Ecophysiological responses of *Terminalia sericea* to fire history in a semi-arid woodland savanna, central Namibia

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A B S T R A C T

Woody vegetation is increasing in savanna ecosystems worldwide. Fire is frequently used as a management tool to decrease bush encroachment, but knowledge regarding the underlying leaf-level ecophysiological responses to fire history is lacking. In southern Africa, *Terminalia sericea* is a dominant encroaching species that resprouts readily following fires. The impact of fire on leaf-level photosynthesis, transpiration, conductance and water use efficiency was investigated using infrared gas analysis. Data were collected in three areas on the Waterberg Plateau with different fire histories (fire occurring 2, 3 and 15 years prior to sampling). Leaf-level photosynthetic rates were comparable to the relatively high rates shown by other encroaching bush species. In contrast to expectations, ecophysiological variables did not differ among plants in areas with different fire histories. However, photosynthetic rates were highly sensitive to variation in light level, suggesting that canopy structural differences may affect carbon fixation and growth rates at the whole-plant level. Encroachment by *T. sericea* may be facilitated, at least in part, by high leaf-level photosynthetic rates that are insensitive to long-term fire history on sandy, low-nutrient soils.

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1. Introduction

Savannas occur throughout the world, accounting for 20% of the earth's land surface and 40% of Africa's surface (Bond and Midgley 2000; Scholes and Walker 1993). Bush encroachment, the increasing abundance and density of woody species at the expense of herbaceous vegetation, affects many savanna ecosystems worldwide (O'Connor et al., 2014). While the drivers of bush encroachment are complex and often interacting, decreased fire frequency can be an important factor in some systems (O'Connor et al., 2014; Scholes and Archer 1997; Trollope et al., 1998; Ward et al., 2014). Fire can curb establishment of woody seedlings and saplings (Higgins et al., 2000; Joubert et al., 2012; Scholes and Archer 1997) and reduce the cover and density of shrubs and trees (Daryanto et al., 2019; Trollope et al., 1998). Complex interactions among grass cover, shrub density, and fire can exist, with fire impacts on shrubs mediated by positive relationships between grass cover and fire intensity (Higgins et al., 2000). As a result, fire has been widely applied as a management tool to combat bush encroachment (Archer et al., 2011; Roques et al., 2001), although the efficacy of fire differs among sites, biotic and abiotic

conditions, and management histories (Lohmann et al., 2014; Roques et al., 2001). When fires are sufficiently intense to topkill stems, many fire-adapted savanna plants respond by resprouting fuelled by retranslocating stored carbohydrate reserves from their roots (Roques et al., 2001). This physiological adaptation is fundamental to the survival of woody species in savannas (Higgins et al., 2000). While considerable information is known about the woody regrowth after fires, less is known about the leaf-level ecophysiological behaviour of regrowing plants. Understanding the long-term physiological impacts of fire on regrowing woody plants is important for developing a comprehensive understanding of the role of fire in affecting bush encroachment in savannas.

Leaf-level ecophysiological studies provide insights on the physiological mechanisms that may drive responses to fire. In particular, the ecophysiological response variables of photosynthetic rate, transpiration rate, conductance, and instantaneous water use efficiency (WUE) provide key functional information regarding plant responses to environmental conditions. Previous studies indicate that fire can enhance leaf-level ecophysiological variables, although there is considerable variation among species and agro-climatic areas in the magnitude and purported mechanistic drivers. For example, fire resulted in increased photosynthetic rates and conductance in *Pinus rigida* in a temperate forest with sandy, low-nutrient soils (Renninger et al., 2013). Similarly, increased photosynthesis and

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conductance in three of four woody species in a mixed temperate forest were attributed to fire-induced increased leaf nitrogen content (Reich et al., 1990). In contrast, increased photosynthetic rate (after fire) in resprouting Holm oak, *Quercus ilex* L., was attributed to increased water availability (Fleck et al., 1998). These examples indicate that fire can lead to changes in resource availability that affect leaf-level ecophysiology at least in the short-term, but the long-term stability of these conditions in the years following fire may differ from these short-term responses.

Bush encroachment is widespread in former savannas in Namibia where it leads to considerable economic and environmental concerns (de Klerk 2004). Although the causes and effects of bush encroachment have received some research attention in Namibia (Christian et al., 2010; de Klerk 2004; Joubert et al., 2014; Joubert et al., 2008; Joubert et al., 2012), to our knowledge no published research has tested the ecophysiological responses of an encroaching woody species to fire in Namibia. This study focuses on the ecophysiological response of a dominant encroaching woody species, *Terminalia sericea* Burch. ex DC. to different fire histories (time since last fire) in a semi-arid woodland savanna with sandy soils at the Waterberg Plateau Park. We selected *T. sericea* due to its importance as a widespread encroacher in rangelands of southern Africa that can detrimentally affect rangeland productivity (Jordaan 2010; Moleele et al., 2002; Shikangalah and Mapani 2020). In addition, to our knowledge there has been no prior assessment of ecophysiological responses of this species to fire. The objectives of the study were 1) to determine the leaf-level ecophysiological characteristics [photosynthetic rates, transpiration rates, conductance, and water use efficiency (WUE)] of *T. sericea* in locations with different fire history (2, 3, and 15 years since a fire) and 2) to determine the photosynthetic light response and diurnal pattern of *T. sericea*. We hypothesized that *T. sericea* individuals would have higher photosynthetic rates in the areas burned 2 or 3 years prior to measurements than in the area burned 15 years prior. Measurement and comparison of photosynthesis, transpiration, conductance and WUE among areas that differ in fire history may provide a better understanding of the effectiveness of current fire measures as a management tool against bush encroachment.

2. Material and methods

2.1. Study site

The study was conducted on the Waterberg Plateau, approximately 80 km east of Otjiwarongo, Namibia. Waterberg Plateau Park (20°30′51" S, 17°14′45" E) was declared a protected area in 1972 with the aim of breeding rare and protected game species (Erb 1993). The park is 40 500 ha, all but 500 ha of which is a plateau (Erb 1993). The plateau is 1550-1850 m above sea level (Erb 1993), roughly 400 m higher than the surrounding plains (Schneider 1998). The soil on the plateau is several metres deep Kalahari sand, transported by wind from the Kalahari Basin (Erb 1993; Schneider 1998). There is no long-term rainfall record on the Plateau prior to September 2011 (Amputu et al., 2019). Mean annual precipitation from 2012-2020 was 406 mm (www.sasscalweathernet.org, station ID 31205), with most rain falling between November and April (Fig. 1A). Mean annual temperature was 19.9 °C with lowest temperatures in June and July (Fig. 1B).

The Waterberg Plateau falls within the tree savanna and woodland vegetation type (Giess 1971). *Terminalia sericea* Burch. ex DC. (Combretaceae) is an encroaching woody species in sandy soils in Namibia (de Klerk 2004) and it is common on the Waterberg Plateau (Schneider 1998). The species is known for its extensive lateral root system (Hipondoka et al., 2003; Hipondoka and Versfeld 2006) resulting in direct competition with grasses for water and nutrients (Hipondoka et al., 2003). It is a deciduous woody plant that will under
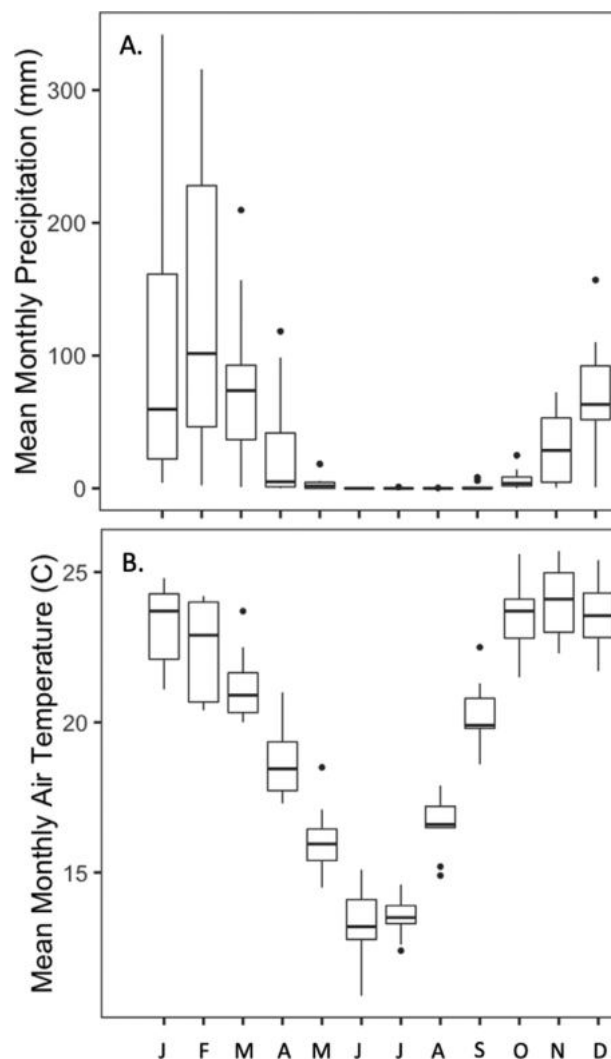

Fig. 1. Box and whisker plots showing monthly A) precipitation and B) temperature and their variability at Waterberg Plateau Park. Monthly values are based on total monthly precipitation and monthly mean air temperature from September 2011 through June 2020 from the SASSCAL meteorological station on the Waterberg Plateau (www.sasscalweathernet.org, station ID 31205). Centre lines indicate medians, lower and upper edges of boxes indicate 25th and 75th percentile values, respectively, and dots indicate outliers.

some conditions remain in a short-statured shrub form and in other conditions will grow in a more tree-like form of up to 8 m in height (Mannheimer and Curtis 2009).

2.2. Fire History

To determine the leaf-level ecophysiological response of *T. sericea* to fire, data were collected on the Waterberg Plateau where fire is used as a management tool (Joubert et al., 2018). Data were collected using a space-for-time substitution in 2000-2500 ha management blocks that burned 2, 3 and 15 years prior to sampling (Joubert et al., 2018). Within each of these "fire treatments", 10-12 *T. sericea* individuals were selected for measurements by using a random number table to select point locations within the fire treatment areas. To minimize transit time, we restricted our sampling to plants that were within 500 m of the location where the three treatments intersected. Once we arrived at a random sampling points, we selected the closest study plant that was representative of the dominant size class and leaf damage (e.g., minor insect herbivory and leaf galls) for each fire treatment. Data collected six months prior to our sampling indicate

Table 1
Mean size of *Terminalia sericea* individuals in fire history treatment blocks at the Waterberg Plateau Park. Data are extracted from Lutebezi (2017) and were collected in the same fire treatment blocks as the ecophysiological measurements, but six months earlier. Values are means from 30 individuals along transects in each of the three fire history treatments. Number of stems is the number of stems per individual plant.

Years Since Fire	Height (m)	Canopy volume (m^3)	Leaf mass (g)	Number of stems
2	0.7	0.8	311	12.0
3	1.2	1.8	545	9.7
15	2.4	4.1	903	2.5

that mean shrub size increased with time since last fire (Table 1; Lutibezi 2017).

Leaf-level gas exchange measurements were conducted on *T. sericea* with a portable photosynthesis system (LI 6400XT; Li-Cor, Lincoln, Nebraska, USA). Measurements were made on 5-9 April 2015, from approximately 10:00 until 18:00 hours. Sampling took place after several weeks of frequent rainfall (23 mm in the prior two weeks) following several months of monthly precipitation well below mean values (monthly precipitation totals of 14.4, 15.5, and 33.2 mm in January, February, and March, respectively). One healthy, fully expanded leaf with no visible herbivory and in full sun exposure was selected for each of the 34 plants chosen for measurements. However, within the area burned 15 years prior to sampling the canopy was denser, with much taller plants. As a consequence, selected leaves in this area may have been shaded for at least part of the day. The cardinal direction of the leaf within the canopy was randomized. Leaf chamber environmental conditions were set to be optimal for photosynthesis (Throop et al., 2012): relative humidity was 40 - 70%, CO_2 concentration was 400 parts per million (ppm), and leaf temperature was 28 - 30° C. An LED light source was used to deliver photosynthetically active radiation (PAR in μmol photons m^{-2} s^{-1}) at specified values. Light curves were performed by subjecting leaves to sequentially decreasing light levels (2500, 2000, 1500, 1000, 750, 500, 250, 125, 75, 50 and 0 μmol photons m^{-2} s^{-1}). Data were logged once photosynthetic rates and leaf chamber CO_2 were stable at each PAR level, allowing the leaf time to respond to changing light levels (Mengistu et al., 2011). Stabilization typically took about three minutes with each change in light level.

Leaves often did not completely fill the 6 cm^2 leaf chamber, so ecophysiological variables were back-calculated based on leaf area in the chamber. This was determined by marking the leaf area in the chamber, excising and scanning leaves, and measuring area with ImageJ 1.48v (National Institutes of Health, USA). The area and dry mass of each leaf portion was used to calculate leaf dry mass per unit leaf area (LMA; g cm^{-2}). Photosynthetic WUE was defined as net instantaneous carbon fixed through photosynthesis per unit water lost through transpiration (Lambers et al., 1998).

2.3. Data analyses

Data were analysed with R version 3.2.0 (R Core Team 2018). For high light conditions, data were used when PAR was 2000 μmol photons m^{-2} s^{-1} and 250 μmol photons m^{-2} s^{-1} was used for low light conditions. To assess diurnal patterns of ecophysiological response variables, data were grouped together in two-hour time intervals.

Two-way analysis of variance (ANOVA) procedures were used to assess how ecophysiological variables (photosynthesis, transpiration, conductance, WUE) responded to the main effects of light and fire treatments and their interaction. A one-way ANOVA was used to assess differences in LMA among fire treatments. Data were transformed prior to analyses to improve normality; transpiration data were subjected to a square root transformation and other ecophysiological response variables were subjected to an arcsine transformation.

3. Results

3.1. Ecophysiological responses to fire and light

Light levels affected some leaf-level ecophysiological variables but fire treatment did not affect any of the ecophysiological variables. Photosynthetic rates did not differ among fire treatments and there was no fire x light interaction, although mean photosynthetic rates in high light conditions were approximately double those of low light conditions (Fig. 2A, Table 2). There was marginally greater transpiration under high than low light levels (Fig. 2B; *P* = 0.08), but no effect of fire treatment and no fire x light interaction was observed. For conductance and WUE there were no differences in response to fire treatment, light level, or their interaction (Fig. 2C-D). No differences in LMA were found among the three fire blocks, so ecophysiological data are reported only on a per area basis.

3.2. Light response curves

Across all three fire treatments (2, 3, and 15 y since fire), photosynthetic rates increased roughly linearly with increasing light availability up to about 750 μmol photons m^{-2} s^{-1} (Fig. 3). At PAR levels exceeding 750 μmol photons m^{-2} s^{-1}, photosynthetic rates began to saturate although complete saturation did not appear to have been reached at the highest measured light level (2000 μmol photons m^{-2} s^{-1}). At lower light levels, net photosynthesis occurred until the compensation point was reached at PAR = 60.7 ± 6.3 μmol photons m^{-2} s^{-1} (n = 34).

3.3. Diurnal patterns

Most ecophysiological variables showed a decreasing trend in late afternoon under both high and low light conditions (Fig. 4). There was generally a greater diurnal decline in physiological activity under high light than low light conditions. For example, mean photosynthetic rate between 10:00-12:00 was 23.8 ± 2.24 μmol CO_2 m^{-2} s^{-1} at high light, compared to 9.19 ± 0.86 μmol CO_2 m^{-2} s^{-1} at low light (n = 5-10 leaves) versus 16:00-18:00 readings of 15.1 ± 3.27 μmol CO_2 m^{-2} s^{-1} at high light and 7.5 ± 3.27 μmol CO_2 m^{-2} s^{-1} at low light (Fig. 4A). In contrast to the other variables, WUE remained relatively stable from 10:00-18:00 under both light conditions (Fig. 4D).

4. Discussion

Leaf-level photosynthetic rate measurements indicate that *T. sericea* has high photosynthetic capacity, similar to that observed for other encroacher bush species. For example, maximum photosynthetic rates under light saturating conditions (PAR > 1000 μmol photons m^{-2} s^{-1}) were 16-20 μmol CO_2 m^{-2} s^{-1} for *T. sericea*, similar to rates for *Colophospermum mopane,* dominating Botswana's Kalahari sandveld (15-22 μmol CO_2 m^{-2} s^{-1} during the rainy season, Veenendaal et al., 2008) and *Prosopis glandulosa*, an encroacher in the southwestern USA (24.8 ± 1.02 CO_2 m^{-2} s^{-1}; Throop et al., 2012). While these rates are consistent with the capacity for rapid growth
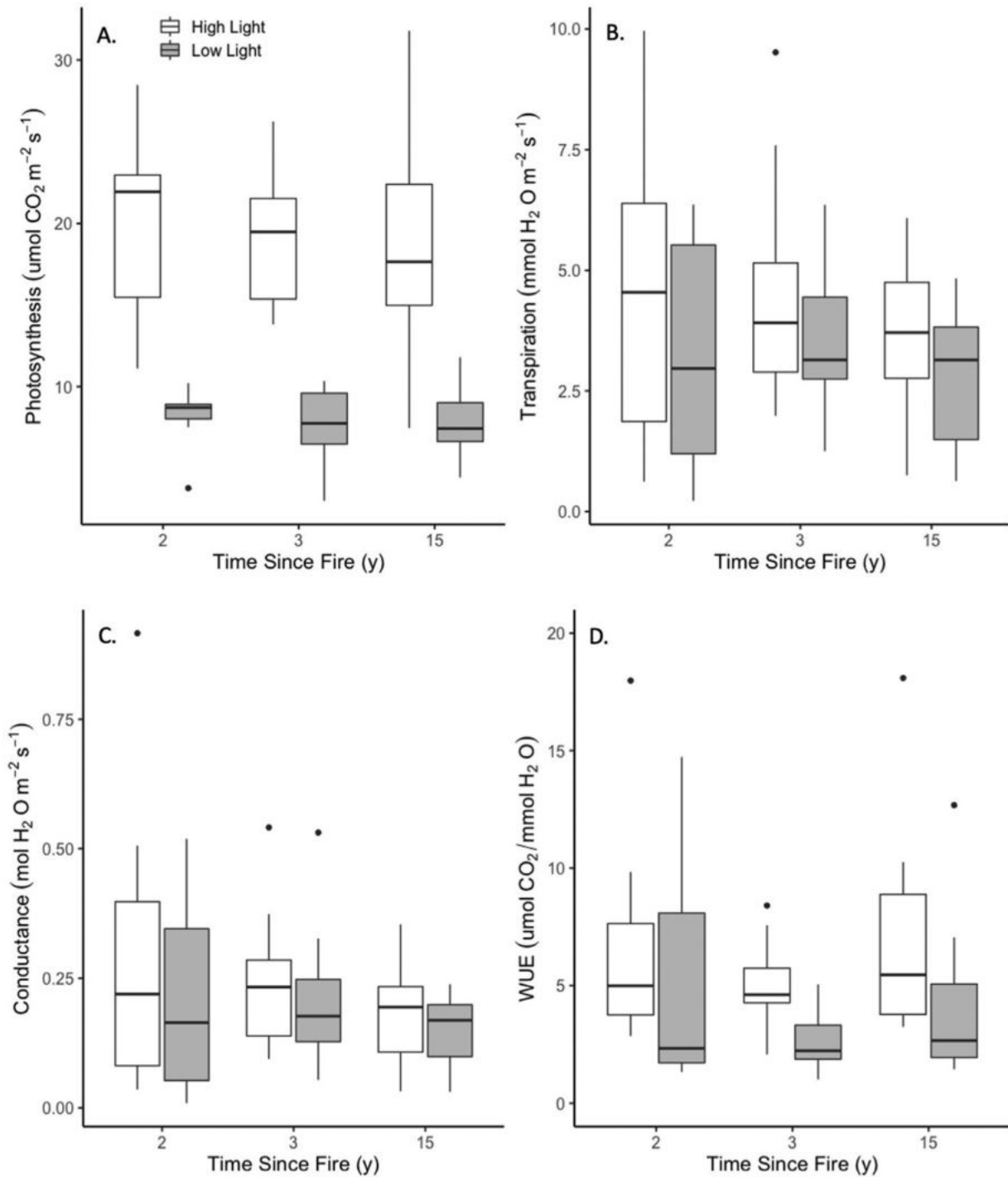
Fig. 2. Ecophysiological responses of *Terminalia sericea* to three different fire history treatments (2, 3, and 15 y prior to study). Data are A) photosynthesis, B) transpiration, C) conductance, and D) water use efficiency (WUE). High light values were measured as PAR = 1500-2500 μmol photons m^{-2} s^{-1} and low light values were measured as PAR = 250 μmol photons m^{-2} s^{-1}. Centre lines indicate medians, lower and upper edges of boxes indicate 25th and 75th percentile values, respectively, and dots indicate possible outliers (N = 10-12 leaves per light condition * fire treatment combination). For all four ecophysiological variables at both high and low light conditions one way ANOVAs for the fire effect showed no significant difference amongst treatments (P > 0.05).

that would enable encroachment, we found no support for our hypothesis that fire history would lead to differences in leaf-level photosynthesis among the blocks.

4.1. Fire influences on physiology

The ecophysiological parameters that we measured all showed little variation among the blocks with different fire histories. Positive responses of leaf-level ecophysiology to fire have been widely reported for woody species, although *T. sericea* is not unique in the lack of response to fire. Several possible mechanisms may explain this observed lack of response. High post-fire photosynthesis in woody plants has been attributed to enhanced soil N availability and subsequent increases in leaf N content (Reich et al., 1990; Veenendaal et al., 2008). We did not measure leaf N content in this study, but several factors suggest that leaf N contents may not have differed among the fire treatments. Prior work on soil nutrient distribution in these treatment blocks indicates that total soil nutrient
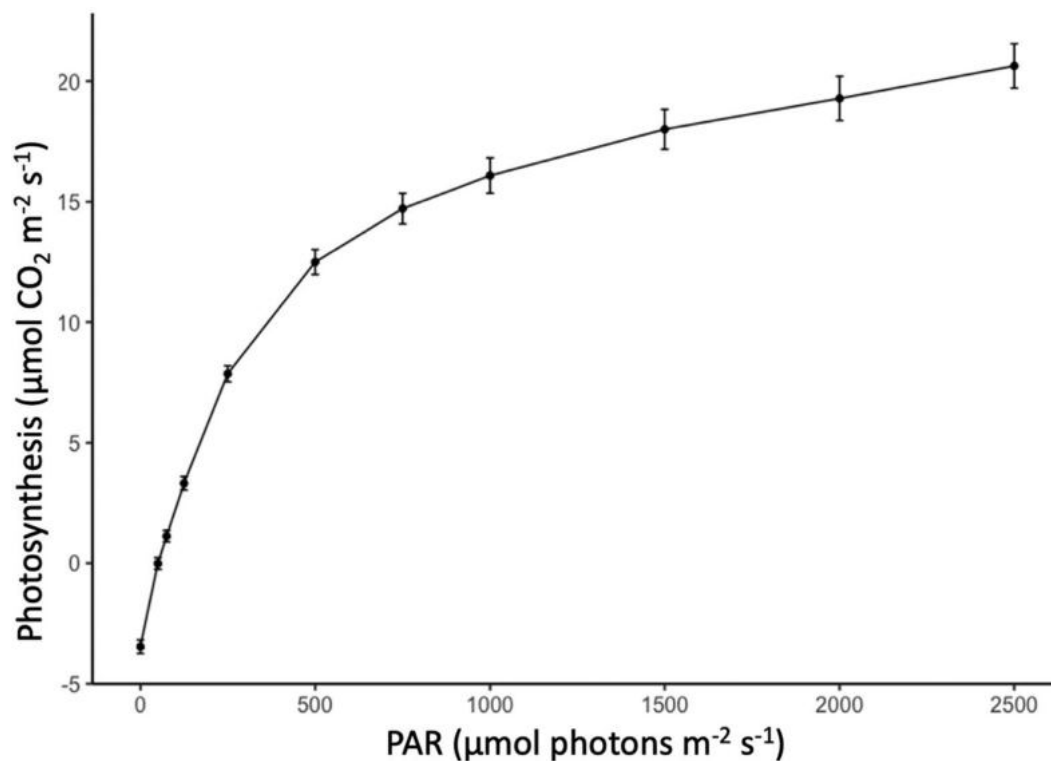
Fig. 3. Photosynthetic light response curve at different photosynthetically active radiation (PAR) levels (mean ± SE, n = 34 leaves on different trees) for all observations, irrespective of fire treatment or time of day.

concentrations, including N, were not enhanced in the most recently burned areas, perhaps due to the limited nutrient holding capacity of the sandy soils (Nghalipo et al., 2019). In addition, the time scale of our measurements may not have captured post-fire increases in N if these are transient responses. High post-fire leaf N and photosynthesis may persist for a growing season or less (Reich et al., 1990), and our measurements took place 2 y or longer after a fire. Measurement of leaf N through time following fire would be needed to assess the role of leaf N in mediating ecophysiological response patterns for *T. sericea*.

An alternative mechanism by which fire may affect leaf-level gas exchange is through changes in water availability. Increased photosynthetic rates in recently burned areas have been linked with greater water availability, which may occur due to decreased cover and water uptake of herbaceous species, decreased canopy interception of rainfall, or decreased woody plant uptake due to leaf area loss (DeSouza et al., 1986; Fleck et al., 1998; Renninger et al., 2013; Saruwatari and Davis 1989). Prior work from our study site found reduced grass cover and biomass in the growing season following fire (Amputu et al., 2019) and greater wet season soil moisture content in the most recently burned areas (Nghalipo and Throop 2021), suggesting that shrubs in our recently burned plots could have had access to greater soil moisture. An alternative, though not mutually exclusive, explanation for greater post-fire gas exchange in other species is that root:shoot ratios would be high following a fire that causes topkill while roots sustain limited damage. This could enable high water exploitation capacity on a leaf-area basis that would decline with time since last burn in concert with aboveground regrowth. Shifting root:shoot through time is almost certainly the case at our study site. Low root mortality from fire is supported by similar soil respiration beneath *T. sericea* canopies among fire blocks (Nghalipo and Throop 2021), while aboveground herbaceous and woody biomass increased at our study site with time since fire (Amputu et al., 2019). An important caveat is that our one-time sampling only captured one set of

abiotic conditions. However, the magnitude of variation in photosynthetic rates in response to light availability relative to the complete lack of difference in response to fire history across a 13 y space-for-time substitution does not provide any evidence that fire history would emerge as an important variable under different time points or environmental conditions. For example, soil moisture content was relatively high during our sampling period (Nghalipo and Throop 2021) following several months of usually dry conditions during the growing season. We cannot rule out the possibility that fire treatment differences could emerge as important under different soil moisture conditions. However, the extensive root system of *T. sericea* (Hipondoka and Versfeld 2006) suggests that this species may be relatively insensitive to changes in soil moisture, even if root:shoot changes. For example, leaf-level physiological parameters were insensitive to large changes in soil moisture in *Prosopis glandulosa* in the southwestern United States, ostensibly the result of root systems that maintained sufficient uptake for xylem water potential to remain stable despite changes in soil moisture content (Throop et al., 2012).

The space-for-time substitution allowed us to compare responses of plants that differ across a 13 y difference in time since last burn but did not allow finer-scale analysis of temporal dynamics. For example, at short time scales of several months following fire, *Vachellia karoo* in South Africa exhibited increased leaf-level photosynthetic rates. These differences were no longer evident six months after the fire, perhaps due to rapid recovery of root carbohydrate reserves in the year following a fire (Schutz et al., 2009). While we do not know whether root carbohydrates were altered by fire in our study plants, total non-structural carbohydrates in *T. sericea* were similar 2, 15, and 25 y following fire (with a slight increase 3 y following fire; Lutibezi 2017), suggesting that any substantial changes in carbon reallocation patterns, if present, may have occurred before we made our measurements. A time series of frequent sampling following fire would be needed to assess temporal patterns of leaf-level response to fire.
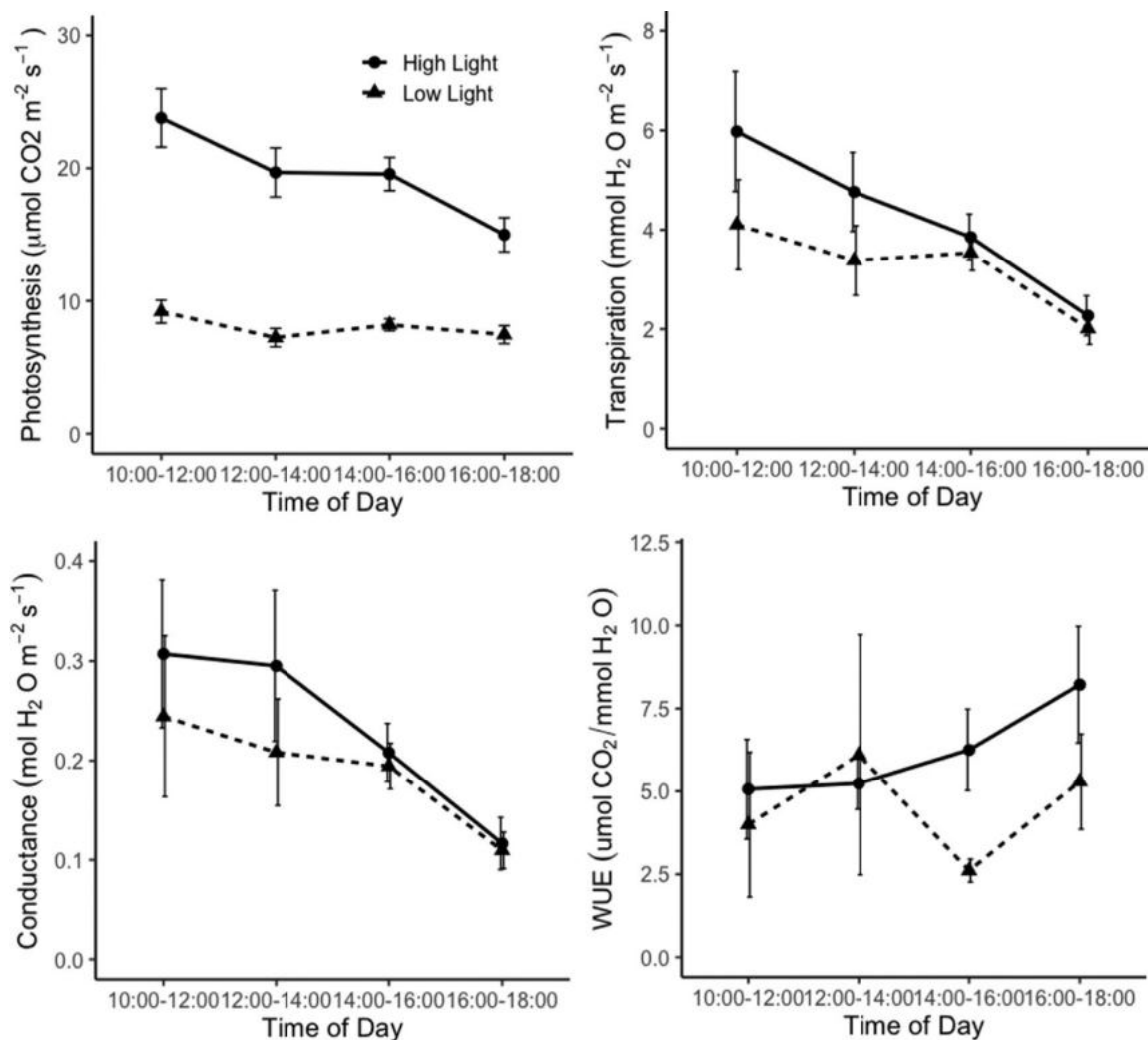
Fig. 4. Diurnal patterns in A) photosynthesis, B) transpiration, C) conductance, and D) water use efficiency (WUE) during different time periods. Data are mean (± SE) for all leaves measuring during that time period, regardless of fire treatment. High light values were those measured when PAR = 1500-2500 μmol photons m^{-2} s^{-1} and low light values were measured when PAR = 250 μmol photons m^{-2} s^{-1}.

4.2. Implications for responses to fire

Our measured ecophysiological responses to light availability suggest that fire may indirectly affect leaf-level physiology by modifying the light environment, despite the lack of direct influence of time since fire on gas exchange. Fire maintains an open canopy in this system (Joubert et al., 2018), which would maintain high leaf-level photosynthetic rates. However, the light environment for individual leaves is a function of plant morphology, which shifts with time since fire for woody plants in fire-prone savannas (Akpoué et al., 2021; Archibald and Bond 2003). At this site, *T. sericea* individuals become on average taller but with fewer stems with increasing time since fire (Amputu et al., 2019; Lutibezi 2017). These patterns are consistent with regrowth of other savanna species (e.g., *Vachellia karroo*) where fire promotes vertical regrowth (Archibald and Bond 2003). This vertical elongation would potentially increase photosynthetic rate through enhanced light availability. Higher light availability led to increased instantaneous photosynthetic rates and greater afternoon water use efficiency, at least for the sun-adapted leaves during the relatively moist soil conditions of this study. The ability to capitalize on high light availability may facilitate rapid regrowth in *T. sericea* following fire, particularly as light saturation of photosynthetic rates occurred at very high light levels. However, selective pressure of fire and browsers may also play an important role in shaping plant

morphology (Archibald and Bond 2003) and subsequent physiological parameters. In our study area, the persistent differences in canopy structure among fire treatments could lead to long-term differences in plant-level carbon fixation and growth if light levels are sufficiently altered. Similarly, land management treatments that alter light availability could also facilitate rapid regrowth in *T. sericea*. For example, rapid regrowth following firewood harvesting, as has been observed for this species in South Africa's Limpopo Province (Neke et al., 2006), could be facilitated by enhanced light availability from canopy thinning.

4.3. Implications for *T. sericea* encroachment

While our data do not indicate differences in leaf-level ecophysiological variables for *T. sericea* in the years following fire, the data provide some insight into the characteristics that influence the success of this species as an encroacher in southern Africa. Despite the low nutrient soils with low water holding capacity at the Waterberg Plateau, photosynthetic rates for *T. sericea* under high light conditions (23.7 ± 2.2 μmol CO2 m^{-2} s^{-1}) were similar to those reported for *Prosopis glandulosa,* a nitrogen-fixing encroaching species in North America (24.8 ± 1.02 μmol CO$_2$ m^{-2} s^{-1}; Throop et al., 2012). Success of *P. glandulosa* relative to native grasses appears to be, at least in part, a function of high photosynthetic rate that is largely insensitive

Table 2

Results of analysis of variance procedures assessing the influence of fire history ("fire"; 2, 3, or 15 y prior to sampling), photosynthetically active radiation ("light"; low or high light conditions), and their interactions on leaf-level ecophysiological variables (photosynthetic rate, transpiration, stomatal conductance, and water use efficiency).

		df	MS	F	P
Photosynthesis	fire	2	0.038	0.42	0.66
	light	1	13.45	148.42	<**0.001**
	fire × light	2	0.008	0.09	0.92
	residuals	62	0.091		
Transpiration	fire	2	0.296	0.91	0.41
	light	1	1.041	3.20	0.08
	fire × light	2	0.029	0.09	0.92
	residuals	62	0.325		
Conductance	fire	2	0.032	1.50	0.23
	light	1	0.035	1.64	0.21
	fire × light	2	0.002	0.11	0.90
	residuals	62	0.021		
WUE	fire	2	0.393	1.02	0.37
	light	1	1.051	2.73	0.10
	fire × light	2	0.032	0.08	0.92
	residuals	62	0.386		

to changes in soil moisture (Throop et al., 2012). Similarly, high photosynthetic rates may be maintained in *T. sericea* given the extensive lateral root systems that facilitates interception of small rain events (O'Donnell et al., 2015). Work in Kruger National Park found that *T. sericea* had consistently higher stomatal conductance than co-occurring woody species, with mean conductance rates (~0.27 mol m^{-2} s^{-1}) (Tobin and Kulmatiski 2018) similar to our findings. These data suggest high physiological capabilities of *T. sericea* may play a role in its success in the absence of disturbances sufficient to cause mortality.

5. Conclusions

Our findings provide an ecophysiological basis for high growth rates and encroachment success of *T. sericea*. Although we did not find that fire led to an increase in carbon fixation as we had hypothesized, *T. sericea* exhibited high photosynthetic rates and stomatal conductance in regrowth in the time span of 2 to 15 y following fire. Furthermore, high light sensitivity of *T. sericea* photosynthesis suggests that fire and other management practices that maintain a high light environment have the potential to indirectly influence leaf-level photosynthetic rates.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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