



Plant measurements on African tropical *Maesopsis eminii* seedlings contradict pioneering water use behaviour



Jackie Epila^{a,b,*}, Wouter H. Maes^{a,c}, Hans Verbeeck^b, Janne Van Camp^a, John Bosco Lamoris Okullo^d, Kathy Steppe^a

^a Laboratory of Plant Ecology, Department of Applied Ecology and Environmental Biology, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, B-9000 Ghent, Belgium

^b CAVElab Computational & Applied Vegetation Ecology, Department of Applied Ecology and Environmental Biology, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, B-9000 Ghent, Belgium

^c Laboratory of Hydrology and Water Management, Department of Forest and Water Management, Faculty of Bioscience Engineering, Ghent University, Coupure Links 653, B-9000 Ghent, Belgium

^d College of Agriculture and Environmental Sciences, Department of Forestry, Biodiversity and Tourism, Makerere University, P.O. Box 7062, Kampala, Uganda

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ABSTRACT

With increased drought events affecting forests globally, little is known about their future impact on Africa's forests. In particular, we need to gain a better understanding of how key African forest species will respond to drought stress. In this study, we investigated functional traits and physiological responses to drought of the light-demanding pioneer species *Maesopsis eminii* Engl. The study involved an experiment on potted *M. eminii* seedlings with three different drought treatments in which sap flow (SF), stem diameter variation (SDV) and stomatal conductance (g_s) were measured. Whereas low g_s rates ($39 \pm 30 \text{ mmol m}^{-2} \text{ s}^{-1}$) and pronounced SF-VPD (vapour pressure deficit) and g_s -VPD hysteresis loops during well-watered conditions indicated conservative stomatal control on water loss, nocturnal sap flow implied *M. eminii* is not able to completely block transpiration. At the onset of drought, the pioneer seedlings retained high stem diameter growth despite highly reduced soil moisture ($> -0.95 \pm 0.03 \text{ MPa}$) and SF rates, indicating that growth was prioritised. Contribution of stored stem water to daily water use was limited both during drought and control conditions, which was confirmed by the absence of time lags between photosynthetic active radiation (PAR)-SDV, PAR-SF and SDV-SF in all treatments. Below a soil water potential of $-0.95 \pm 0.03 \text{ MPa}$, leaves were gradually shed, but diurnal and nocturnal SF did not turn zero, and absolute stem diameter kept decreasing for the entire experimental period (115 days), portraying that *M. eminii* seedlings can survive only limited drought periods. In sum, this study demonstrated that species-specific traits, as opposed to species ecological strategy, govern drought performance. For *M. eminii*, its leaf traits proved pivotal to its drought performance.

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1. Introduction

The increased frequency and severity of drought periods (IPCC, 2007) is placing forest ecosystems under increasing pressure around the globe (Anderegg et al., 2016), and are leading to dieback of less drought-tolerant species and to shifts in vegetation composition, with important long- and short-term impacts on ecosystem functioning (Anderegg et al., 2012, 2016; Avila et al.,

2016; Berdanier and Clark, 2016; Bréda et al., 2006; Clark et al., 2016; Guada et al., 2016; Martin et al., 2015; Pellizzari et al., 2016). For African forests however, the impacts are not well understood. From the meta-analysis of Anderegg et al. (2016) on the link between drought and tree dieback, it is clear that very few studies have been performed in African forests. Furthermore, the few studies looking at the impact of drought on African forests disagree. Based on satellite data, Asefi-Najafabady and Saatchi (2013) found that African forests were remarkably undisturbed by drought events, unlike the Amazon. Zhou et al. (2014) on the other hand, reported a large decrease in Congolese rainforest greenness caused by short-term droughts. Similarly, inventory studies in African forests came to very different conclusions. Fauset et al. (2012) reported that increasing drought was causing a

* Corresponding author at: Laboratory of Plant Ecology, Ghent University, Coupure links 653, B-9000 Ghent, Belgium.

E-mail addresses: Jackie.Epila@UGent.be, epilajackie@yahoo.co.uk (J. Epila), Kathy.Steppe@UGent.be (K. Steppe).

compositional shift in favour of deciduous, light-demanding species in Ghanaian wet evergreen, moist evergreen and moist semi-deciduous forests. Ouédraogo et al. (2013) on the other hand, found that slow growing shade tolerant species were less sensitive to drought compared to fast-growing light-demanding species in M’Baïki Central Africa’s deciduous moist forest.

Based on these skewed observations, it is clear that we need to gain a better knowledge of how key African forest species will respond to drought in order to understand or predict the consequences of climate change-induced drought on African forest species. In particular, we need to assess species’ functional traits and physiological responses and mechanisms that aid in coping with drought (Bazzaz and Pickett, 1980; Choat et al., 2012; Engelbrecht and Kursar, 2003; Gliniars et al., 2013; Lloret et al., 2012; Malhi et al., 2013; Poorter and Markesteijn, 2008; Steppe et al., 2016).

In this study, we report on the plant water relations and drought traits of seedlings of an African pioneer species, *Maesopsis eminii* Engl. *M. eminii* was selected because of its ecological importance in tropical Africa. It is one of the dominant or co-dominant species in a wide range of tropical forests, including shrublands, dry forests, mountain forests, moist deciduous and rain forests (Epila et al., 2016). *M. eminii* also has many economic applications: it is used for timber or firewood, as a medicine or as source of edible oil, and is also used in agroforestry (Binggeli and Hamilton, 1993; Eggeling, 1947; Hall, 2010; Jøker, 2000; Struhsaker, 1987).

M. eminii is an early successional species colonizing forest gaps or clearings (Eggeling, 1947; Hall, 1995) and is shade-intolerant from the age of one year (Binggeli and Hamilton, 1993; Eggeling, 1947), typical of pioneer species (Poorter and Bongers, 2006). It has a low stem wood density of 0.37–0.48 g cm⁻³ (Chave et al., 2009) and has small to medium-sized (2.3–182.3 cm²) palatable leaves (Eggeling, 1947; Raunkier, 1934). It is a semi-deciduous species, becoming deciduous during severe drought (Eggeling, 1947). It can

grow in areas with dry seasons lasting between 2 and 6 months (Ani and Aminah, 2006; Hall, 1995; Jøker, 2000), but its distribution is most pronounced in the tropical rainforest region (Hall, 1995).

Our main hypothesis is that the plant water relations and drought traits of *M. eminii* will be similar to those of other tropical pioneer species. When water is not limiting, pioneer species prioritize fast growth (Ouédraogo et al., 2013; Poorter and Bongers, 2006). This is achieved by forming ‘cheap’ low-density wood and short-lived, mesomorphic leaves (Borchert, 1994; Poorter and Bongers, 2006). The associated high photosynthesis rates go hand in hand with little stomatal control and hence high stomatal conductance and water use (Huc et al., 1994; Nogueira et al., 2004). Hence, when water is not limiting, we hypothesize that (i) absolute (i.e. net day-to-day) stem diameter growth will be high, (ii) daily lost stem water will be recovered, and (iii) water use (transpiration and stomatal conductance) will be high without clear signs of diurnal stomatal control (no clear hysteresis when sap flow or g_s are plotted against vapour pressure deficit).

When soil water availability decreases, (i) limited stomatal control keeps water use relatively high, (ii) the contribution of water in the stem to diel sap flow increases because of the high hydraulic capacitance that is linked to low wood density (Borchert, 1994; Holbrook, 1995; Markesteijn et al., 2011a, 2011b; McCulloh et al., 2011, 2012; Tyree and Yang, 1990), and indirectly gauged by the presence of time lags (Ford et al., 2004; Goldstein et al., 1998; O’Grady et al., 1999; Phillips et al., 2003; Steppe and Lemeur, 2004), and (iii) recovery of lost stem water will still be evident. Hence, we hypothesize that at the onset of drought, (i) growth is still prioritized thus absolute diameter growth remains high, (ii) daily stem water recovery will become more pronounced, (iii) water use will decrease, and (iv) larger time lags will be observed between measured physiological variables (e.g., sap flow and stem diameter variations), and between these variables and environmental

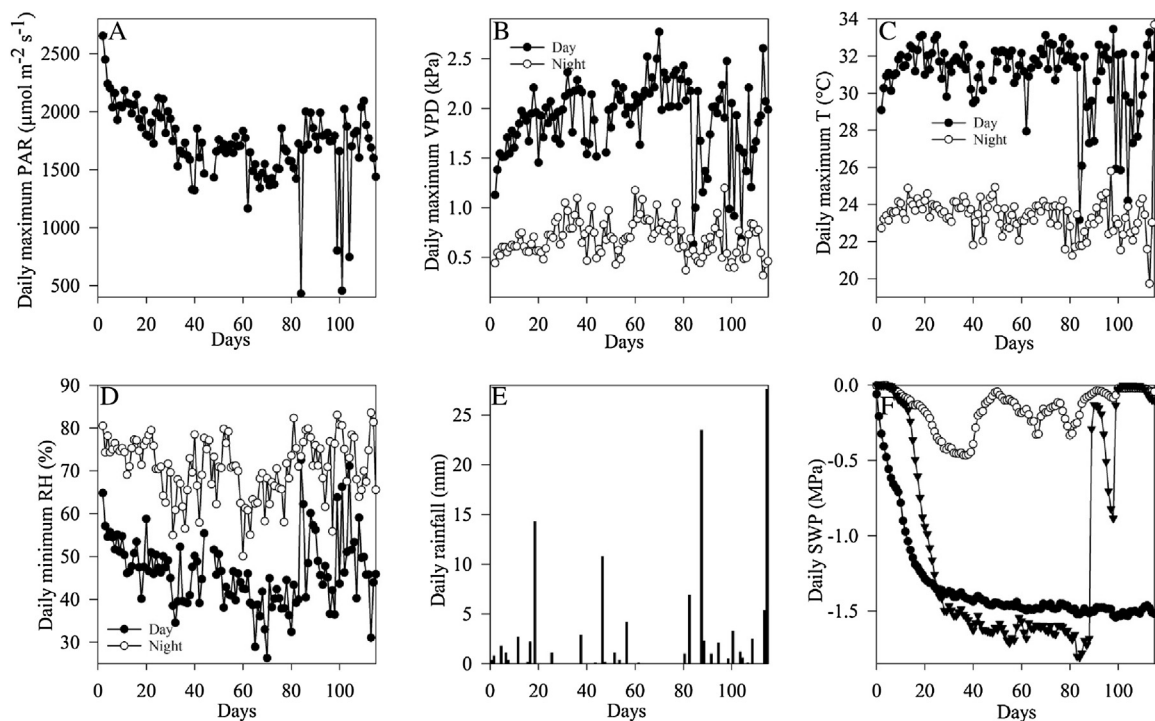


Fig. 1. Daily values of environmental conditions experienced at the experimental site from day zero (8 May 2013) until day 115 (31 August 2013). (A) Maximum photosynthetic active radiation (PAR; ●), (B) maximum vapour pressure deficit (VPD) (day (●) and night (○)), (C) maximum air temperature (T) (day (●) and night (○)), (D) minimum relative humidity (RH) (day (●) and night (○)), (E) daily rainfall and (F) soil water potential (drought (●), control (○) and rain-fed (▼)). Blank spaces for all parameters except rainfall indicate regions with missing data.

variables (i.e., photosynthetic active radiation, relative humidity, temperature, vapour pressure deficit, and soil water potential).

Eventually though, the limited stomatal control of pioneer species leads to a quick depletion of the available water, followed by leaf shedding to avoid further water loss but at the cost of reduced carbon fixation (Borchert, 1994; Eamus 1999; Ouédraogo et al., 2013; Poorter and Bongers, 2006; Poorter and Markesteijn, 2008). Once plant water is depleted, we expect that leaves will be shed rapidly, after which we hypothesize that the water use, the net diameter growth, stem water recovery as well as the daily diameter patterns stop completely.

2. Materials and methods

2.1. Description of the study site

The study was carried out at Muyenga-Bukasa (0°17'05.53"N, 32°37'53.55"E), a residential suburb of Kampala City, Uganda, located on the north-western shore of Lake Victoria. *M. eminii* seeds were collected on 7 February 2012 from mature trees of the Mabira Central Forest Reserve (0°23.357'N, 33°0.344'E), located on the northern shores of Lake Victoria. Seeds were germinated and newly germinated seedlings were placed into moist potting mix (forest soil mixed with clay loam soil) in plastic tubes on 9 March 2012, and raised for 12 months at the nursery of National Forestry Resources Research Institute (NaFORRI) located at 0°21'N, 32°46'E, approximately 1250 m a.s.l. On 2 March 2013, fifteen seedlings were carefully transferred into moist potting mix in ten-litre plastic buckets whose bottom was perforated to allow drainage of excess water. These seedlings were allowed to grow and acclimatize in the buckets at the study site for two more months, and were watered to field capacity twice daily, early in the morning and in the evening.

At this location, the tropical climate has a long rainfall season between March and May, and a highly variable shorter rainfall season between (August-) September and December (Black et al., 2003; Shongwe et al., 2011). Total annual rainfall is 1300 mm, ranging between 1000 and 1500 mm. Daily rainfall data were extracted from the Uganda National Meteorological Authority (UNMA) standard manual splayed-case copper rain gauge (aperture diameter: 127 mm and area 126.7 cm²; Casella Monitor, UK), situated 3.6 km from our study site.

Air temperature (T) and relative humidity (RH) were measured with a ventilated sensor (SHT75, Sensirion Technology, Switzerland) and photosynthetically active radiation (PAR) was measured with a quantum sensor (model QS, Delta-T Devices, UK) installed at 0.93 m height in the middle of the study site.

2.2. Experimental treatments

On 8 May 2013, nine plants were randomly selected from the 15 plants and their mean height (44.4 ± 4.6 cm), root collar diameter (6.4 ± 0.6 mm) and number of leaves (89 ± 13) were measured. The plants were then randomly assigned to one of three drought treatments. These drought treatments were (i) no irrigation at all

(Drought), (ii) daily irrigation at 6 pm with 200 ml of tap water as control (Control), and (iii) rain-fed watering (Rain-fed), which only received water when it rained. All test plants were placed on wooden planks to prevent the possibility of the roots of seedlings out-growing through the holes at the bottom of the bucket and getting access to soil water. Drought and control seedlings were placed within an open wooden rain shelter (2.5 m length × 1.5 m height × 1.5 m width) with a provision for placing a 3 × 6 m black plastic cover that could be anchored down to prevent rain from reaching the seedlings. The cover could be removed manually and was only installed when it rained and during the night (between 19:30–06:30 h, when PAR was 0 μmol m⁻² s⁻¹).

The microclimatic conditions and soil water potential of each treatment during the treatment period are given in Fig. 1 and Table 1. Note that the first month, which should have covered the long rainy season (May), was relatively dry (daily rainfall in May was 1 ± 3 mm day⁻¹), indicating an abnormal rainy season.

2.3. Sap flow and stem diameter variation

All nine seedlings were equipped with sap flow and stem diameter variation sensors for a period of 115 full days, from the start of the drought treatment (9 May) until 31 August 2013. Sap flow dynamics were measured using a home-built non-invasive heat field deformation (mini HFD) sensor, following the design of Hanssens et al. (2013). Each sap flow sensor consisted of three thermocouples (type T copper constantan, Omega engineering limited, Netherlands) and a 100 Ω heater, which were sewn onto an insulating material (Class 0 Armaflex self-adhesive tape). More details on the principle of HFD can be found in Hanssens et al. (2013), Nadezhdina et al. (2012) and Vandegehuchte and Steppe (2012). Axially, two thermocouples (T₁ (above the heater) and T₂ (below the heater)) were placed 1 cm from the heater and the third thermocouple (T₃ (side of the heater)) was placed tangentially at 0.3 cm from the heater. The symmetric (T_s or T₁-T₂) and asymmetric (T_a or T₃-T₂) temperature differences were used to determine parameter K (Eq. (1)) during zero sap flow (T_s=0) by plotting T_s-T_a as a function of T_s/T_a (Hanssens et al., 2013). K was derived as the intercept of the resulting linear fit. The R² values at which K was determined was 0.84 ± 0.15. Once the parameter K was known, the sap flow dynamics (SFD) (–) were computed (Eq. (1)) as in Hanssens et al. (2013).

$$SFDs = (K + (T_s - T_a))T_a^{-1} \quad (1)$$

The relative sap flow dynamic (RSFD) (%) was obtained by normalizing sap flow dynamic values using the highest value observed in the first full day of measurement (May 9) and the lowest value observed throughout the study period per individual to obtain percentages ranging between 0 and >100% (Eq. (2)).

$$RSFD = \left(\frac{SFD_{measured} - SFD_{min}}{SFD_{maxDay1} - SFD_{min}} \right) 100 \quad (2)$$

From here on, RSFDs will be referred to as sap flow. Daily sap flow refers to diel sap flow. Day-time sap flow was observed when

Table 1

Average and standard deviation values for daily maximum photosynthetic active radiation (PAR), vapour pressure deficit (VPD), air temperature (T), daily soil water potential (SWP) and minimum relative humidity (RH). The SWP subscripts imply, drought for drought treatment, control for control treatment and rain-fed for rain-fed treatment.

Parameter	PAR (μmol m ⁻² s ⁻¹)	VPD (kPa)	T (°C)	RH (%)	SWP _{drought} (MPa)	SWP _{control} (MPa)	SWP _{rain-fed} (MPa)	Long rains (mm day ⁻¹) (May)	Dry season (mm day ⁻¹) (June–July)	Short rains (mm day ⁻¹) (August)
Day	1727 ± 330	2.0 ± 0.4	31 ± 2	46 ± 8	-1.3 ± 0.3	-0.2 ± 0.1	-1.0 ± 0.7	1 ± 3	1 ± 2	4 ± 11
Night	0	0.7 ± 0.2	23 ± 1	71 ± 7						

PAR was greater than $0 \mu\text{mol m}^{-2} \text{s}^{-1}$, night-time sap flow when PAR was $0 \mu\text{mol m}^{-2} \text{s}^{-1}$, running from the end of the current day into the next day before PAR became greater than $0 \mu\text{mol m}^{-2} \text{s}^{-1}$. Day one refers to 9 May 2013. To highlight, treatment differences in nocturnal sap flow, SFD_{maxnocDay1} was replaced by nocturnal sap flow (SFD_{maxnocDay1}).

Stem diameter variations (SDV) of each monitored seedling were measured by a calibrated linear variable displacement transducer (LVDT; Solatron Metrology, DF/5.0, UK), secured about 3 cm above the root collar diameter using a home-built holder as described in [Steppe et al. \(2006\)](#). From the SDV data, two variables were calculated per seedling and for each day:

- **absolute growth:** the maximum stem diameter of each day, and
- **daily stem water recovery:** the difference between the following day's maximum stem diameter (wee hours of the morning peak value) and the minimum diameter of the previous day.

Equitensiometers (EQ2x, Delta-T Devices, UK) were used to measure soil water potential (SWP). One sensor per treatment was placed at a soil depth of 12 cm below root collar. SWP data, which were temperature sensitive, were normalized over a 24 h period. Data from all sensors were logged (CR1000, Campbell Scientific Inc., Logan, UT, USA) at 30 s intervals and averaged every 5 min.

2.4. Stomatal conductance

Stomatal conductance (g_s) was measured at the end of July (23, 25–29 July 2013) and the beginning of August (4–7 August 2013) with a calibrated diffusion AP4 porometer (Delta-T Devices Ltd, Cambridge, UK). By then, only the control seedlings had leaves

remaining, so stomatal conductance measurements were confined to the control treatment. Four leaves per seedling were measured in each measurement rounds. Daily measurement rounds were carried out between 06:34 h and 21:38 h ensuring night time g_s was captured, with night time occurring on average between 19:15–06:30 h. Porometer resistance measurements (m s^{-1}) were converted to stomatal conductance ($\text{mmol m}^{-2} \text{s}^{-1}$) using the equations provided by [Bragg et al. \(1991\)](#).

2.5. Statistical analysis

For all statistical tests performed for this study, the significance level (α) was set at 5%. Repeated measures ANOVA with between-subject factor Drought (3 levels) and between-subject factor Time (115 levels) was performed on daily maximum day-time sap flow, daily maximum night-time sap flow, the ratio of daily maximum nocturnal to day-time sap flow, daily absolute growth and daily stem water recovery. If Mauchly's sphericity (ϵ) test statistic was significant ($P < 0.05$), the Greenhouse–Geisser correction was used if $\epsilon < 0.75$, else the Huynh–Feldt correction ($\epsilon > 0.75$) was preferred for the within subjects test. The Bonferroni procedure was used for confidence interval adjustment and post-hoc tests.

Cross correlation (CCR) analyses were performed to identify correlations and time lags between the environmental variables (x : T, RH, VPD, PAR and SWP) and the physiological responses (y : sap flow and stem diameter variations). The 5-min dataset of the first 30 days of drought was used as input for all treatments as all treatment plants still had viable leaves. CCR analyses were performed individually per seedling and analysed per treatment to determine the overall time lags and correlations. A one way ANOVA (univariate analysis) with the drought treatment as factor was performed on the CCR values to yield means and standard

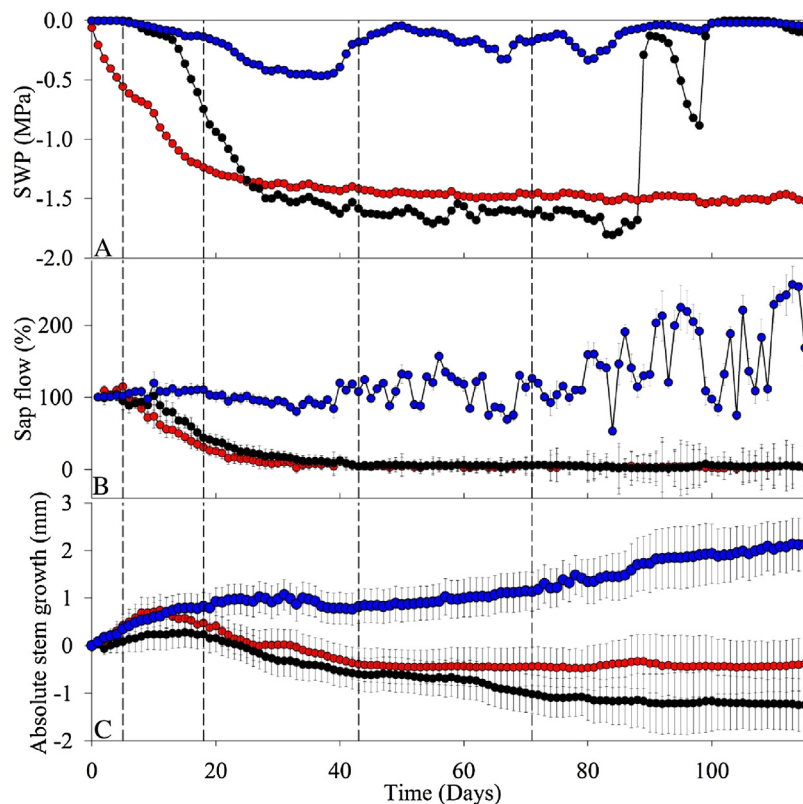


Fig. 2. *M. eminii* seedlings' maximum day-time sap flow (B) and daily absolute stem growth (C), and their respective standard error bars per treatment during different soil moisture conditions (A). Control seedlings are coloured blue, drought is red and the rain-fed is coloured black. The black vertical dashed lines indicate selected days (Days: 5, 18, 43 and 71), which are displayed in [Fig. 3](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

errors and to determine between which group means statistical differences arose. When group sizes were not equal the Scheffe test was used, otherwise the Tukey test was preferred. If Levene's test indicated the equal variance assumption was violated ($P < 0.001$), between groups (ANOVA) and robust test of equality means (Welch and Brown-Forsythe) were checked. If they were significant ($P < 0.001$) then the null hypothesis was rejected as there was a statistically significant difference among the group means. If these were not significant, the Tamhane's T^2 test for unequal variance was used. The between subjects effects (treatment) was checked. If ($P < 0.05$), the null hypothesis was rejected as there was a significant treatment effect. The Post Hoc test indicated where the statistical difference was ($P > 0.05$; not significant; $P < 0.05$ significant). Lower and upper bound 95% confidence intervals for estimated marginal means were checked for overlap.

Stomatal conductance (g_s) for the three control seedlings was split into day and night and correlated with PAR, RH, T and VPD using Spearman's correlation. A two-tailed test was performed and a 95% confidence interval was chosen. All statistical tests were performed using SPSS 23.0 (SPSS, Inc. Chicago, IL, USA).

3. Results

3.1. Soil water potential

Control soil water potential (SWP) decreased slightly during the first 38 days to -0.5 MPa, and then recovered to the original 0 MPa value from day 100 onwards (Fig. 2A).

SWP dropped very rapidly after the onset of the drought treatment to reach -0.75 MPa after 10 days and then decreased further to -1.3 MPa after 24 days. Afterwards, it kept decreasing slightly. The limited amount of rain in the long rainy season caused the rain-fed treatment to be a treatment in between the control and the drought treatment. In the first 12 days, its SWP was the same as the control treatment, but then SWP dropped rapidly, reaching values of about -1.5 MPa after 28 days, after which SWP continued to decrease slowly. It peaked on day 88 when rains returned (Fig. 1) and then fluctuated as rain became periodical again.

3.2. Plant growth

At the end of the experiment, the recorded increase in seedling height was -0.03 ± 0.84 cm for drought, 3.8 ± 1.0 cm for rain-fed and 16.0 ± 5.0 cm for the control treatment. At this point in time, drought and rain-fed plants had completely wilted leaves with the exception of one individual from the rain-fed treatment having five viable green leaves. The control seedlings had gained 55 ± 17 leaves.

3.3. Sap flow

Repeated measures ANOVA revealed that there was a very significant interaction (all $P < 0.001$) between drought treatment and the time factor for daily maximum sap flow (Fig. 2B) and absolute growth (Fig. 2C).

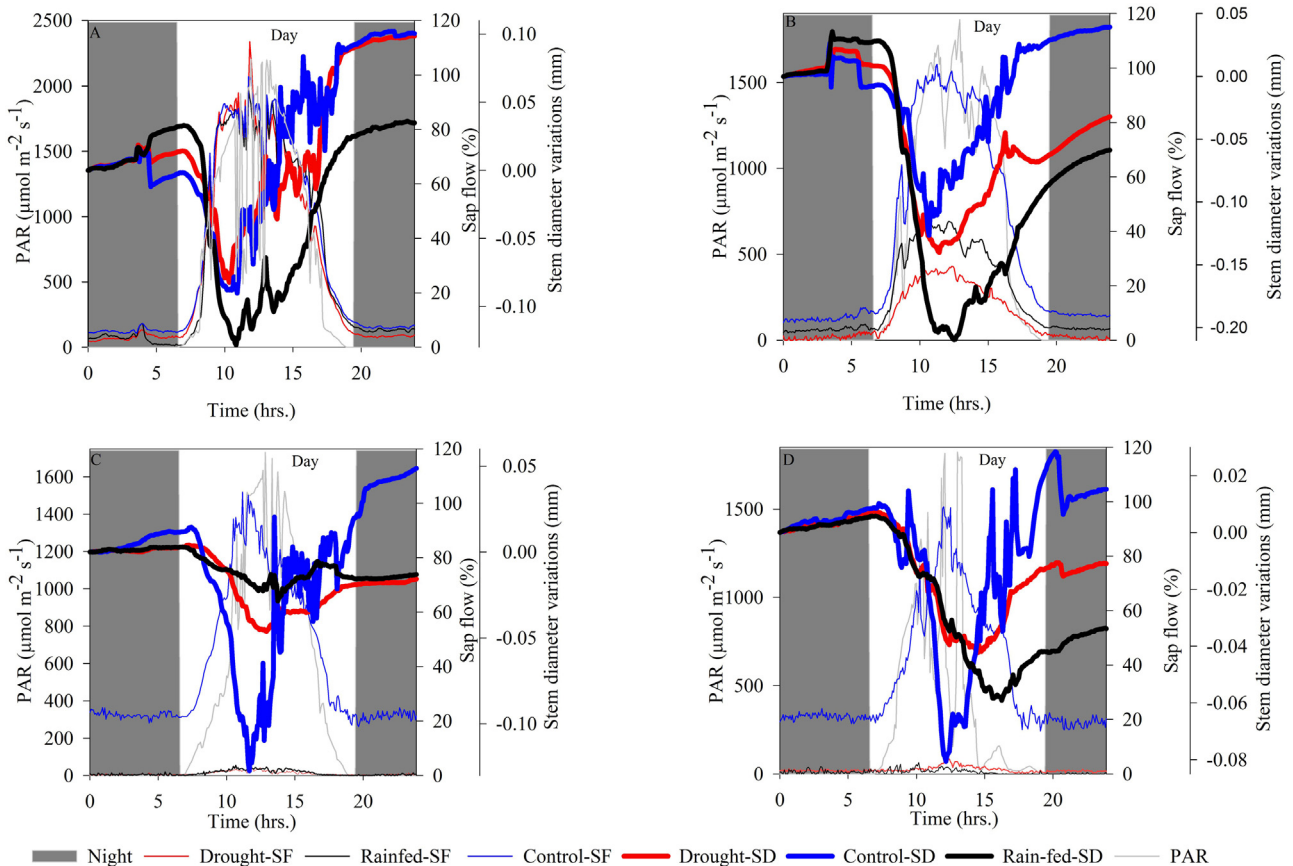


Fig. 3. *M. eminii* mean sap flow and stem diameter variation patterns (shrinkage and swelling) for the three treatments as soil water potential declined on drought days (A) 5, (B) 18, (C) 43 and (D) 71. The photosynthetic active radiation (PAR) is the light grey line, sap flow is coloured lightly and stem diameter variations, darker. For the treatments, drought is red, control is blue and rain-fed is black. Night-time is shown by the dark grey shaded area; the white portion is day-time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

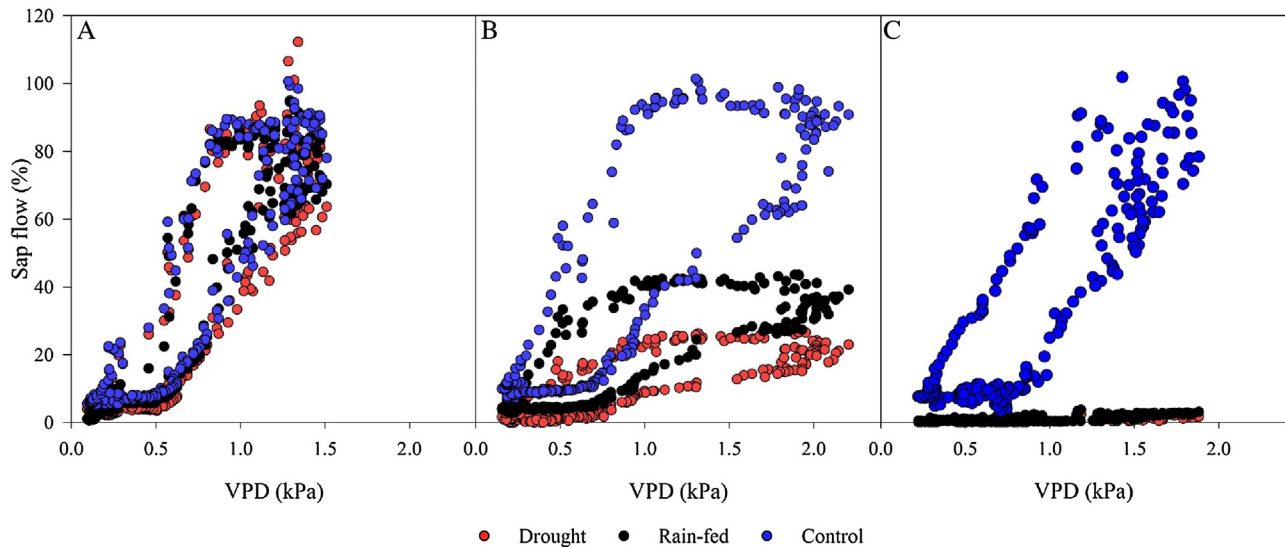


Fig. 4. Clockwise hysteresis loops for *M. eminii* on day 5 (A), 18 (B) and 43 (C) showing that VPD strongly influenced *M. eminii* sap flow behaviour.

In the first few days and despite the immediate drop in SWP of the drought treatment, day-time sap flow (SF) of the three treatments was very similar. SF for drought and rain-fed treatments declined respectively 6 (−0.6 MPa) and 10 (−0.1 MPa) days after the start of the treatment period (Fig. 2B). Control SF remained strongly coupled with atmospheric variables (Figs. 1 and 2 B). Fig. 3 shows the diurnal and nocturnal SF pattern for four different days. The SF pattern was very similar for all treatments on day 5 (Fig. 3A). However, the drought treatments had a strong and increasing impact on the SF on days 18 (Fig. 3B), 43 (Fig. 3C) and 71 (Fig. 3D) noted by decreased stem increment. For the first three selected days (5, 18 and 43), the relation between SF and VPD is plotted in Fig. 4. This shows clockwise hysteresis loops for all days, and all treatments (Fig. 4A and B). Day 43 showed this similar loop for control (Fig. 4C) with the relation for drought and rain-fed

being highly obscured because of the very limited SF. Control SF increases strongly until VPD is about 1 kPa and then levels off.

Based on the 5 min-dataset, SF was highly correlated with all microclimatic variables, and most strongly with PAR (Table 2). No significant time lag was observed between SF and any microclimatic variables, so the plants responded immediately to changes in environmental variables. Correlations between the microclimatic variables and the plants were highest for the control plants. The rain-fed and drought treatment plants were more strongly correlated to SWP.

Nocturnal SF (Fig. 5) was not zero and was strongly influenced by atmospheric conditions. Nocturnal SF pattern for drought (day 6; SWP = −0.6 MPa) and rain-fed (day 10; SWP = −0.1 MPa) plants started declining a day after and on the same day as the diurnal sap flow started decreasing. For the control, there is an increasing trend

Table 2

Averages and standard error values of cross-correlation (CCR) output of 5 min dataset values for the first 30 days of treatment when all seedlings still had leaves computed per seedling and treatment using a one way between groups ANOVA (univariate). The CCRs show how *M. eminii* seedling's sap flow (SF) and stem diameter variations (SDV) correlated between themselves as well as with environmental variables experienced at the study site and how the treatments influenced this correlation. The standard error of the CCR analysis was 0.009. Time lags are measured in minutes. Underlined values are the highest. A 95% confidence interval was used. PAR is photosynthetic active radiation, RH is relative humidity, T is air temperature, VPD is the vapour pressure deficit and SWP is the soil water potential. Letters in superscript indicate significant differences between the drought treatments with ^abeing the highest and ^bthe lowest.

Variable		Sap flow (SF)			Stem diameter variations (SDV)		
		Control	Rain-fed	Drought	Control	Rain-fed	Drought
PAR	R-value	<u>0.9 ± 0.0^a</u>	0.7 ± 0.1 ^{ab}	0.6 ± 0.0 ^b	−0.4 ± 0.1	<u>−0.6 ± 0.1</u>	−0.3 ± 0.1
	Lag	1.5 ± 0.7	2.2 ± 0.0	2.2 ± 0.0	3 ± 2	<u>20 ± 13</u>	7 ± 2
RH	R-value	−0.8 ± 0.0 ^b	−0.4 ± 0.1 ^a	−0.3 ± 0.0 ^a	0.4 ± 0.1	<u>0.6 ± 0.1</u>	0.3 ± 0.1
	Lag	0 ± 0	0 ± 0	0 ± 0	0 ± 4	<u>7 ± 4</u>	0 ± 4
T	R-value	<u>0.9 ± 0.0^a</u>	0.6 ± 0.0 ^{ab}	0.5 ± 0.1 ^b	−0.4 ± 0.1	<u>−0.7 ± 0.1</u>	−0.4 ± 0.1
	Lag	0 ± 0	0 ± 0	0 ± 0	0 ± 4	<u>7 ± 4</u>	0 ± 4
VPD	R-value	<u>0.8 ± 0.0^a</u>	0.5 ± 0.1 ^b	0.4 ± 0.0 ^b	−0.4 ± 0.1	<u>−0.6 ± 0.1</u>	−0.3 ± 0.2
	Lag	0 ± 0	0 ± 0	0 ± 0	0 ± 3	<u>5 ± 3</u>	0 ± 3
SWP	R-value	0.0 ± 0.1 ^b	<u>0.5 ± 0.1^a</u>	<u>0.5 ± 0.1^a</u>	<u>0.2 ± 0.1</u>	0.0 ± 0.1	0.1 ± 0.1
	Lag	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
SDV	R-value	−0.5 ± 0.1	<u>−0.5 ± 0.2</u>	−0.3 ± 0.1			
	Lag	3 ± 4	<u>8 ± 4</u>	7 ± 4			

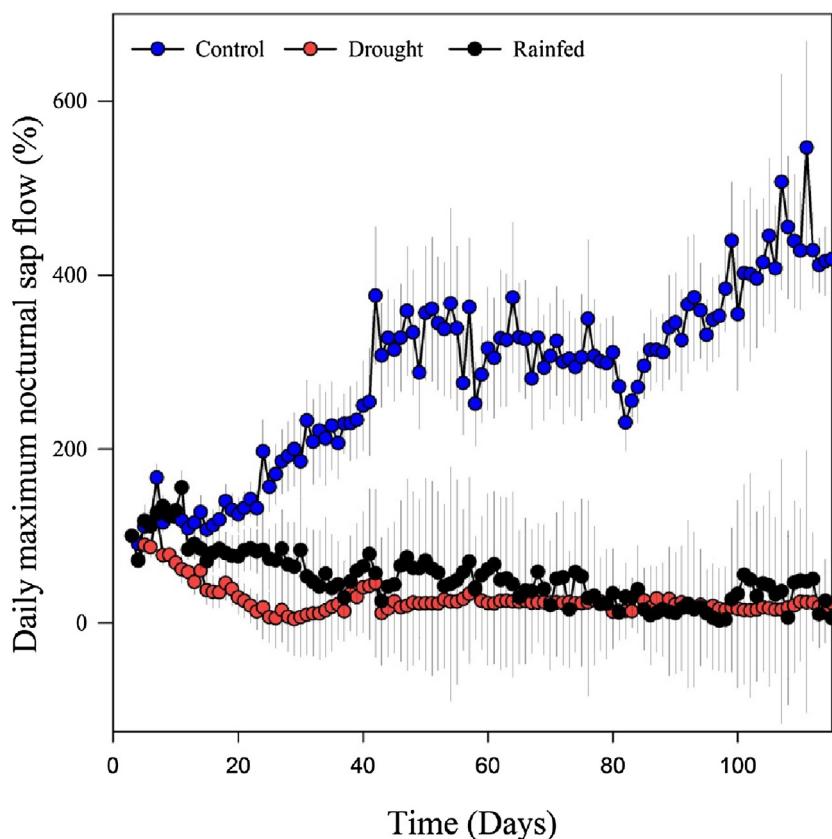


Fig. 5. *M. eminii* seedlings nocturnal sap flow pattern with standard error values for the three different treatments. These values have been renormalized using the first day highest nocturnal SF value setting it to 100% and the rest were relative to it.

of nocturnal SF from the onset, closely following atmospheric conditions, with the highest value recorded on day 110.

3.4. Stem diameter variations

Initially, all treatments had a positive absolute growth trend, although this growth tended to be lower for the rain-fed seedlings than for the control and drought ones (Fig. 2C). Diameter growth of the controls increased the first 18 days and continued regardless of SWP fluctuation, but then stabilized and became more coupled to SWP. Absolute stem growth declined for the drought treatment on day 11 (at SWP of -0.9 MPa), 5 days after SF decline. Absolute stem growth of the rain-fed trees started decreasing on day 15 at SWP of -0.4 MPa, also 5 days after the initial decline in SF (Fig. 2C). The stem diameter patterns did not differ between the treatments on day 5 (Fig. 3A). For all treatments, a strong decrease was observed when sap starts flowing, and a recovery after the sap flow peak was reached. On the three other days, differences in the profiles between the treatments were evident (Fig. 3B–D).

Daily stem water recovery was initially the same for all treatments (Fig. 6). Then recovery of the drought treatment became slightly higher than the control seedlings between days 11 and 18, and this difference was significant for two days (14 and 16) (Fig. 6). After this, it dropped quickly below the values of the control treatment. Daily stem water recovery of the rain-fed treatment did not show this marked increasing trend and dropped below the control treatment values from day 23 (Fig. 6). The deviation profile exhibited by the rain-fed plants immediately before and after day 60 was due to rain water contribution (Figs. 1 and 6). Recovery for the drought treatments never became zero.

Even after 115 days into drought stress, drought-stressed and rain-fed seedlings continued to shrink and still had some sap flow recorded despite not having any viable leaves (Fig. 6). Control recovery fluctuated through the trial period due to strong coupling with atmospheric conditions.

Like the SF data, SDV data were closely correlated to the environmental variables when looking at the 5 min dataset (Table 2), although correlations were lower than for the SF data. There were also small time lags between PAR and SDV for all treatments, and also between SF and SDV responses. Correlations between SDV and SWP were very low.

3.5. Stomatal conductance

M. eminii's stomatal conductance (g_s) as illustrated for a single day (Fig. 7A) had a general incremental profile from predawn up to around 10:50 am after which it reduced as VPD increased. The mean day time g_s value for the selected day was 33 ± 24 $\text{mmol m}^{-2} \text{s}^{-1}$ at VPD of 1.2 ± 0.6 kPa. The mean daily day time value for the entire campaign window of July and August was low: 39 ± 30 $\text{mmol m}^{-2} \text{s}^{-1}$ at VPD of 1.1 ± 0.5 kPa.

Measurements of g_s show that the earlier observed hysteresis loop for all treatments (Fig. 4) was due to stomatal closure (Fig. 7B). Nocturnal g_s was confirmed (Figs. 3 and 7 A). The g_s were much lower during the night (11 ± 4 $\text{mmol m}^{-2} \text{s}^{-1}$ for a VPD range of 0.5 ± 0.2 kPa) than the day (39 ± 30 $\text{mmol m}^{-2} \text{s}^{-1}$ for a VPD range of 1.1 ± 0.5 kPa).

Statistical correlations revealed that day-time g_s were most strongly coupled to PAR followed by T. An exemplified illustration

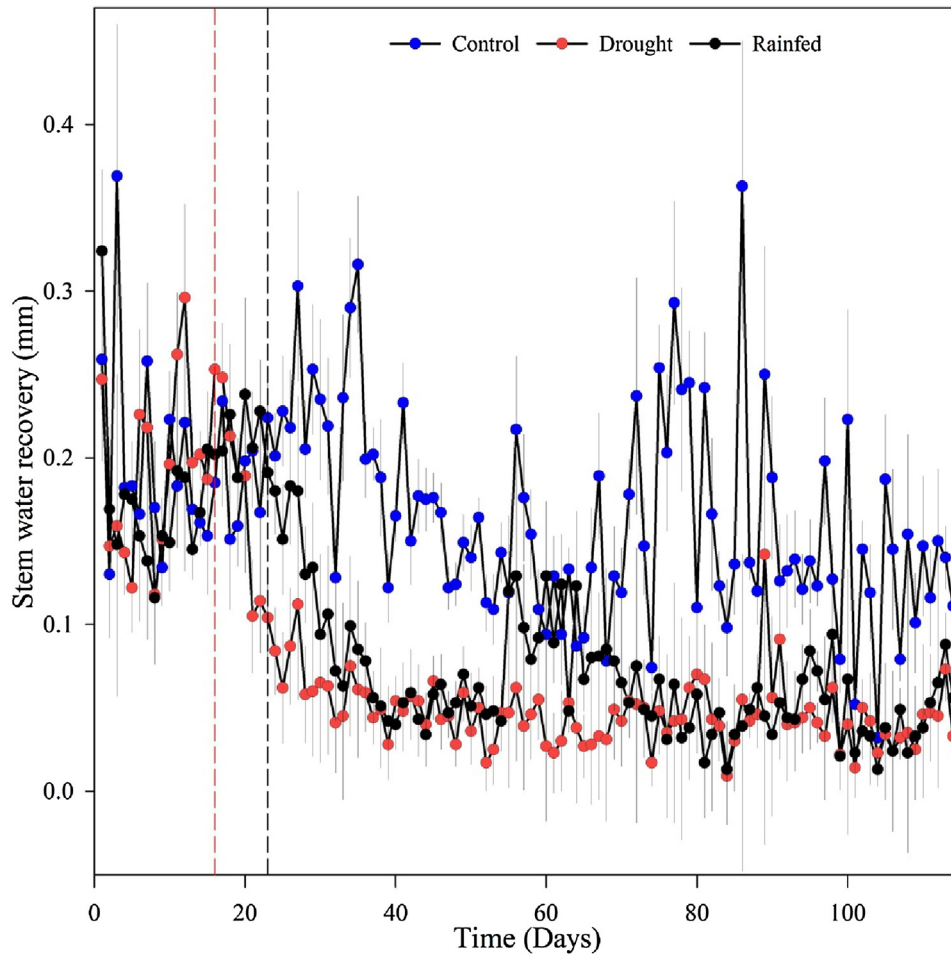


Fig. 6. *M. eminii* seedlings' stem water recovery with standard error values for all treatments. The red vertical dashed line indicates when the drought treatment recovery started declining, and the black is for the rain-fed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of how g_s closely followed PAR is depicted by Fig. 7. In the night, g_s weakly coupled to RH, T and VPD (Table 3).

The typical clockwise hysteresis loops between g_s and VPD and SF and VPD (Fig. 7B) explain the relatively low correlation during

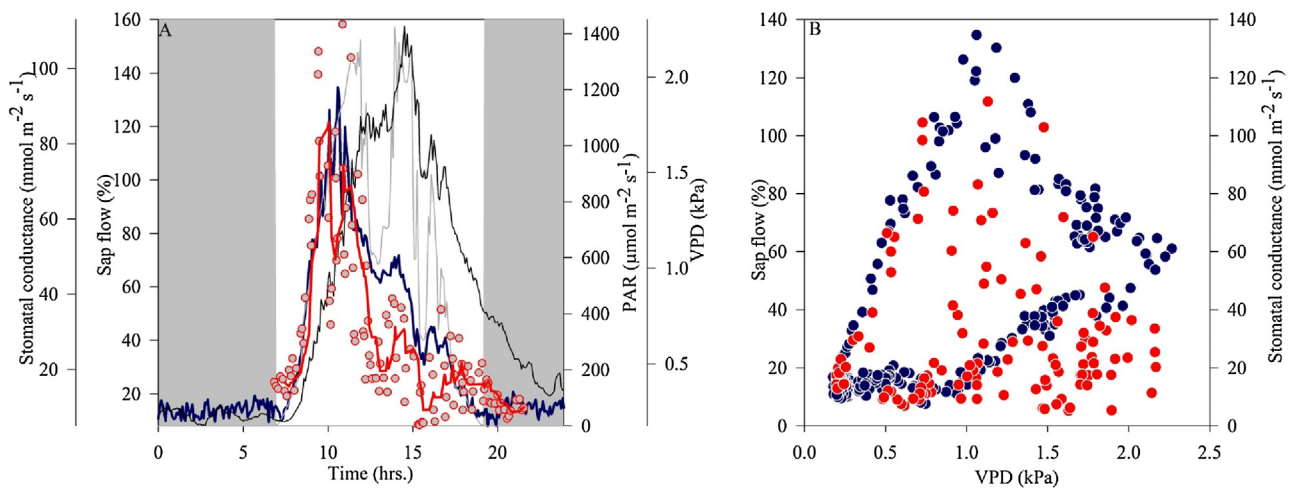


Fig. 7. (A) Representation of a selected sunny day of the control treatment with non-pronounced fluctuating PAR (light grey line; 29 July (82 drought days)) depicting the 5 min sap flow (thick blue line) and 3 min averaged stomatal conductance (g_s ; grey circles with red edging) patterns to follow PAR. Vapour pressure deficit (VPD; black line) is noted to lag behind. A 5 point moving average forecast curve (thick red line) was fitted through the g_s point values. The dark grey portion represents night and the white, day time. (B) Hysteresis loops of 5 min sap flow (blue dots) and 3 min averaged g_s (red dots) plotted as functions of VPD show coherence in *M. eminii* physiological responses to VPD. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3

M. eminii control seedlings' day and night stomatal conductance (g_s) values correlated with climatic variable of T (temperature), RH (relative humidity), VPD (vapour pressure deficit) and PAR (photosynthetically active radiation) using Spearman's bivariate correlation. Flagged values indicate: **correlation is significant at the 0.01 level (2-tailed) and *correlation is significant at the 0.05 level (2-tailed).

	RH (%)	T (°C)	VPD (kPa)	PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	N
Day					
g_s ($\text{mol s}^{-1} \text{m}^{-2}$)	-0.037	0.076**	0.047*	0.307**	2709
Night					
g_s ($\text{mol s}^{-1} \text{m}^{-2}$)	-0.051	0.173**	0.081	-	411

the day compared to night as VPD increase provoked a decline in g_s and SF beyond VPD ranges of 0.9–1.13 kPa.

4. Discussion

4.1. Plant-water relations when water was not limiting

As hypothesized, we observed a relatively fast and persistent growth, in height, leaf number, and in absolute growth diameter for the control treatment seedlings (Fig. 2C). Control stem water recovery is also evident (Fig. 6). Such fast growth strategy is a characteristic of tropical pioneer species (Croat, 1978; McCulloh et al., 2012; Ouédraogo et al., 2013) that enables them to quickly outgrow competitors and escape herbivores (Pearson et al., 2003a, 2003b).

We hypothesized that *M. eminii* would have a high water use without clear signs of diurnal control. However, this was not observed. Instead, we noticed that *M. eminii* had (i) low overall levels of g_s (Fig. 7A), (ii) hysteresis in both sap flow and g_s (Figs. 4 and 7 B), (iii) stomatal closure starting at a VPD threshold of about 1 kPa, typical of low wood density species as a means of maintaining leaf water potentials at high levels to avoid cavitation (Borchert, 1994; Maes et al., 2009). We also observed that *M. eminii* adjusted its leaf angle (parahelionasty) and curled up its leaves, which Maes et al. (2011) observed for *Jatropha* as an effective measure to prevent leaf overheating when g_s is reduced and atmospheric conditions are demanding.

However, the low water use does not imply that this species has low water use for a given assimilation rate. Indeed, despite this conservative water use strategy, the seedlings were not able to avoid water loss. The control plants, like the plants of the other treatments, showed nocturnal sap flow. This was not caused by incorrect calculation of sap flow rates (parameter K setting; see M&M), because (i) the nocturnal sap flow was significantly correlated to climatic conditions (Table 3), and (ii) it was confirmed by nocturnal g_s measurements (Fig. 7A). The control seedlings had increasing nocturnal sap flow throughout the experiment (Fig. 5), despite the fact that nocturnal microclimatic conditions did not systematically become more demanding throughout the experiment (Fig. 1). This study did not allow to distinguish whether this nocturnal water loss was due to water flow through the leaf cuticular layer (despite the potted seedlings growing in natural conditions) or due to poor stomatal control, or a combination of both.

4.2. Plant-water relations at the onset of drought

When sap flow started decreasing as a consequence of reduced soil water availability, drought-stressed and rain-fed seedlings kept growing at high rates for five more days. This confirms the

hypothesis that pioneer *M. eminii* seedlings prioritise growth despite decreases in soil moisture and the coupled down-regulation of sap flow (Fig. 2).

The hypothesis that daily stem water recovery (Fig. 6) becomes more pronounced at the onset of drought (i.e., Fig. 2C) was not confirmed for the rain-fed treatment. For the drought treatment, there was a slight trend of increased recovery. All in all, it appears that the role of hydraulic capacitance or stored stem water for our 15 month old seedlings was small, and that *M. eminii*'s reserves cannot be replenished below -0.95 ± 0.03 MPa. The limited role of stem water for balancing *M. eminii*'s water use was further reflected by small time lags between sap flow and environmental conditions (Table 2), where larger time lags have been related to larger stem water storage (Ford et al., 2004; Goldstein et al., 1998; O'Grady et al., 1999; Phillips et al., 2003; Steppe and Lemeur, 2004). For our 15 month-old seedlings, the potential contribution of stem-stored water to the transpiration stream was minimal. Stem volume estimations showed that the maximum daily volume shrinkage was only about 0.44 cm^3 . Our findings of limited contribution of the stem water to buffering water use are in line with the findings of Maes et al. (2009) for *Jatropha curcas*, and Chapotin et al. (2006) and Van den Bilcke et al. (2013) for Baobab (*Adansonia* sp.).

4.3. Plant-water relations after prolonged period of drought stress

As long as there were leaves left on the plant, diel (Fig. 3) and nocturnal sap flow (Fig. 5) rates of rain-fed and drought-stressed seedlings were still significantly different from zero, even after soil water potential values dropped to very low values. As such, it is clear that the plants were still 'leaking' water through the remaining leaves, not uncommon in mesomorphic leaves (Borchert, 1994). Eventually, as hypothesized, all leaves were shed to avoid further moisture losses. However, even after leaves were shed, the plants were still losing water, as is proven by the low but non-zero values of diel (Fig. 3C and D) and nocturnal (Fig. 5) sap flow, and the small but persistent daily stem diameter patterns (Fig. 3C and D). As a consequence, the seedling diameters of the rain-fed and the drought treatment seedlings kept decreasing further during the entire drought period (Fig. 2C). This steady decrease indicates that *M. eminii* seedlings can only survive prolonged dry seasons for a limited time.

5. Conclusions

The common belief is that a species' drought performance hinges on its ecological strategy cohort (e.g., pioneer). Our study on potted seedlings of the pioneer *M. eminii* has shown that species-specific traits might prove more important. Where we expected *M. eminii* to have a high water use, we observed low levels of g_s and pronounced hysteresis loops in both sap flow and g_s with VPD portraying *M. eminii* as a conservative water user, but with limited control over its nocturnal water losses. At the onset of drought stress, the seedlings were able to prioritize growth despite decreases in both soil moisture and sap flow as expected from a pioneer. Prolonged drought stress eventually caused leaf shedding and a continuous decrease in absolute stem diameter due to low but non-zero sap flow rates.

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