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Seasonal Variation in Transpiration and Stomatal Conductance of Three Savanna Tree Species in Ruma National Park, Kenya

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Abstract: Understanding the seasonal regulation of transpiration and stomatal conductance is critical for evaluating plant water-use strategies in response to environmental variability. This study assessed these physiological traits in three dominant savanna tree species (*Piliostigma thonningii* (Schumach.) Milne-Redh., *Combretum molle* R.Br. ex G.Don, and *Balanites aegyptiaca* (L.) Delile) in Ruma National Park, Kenya. Measurements were taken during wet and dry seasons under varying canopy light conditions (light-exposed vs. shaded leaves) and soil moisture regimes. A randomized design with four treatments and three replicates was employed. Results showed significantly higher transpiration and stomatal conductance during wet seasons, especially in sunlit leaves ($p < 0.05$). *P. thonningii* exhibited the highest rates of transpiration (9 mmol m^{-2} s^{-1}) and stomatal conductance (~2.2 mmol m^{-2} s^{-1}) in light conditions, while *B. aegyptiaca* maintained consistently low values, reflecting a drought-tolerant strategy. *C. molle* demonstrated intermediate responses, suggesting a balance between water conservation and resource use. Despite seasonal trends, low R^2 values indicated that internal physiological regulation outweighed the influence of external climatic drivers. These findings reveal species-specific water-use strategies and highlight the ecological significance of leaf-level responses to light and moisture availability in tropical savannas. The study provides valuable insights for forest management and climate-resilient restoration planning in water-limited ecosystems.

Keywords: transpiration; stomatal conductance; plant water-use strategy; canopy light gradient; tropical savanna; climate adaptation

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1. Introduction

Transpiration and stomatal conductance play critical physiological roles in regulating water loss and carbon dioxide uptake in plants, directly influencing photosynthesis, cooling, and nutrient transport [1,2]. Ecologically, these processes determine plant water-use efficiency and adaptability to environmental stress, especially in water-limited ecosystems.

Stomatal behavior, by mediating gas exchange, helps plants balance growth and survival, shaping species distribution, community structure, and ecosystem productivity under varying climatic conditions [2]. Leaf transpiration plays a vital role in the terrestrial water cycle, constituting a major component of overall evapotranspiration [1]. Plant water use is predominantly regulated by the opening and closing of stomata, which in turn control carbon uptake and water loss across scales, from individual leaves to entire landscapes [2,3]. The movement of stomata is influenced by both biotic and abiotic factors, with significant implications for plant physiological responses under variable environmental conditions [2,4].

A mechanistic understanding of transpiration (Tr) and stomatal conductance (gs) is essential for developing models that predict plant water use at ecosystem, regional, and global scales, especially under projected climate change scenarios. In savanna ecosystems, such models are particularly valuable due to the inherent variability in light, moisture and vegetation structure. Previous studies have identified diverse strategies used by plants to cope with fluctuating light conditions across canopy layers, with canopy position significantly affecting photosynthetic capacity and water-use efficiency [5,6].

Transpiration is known to increase with a rising vapor pressure deficit (VPD), while stomatal behavior is tightly coupled with soil moisture availability. Under dry conditions, stomatal closure serves as a protective mechanism to prevent xylem embolism and conserve water [2,7]. Despite the importance of these processes, empirical data on Tr and gs in East African humid savanna trees, especially at the leaf level, remain scarce. Limited studies suggest that both soil characteristics and atmospheric conditions such as solar radiation, humidity, and wind speed can influence transpiration by affecting leaf temperature and vapor exchange dynamics [8].

In African savannas, several investigations have examined short-term patterns of transpiration and seasonal gs [9]. However, many of these studies rely on indirect micrometeorological extrapolations rather than direct measurements at the leaf or crown level. Additionally, the assumption of uniform light distribution across tree canopies limits the ecological relevance of these assessments [10,11]. The vertical stratification of canopies where younger, light-exposed leaves differ physiologically from shaded, older leaves is seldom considered in such analyses.

Leaf-level physiological traits such as Tr and gs can vary significantly by canopy position, leaf age, and irradiance throughout the day [4,9]. These fine-scale variations are critical for understanding species' ecological strategies and their capacity to survive under fluctuating water and light availability [9]. *Balanites aegyptiaca* has been shown to exhibit strong physiological sensitivity to soil moisture availability, though most data originate from controlled experiments [12]. Some studies in southern Africa indicate that water availability may not directly trigger phenological changes in *Piliostigma thonningii* [13], underscoring the complex relationship between plant physiology and environmental cues.

However, how *C. molle*, *B. aegyptiaca*, and *P. thonningii* physiologically respond to vertical light gradients within their canopies remains poorly understood. This knowledge gap hinders our ability to predict carbon and water fluxes in humid savanna systems, which are characterized by strong temporal variability in resource availability [14]. Prior studies have shown that sun-exposed leaves generally exhibit higher photosynthetic rates, modulated by leaf nitrogen content and light intensity [15], while others have noted reduced biochemical sensitivity in shaded leaves of arid-adapted species [6].

Accordingly, this study addresses two key research questions: How do sunlit and shaded leaves of savanna tree species respond to seasonal microclimatic conditions during the growing season? Are there differences in transpiration and stomatal conductance between top (light-exposed) and bottom (shaded) canopy leaves? These questions are critical for improving our understanding of canopy-level physiological heterogeneity. Although *C. molle*, *B. aegyptiaca*, and *P. thonningii* are widespread in Ruma National Park, Kenya, their seasonal leaf-level gas exchange patterns under field conditions remain undocumented. This study aims to fill that gap, providing insights critical for ecosystem management, climate-resilient restoration, and modeling of plant–water interactions in the East African savannas.

2. Materials and Methods

2.1. Study Site

The study was conducted in Ruma National Park, located in the Lambwe Valley between the Kanyamwa Escarpment and the Gwasi Hills (00°36′28″ S, 34°15′24″ E) at approximately 1400 m above sea level (Figure 1). The park is situated 23 km southwest of Homa Bay Town and 425 km west of Nairobi [16]. A section within the park, managed separately by the National Youth Service (NYS), encompasses approximately 40 ha and has been used for long-term monitoring of savanna vegetation dynamics. Soils in the area are predominantly alkaline black Vertisols. The region experiences a bimodal rainfall pattern, with annual precipitation ranging from 1200 to 1600 mm. The long rainy season occurs from March to May, and the short rains fall between October and December. The experimental work was carried out within a 70 m × 100 m fenced plot, previously subjected to grazing but protected during the study period.

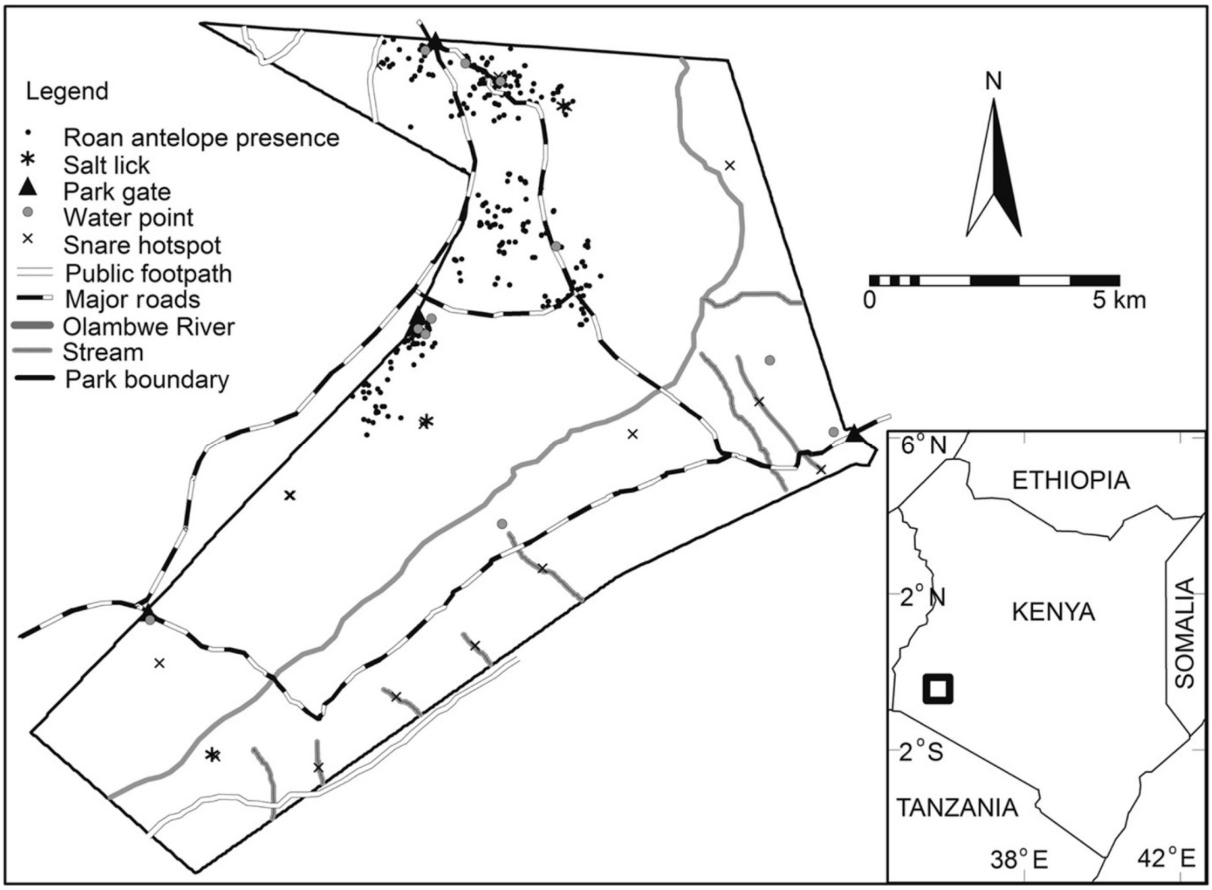

Figure 1. Map of Ruma National Park and surrounding areas (adapted from Kimanzi et al. [16]).

2.2. Experimental Design and Vegetation Sampling

Three dominant savanna tree species, *Piliostigma thonningii* (Schumach.) Milne-Redh., *Combretum molle* R.Br. ex G.Don, and *Balanites aegyptiaca* (L.) Delile, were selected based on their ecological importance (Table 1). Species identification was confirmed through morphological comparison with authenticated herbarium specimens at the Maseno University Herbarium. Voucher specimens were collected and deposited at the University Botanical Garden, Maseno University Herbarium (acronym: MUH), to support species verification and future reference (Supplementary Materials).

Table 1. Description of tree species in Ruma National Park.

Characteristics	*P. thonningii*	*B. aegyptiaca*	*C. mole*
Distribution	Woodland and wooded grasslands of sub-humid Africa	Tropical, dry-land African savanna	Throughout tropical Africa
Life form	Deciduous tree, 4–15 m in height	Spiny shrub or tree, up to 10 m in height	Variable shrub or small semi-deciduous tree, 3–13 m.
Leaf type	Broad-leaved	Compound leaves	Opposite and simple
Leaf Characteristics	Large, simple, two-lobed, leathery leaves (camel foot-like)	Reduced and spirally arranged leaves	Leathery leaves
Stem	Single-stem tree	Multi-branched	Crooked or leaning trunk
Root system	Deep roots	Complex system of strong, diagonally radiating roots	Does not have an aggressive root system

For each species, three individual trees were randomly selected, with heights ranging from 2.0 to 2.8 m and diameters around 0.17 m. All selected individuals were estimated to be older than 15 years.

A completely randomized design was applied, with three individual trees per species, each subjected to four treatments: bottom-lit (BL), bottom-shaded (BD), top-lit (TL), and top-shaded (TD) conditions. From each individual tree, a total of 10 fully expanded leaves (5 sunlit and 5 shaded) were selected for measurements. Leaves were sampled from similar twig positions to minimize variability caused by leaf age or damage.

2.3. Data Collection

2.3.1. Microclimatic Measurements

Microclimatic variables were recorded using an automatic weather station (AWSGP1, Delta-T Devices, Cambridge, UK) mounted 2 m above ground. Parameters recorded included wind direction and speed, precipitation, solar radiation, photosynthetic photon flux density (PPFD), relative humidity (RH), and air temperature. Data were logged every 5 min and averaged over 30 min intervals using a Delta-T logger.

The vapor pressure deficit (VPD) was calculated using standard meteorological formulas based on RH and temperature [2]. As VPD calculation methods are widely established, detailed formulas are not provided here.

2.3.2. Soil Moisture Monitoring

Volumetric soil moisture content was measured with 5TE sensors (Decagon Devices, Pullman, WA, USA) installed at 60 cm soil depth. Three sensors were deployed around each tree within a 50 cm radius. Data were logged at 30 min intervals and daily averages were computed.

2.3.3. Leaf Gas Exchange Measurements

Leaf gas exchange was assessed using a steady-state porometer (LI-1600, LI-COR Biosciences, Lincoln, NE, USA) with a 2 cm circular aperture. Measurements included transpiration rate (Tr), stomatal conductance (gs), leaf temperature, air temperature, RH, and PPFD, all taken on the adaxial surface of leaves.

At each canopy level (upper and lower), measurements were made on five sunlit and five shaded leaves, totaling 10 leaves per tree. Measurements were conducted from sunrise to sunset. During rainy or humid conditions, diurnal measurements were standardized at six time points: 0700, 0900, 1100, 1300, 1500, and 1700 h. Each measurement lasted 20–30 s while keeping the leaves attached to the branch.

To account for diurnal variation in gs, especially under changing VPD conditions, data analyses incorporated the VPD as a covariate in the regression models. Furthermore, leaf gas exchange data were stratified by light conditions (sunlit vs. shaded leaves) using measured PPFD values to assess PAR (photosynthetically active radiation) effects.

Transpiration (Tr) was estimated following standard approaches, and stomatal conductance (gs) was recalculated and expressed in mmol m^{-2} s^{-1} for comparability with literature standards.

The following standard Equations (1) and (2) [2] were applied:

Transpiration rate (Tr):

$$Tr = {}^{E}/_{A} \tag{1}$$

where E is the transpiration rate (mmol H_2O m^{-2} s^{-1}), and A is the leaf area (m^2) of the chamber window.

Stomatal conductance (gs):

$$gs = {}^{E \cdot P}/_{VPD} \tag{2}$$

where E is the transpiration rate, P is atmospheric pressure (kPa), and VPD is the vapor pressure deficit (kPa).

PPFD (photosynthetic photon flux density) values were used to stratify the data into sunlit (>800 µmol m^{-2} s^{-1}) and shaded (<400 µmol m^{-2} s^{-1}) light categories.

2.4. Data Analysis

All statistical analyses were conducted using SPSS v25 (IBM Corp.) and R v4.0.1. Data normality was verified via the Kolmogorov–Smirnov and Shapiro–Wilk tests. Differences in gas exchange parameters (Tr and gs) were analyzed using one-way ANOVA, with significance set at $p < 0.05$. Linear regressions were performed to assess relationships between physiological variables (gs and Tr) and environmental factors (VPD, PAR, and soil moisture), with the VPD incorporated as a covariate where appropriate. Analyses were stratified by species and canopy position. An independent *t*-test was used to compare transpiration and stomatal conductance between different light conditions.

3. Results

3.1. Climatic Conditions

Seasonal variation in climatic conditions at Ruma National Park followed a typical tropical bimodal rainfall pattern (Figure 2). Rainfall peaked in April (261.5 mm) and October (184.75 mm), corresponding to the long and short rainy seasons, respectively. The driest months were January (95 mm) and July (84.8 mm).

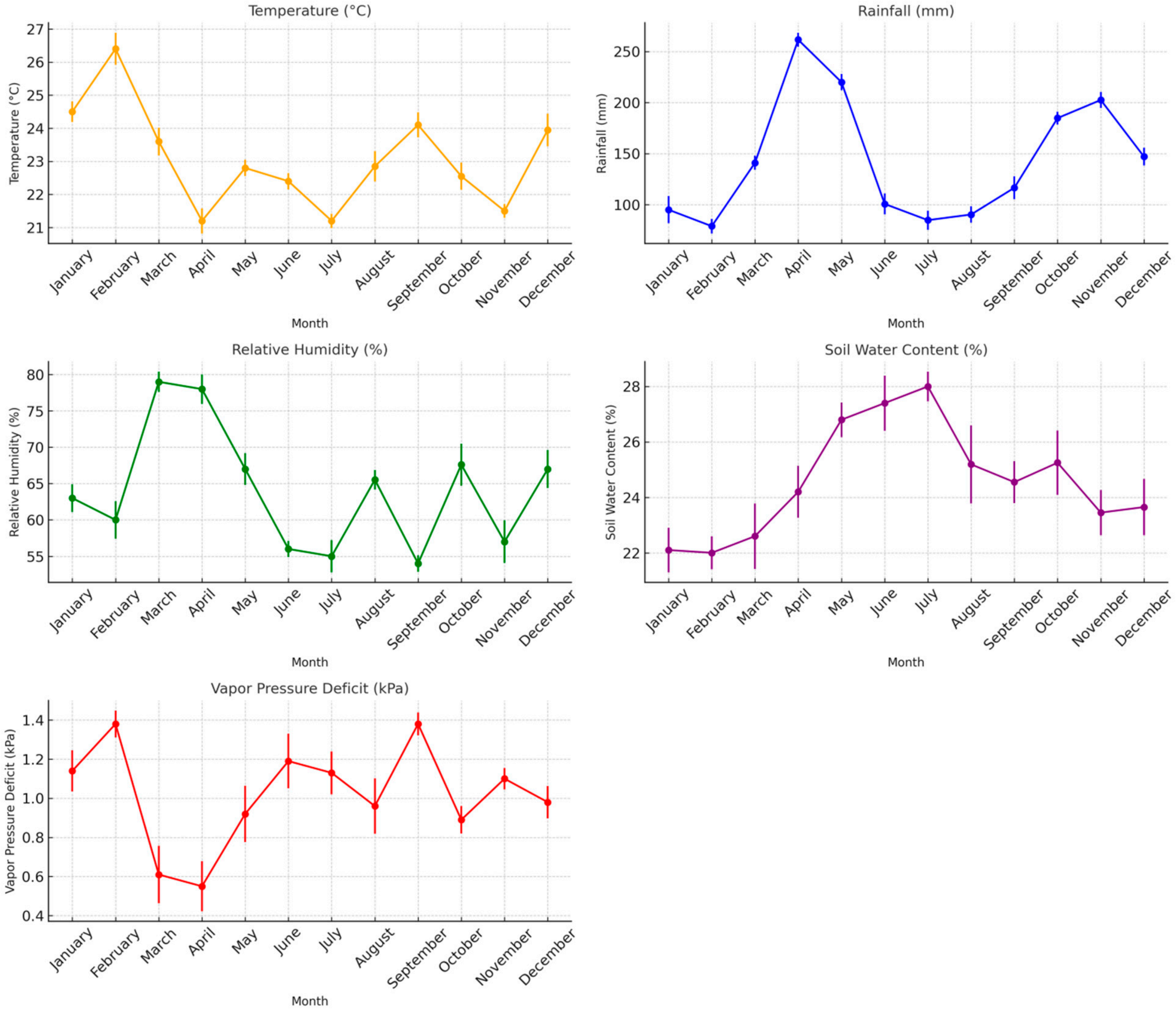

Figure 2. Seasonal variability of climate variables in Ruma National Park.

Air temperature remained relatively stable, ranging from 21.0 °C to 26.4 °C, with higher values recorded in February. Relative humidity (RH) ranged between 54% and 79%, generally higher during wet months and lower during dry seasons. Soil water content (SWC) mirrored rainfall patterns, peaking at 26.8% in May and dropping to 22% in February. The vapor pressure deficit (VPD) inversely tracked RH, with the highest VPD observed during February and September (1.38 kPa) and the lowest in April (0.55 kPa).

3.2. *Stomatal Conductance in Light and Shaded Leaves*

Stomatal conductance (gs, mmol m^{-2} s^{-1}) showed clear differences between light-exposed (TL) and shaded (TD) leaves (Figure 3). In all species, gs was significantly higher under TL conditions compared to the bottom dark (BD) conditions, especially during wet seasons, corresponding with increased soil moisture and photosynthetic activity.

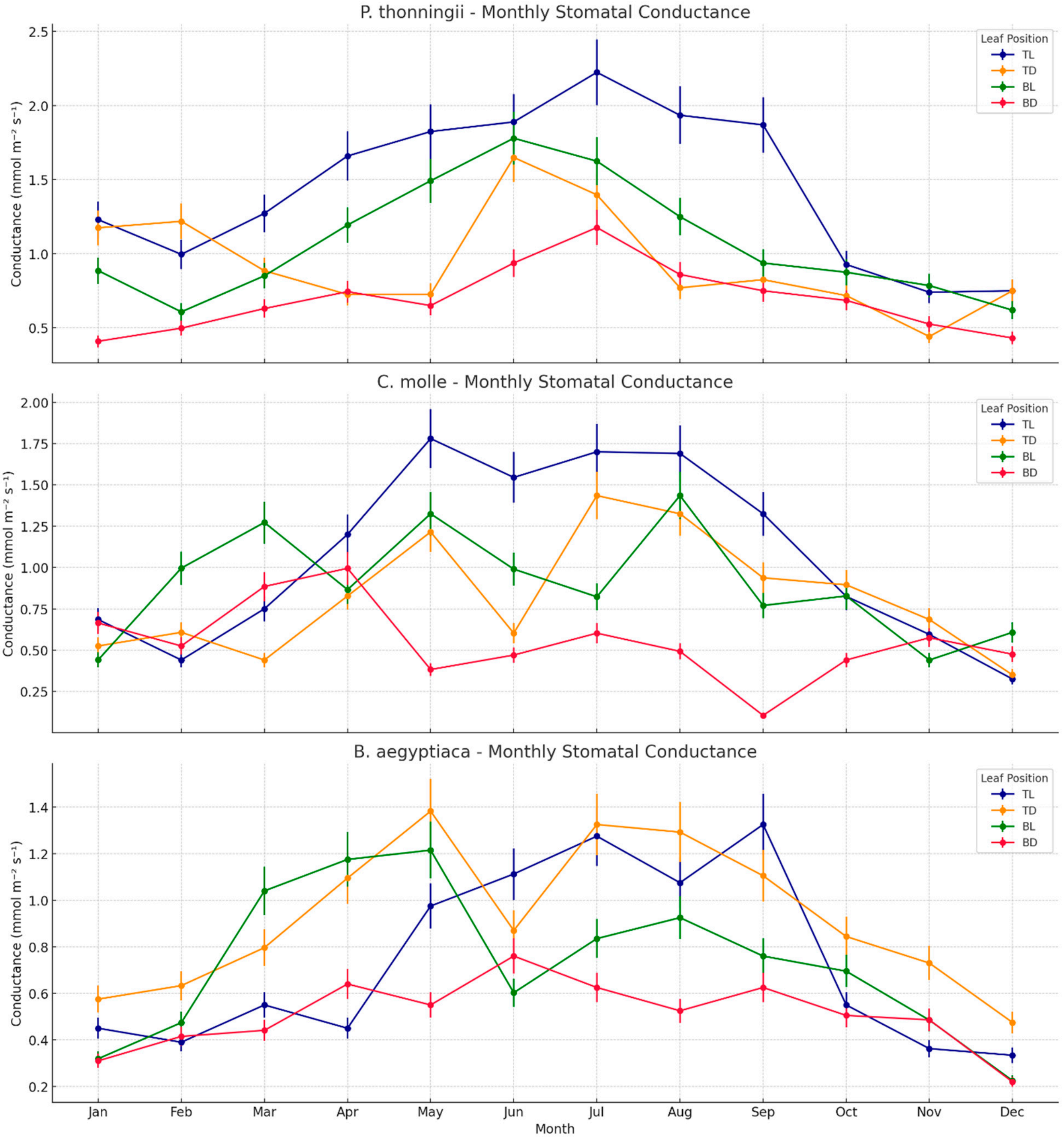

Figure 3. Seasonal variation in stomatal conductance (gs, mmol m^{-2} s^{-1}) in *P. thonningii*, *C. molle* and *B. aegyptiaca.* under light (top light—TL and bottom light—BL) and shaded (top dark—TD and bottom dark—BD) conditions. Error bars represent standard errors (SE).

Among species, *P. thonningii* exhibited the greatest seasonal variation in gs, with the highest peak conductance in July (TL: ~2.2 mmol m^{-2} s^{-1}), while *Balanites aegyptiaca* maintained consistently low transpiration and stomatal conductance values across all treatments and seasons, indicative of a conservative drought-tolerant strategy. This strategy involves sustained stomatal closure to limit water loss, allowing the species to maintain physiological integrity under arid conditions. In contrast, *C. molle* exhibited a bimodal conductance pattern, with elevated values in May and July particularly in TL and TD positions, suggesting a seasonally responsive strategy that optimizes gas exchange during periods of favorable moisture and low vapor pressure deficit. Under TD conditions, all species showed reduced and relatively stable gs.

3.3. Transpiration Patterns in Light and Shaded Leaves

Transpiration rates (Tr, mmol m^{-2} s^{-1}) were consistently higher under TL conditions across all species (Figure 4) compared to dark conditions (TD and BD). Increases in Tr were most pronounced during the wet seasons, reflecting higher soil moisture availability.

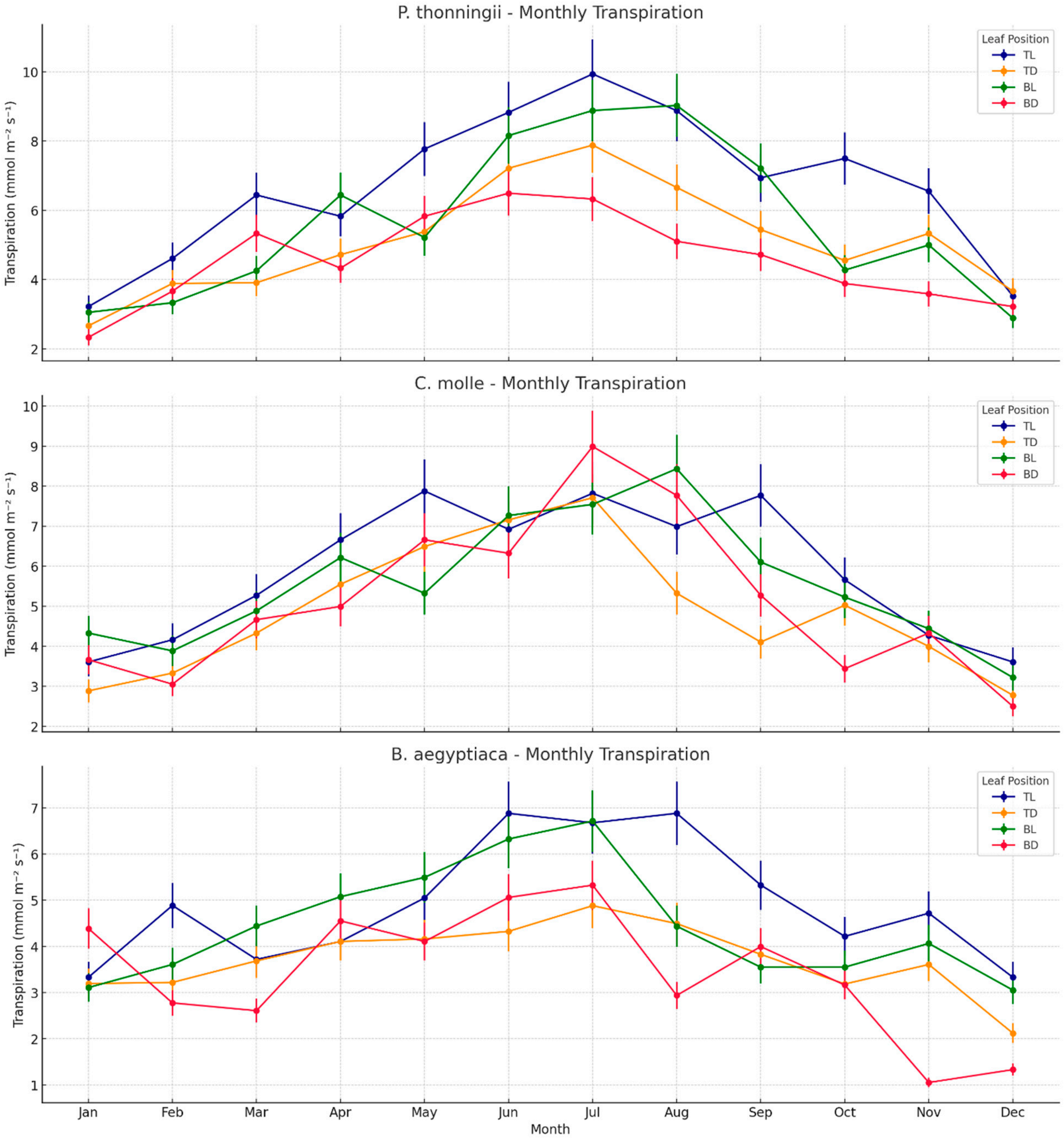

Figure 4. Seasonal variation in transpiration rate (Tr, mmol m^{-2} s^{-1}) in *P. thonningii*, *C. molle* and *B. aegyptiaca* under light (top light—TL and bottom light—BL) and shaded (top dark—TD and bottom dark—BD) conditions. Error bars represent standard errors (SE).

P. thonningii recorded the highest Tr, particularly during rainy periods, reaching 9 mmol m^{-2} s^{-1} in July, while *Balanites aegyptiaca* exhibited low and stable Tr values year-round. *Combretum molle* displayed moderate seasonal variability. During dry seasons, all species experienced reduced Tr that was consistent with declining soil moisture and an increased vapor pressure deficit (VPD), which is a key indicator of atmospheric evaporative demand.

3.4. Relationships Between Stomatal Conductance, VPD, and Soil Moisture

Regression analysis revealed species-specific relationships between gas exchange parameters and key climate variables (Table 2). Under TL conditions, *P. thonningii* showed a moderately strong positive correlation between transpiration and temperature (R^2 = 0.353, p = 0.026), suggesting that warmer conditions significantly enhance its water loss. Relationships with other climatic variables (rainfall, RH, SWC, and VPD) were weak or nonsignificant for this species.

Table 2. Coefficients of determination (R^2) and p-values for relationships between climate variables and leaf gas exchange parameters in *P. thonningii*, *C. molle*, and *B. aegyptiaca* under light and shaded canopy conditions.

Species	Condition	Climate Variable	Transpiration		Stomata Conductance	
			R^2	p-Value	R^2	p-Value
P. thonningii	Light	Temperature (°C)	0.353	0.026	0.020	0.820
P. thonningii	Light	Rainfall (mm)	0.026	0.542	0.137	0.633
P. thonningii	Light	Relative Humidity (%)	0.188	0.158	0.056	0.966
P. thonningii	Light	Soil Water Content (%)	0.285	0.167	0.010	0.966
P. thonningii	Light	Vapor Pressure Deficit (kPa)	0.019	0.729	0.014	0.957
P. thonningii	Dark	Temperature (°C)	0.040	0.527	0.026	0.778
P. thonningii	Dark	Rainfall (mm)	0.229	0.308	0.345	0.022
P. thonningii	Dark	Relative Humidity (%)	0.286	0.009	0.112	0.463
P. thonningii	Dark	Soil Water Content (%)	0.000	0.618	0.003	0.966
P. thonningii	Dark	Vapor Pressure Deficit (kPa)	0.295	0.013	0.129	0.230
C. molle	Light	Temperature (°C)	0.003	0.617	0.115	0.166
C. molle	Light	Rainfall (mm)	0.140	0.379	0.280	0.183
C. molle	Light	Relative Humidity (%)	0.000	0.564	0.421	0.027
C. molle	Light	Soil Water Content (%)	0.039	0.542	0.003	0.863
C. molle	Light	Vapor Pressure Deficit (kPa)	0.001	0.549	0.502	0.006
C. molle	Dark	Temperature (Â °C)	0.014	0.914	0.138	0.409
C. molle	Dark	Rainfall (mm)	0.002	0.471	0.000	0.618
C. molle	Dark	Relative Humidity (%)	0.241	0.051	0.236	0.264
C. molle	Dark	Soil Water Content (%)	0.014	0.880	0.322	0.112
C. molle	Dark	Vapor Pressure Deficit (kPa)	0.251	0.066	0.067	0.820
B. aegyptiaca	Light	Temperature (°C)	0.073	0.564	0.055	0.696
B. aegyptiaca	Light	Rainfall (mm)	0.001	0.863	0.417	0.006
B. aegyptiaca	Light	Relative Humidity (%)	0.227	0.111	0.076	0.534
B. aegyptiaca	Light	Soil Water Content (%)	0.127	0.331	0.003	0.880
B. aegyptiaca	Light	Vapor Pressure Deficit (kPa)	0.297	0.082	0.107	0.372
B. aegyptiaca	Dark	Temperature (°C)	0.056	0.571	0.000	0.914
B. aegyptiaca	Dark	Rainfall (mm)	0.030	0.499	0.042	0.649
B. aegyptiaca	Dark	Relative Humidity (%)	0.123	0.075	0.000	0.422
B. aegyptiaca	Dark	Soil Water Content (%)	0.015	0.795	0.022	0.391
B. aegyptiaca	Dark	Vapor Pressure Deficit (kPa)	0.182	0.077	0.000	0.778

In contrast, *C. molle* and *B. aegyptiaca* demonstrated weaker correlations overall, indicating a conservative water-use strategy characterized by limited seasonal variation in transpiration. Notably, *C. molle* showed a significant relationship between gs and the VPD (R^2 = 0.502, p = 0.006) and RH (R^2 = 0.421, p = 0.027) under light conditions. This indicates that its stomatal function is moderately sensitive to atmospheric moisture demand.

P. thonningii also showed significant correlations between gs and rainfall (R^2 = 0.345, p = 0.022) and the VPD (R^2 = 0.295, p = 0.013) under shaded conditions. However, across all species, shaded leaves generally displayed lower correlations, reflecting limited stomatal responsiveness due to reduced photosynthetic demand.

The low R^2 values for many variables suggest that intrinsic plant mechanisms (e.g., hormonal regulation, leaf anatomy, hydraulic traits) may play a stronger role than external climatic drivers in regulating leaf-level gas exchange.

3.5. Comparison of Tr and gs in Different Light Conditions

The table presents the results of independent *t*-tests comparing transpiration and stomatal conductance between different light conditions; top light (TL) vs. top shaded (TD), and bottom light (BL) vs. bottom shaded (BD) across wet and dry seasons for each species (Table 3). For each comparison, the *p*-value is reported alongside an indication of statistical significance ($p < 0.05$). These results highlight species-specific physiological responses to light exposure and seasonal variation, with significant differences observed in stomatal conductance under wet season TL vs. TD conditions for *P. thonningii*. Most comparisons, however, did not yield statistically significant differences, suggesting a generally conservative water-use response to light variation across seasons.

Table 3. Statistical significance comparing light conditions (e.g., TL vs. TD, BL vs. BD) across wet and dry seasons for each species and both transpiration and stomatal conductance.

Species	Measure	Comparison	Season	*p*-Value	Significant
P. thonningii	Transpiration	TL vs. TD	Wet	0.0528	No
P. thonningii	Transpiration	TL vs.TD	Dry	0.178	No
P. thonningii	Transpiration	BL vs. BD	Wet	0.8666	No
P. thonningii	Transpiration	BL vs. BD	Dry	0.179	No
P. thonningii	Stomatal Conductance	TL vs. TD	Wet	0.0292	Yes
P. thonningii	Stomatal Conductance	TL vs. TD	Dry	0.1062	No
P. thonningii	Stomatal Conductance	BL vs. BD	Wet	0.1078	No
P. thonningii	Stomatal Conductance	BL vs. BD	Dry	0.0574	No
C. mole	Transpiration	TL vs. TD	Wet	0.3086	No
C. mole	Transpiration	TL vs. TD	Dry	0.2755	No
C. mole	Transpiration	BL vs. BD	Wet	0.9645	No
C. mole	Transpiration	BL vs. BD	Dry	0.5638	No
C. mole	Stomatal Conductance	TL vs. TD	Wet	0.3316	No
C. mole	Stomatal Conductance	TL vs. TD	Dry	0.3883	No
C. mole	Stomatal Conductance	BL vs. BD	Wet	0.1723	No
C. mole	Stomatal Conductance	BL vs. BD	Dry	0.0149	Yes
B. aegyptiaca	Transpiration	TL vs. TD	Wet	0.5289	No
B. aegyptiaca	Transpiration	TL vs. TD	Dry	0.018	Yes
B. aegyptiaca	Transpiration	BL vs. BD	Wet	0.1559	No
B. aegyptiaca	Transpiration	BL vs. BD	Dry	0.1868	No
B. aegyptiaca	Stomatal Conductance	TL vs. TD	Wet	0.1377	No
B. aegyptiaca	Stomatal Conductance	TL vs. TD	Dry	0.5434	No
B. aegyptiaca	Stomatal Conductance	BL vs. BD	Wet	0.0016	Yes
B. aegyptiaca	Stomatal Conductance	BL vs. BD	Dry	0.3422	No

4. Discussion

4.1. Seasonal Responses and Species Adaptations

This study examined the seasonal dynamics of transpiration and stomatal conductance in three dominant savanna tree species, *Piliostigma thonningii*, *Combretum molle*, and *Balanites aegyptiaca*, under varying light and soil moisture conditions. The findings revealed distinct species-specific adaptations, largely shaped by differences in light exposure, canopy position, and water availability. All three species exhibited increased transpiration and stomatal conductance during the wet seasons, particularly in light-exposed leaves, due to enhanced water availability and favorable environmental conditions for photosynthesis [9]. Conversely, reductions in both parameters during the dry season reflected adaptive water conservation strategies. These seasonal trends were most pronounced in *P. thonningii*, which demonstrated strong physiological plasticity and the abilty to maximize water use during favorable periods. Furthermore, these findings reflected species-specific strategies, with *P. thonningii* and *C. molle* showing high seasonal responsiveness, while *B. aegyptiaca* adopted a more conservative and stable water-use pattern.

The statistical analysis revealed that light conditions and seasonal variation influenced gas exchange parameters differently across the three tree species. Notably, *P. thonningii* exhibited a significant difference in stomatal conductance between top light (TL) and top shaded (TD) conditions during the wet season, reflecting its sensitivity to light availability when soil moisture is sufficient. However, most comparisons across species and seasons were not statistically significant, particularly for *C. molle* and *B. aegyptiaca*, suggesting a more conservative or stable physiological response regardless of light position. These findings underscore interspecific differences in light responsiveness, with *P. thonningii* adopting a more opportunistic strategy, while *C. molle* and *B. aegyptiaca* maintain consistent gas exchange as part of their drought-adaptive strategies.

4.2. Influence of Light Conditions on Gas Exchange

Light availability played a central role in regulating gas exchange, with consistently higher rates of transpiration and stomatal conductance recorded in sunlit leaves across all species. For all three species, the bottom-down (BD) position consistently recorded the lowest transpiration, likely due to reduced light exposure and photosynthetic demand. This is consistent with the role of light in stimulating stomatal opening to enable CO_2 uptake for photosynthesis [17]. Under shaded conditions, all species exhibited reduced gas exchange, indicating efficient stomatal regulation aimed at minimizing water loss in the absence of high photosynthetic demand [18]. Interestingly, *C. molle* maintained relatively higher transpiration under shade compared to the other species, suggesting a physiological mechanism supporting minimal hydration or nutrient transport even under low light.

4.3. Climatic Drivers of Gas Exchange

Regression analyses revealed that temperature was the most consistent climatic driver of transpiration, especially in *P. thonningii* under light-exposed conditions. This finding aligns with previous studies linking higher evaporative demand to increased stomatal activity [18]. In contrast, other environmental variables such as rainfall, relative humidity, and soil water content exhibited weaker or non-significant relationships with gas exchange parameters. These results suggest that, in this humid savanna system, intrinsic physiological controls may override external climatic cues in regulating transpiration rates.

P. thonningii exhibited a moderately strong positive correlation between transpiration and temperature under top light (TL) conditions, indicating increased water loss with rising temperatures. Additionally, its stomatal conductance correlated significantly with rainfall and the VPD under shaded conditions, suggesting responsiveness to both water availability and atmospheric demand. In contrast, *Combretum molle* and *Balanites aegyptiaca* showed weaker correlations with most climatic variables, consistent with a conservative water-use strategy.

The relationship between stomatal conductance and climatic variables was generally weak across species, particularly under shaded conditions. This observation indicates that stomatal behavior may be governed more strongly by internal regulatory mechanisms, such as abscisic acid signaling or hydraulic feedback [19], rather than by direct responses to environmental fluctuations. Similar patterns have been reported in other woody species, where drought tolerance is associated with traits such as xylem resistance, plant water storage capacity, and root system architecture [20].

4.4. Interspecific Variation in Water-Use Strategies

The three species showed contrasting ecological strategies that reflect their spatial distribution and functional adaptations in relation to soil moisture and the vapor pressure deficit (VPD). For instance, *B. aegyptiaca* demonstrated a highly conservative water-use strategy, maintaining low transpiration and stomatal conductance regardless of season or light condition. This species is typically found in savanna plains characterized by low soil moisture and a high VPD [14]. Regression analyses revealed a weak correlation between its gas exchange parameters and soil moisture or the VPD, suggesting a limited physiological response to external water availability or atmospheric demand. This insensitivity is ecologically advantageous in its typical habitat of savanna plains with low soil water content and a high VPD, where a deep root system and small leaf area help reduce water loss and enable survival during extended drought. The lack of seasonal fluctuation in Tr and gs supports its strategy of water conservation over productivity, ensuring persistence rather than performance under stress.

C. molle, dominant on the slopes, exhibited an intermediate strategy. Its moderate gas exchange rates suggest a balance between water conservation and opportunistic resource use. Slopes in this ecosystem provide better drainage and intermittent moisture, which likely favor this flexible response [14]. Weak correlations with soil moisture suggested that atmospheric conditions played a more influential role in regulating its water use. This flexible physiological behavior likely reflects the intermediate water availability on slopes, where intermittent rainfall and good drainage favor opportunistic gas exchange during moisture pulses while minimizing drought exposure. The species' moderate sensitivity to relative humidity and soil moisture suggests a capacity to optimize performance across a range of conditions [20].

P. thonningii, also occupying slope habitats, displayed a highly responsive strategy, maximizing water use and gas exchange during favorable periods. Its high transpiration and stomatal conductance in light conditions reflect its fast growth and competitive advantage during wet seasons. Regression results showed strong positive correlations with soil moisture and negative relationships with VPD, confirming that this species maximizes gas exchange under favorable conditions but restricts water loss during dry periods. However, this reliance on external moisture makes it less drought-resilient than *B. aegyptiaca*, likely confining its success to microenvironments with more consistent water availability [19].

4.5. Canopy Position and Physiological Plasticity

The observed differences between top (light-exposed) and bottom (shaded) canopy leaves across all species underscore the physiological plasticity associated with light gradients. In all cases, transpiration and stomatal conductance were significantly higher in the upper canopy, where irradiance and photosynthetic demand are greatest [7]. *P. thonningii* showed the highest rates under these conditions, reinforcing its light-dependent strategy. By contrast, *C. molle* maintained moderate gas exchange in both canopy layers, demonstrating its adaptability to fluctuating light and moisture availability. *B. aegyptiaca* showed minimal variation between canopy positions, which is consistent with its conservative water-use strategy and tight stomatal regulation [21,22].

Shaded leaves across all species exhibited significantly reduced stomatal conductance, reflecting lower photosynthetic activity and an emphasis on water conservation. *P. thonningii* experienced the steepest decline in gs under shade, further highlighting its sensitivity to irradiance [23]. *C. molle* showed moderate reductions, while *B. aegyptiaca* remained largely unresponsive, underscoring its low physiological plasticity.

4.6. Ecological Implications and Broader Relevance

The species-specific responses observed in this study reflect evolutionary adaptations to distinct ecological niches within the humid savanna. These physiological strategies ranging from opportunistic to conservative enable coexistence and resilience in an environment characterized by intermittent resource availability. Importantly, the study highlights the dominant role of intrinsic traits and microhabitat preferences in shaping gas exchange dynamics. While climate variables do influence transpiration and stomatal behavior, their impact is modulated by internal regulation and species-specific architecture. These insights are critical for developing species-specific models of plant water use and for informing management practices aimed at restoring or conserving savanna ecosystems under climate variability. Understanding how native species partition water resources across microenvironments can guide selection for afforestation, ecological restoration, and climate-resilient landscape planning.

5. Conclusions

This study demonstrates the critical role of light availability and seasonal moisture variation in shaping leaf-level physiological responses among three key savanna tree species. *P. thonningii* exhibited strong light dependency, with marked differences in transpiration and stomatal conductance between sunlit and shaded leaves. This suggests a resource-acquisitive strategy that enables it to thrive under favorable conditions with ample light and moisture. In contrast, *C. molle* showed moderate physiological differentiation between canopy positions, reflecting its capacity to balance water use and conservation. This intermediate response indicates ecological flexibility, enabling survival in environments with fluctuating light and soil water availability. *B. aegyptiaca* exhibited the least variation between light conditions, consistent with its conservative water-use strategy. Its low and stable transpiration and stomatal conductance, regardless of environmental variation, suggest strong physiological control that supports survival in arid and high-stress habitats.

These species-specific differences underscore the importance of intrinsic adaptations in regulating water use strategies in tropical savannas. Light availability emerged as a dominant factor influencing gas exchange, while seasonal water dynamics played a supporting role. Collectively, these traits determine each species' ecological niche and resilience under climate variability. Future research should integrate additional functional traits, such as leaf hydraulic properties, xylem vulnerability, and rooting depth to deepen our understanding of plant water regulation. Additionally, incorporating multi-depth soil moisture profiling will capture species-specific water uptake patterns. Long-term, cross-ecosystem studies are also needed to assess the adaptability and persistence of these species under shifting climatic regimes. The findings of this study provide valuable insights for forest management, conservation planning, and restoration efforts in water-limited ecosystems, particularly those facing increased variability in light and moisture due to climate change.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f16060999/s1.

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