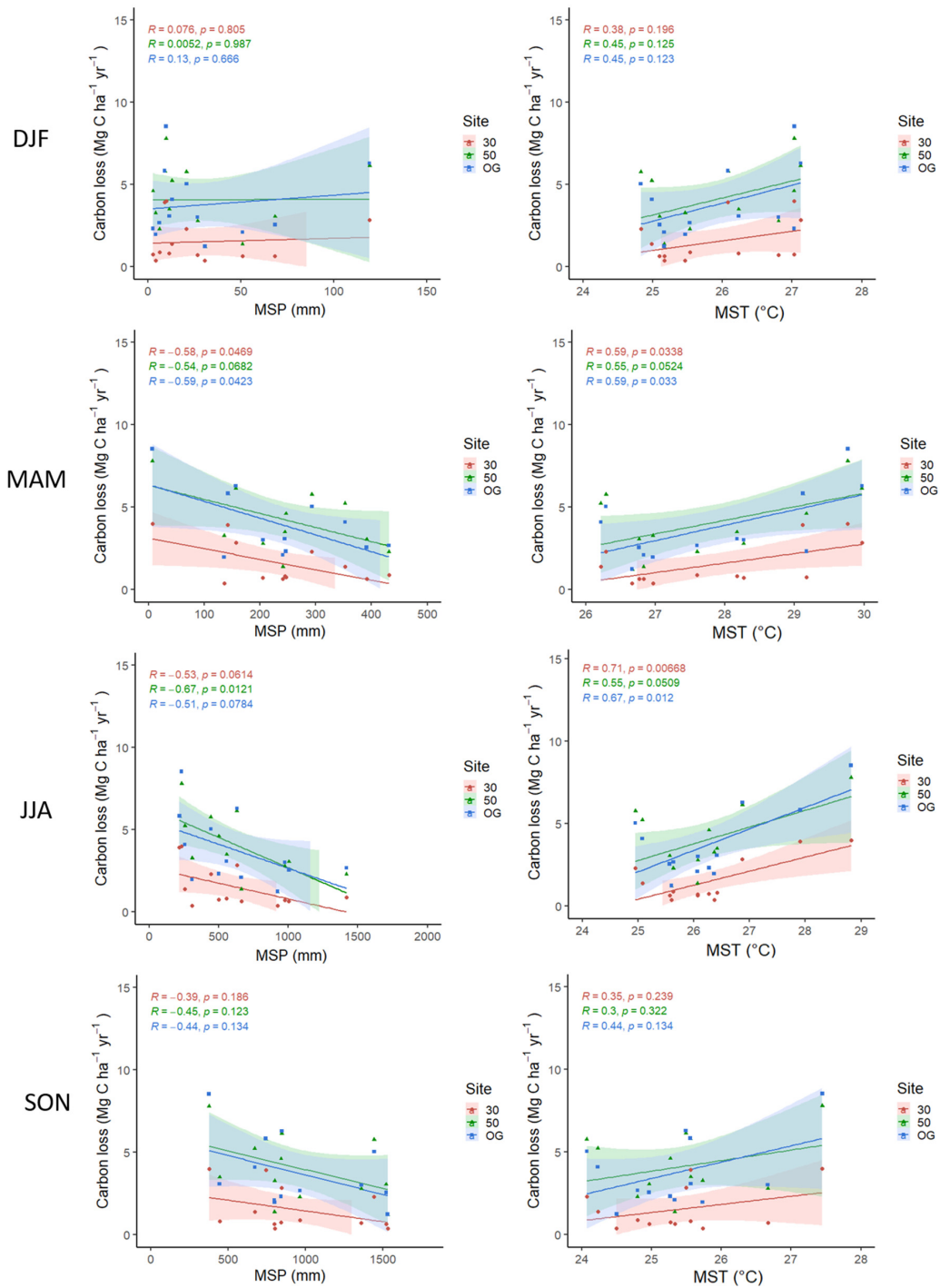


Figure 6. Linear relationship between carbon losses, mean seasonal temperature (MST), and mean seasonal precipitation (MSP) in Santa Rosa National Park SRNP. DJF (December to February), MAM (March to May), JJA (June to August), SON (September to November), and DJF (December to February).

4. Discussion

4.1. Forests Biomass and Carbon Sequestration Dynamics

Biomass and carbon storage increased through time at both of our TDF sites under study, which is an indicator of forest recovery of these ecosystems from human disturbances; however, these increases are not statistically significant. Average annual increment in total biomass storage ranged from $4.0 \text{ Mg ha}^{-1} \text{ y}^{-1}$ in the younger forest to $0.2\text{--}0.7 \text{ Mg ha}^{-1} \text{ y}^{-1}$ in the mature forest in the Brazilian TDF and from $0.5 \text{ Mg ha}^{-1} \text{ y}^{-1}$ in the younger forest to $2.0\text{--}2.87$ in the mature Costa Rican TDF. The Intergovernmental Panel on Climate Change (IPCC) [42] reported for the Americas an average annual increment in AGB of 1 to 4 Mg ha^{-1} for TDF and tropical moist forests with a long dry season. Another study that compared AGB dynamics of dry and wet tropical forests across the Americas obtained lower annual increments in AGB in TDF, with 2.3 and $1.9 \text{ Mg ha}^{-1} \text{ y}^{-1}$ after 5–15 and 15–25 year after abandonment, respectively, than in younger wet forests (4.7 and $6.1 \text{ Mg ha}^{-1} \text{ y}^{-1}$) [43]. In addition, in their study biomass changes were driven mainly by tree growth, which contributed to $>48\%$ of the changes in biomass across forest types and age classes. Mortality also contributed to changes in biomass in the wet forests that were 5–15-year-old, but in TDF, mortality became more important later in the succession [43].

Regarding the carbon accumulation, at both TDFs the components with the highest contribution were AGC followed by litterfall. Other components such as BGC might be underestimated because the root-to-shoot ratio used in this study has some major limitations. Few studies that report total ecosystem carbon accumulation measured components of belowground production [44]. From our estimates, belowground biomass consisted mostly of the standing stock of woody biomass, but this estimation does not capture fine root production and growth, which makes up a great part of the total net primary productivity (NPP) [44]. Woody NPP estimated from the sum of aboveground and belowground components have been estimated to be around $11\text{--}14 \text{ Mg ha}^{-1} \text{ year}^{-1}$ in Mexican TDF, of which about 44% on average was allocated belowground [45]. Modeled aboveground net primary productivity (ANPP) in SRNP using the CASA model (Carnegie–Ames–Stanford Approach, [46]) in the same area as our study showed the same successional trends with some overestimation, where ANPP values for the 30-year-old, 50-year-old, and old-growth forest were of $3.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, $8.9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, and $7.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, respectively [46], compared with our respective carbon accumulation results of $2.6 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, $6.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$, and $5.2 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$.

The linear models that were built to test the influence of forest structure and composition on carbon dynamics showed that time since abandonment and number of stems per plot were the best predictors of carbon storage. For carbon gains, the number of stems per plot was the best predictor, and for carbon losses, time since abandonment and number of species per plot were best predictors. Time since abandonment is an important driver of carbon dynamics because the disturbance history, recovery of soil properties, and recovery of forest structure are reflected within it [25,26]. Former studies that evaluated biomass across successional gradients in seasonal forests in the Yucatan Peninsula in Mexico and Guanacaste Province in Costa Rica found that stand age explained much of the variation in biomass and basal area [47,48].

4.2. Effects of Climate Variability on Carbon Sequestration

We found significant correlations between seasonal climatic variables and annual tree mortality and carbon losses at our study sites. Climatic variables such as temperature, precipitation, number of rainy days, the ONI index and potential evapotranspiration can be important predictors of carbon losses under extreme climatic events such as the ENSO. When successional stages were separated, we found a significant relationship with carbon losses and rising seasonal temperature and seasonal precipitation. However, the significance of this relationship varied across successional stages and also across seasons. For the Brazilian site, stronger relationships were found for carbon losses and seasonal climatic variables (MST) from September to February, covering the beginning of the wet

season. The same is observed for the Costa Rican site, where the strongest relationships were found for carbon losses and seasonal climatic variables (MST and MSP) from March to August, covering part of the dry season and the start of the wet season. This indicates that the extension and intensity of the drought in the dry season has an important effect on mortality and carbon losses. However, mortality and carbon losses can increase during years of high precipitation (years with hurricanes, floods, or wind storms). Both dry years and very rainy years can have profound consequences for the demographic rates and carbon dynamics of TDF.

The carbon losses at the SRNP forest stands were more strongly related to climate variables than the MSSP, even though the MSSP is a drier TDF with lower annual precipitation. Increases in forest mortality related to the intensification of droughts and temperature in tropical forests have been reported in the literature [49–51]. In a TDF in Mexico, prolonged and severe droughts led to increases in tree mortality rates after ENSO events [51,52]. At a TDF in Chamela-Cuixmala Mexico, the work [52] also found that the regenerative community (seedlings, saplings and resprouts) at different stages of forest succession, tree mortality and rates of species loss increased as annual rainfall decreased. In particular, mortality and rate of species loss peaked in the ENSO of 2005, and they were still high in the following year. However, they observed recovery from the ENSO effects after subsequent rainy years, where mortality rates returned to normal levels, which led to a net increase in plant density and species density, especially in young forests [52].

Under El Niño events, a reduction in photosynthesis rates and increased ecosystem respiration rates have been observed [53–55], affecting the overall annual carbon sink [56]. Another study in SRNP at the 50-year-old forest stands reported for the net ecosystem exchange an ecosystem uptake between 6.6 and 3.6 Mg C ha⁻¹ for the growing seasons during the period 2013–2016; the lowest net ecosystem exchange (~40% less than previous year) occurred in 2015 (−3.6 Mg C ha⁻¹) when a strong El Niño event affected the area [18]. Additionally, the research [57] found significant interannual and seasonal variations due to seasonal precipitation differences in a TDF in northwest Mexico, where less precipitation switched the annual ecosystem carbon balance to a net source (+1.02 Mg C ha⁻¹ y⁻¹), and higher precipitation led to a net sink (−2.49 Mg C ha⁻¹ y⁻¹). Nonetheless, more information and long-term studies are needed in order to understand how tropical dry forests will cope in the future with predicted climate changes.

5. Conclusions

Our results showed that carbon dynamics in TDFs were strongly influenced by time since abandonment and climate variation. Depending on their location, some dry forests are more influenced by climate variability than others, and differences between secondary stages are observed. In the future, we expect to see far greater carbon losses caused by increases in severe droughts and hurricane events. These events can modify TDF carbon sequestration capacity and the recovery rates of secondary TDFs in carbon storage, forest structure, and diversity. Under predicted increases in extreme drought events, these changes will jeopardize the ability of secondary TDFs to recover faster after human intervention, especially under extreme climatic events such as El Niño.

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Appendix A

Table A1. Linear models to evaluate the effects of time since abandonment (TSA), number of species and stems per plot and average annual litterfall per plot on carbon storage, carbon losses, and carbon gains.

		Estimate	Std. Error	t Value	Pr(> t)	Model
	(Intercept)	−0.18	0.13	0.00		R ² = 0.58
	TSA	0.35	0.16	2.28	<0.05	p < 0.001
	Species	0.57	0.15	3.87	<0.001	
	Litterfall	−0.19	0.14	−1.39		
carbon gain	(Intercept)	−0.00	0.16	0.00		R ² = 0.33
	Stems	0.54	0.16	3.38	<0.05	p < 0.05
	Litterfall	2.54	0.16	1.58		
carbon storage	(Intercept)	−0.00	0.08	0.00		R ² = 0.79
	TSA	0.57	0.12	4.67	<0.001	p < 0.001
	Stems	0.40	0.12	3.26	<0.05	

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