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# Savanna tree-grass interactions: A phenological investigation of green-up in relation to water availability over three seasons

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ABSTRACT

Phenology of African savannas is considered to have high temporal variability, yet few studies have quantified this variation between seasons. This study assessed the weekly green-up phenology of trees, as well as below- and between-canopy grasses in a broad-leaved savanna woodland in the Nylsvley Nature Reserve (NNR), South Africa over three growing seasons (2012–2014). Tree green-up start dates were highly variable in comparison to the grasses, whose green-up showed close ties to the availability of water, particularly rainfall. Early green-up of *Burkea africana* trees occurred if rainfall onset was after mid-October, thus long-term rainfall records indicate that trees would benefit from early-greening approximately 46% of the time in the NNR. The effects of tree canopies on the growth and biomass accumulation of below-canopy grasses showed that during periods of irrigation when water was not limited, light availability became the limiting factor for grass growth, with grasses below the higher shading of *B. africana* producing significantly lower biomass than those below the less shaded *Terminalia sericea* canopies. Access to higher light conditions at the start of the growing season potentially drives the 2–5 days faster green-up of below-canopy grasses compared to the between-canopy grasses. A comparison of the above phenological data to the remotely sensed normalized difference vegetation index (NDVI) was made, to determine if it was possible to detect an early-greening signal from the trees, which the sensor was able to effectively distinguish. This study highlights the variability in temporal separation between tree and grass phenology in an African savanna. Trees take advantage of periods of low competition from herbaceous neighbours at the end of the dry season prior to the onset of seasonal rainfall, and potentially at the end of the growing season when seasonal rainfall concludes through the uncoupling of their green-up cue from seasonal water availability.



## 1. Introduction

Understanding and investigating phenology of ecosystems is important for identifying any future changes in response to changing climates (Menzel, 2002; Cleland et al., 2007; Polgar and Primack, 2011; Chambers et al., 2013; Buitenwerf et al., 2015; Fitchett et al., 2015). Phenology is the study of the timing of biological events, for example the date at which trees commence the flushing of new leaves each year (Lieth, 1974). The phenology of African savannas has been shown to be unpredictable, partly due to the high variability in seasonal rainfall which acts as one of the major environmental drivers of green-up in this ecosystem (Eamus et al., 1999; Lehmann et al., 2011; Whitecross et al., 2016a). Savannas are most broadly defined as a mixture of a homogeneous grass layer with a discontinuous tree layer which can vary in density (Huntley and Walker, 1982; Scholes and Archer, 1997). Tree/grass ratios in savannas are driven by several abiotic factors including climate, geology and topography, as well as disturbances such as fire, herbivory and frost (Huntley and Walker, 1982; Scholes and Walker, 1993; Whitecross et al., 2012; Lehmann et al., 2014). Numerous studies have investigated the physical impacts of disturbances such as fire on savanna vegetation (Gandar, 1982; Higgins et al., 2000; Kennedy and Potgieter, 2003; Wilson and Witkowski, 2003; Furley et al., 2008; Ryan and Williams, 2011), however, only a few studies have shown the impacts of these disturbances on savanna plant phenology (Coutinho, 1982; Trollope, 1982; Whitecross et al., 2016a). Wade and Johansen (1986) proposed the 'tree physiology hypothesis' wherein seasonal changes in tree physiology play an important role in influencing trees' susceptibility to fire. Kennedy and Potgieter (2003) supported this hypothesis when they showed that in the dry season (May to August) dormant broad-leaved deciduous trees were more tolerant of fires, whereas in the early growing season (September–October) when physiological activity increased, so too did the risk of fire-related damage. Understanding the phenology of savannas is difficult as the two dominant life-forms – trees and grasses – show different seasonal dynamics and seem to respond to different environmental cues (Rutherford and Panagos, 1982; Childes, 1989; De Bie et al.,

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1998; Archibald and Scholes, 2007; Higgins et al., 2011; Buitenwerf et al., 2015).

The phenology of semi-arid savanna vegetation is closely linked to the availability of water, with deciduous vegetation flushing new leaves after the onset of the first substantial (>15 mm) seasonal rainfall event (Huntley and Walker, 1982; Scholes and Archer, 1997; Chidumayo, 2001; Jolly and Running, 2004; Archibald and Scholes, 2007; Hachigonta et al., 2008). The arrival of these storm systems is highly variable both temporally and spatially between seasons (Huntley and Walker, 1982). Although the first rains represent the end of the "dormant season" in these tropical and sub-tropical systems, some tree species are able to flush new leaves prior to the arrival of seasonal rainfall which enables them to grow during a period of limited competition for resources from their herbaceous and non-early-greening woody neighbours (Childes, 1989; Scholes and Walker, 1993; De Bie et al., 1998; Chidumayo, 2001; Higgins et al., 2011; February and Higgins, 2016; Whitecross et al., 2016a). Unlike trees, the phenology of savanna grasses is closely linked to water availability (Dye and Walker, 1987; Prins, 1988; Scholes and Walker, 1993; Archibald and Scholes, 2007; February et al., 2013).

The patchy distribution of trees across the savanna landscape results in grasses growing either below or between tree canopies. Grasses found below canopies benefit from a concentrated source of nutrients through litterfall and an improvement in water use as temperatures are lower under the canopy's microclimate (Belsky, 1994; Durr and Rangel, 2000; Ludwig et al., 2001). However, below-canopy grasses face reduced light availability through shading and direct competition with trees for available resources (Knoop and Walker, 1985; Scholes and Archer, 1997; Ludwig et al., 2001; February et al., 2013). Light-limited grasses growing below canopies have shown differences in growth rates, biomass accumulation and expansion of leaf area compared with between-canopy grasses (Belsky, 1994; Durr and Rangel, 2000; Ludwig et al., 2001). Grasses growing between canopies experience less competition from trees and compete directly with other grasses for limited nutrients and space to grow (Rutherford, 1983; Belsky, 1994). Few studies have investigated the effect of tree canopies on the phenology of below- and between-canopy grasses (Dye and Walker, 1987; Prins, 1988), with the majority of the research tending towards investigations into growth and biomass accumulation (Scholes and Walker, 1993; Belsky, 1994; Ludwig et al., 2001). Understanding the effect that canopies have on grass phenology can assist in furthering knowledge about phenological dynamics in the complex savanna ecosystems.

Many studies demonstrate the usefulness of long-term remotely sensed indices of vegetation greenness from AVHRR and MODIS data for tracking phenological shifts (Myneni et al., 1997; Schwartz, 1998; Poulter and Cramer, 2009; Richardson et al., 2013; Buitenwerf et al., 2015). However, remote sensing of phenology is most useful when integrated with field measurements which can validate and inform the vegetation indices acquired from satellite data (Fitchett et al., 2015). This is particularly important in systems with high ecosystem-level variation in phenological patterns, such as savannas, where the coarse scale of the remotely sensed data often obscures much of the system dynamics such as the specific greening of trees or grasses (Scholes and Walker, 1993; Chidumayo, 2001; Scanlon et al., 2002; Jolly and Running, 2004; Simioni et al., 2004; Archibald and Scholes, 2007; Higgins et al., 2011). In these situations long-term field measurements and phenological networks are still essential but are currently lacking in the majority of the world's savannas, particularly those in Africa (Chambers et al., 2013).

Without detailed ground-based studies it will be challenging to develop generalised theories on the phenology of savannas and their different life forms. Few studies have shown the phenological changes which occur in savannas at more than a monthly temporal scale, which often obscures complex processes occurring rapidly at the start of the season (Childes, 1989; Scholes and Walker, 1993; De Bie et al., 1998; Chidumayo, 2001). The aim of this study was to investigate the relative responsiveness of trees and grasses in a broad-leaved savanna to the timing of water availability at a weekly scale over the 2012, 2013 and 2014 green-up periods (August–December). We compared differences in growth onset and rates of below- and between-canopy grasses and tested the response of grasses when additional water was provided through irrigation. We hypothesized that additional water would result in an earlier onset of grass growth and faster growth rates. We then compared the onset of green-up between the trees and grasses and compared our findings to remotely sensed normalized difference vegetation index (NDVI) data to determine whether the onset of green-up was accurately detected by the satellite imagery. Through this study we hope to further the understanding of how these coexisting floral life-forms are competing at various temporal and spatial scales.

## 2. Materials and methods

This study was run in conjunction with Whitecross et al.'s (2016a) study and conducted from the beginning of August 2012 until the end of May 2014. Full details regarding the layout of the irrigation and tree phenology aspects of the study are reported in Whitecross et al. (2016a).

### *2.1. Study site*

This study was conducted in the broad-leaved savanna of the Nylsvley Nature Reserve (NNR), Mookgophong, Limpopo Province, South Africa (24°39′ S, 28°42′ E; 3975 ha). The vegetation type is classified as central sandy bushveld within the savanna biome (Rutherford et al., 2006). The NNR has a seasonal climate with hot, wet summers in which an average of 85% of the 623 mm mean annual precipitation (MAP) falls between October and March (Huntley and Morris, 1982). Further details on the rainfall during the study period are presented below. On the 19th September 2013, a severe unplanned fire burnt 85% the NNR, damaging many adult trees and incinerating all aboveground grass (and herbaceous) biomass (more details in Whitecross et al., 2016a). The irrigation system was also destroyed, but reinstalled one week thereafter. The study area was fenced to remove the effects of mammalian herbivory.

### *2.2. Study species*

#### *2.2.1. Trees*

Two of the dominant broad-leaved savanna trees in the NNR were chosen for this study. *Burkea africana* (Hook.) (Caesalpiniaceae) has been recorded as an early-greener – flushing new leaves prior to the start of seasonal rainfall (Childes, 1989; De Bie et al., 1998). Its green-up period in the NNR is recorded as an average of 8 weeks, generally commencing in late September (Rutherford and Panagos, 1982). It is a medium-sized deciduous, leguminous tree and stands at an average of 10–12 m in height (Maroyi, 2010). Its distribution is vast, ranging throughout central and southern Africa (Maroyi, 2010).

*Terminalia sericea* (Burch. ex DC.) (Combretaceae) occasionally demonstrates early-greening as new leaves are flushed just before or immediately after the arrival of seasonal rainfall (Childes, 1989; Moyo et al., 2015). It is a small to medium-sized, deciduous tree with a mean height of 9 m and is distributed throughout southern African savannas (Lemmens, 2009).

#### *2.2.2. Grasses*

Grass plots were marked out under *B. africana* and *T. sericea* canopies and also between these tree canopies with no shade from woody plants. The dominant grasses associated with the *B. africana* plots were *Setaria sphacelata* var. *sphacelata* (Schumach.), *Eragrostis curvula* (Schrad.) and *Sporobolus africanus* (Poir.). Under the *T. sericea* canopies, plots were dominated by *Trachypogon spicatus* (Kuntze) and *Sporobolus africanus*.