LETTER

Integrating proximal broad-band vegetation indices and carbon fluxes to model gross primary productivity in a tropical dry forest

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Keywords: carbon monitoring, eddy covariance, NDVI, EVI2, proximal remote sensing, fAPAR

Supplementary material for this article is available online

Abstract

The measurement of carbon exchange between vegetation and the atmosphere is vital to quantify the impact of environmental variables on the carbon sequestration capacity of forests, and to predict how they will respond to future climate. In this study we use proximal remote sensing, defined as observations made from non-contact radiometric or imaging sensors in close proximity to the forest canopy (10–20 m), as an intermediate upscaling tool between direct measurements of carbon fluxes and satellite-derived estimations of primary productivity in a tropical dry forest (TDF) in Jalisco, Mexico. Two broad-band vegetation indices (VIs), the normalized difference VI and the enhanced vegetation index 2 (EVI2), were calculated from proximally sensed canopy properties, validated with field estimates of the fraction of absorbed photosynthetically active radiation by photosynthetic tissue (fAPARgreen), and compared to estimates of gross primary productivity (GPP) and net ecosystem exchange of CO₂, measured from a flux tower. The VIs captured the phenology of the TDF, both under typical summer rainfall and during an atypically-dry wet season in El Niño of 2009. The VIs also tracked a secondary leaf-flushing in the dry season of 2010. Our study suggests that (1) VIs are the best predictors of gross carbon uptake, able to explain up to 86% of variations in GPP; (2) VIs are accurate predictors of the photosynthetic capacity of green tissue, able to explain up to 99% of fAPARgreen variation; and (3) VIs and soil water content can be used to develop an empirical model that captures the seasonal trajectory of GPP from high respiration after the rain pulses, to rapid leaf development, and finally to slow senescence as the soil dries out. Proximal remote sensing constitutes a useful tool to link field-base measurements of carbon fluxes to satellite- or airborne-derived estimates of carbon exchange.

1. Introduction

The balance between carbon sequestration in forest biomass and carbon release through respiration, i.e. the net primary production of forests, is both a provisioning ecosystem service that drives the supply of food and wood for human consumption, and a regulatory ecosystem service as it reduces the amount of CO₂ in the atmosphere, and thus mitigates climate change. The quantification of the temporal and spatial variations of carbon stocks and carbon exchange between forests and the atmosphere is therefore essential to our understanding of the global carbon cycle, and to our ability to predict future climate. At the national and regional levels, carbon monitoring is usually based on a combination of field-based forest inventories and
remote sensing of structural attributes of forests, such as aboveground biomass, canopy cover or changes in amount of forested land (e.g. Urbazaeve et al. 2016). This approach, combined with process or empirical models, may be sufficient to develop nationwide greenhouse gas inventories or carbon stock estimations. However, research-intensive sites that combine field plots, flux towers and remote sensing techniques can be deployed to produce detailed information on carbon dynamics at local and regional levels (Birdsey et al. 2014). Such information may be used to generate and test physiological parameters that inform model parameterizations, or to generate emission factors, which in turn may be applied to assess carbon gains and losses in similar forests climate conditions, where implementing a detailed carbon monitoring program is unfeasible.

The majority of flux monitoring sites are located in temperate and boreal ecosystems, with a smaller number of sites situated in evergreen forests of the humid tropics and in tropical savannas (ORNL DAAC 2013). At the global scale, recent work indicates that the drought-sensitive vegetation of mesic biomes (e.g. tropical and temperate rainforests) determines the strength of the land carbon sink. However, there is increasing evidence that drought-adapted vegetation of low latitudes has a dominant effect on both the year-to-year variations of carbon exchange and land greening trends (Ahlstrom et al. 2015, Haverd et al. 2017, Poulter et al. 2014), and that the response of tropical biomes to water availability underlies their sensitivity to temperature and may control the variation of the terrestrial carbon balance (Wang et al. 2014, Jung et al. 2017). Among ecosystems where drought-adapted vegetation dominates, tropical dry forests (TDFs) have received very little attention from the flux community and their contribution to the global carbon balance is still poorly understood. As of today only five of 517 FLUXNET sites are reportedly situated in this type of vegetation (ORNL DAAC 2013b). This contrasts directly to the importance, extent, and vulnerability of TDFs to disturbance (Portillo-Quintero and Sanchez-Azofeifa 2010, Portillo et al. 2015, Calvo-Rodriguez et al. 2017). In the Americas alone, their current extent is approximately 500,000 km², but compared to their potential extent, 66% of these forests have already been converted to other land uses (Portillo-Quintero and Sanchez-Azofeifa 2010). Moreover, estimates of aboveground biomass and CO₂ emissions to the atmosphere during conversion to other land uses suggest these forests might be sites of substantial CO₂ exchange (Kauffman et al. 2003, Martínez-Yrízar et al. 1996).

At larger spatial scales, neither the magnitude of primary production of TDFs nor their sensitivity to environmental drivers is adequately characterized via remote sensing. The widely used MODIS product for the gross and net primary production (GPP/NPP) of Earth’s vegetated land surface (Friedl et al. 2010, Running et al. 2004) relies on the light use efficiency model first proposed by Monteith (1972). In the MODIS algorithm, a biome-specific parameter is extracted from the Biome Property Lookup Table for different vegetation types derived from five land cover classification schemes (Friedl et al. 2010), none of which recognize TDF as a distinct vegetation type, since areas classified by Miles et al. (2006) as TDF appear either as broadleaf deciduous forests or as savannas in these schemes, and therefore the ecophysiological particularities of tree drought-deciduousness in the tropics are disregarded.

There is growing interest in using carbon flux data to validate and refine the parameters used in satellite-based estimates of primary production (e.g. Canadell et al. 2000, Heinsch et al. 2006, Yuan et al. 2007). A key challenge is the inherent mismatch of the spatial and temporal scales of optical and flux measurements. Fluxes are sampled at high temporal frequency but the size of the source area for a given eddy covariance (EC) system typically ranges from hundreds of square meters to 1–2 km², and varies with atmospheric stability and wind speed (Göckede et al. 2004, Schmid 1994). Meanwhile, satellite-borne sensors view a much larger scene at any given time but have limited spatial and temporal resolution.

Recently, many flux sites have deployed optical sampling devices at ground level, above the canopy, as a way to overcome the mismatch between Earth observation platforms and flux measurements (Huemmrich et al. 1999, Eklundh et al. 2011, Gamon 2015). This proximal remote sensing of the optical properties of the canopy (also referred to as in situ, ground-based, or near-surface remote sensing) provides a closer spatial and temporal match to fluxes while remaining directly scalable to optical satellite products. It is also less affected by atmospheric conditions and the cloud contamination that pervades satellite and aerial observations in tropical ecosystems (Sanchez-Azofeifa et al. 2017). Huemmrich et al. (1999) first demonstrated the use of above-canopy reflectances in the photosynthetically active radiation (PAR) and near-infrared regions to derive a daily broad-band normalized difference vegetation index (NDVI) to track phenology in boreal sites. Since then, proximal broad-band indices have been used to monitor the seasonality of vegetation in a wide range of ecosystems (e.g. Soudani et al. 2012, Wilson and Meyers 2007), compared to satellite-derived estimates of productivity (Fensholt et al. 2004, Tittebrand et al. 2009, Wilson and Meyers 2007), and used as proxy data to fill missing periods in flux records (Nestola et al. 2016, Wohlfahrt et al. 2010). As of today, no similar studies have been implemented for a TDF.

In this study we concurrently measured the carbon exchange of a pristine TDF and the phenological changes in its photosynthetic capacity using vegetation indices (VIs) derived from proximal remote sensing. We aimed to answer the following questions: (1) can
Broad-band VIs be used to track the dynamics of carbon fluxes in a TDF over seasonal to annual time scales?, (2) how well do broad-band VIs correlate with a ground-based physiological parameter like $f_{\text{APARgreen}}$, and (3) can broad-band VIs be used as predictors of carbon fluxes and aid in the gap-filling process of flux time series, and ultimately in the parameterization of models that predict the GPP in similar types of forests and climate conditions?

2. Materials and methods

2.1. Site description and instrumentation

A micrometeorological tower equipped with an EC system for flux monitoring, and proximal remote sensing instruments were installed at Estación de Biología Chamela (EBCh) (19.5095° N, 105.0401° W) of Universidad Nacional Autónoma de México, 3 km inland from the Pacific coastline, in Jalisco, Mexico (figure 1), and operated between 2007 and 2015. The climate at EBCh is warm and sub-humid, with summer rains and an isothermal regime (Garcia 1988). Annual temperature averages at 25.8 °C (1982–2015). Mean annual precipitation is 844 mm (1977–2015), 89% of which falls from May to October. The tower is surrounded by low convex hills covered by old-growth, highly diverse TDF (Bullock and Solís-Magallanes 1990). Canopy height at the tower location is ~10.5 m, with a dense understory.

The EC system was installed on a steel tower, 12.5 m above ground level. The system consisted of a 3D sonic anemometer and an open-path CO$_2$/H$_2$O infrared gas analyzer (IRGA) (table 1). Wind velocity components, sonic temperature and gas concentrations were measured at a frequency of 10 Hz. We also recorded 30 min averages of ancillary meteorological variables (table 1). Daily precipitation was measured with a standard rain gauge at the meteorological station of EBCh, 1.5 km away from the tower site.

A detailed explanation of the methods used to estimate carbon fluxes can be found in Gonzalez del Castillo et al (2018). Additional information on flux partitioning, gap filling, proximal broad-band indices, fractions of absorbed PAR and GPP modeling can be found as supplementary material available at stacks.iop.org/ERL/13/065017/mmedia.

3. Results and discussion

3.1. Environmental drivers of the temporal patterns of carbon flux

In spite of the high variability of carbon exchange in this TDF, a consistent temporal correlation between rainfall, greenness, and carbon fluxes can be discerned from the time series in figures 2 and 3. Precipitation during the rainy season of 2008 (May–October) was 35% above the 30 yr average (1981–2010, 805 mm) for our site. Due to a moderate warm phase of El Niño–Southern Oscillation, which prevailed from June 2009–May 2010, cumulative rainfall for the rainy season of 2009 was 23% below the long-term mean (720 mm), but 3.2 times the average (86 mm) for the dry season (November 2009–April 2010). Accordingly, the midday average of the net ecosystem exchange of CO$_2$ (NEE$_{md}$) and the daily NEE were respectively 16% and 8% lower during the summer of 2009 compared to those at the beginning of the rainy season in 2008, and 44% and 30% lower than the respective rates during the summer of 2010. The rains in February 2010 triggered a flush of new leaves in the middle of the dry season that resulted in sustained C gains until the end of April. The average daily NEE during this brief growing period ($-2.4 \pm 1.2$ g C m$^{-2}$ d$^{-1}$) was comparable to the average daily NEE for the...
### Table 1. Flux measurement system, meteorological, and optical phenology variables measured at the ERCh flux site.

| System                  | Variable(s)                        | Instrument     | Manufacturer              | Position              |
|-------------------------|------------------------------------|----------------|---------------------------|-----------------------|
| Eddy covariance         | Horizontal, transversal and vertical wind velocities | CSAT3          | Campbell Sci. Inc. (Logan, UT, USA) | 12.5 m height, 220° azimuth |
|                         | CO₂/H₂O concentrations             | LI-7500        | (Li-Cor, Lincoln, NE, USA) | 12.5 m height          |
|                         |                                    |                | Campbell Sci. Inc. (Logan, UT, USA) | Base of tower         |
| Meteorology             | Air temperature (\(T_a\)) and relative humidity (RH) | HMP45C         | Vaisala Oyj (Helsinki, Finland) | 12.5 m height          |
|                         | Barometric pressure                 | 61205 V        | RM Young (Traverse City, MI, USA) | —                     |
|                         | Net radiation                       | NR-Lite        | Kipp and Zonen (Delft, Netherlands) | 17 m height           |
|                         | Soil heat flux                      | HFT3           | REBS (Seattle, WA, USA) | 8 cm depth            |
|                         | Soil temperature (\(T_{\text{soil}}\)) | TCAV           | Campbell Sci. Inc. (Logan, UT, USA) | 4 cm depth           |
|                         | Volumetric soil water content (SWC)| T107           | —                          | 15, 25 and 40 cm depth |
|                         |                                    | CS616          | —                          | 2.5 cm depth          |
| Proximal remote sensing | Incident PAR (\(\text{PAR}_{\text{in}}\)) | HOBO S-LIA     | —                          | 18 m height, upward   |
|                         | Reflected PAR (\(\text{PAR}_{\text{ref}}\)) | HOBO S-LIA     | —                          | 18 m height, downward |
|                         | Incident solar radiation (\(\text{SR}_{\text{in}}\)) | HOBO S-LIB     | Onset Computer (Bourne, MA, USA) | 18 m height, upward   |
|                         | Reflected solar radiation (\(\text{SR}_{\text{ref}}\)) | HOBO S-LIB     | —                          | 18 m height, downward |
|                         |                                    | HOBO H21-001   | —                          | Base of tower         |
|                         |                                     | datalogger     | —                          |                       |

**Figure 2.** Carbon fluxes and meteorological drivers from November 2007–September 2010 at the TDF of Chamela. From top to bottom: midday average of net ecosystem exchange of CO₂ (NEE\(_{\text{md}}\), dark green), daily NEE (NEE\(_d\), yellow), daily gross primary productivity (GPP, dark blue) and ecosystem respiration (\(R_{\text{eco}}\), red), daily average of air temperature (orange) and vapor pressure deficit (light blue), soil temperature (green) and soil water content (brown), and total daily precipitation in summer and fall (dark blue) and winter and spring (light blue). Bars indicate the daily range of each variable.
summer of 2009 $(-1.3 \pm 1.4 \text{ g C m}^{-2} \text{ d}^{-1})$ and 2010 $(-2.8 \pm 1.4 \text{ g C m}^{-2} \text{ d}^{-1})$ (figure 2).

Four to nine days after the first appreciable rains in June 2008, June 2009, July 2010, and February 2010, carbon exchange was dominated by respiration, as evidenced by positive NEE even at midday (figure 2). In the summer of 2009, whenever rain pulses interrupted short intra-seasonal dry spells, net daily C loss persisted longer ($\sim 15$–$20$ days). Large respiratory fluxes after soil rewetting—the so-called ’Birch effect’ (Jarvis et al. 2007)—have been previously reported for numerous dry seasonal environments, including TDFs (e.g. Jarvis et al. 2007, Verduzco et al. 2015, Waring and Powers 2016), and may significantly influence their overall carbon balance. For example, Verduzco et al. (2015) found that the respiration-dominated flux accounted for 36%–148% of the total C fixed during the wet season in a TDF, and determined whether the system acted as a source or a sink of C in a given year. Several non-exclusive mechanisms have been proposed for these transient CO$_2$ outbursts, among them physical displacement of air from soil pores by water (Unger et al. 2010), and rapid decomposition and mineralization of organic C pools by soil heterotrophs (Tang and Baldocchi 2005, Unger et al. 2010, Xu et al. 2004). EC data cannot be used to unequivocally ascertain the origin of the CO$_2$ efflux, but the signal of an immediate physical expulsion of air from soil is likely missed because such flux would be small and transient (Unger et al. 2010), and data gathered during the rain event itself and until the open-path IRGA dries out are discarded. NEE partition reveals that after the initial CO$_2$ outburst, GPP grew at a slower pace, and its peak lagged behind $R_{\text{eco}}$ by 8 days on average in summer 2008, summer 2009 and winter 2010 (figure 2). This suggests that $R_{\text{eco}}$ was at first dominated by the activation of heterotrophic respiration of labile C substrates accumulated on the forest floor during the long dry season. Indeed in this same TDF, Anaya et al. (2012) found that rain events $>10$ mm were positively correlated to the decomposition rates of litterfall. Tissue construction and transport of recent photosynthate to the soil take longer and may not start until deeper roots have access to water (Carbone et al. 2011, Huxman et al. 2004), so the contribution from autotrophic respiration may increase over the days following a rain event. CO$_2$ uptake also lags behind $R_{\text{eco}}$ since it depends on leaf expansion and maturation. We found that the increase in GPP was closely matched by the rise in the proximal greenness indices (EVI$_{\text{md}}$ and NDVI$_{\text{md}}$) from their dry season minima to their peak in $\sim 13$ days on average, as leaves expanded and the canopy closed (figure 3).

The amplitude of the annual thermal oscillation was small; average daily temperatures dropped to $20 \pm 3^\circ \text{C}$ from November through mid-April and went up to $27 \pm 3^\circ \text{C}$ from June to late October (figure 2). Half-hourly minimum temperatures during the study ($10^\circ \text{C}$–$12^\circ \text{C}$) were registered in early March 2008 due to the passage of a cold front, while maximum temperatures of $33^\circ \text{C}$–$35^\circ \text{C}$ were recorded for several days from July to September 2009. Due to the constant supply of water vapor from the nearby ocean, relative humidity was high throughout the year; only 12% of half-hourly values fell below 0.60. As a consequence, the vapor pressure deficit (VPD) generally remained low (0.2–1.7 kPa) (figure 2).

Every year soil temperature rose as the dry season advanced, reaching daily maxima of $35^\circ \text{C}$–$39^\circ \text{C}$ right before the onset of the rains, during periods when almost negligible NEE was observed. Then, in June 2008, June 2009 and late July 2010, the average $T_{\text{soil}}$ cooled overnight by $3^\circ \text{C}$–$5^\circ \text{C}$ after the first substantial rain fell (figure 2). The daily $T_{\text{soil}}$ range also diminished from an average of $4^\circ \text{C}$ prior to the rains to less than $1.5^\circ \text{C}$ during the rainy season. After the drop, the average $T_{\text{soil}}$ slowly diminished again toward its annual winter minimum. The negative correlation of $T_{\text{soil}}$ with the volumetric soil water content (SWC) and its limited variability made it an unsuitable predictor of nighttime $R_{\text{eco}}$, as reported for other tropical locations (Davidson et al. 2000, Hutyra et al. 2007); thus, SWC was preferred for NEE partitioning. The seemingly small effect of $T_{\text{soil}}$ on C fluxes was nevertheless incorporated into $R_{\text{eco}}$ modeling since a separate equation for the relation SWC–$R_{\text{eco}}$ was fitted for different
T_{soil} bins (table 2). After the rains in the dry season of 2010, SWC reached the same level of wet season rain pulses, but lower estimates for R_{eco} at the lowest T_{soil} class resulted in lower daily R_{eco} rates, since it coincided with the annual minimum T_{soil}. During this period, canopy greenness peaked at an EVI2_{md} of only 0.45, which is 30% lower than the average summer–fall maximum (0.65) (figure 3), but net C fixation rates were similar to those of the drier-than-average summer and fall of 2009, because the smaller respiratory losses at cooler T_{soil} were soon exceeded by the daily GPP.

As could be expected from the described asynchrony between these factors and the C exchange at Chamela, T_{a}, VPD, PAR and T_{soil} exhibit low (some non-significant) correlations with C flux (table 3). In contrast, SWC is able to explain 79% and 58% of R_{eco} and GPP variation, respectively; the strong correlation between soil humidity and C fluxes is expected since they were partially modeled based on SWC. Less predictably, SWC alone is also able to explain almost 40% of NEE_{md} variability.

| T_{soil} quartile | Coefficient Estimate (SE) | P-statistic | P-value | Adj. r^2 |
|------------------|---------------------------|-------------|--------|---------|
| 1                | A                         | 1.24 (0.27) | 4.60   | 0.000   | 0.35    |
|                  | B                         | 4.71 (0.69) | 6.82   | 0.000   | 0.79    |
| 2                | A                         | 3.24 (0.28) | 11.59  | 0.000   | 0.79    |
|                  | B                         | 10.14 (0.68) | 14.97 | 0.000   | 0.79    |
| 3                | A                         | 4.65 (0.35) | 13.30  | 0.000   | 0.83    |
|                  | B                         | 14.13 (0.80) | 17.67 | 0.000   | 0.79    |
| 4                | A                         | 2.24 (0.23) | 9.53   | 0.000   | 0.73    |
|                  | B                         | 7.31 (0.64) | 11.47  | 0.000   | 0.73    |

3.2. Proximal VIs as predictors of carbon fluxes

Proximal, broad-band VIs were able to capture the vegetative phenophases of the deciduous canopy at the Chamela Biological Station (figure 3). Both NDVI_{md} and EVI2_{md} rose from their dry-season minima (around 0.44 and 0.25, respectively) to their peaks (0.78 and 0.65) during quick green-up periods of 14, 11 and 14 days after the first rains in June 2008, June 2009, and July 2010, respectively. In the wet season of 2008, the fully developed, mature canopy, maintained a level of greenness close to peak values until late October. Leaves then senesced and fell, and the VIs gradually descended and reached their annual minima in April 2009. After the dry-season rains in February 2010, NDVI_{md} and EVI2_{md} increased from higher minimal values (0.51 and 0.27) since the canopy was not completely leafless, and reached lower maxima of 0.68 and 0.46, respectively. Both indices captured interannual variation in canopy development; the peak NDVI_{md} and EVI2_{md} values for the drier wet season of 2009 were lower than those in 2008 and 2010, but EVI2_{md} showed more intra-seasonal variability at the fully developed canopy stage than NDVI. At high values, EVI2_{md} also exhibited more day-to-day noise than NDVI_{md}.

Proximal EVI2_{md} and NDVI_{md} were the most important predictors of C exchange, statistically explaining, respectively, 77% and 71% of NEE_{md}, and 86% and 81% of daily GPP, but only 59% and 53% of R_{eco} variations (table 3, figure 4). Over seasonal and annual time scales, a strong influence of the photosynthetic capacity of the canopy on R_{eco} is to be expected, as root respiration depends on the allocation of photosynthates recently produced by the aerial parts of the plant (Högberg et al 2005, Janssens et al 2001). However, controls exerted on the heterotrophic component of R_{eco} may dominate over shorter periods, as discussed in section 3.1. An inspection of the high R_{eco} data points that depart from the bulk of the dispersion at EVI2_{md}<0.45 and NDVI_{md}<0.65 reveals that they correspond to periods of steep increase in VIs after the first rains, before peak photosynthetic capacity is reached. It is likely that in these conditions high R_{eco} is produced by elevated metabolic rates during the active construction of new plant tissues combined with large heterotrophic CO2 efflux driven by high SWC. Not surprising either is the low correlation of daily NEE to VIs, since NEE carries the signal of two opposing processes (GPP and R_{eco}) that summed over diurnal cycles are of almost equal magnitude (Reichstein et al 2005).

We also explored the possibility of multiplicative effects of environmental variables over the single best predictor (EVI2_{md}) of GPP; none of the direct products of EVI2_{md} with PAR, T_{soil}, or SWC improved the obtained correlation to EVI2_{md} alone (table 3).

The advantage of using EVI2 over the most widely used NDVI is illustrated in figure 4. Some saturation of EVI2_{md} at high levels of GPP was evident; variations in the photosynthetic capacity of the forest at the peak of the growing season were not matched by variations in the optical properties of the canopy. However, the relationships of the main C fluxes to EVI2_{md} were mostly linear. In contrast, NEE_{md}, R_{eco} and GPP exhibit good sensitivity to changes in NDVI_{md}<0.7, but above this value the VI is almost invariant while the dynamic range of C fluxes may span 6–8 g m^{-2} d^{-1} for GPP and R_{eco} respectively, and up to 17 µmol m^{-2} s^{-1} for NEE_{md}.

3.3. Ground-based measurements of radiation absorption

Field estimates of f_{APAR} and f_{APAR_Green} identified senescence in late 2009 and winter growth, green-up, and maturity peak phenophases in the wet season of 2010 (figure 5). However, f_{APAR_Green} dropped more significantly in the fall and winter of 2009, better mirroring the behavior of the VIs.

There were large temporal variations in the spatial repeatability of f_{APAR} and f_{APAR_Green}: the SDs of both estimates decreased five to six times from the dry to the wet season (figure 5). This points to a mismatch between the footprint of the sensors at the tower and the spectrometer on the ground, which
Figure 4. Carbon fluxes at the Chamela TDF in relation to daily averages of EVI$_{2\text{md}}$ (left) and NDVI$_{\text{md}}$ (right). Colors indicate different growing phenophases.

Table 3. Pearson’s correlation coefficients between carbon fluxes and environmental variables and their combinations. Correlation coefficients higher than 0.75 are emphasized in bold.

| Predictor         | NEE$_{\text{md}}$ | NEE$_{\text{d}}$ | R$_{\text{eco}}$ | GPP   |
|------------------|-------------------|-------------------|-----------------|-------|
|                  | r  | P-value | r  | P-value | r  | P-value | r  | P-value |
| $T_{\text{air}}$ | $-0.41$ | 0.000 | $-0.21$ | 0.000 | $0.49$ | 0.000 | $-0.47$ | 0.000 |
| VPD              | 0.05 | 0.246 | $-0.05$ | 0.238 | $-0.08$ | 0.057 | 0.02 | 0.572 |
| PAR              | 0.11 | 0.019 | $-0.10$ | 0.017 | $-0.32$ | 0.000 | 0.16 | 0.000 |
| $T_{\text{soil}}$ | 0.10 | 0.015 | 0.13 | 0.002 | $-0.06$ | 0.140 | 0.12 | 0.002 |
| SWC              | $-0.61$ | 0.000 | $-0.21$ | 0.000 | 0.89 | 0.000 | $-0.76$ | 0.000 |
| EVI$_{2\text{md}}$ | $-0.88$ | 0.000 | $-0.60$ | 0.000 | 0.77 | 0.000 | $-0.93$ | 0.000 |
| EVI$_{2\text{md}}$ | $-0.84$ | 0.000 | $-0.60$ | 0.000 | 0.73 | 0.000 | $-0.90$ | 0.000 |
| EVI$_{2\text{md}}$ | $-0.78$ | 0.000 | $-0.65$ | 0.000 | 0.57 | 0.000 | $-0.82$ | 0.000 |
| EVI$_{2\text{md}}$ | $-0.87$ | 0.000 | $-0.59$ | 0.000 | 0.76 | 0.000 | $-0.91$ | 0.000 |
| EVI$_{2\text{md}}$ | $-0.81$ | 0.000 | $-0.42$ | 0.000 | 0.88 | 0.000 | $-0.90$ | 0.000 |
is difficult to circumvent. Down-looking instruments above the canopy sense a mixture of the radiation reflected by numerous individual elements of the vegetation and the ground within their field of view. At ground level this mixture is sampled at discrete locations, so a topographical feature, a large tree, or a bare patch of soil may disproportionately influence the small area seen by the ceptometer at any given sampling point. The influence of such point-to-point variation is larger during the dry season and under thinner canopies compared to the uniform shade provided by full foliage.

Weighted regressions (figure 5, table 4) show that there is an apparent non-linearity of the EVI2ₘd–fAPAR relationship that disappears for fAPARgreen, which confirms the greater ability of fAPARgreen to capture the canopy photosynthetic capacity, without the influence of PAR absorption by non-photosynthetic tissues (Gitelson and Gamon 2015, Nestola et al 2016). Narrow-band NDVI and EVI2 exhibit an asymptotic relationship with fAPARgreen in crops, becoming insensitive to fAPARgreen changes for NDVI > 0.7 and EVI2 > 0.6, respectively (Goward and Huemmrich 1992, Viña and Gitelson 2005). The dynamic range of the broad-band VIs at Chamela fell almost entirely within the linear portion of the VI–fAPARgreen relationship, so both indices were accurate predictors of fAPARgreen (figure 5).

### 3.4. Potential of proximal VIs for GPP modeling

We found moderate correlations between the parameters of the light response curve and EVI2ₘd (figure 6). The relation to the apparent quantum yield (α) was linear, but in contrast to Wohlfahrt et al (2010), both the photosynthetic rate at the saturating PAR in (β) and daytime Rₜₚ (Rₑₑₒ₋ₜₚ) showed an asymptotic response to EVI2ₘd (table 5). Correlation coefficients (−0.74, −0.85 and 0.71 for α, β and Rₑₑₒ₋ₜₚ, respectively) are within the range found by Wohlfahrt et al (2010) for two mountain grassland sites.

From June 2009 to February 2010, absorbed radiation (APAR) derived from EVI2ₘd was able to explain less GPP variability than EVI2ₘd directly (57% and 72%, respectively), although the relation APAR–GPP was more linear (figure 7). The addition of the second best predictor (SWC) reveals a U-shaped trajectory response: starting from the right, upper, back side of the curve in figure 7, the cubical points (dark green) that depart clearly from the rest of the data correspond to the initial CO₂ released immediately after the first rains but before canopy closure. The trajectory then depicts an increase toward higher photosynthetic activity (high APAR, lower GPP) as the canopy developed rapidly (dark to medium green dots) under high SWC. Later, as soil dried and photosynthetic capacity diminished, C fixation was reduced during the senescence phase (light green to orange to pink dots).

### Table 4. Weighted linear regression coefficients and statistics for the relationship of night-time fAPAR and fAPARgreen to the average of proximal vegetation indices EVI2ₘd and NDVIₘd.

| Predictor Coefficient | Estimate (SE) | t-statistic | P-value | Adjusted r² |
|-----------------------|--------------|-------------|---------|-------------|
| fAPAR                 | EVI2ₘd slope | 1.02 (0.08) | 12.44   | 0.000       | 0.94        |
|                       | intercept    | 0.31 (0.04) | 7.39    | 0.000       |
|                       | EVI2ₘd slope | 1.31 (0.09) | 14.97   | 0.000       | 0.96        |
|                       | intercept    | −0.07 (0.06) | −1.18  | 0.27        |
|                       | NDVIₘd slope | 1.26 (0.05) | 23.84   | 0.000       | 0.98        |
|                       | intercept    | 0.07 (0.03) | 2.88    | 0.018       |
|                       | fAPARgreen NDVIₘd slope | 1.60 (0.05) | 29.52   | 0.000       | 0.99        |
|                       | intercept    | −0.38 (0.04) | −10.74 | 0.000       |

\[ \text{Table 4. Weighted linear regression coefficients and statistics for the relationship of night-time } f_{\text{APAR}} \text{ and } f_{\text{APARgreen}} \text{ to the average of proximal vegetation indices } \text{EVI2}_{\text{md}} \text{ and } \text{NDVI}_{\text{md}}. \]
Figure 6. Relation of EVI2\textsubscript{md} to the parameters of light response curve obtained by regressing NEE against PAR over 15 days windows. Colors indicate different growing phenophases.

Table 5. Regression coefficients and statistics for the relationship of EVI2\textsubscript{md} to parameters of the NEE–PAR response curve.

| Parameter                     | Best-fit equation | Coefficient | Estimate (SE) | t-statistic | P-value | Adj. \( r^2 \) |
|-------------------------------|-------------------|-------------|---------------|-------------|---------|----------------|
| Apparent quantum yield (\( \alpha \)) | \( \alpha = b_1 (\text{EVI2} \text{md}) + b_0 \) | \( b_1 \) | -0.17 (0.02) | -7.09 | 0.000 | 0.55 |
| Maximum photosynthetic rate (\( \beta \)) | \( \beta = 1 - e^{-A(\text{EVI2} \text{md})} \) | \( A \) | -5.84 (0.08) | -70.77 | 0.000 | 0.72 |
| Daytime ecosystem respiration (\( R_{\text{eco-dt}} \)) | \( R_{\text{eco-dt}} = e^{A \text{EVI2} \text{md} + B} \) | \( A \) | 6.39 (1.15) | 5.35 | 0.000 | 0.51 |
|                              | \( B \) | -2.04 (0.66) | -3.06 | 0.004 |

Table 6. Coefficients of the surface response of daily GPP to the product \( f_{\text{PARgreen}} \cdot \text{PAR} \) and SWC for the growing season of 2009.

| Equation                                                                 | Coefficient     | Estimate (SE) | t-statistic | P-value |
|--------------------------------------------------------------------------|-----------------|---------------|-------------|---------|
| GPP = \( A \left[ e^{-\frac{(x-x_c)^2}{2w_1}}\cdot e^{\frac{(y-y_c)^2}{2w_2}} \right] \) | \( A \) | -8.65 (1.20) | -7.21 | 0.000 |
|                                                                            | \( x_c \) | 11.82 (2.42) | 4.87 | 0.000 |
|                                                                            | \( w_1 \) | 6.48 (1.46) | 4.45 | 0.000 |
|                                                                            | \( \gamma_c \) | 0.19 (0.00) | 51.04 | 0.000 |
|                                                                            | \( w_2 \) | 0.09 (0.00) | 16.75 | 0.000 |
Figure 7. Left: bivariate relation of daily GPP to the product of $f_{\text{PAR}_{\text{green}}}$-PAR (derived from EVI2 md) for the growing season of 2009. Right: average SWC is added as second predictor. The gray mesh is the surface response of the equation in table 6. Cubical points indicate high $R_{\text{eco}}$ during green-up. The colors reflect the time progression of the growing season (see text).

Figure 8. Daily estimates of GPP obtained by the standard method of gap filling using look-up tables versus GPP modeling that incorporated proximal EVI2 md as predictor (left and middle) or that derived from standard light response parameterization (right). Orange cubes represent respiration-dominated days when rain pulses interrupted intra-seasonal dry spells. This trajectory was consistent among all seasons (not shown). When the relationship of GPP with APAR derived from EVI2 md is examined with the exclusion of SWC, the cubical points are not distinguishable from the rest of the points in the scatterplot; the fact that they clearly stand out when the SWC is considered, reveals that different mechanisms contribute to low uptake at the beginning of the rainy season and at the end of the senescing phase, and adds complexity to our understanding of C dynamics’ dependence on water availability.

The best-fit surface for this relation is a Gaussian model with slightly higher explanatory power (77%) than EVI2 md alone (table 6). This model, although purely statistical and therefore site-specific, produced GPP estimates that closely compared to GPP series gap-filled using look-up tables of observed fluxes (figure 8, left), while the procedures that modeled the light response curve based on EVI2 md (figure 8, middle) or directly based on PAR (figure 8, right) tended to overestimate high GPP and underestimate low GPP (figure 8, table 7). Because large data gaps remained in the record (Gonzalez del Castillo, unpublished results), we did not attempt to obtain seasonal or annual sums of C fluxes, but if the tendencies depicted in figure 8 prevailed for the whole data sets, models relying on the light response curve would likely overestimate C gained during the summer but would underestimates late-fall fixation rates.

4. Conclusions

Our study provided two important conclusions for TDFs in this region. The first conclusion is mechanistic in nature. As expected for these ecosystems—but not fully documented or linked to carbon fluxes—there is a clear controlling influence of precipitation and soil moisture on carbon release and uptake. Water availability drives both the respiratory release of
carbon from soils at the onset of the rains and the photosynthetic capacity of the canopy throughout the growing period. The response of the TDF to the atypical rains at the peak of the dry season is a clear example of this dependence. Our second conclusion is related to the role that proximal remote sensing plays as a tool to estimate carbon fluxes in a TDF environment. The integration of proximal remote sensing indices with the flux and meteorological data showed two main advantages: (1) it yielded a more complex picture of the way water availability controls carbon flux in this ecosystem, and (2) it allowed the prediction of GPP values comparable to those obtained using past relations between meteorological drivers and observed fluxes, and therefore may be used as a valuable tool in GPP gap-filling and modeling. It is fundamentally clear that, once spectral vegetation indices have been properly validated against field estimates of light absorption and conversion to biomass in a particular forest, they show good promise as aids in thorough carbon monitoring programs at the local scale.

Acknowledgments

This work was supported by the Inter-American Institute for Global Change Research, through grants CRN2 and CRN3-025 (Grant GEO-0452325), a CONACYT-UCMexus scholarship (175725) awarded to EGC. Support was also provided by the Natural Sciences and Engineering Research Council of Canada’s Discovery Grant Program. Partial support was also obtained from a National Science Foundation award EF1137306/MIT subaward 5710003122 to the University of California National Science Foundation award EF1137306/MIT. Partial support was also obtained from the Engineering Research Council of Canada and CRN3-025 (Grant GEO-0452325), a CONACyT-Mexicus scholarship (175725) awarded to EGC.

References

Anaya C A, Jaramillo V J, Martinez-Yrizar A and Garcia-Oliva F 2012 Large rainfall pulses control litter decomposition in a tropical dry forest: evidence from an 8 year study Ecosystems 15 652–63

Ashstrom A et al 2015 The dominant role of semi-arid ecosystems in the trend and variability of the land CO2 sink Science 348 895–9

Birdsey R, Angeles-Perez A, Kurz W A, Lister A, Olguin M, Pan Y, Wayson C, Wilson B and Johnson K 2014 Approaches to monitoring changes in carbon stocks for REDD+ Carbon Manage. 4 319–37

Bullock S H and Solis-Magallanes J A 1990 Phenology of canopy trees of a tropical deciduous forest in Mexico Biotropica 22 22–35

Calvo-Rodriguez S, Sanchez-Azofeifa G A and Duran S M and Santo M M 2017 Assessing ecosystem services in tropical dry forests: a systematic review Environ. Conserv. 44 54–63

Canadell J G et al 2000 Carbon metabolism of the terrestrial biosphere: a multi-technique approach for improved understanding Ecosystems 3 115–30

Carbone M S, Still C J, Ambrose A R, Dawson T E, Williams A P, Boot C M, Schaeffer S M and Schimel S P 2010 Seasonal and episodic moisture controls on plant and microbial contributions to soil respiration Oecologia 167 265–78

Davidson E A, Verchot L V, Catánini J H, Ackerman I L and Carvalho J E M 2000 Effects of soil water content on soil respiration in forests and cattle pastures of eastern Amazonia Biogeochemistry 48 53–69

Eklandt L, Hongxiao J, Schubert P, Guzinski R and Heliasz M 2011 An optical sensor network for vegetation phenology monitoring and satellite data calibration Sensors 11 7678–709

Fensholt R and Sandholt I and Rasmussen M 2004 Evaluation of MODIS LAI, fAPAR and the relation between fAPAR and NDVI in a semi-arid environment using in situ measurements Remote Sens. Environ. 91 490–507

Friedl M A, Sulla-Menashe D, Tan B, Schneider A, Ramankutty N, Sibley A and Huang X 2010 MODIS Collection 5 global land cover: algorithm refinements and characterization of new datasets Remote Sens. Environ. 114 168–82

Gamon J A 2015 Reviews and syntheses: optical sampling of the flux tower footprint Biogeosciences 12 4309–23

Garcia E 1988 Modificaciones al Sistema de Clasificación Climática de Köppen (para adaptarlo a las condiciones de la República Mexicana) 4th edn (Mexico City: UNAM)

Gitelson A A and Gamon J A 2015 The need for a common basis for defining light-use efficiency: implications for productivity estimation Remote Sens. Environ. 156 196–201

Gockede M, Rebmann C and Foken T 2004 A combination of quality assessment tools for eddy covariance measurements with footprint modelling for the characterization of complex sites Agric. Forest Meteorol. 127 173–88

Gonzalez del Castillo E, Paw U K T, Sanchez-Azofeifa G A and Quesada-Avendaño M 2018 Turbulence scales for eddy covariance quality control over a tropical dry forest in complex terrain Agric. Forest Meteorol. 249 390–406

Table 7. Linear regression coefficients and statistics for the relationship between daily GPP that was gap-filled using different procedures and daily GPP gap-filled using standard look-up tables of half-hourly PAR and SWC.

| Gap-filling procedure | Coefficient | Estimate (SE) | r-statistic | P-value | Adjusted r² |
|-----------------------|-------------|---------------|-------------|---------|-------------|
| fAPARgreen–PAR–SWC surface: fAPARgreen is EVI2_md–derived | slope intercept | 1.02 (0.05) | 21.14 | 0.000 | 0.78 |
| EVI2_md–derived light response curve coefficients | slope intercept | 0.76 (0.02) | 34.53 | 0.000 | 0.90 |
| PAR-based light response curve coefficients | slope intercept | 0.71 (0.02) | 31.54 | 0.000 | 0.87 |

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Goward S N and Huemmrich K F 1992 Vegetation canopy PAR absorptance and the normalized difference vegetation index: an assessment using the SAIL model Remote Sens. Environ. 39 119–40

Haverd V, Ahlström A, Smith B and Canadell J G et al 2017 Carbon cycle responses of semi-arid ecosystems to positive asymmetry in rainfall Glob. Change Biol. 23 793–800

Heinsch F A et al 2006 Evaluation of remote sensing based terrestrial production from MODIS using Ameriflux eddy tower flux network observations IEEE. Trans. Geosci. Remote Sens. 44 1908–23

Högberg P, Nordgren A, Högberg M N, Ottosson-Löfvenius M, Jarvis P G, McCaughey J H and Hall F G 1999 High temporal resolution NDVI phenology from micrometeorological radiation sensors J. Geophys. Res. 104 27935–44

Hutyra L R, Munger J W, Saleeza S R, Gottlieb E, Daube B C, Dunn A L, Amaral D F, de Camargo P B and Wolsky S C 2007 Seasonal controls on the exchange of carbon and water in an Amazonian rain forest J. Geophys. Res. 112 G03S08

Huxman T, Snyder K, Tissue D, Leffler A J, Ogle K, Pockman W, Sandquist D, Potts D and Schwinnning S 2004 Precipitation pulses and carbon fluxes in semiarid and arid ecosystems Oecologia 141 254–68

Janssens I A et al 2001 Productivity overshadows temperature in determining soil and ecosystem respiration across European forests Glob. Change Biol. 7 269–78

Jarvis P et al 2007 Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the ‘Birch effect’ Tree Physiol. 27 929–40

Jung M et al 2017 Compensatory water effects link yearly global land CO2 sink changes to temperature Nature 541 516–20

Kaufman J B, Steele M D, Cummings D L and Jaramillo V J 2003 Biomass dynamics associated with deforestation, fire, and conversion to cattle pasture in a Mexican tropical dry forest Forest Ecol. Manage. 176 1–12

Martinez-Yrezar A, Maas J M, Pérez-Jiménez J A and Sarukhán J 1996 Net primary productivity of a tropical deciduous forest ecosystem in western Mexico J. Trop. Ecol. 12 169–75

Miles L, Newton A C, DeFries R S, Ravilious C, May J, Blyth S, Kapso V and Gordon J E 2006 A global overview of the conservation status of tropical dry forests J. Biogeog. 33 491–505

Monterith J L 1972 Solar-radiation and productivity in tropical ecosystems J. Appl. Ecol. 9 747–66

Nestola E, Callapierta C, Emmerton C A, Wong C Y S, Thayer D R and Gamon J A 2016 Monitoring grassland seasonal carbon dynamics, by integrating MODIS NDVI, proximal optical sampling, and eddy covariance measurements Remote Sens. 8 260

Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) 2013 FLUXNET Maps and Graphics (http://fluxnet.ornl.gov/maps-graphics) (Accessed: 21 May 2016)

Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) 2013b FLUXNET WebGIS (http://webgis.ornl.gov/webgis/fluxnet) (Accessed: 21 May 2016)

Portillo C and Sanchez-Azofeifa G A 2010 Extent and conservation of tropical dry forests in the Americas Biol. Conserv. 143 144–53

Portillo C, Sanchez-Azofeifa G A, Calvo-Alvarado J C, Quesada M and Espiritu Santo M M 2015 The role of tropical dry forests for biodiversity, carbon and water conservation in the neotropics: lessons learned and opportunities for sustainable management Reg. Environ. Change 15 1039–49

Poulter B et al 2014 Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle Nature 509 660–4

Reichstein M et al 2005 On the separation of net ecosystem exchange into assimilation and ecosystem respiration: review and improved algorithm Glob. Change Biol. 11 1424–39

Running S W, Nemani R R, Heinsch F A, Zhao M, Reeves M and Hashimoto H 2004 A continuous satellite-derived measure of global terrestrial primary production BioScience 54 574–60

Sanchez-Azofeifa A, Guzmán J A, Campos C A, Castro S, Garcia-Millan V, Nightingale J and Rankine C 2017 Twenty-first century remote sensing technologies are revolutionizing the study of tropical forests Biotropica 49 604–19

Schmid H P 1994 Source areas for scalars and scalar fluxes Bound.-Layer Meteorol. 67 293–318

Soudani K et al 2012 Ground-based network of NDVI measurements for tracking temporal dynamics of canopy structure and vegetation phenology in different biomes Remote Sens. Environ. 123 234–45

Tang J and Baldocchi D D 2005 Spatial–temporal variation in soil respiration in an oak–grass savanna ecosystem in California and its partitioning into autotrophic and heterotrophic components Biogeochemistry 73 183–207

Tietzebrand A, Spank U and Berhofer C H 2009 Comparison of satellite- and ground-based NDVI above different land-use types Theor. Appl. Climatol. 98 171–86

Unger S, Máguez C, Perera J S, David T S and Werner C 2010 The influence of precipitation pulses on soil respiration: assessing the ‘Birch effect’ by stable carbon isotopes Soil Biol. Biochem. 42 1800–10

Urbaezav M, Thiel C, Migliavacca M, Reichstein M, Rodríguez-veiga P and Schmullius C 2016 Improved multi-sensor satellite-based aboveground biomass estimation by selecting temporally stable forest inventory plots using NDVI time series Forests 7 169

Verduzco V S, Garatuz-Payán J, Yépez E A, Watts C J, Rodríguez J C, Robles-Moria A and Vivoni E R 2015 Variations of net ecosystem production due to seasonal precipitation differences in a tropical dry forest of northwest Mexico J. Geophys. Res. Biogeosci. 120 2081–94

Viña A and Gitelson A A 2005 New developments in the remote estimation of the fraction of absorbed photosynthetically active radiation in crops Geophys. Res. Lett. 32 L17403

Wang X et al 2014 A two-fold increase of carbon cycle sensitivity to tropical temperature variations Nature 506 212–5

Waring B G and Powers J S 2016 Unraveling the mechanisms underlying pulse dynamics of soil respiration in tropical dry forests Environ. Res. Lett. 11 105005

Wilson T B and Meyers T P 2007 Determining vegetation indices from solar and photosynthetically active radiation fluxes Agric. Forest Meteorol. 144 160–79

Wolffhaut G, Pillon S, Hörttaui L and Hammel A 2010 Estimating carbon dioxide fluxes from temperate mountain grasslands using broadband vegetation indices Biogeosciences 7 683–94

Xu L, Baldocchi D D and Tang J 2004 How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature Glob. Biogeochem. Cycles 18 GB4002

Yuan W et al 2007 Deriving a light use efficiency model from eddy covariance flux data for predicting daily gross primary production across biomes Agric. Forest Meteorol. 143 189–207