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Leaf green-up in a semi-arid African savanna – separating tree and grass responses to environmental cues

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Abstract

Question: Can satellite time series be used to identify tree and grass green-up dates in a semi-arid savanna system, and are there predictable environmental cues for green-up for each life form?

Location: *Acacia nigrescens*/*Combretum apiculatum* savanna, Kruger National Park, South Africa (25° S, 31° E).

Methods: Remotely-sensed data from the MODIS sensor were used to provide a five year record of greenness (NDVI) between 2000 and 2005. The seasonal and inter-annual patterns of leaf display of trees and grasses were described, using additional ecological information to separate the greening signal of each life form from the satellite time series. Linking this data to daily meteorological and soil moisture data allowed the cues responsible for leaf flush in trees and grasses to be identified and a predictive model of savanna leaf-out was developed. This was tested on a 22-year NDVI dataset from the Advanced Very High Resolution Radiometer.

A day length cue for tree green-up predicted 86% of the green-ups with an accuracy better than one month. A soil moisture and day length cue for grass green-up predicted 73% of the green-ups with an accuracy better than a month, and 82% within 45 days. This accuracy could be improved if the temporal resolution of the satellite data was shortened from the current two weeks.

Conclusions: The data show that at a landscape scale savanna trees have a less variable phenological cycle (within and between years) than grasses. Realistic biophysical models of savanna systems need to take this into account. Using climatic data to predict these dynamics is a feasible approach.

Keywords: Biophysical model; *Combretum apiculatum*; Environmental predictor; MODIS; NDVI; Phenology.

Abbreviations: AVHRR = Advanced Very High Resolution Radiometer; MODIS = Moderate Resolution Imaging Spectroradiometer; NDVI = Normalized Difference Vegetation Index; PET = Potential evapotranspiration.

Introduction

The recognition of human-induced global climatic change has renewed scientific interest in the environmental controls of vegetation dynamics – particularly the cues for leaf flush and leaf fall (Chase et al. 1996; Jolly et al. 2005; Menzel 2002). Small changes in temperature can result in large changes in the timing and duration of leaf display, which in turn, feed back to large changes in global CO_2 cycles (Keeling et al. 1996; Myneni et al. 1997). Reliable phenology models are therefore essential for predicting global change (Chase et al. 1996).

Furthermore, the timing and duration of leaf display affect a range of ecosystem processes – from carbon, water and energy exchange to forage availability. A delay of a few weeks in the production of new leaves can make a difference to the survival and reproductive success of the herbivores that depend on them (Owen-Smith & Cooper 1989). Thus, climatic changes, by altering the length of the growing season, can have cascading effects on other ecosystem processes.

Environmental cues of leaf phenology are well understood in temperate systems (Cannell & Smith 1983; Chuine & Cour 1999; Nizinski & Saugier 1988; Seiwa 1999). Temperature and photoperiod (day length) control phenology in the high latitudes, but there are conflicting opinions on their importance in systems like tropical savannas where water, not temperature or light, is often the limiting factor for growth (Scholes & Walker 1993). Savannas cover about a sixth of the global land surface (Scholes & Hall 1996) and are second only to forests in their carbon fluxes and storage, so a robust understanding of their phenology has implications for the global carbon cycle.

Predicting savanna phenological patterns is complicated for two reasons. Firstly, although water availability is identified as an important seasonal driver (Reich & Borchert 1984; Singh & Kushwaha 2005), it is difficult to measure at regional scales, and no phenology models have yet been developed that adequately incorporate soil moisture. Rainfall data and calculations of potential evapotranspiration (PET) both fall short – rainfall because it reflects only the input side of the water balance and

is an episodic rather than continuous variable, and PET because it is not known how much water is present to be evaporated.

Unlike in temperate systems – where low winter temperatures pose a barrier to growth of most plant-types – in rainfall-driven systems there is the potential for a range of different strategies, depending on an organism's ability to store/access water. Thus seasonal responses of savanna plant species are closely linked to their structure and function. Many tree species are known to put on leaves before the first rains of the season (Do et al. 2004; Schackleton 1999; Milton 1989) whereas growth of grasses is always limited by water availability (Dye & Walker 1987; Prins 1988).

Because trees and grasses have different seasonal patterns of leaf display a generalised phenology model for savannas needs to incorporate both responses. The large-scale, long term datasets provided by satellite imagery (Reed et al. 1994) are of little use in savannas unless it is possible to separate the contributions of these two main functional types to the landscape greenness.

The problem of separating trees and grasses has not been adequately addressed in remote sensing studies of savannas. Jolly & Running (2004) ignored the grass component entirely, which resulted in over-prediction of early green-up in sites with a high grass cover. Chidumayo (2001) assumed that tree and grass green-up times are distinctly separated – that before December, increases in the Normalised Difference Vegetation Index (NDVI) are due to tree leaf-out, and after December, due to grass growth. This is clearly not true: Van Rooyen et al. (1986a) report grass growth to begin as early as August in some years, while some trees only reached full leaf late in December.

Describing soil moisture availability and separating tree and grass responses have been identified as the two main factors limiting our ability to model canopy dynamics in savanna systems (Jolly & Running 2004). This study attempts to resolve both of these issues.

Firstly, instead of using rainfall or PET as surrogates for water availability, a soil moisture model was developed, which was tested using a four year soil moisture dataset. The modelled soil moisture provides a realistic measure of water availability at a daily time-step over a 40 year period.

Secondly, ecological theory and data was used to separate tree and grass phenological patterns from a single remotely-sensed signal of greenness (NDVI). Trees have a much more deterministic pattern of growth: stored water reserves make them less dependent on the timing of rainfall than grasses and their maximum leaf area is limited by hydraulic and architectural constraints (Berninger et al. 1995; Woodward 1987). Our approach therefore involved quantifying the key characteristics of tree green-up, and using that to extract the more variable grass response from a time-series of NDVI data at a site near Skukuza in the Kruger Park, South Africa. The environmental conditions associated with leaf flush of trees and grasses were then identified, and the results were tested on a 22 year NDVI time-series from the same site.

This approach aims to use the great amount of facts that *is* known about savanna tree and grass ecology in order to add meaning to datasets that provide large-scale and long-term information. The ultimate goal is a predictive model of tree and grass phenology that accurately represents the ecology of the system but is broad enough to apply at a regional level.

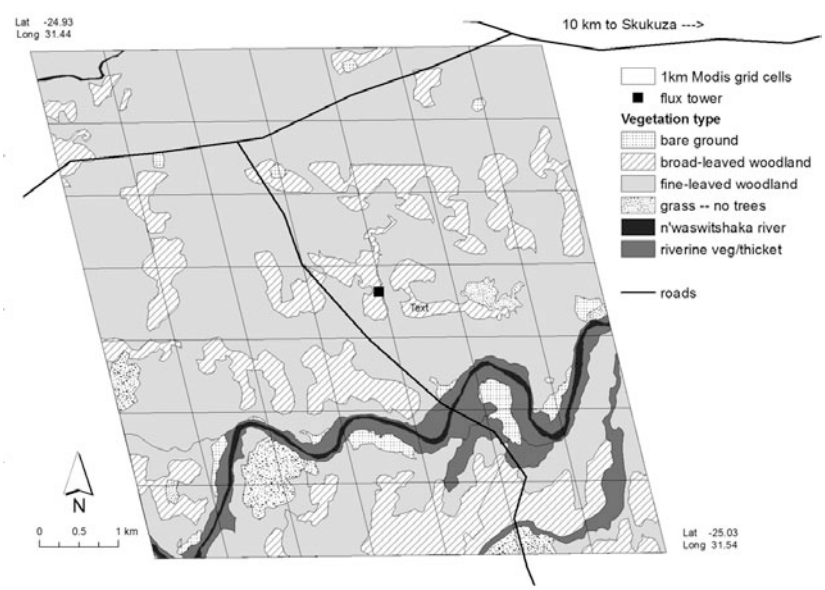

Fig. 1. Study site at the flux tower near Skukuza, in the Kruger park. The broad-leafed *Combretum* and fine-leafed *Acacia* vegetation types (associated with sand and clay soils respectively) are distributed patchily through the landscape, according to the catenal sequence. The flux tower is placed at a transition between vegetation types (Scholes et al. 2001).

Material and Methods

Study area

The Skukuza area of the Kruger National Park is a semi-arid savanna system (570 mm mean annual rainfall, 22ºC mean annual temperature). The 7 km × 7 km landscape block for which regular MODIS imagery was collected is centred on a flux tower, 19 km WSW of Skukuza village (Fig. 1) which was set up in 2000 (Scholes et al. 2001).

The gently-rolling granite-based landscape is composed of two main vegetation and soil associations: the soils on the ridge crests are sandy, and support a broad-leafed savanna dominated by *Combretum apiculatum*. Some distance down the slope, a sharp transition, marked by a narrow seepline, to *Acacia nigrescens*-dominated fine-leafed savannas occurs. *Sclerocarya birrea* is a common tree on both soil types. There is a narrow strip of riparian vegetation associated with the N'waswitshaka river at the bottom of the slope.

The flux tower is located on the boundary between the two vegetation types. Instruments on the tower measure a range of meteorological variables, as well as net ecosystem exchange of CO_2, water and energy, at 30 minute intervals. Soil probes measure soil water and temperature at four depths in the *Combretum* and five in the *Acacia* savanna.

Daily weather data for the period 1960 to 2005 is available for Skukuza village from the South African Weather Bureau. The climate is characterised by a dry season which coincides with decreased winter temperatures (April to November), and between-year variation in rainfall is high. In this it is typical of many tropical savanna systems.

Data acquisition

Satellite data

While Leaf Area Index (LAI) is the most accurate measure of the photosynthetic capacity of vegetation it is difficult to measure remotely, and there are no accurate LAI products yet available for savanna systems. The Normalised Difference Vegetation Index (NDVI) (Reed et al. 1994) is a good indicator of leaf area, especially in open systems like savannas where it never reaches saturation values. Using NDVI as the measure of phenology also means long-term AVHRR datasets can be used to test results.

Training dataset

NDVI was calculated (near infrared-red)/(near infrared+red) from 16-day MODIS NBAR (MOD43B4) reflectance data for the Skukuza Flux site, obtained from the Oak Ridge National Laboratory ASCII subsets (www.Modis.ornl.gov/Modis). This product is Bidirectional Reflectance Distribution Function (BRDF) corrected, and the algorithm excludes cloud-contaminated pixels. Only those data points classified as 'good quality' by the QA flag were used.

The BRDF-adjusted dataset is a 16-day composite which is a rather coarse time-interval with which to study seasonal changes in phenology. However, year-to-year climatic variability at the site shifts the growing season by as much as three months, so even a 16-day resolution should be sensitive to the main cues. The MODIS bands used in calculating NDVI have a fundamental resolution of 250 m, but the spatial data resolution of the available product was 1 km. To further reduce variation, the 49 pixels in the 7 km × 7 km study area were averaged to produce one value for each time step (see Kang et al. 2003).

This 5-year MODIS NDVI was used as a training dataset to find the environmental cues for green-up.

Validation dataset

A long-term 22-year NDVI dataset was used to test the predictive ability of the green-up cues. The Global Inventory Modelling and Mapping Studies (GIMMS) fifteen-day Advanced Very High Resolution Radiometer (AVHRR) NDVI data was used (Tucker et al. 2004). Because the data come from several different satellites in the NOAA series, there are problems with using AVHRR data for time-series comparisons (DeFries et al. 2000). The GIMMS data provide the best available corrections for calibration, view geometry, aerosols, and are corrected for sensor drift. The moving average method used to determine green-up date avoided some of the problems associated with sensor drift as it did not depend on minimum or maximum values. This method also meant that we could use data from two different sensors for training and validation without increasing potential error sources due to slight differences in NDVI between MODIS and AVHRR (Gallo et al. 2004).

High-resolution satellite data

A 1 m resolution Ikonos image (available for the site through the Safari 2000 project) was used to quantify the percentage cover of tree, grass and bare ground in each 1000 m MODIS pixel in March 2002 (end of the growing season).

Soil moisture modelling

A simple water-balance model was developed to provide a daily measure of soil moisture. Potential evapotranspiration was calculated from air temperature, humidity, wind-speed and radiation data using the Penman-Monteith method. Daily rainfall and vegetation cover data (NDVI) were used as inputs in a four-layer bucket model calibrated to the soil properties at the site. This modelled data fit well with the available soil moisture data at the site.

Using NDVI data as an input to the soil moisture model (one of the predictor variables), as well as the measure of LAI (dependent variable) is unavoidable as it is the only long-term measure of greenness available. However, there are several reasons why this should not invalidate the predictive power of the analysis:

- The relationship between NDVI and soil moisture in the model is non-linear, and mediated by numerous other independent factors.
- NDVI is used as an indication of the amount of transpiration that is occurring in the soil moisture model. Transpiration can only occur once vegetation has flushed. In this instance soil moisture is used as a predictor of vegetation flush, under conditions where there is no transpiration subroutine, and therefore, no circularity.
- Finally, the analysis was also run using the five years of available soil moisture data at the site with exactly the same results, indicating that the relationships found were real, and not artefacts of the NDVI data input.

Environmental cues of leaf flush

Daily meteorological data from Skukuza village was used to collate a dataset of all environmental conditions potentially affecting leaf phenology. Previous studies have identified temperature, day length, relative humidity, and soil moisture as cues for leaf flush in savanna trees (Chidumayo 2001; Childes 1989; Do et al. 2005; Dye & Walker 1987; Jolly & Running 2004; Rutherford & Panagos 1982; Van Rooyen et al. 1986b). There is a lot of evidence that grass growth patterns are linked to water availability (Dye & Walker 1987; Prins 1988), but there could also be a temperature constraint (Leigh 1960).

Cues found to be important in more temperate areas (Cannell & Smith 1983; Chuine & Cour 1999; Nizinski & Saugier 1988; Seiwa 1999) were also included. In total, eight factors were considered: day length, degree-days (cumulative average temperature starting July 1), minimum temperature, maximum temperature, rainfall, cumulative rainfall, soil moisture, and relative humidity (Table 1).

As the time step of the satellite data was two weeks, 15 day averages for the relevant variables were also calculated, to see whether this improved the predictive capacity of the model.

Field data collection

The pattern of tree green-up at the study site was monitored from September to January in 2005-2006 using two methods.

Table 1. Summary of environmental variables tested as potential green-up cues in a semi-arid savanna system in the Kruger National Park, South Africa. Temperature, soil water, and relative humidity variables were averaged to encompass the conditions over the 2-week NDVI time step.

Environmental factor	Variable used in analysis	Reference
Photoperiod	Daylength	Number of hours of sunlight. Found to be important in temperate systems, potentially important in savanna trees (Milton 1987; Van Rooyen et al. 1986b)
Temperature	Tmin	Minimum temperature. Possibly important in preventing growth during un-seasonal mid-winter rainfall events (Everson & Everson 1987; Leigh 1960)
	Tmax	Maximum temperature — hypothesised as important in savanna tree green-up (Milton 1987; Rutherford & Panagos 1982)
	15DayAvgMinT	15 day moving average
	15DayAvgMaxT	15 day moving average
	DegreeDay	Cumulative average temperature (starting July 1). Found to be an important cue in temperate systems (Cannell & Smith 1983; Chuine & Cour 1999)
Soil moisture	Rainfall	Daily rainfall. Affects soil moisture but not a good indication of water availability to plants on a daily level
	15DayAvgRain	15 day moving average
	CumRain	Cumulative average rainfall (starting July 1). Suggested as a potential cue in savanna systems (Fuller 1999; Prins 1988)
	SM	Soil moisture. Thought to be the driver of grass green-up (French 1974; Prins 1988). Potentially important for tree green-up (Borchert 1994; Childes 1989; Jolly & Running 2004; Prins 1988)
	15DayAvgSM	15 day moving average
Atmospheric conditions	RH	Relative Humidity – found to be a predictor of tree green-up in *Acacia tortilis* in West Africa (Do et al. 2005).
	15DayAvgRH	15 day moving average

1. Eight trees of the four major species (*Combretum apiculatum, Sclerocarya birrea, Acacia nigrescens,* and *Acacia nilotica*) were marked and photographed once a week. The amount of green leaves on each tree was classified as: 0 (no green leaves) 1 (a few green leaves) 2 (some green leaves) 3 (half of the tree is green) 4 (more than half of the tree is green) and 5 (in full leaf). These data were summed each week to give a green-up curve for the season.
2. Eight oblique photographs were taken from the top of the 20 m flux tower each week. These were superimposed in image processing software and the greenness of each tree in the picture monitored using the same method as above. Trees were categorised as shrubs (< 2 m), small trees (2-6 m) or large trees (> 6 m). A green-up curve was produced for the entire landscape by multiplying the size of the tree by the greenness of the tree at each sampling date, and summing the values.

Data analysis

Extracting green-up dates

Different methods for extracting green-up dates have been reported in the literature. White et al. (1997) used a seasonal time-course of AVHRR NDVI data, and defined the green-up date as the day of year when NDVI rose above a threshold of 0.5 of the maximum NDVI. Kang et al. (2003) expanded this technique using different green-up thresholds. Zhang et al. (2003) fitted a logistic function to each green-up period and looked for rates of maximum change in the derivative of the curve (local maxima in the second derivative).

This analysis used a method modified from Reed et al. (1994). A moving average of the previous four time steps was compared with the raw NDVI data. Tree green-up date was defined as the first date after July 1 when the real-time NDVI value was greater than the moving average (Fig. 2). This method identifies times when the NDVI showed a sudden increase, a signal of the beginning of photosynthetic activity.

For the Skukuza landscape and data this method is superior to other methods because it does not require the maximum and minimum NDVI values to be defined *a priori*. In savannas inter-annual variation in rainfall results in highly variable LAI between years. It is therefore not possible to determine a maximum or minimum value which applies for all years.

Finally, the aim was not to isolate the period of most rapid change in NDVI (e.g. White et al. 1997) but the moment when green leaves first appear in the landscape. Reed et al. (1994) used a nine time-step moving average. However, in savannas many trees hold on to their leaves until late in the dry season, and the NDVI drops to its lowest value for only ca. 2 months. A shorter moving mean period of four time steps (2 months) was better able to represent the dry season values in the study system.

Tree-grass separation

In its simplest (linear) form a green-up curve can be defined by three variables: the date at which bud-burst occurs, the maximum LAI attained, and the time taken to get fully green. These values can easily be extracted from NDVI satellite data in homogeneous vegetation types. However, savannas consist of a quasi-continuous grass layer, overlaid by a discontinuous tree layer. The NDVI value recorded by the satellite at a spatial resolution of hundreds of metres is therefore a combination of the contributions by trees and grasses. It is not valid to use NDVI as a measure of leaf phenology in savannas unless its composite parts can be un-mixed.

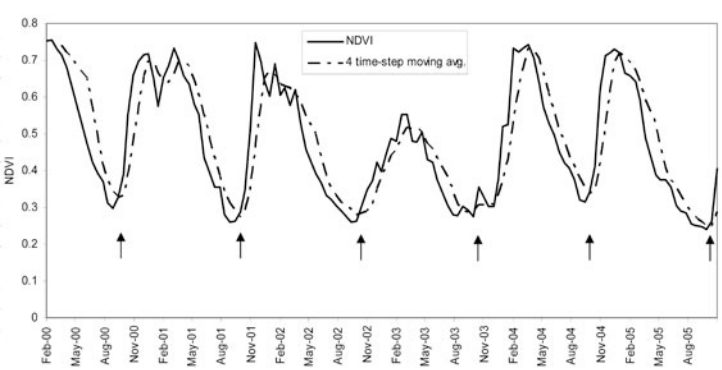

Fig. 2. A five-year time series of MODIS NDVI data showing the method for determining green-up date. Unlike the more deterministic temperate and arctic vegetation types, the shape of the NDVI curve in tropical savannas varies greatly between years (2002/2003 was a drought year). When the NDVI time series crosses a moving average of the previous four time steps, green-up is said to have occurred – indicated by arrows in the figure.

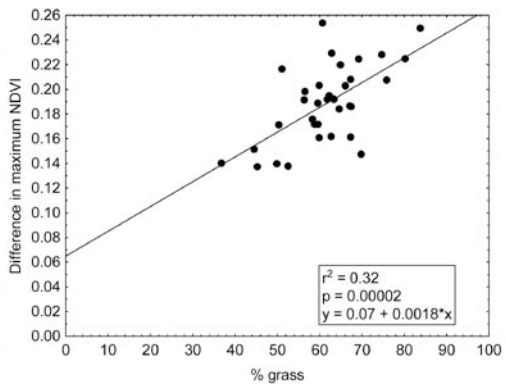

Fig. 3. Change in maximum growing season NDVI values between a very wet year (2004: MAR 760 mm) and a very dry year (2002: MAR 300 mm) shows a positive correlation with the percentage of grass in a plot. Extrapolating the fit back to 0 percent grass (100 percent tree) gives a difference in NDVI of 0.07, but a 60% grass layer can result in variations in NDVI of almost 0.2 between years. This suggests that the grass layer is the major cause of variation between years.

There are various characteristic differences in the biology of trees and grasses that might make this possible: Grasses cannot start leaf expansion until there is water available in the soil, whereas many trees rely on water stored in the tree stem, or possibly very deep soil layers, to start greening up before the first rains (Borchert 1994, 1999; Reich & Borchert 1984). Conversely, the leaf area that trees can support on a given stem in a single season is constrained by the cross sectional area and hydraulic conductivity of the sapwood and the number of active bud initials (Berninger et al. 1995; Woodward 1987). Grasses, on the other hand, can continue amassing leaf area until the self-shading limit is reached, because although each grass tiller has a limited leaf number, new tillers are easily produced throughout the season if conditions permit (O'Connor 1993).

With this information, three basic assumptions about tree phenology can be made:

- *The first greening signal shown by the NDVI data is due to tree leaf flush*. This is a reasonable assumption except in very unusual years when rainfall occurs 2-3 months earlier than usual (this happened only twice in the 46 year rainfall record available).
- *Maximum tree greenness values are constant between years*. A regression of variance in maximum NDVI against percentage tree cover (Fig. 3) shows that most of the variation in greenness between years is contributed by the grass layer (Scanlon et al. 2002). Field measurements of NDVI for individual trees in full leaf, combined with information on the percentage cover of trees at the site can therefore be used to calculate the maximum NDVI contributed by trees (see App. 1), and this can be considered to be constant between years.
- *Tree green-up rates are constant between years*. A 10-year dataset of tree phenology records from Nylsvlei Nature reserve corroborate this assumption (unpubl. data, Scholes & Walker 1993). What is not known is whether tree green-up rates are similar between sites, so field data was used to determine the green-up rate for trees at the Skukuza site.

Thus the three key green-up variables for the tree layer at the Skukuza site were identified: *green-up date* (directly from the satellite data), *maximum greenness* (measured values of tree NDVI modified by the percentage tree cover in a pixel), and *green-up rate* (quantified from data collected at the site during 2005). The green-up curve for grass could then be backed out of the NDVI data by subtracting the contribution of the tree layer (see Fig. 4).

Because of the multiple scattering of radiances within a multi-layered plant cover one should be cautious in using linear un-mixing to extract the different components of NDVI signals (Huete 1986; Myneni et al. 1995). However, one can approximate green-up dynamics by assuming that the total NDVI of a landscape is made up of the fractional NDVI sum of the of various cover types: trees, grass, and bare ground – because the overall leaf area is relatively low, as is the tree cover percentage.

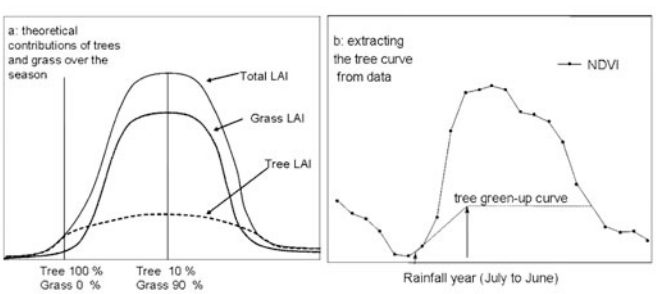

Fig. 4. a. Theoretical contributions of trees and grass to total landscape LAI over a growing season. Trees go green earlier, and stay green for longer, but grasses have a higher LAI at the height of the growing season. b. Schematic showing how to extract the tree green-up curve from satellite NDVI data. The parameters required to derive a tree phenology curve are: (1) tree green-up date (the first sign of increased NDVI in spring); (2) the maximum greenness trees can attain in the landscape (calculated from the percentage of tree cover) and (3) the time taken to get from green-up to full leaf (green-up rate – observed from field data).

Table 2. Green-up statistics for the three main species at the Skukuza study site. Photographs of about eight individuals of each species were taken once a week over the 2005/6 growing season and classified on a scale of 0 (no leaves) to 5 (full leaf).

	Green-up date		Green-up time (weeks)		
	average	std dev	average	std dev	*n*
Sclerocarya birrea	15 Oct 2005	3 days	8.4	0.5	7
Acacia nigrescens	22 Oct 2005	17 days	7.9	2.1	9
Combretum apiculatum	11 Nov 2005	10 days	5.6	1.6	8

Determining environmental cues

Rather than looking for general correlations between NDVI and environmental data (e.g. Chidumayo 2001; Do et al. 2005) the aims of this research were more specific: first to identify the green-up date for trees and grasses and discover whether these were clearly associated with an environmental factor which could then be assumed to be a green-up cue. Second, to see how accurately this identified cue could predict green-up in a different NDVI dataset.

A classification tree approach was used to isolate the conditions necessary for green-up. A classification (or decision) tree is a non-parametric procedure that uses hierarchical decision-making to predict the occurrence of a certain condition based on the values of various predictor variables (Breiman et al. 1984; Anon. 2005). In this instance the procedure systematically searches for values of the predictor variables, which would separate 'green-up' from 'non green-up'.

Environmental conditions on all dates prior to and including green-up date were used as inputs, and each date was classified as 1 (green-up) or 0 (no green-up).

The classification method used was a Classification and Regression Trees (C&RT-style) exhaustive search for univariate splits (Anon. 2005). Fact-style directive stopping was used (Loh & Vanichestakul 1988), and the classification stopped when < 0.01 of the sample was misclassified. The probability of a green-up event was determined from the proportion of 1's and 0's in the dataset (i.e. about 1:10).

Results

Measured green-up characteristics of the tree layer

The first significant rains in the 2005-2006 growing season (86 mm overnight) fell on November 5. All tree species monitored at the site had already started to put on leaves before this date, except for *Combretum apiculatum* and *C. zeyheri* which started greening up at the same time as the grasses (16 November); see Fig. 5.

Species varied in their dates of bud-burst and reaching full leaf-out (Table 2). Trees such as *Combretum apiculatum* that started greening later in the season took a shorter time to get to full leaf than the early flushers, e.g. *Acacia nigrescens*. A regression of green-up date against green-up time had an r^2 of 0.87 ($P < 0.01$; $n = 24$). Thus, despite differences in leaf out date, most trees reached full leaf at about the same date (16 December).

It took 8 weeks from the date the first trees started leafing until all trees in the landscape were in full leaf. (Rutherford & Panagos 1982), in a similar savanna system, also found a tree green-up period of 8 weeks.

Although the green-up curve for each species was functionally linear (Fig. 5), inter-species differences in date of first green-up meant that the tree layer overall displayed a sigmoidal green-up curve. Therefore the proportion of late-greening species like C*ombretum apiculatum* in a landscape is likely to affect the shape of the green-up curve. The analysis in this paper used a linear simplification to describe the green-up curve, but this could be modified to fit the data more precisely.

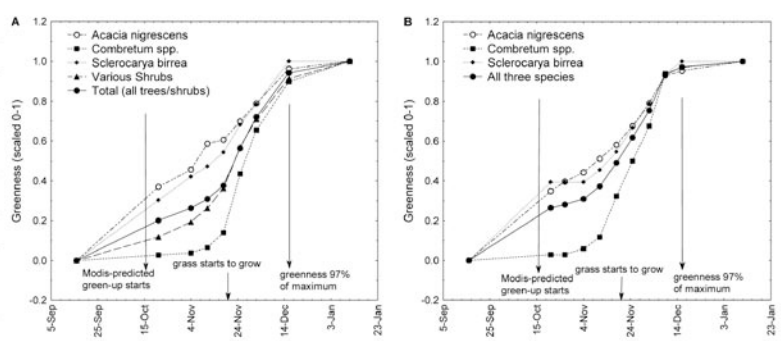

Fig. 5. Showing tree green-up pattern over the 2005 rainfall year at the Skukuza flux site. Although varying in dates when green-up started, all species were fully green by mid December. Data were extracted from weekly photographs taken at the site. A. Landscape analysis (aerial photographs); B. species-specific analysis (individual photographs of the three dominant species).

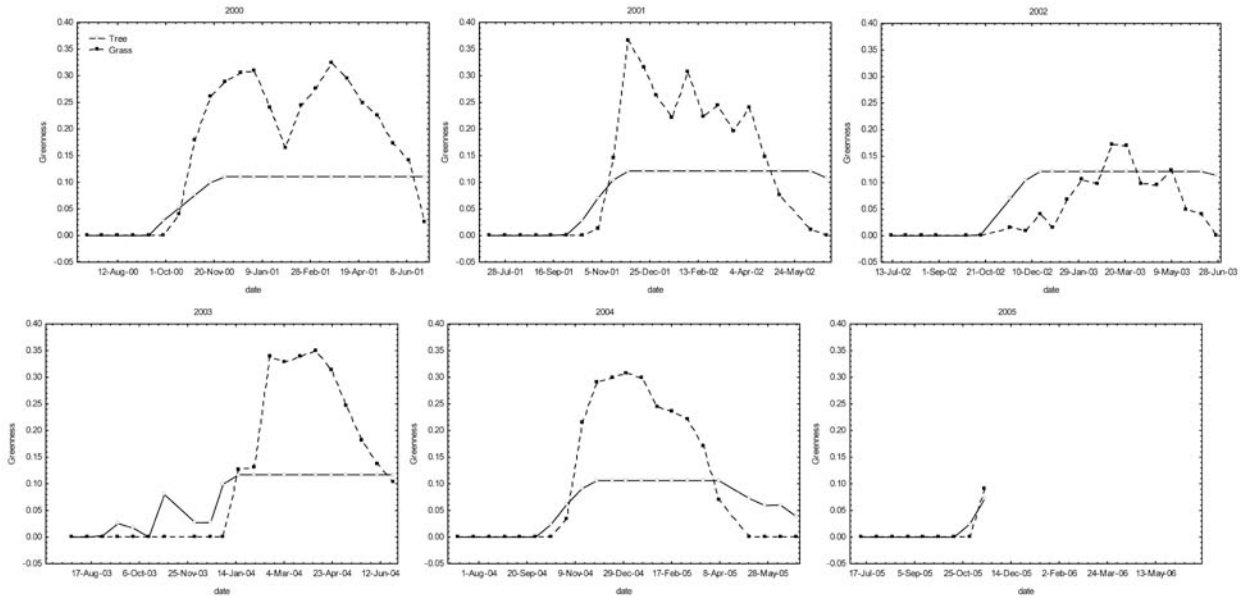

Fig. 6. Tree and Grass green-up curves for each year of the MODIS NDVI dataset. The tree green-up curve was extracted from the raw data using field observations of green-up rates and theoretical computation of maximum greenness values for trees in the landscape. This was then subtracted from the total landscape NDVI to obtain the grass curve. In 2002 there was a drought, and very little grass growth occurred.

Green-up date

The moving average algorithm identified the first greening signal in the NDVI data to occur consistently between the 29.09 and 16.10 (17 days – Table 3). Considering that the time step of observation was 16 days this represents a remarkable regularity in the timing of leaf flush for savanna trees at the site. Where field data was available (2005), it corroborated the tree green-up date identified from the NDVI signal (Fig. 5).

The tree green-up curve was then defined using methods described above, which allowed the grass green-up curve to be extracted from the NDVI signal (Fig. 6).

The moving average algorithm was re-run to determine the grass green-up date. This data was much more variable between years – as would be expected from a life form that depends on rainfall for growth. The earliest grass green-up date identified was October 31 and the latest January 17 — a range of 78 days, or nearly three months (Table 3).

Environmental cues for green-up

A classification tree procedure was used to see whether the green-up dates identified with the NDVI time series could be predicted from environmental data. The 6 year MODIS time series was used as training data, and the 22-year GIMMS time series was used as testing data for the classification tree.

Developing a predictive model

The classification tree identified a mean soil moisture > 0.09 cm^3/cm^3 to be the threshold above which grass green-up will occur. This method correctly classified all six grass green-up events in the 6-year MODIS time series and falsely identified four green-up events. (N = 60, prior probabilities estimated from data, analysis stopped when < 0.5 % of sample was misclassified).

Day length was the most important predictor of tree green-up. A threshold day length of greater than 12.1 hours correctly identified all tree green-up events, but also generated three false green-up events (N = 43, prior

Table 3. Green-up dates for trees and grasses at Skukuza – calculated from NDVI data by extracting the tree green-up curve from the raw data and running the green-up algorithm on the remaining data to find the grass green-up date. Grasses vary more than trees do in the timing of green-up between years.

	Tree green-up		Grass green-up	
Year	Date	Day of year	Date	Day of year
2000	29.09.2000	91	31.10.2000	123
2001	30.09.2001	92	17.11.2001	140
2002	16.10.2002	108	19.12.2003	172
2003	16.10.2003	108	17.01.2004	201
2004	29.09.2004	91	16.11.2004	139
2005	16.10.2005	108	17.11.2005	140
Average	07.10	100	30.11	153
Range	17 days		78 days	
SD	9 days		29 days	

probabilities estimated from data, 0.5% misclassification threshold).

Importance values of the different environmental variables (Table 4) show the differences between the two life forms. Day length clearly emerges as the most important factor for tree green-up, followed by various indicators of temperature. Rainfall and soil moisture indicators were not important for tree green-up. Soil moisture and relative humidity were most important for grass green-up, followed by day length.

Many environmental factors co-vary, and one would expect them to have similar importance values. Day length and temperature are an example. Interestingly, although it was not included in the final classification tree, relative humidity came out as the most important predictor for grass green-up. Relative humidity and soil moisture are significantly correlated (Table 4B).

Testing the model

When the classification trees were applied to the 22-year GIMMS time series, 73% of the grass green-up events were predicted to within 1 month (2 time steps) and 6 were predicted exactly (Fig. 7). The prediction was out by more than 2 months only 3 times in the 22 years. Two of these were in severe drought years (1982 and 1991), where no green-up for grass was predicted from environmental data at all. In these cases, it is likely the un-mixing of the satellite data is in error, and that in fact there was no grass green-up (Walker et al. 1987).

Tree green-up was exactly predicted four out of 22 times in the GIMMS data. Thirteen of the 22 times the prediction was within one time step (15 days) of the satellite-observed green-up, and 86% (19/22) of the predicted green-ups were within a month of the observed date (Fig. 7). The outliers were three very early (August) green-ups in 1984, 1987, and 1990. In these years there were early rains, and soil moisture values rose above 0.09 cm^3/cm^3 in August. Therefore grasses could have been responsible for the first green-up seen in the data, which would have invalidated the analysis technique used which always assumes trees green-up first.

Discussion

This analysis shows, and other research has suggested, that trees and grasses in savanna systems have different seasonal leaf area dynamics, controlled by different environmental cues. Despite the coarse temporal resolution of the satellite time series, clear patterns emerge from the long-term data, and the environmental cues identified were 70-80 % correct in identifying green-up to within two time steps of the observed date. If higher

Table 4. A. Importance values of each environmental factor determined from a classification tree run in STATISTICA software (Anon. 2005). It reflects how well each predictor performs in simplifying the tree into homogeneous groups and is calculated by summing the drop in node impurity for all nodes in the tree. Importance is a relative measure: the value of each predictor is scaled relative to the value of the predictor which decreases the impurity the most (which is given a value of 100). It is possible for a predictor to have a high importance value while not appearing in the final classification tree, as is the case with relative humidity in our analysis. **B.** Correlation matrix showing which variables co-vary. Significant correlations marked in bold. See Table 1 for abbreviations.

A.	Tree green-up	Grass green-up
DayLength	100	83
Tmin	56	72
Tmax	68	13
15DayAvgMinT	79	66
15DayAvgMaxT	66	40
DegreeDay	79	35
Rainfall	16	63
15DayAvgRain	30	88
CumRain	34	33
SM	43	74
15DayAvgSM	38	97
RH	41	97
15DayAvgRH	32	100

B.	DayLength	*T*max	*T*min	Rainfall	RH	SM
DayLength	—	**0.44**	**0.68**	**0.19**	0.04	0.09
Tmax		—	0.09	0.00	**–0.63**	–0.13
Tmin			—	**0.20**	**0.49**	**0.21**
Rainfall				—	**0.24**	**0.35**
RH					—	**0.35**
SM						

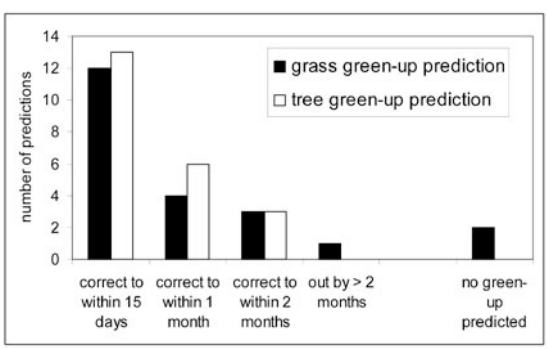

Fig. 7. Frequency distribution of green-up dates predicted for the GIMMS time series using classification trees developed from the MODIS time series (y-axis shows number of green-up events); 16 out of 22 (73%) of the predicted grass green-up events were within two time steps (one month) of the green-up date determined from satellite imagery; 19 out of 22 (86%) of the predicted tree green-up events were within two time steps (one month) of the date determined from satellite imagery. In the drought years of 1982 and 1991 the soil moisture data did not predict a green-up event for grass, and this is likely to be more realistic than the green-up algorithm, which always finds a green-up date each year.

time-resolution data were available, they would in all probability improve this predictive power.

In this analysis, day length was the best predictor of initial tree green-up, as suggested by the small variation between years in the date of first leaf flush (Table 3). Considering the risks of early or late bud-break in relation to the high variability in the onset of good growing conditions in savanna systems, the results are slightly surprising: plants such as trees, which are able to store water and carbohydrate reserves, can have deterministic phenological cycles even in these highly variable biomes, and apparently there is a selective advantage in doing so. Grasses are much more dependent on rainfall for their seasonal growth patterns and are the main source of the large variation between years in NDVI signals in savannas (Scanlon et al. 2002). When the grasses start to grow, the slope of the NDVI curve increases dramatically. The un-mixing analysis was able to pick up the start of this period of rapid grass leaf expansion (Fig. 6), and this date varies greatly between years.

The noisy NDVI signal in savanna systems is therefore hiding two important dates for savanna green-up: the date when the first trees start putting on leaves, and the timing of the rapid increase in NDVI when the grasses start growing. Methods for analysing greening patterns in these systems must be able to extract both values.

Satellite-based phenology studies cannot have a mechanistic basis – there is no proof that environmental cues identified are related to the physiological controls on leaf flush. Results presented here support the general consensus in the literature that soil moisture controls the timing of grass growth (French & Sauer 1974; Pitt & Wikeem 1990; Prins 1988). However, it is likely that another phenological control prevents grasses from greening up during unseasonable wet periods in the middle of winter. Day length was the second most important predictor of grass green-up identified by the classification tree. Because day length and temperature are correlated (Table 4B), the causal factor behind this cue could also be temperature.

Temperature limitations on grass growth have been found in field and laboratory experiments (Everson & Everson 1987; Leigh 1960), but at the Skukuza study site temperatures might never fall low enough to prevent grass growth (mean minimum temperature in June is 5.6 °C).

Similarly, the results presented here do not conclusively show whether trees that flush before the first rains are cued by day length, temperature, or some co-varying factor like relative humidity. Performing this analysis at a regional scale could help to separate the roles played by temperature and day length; for instance by comparing green-up dates at sites on the same latitude, but higher elevations.

Tropical trees have been shown to display a range of different strategies for dealing with their seasonally-arid and highly variable environment (Singh & Kushwaha 2005). Thus evergreen, deciduous, semi-deciduous, and facultatively deciduous trees can be found in the same plant community (Borchert 1999). Moreover, it is likely that tree size, soil type, and landscape position affect the timing of green-up for individual trees (Novellie 1989; Seiwa 1999; Shackleton 1999). This poses a challenge for landscape level descriptions of phenology, which cannot represent the growth patterns of each individual.

While our observational data showed variation between individuals and between species in green-up dates and green-up rates (Fig. 5) it was possible to define a generalised green-up curve for the tree community at the site. Further studies might choose to split the tree layer into two functional types – those cued by soil moisture and those cued by day length.

Savanna phenology and global change

Organisms adapted to the variability displayed in savanna systems might be expected to adapt well to further rapid changes associated with global change. However, our results show that for many tree species in this system, green-up is uncoupled from water – the main limiting resource. They therefore run the risk of allocating resources to green leaves in an environment where they will not be able to support them. If rains are late, early flushing trees reportedly drop their first leaves, and re-flush after the first rain (Owen-Smith pers. obs.; Do et al. 2005). It is not known how often this happens in different savanna environments, and what the costs are to a tree (research in temperate tree species shows that they are able to regrow their entire leaf area twice before using up their stored reserves (Kaitaniemi et al 1999).

At Skukuza trees always flush in mid-October. The probability of having had good rains within two months (by the middle of December) can be calculated using the 46 year rainfall record; 98% of the years had received more than 50 mm of rain by 15.12, and 83 % had received more than 100 mm. Under Skukuza's current rainfall regime, therefore, the risks of early flushing do not seem too great. Productive future research would involve determining the energetic costs of failed green-up events, and their probability in different savanna environments and climate change scenarios.

The early flushing of savanna trees has been explained as a strategy to make the most out of the pulse of nutrients that is released in these systems with the onset of the first rains (Scholes & Walker 1993). Compared with grasses, which still need to amass leaf material, early-flushing trees are ready to start photosynthesising the moment conditions become suitable. Other explanations involve

extending of the growing season (Fuller 1999). However, preliminary sap flow data from the site suggests that very little photosynthesis occurs in these trees before the first rains (M. Gush unpubl. data).

At a system level, the fact that the phenology of many tree species is uncoupled from the key environmental driver could make the ecosystem more resilient. Early flushing trees have been shown to be vital for the nutritional ecology of kudu in a southern African savanna (Owen-Smith & Cooper 1989). These new leaves were the major source of food for these browsers (and probably most other browsers) at the end of the dry season, a time when all herbivores are struggling to fulfil their metabolic requirements. Even grazers probably make use of the new leaves offered by trees at this time of year (Botha & Stock 2005). The deterministic pattern of leaf flush shown by tree species means herbivores are assured of a food source in all years, and could buffer the system from the effects of variable, or changing climates.

Conclusion

This paper has demonstrated that it is possible to use satellite imagery to describe tree and grass phenologies, and that historical patterns of leaf flush can be predicted using climatic data. Due to the covariance of several of the predictors, more information on the causal mechanisms involved is needed before confident predictions about long-term future patterns can be made. Ongoing work at this site involves reaching a similar level of understanding regarding the prediction of leaf-fall in trees and grasses with the aim of developing a regional phenology model.

Resolving some of the questions raised in this paper requires repetition of this analysis at a regional scale, as well as large-scale phenology networks within African savanna systems. Including three different functional types – grasses, early-flushing tree species, and soil-moisture-induced tree species – might also improve the accuracy of the model, but using satellite data with a finer temporal resolution is likely to make more of a difference.

Biophysical models that ignore the differences in tree and grass leaf dynamics are unlikely to be reliable in savanna systems.

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