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Spatial patterns and temporal dynamics in savanna vegetation phenology across the North Australian Tropical Transect

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ABSTRACT

The phenology of a landscape is a key parameter in climate and biogeochemical cycle models and its correct representation is central to the accurate simulation of carbon, water and energy exchange between the land surface and the atmosphere. Whereas biogeographic phenological patterns and shifts have received much attention in temperate ecosystems, much less is known about the phenology of savannas, despite their sensitivity to climate change and their coverage of approximately one eighth of the global land surface. Savannas are complex assemblages of multiple tree, shrub, and grass vegetation strata, each with variable phenological responses to seasonal climate and environmental variables. The objectives of this study were to investigate biogeographical and inter-annual patterns in savanna phenology along a 1100 km ecological rainfall gradient, known as North Australian Tropical Transect (NATT), encompassing humid coastal *Eucalyptus* forests and woodlands to xeric inland *Acacia* woodlands and shrublands. Key phenology transition dates (start, peak, end, and length of seasonal greening periods) were extracted from 13 years (2000–2012) of Moderate Resolution Imaging Spectroradiometer (MODIS) Enhanced Vegetation Index (EVI) data using Singular Spectrum Analysis (SSA).

Two distinct biogeographical patterns in phenology were observed, controlled by different climate systems. The northern (mesic) portion of the transect, from 12°S, to around 17.7°S, was influenced by the Inter-Tropical Convergence Zone (ITCZ) seasonal monsoon climate system, resulting in strong latitudinal shifts in phenology patterns, primarily associated with the functional response of the C4 grass layer. Both the start and end of the greening (enhanced vegetation activity) season occurred earlier in the northern tropical savannas and were progressively delayed towards the southern limit of the *Eucalyptus*-dominated savannas resulting in relatively stable length of greening periods. In contrast, the southern xeric portion of the study area was largely decoupled from monsoonal influences and exhibited highly variable phenology that was largely rainfall pulse driven. The seasonal greening periods were generally shorter but fluctuated widely from no detectable greening during extended drought periods to length of greening seasons that exceeded those in the more mesic northern savannas in some wet years. This was in part due to more extreme rainfall variability, as well as a C3/C4 grass-forb understory that provided the potential for extended greening periods. Phenology of *Acacia* dominated savannas displayed a much greater overall responsiveness to hydroclimatic variability. The variance in annual precipitation alone could explain 80% of the variances in the length of greening season across the major vegetation groups. We also found that increased variation in the timing of phenology was coupled with a decreasing tree-grass ratio. We further compared the satellite-based phenology results with tower-derived measures of Gross Ecosystem Production (GEP) fluxes at three sites over two contrasting savanna classes. We found good convergence between MODIS EVI and tower GEP, thereby confirming the potential to link these two independent data sources to better understand savanna ecosystem functioning.

1. Introduction

Phenology is the study and analysis of the life cycles of flora and fauna and their interactions with climate and other seasonal

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environmental drivers (White & Thornton, 1997). Studies involving species-level phenology as well as at community-level, ecosystem and biome scales, are important in global land-surface change research. As an integrative indicator of climate variability and vegetation growth responses to climate change, understanding the timing and drivers of phenological patterns is also required to better simulate the carbon, water, and energy exchanges between atmosphere and land surface (Running & Hunt, 1993).

Phenological studies of vegetation can be carried out at the species level (bud break, flowering, leaf flush, etc.) using in-situ field techniques (Menzel et al., 2006; Williams, Myers, Muller, Duff, & Eamus, 1997). However, remote sensing provides the only feasible means of phenology monitoring over landscape, continental and global scales (Ahl et al., 2006; Glenn, Huete, Nagler, & Nelson, 2008; Huete et al., 2002; Stockli & Vidale, 2004; Zhang et al., 2003). Space-borne optical sensors such as NOAA-AVHRR and NASA-MODIS provide daily measurements of a variety of biophysical and biochemical satellite-based parameters of the land surface (Friedl et al., 2002; Huete et al., 2002; Tucker, Townshend, & Goff, 1985). These earth observation systems examine broader scale phenomena that allow retrievals of whole-system phenological metrics, such as the timing and magnitudes of greening, peak activity, and drying phases of the growing season (Zhang et al., 2003).

Many remote sensing phenology studies have been conducted in northern mid- to high-latitude temperate regions in which the timing and duration of the growing season is tightly correlated with temperature (Chen, Hu, & Yu, 2005; de Beurs & Henebry, 2005; Piao, Fang, Zhou, Ciais, & Zhu, 2006; White et al., 2009; Zhang, Friedl, Schaaf, & Strahler, 2004). In contrast to temperature-driven patterns in vegetation phenology, there have been fewer studies conducted in tropical water- or light- limited/driven ecosystems. The start of the rainy season has been found to be the best predictor of the onset of vegetation green-up in drier areas where water availability is the primary driver of vegetation growth (Brown, de Beurs, & Vrieling, 2010; Zhang, Friedl, Schaaf, Strahler, & Liu, 2005). In light-limited areas of the Amazon Basin, the green-up phenophase in rainforests was found to be synchronized with the dry season, when sunlight availability increases (Huete et al., 2006).

"Savanna" as an ecological term has various definitions (Gillison, 1981; Walker & Gillison, 1982; Frost et al., 1986; Scholes & Walker, 1993; Eamus & Prior, 2001). In this study, we adopted a definition after Walker and Gillison (1982), who defined savannas as wooded communities with a conspicuous perennial or annual graminoid component. In an Australian context, such a definition has been further extended to include woodland savanna (single-stemmed woody) and shrub savanna (multi-stemmed woody) ecosystems (Walker & Gillison, 1982). We adopted such a definition due to its recognition of varying mixtures of trees, shrubs and graminoids that form a structural continuum (Walker & Gillison, 1982).

The tree-shrub-grass layers of savanna have distinct physiological characteristics, expressed as multiple plant functional types with tree and grass ratios of cover and leaf area index varying significantly among different savanna classes (Scholes & Archer, 1997). The phenology of mixed physiognomy savanna ecosystems is distinct from those of forests and grasslands. The multi-stratum nature of savannas results in a more complex and dynamic landscape with each layer exhibits unique functional responses and interactions to seasonal rainfall and other environmental variables (Scholes & Archer, 1997).

Savanna phenology has been investigated at species and community scales (Seghieri et al., 2009; Williams et al., 1997). For example, at a site near Darwin (Northern Territory, Australia), ground observations showed evergreen species continued to flush and produce leaves throughout the dry season, and that leafing in brevi- and semi-deciduous species commenced prior to the arrival of rainfall (Williams et al., 1997). In contrast, the fully deciduous species displayed a range of behaviors: some flushed before the first rain, while others flushed after ~25 mm of rain had fallen (Williams et al., 1997). A study conducted at Kruger National Park in South Africa identified two distinct phenological syndromes where leaf flushing of trees occurred prior to rainfall but grasses flush followed the rain (Higgins, Cartay, February, & Combrink, 2011).

At regional scales, savanna phenology has also been investigated using remote sensing (Archibald & Scholes, 2007; Chidumayo, 2001; Ferreira & Huete, 2013; Higgins et al., 2011; Ratana, Huete, & Ferreira 2005). In South African savannas, a model based on AVHRR and MODIS observations can predict 86% of the onset of tree species green-up from day length alone, while with the incorporation of soil moisture the model could predict 73% of the grass green-up, both to within an accuracy of less than one month (Archibald & Scholes, 2007). However, Seghieri et al. (2009) found the phenophases of most Sahelian woody species to be correlated with temperature rather than rainfall. In central Brazil, temporal profiles of vegetation indices over the cerrado exhibited high wet-dry season contrasts, and variations in seasonal vegetation indices (VI) were negatively correlated with woody cover (Ratana et al., 2005). Hill et al. (2011) investigated the utility of MODIS VIs to classify global savanna ecoregions based on annual average phenological profiles. Based on in-situ survey and satellite observations, Hüttich et al. (2009) classified savanna vegetation in South Africa using phenological metrics. Donohue, McVicar, and Roderick (2009) recognized the distinct seasonal contributions of the tree and grass layers in Australian savannas and decomposed AVHRR-NDVI (Normalized Difference Vegetation Index) into recurrent and persistent components, as surrogates of the herbaceous understorey and evergreen woody overstorey, respectively.

However, accurate and robust regional-scale retrievals of savanna phenology metrics remain a challenge using remote sensing methods. For example, in African savannas, Hmimina et al. (2013) found that NDVI time series could not be modeled with sigmoidal functions, as commonly applied to VI time series in temperate biomes (Soudani et al., 2008; Zhang et al., 2003). This was attributed to irregular rainfall driven temporal vegetation growth patterns in savannas, thus requiring use of non-parametric methods, such cubic spline methods, to smooth the VI time series for retrieval of phenology metrics (Hmimina et al., 2013). Jin et al. (2013) coupled flux tower measurements of productivity with MODIS data and similarly found existing phenology retrieval methods were highly unstable across different savanna woodlands sites. These studies suggest a need to consider the limitations of current methodologies and develop more robust and accurate remote sensing methods to retrieve phenological information in savannas landscapes.

Savannas are most commonly found in the tropics and sub-tropics and are present in both mesic and xeric regions (Eamus & Prior, 2001; Frost et al., 1986). Savannas typically experience highly seasonal rainfall and prominent inter-annual climate variability, making them one of the most dynamic global biomes (Frost et al., 1986). With their distinct rainy season and pronounced dry season, they are also considered particularly vulnerable to climate change (Field, Lobell, Peters, & Chiariello, 2007). The biotic and abiotic controls on savanna productivity exhibit high spatial variability and complex interactions that create considerable challenges to accurate simulation of savanna-atmosphere exchange processes (Kanniah, Beringer, & Hutley, 2010; Whitley et al., 2011).

Savannas cover one eighth of the global land area (Scholes & Archer, 1997) and contribute approximately 30% of all terrestrial ecosystem gross primary productivity (House & Hall, 2001). Most importantly, savannas support a vast and ever increasing human population that is supported by livestock grazing activities (Scholes & Archer, 1997). Land degradation in savanna regions has resulted in altered species composition and declines in productivity, which pose concerns for their fate, functioning, and resilience under future climate change (Scheiter et al., 2012), as well as their continued capacity to support human livelihoods and biodiversity (Frost et al., 1986; Hanan & Lehmann, 2011; Scholes & Archer, 1997).