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'Pre-rain green-up is ubiquitous across southern tropical Africa: implications for temporal niche separation and model representation

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2 temporal niche separation and model representation 3 4 Short running title: The precocious phenology of southern Africa Casey M Ryan*, Mathew Williams, John Grace, Emily Woollen, Caroline E. R. 5 6 Lehmann 7 School of GeoSciences University of Edinburgh 8 Crew Building, King's Buildings 9 10 Alexander Crum Brown Road, Edinburgh 11 EH9 3FF, UK 12 * corresponding author - casey.ryan@ed.ac.uk; +44 (0)131 650 7722 13 14 15 length: 3710 words (excluding captions) 16

Pre-rain green-up is ubiquitous across southern tropical Africa: implications for

Summary

- Tree phenology mediates land-atmosphere mass and energy exchange
 and is a determinant of ecosystem structure and function. In the dry
 tropics, including African savannas, many trees grow new leaves during
 the dry season weeks or months before the rains typically start. This
 syndrome of pre-rain green-up has long been recognised at small scales,
 but the high spatial and interspecific variability in leaf phenology has
 precluded regional generalisations
 - We use remote sensing data to show that this precocious phenology is ubiquitous across the woodlands and savannas of southern tropical Africa.
 - In 70% of the study area, green-up preceded rain onset by > 20 days (42% >40 days). All the main vegetation formations exhibit pre-rain green-up, by as much as 53 ± 18 days (in the wet miombo). Green-up shows low interannual variability (SD between years = 11 days), and high spatial variability (>100 days)
 - These results are consistent with a high degree of local phenological adaptation, and an insolation trigger of green-up. Tree-tree competition and niche separation may explain the ubiquity of this precocious phenology. The ubiquity of pre-rain green-up described here challenges existing model representations and suggests resistance (but not necessarily resilience) to the delay in rain onset predicted under climate change.

Keywords: Leaf phenology, rain onset, miombo, mopane, tree-tree competition, tree-grass competition

Introduction

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45 The timing of leaf emergence in tree species mediates land-atmosphere 46 mass and energy exchanges and is an important determinant of ecosystem 47 structure and function (Richardson et al., 2013; Xia et al., 2015). However, in the dry tropics, phenological data are sparse and the processes controlling leaf 48 49 emergence are not well understood (Richardson et al., 2013). Existing work 50 documents a wide range of phenological syndromes ranging from deciduous 51 through brevideciduous to evergreen (Williams et al., 1997; de Bie et al., 1998; 52 Singh & Kushwaha, 2005) and a large degree of spatial, inter- and intra-specific 53 variability (de Bie et al., 1998; Shackleton, 1999; Higgins et al., 2011) 54 Many ecological studies report the intriguing (Borchert, 1994; Archibald 55 & Scholes, 2007) phenomenon of *pre-rain green-up* i.e. the appearance of new 56 leaves towards the end of the dry season, but before the start of the wet season. 57 This phenological syndrome has been recorded in the dry forests of the 58 Neotropics (Borchert, 1994), South East Asia (Elliott et al., 2006) and in the 59 savanna woodlands of Australia (Williams et al., 1997; Myers et al., 1998). In 60 Africa, studies have documented pre-rain green-up in mesic woodlands (Ernst & 61 Walker, 1973; Hall-Martin & Fuller, 1974; Malaisse, 1974; Guy et al., 1979; Frost 62 & Campbell, 1996; Devineau, 1999; Chidumayo, 2001; Simioni *et al.*, 2004; Ryan 63 et al., 2014), semi-arid savannas (Childes, 1988; de Bie et al., 1998; Archibald & 64 Scholes, 2007; Higgins et al., 2011) and arid savannas (Do et al., 2005). 65 The reasons for pre-rain green-up are not fully understood. However, the 66 suggested benefits include: 1) The avoidance of herbivory during the vulnerable 67 stage of leaf expansion, due to reduced insect activity in the dry season (Aide, 68 1988); 2) avoidance of rain-induced leaching of the nutrient-rich, immature 69 leaves (Sarmiento et al., 1985); 3) optimisation of photosynthetic gain during the 70 wet season (Kikuzawa, 1995; Reich, 1995); 4) being ready to fully exploit, and 71 compete for, rain-induced soil nutrient availability (Scholes & Walker, 2004; 72 Archibald & Scholes, 2007); 5) a longer growing season (Scholes & Walker, 73 2004). However, several costs must be set against these benefits: pre-rain green-74 up has been linked to the ability to access deep soil moisture (Borchert, 1994) or 75 groundwater (Do et al., 2008), and to the storage of water in tree stems

(Borchert, 1994), but these mechanisms require substantial investments in hydraulic architecture and therefore confer large construction and maintenance costs. Furthermore, utilising deep water at the height of the dry season requires a costly, embolism-resistant hydraulic system (Eamus, 1999). Most seasonally dry ecosystems are highly flammable in the late dry season, presenting an additional risk to new leaves (Frost & Campbell, 1996).

Understanding the extent and frequency of pre-rain green-up is important for several reasons. Firstly, prognostic models of the land surface need to be able to represent tree leaf phenology if they are to accurately describe landatmosphere fluxes (Richardson et al., 2013). Currently, because of weak process understanding, even "state of the art" Africa-specific dynamic global vegetation models (DGVMs) assume all trees are facultatively deciduous, even though the many observations of pre-rain green-up suggest that some trees may be obligately deciduous (Scheiter & Higgins, 2009); other models use a simple soil water threshold (Cramer et al., 2001). Neither of these approaches can be expected to represent the relationship between tree leaf phenology and a changing climate (Seth *et al.*, 2013) in a system where pre-rain green-up is common. Finally, temporal niche separation is a fundamental process by which inter-specific competition structures tropical ecosystems (Pau et al., 2011). Both tree-tree and tree-grass competition are likely to play a role in the phenology of savanna ecosystems, but as yet there has been no regional analysis comparing pre-rain green-up in floristically different savanna systems.

As a step towards improved understanding of pre-rain green-up, and thus process-based modelling, a better understanding of its biogeography is needed (Guan *et al.*, 2014b). To date this has been hindered by the high variability in phenological characteristics: which vary between and within species (de Bie *et al.*, 1998), with climate (White, 1983; Chidumayo, 2001), short term weather patterns like droughts (Borchert, 2008) and catenary position (Shackleton, 1999; Fuller, 1999). These multiple scales of temporal and spatial variability have hindered our ability to draw broad regional conclusions from field studies, and highlight the need for regional-scale analyses (Archibald & Scholes, 2007). Here we present such an analysis, using the methods developed by Ryan *et al.*

108 (2014) to examine pre-rain green-up in Southern tropical Africa and analyse its 109 occurrence in different vegetation formations. Specifically, we ask: 110 1. What is the leaf phenology of the major floristic assemblages in southern 111 tropical Africa and how does it vary in time and space? 112 2. How common in time and space is the occurrence of pre-rain green-up? 113 3. For each floristic assemblage, what is the interannual and spatial variability 114 in green-up dates, and what factors can explain this variation? 115 We interpret the results of the study using ecological and evolutionary 116 explanations of phenological niche separation (Pau et al., 2011) and theories of 117 savanna tree-grass coexistence (Chesson, 1985; Walker, 1987). 118 **Methods** 119 To understand the prevalence of pre-rain green-up we conducted a remote 120 sensing analysis of green-up dates and rain onset dates from 2°S to 23°S for the 121 African mainland, for each March-March year (2002-2014) using MODIS EVI (the 122 enhanced vegetation index acquired from the Moderate Resolution Imaging 123 Spectroradiometers; Huete 2002) and TRMM rainfall data (Tropical Rainfall 124 Measuring Mission; Kummerow et al. 1998). 125 **Green-up dates** 126 The definition and estimation of green-up dates uses the method corroborated in these ecosystems by Ryan et al. (2014). The method utilises the fact that the land 127 128 surface phenology signal detected by satellite-borne sensors is closely related to 129 the tree leaf phenology in the period before the rains. This is because before the 130 rains, no substantial grass growth is possible (Chidumayo, 2001; Archibald & 131 Scholes, 2007). Given this, the method looks for the first detectable increase in 132 vegetation greenness (represented by EVI) each year. We use MODIS EVI 133 aggregated to a 0.05° lat/long grid (MOD and MYD 13C1.5, available from 134 LPDAAC). These two MODIS products, obtained by the Terra and Aqua satellites 135 respectively, composite daily acquisitions over 16 day periods, 8 days out of 136 synchrony with each other. We interleave the 16 day composites to improve the

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temporal resolution of the time series.

Many definitions have been used to derive day of year of green-up (G_{DOY}) dates from reflectance and/or EVI data (Reed et al., 1994; Zhang, 2005; Archibald & Scholes, 2007; Bachoo & Archibald, 2007; Guan et al., 2014a; Buitenwerf et al., 2015), with no consensus as to techniques. To help resolve this, Ryan et al. (2014) tested four different methods of estimating G_{DOY} from EVI data and compared them to ground-based hemispherical canopy photography at a site in the woodlands of Mozambique. This showed that when using MODIS EVI data the i) choice of G_{DOY} definition made only small differences to the estimated G_{DOY} (max range 15 days), ii) that all methods were capable of detecting G_{DOY} at some point between the annual min and 10% of the annual max in over 80% of pixel-years, iii) that the backwards looking moving average definition of Archibald & Scholes (2007) was most reliable at detecting G_{DOY} when used with EVI data, and was conservative, tending to give later green-up dates than the ground data. Thus in this study we present the results using the Archibald & Scholes (2007) definition of green-up.

The estimation of day of year of green-up (G_{DOY}) is done for each pixel and for each annual (March-March) time series (Archibald & Scholes, 2007; Ryan et al., 2014). First the data are smoothed with a Savatsky-Golay filter, using only data with 'good' or 'marginal' pixel reliability. The Savatsky-Golay filter was chosen as it minimised the tendency of some smoothing filters to shift green-up to earlier dates. The smoothed data are fitted with a piecewise cubic Hermite interpolation and the year's minimum value is found. Based on Archibald & Scholes (2007), searching forward from this point, G_{DOY} is indicated as occurring at measurement i, when:

 $p_i > \overline{p_{\iota-1\ldots\iota-4}}$

where p_i is the EVI value at time i and $\overline{p_{i-1...i-4}}$ is the mean EVI of the past four observations.

This procedure was executed for each 0.05° pixel. D, the number of days between green-up and rain onset, was calculated at the 0.05° resolution of the MODIS data, with the 0.25° rainfall data (see below) interpolated using a cubic spline.

Rain onset dates

For rainfall estimates we use data from the Tropical Rainfall Measuring Mission (TRMM, Kummerow *et al.*, 1998). The 3B42 daily product uses a combination of infra-red and microwave observations scaled to match monthly rain gauge analyses (Huffman *et al.*, 2007). Data are available at 0.25° spatial resolution and were extracted for the period 2002-2014 from the NASA Goddard Earth Sciences Data and Information Services Center.

For rain onset detection, an approach similar to that for green-up dates was followed. We use the daily TRMM data from 2002 (when data from both MODIS sensors became available) to 2014 (when one instrument aboard TRMM was switched off). For each year (March-March) and for each pixel, the month of minimum rainfall is located, and the remainder of the time series is evaluated until two criteria are met. The criteria are: (a) 10 days during which a total of 25 mm of rain falls, followed by (b) 20 days with > 20 mm total rain. These criteria are based on Tadross (2005) and are designed to detect rainfall that allows the start of maize cultivation. Thus we believe they are conservative with respect to tree water requirements, but approximate those of grasses.

Green-up and rain onset frequencies were analysed by the major floristic assemblages defined by the map of White (1983), which was created before satellite data was available and is thus independent of the MODIS data. White's map was downsampled from its original resolution of 30" by taking the mode to 0.25° resolution for comparison to the rainfall data, and to 0.05° for the comparison to EVI and the estimation of the pre-rain green-up period (~ 5.4 km at the centre of the study area). A description of the floristics and structure of each vegetation type is included in supplementary Table S1.

We masked from our analysis pixels where we expect few trees to be present, namely pixels that had more than 10% water; pixels with a maximum EVI < 0.4; and pixels classed as wetlands, agriculture or urban in the MODIS 12C1 land cover product for 2001. Pixels with low seasonal variation in EVI (range < 0.2) were also excluded, as evergreen systems are not amenable to the analysis presented here. In areas without a distinct rainy season, the rain onset

algorithm detects no R_{DOY} – pixels where this occurred more than eight times were also masked from the analysis.

Results

Pre-rain green-up is widespread across southern tropical Africa (Fig. 1 and 2). All the major vegetation types with a strong seasonal cycle of EVI show pre-rain green-up, and the period between G_{DOY} and R_{DOY} , D, varied from a mean of 27 ± 25 to 53 ± 18 days for the major vegetation types (Table 1). The number of days by which green-up preceded rain onset on average (D), was > 0 days for 78% of the terrestrial study area; > 20 days for 70% of the study area; and > 40 days for 42% of the study area. 19% of the study area was masked, mainly because of low EVI (9%) or low interannual variation in EVI (5%), anthropic land cover (3%). R_{DOY} could not be detected in > 8 years (of 13) in 2% of the region.

Each year, the rains spread southeast from the Congo Basin arriving in most of central southern Africa by DOY 300, and reaching the northeast and southwest of the region last, around DOY 330 (Fig. 2). Northern Angola and the Congo basin have earliest R_{DOY} from around DOY 250. Standard deviation (SD) in R_{DOY} between the 13 years was <20 days for most of central southern Africa, but more variable in the northeast and southwest coastal regions.

Green-up DOY (G_{DOY}) followed a broadly similar, but earlier, pattern, occurring first in Angola, the Congo basin and parts of Zambia ($G_{DOY} \sim 200$) and then moving south and east, reaching Zimbabwe, Botswana and Mozambique by DOY 250-280 and occurring last along the Indian Ocean coast (DOY >300) (Fig. 2). Similar to R_{DOY} , G_{DOY} was least variable in the northwest and centre of the study area (SD \sim 10 days), and SD was <30 days for all the study area except the equatorial rainforest, and the southwest shrublands and semi-deserts.

Differences between vegetation types

Each (floristic) vegetation type had a distinctive time series of EVI, varying from the relatively aseasonal rainforest (Fig. 1a), to the highly seasonal woodlands and savannas (Fig. 1b-e). The wet miombo woodlands showed a clear and sustained increase in EVI up to 2 months before rain onset, at which point there

was a much more rapid increase in EVI (Fig. 1b). The drier (miombo, undifferentiated and mopane) woodlands had a less distinct pre-rain green-up, but EVI still increased before $R_{DOY}(D=39\pm17,33\pm16 \text{ and }35\pm15 \text{ respectively})$. The *Acacia* savannas had by far the highest interannual variability in rain onset date (23 days) and also green-up (34 days), but still on average showed pre-rain green-up of 41 ± 14 days.

Within vegetation types, *GDOY* was much more variable spatially than between years (compare the widths of the pdfs to the vertical range of the dashed lines in Fig. 3), with for example, wet miombo showing low interannual variability (SD 11 days), but spatial variability in *GDOY* from 205-297. Interannual variability in *GDOY*, expressed as the standard deviation of the 13 years of observations, ranged from 11 days for wet miombo to 34 days for the *Acacia* savannas (Table 1). For *RDOY*, interannual variability ranged from 14 days in wet miombo to 23 days in the Acacia savannas. In the miombo and lowland rainforests, for a given pixel, green-up and rain onset dates showed no relationship with each other (slope 0.01-0.06), whilst in the *Acacia* woodlands types there was a weak relationship (slope 0.2-0.37), suggesting more plasticity in these more arid and variable systems.

Our analysis used the rescaled vegetation map at 0.05° for the estimation of green-up dates of each vegetation class (see methods). This resulted in 10% of the 1 unmasked study area being comprised of pixels with a mixture of two vegetation types. To check if these mixed pixels were different from the rest of the vegetation type, we reran the analysis with and without the mixed pixels. This showed that the mixed pixels had on average a similar green-up date to the whole vegetation class, with the difference only exceeding 6 days for the drier rain forests (where the mixed pixels G_{DOY} was 18 ± 45 (mean \pm SD) and the whole vegetation type averaged 4 ± 48).

Discussion

Our results demonstrate that the precocious phenology of pre-rain greenup is widespread across the region and occurs in all the major vegetation types. There is high spatial variation in green-up dates within each vegetation type, consistent with local adaptation, and, in the wetter parts of the region, there is low interannual variability, suggesting an insolation (i.e. photoperiod or irradiance) cue rather than a meteorological cue of green-up. These results, alongside previous ground-based studies in the region (Hall-Martin & Fuller, 1974; Malaisse, 1974; Guy et al., 1979; Childes, 1988; Chidumayo, 1994, 2001, 2015; Frost & Campbell, 1996; Archibald & Scholes, 2007; Richer, 2008a; Higgins et al., 2011; Ryan et al., 2014) and one other remote sensing study (Guan et al., 2014b), build a coherent picture of ubiquitous pre-rain green-up in the region. This provides several challenges to current understanding and modelling of this region's vegetation.

Firstly, the fact that trees are able to display leaves in very dry conditions, e.g. 4-5 months since the last substantive rainfall, raises questions about tree water use and access in the dry season. Leaf display in the dry season implies substantial quantities of water stored in the tree or deep root access to groundwater must be common. This in turn suggests that models of tree leaf phenology based on surface soil moisture (e.g. in many DVGMs, Cramer 2001) cannot capture the dominant tree phenology of the region, as clearly surface soil moisture is weakly tied to leaf display across much of southern Africa (Fig 1). Such models need to be adapted to incorporate pre-rain green-up to skilfully represent land-atmosphere interactions in the late dry season.

Secondly, there appears to be an internal control on phenology unrelated to weather conditions in most of the study region. This is evidenced by the low interannual variability of green-up across the region (Fig 1) particular in the wetter areas. We consider it implausible that a weather-related cue could have such low interannual variability over a 13-year period as to lead to the mean of 11 days interannual variability in green-up in the wet miombo. This internal control could be cued by insolation e.g. day length, or a related property such as the timing of peak insolation (Rivera *et al.*, 2002; Borchert *et al.*, 2005). The large spatial variability in green-up dates, even in vegetation types which are known to be dominated by the same genera across their entire range (such as the miombo (Frost & Campbell 1996)), is consistent with a high degree of local adaptation (Phillimore *et al.*, 2010) to the timing of the rains. This is supported by the fact

that in the wetter vegetation types, mean dates of green-up and rain-onset are correlated (e.g. in the wet miombo $G_{DOY} = 1.0 \times R_{DOY} - 55$, p $\ll 0.01$, $r^2 = 0.46$; Table 1). The implications are intriguing: trees that have an insolation cue and a high level of local adaptation are likely to show little change in green-up dates in response to the predicted delays in rain onset resulting from climate change-driven alterations to the African monsoon (Seth *et al.*, 2013), at least until some ecophysiological threshold is exceeded (Richer, 2008b). Support for this idea comes from a global analyses of phenological change which shows that African woodlands have undergone comparatively little phenological change over the last three decades (Buitenwerf *et al.*, 2015). Such resistance to climate change does not imply resilience; the fitness consequences of delayed rain onset may be significant, and might cause species turnover.

Thirdly, these observations show that the fundamental temporal niche for savanna and woodland tree leaf display is rather large and includes the driest, hottest part of the year. The realised temporal niche of many tree species is much more restricted, i.e. Fig 1 shows sub-maximal leaf display for much of the year in all vegetation types. Although precocious phenology is mostly discussed in terms of its costs and benefits compared to rain-induced green-up (see references in introduction), we discuss it here in terms of niche differentiation leading to competitive advantage.

Two frameworks for thinking about competitive interactions and phenology are the conceptual model of abiotic and biotic controls on phenology presented in Pau et al. (2011), and the long-standing (Chesson, 1985; Walker, 1987; Scholes & Walker, 2004) temporal niche separation hypothesis sometimes invoked to explain tree-grass coexistence in savannas. Under the Pau et al (2011) conceptual model, leaf display is presented as having fundamental limitations imposed by abiotic factors (primarily climate) but, where these are not limiting, being driven by inter-specific competitive processes, which drive temporal niche separation. The abiotic factors are typically well represented in models (Jolly *et al.*, 2005; Richardson *et al.*, 2013) and often invoked in the description of the study region as "rain green" (Friend *et al.*, 2007) or "drought deciduous". Such abiotic models are however not sufficient in tropical systems

such as the study area: the ubiquity of pre-rain green-up implies no fundamental limitation to the timing and period of tree leaf display in these systems. In the (humid, equatorial) tropics, Pau et al's model invokes biotic competition to explain the distinct phenological niche that most species occupy, which also explains the predominance of solar radiation-driven phenological cues, as this is the only reliable cue in the wet tropics (Borchert et al., 2005). Such biotic processes can be invoked to explain the patterns presented here: competition pushes tree leaf display into the unfavourable, but feasible, dry season. This could be competition between trees and grasses or between tree species. An "arms race" might result, in which some trees specialise in pre-rain green-up, in an attempt to avoid competition for nutrient, water or carbon acquisition. The savanna temporal niche hypothesis would suggest that this is driven by treegrass competition for the rain-induced flush of nutrients (February & Higgins, 2016) rather than extending the photosynthetic period (Scholes & Walker, 2004); plausible given the dystrophia of the study region. However pre-rain green-up is observed in dry forests and other ecosystems with no grass layer. We therefore hypothesise that rain-green, facultatively deciduous, trees possess traits that allow effective resource acquisition in the wet season only, whilst others, obligately deciduous, species compromise this by investing in precocious nutrient (and possibly carbon) acquisition which requires a more embolismresistant hydraulic system; stem or root water storage; or deep roots. In summary, one explanation for the ubiquity of pre-rain green-up is that leaf display is determined by biotic competitive processes, and not solely by abiotic limitations.

Conclusions

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- We have shown that pre-rain green-up is widespread across the region, and is present in all the major vegetation types. The period between leaf out and rain onset varies from 53 to 27 days in different vegetation types, and occurs in vegetation types that have a wide range of mean annual rainfall and interannual variability in rain onset
- Interannual variability in green-up is low, particularly in the woodlands, but for a given vegetation type, spatial variation can be very high, consistent with

358 high levels of local adaptation, a solar radiation trigger, and resistance (if not 359 resilience) to predicted shifts in rainfall patterns 360 Models of phenology will need to incorporate extra processes if they are to accurately describe the observed leaf phenologies of southern Africa 361 362 reported here. Rainfall, and thus surface soil moisture, cannot be used to 363 explain green-up. 364 The ubiquity of pre-rain green-up can be explained by a conceptual model of 365 abiotic and biotic temporal niche separation, which may be driven by tree-366 tree or tree-grass competition for nutrients or other resources 367 **Acknowledgements** 368 NASA for MODIS and TRMM data. Thanks to Meg Coates Palgrave for helpful 369 comments and Tristan Quaife, Rob Clement, Tim Hill and Sophie Bertin for useful 370 discussions. This work was partly supported by the Ecosystem Services for 371 Poverty Alleviation (ESPA) programme (ACES project, NE/K010395/1). The 372 ESPA programme is funded by the Department for International Development 373 (DFID), the Economic and Social Research Council (ESRC) and the Natural 374 Environment Research Council (NERC). - See more at: http://www.espa.ac.uk 375 **Author Contribution** 376 CMR developed the methods, implemented the analysis and drafted the 377 manuscript; MW, JG, EW and CERL other authors contributed to revising the 378 manuscript and developing the interpretation of the results. MW initiated the 379 study of tree phenology at the Nhambita (Mozambique) site, the results from 380 which provided the impetus for this work. 381 References 382 **Aide TM**. **1988**. Herbivory as a selective agent on the timing of leaf 383 production in a tropical understory community. *Nature* **336**: 574–575. 384 **Archibald S, Scholes R. 2007.** Leaf green-up in a semi-arid African savannaseparating tree and grass responses to environmental cues. *Journal of Vegetation* 385 386 Science 18: 583-594. 387 Bachoo A, Archibald S. 2007. Influence of Using Date-Specific Values when Extracting Phenological Metrics from 8-day Composite NDVI Data. International 388 389 Workshop on the Analysis of Multi-temporal Remote Sensing Images, 2007.

390	MultiTemp 2007. Leuven, Belgium: IEEE, 1–4.
391 392	de Bie S, Ketner P, Paasse M, Geerling C, Ecology T. 1998. Woody plant phenology in the West Africa savanna. <i>Journal of Biogeography</i> 25: 883–900.
393 394	Borchert R. 1994. Soil and stem water storage determine phenology and distribution of tropical dry forest trees. <i>Ecology</i> 75 : 1437–1449.
395 396	Borchert R. 2008 . Modification of Vegetative Phenology in a Tropical Semi-deciduous Forest by Abnormal Drought and Rain'. <i>Biotropica</i> 34 : 27–39.
397 398 399	Borchert R, Renner SS, Calle Z, Navarrete D, Tye A, Gautier L, Spichiger R, von Hildebrand P. 2005. Photoperiodic induction of synchronous flowering near the Equator. <i>Nature</i> 433: 627–629.
400 401	Buitenwerf R, Rose L, Higgins SI . 2015 . Three decades of multidimensional change in global leaf phenology. <i>Nature Climate Change</i> : 1–5.
402 403 404	Chesson PL. 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability. <i>Theoretical Population Biology</i> 28 : 263–287.
405 406	Chidumayo EN . 1994 . Phenology and Nutrition of Miombo Woodland Trees in Zambia. <i>Trees-Structure and Function</i> 9 : 67–72.
407 408	Chidumayo EN . 2001 . Climate and phenology of savanna vegetation in southern Africa. <i>Journal of Vegetation Science</i> 12 : 347–354.
409 410 411	Chidumayo E. 2015. Dry season watering alters the significance of climate factors influencing phenology and growth of saplings of savanna woody species in central Zambia, southern Africa. <i>Austral Ecology</i> 40 : 794–805.
412 413	Childes SL. 1988 . Phenology of nine common woody species in semi-arid, deciduous Kalahari Sand vegetation. <i>Vegetatio</i> 79 : 151–163.
414 415 416	Cramer W. 2001. Global response of terrestrial ecosystem structure and function to CO 2 and climate change: results from six dynamic global vegetation models. <i>Glob. Change Biol.</i> 7 : 357–373.
417 418 419 420	Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, <i>et al.</i> 2001. Global response of terrestrial ecosystem structure and function to CO2 and climate change: results from six dynamic global vegetation models. <i>Global Change Biology</i> 7: 357–373.
421 422 423	Devineau J-L. 1999. Seasonal rhythms and phenological plasticity of savanna woody species in a fallow farming system (south-west Burkina Faso). <i>Journal of Tropical Ecology</i> 15 : 497–513.
424 425 426	Do FC, Goudiaby VA, Gimenez O, Diagne AL, Diouf M, Rocheteau a, Akpo LE. 2005 . Environmental influence on canopy phenology in the dry tropics. <i>Forest Ecology And Management</i> 215 : 319–328.
427 428 429	Do FC, Rocheteau A, Diagne AL, Goudiaby V, Granier A, Lhomme J-P. 2008. Stable annual pattern of water use by Acacia tortilis in Sahelian Africa. <i>Tree physiology</i> 28: 95–104.
430	Eamus D. 1999. Ecophysiological traits of deciduous and evergreen woody

- 431 species in the seasonally dry tropics. *Trends in Ecology & Evolution* **14**: 11–16. 432 **Elliott S, Baker PJ, Borchert R. 2006.** Leaf flushing during the dry season: 433 the paradox of Asian monsoon forests. Global Ecology and Biogeography 15: 434 248-257. 435 Ernst W, Walker BH. 1973. Studies on the Hydrature of Trees in the 436 Miombo Woodland in South Central Africa. *The Journal of Ecology* **61**: 667–673. 437 February EC, Higgins SI. 2016. Rapid Leaf Deployment Strategies in a Deciduous Savanna. PLOS ONE 11: e0157833. 438 439 Frost P, Campbell BM. 1996. The ecology of Miombo woodlands. In: 440 Campbell BM, ed. The Miombo in transition: Woodlands and welfare in Africa. 441 Bogor, Indonesia: Center for International Forestry Research, 11–55. Fuller DO. 1999. Canopy phenology of some mopane and miombo 442 443 woodlands in eastern Zambia. *Global Ecology and Biogeography* **8**: 199–209. 444 Guan K, Medvigy D, Wood EF, Caylor KK, Li S, Jeong S. 2014a. Deriving 445 Vegetation Phenological Time and Trajectory Information Over Africa Using 446 SEVIRI Daily LAI. *IEEE Transactions on Geoscience and Remote Sensing* **52**: 1113-1130. 447 448 Guan K, Wood EF, Medvigy D, Kimball J, Pan M, Caylor KK, Sheffield J, Xu X, **Iones MO. 2014b.** Terrestrial hydrological controls on land surface phenology of 449 450 African savannas and woodlands. *Journal of Geophysical Research:* 451 Biogeosciences 119: 1652-1669. 452 Guy PR, Mahlangu Z, Charidza H. 1979. Phenology of some trees and 453 shrubs in the Sengwa Wild Life Research Area, Zimbabwe-Rhodesia. S.A.J. Wildl. 454 *Res* **9**: 47–54. 455 Hall-Martin AJ, Fuller NG. 1974. Observations on the phenology of trees 456 and shrubs of the Lengwe National Park, Malawi. J.S. Aft. Wildl. Mgmt. Ass. 5: 83-457 458 Higgins SI, Delgado-Cartay MD, February EC, Combrink HJ. 2011. Is there a 459 temporal niche separation in the leaf phenology of savanna trees and grasses? Journal of Biogeography 38: 2165–2175. 460 461 **Huete a. 2002.** Overview of the radiometric and biophysical performance 462 of the MODIS vegetation indices. *Remote Sensing of Environment* **83**: 195–213. 463 Jolly WM, Nemani R, Running SW. 2005. A generalized, bioclimatic index to 464 predict foliar phenology in response to climate. Global Change Biology 11: 619-465 632. 466 Kikuzawa K. 1995. Leaf phenology as an optimal strategy for carbon gain 467 in plants. Canadian Journal of Botany 73: 158-163. 468 Kummerow C, Barnes W, Kozu T, Shiue J, Simpson J. 1998. The Tropical
 - emphasis on the miombo ecosystem. In: Lieth H, ed. Phenology and seasonality

Rainfall Measuring Mission (TRMM) Sensor Package. Journal of Atmospheric and

Malaisse FP. 1974. Phenology of the Zambezian woodland area with

469

470

471

472

Oceanic Technology 15: 809-817.

4/3	modeling. New York: Springer Science+Business Media, 269–286.
474 475 476	Myers B a., Williams RJ, Fordyce I, Duff G a., Eamus D. 1998 . Does irrigation affect leaf phenology in deciduous and evergreen trees of the savannas of northern Australia? <i>Australian Journal of Ecology</i> 23 : 329–339.
477 478 479	Pau S, Wolkovich EM, Cook BI, Davies TJ, Kraft NJB, Bolmgren K, Betancourt JL, Cleland EE. 2011. Predicting phenology by integrating ecology, evolution and climate science. <i>Global Change Biology</i> 17: 3633–3643.
480 481 482 483	Phillimore AB, Hadfield JD, Jones OR, Smithers RJ. 2010. Differences in spawning date between populations of common frog reveal local adaptation. <i>Proceedings of the National Academy of Sciences of the United States of America</i> 107: 8292–7.
484 485 486	Reed BC, Brown JF, VanderZee D, Loveland TR, Merchant JW, Ohlen DO. 1994. Measuring phenological variability from satellite imagery. <i>Journal of Vegetation Science</i> 5: 703–714.
487 488	Reich PB. 1995 . Phenology of tropical forests: patterns, causes, and consequences 1. 174 : 164–174.
489 490 491 492	Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M. 2013 . Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. <i>Agricultural and Forest Meteorology</i> 169 : 156–173.
493 494	Richer RA . 2008a . Leaf phenology and carbon dynamics in six leguminous trees. <i>African Journal of Ecology</i> 46 : 88–95.
495 496	Richer RA . 2008b . Shading delays bud break in Brachsyegia spiciformis. <i>African Journal of Ecology</i> 46 : 556–564.
497 498 499	Rivera G, Elliott S, Caldas LS, Nicolossi G, Coradin VTR, Borchert R. 2002. Increasing day-length induces spring flushing of tropical dry forest trees in the absence of rain. <i>Trees</i> 16: 445–456.
500 501 502 503	Ryan CM, Williams M, Hill TC, Grace J, Woodhouse IH. 2014. Assessing the Phenology of Southern Tropical Africa: A Comparison of Hemispherical Photography, Scatterometry, and Optical/NIR Remote Sensing. <i>IEEE Transactions on Geoscience and Remote Sensing</i> 52: 519–528.
504 505	Sarmiento G, Goldstein G, Meinzer F. 1985 . Adaptive Strategies of Woody Species in Neotropical Savannas. <i>Biological Reviews</i> 60 : 315–355.
506 507 508	Scheiter S, Higgins SI . 2009 . Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. <i>Global Change Biology</i> 15 : 2224–2246.
509 510	Scholes RJ, Walker BH. 2004. An African savanna: synthesis of the Nylsvley study. Cambridge, UK: Cambridge University Press.
511 512 513	Seth A, Rauscher SA, Biasutti M, Giannini A, Camargo SJ, Rojas M. 2013. CMIP5 projected changes in the annual cycle of precipitation in monsoon regions. <i>Journal of Climate</i> 26: 7328–7351.
514	Shackleton CM. 1999. Rainfall and topo-edaphic influences on woody

515 516	community phenology in South African savannas. <i>Global Ecology and Biogeography</i> 8 : 125–136.
517 518 519	Simioni G, Gignoux J, Roux XLE, Benest D. 2004. Spatial and temporal variations in leaf area index, specific leaf area and leaf nitrogen of two cooccurring savanna tree species. <i>Tree Physiology</i> 24 : 205–216.
520 521 522	Walker BH. 1987 . <i>Determinants of tropical savannas : presentations made by savanna researchers at a workshop in Harare, Zimbabwe, 1985</i> . Oxford: IRL Press.
523 524 525	White F. 1983 . <i>Vegetation of Africa - a descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa</i> . 7 Place de Fontenoy, 75700 Paris, France.
526 527 528	Williams RJ, Myers BA, Muller WJ, Duff GA, Eamus D, Dec N. 1997. Leaf phenology of woody species in a North Australian tropical savanna. <i>Ecology</i> 78: 2542–2558.
529 530 531 532	Xia J, Niu S, Ciais P, Janssens I., Chen J, Ammann C, Arain A, Blanken PD, Cescatti A, Bonal D, <i>et al.</i> 2015. Joint control of terrestrial gross primary productivity by plant phenology and physiology. <i>Proceedings of the National Academy of Sciences</i> 112: 201413090.
533 534 535	Zhang X . 2005 . Monitoring the response of vegetation phenology to precipitation in Africa by coupling MODIS and TRMM instruments. <i>Journal of Geophysical Research</i> 110 : D12103.
536	
537 538	The following Supporting Information is available for this article:
539	Table S1 A description of the main vegetation types analysed in this study

Table 1. The vegetation phenology and rainfall regime of southern tropical Africa, including its spatial and interannual variability (IAV). Day of year of green-up (G_{DOY}) and rain onset (R_{DOY}) , and the difference between them (D) are summarised for the major vegetation types of the region (based on White 1983). To look at the relationship between IAV in G_{DOY} and IAV in R_{DOY} , the parameters of a regression for each pixel between G_{DOY} and R_{DOY} are also shown. Descriptive statistics of the rainfall regime in each vegetation type are also included. Spatial variability is presented as the 95% interval for each vegetation type, and interannual variability is the per pixel standard deviation (SD) of the thirteen years of data. A dry month is defined as a month with < 15 mm rain. A description of the floristics and structure of each vegetation type is included in supplementary Table S1.

Vegetation type [‡]	No. 0.05° pixels (1000s)	Mean day of year of green-up. $G_{\rm DOY}$, days (spatial variability)	Mean IAV in GDOY, days	Mean day of year of rain onset, R _{DOY} , days (spatial variability)	Mean IAV in RDOY, days	Mean difference between GDOY and RDOY	Mean annual rainfall, mm (Coefficient of Variation)	Mean no. dry months ±SD	Mean regressio n slope ±SD	Mean regression intercept ±SD
Wet miombo woodland	47.7	245 (205-297)	11	297 (262-327)	14	53±18	1050 (21%)	4.7 ±0.8	0.01 ±0.30	243 ±92
Dry miombo woodland	27	276 (235-309)	18	315 (298-332)	17	39±17	904 (18%)	5.0 ± 0.6	0.02 ± 0.40	271 ±124
Lowland rain forest	23	230 (196-273)	15	268 (245-296)	15	38±15	1382 (20%)	3.1 ±0.7	0.06 ±0.64	213 ±176
Mopane woodland	18.6	281 (251-306)	24	316 (301-333)	19	35±15	597 (28%)	5.6 ± 0.4	0.13 ± 0.47	240 ±146
Undifferentiated woodland	14.4	273 (223-307)	21	305 (278-327)	17	33±16	724 (24%)	4.9 ± 0.6	0.12 ±0.52	236 ±157
Kalahari <i>Acacia</i> wooded grassland	11.8	274 (244-302)	34	316 (294-342)	23	41±14	443 (33%)	5.4 ± 0.4	0.37 ±0.51	160 ± 159
East African coastal mosaic	11.4	290 (263-326)	23	323 (298-343)	21	33±17	928 (23%)	4.6 ± 0.6	0.12 ±0.44	250 ±140
Undifferentiated woodland transition to A. bushland & wooded grassland	11.2	274 (252-296)	29	319 (303-334)	20	43±12	521 (33%)	5.7 ±0.3	0.20 ±0.47	214 ±150
Rain forest: drier types	10.9	238 (195-310)	23	265 (239-288)	13	27±25	1487 (19%)	2.9 ± 0.6	0.16 ±1.33	196 ±363
Dry deciduous forest & grassland	8.8	263 (231-288)	19	314 (304-327)	16	51±14	651 (30%)	5.6 ± 0.3	0.07 ± 0.47	240 ±144

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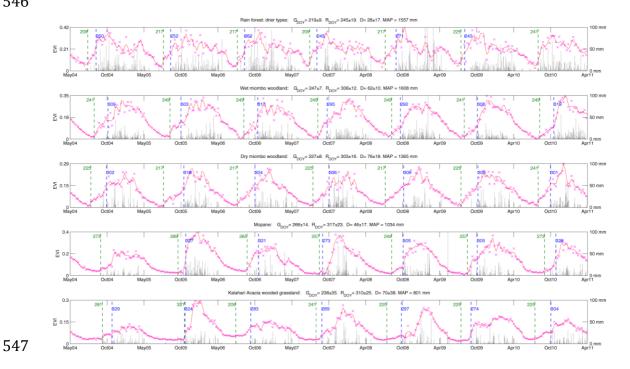


Figure 1. Examples of EVI (Enhanced Vegetation Index) and rainfall time series for randomly chosen locations in 5 major vegetation types in southern Africa. EVI data points are shown with crosses, and the smoothed fit with a pink line. Vertical lines show the day of green-up (G_{DOY} , dashed green line, green numbers) and the start of the rainy season (R_{DOY} , dashed blue line, blue numbers) as detected by our algorithms. Daily rainfall (mm) is shown with grey bars. For clarity only the middle 8 years of the time series are shown.

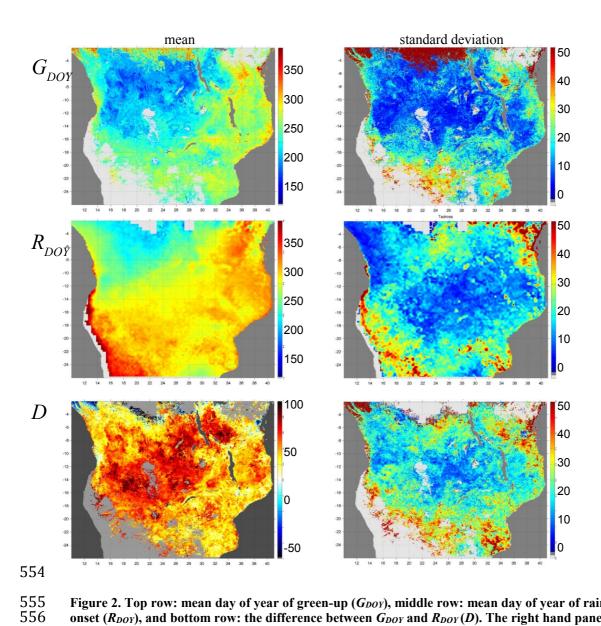


Figure 2. Top row: mean day of year of green-up (G_{DOY}) , middle row: mean day of year of rainonset (R_{DOY}) , and bottom row: the difference between G_{DOY} and $R_{DOY}(D)$. The right hand panels show the standard deviation of the 13 years of data, 2002-14 (inclusive). Grey areas indicate regions that were not included in the analysis because of very sparse or evergreen vegetation, or for which no green-up was detected. Grids and ticks mark 2° lat/long intervals.

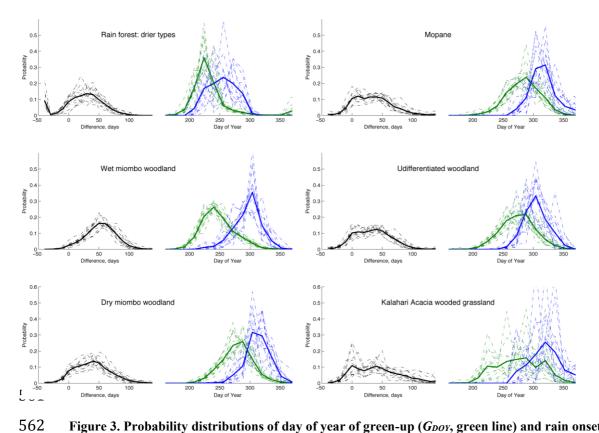


Figure 3. Probability distributions of day of year of green-up (G_{DOY} , green line) and rain onset (R_{DOY} , blue line), are shown on the right axes and the difference (R_{DOY} - G_{DOY}) on a per pixel basis (D, black line) on the left axes, for the major vegetation types of southern Africa. The dashed lines show each of the 13 years of analysis and the thicker line the mean. Frequencies are calculated for 16 day bins and are for pixels at their original resolution.