

# Will trees or grasses profit from changing rainfall regimes in savannas?

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## Summary

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- Increasing rainfall variability is widely expected under future climate change scenarios. How will savanna trees and grasses be affected by growing season dry spells and altered seasonality and how tightly coupled are tree–grass phenologies with rainfall?
- We measured tree and grass responses to growing season dry spells and dry season rainfall. We also tested whether the phenologies of 17 deciduous woody species and the Soil Adjusted Vegetation Index of grasses were related to rainfall between 2019 and 2023.
- Tree and grass growth was significantly reduced during growing season dry spells. Tree growth was strongly related to growing season soil water potentials and limited to the wet season. Grasses can rapidly recover after growing season dry spells and grass evapotranspiration was significantly related to soil water potentials in both the wet and dry seasons. Tree leaf flushing commenced before the rainfall onset date with little subsequent leaf flushing. Grasses grew when moisture became available regardless of season.
- Our findings suggest that increased dry spell length and frequency in the growing season may slow down tree growth in some savannas, which together with longer growing seasons may allow grasses an advantage over C<sub>3</sub> plants that are advantaged by rising CO<sub>2</sub> levels.

## Introduction

A characteristic of tropical savanna is the co-dominance of trees and grasses (Frost *et al.*, 1986). In savannas, diurnal temperatures are high and rainfall is distinctly seasonal with a warm wet season and a cool dry season during which soil moisture in the upper layers of the soil falls by as much as 80% (Williams *et al.*, 1997; Oliveira *et al.*, 2005; Archibald *et al.*, 2019). Trees and grasses have adapted to this seasonality through multiple interactions that ensure that neither exclude the other; these interactions are governed by belowground processes such as water and nutrient uptake and aboveground processes such as fire and herbivory (Bond, 2008). With plant growth restricted to a clearly defined wet season, there has long been debate about the importance of competition for water in determining tree–grass coexistence (Higgins *et al.*, 2000; Jeltsch *et al.*, 2000; Bond, 2008). One popular mechanism suggests that coexistence is possible because trees and grasses use water from different soil depths (Walter's two-layer hypothesis; Walter, 1939; Walker & Noy-Meir, 1982). Recent research, however, proposes that trees and grasses have a large proportion of their roots at the same soil depth and that competition for water is much more nuanced (Schenk & Jackson, 2002; February *et al.*, 2013a; Kulmatiski & Beard, 2013a; Mazzacavallo & Kulmatiski, 2015;

Kulmatiski *et al.*, 2020), with grasses often superior competitors for water (February *et al.*, 2013b; Morrison *et al.*, 2019; Belovitch *et al.*, 2023). Despite spatial overlap with grasses in rooting depth and the shared use of water in the upper layers of the soil, trees may root deeper if soils are deep, enabling them to outperform grasses when shallower soil water dries up (Kulmatiski & Beard, 2013a; Kulmatiski *et al.*, 2020; Rossatto & Franco, 2023). There are however, exceptions, such as on well-drained Oxisols in Brazil, the soils are deep enough to allow for complete separation of tree–grass rooting depths. At this site, the grasses did not appear to compete with trees for soil water regardless of season (although grasses did compete with forbs; Rossatto *et al.*, 2013).

Both climate simulations and direct observations have shown an increase in precipitation intensity and rainfall variability over the last century for terrestrial ecosystems world-wide (Donat *et al.*, 2016; Masson-Delmotte *et al.*, 2021). Increased rainfall variability includes increases in extreme daily precipitation (e.g. R95pTOT, RX1day and RX5day) across the globe (Alexander *et al.*, 2006; Min *et al.*, 2011; Kharin *et al.*, 2013; Westra *et al.*, 2013, 2014; Donat *et al.*, 2016) and increased length and frequency of dry spells in eastern, central and southern Europe, western and south-western United States, South America, parts of Asia and parts of Africa (Bouagila & Sushama, 2013; Jacob

*et al.*, 2014; Singh *et al.*, 2014; Marengo *et al.*, 2016; Breinl *et al.*, 2020). Increased rainfall variability may also interact with increased temperatures and evapotranspiration (ET) to further compound changes in water availability (Konapala *et al.*, 2020). Globally, changes in timing and duration of rainfall (i.e. onset and end of the rainy season) are less clear, with no changes, later and earlier onsets, as well as longer and shorter growing seasons predicted (Feng *et al.*, 2013; Hajek & Knapp, 2022). For savannas, future predictions of total rainfall using Coupled Model Intercomparison Project (e.g. CMIP5 and CMIP6) models are not consistent. The predictions vary from no change to increased or decreased total rainfall depending on the model, continent and the greenhouse gas scenario used (Pinto *et al.*, 2016; Pohl *et al.*, 2017; Dunning *et al.*, 2018; Deegala *et al.*, 2023). However, many studies have shown that how rain is received has changed and will continue to change; with a decrease in the number of rainy days (Sillmann *et al.*, 2013; Pohl *et al.*, 2017; Dunning *et al.*, 2018) and an increase in the average rainfall amount per rain day (Pinto *et al.*, 2016; Bao *et al.*, 2017; Dunning *et al.*, 2018; Konapala *et al.*, 2020), which together will result in increased precipitation intensity (Pinto *et al.*, 2016; Kotz *et al.*, 2024). An increase in the length of time between rainfall events, frequency of dry spells and higher temperatures in the growing season will have important consequences for plant water availability. Such changes will result in higher potential ET, driven by the exponential relationship between air temperature and atmospheric vapour pressure deficits (Hajek & Knapp, 2022). The nature of this thermodynamic relationship therefore has the potential to alter patterns of seasonal water availability without any change in total precipitation amount (Padrón *et al.*, 2020).

What are the likely consequences of increased precipitation intensity and rainfall variability for savanna ecosystems? Rainfall variability has been shown to maintain coexistence among different species of dominant grasses (Adler *et al.*, 2006), between grasses and forbs (Hallett *et al.*, 2019) and between grasses and trees (Holmgren *et al.*, 2013; D'Onofrio *et al.*, 2015, 2019; Yu *et al.*, 2017). Both models and empirical studies show that increased precipitation intensity has the potential to give rise to wetter soils in semi-arid systems when soils are deep, as it would allow water to move to deep soil layers before it is lost as evaporation (Knapp *et al.*, 2008; Berry & Kulmatiski, 2017). Mesic systems, on the contrary, where soils are usually wet in the growing season, will experience greater drying of the soil with more infrequent but larger events (Knapp *et al.*, 2008). These changes were shown experimentally to alter aboveground net productivity (ANPP) of grassland, with higher ANPP associated with fewer but larger events in semi-arid grassland (e.g. semi-arid steppe and mixed-grass prairie) while mesic grassland had reduced ANPP (e.g. mesic tall-grass prairie; Heisler-White *et al.*, 2009; Zeppel *et al.*, 2014). Although the deeper recharge of soil water with increased precipitation intensity may benefit trees more than grasses (Kulmatiski & Beard, 2013b), the realized competitive effects depend on species involved, life stage, mean annual precipitation, soil types and depths and interactions with other climate variables such as increased temperature (Volder *et al.*, 2013; Xu *et al.*, 2015; Case & Staver, 2018; D'Onofrio *et al.*, 2019; Palmquist *et al.*, 2021;

Rossatto & Franco, 2023) as well as interactions with disturbances such as fire and herbivory (Yu *et al.*, 2017).

Temporal niche separation, driven by the seasonal patterns of rainfall inherent to savannas, has been proposed as a mechanism for tree–grass coexistence (Scholes & Walker, 2004; Higgins *et al.*, 2011; Holdo & Nippert, 2023). While the role of spatial niche partitioning is widely acknowledged, as can be seen in a recent review of tree–grass coexistence in savannas (Holdo & Nippert, 2023), the potential role of temporal niche separation in contributing to tree–grass coexistence is often overlooked. Prerain green-up is widespread across savannas (Williams *et al.*, 1997; Rossatto *et al.*, 2009; Higgins *et al.*, 2011; Ryan *et al.*, 2017; Adole *et al.*, 2018). Scholes & Walker (1993) and Scholes & Walker (2004) were the first studies to suggest that trees avoid competing with grasses for water and nutrients by flushing leaves before the onset of the growing season, allowing temporal niche separation (Scholes & Walker, 1993; Higgins *et al.*, 2011; February & Higgins, 2016; Adole *et al.*, 2018). This is because early leaf flushing extends the effective growing season (Higgins *et al.*, 2011) of trees creating a period of up to 2 months with no competition from grasses, although some studies have found much shorter periods of 10–30 d (Higgins *et al.*, 2011; Ryan *et al.*, 2017; Adole *et al.*, 2018). Expanding on this concept, Xu *et al.* (2015) proposed a trade-off between trees and grasses, with grasses growing faster under wet conditions and trees growing better under dry conditions. More recently, Belovitch *et al.* (2023), using a trait-based approach under controlled conditions, proposed that savanna grasses are more drought tolerant but can also exploit water more efficiently than tree seedlings when it is available. Similarly, previous work that considered competition between grasses and trees when root space is shared (e.g. juvenile trees or shallow soils) indicates that grasses have a competitive advantage over trees (February *et al.*, 2013b; Campbell & Holdo, 2017).

We used a time series approach to examine how grasses and trees in a semi-arid savanna responded to natural variation in rainfall. The study period reported here was characterized by two extended dry spells during the wet season of both 2021 and 2022 and an extended wet spell into the 2021 dry season. The first dry spell was from the end of January to the middle of March (6 wk) during the 2021 wet season, which was followed by an unusually wet 'dry' season with continuously low (close to zero) soil water potentials for most of the 2021 dry season. In 2022, some early rains fell before the wet season began (i.e. in September), but this was followed by mostly dry conditions until mid-December (only 88 mm of rain fell in the first 11 wk of the wet season followed by 705 mm in the remaining 15 wk). The 2022 dry season was also more typical with average soil water potentials mostly below –1500 kPa. Here, we quantify the effects of these wet-season dry spells and dry-season rainfall on savanna trees and grasses to ascertain the extent to which they are able to adapt to possible changes in rainfall seasonality. By measuring the physiological activity of trees and grasses throughout the relevant period, combined with longer term phenology data sets, we address the following specific questions. (1) How do trees and grasses respond to and recover from growing season dry spells? (2) How tightly are tree and grass phenologies (and growth) linked to rainfall amount and

seasonality? Finally, we discuss some of the implications of changing rainfall patterns for tree–grass coexistence in savannas, particularly in relation to the expected increases in both the number and length of dry spells and changes in the seasonality of rainfall.

## Materials and Methods

### Study site

The study site is 365 m above sea level in the Skukuza region of the Kruger National Park (KNP), South Africa, with annual rainfall of 550 mm which typically falls between October and March. Mean annual minimum and maximum temperatures are 14.3°C and 29.5°C, respectively. Soils are granite-derived and typically shallow (*c.* 0.5 m) with high sand content (> 65%). The Skukuza landscape is mainly open woodland dominated by a mix of broad-leaved bushwillow (*Combretum*) and acacia (*Senegalia* and *Vachellia*) savanna types. As the study site is situated in a national park with large mammals present that could potentially damage our research equipment, we used two fenced locations for the experimental work; the first is the Skukuza airport (−25.01016299S and 31.92083898E) and the second, the campus of the Skukuza Science Leadership Initiative (SSLI; −24.995608S and 31.588140E). Neither of the two locations were burnt during the study period. In this study, we used a combination of several data sets: (1) A 2-yr data set (2021 and 2022 rainfall years) of tree growth and xylem pressure potentials (XPPs; six species, 54 trees) from the Skukuza airport study site to determine how growing season dry spells and season affect tree growth and XPPs. (2) A lysimeter experiment (six lysimeters) was set up at the SSLI campus to determine how grass ET rates are affected by growing season dry spells and season for the same period as 1 above. (3) We use a 5-yr (2019–2023) phenology data set from the Skukuza region to determine when the dominant deciduous species (17 species, 260 trees) flush and drop leaves and how this relates to rainfall and season. (4) We use Soil Adjusted Vegetation Index (SAVI) measurements from open grassy (14 nonwooded sites) areas to the northwest and northeast of the Skukuza airport study site (e.g. −24.952020S and 31.589545E) to determine grass phenologies and how these relate to rainfall and season for the same period as 3 above. 5. A > 100 yr record of daily rainfall data for Skukuza to explore long-term trends in rainfall onset and ending dates as well as the frequency of dry spells in the growing season.

### Tree growth rates

The six dominant tree species at our study site (Supporting Information Table S1) were selected for growth rate measurements. For each species, nine individuals (a total of 54 trees) were selected. The species selected provide a reasonable sample of the functional diversity of trees in the region (see Table S1). Each of the 54 trees was fitted with a manual band dendrometer (Agricultural Electronics Corp., Tucson, AZ, USA). These band dendrometers consist of 3 mm × 0.75 mm metal bands placed around the tree and are held in place by a spring-loaded vernier gauge (Palmer & Ogden, 1983). Changes in tree diameter resulting

from growth or shrinkage are translated through the metal band to the vernier, thereby allowing changes in tree circumference to be read to the nearest 0.1 mm. Dendrometer bands were installed on all 54 trees in mid-October 2021 and then left for 4 wk to settle. Manual readings of the verniers were subsequently recorded every 2–3 wk until the end of September 2023. A drought experiment using rain-out shelters was initiated at the start of the 2022 rainfall year. We have therefore only used growth data for the untreated replicates (three trees for each of the six species) for the second growing season. For each study tree, we measured the initial stem diameter at the height at which the dendrometer was installed. For the purposes of this study, we make the assumption that changes in stem diameter (i.e. net stem increment) can be used as a proxy for tree growth. Dendroband readings were consistently taken at the same time in the early morning by the same person to improve accuracy and to avoid possible differences in stem diameter due to daily fluctuations (e.g. capacitance). We acknowledge that water uptake can result in stem increments but expect contraction during dryer periods with the net increment over a rainfall year equalling growth (Downes *et al.*, 1999). An ATMOS-41 (Meter Group, Pullman, WA, USA) weather station was installed at the initiation of the experiment at the Skukuza airport study site. The weather station recorded rainfall, temperature, humidity and wind speed every 5 min, and these data were stored on a ZL-6 data logger (Meter Group). An additional three TEROS-21 water potential sensors (Meter Group) were buried at three depths (15, 30 and 45 cm) in the centre of the study site and were connected to the same data logger as the weather station.

### Xylem pressure potentials

Xylem pressure potentials can be used to provide an instantaneous estimate of plant water stress (Scholander *et al.*, 1965). We measured monthly predawn XPPs using a Scholander-type pressure chamber (PMS Instrument Co., Albany, OR, USA) at the Skukuza airport study site, using freshly clipped twigs that contained fully expanded healthy leaves from each of the 54 study trees. As per the tree growth measurements, we only included nondroughted trees in our analyses of the 2022 wet season.

### Grass evapotranspiration measurements

Six weighing lysimeters were built in December 2021 to measure grass ET rates. Each lysimeter consisted of a weighing platform custom-built by a commercial company (Richter Scales, Pretoria, South Africa). Briefly, a solid metal base (1.2 × 1.2 m) with four loadcell feet was fitted with four load cells (Zemic H8C 250 kg), which were wired to a four-way junction box. The voltage signal of the load cells was measured using an analogue signal amplifier (SparkFun HX711 Load Cell Amplifier) and an Arduino Nano 33 microcontroller. A manual calibration using known weights was used to construct a voltage–weight linear regression equation for each lysimeter. A plastic bin with internal dimensions of 1196 mm × 996 mm × 400 mm (Mpact, 4 WAY JUMBO BIN SOLID) was then placed on each weighing platform and filled with soil. For each of the six lysimeters, we transplanted a

randomly selected 1196 × 996 × 400 mm soil monolith with its intact grass community. The six grass communities were taken from the Skukuza airport site; three from areas between tree canopies; and three from areas under tree canopies. The lysimeters were artificially watered once at the time of planting to mitigate transplantation stress and once at the end of February 2022 after an extended growing season dry spell to prevent the grasses from dying. Due to the strong coupling between transpiration and CO<sub>2</sub> assimilation, ET is intimately linked to carbon uptake, which in turn linked to plant growth (Major, 1967; Rosenzweig, 1968; Feng *et al.*, 2012). We found a strong correlation between ET and high-resolution NDVI measurements taken on each lysimeter on a two-weekly basis for > 1 yr (Fig. S1). We therefore used grass ET rates as a proxy for grass growth. In December 2021, an additional ATMOS-41 (Meter Group) weather station was installed at the SSLI campus study site.

The weather station records rainfall, temperature, humidity and wind speed every 5 min, and these data are stored on a ZL-6 data logger (Meter Group). Three TERSOS-21 water potential sensors (Meter Group) were buried at three depths in one of the lysimeters (10, 20 and 30 cm) and were connected to the same data logger as the weather station. We used a Parrot Sequoia multispectral camera to manually take high-resolution images of each lysimeter on a two-weekly basis between September 2022 and September 2023. These images were processed (see Methods S1 for detailed methods) and used to calculate NDVI values for the lysimeters on each of the image acquisition dates.

### Grass Soil Adjusted Vegetation Index measurements

Many of the private game reserves surrounding KNP manually clear woody vegetation to enhance tourist game viewing opportunities. As KNP has very few areas on granite-derived soils where trees are absent, we selected 14 open grassy areas in the Sabi Sands Game Reserve that were within 3 km of the Skukuza airport site. SAVI values were measured on the selected sites between June 2019 and September 2023 using satellite imagery. The grass sites covered an area of *c.* 6500 m<sup>2</sup>. A time series analysis was performed using Level 2A Sentinel-2 data in the Google Earth Engine cloud-computing environment. Preprocessing of the data included the following steps: (1) removing clouds by filtering scenes with < 30% cloud coverage and masking out remaining cloud pixels, making use of the S2 cloud probability data set (s2cloudless); (2) correction of illumination conditions using the bidirectional reflectance distribution function (BRDF); (3) co-registration to account for misalignment of pixels; and (4) clipping images to area of interest. BRDF Correction and co-registration were performed following Nguyen *et al.* (2020). To avoid major biases due to the spectral mixing of edge pixels, the areas were manually adjusted to the pixels of Sentinel-2. However, point spread function (PSF) effects, stemming from sensor characteristics, still introduce bias by involving neighbouring pixels in the observation. Since PSF effects are generally considered rather small (Huang *et al.*, 2002) and may be more important in heterogeneous landscapes (Wang & Atkinson, 2017), this bias is tolerated in our analysis. After preprocessing, the image collection consisted of 169 timesteps over

48 months. To monitor the effect of missing values due to cloud cover, a pixel count was performed and images with < 80% of the full pixel number were eliminated. The final data set therefore consisted of 142 timesteps. The SAVI has been shown to be strongly correlated with herbaceous aboveground biomass in savannas (Svinurai *et al.*, 2018; Munyati, 2022). We therefore chose SAVI to monitor grass growth during the study period, using the near-infrared and the red band of Sentinel-2 (Huete, 1988). The correction factor L was set to 0.5. Median SAVI values and standard deviations were calculated for each of the 14 grass plots at each timestep. The workflow and the equation used to calculate SAVI can be found in Fig. S2.

### Tree phenology monitoring

We used data from an ongoing study that monitors the phenology of the dominant deciduous woody species in the Skukuza region of KNP. In August 2015, 10 individuals each of the common species (a total of 260 trees from 17 species) were tagged at three sites in southern Kruger National Park. At Nkuhlu (−24.9808S, 31.78026E), the following species were included: *Acacia exuvialis* (I. Verd.) Kyal. & Boatwr., *A. nigrescens* (Oliv.) P.J.H. Hurter, *Combretum apiculatum* (Sond.) subsp. *apiculatum*, *C. hereroense* Schinz., *Grewia flavescens* Juss., *Sclerocarya birrea* (A. Rich.) Hochst. subsp. *Caffra* (Sond.) *Kokwaro*, *Terminalia sericea* Burch. Ex DC. and *Ziziphus mucronata* Willd. At Skukuza (−24.9851S, 31.5854E), the following species were included: *Acacia exuvialis*, *A. grandicornuta* (Gerstner) Seigler & Ebinger, *A. nigrescens*, *A. tortilis* (Forssk.) Gallaso & Banfi, *Combretum apiculatum*, *Grewia bicolor*, *Grewia flavescens*, *Kigelia africana* (Lam.) Benth., *Sclerocarya birrea* and *Ziziphus mucronata*. At the southern granite super-site (Smit *et al.*, 2013; −24.9938S and 31.5927E), the following species were included: *Acacia gerrardii* (Benth.) P.J.H. Hurter subsp. *gerrardii*, *A. nigrescens*, *A. nilotica* (L.) P.J.H. Hurter & Mabb. subsp. *kraussiana* (Benth) Kyal. & Boatwr., *Combretum hereroense*, *C. zeyheri* Sond., *Lannea schweinfurthii* (Engl.) var. *stuhlmannii* (Engl.) *Kokwaro*, *Terminalia sericea* and *Ziziphus mucronata*. Each of the tagged trees was inspected on a monthly basis and the proportion of flushing leaves, mature leaves, leaves changing colour and leaves shed were recorded using five categories as per (Fournier, 1974): (0 = none present, 1 = between 1 and 25% of canopy, 2 = between 26 and 50% of canopy, 3 = between 51 and 75% of canopy, 4 > 75% of canopy). In this study, we examined the patterns of leaf flushing and leaf senescence (changes in colour before being shed) for the 17 deciduous species.

### Analyses of long-term rainfall records

Because the growing season at our study site spans two calendar years, we have performed all analyses using rainfall years (i.e. a rainfall year runs from the beginning of October to the end of the following September) rather than calendar years. We have further divided rainfall years into two seasons according to Schulze (1997), whereby the dry season includes the months from April to September and the wet season includes the months from October to the end of the following March. The rainfall data set was provided by

the Scientific Services Department of SANParks, Skukuza. Rainfall has been collected daily since 1920 in Skukuza by Conservation Services staff using a rain gauge and recording readings manually. All rainfall data are then collated and stored in digital format by Scientific Services. We calculated the date of rain onset for each year according to the two criteria outlined by Ryan *et al.* (2017): 10 d in which a total of 25 mm of rain is recorded, followed by 20 d in which > 20 mm of additional rain is recorded. The end of the wet season was defined as the date after the start of the wet season when no rain occurred for a period of 20 consecutive days following (Zhang *et al.*, 2005; Adole *et al.*, 2018). Mengistu *et al.* (2021) and Usman & Reason (2004) have previously analysed how mid-growing season dry spells are likely to affect the dryland production of maize in the summer rainfall parts of Southern Africa using pentad analyses. We suggest that savanna vegetation, especially the grass component, should be similar to maize in their response to rainfall patterns and have therefore adopted their approach and defined a dry spell as a period of 5 d (a pentad) during which rainfall totals were < 5 mm. The growing season was split into 36 pentads and the total rainfall for each pentad for each rainfall year was calculated. We then calculated the total number of pentads with totals < 5 mm and the number of times there were at least four or more consecutive pentads with rainfall < 5 mm (i.e. a dry spell of > 20 d) for each rainfall year of the 102 yr record. To determine whether there are any long-term patterns evident in the total number and length of dry spells during the wet seasons we calculated the anomalies (differences from the long-term mean) for the total number of dry pentads and number of dry periods > 20 d and plotted these for each rainfall year (Fig. S3a,b). We then fitted a locally weighted scatterplot smoothing (LOESS) function to the dry spell time series data. This nonparametric regression technique allows for a smooth curve to be fitted onto time series data that does not follow a simple linear or polynomial form (Cleveland & Devlin, 1988).

## Data analyses

All analyses were performed using R v.3.4.2 (R Core Team, 2022). Tree dendrometer data were converted to daily changes in stem diameter and the cumulative stem diameter was calculated for each tree (Fig. 1). Grass ET rates were calculated according to the following steps: A mean absolute deviation filter was used to remove outliers, after which a rolling mean filter was applied to smooth the weights measured by the lysimeter. Linear interpolation (using the R-base linear interpolation function, `approx`) was used to derive a weight estimate for the time points when the weather station data were logged. We then calculated ET assuming a simple water balance model,

$$ET_t = \Delta w_t - r_t \quad \text{Eqn 1}$$

where  $\Delta w_t$  is the weight change measured by the lysimeter in time interval  $t$  and  $r_t$  is the rainfall in time interval  $t$  measured by the weather station. The time step used by the weather station was 5 min. The estimates for these time intervals were then summed to yield hourly and daily estimates of ET for each lysimeter. Although

ET measures both transpiration from vegetation and evaporation from soil, we assume that the overwhelming majority of ET is transpiration (Hutley *et al.*, 2001; Jasechko *et al.*, 2013).

Daily ET rates and tree growth rates by season  $\times$  rainfall year failed the Shapiro–Wilk test for normality; we therefore used the `dunn.test` to test for differences in grass ET and tree growth rates between seasons and rainfall years (Fig. 2). Predawn XPPs were log-transformed before we ran an ANOVA to compare XPPs during the growing season dry spells vs normal wet season measurements (Fig. 3).

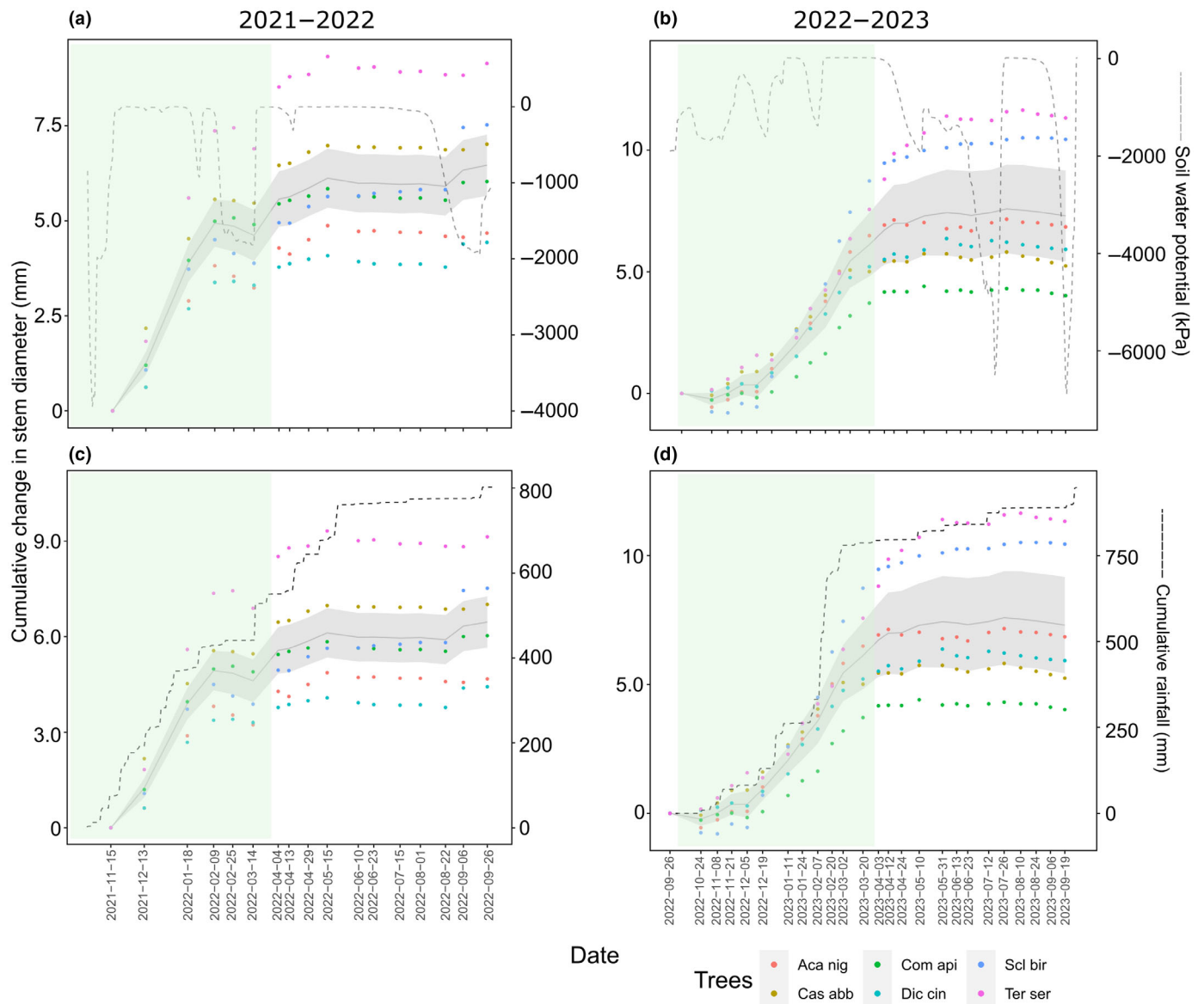
To test whether daily grass ET rates were related to soil water potentials we transformed ET rates using the `transformTukey` function in the `RCOMPANION` package in R (Mangiafico, 2019). We partitioned our data by season (wet and dry) and modelled ET rates as a function of lysimeter soil water potentials (average of 10, 20 and 30 cm depths) using generalized linear mixed models executed with the `GLMMTMB` package in R (Brooks *et al.*, 2017). Separate models were fitted for the growing and dry seasons using a Gamma distribution with a log link with the lysimeter identity (1–6) set as a random effect (Fig. 4a). The `r.squaredGLMM` function in the `MUMIN` package (Barton, 2013) was used to calculate marginal and conditional  $R$ -squared values for each of the models. We tested for differences in tree growth rates between three different growth periods in both the 2021 and 2022 rainfall years (growing season, growing season dry spell and dry season) using `dunn.test` in the `DUNN.TEST` package for R (Dinno & Dinno, 2017) which uses a  $Z$ -test with a Bonferroni correction to account for multiple comparisons (Fig. 4b). We calculated the average daily soil water potential of the three measured depths (10, 20 and 30 cm) in the lysimeters (Fig. 5).

To test for any changes in the onset and end dates of rainfall over the past 102 yr, we fitted linear models to our long-term rainfall onset and rainfall ending data, we assumed that each rainfall year was independent of previous observations and therefore did not need to account for the potential effects of temporal autocorrelation in our time series data. A plot of the fitted values against the standardized residuals was used to assess the assumption of normality for each of the models we ran (rainfall onset and end dates  $\sim$  rainfall year).

## Results

### How do trees and grasses respond to and recover from growing season dry spells?

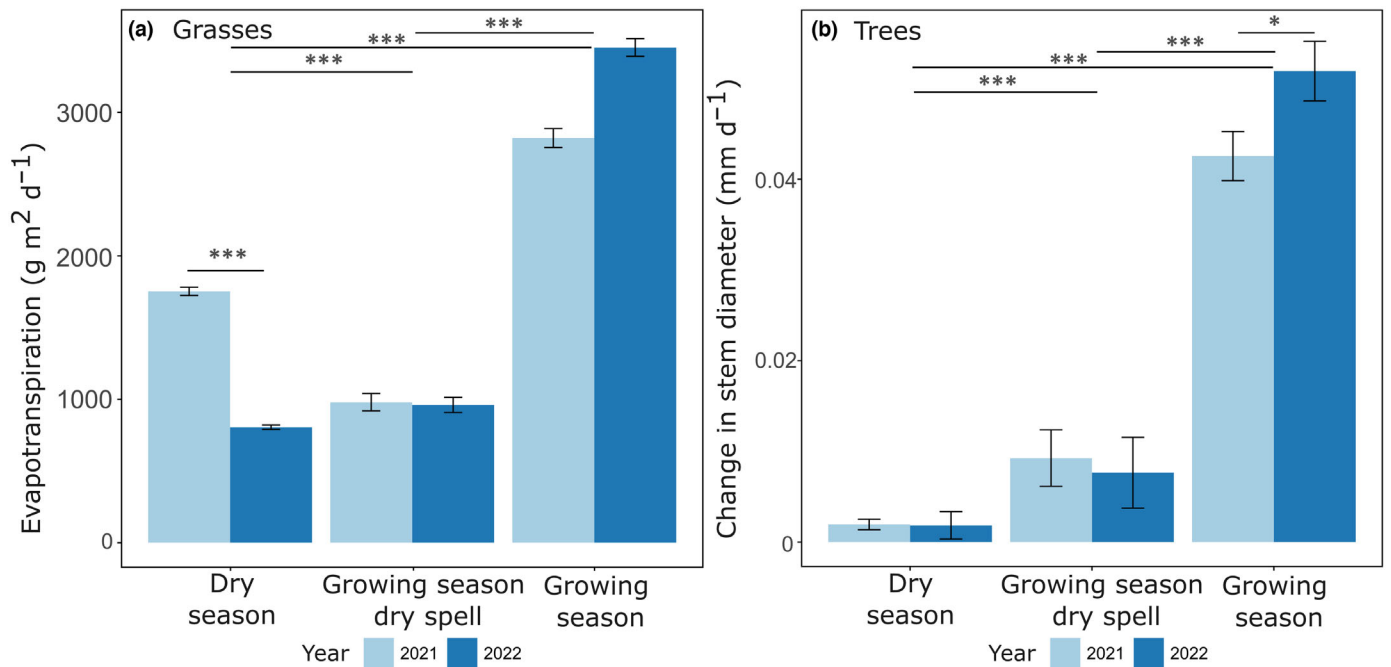
Growth of all six tree species at the Skukuza study site was significantly affected by both the growing season dry spells of 2021 and 2022 with no or negative stem increment growth during these periods (Fig. 1). During the 2021 growing season dry spell, the average soil water potential (measured at 15, 30 and 45 cm) at the Skukuza airport site dropped below 1500 kPa (Fig. 1a). During the early 2022 wet season, the soil water potentials were more variable but remained below 1500 kPa between October and November 2022 and again in early December (Fig. 1b). Dry season daily grass ET rates were significantly lower ( $P < 0.0001$ ) during the 2022 rainfall year than the 2021 rainfall year



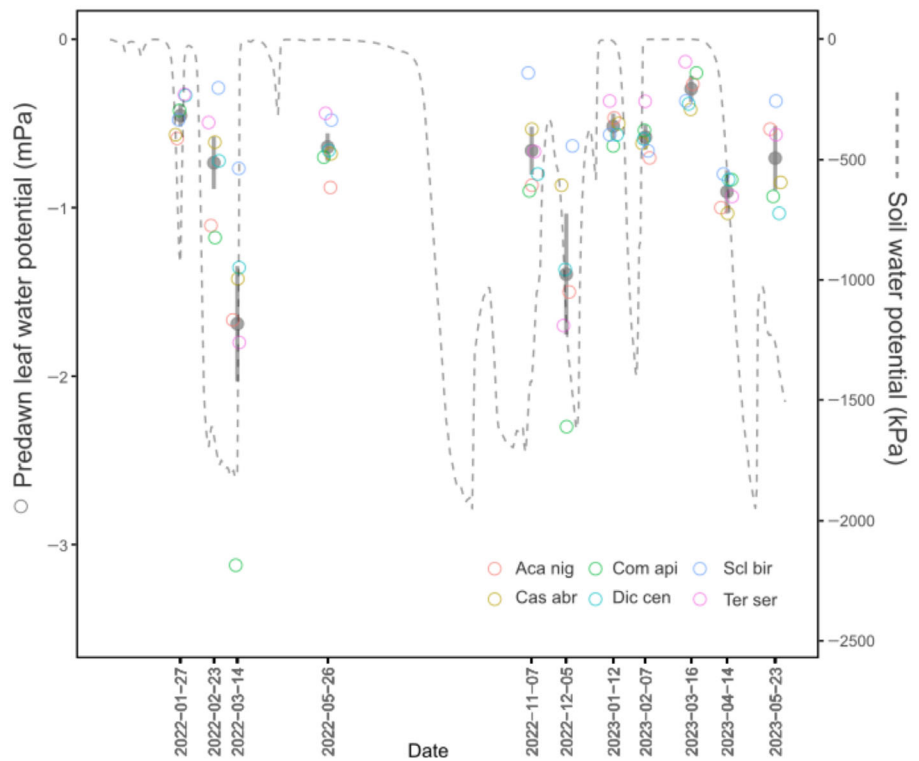
**Fig. 1** Mean growth rates  $\pm 95\%$  *ci* during the 2021 and 2022 rainfall years for the six tree species growing at the Skukuza airport site. An extended dry spell occurred between the end of January 2022 and the middle of March 2022 in the 2021 rainfall year and several dry spells occurred between mid-October 2022 and mid-December 2022 in the 2022 rainfall year. (a) Cumulative growth relative to the average soil water potential measured at three depths (15, 30 and 45 cm) for the 2021 rainfall year; (b) cumulative growth relative to the average soil water potential measured at three depths (15, 30 and 45 cm) for the 2022 rainfall year; (c) cumulative growth relative to cumulative rainfall for the 2021 rainfall year; (d) cumulative growth relative to cumulative rainfall for the 2022 rainfall year. The periods shaded in green indicate the wet season months. *Aca nig*, *Acacia nigrescens*; *Cas abb*, *Cassia abbreviata*; *Com api*, *Combretum apiculatum*; *Dic cin*, *Dicrostachys cinerea*; *Scl bir*, *Sclerocarya birrea*; *Ter ser*, *Terminalia sericea*.

(Fig. 2a), corresponding to lower soil water potentials during the 2022 rainfall year winter months (i.e. compare soil kPa values of April–August 2022 to April–August 2023; Fig. 5a). Grass ET rates during the growing season dry spells were similar for both the 2021 and 2022 rainfall years. Growing season grass ET rates did not significantly differ ( $P=0.66$ ) between the two rainfall years (Fig. 2a). Average daily grass ET rates over the 2-yr period were lowest during the growing season dry spells, slightly higher during the dry season and highest in the wet season. Differences between these three periods were all highly significant ( $P < 0.001$ ; Fig. 2a).

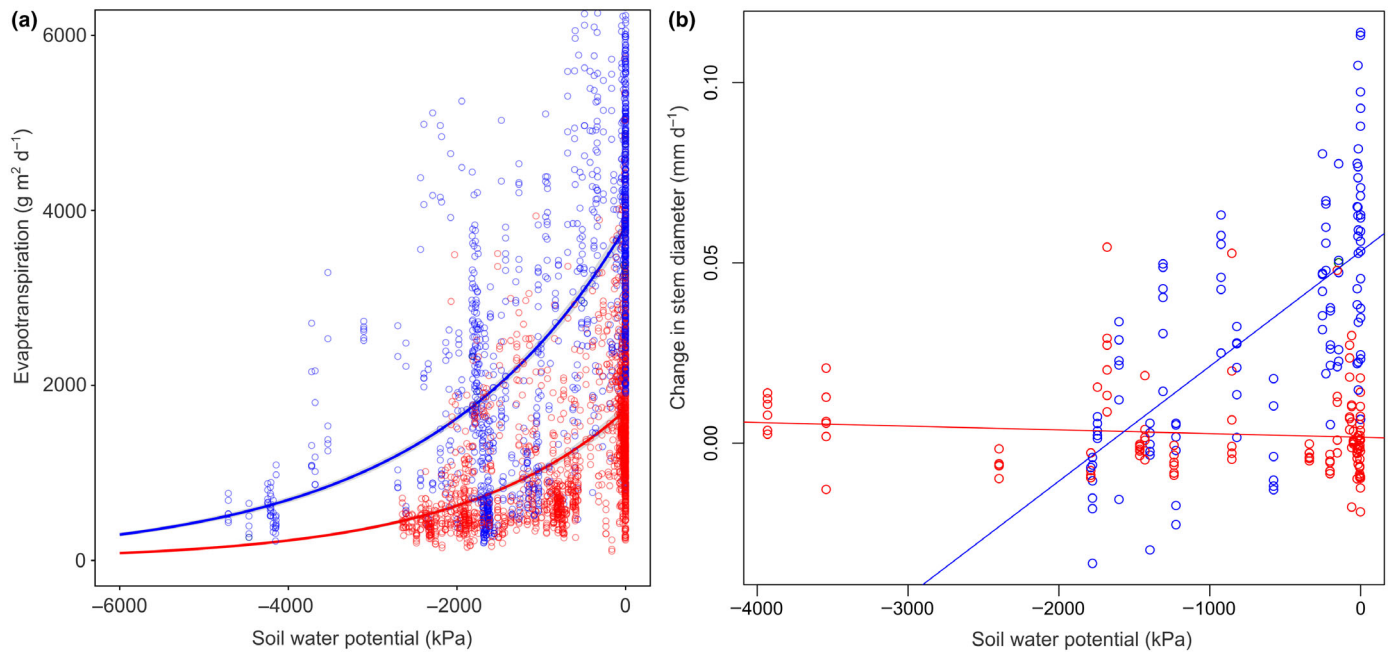
As expected, tree growth rates were the lowest in the dry season, slightly higher during the growing season dry spells and highest in the wet season (Fig. 2b). Tree growth rates were all highly significantly different from each other during the three periods ( $P < 0.001$ ) but showed no difference between years in the dry season and growing season dry spell. The average daily growth rate during the growing season was higher (chi-squared = 5.46,  $df = 1$ ,  $P$ -value = 0.01946) in 2022 than in 2021 (Fig. 2b). Predawn xylem water potentials show a similar pattern with significantly higher (more negative) values for all species during both of the growing season dry spells ( $F = 124.5$ ,



**Fig. 2** (a) Mean  $\pm$  SE daily evapotranspiration rates measured for grasses in the six lysimeters at the Skukuza Science Leadership Initiative (SSLI) study site during the dry season, growing season dry spells and wet seasons of the 2021 and 2022 rainfall years; (b) mean  $\pm$  SE growth rates for the six tree species growing at the Skukuza airport study during the same period. The three categories correspond to the following dates: Dry season = April to September, Wet season = October to March. An extended dry spell occurred between the end of January 2022 and the middle of March 2022 in the 2021 rainfall year and several dry spells occurred between mid-October 2022 and mid-December 2022 in the 2022 rainfall year. Significance levels are \*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ . Seasonal differences in grass evapotranspiration rates and tree growth rates during the 2021 and 2022 rainfall years.



**Fig. 3** Mean  $\pm$  95% confidence interval (CI) predawn xylem water potentials measured on the 54 trees growing at the Skukuza airport site during the growing seasons of the 2021 and 2022 rainfall years. Species means are also shown. Average soil water potentials measured at three depths (15, 30 and 45 cm) at the Skukuza airport site are also plotted. Aca nig, *Acacia nigrescens*; Cas abr, *Cassia abbreviata*; Com api, *Combretum apiculatum*; Dic cin, *Dicrostachys cinerea*; Scl bir, *Sclerocarya birrea*; Ter ser, *Terminalia sericea*.



**Fig. 4** (a) Relationships between grass evapotranspiration rates and soil water potential during the growing season (blue) and dry season (red). Glimm model fits were highly significant ( $P < 0.0001$ ) for both the growing season and the dry season. (b) Relationships between the mean change in stem diameter for the six tree species and mean soil water potentials during the growing season (blue) and dry season (red). Changes in stem diameter were positively related to soil water potentials (higher growth at higher soil water potentials) during the growing season ( $F = 17.09$ ,  $P < 0.001$ ,  $R^2 = 0.5$ ), but showed no relationship with soil water potential ( $F = 0.1$ ,  $P = 0.75$ ,  $R^2 = -0.05$ ) during the dry season. Dry season = April to September, Wet season = October to March. Seasonal differences in the relationships between grass evapotranspiration rates and soil water potentials and tree growth rates and soil water potentials.

df = 1,  $P$ -value < 0.0001; Fig. 3). Almost no growth was evident during the dry season months in all six tree species (Figs 2b, 4b; Table S2), despite unusually high soil moisture availability during the dry season months (May to August in the 2021 rainfall year). Soil water potentials remained close to zero during this period (Fig. 1). Total annual growth (changes in stem diameter) varied by between 1 and 3 mm between the two rainfall years for all of the species, the two fastest growing species, *Sclerocarya birrea* and *Terminalia sericea*, showed an average annual diameter increase of 8.98 and 10.23 mm respectively. The average for the four remaining species *Acacia nigrescens*, *Cassia abbreviata*, *Combretum apiculatum* and *Dicrostachys cinerea* ranged between 5.02 and 6.13 mm per annum (Table S2).

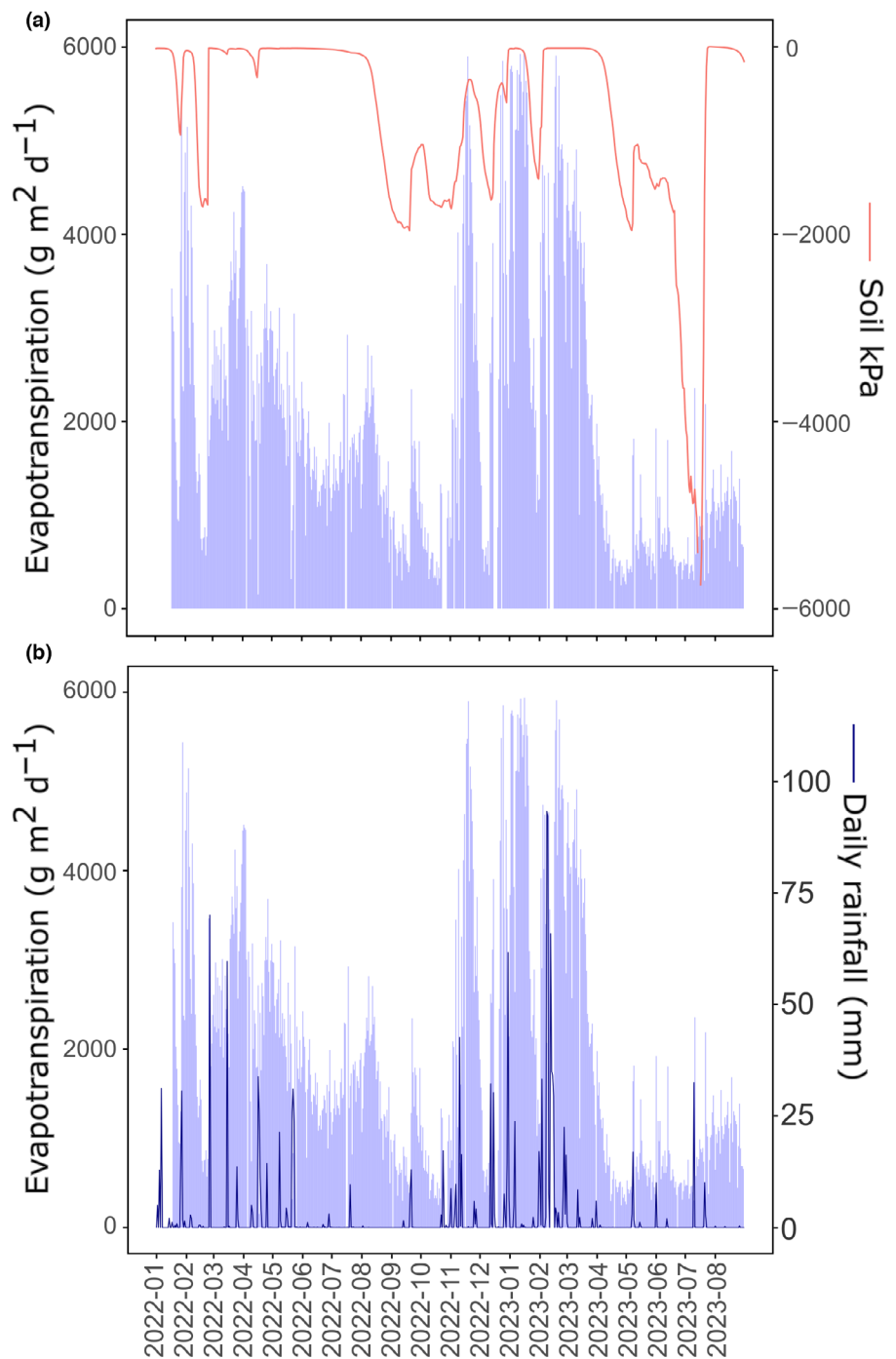
The measured daily ET rates of grasses at the SSLI campus site showed that grasses were also strongly affected by growing season dry spells. Daily ET rates showed steady decreases (from > 5000 to < 1000 g m<sup>-2</sup> d<sup>-1</sup>) during both dry spells that occurred in February/March 2022 and November/December 2022 (Fig. 5a,b). However, in contrast to trees, grasses recovered rapidly (< 1 wk) when soil moisture became available again (Fig. 5a,b).

#### How tightly are tree and grass phenologies linked to rainfall and season?

Analyses of the past 4 yr of phenology data showed that on average trees began to flush new leaves before the onset of the rains in

August or September with peak flushing occurring in November for the first 2 yr and in October thereafter (Fig. 6b). Leaves on the 17 tree species typically started to senesce in April, with leaf senescence peaking in June or July (Fig. 6b). Dendroband data for the six species at the airport study site showed that most of the trees stopped growing at the end of the growing season (April in both rainfall years) regardless of continued high soil water availability throughout the 2021 dry season (May–August 2022, Fig. 1). Grass growth (ET and NDVI), on the contrary, were found to be tightly coupled with soil water potentials regardless of season. The fixed effect of soil kPa was significantly related to ET during both the growing season (Estimate = 0.0427, SE = 0.0014,  $z = 30.58$ ,  $P < 0.0001$ ) and the dry season (Estimate = 0.0505, SE = 0.0015,  $z = 33.77$ ,  $P < 0.0001$ ; Fig. 4a). Tree growth rates were strongly correlated with soil water potentials ( $F = 17.09$ , df = 15,  $r^2 = 0.5$ ,  $P < 0.001$ ) during the wet season but completely unrelated ( $F = 0.1$ , df = 19,  $r^2 = -0.05$ ,  $P = 0.75$ ) with soil water potentials during the dry season (Fig. 4b). The intercept (i.e. at soil saturation) of the growing season model (ET = 3815 g m<sup>-2</sup> d<sup>-1</sup>) was higher than the dry season model (ET = 1719 g m<sup>-2</sup> d<sup>-1</sup>). The random effect (i.e. lysimeter identity) accounted for very low proportions of the variance (< 0.02) in both models. The SAVI values for the 14 grass sites (Fig. 6a) and ET rates (Fig. 5a,b) show that grasses start growing rapidly after rainfall and continue to grow as long as soil moisture is available regardless of season.



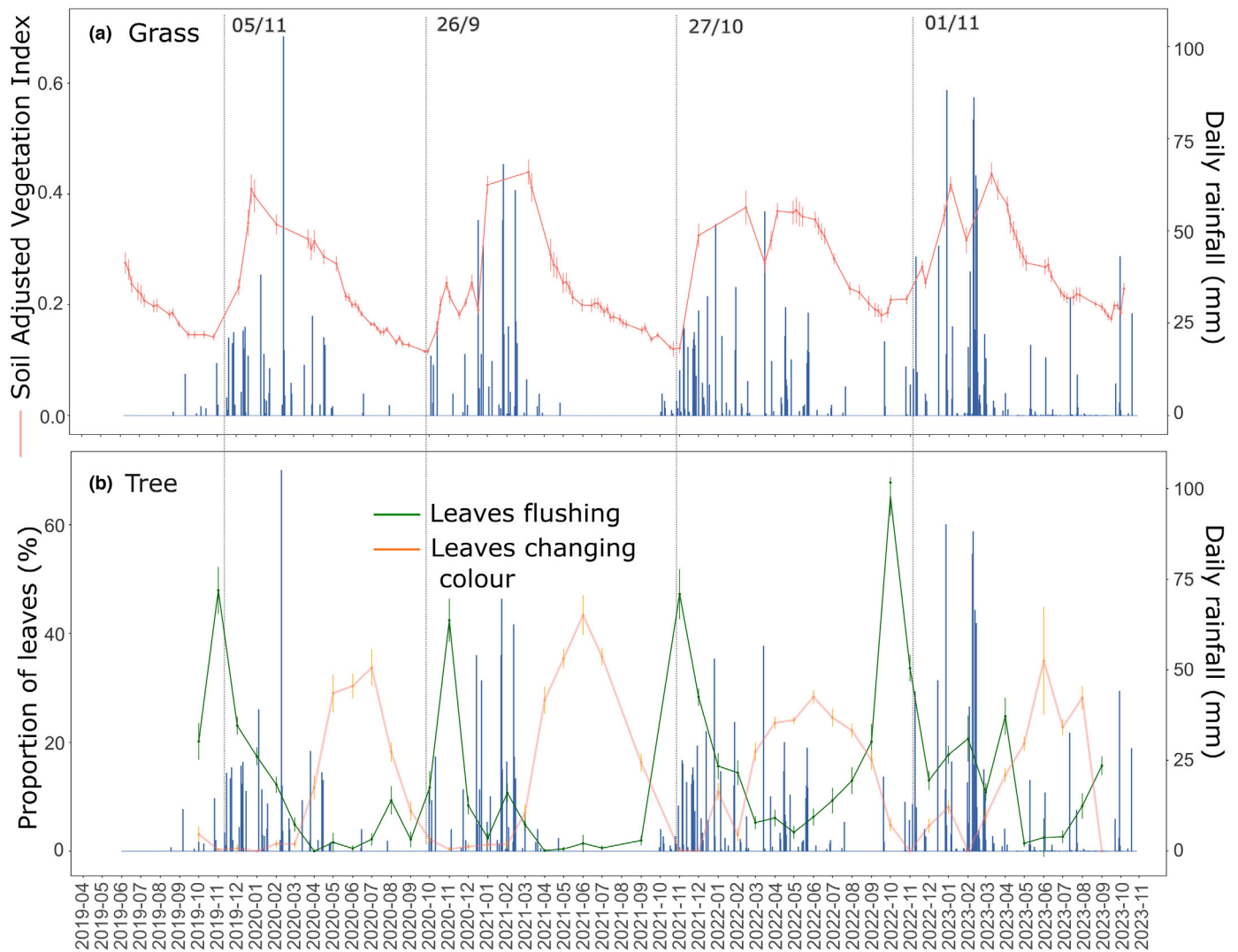


**Fig. 5** Mean daily evapotranspiration (ET) rates measured for grasses growing in six weighing lysimeters at the Skukuza Science Leadership Initiative (SSL) campus site. (a) Daily ET rates and average soil water potential measured at three depths (10, 20 and 30 cm) between January 2022 and September 2023; (b) daily ET rates and daily rainfall for the same period.

### Rainfall patterns

Our model shows a marginally significant decrease, that is, day of rainfall onset became earlier (Estimate =  $-0.1987$ ,  $df = 99$ ,  $F = 2.876$ ,  $P = 0.09$ ) in the day of rainfall onset over the past century, shifting from *c.* Day 308 (4th November) in 1920 to Day 288 (15 October) in 2022, corresponding to a shift of 20 d (Fig. 7a). The modelled day of rainfall end showed the opposite trend, with a significant increase, that is the end of the wet season became later (Estimate =  $0.2464$ ,  $df = 99$ ,  $F = 4.627$ ,  $P = 0.0339$ ).

The estimated day of rainfall end moved from 5 April in 1920 to 25 April in 2022 (Fig. 7b). This corresponds to a shift of *c.* 20 d. These results together suggest that on average, the growing season has increased over the past century, but there are consistently high levels of interannual variability in both the day of rainfall onset and ending (Fig. 7). Our pentad analyses showed that short dry spells (5 d) are common at our study site with a long-term average of *c.* 21 per wet season. The total number of dry pentads during the wet season showed a decreasing trend during the first 50 yr of the record. The opposite trend is however evident for the



**Fig. 6** (a) Median  $\pm$  SD of the calculated Soil Adjusted Vegetation Index (SAVI) values for grasses growing at 14 sites near to the Skukuza airport study site; (b) Proportion  $\pm$  SE of leaves flushing and changing colour (i.e. senescing) for the past four growing seasons (June 2019 to October 2023). Means of the 17 species growing at the three phenology monitoring sites are plotted. The date of wet season onset as defined by Ryan *et al.* (2017) is given for each year. Values are plotted for the same four growing seasons depicted in (a). Grass and tree phenologies in relation to rainfall for the years 2019 to 2023.

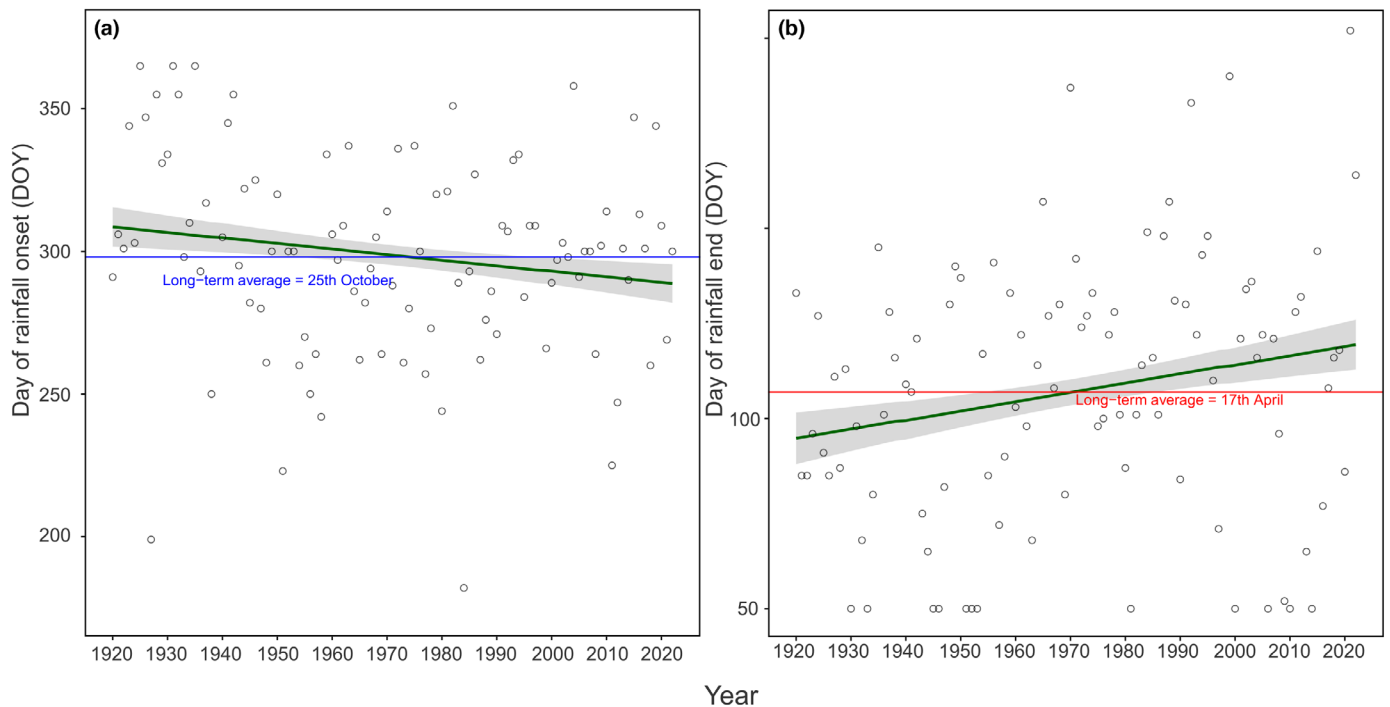
second half of the record showing a steady increase until the early 2020's, ending at least 1 pentad higher than the long-term average of 21 dry pentads (Fig. S3a). Our results also show that longer dry spells (i.e.  $> 20$  dry days) are also fairly common at our study site, occurring almost twice per growing season on average with an increasing trend during the past 50 yr, moving from well below the long-term average (1.8) to *c.* 2.3 in the 2020s (Fig. S3b).

## Discussion

Our results show the following: (1) both trees and grasses are negatively impacted by growing season dry spells, but (2) grasses are very responsive to rainfall and will grow at any time of the year as long as there is moisture in the soil; (3) trees typically initiate growth (measured as leaf flush) in October, regardless of

rainfall onset and stopped growing in April (measured as leaf senescence and change in stem diameter); (4) tree growth (measured as leaf flushing and changes in stem diameter) is predominantly constrained to the wet growing season (i.e. trees did not take advantage of wet conditions in the dry season); and (5) the potential growing season has become longer at our study site over the past century (i.e. earlier onset and later ending of rainfall) and that both short and long dry spells in the growing season have been increasing since the 1980s.

During the 2021 growing season dry spell, tree radial growth was significantly and negatively impacted and never fully recovered predry spell growth rates, even after soil water potentials approached saturation. Trees mostly stopped growing at the end of the wet season (April 2022), despite continued high soil water availability until August 2022. During the second growing season (2022), tree growth was limited during the initial months



**Fig. 7** Analyses of 102 yr of rainfall data at the Skukuza study site showing (a) the day of rainfall onset calculated according to the two criteria outlined by Ryan *et al.* (2017) with the modelled fit (green solid line)  $\pm$  SE (shaded grey area) ( $P = 0.09$ ) shown for each year and the long-term average, (b) mean day of rainfall ending as defined by Adole *et al.* (2018) with the modelled fit (green solid line)  $\pm$  SE (shaded grey area) ( $P = 0.03$ ) shown for each year and the long-term average. DOY, day of the year.

(October–December) due to several dry spells during that period but when adequate soil moisture became available during the core of the wet season (January–March 2023), growth rates (i.e. increased stem growth) recovered with trees growing steadily until the end of the wet season (April 2023). With the exception of *Terminalia sericea* (which continued growth until May in both years), all of the species stopped growing in April in both years.

One caveat relevant to this study is that we used manual band dendrometers to measure growth. Even though many studies that have quantified tree growth used band dendrometers (or manual measurements of DBH; Worbes, 1995; Callado *et al.*, 2013), band dendrometers cannot separate cambial growth from capacitance, and some of the initial stem growth at the beginning of the growing season can be due to rehydration of the trunk (Kozłowski, 1963; Borchert, 1999) and not true cambial growth. Surprisingly, few studies have empirically measured when savanna trees grow. What studies there are suggest that stem growth is closely associated with whole plant physiology and associated phenology (Prior *et al.*, 2004; Callado *et al.*, 2013). Whether cambium is dormant or growing depends on environmental factors associated with phytogeography, which may include temperature, day length and precipitation (Begum *et al.*, 2018; Rahman *et al.*, 2019). Previous studies from South American and Australian savannas (using both stem increment growth as well as methods to detect cambial activity) show that trees grow in the wet season, although they can start growing before the rains (Prior *et al.*, 2004; Rossatto *et al.*, 2009; Marcati *et al.*, 2016). Rossatto *et al.* (2009) found that stem growth started

towards the end of the growing season (in August) and continued until February in Cerrado trees (using band dendrometers on 12 savanna species in a system where the wet season normally starts in October and lasts to April). They suggested (but did not test) that the weak relationship between stem growth and monthly rainfall towards the end of the growing season when water was still abundant, meant that assimilates were being diverted to carbohydrate stores and/or root growth. The stem diameters of *Sclerocarya birrea* did show some increases before the 2022 wet season (Fig. 1) in our study; however, the majority of the gained diameter was subsequently lost (i.e. shrinkage), after which growth continued linearly for the rest of the wet season. It is thus unlikely that *S. birrea* was actively growing at the beginning of the season, but more likely redistributing water within the stem. This behaviour is consistent with the stem succulent strategy described by Borchert & Rivera (2001).

For trees, our measurements of predawn XPPs during both the 2021 and 2022 growing season dry spells, were significantly lower than the months preceding and following the dry spells, in all species for both years. These results combined with the shallow soils suggest that only a limited amount of deeper soil water is available to trees at our study site. The low soil water potentials ( $< -1500$  kPa) throughout the soil profile, together with significantly depressed XPPs and strong decreases in growth during the dry spells, in all species including those known to be deep-rooted (e.g. *Sclerocarya birrea*), suggest that the trees did not have access to significant amounts of deeper soil water. Furthermore, our soil water potential measurements showed that the available

soil moisture at all the depths we measured is rapidly depleted during growing season dry spells (within a few weeks; e.g. see Fig. 1; January–February 2022 and 2023). While the soils at our study site are relatively shallow (c. 0.5 m), which could partly account for these findings, the implications are important as large parts of the world's savannas occur on shallow soils (Oliveras & Malhi, 2016; Leenaars *et al.*, 2018; Malone & Searle, 2020).

Prerain green-up of tropical systems, including savannas and deciduous/semi-deciduous forest, is a well-known phenomenon (Rivera *et al.*, 2002; Kushwaha & Singh, 2005; Adole *et al.*, 2018). Similarly for the 17 deciduous, savanna tree species monitored, leaf flushing typically began in August or September across all years, reaching a peak in October or November. Peak leaf flushing showed no relationship with rainfall onset, occurring before (2019, 2022), at (2021) or after (2020) the rainfall onset date (Fig. 6b). Studies from South American savannas have also shown that leaf flushing of deciduous trees can be concentrated (within a month or two) early in the growing season with flushing commencing before the first significant rain (Rossatto *et al.*, 2009; Lacerda *et al.*, 2018). In this study, we found limited evidence for new leaf flushing events after the late growing season dry spell in the 2021 rainfall year despite an increase in leaf shedding during the dry spell (February–March 2022). There was however, some new flushing after the earlier growing season dry spell in the 2022 rainfall year (see January–February 2023; Fig. 6b). Leaf flushing throughout the growing season is not uncommon in savannas and has been reported from African (Moyo *et al.*, 2015; Masia *et al.*, 2018), Asian (Elliott *et al.*, 2006), Australian (Williams *et al.*, 1997) and South American savannas (de Camargo *et al.*, 2018). This work and our results would suggest that deciduous savanna trees can flush new leaves after a growing season dry spell, but this likely depends on when in the growing season the dry spell took place, the duration of the dry spell and how many resources were available to the trees in the preceding months.

Consistent with previous work, grasses at our study site were very responsive to soil moisture availability (Archibald & Scholes, 2007; Belovitch *et al.*, 2023). Furthermore, grasses responded regardless of season. This is not an uncommon phenomenon; for instance, Peters *et al.* (2014) compared aboveground annual productivity (ANPP) in grasslands and shrublands in an arid system in Southern New Mexico and showed that ANPP was linearly related to precipitation regardless of rainfall period, primarily as a result of stolon recruitment by a dominant grass. Grasses can also take advantage of nongrowing (e.g. colder or drier) season precipitation (Köchy & Wilson, 2004; de Jesus *et al.*, 2021), and in some cases, this may be more important in governing ANPP than growing season rainfall (Milchunas *et al.*, 1998). Grass productivity during the nongrowing season may contribute significantly to ANPP in tropical systems where nongrowing season temperatures and fertility are high enough (Queiroz *et al.*, 2012; Silva *et al.*, 2012; de Jesus *et al.*, 2021). Mid-growing season drought may, however, result in reduced flowering in grasses with potential longer term recruitment effects (Dietrich & Smith, 2016).

Rainfall variability can be measured in several ways, commonly used measures include total annual precipitation, number of days with rain (with varied minimum cut-offs) and intensity of rain

(average or maximum size of rainfall events; Kruger & Nxumalo, 2017). The majority of the savanna biome's global distribution has highly variable rainfall, both within and across years, and this variability is predicted to increase with climate change (Krishna Prabhakar, 2022). Studies across the globe (Jacob *et al.*, 2014; Singh *et al.*, 2014; Marengo *et al.*, 2016; Breinl *et al.*, 2020), including Africa (Usman & Reason, 2004; MacKellar *et al.*, 2014; Mengistu *et al.*, 2021), have shown a decrease in the number of rainy days and an increase in the frequency of growing season dry spells. While the mechanisms of how prerain green-up provides an opportunity for trees to grow without competition from grasses (temporal niche separation) and contributes to tree–grass coexistence have been relatively well documented in savannas (Scholes & Walker, 2004; Higgins *et al.*, 2011; Holdo & Nippert, 2023), only a few studies have explored how tree–grass interactions are likely to be affected by the increased variability in rainfall patterns expected with climate change. Some studies have suggested that more intense rainfall in sub-Saharan savannas (< 1200 mm yr<sup>-1</sup>) is more advantageous for trees as more intense rainfall events would result in wetter soils at depth while less intense, but more frequent rainfall would advantage grasses as the upper soil layers will be wet more frequently (D'Onofrio *et al.*, 2019). Yu *et al.* (2017), working on a rainfall gradient (i.e. Kalahari transect) across southern Africa, suggested that increased intensity of rainfall will advantage trees at lower MAP (> 900–1000 mm yr<sup>-1</sup>), but grasses will be advantaged at higher rainfall because of increased fire-related mortality to trees.

Previous studies that have suggested that trees will be advantaged by increased rainfall variability (especially higher rainfall intensities) are based on the well-established root niche separation theory (Walter, 1971; Kulmatiski & Beard, 2013b; Holdo & Nippert, 2023), which posits that tree roots are more deeply distributed than grassroots and can take advantage of deeper soil moisture when surface soils dry out. These findings, however, were not supported by a remote sensing study across African savannas, which found that maximum tree cover decreased with increasing rainfall intensity (Good & Caylor, 2011), especially at MAP of 500–800 mm yr<sup>-1</sup>. Good & Caylor (2011)'s study prompted Xu *et al.* (2015) to see whether they could use a biophysical tree–grass competition model to test whether differentiated tree and grass water use strategies can explain the observed negative relation between maximum tree abundance and rainfall intensity. They suggest that the aggressive water use of grasses confers a growth advantage to C<sub>4</sub> grasses in wet periods. In other words, the growth advantage of C<sub>4</sub> grasses in wet periods is larger than the advantage of deeper-rooted trees in dry periods. The findings of these studies (Good & Caylor, 2011; Xu *et al.*, 2015) suggest that increases in rainfall intensity (which would equate to more frequent dry spells) would benefit grasses more than trees in the savanna biome. Analyses of long-term rainfall records at our study site did not reveal any strong trends that suggest a change in total annual rainfall (data not shown). Our analyses did however suggest that the onset of rain has become earlier and the end of the rains later on average, suggesting that the growing season has become longer at our study site. The total number of both short

(> 5 d) and long (> 20 d) growing season dry spells showed a decreasing trend during the first half of the record, but have been steadily increasing since the 1980s. Should all of the above trends continue into the future we can expect that rainfall events will be further apart and more intense, and dry spells will become more frequent and protracted as has been predicted by many studies.

A number of important consequences are likely to affect tree–grass coexistence if growing season dry spells become more common and rainfall seasonality becomes less predictable in the future: (1) The effective growing season of trees may be significantly reduced compared with grasses because grasses can recover more effectively and quickly from mid-growing season dry spells and grasses can continue growing throughout the dry season, as long as temperatures are high enough, which seem likely under future climate. In other words, for grasses, phenological events are governed by moisture availability and grasses are able to flush when moisture becomes available (Bhat & Murali, 2001). (2) The assumption that trees outperform grasses under dry conditions lacks support as grasses can recover more rapidly after drought (Xu *et al.*, 2015; Holdo & Nippert, 2023). Our findings suggest that savanna trees growing on shallow soils will most likely be negatively impacted by more frequent growing season dry spells in the future. (3) If the onset of leaf flushing in trees is hardwired to a static cue such as the day of the year as is frequently found in tropical systems (Pau *et al.*, 2011), an earlier onset of rainfall in the future would benefit grasses more than trees as it would decrease the length of time that trees would not be competing with grasses (i.e. decreased temporal niche separation) as grasses are able to rapidly respond to rainfall onset. Additionally, if the day of rainfall ending becomes later, it will also benefit grasses as trees do not appear to be able to take advantage of dry season rainfall.

Our findings suggest that grasses should be advantaged by the predicted changes in rainfall variability expected with climate change. Yet trees are still thriving in many of the world's savannas (e.g. Stevens *et al.*, 2017; García Criado *et al.*, 2020). This pattern is probably due to factors unrelated to rainfall, which include fire suppression (Durigan & Ratter, 2016; Andela *et al.*, 2017; Stevens *et al.*, 2017; Moura *et al.*, 2019) and increased CO<sub>2</sub> (Buitenwerf *et al.*, 2012). However, the fertilizing effect of CO<sub>2</sub> may itself be contingent on adequate soil moisture availability (Nackley *et al.*, 2018). We suggest that future research should attempt to determine the conditions under which trees are likely to become more severely impacted by rainfall variability. For example, is rainfall frequency, rainfall intensity or rainfall seasonality more important for tree growth, and how will these ultimately interact with disturbances such as fire and grazing? A better understanding of the role of stored resources in tolerating growing season dry spells in trees and grasses is needed, that is trees have higher potential storage than grasses. There is also a need to more clearly separate leaf deployment, onset of gas exchange and onset of growth as different phenological events and measure these more effectively across savannas. Finally, a better understanding of the cues that trees use for leaf onset and senescence and the prevalence of polycyclism in savanna trees needs to be determined in order to determine whether savanna trees will

be able to adjust their phenologies to changing rainfall seasonality and be able to survive more frequent growing season dry spells. Some anecdotal evidence suggests that certain species (e.g. *Terminalia sericea*) are able to flush more than once in a growing season or adapt their phenologies according to water availability. This could partially account for why such species are more successful encroachers than others, making them likely winners under future climate change scenarios.

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## Competing interests

None declared.

## Author contributions

BW, SH and CC conceived the ideas and designed the methodology. BW, SH, CC, EF and SD collected the data. BW, SH and SD analysed the data. BW and CC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Data availability

The data that support the findings of this study are openly available in Dryad at doi: [10.5061/dryad.dbrv15f7w](https://doi.org/10.5061/dryad.dbrv15f7w).

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Overview of the workflow including the equation used to calculate Soil Adjusted Vegetation Index for the 14 grassy sites.

**Fig. S2** Pentad analyses of the long-term rainfall records from Skukuza.

**Fig. S3** Relationship between daily grass evapotranspiration rates and the normalized difference vegetation index.

**Methods S1** Methods used to calculate Soil Adjusted Vegetation Index values for the 14 grassy sites.

**Table S1** Six selected study species and their characteristics.

**Table S2** Mean cumulative changes in stem diameter for the two rainfall years by season for each of the six study species.

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