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RESEARCH ARTICLE

Differential climatic conditions drive growth of *Acacia tortilis* tree in its range edges in Africa and Asia

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Abstract

Premise: Tree growth is a fundamental biological process that is essential to ecosystem functioning and water and element cycling. Climate exerts a major impact on tree growth, with tree species often requiring a unique set of conditions to initiate and maintain growth throughout the growing season. Still, little is known about the specific climatic factors that enable tree growth in savannah and desert tree species. Among the global tree species, *Acacia tortilis* occupies one of the largest distribution ranges (crossing 6500 km and 54 latitudes), spanning large parts of Africa and into the Middle East and Asia.

Methods: Here we collected climate data and monitored *Acacia tortilis* tree growth (continuous measurements of stem circumference) in its southern and northern range edges in South Africa (SA) and Israel (IL), respectively, to elucidate whether the growth–climate interactions were similar in both edges.

Results: Growth occurred during the summer (between December and March) in SA and in IL during early summer and autumn (April–June and October–November, respectively). Surprisingly, annual growth was 40% higher in IL than in SA. Within the wide distribution range of *Acacia tortilis*, our statistical model showed that climatic drivers of tree growth differed between the two sites.

Conclusions: High temperatures facilitated growth at the hot and arid IL site, while high humidity permitted growth at the more humid SA site. Our results confer an additional understanding of tree growth adaptation to extreme conditions in *Acacia*'s world range edges, a major point of interest with ongoing climate change.

KEYWORDS

Acacia tortilis, desert, distribution, growth season, growth variation, savannah

Tree growth is a fundamental mechanism in natural ecosystems that involves water and nutrient cycles, and atmospheric changes and influences other trophic levels (Hilty et al., 2021). The intriguing process of tree growth has captivated scientists for centuries. Thanks to that, we now know that cambial growth in trees (xylogenesis) involves cell division, cell enlargement, and cell wall synthesis and that the rates of these processes are influenced by environmental conditions (Deleuze and Houllier, 1998; Vaganov et al., 2006; Rossi et al., 2008). Moreover, trees can adjust their anatomical (David-Schwartz et al., 2016), physiological (Klein et al., 2013), and phenological (Stevens et al., 2016; Figueiredo-Lima et al., 2018) traits in response to changes in environmental conditions, allowing survival and growth across a wide range of conditions within their distribution.

The shape and size of species distributions are thought to be determined by a lack of adaptation to novel ecological conditions (including competition) beyond the edge (Sexton et al., 2009; Hargreaves et al., 2014) or by physical barriers (Kerr et al., 2007). Climate has a strong influence on the geographical distribution of trees via specific thresholds of temperature and water availability (Woodward and Woodward, 1987). The ability of trees to adjust their growth in accordance with climatic conditions is especially important at the edges of their geographical distribution (Andreu et al., 2007; Fady et al., 2016), where climatic conditions might be at their most extreme (Abeli et al., 2014). Duration of tree growth activity is strongly controlled by climate; for example, in conifer trees, the duration of the growing season is ~40 days in the northernmost boreal forest (70°N), ~100 days in the forest-steppe zone (50°N), and up to ~155 days in the subtropical zone (Vaganov et al., 2006). A study of phenological differences in *Pinus halepensis* across its distribution, from the temperate climate in its northern range to the semiarid climate in its southern range, revealed that the length of the growing season decreased with a reduction in precipitation (Klein et al., 2013). Not only does the duration of growth change with climate, but also the rate of growth varies across climate conditions (Ettl and Peterson, 1995; Andreu et al., 2007; Henderson and Grissino-Mayer, 2009; Voltas Velasco et al., 2018; Patsiou et al., 2020). In the Mediterranean basin, Patsiou et al. (2020) showed that the height of *P. halepensis* trees increased 2.5-fold with increasing precipitation (from 300 to 800 mm year^{-1}) and temperature (mean annual temperature increasing from 11° to 20°C) in 30 years. Another study on pine species found that the timing and duration of growth varied among species, sites and years, while the temperatures for growth were stable for all the studied species (Rossi et al., 2008).

However, most of the research regarding tree growth in different geographical distribution range edges has been performed within biomes of the northern hemisphere (Way and Oren, 2010; Klein et al., 2013, 2016; David-Schwartz et al., 2016; Fréjaville et al., 2020). There is still a lack of knowledge regarding growth patterns in range-edge tree populations outside boreal and temperate biomes such as arid deserts and tropical savannahs. Here, we investigated *Acacia* trees, a keystone genus of the Fabaceae family, that supports other organisms (Munzbergova and Ward, 2002), with a very wide global distribution, mostly in the southern hemisphere (Maslin et al., 2003).

The global distribution of trees within the genus *Acacia* (officially recognized as *Vachellia*[1]) demonstrates their capacity to live and adjust to a wide range of climatic conditions—from the tropic equator through the African savannahs and even to the most arid deserts of Africa and the Middle East (Munzbergova and Ward, 2002; Ludwig et al., 2003; Maslin et al., 2003; Bouchenak-Khelladi et al., 2010). Of the 1350 species of *Acacia* (Maslin et al., 2003), *Acacia tortilis* is the most widespread, drought-resistant, and heat-tolerant (Halevy and Orshan, 1972; Boulos, 1999). *Acacia tortilis* has been subdivided into four distinct subspecies, *A. tortilis* subsp. *tortilis* (Forssk.) Hayne, *A. tortilis* subsp. *raddiana* (Savi), *A. tortilis* subsp. *spirocarpa* (Hochst. ex. A.Rich) and *A. tortilis* subsp. *heteracantha* (Burch.) (Wickens et al., 1995; Kyalangalilwa et al., 2013). The northern limit of this species is in the Negev and Arava deserts of Israel, where *A. tortilis* subsp. *tortilis* and *A. tortilis* subsp. *raddiana* are abundant (Halevy and Orshan, 1972; Ross, 1981; Danin, 1983). Its southern limit is in South Africa (Maslin et al., 2003), where *A. tortilis* subsp. *heteracantha* is abundant. These opposing distribution edges are distinct in their climatic conditions; the northern is a hyperarid desert, whereas the southern is a subtropical savannah. Thus, they provide an opportunity to explore the ecophysiological adaptations of individuals of the same species to two drastically different environments.

Despite the presence of *Acacia* species in numerous ecosystems, there is very limited knowledge of how different climatic conditions influence its growth. Locally, we know that in Israel, stem activity and extension growth of *A. tortilis* subsp. *raddiana* saplings are strongly dependent on relatively high temperatures and mostly occurs during April and May (Fahn et al., 1968). Winters et al. (2018) found that stem growth of *A. tortilis* subspecies in the desert of Israel was highly seasonal, with fast increments during the hottest months (May–June and August) and again in the driest month (November). However, more research is needed to understand, identify, and characterize the ways by which *Acacia* trees survive and grow in dry conditions.

Here, we measured *Acacia* tree growth (stem circumference) over 2 years at the geographical peripheries of the distribution of *A. tortilis* in Israel (IL) and South Africa (SA), aiming to investigate the growth dynamics under different climatic conditions. Our objective was to elucidate the climatic drivers of stem growth at both edges and evaluate whether these were similar or different. We hypothesized that (1) annual growth will be higher and the growing season longer in the mesic conditions in SA than in the arid conditions in IL and that (2) the growing season in each location will correspond to the periods when the local conditions include mild temperature (20–25°C) and high water availability.

MATERIALS AND METHODS

Study sites and tree species

The study was conducted at the two distributional edges of *Acacia tortilis*, the northern range edge at Wadi Sheizaf in the Arava Valley (Israel), and the southern range edge at Skukuza, Kruger National Park (KNP) in South Africa (Figure 1A) between July 2019 and July 2021. In both sites, *Acacia* trees are considered keystone species. The two study sites differ in their climatic conditions: the northern range edge site is a hyperarid desert characterized by mean annual rainfall of ~25–70 mm (Shalev et al., 2011; Winters et al., 2018), whilst the southern

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[1] The genus (*Acacia*) was split into two different genera, *Vachellia* and *Acacia*. While the original name (*Acacia* = Latin for "thorn") 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*.

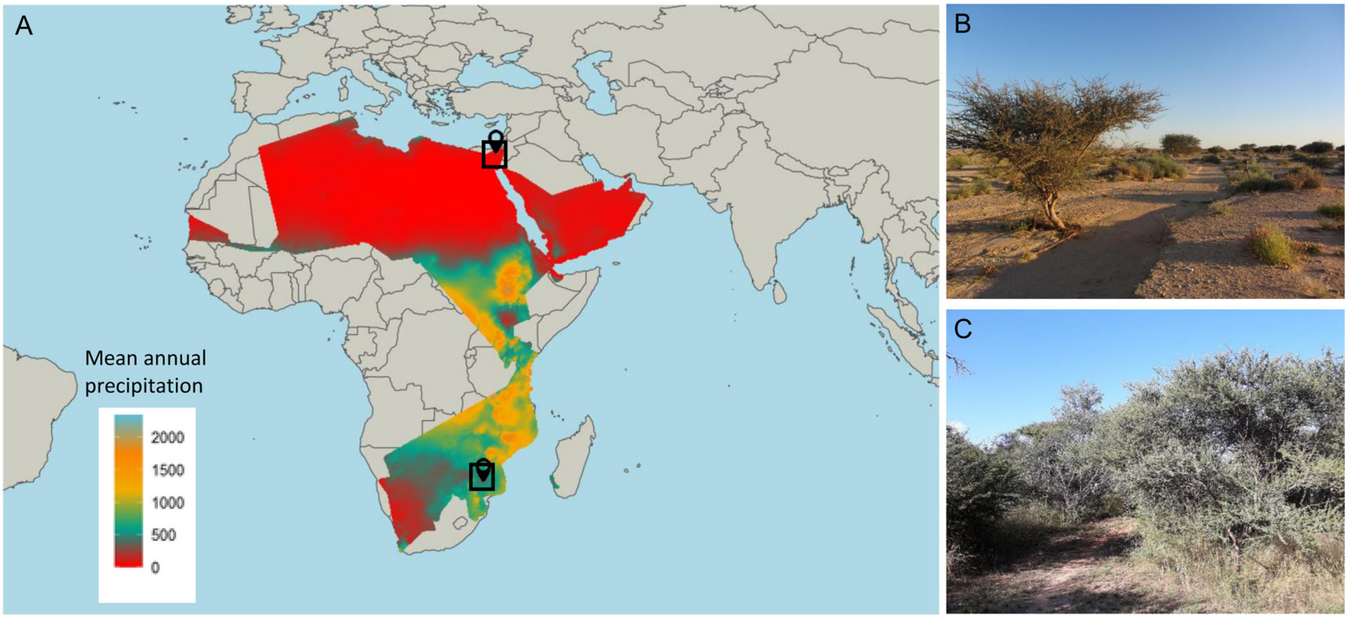

FIGURE 1 (A) Map of *Acacia tortilis* geographical distribution obtained from the Global Biodiversity Information Facility (GBIF) database (https://www.gbif.org/). The color gradient represents mean annual rain (mm; WorldClim data set). Examples of typical *A. tortilis* tree in (B) its northern range edge desert site in Israel and (C) its southern range edge savannah site in South Africa.

range edge site is characterized by mean annual rainfall of ~565 mm (Smit et al., 2013). In both study sites, the rainy season occurs between November and May, resulting in winter rain in the cold season in IL and summer rain in the warm season in SA.

The research site at Wadi Sheizaf is a dry sandy streambed (i.e., wadi) in the northern edge of the Arava Valley, southern Israel (30.721222°N, 35.268366°E; elevation –137 m a.s.l.), a site defined as a "hot desert climate" (Koppen, 1936), with aridity index (AI) of 0.02—a hyperarid ecosystem (Trabucco and Zomer, 2018). Most of the rain events are local, intense, and short period, sometimes causing flash floods (Shalev et al., 2011). In a flash flood, there is a high input of water into the Wadi system, locally increasing the soil moisture regime experienced by *A. tortilis* trees. In general, the lithological cross section under the streambed in the IL study area is composed of coarse alluvial deposits. Streambeds of ephemeral rivers are largely composed of permeable, coarse alluvial sediments that promote relatively rapid infiltration of floodwater and therefore low availability of water in the first 5–7 m (Dahan et al., 2007; Winters et al., 2015). The vegetation in the site includes sparse ephemeral vegetation and *A. tortilis* trees that are scattered throughout the wadi, but never forming a continuous canopy.

The site in South Africa in the Skukuza research camp, Kruger National Park (–24.993014°S, 31.583957°E; elevation 276 m a.s.l.) is defined as a subtropical savannah with aridity index (AI) value of 0.38—semiarid climate. The site is around 90 m from the seasonal Nwaswitshaka River, which flows only during years with high rain, and then only for a couple of weeks (however, subsurface water is present in the riverbed for longer periods). The area is underlain by granitic rocks, giving rise to nutrient-poor sandy soils. The area is characterized by a largely continuous herbaceous layer, with a rather dense woody canopy cover of a range of woody species, most commonly from the genus *Acacia* and *Combretum*. Kruger National Park contains the full complement of herbivores and predators expected in protected African savannahs, and diverse species from other taxonomic groups (e.g., birds, reptiles). However, our study site was in an enclosed area to exclude animal interference (both in terms of selected trees being pushed over by elephants and inquisitive animals tampering with the dendrometers).

At each site, we selected 10 representative *A. tortilis* trees in a plot of 1 ha. The selected trees were similar in diameter at breast height (DBH; Appendix S1, Table S1) and growing in similar microclimates (elevation, distance from other plants, soil properties), we monitored also one dead tree in each site as a control for our measuring devices. In the South African study site, we selected the subspecies present there: *A. tortilis* subsp. *heteracantha* (Burch.). In the Israeli site, we selected an equal number (five trees) for each of the two subspecies present; *A. tortilis* (Forssk.) Hayne subsp. *tortilis* and *A. tortilis* subsp. *raddiana* (Savi). We monitored daily stem circumference and environmental conditions to investigate their ecophysiology in their natural habitat of the two distribution edges.

Species distribution map

To learn about the relative location of our field sites within the species distribution, we created a distribution map of

A. tortilis. We downloaded a data set of *A. tortilis* occurrences from the open-source data set Global Biodiversity Information Facility (GBIF https://www.gbif.org/) (Hijmans et al., 2005). We used R scripts for a cleaning pipeline to filter out (1) any occurrence that had an uncertainty of more than 100 km, (2) any records based on fossils, and (3) any record with an unknown source. We then used the R package CoordinateCleaner (Zizka et al., 2019) to remove (4) any occurrence that showed zero coordinates and equal *x* and *y* coordinates, (5) duplicates, (6) occurrences at sea, and (7) coordinates at capitals and centroids. We identified two occurrence points in India, both annotated through human observation. After investigating their annotation in GBIF and through a literature review, we decided to account for these as false positives and removed them. A final data set of 450 data points was generated. A concave hull was then formed around the occurrence points with the R package concaveman (Park and Oh, 2012) and concavity value of 1.5. Climatic values were downloaded from WorldClim (Hijmans et al., 2005), and the annual rainfall was mapped onto the species distribution map.

Stem growth

In both sites, stem circumference of each tree was continuously measured by an automatic high-resolution radial dendrometer (DRL26, EMS, Brno, Czech Republic; Urban et al., 2013), recording variations of up to 1 μm resolution and logging data into a built-in data logger once per hour. Hourly data represent not only stem growth, but also the shrinking and expansion of the tree stem as a function of temperature and water transfer in the xylem (Zweifel et al., 2016). Therefore, for consistency, we always used the stem circumference at 00:00 hours (when the tree–soil water relations are balanced) and compared it to the stem circumference on the next day or week at 00:00 hours. Thus, we were able to follow only the net changes in the stem increment (growth) and neglect the diurnal cycles of shrinking and expansion that are reflected by the hourly data. We used the values measured by the dendrometers (stem circumference at 00:00) to analyze the radial stem growth of each tree. Three indicators of stem growth were calculated: (1) diurnal stem growth (mm day^{-1}), calculated by subtracting the circumference on a given day from the circumference on the previous day; (2) weekly stem growth (mm week^{-1}), calculated by subtracting circumference on a given day from the circumference value 7 days earlier; and (3) cumulative weekly stem growth, calculated by subtracting the stem circumference value every 7 days from the stem circumference on 1 July 2019 and 1 July 2020 (i.e., using these dates as "zero values"). These calculations allowed us to analyze trends at daily and weekly scales and relate them to the climate conditions on similar temporal scales. Each year, 1 July was selected as the reference onset point because it falls outside of the growing seasons at both study sites. Data were collected for two consecutive years, from 1 July 2019 to 30 June 2021.

Meteorological data

Hourly meteorological data on temperature (°C), relative humidity in the air (%; RH), radiation (Watt/m^2), and rain were collected at both study sites. For the IL site, meteorological data were from the Israeli Meteorological Service station in Hatzeva, 7 km north of the study site (www.ims.gov.il; from 1 July 2019 to 30 June 2021; accessed on 18 September 2021). Solar radiation data (W m^{-2}) were missing at this station; hence, they were obtained from the meteorological station in Eilat (130 km south of the study site). Despite the distance, both stations are at similar elevations and operate under hyperarid conditions, i.e., clear skies at most times. At the SA study site, we combined data from three Ileaf weather stations (www.ileaf.co.za): (1) Skukuza, within the study plot; (2) Sabi-Sabi, 15 km west of the study site, and (3) Riverside Oos-Eind, 50 km west of the study site. Data was taken from the closest station (Skukuza) whenever possible, and when data were missing from the Skukuza station, data came from either Sabi-Sabi or Riverside). Temperature (°C) and RH (%) data were available from the Skukuza station only from November 2019 onward; hence, data from the Riverside station were used for the preceding period. Exploring the relationships between these two stations, we found a high correlation ($R^2 = 0.93$ for temperature, $R^2 = 0.92$ for RH) for the period when data from both these weather stations were available (February 2020–July 2020) (Appendix S2, Figure S1). Solar radiation data were unavailable at Skukuza and were not continuous for either of the two other stations. Data were obtained from Riverside from July 2019 to February 2020 and from Sabi-Sabi from March 2020 onward. Finally, we compiled a database of hourly meteorological data for both sites for the entire study period. To compare between sites and to analyze the data at the same timescale of the dendrometers (daily growth), we chose temperature, RH, and radiation at noontime, roughly representing the daily maximum temperature and radiation. To analyze the growth of the trees in relation to the climatic conditions, we paired temperature, RH, and radiation data from the same dates as the data from the dendrometer data. When comparing the weekly growth of the trees, we used averages of the climatic variables during this week.

Statistical analyses

We tested the effect of climatic variables (RH, temperature, radiation, and rain) on the weekly stem growth of *Acacia* trees at both sites combined using generalized linear mixed models (GLMMs) with restricted maximum likelihood and Gaussian distribution of error. In a model that included all climatic variables, we tested whether their effect differed between the two sites (IL and SA) using site as a fixed effect (Table 1: Model 1, M1). We also tested the interactions between each climatic variable and site (M2) to better understand the effect differences between sites. After finding strong significant interactions between all climatic variables and site and a lower AIC for M2, we elucidated the specific effects in each site (M3 for SA and M4 and M5 for IL). For IL, we also compared the effect of the climatic variables with (M4) and without (M5) the inclusion of rain, since rain events were too scarce and stochastic at the IL site and selected the most parsimonious of the two models using AIC. For all models, we included repeats (individual trees) as a random variable. All climatic variables were scaled to a mean of zero and a standard deviation of one, and stem growth was expressed in the model as a rate and not as a cumulative value. We tested both the linear and quadratic effects of temperature to look for a unimodal response of the weekly growth to increasing temperatures. We calculated Pearson correlations amongst all climatic variables to assess collinearity between the three main climatic variables and used variance inflation factor (VIF) with a cut-off threshold of 3 to test for multi-collinearity (Appendix S1, Table S2). Given the correlation between the three climatic variables, we compared models M3, M4, and M5 to models in which we excluded one of the collinear variables at a time for each site (e.g., radiation and temperature in SA). We found that the partial models were less parsimonious than models that included all variables based on AIC values (Appendix S1, Table S3). Finally, to test for a lagged response of stem growth to climatic conditions, we matched the growth rate with the climatic data for the preceding week and repeated the same set of statistical models. This is because rain events are often associated with cloudy days and reduced solar radiation, reducing photosynthesis and delaying growth by up to a week (Table 2). All statistical analyses were conducted using R version 4.2 (R Core Team, 2013), and jamovi version 2.2.5 (Gallucci, 2019; jamovi project, 2020). Plots were created using the R package ggplot2 (Wickham, 2016). All model equations are in Appendix S1, Table S4.

TABLE 1 Models (M1–M5) to predict stem growth rate of *Acacia tortilis* in response to climate at two sites. Significant effects are in bold. AIC, Akaike information criterion; IL, Israel; SA, South Africa.

Country	Model	AIC	R^2	Fixed effect	Standard coefficient	P
IL + SA	M1	3035	0.205	**Site**	**−0.825**	**<0.001**
				RH	**0.0213**	**<0.001**
				Radiation	**4.19e-4**	**0.014**
				Temperature	**−0.005**	**<0.001**
				Rain	**0.005**	**0.002**
IL + SA	M2	2889	0.301	**Site**	**−0.701**	**<0.001**
				RH	**0.015**	**<0.001**
				Radiation	**−0.001**	**<0.001**
				Temperature	0.057	0.347
				Temperature^2	−3.97e-4	0.713
				Rain	**0.005**	**0.034**
				Site × RH	**0.042**	**<0.001**
				Site × Radiation	**−0.002**	**<0.001**
				Site × Temperature	**0.713**	**<0.001**
				Site × Temperature^2	**0.013**	**<0.001**
				Site × Rain	0.007	0.189
SA	M3	1343	0.323	**RH**	**0.036**	**<0.001**
				Radiation	**−0.002**	**<0.001**
				Temperature	**0.006**	**0.011**
				Temperature^2	−0.200	0.110
				Rain	0.002	0.35
IL	M4	1421	0.253	RH	−0.006	0.084
				Radiation	−2.75e-4	0.088
				Temperature	**0.414**	**<0.001**
				Temperature^2	**−0.007**	**<0.001**
				Rain	0.009	0.242
IL	M5	1342	0.322	RH	−0.003	0.337
				Radiation	−1.93e-4	0.219
				Temperature	**0.404**	**<0.001**
				Temperature^2	**−0.007**	**<0.001**

RESULTS

At both the Israeli and South African study sites, all climatic variables (including rain) were distinctly marked by seasonality (Figure 2). The seasons in SA occur inversely to IL seasons, given the opposing hemispheres of the two sites, as manifested by mirror images of temperature and radiation between the two sites (Figure 2A,B). Overall, seasonal variations in temperature and radiation were mildly larger in IL than in SA, with peak values exceeding 45°C and 1000 W m^{-2} in IL summer. In contrast, rain and relative humidity (RH) peaked during the same period at both sites (December to April); thus, in SA, the rainy season occurs in the (warm) summer, but in the (cool) winter in IL (Figure 2C,D). Moreover, rain at IL (78 mm in the first year and only 23 mm in the second year) was an order of magnitude lower than that in SA (525 mm in the first year and 471 mm in the second year). Another difference between the sites was in RH, which was almost consistently ~15% higher at the SA site than at IL (Figure 2C). These differences caused a positive correlation between temperature and rain in SA, compared to a negative correlation between the same variables in IL (Appendix S2, Figure S2). Another difference between conditions in the two sites, was

TABLE 2 Models (M6–M10) to predict stem growth rate of *Acacia tortilis* with 1-week lag in the climatic effect. Significant effects are in bold. AIC, Akaike information criterion; IL, Israel; SA, South Africa.

Country	Model	AIC	R^2	Fixed effect	Standard coefficient	P
IL + SA	M6	3138	0.120	**Site**	**−0.026**	**0.039**
				RH	−0.001	0.657
				Radiation	5.29e-4	0.007
				Temperature	**0.300**	**<0.001**
				Rain	**0.008**	**<0.001**
IL + SA	M7	2973	0.230	Site	0.237	0.079
				RH	**−0.007**	**0.014**
				Radiation	1.37e-4	0.527
				Temperature	−0.066	0.301
				Temperature^2	0.001	0.105
				Rain	0.004	0.132
				Site × RH	−0.001	0.833
				Site × Radiation	7.52e-4	0.083
				Site × Temperature	**−0.951**	**<0.001**
				Site × Temperature^2	**0.018**	**<0.001**
				Site × Rain	**0.011**	**0.037**
SA	M8	1401	0.208	RH	0.004	0.087
				Radiation	5.30e-4	0.256
				Temperature	**−0.054**	**<0.001**
				Temperature^2	**0.010**	**<0.001**
				Rain	**0.010**	**<0.001**
IL	M9	1405	0.252	RH	−0.006	0.070
				Radiation	−2.35e-4	0.200
				Temperature	**0.409**	**<0.001**
				Temperature^2	**−0.001**	**<0.001**
				Rain	−0.001	0.694
IL	M10	1403	0.253	RH	−0.007	0.034
				Radiation	−2.53e-4	0.156
				Temperature	**0.411**	**<0.001**
				Temperature^2	**−0.007**	**<0.001**

the larger variability in radiation values in SA, compared to the more stable radiation values in IL; the high frequency of cloudy days in SA, might be related to the geographical proximity to the Indian and the Atlantic oceans, which in turn causes higher RH (forming clouds), decreasing radiation intensity.

To investigate the adaptation of *A. tortilis* to the opposing conditions at its two range edges, we compared the dynamic of the growth increment of the radial stem ("growth" hereafter) between the two sites for two consecutive years (2019–2021) (Figure 3). Annual growth was unrelated to initial stem circumference in both sites (IL: $R^2 = 0.003$; SA: $R^2 = 0.09$), and, therefore, growth is presented in millimeters and not as percentage stem increase, despite the variation in individual tree sizes. To determine which trees were actively growing in a current year, we used a threshold of >1 mm increase in stem circumference by the end of the year. During the first year, the *A. tortilis* population in SA had less annual growth compared with the IL population, although not significantly ($P = 0.187$). This reduced growth of the SA trees was reflected in the number of actively growing trees (30% in SA vs. 100% in IL; Figure 3) and annual growth (mm year^{-1}) of the actively growing trees (SA: 10.09 ± 1.77 mm tree^{-1}, IL: 18.4 ± 2.03 mm tree^{-1}; Figure 4). During the second year, more trees in the SA population were growing (60%) than in the first year. The three trees that grew in the first year were also growing in the second year, plus three additional trees that did not grow in the first year. Unfortunately, four dendrometers of the IL trees failed during the second year, and we obtained data for the remaining six trees, all of which grew. The average annual growth in the second year was still higher in the IL population (17.6 ± 2.3 mm tree^{-1}) compared to the SA population (13.02 ± 1.5 mm tree^{-1}). Over the entire 2 years, the average growth of the IL population was 51% higher than that of the SA population.

In SA trees, although there were differences between years in the amount of growth, the timing of growth was similar in both years (Figure 4B). Growth occurred during the SA summer between December and March when both temperatures and rain peaked. However, in IL trees, only slight differences in growth dynamic were observed between the 2 years. Stem growth in the first year occurred for all trees between April (spring) and June (early summer) (Figure 3A), once the rainy season had ended and temperature and radiation increased. In addition, a small fraction of trees (30%) grew also between October at the end of summer and November (Figure 3A) before the beginning of the winter rain season, when temperatures started to decrease and relative humidity increased (Figure 2). In the second year, only two of six trees grew between April and June, whereas most of the trees (five trees) grew between October and November (Figure 3). Although *A. tortilis* subsp. *raddiana* trees were larger than *A. tortilis* subsp. *tortilis* trees ($t = 3.8579$, $P = 0.0048$), there was no difference in stem growth between the two subspecies (Figure 3A). Even though annual rain at the IL site was 2.3-fold higher the first year, the annual growth of trees was not significantly different between the years (Figure 4A; an average of 18.4 mm tree^{-1} in the first year and 17.6 mm tree^{-1} in the second year; $P = 0.413$). We found similar growth for the SA trees with both the smallest and largest initial stem diameter in the first year, suggesting that growth patterns were not directly related to tree size. Contrary to the observations at IL, SA trees

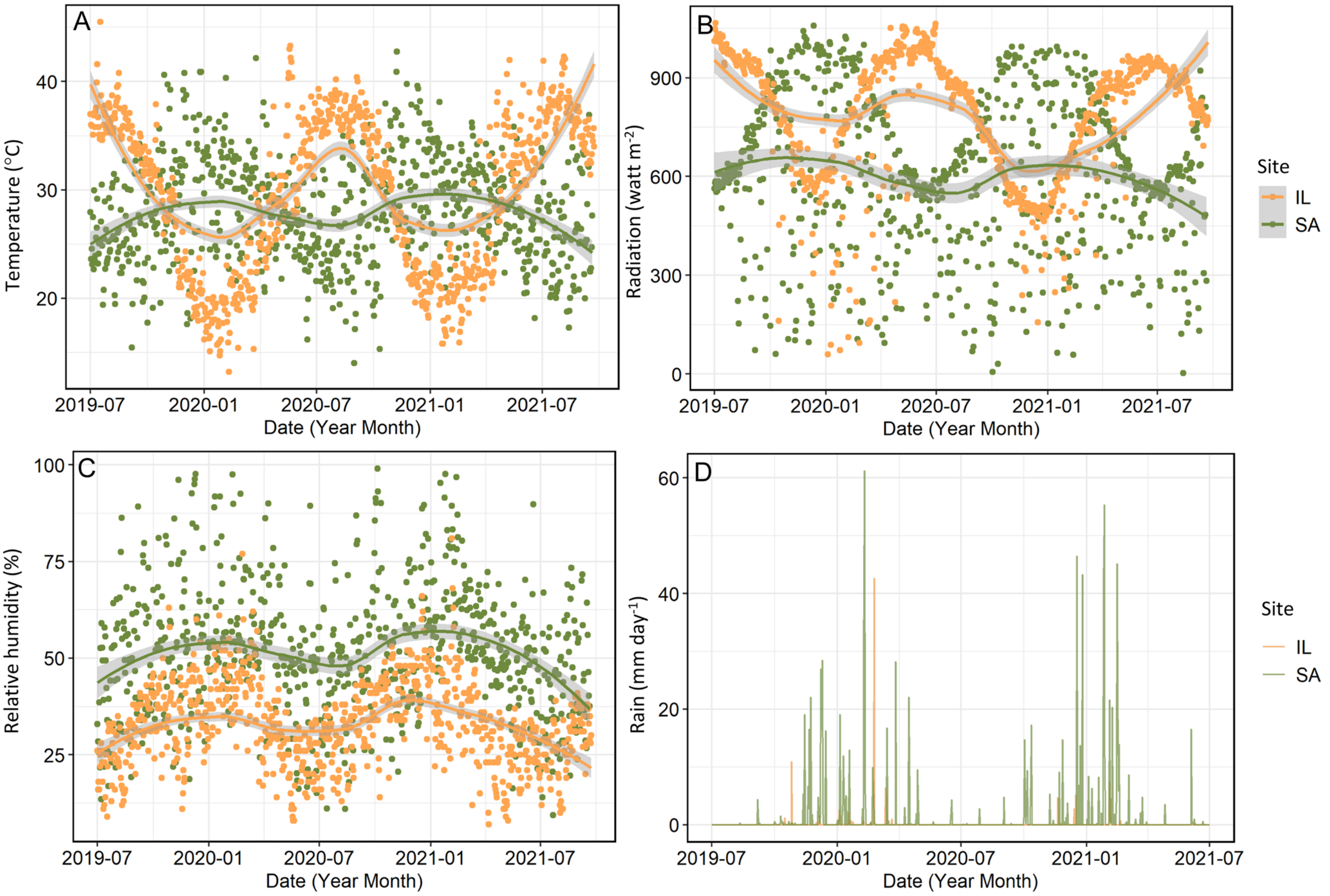

FIGURE 2 Meteorological conditions at the northern and southern range edges of *Acacia tortilis*. (A) Temperature, (B) radiation, (C) relative humidity, (D) and rain in Kruger NP, South Africa (green), and Arava Valley, Israel (orange). Each point represents a midday diurnal measurement from July 2019 to July 2021.

expanded and contracted more notably (Figure 3). This dynamic was synchronized within all the trees in the studied population. One SA individual tree outgrew the population, and in early March 2020, its diameter exceeded the dendrometer capacity, resulting in the loss of its growth data thereafter.

We found a significant difference between the effects of climate on the growth of *Acacia* trees at the SA and IL sites (Table 1: M1, M2). The temperature had a significant effect on the weekly growth rate across sites (Table 1: M3–M5), with maximal growth at optimal temperatures of ~27.5°C and decreasing at higher and lower temperatures (Figure 5A). At IL, the temperature was the only climatic variable explaining variation in weekly growth (Table 1: M5), whereas at SA, growth was positively affected by RH (Figure 5C) and temperature but negatively affected by radiation (Figure 5B) (M3). The effect of temperature on growth was positive and weak throughout the temperature range at SA, whereas at IL, we found a unimodal response: a positive effect up to 27.5°C and negative for temperatures exceeding this threshold. Standard coefficients reflect the size of effects; hence, tree growth was driven mainly by increasing temperature at IL and by increasing RH at SA (higher standard coefficients in Table 1: M3, M4). The interaction between the effects of temperature and RH was not significant ($F = 0.901$, $P = 0.343$). When accounting for a weekly lagging effect on growth (Table 2), temperature and rain had significant effects when both sites were analyzed together (Table 2: M6). When each site was tested separately, temperature was the only strong predictor of growth at both sites (Table 2: M8–M10; Appendix S2, Figure S3), showing a robust response to temperature at the IL site and a possible lagging effect at the SA.

DISCUSSION

In this study, to elucidate the climatic conditions that drive the growth of the same tree species under different climatic conditions, we monitored stem radial growth of trees over two consecutive years at the northern and southern distribution edges of *Acacia tortilis* to investigate its growth dynamics in the different climatic conditions. We hypothesized that (1) the total annual growth will be higher and the growing season will be longer at the SA site due to the more mesic conditions (i.e., characterized by moderate heat and humidity and seasonal

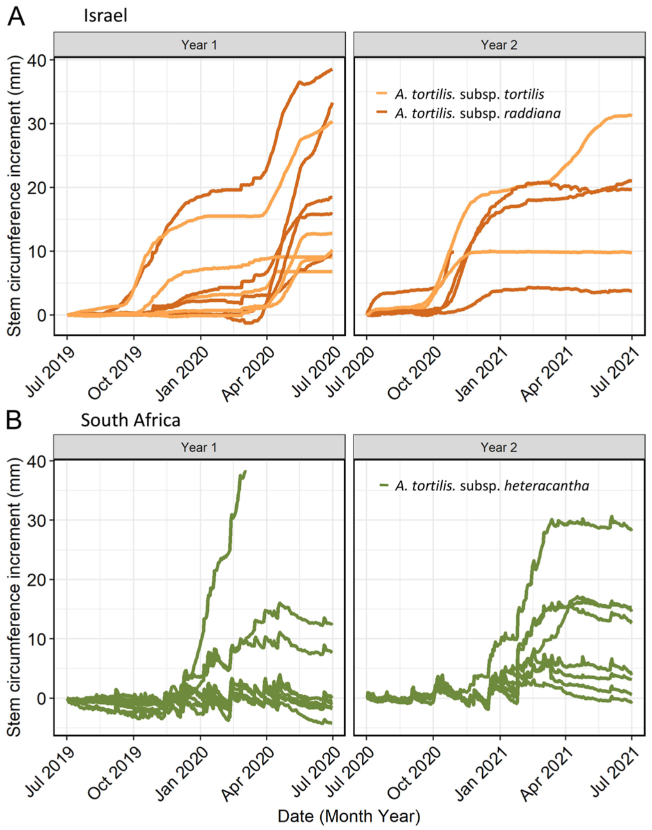

FIGURE 3 Daily cumulative stem growth of *Acacia tortilis* in (A) its northern edge at Wadi Sheizaf (Arava Valley, Israel) and (B) its southern range edge at Skukuza (Kruger NP, South Africa) from July 2019 to July 2021. Each line represents a single tree ($N = 10$).

supply of moisture) in comparison to the extreme hot and dry conditions at the IL site and (2) that the growing season of the trees at each location will correspond with the optimal local conditions for growth, mild temperatures of 20–25°C, and high water availability. Counterintuitively, our results showed that (1) growth was higher at IL than at SA and that (2) high temperatures (optimum of 27.5°C) facilitated growth at the arid IL site, while high humidity favored growth at the more humid SA site.

Higher annual growth in desert vs. savannah

Why was growth halted and 51% lower at the SA site than at the IL? And why were fewer trees actively growing at SA than IL (Figures 3 and 4)? Although tree intrinsic factors might offer an explanation, we cannot assume that the growth potential of *A. tortilis* subsp. *heteracantha* is lower than that of the other subspecies, especially since the cumulative growth of some of the *A. tortilis* subsp. *heteracantha* trees at SA was similar to that of the subspecies at IL. In addition, climatic factors were not more limiting in SA than in IL (below). We rather propose that it was an indirect effect of climate that caused this result. The humid and adequate conditions at SA (Figure 2D) allow other plant species to develop in this environment, producing a savannah with thickets of various tree canopies, thereby competing with the studied trees. Indeed, woody vegetation cover at the SA savannah site is far denser than the vegetation surrounding *Acacia* trees in the sparse IL desert site. While at both sites, *A. tortilis* trees were 5–20 m apart, gaps at the IL site were devoid of trees (Figure 1B), but they were largely occupied at the SA site by other trees and shrubs of similar or taller stature by an herbaceous layer (Figure 1C). It is therefore possible that the higher competition (e.g., for soil moisture and light) might have stunted *A. tortilis* growth at the SA site. For example, in a semi-arid forest site 80 km northwest of the IL site, tree growth doubled after trees were thinned from 300 to 100 ha^{-1} (Tsamir et al., 2019). The contrast between our two sites is even greater, with ~10 trees ha^{-1} at the Arava site in IL (Nezer et al., 2017) vs. 600–800 trees ha^{-1} at the KNP site in SA (Brits et al., 2002). Tree–tree competition, either interspecific (Bacelar et al., 2014) or intraspecific (Gouveia and Freitas, 2008), is a major force in shaping savannah vegetation, especially in Africa (Staver et al., 2019). Herbaceous vegetation (especially early in establishment) strongly competes with woody vegetation in African savannahs (Knoop and Walker, 1984) and could be an additional contributing factor for the limited growth of SA *Acacia* trees compared to IL. For example, February et al. (2013) found that grass removal in experimental plots within KNP significantly increased growth of juvenile trees (height and basal area). *Acacia* trees have the ability to develop a wide,

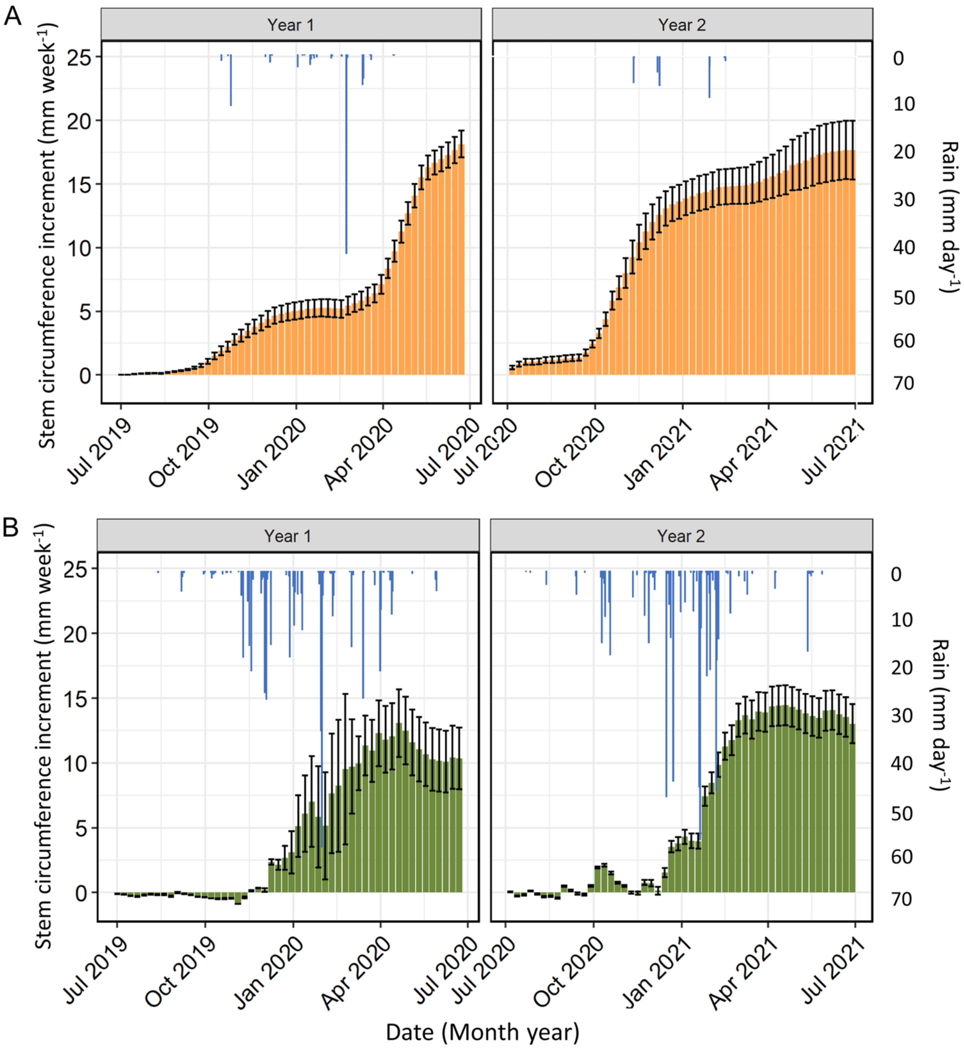

FIGURE 4 *Acacia tortilis* cumulative weekly stem growth in (A) Wadi Sheizaf (Arava Valley, Israel) and (B) Skukuza (Kruger NP, South Africa) from July 2019 to July 2021. Vertical blue bars represent local rain events.

deep root system that allows them to reach deep soil water reservoirs (Stave et al., 2005; Do et al., 2008; Sher et al., 2010; Winters et al., 2018). Studies from the hyperarid Arava (IL) suggest that the root system of acacia trees reach a depth of 7–10 m based on $^{18}O/^{16}O$ isotopic ratios in water samples extracted from *Acacia* twigs compared with those from nearby water sources (Sher et al., 2010) and on mapping electrical resistivity of belowground soil layers using electrical resistivity tomography (ERT) (Winters et al., 2015). In addition to facilitating growth under extreme aridity, reduced competition aboveground is as important belowground (Rog et al., 2021).

Another major difference between the tree growth dynamics of the desert (IL) vs. savannah (SA) was that stems of SA trees expanded and contracted more notably than IL trees (Figure 3). We suggest that this behavior is a result of higher rain and RH at the SA site because water content in the tree is linearly coupled to fluctuations in the stem radius (Zweifel et al., 2016). Variations in daily stem diameters also indicate that the physiological processes involved differ among species (Vandegehuchte et al., 2014). Therefore, we assume that higher water availability in the SA trees caused stem fluctuations, while the IL trees had a constant source of underground water (Winters et al., 2015) that allowed them to grow more and fluctuate less. Soil water availability is essential for tree growth (Reich et al., 2018; Flo Sierra, 2021); however, in trees in their natural habitat, following the roots to the depth they reach water is challenging. Therefore, we were not able to include soil water as an explanatory factor in this work.

Variation in tree growth among *Acacia* populations

Trees grew at the SA site during the summer between December and March and at the IL in the fall during October and November and resumed between April (spring) and June (early summer). At SA, growth began in December following

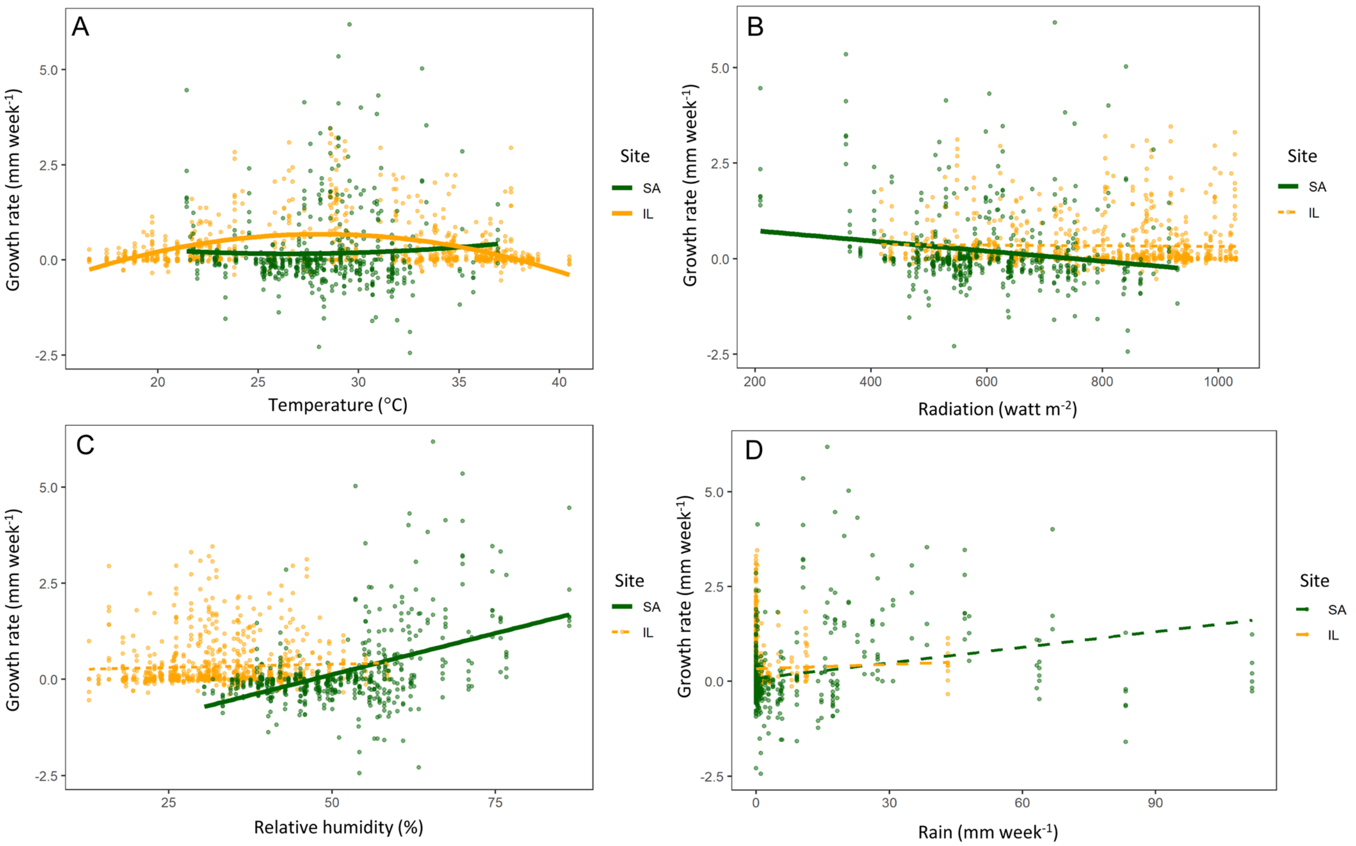

FIGURE 5 *Acacia tortilis* weekly growth rate as a function of climatic predictors (A) temperature, (B) radiation, (C) relative humidity, (D) and rain (D) in Israel (yellow) and South Africa (green). Solid fitted lines represent the significant fitted lines based on GLMMs M3 and M4 (Table 1). Nonsignificant effects are presented in dashed lines.

the start of the rains until the end of the rainy season in April and May. At IL, the stem growth dynamics presented in this study for *A. tortilis* subp. *tortilis* and subsp. *raddiana* are very similar to those presented in our previous study (Winters et al., 2018), showing no association with rain events. Summer tree growth in IL is an exception for hot deserts rather than the norm, and trees tend not to grow in the summer, considering that it coincides with the dry season (Turner, 1963; Klein et al., 2013). In contrast, summer in SA coincides with the wet season (Figure 2D), as it does across the East African savannahs (Kniveton et al., 2009), ensuring suitable water supply and warm temperatures for tree activity. Therefore, growth in the summer might be genetically programmed in *A. tortilis* and reflect its origin in the southern hemisphere (Shrestha et al., 2002). Genetic control over growth is known in trees, e.g., in the case of pines in IL, which grow new needles in the summer, despite the 6-month seasonal drought (Klein et al., 2005).

The summer growth of the IL population might also be related to the higher seasonal variability in climate compared to that in SA. The climatic variability hypothesis states that terrestrial organisms distributed in highly variable environments (e.g., high latitudes or elevations) are adapted to withstand a broader range of climatic conditions than organisms in less variable environments (Stevens, 1989). The higher growth and unusual seasonality at the IL site can also be explained by yet another hypothesis. In edge populations, especially at the hyperarid IL site, selective pressure on the trees is high. Along the pathway of migration from the center of distribution toward the edges (Rodger et al., 2018), only the individuals adapted to extremely high temperatures and low water availably survived. Those individuals that founded edge populations such as the IL population are adapted to grow at high temperatures with low rainfall. In this context, the diurnal minimum temperature is also an important factor limiting tree growth. The daily fluctuation of temperature at the SA sitewas stronger than at the IL site, especially during the winter. While the minimum temperature at IL was always >5°C, at SA, the temperature on most winter nights was <5°C and even reached 0°C in June (Appendix S2, Figure S4). Frost is one of the most limiting factors for plant growth, sometimes inducing dormancy to protect against night frost (Carevic et al., 2015).

Differential climatic drivers of *Acacia tortilis* growth in its opposite range edges

In our statistical analyses, we included all climatic variables at both sites to test whether their effect differed between the two sites. We found a significant difference between sites and in the interactions of sites with climatic variables, meaning that climatic conditions affected stem growth differently at the two sites. Tree growth was driven by a unimodal effect of increasing temperature at the IL site with a peak at 27.5°C and by increasing relative humidity at SA, especially when RH > ~55%. Rain was a problematic variable for several reasons. At the IL study site, the rain regime differed greatly between the 2 years, but the annual growth increment of the trees did not significantly differ between the years (18.4 vs. 17.6 mm tree^{-1}). We suggest that the alluvial and drainage characteristics of the Sheizaf Wadi influence the storage of moisture—and therefore the amount of rain does not necessarily reflect the soil moisture regime experienced by *A. tortilis* trees in the wadi (Winters et al., 2018).

Another way to test tree-growth–climate interactions is by determining thresholds. Our analysis showed active *Acacia* growth (>0.1 mm week^{-1}) at IL when solar radiation was greater than 500 watt m^{-2} and temperatures higher than 22°C and lower than 39°C. At SA, trees grew when solar radiation was less than 600 watt m^{-2}, the temperatures wad higher than 26°C but lower than 37°C, and relative humidity was 48–65%. The overlap between these thresholds at IL and SA is at a narrow solar radiation range of 500–600 watt m^{-2} and narrower (SA) temperature range of 26–37°C. Overall, IL trees grew at higher radiations and higher temperatures. Generally, under a similar RH, trees from cooler environments may benefit from mild warming, but trees from warmer environments will not (Way and Oren, 2010). The finding of a warmer low-temperature threshold of *Acacia* growth at the SA site compared with that of the IL (26°C vs. 22°C, respectively) supports this general trend.

Implications for tree growth as climate changes

With the expected movement of species both north- and southward in the present and predicted climate (Chen et al., 2011; Lawler et al., 2013; Boisvert-Marsh et al., 2014), conserving tree populations at the edges of their geographical distributions and deciphering their growth patterns are especially important (Gibson et al., 2009). Here, we monitored the growth of *A. tortilis* across 6500 km and 54 latitudes and variations in climatic conditions. We found that tree growth–climate interactions changed between the different edges of distribution. For example, if the trees of the SA population, which were mostly affected by air humidity (RH%) was growing at the IL site with low RH%, they would have a very narrow window for growth and would probably not be able to complete a growing season. Vice versa, if the IL populations, which were mostly affected by high temperatures, were growing at the SA site, their growth would be suboptimal. Given the fast climatic changes, which influence populations in the edges of the distribution (as our studied *Acacia*) (Lawal et al., 2019; Lyam et al., 2022), we suggest two possible future scenarios: First, *A. tortilis* will expand into mesic sites, which will become warmer and drier. Alternatively, different phenotypes will develop, an important mechanism for species to adapt to fast-changing environmental conditions. We will test this possibility using a common garden experiment with seeds from the species' distributional edges as part of our follow-up research on this topic. Other questions concern the *A. tortilis* core populations in East Africa. Is their growth driven by temperature or by humidity? And where in the distributional range do drivers of growth shift? At the savannah–desert border or by latitude? These questions remain to be answered. Finally, climate was not the sole driver of these growth patterns, as the higher growth in the IL desert site might be explained by reduced competition. Adding species interactions is important to better understand and simulate the fundamental ecophysiological phenomenon of tree growth, increasing the complexity of our analyses and models.

AUTHOR CONTRIBUTIONS

G.W. and T.K. established the monitoring plots in Israel and South Africa. D.U. performed the data and statistical analyses under the guidance of E.S., T.K., and G.W. I.S. and D.M. coordinated measurements in South Africa. D.L. created the distribution map. D.U., T.K., and D.L. wrote the paper with help from all coauthors.

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COMPETING INTERESTS

Authors declare that they have no competing interests.

DATA AVAILABILITY STATEMENT

The full data are available on Figshare at https://doi.org/10.6084/m9.figshare.21779819.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

APPENDIX S1. Supplementary tables.

APPENDIX S2. Supplementary figures.

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