



Tree growth and water-use in hyper-arid *Acacia* occurs during the hottest and driest season

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Abstract

Drought-induced tree mortality has been recently increasing and is expected to increase further under warming climate. Conversely, tree species that survive under arid conditions might provide vital information on successful drought resistance strategies. Although *Acacia* (*Vachellia*) species dominate many of the globe's deserts, little is known about their growth dynamics and water-use in situ. Stem diameter dynamics, leaf phenology, and sap flow were monitored during 3 consecutive years in five *Acacia raddiana* trees and five *Acacia tortilis* trees in the Arid Arava Valley, southern Israel (annual precipitation 20–70 mm, restricted to October–May). We hypothesized that stem growth and other tree activities are synchronized with, and limited to single rainfall or flashflood events. Unexpectedly, cambial growth of both *Acacia* species was arrested during the wet season, and occurred during most of the dry season, coinciding with maximum daily temperatures as high as 45 °C and vapor pressure deficit of up to 9 kPa. Summer growth was correlated with peak sap flow in June, with almost year-round activity and foliage cover. To the best of our knowledge, these are the harshest drought conditions ever documented permitting cambial growth. These findings point to the possibility that summer cambial growth in *Acacia* under hyper-arid conditions relies on concurrent leaf gas exchange, which is in turn permitted by access to deep soil water. Soil water can support low-density tree populations despite heat and drought, as long as recharge is kept above a minimum threshold.

Keywords *Acacia raddiana* · *Acacia tortilis* · Leaf phenology · Sap flow · Desert · Global warming · Tree drought resistance · Arava

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Introduction

Drought-induced tree mortality has been increasing in recent decades (Klein 2015; Anderegg et al. 2016), and is expected to increase further due to global warming and desertification, especially in already dry ecosystems (Steinkamp and Hickler 2015). Conversely, tree species which already survive under arid conditions could provide vital information on successful drought resistance strategies (Schwinning and Ehleringer 2001). Indeed, there is growing interest to elucidate some of these strategies, as demonstrated by recent studies on *Tamarix* and *Populus* in the Taklamakan desert (Gries et al. 2003; Lang et al. 2016) and *Prosopis* in the Atacama desert (Garrido et al. 2016). Water scarcity and high temperatures often interact to exacerbate drought stress on tree physiology (Ruehr et al. 2016). Hence, resolving tree drought resistance strategies, and specifically in arid environments, is a major interest of scientists and stakeholders alike (Hartmann et al. 2015; Cobb et al. 2018). In deserts, trees such as *Acacia*,

Tamarix, *Populus*, and *Prosopis* are often the only woody species, and as such, they are considered keystone species (Ward and Rohner 1997). Successful desert trees are essential locally for their associated ecosystems and important globally for their unique eco-physiology.

Among living tree species, *Acacia raddiana* and *Acacia tortilis* (the genus name changed to *Vachellia*¹) inhabit some of the hottest and driest places on Earth. These *Acacia* trees are major components of savannas and open woodlands in many arid regions of Africa and the Middle East (Maslin et al. 2003). Within the arid Arava valley, along the Syrian–African transform (Great Rift valley) in southern Israel and Jordan, *A. raddiana* and *A. tortilis* are the two most abundant and, in many places, the only tree species present (Danin 1983). In these arid habitats, *Acacia* trees are found mostly growing in the channels of ephemeral river beds (“wadis”, a term from Arabic; Ward et al. 1993; Munzbergova and Ward 2002). Here, both *A. raddiana* and *A. tortilis* are considered keystone species that support the majority of the biodiversity surrounding them and locally improve soil conditions for other plant species (Milton and Dean 1995; Ward and Rohner 1997; Munzbergova and Ward 2002).

Although *Acacia* species dominate many of Earth’s hottest and driest deserts, little is known about their growth dynamics in situ. Some knowledge of related eco-physiological parameters does exist but not for *Acacia* trees growing in situ and in arid environments. Water relations were studied extensively for *A. tortilis*, but not in hyper-arid conditions; for example, Do et al. (2008) studied water-use of *A. tortilis* in the northern Sahel, where annual rainfall ranged between 146 and 367 mm. Ludwig et al. (2003) studied hydraulic lift in *A. tortilis* trees on an East African savanna where the climate is tropical seasonal (650 ± 272 mm year⁻¹). Studies by Otieno et al. (2003, 2005a) were based on seeds that were collected in Kenya but brought back to Germany where they were germinated and grown under controlled conditions. Both Otieno et al. (2005b) and Do et al. (2008) showed the high drought resistance of this species, including physiological and morphological adaptations, in semi-arid environments, which do not represent the real extreme environments that some Acacias can tolerate. In the more arid

Eastern Desert of Egypt (North Africa), wood anatomy of *A. raddiana* was studied using ¹⁴C, due to the lack of annual tree-rings (Andersen and Krzywinski 2007). In the Arava valley of Southern Israel, *A. raddiana* cambial activity was studied in seedlings and in shoots of mature trees (Fahn et al. 1968; Arzee et al. 1970). Several other studies have tried to address the challenging task of identifying water source(s) sustaining *Acacia* populations in the Arava. This topic has drawn particular attention, especially following mortality events due to consecutive drought years in the 1980s (Peled 1988; Shrestha et al. 2003). Based on the dynamics of *A. raddiana* shoot water potential across sites and seasons, it was suggested that surface floods are the major water source for populations in the Arava (Shrestha et al. 2003). Such a strategy is typical of pulse-driven arid ecosystems (Schwinning and Ehleringer 2001). Studying the water source for *Acacia* trees in situ has been done by exposing their root systems (Peled 1988), comparing the ¹⁸O/¹⁶O isotopic ratios in water samples extracted from *Acacia* twigs and from nearby water sources (Sher et al. 2010), and using Electrical Resistivity Tomography (ERT; Winters et al. 2015). Yet, none of these studies monitored in situ *Acacia* growth and water-use in stems and leaves to observe their temporal dynamics and relationships to local meteorological conditions.

Here, we aimed to decipher the eco-physiological dynamics of both *A. raddiana* and *A. tortilis*, the dominant tree species in the hyper-arid regions of North Africa and the Middle East, as a case of tree growth at the hot and dry extreme. We hypothesized that stem growth and other tree activities are synchronized with rainfall or flashflood events. We took advantage of state-of-the-art monitoring technologies, and used a high-resolution, long-term, and continuous observation approach. Electronic dendrometers, sap flow sensors, and phenology cameras were connected to individual trees, to produce an accurate and detailed representation of *Acacia* survival and growth in one of Earth’s most hostile environments.

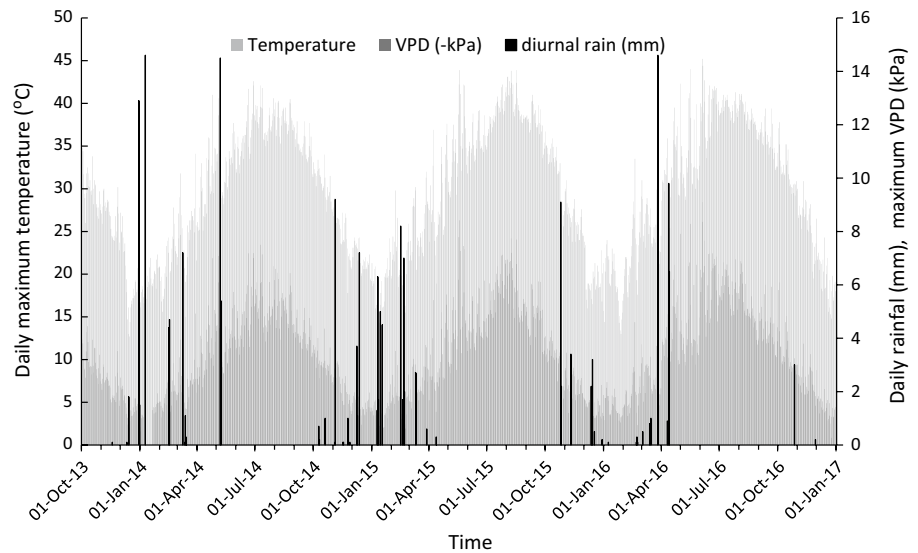
Materials and methods

Site and climate

Our study was conducted in Wadi Sheizaf, a dry sandy streambed at the northern edge of the Arid Arava Valley, southern Israel (Fig S1; 30°44’N, 35°14’E; elevation 137 below sea level). Meteorological data were obtained from the Israeli Meteorological Service for station 340528 in Hatzeva, located 7 km north of Wadi Sheizaf. The climate here is hot and dry: 30-year average minimum, mean, and maximum temperature of the hottest month were 26.2 °C, 33.2 °C, and 40.2 °C, respectively; average minimum, mean, and maximum temperature of the coolest month was recorded

¹ The genus (*Acacia*) was recently split (Kyalangalilwa et al. 2013) into two different genera, *Vachellia* and *Acacia*. While the original name (*Acacia* = “thorn” in latin) was reserved for the Australian (thornless) *Acacia* trees, the new name, *Vachellia*, was reserved for the *Acacias* from the rest of the world, with thorns. Searching the web science for scientific papers published from 2015 to June 2016 showed that only 2.6% from the 346 *Acacia* papers published during this period chose to use the new name. A short survey among Israel’s botanists also demonstrates that it is preferable to continue to use the genera name *Acacia* (see for example Winters et al. 2015; Nothers et al. 2017; Rodger et al. 2018). For these reasons, we chose to use the genera *Acacia*.

Fig. 1 Meteorological conditions at Hatzeva, 7 km north of Wadi Sheizaf (Arava valley, Israel; Fig. S1) in 2014–2016. During the 3 observation years, there were 77 days when temperature was $> 40\text{ }^{\circ}\text{C}$, 26 days when vapor pressure deficit (VPD) was $> 7\text{ kPa}$, and only 4 days when rainfall was $> 10\text{ mm}$



as $9.1\text{ }^{\circ}\text{C}$, $14.4\text{ }^{\circ}\text{C}$, and $19.6\text{ }^{\circ}\text{C}$, respectively, and annual precipitation of only 20–70 mm is restricted to the period between October and May (Fig. 1). Multiple individual trees of *A. raddiana* and *A. tortilis* are scattered throughout the wadi, but never forming a continuous canopy (Fig. S1).

Stem growth

Stem circumference was measured continuously with automatic high-resolution radial dendrometers (DRL26, EMS, Brno, Czech Republic; Urban et al. 2013). These dendrometers measured circumference variations of less than $1\text{ }\mu\text{m}$ and logged the data into a built-in memory once per hour. In October–November 2013, dendrometers were installed on four *A. raddiana* trees, followed by two *A. tortilis* trees in April–June 2014. Later, in 2014, this setup was increased to five *A. raddiana* trees and six *A. tortilis* trees. Basal stem circumferences of the five *A. raddiana* trees were 111 cm, 129 cm, 47 cm, 104 cm, and 165 cm, and those of the six *A. tortilis* trees were 38 cm, 52 cm, 38 cm, 34 cm, 44 cm, and 51 cm. To ensure that circumference variations were not affected by the frequent temperature and radiation gradients, a 12th dendrometer was installed on a dead *A. raddiana* tree in December 2015. This dendrometer showed minimal changes, confirming the robustness of the dendrometer sensor. In the data analysis stage, all dendrometer values were set to zero on January 1st of each year. Tree-specific dendrometer data were used in four types of analyses: (1) diurnal stem growth (mm) during a given year, produced by zeroing readings on January 1st of each year; (2) relative stem growth (between 0 and 1), produced by dividing the values in (1) by the tree-specific total annual growth; (3) stem growth rate (mm day^{-1}), produced by subtracting the values in (1) from the values of the following day; (4)

diurnal stem circumference variations (mm), produced by plotting the readings at hourly temporal resolution, and zeroing at midnight of each day.

Sap flow

Sap flow has been monitored continuously in six of the study trees (two *A. raddiana* and four *A. tortilis* trees) since November 2015. Thermal dissipation sensors ($n=6$) prepared in workshops at the University of Bayreuth (Germany) and at ARO Volcani center (Israel) were installed in the lower 30 cm of the stem, below the lowest branches, in the outer 2 cm of xylem, and connected to data loggers (CR1000, Campbell Scientific, UT, USA; and DL2e, Delta-T Devices, Cambridge, UK) and constant current power supplies. Probes were insulated by filling aluminum foil wraps tied around the stems and probes with polyurethane foam. Power was from solar charged 12 V car batteries. Sap flow measurement and analysis followed Granier and Loustau (1994). Stem circumference, which averaged 44 cm, was used to calculate sapwood area for each tree, assuming a linear decrease in flux density with depth, as described in Paudel et al. (2013) and Kanety (2014). We estimated zero flux to be 5 cm into the xylem, as found for many broad-leaf, diffuse-porous tree species (Cohen et al. 2008). Sap flow (L h^{-1}) was calculated assuming zero flux at times of maximum temperature differentials measured during the 24 h period, which was typically found predawn. No further calibration factor was applied.

Foliage dynamics

To follow changes in tree phenology, all study trees (5 *A. raddiana* and 6 *A. tortilis*) were photographed monthly in

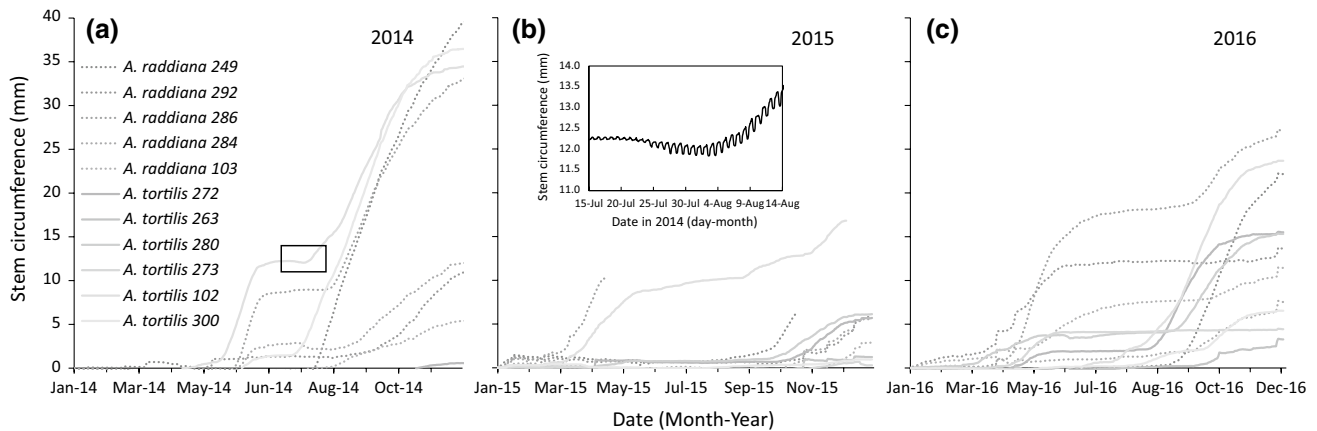


Fig. 2 *Acacia* stem growth in Wadi Sheizaf (Arava valley, Israel) in 2014–2016, **a–c**, respectively. Missing or truncated curves are due to measurement failures. Inset figure in **b** shows a zoom in on *A. tortilis* 102 during 15 July–15 August 2014 (see rectangle on the seasonal

curve of summer 2014). Most of the cambial growth occurred in May–June and August–November, coinciding with some of the hottest and driest days

Wadi Sheizaf under natural irradiances. Photographs were taken between January 2016 and December 2016 from a marked spot and at consistent height and angle (from south to north, using the digital compass within the camera) and using a single camera (Nikon AW110, Japan). Photographs included a Kodak grey scale in the image, which was used for testing the effect of different time of day/season on color intensity.

Photographs were analyzed in R (R core Team 2013) using the recently described Phenopix (Filippa et al. 2016), an R package that allows for the extraction of phenological information from time-lapse digital photography of vegetation cover. A region of interest (ROI) was drawn onto an imported image and used to extract Red (R), Green (G), and Blue (B) (RGB) digital numbers (DN—range between 0 and 254), which allowed us to depict the greenness index (intensity of the Green channel/Red + Green + Blue) represented by the Green Chromatic Coordinate (GCC—range between 0 and 1). The ROI in Phenopix (Filippa et al. 2016) represented vector locations allowing for images that were taken from the same exact location/distance and angle to be automatically assessed for the same ROI, allowing us to process hundreds of images within minutes. To ensure that the dynamics of GCC of the trees showed real changes, we calculated the GCC of the grey patch [grey 182 (R = G = B = 182)] of the Kodak grey scale (Fig. S2). As the grey scale was placed at different locations of the images, the analysis was performed manually in ImageJ. To analyze the seasonal dynamics of the GCC, we fitted a generalized additive model (GAM) (Hastie and Tibshirani 1990). A GAM is a non-linear additive model that describes the relationship between the predictor and the response variable as a smooth function. We fitted different smoothing functions per species and allowed for random differences between trees.

Results

Acacia stem growth dynamics

Annual increments in *Acacia* stem circumference were between 0 and 40 mm, with large variations between individual trees and different years (Fig. 2). Differences between individual trees were not related to stem diameter (correlation $r^2 < 0.01$), i.e., trees with large annual increments included both larger and smaller individuals. There were no clear differences in stem growth between *A. raddiana* and *A. tortilis* trees. Stem growth in 2015 was smaller than in 2014 and 2016 (Fig. 2). In 2014 specifically, four of eight monitored trees grew > 30 mm, an annual increment that did not recur in the consecutive years. Stem growth was highly seasonal, with fast increments during May–June and again in August–November, and close to zero growth in December–April and in July. Interestingly, growth was decoupled from rainfall or flashflood events (Fig. 1), which are also restricted to November–April. Instead, trees were actively growing mostly when daily maximum temperature was > 27 °C, and up to 45 °C (June 2016). Except for the growth arrest in July, most of the annual stem increment was completed during such hot and dry days, with vapor pressure deficit (VPD) of up to 9 kPa, a combination of the very high air temperature and a very low relative humidity value of 6%. Except for a few days per year, stem circumference changes reflected growth per se and not elastic water-induced changes, typically identified by stem swelling and shrinking. For example, *A. tortilis* 102 showed a 0.2 mm decrease during late July 2014 (Fig. 2, inset), which was in turn dwarfed by a continuous increase of 22 mm during the following months.

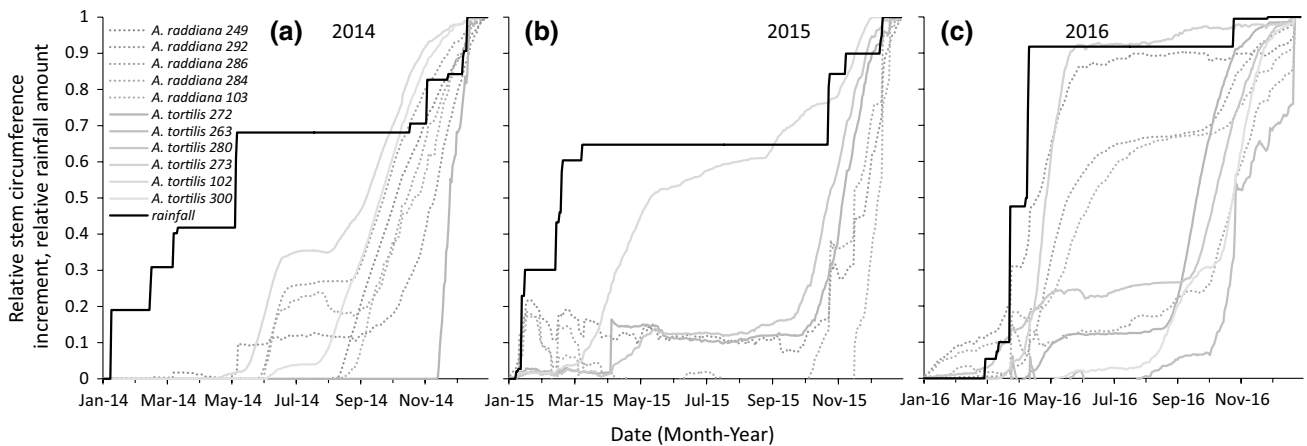


Fig. 3 Cumulative relative rainfall amount and *Acacia* stem growth in Wadi Shezaf (Arava valley, Israel) in 2014–2016, **a–c**, respectively. Missing or truncated curves are due to measurement failures. Curves

represent the fraction of the annual total stem increment per tree or rainfall amount

To test the sensitivity of stem growth to rainfall, relative growth curves and the cumulative rainfall amount (fractions of the annual totals) were superimposed (Fig. 3). In 2014 and 2015, stem growth took place mostly in spring and autumn, months after the majority of the rainfall amount had already been precipitated. However, in 2016, stem growth onset in many trees seemed to synchronize with the rain events (Fig. 3c). It is not clear whether the apparent co-occurrence in 2016 was the result of the delayed rains, or the earlier growth, compared to the two preceding years. In most trees and across the years, stem growth onset was usually not before 40% of the annual rain water input. However, overall, precipitation patterns alone could not sufficiently explain stem growth trends, such as the growth enhancement in August 2014 in most trees and the lack of growth before autumn 2015 despite the winter rains. Interestingly, the studied trees showed almost no stem shrinkage, which is often observed in dendrometry during periods of sub-optimal conditions (Chan et al. 2016; Zweifel et al. 2016). On an hourly scale, the diurnal stem circumference variations showed the expected daytime shrinking and nighttime swelling (Fig. S3), reflecting the changes in plant tissue water potential during the day (Steppe et al. 2015). The diurnal amplitude was ~ 0.3 mm during the growing season and < 0.1 mm outside the season (Fig. S3). *A. raddiana* had slightly larger amplitudes than *A. tortilis*.

The diurnal stem circumference increment was typically between 0 and 0.4 mm (Fig. 4). Short-term spikes of up to 1 mm day^{-1} were mostly related to tissue swelling during rain events, and, hence, do not represent growth per se. In each of the 3 study years, there were roughly two growth periods, separated by two no-growth periods, in peak winter and peak summer, respectively. 2014 had the highest growth rates, but 2016 had the longest growth

season, stopping only for periods of 5–20 days in February, April, August, and December (Fig. 4c). Summer growth was recorded in all 3 years in June, in July 2016, and in August 2014 and 2016. Among species, growth rates were mostly higher in *A. tortilis* in 2015, and in *A. raddiana* in 2016.

Plotting stem growth rate against meteorological conditions yielded no clear relationships, and hence, correlations were not significant (Fig. 5). Yet, it was clear that: (1) growth was not higher during rainy days; (2) most *A. raddiana* growth peaks followed rainy days, but were not related to rainfall amount; (3) growth of *A. raddiana* and *A. tortilis* was generally higher around 33 °C and 35 °C and around VPD of 3.8 kPa and 4.0 kPa, respectively, with local peaks in *A. raddiana* at lower temperature and VPD values.

Acacia sap flow dynamics

There was relatively little seasonal variability in the diurnal sap flow amounts (Fig. 6), and sap flow rates were 2–3 L h^{-1} during mid-day hours on most days. The diurnal sap flux was around 12 L day^{-1} year-round, increasing to over 13 L day^{-1} in May–June and November, and decreasing to 7.4 L day^{-1} at the end August (Fig. 6, inset). A morning spike reflecting high sap flow rates following sunrise was evident in most days and was up to 10 L h^{-1} on cooler days, i.e., during November–February. The highest diurnal water-use was recorded in October–November (Fig. 6), and the second highest in May–June. Evidently, the highest sap flow activity coincided with the hottest and driest times, whereas lower activity was recorded on cooler, milder days, such as in March.

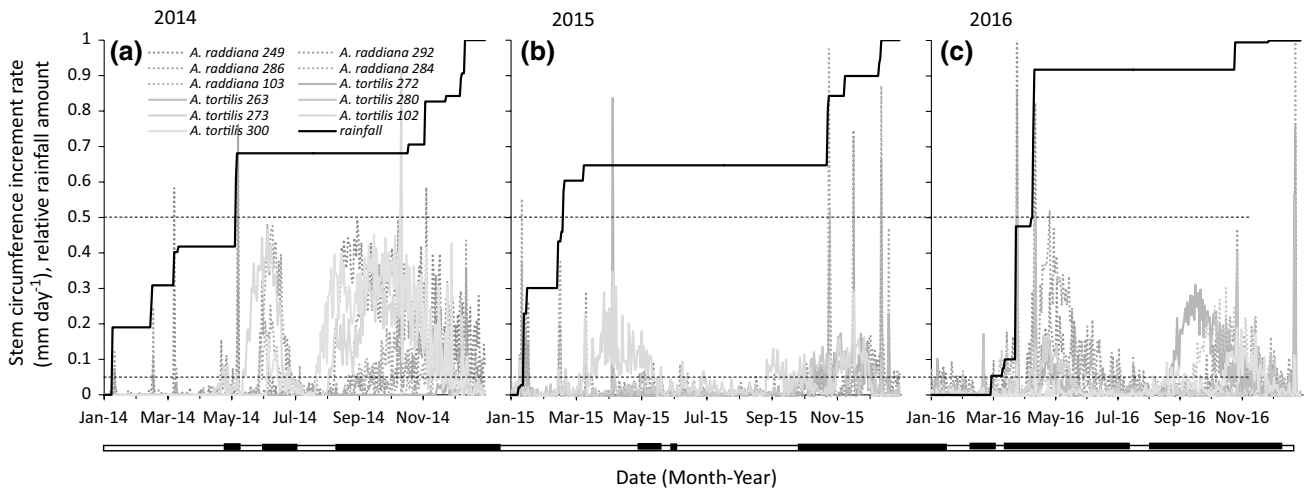


Fig. 4 *Acacia* stem growth rate and cumulative relative rainfall amount in Wadi Sheizaf (Arava valley, Israel) in 2014–2016, **a–c**, respectively. Missing or truncated curves are due to measurement failures. The dashed horizontal lines at 0.05 and 0.5 mm day⁻¹ were

used to filter out periods of no-growth and rain-driven tissue swelling, respectively, in estimating growth periods (black bars in the bottom). A growth period was defined when at least two individual trees were growing at a rate >0.05 mm day⁻¹ (but <0.5 mm day⁻¹)

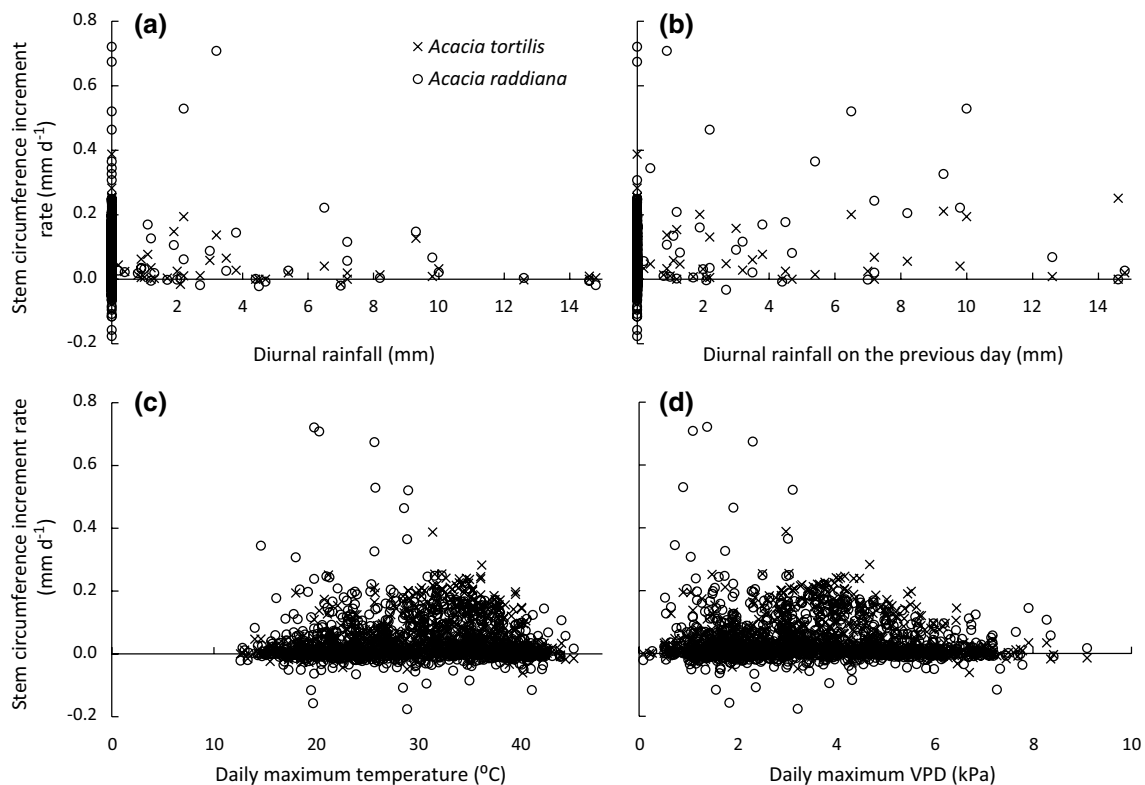


Fig. 5 Relationships between *Acacia* stem growth rate and meteorological conditions in Wadi Sheizaf (Arava valley, Israel) in 2014–2016. Each data point is a mean of 5 (6) trees of *A. raddiana* (*A. tortilis*)

Acacia leaf phenology

Crown foliage was maintained almost all year-round in both *A. raddiana* and *A. tortilis* (Fig. 7; Supplementary

Information Video S1). In the two species, new leaves emerged two times a year, in early March, and again in late October. The leaf shedding period was relatively short and timed to July (*A. raddiana*) or August (*A. tortilis*). In

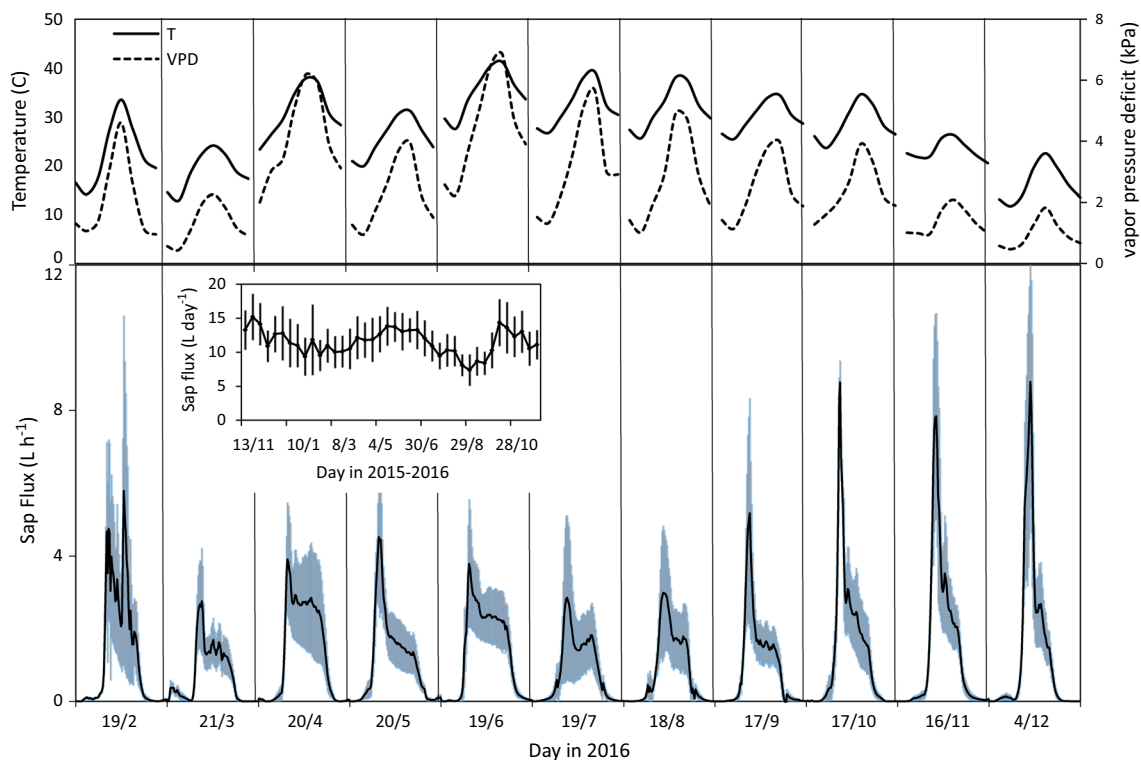


Fig. 6 Diurnal courses of *A. tortilis* sap flow, air temperature (°C) and vapor pressure deficit (VPD) in Wadi Sheizaf (Arava valley, Israel) during 11 days in February–December 2016 ($n=6$). An annual curve with 10-day average \pm SE is in the inset. Sap flow morning

spikes occurred on cooler days, but the activity was roughly similar year-round, with the largest water-use at the hottest and driest days, in June

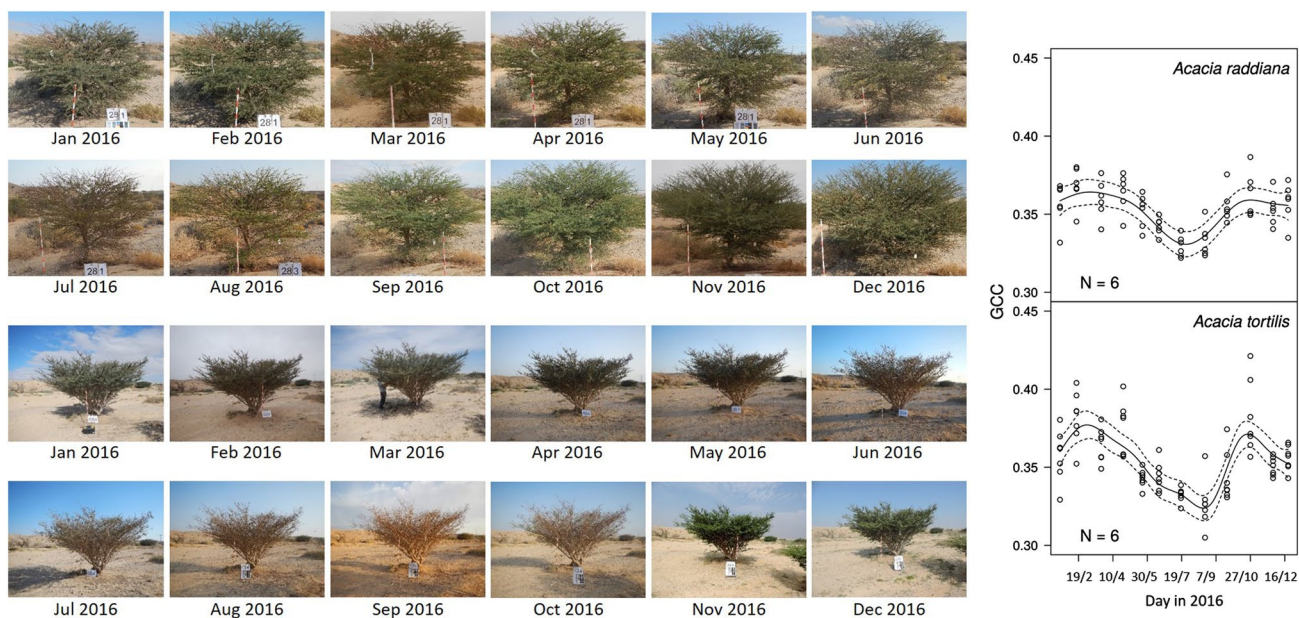


Fig. 7 Leaf phenology of *A. raddiana* (top) and *A. tortilis* (bottom) in Wadi Sheizaf (Arava valley, Israel). Monthly photographs (shown here are examples of for *A. raddiana* 281 and *A. tortilis* 24) from six trees of each species were analyzed for the calculation of the greenness index represented by Green Chromatic Coordinate (GCC; dia-

grams on right-hand side). Both species had close to evergreen leaf habit, with two annual flushing events (early March and late October) and a short shedding period in July (*A. raddiana*; **a**) or August (*A. tortilis*; **b**) (color figure online)

general, seasonal changes in the foliage, and the resulting dynamics in greenness [Green Chromatic Coordinate (GCC)] were more pronounced in *A. tortilis* than *A. raddiana* (Fig. 7). The GCC changed between 0.36 (spring and autumn maxima points) and 0.33 (summer minima) in *A. raddiana*, and between 0.37 and 0.32 in *A. tortilis*. Leaf flushing was unrelated to water inputs, since the early March flushing preceded the two major rain events in late March and early April 2016, and the late October flushing coincided with only a 3 mm rain event (Fig. 1). The GCC of the grey scale (grey 182) hardly showed any seasonal effect (Fig. S2). This is in accordance with other studies that reported that GCC was relatively robust to variations in illumination (e.g., Toomey et al. 2015).

Discussion

Acacia year-round activity and summer growth

This study explored tree eco-physiology at the hot and dry edge of tree existence. The Arava valley in Israel offers some of the hottest and driest conditions on the planet, while still permitting *Acacia* tree year-round growth. The local climate is also characterized by large seasonal differences, with daily maximum temperatures spanning over an amplitude of 30 °C (Fig. 1) and large year-to-year variations in the amount and the timing of local rain events. In spite of these large variations, there was year-round growth activity in these trees. The diurnal sap flow curves showed robust water-use by the trees throughout the year (Fig. 6), and the crown foliage cover was close to evergreen, especially in *A. raddiana* (Fig. 7). On top of this remarkable persistence in a hostile environment, stem growth was unexpectedly timed to the hotter and drier months of the year (Figs. 2, 4). Therefore, our hypothesis of synchronization with single rainfall or flashflood events, also relying on the previous observations at the site (Shrestha et al. 2003), was rejected.

The early studies on wood anatomy of *A. raddiana* have already shown that cambial activity in twigs peaked in May and persisted until September, with very little growth in the cooler months (Fahn et al. 1968; Arzee et al. 1970). Using anatomical methods combined with ^{14}C labelling, it was shown that May and August were the only months when both the cambium and phellogen were active (Fahn et al. 1968; Arzee et al. 1970). Our ultra-sensitive dendrometers confirm these previous observations in twigs, albeit in mature trees in the field, with continuous dynamics over 3 consecutive years.

The *Acacia* species studied here are of tropical origin and, hence, display thermophilic behavior (Otieno et al. 2005a, b). Indeed, cambial growth in our study was restricted to days with daily maximum temperature > 27 °C. Among the

two species, the more drought-resistant *A. tortilis* (Otieno et al. 2003) grew faster than *A. raddiana* during the harsher 2015 (and slower in the following, better, year). *A. tortilis* growth rate peaked around 35 °C and was unrelated to rainfall (Fig. 5a, b). Why then was growth temporarily arrested in most trees during July or August? This was not related to harsher conditions in either of the months than in June, i.e., there was no temperature or VPD threshold limiting growth during these months. One possible explanation can be found in leaf phenology: leaf shedding and minimum greenness were observed in late July in *A. raddiana* and in early August in *A. tortilis* (Fig. 7; Video S1). The seasonal minimum in greenness corresponded with that of sap flow (Fig. 6, inset). If cambial growth relies on concurrent photosynthesis (see below), then leaf phenology has a direct limitation on growth. Defoliation decreases growth as well as tissue carbon reserves (Landhäusser and Lieffers 2012). Leaf shedding in high summer might be related to cumulative photo-damage, as shown in the pine *Pinus halepensis* growing on the edge of the Arava, 75 km north of Wadi Sheizaf (Yatir forest, 650 m above sea level; Maseyk et al. 2008). The global solar radiation in our site reaches over 1000 W m⁻² at noon in summer, and irreversible damage to the fully exposed photosynthetic tissue is probably unavoidable (Wittenberg et al. 2014). Yet, the controls of stem growth phenology seem to be more complex. For example, some *A. tortilis* trees were growing during September, in spite of the low foliage cover.

Inter-annual growth variations

Stem growth in 2015 was lower than in 2016, which was in turn lower than in 2014 (Fig. 2). Our analysis yielded limited sensitivity of stem growth to rain events (Fig. 3), with other factors such as temperature being involved. Yet, sensitivity to climate might act at longer time-scales. Summing the winter rainfall amounts preceding these summer seasons shows a rather similar inter-annual water input, with 69 mm, 66 mm, and 58 mm in 2014, 2015, and 2016, respectively. In general, inter-annual variation in precipitation in the Arava can be much larger (Ginat et al. 2011). Why then was growth so different between the years? In arid environments, the total rainfall amount might be less important than the temporal rainfall distribution (Raz-Yaseef et al. 2010a, b; Klein et al. 2014) or the spatial distribution (Isaacson et al. 2017). Our measurements are in agreement with the previous observations at the site, showing higher tree water stress following a dry winter than during the dry, hot summer (Shrestha et al. 2003). The ranking of growth by years 2014 > 2016 > 2015 correlates with two such observations: (1) the last substantial rain event (“spring rain”) was 7th May 2014 > 12th April 2016 > 28th March 2015. This entails over a month of inter-annual differences in soil water conditions;

(2) the number of days with rainfall > 10 mm was 3 > 1 > 0 in 2014, 2016, and 2015, respectively. This means higher percolation and lower losses to surface evaporation in 2014. The role of indirect water inputs must be considered too. Belowground flows can feed an aquifer which the *Acacia* roots may have access to (Winters et al. 2015), but this is yet to be studied.

Carbon source for growth

Can concurrent photosynthesis explain the summer cambial growth? Active carbon uptake at temperature > 40 °C and VPD > 8 kPa is hard to imagine. Trees typically cease growth at temperature > 40 °C and VPD > 6 kPa (Ruehr et al. 2016). However, in our trees, leaves were there almost all year-round and the trees maintained relatively moderate and stable sap flow rates during the entire experimental period. The desert environment causes large seasonal amplitudes (Fig. 1), as well as large diurnal amplitudes. For example, VPD < 2 kPa was recorded almost every night throughout the year, including summer (Fig. 6). In a typical day in May 2016, VPD was 1.74 kPa and 2.61 kPa at 8:00 and 11:00, respectively. In addition, in a typical day in August 2016, VPD was 1.93 kPa and 2.90 kPa in 8:00 and 11:00, respectively. These VPD levels usually permit some stomatal conductance, and hence, photosynthetic activity could take place for 4 h or more every morning (Klein et al. 2016). It is possible that during a summer day stomata shut down in late morning, while sap flow continues until sunset (Fig. 6), to refill water storage in woody or leaf tissues, or even embolisms in the xylem (Klein et al. 2016). Such physiological regulation can be regarded as drought avoidance at a fine temporal scale.

Water source for growth

Our sap flow measurements suggest a rich and constant year-round water source for *Acacia* growing in the desert. Studying the roles and interactions of soil water, ground water, and *Acacia* root accessibility was beyond the scope of this current research. Nevertheless, we have indications of significant water amounts at 7–10 m depth in a nearby site (7 km to the north; Winters et al. 2015), and their use by *A. raddiana* (Sher et al. 2010). Accessible ground water support *Prosopis* trees even in the Atacama, the driest desert on Earth, as well as *Tamarix* and *Populus* in the Taklamakan, with water table depth playing a major role in tree function (Garrido et al. 2016; Gries et al. 2003, respectively). Desert trees have the deepest roots in the plant kingdom (Canadell et al. 1996), and *Acacia* species rank high among them, e.g., records of *A. raddiana* roots at 35 m below surface (Stone and Kalisz 1991). In the Mojave Desert, deep-rooted plants were less vulnerable to drought than others on soils that

allowed for deep-water percolation (Munson et al. 2015). *Acacia* roots go deep, as well as far from the stem, to collect water from a large area as possible. In a road construction site in the Arava valley, 120 km south of Wadi Sheizaf, there was an attempt to conserve *A. tortilis* trees by digging around trees, leaving them on 2–3 m wide, 7–8 m tall poles (Fig. S4). Failure of this attempt and the resulting *Acacia* tree die-off indicates the significant role of lateral roots for their survival.

The observed inter-annual variation in growth and its relation to rainfall distribution (Fig. 2) indicates that the water source for these trees, as deep as it may be, is also sensitive to climate. Soil water can support low-density tree populations despite heat and drought, as long as recharge is kept above a minimum, yet unknown, threshold. Furthermore, the variation among individual trees in 2014 suggests different access to water, either due to source patchiness (water pockets), or root system architecture. Hydrological niche segregation is a widespread phenomenon across terrestrial biomes, but, so far, only arid plant communities have demonstrated temporal partitioning that promotes coexistence (Silvertown et al. 2015). *Acacia* trees, typically growing in savanna ecosystems, are used to competition with grass species over water resources (Cramer et al. 2010). In that sense, desert ecosystems, with only limited grass growth, offer an advantage for *Acacia* growth.

In pulse-driven arid ecosystems, four major plant forms have evolved: winter annuals, drought-deciduous perennials, evergreen perennials, and stem succulents (Schwinning and Ehleringer 2001). The third category fits best the *Acacia* studied here, and predicts large root/shoot ratio, deep root system, and lower leaf conductance with low stomatal sensitivity, as adaptations that maximize deeper soil water-use (Schwinning and Ehleringer 2001). In the case of *Acacia* in the hyper-arid Arava, while some indications exist for deep soil water-use (Sher et al. 2010; Winters et al. 2015), predictions for the other traits should be used as major hypotheses for future research at our site.

Implications for arid ecosystems under climate change

In face of climate change and its threats to forests worldwide, our study points to the potential advantage of low-density woodland over a forest, allowing each individual tree to exploit a large area by growing proliferate root systems. Under future drying and warming scenarios, such sparse woodlands might survive climate change better than dense forests. On an ecological perspective, we demonstrate that in spite of flashflood and rainfall pulses, deep soil water in our hyper-arid ecosystem had a larger effect on *Acacia* growth. This also indicates that terrestrial vegetation models must account for belowground conditions to capture ecosystem

dynamics. In addition, future research should quantify the hydrological threshold for *Acacia* growth and survival, to facilitate better predictions under climate change.

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Author contribution statement GW initiated the study in 2013, with monitoring operated together with GR. DO, SC, and TK joined the study in 2015, with YW, IR, IP, and CB joining in 2016. TK started the analysis and manuscript drafting, with contributions from all authors.

Data accessibility Data used in this paper will be archived in Figshare.

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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