



Peak photosynthesis at summer midday in *Acacia* trees growing in a hyper-arid habitat

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Abstract

Key message Desert *Acacia* trees photosynthesize during the hot dry summer, and use stored carbon for summer growth.

Trees that grow in hyper-arid environments can provide important insight into the role of carbon use and carbon storage for tree survival and growth in extreme conditions. *Acacia* trees, in particular, experience some of the most arid conditions in which trees can grow on the planet, enduring high temperatures, high radiation and drought. Here we measured for two years photosynthesis along the day, stem circumference growth, and seasonal changes in non-structural carbohydrates in adult *Acacia* trees in their natural hyper-arid habitat (Arava desert, southern Israel). The peak of net CO₂ assimilation was at midday in all seasons, even during summer when vapor pressure deficit was at maximum of 6 kPa and light intensities were at high levels (1800 μmol photons m⁻² s⁻¹). Tree growth started in the spring and increased in the hot summer season and during the dry fall season (autumn). Starch concentrations in the branches were highest in the winter and spring (17% in dry matter) decreasing in the summer and fall (7% in dry matter). Our observations indicated that carbon assimilated during the winter was stored in the branches as starch reserves, which were later used for tree growth in summer. Still, most of the growth was subsidized by concurrent assimilation during the dry season. These findings show that *Acacia* trees are able to photosynthesize in conditions that other trees cannot, indicating a strong potential to contribute to ecosystem carbon sequestration in warming and drying climates.

Keywords Tree growth · Desert · *Acacia* · Photosynthesis · Carbon

Introduction

Three major environmental factors limit plant growth and photosynthesis: light (Barber and Andersson 1992; Gururani et al. 2015), temperature (Berry and Bjorkman 1980; Slot and Winter 2017), and water availability (Fan et al. 2017). Climatic changes are predicted to drive much of the natural and agricultural habitats globally towards the limits of these environmental conditions (Christensen et al. 2007). Therefore, identifying tree species that are able to survive and even prosper under these predicted conditions has an ecological and societal value. Hot desert ecosystems are characterized by low availability of water and high temperatures. Heat combined with drought results in a high vapor pressure deficit (VPD) in the air, which increases plant water loss via transpiration (Chaves et al. 2003; Sanginés de Cárcer et al. 2018). In addition, plants in deserts are exposed to high radiation which results in long periods of photosynthetically active radiation (PAR) exceeding 1300 μmol photons

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$\text{m}^{-2} \text{s}^{-1}$, a level that can damage photosynthetic processes (Treves et al. 2016).

Despite this combined effect of high temperature, high PAR, and low water availability, there is a tree genus that populates some of the hottest and driest deserts around the globe. *Acacia*¹ trees are distributed in the Namib desert (Schulze et al. 1991), the Sahara desert (Essendoubi et al. 2007), the Australian desert (Adams et al. 2016), and the Arabian deserts (Seleem et al. 2013), where they are considered keystone species. Recently, in the Israeli desert, two species of *Acacia* were found to grow predominantly during the hot, dry season when environmental conditions are at their extreme heat and drought (Winters et al. 2018). Tree growth and other biochemical processes depend mainly on photosynthetic uptake of CO_2 (assimilation) from the atmosphere (Dickson 1989; Ericsson et al. 1996; Klein et al. 2011, 2016; Klein 2015; Klein and Hoch 2015). However, CO_2 assimilation (via opening of the stomata) entails a high cost of water loss, especially in dry environments. Therefore, trees have developed the ability to buffer carbon availability by producing carbon reserves, as non-structural carbohydrates (NSC), to be consumed up to months, seasons and years later. These NSCs (mainly sugars and starch) are the long-term storage of C, produced by the plant to ensure survival when CO_2 assimilation is limited (Wiley and Helliker 2012; Klein and Hoch 2015).

Trees that live in a hyper-arid environment can provide important insight into the role of carbon use and storage for tree survival and growth. Therefore, we ask: What are the environmental conditions (temperature, PAR, and humidity) that control leaf gas exchange and allow *Acacia* trees to grow in the hot dry summer? And does *Acacia* tree growth depend on direct C inputs from photosynthesis (net CO_2 assimilation) or on the usage of C reserves (NSC)? We performed two years of diurnal measurements of photosynthesis, stem circumference growth, and seasonal measurements of NSC in adult *Acacia* trees in their natural hyper-arid habitat. Although other C sinks exist (respiration, fruit production, etc.), source-storage-growth relationships still represent intrinsic tree C management. We use this extensive field dataset to test two hypotheses: (1) CO_2 assimilation is constrained during midday and summer, by a combination of high temperatures, high VPD, and PAR approaching 2000 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$; (2) Carbon reserves accumulate

in the branches during the wintertime, and these C stores are used for stem growth during the summer.

Materials and methods

Study species and field site

Trees of the genus *Acacia* (nowadays separated into *Acacia* and *Vachellia*) consist of about 1,300 species that are distributed all around the southern hemisphere including the most arid environments on Earth (Maslin et al. 2003). The species *Acacia tortilis*, considered as the most thermophilic *Acacia* species (Boulos 1999), has been subdivided into four distinct subspecies: *A. tortilis* subsp. *tortilis*, *A. tortilis* subsp. *raddiana*, *A. tortilis* subsp. *spirocarpa* and *A. tortilis* subsp. *heteracantha* (Wickens et al. 1995). The northern limit of this species is in the Negev and Arava deserts of Israel, where *A. tortilis* subsp. *tortilis* (Forssk.) Hayne (Fig. 1b) and *A. tortilis* subsp. *raddiana* Savi (Fig. 1c), are the two dominant (and sometimes the only) tree species existing (Zohary and Orshan 1956; Halevy and Orshan 1972; Ross 1981; Winters et al. 2018). Surrounded by coexisting shrub species, these *Acacias* have a true tree form, growing up to 5 m in height, which is the maximum potential tree height due to hydraulic limitation (Klein et al. 2015). For simplicity, we term here *Acacia tortilis tortilis* as *Acacia tortilis* and *A. tortilis raddiana* as *A. raddiana*. There are visible morphological differences between the two subspecies; *A. raddiana* trees have one stem, twice as large smooth leaves, and larger fruits than *A. tortilis* trees which have multiple stems, smaller hairy leaves and smaller hairy fruits. While the general shape of *A. tortilis* is of an upside down pyramid (Fig. 1c), *A. raddiana* has a round crown (Fig. 1d). There are also phenological differences in the timing of fruit ripening which starts earlier in *A. raddiana*.

This study was conducted in Wadi Sheizaf, a dry sandy ephemeral streambed in the northern edge of the Arava Valley, southern Israel (30.721222°N, 35.268366°E; elevation – 137 m a.s.l.) (Fig. 1a). Climate in the site is hot and dry; the 30-year average diurnal temperatures of the hottest and coolest months are 33.2 °C and 14.4 °C, respectively (Winters et al. 2018). The mean annual precipitation ranges 20–70 mm, and most of the rain events are local and strong, occurring within a short time and causing flash floods. Both *Acacia* subspecies—*A. tortilis* and *A. raddiana*—are distributed along the Sheizaf wadi at distances of 5–20 m between each other. Circumference of *Acacia* trees in this wadi ranged 60–100 cm (in the multi-stemmed *A. tortilis* this refers to the thickest stem) (Data not shown). Both subspecies have close to evergreen leaf canopy, with two annual flushing events (early March and late October) and a short shedding period in July (*A. raddiana*) or August (*A.*

¹ The genus (*Acacia*) was split into two different genera, *Vachellia* and *Acacia*. While the original name (*Acacia* = "thorn" in latin) has been reserved for the species in Australia (thornless), the new name, *Vachellia*, has been reserved for the species in the rest of the world (with thorns). However, most published studies and researchers continue to use the old name. We therefore chose to use the old genus name *Acacia*.

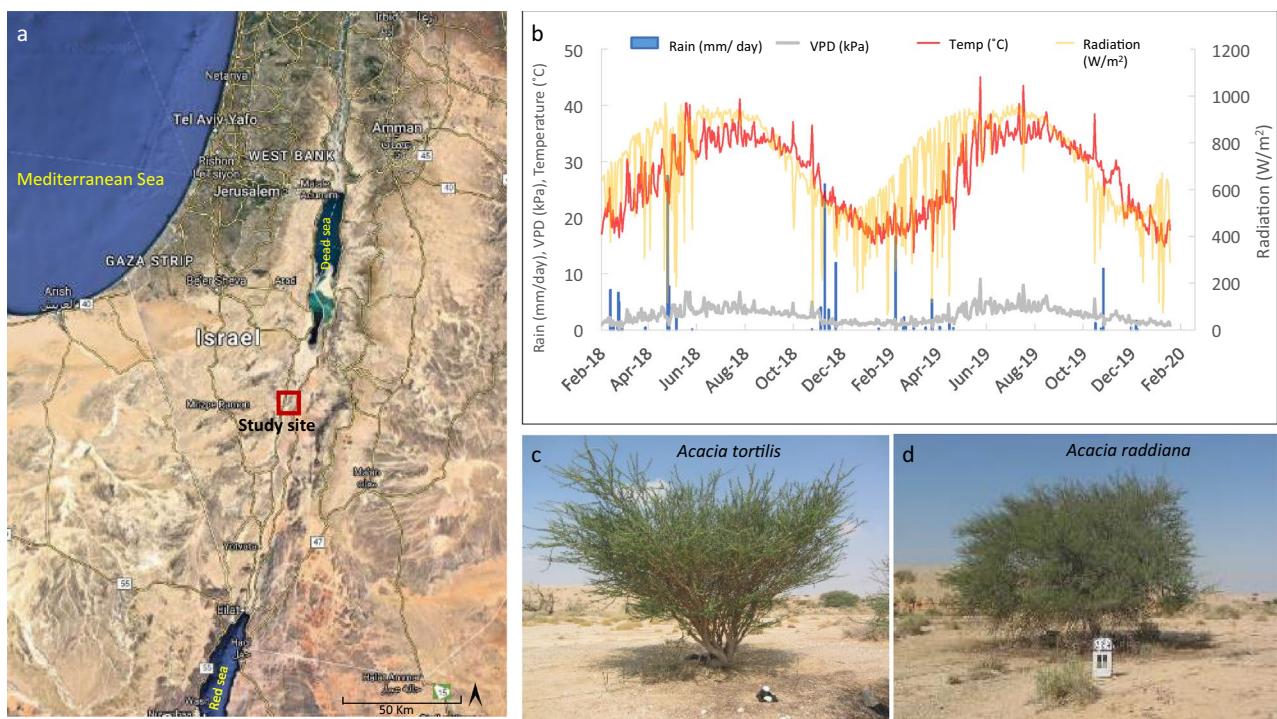


Fig. 1 **a** The Arava valley region (Israel) and the location of the study site (red square). **b** Rainfall and atmospheric conditions during the study period were recorded in Hatzeva meteorological station (7 km

north of the study site). Typical *Acacia tortilis* tree (**c**) and *Acacia raddiana* tree (**d**) in the study site

tortilis), however, shedding periods are water dependent, and can vary between years and drought periods (Winters et al. 2018). We selected five individual trees of each subspecies for monthly measurements of photosynthesis, stem growth, and NSC. Monthly measurement campaigns were carried out for two consecutive years (Jan 2018–2020).

Rate of photosynthesis

To examine seasonal and diurnal patterns of photosynthesis (via net CO_2 assimilation), each month we measured leaf gas exchange and stomatal conductance (g_s) at three time-points during the day—morning (one hour after sunrise), midday (solar noon when the sun reaches its highest position in the sky), and afternoon (two hours before sunset). At each daily time-point of each monthly measurement, we pruned two sun-branches from the south-facing side of the canopy and immediately transferred them in a controlled closed and humid box to the measuring system (2–5 min depending on transfer distance). From the pruned branches from each tree, we selected four fully developed leaves and measured their rate of photosynthesis and g_s using an Infra-Red Gas Analyzer (IRGA) photosynthesis system (GFS 3000, WALZ, Germany). Measurements of leaf net CO_2 assimilation in the IRGA chamber simulated open-air conditions (400 ppm CO_2 , air temperature, and relative humidity (RH) adjusted

according to ambient conditions at the time of measurement). Light conditions within the IRGA chamber were adjusted each time to the natural levels of PAR at the time of measurement (using the IRGA internal LED Light Source 3041-L LED array providing wavelength of 400–700 nm). The rate of photosynthesis ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was recorded after 3 min, once gas exchange in the chamber has stabilized. Leaves were then removed from the IRGA chamber and photographed with a known scale. Photographs were used to calculate leaf surface area (cm^2) using image J (Rasband 1997). We used the measured surface area of all measured leaves to standardize the rate of photosynthesis and g_s per unit of leaf area ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ of measured leaf s}^{-1}$). We calculated the maximum g_s value ($g_{s \text{ max}}$) for each month by the average of morning g_s which was the highest of the day consistently for the two measured years. Based on this value ($g_{s \text{ max}}$) we could reveal the percentage of stomatal closure at noon and afternoon times. For testing the effects of detaching the leaves we compared the measurements of detached leaves to measurements of the rate of photosynthesis *in-situ* in attached leaves, on autumn midday ($n=5$ attached and detached leaves for each of the two species, $N=20$). Although we found slightly higher photosynthetic rates in attached vs. detached leaves of *A. tortilis* (6.1 ± 1.8 and $4.6 \pm 1.03 \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively), this difference was not statistically significant. Almost no differences were

found between photosynthetic rates in attached and detached leaves of *A. raddiana* (7.0 ± 2.2 and $6.6 \pm 2.8 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, respectively). This indicated a negligible effect of leaf detachment and transfer.

Stem growth

We measured stem circumference continuously with automatic high-resolution radial dendrometers (DRL26, EMS, Brno, Czech Republic; (Urban et al. 2013)). These dendrometers measured circumference variations of up to $1 \text{ }\mu\text{m}$ resolution and logged hourly data into a built-in data logger. Dendrometers were installed on five *A. tortilis* trees and five *A. raddiana* trees. Data from dendrometers were used in two types of analyses: (1) diurnal stem growth (mm day^{-1}) during the given year; for this analysis readings were set to zero in Jan 2018 and again in Jan 2019; (2) seasonal stem growth (mm/season). For this, readings were set to zero at the onset of each season. This was followed by subtracting the value measured at the end of the season from the first value of the next season (Fig. 5b). Seasons were defined, for simplicity, as winter (1st January–31st March); spring (1st April–30th June); summer (1st July–30th September); and fall (1st October–31st December) (2018 and 2019).

Nonstructural carbohydrates in branches and roots

Plant materials for non-structural carbohydrate (NSC) analysis were sampled once a season for two years (in February, May, August, and November) from the same set of focal *A. raddiana* ($n=5$) and *A. tortilis* ($n=5$) trees. Branches (2–3 mm) were cut at 1–2 m height and fine roots (0.5–1.0 mm) were sampled at 10–50 cm depth. All plant materials were microwaved at a nearby village to stop further enzymatic activity, and then oven-dried at $60 \text{ }^{\circ}\text{C}$ for 48 h. Samples were then ground using a mortar and pestle and a ball mill (MM301; Retsch GmbH, Haan, Germany) until tissues turned into fine powder. NSC analysis was performed following protocols S1, S2, and S3 of Landhäusser et al. (2018) with minor adjustments. Shortly, $30 \pm 1 \text{ mg}$ of dry tissue was used for the extraction of soluble sugars and starch, using 80% ethanol at $90 \text{ }^{\circ}\text{C}$. Starch was later digested by α -amylase ($85 \text{ }^{\circ}\text{C}, 60 \text{ min}$) and amyloglucosidase ($55 \text{ }^{\circ}\text{C}, 30 \text{ min}$) enzymes (Sigma-Aldrich). Different NSC components (soluble sugars and glucose-hydrolysate) were detected and quantified using an analytical high-performance liquid chromatography (HPLC) system (Shimadzu Scientific Instruments, Kyoto, Japan) fitted with an Aminex HPX-87C Column ($300 \times 7.8 \text{ mm}$, $9 \text{ }\mu\text{m}$ particle, Bio-Rad, California, USA). Sugars separation occurred under the following conditions: $84 \text{ }^{\circ}\text{C}$ column temperature, water as mobile phase, 0.6 mL/min flow rate (according to manufacturer recommendations). Glucose, sucrose, and fructose standard curves

were used to quantify extracted and hydrolyzed NSC samples. All standards were purchased from Sigma-Aldrich (Sigma cat. 47,829, 47,289, and F2793, respectively).

Meteorological data

We used meteorological data to test the influence of environmental conditions on photosynthetic rates of *Acacia* trees in the field, including air temperature ($^{\circ}\text{C}$), relative air humidity (%), irradiance (i.e., light, W m^{-2}) and daily rainfall (mm day^{-1}) (Fig. 1b). We collected all data from the Israeli Meteorological Service (www.ims.gov.il) station in Hatzeva, 7 km north of the study site.

Thermal Infra-Red imaging

Thermal Infra-Red (TIR) images were taken in the field using a FLIR T1030sc camera (FLIR Systems Inc., Wilsonville, OR, USA), with 14-bit, 1027×768 -pixel resolution, 30 frame rate per second, accuracy of $\pm 1 \text{ }^{\circ}\text{C}$ or 1% of the temperature reading between 5 to $150 \text{ }^{\circ}\text{C}$, $7.5\text{--}14 \text{ }\mu\text{m}$ spectral range, 24.6 mm focal length, $21^{\circ} \times 28^{\circ}$ field of view and built-in 5Mpixel digital camera, adapted to the IR lens (technical data taken from the Manufacturer). In the April – September campaigns the camera was placed in a fixed position at a known distance (7 m) from an *Acacia tortilis* tree at the height of 1.5 m in 90° from the soil to capture a full image of the tree canopy. Values of relative humidity and air temperature were set for each image, based on the measurements from the nearby meteorological station. The emissivity was set to a value of 0.98, as recommended by Idso et al. (1969). TIR images were processed using FLIR ResearchIR Max software (FLIR Systems Inc., Wilsonville, OR, USA). Data represent the average of five different regions of the crown foliage and the stem.

Statistical analyses

We tested how the rates of photosynthesis in adult trees in the field are influenced by the species of *Acacia*, the month of the year, and daytime, and the interactions between these independent variables, using repeated-measures ANOVA (2 species, 24 months, 3 daytimes, 5 replicates per species). To test the influence of season on stem growth, photosynthesis, and NSCs concentrations we tested the correlation between seasonal growth and the seasonal photosynthesis and concentrations of starch and sugars reserves in stems and roots, using the same monthly composition for each season: winter (JFM), spring (AMJ), summer (JAS) and fall (OND), then we correlate the seasonal growth to the seasonal photosynthesis and starch and sugars reserves. Statistical analysis was performed using R (R Development Core Team 2006) and the interface R Studio, with packages nlme (linear and

Table 1 A comparison among alternative models for the effects of environmental variables on the rates of photosynthesis in adult *Acacia* trees in the field

Model	Effect variable	No. of parameters	AIC _c	Slope	R ²
1. Linear	Temperature	3	5126	1.000	0.004
2. Linear	RH	3	5130	0.999	0.000
3. Linear	VPD	3	5130	0.999	0.000
4. Linear	Light (PAR)	3	4803	0.999	0.259
5. Saturation	Temperature	4	5121	0.996	0.010
6. Saturation	RH	4	5132	1.000	0.006
7. Saturation	VPD	4	5122	0.995	0.009
8. Saturation	Light (PAR)	4	4778	0.999	0.277
9. Saturation with 0000interaction	Light (PAR) + Temperature	4	4913	0.999	0.182
10. Non-rectangular 0000hyperbola	Light (PAR)	4	4736	0.999	0.304
11. Non-rectangular 0000hyperbola	Light (PAR) and species	7	4720	1.001	0.319

nonlinear mixed-effects models; version 3.1) and car (companion to applied regression; version 3.0).

We used inverse modeling and maximum likelihood estimation to find the most parsimonious model of the effect of environmental variables (temperature, RH, VPD, and PAR) on photosynthesis, and the most likely set of parameters for this model, given our large empirical dataset (Johnson and Omland 2004; Sheffer et al. 2013, 2020). The inverse modeling approach is used to compare a set of alternative models (e.g., different functional forms) to test the strength of support for different hypotheses. We compared the following set of models representing alternative hypotheses for the effects of environmental factors on photosynthesis: (1) linear models, which test a continuous linear effect of each of the environmental variables alone (models 1–4). (2) Saturation models, which test a Michaelis–Menten type effect of each of the environmental variables alone, to take into account the biochemical limitation of photosynthetic enzymes (models 5–8). (3) Interaction models, which test a multiplicative effect of temperature on the saturating effect of PAR (model 5); and (4) non-rectangular hyperbola model, which tests the response of photosynthesis to PAR including the effect of light-saturation followed by photo-inhibition (model 10–11 in Table 1).

To understand the relative importance of each of the independent environmental variables, we searched for the most parsimonious grouping of environmental effects and different partial combinations of them, using model comparison methods. We compared the strength of evidence for a model that includes one set of parameters for the results of both species and a model with two species-specific sets of parameters. We solved for the maximum likelihood parameter values using simulated annealing in the “likelihood” package in R (Murphy 2012). Residuals (ϵ) for the different variables were normally distributed, so the error terms were modeled

accordingly. We compared alternative models based on the Akaike information criterion corrected for a small sample size (AIC_c) which allowed to find the most parsimonious model (lower AIC_c). To evaluate each alternate model, we calculated the slope and the R² of the regression of observed vs. predicted as measures of model bias and goodness of fit, respectively. All analyses were done using the R programming environment version 1.2.5033 (R Development Core Team 2006).

Results

Two years of monthly measurements in the field (Fig. 2a) showed that photosynthesis (net CO₂ assimilation) was low during the morning, peaked at midday (solar noon), and decreased again in the afternoon (average \pm SE values of 1.5 ± 0.06 , 5.0 ± 0.15 and 1.3 ± 0.07 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, respectively). The same diurnal pattern was found across seasons, including the dry and hot months of April–October (Fig. 1b). There was no significant difference in the rates of photosynthesis between the two subspecies of *Acacia* ($F_{1,22} = 0.145$, $p = 0.703$). There was, however, a significant difference in the rates of photosynthesis among daytimes ($F_{2,22} = 378.423$, $p < 0.001$) and months ($F_{11,22} = 5.215$, $p < 0.001$). Unexpectedly, the rates of photosynthesis were the highest during conditions of extremely dry and hot air (VPD = 4–6 kPa) and very high PAR intensities (1800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) (Fig. 2b).

During the two study years, air temperatures ranged 10–40 °C (Figs. 1b, 3), RH ranged 14%–65% and PAR ranged 100–1800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, with the highest values measured at midday during the summer (when the sun is in the northern hemisphere). At midday (solar noon) PAR varied from 800 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in the

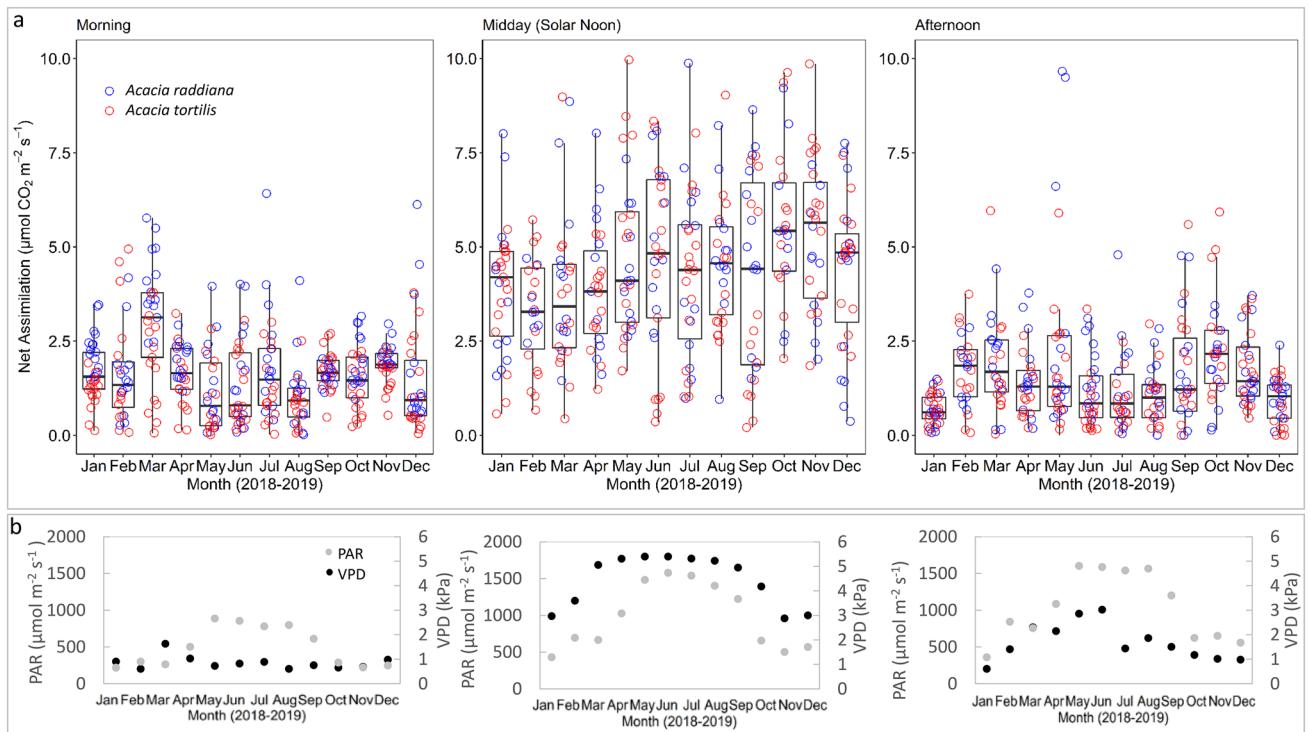


Fig. 2 **a** Two years dynamics of monthly rates of photosynthesis (net CO_2 assimilation) in adult *Acacia raddiana* (blue) and *A. tortilis* (red) trees in the field in the morning, midday (when the sun reached its highest position in the sky) and afternoon. Monthly measurements include two consecutive years. Each point represents one measuring

date and time of an individual tree ($n=5$ for each species; 24 measurement days). Boxplots represent first to third quantiles; the middle line represents the median. **b** Two years average of photosynthetically active radiation (PAR) and at the time of photosynthesis measurement

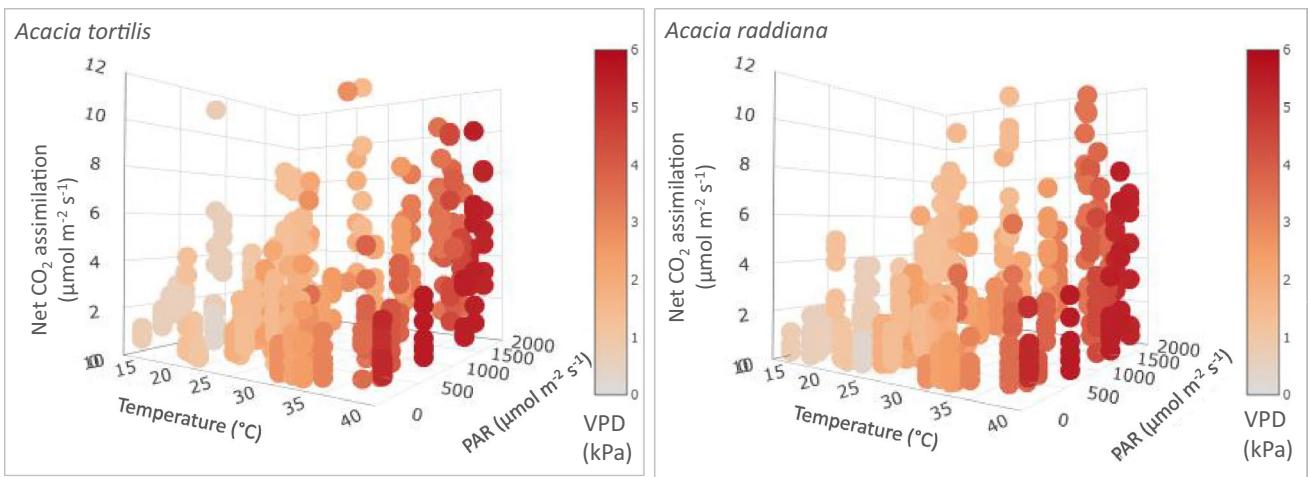


Fig. 3 **a** Rates of photosynthesis as a function of temperature, light (measured as photosynthetically active radiation; PAR), and vapor pressure deficit (VPD) in adult *A. raddiana* (top) and *A. tortilis* (bottom).

b A comparison among alternative models for the effects of environmental variables on the rates of photosynthesis in adult *Acacia* trees in the field

winter to $1800 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in the summer. At the same time, photosynthesis (net CO_2 assimilation) rates were $2-12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, which is two-fold higher compared to the rates measured during mornings and

afternoons. In both species, the rates of photosynthesis increased with temperature and PAR (Fig. 3). Thermal IR images show the mean temperatures of the tree leaves (foliage), tree stem, and the ambient air at 06:00 (morning)

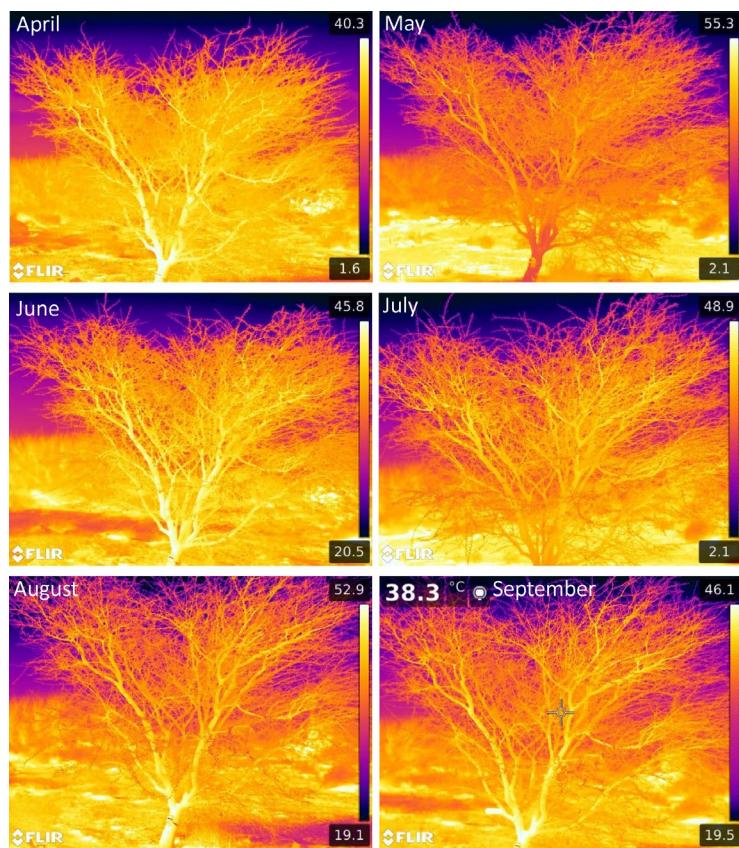


Fig. 4 Thermal infra-red (TIR) images at noontime in the hottest months in the hyper-arid site. Graphs show the mean \pm SE of the tree foliage temperature (green), tree stem temperature (brown) and the

ambient air temperature (blue, taken for metrological station) ($n=5$) at morning (upper plot) and noon (lower plot)

and 12:00 (noon) throughout the summer months (Fig. 4). Foliage noon temperature was similar to air noon temperature constantly, ranging from 30.7 °C in April to 39.3 °C in August (p value = 0.411). By contrast, the stem temperature was significantly higher than air temperature at noontime by 40% (p value = 0.001), ranging from 45.5 °C in April to 51.0 °C in June and 46 °C in September. Thus, the transpiring tissue (foliage) was able to cool-down itself to air temperature while the non-transpiring tissue (stem) was overheated (Fig. 4).

We used maximum likelihood estimation and model comparison to examine the effect of atmospheric variables (temperature, RH, VPD, and PAR) on the rates of photosynthesis in acacias (Table 1). Each model resulted in an AIC score, smaller AIC scores entailing the model explain better the results. The AICc scores in Table 1 showed greater support for models that included the effect of PAR (AICc scores 4803 and 4778 for models 4, 8 respectively). Models that included the effects of temperature, VPD, and RH were not parsimonious (higher AICc scores of 5126 and 5122 for models 1, 7 respectively). The most parsimonious model contained the effect of PAR only, using a non-rectangular

hyperbola, with a different set of parameters for each of the species (model 11, AICc = 4720; Table 1).

The continuous measurement of radial stem growth in our *A. tortilis* and *A. raddiana* trees (Fig. 5) showed that there were significant differences among seasons ($p=0.008$), while there were no significant differences between tree species ($p=0.411$). During the first year of measurements (2018) all the trees from both species grew with an annual average growth of 21.91 ± 2.09 mm in *A. tortilis* and 30.05 ± 3.004 in *A. raddiana*. In the second year (2019) growth was lower and occurred only in 70% of the trees, with an annual average growth of 12.62 ± 3.95 mm in *A. tortilis* and 11.04 ± 1.60 in *A. raddiana* (Fig. 5a). Despite the differences in growth between the years ($p < 0.001$), the seasonal timing of growth was similar. A first growth phase occurred in May, and a second phase in September. An analysis of seasonal stem growth showed that growth rates were higher during the hot summer and dry fall compared to winter in both species (74 and 89% of the annual growth for *A. raddiana* and *A. tortilis* respectively) (Fig. 5b).

We analyzed the seasonal dynamics of non-structural carbohydrate (NSC) and soluble sugars in the branches

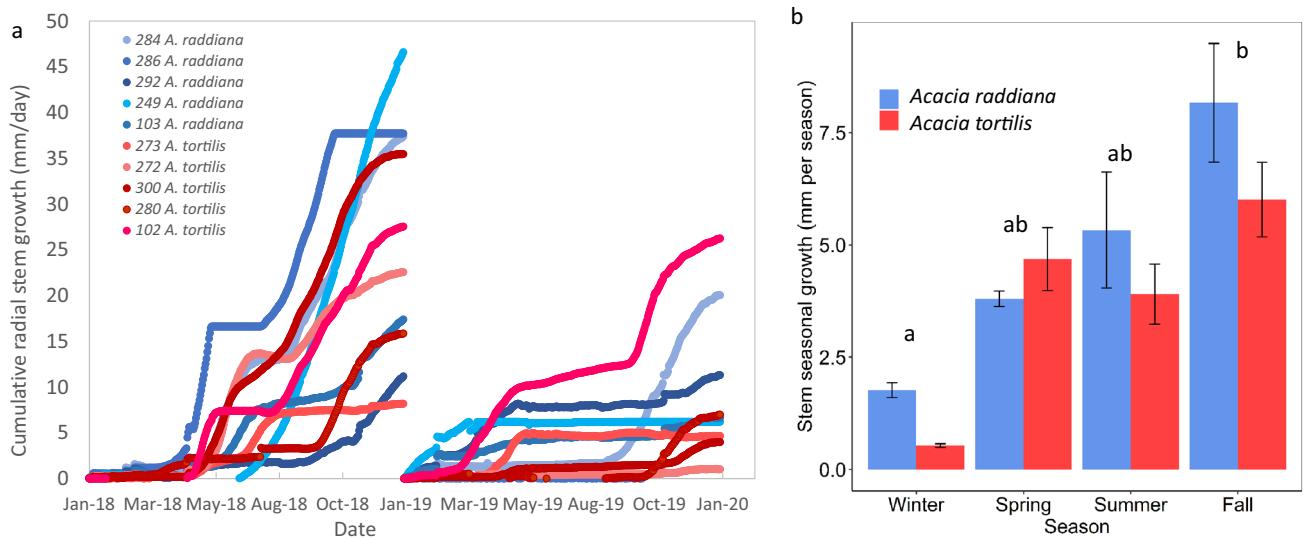


Fig. 5 a Adult *Acacia* stem growth in Wadi Sheizaf (Arava valley, Israel) in 2018–2019. Missing or truncated curves are due to sensor failures. **b** Two years average of seasonal stem growth by season. For each season all trees from the same species ($n=5$) were averaged.

Error bars represent SE. Groups were compared using Tukey's Honest Significance test; different letters above bars represent significant differences among seasons; $p < 0.05$. $n=5$ trees per subspecies

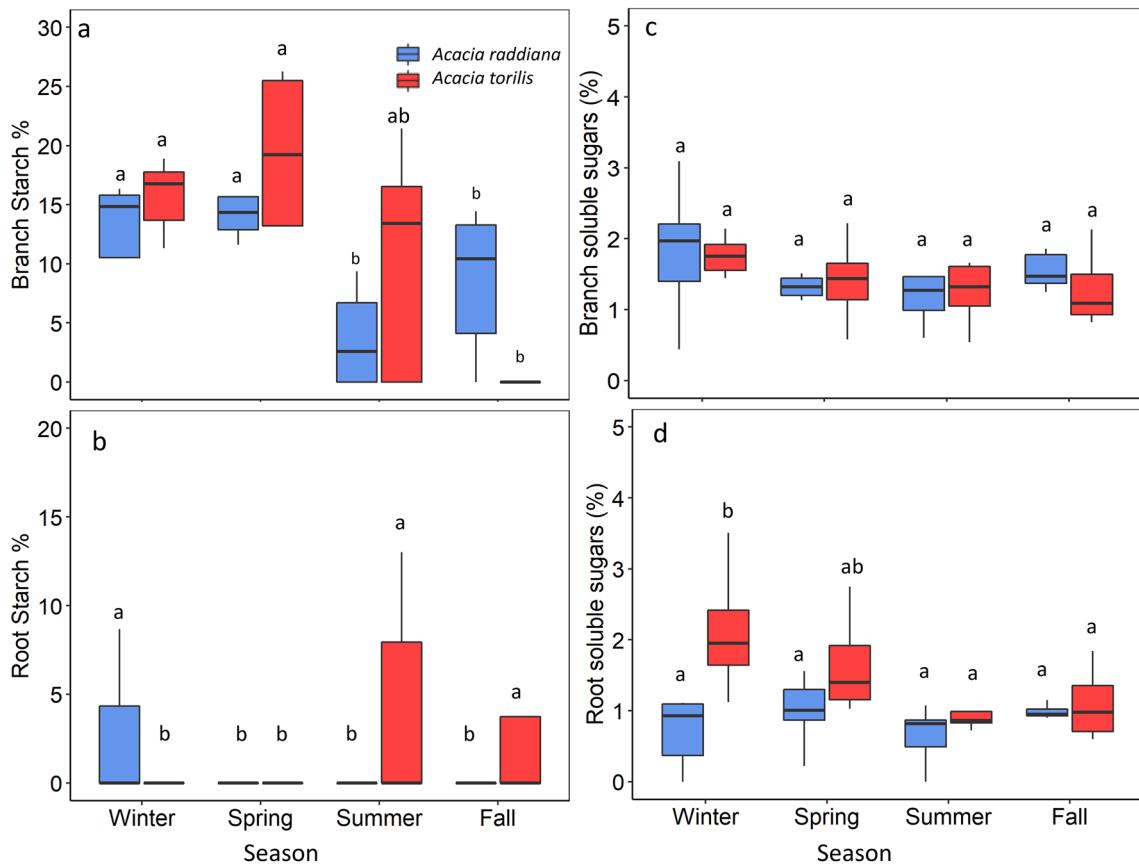


Fig. 6 Nonstructural carbohydrate (NSC) content (in percent of dry matter) in branches (**a, b**) and roots (**c, d**) of adult *Acacia raddiana* (blue) and *Acacia tortilis* (red). Boxplot represents the average of two years (2018–2019) ($n=5$ of each species). Groups were com-

pared using Tukey's Honest Significance test; different letters above boxplots represent significant differences among seasons and species; $p < 0.05$. $n=5$ trees per subspecies

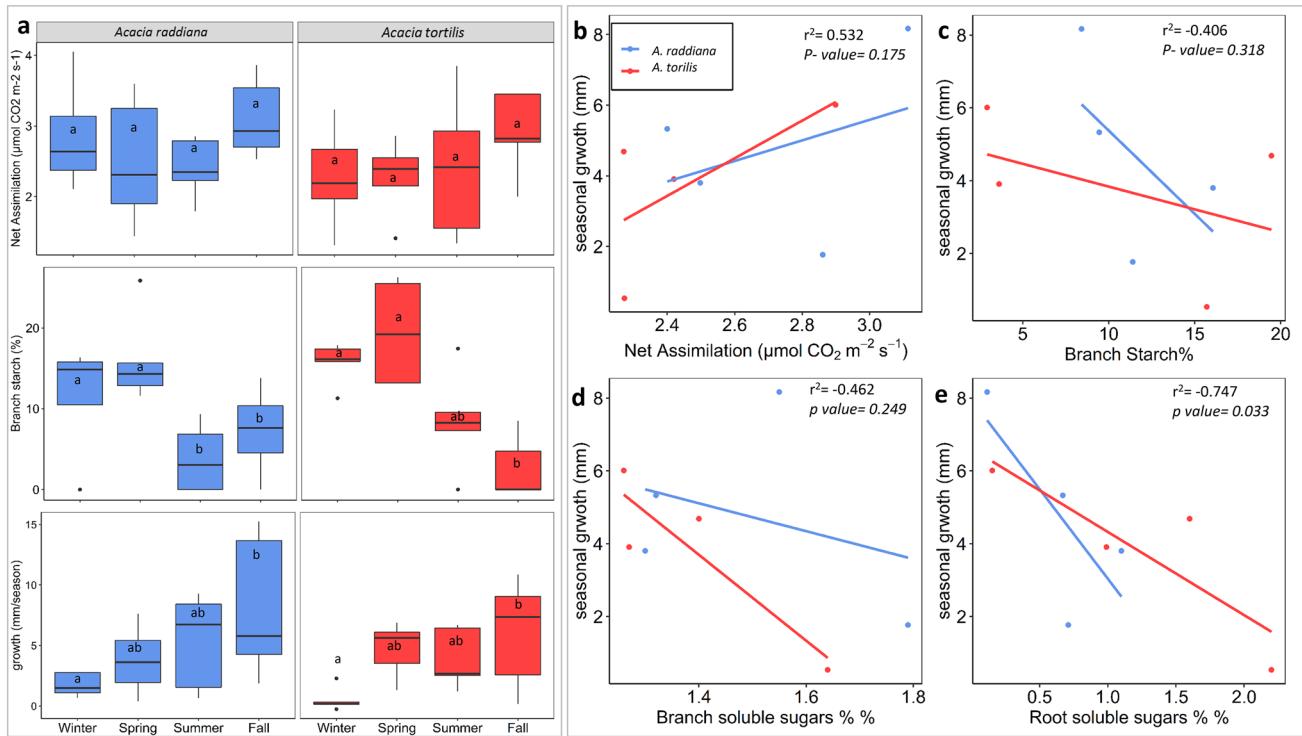


Fig. 7 **a** Seasonal patterns of photosynthesis, branch starch concentration, and the stem growth of adult *Acacia raddiana* (blue) and *Acacia tortilis* (red). Correlations between seasonal growth and photosynthesis (**b**), branch starch (**c**), branch sucrose (**d**), and root sucrose (**e**).

Groups were compared using Tukey's Honest Significance test; different letters above boxplots represent significant differences among seasons for each subspecies separately; $p < 0.05$. $n = 5$ trees per subspecies

and roots of the measured trees (Fig. 6). The concentration of starch in the branches was the highest in the winter and spring (16% in *A. raddiana* and 18% in *A. tortilis*) compared to the low levels in the summer and fall (8% in *A. raddiana* and 5.5% in *A. tortilis*) (Fig. 6a). In both species the concentrations of root starch reserves were low, less than 5% throughout the year (Fig. 6b). Examination of the concentrations of soluble sugars in the samples showed that 98% of them were sucrose (data not shown) and that glucose and fructose composed only 2% of soluble sugars. The concentration of soluble sugars in the branches was almost constant along the year (average of 1.5%) (Fig. 6c), while in the roots of *A. tortilis* they were higher in the winter (2%) and lower in fall (1%). No seasonal changes in the content of soluble sugars were found in *A. raddiana* roots (Fig. 6d). We evaluated how tree growth is related to the tree carbon reserves by analyzing on a seasonal scale photosynthesis, sugars reserves, and growth (Fig. 7a) and tested whether seasonal growth correlates with seasonal photosynthesis, and the concentrations of starch and soluble sugar reserves (Fig. 7b,c,d,e). Looking at the seasonal change in growth, photosynthesis, and starch percentage in the branches (Fig. 7a) shows that photosynthesis occurs all year round, starch in the branches is accumulated in the winter and spring and decreases in the summer, and tree growth begins in the spring and increase in

the summer and fall. We found a significant negative correlation between growth and soluble sugars in the roots (Fig. 7e; $r^2 = -0.747$): growth increased as root sugars decreased. Other correlations were not significant, probably due to the small sample size, yet hinted to a similar tradeoff between growth and NSC.

Discussion

Two years of photosynthesis (net CO_2 assimilation) measurements in adult *Acacia* trees measured in situ in their hyperarid habitat (Fig. 1) showed that the peak of photosynthesis was at midday in all seasons (Fig. 2a) when light intensities and VPD are at their maximum (Fig. 2b). Surprisingly, and against our hypothesis, the rate of photosynthesis was not influenced by the VPD, i.e., stomatal conductance was above $100 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ in high VPD ($> 4 \text{ kPa}$) (Fig. S1). This might be explained by the ability of *Acacia* trees to develop a wide and deep root system that allows them to reach deep soil water reservoirs year round (Do et al. 2008; Winters et al. 2018). Even after six months of a rainless summer with VPD of 4 kPa and more (Fig. 1b), we found no evidence for water stress in the studied trees, i.e., predawn measurements of leaf water potential ranged between -0.5

to ~ 0.9 MPa (data not shown). Peak of photosynthesis at midday in all seasons (Fig. 2) together with summer growth (Fig. 5) and cooling effect (Fig. 4) reinforce the claim that these trees are capable of reaching constant water source in the dry desert all year, as suggested previously by Winters et al. (2015) that showed the presence of a perched aquifer at a depth of ~ 7 –10 m in a nearby site.

Summer noon photosynthesis in an arid environment—unique for *Acacia*

The photosynthetic activity during noon time found in the current research (Fig. 2a) is opposed to the common activity pattern in dryland tree species, which minimize their gas exchange activity when exposed to high VPD (Klein 2014). For example, pine trees (*Pinus halepensis*) that grow in the semi-arid region of Israel, ~ 80 km NW of our site, exhibit noon assimilation that is higher only in fall and winter ($10 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and decreases to minimal activity during summer (0 – $1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Maseyk et al. 2008). In addition, the diurnal curve of CO_2 assimilation during the dry season for these pine trees shows a morning peak ($3 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) followed by a midday depression and a smaller afternoon peak ($1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) (Klein et al. 2016). Another example of minimizing activity at high VPD was demonstrated in *Eucalyptus globulus* trees that grow in a semi-arid site in Portugal. CO_2 assimilation of those trees was highest ($12 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in the spring, reduced in the winter, and strongly depressed by the middle of the summer when severe drought conditions prevailed (Pereira et al. 1986). Olive trees in Spain partially close stomata before noon to reduce leaf photosynthesis, in spring, summer and autumn. Midday stomatal closure appears to be related mainly to VPD and air temperature (Gimenez et al. 1996). *Ziziphus spina-christi*, a desert tree that grows in our site, exhibited maximum photosynthesis during the spring (VPD = ~ 2.5 kPa), declined photosynthesis during the summer (VPD = ~ 4 kPa) and slightly increased photosynthesis during the fall (VPD = ~ 3 kPa) (Zait and Schwartz 2018). In comparison, *Acacia* trees seem to stand out in their ability to keep their stomata open even in the middle of a hot summer day in the dry desert (Fig. S2). During summer noon (June–September), g_s values remained high (48% of the measured $g_{s \text{ max}}$), while in the afternoon (two hours before sunset), stomata closed to 10% of $g_{s \text{ max}}$ due to reduced PAR. Keeping the stomata open enables assimilation of CO_2 during noontime across seasons as shown in Fig. 2a and Fig. 7a. This unique behavior can be explained by the cooling effect hypothesis: When water is transpired, evaporative cooling of the leaves occurs (Crawford et al. 2012; Lapidot et al. 2019; Aparecido et al. 2020). To cope with high temperatures of 40°C and occasional heat waves when temperatures reach 47°C , transpiration aids in cooling the *Acacia*. Evaporative

cooling can take effect in the desert acacias given that they have access to deep-water reservoirs and therefore are not exposed to severe water stress, and do not shut their gas exchange activity (Fig. 2, Fig. S1, S2). Comparing the foliage, stem, and the air temperatures validated that the tree cools via transpiration at the hottest hours (12:00). The results indicated that indeed during noontime the tree foliage temperature and the air temperature were significantly similar (Fig. 4), measuring up to 15°C cooler than the stem surface. Such evaporative cooling is exceptional for a broadleaf tree species, and is more typical of conifer needles (Lapidot et al. 2019). Another optional hypothesis to explain the high gas exchange and photosynthesis relates to nitrogen fixation ability of the trees. *Acacias* associate with dinitrogen-fixing rhizobia via root symbiosis, and therefore increase the concentration of nitrogen in the leaves (Sprent 1995). High contents of nitrogen in the leaves can support higher concentrations of chlorophyll, therefore sustaining efficient photosynthesis (Adams et al. 2016). In addition, dinitrogen-fixing bacteria in the root system can be a large sink for carbon, in turn increasing the demand for photosynthates.

High light and temperature resistance in *Acacia* trees

Another surprising finding of this research is that the predominant environmental factor that limited photosynthesis was light (PAR) (Fig. 3, Table 1). Why would light be a limiting factor in a desert environment with almost year-round light availability? It is known that high PAR intensities of above $1300 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ can cause photooxidative damage to the photosynthetic apparatus (Barber and Andersson 1992; Long et al. 1994; Müller et al. 2001; Murchie and Niyogi 2011; Takahashi and Badger 2011; Treves et al. 2016). However, the trees in our field are exposed to $\sim 1800 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ in the summer, and together with the light reflected by the white desert soil desert (Stern et al. 2020) acacias experience high PAR intensities, far beyond the photo-inhibition threshold known for most trees. We assume that the *Acacia* trees have developed a defense mechanism to protect themselves from photo-damage. Therefore we suggest the potential existence of a “defense layer” (which is still unknown) that decreases the actual PAR intensity for the surface of the leaves. In this scenario, the leaves are “starving” for photons, and higher PAR is needed for photosynthesis. More research is needed to elucidate the mechanism that allows exceptional light tolerance in *A. raddiana* and *A. tortilis*. In turn, this knowledge can serve to design improved plant varieties, e.g., new light-tolerant crops and timber trees.

High tolerance to heat is also needed to survive the hyper-arid conditions, as high temperatures may lead to direct thermal damage or mortality (O’sullivan et al. 2017). Extreme

temperatures combined with long drought have been associated with tree mortality in forests (Allen et al. 2015). However, the *Acacia* trees in this study grow and thrive under regularly high temperatures (Figs. 1, 3). We suggest that the tolerance of desert acacias to heat is related also to their small leaf and leaflet sizes: the surface area of ~ 200 leaflets is $2.05 \pm 0.05 \text{ cm}^2$ in *A. raddiana* and $1.12 \pm 0.04 \text{ cm}^2$ in *A. tortilis*, contributing to leaf thermal regulation through tight coupling with air (Givnish and Vermeij 1976; Ackerly et al. 2002; Wright et al. 2004). In addition, the bipinnate leaf structure results in high surface area of the canopy. Increased thickness of the boundary layer of the canopy allows more turbulent wind flow through the canopy which causes better heat transfer via convection (Ackerly et al. 2002; Leigh et al. 2017). Generally, the small leaves of the *Acacia* are advantageous in hot and dry environments and at high intensities of solar radiation (Niinemets et al. 2007; Tozer et al. 2015), as found also in Okajima et al. (2012) that showed how in warm environments the rate of photosynthesis per unit leaf area increases with the decrease in leaf size.

Carbon dynamics in *Acacia* trees

In our desert acacias, most stem growth occurred during the summer (hottest months) and fall (driest months) (Fig. 5b). These results are in agreement with a previous study on these trees that showed that cambial growth was arrested during the wet season and occurred during most of the dry season (Winters et al. 2018). Here we examined whether this summer growth is based on the use of carbon reserves rather than assimilated carbon. Although other C sinks exist (respiration, fruit production, etc.), the source-storage-growth relationships studied here still represent intrinsic tree C management. Seasonal dynamics of NSC have been studied extensively in many forest ecosystems, however, there is almost no data on the dynamics of C reserves in *Acacia* species (Wigley et al. 2009; Ward 2016) and even less data on NSC in mature *Acacia* trees in the desert. We found high concentrations of starch in the branches (up to 20% in the winter and spring). The seasonal patterns of the concentrations of starch, stem growth, and photosynthesis (Fig. 7a) showed that starch accumulated primarily in the winter and spring and later decreased in the summer. Tree growth started in the spring and increased in the summer and fall, while photosynthesis was almost constant throughout the year. Based on these findings we suggest that the carbon that is assimilated during the winter is stored in the branches as starch reserves which later on drives tree growth in the summer. Still, most biomass was produced during summer, and moreover during fall, probably using concurrent assimilate. High levels of starch may explain why *Acacia* branches and leaves are the main source of food for elephants and giraffes in the African savanna (Lamprey et al. 1974; Pellew 1983).

That said, and despite belonging to the same species, starch concentration in *Acacia* trees in the Arava doesn't necessarily represent the starch levels in the African *Acacia* trees. At our site, *Acacia* is a major food source for gazelles (*Gazella dorcas*), among other species.

A. raddiana and A. tortilis comparison

Although the *A. raddiana* is considered a subspecies of *A. tortilis* (Wickens et al. 1995), in this paper we examined them as two different species as suggested in our regions due to visible morphological differences that might affect their ecophysiology. For example, *A. raddiana* trees have one stem, twice as larger smooth leaves, and larger fruits, while *A. tortilis* trees have multiple stems, smaller hairy leaves and smaller hairy fruits. There are also phenological differences in the timing of fruit ripening which starts earlier in *A. raddiana*. In terms of photosynthesis, stem growth, NSC and sugars, we found only slight but non-significant differences between the species. Stem growth was higher in *A. raddiana* compared to *A. tortilis* in all seasons except for springtime (when *A. tortilis* trees grew 1.8 mm more). The dynamics of starch concentrations in the branches differed between the two species, as in *A. raddiana* concentrations were lower in the summer and higher in the fall, compared to *A. tortilis* (Figs. 6a, 7a). This observation can be explained by the time of fruit development that starts early (June) in *A. raddiana* and later (August) in *A. tortilis*. Flowering and fruit formation are known as carbon-demanding processes and therefore can explain the earlier decrease in starch reserves in the branch in *A. raddiana* compared to *A. tortilis*.

The current study highlights some of the gaps concerning *Acacia* trees and their carbon use in hyper-arid deserts. Understanding the diurnal and seasonal changes in temperature, radiation and VPD, and how they influence CO₂ assimilation, NSC and growth provides us with a good study case for tree ecophysiology in extremely dry and hot conditions. Such conditions are predicted to be more prevalent in the coming decades (Vicente-Serrano et al. 2010; Pachauri et al. 2014). These findings suggest a strong potential for *Acacia* trees to contribute to ecosystem carbon sequestration in warming and drying climates.

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Declarations

Conflict of interests Authors declare no competing interests.

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