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Diurnal Variation in the Photosynthetic Traits of *Sclerocarya birrea* (Marula) Trees in North Namibia

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ABSTRACT

Sclerocarya birrea (marula) trees are important components of dry and semi-dry African savanna environments due to their ecological and economical importance, including carbon storage. However, functional characteristics of these dioecious trees, such as their photosynthetic rates, remain largely unstudied. We quantified the diurnal cycle in leaf-level net photosynthetic rate (A), stomatal conductance (g_{sw}) and transpiration (E) in sun and shade leaves of male and female individuals of 14 *Sclerocarya birrea* trees in a northern Namibian semi-arid agroforestry system and explained the observed trends by three environmental drivers (light, temperature and humidity). A generalised additive model with a thin-plate regression spline smoother was applied to describe non-linear diurnal variation in A, g_{sw} and E. Results revealed a pronounced pre-midday decline in A for sun leaves, from 5.5 μmol CO_2 $m^{-2} s^{-1}$ in the morning to 2.4 μmol CO_2 $m^{-2} s^{-1}$ in the late afternoon, while shade leaves showed a continuous decrease from 3.0 to 1.8 μmol CO_2 $m^{-2} s^{-1}$. Correspondingly, g_{sw} declined from 0.07 to 0.04 mol $m^{-2} s^{-1}$, and E from 0.0012 to 0.0008 mol $m^{-2} s^{-1}$ between morning and afternoon hours for sun leaves. Male trees exhibited higher A, g_{sw} and E than females, suggesting secondary sexual dimorphism in gas-exchange traits. Light was the best predictor of net photosynthetic rate and transpiration, whereas temperature was the best predictor of stomatal conductance. These findings highlight the complex interplay between environmental factors, leaf position and tree-specific traits in shaping the photosynthetic performance of *Sclerocarya birrea*. Consequently, this knowledge enables better-informed management and conservation strategies for this key savanna species.

1 | Introduction

The savanna ecosystem features an open tree canopy above a dense grass layer and represents one of the world's major biomes (Beerling and Osborne 2006; Sankaran et al. 2008; Ratnam et al. 2011; Whitley et al. 2017). Even though savannas are widespread, occupying 3106 km^2 in West Africa alone, there is still a dearth of information regarding the vegetation functioning. Although previous studies have measured leaf-level net photosynthetic rate, stomatal conductance and transpiration rates in savanna trees, particularly in Australia (Eamus et al. 2001), comprehensive global data on the photosynthetic traits of common savanna tree species are still lacking (Schulze et al. 1994; Woodward and Smith 1994; Quansah et al. 2014). Moreover, there remain significant gaps in understanding how these measurements scale temporally, driven by strong diurnal variation in air temperature and humidity, as well as seasonal climatic cycles (Eamus and Prior 2001). Such data are essential for improving understanding of leaf photosynthetic performance in savanna trees, providing baseline information for assessing the contribution of savannas to regional and global carbon dynamics (Denmead et al. 1993; Barford et al. 2001; Clark et al. 2003).

Leaves in a canopy encounter varying light and microclimatic conditions and may thus exhibit varying physiological responses depending on their position (sun vs. shaded leaves). The differentiation between sun and shade leaves represents a suite of coordinated traits optimised for their specific light environments (Niinemets 2007), that is, a leaf can fall anywhere on a sun-shade leaf spectrum, a continuum from extreme sun-leaf to deep shade-leaf, depending on the exact light level it developed in. Sun-shade leaf spectrum is not a fixed genetic adaptation but an acclimation, though the ability to acclimate is itself an adaptation. Sun leaves are typically thicker, with a higher stomatal density and nitrogen content per unit area, allowing for a higher light saturation point and greater photosynthetic capacity (Terashima et al. 2011). This high-resource strategy comes at the cost of a shorter leaf lifespan, positioning sun leaves on the fast-return end of the leaf economics spectrum (Wright et al. 2004), but is also coupled with enhanced photoprotective mechanisms that confer greater resistance to photoinhibition, a key difference from shade leaves (Goss and Lepetit 2015).

Biological characteristics like plant sex also affect plant physiological responses (Niinemets et al. 2015; Korgiopoulou et al. 2019). Sexually dimorphic plants often exhibit different reproductive costs due to their distinct reproductive roles; female plants typically invest more resources in reproduction during the growing season compared to males (Sánchez-Vilas and Retuerto 2011; Rakočević et al. 2025). These sex-specific trade-offs, together with variability within the canopy, complicate the scaling of leaf-level measurements to tree-level processes (Niinemets 2010). However, leaf-level information is still crucial for understanding how trees function in disparate environmental settings, especially in semi-arid savanna ecosystems with significant seasonal and diurnal variations (Williams and Rastetter 1999).

The *Sclerocarya birrea* (A.Rich.) Hochst. (commonly known as marula) is a dimorphic tree species native to the semi-arid regions of sub-Saharan Africa, and ecologically and economically a significant component of African agroforestry systems (Shackleton 2002). It is one of the dominant tree species in Southern African woodlands, comprising more than 20% of total woody biomass (Helm 2011). Its large canopy size results in a cooler subcanopy microenvironment beneficial for other plant and animal species (Muok et al. 2011). Its ability to provide people with their fundamental needs, such as food and medicine, and its potential to generate cash income for smallholder agriculture make it particularly important. Despite these important roles, its ecophysiological characteristics, including leaf-level net photosynthetic rates, remain poorly understood.

The aim of this study was to quantify the diurnal trends of the photosynthetic traits (net photosynthetic rate, stomatal conductance for water vapour and transpiration rate) of *S. birrea* trees in their natural environment in Northern Namibian agroforestry fields and to explain the trends by the main environmental drivers. Additionally, we were interested in sex-specific differences in leaf-level photosynthetic traits. Due to the pronounced diurnal cycle not only in light but also in temperature and humidity conditions in the area, we expected *S. birrea* leaves to show a clear diurnal cycle in their photosynthetic traits reflecting these conditions, net photosynthetic rate reaching its maximum in the morning and decreasing towards the afternoon. Male trees were expected to exhibit higher photosynthetic rates, stomatal conductance and transpiration than female trees due to females' stronger resource investment in reproduction. To quantify and explain these relationships, also in terms of air temperature and relative air humidity, leaf-level gas exchange of trees was measured throughout the day, for sun and shade leaves separately and related to the local weather data. Photosynthetic traits between male and female trees were also compared.

2 | Methodology

2.1 | The Study Area and the Species

The study was conducted at Ogongo Campus of the University of Namibia, in Ogongo (−17.70° S, 15.31° E), North Namibia in March—April 2023, corresponding to the mid-to-late growing season (Figure 1). Ogongo area has a semi-arid climate (Kopij 2024). The temperature has a strong seasonal variation, maximum summer temperatures going to 36°C and winter temperature falling to 6°C (Hove et al. 2021). The rainfall is strongly seasonal, falling mostly between November and April, with the average annual amount ranging from 450 to 500 mm (Awala et al. 2019).

Sclerocarya birrea is a dioecious tree, with pinnately compound leaves clustered at branch ends and a broad, spreading crown with male and female flowers occurring on separate individuals. In the study area, *S. birrea* trees grow sparsely distributed within other tree and shrub vegetation, such as *Vachellia erioloba, V. nilotica, Senegalia fleckii, S. mellifera, Albizia anthelmintica, Dichrostachys cinerea, Colophospermum mopane, Combretum* spp., *Commiphora* spp., *Grewia* spp., *Ficus sycomorus, Boscia albitrunca, Terminalia sericea, Zyzyphus mucronata* and *Hyphaene petersiana*. The minimum distance between the measured trees was 10 m, and the maximum distance between them was 1500 m (Figure 1). Seven of the measured trees were female and seven were male. Tree height of the measured trees ranged from 15.8 to 30.1 m and diameters at breast height (DBH) from 18.6 to 157.9 cm.

2.2 | Gas Exchange Measurements

We measured gas exchange from mature, healthy leaves of 14 naturally growing *Sclerocarya birrea* trees with a LI-6800 Portable Photosynthesis System (LI-COR Inc., Lincoln, NE, USA) using a standard $2 \times 3\,\text{cm}^2$ LED chamber. Each tree was subjected to a 1-day measurement cycle (8 AM–4 PM). Twelve leaves were measured per hour, six of which were exposed to the sun and six of which were shaded (giving 84 leaves per tree). The sun position at the moment of the measurement was used to classify the leaf as sun or shade leaf. Naturally weeping branches, accessible from the ground level with the tripod mounted LI-6800 equipment (max 2 m above the ground), were measured. The sun leaves were usually located in the outer canopy and the shaded leaves in the inner or outer canopy. The measurement conditions

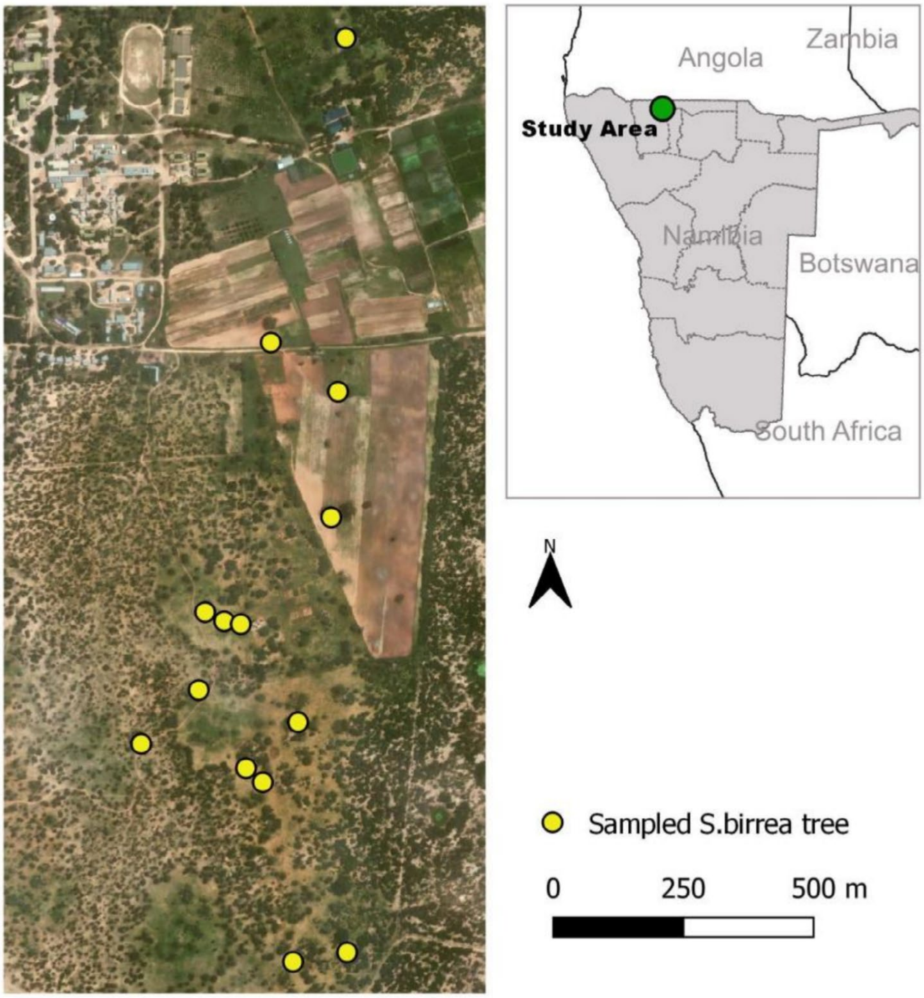

FIGURE 1 | Map of the study area, Ogongo Campus of the University of Namibia, in Ogongo (−17.70° S, 15.31° E) North Namibia.

TABLE 1 | Environmental control for sun leaves at each time interval during the diurnal measurement cycle.

Time	Irradiance (W m^{-2})	PAR (PPFD) μmol m^{-2} s^{-1}	RH %	Leaf T °C
08–09	97	229	60	22
09–10	272	640	55	24
10–11	469	1103	55	26
11–12	638	1498	50	27
13–14	826	1941	40	29
14–15	800	1880	40	30
15–16	706	1660	40	31

Note: Irradiance values were taken from the local weather station and transformed to PAR s. RH = Relative air humidity and LeafT = Leaf temperature, used as leaf chamber setting during the measurements. The shade leaves were measured in 194 μmol m^{-2} s^{-1} (83 W m^{-2}) throughout the day following the same diurnal cycle in RH and LeafT as sun leaves.

(environmental control) were set stable, simulating as closely as possible the average local diurnal cycle in light conditions, air temperature and air humidity. The light conditions for sun leaves were taken from the local weather station data (Ogongo SASSCAL Weathernet, −17.68° S, 15.29° E) and for shade leaves from the HOBO Pendant Temperature/Light data loggers (Onset Computer Corporation, Bourne, MA, USA) installed in the inner canopy of six measured trees, 2–3 m above the ground, recording data in every 15 min. The hourly-based values of solar irradiance from the Ogongo weather station were extracted from March to April 2021, which was the closest year that complete solar irradiance data was available for these months. Mean values per hour during this period were used in the analysis. The data was transformed from irradiance (W m^{-2}) to the photosynthetic photon flux density, PPFD (μmol m^{-2} s^{-1}) using 600 nm wavelength and expecting first that two-thirds of the irradiance is photosynthetically active, and later on corrected to correspond the fraction of 47% of photosynthetically active radiation (PAR) (McRee 1972; Ross and Sulev 2000). The measurements were carried out in the former light conditions; thus, the values were posteriorly scaled to correspond to the 47% PAR fraction. The scaling was performed using a function derived from the non-rectangular hyperbola model for photosynthetic light-response curves (Prioul and Chartier 1977), by assuming that 85% of the maximum assimilation ($A_{\max}$) was achieved in the original light intensity. The corrected light values of photon flux density (PPFD) ranged from 229 to 1941 μmol m^{-2} s^{-1} for sun leaves. For shade leaves, the PPFD was averagely 194 μmol m^{-2} s^{-1} throughout the day (Table 1). This setting follows the diurnal cycle of naturally occurring solar irradiance in the study area. During the measurements, we occasionally also registered higher natural PAR values, up to 2100 μmol m^{-2} s^{-1}. The leaf temperature (LeafT) was set to 22°C–31°C and relative air humidity (RH) to 60%–40% throughout the day, based on the averaged SASSCAL weather data at the Ogongo station during March–April 2023 (Table 1). CO$_2$ concentration was set to 430 μmol mol^{-1}, which is an average level of atmospheric CO$_2$ concentration currently in Namibia. The mixing fan was set at 10,000 rpm and the flow to 500 μmol s^{-1}. Steady-state gas exchange rates were recorded from each leaf after ~4–5 min of stabilisation.

3 | Analysis

3.1 | Modelling Diurnal Variation

Variation in net photosynthetic rate (A), stomatal conductance for water vapour (g_{sw}) and transpiration (E) was analysed with generalised additive models (GAMs) to assess the nonlinear relationship between these variables and time using the 'mgcv' package in R software version 4.4.2, within the RStudio IDE version 2024.12.0 (R Core Team 2024). We fitted a smooth term for time (s(Time)) using a thin-plate regression spline (TPRS) with the default smoothing penalty (gamma = 1) and a control of the wiggliness of the smooth (k = 4). TPRS is a default spline basis that estimates flexible, isotropic smooth functions between predictors and the response variable, accommodating complex ecological patterns without requiring strict parametric assumptions. Model fitting was performed using restricted maximum likelihood (REML). We fitted the models separately for sun and shade leaves and visualised the fitted relationship by generating model predictions across a sequence of time values. We calculated 95% confidence intervals for the predictions using the standard error of the predicted values. The final plots included the fitted spline curves with their confidence intervals and overlaid raw data points for reference (Figure 2). All plots were produced using the 'ggplot2' package in R software.

3.2 | Quantifying Partial Effects of Environmental Predictors

To analyse more specifically the effects of environmental drivers (light intensity, air temperature and relative air humidity) on net leaf photosynthetic rate (A), stomatal conductance (g_{sw}) and transpiration (E), we used GAMs fitting smooth terms (TPRS) for environmental predictors (light intensity, temperature and humidity) for all the data, that is, sun and shade leaves together, using the 'mgcv' package in R software. We first looked at the correlations between the environmental variables and dropped out relative air humidity due to its strong correlation with air temperature. Then we fitted GAMs using

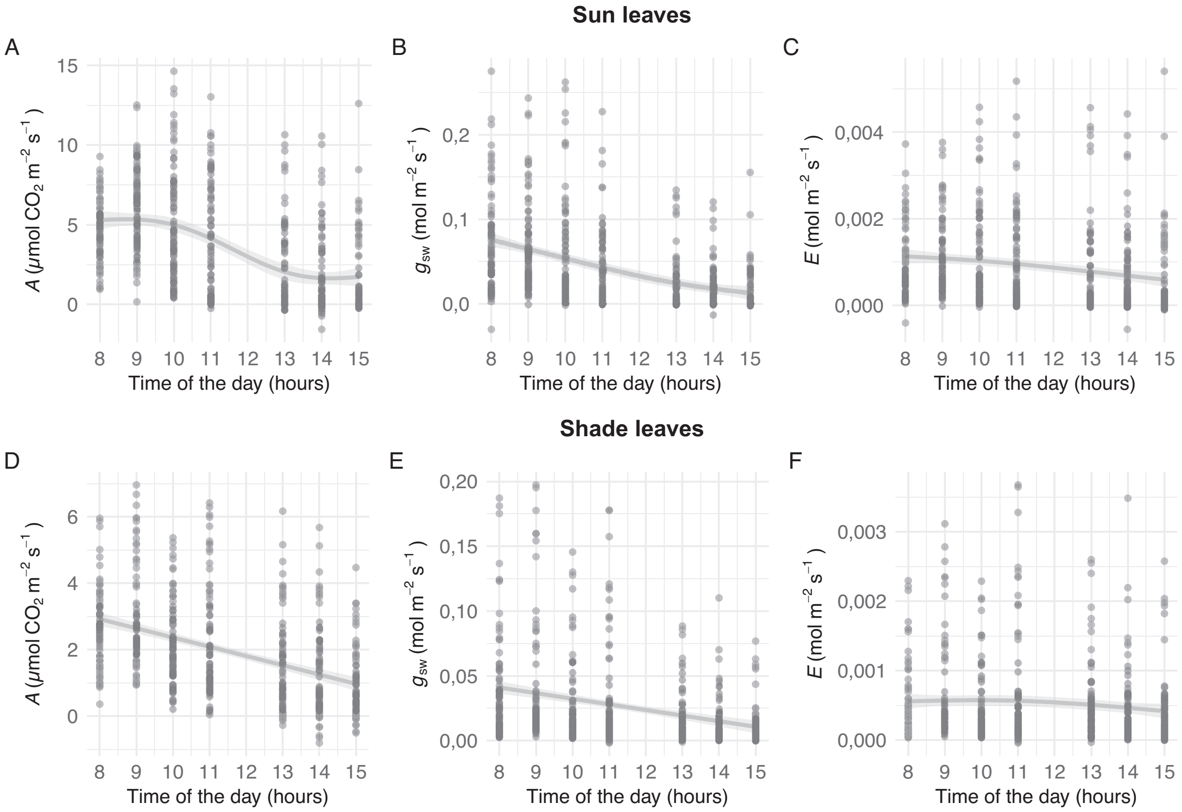

FIGURE 2 | Diurnal variation of leaf photosynthetic traits of *Sclerocarya birrea* trees for sun and shade leaves separately, fitted with GAM using smooth terms for time, and 95% confidence intervals (grey colour around the trend line). Grey dots are the original measurements expressing the variability of the data. A = net photosynthetic rate, g_{sw} = stomatal conductance for water vapour, E = transpiration. Subplot A–C are for sun leaves: (A) A versus time ($R^2 = 0.23$, $p < 0.001$); (B) g_{sw} versus time ($R^2 = 0.19$, $p < 0.001$); (C) E versus time ($R^2 = 0.04$, $p < 0.001$). Subplots D–F are for shade leaves: (D) A versus time ($R^2 = 0.19$, $p < 0.001$); (E) g_{sw} versus time ($R^2 = 0.09$, $p < 0.001$), (F) E vs. time ($R^2 = 0.008$, $p = 0.08$).

light intensity, temperature and their interaction as predictors. The variable *Tree* was included as a random effect in the models (s (Tree, bs = "re")) to account for repeated measurements within individual trees. The partial effects of the environmental variables accounted for a response to an 'average' tree with zero random effect, and they were centred around zero. Our models, however, showed high concurvity when both light intensity and temperature were included, even though these variables were not correlated in a simple correlation test. Thus, to ensure model parsimony and avoid overfitting, we fitted our final models with a single smooth term for either light intensity, temperature or humidity, along with a random effect for individual trees (s (Tree, bs = "re")). Smoothness was controlled by setting the basis dimension (k) for each predictor separately ($k = 5$ for light, $k = 5$ for temperature and $k = 4$ for humidity). Additionally, to prevent overfitting, the smoothness penalty was increased (gamma = 1.3). These values were chosen to balance model flexibility with parsimony. To evaluate the relative importance of light, temperature and humidity on photosynthetic performance of *S. birrea* leaves, we compared the GAMs fitted separately for net photosynthetic rate (A), stomatal conductance (g_{sw}) and transpiration (E), based on Akaike's Information Criterion (AIC).

3.3 | Sex-Specific Differences

To compare sex-specific differences in photosynthetic traits, we used the data on sun-exposed leaves during morning hours (8–11 AM). The analysis included one fixed factor, sex, with two levels (male and female trees). The response variables were net photosynthetic rate (A), stomatal conductance (g_{sw}) and transpiration rate (E). The data for A were square-root transformed to meet the assumptions of normality and homoscedasticity of residuals and subsequently analysed using an independent sample t-test. The data for g_{sw} and E violated parametric assumptions even after transformation and were therefore analysed using the non-parametric Wilcoxon rank-sum test.

4 | Results

4.1 | Daily Variation

Photosynthetic performance of *Sclerocarya birrea* showed a diurnal cycle, net leaf photosynthetic rates being higher during the morning compared to the afternoon, both in sun and shade leaves. Sun leaves had higher rates of leaf net photosynthesis and they also showed a stronger decline in photosynthesis towards afternoon than shade leaves. The strongest net leaf photosynthesis rate decline happened between 11 AM and 1 PM, especially in sun leaves (Figure 2A). Shade leaves showed a gentler declining curve due to generally lower photosynthetic rates, especially in the morning (Figure 2D). The average leaf net photosynthetic rate varied from 5.5 ± 4.8 (mean ± SE) μmol CO_2 $m^{-2} s^{-1}$ in the morning to 2.4 ± 2.3 (mean ± SE) μmol CO_2 $m^{-2} s^{-1}$ in late afternoon for sun leaves (Figure 2A). A less pronounced and continuous declining trend was observed for shade leaves, from 3.0 ± 2.1 (mean ± SE) μmol CO_2 $m^{-2} s^{-1}$ in the morning to 1.8 ± 1.0 (mean ± SE) μmol CO_2 $m^{-2} s^{-1}$ in the afternoon (Figure 2D). Stomatal conductance declined from 0.07 ± 0.05 (mean ± SE) mol $m^{-2} s^{-1}$ in the morning to 0.04 ± 0.025 (mean ± SE) mol $m^{-2} s^{-1}$ in the afternoon for the sun leaves (Figure 2B), and from 0.04 ± 0.02 (mean ± SE) mol $m^{-2} s^{-1}$ in the morning to 0.02 ± 0.01 (mean ± SE) mol $m^{-2} s^{-1}$ in the afternoon for the shaded leaves (Figure 2E). Transpiration declined from 0.0012 ± 0.001 (mean ± SE) mol $m^{-2} s^{-1}$ (corresponding to 52.8 W m^{-2}) in the morning to 0.0008 ± 0.0006 (mean ± SE) mol $m^{-2} s^{-1}$ (corresponding to 44 W m^{-2}) in the afternoon for sun leaves (Figure 2C), while shade leaves showed only a slight decrease from 0.0006 ± 0.0007 (mean ± SE) mol $m^{-2} s^{-1}$ (corresponding to 26.4 W m^{-2}) in the morning to 0.0005 ± 0.0004 (mean ± SE) mol $m^{-2} s^{-1}$ (corresponding to 17.6 W m^{-2}) in the afternoon (Figure 2F). All the fitted GAMs with a smooth term for time were statistically significant, except transpiration (E) in shaded leaves, which was only nearly significant. The explanatory power was the highest for the net photosynthetic rate (A) in both sun and shade leaf models ($R^2 = 0.23$, $p < 0.001$ and $R^2 = 0.19$, $p < 0.001$, respectively), and for stomatal conductance (g_{sw}) in the sun leaf model ($R^2 = 0.19$, $p < 0.001$). For the rest of the models the explanatory power was lower (Figure 2).

4.2 | The Role of Environmental Factors

The role of environmental factors (light, temperature and humidity) on leaf-level photosynthetic traits of *Sclerocarya birrea* was studied in separate GAM models. The inclusion of a variable *Tree* as a random factor to the models significantly improved the model fit and explained a substantial proportion of variation, as evidenced by comparisons with equivalent models lacking the random term. Models without *Tree* explained only 18%–27% of the variation in the leaf net photosynthetic rate, while when including *Tree* in the model, the proportion of explained variation increased to 60%–64%. For stomatal conductance and transpiration, the corresponding proportions were 13%–15% versus 66%–70% and 2%–7% versus 71%–74% (Table 2). This indicates a substantial difference between trees in their photosynthetic traits. All the models, where the random factor *Tree* was included, were significant and in general quite similar in their explanatory power, regardless of whether they had light intensity, air temperature or relative air humidity as a fixed effect explanatory variable (Table 2). In case of net photosynthetic rate and transpiration, the AIC test gave the best support for the model having light intensity as a predictor, while for stomatal conductance the best support was achieved from the model where temperature was used as a predictor (Table 2).

The partial effects of the models, that is, the responses of light intensity, temperature and humidity for net photosynthetic rate, stomatal conductance and transpiration of an 'average' tree, are shown in Figure 3. All photosynthetic traits (A, g_{sw} and E) showed an optimum curve in response to light, maximum values occurring at around 750 μmol $m^{-2} s^{-1}$ of PPFD. In response to temperature, the maximum values were reached at 24.0°C for A, at 22°C for g_{sw}, and at 24.5°C for E. In the case of humidity, the response showed an optimum curve only for A and

TABLE 2 | Comparison of the single variable smooth-term GAM models carried out for net photosynthetic rate (A), stomatal conductance (g_{sw}) and transpiration rate (E), including tree as a random factor.

Model	Env. variable (edf Ref.df^{-1})	Tree (edf Ref.df^{-1})	R^2 (adj)	AIC	ΔAIC
A~s (Light_scaled, $k=5$) + s (Tree, bs = "re")	**3.89/3.99**	**11.86/12.00**	**0.65**	**4164.6**	**0.0**
A~s(Temp_scaled, $k=5$) + s(Tree, bs = "re")	3.70/3.95	11.85/12.00	0.61	4269.8	105.2
A~s(Hum_scaled, $k=4$) + s(Tree, bs = "re")	2.82/2.97	11.84/12.00	0.60	4292.5	127.9
g_{sw}~s(Light_scaled, $k=5$) + s(Tree, bs = "re")	3.82/3.98	11.90/12.00	0.67	−4856.3	114.4
g_{sw}~s(Temp_scaled, $k=5$) + s(Tree, bs = "re")	**3.33/3.77**	**11.91/12.00**	**0.70**	**−4970.6**	**0.0**
g_{sw}~s(Hum_scaled, $k=4$) + s(Tree, bs = "re")	1.00/1.00	11.91/12.00	0.69	−4945.0	25.6
E~s(Light_scaled, $k=5$) + s(Tree, bs = "re")	**3.71/3.95**	**11.94/12.00**	**0.74**	**−13758.2**	**0.0**
E~s(Temp_scaled, $k=5$) + s(Tree, bs = "re")	3.04/3.55	11.93/12.00	0.71	−13608.6	149.6
E~s(Hum_scaled, $k=4$) + s(Tree, bs = "re")	2.42/2.74	11.93/12.00	0.70	−13603.4	154.9

Note: Effective degrees of freedom (edf) quantify curve complexity (edf = 1 indicating a linear relationship and higher values increasing nonlinearity). Ref.df shows the maximum possible complexity allowed by the model. R^2 (adj) expresses the explanatory power of the model. AIC and ΔAIC values indicate the best model in each of the comparisons (marked in bold).

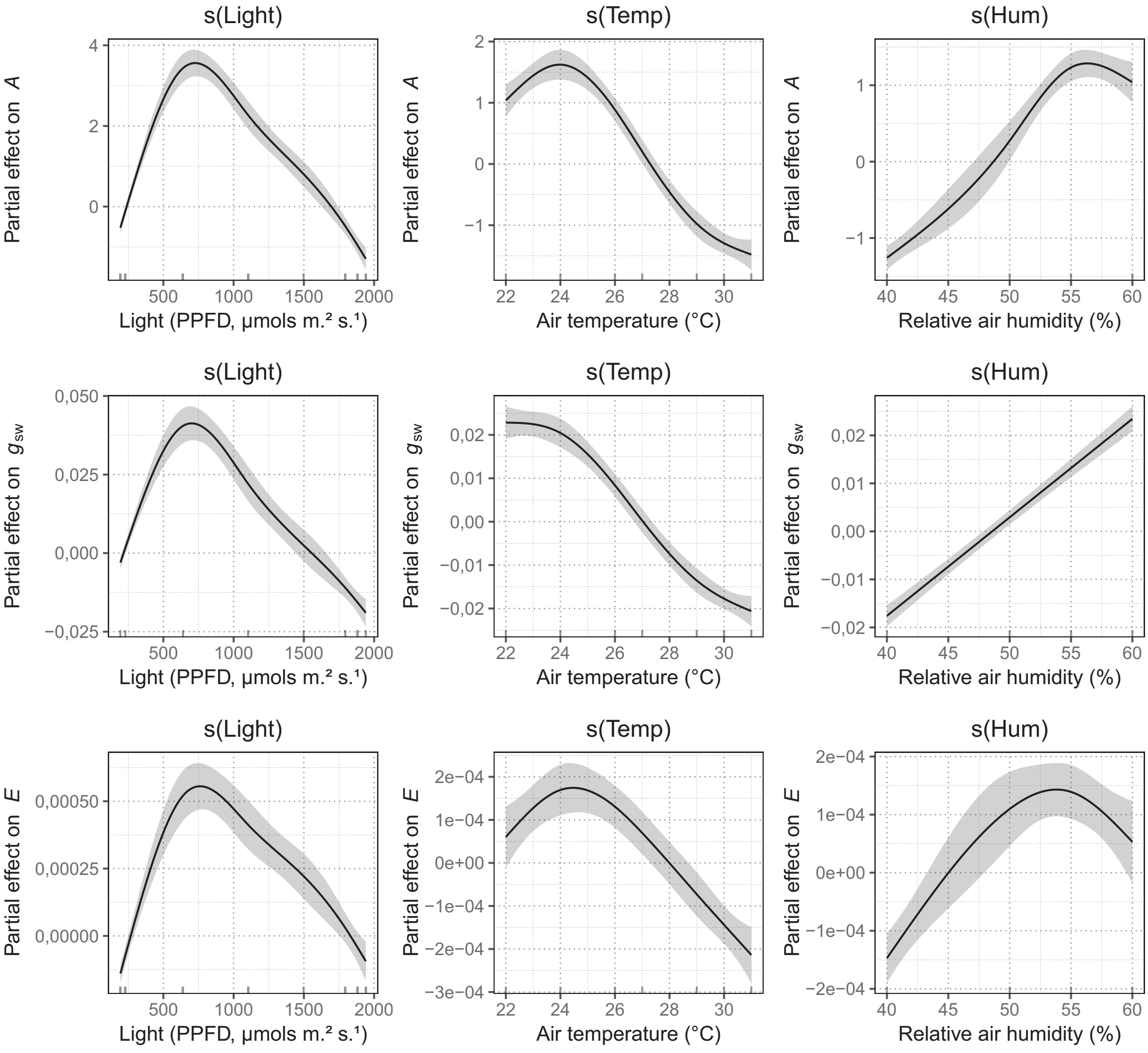

FIGURE 3 | GAM spline smooth-term plots showing the partial effects of light intensity (PPFD, µmol m^{-2} s^{-1}), temperature (°C) and humidity (RH, %) on the net photosynthesis rate (A), stomatal conductance (g_{ws}) and transpiration rate (E) of *Sclerocarya birrea* leaves. Light grey colour around the trend line represents 95% confidence intervals.

E, maximum values occurring at 56.5% and 54% of RH, respectively. For g_{sw}, the response to humidity was linear, increasing continuously from 40% to 60% of RH (Figure 3).

4.3 | Sex-Specific Photosynthetic Performance

Sclerocarya birrea trees showed sex-specific differences in their leaf-level net photosynthetic performance. Male trees had higher net photosynthetic rate, stomatal conductance and transpiration than female trees (Figure 4). The mean leaf net photosynthetic rate was 5.97 ± 2.90 (mean ± SD) μmol CO_2 $m^{-2} s^{-1}$ for male trees and 4.75 ± 2.76 (mean ± SD) μmol CO_2 $m^{-2} s^{-1}$ for female trees. Stomatal conductance was 0.084 ± 0.072 (mean ± SD) mol $m^{-2} s^{-1}$ and 0.052 ± 0.044 (mean ± SD) mol $m^{-2} s^{-1}$ for female trees. Transpiration was 0.0014 ± 0.0011 (mean ± SD) mol $m^{-2} s^{-1}$ for male trees and 0.0009 ± 0.0007 (mean ± SD) mol $m^{-2} s^{-1}$ for female trees, corresponding to 50.4 and 29.3 W m^{-2} respectively, in latent heat flux.

5 | Discussion

This study offers the first thorough evaluation of diurnal variations in *Sclerocarya birrea* leaf-level photosynthetic rates in response to environmental conditions in northern Namibian semi-arid savanna agroforestry systems. Our findings show distinct daily cycles in leaf net photosynthesis rate, stomatal conductance and transpiration, with substantial differences between sun and shade leaves (Figure 2). Net leaf photosynthetic rates were higher during the morning compared to the afternoon, both in sun and shade leaves. Similar diurnal cycles have been documented in *S. birrea* seedlings populations in South Africa, where leaf-level net photosynthesis was highest in the morning and declined sharply under midday stress (Li et al. 2015; Wilken et al. 2024). Other semi-arid savanna tree species also show similar diurnal patterns in leaf net photosynthesis (Eamus et al. 1999; Eamus and Prior 2001; Hoffmann et al. 2005). Our study also showed that sun leaves had higher absolute rates of leaf net photosynthesis than shade leaves, and a stronger decline in net photosynthesis towards afternoon. The strongest decline happened between 11 AM and 1 PM (Figure 2A), likely resulting from the combined impacts of lowered humidity, rising leaf temperature and high irradiance, all of which limit stomatal opening (Veste et al. 2000; Naumburg and Ellsworth 2002; Ribeiro et al. 2009; Liu et al. 2010; Urban et al. 2012). This pre-midday decline of the net photosynthesis of sun leaves may represent an adaptive strategy of the species to limit water loss and thermal stress in the semi-arid environment. Stomatal conductance and transpiration, being highly correlated with the net photosynthesis rate, followed a similar but more continuous decline from the early morning to late afternoon (Figure 2B,C). Although transpiration represents water loss at the leaf level, it also plays an essential role in controlling local and regional climate by facilitating energy dissipation and maintaining the short-term water cycle, thereby balancing temperature variations in the tree canopy and surrounding area (Ellison et al. 2017). Photosynthetic traits of shade leaves didn't show as clear a diurnal cycle as the traits of sun leaves did, even though the general trends were also decreasing from morning to afternoon (Figure 2D–F). These results demonstrate how sun and shade foliage work differently to control carbon uptake at the crown level. Quantifying and understanding these leaf-level variations are the first steps towards a more complete understanding of tree-level CO_2 assimilation in dry and semi-dry savanna systems.

In general, the responses of each photosynthetic trait (A, g_{sw}, E) to environmental factors (light, temperature and humidity) followed similar hump-shaped patterns, except the linear response of g_{sw} to humidity, indicating that our diurnal measurement cycle managed to capture the daily optima for each trait along the three environmental dimensions (Figure 3). Leaf net photosynthetic rate, stomatal conductance and transpiration all reached their optima at ~750 μmol photons $m^{-2} s^{-1}$. This corresponds to the morning hours around 10 AM. The temperature optima for the traits were reached at 22.0°C–24.5°C. These temperatures occurred early in the morning, between 8 and 10 AM. Humidity optimum occurred even earlier, between 8 and 9 AM.

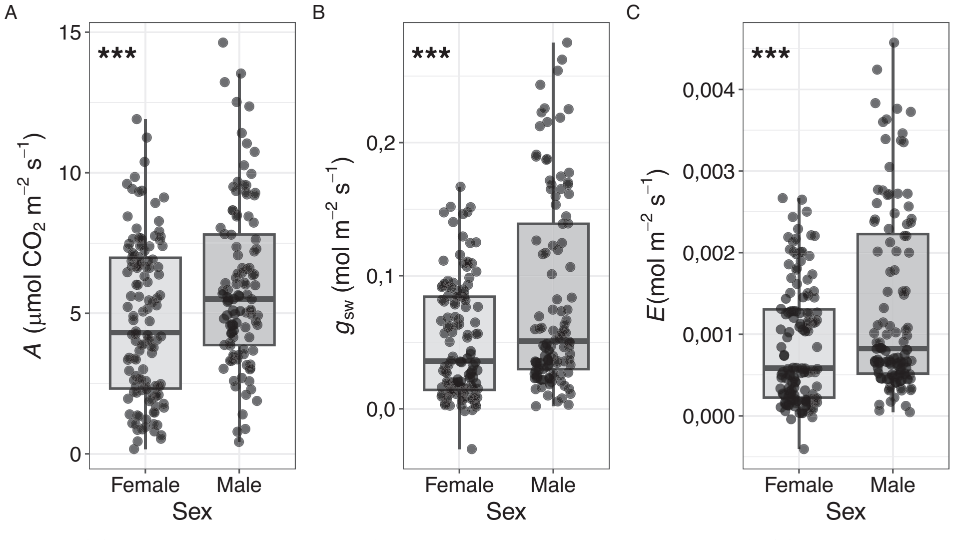

FIGURE 4 | Difference in (A) net photosynthetic rate, A (T-test: $T = -35{,}259$, df = 231,74, $p < 0.001$), (B) stomatal conductance, g_{sw} (Wilcoxon rank-sum test: $W = 4993$, $p < 0.001$) and (C) transpiration, E (Wilcoxon rank-sum test: $W = 5007$, $p < 0.001$) in the morning hours (08–11 AM) between female and male trees (n for Female = 126; n for Male = 108).

This means that when the light conditions are optimal, the temperature and humidity optima have already passed. Thus, a real diurnal photosynthetic optimum condition for *S. birrea* trees is a complex interplay between these three factors. These optima are in line with studies carried out in other savanna tree species (Veste et al. 2000; Naumburg and Ellsworth 2002; Urban et al. 2012).

To explore the best environmental predictors for the diurnal cycle of the photosynthetic traits, we fitted the GAMs using smooth terms separately for each trait. To balance between model flexibility and parsimony, and to avoid overfitting, we fitted the final models with only one environmental predictor at a time (either light, temperature or humidity). Our data showed significant variation in leaf photosynthetic traits between individual trees. Thus, it was crucial to include *Tree* as a random factor in each model to account for this variability. A strong tree-to-tree variation may arise from several reasons, for example from crown architecture or microclimate (Niinemets and Valladares 2004), soil conditions or sex-specific traits, males investing less in reproduction than females and are therefore able to retain more resources for photosynthesis and growth (Wheelwright and Logan 2004). Our results supported the sex-specific differences, male *S. birrea* trees having higher net leaf photosynthetic rate, stomatal conductance and transpiration rate than female trees (Figure 4). To evaluate the relative importance of light, temperature and humidity on photosynthetic traits of *S. birrea* leaves, we compared the models by AIC. Our results showed light as the best predictor for the net photosynthetic rate (A) and transpiration (E). This aligns with studies on other tropical and savanna species, showing light as the main driver of photosynthesis and temperature and humidity modulating rates indirectly via stomatal function (Lawlor 1995; Han 2001; Kanniah et al. 2013). The best predictor for stomatal conductance (g_{sw}) was temperature, which has also previously been noted to have an important role in controlling stomatal behaviour (Dai et al. 1992; McAdam and Brodribb 2015; Kruse et al. 2019; Grossiord et al. 2020). This highlights trait-specific environmental sensitivity in *S. birrea* by showing that stomatal function responds more strongly to temperature than to light.

6 | Conclusion

Our findings emphasise a strong diurnal variation in the leaf-level photosynthetic traits of *Sclerocarya birrea* trees, remarkable differences between sun and shade leaves, and a complex interplay between environmental variables in modulating the physiological responses of leaves to a strong diurnal cycle of the environmental conditions. The sex-specific differences reflected secondary sexual dimorphism, where males outperformed the female trees in leaf-level photosynthetic activity. The results also point out a substantial tree-to-tree variation in the photosynthetic traits, highlighting the need for further research to better understand the dynamic responses of the leaf and tree-level photosynthesis to the diurnal light, temperature and humidity cycles in a semi-dry savanna environment. Accounting for within and between tree variation in photosynthetic traits is important to be able to estimate net photosynthetic rate not only at the whole tree level but also in a larger spatial context.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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