



Determining the K coefficient to leaf area index estimations in a tropical dry forest

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Received: 15 August 2017 / Revised: 23 February 2018 / Accepted: 27 February 2018
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Abstract

Vegetation indices are useful tools to remotely estimate several important parameters related to ecosystem functioning. However, improving and validating estimations for a wide range of vegetation types are necessary. In this study, we provide a methodology for the estimation of the leaf area index (LAI) in a tropical dry forest (TDF) using the light diffusion through the canopy as a function of the successional stage. For this purpose, we estimated the K coefficient, a parameter that relates the normalized difference vegetation index (NDVI) to LAI, based on photosynthetically active radiation (PAR) and solar radiation. The study was conducted in the Mata Seca State Park, in southeastern Brazil, from 2012 to 2013. We defined four successional stages (very early, early, intermediate, and late) and established one optical phenology tower at one plot of 20×20 m per stage. Towers measured the incoming and reflected solar radiation and PAR for NDVI calculation. For each plot, we established 24 points for LAI sampling through hemispherical photographs. Because leaf cover is highly seasonal in TDFs, we determined ΔK (leaf growth phase) and K_{\max} (leaf maturity phase). We detected a strong correlation between NDVI and LAI, which is necessary for a reliable determination of the K coefficient. Both NDVI and LAI varied significantly between successional stages, indicating sensitivity to structural changes in forest regeneration. Furthermore, the K values differed between successional stages and correlated significantly with other environmental variables such as air temperature and humidity, fraction of absorbed PAR, and soil moisture. Thus, we established a model based on spectral properties of the vegetation coupled with biophysical characteristics in a TDF that makes possible to estimate LAI from NDVI values. The application of the K coefficient can improve remote estimations of forest primary productivity and gases and energy exchanges between vegetation and atmosphere. This model can be applied to distinguish different successional stages of TDFs, supporting environmental monitoring and conservation policies towards this biome.

Keywords Spectral vegetation indices · Leaf area · Remote monitoring · Tropical dry forest · Secondary succession · Phenology

Introduction

The energy, water, and carbon exchange between the vegetation and the atmosphere can be influenced by the amount of

forest biomass, which is indirectly measured by several parameters, such as plant canopy height, tree basal area, litterfall, and leaf area (Campbell and Norman 1998; Asner et al. 2003; Wilson and Meyers 2007). Determining the contribution of vegetation to matter exchange flows in the atmosphere depends on monitoring phenological processes such as leaf production, growth, and senescence (Campbell and Norman 1998; Wilson and Meyers 2007). Spectral vegetation indices (VIs) are useful tools to monitor these phenophases (Asner et al. 1998; Pettorelli et al. 2005). VIs are obtained through combinations of different types of measurements of leaf radiation reflectance (Campbell and Norman 1998; Kalácska et al. 2004a), which are sensitive to joint effects of leaf and forest traits, including chlorophyll concentration, leaf area, leaf clumping, and plant canopy architecture (Turner et al. 1999).

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The normalized difference vegetation index (NDVI) (Wilson and Meyers 2007) has been widely used in studies on vegetation monitoring, due to its strong correlation with plant biomass (Carlson and Ripley 1997; Turner et al. 1999). The NDVI is determined by the difference between the amount of reflected near-infrared (NIR) and red (VIS) regions of the electromagnetic spectrum normalized by its sum. It comprises the range of photosynthetically active radiation (PAR), with the NIR being strongly reflected or transmitted and the VIS strongly absorbed by the plant canopy (Carlson and Ripley 1997; Campbell and Norman 1998). NDVI values range between -1 and 1 , and values closer to 1 indicate a higher NIR reflectance and higher VIS absorption (Kalácska et al. 2004a), which are generally associated with a larger amount of biomass in almost every vegetation type worldwide (Campbell and Norman 1998; Turner et al. 1999; Pontauiller et al. 2003; Kalácska et al. 2004a; Wilson and Meyers 2007; Goswami et al. 2015).

Despite having a good relationship with the biomass amount, VIs such as NDVI do not provide quantitative information about biological or environmental factors contributing to the PAR absorption, such as leaf area and chlorophyll content (Jacquemoud et al. 1992; Asner et al. 1998; Campbell and Norman 1998). However, VIs have shown a good correlation with the leaf area index (LAI), defined as half the total leaf surface area per unit of horizontal surface (Asner et al. 2003; Yang 2006). LAI can be used to indirectly estimate forest productivity and has been widely used in ecological monitoring and environmental conservation studies (Carlson and Ripley 1997). Leaf area is one of the main regulators of microclimatic conditions below the plant canopy, controlling water interception, carbon exchange, and solar radiation absorption and transmission (Bonan 1995; Bréda 2003; Fournier et al. 2003; Van Wijk and Williams 2005; Clark et al. 2008). Since vegetation is dominated by leaves, where most chlorophyll is stored (Fournier et al. 2003), we can then consider that LAI is a useful and well-established tool for estimating forest photosynthetic rates (Asner et al. 2003; Gonsamo 2009). Thus, LAI temporal and spatial changes in the tree canopy, either by natural or by anthropogenic effects, result in changes in forest primary productivity (Bréda 2003) and, consequently, in ecosystem functioning.

The LAI can be obtained by indirect measurements through optical devices (i.e., LAI-2000, plant canopy analyzer, LICOR®) or by estimating the amount of leaves on the canopy based on pixel analyses (White et al. 2000; Asner et al. 2003; Fournier et al. 2003). Although it is a very useful tool for environmental monitoring, reliable LAI data requires training and several incursions into the field (Carlson and Ripley 1997; Manninen et al. 2005). However, the strong correlation between LAI and VIs is an incentive to create models based on spectral indices characterizing biomass vegetation (Wilson and Meyers 2007). In this context, Wilson and Meyers

(2007) proposed an equation to estimate LAI using NDVI data, based on PAR and solar radiation measured by flux towers, using a coefficient termed as K . Thus, since NDVI and LAI data are obtained, it is possible to obtain K values to further apply in the equation established by Wilson and Meyers (2007) and estimate LAI automatically. As of today, this method has only been implemented in desert grasslands, temperate grasslands, crops, temperate deciduous forests, evergreen, and pine forests of North America (Pontauiller et al. 2003; Wilson and Meyers 2007). At present, estimates of the K coefficient do not exist for tropical dry forests (TDFs) in Brazil or any tropical forest in South America. Besides, most studies only utilized a single dataset to establish LAI-NDVI relationships and have not taken the seasonal dynamics into account.

Once these models are successfully established and tested, the monitoring of endangered forests such as TDFs (Sánchez-Azofeifa et al. 2005) would be automated, with lower costs and higher efficiency. The highest deforestation rates of TDFs were recorded for South America between 1980 and 2000 (Miles et al. 2006). Throughout the tropics, land use and further abandonment turned this forest type into vegetation mosaics in different stages of natural regeneration (Arroyo-Mora et al. 2005). As the structure and function (i.e., productivity, water balance, nutrient cycling) of these secondary TDFs vary with forest age, it is likely that successional stages can be remotely differentiated via satellite imagery (Gallardo-Cruz et al. 2012). Therefore, improving remote sensing techniques focused on TDF natural regeneration can provide useful information to policy-makers and support the development of policies for environmental monitoring, management, and sustainable use in this ecosystem (Quesada et al. 2009; Hesketh and Sánchez-Azofeifa 2014; Espírito-Santo et al. 2014). The present study aimed to determine the K coefficient for different successional stages in a Brazilian TDF using field measurements of LAI and VIs. We intend to answer the following question: is the K coefficient an effective tool to identify leaf development (as indicated by LAI) and different successional stages?

Materials and methods

Study area

This study was conducted in the Mata Seca State Park (MSSP) in Brazil (Fig. 1). The MSSP is located in the valley of the São Francisco River ($14^{\circ} 50'$, $44^{\circ} 00' W$), in the municipality of Manga, Minas Gerais State, Brazil. It has a semi-arid tropical climate (Aw) according to Köppen's classification (modified by Peel et al. (2007)), characterized by a well-defined dry season. The average temperature in this region is $24^{\circ} C$, with average annual precipitation of 871 mm (Antunes 1994). The

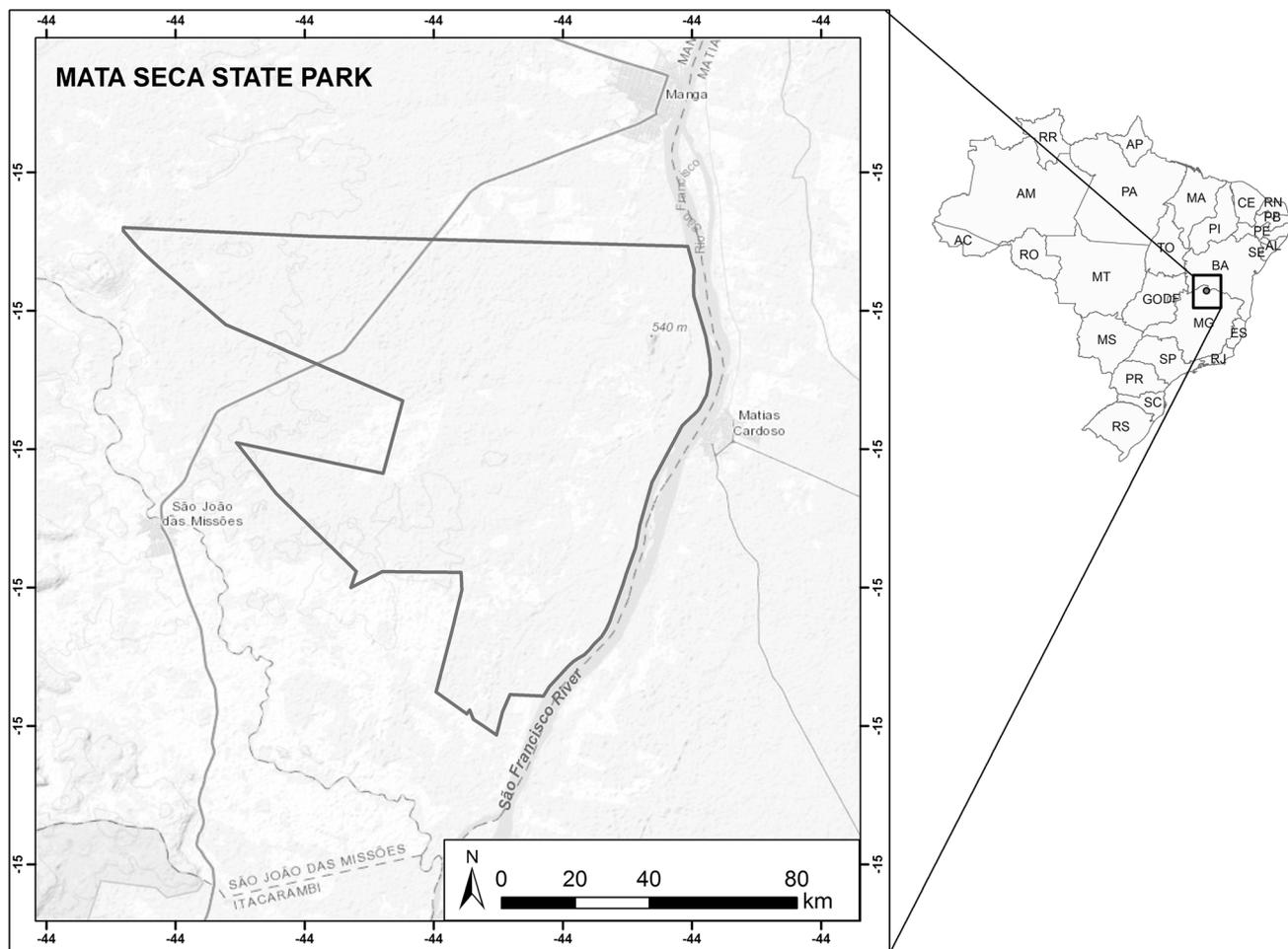


Fig. 1 Location of the Mata Seca State Park, in northern Minas Gerais, Brazil

MSSP is mainly covered by deciduous vegetation (Sánchez-Azofeifa et al. 2005), with approximately 90–95% leaf loss during the dry season (May–October) (Pezzini et al. 2008, 2014). Due to the land use before the creation of the park (i.e., agriculture and pasture), these TDFs constitute a mosaic of different successional stages. Based on time since abandonment and vertical (tree height and number of strata) and horizontal (tree density and basal area) forest structures (Madeira et al. 2009; Kalácska et al. 2004b), we categorized different forest areas as very early, early, intermediate, and late stages of secondary succession (Table 1). The data obtained in the present study demonstrated that canopy openness is different among all the four stages ($p < 0.05$; except between the very early and late stages), corroborating our separation based in forest structure.

Sampling design

Optical phenology towers

At each successional stage, one optical phenology tower (Pastorello et al. 2011) with a set of radiation sensors was

assembled between 2007 and 2013. Two pyranometers (Onset®- LIA and LIB) (PYR, measuring the solar radiation flux density) and two photosynthetically active radiation (PAR) (Onset®- LIA and LIB) sensors (measuring the radiation between 400 and 700 nm) were installed per tower. Tower extension depended on the canopy height, in such a way that sensors were always positioned at 5 m above the canopy. Each group of four sensors had a pair of PYR-PAR sensors facing up and down to measure the incoming and reflected radiation, respectively. Synchronized above-canopy radiometric observations were sampled every 30 s, averaged, and logged at 15-min intervals (Rankine et al. 2017). The field-of-view of the sensors was approximately 100 m in radius (Rankine et al. 2017). We only considered the measurements obtained between 10 and 14 h in our analyses, to avoid the inference of bidirectional reflectance distribution function (BRDF) that occurs when the solar zenith angle is less than 30° (Disney et al. 2004). With these radiation measures (near-infrared— R_{nr} and visible— R_{vis}), we calculated the NDVI according to the following equation (Campbell and Norman 1998):

$$\text{NDVI} = (R_{\text{nr}} - R_{\text{vis}}) / (R_{\text{nr}} + R_{\text{vis}}) \quad (1)$$

Table 1 Characterization of the vegetation structure and land use history for the four successional stages studied in the Mata Seca State Park, southeastern Brazil

Stages	Forest structure	Land use history
Very early	Presence of patches of sparse vegetation, canopy reaching 5 m in height, and an understory consisting of an herbaceous-shrub stratum. Canopy openness: 14%.	Used as pasture for about 20 years and abandoned in 2000, but occasionally used by free-ranging cattle until 2006.
Early	Presence of patches of sparse vegetation, canopy reaching 7 m in height, and an understory consisting of an herbaceous-shrub stratum. Canopy openness: 26%.	Used as pasture for about 20 years and abandoned in 1990. Forest regeneration occurred mainly through tree resprouting.
Intermediate	Presence of two vegetation layers: a canopy stratum averaging 8 m in height with some emergent trees over 15 m, and a dense tree-shrub layer consisting of young trees and abundant lianas. Canopy openness: 20%.	Used for pasture before 1970, but is under regeneration since then, with low-intensity, occasional selective logging and use by free-ranging cattle until 2006.
Late	Presence of two well-defined strata: a tree stratum with a closed canopy reaching 10–12 m, with some emergent trees over 18 m and a sparse shrub layer with a low density of saplings and lianas. Canopy openness: 16%.	No records of clear-cutting, but with a low-intensity, occasional selective logging and presence of sparse free-ranging cattle until 2006.

Each tower was also equipped with a meteorological station (HOBO Microstation) measuring air temperature and humidity (Onset S-THB-M00x). Below the canopy, an array of sensors was used to measure transmitted PAR (Apogee SQ-110) and soil moisture (Decagon ECH2O EC-5 at 20-cm depth) in the forest understory (Pastorello et al. 2011). The fraction of absorbed PAR (fPAR) was calculated from the incident PAR, reflected PAR from the canopy, and transmitted PAR from the forest understory (Jenkins et al. 2007).

Obtaining the LAI

We delimited a plot of 20 m × 20 m surrounding the optical phenology tower established in each successional stage, totaling four plots (with the tower in the center of these quadrats). For each plot, we established 24 points for LAI sampling within the field-of-view limit (10-m radius) of the PAR and PYR sensors. LAI was obtained through hemispherical photographs taken from November 2012 to June 2013 in the very early-, early-, intermediate-, and late-stage plots. We considered three phases of leaf development: (i) leaf growth, which lasts from leaf bud production, leaf unfolding, and blade expansion until reaching its full size; (ii) leaf maturity, during which the leaf blade maintains a constant size and the predominant green color; and (iii) leaf senescence, when nutrient resorption from leaves starts, causing changes in leaf color and size (Lim et al. 2007) until leaf fall.

We took hemispherical photographs on a daily basis to obtain plant area index (PAI) throughout the phase of leaf growth, from November 12th to 25th. After this period, leaves were fully developed and expanded, and the leaf maturity phase lasted from December to March, when we conducted six samplings of hemispherical photographs at approximately 20-day intervals. With the onset of the dry season, leaf senescence started and lasted from April to June. During this phase, we conducted monthly PAI measurements, until complete leaf

abscission was observed. Finally, we calculated the specific LAI by removing the contribution of wood area index (WAI) (see below) from PAI values (Kalácska et al. 2005a).

We also obtained hemispherical photographs when trees were leafless, to calculate the WAI in all four successional stages. WAI values were obtained at the peak of the dry season in September 2012. Photographs were taken using a camera (Pentax-SR) with a 180° lens (fish-eye) directed to the sky at the height of 1.30 m above the ground, under conditions of diffuse light during sunrise or sunset, or on cloudy days to prevent the direct incidence of sunlight on the hemispherical lens. These photographs produced circular images that recorded the size, shape, and location of gaps in the forest canopy. Such images were converted to bitmaps and analyzed using the Hemispherical Photo Analyzer software (Opie 2010). Image processing involves transforming positions of image pixels in angular coordinates, dividing the intensity of the pixels into classes representing the sky and the vegetation, and the computation of the distribution of the brightness of the sky (Opie 2010). With the same photographs, we used the Gap Light Analyzer software to estimate canopy openness (Frazer et al. 1999).

Calculation of the coefficient K

After obtaining the NDVI and the LAI, all indices were applied to the following equation (Wilson and Meyers 2007):

$$\text{LAI} = -K * \log(b) \quad (2)$$

where b is given by $(\text{NDVI}_{\max} - \text{NDVI}_i) / (\text{NDVI}_{\max} - \text{NDVI}_{\min})$ according to Campbell and Norman (1998); NDVI_{\max} corresponds to the average of NDVI values when the vegetation is dense, NDVI_{\min} is the average of NDVI minimum values when there is little or no contribution of leaves to the absorption or reflectance of the radiation, and

$NDVI_t$ is the mean of all changes in NDVI values during the rainy season. The LAI is determined by the average of LAI values for all sampling points in a given plot. The value of the K coefficient was then determined per plot for each sampling date by rearranging the Eq. (2):

$$K = -\frac{LAI}{\log(b)} \quad (3)$$

During the leaf growth phase, the K coefficient values varied with the increase in leaf area. We calculated such variation (ΔK) as the slope of the straight-line equation obtained from a linear regression analysis, with the K value as a function of time (in days) of the growth phase. We also calculated the average maximum value of the K coefficient (K_{max}), using the measurements taken during the leaf maturity phase, at the peak of the rainy season, when the K values showed less variation.

Statistical analyses

We performed regression analyses to assess the strength of the correlation between the LAI and NDVI. These analyses were performed as a prerequisite to calculate the K coefficient. If there were no significant correlations between the LAI and NDVI, the determination of the K coefficient from LAI values would not be valid. To compare LAI and PAI among successional stages and phenophases, we constructed linear mixed effect models (LME). Measurements were repeatedly taken through time at the same sampling points, which violates the assumption of sampling independence. To overcome this problem, the LAI and PAI data were grouped by sampling point, and the error variances were calculated for each different group. In this case, the response is not the individual measure, but the sequence of measures at a given point (Crawley 2002). The successional stages and phenophases were used as independent variables (fixed effects), whereas the resulting groups per point were treated as random effects. After the construction of LMEs, we performed an analysis of variance (ANOVA), followed by contrast analysis, to test the difference between LAI and PAI among successional stages and phenophases. An ANOVA with repeated measurements was used to compare the variation of the K coefficient among the four successional stages over the study period. Data were log-transformed when the ANOVA assumptions of normality and homoscedasticity were not satisfied. We used Pearson correlations between the K coefficient at each stage and the daily average of the following environmental variables: air temperature, air humidity, soil moisture, and fPAR. These data were obtained from the meteorological stations situated at each tower and at the forest understory. The significance of the correlations was tested with an alpha of 0.05. We conducted all analyses in the software R 2.11

(R Development Core Team 2010). All values are given as mean \pm standard error.

Results

Temporal and successional variations in vegetation indices

The mean values of the spectral indices varied according to the seasonality and the successional stages (Table 2). Almost all the indices considered here showed the highest values in the early and intermediate stages, except for the $NDVI_t$ (i.e., mean change during the rainy season), which was higher in the late stage (Table 2). The PAI and LAI showed large variations over the study period for all successional stages (Fig. 2a, b). In general, both indices indicated synchronous patterns of leaf production, growth, and senescence. As a whole, both PAI and LAI differed between the phenophases considered here ($p < 0.01$) (Table 3). The lowest values of both indices were observed for the leaf growth phase and the highest values for the leaf maturity phase in all stages (Fig. 2a, b). PAI and LAI also differed between successional stages along the phenophases. During the leaf growth phase, the intermediate stage showed the highest PAI, but in the leaf maturity phase, the greatest PAI was observed for the early stage, followed by the late stage. Finally, leaf senescence was slower in the intermediate stage, whereas the other stages exhibited a sharp drop in PAI values during this phase (Fig. 2a). For LAI values, the pattern of temporal variation among stages was different from the observed for PAI, with the early stage showing the highest values during the leaf growth phase, a trend also observed in the leaf maturity phase. On the other hand, during leaf senescence, the same successional pattern observed for PAI values was recorded for LAI: the intermediate stage exhibited slower leaf fall, whereas the other stages showed an abrupt decline in LAI (Fig. 2b).

Determination of the K coefficient

The NDVI showed a significant relationship with LAI ($R^2 = 0.81$) (Fig. 3) in all successional stages, indicating that the determination of the K coefficient from LAI and NDVI values is statistically reliable. The temporal variation of the K coefficient showed the same trend in all successional stages, increasing during the leaf growth phase and stabilizing in the leaf maturity phase (Fig. 4). K values differed among successional stages over the study period ($p < 0.001$). Both the K_{max} (obtained during the leaf maturity phase) and ΔK (that reflects the leaf growth phenophase) were higher at the early stage and lower at the late stage in the studied TDF (Table 2).

The temporal variations in the K coefficient were significantly correlated with all environmental variables tested in this

Table 2 The stage-based maximum (NDVI_{max}), minimum (NDVI_{min}), and seasonal changes (NDVI) on NDVI used to determine the *K* value during two leaf phenophases: leaf maturity (*K*_{max}) and leaf growth (ΔK)

Stage	NDVI _{min}	NDVI _{max}	NDVI _i	<i>K</i> _{max}	ΔK
Very early	0.541	0.796	0.696	3.09	0.183
Early	0.574	0.881	0.744	5.87	0.329
Intermediate	0.553	0.846	0.715	3.72	0.235
Late	0.533	0.846	0.778	2.76	0.135

study, except for the air temperature in the intermediate stage (Table 4). The significant correlation coefficients were always

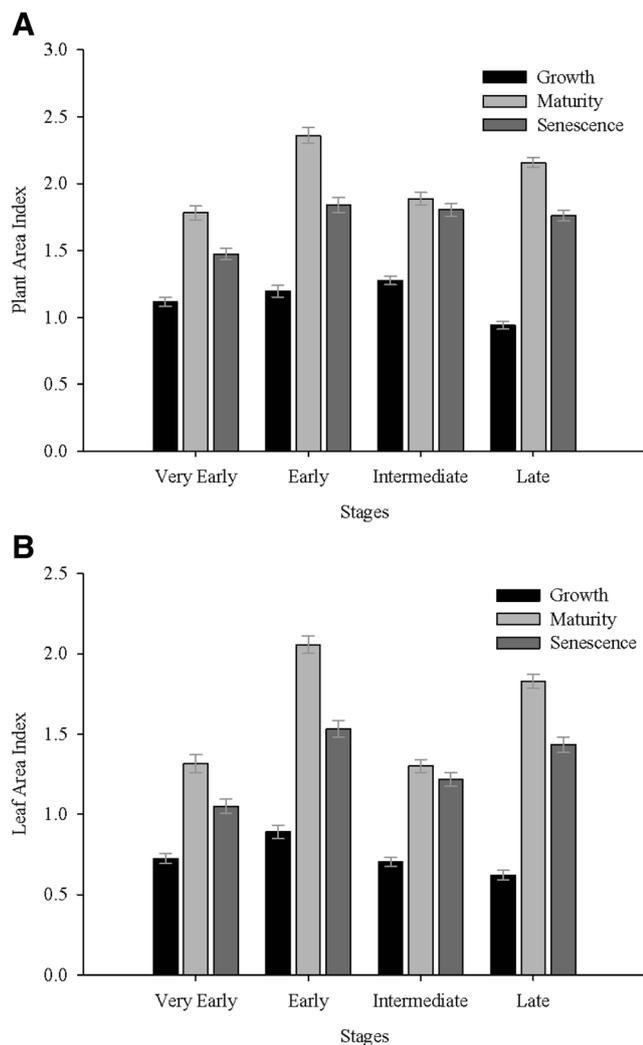


Fig. 2 Plant (a) and leaf (b) area indices in the very early, early, intermediate, and late successional stages along leaf phenophases. Different letters above the bars indicate statistically significant differences in PAI and LAI among phenological phases within each stage. Different numbers indicate statistical differences in PAI and LAI among successional stages. *N* = 216 for the leaf growth phase (24 points \times 9 days of LAI and PAI measurements for each stage), 120 for the leaf maturity phase (24 points \times 5 days of measurements), and 96 for the leaf senescence phase (24 points \times 4 days of measurements). All values are given as mean \pm standard error

Table 3 Summary statistics for the linear mixed effects models constructed to test the differences in LAI and PAI among four successional stages (very early, early, intermediate, and late) and three phenophases in a Brazilian tropical dry forest

Response variable	Explanatory variable	DF	<i>F</i> -value	<i>p</i> value
LAI	Stage	3	6.482	< 0.0001
	Phenophase	2	756.172	< 0.0001
	Stage: phenophase	6	29.479	< 0.0001
PAI	Stage	3	3.365	< 0.05
	Phenophase	2	808.607	< 0.0001
	Stage: phenophase	6	26.1736	< 0.0001

negative for air temperature and positive for air humidity, soil moisture, and fPAR. The strength of the correlations between *K* and the environmental variables varied across stages, being higher for the late stage, followed by the very early, early, and intermediate stages. The *K* coefficient showed a stronger correlation with the fPAR and with air humidity in the very early, early, and late stages (Table 4).

Discussion

Temporal and successional variations in vegetation indices

TDFs are highly seasonal ecosystems, with a short rainy season (4–6 months) when leaves are produced and lost very quickly (Lopezaraiza-Mikel et al. 2014). Such sharp variations were expressed in the NDVI obtained in the present study, which is strongly driven by changes in leaf number and size during the rainy season but may also reflect differences in pigment concentration along plant vegetative phenophases. Such physiological alterations are visible in distinct shades of green of the leaves, resulting in a change in reflectance values (Hesketh and Sánchez-Azofeifa 2014). Besides the sensitivity to forest phenology, it is also important to highlight the sensitivity of VIs to the forest structural changes along the successional gradient.

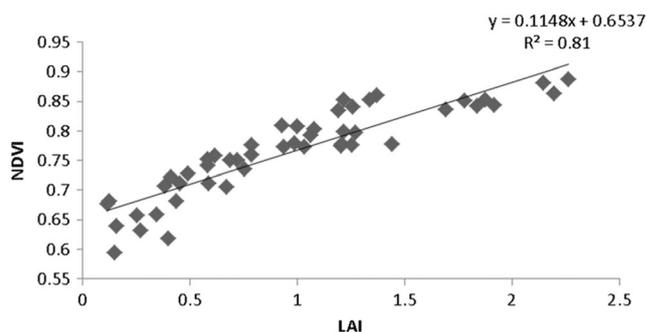


Fig. 3 Relationship between NDVI and LAI (considering all successional stages together) during the leaf growth and leaf maturity phases in a tropical dry forest

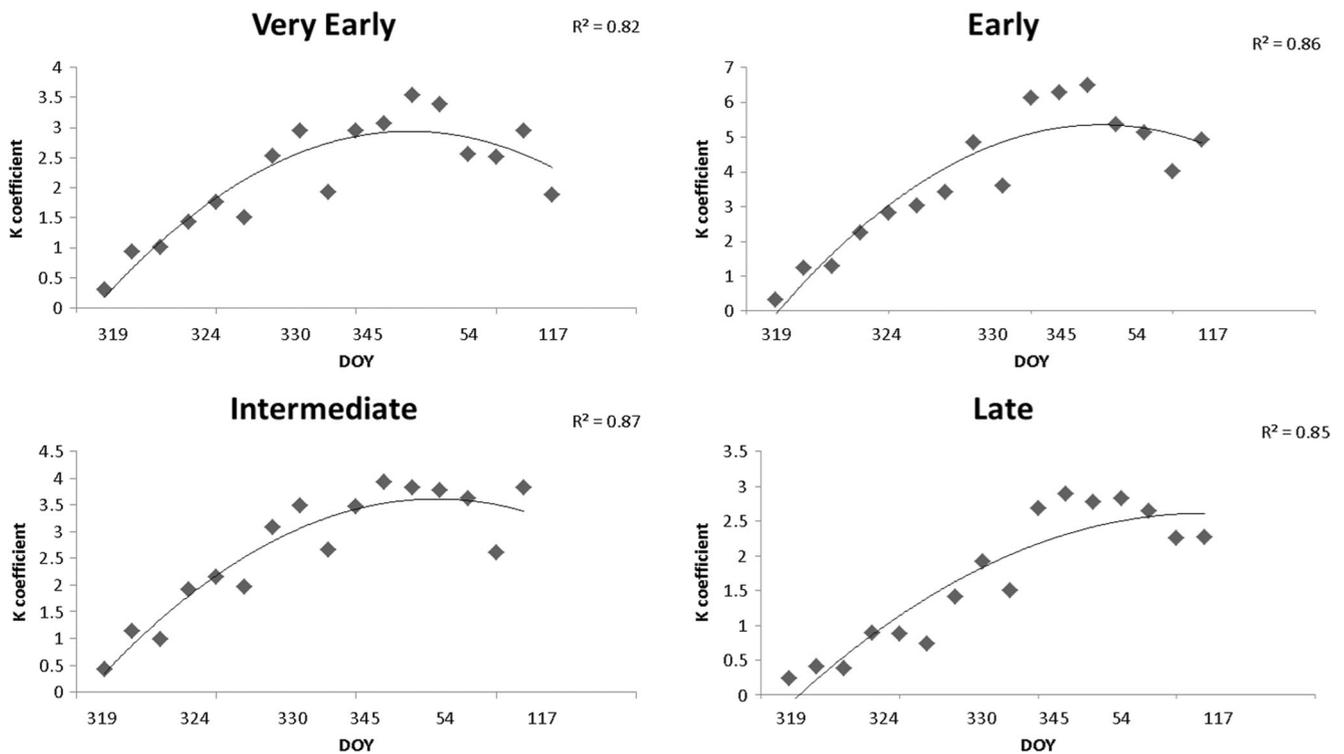


Fig. 4 *K* coefficient variation during the leaf growth and leaf maturity phases at four successional stages in a tropical dry forest. *DOY* day of the year

As the structure and function of these secondary TDFs vary with forest age (Gallardo-Cruz et al. 2012), VIs sensitivity to structural changes indicates their usefulness to distinguish stages of natural regeneration. Regarding NDVI, this study adds to other studies that have shown satisfactory results with the application of NDVI for the differentiation of successional stages in secondary forests (Arroyo-Mora et al. 2005; Gallardo-Cruz et al. 2012).

Although the maximum values of NDVI were higher in the early stage, the overall variation showed higher values during the rainy season in the late stage. This variation suggests an overestimation of the spectral indices in the early stage, associated to the fact that the higher canopy openness at this stage increases soil exposure, affecting the type of radiation that is reflected (Kalácska et al. 2005b). The early-stage forest grows on red oxisols, with the upper surface horizon characterized by a dark red-gray coloration (Vasques et al. 2016). Darker

soils also absorb radiation in the visible range, reducing the amount of radiation that is sent to the sensors. As NDVI is based on the difference between R_{nir} and R_{vis} , the reduction in reflectance values results in increased values of both spectral indices (Campbell and Norman 1998).

The differences in PAI and LAI in the phases of leaf development also reflect the strong seasonality of the studied TDF. Furthermore, the observed differences in the values of PAI and LAI among stages are probably caused by contrasts in vertical canopy structure, indicating that, along with NDVI, these indices are also useful to discriminate TDF successional stages (Kalácska et al. 2005b). The highest average of PAI in the intermediate stage during the growth phase can be attributed to the greater contribution of the wood area index (WAI) in this stage (Sánchez-Azofeifa et al. 2009). At the MSSP, the intermediate stage is characterized by the abundant presence of lianas (Sánchez-Azofeifa et al. 2009), increasing the wood

Table 4 Summary statistics for the Pearson correlation tests to determine the effects of environmental conditions on the *K* coefficient at each successional stage. Pearson's correlation coefficient is denoted by *r*

Variable	Successional stage							
	Very early		Early		Intermediate		Late	
	<i>r</i>	<i>p</i> value	<i>r</i>	<i>p</i> value	<i>r</i>	<i>p</i> value	<i>r</i>	<i>p</i> value
Soil moisture	0.752	< 0.05	0.669	< 0.05	0.565	< 0.05	0.802	< 0.05
fPAR	0.811	< 0.05	0.786	< 0.05	0.757	< 0.05	0.876	< 0.05
Air temperature	-0.501	< 0.05	-0.525	< 0.05	-0.404	0.121	-0.718	< 0.05
Air humidity	0.749	< 0.05	0.680	< 0.05	0.632	< 0.05	0.817	< 0.05

volume of the forest compared to other stages. However, LAI did not differ between the intermediate and the very early stage, indicating that the leaf contribution of lianas is not expressive. The late stage showed the lowest values of PAI and LAI along the leaf growth phase, probably due to a slight lack of synchrony in leaf flushing between its two well-defined vertical strata, with canopy greening occurring after the understory greening.

Differences observed in LAI values among successional stages were expected due to dissimilarity in species composition, richness and dominance, canopy structure, land use history, seasonality, soil moisture, and microclimate (Kalácska et al. 2005a; Sánchez-Azofeifa et al. 2009). In general, average values of LAI for the leaf maturity phase during the peak of the rainy season were very close to values reported for other TDFs in the rainy season. For instance, Kalácska et al. (2005a) reported values of 2.8 in the early stage, 4.6 in the intermediate stage, and 2.5 in the late stage for plots at the Santa Rosa National Park in Costa Rica. Huang et al. (2014) reported values between 1.26 and 2.17 for the early-stage plots, between 1.21 and 3.64 for the intermediate, and from 1.14 to 3.88 for the late successional stage plots in the TDF of Chamela-Cuixmala Biosphere Reserve in Mexico.

In the leaf maturity phase, the PAI and LAI increased with succession (very early < intermediate < late), except for the early stage. Contrary to the expected, the early stage had the highest PAI and LAI, although structural variables in the MSSP have been shown to increase along the successional gradient (Madeira et al. 2009; Espírito-Santo et al. 2014). This may be associated with a possible LAI overestimation due to the height where hemispherical photographs were obtained (1.30 m), which is very close to the understory in the early stage.

In the senescence phenophase, values of PAI and LAI showed a sharp decrease for all but the intermediate stage. Kalácska et al. (2005a) also observed a similar pattern in the leaf fall at the intermediate stage compared to other successional stages in the Santa Rosa National Park in Costa Rica. Leaf lifespan is a result of plant responses to light, nutrient, and water availability, among other biotic and abiotic factors (Reich et al. 1992). The intermediate-stage forest is located on a relatively poorer soil, where nutrient levels, base saturation, and cation exchange capacity are significantly lower (Espírito-Santo et al. 2014). Thus, it is possible that the cost of leaf production is higher at this stage, resulting in slower leaf abscission and more efficient use of nutrients. On the other hand, clay content in the soil is higher in the plots at the intermediate stage, and this parameter is directly related to soil water holding capacity (Manrique et al. 1991). Indeed, a previous study in the same plots indicated that litterfall deposition is lower in the intermediate stage and negatively correlated with clay content (Souza 2014). Therefore, it is likely that the longer leaf

retention observed for the plants in the intermediate stage is related to its higher soil water holding capacity.

Determination of the *K* coefficient

The strong correlation between NDVI and LAI demonstrates that it is possible to obtain continuous LAI measurements derived from towers deployed in different successional stages. The value of R^2 found here is similar to that found by Kalácska and co-workers (2004a) in the Santa Rosa National Park in Costa Rica. VIs such as NDVI are sensitive to different ranges of LAI and can saturate asymptotically in vegetation types with LAI above 5.0 (Kalácska et al. 2004a). In the MSSP, the greatest value of LAI was below 3.0. Thus, the NDVI is considered adequate to detect variations in LAI for this ecosystem. Therefore, the *K* coefficient determined in this study, based on NDVI and LAI, is likely a reliable way to monitor the production of biomass in different successional stages in TDFs, although further validation is necessary.

Because the study areas are highly seasonal TDFs, the growth phase is short and extremely variable, followed by apparent stability in the leaf maturity phase. We considered that it would be unrealistic to define a single *K* coefficient to estimate the LAI for the whole phase of leaf development throughout the rainy season. Values of *K* were variable throughout the year, and in the rainy season, they tended to be higher (Table 2). This explains the high positive correlation between the *K* coefficient and the fPAR since a higher amount of light is intercepted and absorbed by the canopy when leaves start growing and reach the leaf maturity phase. A positive correlation between the *K* coefficient and soil moisture and humidity was also expected, since both these variables increase in the rainy season, and on the contrary, temperature slightly decreases in the rainy season.

K coefficients derived from LAI and NDVI and with values greater than 1 have been reported in the literature: Wilson and Meyers (2007) found *K* values of 4.3 in a temperate deciduous forest and of 1.0 to 1.8 in temperate grasslands. Calvo-Rodriguez and Sanchez-Azofeifa (2016) found *K* values of 3.01 in early-stage plots and of 4.93 in intermediate-stage plots in a TDF at the Santa Rosa National Park in Costa Rica. Both these studies used optical phenology towers and followed an approach similar to our study. The *K* coefficient also varied along the successional gradient (see Table 3), indicating its usefulness for monitoring studies in secondary forests. Thus, our study is innovative not only for defining the *K* coefficient for different successional stages in a TDF but also for indicating that, in seasonal ecosystems, the *K* coefficient should be defined by ΔK and K_{\max} to obtain more reliable values of LAI for each one of the different phenological phases. Also, such procedure can reduce serious deviations in the LAI estimation in TDFs and, thereby, in estimates of carbon balances and primary productivity. However,

because we obtained a significant correlation between the K coefficient and climatic variables in our study, it is necessary to deeply explore the effects of environmental conditions (e.g., soil water moisture, air humidity, and temperature) on this parameter in TDFs. Such an approach would allow LAI estimations to be used in future-expected climatic scenarios that can alter patterns of vegetative growth and phenology (Allen et al. 2017). Changes in climatic conditions also cause canopy stress, leading to multiyear differences in the phenophases (Rankine et al. 2017). The sensitivity of LAI and the K coefficient to significant changes in the environmental conditions such as droughts or ENSO effects needs to be further investigated.

Conclusions

Our study pioneers in the attempt to determine a K coefficient that estimates LAI in different successional stages of a TDF accurately and efficiently. The daily, real-time monitoring performed by in situ meteorological sensors provides consistent NDVI data from which we can now obtain more reliable measures of LAI. The potential use of the K coefficient is enormous, representing an advance in the estimation of forest ecosystem services such as primary productivity and fluxes of energy, water, and carbon, in addition to complementing and validating satellite data. Once the K coefficient is validated, it could be used to obtain accurate and automated LAI. The calculation of this variable enables the remote differentiation of successional stages and consists in an important approach for the management and conservation of the Brazilian TDFs. Taking into account that Brazilian laws restrict the clearing of TDFs at advanced stages of regeneration (Espírito-Santo et al. 2014), we can provide to policy-makers a new tool to improve the effective enforcement of environmental laws.

Acknowledgements The authors thank L. A. D. Falcão and R. Reis Jr. for their assistance in statistical analyses. We gratefully acknowledge the staff of the Instituto Estadual de Florestas (IEF-MG) for allowing us to stay and work at Mata Seca State Park (MSSP). S. F. Magalhães and MM Espírito-Santo greatly acknowledge a research scholarship from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and CNPq, respectively. We thank the National Science and Engineering Research Council of Canada (NSERC) for the financial support through its Discovery grant program. This study was in partial fulfillment of requirements for the Master degree at the Universidade Estadual de Montes Claros.

Funding information This work was carried out with the aid of a grant from Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq -563304/2010-3 and 562955/2010-0), Fundação de Amparo à Pesquisa de Minas Gerais - FAPEMIG, and the Inter-American Institute for Global Change Research (IAI - CRN 2021 and CRN 3025).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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