

Is there a temporal niche separation in the leaf phenology of savanna trees and grasses?

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ABSTRACT

Aim It has been proposed that, in tropical savannas, trees deploy their leaves earlier in the growing season and grasses deploy their leaves later. This hypothesis implies a mechanism that facilitates the coexistence of trees and grasses in savannas. If true, this hypothesis would also allow algorithms to use differences in the phenological timing of grass and tree leaves to partition the relative contribution of grasses and trees to net primary production. In this study we examine whether a temporal niche separation between grasses and trees exists in savanna.

Location A semi-arid, subtropical savanna, Kruger National Park, South Africa.

Methods We use a multi-spectral camera to track through an entire growing season the normalized difference vegetation index (NDVI) of individual canopies of grasses and trees at eight sites arranged along a precipitation and temperature gradient.

Results Among trees, we identified two distinct phenological syndromes: an early flushing syndrome and a late-flushing syndrome. Leaf flush in the tree strategies appears to pre-empt rainfall, whereas grass leaf flush follows the rain. The growing season of trees is 20 (late-flushing trees) to 27 (early flushing trees) days longer than that of the grasses.

Main conclusions We show that grasses and trees have different leaf deployment strategies. Trees deployed leaves at lower temperatures than grasses and retained them for longer at the end of the growing season. The timing of the increase in NDVI is, however, similar between grasses and late-flushing trees and this complicates the separation of grass and tree signals from multi-spectral satellite imagery.

Keywords

Grass–tree competition, growing season length, Kruger National Park, NDVI, phenology, savanna, South Africa, temporal niche hypothesis.

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INTRODUCTION

The growing season length is, along with the absorbed fraction of photosynthetically active radiation and the light-use efficiency, a fundamental determinant of an ecosystem's primary productivity (Eamus, 1999; Larcher, 2003). These observations are the basis of a family of methods that use remotely sensed data to estimate and/or monitor primary productivity in ecosystems (Grace *et al.*, 2007; Hilker *et al.*, 2008). Such estimates are important for monitoring how

terrestrial ecosystems are responding to climate change, projecting the carbon sequestration potential of terrestrial ecosystems, as well as for evaluating how well models (e.g. Cramer *et al.*, 2001) predict such changes.

These methods based on remote sensing are, however, still in development. One problem is that subgrid heterogeneity has the potential to bias the interpretation of satellite metrics of growing season length and productivity (Fisher & Mustard, 2007). In savannas, the focus of this study, an important source of subgrid heterogeneity is the ratio of grass to tree

cover. Many remotely sensed products of savannas are therefore difficult to interpret because they integrate the signals of two life-forms that potentially respond in fundamentally different ways to environmental forcing variables (Scheiter & Higgins, 2009). Even in forested ecosystems the behaviour of the understorey has been recognized as an important bias when using remote sensing products to project the length of the growing season (Stöckli *et al.*, 2008).

It has also been argued that grasses and trees in savannas differ in their growing season lengths. Such differences in the phenologies of grasses and trees are thought to be crucial for understanding competitive interactions in savannas. Specifically, it has been proposed that a temporal niche separation ameliorates the effects of grass and tree competition (Scholes & Walker, 1993). This temporal niche separation hypothesis proposes that trees, due to stored carbon reserves, can deploy leaves earlier in the growing season than grasses can and this allows trees a period of growth in which grass competition is reduced (Scholes & Walker, 1993). Even though phenological differences between grasses and trees might be central to understanding the dynamics of savanna ecosystems, only a few studies (Chidumayo, 2001; Simioni *et al.*, 2004; Archibald & Scholes, 2007) have discussed phenological patterns in savannas in the context of the temporal niche separation hypothesis. We are not aware of a study that has provided a quantitative estimate of the extent of this putative niche partitioning.

Only a handful of studies have used remote sensing to examine the growing season length of savannas. Chidumayo (2001) assumed that savanna tree leaf phenology was advanced relative to that of grasses and used this to separate the grass and tree components in a normalized difference vegetation index (NDVI) time series. Jolly & Running (2004) used a water balance model to predict savanna phenology and compared the model with a 3-year NDVI time series. The deviation between the onset of leaf flush predicted by the model and empirical data was between 10 and 40 days. Archibald & Scholes (2007) developed an intricate algorithm that used Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI products and field-based parameter estimates to untangle the grass and tree components at a site in the Kruger National Park, South Africa. The resulting statistical model predicts green-up dates for grass and tree components with similar precision to the process-based model of Jolly & Running (2004). The performance of these savanna phenology models is poor relative to similar studies conducted in other regions. For instance, White *et al.* (1997) achieve a 6–7-day accuracy in green-up forecasts for continental North America.

In this study, at eight sites that follow an environmental gradient in precipitation and temperature, we captured a high spatial resolution (c. 18 cm pixel size), high temporal resolution (weekly early in the season, less frequently later) multi-spectral data set and linked this with site-specific meteorological measurements. These data allow us to construct a time series of tree and grass activity over a growing season. We ask the following questions: (1) Do trees and grasses have distinct phenological strategies? (2) Is there evidence that trees and

grasses respond to different environmental cues for the initiation of leaf growth and for leaf abscission? (3) Do grasses and trees have different growing season lengths, and if so are these differences attributed to differences at the start or at the end of the growing season?

MATERIALS AND METHODS

Study area

The study site is located in the Kruger National Park, South Africa. The eight sites we investigate form a c. 50 km transect that traverses two vegetation types in Gertenbach's landscapes of the Kruger National Park (Gertenbach, 1983), the Lowveld Sour Bushveld of Pretoriuskop and the Bushwillow and Large-fruited Bushwillow Woodland. The transect starts south of Skukuza and ends close to Pretoriuskop. Historical climate diagrams for Skukuza, Pretoriuskop and for the study transect for the period of study are shown in Fig. 1. The coordinates (latitude, longitude and elevation) of the eight sites are listed in Table 1.

The descriptions of the two Gertenbach landscapes in the following paragraphs follow largely from Gertenbach (1983). Both landscape types have undulating landforms with distinct catenal sequences which overlay archaean granite and gneiss. The soils of both landscapes are red to yellow-brown in colour and vary from a sand to a sandy loam and are deeply leached. The soils are classified as Hutton and Clovelly forms. The soils of the Bushwillow Woodland landscapes are deeper and better drained than those of the Sour Bushveld.

The species compositions of the landscapes are similar (nomenclature follows Palgrave, 1983 for trees and Gibbs Russell *et al.*, 1987 for grasses). Structurally they are described as a tree savanna with low shrubs. The most common tree species are *Terminalia sericea* (more common in the Sour Bushveld) and *Combretum apiculatum* (more common in the Bushwillow woodland). Other common woody species are *Sclerocarya birrea*, *Dichrostachys cinerea* subsp. *Nyassana*, *Strychnos madagascariensis*, *Peltophorum africanum*, *Combretum collinum* subsp. *suluense*, *Combretum zeyheri* and *Maytenus heterophylla*. All of these common species are deciduous.

The grass layer of the Sour Bushveld is tall (1–2) with high (70%) cover. Sour grass species dominate (*Hyperthelia dissoluta*, *Elionurus argenteus*, *Hyparrhenia hirta*, *Setaria perennis*, *Heteropogon contortus* and *Pogonarthria squarrosa*). The grass layer of the Bushwillow woodland is shorter (1 m) and has a lower cover (typically < 70%). The dominant species are *Pogonarthria squarrosa*, *Hyperthelia dissoluta*, *Setaria flabellata*, *Loudetia simplex*, *Eragrostis rigidior*, *Digitaria eriantha*, *Panicum maximum* and *Heteropogon contortus*.

Study sites and their instrumentation

Eight meteorological stations were established over the rainfall gradient between Skukuza and Pretoriuskop during September 2007. The following instruments were installed at each station.

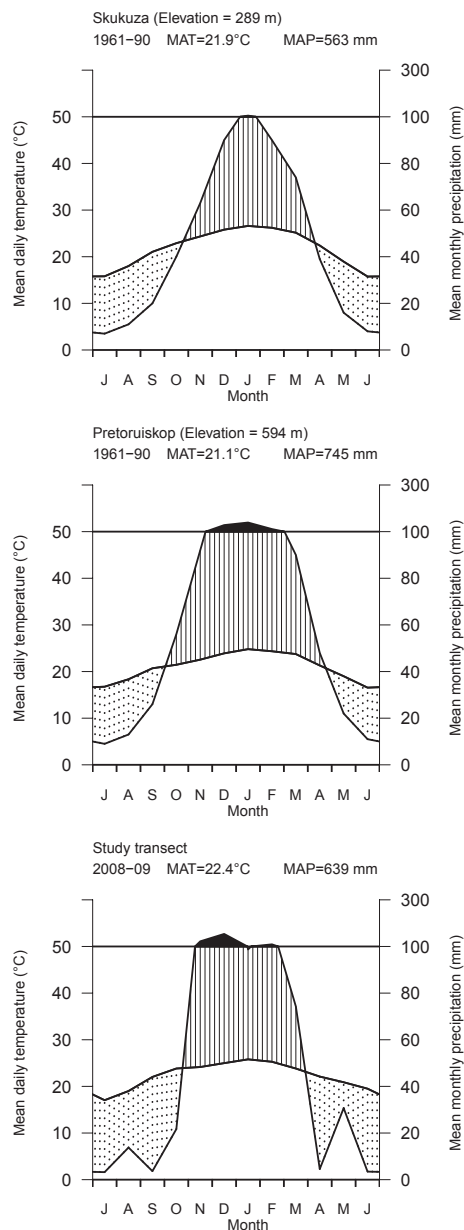


Figure 1 Climate diagrams for Skukuza and Pretoriuskop, Kruger National Park, for the period 1961–90 and a climate diagram (averaged for the eight study sites) for the study period (September 2008 to August 2009). MAT indicates the mean annual temperature and MAP the mean annual precipitation at a site.

A Decagon Devices EC-5 soil moisture probe, a Pronamic Rain-O-Matic Professional tipping bucket rain gauge, a Vaisala HMP50 temperature and humidity sensor, an Apogee Instrument Inc. QS0-S Quantum Sensor, an Apogee Instrument Inc. SP-110 pyranometer and a R. M. Young 0301 anemometer. The instrument array was powered and controlled with a CR200 (Campbell Scientific Inc., Logan, UT, USA) data logger, which was powered by a rechargeable lead acid battery connected to a voltage-regulated solar panel.

To prevent animal damage, the instrument array was mounted on a customized bracket system (Campbell Scientific

Table 1 Latitude, longitude (in decimal degrees), elevation and estimated cover of the three phenological types [early flushing trees (EFT), late-flushing trees (LFT) and grasses] at the eight study sites in Kruger National Park, South Africa.

Site	Latitude (°S)	Longitude (°E)	Elevation (m)	Cover		
				EFT	LFT	Grass
1	25.073	31.607	399	0.12	0.44	0.45
2	25.074	31.545	398	0.30	0.22	0.49
3	25.111	31.515	415	0.22	0.24	0.54
4	25.094	31.470	440	0.18	0.30	0.52
5	25.136	31.417	477	0.07	0.20	0.73
6	25.091	31.381	491	0.21	0.32	0.47
7	25.144	31.355	510	0.08	0.53	0.39
8	25.197	31.249	574	0.41	0.31	0.28

Inc.) attached to a 4-m wooden mounting pole. The mounting pole was supported by three struts that were fenced to create a triangular enclosure for the station power supply, control and logging equipment. All instruments were levelled and orientated in an east–west direction to prevent shadow interference. The soil moisture probe was installed at a depth of 20 cm in a horizontal position 5 m from the station. The weather stations were operational 12 months before the start of NDVI measurements, that is, they provide data on conditions antecedent to the NDVI measurement campaign. Sensor data were logged every half hour for the duration of the study.

Image capture and processing

Multi-spectral images were captured with a 3.2 megapixel (CMOS sensor, 2048 × 1536 pixel) camera that senses green (520–620 nm), red (650–750 nm) and near-infrared (750–950 nm) bands that approximate the Landsat Thematic Mapper's bands 2, 3 and 4 (ADC-Air, Tetracam, Chatsworth, CA, USA; Steltzer & Welker, 2006, provide an example of the use of this camera for describing NDVI). The camera was mounted on a South African National Parks helicopter. Ten flights were scheduled between 4 November 2008 and 10 July 2009. The flight dates were 4 November 2008, 11 November 2008, 28 November 2008, 12 December 2008, 14 January 2009, 17 March 2009, 11 May 2009, 3 June 2009 and 10 July 2009. Flight frequency was adapted to phenological activity (i.e. flights were more frequent initially and less frequent later).

At each sample date one image was captured 450 m above ground level at each of the eight study sites, thus covering an approximate area of 376 m × 282 m (c. 10.6 ha) with an approximate pixel resolution of 18 cm. All flights were conducted on clear days close to noon to reduce the area cast by shadows. Images were taken at a nadir view angle to minimize bidirectional effects on the reflectance measurements. We used the automatic exposure mode of the camera to correct for changing light conditions during the flight. Images of a barium sulphate white standard (99% reflectance) were taken every 20 min during each flight.

Pre-processing of images involved several steps. Because images obtained with the ADC camera are grey-scale images containing raw pixel values they need to be colour processed prior to analysis. This was done by applying a standard colour matrix to the raw Bayer pattern images obtained with the camera, using PIXELWRENCH2 (Tetracam, Chatsworth, CA, USA) software. The images were then separated into the green, red and near-infrared bands. The nearest in time image of the reflectance standard was used to normalize the bands to account for variance in incoming radiation and to calculate the reflectances (in practice the differences between the uncalibrated and calibrated images were small). NDVI was calculated as $(\text{near-infrared-reflectance} - \text{red-reflectance})/(\text{near-infrared-reflectance} + \text{red-reflectance})$.

Individual canopies of trees and grasses were tracked through time at each of the eight sites. For grasses, a canopy was defined as a circular plot of diameter 3.5 m. The grass canopies were selected to be at least 3 m from the nearest tree. For trees, a canopy was defined as a circle centred within an actual tree canopy. Small trees and trees with damaged canopies were not sampled. Edge effects were avoided by ensuring that the diameter of this circle was always smaller than the actual canopy diameter. Typical sampled tree canopy diameters were 1.5–3.5 m, ensuring that we sampled 50–300 pixels per tree canopy. Tracking of canopies was achieved by georeferencing images from the first flight by using the locations of known points (structures, road intersections, markers) and all subsequent images were co-registered to these first images. The root mean square (RMS) error in these co-registered images was typically 54–72 cm (three to four pixels); this was sufficient quality to obtain a reliable sample of the c. 50–300 pixels that constitute an individual canopy. Preliminary analyses of the images revealed that two distinct phenological syndromes could be identified amongst the trees. The first syndrome we call early flushing trees (EFT) and the second we call late-flushing trees (LFT). We followed 10 grass, 10 EFT and 10 LFT canopies at each of eight sites (240 sample points for each of 10 surveys). The relative cover of EFT, LFT and grass at the eight study sites is listed in Table 1.

Canopies were delimited through visual interpretation of false-colour composites of the near-infrared, red and green bands. This involved selecting EFT from the first images, where no LFT or grasses had flushed their leaves. Grass and LFT canopies were selected from mid-season images when the vegetation had reached its maximum greenness. To avoid misclassification of EFT as LFT, only the tree canopies that had full canopies in the mid-season images and no leaves at the beginning of the season were classified as LFT. Selecting the grass canopies in the mid-season images ensured that bare ground areas were avoided. For each canopy we extracted the NDVI values for each pixel in the canopy. The mean NDVI value of this canopy was used in the analyses. EFTs accounted for c. 20% of the woody canopy cover in our study sites (LFTs for the remaining 80%).

This separation into three phenological strategies ignores the fact that grasses below the tree canopy might constitute a

fourth type. Our data, however, do not allow us to examine whether this statement is true. Moreover, our analysis implicitly assumes that grass below the tree canopy does not significantly contaminate the tree NDVI signal. One would expect low contamination for high leaf area index (LAI) tree canopies, as the transmittance through such canopies would be low, and any subsequent interception of reflected radiation by these canopies would be high (Fuller *et al.*, 1997). Our sampling programme avoided sampling small trees and indistinct tree canopies, that is the tree canopies in our study had relatively high LAI (Simioni *et al.*, 2004 report mean single tree canopy LAI > 2 in a West African savanna and Scholes *et al.*, 2004 estimated a mean tree LAI of 1.5 for a savanna in Botswana with 630 mm mean annual precipitation).

Statistical analyses

The mean canopy NDVI values described in the previous section were used as a response variable. In a first analysis we summarize the empirically observed pattern of NDVI development over the course of the observation period using a back-to-back sigmoid curve

$$f_1(x; l_1, l_2, s_1, s_2, a, b) = 2b - a + \frac{a - b}{1 + \exp[s_1(l_1 - x)]} + \frac{a - b}{1 + \exp[s_2(x - l_2)]}. \quad (1)$$

This equation, although cumbersome, provides a means to estimate parameters that provide intuitive descriptions of the seasonal NDVI development. It assumes that a baseline level of NDVI (b) exists in the dormant season and that a peak NDVI (a) is attained during the growing season. The exponential terms describe the change in NDVI and two phases are recognized: an increase in NDVI and a decrease in NDVI. The variable x is the independent variable; in this case it is a cumulative day counter (day 0 was arbitrarily set to 1 September 2008). The parameter l_1 describes the day on which the midpoint of the increase in NDVI is attained, and s_1 describes how rapidly NDVI changes as day number increases around point l_1 . The parameters l_2 and s_2 perform analogous roles except that they describe the pattern of decrease in NDVI at the end of the growing season.

In a second series of analyses we use the weather station data as forcing variables for the seasonal development of NDVI. Here we use the equation

$$f_2(x; l, s, a, b) = b + \frac{a - b}{1 + \exp[s(1 - x)]}, \quad (2)$$

where the parameter x is the forcing variable. Equation 2 is a sigmoidal function that describes, for both the onset and the decline of the growing season, how NDVI changes as a function of the forcing variable (see equation 4 for a description of how the parameters are estimated for both the onset and decline of the growing season). In preliminary analyses we selected between related candidate forcing variables, that is minimum daily temperature rather than mean daily or

maximum daily temperature, day length rather than photosynthetically active radiation or solar radiation. For soil moisture content we used a 7-day running mean. Instead of relative humidity metrics we used vapour pressure deficit (VPD, calculated following Allen *et al.*, 1998, from relative humidity and temperature measurements). The parameter l describes the location (in units of the independent variable x) of the midpoint of the change in NDVI, and s describes how rapidly NDVI changes as x changes around point l . The parameters a and b have the same interpretation as in equation 1.

We estimate the parameters using a Bayesian method. For model 1, the parameters s_1 , s_2 , l_1 , l_2 and a are treated as fixed effects of phenological type (factor F_i with three levels: EFT, LFT, grass). The parameter b describes the random effect of the individual canopy (factor C_i with 240 levels) on NDVI. The model can be summarized as,

$$\begin{aligned} y_i &\sim \text{normal}(\mu_i, \sigma) \\ \mu_i &= f_1(x; l_1[F_i], l_2[F_i], s_1[F_i], s_2[F_i], a[F_i], b[C_i]). \end{aligned} \quad (3)$$

For fitting model 2 the parameters s and l are treated as fixed effects of phenological type (factor F_i with three levels: EFT, LFT, grass) and phenological phase (factor P_i with two levels: onset and decline of the growing season). Parameter a is a fixed effect of phenological type (factor F_i with three levels: EFT, LFT, grass) and parameter b describes the random effect of the individual canopy (factor C_i with 240 levels) on NDVI. This model can be summarized as

$$\begin{aligned} y_i &\sim \text{normal}(\mu_i, \sigma) \\ \mu_i &= f_2(x; l[F_i, P_i], s[F_i, P_i], a[F_i], b[C_i]). \end{aligned} \quad (4)$$

All coefficients are assumed to have normal and uninformative priors. The variances of these priors are in turn assumed to have uniform and uninformative priors. We fitted the models using JAGS v. 1.03 (Plummer, 2009). JAGS is a program for the analysis of Bayesian models using Markov chain Monte Carlo (MCMC) simulation. The chains produced by JAGS were analysed using the coda package (Plummer *et al.*, 2009) of the R statistical language (R Development Core Team, 2009).

For each analysis multiple chains (each with 30,000 iteration burn-in followed by 20,000 updates) were run and visual examinations of diagnostic plots were used to confirm that chains had converged. The credible intervals (sometimes referred to as Bayesian confidence intervals) were estimated from the MCMC sample of the posterior distributions. To provide an approximate estimate of the how well the fitted models describe the data we calculate the R^2 statistics for all fitted models.

RESULTS

The results are summarized in two figures. Figure 2 shows the NDVI responses of the individual canopies plotted against a series of candidate driving variables, overlaid with the models

fitted to these data. Figure 3 shows the posterior parameter estimates of the model parameters. In the narration of the results, we describe differences between parameters as being significant if the 95% credible intervals of the parameters do not overlap (the 95% credible intervals are plotted in Fig. 3).

A plot of NDVI development over time (Fig. 2) reveals that there is a rapid onset of NDVI, which peaks 40–50 days after the onset of greening. This is followed by a gentle decline in NDVI, which is indicative of a slow but steady loss of leaves. The peak NDVI was significantly lower for grasses than for trees, and LFT had slightly higher (0.74 vs. 0.69) NDVI values than EFT (Fig. 3). The day of onset of NDVI was approximately 10 days earlier for EFT than it was for grasses or for LFT. That is, LFT and grasses did not differ significantly in the date of onset of leaf flushing. The decline in NDVI at the end of the growing season started approximately 16 days earlier for grasses than it did for LFT and EFT. The difference in the timing of decline in NDVI for the two tree syndromes was not significant. Taken together, the start of growing season and end of growing season differences mean that EFT have a 27-day and LFT a 20-day longer growing season than grasses. The rate of change in the onset period was fastest for grasses and slowest for EFT, although the difference between EFT and LFT was not significant. The fact that the rate of increase in NDVI was slowest for the EFT and fastest for the grasses ensured that all three strategies obtained their peak NDVI values at a similar point in time. The decline in NDVI at the end of the growing season generally occurred slowly, and there were no detectable differences in these rates between the three strategies. The R^2 of this fitted model was 0.735.

The relationship between NDVI and the 7-day running mean of minimum daily temperature (Figs 2 & 3) shows that EFT initiated their leaf deployment at temperatures approximately 0.86 °C lower than LFT and 1.8 °C lower than grasses. The slope of the NDVI response to increases in minimum temperature was steep for grasses, intermediate for LFT and shallow for EFT. The decline in NDVI at the end of the growing season was located at a higher temperature for grasses than for the two tree strategies. The two tree strategies did not differ in the location of the decline of NDVI. The rate of decline in NDVI as minimum temperature changed was more gentle than the rate of onset, and the differences between the three strategies were not significant. The R^2 of this fitted model was 0.584.

There was a rapid increase in NDVI as day length increased and a relatively slow decline in NDVI as day length shortened (Figs 2 & 3). The midpoint of the increase in NDVI was located at a day length of 12 h 58 min for EFT, 13 h 3 min for LFT and 13 h 9 min for grasses. The differences in the increase in NDVI in response to day length between the two tree syndromes were not significant, but the grasses did differ significantly from the trees. The slope of the response of NDVI to increasing day length was shallowest for the EFT, intermediate for LFT and steepest for grasses. The decline in NDVI in response to reductions in day length suggested that LFT delayed leaf abscission; this is evidenced by their significantly

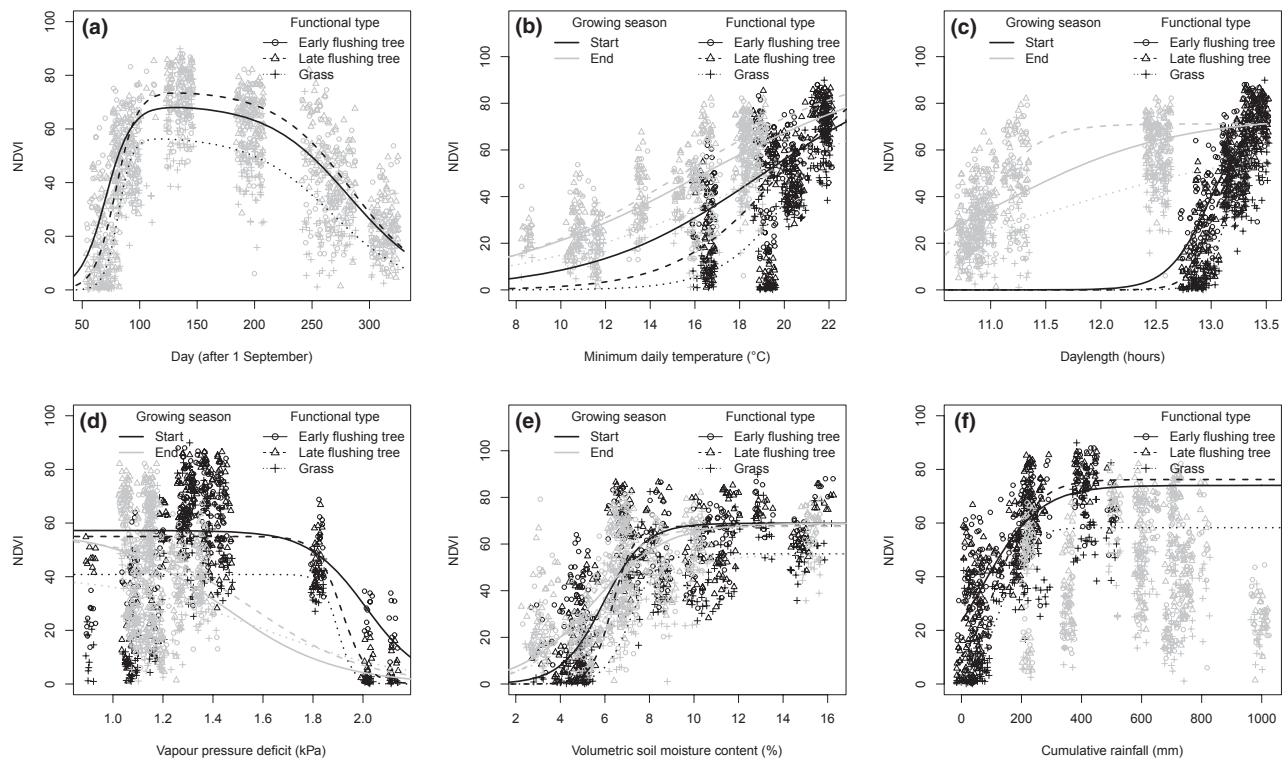


Figure 2 The response of normalized difference vegetation index (NDVI; expressed as a percentage) to (a) time (day of year), (b) minimum daily temperature, (c) day length, (d) vapour pressure deficit (VPD), (e) volumetric soil moisture content, and (f) cumulative rainfall at eight sites in Kruger National Park, South Africa. The responses of three different strategies (early flushing trees, late-flushing trees and grasses) are illustrated. The temperature, VPD and soil moisture variables are the mean of the preceding 7 days of measurements. For cumulative rainfall we only fitted the response surfaces to the start of the growing season data. The lines represent the model fits to the data. To prevent data points from being plotted on top of one another we added a small amount of noise to the position of the data points in relation to the *x*-axis. Each environmental driving variable increases as the growing season starts and decreases as the growing season ends (the exception being VPD, where the changes are the other way around).

steeper decline in NDVI, which was initiated only once day length was shorter than 11 h 30 min. The R^2 of this fitted model was 0.719.

The increase in NDVI was located at a VPD of 2.01 for EFT, 1.91 for LFT and at 1.89 for grasses (Figs 2 & 3). That is, grasses and LFT only initiated the leaf flush once the VPD had declined, whereas EFT trees initiated leaf flush under drier atmospheric conditions than the other two types. The rate of increase in NDVI as VPD declines was similar for grasses and LFT, and significantly slower for EFT. The location and slope of the decline in VPD did not differ significantly between the three strategies. The R^2 of this fitted model was 0.285. This poor fit can be explained by the fact that variance in NDVI is poorly explained for VPD values of less than 1.6.

An analysis of the effect of the 7-day running mean of soil moisture on the seasonal NDVI development (Figs 2 & 3) reveals that EFT deployed leaves at lower soil moisture

contents than LFT, which in turn deploy leaves at lower soil moisture contents than grasses. Although these differences were not significant, the fact that the slope of the NDVI response to soil moisture was lower for EFT than for the other two strategies was significant. The soil moisture contents at which NDVI declined did not differ between the three strategies, nor did the rate of decline. The slopes of the decline in NDVI as soil moisture decreased were substantially lower than the rates of increase. The R^2 of this fitted model was 0.533.

In a final analysis we examined how the increase in NDVI is influenced by cumulative rainfall (from 1 August 2008); only data from the first four surveys were analysed (Figs 2 & 3). We fitted a reduced version of the model described in equation 4. The parameters l and s are now only influenced by phenological type (F) because only the initial phenological phase (P) is considered. The NDVI increase in the EFT is initiated before

Figure 3 Summary of the posterior parameter estimates of the statistical models illustrated in Fig. 2: (a) time (day of year), (b) minimum daily temperature, (c) day length, (d) vapour pressure deficit, (e) volumetric soil moisture content, and (f) cumulative rainfall. The tick point indicates the location of the mean parameter estimate, the broad bar spans the 90% credible interval and the whisker bar spans the 95% credible interval. For further details see Fig. 2.

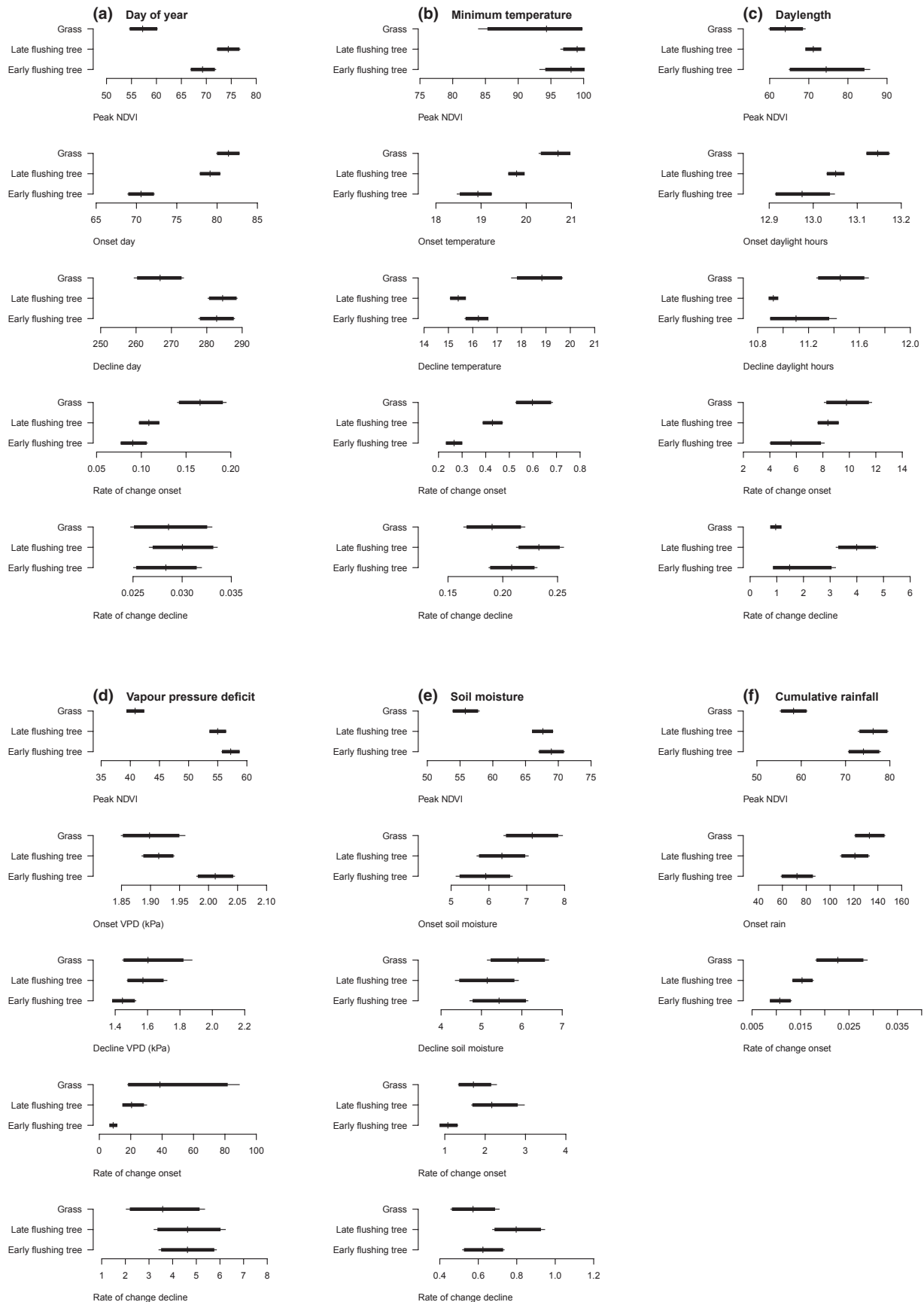


Table 2 Matrices of Pearson correlation coefficients between the forcing variables used in this study for the entire growing season in Kruger National Park and for the start and end of the growing season separately. The temperature, soil moisture and vapour pressure deficit (VPD) variables are the 7-day running means.

	Day length	Min. temp.	Soil moisture	VPD	Cum. rain
Entire growing season					
Day length	1.000	0.931	0.460	-0.412	-0.595
Min. temp.	0.931	1.000	0.558	-0.397	-0.527
Soil moisture	0.460	0.558	1.000	-0.387	-0.024
VPD	-0.412	-0.397	-0.387	1.000	-0.117
Cum. rain	-0.595	-0.527	-0.024	-0.117	1.000
Start of growing season					
Day length	1.000	0.823	0.696	-0.835	0.840
Min. temp.	0.823	1.000	0.643	-0.644	0.714
Soil moisture	0.696	0.643	1.000	-0.598	0.563
VPD	-0.835	-0.644	-0.598	1.000	-0.690
Cum. rain	0.840	0.714	0.563	-0.690	1.000
End of growing season					
Day length	1.000	0.897	0.628	-0.658	-0.019
Min. temp.	0.897	1.000	0.650	-0.444	-0.203
Soil moisture	0.628	0.650	1.000	-0.203	-0.055
VPD	-0.658	-0.444	-0.203	1.000	-0.052
Cum. rain	-0.019	-0.203	-0.055	-0.052	1.000

Cum. rain, cumulative rainfall from 1 August 2008.

rainfall starts. When the cumulative rainfall (Fig. 2) is zero, the 95% credible intervals of the EFT NDVI are 25–32% of their peak NDVI. LFT, although they reach 50% of their NDVI when the cumulative rainfall is some 48 mm higher than for EFT, also appear to initiate leaf flush before the rains start (at a cumulative rainfall of zero, the 95% credible intervals of their NDVI are 10–15% of their peak NDVI). Grasses initiate leaf deployment only after an additional 12 mm of rainfall and do not appear to pre-empt rainfall (the credible intervals of the NDVI estimates at zero rainfall are only 2–7% of the peak grass NDVI). The rate of increase in NDVI in response to rainfall is fastest for grasses. The consequence of this is that grasses and LFT reach 50% of the peak NDVI at similar levels of cumulative rainfall. The R^2 of this fitted model was 0.831.

There was a complex correlation structure between the forcing variables (Table 2). Some variables were strongly correlated at the onset of the growing season, yet weakly correlated at the end of the growing season. Strong correlations exist between minimum temperature and day length. VPD is weakly correlated with the other variables over the entire year, although it is well correlated with day length and cumulative rainfall at the start of the growing season.

DISCUSSION

Although the correlation structure between the forcing variables makes it difficult to interpret which variable is primarily driving the seasonal phenological patterns, there are several conclusions we can draw from these analyses. Rainfall clearly

did not, in this study, drive the deployment of the leaves of trees. Both tree syndromes we examined had already deployed leaves when the cumulative seasonal rainfall was still zero. These findings agree with results from other seasonally dry tropical systems. Williams *et al.* (1997) concluded that leaf flush was initiated before the onset of the wet season and Simioni *et al.* (2004) found that leaf flush was initiated under unfavourable soil conditions. Similarly, Borchert & Rivera (2001) reported phenological strategies that were not responsive to available moisture and de Bie *et al.* (1998) reported deciduous strategies where leaf expansion is initiated before the onset of the first rains. In contrast to the trees, grass green-up was closely associated with the onset of the first rains.

A strategy that pre-empt rainfall must rely on a cue other than precipitation. It is, however, difficult to identify this cue. We could, for instance, use the proportion of the variance explained by a statistical relationship between a candidate driver of NDVI to rank the candidate drivers. This would, for our study, identify day length and cumulative rainfall as the most likely forcing variables. One problem with this is that a putative driver might explain the cue for a phenological event poorly, yet might explain the subsequent development of that phenological phase well. For example, in our study rainfall cannot explain the timing of leaf deployment because it is clearly initiated before the rains, yet cumulative rainfall does the best job of statistically describing the subsequent pattern of increase in NDVI. An alternative, to focusing on variance explained is to focus on the magnitude of the responses. That is the response of NDVI at the start of the growing season to temperature is shallow, the response to soil moisture, daylight and VPD are steep and that the response to cumulative rainfall is intermediate. The very steep response of NDVI to changes in day length suggests that day length is an important driver of leaf deployment. Day length as the driver of NDVI is consistent with several previous studies of tree phenology in seasonally dry tropical and subtropical ecosystems. Borchert & Rivera (2001) concluded that photoperiod is frequently the cue for leaf phenological events in dry tropical ecosystems, while Williams *et al.* (2008) found that leaf flushing was often (38% of 24 species in a seasonal forest in Thailand) associated with changes in photoperiod. Similarly, Archibald & Scholes (2007) reported that the leaf phenological events of trees were remarkably consistent between years, implicating day length as the likely cue. However, in temperate systems Menzel *et al.* (2005) reported considerable variability in green-up dates, which suggests that green-up is not uniquely defined by day length in temperate systems. Day length as a cue for leaf initiation implies local adaptation, something which providence trials have demonstrated in other systems (e.g. Chmura & Rozkowski, 2002). We further wish to draw attention to the fact that although NDVI responded diffusely to changes in VPD, it did respond strongly to VPD changes in the 2.2–1.8 kPa range. That is, although our NDVI–VPD data are inconclusive, we suggest that future studies should examine whether changes in VPD may be a cue for the approaching rainy season.

The decrease in NDVI at the end of the growing season was less clearly linked to any of the candidate driving variables. There was a gentle decrease in NDVI with temperature, day length and VPD, suggesting that none of the variables controlled abscission. The decrease in NDVI responded more strongly to decreases in soil moisture. The rather lethargic and diffuse response of end of season NDVI is consistent with the work of Stöckli *et al.* (2008) who report that end of season events are often associated with more variance. The contrasting nature of the pattern of NDVI increase with the pattern of NDVI decrease implies either that there is a hysteresis effect, or more probably, the processes that drive leaf deployment differ from those that drive leaf abscission. Overall, our results suggest that all strategies we investigated were characterized by a steep increase in NDVI at the start of the growing season; the end of the growing season was in contrast characterized by a gradual and continuous decrease in NDVI.

We found it useful to distinguish between three different phenological strategies that differ in the extent to which leaf deployment pre-empts rainfall. Differences in leaf abscission strategies were less apparent. The EFT clearly pre-empted rainfall, the LFT to a lesser degree, while the grasses appeared to deploy leaves only after the initial rains. All trees in this study appear to fit into Singh & Kushwaha's (2005) '> 4 month deciduous/spring flushing' strategy whereas the grasses fit the '> 4 month deciduous/rainy flushing' strategy. Borchert & Rivera (2001) distinguished two phenological strategies amongst trees in a seasonally dry tropical forest. Their deciduous strategy is defined as 'species (that) shed their mesic leaves during the early dry season, remain desiccated during the remainder of the dry season, and flush synchronously after the first major rains have caused re-hydration of the top soil during the early wet season' (Borchert & Rivera, 2001, p. 213). Their stem succulent strategy initiates leaf expansion 'weeks before the first major rains' and leaf abscission is synchronous (Borchert & Rivera, 2001, p. 213). Our 'early-flushing strategy' is similar to their stem succulent strategy, yet does not exhibit synchronous leaf abscission. Our late-flushing strategy although similar to their deciduous strategy, appears to flush leaves before the first major rains (we found that 10–15% of the peak NDVI of LFT is achieved before the onset of the rain season). Hence, although the Borchert & Rivera (2001) system provides a useful framework for thinking about leaf phenology in seasonally dry deciduous systems, our two tree strategies do not perfectly match their classification.

The early and late-flushing strategies we report resemble more closely the two phenological strategies described by Rossatto *et al.* (2009) in Brazilian savannas. They examined congeneric pairs of savanna and forest tree species growing in savanna conditions and found that leaf deployment in both groups occurred before the rains, with the savanna trees deploying their leaves earlier than the forest trees, analogous to our EFT and LFT. In further agreement with our study, Rossatto *et al.* (2009) report that neither group differed in the

timing of leaf abscission. Rossatto *et al.* (2009) argue that early flushing in savanna trees is a strategy to avoid nutrient losses by pre-empting insect phenology and thereby reducing exposure to herbivory at a critical phase in leaf development. This herbivory hypothesis is unlikely to be valid in our study area where one would expect large mammalian herbivores to target EFT. An alternative hypothesis suggested by Rossatto *et al.* (2009) was that EFT might avoid rainfall-induced nutrient leaching.

Most studies of leaf phenology concentrate on single phenological events and fewer examine the growing season length (Menzel & Fabian, 1999; Stöckli *et al.*, 2008). Moreover, the temporal niche separation hypothesis (Scholes & Walker, 1993) has emphasized differences in tree and grass phenology at the start of the growing season. For example, in miombo savanna Chidumayo (2001) showed that dominant tree species initiated leaf growth earlier than grasses, but he did not examine the leaf abscission phase. By following an entire phenological cycle, we show that EFT have a growing season length of 212 days, LFT a growing season length of 205 days and grasses a growing season length of 185 days. The implication is that EFT in our study area have a 27-day period when they are not exposed to grass competition and only a 7-day period when not exposed to competition from LFT. LFT, by contrast, have a 20-day period in which they are free of intense grass competition. The asymmetry in the seasonal NDVI cycle means that temporal niche separation may be more pronounced at the end of the growing season, where trees appear to delay leaf abscission. This statement, however, assumes that the resource axis is time. In reality, time in the temporal niche hypothesis is a proxy for some undefined resource or suite of resources that vary in availability over time. This study has merely identified periods when grasses and trees differ in their phenological activity. The next step for developing the temporal niche hypothesis is to examine how these differences in phenological activities influence the availability and uptake of limiting resources over a seasonal cycle.

It would be convenient for remote sensing studies of savanna phenology if trees produced leaves before grasses did, as this would allow one to separate the grass and tree signals in satellite imagery (Chidumayo, 2001; Archibald & Scholes, 2007). Our study illustrates, however, that the timing of leaf flushing in grasses and LFT (which in our study area constituted 80% of tree cover, Table 1) were indistinguishable on a temporal and on a cumulative rainfall axis. However, we find separation in phenological behaviour on the minimum temperature and day-length axes, which suggests that LFT and grasses have different phenological strategies.

In conclusion, we have shown that grasses and trees have different leaf deployment strategies. Trees deployed leaves at lower temperatures than grasses and retained them for longer at the end of the growing season. The differences in leaf deployment were more exaggerated at the end of the growing season. Although we could rule out rainfall as a cue for the deployment of tree leaves, we could not identify the

environmental cues for leaf phenological events, nor could we illustrate whether the identity of the cues differed for grasses and trees.

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BIOSKETCH

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