Effect of drought on productivity in a Costa Rican tropical dry forest

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Abstract

Climate models predict that precipitation patterns in tropical dry forests (TDFs) will change, with an overall reduction in rainfall amount and intensification of dry intervals, leading to greater susceptibility to drought. In this paper, we explore the effect of drought on phenology and carbon dynamics of a secondary TDF located in the Santa Rosa National Park (SRNP), Costa Rica. Through the use of optical sensors and an eddy covariance flux tower, seasonal phenology and carbon fluxes were monitored over a four-year period (2013–2016). Over this time frame, annual precipitation varied considerably. Total precipitation amounts for the 2013–2016 seasons equaled 1591.8 mm (+14.4 mm SD), 1112.9 mm (+9.9 mm SD), 600.8 mm (+7.6 mm SD), and 1762.2 mm (+13.9 mm SD), respectively. The 2014 and 2015 (ENSO) seasonal precipitation amounts represent a 30% and 63% reduction in precipitation, respectively, and were designated as drought seasons. Phenology was affected by precipitation patterns and availability. The onset of green-up was closely associated with pre-seasonal rains. Drought events lead to seasonal NDVI minimums and changes in phenologic cycle length. Carbon fluxes, assimilation, and photosynthetic light use efficiency were negatively affected by drought. Seasonal minimums in photosynthetic rates and light use efficiency were observed during drought events, and gross primary productivity was reduced by 13% and 42% during drought seasons 2014 and 2015, respectively. However, all four growth seasons were net carbon sinks. Results from this study contribute towards a deeper understanding of the impact of drought on TDF phenology and carbon dynamics.

1. Introduction

Tropical dry forests (TDFs) hold a strong economic and cultural connection to human development in the neotropics (Maass et al. 2005). TDFs not only provide a source of agricultural and urban land but also an important source of goods and ecosystem services for the communities that live around them (Balvanera et al. 2011, Castillo et al. 2005, Fajardo et al. 2005). Such is the close connection of TDFs to human activity that they are considered the most heavily utilized and disturbed ecosystem in the world (Janzen 1988, Sanchez-Azofeifa et al. 2005). Tropical forests have been estimated to account for a third of global metabolic activity (Malhi 2012), and TDF may account for roughly 42% of all tropical ecosystems (Quesada et al. 2009, Murphy and Lugo 1986). However, TDFs are surprisingly understudied and currently represents only a fraction of research on tropical ecosystem (Sanchez-Azofeifa et al. 2005). The former has contributed to the fact that we still have a poor understanding of TDF response to climatic factors, including moisture dynamics, which are needed to understand ecosystem responses to climate change.

The eddy covariance technique has become the backbone for regional and continental carbon balance modeling efforts (Papale and Valentini 2003, Reichstein et al. 2003) as well as validation and calibration of ecosystem models (Baldocchi 1997, Hanan et al. 2002, Hanson et al. 2004, Reichstein et al. 2002, 2003).
However, as global modeling has progressed, there remains an underrepresentation of tropical ecosystems. Fluxnet-Multi-Tree Ensemble upscaling efforts in detecting global variability in terrestrial carbon and water cycles indicated a high index of extrapolation in tropical areas (Jung et al 2009). A more recent Fluxnet (2015) summary report on global fluxes, reported insufficient flux measurements in the tropical ecosystems (Kumar et al 2016), leading to an underestimate of gross primary productivity (GPP) in these regions.

Global climate models project precipitation regimes in tropical regions to change (Feng et al 2013) with increasing in seasonality and variability as main outcomes. Rainfall patterns are predicted to move towards more extreme events and lead to an overall reduction in the amount and an extension of the dry intervals (Chadwick et al 2016, Malhi et al 2008, Zelazowski et al 2011). Changes in precipitation regimes are of particular importance to tropical dry forests as water dynamics determine the alternating seasonality between wet and dry seasons. As such, the issue of how TDFs will respond to the predicted drier conditions has become important to consider. A recent synthesis by Allen et al (2017) reviewed multiple data sources including seedling, dendrochronology and modeling data to suggest changes in structure and functionality, including a reduction in carbon storage, as drought frequency increases and precipitation becomes more variable.

In this context, the objective of this study is to contribute to the discussion of how TDFs will respond to changes in rainfall regimes, specifically in the context of phenology and ecosystem carbon exchange. Through the use of eddy covariance measurements, optical phenology, and meteorological data collected through four growing seasons (2013–2016), including a drought (2014) and an ENSO severe drought season (2015), we explored the following questions: (1) how are phenology and carbon exchange in a TDF impacted by drought? (2) What drives seasonal variations of GPP and respiration under ‘normal’ and drought conditions? This analysis will contribute towards a deeper understanding of the mechanisms controlling ecosystem productivity and explores TDFs sensitivity and resilience to drought in the face of changing climate.

2. Methods

2.1. Site description

The study was conducted within the Santa Rosa National Park Environmental Monitoring Super Site (SRNP-EMSS), Guanacaste, Costa Rica. The SRNP-EMSS is located in the northwest of Costa Rica, near the border with Nicaragua and is part of a broader conservation area called Area de Conservacion Guanacaste (ACG) (figure 1). The park area consists of a series of plateaus ranging from 300 masl to sea level and covered by a mosaic of pasture and tropical dry forest in various stages of regeneration (Janzen 2000, Sen and Sanchez-Azofeifa 2017). The study plot is located at 10°44.206’ N, 85°37.034 W with an altitude of 290 masl, and is characterized as an intermediate successional stage tropical dry forest with average tree height of 13 m (Li et al 2017) (figure 1). Its topography is slightly sloping (<2%) in the north direction, and the predominant wind direction is from the north-west. The mean annual air temperature for the area is 25 °C and mean annual precipitation over the past 26 years is 1575 mm, with 85%–97% of precipitation falling between May and November. The natural phenologic cycle initiates during the onset of rains (May) and extends, through a prolonged senescence, into late February of the following calendar year.

2.2. General Instrumentation

The study site has been monitored with an eddy covariance system and meteorological station installed on a 35 m 0.70 m × 2.0 m-section triangular steel tower located within the forest stand. The eddy covariance (EC) method (Aubinet et al 1999, Baldocchi et al 1988, Moncrieff et al 1997) provided measurements of net ecosystem CO2 exchange (NEE) (mg m−2 s−1), latent heat flux (LE) (W m−2), and sensible heat (H) (W m−2) fluxes continuously from 2013–2016. Further detail on the eddy covariance instrumentation and data processing can be found in the supplementary methods section available at stacks.iop.org/ERL/13/045001/mmedia.

Proximal remote sensing sensors mounted on south-facing arms extending from the steel tower allow the tracking of forest stand phenology progression. A broadband NDVI was derived from the two-band spot radiometers following a revised method of the Huemmrich et al (1999) method. NDVI seasonal changes were used to calculate the phenological cycle and its stages, green-up, maturity, and senescence. Dates for the start of the season, end of season, as well as transitions between stages were determined by analyzing the rate of change throughout the time series, using second derivative functions. Additionally, a meteorological station provided ancillary climate variables including temperature (T), vapor pressure deficit (VPD), relative humidity (RH) measurements and volumetric soil water content (VWC). More detailed information on sensor deployment can be found in the supplementary methods section.

2.3. Eddy covariance partitioning

Measurements of NEE was partitioned into its two components: GPP (mg m−2 s−1) and total ecosystem respiration (Reco) (mg m−2 s−1). Reco was estimated using night-time fluxes based on the approach suggested by Reichstein et al (2005). Additionally, a light-response curve model, independent of temperature by relying solely on characterizing carbon
assimilation as a function of light, was used as an independent method for estimating Reco and GPP. A series of hyperbolic functions were used to assess the response of photosynthesis to incident radiation, following the methods outlined by Hutyra et al (2007) used in tropical forests (equations and detailed explanation found in supplementary material section).

2.4. Analysis of relative importance
A stepwise multiple regression model was used to identify the environmental drivers most affecting the temporal variability in GPP. The identified regression and predictors are expressed by the following formula:

\[ \text{GLM} = \text{GPP} \sim \text{PAR} + \text{VWC} + \text{VPD} + \text{LE} \]  

where gross primary productivity (GPP) is a product of photosynthetically active radiation (PAR), volumetric soil water content (VWC), vapor pressure deficit (VPD), relative humidity (RH), temperature (T), and latent heat flux (LE).

A relative importance analysis based on the multiple regression framework of these combined variables provided the strength of each predictor in relation to seasonal GPP (2013–2016). Four different relative importance techniques were used including the LMG (Chevan and Sutherland 1991, Lindeman et al 1980), First, Genizi (Genizi 1993), and CAR (Zuber and Strimmer 2010) models. All models were bootstrapped using 1000 replicates producing 95% confidence intervals. The LMG model has been described as the most robust method as it takes into account the direct and adjusted effects of each regressor allowing more effective \( R^2 \) decomposition. Further details on the stepwise multiple regression and relative importance model can be found within the supplementary material section.

3. Results

3.1. Comparison of meteorological conditions
Total seasonal precipitation during the four monitored growing seasons was 1591.8 mm (+14.4 mm SD), 1112.9 mm (+9.9 mm SD), 600.8 mm (+7.6 mm SD), and 1762.2 mm (+13.9 mm SD) during 2013, 2014, 2015, and 2016, respectively. Precipitation accumulation for the 2013 and 2016 years was comparable to published seasonal totals (Gillespie et al 2000), and therefore, these seasons were treated as receiving ‘normal’ precipitation amounts. In contrast, accumulation amounts during the 2014 drought and 2015 ENSO drought represented 30%, and 62% declines, respectively, from 2013 ‘normal’ levels (figure 2). Interseasonal variability in precipitation patterns was also observed; results can be found in the supplementary results section. Precipitation amounts were
Figure 2. Monthly precipitation for 2013, 2014, 2015, and 2016 growing seasons.

Figure 3. Pre-season precipitation patterns and NDVI changes for the (a) 2013 season, (b) 2014 season, (c) 2015 season, and (d) 2016 season. NDVI and precipitation patterns are shown for periods leading up to the start of season (gray line) and into green-up.

Table 1. Precipitation totals (mm) grouped by phenologic stage.

|              | 2013     | 2014     | 2015     | 2016     |
|--------------|----------|----------|----------|----------|
| Green-up     | 531.1    | 101.7    | 159.5    | 221.4    |
| Maturity     | 1219.8   | 993.0    | 433.0    | 1504.3   |
| Senescence   | 0.0      | 1.6      | 8.3      | 1.0      |
| Seasonal total | 1570.9  | 1096.0   | 600.8    | 1726.6   |
| Pre-Season total | 20.5    | 18.2     | 74.0     | 72.6     |

Main temporal changes in PAR, T, RH, and VPD were driven by seasonality (figure 4). PAR, T and VPD maximums occur during the dry season and minimums during the wet season, when cloud cover and precipitation are common, and RH values reach maximums. Temporal patterns of VWC were connected to precipitation frequencies. VWC spiked with precipitation events and plateaued during dry periods. Interannual variability associated with drought was observed in all meteorological parameters (table 2). Average seasonal values of PAR (1082.64 $\mu$mol m$^{-2}$ s$^{-1}$), T (28.05 °C), VPD (11.79 hPa), and VWC (15.12%) were highest during the 2015 severe drought season, compared to 2013, 2014, and 2016 season values. The 2013 season had the lowest VPD and RH quantities and spanned the greatest range (table 2). During each season, minimum values of VPD approached zero during peak precipitation periods (common in September and October months).
Figure 4. Time series of mean daytime (a) VPD, (b) VWC, (c) RH, (d) T, and (e) PAR, with daily cumulative precipitation.

Table 2. Summary of seasonal maximums, minimums, mean, and standard deviation values of meteorological parameters PAR, VWC, VPD, RH, and T.

|       | 2013          | 2014          |       |       |       |       | 2015          | 2016          |
|-------|---------------|---------------|-------|-------|-------|-------|---------------|---------------|
|       | Max.          | Min.          | Mean. | SD    | Max.  | Min.  | Mean.         | SD            |
| PAR (\(\mu \text{mol m}^{-2} \text{s}^{-1}\)) | 1387.43       | 283.67        | 996.83| 239.94| 1613.01| 367.42| 1060.75       | 266.22        |
| VWC (%)| 42.87         | 10.33         | 25.76 | 9.23  | 40.42 | 7.4   | 19.65         | 7.1           |
| VPD (hPa)| 28.22        | 0.65          | 8.58  | 4.44  | 22.17 | 0.42  | 11.22         | 4.55          |
| RH (%) | 97.84         | 38.08         | 76.84 | 11.14 | 98.57 | 48.69 | 70.82         | 10.73         |
| Temp (°C)| 30.59        | 22.99         | 26.65 | 1.17  | 29.86 | 23.53 | 24.72         | 1.31          |

|       | 2015          | 2016          |       |       |       |       | Max.          | 2016          |
|-------|---------------|---------------|-------|-------|-------|-------|---------------|---------------|
|       | Min.          | Mean.         | SD    | Max.  | Min.  | Mean. | SD            |               |
| PAR (\(\mu \text{mol m}^{-2} \text{s}^{-1}\)) | 1390.75       | 1082.64       | 192.94| 5.33  | 1276.25| 158.75| 877.88        | 235.24        |
| VWC (%)| 31.65         | 15.12         | 5.48  | 13.54 | 20.76 | 13.54 | 20.76         |               |
| VPD (hPa)| 21.57        | 11.79         | 3.55  | 0.58  | 23.64 | 0.58  | 9.87          | 4.79          |
| RH (%) | 90.7          | 70.14         | 8.19  | 40.48 | 73.58 | 11.58 |               |               |
| Temp (°C)| 30.42        | 28.05         | 1.04  | 26.91 | 4.17  |       |               |               |
Figure 5. Time series of (a) phenologic cycle derived from mean daily NDVI values and (b) seasonal precipitation (mm) throughout the four-year period. Precipitation data were collected manually and corroborated with electronic tipping bucket precipitation measurements.

Table 3. Dates and changes (Δ) in green-up, maturity, senescence, and total season length in days using 2013 for length comparisons.

|             | 2013     | 2014     | 2015     | 2016     | Δ (2013–2014) | Δ (2013–2015) | Δ (2013–2016) |
|-------------|----------|----------|----------|----------|--------------|--------------|--------------|
| Start of green-up | 20-May   | 09-May   | 09-June | 01-May   | 11           | −20          | 19           |
| Start of maturity   | 10-June  | 28-May   | 27-June | 06-June  | 13           | −17          | 4            |
| Start of senescence | 27-December | 02-January | 24-November | 20-January | −6           | 33           | −24          |
| End of season      | 03-March | 06-April | 09-February | 23-April | −34          | 22           | −51          |

Table 4. Length of each phenology stage (days) for each growth season within the four-year study period (2013–2016).

|          | 2013 | 2014 | 2015 | 2016 |
|----------|------|------|------|------|
| Green-up | 21   | 19   | 18   | 36   |
| Maturity | 200  | 219  | 150  | 228  |
| Senescence | 66  | 94   | 77   | 94   |
| Total season | 287 | 332  | 245  | 358  |

3.2. Changes in phenology

Seasonal phenology was monitored by tracking changes in canopy NDVI and phenologic stages, green-up, maturity, and senescence, were identified (figure 5). Phenologic stages represented consistent time periods. Greenup, Maturity, and Senescence accounted for approximately 7% (+3%), 65% (+4%), and 27% (+4%) of the total phenologic cycle, respectively. The duration of phenologic stages varied from year to year. Drought seasons 2014 and 2015 were 34 days longer and 22 days shorter, respectively, than the 2013 season; while the 2016 season was 51 days longer (table 3). Comparison of seasonal NDVI showed maximum values during 2013 (0.85) and consistently decreased during 2014 (0.82) and 2015 (0.80) drought years, before stabilizing during 2016 (0.80).

The start of season date also varied interannually, with green-up initiating shortly after the start of seasonal rains (figure 5). Following green-up, a rapid transition from green-up to maturity was observed, lasting between 18–36 days. Proportionally, the majority of the growing season was spent within maturity and comparison between the four years showed this period as having the most variability between these seasons. Using the 2013 season as a standard for comparison, the 2014 and 2016 phenologic cycles were longer (332 and 358 total days, respectively), while the 2015 phenologic cycle was shorter (150 total days) (table 4).

Seasons with longer maturity periods coincided with late-season rain events (figure 2). Intra-seasonal NDVI variability was also greatest during maturity due to droughts occurring during this stage. Large decreases in NDVI, amounting to approximately 0.1, were observed during July and August months in
drought years 2014 and 2015, indicating marked losses of canopy greenness. Drought months were characterized by low variability in daily NDVI values, showing consistency in depressed quantities. During the second half of the 2013 maturity, instrument error affected data quality and is likely the cause for the sudden observed decrease in NDVI and high spike in measurement variability.

3.3. Ecosystem carbon fluxes

Common patterns emerged from the evaluation of carbon fluxes of ‘normal’ precipitation years (2013 and 2016). GPP increased consistently from green-up to maturity, plateaued during peak precipitation months (September and October). This is followed by steady GPP declines into senescence and the dry season (figure 6(b)). Drought years 2014 and 2015 deviated from this pattern by displaying GPP reductions during drought months (July and August). Following the return of rainfall events, GPP increased to pre-drought levels. Total accumulated GPP was greatest during the 2016 season, amounting to 1453.53 g C m\(^{-2}\) season\(^{-1}\), a 29% increase from 2013 (1125.30 g C m\(^{-2}\) season\(^{-1}\)) (figure 7(b)). GPP levels were significantly reduced during drought years, totaling 949.97 g C m\(^{-2}\) season\(^{-1}\) in 2014 and 636.41 g CO\(_2\) m\(^{-2}\) season\(^{-1}\) in 2015, a 16% and 43% decrease, respectively (figure 7(b)). Accumulated NEE quantities for both ‘normal’ precipitation and drought seasons showed net carbon sequestration to the amounts of \(-659.20\) g C m\(^{-2}\) season\(^{-1}\), \(-577.97\) g C m\(^{-2}\) season\(^{-1}\), \(-361.69\) g C m\(^{-2}\) season\(^{-1}\), and \(-581.84\) g C m\(^{-2}\) season\(^{-1}\), for 2013–2016 seasons respectively (figure 7(a)).

High levels of respiration were observed at the onset of the 2013, 2014, and 2015 seasons (0.41 ± 0.02, 0.22 ± 0.03, and 0.31 ± 0.13 mg m\(^{-2}\) s\(^{-1}\), respectively) (figure 8(b)). Following the initial burst of respiration in 2013, levels decreased steadily until dormancy. During 2016, respiration initiated at a low 0.08 ± 0.04 mg m\(^{-2}\) s\(^{-1}\), then increased and plateaued at elevated levels (0.33 ± 0.02 mg m\(^{-2}\) s\(^{-1}\)) for much of the remainder of the season. Drought months (July and August) of 2014 and 2015 seasons showed sharp declines in respiration rates. 2015 drought levels (0.050 ± 0.01 mg m\(^{-2}\) s\(^{-1}\)) were comparable to dry season rates (0.052 ± 0.02 mg m\(^{-2}\) s\(^{-1}\)).

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**Figure 6.** Monthly time series of average (a) \(R_{eco}\) (mg m\(^{-2}\) s\(^{-1}\)), (b) GPP (mg m\(^{-2}\) s\(^{-1}\)), and (c) NEE (mg m\(^{-2}\) s\(^{-1}\)). Shaded patterns indicate wet or dry season. Precipitation histogram (mm) is shown in blue.
Following droughts, respiration rates recovered, followed by steady decreases into dry season (figure 6(a)).

3.4. Controls on carbon fluxes
Relative importance analysis showed strong agreement in importance ranking of predictors using the LMG, Genizi, and CAR models, across all growth seasons. In 2013, the set of environmental drivers within the multiple linear regression accounted for 80.1% of GPP variance. LE and VPD combined for over 69% of the LMG, Genizi, and CAR models’ $R^2$, with LE having the highest relative importance (37%–39%) (figure 9(a)).

The 'First' method showed slightly different results, showing VPD as the variable of highest importance followed by LE. Differences in results should be interpreted in the context of the model. The 'First' metric is derived by adding correlations by a regressor individual, ignoring adjustments based on the combined weight of other regressors within the model, thus producing less robust sets of results. Notwithstanding, atmospheric evaporative power (represented by LE and VPD) still remains the main driving mechanism affecting GPP. Analysis of the 2016 data showed similar patterns to the 2013 season, with LE and VPD, as the

Figure 7. Time series of (a) seasonal cumulative net ecosystem CO$_2$ exchange (NEE g C m$^{-2}$), (b) seasonal cumulative gross primary productivity (GPP g C m$^{-2}$), and (c) cumulative precipitation (mm), for 2013, 2014, 2015, and 2016 seasons.
Figure 8. Monthly mean seasonal (2013–2016) comparison of (a) gross primary productivity (GPP mg m$^{-2}$ s$^{-1}$), and (b) ecosystem respiration ($R_{eco}$ mg m$^{-2}$ s$^{-1}$).

Figure 9. Relative importance analysis of environmental parameters PAR, VWC, VPD, and LE about GPP for (a) 2013, (b) 2014, (c) 2015, and (d) 2016 growing seasons. Four relative importance models were used including LMG, First, Genizi, and CAR. GLM accounted for 80.01%, 89.91%, 84.34%, and 72.65% of 2013, 2014, 2015, and 2016 GPP variability, respectively.
Figure 10. Relative importance analysis of GLM GPP = PAR + VWC + VPD + LE for drought event in (a) 2014 and (b) 2015. Four relative importance models were used including LMG, First, Genizi, and CAR. GLM accounted for 93.42% and 94.29% of 2014 and 2015 GPP variability, respectively.

main driving variables accounting for over 76% of the models correlation to GPP. Latent heat flux displayed the largest relative importance metric of 43%–58% (figure 9(d)). The combined set of predictors accounted a total of 72.65% of GPP variability. Drought seasons 2014 and 2015 displayed an increase in predictive power by VWC compared to the 2013 and 2016 seasons, especially during the 2015 severe drought year (figure 9(b–c)). Closer analysis of the relative importance of parameters solely during the drought months (figure 10) in 2014 and 2015 seasons show VWC as the main predictor metric. During the 2014 season, VWC had a relative importance contribution of 56%–76% to the models’ predictive power. The second ranked predictor was LE with 20%–36%. Combined variables accounted for 93.42% of GPP variability. In the 2015 ENSO year, we also see VWC as the main predictor, accounting for 60%–83% model predictive power. Latent heat flux represented the second highest relative importance and represented 11%–28% of models \( R^2 \). All combined variables accounted 94.29% of GPP variability observed during the 2015 drought months.

4. Discussion

4.1. Water relations and phenology

Preseason precipitation appears to play a significant role in the initiation of the phenologic cycle of this secondary tropical dry forest. However, since tree water status was not monitored for this study, we cannot conclusively identify the ecophysiological mechanism by which trees respond to the onset of water availability. Nevertheless, results (shown in supplementary section) from relative importance analysis comparing various environmental drivers (PAR, VWC, VPD, and LE) to NDVI changes during green-up can be used to indicate some of the processes at hand. Throughout all seasons, volumetric soil water was consistently ranked with the most important variable during green-up. The correlation between the onset of precipitation events and VWC (figure 1, table 1 of supplementary results), as well the importance of VWC during the start of the season would complement observations by Borchert (1994) where irrigation experiments led to stem recharge and leaf flush within one week of application. Reich and Borchert (1984) also reported rapid girth growth but only in response to heavy rains, suggesting a presence of a minimum rehydration threshold for bud break; the threshold varying with the degree of previous dehydration of soil and trees. This threshold variability would in part explain the different pre-season precipitation amounts observed during the four-year study. During the 2013 and 2014 seasons, 18–21 mm of rainfall was observed before bud break. However, pre-season amounts increased to +70 mm for both the 2015 and 2016 seasons. During the 2015 dry season, a series of small rainfall events of less than 9 mm were observed before a heavy rainfall event of 49 mm, which appeared to trigger the start of the growing season. It is unclear if a higher threshold was required to achieve complete stem recharge or if the smaller precipitation events were not sufficient to reach total rehydration. In contrast, the 2016 season did see a pre-season heavy precipitation event of 26 mm that did not trigger bud break. This seeming higher threshold may suggest a strongly water-stressed ecosystem as consequence of the 2015 severe drought conditions. Similar reported results (Daubenmire 1972, Lieberman 1982, Reich and Borchert 1982) indicate rainfalls of 20–40 mm caused bud break in moderately but not strongly water-stressed trees, and rainfall greater than 50–60 mm trigger most trees. Our results are in line with the concept that pre-season precipitation serves as a primer for bud-break and the threshold required to trigger stem recharge varies as a result of prior dehydration of soil and trees (Eamus and Prior 2001).

Analysis of the NDVI time series showed the effect of drought on phenology. During the 2014
and 2015 drought months' seasonal minimums were observed during periods where maximums are the norm. Drought decreases in NDVI are likely associated with decreases in nitrogen and chlorophyll contents. Personal correspondence with members of the Area de Conservación Guanacaste (ACG) confirmed, through visual inspection, the yellowing of canopy leaves during the extended drought periods. And, although a qualitative observation, this would confirm changes in leaf greenness observed during drought. The initiation of senescence showed by the decline in NDVI, coincided with low precipitation and high evapotranspiration demand (figure 3 of supplementary results). Leaf fall would then be associated with depleting water levels stored in trees as observed in previous studies (Borchert 1994, Reich and Borchert 1984). Substantial rainfall events were observed during the latter part of the 2016 growing seasons. These events lead to high soil water moisture levels and likely delayed leaf drop (Whigham et al 1990).

4.2. Seasonal carbon balance patterns
The impact of drought on carbon fluxes was substantial. Decreases in precipitation during the 2014 and 2015 drought months were accompanied reductions in GPP, NEE, and Reco. Low drought productivity suggests that precipitation accumulated before intra-seasonal drought events did not provide sufficient moisture (soil or atmospheric) to maintain peak productivity levels over the drought periods. Late dry-season periods following drought years acted as mean carbon sources. These episodes may demarcate the limits of drought-adapted vegetation, perhaps due to depletion of moisture reserves in plant tissue and soil layers. However, it’s important to note that this ecosystem still acted as a mean carbon sink, even when confronted with severe drought (figure 7(a)). Our study suggests that this secondary tropical dry forest was sensitive to precipitation anomalies, particularly during El Niño severe drought events.

The first precipitation events that marked the end of the dry season were followed by a sudden emission of carbon dioxide through the four-year period (figure 8(b)), indicating that the onset of respiration is dependent on water dynamics. The wetting of dry soils and the subsequent pulse of CO₂ release and nitrogen mineralization is known as the 'Birch effect' (Birch 1958), which was observed interannually at the ecosystem level through eddy covariance methods in this study. The magnitude of the precipitation-induced carbon pulse is dependent on the amount of stored carbon in the forest soils as well as the severity of the dry season (Jarvis et al 2007). The observed pulse sizes could indicate a potential reduction in carbon pool size over drought years (2014–2015) relative to a ‘normal’ year (2013), possibly due to reduced litterfall for decomposition through the previous drought-afflicted growing season (figure 6(a)). The 'Birch effect' has been recently observed in another tropical dry forest site in Guanacaste, however on a smaller spatial scale using simulated precipitation and chamber-based measurements (Waring and Powers 2016).

The results of our study fit well into the body of research on how drought affects the carbon fluxes of other tropical ecosystems. Hutyra et al (2007) performed a similar four-year study in tropical rainforest (Tapajos National Forest, Para, Brazil), examining the controls of CO₂ exchange and the possible effects of water limitation. Tapajos National Forest is classified as primary rain forest, with distinct seasonal meteorology including an approximate five-month dry season (July–September). However, dry season in the Tapajos rainforest still receives an order of magnitude more seasonal precipitation than our study site (~300–400 mm vs. ~20–30 mm).

The seasonal patterns and magnitudes of carbon fluxes from tropical dry and rainforest overlap and diverge in some aspects. The severity TDF dry season is reflected in our site by the progressive decline of respiration and GPP throughout the dry season (figure 6). NEE remained negative during the dry season for non-drought years and acted as a carbon sink, possibly due to the presence of evergreen trees with deep root systems. However, NEE tapers off with progress into the end of the dry season, switching to a carbon source at the end of the season. In contrast, rainforests have been shown to sustain high levels of productivity during its dry season with highest uptake values occurring during its driest period, coinciding with peak levels of PAR (Goudien et al 2004, Huete et al 2006). Light has been shown to be a consistent control of rainforest fluxes, resulting in increases in carbon sequestration during seasonal drought (Bonal et al 2016). This is a notable difference from tropical dry forest productivity, which is largely controlled by seasonally dictated water availability. Our studied TDF was also found to have higher peak rates of GPP (>13 µmol m⁻² s⁻¹) than the Tapajos rain forest (~8 µmol m⁻² s⁻¹) during its wet season (Hutyra et al 2007).

Respiration rates of rainforest have been found to decrease during the dry season, attributed to the drying of surface litter. Thus, the aridity of the dry season in rainforest may be sufficient to suppress respiration, but insufficient to inhibit productivity. The net effect is a negative NEE through the dry season, implying that it is a carbon sink during this phenologic period (Hutyra et al 2007). During the wet season, both rain and dry forest (for non-drought years) follow a similar hill-shaped pattern of productivity where GPP increases at the onset of the rains, peaks in mid-season, then declines for the rest of the season. This pattern and magnitudes of respiration agree with a study of similar timescale on a tropical dry forest site in northwest Mexico, where pulses of CO₂ were observed at the onset of the growing seasons (Verduzco et al 2015). Tropical savanna, while much less dense in woody plants, has shown similar responses of ecosystem respiration to drought (Kutsch et al 2008).
4.3. Controls on gross primary production

The relative importance analysis was used to discern primary factors affecting carbon fluxes in TDF. A previous study by Becknell et al. (2012) showed precipitation to account for 55% of the variation in biomass among mature TDF sites. Other analyses into the interrelations of environmental conditions showed water balance depended on soil moisture availability, atmospheric evaporative demand, and the transpiration capacity of the tree (Reich and Borchert 1982). The interplay of environmental parameters makes controls difficult to identify individually. The 2013 and 2016 seasons showed parallel drivers (LE and VPD) accounting for the majority of GPP variability. This indicates atmospheric evaporation demand as the principal controlling factor of productivity and water balance status during these seasons. Conversely, focus on the drought events of 2014 and 2015 show a shift in importance towards soil water moisture. Latent heat flux, representing the evaporative demand, still had noticeable contributions during drought periods. Assuming active regulation by vegetation to minimize water loss through evaporation during water scarcity (Borchert 1994, Reich and Borchert 1988, Reich 1995, Sobrado 1997), the presence of LE as a governing factor during drought may represent the minimum evaporative regulation demand. The high relative importance of VWC across both drought periods could point towards a common regulation mechanism and strategy in response to drought.

Whole season analysis of 2014 and 2015 drought years showed similar results to non-drought years, where the interplay of a suite of environmental variables informed GPP patterns. The main difference in parameter importance was an increasing importance of soil moisture during drought. The shifting in variable importance about ecosystem productivity (from soil water moisture during droughts to evaporative demands during non-drought periods) demonstrates the ability of this TDF to adjust to limited water resources. These observations align with functional convergence theory (Bloom et al. 1985, Field 1991, Mooney and Gulmon 1979, 1982) which states that investment on CO₂ fixation will vary with resource availability, resulting in productivity being curtailed when faced with limiting resource availability that prevents utilization of additional capacity.

5. Conclusions

This study assessed the effect of drought on phenology and carbon dynamics. Our results show significant changes in phenology closely linked to seasonal water availability patterns. Water limitations had important effects on start of season, drought recovery, and senescence. Water status should not be interpreted as a cause to phenology, but rather an alteration to the timing of the progression between phenologic cycles. Forest carbon dynamics were also affected by water scarcity and drought severity. Reductions in seasonal productivity were observed during both drought years. The 2014 season showed post-drought recovery levels comparable to non-drought states that point to a notable drought resilience capacity. However, the severity of the 2015 drought did not allow in-season recovery. Instead, the recovery was observed during the 2016 season, where we observed higher productivity and an extended phenologic cycle. Alterations to phenology and forest productivity appear to be important drought coping strategies for tropical dry forests. The magnitude of the fluxes and the duration of phases can be readily applied toward refinement of larger scale flux estimates as well as vegetation model parametrization and validation.

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