Spatiotemporal partitioning of savanna plant functional type productivity along NATT

Xuanlong Ma\textsuperscript{a,b,*}, Alfredo Huete\textsuperscript{a}, Caitlin E. Moore\textsuperscript{c}, James Cleverly\textsuperscript{a}, Lindsay B. Hutley\textsuperscript{d}, Jason Beringer\textsuperscript{e}, Song Leng\textsuperscript{a}, Zunyi Xie\textsuperscript{f}, Qiang Yu\textsuperscript{b,g}, Derek Eamus\textsuperscript{a}

\textsuperscript{a} School of Life Sciences, University of Technology Sydney, Ultimo, NSW, Australia
\textsuperscript{b} College of Earth and Environmental Sciences, Lanzhou University, Lanzhou, Gansu, China
\textsuperscript{c} Genomic Ecology of Global Change, Carl R. Woese Institute for Genomic Biology, University of Illinois, Urbana, IL, USA
\textsuperscript{d} Research Institute for the Environment and Livelihoods, Charles Darwin University, Casuarina, NT, Australia
\textsuperscript{e} School of Agriculture and Environment, University of Western Australia, Crawley, WA, Australia
\textsuperscript{f} Centre for Biodiversity and Conservation Science, School of Earth and Environmental Sciences, The University of Queensland, Brisbane, QLD, Australia
\textsuperscript{g} State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A\&F University, Yangling, Shanxi, China

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ABSTRACT

Realistic representations and simulation of mass and energy exchanges across heterogeneous landscapes can be a challenge in land surface and dynamic vegetation models. For mixed life-form biomes such as savannas, plant function is very difficult to parameterise due to the distinct physiological characteristics of tree and grass plant functional types (PFTs) that vary dramatically across space and time. The partitioning of their fractional contributions to ecosystem gross primary production (GPP) remains to be achieved at regional scale using remote sensing. The objective of this study was to partition savanna gross primary production (GPP) into tree and grass functional components based on their distinctive phenological characteristics. Comparison of the remote sensing partitioned GPP\textsubscript{tree} and GPP\textsubscript{grass} against field measurements from eddy covariance (EC) towers showed an overall good agreement in terms of both GPP seasonality and magnitude. We found total GPP, as well as its tree and grass components, decreased dramatically with rainfall over the North Australian Tropical Transect (NATT), from the \textit{Eucalyptus} forest and woodland in the northern humid coast to the grasslands, \textit{Acacia} woodlands and shrublands in the southern xeric interior. Spatially, GPP\textsubscript{tree} showed a steeper decrease with precipitation along the NATT compared to GPP\textsubscript{grass}, thus tree/grass GPP ratios also decreased from the northern mesic region to the arid south region of the NATT. However, results also showed a second trend at the southern part of the transect, where tree-grass ratios and total GPP increased with decreasing mean annual precipitation, and this occurred in the physiognomic transition from hummock grasslands to \textit{Acacia} woodland savannas. Total GPP and tree-grass GPP ratios across climate extremes were found to be primarily driven by grass layer response to rainfall dynamics. The grass-containing xeric savannas exhibited a higher hydroclimatic sensitivity, whereas GPP in the northern mesic savannas was fairly stable across years despite large variations in rainfall amount. The pronounced spatiotemporal variations in savanna vegetation productivity encountered along the NATT study area suggests that the savanna biome is particularly sensitive and vulnerable to predicted future climate change and hydroclimatic variability.

1. Introduction

Tropical savannas dominate the wet-dry tropics and are defined by mixtures of co-existing trees, shrubs, and grasses (Walker and Gillison, 1982a, 1982b). Over a broad rainfall gradient, savanna structure can vary from grass dominant to woody dominant (Hill and Hanan, 2013; Hutley and Setterfield, 2008). The tree-shrub-grass layers of savannas consist of multiple plant functional types and their relative fractions vary greatly in space and time (Scholes and Archer, 1997), making savannas a highly complex biome type with high structural heterogeneity (Asner et al., 1998; Jeltsch and Milton, 1996).

Savannas cover one-fifth of the global land area (Hutley and Setterfield, 2008) and contribute approximately 30% of all terrestrial ecosystem gross primary productivity (Grace et al., 2006). In South
America, the Brazilian cerrado and the Colombian and Venezuelan llanos have a rich and diverse flora, with ground layer dominated by perennial herbs and woody layer dominated by trees and shrubs which can remain alive at relative short heights for many years (Ratter et al., 1997). In Africa, savannas cover 50% of the continent, encompassing diverse ecosystems with a wide range of woody cover, from densely wooded Miombo woodlands to Serengeti grasslands with scattered trees (Osborne et al., 2018). In Australia, savannas occur across the northern third of the continent and feature woody overstorey strata dominated by evergreen Eucalyptus and Corymbia tree species and an understorey dominated by annual and perennial C4 grasses (Egan and Williams, 1996; Hutley et al., 2011). In Asia, the savanna is fairly extensive in the Indian subcontinent and also widely distributed in Southeast Asia. The dry dipterocarp forest occurs in Southeast Asia and is dominated by the deciduous Dipterocarpus species over a dense grass and herb layer (Hutley and Setterfield, 2008). Tree-grass mixtures can also be found in temperate regions such as in North America, Mediterranean Europe, and Russia.

To achieve a more realistic representation of savanna ecosystem functioning and predict their responses to disturbances and future climate change, it is of particular importance to partition key ecosystem processes, including carbon, water, and energy fluxes into their plant functional types of C3 tree and C4 grass sources to further investigate the distinct response of savannas to environmental factors. Although such partitioning is very important, to date it remains to be achieved at regional scales using remote sensing observations or at local scales using Eddy-Covariance (EC) flux towers measurements (Moore et al., 2016, 2018).

Remote sensing-based studies on savanna vegetation structure and function primarily utilise the information from three perspectives: the electromagnetic spectrum, 3-D geometry, and phenological profiles. Spectral mixture analysis has been applied to distinguish trees, grasses and bare soil using hyperspectral images acquired from airborne or space-borne sensors (Bateson et al., 2000; Asser et al., 2003; Chen and Vierling, 2006; Meyer and Okin, 2015). High spatial resolution aerial photograph has also been used to derive the changes in woody cover across time (Hudak and Wessman, 1999; Fensham et al., 2003). Aside from differences in spectral and geometric perspectives, there is also valuable information embedded in the phenological profiles as depicted by continuous satellite observations.

In comparison to savannas in other global regions, Australian savannas are largely ecologically intact with relatively low levels of fragmentation (Beringer et al., 2011), which can be considered as a “living laboratory” (Hutley et al., 2011) to investigate the environmental determinants on their structure and functioning. The woody layer of Australian savannas is predominantly evergreen C4 tree species (Eucalyptus, Corymbia and Acacia) (Walker et al., 1999) with lengthy root systems that facilitate access to soil content in the deep soil layers (Eamus et al., 2000). This functional trait means trees gain access to water year round, even in dry or drought periods (O’Grady et al., 2009; Eamus et al., 2013). Continued tree functioning is facilitated by this access to water, along with a lack of a dormant period, no freezing temperatures below 5°C in northern tropical zones, and no periods of apparent leaflessness (Williams et al., 1997; Eamus et al., 2013). In contrast, annual and perennial species (primarily C4 photosynthetic pathway) make up the understory grass and forb layers and these grasses typically have shallow roots and hence highly responsive to seasonal rainfall patterns (Hutley et al., 2001; Whitley et al., 2011; Eamus et al., 2013).

Such unique phenological characteristics have driven the need for sub-pixel tree/grass partitions using continuous satellite observations. For example, Roderick et al. (1999) estimated the foliage projective cover (FPC) of evergreen woody layer over Australia from AVHRR-NDVI time series. By incorporation of climatology data, Berry and Roderick (2002) and Beringer et al. (2016) decomposed the satellite signal into three leaf types, namely “turgor”, “mesic”, and “sclerophyll”. Lu et al. (2003) further developed a model for decomposition of the satellite derived FPC into woody and herbaceous components. Most recently, a study showed an increasing trend in evergreen trees decomposed from AVHRR-NDVI time series across continental Australia over the past several decades (Donohue et al., 2009).

Previous tree-grass decomposition studies have primarily focused on the structural (e.g., LAI and FPC) (Roderick et al., 1999), or intermediate functional variables (e.g., fractional absorbed photosynthetic active radiation, or fAPAR) (Donohue et al., 2009). These variables are useful in quantifying the varying structure and functioning of the savanna biome as well as for studying climate-related changes in savanna composition of trees and grasses (Donohue et al., 2009; Gill et al., 2009; Donohue et al., 2013). The direct partitioning of several key ecosystem processes, such as Gross Primary Production (GPP) or evapotranspiration (ET), however, has not been accomplished yet with remote sensing. This study was aimed to obtain the direct partition of savanna GPP into components of C3 trees and C4 grasses, the two contrasting plant functional types.

Over recent decades, several EC flux towers have been established across north Australian savannas. With more than 25 site-years of data available from 2010 to 2018, there is an opportunity to directly partition carbon fluxes in savannas into PFTs of C3 trees and C4 grasses across space and time by coupling of satellite remote sensing and landscape flux measurements. The objectives of this study were to: (1) functionally partition savanna GPP into components of trees and grasses; (2) assess spatial variations in savanna GPP per plant functional type across northern Australian mesic to xeric savannas; and (3) investigate the responses of savanna ecosystems to rainfall variations across seasons and between years, with particular emphasis on the examination of different sensitivities of tree and grass components to decadal scale hydroclimatic variability including wet and drought extremes.

2. Data and method

2.1. The NATT study area

The North Australian Tropical Transect (NATT) study area is a 1100 km distance sub-continental scale rainfall gradient (Koch et al., 1995) (Fig. 1). The vegetation varies from Eucalyptus and Corymbia savannas in the northern humid areas (above 700 mm annual precipitation) to hummock grasslands and Acacia savannas to the south arid areas (Walker et al., 1999; Hutley et al., 2011). More detailed description of the vegetation, climate, and soil of the NATT study area can be found in Ma et al. (2013) and Hutley et al. (2011).

2.2. Eddy covariance data

We used in-situ measurements of carbon flux from six EC flux towers sites in the study area (Fig. 1) (Beringer et al., 2016). The site details and the technical procedures applied for partitioning original net ecosystem exchange (NEE) time series into GPP and ecosystem respiration can be found in Ma et al. (2014). To match MODIS observations, daily GPP values were aggregated to 16-days.

2.3. MODIS reflectance data and vegetation indices data

We used approximately 13.5 years (Jul 2002 – June 2018) of 16-day 250 m MODIS Vegetation Index product (MYD13Q1, Collection 6, tiles h30v10 and h30v11) (Huete et al., 2002) and 16-day 0.05° resolution Vegetation Index (VI) product (MYD13C1, Collection 6) (obtained from https://lpdaac.usgs.gov/data_access). For site-level analyses we used 500 m resolution product and for regional analyses we used the 0.05° resolution product (MCD13C1). We used the Quality Assurance (QA) fields from the MYD13Q1 and MCD13C1 products to filter out the cloud
and aerosol contaminated observations. The EVI (Enhanced Vegetation Index) is defined as (Huete et al., 2002):

\[
\text{EVI} = 2.5 \frac{\rho_{\text{nir}} - \rho_{\text{red}}}{\rho_{\text{nir}} + 6\rho_{\text{red}} - 7.5\rho_{\text{blue}} + 1}
\]

(1)

where \(\rho_{\text{nir}}, \rho_{\text{red}}\) and \(\rho_{\text{blue}}\) are reflectances are the MODIS 841–876 nm (NIR), 620–670 nm (Red), and 459–479 nm (Blue) bands respectively.

2.4. Gridded rainfall data

We obtained the Australian monthly precipitation data at 0.05° spatial resolution from the TERN AusCover Data Facility (http://www.auscover.org.au). These data were produced by National Climate Centre of Australia (http://www.bom.gov.au/climate/) through interpolation from spatially distributed ground stations (Jones et al., 2009).

2.5. Tree-grass partition model

A time series-based method was used to partition the EVI (greenness) time series into components of C3 trees and C4 grasses based on their distinctive phenological characteristics. Fig. 2 is a graphical flowchart showing the overview of the entire workflow described below. The primary assumption of the partitioning is that the temporal variation of the C3 evergreen trees should follow the dry season baseline of the EVI time series with most of the seasonal variations are contributed from C4 grasses. The tree-grass partition model we used was first proposed by Lu et al. (2003) for decomposing AVHRR NDVI time series and was updated in this study for partitioning of MODIS EVI time series. A refinement to the original model in this study was to update the tree seasonality parameter, which was calibrated from a very low value considering the relatively stable structure of evergreen tree species, to a much higher value that better reflected the pronounced seasonality of the tree layer as indicated by our in-situ measurements. This update ensured our model partitioned results more realistically represented savanna tree and grass GPP seasonal dynamics.

First, assuming the contributions from trees, \(\text{EVI}_{\text{tree}}(t)\), and grasses, \(\text{EVI}_{\text{grass}}(t)\), to time series of EVI are (Lu et al., 2003):

\[
\text{EVI}(t) = \text{EVI}_{\text{tree}}(t) + \text{EVI}_{\text{grass}}(t)
\]

(2)

The \(\text{EVI}_{\text{tree}}(t)\) and \(\text{EVI}_{\text{grass}}(t)\) in Eq. 2 can be expressed as following equations by considering the weak annual phenological magnitude of evergreen tree canopy and strong annual phenological magnitude of ephemeral grass understorey (Lu et al., 2003):

\[
\text{EVI}_{\text{tree}}(t) = [1 + 2S(t)]\text{EVI}_{\text{tree}}(t) \\
\text{EVI}_{\text{grass}}(t) = S(t)\text{EVI}_{\text{grass}}(t)
\]

(3)

where \(\text{EVI}_{\text{tree}}(t)\) is the baseline of the \(\text{EVI}_{\text{tree}}(t)\); \(\text{EVI}_{\text{grass}}(t)\) is the time-varying peak value of the grass component \(\text{EVI}_{\text{grass}}(t)\); \(S(t)\) is the dimensionless shape factor that describes the annual phenological cycle \((0 \leq S(t) \leq 1)\); \(\lambda\) defines the magnitude of the annual phenological cycle.
cycle for EVI$_{tree}$(t), as induced by the enhanced growth during the rainy season, relative the baseline value during the dry season (Lu et al., 2003). The model parameter $\lambda$ was determined as 0.6 to best capture the GPP$_{tree}$ seasonality from flux tower measurements at Howard Springs in the NATT area (Moore et al., 2016).

Fig. 3 depicts the concept of adjusting the slowing varying EVI$_{treeB}$(t) and EVI$_{grassA}$(t) to EVI$_{tree}$(t) and EVI$_{grass}$(t) using the phenological cycle shape factor $S(t)$. For the tree-grass decomposition approach we implemented here, we intended to decompose the whole time series instead of only obtaining a single ratio between tree and grass at any given time (e.g., during the peak season). Our methodology relies on the assumption that the tree layer should follow the time-varying baseline of the original time series (EVI$_{treeB}$(t)), and the grass layer should follow the time-varying peak value of the original time series (EVI$_{grassA}$(t)) (Fig. 3). EVI$_{grassA}$(t) can be further computed by adjusting EVI$_{grassA}$(t) with the dimensionless shape factor $S(t)$ describing the annual phenology cycle ($0 \leq S(t) \leq 1$) and EVI$_{tree}$ can be computed by adjusting EVI$_{treeB}$ with the product of $S(t)$ and the tree seasonality multiplier $\lambda$, following the Eq. 3.

Then, the EVI$_{treeB}$(t) and EVI$_{grassA}$(t) were computed as (Lu et al., 2003)

$$\text{EVI}_{treeB} = \text{EVI}_T - s\text{EVI}_A$$
$$\text{EVI}_{grassA} = (1 + \lambda s)\text{EVI}_A - \lambda\text{EVI}_T$$

(4)

where EVI$_T$ corresponds to the long term trend of the EVI(t), EVI$_A$ is the annual amplitude of the EVI(t), and $s$ is the mean of the $S(t)$ (Lu et al., 2003).

We applied Singular Spectrum Analysis (SSA) to decompose the EVI(t) into trend (EVI$_T$) and cyclic (EVI$_C$) signals (Alexandrov et al., 2012). Following Ma et al. (2013), we used the window length of 37 composite periods ($37 \times 16 / 365 \approx 1.6$ years) that was found to best capture the periodicity of the savanna vegetation dynamics over the NATT study area. With the window length set as 37, there were 37 components generated by the singular vector decomposition (SVD). The 1st leading SVD component was used to reconstruct the long-term trend EVI$_T$, while the additive of the 2nd to the 14th components was used to reconstruct the cyclic signal EVI$_C$. The number of 14 was decided based on a 99% variance explained thresholding approach using data from six flux tower sites located along the NATT. The remaining components from SVD (15th to 37th) were considered as noises and hence were not used in the analyses. We implemented SSA using the R package Rssa - A collection of methods for singular spectrum analysis (Golyandina et al., 2015). Combining the Eq. 3 and Eq. 4, the equation for calculating
EVI_{tree}(t) and EVI_{grass}(t) (Lu et al., 2003) is obtained:

\[
EVI_{\text{tree}} = (1 + \lambda S(t))[(EVI_{t} - sEVIA - EVI_{\text{soil}})]
\]
\[
EVI_{\text{grass}} = S(t)[(1 + \lambda s)EVIA - \lambda EVI_{t} + \lambda S(t)EVIS]
\]

The EVI_{soil} in Eq. (5) is the soil background contribution to EVI, which is estimated as 0.08 using MODIS EVI and EC-tower GPP measurements (Ma et al., 2014). It should be noted that the value we assigned for EVI_{soil} was an approximation and hence an assumption was made to use this value to represent all soil types in this region. A sensitivity analysis of the model partitioned results to the change in EVI_{soil} was performed and the results are included in the Appendix A.

Then, to obtain the time-varying peak-to-trough amplitude EVIA that was used in Eq. (4)–(5), a three-passes digital filter was applied to the cyclic component of the original EVI time series (Lu et al., 2003):

\[
EVIA = EVIC_{(\text{max})}(t) - EVIC_{(\text{min})}(t)
\]
\[
EVIC_{(\text{min})}(t) = \min \left[ EVIC(t), \frac{p}{2-p}EVIC_{(\text{min})}(t - \Delta t) + \frac{1-p}{2-p}EVIC(t) \right]
\]
\[
EVIC_{(\text{max})}(t) = \max \left[ EVIC(t), \frac{p}{2-p}EVIC_{(\text{max})}(t - \Delta t) + \frac{1-p}{2-p}EVIC(t) \right]
\]

where \(\Delta t\) is the temporal resolution of EVI time series (16-days), and \(p\) is the parameter of the digital filter which was assigned as 0.99 following Lu et al. (2003). EVIC is the cyclic component of the original EVI time series. EVIC was obtained by decomposing the original EVI time series using the SSA (Singular Spectrum Analysis), with the additive of the 2nd and the 14th components corresponding to EVIC. EVIC_{(max)} and EVIC_{(min)} are the time-varying peak and trough values of EVIC. The digital filter in Eq. 6 was applied in three passes, with the first and the third passes in ascending time order, while the second in descending time order, replacing \(t + \Delta t\) with \(t - \Delta t\) (Lu et al., 2003).

Finally, it is possible to define the shape factor \(S(t)\) of annual vegetation growth cycle as (Lu et al., 2003):

\[
S(t) = \frac{EVIC(t) - EVIC_{(\text{min})}(t)}{EVIC_{(\text{max})}(t) - EVIC_{(\text{min})}(t)}
\]

the definition of EVIC, EVIA, EVIC and \(S(t)\) and its mean, \(s\), are as same as before.

2.6. Functional interpretation of the decomposed tree and grass EVI components

An ecosystem light-use-efficiency (eLUE) model has been proposed in a previous study to simplify the upscaling of savanna GPP from tower sites to regional scale using MODIS EVI (Ma et al., 2014). The eLUE model integrates the effects of variations in canopy photosynthetic capacity (fAPAR) and efficiency (LUE), thus simplifying the up-scaling of savanna GPP from tower to regional scale (Ma et al., 2014). In recognizing the highly complex multi-layer structure of savannas, in this study we further advanced the eLUE concept from modelling the ecosystem-level total GPP to modelling the individual plant functional type GPP. The eLUE model is formulated as (Ma et al., 2014):

\[
eLUE = \frac{\text{GPP}}{\text{PAR}} = f(EVI)
\]

where eLUE (g C MJ\(^{-1}\)) was computed by using GPP and PAR (photosynthetic active radiation); \(f(EVI)\) was estimated by a linear regression model of EVI in relation to eLUE. As EVI has been decomposed to tree and grass components, Eq. (8) can be rewritten to:

\[
\text{GPP} = f(EVI) \times \text{PAR} = f(EVI_{\text{tree}} + EVI_{\text{grass}}) \times \text{PAR}
\]

We can then approximate GPP components of tree and grass as following:

\[
\text{GPP}_{\text{tree}} = f(EVI_{\text{tree}}) \times \text{PAR}
\]
\[
\text{GPP}_{\text{grass}} = f(EVI_{\text{grass}}) \times \text{PAR}
\]

where GPP_{tree} and GPP_{grass} are the contributions from tree and grass to the total GPP respectively.

We defined eLUE from top-of-atmosphere PAR (PAR_{TOA}) instead of PAR measured by flux tower at the top-of-canopy since a previous study showed that eLUE defined and computed from PAR_{TOA} provided better performances in modelling GPP (Ma et al., 2014). PAR_{TOA} can be approximated using top-of-atmosphere solar radiation (R_{TOA}, MJ m\(^{-2}\) d\(^{-1}\)) as PAR_{TOA} = 0.4 * R_{TOA} (Monteith & Unsworth, 2013).

To calibrate and validate the linear regression model for predicting eLUE using EVI, we performed a stratified leave-one-site-out cross-validation, running 6 times with each time the data from 5 sites used as calibration subset and the data from the other site used as validation subset. In total 713 samples from six flux tower sites were used in the cross-validation. The cross-validation is implemented in R using the package caret - Classification and Regression Training (Kuhn, 2020). The model performance was evaluated using validation dataset based
on the statistical measures $R^2$ CV and RMSE CV, with subscript CV denoting cross-validation. Fig. 4 presents the cross-validation results for predicting eLUE using MODIS EVI and also for predicting GPP using EVI-based eLUE model. The model performs well in predicting flux tower derived eLUE using MODIS EVI, with cross-validation $R^2$ to be 0.7 and RMSE to be 0.06 g C MJ$^{-1}$. These results suggested that MODIS EVI can be used as a robust measure of eLUE for upscaling flux tower derived GPP from point to regional scale.

The model for predicting eLUE using EVI was estimated as:

$$\text{eLUE} = 1.23 \times (\text{EVI} - \text{d})$$  \hspace{1cm} (11)

where $\text{d}$ (0.08) is soil background EVI and it was estimated through inversion of the linear regression model $\text{GPP}_{\text{EC}} \sim \text{EVI}$ (Ma et al., 2014).

Finally, the eLUE model was constructed for estimating GPP using EVI and PAR$_{\text{TOA}}$:

$$\text{GPP} = [1.23 \times (\text{EVI} - \text{d})] \times \text{PAR}_{\text{TOA}}$$  \hspace{1cm} (12)

Overall, eLUE model demonstrated good performance in simulating GPP$_{\text{EC}}$ across six NATT sites (Fig. 4B), with cross-validation $R^2$ to be 0.78 and RMSE to be 0.82 g C m$^{-2}$ d$^{-1}$. In addition, data from all six sites that located along the NATT transect fall onto the 1:1 symmetric line without major deviation at either the northern humid savannas (Howard Springs) or the southern dry savannas (Ti Tree) (Fig. 4B).

We continued our analysis by translating model decomposed tree and grass EVI as eLUE and further converted to GPP of tree and grass component. The equations for computation of GPP$_{\text{tree}}$ and GPP$_{\text{grass}}$ are

$$\text{GPP}_{\text{tree}} = [1.23 \times \text{EVI}_{\text{tree}}] \times \text{PAR}_{\text{TOA}}$$

$$\text{GPP}_{\text{grass}} = [1.23 \times \text{EVI}_{\text{grass}}] \times \text{PAR}_{\text{TOA}}$$  \hspace{1cm} (13)

Note that in Eq. 13, we did not further subtract soil background ($\text{d}$) from EVI$_{\text{tree}}$ and EVI$_{\text{grass}}$ as contribution from soil to EVI has been explicitly subtracted during the tree-grass decomposition process (see Eq. 5 in Section 2.5). Eq. 13 will be used to translate EVI$_{\text{tree}}$ and EVI$_{\text{grass}}$ to GPP$_{\text{tree}}$ and GPP$_{\text{grass}}$ for the following analyses of variations in savanna GPP per plant functional type over the NATT study area.

Notice that we used partitioned EVI to estimate eLUE for both C$_3$ trees and C$_4$ grasses despite the difference in plant physiology and vegetation structure between the two layers. This can be justified by the single linear relationship we obtained between flux tower eLUE and MODIS EVI across multiple sites along the 1100 km rainfall gradient with varying mixtures of C$_3$ and C$_4$ species (Fig. 4A). The convergence to a single eLUE~EVI relationship implies that at canopy level EVI scales linearly with eLUE (IPAR x LUE) regardless of being dominated by C$_3$ or C$_4$ species. This can be explained by the fact that eLUE integrates IPAR and LUE, and hence its variation is not only driven by plant physiology (LUE) but also canopy structure (IPAR). At very short time scales (e.g., sub-daily), the variation in eLUE can be mainly attributed to the variation in LUE. However, at longer time scale that we are looking at in this study (weekly to monthly), the role of IPAR increases and EVI has been proven to be a reliable measure of chlorophyll fraction of IPAR (Xiao et al. 2004; Restrepo-Coupe et al., 2016; Zhang et al., 2018). As such, we conclude that the model partitioned EVI$_{\text{tree}}$ and EVI$_{\text{grass}}$ can be used to estimate eLUE$_{\text{tree}}$ and eLUE$_{\text{grass}}$ and further used to model GPP$_{\text{tree}}$ and GPP$_{\text{grass}}$.

To quantify the proportion between C$_3$ trees and C$_4$ grasses in terms of GPP, and facilitate the comparison across space and time, we propose the Tree-Grass Index (TGI) that can be computed as,

$$\text{TGI} = \frac{\text{GPP}_{\text{tree}} - \text{GPP}_{\text{grass}}}{\text{GPP}_{\text{tree}} + \text{GPP}_{\text{grass}}}$$  \hspace{1cm} (14)

where GPP$_{\text{tree}}$ and GPP$_{\text{grass}}$ are the ecosystem GPP contributed from C$_3$ trees and C$_4$ grasses respectively. The lower and upper limits of TGI are $-1$ and $+1$, corresponding to the conditions that GPP are 100% contributed from C$_4$ grasses (TGI $= -1$) or 100% from C$_3$ trees (TGI $= 1$) or equally from each layer (TGI $= 0$). TGI is functionally, but not linearly, related to the simple ratio between GPP$_{\text{tree}}$ and GPP$_{\text{grass}}$ but has an advantage of being mathematically finite ($-1$ to $+1$).

Fig. 5 shows the decomposed and modelled tree and grass GPP time series alongside with TGI at Howard Springs from July 2000 to June 2018.
contributed to strong seasonality ecosystem-level total GPP had strong seasonality driven by dry to wet season rainfall difference (Fig. 5). During the dry season, ecosystem GPP is dominated by C3 tree layer, as reflected also by the high TGI (Fig. 5). The contribution of C4 grasses to ecosystem GPP increased during the wet season, but still less than the contribution from C3 tree layer except during most of the years (except 2014–15) (Fig. 5).

2.7. Verification of the satellite decomposed result using in-situ measurements

To evaluate the performance of tree and grass GPP decomposition model, we compared satellite decomposed result with tree and grass GPP measured from in-situ flux towers at Howard Springs, a site located at northern part of the NATT (Moore et al. 2016, 2018). Two flux towers next to each other were installed at Howard Springs in 2001 and 2012 respectively, while the first flux tower measures the carbon fluxes for the whole ecosystem and the second flux tower measures the carbon fluxes for the understory layer (Beringer et al., 2016; Eamus et al., 2001). Using these two towers, it is possible to partition ecosystem carbon fluxes into contributions from overstory and understory layers (Moore et al. 2016). Here we used the partitioned daily GPP data for understory grass and overstory trees from Howard Springs extended from September 2012 to May 2019. The daily data was then aggregated to 16-day to match the temporal resolution of MODIS data.

Fig. 6 presents comparisons between satellite decomposed GPPtree and GPPgrass with field measurements of GPPtree and GPPgrass at Howard Springs. Overall, seasonal variations in GPPtree and GPPgrass agreed well between decomposed and measured data (Fig. 6A-B). Seasonal patterns of GPPtree and GPPgrass in field measurements were largely captured by the satellite decomposition (Fig. 6). Statistical analysis indicated a moderate correlation between decomposed and measured GPPtree \( r = 0.55, p < .0001 \) and a strong correlation between decomposed and measured GPPgrass \( r = 0.86, p < .0001 \) (Fig. 6C-D). The absolute uncertainties were similar for estimating GPPtree and GPPgrass, with RMSE being 0.89 and 0.9 g C m\(^{-2}\) d\(^{-1}\) respectively. The relative uncertainty was higher for GPPgrass with normalised RMSE being 35% compared to 27% for GPPtree. To further assess the model performance with respect to inter-annual rainfall variability, we compared model decomposed and in-situ measured GPPtree and GPPgrass for the wettest year (2016–17, annual precipitation 2163 mm) and the driest year (2018–19, 1170 mm) respectively. (Fig. 6E-F) As Fig. 6 shows, the GPPtree was largely immune to the nearly 1000 mm difference in annual precipitation (Fig. 6E). For understory grass layer, an advance of the onset of growing season is observed from the measured data for the wet year, and this was well captured by the model decomposed result (Fig. 6F). A slight underestimation for GPPgrass is noticed for the driest year, with model decomposed GPPgrass being lower than in-situ measured GPPgrass in the first half of the growing season (Fig. 6F). There was no apparent deviation in terms of seasonal magnitude for GPPgrass, between the driest and the wettest years, likely due to the fact that vegetation functioning is less limited by water for this humid site (2000–2019 mean annual precipitation = 1684 mm).

3. Results

3.1. Seasonal variation in GPP partitioned into PFTs at local sites

Fig. 7 presents monthly average variations in GPPtree and GPPgrass and their ratios for the six local sites. Both plant functional types of savannas showed significant seasonal variations with higher values during the wet season than those obtained from the dry season (Fig. 7A-F). The seasonal profiles of GPPtree for Howard Springs, Daly River and Dry River were similar in magnitude, despite large differences in the magnitude and timing of GPPgrass across these three sites (Fig. 7). Interestingly, the Adelaide River site had a much lower GPPtree across seasons than Dry River, despite over 600 mm higher mean annual precipitation at Adelaide River than at Dry River (Fig. 7). Seasonal variations in Tree-Grass Index (TGI) of six local sites were presented for within-sites comparison of the temporal profiles of the tree-grass ratios (Fig. 7G). The highest annual mean tree-grass ratio was found at Dry River (TGI = 0.67) and Daly River (0.57), and the lowest tree-grass ratio was found at Sturt Plains (TGI = 0.14) (Fig. 7). Tree-grass ratios also varied considerably across wet and dry seasons, with the highest tree-grass ratio found during the dry season when the grasses were senescent (Fig. 7G). The contributions of C4 grasses to total GPP increased gradually from dry season to wet season following the greening of understory grasses (Fig. 7G).

3.2. Biogeographic patterns of savanna GPP partitioned into PFTs across wet and dry seasons

Fig. 8 and Fig. 9 present biogeographic patterns of mean daily total GPP, GPPtree, GPPgrass and TGI over the NATT study area. The wet season (January to March) and the dry season (July to September) were estimated based on the intra-annual rainfall distribution.

We found that GPPtree during the wet season decreased dramatically from around 5 g C m\(^{-2}\) d\(^{-1}\) in the Eucalyptus dominated savannas in the north to less than 1 g C m\(^{-2}\) d\(^{-1}\) in grasslands and Acacia dominated shrublands and woodlands in the south (Fig. 8A). During the dry season, the northern humid savannas still maintained GPP of 2–3 g C m\(^{-2}\) d\(^{-1}\), mostly due to GPPgrass (Fig. 8B). Fig. 7 also shows very large seasonal differences in GPPgrass. Mean daily wet season GPPgrass decreased from around 4 g C m\(^{-2}\) d\(^{-1}\) in the humid savannas to less than 1 g C m\(^{-2}\) d\(^{-1}\) over the xeric savannas (Fig. 8C). Wet-season GPPgrass was intermediate in the central-eastern tussock grasslands (2 g C m\(^{-2}\) d\(^{-1}\); Fig. 8D). During the dry season, dramatic declines in GPPgrass were observed, in which mean daily GPPgrass dropped to 0.5 g C m\(^{-2}\) d\(^{-1}\) (Fig. 8D). GPPgrass averaged across the whole area in the wet season was 1.15 ± 0.65 g C m\(^{-2}\) d\(^{-1}\) and in the dry season it decreased to only 0.34 ± 0.14 g C m\(^{-2}\) d\(^{-1}\).

Mean daily GPPtotal decreased from 8 g C m\(^{-2}\) d\(^{-1}\) in the coastal humid regions to less than 2 g C m\(^{-2}\) d\(^{-1}\) over the southern most dry areas in the wet season (Fig. 9A). However, during the dry season, the difference in GPPtotal was small between the northern and southern extremes of the NATT, largely due to sharply declining dry-season GPPtotal in the North (Fig. 9B). The daily GPPtotal during the wet season, averaged across the whole study area (2.80 ± 1.50 g C m\(^{-2}\) d\(^{-1}\)) was nearly twice as large as dry season mean daily GPPtotal (1.34 ± 0.69 g C m\(^{-2}\) d\(^{-1}\)).

Variations in GPPtree and GPPgrass across the wet-dry seasons resulted in fluctuating TGI over the NATT study area, from a weak C3 tree dominance in the wet season (TGI = 0.15 ± 0.28; Fig. 9C) to a strong C3 tree dominance in the dry season (TGI = 0.39 ± 0.28; Fig. 9D). Latitudinal variations in 15-year average GPPtotal, GPPtree, GPPgrass and TGI are shown in Fig. 10. The GPPtotal decreased from ca. 6 g C m\(^{-2}\) d\(^{-1}\) at north end of NATT to ca. 2 g C m\(^{-2}\) d\(^{-1}\) at south end of the NATT in the wet season (Fig. 10A). In the dry season, the GPPtotal decreased more conspicuously in the northern humid section compared to the southern xeric section, resulting in a much shallower latitudinal gradient along the NATT (Fig. 10A).

GPPtree showed less variations across wet and dry seasons along the entire transect (Fig. 10B). In the wet season, the GPPtree decreased from ca. 4 g C m\(^{-2}\) d\(^{-1}\) in the north to ca. 1 g C m\(^{-2}\) d\(^{-1}\) in the central and south regions of the NATT (Fig. 10B). On average, the magnitude of seasonal variation in GPPtree was larger in the northern humid regions and remained low in the southern xeric regions year-round (Fig. 10B).

GPPgrass exhibited larger seasonal variation, particularly at the northern humid savannas (Fig. 10C). GPPgrass in the wet season decreased from ca. 3.5 g C m\(^{-2}\) d\(^{-1}\) in the north to ca. 1 g C m\(^{-2}\) d\(^{-1}\) in the south (Fig. 10C). However, during the dry season, the GPPgrass significantly dropped to less than 1 g C m\(^{-2}\) d\(^{-1}\) over the entire...
transect (Fig. 10C). Interestingly, the highest GPP of grass during the dry season was found in the hummock grasslands of the central NATT (17°S-21°S) (Fig. 10C), possibly due to the highly sclerophyll and drought tolerant characteristics of the Triodia specie (a.k.a spinifex).

Pronounced variation in TGI across wet and dry seasons was observed along the NATT (Fig. 10D). In the dry season, TGI of the entire NATT except in some of the hummock grasslands, stayed positive, implying C3 tree dominated (Fig. 10D). In contrast, the TGI reached between 0.2 and −0.2 over nearly 50% of the areas of the NATT in the wet season, reflected the increase in the contribution of C4 grasses to ecosystem GPP in the wet season (Fig. 10D).

In addition, multiple trends in the tree-grass ratio, as well as the determination of savanna vegetation classes on the tree-grass ratio, were clearly depicted by Fig. 10D. In both wet and dry season, TGI first decreased from northern Eucalyptus dominated savannas (12.5°S to 17°S) towards the southern arid regions of the NATT (Fig. 10D). However, a sharp transition in TGI occurred at 17°S, coinciding with the spatial extent of hummock grasslands (Fig. 10D). TGI increased again at the xeric end of the NATT to the south of the transition from hummock grasslands to Acacia woodlands and shrublands (Fig. 10D).

Overall, the entire 1100 km distance NATT can be roughly dissected into three primary sections according to TGI: the northern tree dominated region (12°S - 17°S) (Fig. 10D), central-south grass dominated or tree-grass balanced region (17°S - 21°S), and south-end tree dominated (21°S - 23°S) (Fig. 10D).

3.3. The responses of savanna GPP partitioned into PFTs to decadal wet and drought extremes

To highlight the inter-annual GPP variation over the NATT study area and to separate the impacts of the drought and wet extremes for tree and grass components, we presented the latitudinal gradient of GPP_total, GPP_tree and GPP_grass and TGI for the wettest and driest years of each transect sample during the 2002–2018 time period respectively (Fig. 11).

Overall, the entire 1100 km distance NATT was not sensitive to the changes in rainfall amount (Fig. 11A). In contrast, GPP at southern NATT was highly responsive to the change in rainfall amount (Fig. 11A). The location of the divergence was at around 16–17°S, where Eucalyptus savanna transitions to dryland ecosystems, hummock grasslands and...
Acacia savanna (Fig. 11A). South of 17°S, large differences in annual GPP were found between the wettest and driest years (Fig. 11A). Fig. 11 also shows the dominance of C3 trees over northern NATT (12°S - 17°S) was relatively stable despite changes in rainfall amount. In contrast, the inter-annual pattern in TGI over the central part of the transect was more complicated (Fig. 11D). Over the southern part of the transect, a general declining trend in TGI (shifted tree-grass balance towards grass-dominated) from the driest year to the wettest year was observed (Fig. 11D).

4. Discussion

4.1. Highly variable savanna vegetation productivity and tree-grass ratios across space

In this study, we achieved a functional partitioning of savanna GPP into C3 tree and C4 grass plant functional types. In comparison with previous studies that primarily focused on structural variables (e.g., LAI or FPC) (Roderick et al., 1999; Lu et al., 2003), or intermediate functional variables (e.g., fAPAR) (Donohue et al., 2009), by coupling satellite remote sensing and landscape flux measurements of ecosystem function, we were able to accomplish a direct functional tree-grass partition in terms of GPP by coupling satellite remote sensing and landscape flux measurements.

Across the NATT, annual GPP decreased gradually from the humid savannas in the north to the xeric savannas in the south. The decreasing trend in annual GPP from 12.5°S to 18°S observed in this study agreed with the trend as reported by Kanniah et al. (2011). In this study, we found that GPP components of C3 trees and C4 grasses also showed a decreasing trend from north to south along the transect. GPPtree decreased dramatically from more than c.a. 1000 g C m⁻² yr⁻¹ at the northern humid end to less than 500 g C m⁻² yr⁻¹ over most areas of the southern xeric regions. This coincided with declining canopy cover and woody LAI along the NATT (Bowman, 1996; Sea et al., 2011). Additionally, we found GPPtree to be smaller than 300 g C m⁻² yr⁻¹ in the hummock grasslands from 18.5°S to 21°S, corresponding with minimal tree cover in this region. These results suggest that the spatial patterns in GPPtree as derived from satellite-based observations, were consistent with those from ground-based measurements.

Compared with tree cover, there are much less studies on the biogeographic pattern of the structure and function of understorey grasses over the NATT study area, with the exception of Howard Springs (Moore et al. 2016, 2017 & 2018). This is likely due to the considerable seasonal variations which demand multiple measurements within a single growth cycle and is therefore more challenging to be applied over the entire transect. Over the NATT study area, we found that GPPgrass decreased gradually from around c.a. 600 g C m⁻² yr⁻¹ in the north to around 200 g C m⁻² yr⁻¹ in the south. We also found that the slope of the decreasing trend in GPPgrass as a function of altitude (4.12 g C m⁻² yr⁻¹ per latitude degree, R² = 0.78, p < .0001) was much smaller compared with the slope of GPPtree (8.09 g C m⁻² yr⁻¹ per latitude degree, R² = 0.80, p < .0001). This was primarily due to the sharp decline in GPPtree in the hummock grassland at ca. 17°S. Consequently, the larger fraction (68%) of the overall decreasing trend in GPPtotal extending the 1100 km NATT transect was attributed to decreases in GPPtree.

Based on the analysis of the spatial pattern of tree-grass ratios as depicted by Tree-Grass Index (TGI), we found that the NATT study area can be roughly divided into three biogeographic regions bisected by 17°S and 21°S respectively. At northern NATT (12.5°S - 17°S), the annual GPP was dominated by C3 trees, but the dominance of C3 trees gradually decreased towards the south, and C4 grasses dominated, or contributed to ecosystem GPP equally as C3 trees, across 17°S - 21°S. At the southern xeric end of the NATT (21°S-23°S), the contributions of GPP from C3 trees increased until the C3 trees dominated annual GPP again. Such multiple spatial trends in TGI resulted in an overall v-shaped pattern in terms of tree-grass ratio along the entire 1100 km NATT, despite a constant decrease in mean annual precipitation alone the NATT.

4.2. Environmental determination on spatiotemporal savanna tree-grass dynamics

The dominance of C3 trees or C4 grasses across different spatial extents of the NATT transect reflected regional climatic patterns. The maintenance of the photosynthesis and transpiration of trees requires constant access to soil or groundwater sources during the extended dry season or drought periods (Eamus et al., 2013). As suggested by Egan and Williams (1996), the likelihood that rainfall will not be received in any given year increases as latitude increases, since the penetration of the Australian summer monsoon weakens with increasing latitudes (Suppiah, 1992; Cook and Heerdegen, 2001). This might explain the sharp decline in tree cover after 17°S, since 18°S-20°S is southern limit of reliable rainfall from the monsoonal influence (Bowman, 1996; Burgidge, 1960). Additional factors that may be responsible for the change in tree/grass ratio include soil texture factor (Williams et al., 1996; McKenzie et al. 2004), temperature (Bowman et al. 1996), and fire (Scholes and Archer, 1997; Beringer et al. 2007; Russell-Smith et al. 2003).

Despite the overall decreasing trends, we observed a second trend at the south xeric end of the NATT where both total tree-grass GPP components and their ratios increased despite the constant decrease in rainfall amount. This increase coincided with the physiognomic transition from hummock grasslands (spinifex) to Acacia shrublands/woodlands (mulga). Bowman (1996) found that the environmental heterogeneity associated with mountainous terrain increased in central Australia and could promote the diversity of woody species. The topographic fire protection effect in mountains (Bowman and Latz, 1993) might also be important for the transition from spinifex to mulga as it is known that spinifex is pyrophytic and mulga is highly fire sensitive while also acting as a fire retardant (Murphy et al., 2010; Nicholas et al., 2011). In addition, soil characteristics could be another candidate explanation for the spinifex-mulga transition, as compared with spinifex, mulga grows on soils that are more acidic, clayey and gravelly (Bowman et al., 1995; Nano and Clarke, 2008; Nicholas et al., 2009), and the floristic distinctions between mulga and spinifex are mostly found with edaphic boundaries (Nicholas et al., 2011; Nano and Clarke, 2008).

The semi-arid mulga was particularly important for central Australian carbon balance. At Ti Tree site, Cleverly et al. (2013) found that the large carbon sink was created due to the responses to C4 vegetation in the wet year, and photosynthesis of C3 canopy during the dry periods through the utilisation of deep soil moisture essentially prevent the mulga to be a carbon source as observed in other semi-arid regions. Nevertheless, large reductions in carbon production during extreme drought years were observed in the mulga savannas in this study, suggesting that the positive carbon balance as observed during the wet years (e.g., 2010–2011, 2016–2017) could be balanced out.
Fig. 8. Spatial distribution of GPP variations between wet and dry seasons in the NATT area. (A) Mean daily wet season GPP_{tree} (g C m\(^{-2}\) d\(^{-1}\)); (B) mean daily dry season GPP_{tree}; (C) Mean daily wet season GPP_{grass} (g C m\(^{-2}\) d\(^{-1}\)); (D) mean daily dry season GPP_{grass}.
Fig. 9. Spatial distribution of ecosystem-level total GPP and Tree-Grass Index between wet and dry seasons in the NATT area. (A) Mean wet season GPP_{total} (g C m^{-2} d^{-1}); (B) dry season GPP_{total}; (C) wet season TGI; (D) dry season TGI.
Fig. 10. Latitudinal gradient of the 2002–2018 (A) averaged total GPP, GPP_{tree}, GPP_{grass}, and (B) averaged Tree-Grass Index (TGI) from the north end (131.09°E, 12.171°S) to the south end (133.43°E, 22.9°S) along the 100 NATT transect samples.
Fig. 11. Latitudinal gradients in GPP partitioned into (A) C₃ trees and (B) C₄ grasses, and (C) Tree-Grass Index during the wettest year and the driest year within 2002–2018 time period of 100 transect samples from the north end (131.09°E, 12.171°S) to the south end (133.43°E, 22.9°S) along the 1100 km NATT transect.
under these region-wide severe droughts (e.g., 2004–2005, 2007–2008, 2012–2013) (Poulter et al., 2014; Ma et al., 2016). Therefore, long-term observations on the carbon fluxes at spinifex and mulga are urgently needed to reduce the uncertainties related with the source and sink of carbon at these two prevalent vegetation types in semi-arid and arid interior Australia, a combined total land area of c.a. 3 million km² (Eamus et al., 2013; Nicholas et al., 2011).

We found a contrasting sensitivity to rainfall variability between the northern half and the southern half of the NATT. Vegetation productivity in the northern humid region, where vegetation was classified as Eucalyptus dominated forests and woodlands, was resilient to inter-annual rainfall variability. In contrast, large inter-annual variations in GPP and the tree-grass ratio, were observed over the southern semi-arid and arid ecosystems (Fig. 11). During drought periods, carbon production of the southern NATT declined significantly, and the wet periods such as the 2010–2011 La Niña year resulted in a large pulse in annual GPP from the southern NATT, suggesting that these regions are particularly sensitive to hydroclimatic variability.

4.3. Limitations and future perspectives

Several limitations exist and much work can be done in future to refine our approach. A primary limitation is the reliance on distinct tree and grass phenology, which limits the application of our approach to other global tree-grass systems where deciduous tree species become more abundant. If this is the case, then the modelling structure must be revised to account for varying degree of tree deciduousness as well as non-synchronized tree and grass seasonal & inter-annual variations. In addition to phenology information, additional spectral, structural, and spatial textural information from spaceborne sensors, such as those from radar, LiDAR and hyperspectral sensors, can also be explored. Besides, in this study we used ground validation data from only one site, and hence to better calibrate the tree-grass decomposition model and validate the remote sensing-based results more ground measurements of tree and grass carbon fluxes can be planned in future along the transect.

In this study, a universal value was assigned to EVI\textsubscript{soil} (soil background contribution to EVI) over the entire study area and across all time. This is a necessary simplification to be able to apply the model to the entire region. Comparing to assigning EVI\textsubscript{soil} an arbitrary value, our approach is better as the value was calibrated using MODIS and in-situ flux tower measurements (Ma et al., 2014). Nonetheless, it must be admitted that over such a large geographical extent, soil type can vary and hence the contribution of soil to EVI signal is also expected to vary across space. A universal EVI\textsubscript{soil} ignores such variation and hence brings potential uncertainties in the decomposed tree and grass signals. A sensitivity analysis shows that the partitioned GPP\textsubscript{tree} is more sensitive than GPP\textsubscript{grass} to the varying EVI\textsubscript{soil} and the relative change in GPP\textsubscript{tree} can be as much as 76% with a minor increase in EVI\textsubscript{soil} from 0.08 to 0.10 (see Fig. A.1 in Appendix). Future efforts can be dedicated to achieving a better calibration of soil contribution to EVI to reduce the uncertainties in estimating savanna GPP and other vegetation properties.

Lastly, it would be of interest to know to what extent the cross-site or spatial variation in tree-grass ratio in terms of GPP is driven by the tree-grass ratio in terms of fractional cover. However, this is not possible at this stage because there is not enough repeated sample of tree and grass fractional cover data with the sampling size being comparable to the size of a MODIS pixel (250 m × 250 m). As such, this question may be investigated in a future study by systematically collecting samples of tree and grass fractional cover across space and time.

5. Conclusions

Realistic representation and simulation of carbon fluxes across heterogeneous landscapes such as savannas have been a great challenge for land surface and dynamic vegetation models. In this study, we proposed an innovative and operational workflow for partitioning savanna GPP into components of C\textsubscript{t} trees and C\textsubscript{g} grasses by coupling 14 years of satellite remote sensing and in-situ flux tower measurements. Our efforts may represent a valuable advance in comparison to previous studies that targeted structural variables (e.g., LAI). Validation against several years of in-situ measured tree and grass GPP confirmed that the workflow we proposed performed well in capturing the seasonal and inter-annual variations of each functional layer.

Additional spectral, structural, and spatial textural information from spaceborne sensors can be used in future work to complement phenological information. This would enable the tree-grass partition model to be applied to other global tree-grass systems where the difference in phenology between tree and grass layer is not as significant as in Australian savannas. Furthermore, soil contributions to EVI can be better calibrated to account for varying soil types across space. Lastly, more ground measurements of tree and grass carbon fluxes can be planned in future along such transects to continue to develop models and provide validation data.

The results from this study have several potential applications. First, there is currently a lack of observation-based tree and grass GPP data for validating land surface and dynamic vegetation models. Our observation-based results can therefore provide a good benchmark for assessing if the models only predicted correctly the lumped ecosystem GPP, or if they also capture the dynamics of each individual functional layer. Second, the spatiotemporal tree-grass partition also facilitates savanna management such as the estimation of forage resources and fire fuel loading. Getting this partitioning correct over a significant rainfall (and fire frequency) gradient is essential to effectively predict long-term carbon storage or loss in savannas. Manipulation of fire regimes and fuel loads is currently an important emissions reduction and potentially a biosequestration activity in north Australia. Predicting spatiotemporal patterns of longer-term carbon storage (trees) and fuels (grasses) as a function of current and/or future impacts from fire management interventions will provide a potentially important monitoring tool. From a carbon science perspective, prediction of the relative size of stable (trees) and variable (grasses) carbon pools would greatly improve our understanding of savanna biogeochemical cycling.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

A.1. Sensitivity of the model partitioned GPP\textsubscript{tree}, GPP\textsubscript{grass}, and TGI to the change in EVI\textsubscript{soil}

To assess the sensitivity of the model partitioned results to the change in soil background contribution to EVI (EVI\textsubscript{soil}), we performed additional sensitive test over the six local sites. Specifically, we assessed how the change in EVI\textsubscript{soil} from 0.08 to 0.10 could affect the derived mean annual values of GPP\textsubscript{tree}, GPP\textsubscript{grass}, and the Tree-Grass Index (TGI).

Fig. A.1. Cross-site comparison of the mean annual values of GPP\textsubscript{tree}, GPP\textsubscript{grass} and Tree-Grass Index (TGI) across the six local sites with EVI\textsubscript{soil} = 0.08 (x-axis) and EVI\textsubscript{soil} = 0.10 (y-axis) respectively.

Fig. A.1 shows that the change in EVI\textsubscript{soil} from 0.08 to 0.10 can cause changes in the derived GPP\textsubscript{tree}, GPP\textsubscript{grass} and the TGI. As expected, the increase in EVI\textsubscript{soil} from 0.08 to 0.10 decreased GPP\textsubscript{tree} by 12% to 76%. This is because the methodology we applied here assuming that the baseline value of EVI time series corresponds to EVI of tree layer during the dry season. By assigning EVI\textsubscript{soil} to a higher value, the EVI of tree layer during the dry season is effectively reduced and hence the derived GPP\textsubscript{tree} is also reduced, further causing a decline in TGI. The relative sensitivity of GPP\textsubscript{tree} to EVI\textsubscript{soil} is particularly high over the southern xeric savannas. By contrast, the decomposed GPP\textsubscript{grass} is much less sensitive to EVI\textsubscript{soil}, with the percent change in GPP\textsubscript{grass} to range from 5% to 14%.

References


