Research paper

A montane species treeline is defined by both temperature and drought effects on growth season length

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Montane treelines are defined by a threshold low temperature. However, what are the dynamics when the snow-free summer growth season coincides with a 6-month seasonal drought? We tested this fundamental question by measuring tree growth and leaf activity across elevations in Mt Hermon (2814 m; in Israel and Syria), where oak trees (*Quercus look* and *Quercus boissieri*) form an observed treeline at 1900 m. While in theory, individuals can be established at higher elevations (minimum daily temperature >6.5 °C for >4 months even at the summit), soil drying and vapor pressure deficit in summer enforces growth cessation in August, leaving only 2–3 months for tree growth. At lower elevations, *Q. look* Kotschy is replaced by *Quercus cerris* L. (1300 m) and *Quercus calliprinos* Webb (1000 m) in accompanying *Q. boissieri* Reut., and growth season length (GSL) is longer due to an earlier start in April. Leaf gas exchange continues during autumn, but assimilates are no longer utilized in growth. Interestingly, the growth and activity of *Q. boissieri* were equivalent to that of each of the other three species across the ~1 km elevation gradient. A planting experiment at 2100 m showed that seedlings of the four oak species survived the cold winter and showed budding of leaves in summer, but wilted in August. Our unique mountain site in the Eastern Mediterranean introduces a new factor to the formation of treelines, involving a drought limitation on GSL. This site presents the elevation edge for each species and the southern distribution edge for both the endemic *Q. look* and the broad-range *Q. cerris*. With ongoing warming, *Q. look* and *Q. boissieri* are slowly expanding to higher elevations, while *Q. cerris* is at risk of future extirpation.

Keywords: cambial growth, endemic oak, growth season length, high elevation, leaf activity, Levant.

Introduction

Montane treelines

There has been extensive exploration of the biotic and abiotic conditions that determine the elevation above which trees cease to grow. Forests are limited in growth at high elevation by a line above which tree growth is absent or stunted. This line, often referred to as the treeline, can be quite visible. In other cases, rather than a clear-cut, definitive boundary, it is a less distinct, gradual change along a steep gradient, from a closed canopy forest to fragmented stands (Körner and Paulsen 2004). Soil and climate are traditionally thought to be the major factors determining the distribution of plant communities and species. Availability of light and water determines photosynthetic rates,

thus setting an upper limit to biomass growth. At the same time, historical variables such as human intervention and biotic factors are also known to strongly influence plant distribution (Hättenschwiler and Körner 1995). Bader et al. (2007) mention different factors, such as low temperatures, competition, soil properties, fires, dispersal ability and excess solar radiation, as limiting the ability of trees to grow in alpine environments. Körner and Hoch (2006) suggested soil temperature as a decisive factor: temperatures below 6–7 °C, whether in root or stem, will prevent tree growth because of insufficient meristem activity. Körner et al. (2016) suggested that temperature, light and wind speed can be integrated to define the time span, or the number of days, permitting tree growth per year. To complete a

growth cycle, trees would need ~100 days with temperatures exceeding 6–7 °C. Seed availability may be another factor affecting the dispersal of trees above the treeline. Loranger et al. (2016) examined the effect of soil temperature and moisture on germination and seedling establishment in five European treeline species. They found that these growth parameters are limited by either temperature or moisture, and that idiosyncratic responses characterized the different tree species. Indeed, not more than 100 tree species worldwide are capable of living as trees at the climatic treeline, i.e., where temperatures exceed 6–7 °C for only ~100 days per year. The world's highest treelines are inhabited by the angiosperm *Polylepis tarpacana* (Rosaceae) at 4810 m elevation in the Bolivian Andes (Rada et al. 2001, Hoch and Körner 2005), and by gymnosperm *Juniperus* spp. (Cupressaceae) in Tibet, forming trees between 4700 and 4900 m elevation (Bosheng 1993, Miehe et al. 2007). Treeline elevation decreases at higher latitude, but sometimes observed treelines of the dominant tree species are found at elevations lower than would be predicted based on climate conditions alone, suggesting a widespread and strong role of past human influence. *Fagus sylvatica* treelines at 1700–1900 m in the Apennine Mountains (Italy; Vitali et al. 2017); the 1900 m treeline in Amanos Mountains (Turkey; Türkmen and Düzenli 1998); and a *Quercus macranthera* treeline at 2850 m in the Alborz Mountains (Iran; Noroozi and Körner 2018) belong to such 'anthropogenic' treelines. The poorer and younger the local flora, and the more isolated it is from cold regions, the more likely will treeline tree taxa be missing.

Montane treelines under climate change

Montane flora and treelines are expected to change and shift with global warming and climate change. Warming-induced expansion of trees and shrubs is observed and predicted in other cold-limited regions like the Greenland tundra (Normand et al. 2013). Whether ongoing warming will induce a re-colonization by a rich woody flora depends on the roles of local climate and migration limitations in shaping species ranges. Pauli et al. (2012) examined changes in vascular plant species richness in summits across Europe along the past decades. They found that in boreal-temperate regions, species richness in sum-mits increased by 3.9 species on average, and in Mediterranean regions, it decreased by 1.4 species, on average. This difference in species richness can be explained by the positive effect of warming in Northern Europe and the decreased water availabil-ity in Southern Europe. Harsch et al. (2009) examined 166 sites across the globe where treeline information was available since 1900 and found that in 52% of the cases, the treeline advanced, whereas, in only 1% of the cases, the treeline receded. They also found that treelines with a diffuse form were more likely to advance than those with abrupt form. By examining high elevation tree rings in bristlecone pines (*Pinus longaeva*), Salzer et al. (2014) found that since the mid-1990s, south-facing trees

in the White Mountains of California experienced a decline in growth rates, possibly reflecting climate change. Peñuelas and Boada (2003) describe an elevational upward shift of ~70 m in beech (*Fagus sylvatica*) forest and heather (*Calluna vulgaris*) shrublands at the highest elevations, which, in turn, are being replaced by holm oak (*Quercus ilex*) forest at medium elevations, in North East Spain. Across Western and Central Asia, treelines are typically formed by species of the conifer genus *Juniperus* (Noroozi and Körner 2018). In the Alborz Mountains of Iran, the absence of trees between 2850 and 3300 m was explained by the eradication of *Juniperus excelsa*. In these regions, growth of montane vegetation is limited by both temperature and aridity. For example, *Lagochilus olgae* shrubs growing at 1850 m in the Nuratau Mountains of Uzbekistan showed loss of regeneration in drought years (Akhmedov et al. 2021). The parallel 3.5‰ increase in $\delta^{13}C$ in leaves of these shrubs indicates that severe water stress affects its growth even at high elevations. Al-Qaddi et al. (2017) investigated current and future distributions of *Quercus coccifera* in the Eastern Mediterranean. By employ-ing ecological niche modeling, a considerable shrinking of *Q. coccifera* range is projected in 2050–2070, however with an upward elevational shift (Al-Qaddi et al. 2017). In the montane parts of the Mediterranean, an ongoing increase in temperature, with no increase in precipitation, means that both evergreen and deciduous oak species (*Q. ilex* and *Quercus pyrenaica*, respectively) will decrease in productivity (Gea-Izquierdo et al. 2013). While the more drought tolerant *Q. ilex* may profit from warming at cold northern locations, the two species would reduce productivity at warm, dry locations. Finally, models of treeline response to global change in the Mediterranean area should account for land-use history (Vitali et al. 2017).

Tree response to prolonged seasonal drought in montane and Mediterranean forests

In Mediterranean environments, the growth and productivity of deciduous oaks are linked to late-spring–early-summer hydrologic balance (Di Filippo et al. 2010, Kopler and Bar-Shalom 2019); at both annual and decadal timescales, oak growth decline is associated with a delayed response to climate (Limousin et al. 2010). The past century (1917–2016) has seen the highest average temperatures in the last 11,000 years (Bailey et al. 2021), and the decade 2000–09 was the warmest since the beginning of climatic measurements (Gottfried et al. 2012). Being sessile, long-lived species, trees are facing changes at unprecedented rates (Klein 2020). Trees growing under prolonged seasonal drought in the hot and dry fringes of the Mediterranean should be well-adapted to such changes (Rog et al. 2021). For example, in the evergreen *Q. ilex*, stem growth is dually controlled by winter temperature and summer drought (Lempereur et al. 2017). Physiological responses include frequent and prolonged stomatal closure (Wagner et al. 2021) and reliance on intrinsic carbon reserves

(Tsamir-Rimon et al. 2021). At the upper treeline, trees are growing at their physiological range limit, and thus the upper forest belt is useful to study climate–vegetation interactions (Bailey et al. 2021). Körner et al. (2016) suggested that individuals of a (tree, in this case) species can act as 'natural experiments' examining survival under unusual circumstances. Several studies made in montane areas suggested warming-induced upward range shifts of animals and plants (Gottfried et al. 2012), with evidence of the decline of cold-adapted species and increased warm adapted species occurrence. They describe this process as thermophilization. Salzer et al. (2014) examined bristlecone pine tree rings from the White Mountains of California. They found a positive growth response to warming climate at the treeline, and no such response below this line.

Research objective and hypotheses

The concept of temperature limitation on growth season length (GSL) allowed Körner et al. (2016) to estimate global treeline elevations. Notably, the treeline of Mt Hermon in the Levant (1900 m; see Figure S2 available as Supplementary data at *Tree Physiology* Online) is significantly lower than expected (3300 m). Seedling establishment below 1900 m is evidence for seed viability; the area has been protected for the past five decades, but deforestation might have occurred earlier, potentially removing trees at higher elevations. This research aimed to gain knowledge on the ecology of the dominant woody species (the deciduous *Quercus boissieri* Reut., *Q. look* Kotschy and *Q. cerris* L., and the evergreen *Quercus calliprinos* Webb.) on different elevational forest belts in a Levant mountain and specifically investigate the causes of the seemingly unexpected lower elevation of its treeline. Our objectives were as follows. (i) To Characterize the phenology of growth, cambial and leaf activity, and water status of each of the four oak species native to Mt Hermon. (ii) To calculate the GSL for each species at the corresponding elevation and link it to the local meteorological and soil conditions. (iii) To decipher the lack of trees at elevations > 1900 m. Our respective hypotheses were that (i) growth, cambial and leaf activity peak in early summer are lower in *Q. boissieri* (the generalist species) than its companion oak species (specialist species); (ii) GSL shortens with elevation due to later start in spring temperature limitation, and ends in summer when soil moisture declines; and (iii) the apparent low treeline is rather a species treeline shaped by millennia of deforestation and forest degradation and the lack of 'true' (climatic) treeline species to populate the physical treeline.

Materials and methods

Mt Hermon: geography, vegetation and climate

Mt Hermon is located in southwest Syria and north-eastern Israel (33°25′N, 35°48′E) along the border with Lebanon. It is an elongated anticline that extends NE-SSW for 55 km long and 25 km wide (see Figure S1 available as Supplementary data at *Tree Physiology* Online; Shamir et al. 2016) of which precipitation above 1500 m consists mostly of snow (Auerbach and Shmida 1993). Mt Hermon's elevation extends from 300 to 2814 m. Its bedrock is Jurassic limestone, and the terrain is characterized by rocky cliffs (Auerbach and Shmida 1993). Most of Mt Hermon's climate is defined as Mediterranean with two apparent seasons—long, dry and hot summer in contrast to cold, strong winds, rainy and snowy winter. The temperature range is quite broad, from up to 33 °C in September to −5 °C in February at 1500 m. Solar radiation and precipitation increase with elevation (Rimmer and Salingar 2006), while temperature decreases. Mt Hermon average annual precipitation is ∼1200 mm (Shamir et al. 2016). The Hermon Mountain range contributes to ∼70% of the water inflow to Sea of Galilee (Zohary et al. 2014). The mountain Flora is quite diverse, including 903 species thriving between 300 and 2800 m while some are endemic to the Hermon region. The specimens of the floristic species were found and collected in past floristic studies (Shmida 1977, 1980). Flora at the upper subalpine belt (1900–2800 m) is sparse, consisting of shrubs, geophytes and herbaceous plants. The mid floristic belt (1300–1900 m) is mainly characterized by deciduous oak trees (*Q. boissieri*, *Q. look* and *Q. cerris*) accompanied by shrubs and geophytes. The lower vegetation belt (300–1300 m) is mainly dominated by evergreen oak, *Q. calliprinos*, accompanied by deciduous *Q. boissieri* and evergreen shrubs (Auerbach and Shmida 1993). The research was carried out for almost 2 years in three vegetative belts on Mt Hermon: a subalpine tragacanth belt at 1900–2800 m, a xero-montane open forest extending over elevations of 1300–1900 m, and an evergreen Mediterranean maquis, which extends to an elevation of 300–1300 m (Figure 1).

Oak species of Mt Hermon in the Levant

Within the remarkable diversity of the genus *Quercus*, several species inhabit the Eastern Mediterranean. This region served as oak refugia and as a source for ancient westward range expansions (Bagnoli et al. 2016). Indeed, the genetic diversity of *Q. cerris*, a wide-range species in the subgenus cerris, section cerris, is higher in the Levant than elsewhere. Its endemic relative, *Q. look*, differentiated from it only during the Pliocene, and is also closely related to *Quercus libani* (Simeone et al. 2018, Hipp et al. 2020). Other species in the subgenus cerris, yet in the section ilex, include the sclerophyllus evergreen *Q. calliprinos*, the Levant vicarious species to the western Mediterranean *Q. coccifera*; the two differentiated from each other also during the Pliocene. In the subgenus quercus, section quercus, *Q. boissieri* inhabits the south Levant, and was differentiated from *Q. infectoria*, now inhabiting the North Levant, only during the Pleistocene (Stephan et al. 2016, Hipp et al. 2020). In the southern Levant, annual rainfall is high on the coast and in the North, and
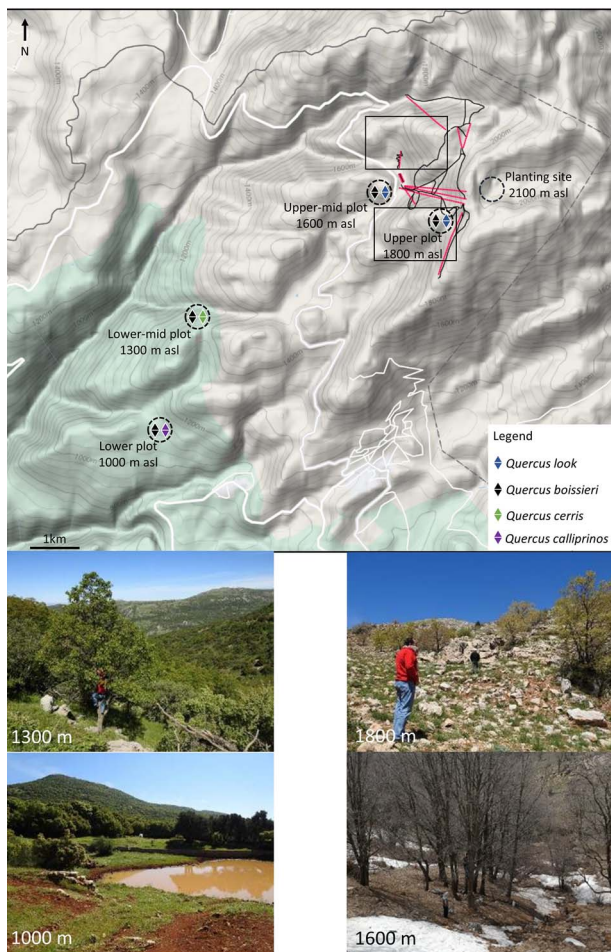
Figure 1. Terrain image of the study area on the southern slopes of Mt Hermon (acquired using Google maps). Circles indicate the four research plots and a planting site, with photographs in lower panels. Rhombuses denote the four species of the naturally occurring oaks in each plot at different elevations on the mountain. All research plots are ~1000 m² in size. Rectangles denote regions where tree cover was monitored by remote sensing methods (see Figure 10). Photographs were taken in May 2020, except for 1600 m (March 2019).

diminishes eastwards and southwards (Langgut et al. 2015). Archaeobotanical studies revealed that, in prehistoric times, large parts of the landscape in the southern Levant were covered by forests, in which several species of oak were present (Rosenberg 2008). *Quercus ithaburensis*, *Q. boisierri*, *Q. calliprinos*, *Q. cerris* and *Q. look* are reaching their southernmost distribution in the Levant. The latter two species are limited in Israel to Mt Hermon, in Northern Israel (Figures S1 and S2 available as Supplementary data at *Tree Physiology* Online). *Quercus calliprinos*, alongside *Phillyrea latifolia*, and few other species, define the southernmost extent of maquis in Israel and the Middle East.

Meteorological data

Meteorological data were obtained from two meteorological stations. The first station is located adjacent to the planting site (33°18′27″N, 35°47′07″E, Hermon ski site, 2048 m), and belongs to Tel Aviv University. Meteorological data consisted of minimum and maximum air temperature (HUMICAP 180R sensor, Vaisala, Vantaa, Finland). We installed the second meteorological station (Meteorological station model—iMETOS 3.3, by Pessl Instruments GmbH, Weiz, Austria) in the lower mid plot (33°17′18″N, 35°44′21″E, ~1300 m). The station was powered by a solar panel and included a rain gauge, wind speed, air temperature and relative humidity sensors (RH, %). Meteorological data were uploaded to the cloud from the data logger by a cellular modem. The measuring interval was set to 5 min by default. In addition, temperature, relative humidity and vapor pressure deficit (VPD) were measured in each of the four plots during measurement campaigns by the infra-red gas analyzer (IRGA; see below). These in-situ data were used in all analyses of leaf activity.

Research plots

The research included five research plots along an elevation gradient (Figure 1; Table 1). At the highest elevation of the Israeli mountain (2100 m), above the species treeline, a planting experiment was conducted at a planting site. Other than this site, the other four measuring plots were located within natural maquis or forest. At the planting site, seedlings were planted in a small array of 3 × 10 m at 2048 m (hereafter referred to as 2100 m), at a flat surface with shallow fine-grained leached soil filled with limestone rocks and stones (Auerbach and Shmida 1993). The planting site is located 200 m east to the upper cable station, and next to a research facility of Tel Aviv University (Figure 1). Measurements for lower plots (1075, 1353, 1623 m a.s.l. hereafter referred to as 1000, 1300, 1600 m) commenced during May 2019, with the exception of the 1787 m a.s.l. (hereafter referred to as 1800 m) plot, where measurements started during May 2020. The plots' locations were chosen based on elevation and representation of the dominant oak species (Figure 1; Table 1). Average size of the four measurement plots was 1000 m² at a relatively square shape. Ten trees were randomly sampled in each plot and marked, 5 trees of each dominant oak species; in total, 40 trees were measured throughout the research. Stand density was calculated by stretching two 33 m lines in 90° to each other. Two people walked in each side of the plot, counting in each direction all tree genera that were at least 3 m high. The total number of counted trees per plot was multiplied by 10 in order to get density estimation in hectare.

Continuous soil moisture measurements

Volumetric soil water content (SWC) was measured once an hour using a Phytech soil moisture sensor (Phytech Company, Rosh Haain, Israel) with a range of 0–57% of volumetric water content. Six sensors were installed at each plot, at three different locations; two in an open area and four for sampled oak species.

Table 1. Main characteristics of four research plots on Mt Hermon. Tree height and diameter at breat height (DBH) values for the oak species are means $\pm$ SE ($n = 5$).

Plot	Aspect	Species	Density (trees ha^{-1})	Tree height (m)	Tree DBH (cm)
1800 m	South	*Q. look*	250	5.6 ± 0.4	17.8 ± 1.7
		Q. boissieri	250	5.8 ± 0.3	21.3 ± 2.0
1600 m	Northwest	*Q. look*	80	10.0 ± 1.2	25.2 ± 3.0
		Q. boissieri	120	10.2 ± 0.6	30.4 ± 5.1
		Crataegus aronia	310		
1300 m	Northwest	*Q. cerris*	70	13.6 ± 3.4	63.9 ± 27.4
		Q. boissieri	120	6.9 ± 1.5	24.0 ± 8.1
		C. aronia	180		
		Pyrus syriaca	200		
1000 m	South	*Q. calliprinos*	520	7.1 ± 0.8	29.8 ± 7.7
		Q. boissieri	440	6.9 ± 1.0	21.8 ± 3.2
		P. syriaca	330		

In each location, two sensors were installed at two soil depths; $\sim$10 and $\sim$30 cm and $\sim$20 cm at the 1800 m plot, at the root zone, i.e., a single sensor for each location/depth combination. The sensors next to the trees were installed up to 50 cm away from the stem. The data for SWC were sent to the cloud system by Phytech's cellular modem data logger; the raw data were downloaded and analyzed to create SWC (%) graph at each plot.

Continuous branch growth measurements

Cambial branch growth was estimated by monitoring diameter changes at main branches of selected trees of the four oak species during 2019–20 (at 1800 m during 2020 only). Installation on the stem suffered damage and theft, and hence we installed the sensors out of reach, on a main branch at 2–4 m height of each tree. Measured branches were 11.0 ± 0.5 cm in diameter, and overall between 6.1 and 21.7 cm. We used automatic point dendrometers (Phytech Company): point position sensors equipped with an invasive stainless-steel bolt fixed to the outer xylem measured length variations once an hour (accuracy 3 μm). The timing of cambial growth onset was defined as the first date where branch radius increased continuously for over a week (i.e., irreversibly). The timing of cambial growth cessation was defined as the first date where branch radius change changed from positive to negative. For this analysis, we considered in 2019 15 trees, while 12 trees were excluded for negligible or no growth, and two trees were excluded for continuous growth. In 2020, we considered 25 trees, while 7 trees were excluded for negligible or no growth, and a single tree was excluded for continuous growth.

Leaf phenology estimation

Leaf phenology was estimated in the three deciduous species by observing images taken by the research group during measurement days. Phenology data for the winter and spring months were mostly captured by research group members during visits.

However, to improve our temporal resolution, our dataset was complemented by observing online photos (https://www.facebook.com/skihermon) taken across elevations during recent years (2018–21). In each image, elevation was determined according to visual identification of manmade structures in the relatively small research area (Figure 1; mainly in the ski resort). Species were visually differentiated by their unique bark features. On each image, oak trees were identified, and the leaf phenology was determined by identifying whether leaves are present, budding or shedding.

Leaf gas exchange and water potential

In-situ gas exchange measurements were carried out by a portable IRGA system GFS-3000 (Heinz Walz GmbH, Effeltrich, Germany). The sensor head of the system was equipped with a red–blue LED light source inside a standard leaf chamber (8 cm^2). Net assimilation (A; μmol CO_2 m^{-2} S^{-1}), leaf transpiration (E; mmol H_2O m^{-2} S^{-1}) and stomatal conductance (gs; mmol H_2O m^{-2} s^{-1}) were measured at all plots and trees ($n = 10$ per plot, 40 overall), approximately every month during the growth season (May–November), in day time (10:00–15:00 h). Ambient temperature, RH and VPD were recorded during measurements, the flow rate of the chamber was set to 750 μmol s^{-1} and the CO_2 level in the leaf chamber was set to 400 p.p.m. constant concentration. The light intensity in the leaf chamber was set to the photosynthetic photon flux density (PPFD) recorded in an unshaded area in each specific plot at the starting time of the measurement. Each measurement was taken on a single leaf of a branch that was cut from the sunlit side of the tree using a telescopic $\sim$3–6 m tree lopper (pruning shears with a telescopic extension pole) and placed within 3 min after cutting in the IRGA leaf chamber. Gas exchange rates of sampled trees were averaged for each oak species at each month and analyzed in order to estimate the yearly and seasonal leaf gas exchange dynamics of the different oak species in

the different plots. The gas exchange rates for *Q. calliprinos* leaves were normalized to 8 cm² (IRGA leaf chamber area) due to its leaves being the only ones smaller than the chamber area. Normalization was done by taking 30 leaves from each *Q. calliprinos* tree (10 from each sunlit branch). This was done once (rather than routinely), to minimize leaf sampling banned by the Nature Reserves Authority. The leaves were scanned, and the leaf area was analyzed using ImageJ (image processing and analysis software). The area of the leaves was averaged for each tree, and a ratio between the average leaf area of the tree and the chamber area was calculated. This ratio was used to normalize the leaf gas exchange rates. Leaf water potential (LWP) was measured using a Scholander-type pressure chamber (PMS Instrument Company, Albany, OR, USA). Measurements were done at midday to capture the diurnal minimum, to detect whether trees reach LWP values risking in xylem embolism. Midday LWP was measured monthly between April and November for ($n = 5$ per species, 10 per plot, 40 overall). The LWP was measured within 3 min after cutting off a branch that was removed from the sunlit side of the tree using a telescopic $\sim$ 3–6 m tree lopper and thereafter cutting off a live twig with leaves that fit in the pressure chamber ($\sim$10 cm in length).

Seedling survival experiment

In order to examine seedling survival beyond the treeline limit, we planted 34 seedlings of four oak species in November 2019; (15 *Q. calliprinos,* 11 *Q. boissieri,* 4 *Q. cerris,* 4 *Q. look*). The seedlings were germinated from acorns from different sources and were grown in the Barnea Oak Nursery in Herev Le'et, Israel. Although study trees produced acorns, their collection was banned by the Nature Reserves Authority (see above), and hence seed sources were outside the site (except for *Q. look* that was under special permit). The sources of the acorns were: *Q. calliprinos*—various sites in Israel, *Q. boissieri*—various sites in Israel, *Q. cerris*—Berlin botanical gardens, *Q. look*—Mt Hermon. The seedlings were planted in $\sim$15 cm deep holes in the ground and each of the planted seedlings was watered with $\sim$5 l of water. The seedling's stem elasticity, leaves and buds occurrences were documented, and their height was measured throughout the growth season in order to examine their survival and growth.

Tree distribution dynamics through aerial and satellite images

Past aerial images of Mt Hermon ridge captured by the mapping department of The Survey of Israel were acquired for 1971–92. Aerial Images were georeferenced relative to a Google Earth satellite image of the examined area from 2014, acquired by a CNES airbus satellite. The high-elevation region in that satellite image was analyzed by a human interpreter to detect existing tree stands. Once a tree stand was found, its exact location was first examined in the earliest aerial footage (1971) and then in subsequent aerial footage to identify whether tree stands existed in past images. Two distinct areas with sparse tree stands were selected for analysis using a time series of all the images. Change detection along five decades in tree occurrences was performed.

Statistical analysis

Statistical analysis was conducted to test the effects of elevation, species, and month, nested in year, on oak leaf activity in 2019 and 2020. A least-square mean (LSM) model was conducted without the random variable (month), by elevation and separately for the 2 years of the study (2019, 2020). Prior to the LSM model test, a Levene variance test was performed and it was found that the variances were equal. Effect test of explaining variables (VPD, Species, Species × VPD) was then used in order to determine the significance of differences in each of the examined parameters (A, E, gs and LWP). Species comparisons were made for one to two elevations according to species elevational ranges. All statistical analysis was performed using JMP statistical analysis computer software (version 1.8; SAS, Cary, NC, USA).

Results

Meteorological conditions on Mt Hermon 2019–20

During the research period (July 2019–December 2020), the average diurnal maximum air temperature at 2100 m was 13.9 °C (note the missing data on 27.1.20–6.5.20, sensor malfunction during winter; Figure 2A). During summer, temperatures reached up to 30 °C in 2019 and above that in 2020. Two distinct heatwave events were recorded during July and September 2020. During wintertime, the lowest temperature measured at 2100 m was −4.8 °C, in late January at night, while data were missing for the rest of winter. Precipitation at this elevation is mostly in the form of snowfall in winter, albeit measurements were not available. At 1300 m, the average diurnal maximum air temperature was 16.1 °C (Figure 2B). During a September heatwave, the average VPD reached 5 kPa. The lowest measured temperature at 1300 m was −5.8 °C during the night in early February. Total precipitation during 2020 was 1382 mm, higher than the annual average of $\sim$1200 mm. Despite these seemingly wet conditions, the dry season lasted from the end of May until the end of October, with only 68.6 mm of rain in 5 months. This long seasonal drought was prevalent across the entire mountain area, from base to summit. Solar radiation from April to September was $\sim$1100 W m⁻², and between October and May—not higher than $\sim$400 W m⁻², due to the high cloud cover (Figure 2C). In the long-term, there has been an increase in the mean annual temperature anomaly during the past three decades, as recorded in the Meteorological station in Safed, 60 km SW of Mt Hermon, at an elevation of 900 m (Figure 2A, inset). At the most extreme, the year of 2010 was 3.4 °C warmer than the year of 1992.
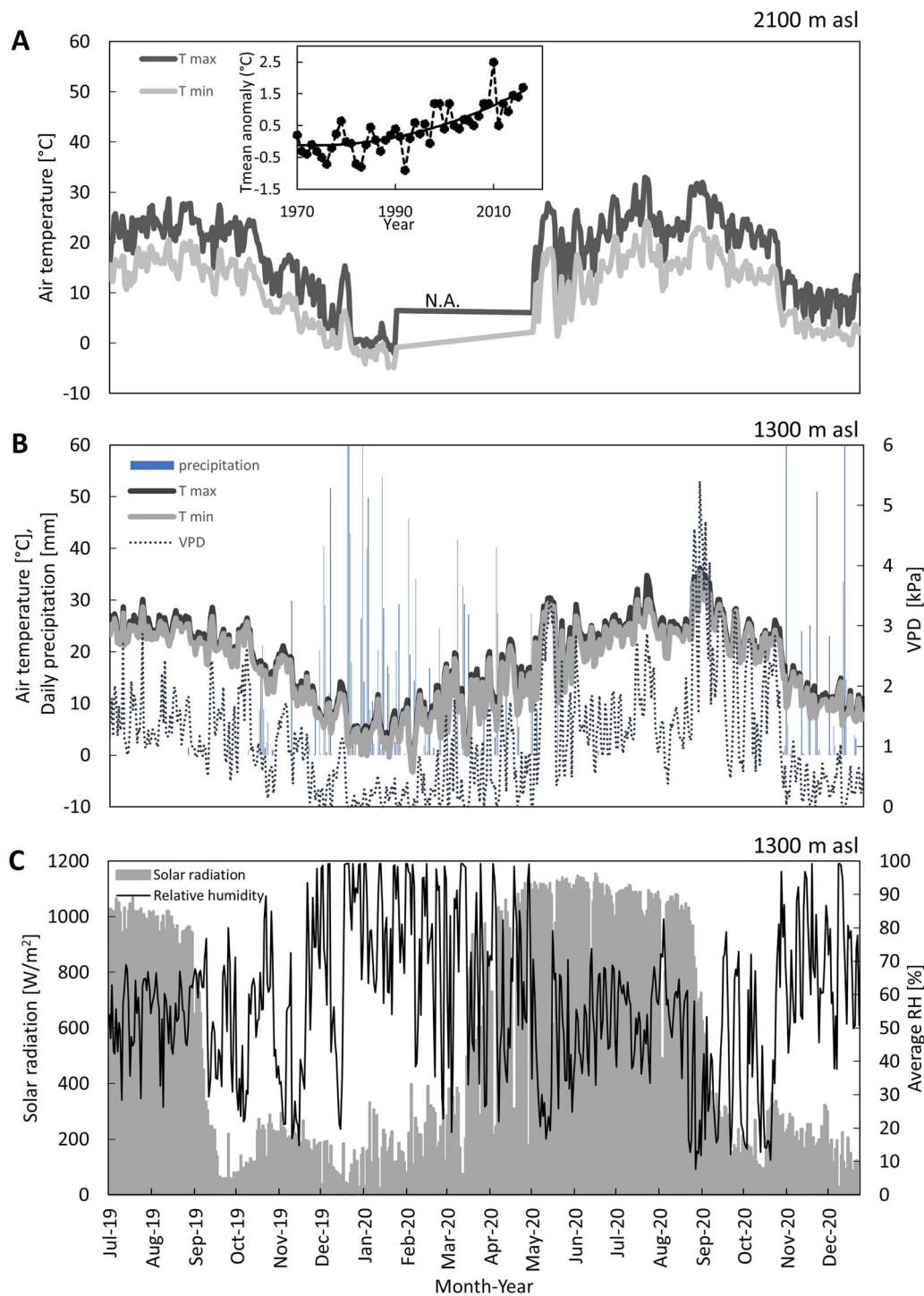
Figure 2. Meteorological conditions in Mt Hermon (1300, 2100 m a.s.l.) in 2019–2020, and mean temperature anomalies for the past 50 years in a nearby mountain site (60 km SW; inset). (A) Daily maximum and minimum air temperature at 2100 m. (B) Daily maximum and minimum air temperature, noontime VPD and daily precipitation at 1300 m. (C) Daily noontime solar radiation and relative humidity at 1300 m.

Yet, also on the multi-annual trend, the recent years were 1.5 °C warmer than those of the 1970s and the 1980s.

Soil moisture dynamics on Mt Hermon

Soil water content was measured continuously in 2019 (see Figure S3 available as Supplementary data at *Tree Physiology*

Online) and in 2020 (Figure 3), with interruptions due to malfunctions in winter (December–April). Measurements were performed at two depths at each plot (at single depth at 1800 m) in locations adjacent to trees of the dominant species, or in a forest open area. In 2020, SWC fluctuated around 30%, with an absolute minimum of 4% in the deep layer (30 cm)
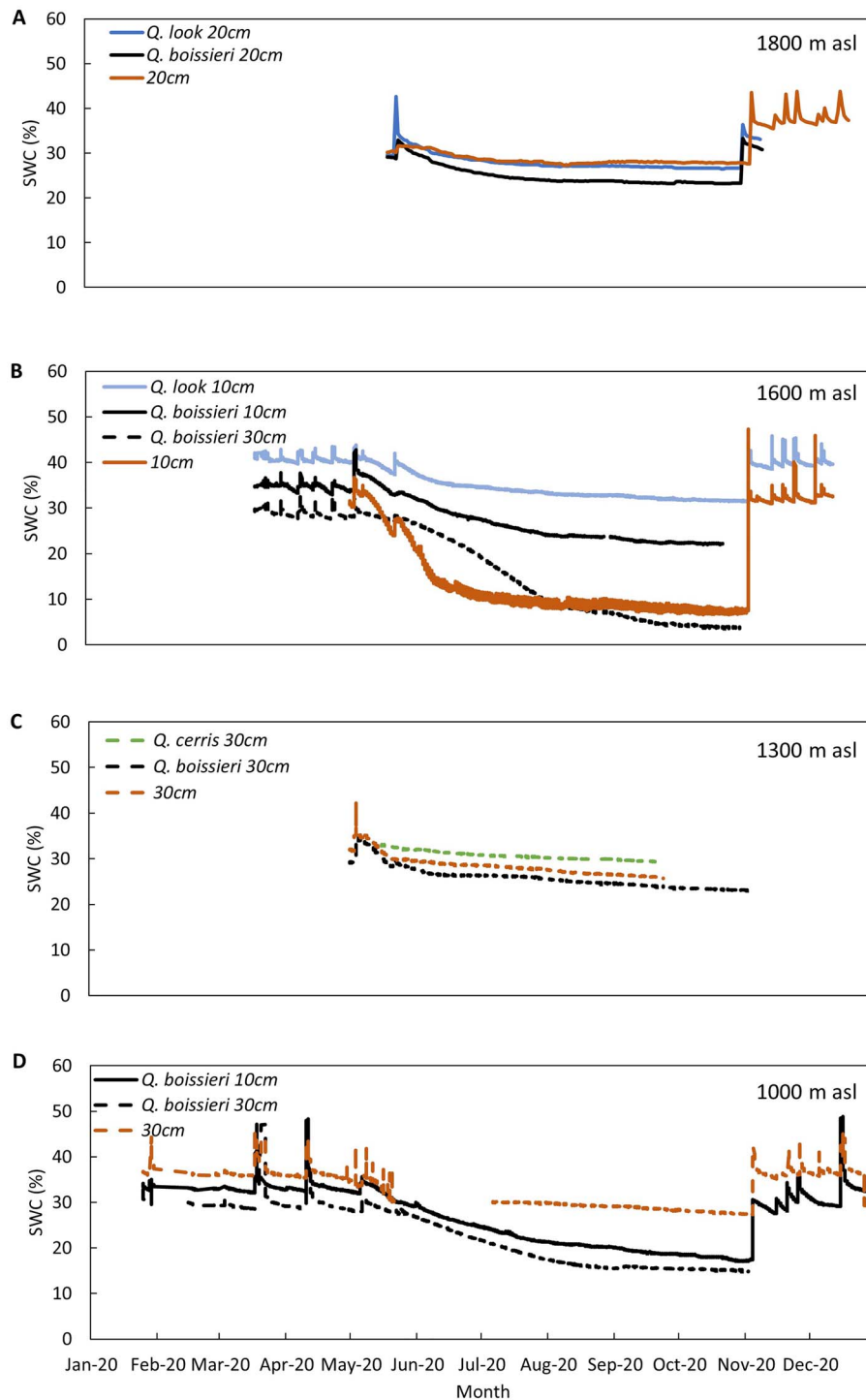
Figure 3. Soil water content in Mt Hermon during 2020, in four research plots at four elevations (1000, 1300, 1600, 1800 m a.s.l.) in two depths (10 cm, 30 cm below surface) next to trees (species indicated) and in an open area.

at the end of October in the 1600 m plot (Figure 3). Due to the negligible precipitation during summer, SWC decreased from late April to late October. These seasonal fluctuations were larger at 1600 and 1000 m, and smaller at 1300 and 1800 m. Among species, SWC was consistently lower adjacent to *Q. boissieri*. Differences in SWC between soil depths and between forest and open area were not consistent. The lowest SWC was measured adjacent to *Q. boissieri* at the 30 cm layer reaching a minimum of 4% at the end of October, while in the open, unshaded area, SWC was 8% (Figure 3B). At 1300 m, the highest SWC measured was in the open area during early May (36%), declining to 30% by the end of May. The sensor that

showed highest SWC throughout the year was adjacent to a *Q. cerris* tree in the 30 cm layer, with 32% in mid-May. At 1000 m, SWC adjacent to *Q. boissieri* gradually decreased for both layers (10, 30 cm) between May to end of October, from ~30% to ~16% with slightly higher values for the top soil. In comparison, the 30 cm layer in the open area showed a minor decrese of SWC between May and end of October from 33% to 27%. In 2019, The shallow soil (10 cm) throughout the measured months showed the lowest SWC in all plots (Figure S3 available as Supplementary data at *Tree Physiology* Online). In that year, at 1300 m the sensors in the deep layer (30 cm) next to the trees seemed to maintain their SWC from end of May to end of September decreasing no more than 4% during the dry season (Figure S3b available as Supplementary data at *Tree Physiology* Online). Overall, SWC in 2020 was very low (<12%) at 1600 m, at 30 cm soil depth near *Q. boissieri*, starting from July, and earlier at 10 cm soil depth away from trees (Figure 3B available as Supplementary data at *Tree Physiology* Online). In 2019, these situations were more common: at both 1000 and 1300 m, at 10 cm depth in the open and near *Q. boissieri*, during the entire dry season (Figure S3b and c available as Supplementary data at *Tree Physiology* Online).

Tree growth across four oak species along an elevation gradient on Mt Hermon

Cambial growth, measured as the diameter change of major branches, varied among tree individuals and ranged between 0 and 4 mm during 2020 (Figure S4 available as Supplementary data at *Tree Physiology* Online). Growth season at all plots initiated at mid-spring (April–May) and lasted until mid-summer (July–August) and rarely after the end of August. Large fluctuations in branch diameter were measured in all plots during the autumn and winter months following precipitation events, probably reflecting changes in bark moisture. For some of the plots, tree sensors did not measure for the whole year due to malfunction in wintertime (January–March, 1600 m). Branch diameter change during 2020 correlated poorly with either tree height, stem diameter or branch diameter (r^2 = −0.33, −0.18, −0.06, respectively).

At 1800 m, the highest growth was of two *Q. look* trees, which grew ~3.5 mm a year, and the lowest were two *Q. boissieri*, which grew only ~0.45 mm a year (Figure S4a available as Supplementary data at *Tree Physiology* Online). At 1600 m, the highest growth was measured for *Q. look*, reaching up to 3.6 mm a year. In comparison, the highest growth among *Q. boissieri* reached only ~1.6 mm. At this elevation, two trees showed no growth at all, one of each species (Figure S4b available as Supplementary data at *Tree Physiology* Online). Overall, *Q. look* grew more (2.26 ± 0.52 and 1.62 ± 0.68 mm at 1800 and 1600 m) than *Q. boissieri* (1.13 ± 0.37 and 0.58 ± 0.33 mm at 1800 and 1600 m). At 1300 m, the lowest growth was recorded for *Q. cerris*, while all but one *Q. boissieri* trees showed an annual growth of ~1.5–2 mm (Figure S4c available as Supplementary data at *Tree Physiology* Online). At 1000 m, overall annual growth was lower than that of trees at higher elevations. The highest growth was measured for *Q. calliprinos* (~2.2 mm; Figure S4d available as Supplementary data at *Tree Physiology* Online). Most trees showed similar growth patterns throughout the year, except for two trees of *Q. calliprinos*, which did not exhibit significant growth. Overall, *Q. boissieri* grew more (2.18 ± 0.42 and 1.10 ± 0.32 mm at 1300 and 1000 m) than both *Q. cerris* (1.26 ± 0.47 mm) and *Q. calliprinos* (0.60 ± 0.37 mm;), however, due to large intraspecific variations, these differences were not significant. Growth during 2019 was highly variable among plots and individual trees. At 1600 m most trees showed growth of ~1–1.5 mm. Sensors stopped in October due to malfunction (Figure S5a available as Supplementary data at *Tree Physiology* Online). At 1300 m, *Q. cerris* showed relatively steady growth and *Q. boissieri* exhibited large fluctuations (Figure S5b available as Supplementary data at *Tree Physiology* Online). At 1000 m, growth patterns among species and individuals visibly resembled each other, with growth limited to ~1 mm and three individuals showing a decrease in diameter (Figure S5c available as Supplementary data at *Tree Physiology* Online). Tree growth in 2019 was mildly lower than in 2020, except for *Q. boissieri* at 1600 m, with 1.74 ± 0.58 mm in 2019 compared with 0.58 ± 0.33 mm in 2020.

Cambial growth cessation was associated with VPD dynamics in 2019, whereby trees at different elevations stopped growing on dates with relatively high VPD, mostly during August (Figure 4). The relatively mild conditions in 2019 facilitated growth of two trees up until a dry day in mid-September, and a single tree (at 1300 m) up until mid-October, following a high-VPD period. In the hotter summer of 2020, many trees at the two lower elevations stopped growing in early July (Figure 4). Two trees stopped growing during heatwaves in late July, while most trees at the two higher elevations continued growing up until mid-August, when VPD was increasing following milder weather. Three trees (two at 1000 m and one at 1800 m) continued growing up until the exceptionally high-VPD heatwave of early September 2020. Temperature dynamics did not line up with growth cessation events as well as VPD did. Many of these events were in August (Figure 4), potentially indicating high temperature as a growth limitation. However, some cessation events were in autumn, when temperatures decreased (Figure 2). It was hence the combined effect of low humidity and high temperature (i.e., high VPD) that best explained growth cessation. Another indication for the limitation induced by high VPD was in the exponential decrease of photosynthesis, whereby net carbon assimilation decreased to near-zero at VPD of 3 kPa (Figure 4).
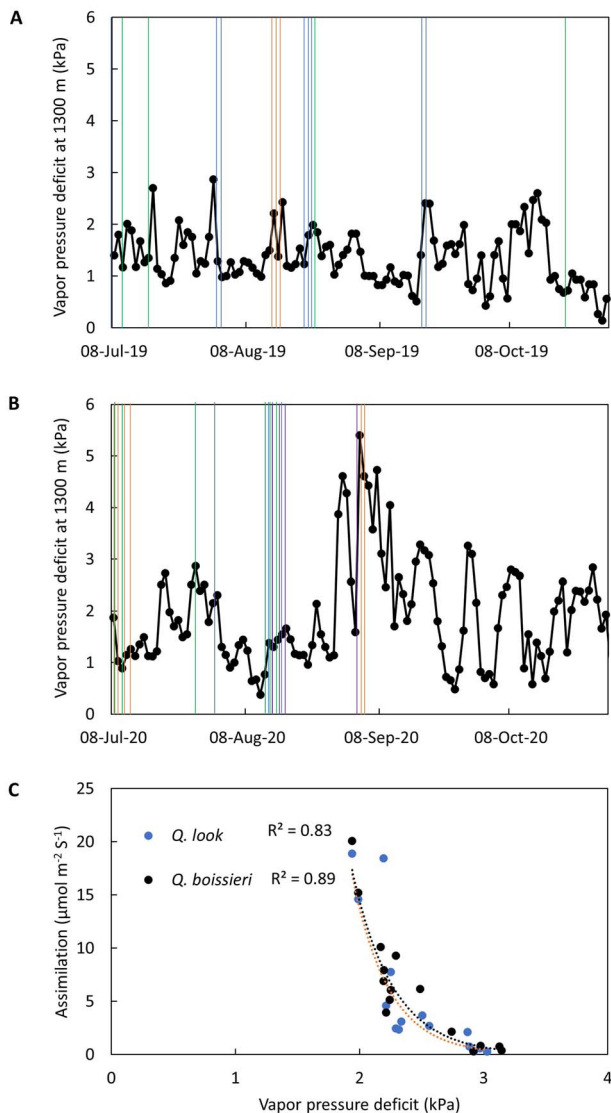
Figure 4. Sensitivity of growth and carbon assimilation of Mt Hermon oaks to VPD. The timing of cambial growth cessation as function of VPD (measured at 1300 m) in summer 2019 (A) and 2020 (B). Vertical lines represent the date of cambial growth cessation for individual trees at 1000 m (orange); 1300 m (green); 1600 m (blue) and 1800 m (purple). Relationships between carbon assimilation and VPD measured in situ at 1800 m during May, July and October 2020 (C). Each data-point represents an individual tree; curves are exponential fits ($a = 12{,}085^{-3.4*VPD}$ and $a = 6351^{-3*VPD}$ for *Q. look* and *Q. boissieri*, respectively).

Growth season length across four oak species along an elevation gradient on Mt Hermon

Leaf and cambial growth phenologies were summarized at half-monthly resolution, due to differences between individuals and the frequency of leaf observations. Growth season length exhibited differences among elevations and species (Figure 5). Cambial growth was restricted to April–August, with an expected extended growth season at lower elevation. Overall, while the end-season was rather ubiquitous in mid or end of

August, season initiation was delayed with elevation. The most extended growth season was at 1000 m for *Q. calliprinos*, lasting for 5 months, while the shortest season was at 1800 m for *Q. boissieri*, lasting for half that time, i.e., 2.5 months. *Quercus cerris* had a 3.5-month growth season at 1300 m, which was notably shorter than its neighboring *Q. boissieri*, and even shorter than *Q. boissieri* and *Q. look* growing at 1600 m (Figure 5A). At growth initiation, tree crowns were typically covered with foliage, or at least partly covered (at 1600 m). In contrast, at 1000 m, *Q. boissieri* growth seemed to precede leafout. Leaf shedding occurred around mid-November (1600–1800 m) or mid-December (1000–1300 m).

Oak seedling survival above the species treeline

We tested seedling survival beyond the treeline (2100 m). Seedlings were planted in November 2019 to avoid the summer heat and drought, leaving 1–2 months for seedlings to acclimate and grow roots. Following the winter, in early May 2020, most seedlings of *Q. cerris* and *Q. look* had living buds and a few green leaves, while only a few seedlings of *Q. calliprinos* and *Q. boissieri* survived (Figure 6). Seedlings of all species had broken branches due to windbreak and snow load. By early July 2020, none of the *Q. boissieri* and *Q. cerris* seedlings had survived, while all *Q. calliprinos* and *Q. look* seedlings that were observed earlier in May persisted. By late August, no seedling of any species showed vital signs. Most of the seedlings were either dried out or physically damaged (broken stem) without any vital buds.

Oak leaf activity across four oak species along an elevation gradient on Mt Hermon

Leaf gas exchange of the four oak species varied among months and years. In 2019, differences in assimilation rates between *Q. boissieri* and its neighboring species were small, yet significant across the two lower plots (Table 2). Assimilation rates differed across elevations, with the highest rates measured at 1600 m in September and at 1300 m in July and no significant difference between species (Figure 7). Gas exchange rates of leaves of the four oak species were measured in 2020 across all elevations in May, July, October and November. The highest rates of assimilation were observed in July, peaking at 18.9 μmol m^{-2} s^{-1} for *Q. boissieri* at 1000 m (Figure 7). In May 2020, *Q. boissieri* exhibited higher assimilation rates than its neighbor species at 1800, 1600 and 1300 m while a significant difference between the species was found only for the 1300 m plot ($P < 0.0001$). The lowest rates measured were in October with an average of 0.53 μmol m^{-2} s^{-1} for *Q. boissieri* at 1000 m. Overall increase in assimilation rates was observed in November in all plots and species, just before winter. In 2020, VPD correlated with assimilation in the 1000, 1300 and 1600 m but not in the 1800 m plot (Table 2).

A

Elevation (m a.s.l.)	Month\ Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
1800	*Quercus look*				→							←	
	Quercus boissieri				→							←	
1600	*Quercus look*				→							←	
	Quercus boissieri				→							←	
1300	*Quercus cerris*				→								←
	Quercus boissieri				→								←
1000	*Quercus calliprinos*												
	Quercus boissieri				→								←

Legend   ■ Branch growth   ■ No growth   □ No data

Figure 5. Cambial growth phenology (A) of four oak species in Mt Hermon in four research plots at four elevations (1000, 1300, 1600, 1800 m a.s.l.). Segments between arrows represent the periods of full crown foliage for each species and elevation (except for the evergreen *Q. calliprinos*). Photographs show the 1600 m plot during February 2021 (B) and the leaf flush gradient during April 2020 (C), with full crown flush at 1600 m, and leaf flush frontier around 1700 m.

The transpiration of oak leaves in 2019 was measured in 1600 and 1300 m throughout the growth season. The highest rates were measured for *Q. look* at 1600 m, 4.38 mmol m^{-2} s^{-1} in July, with no significant difference between species (Figure 8; Table 2). The lowest rates were measured for *Q. cerris* in August with no apparent difference from *Q. boissieri* (2.59 μmol m^{-2} s^{-1}). Transpiration rates during 2020 peaked early in the growth season (May and July), with *Q. boissieri* at 1000 m transpiring 2.87 mmol m^{-2} s^{-1} (Figure 8). Lowest transpiration rates were observed in October across species and elevations, followed by a mild increase in November. In 2020, VPD was correlated with transpiration only in the 1000 m plot (Table 2; Figure 8). Throughout 2020, leaf activity of *Q. boissieri* was either higher or roughly equivalent to that of neighboring oak species at all months and elevations (Figures 7 and 8). There was a significant interaction between species and transpiration in the 1300 m plot (Table 2).

The LWP in 2019 was measured at 1600 m along the growth season, showing moderate values in May, and a seasonal minimum in July, with values approaching −3 and −4 MPa for *Q. look* and *Q. boissieri*, respectively (Figure 9). In August and September, LWP increased gradually, while at the lower plots (1000, 1300 m), values of −3 MPa were maintained for all species. The LWP in 2019 was not found to change with VPD, nor with species (Table 2). In October 2020, LWP was between −3.0 and −3.7 MPa for neighboring species across plots (Figure 9; notice missing measurement of *Q. boissieri* at 1000 m). There was an increase in LWP to ∼−1 in November 2020 at all plots and species (Figure 9).

Semi-centennial oak tree distribution dynamics on Mt Hermon

Change detection using aerial images from 1971, 1976, 1986 and 1992, and a satellite image from 2014 was carried out (Figure 10; Figure S6 available as Supplementary data at *Tree Physiology* Online). We focused on tree stands occurrences across the research area in higher elevations (1700–1930 m a.s.l.). At 1830 and 1930 m, we identified two tree stands

Table 2. Significance of the effects of VPD, tree species, and their interaction on oak leaf activity parameters across four elevations on Mt Hermon in 2019 and 2020.

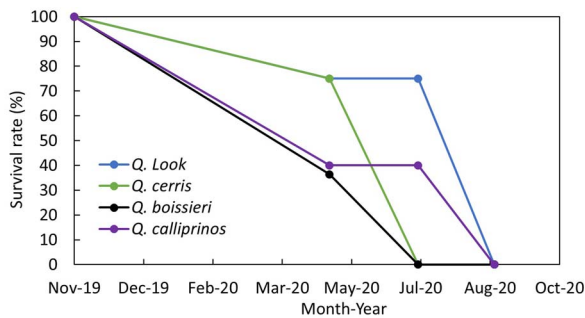| Elevation (m a.s.l.)	1800					
Year	2020					
	VPD	Species × VPD	Species			
Assimilation	0.6886	0.0852	0.5042			
Transpiration	0.8248	0.9869	0.6232			
LWP	<0.0001**	0.9292	0.6016			
Stomatal conductance	<0.0001**	0.8356	0.2853			
Elevation (m a.s.l.)	1600					
Year	2020			2019		
	VPD	Species × VPD	Species	VPD	Species × VPD	Species
Assimilation	0.0053**	0.4692	0.0915	0.1982	0.1890	0.7944
Transpiration	0.3495	0.7014	0.2651	0.9635	0.4147	0.8198
LWP	<0.0001**	0.0162*	0.0098**	0.2480	0.2427	0.7163
Stomatal conductance	<0.0001**	0.4929	0.1099	0.6120	0.9393	0.8898
Elevation (m a.s.l.)	1300					
Year	2020			2019		
Assimilation	0.0163*	0.0584	<0.0001**	0.0021**	0.0071**	0.0390*
Transpiration	0.9591	0.4563	0.0002**	0.0049**	0.0069**	0.2623
LWP	<0.0001**	0.0811	0.1485	0.2341	0.8495	0.3147
Stomatal conductance	<0.0001**	0.2930	0.0003**	<0.0001**	0.0254*	0.1200
Elevation (m a.s.l.)	1000					
Year	2020			2019		
Assimilation	<0.0001**	0.2643	0.7748	0.3175	0.0784	0.0065**
Transpiration	0.0045**	0.2923	0.2771	0.6746	0.8143	0.1266
LWP	0.3928	0.0644	0.3434	0.4478	0.4659	0.3717
Stomatal conductance	<0.0001**	0.2682	0.9036	0.0625	0.4830	0.0500

Figure 6. Survival rates of four oak species seedlings planted in Mt Hermon planting site (2100 m a.s.l.) along one observation year. Values are means ± SE ($n = 5$). Photos show seedlings at planting and in the following summer.

with sparse occurrence in 1971 that gradually increased in density through the years (white circles in Figure 10; note increase in aerial footage resolution). In 1992 and 2014, it is visible that the marked white circles include more trees than the earlier acquired image (Figure 10). For comparison, at a lower elevation of 1780 m, trees were identified continuously from 1971 to 2014 (black circles in Figure 10). Around our highest research plot (1800 m), three locations were examined for qualitative differences in tree stands. At 1650 m (black circles in Figure S6 available as Supplementary data at *Tree Physiology* Online), a stand of oak trees was present in all images, with a slight increase in tree density throughout the years. In contrast, the two white circles in the aerial images of 1971 and 1976 showed almost no trees. In comparison, in 1992 and 2014, dense tree stands, with more than five individuals in each, were identified (Figure S6 available as Supplementary data at *Tree Physiology* Online). In addition to new trees' recruitment on the mountain, an increase in occurrences and recruitment of lower vegetation forms such as woody shrubs and bushes was visible to some extent (Figure 10; Figure S6 available as Supplementary data at *Tree Physiology* Online).

Discussion

The current study describes the first eco-physiological treeline study in the Levant, which is also the first eco-physiological study of the endemic *Q. look* and the first to investigate *Q. cerris* at its southern distribution range edge. We confirmed our first hypothesis, i.e., that cambial and leaf activity and growth
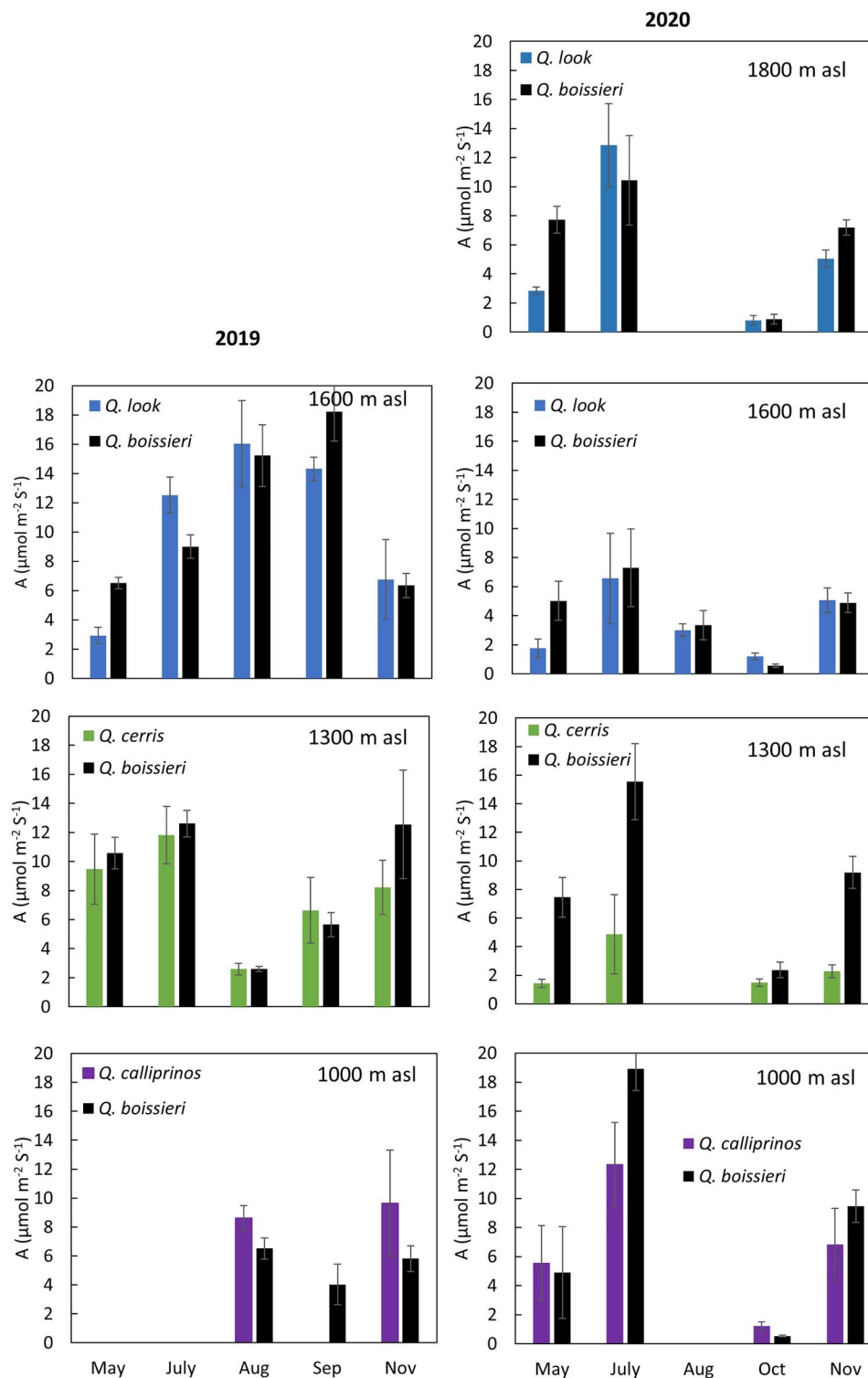
Figure 7. Net assimilation (A) of four oak species in Mt Hermon in four research plots at four elevations (1000, 1300, 1600, 1800 m a.s.l.) during measurement campaign days throughout 2020. Values are means ± SE (*n* = 5).

peaked in early summer (Figures 4, 5, 7–9). Contrary to our hypothesis, they were not lower in *Q. boissieri* (the generalist species) than its companion oak species (specialist species). We confirmed the second hypothesis, that GSL shortens with

elevation due to a later start in spring due to temperature limitation (Figure 5). The end of the growth season in summer was not directly linked to air temperature, but rather to soil drying (Figure 3) and, primarily, high VPD (Figure 4). Finally, the
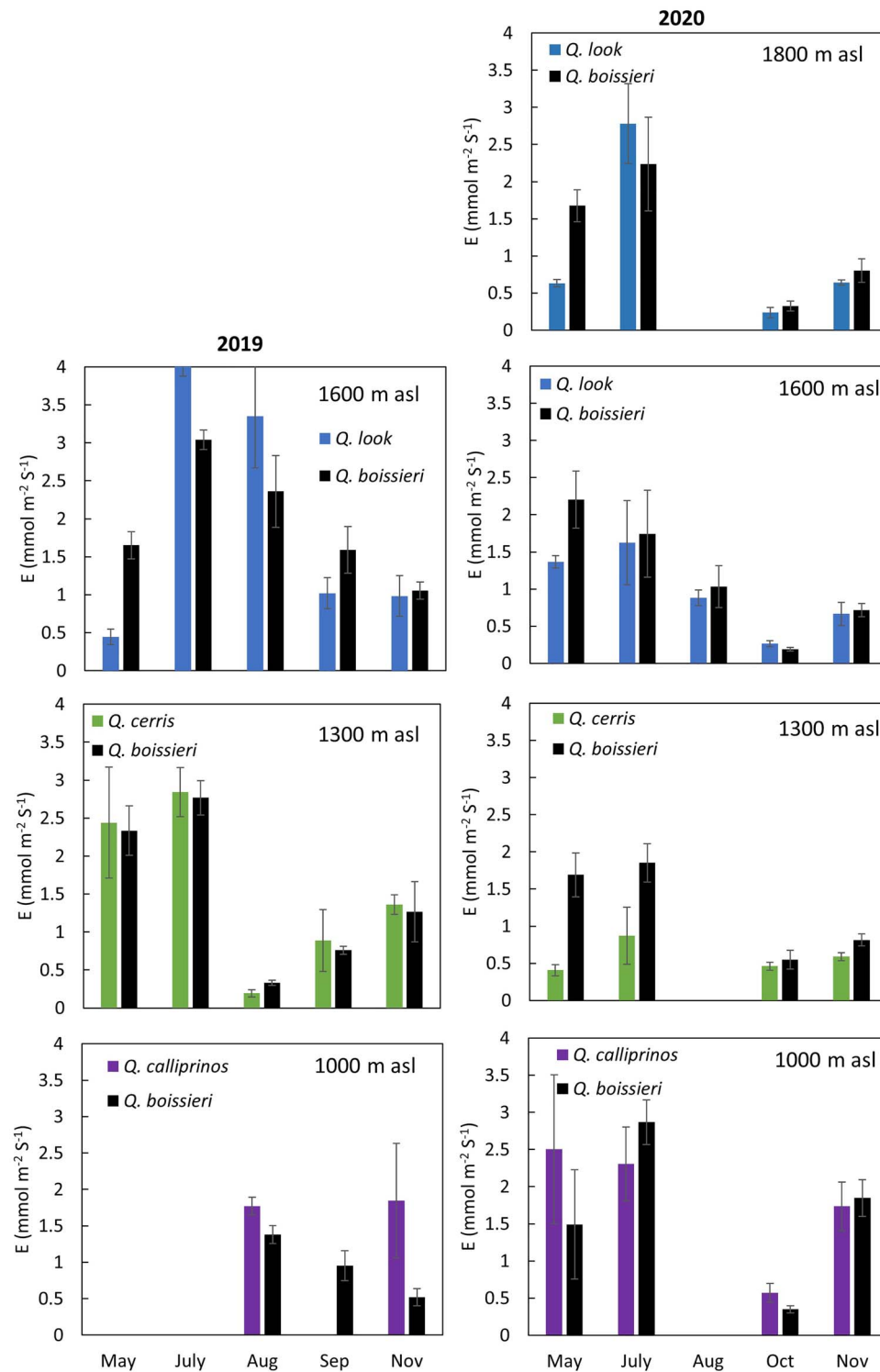
Figure 8. Transpiration (E) of four oak species in Mt Hermon in four research plots at four elevations (1000, 1300, 1600, 1800 m a.s.l.) during measurement campaign days throughout 2020. Values are means ± SE ($n = 5$).

third hypothesis, which explains the unexpectedly low treeline on Mt Hermon by deforestation and absence of 'true' treeline species, was not confirmed (supplementary text; in present days *Juniperus* species grow below the treeline on Mt Hermon, and we found no evidence for their dominance in the late 20th century).

Instead, we found that the current oak treeline is not a stationary one but is rather slowly moving upwards (Figure 10; Figure S6 available as Supplementary data at *Tree Physiology* Online). Oak seedlings planted above the treeline survived the winter, yet wilted before or after July (depending on the species; Figure 6).
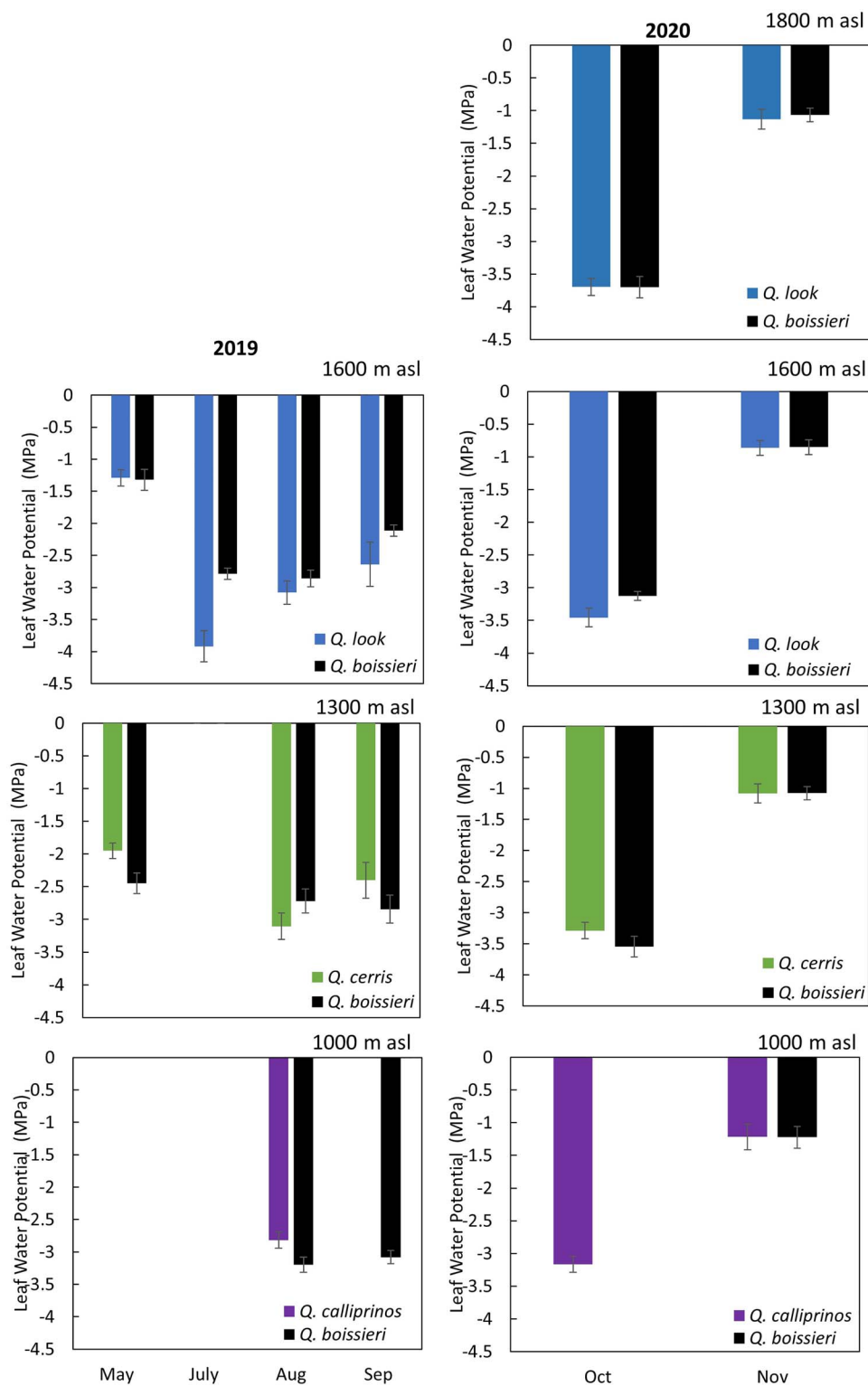
Figure 9. Leaf water potential of four oak species in Mt Hermon in four research plots at four elevations (1000, 1300, 1600, 1800 m a.s.l.) during measurement campaign days throughout 2020. Values are means ± SE (n = 5).

A species treeline defined by dual-limited growth season length

Montane treelines are defined by the threshold temperature of 6–7 °C ([Körner and Hoch 2006](#)). Thus in theory, *Q. look* and *Q. boissieri* could populate higher elevations on Mt Hermon (minimum daily temperature >7 °C for >4 months even at the summit). However, the snow-free summer growth season coincides with a 6-month seasonal drought inducing low SWC
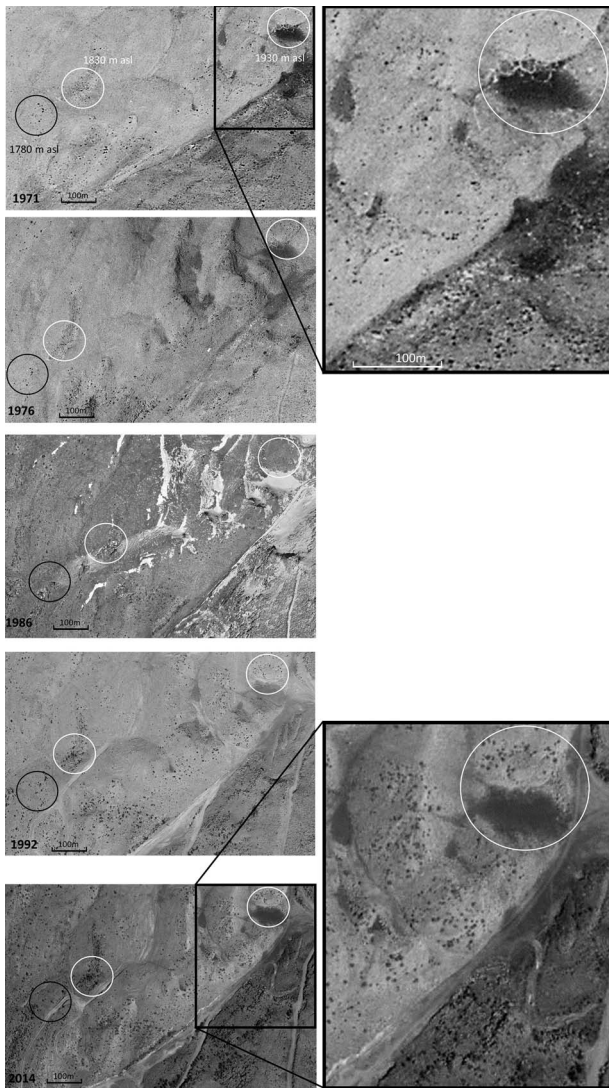
Figure 10. Aerial photos (1971–92) and satellite images (CNES Airbus image; 2014) of three locations on the slopes of Mt Hermon. Black circles indicate the occurrence of oak tree stands in a lower elevation; white circles indicate a change in oak tree stands occurrence in higher elevations along five decades. Aerial photos capture dates and scales are 16 August 1971 (1:46,000); 17 September 1976 (1:23,979); 6 December 1986 (1:22,000) and 2 October 1992 (1:12,500).

and high VPD which enforces growth cessation in August, leaving only 2–3 months for tree growth. Such a short period is insufficient for long-term growth at the treeline (Li et al. 2017), and particularly for oak species (Pérez-de-Lis et al. 2017). The SWC decreased during late spring and summer, and more so around *Q. boissieri*, suggesting a possible limitation in late summer (Figure 3; Figure S3 available as Supplementary data at *Tree Physiology* Online). Maximum VPD in mid-July 2019 reached 3.5 kPa and during the two major heatwaves in 2020, VPD reached 3.4 kPa in early May and up to 5.4 kPa in the second prolonged heatwave in early September. Smaller heatwaves followed during September, with VPD values > 3 kPa

(Figure 4). Previous studies determined that high VPD limits growth and postulated that tree growth happens mainly at night when VPD values are lowest (Zweifel et al. 2021). In general, tree growth is negatively correlated with VPD across different latitudes and elevations (Restaino et al. 2016). It is hence possible that high VPD values during the summer months are the leading cause of the growth cessation observed in summer on Mt Hermon, as they also limit photosynthesis (Figure 4). Under high VPD, trees tend to close their stomata in order to protect their xylem from being embolized (Restaino et al. 2016, Wagner et al. 2021, 2022). Here we showed that gas exchange is resumed in autumn when VPD decreases and despite of the low SWC, probably through deep roots (Väänänen et al. 2020, Rog et al. 2021). It is possible that assimilation measured during autumn and until entering dormancy (Figure 7) is being used for the production of nonstructural carbohydrates in order to replenish sugar reserves for leaf-out in the following spring, as observed in a temperate forest (Klein et al. 2016).

A planting experiment at 2100 m showed that a number of the seedlings of the four oak species survived the cold winter and grew new leaves in summer, yet wilted in August (Figure 6). Among the four species, *Q. cerris* and *Q. look* were under-represented, and only *Q. look* acorns were native to the site, and hence seedlings' responses can vary from those of seedlings germinating locally. Such ecotypic variations exist e.g., in *Pyrus syriaca*, another deciduous tree species in Mt Hermon (Table 1; Paudel et al. 2021). It is possible that the seedlings could not survive their first summer due to the low SWC, combined with a limited root system. Although precipitation is relatively high, increasing with elevation (817 mm year^{-1} at 1130 m; 1353 mm year^{-1} at 1640 m) and increasing even further in higher elevation, but it is mostly restricted to the form of winter snow. Cohen et al. (1981) suggested that potential evapotranspiration increases with elevation in Mt Hermon, mostly because leaf energy balance increases due to radiation. This means that the actual VPD sensed by the oak leaves is higher than the calculated VPD. In addition, among Mediterranean tree species, oak has the highest leaf temperature, 3–7 °C higher than air temperature (Lapidot et al. 2019; for comparison, pine needles were cooler than air under similar conditions). Lastly, vapor pressure becomes lower as air pressure decreases with elevation, further increasing aridity. In spite of the abovementioned limiting factors, growth did not gradually decrease with elevation (Figure S4 available as Supplementary data at *Tree Physiology* Online). We suggest that (i) as growth season shortens with elevation, growth rate increases as a compensation mechanism for the pressing time (see the increase in growth curves' slopes in Figures S4 and S5 available as Supplementary data at *Tree Physiology* Online) and (ii) since stand density decreases with elevation, competition for light, water and nutrients is relieved, and growth increases. Cases of dual limitation of GSL are known for Mediterranean

evergreen species like *Q. ilex* (Lempereur et al. 2017), but less so in montane forests. A potential example for a dual-limited treeline is around Lake Zeribar in Iran (1285 m), where *Q. aegilops* and two other species are tolerant of aridity and low temperatures but sensitive to heavy snowfall. Forest expansion is generally limited by the inability of seedlings to survive the 4-month summer drought (El-Moslimany 1986). However, dual-limited treelines are probably uncommon, as forested mountains typically occur in wet climates, or otherwise, mountains are devoid of forests at all.

The high plasticity of Q. boissieri

Contradictory to our expectation, *Q. boissieri* performed at studied parameters either better or similar to each of its three companion species across a ~1 km elevational gradient. This observation can be linked to other evidences from previous research in nearby sites. For example, (i) *Q. boissieri* xylem can shift from ring-porous to semi-ring-porous in dry years (Castagneri et al. 2020). (ii) The Mt Hermon population of *Q. boissieri* (sampled at 1450 m) is genetically homogeneous with populations growing at lower elevations to the south, all possibly remnants of a larger past population (Schiller et al. 2004), reinforcing its plasticity across a wide range of conditions. (iii) *Q. boissieri* and *Q. calliprinos*, studied in the nearby Golan Heights (967 m, and with lower precipitation than in Mt Hermon), showed no water stress under summer drought (shoot WP mostly above −2.5 MPa), unlike *Q. ithaburensis* in lower elevations (40, 320 m), showing drought-induced mortality (Kopler and Bar-Shalom 2019). *Quercus boissieri*'s northern relative, *Q. infectoria*, showed a higher elevational range than the other six oak species in Lebanon, growing anywhere between 1100 and 1500 m, sometimes as high as 1800 m (Stephan et al. 2016). This was riveled only by *Q. calliprinos*, with an elevational range of 600–1300 m, however solely limited to sites excluding freezing (Stephan et al. 2016), similar to findings in Israel (Rog et al. 2021). Here we showed, unexpectedly, that *Q. calliprinos* seedlings can survive well below zero, at 2100 m, hence proving to be freeze tolerant (Figure 6). Unlike *Q. boissieri*, much is known about the drought resistance strategy of *Q. calliprinos*. At a low elevation site (120 m), mature *Q. calliprinos* trees had a minimum LWP of −4.2 MPa (lower than measured here) and maintained turgor under complete stomatal closure at the end of the dry summer (Väänänen et al. 2020). Combining the aforementioned studies, the minimum seasonal LWP of *Q. calliprinos* was −4.2, −2.7 and −2.5 MPa at 120, 320 and 970 m elevations. On Mt Hermon, we measured a minimum of −3.2 MPa. This may confirm the hypothesis of higher aridity on Mt Hermon than mid-elevation Mediterranean sites (Cohen et al. 1981). Finally, a limitation to our study is the variation in plot aspect (Table 1), which confounds the effects of elevation: the lowest and highest plots had a south aspect, while the middle plots, a northwest aspect. As a result, microclimate was milder

than the average for the specific elevations at the two middle plots. Considering the very small size of the site, and more so, the forest area (Figure 1), alternative plots were in short supply, and hence this issue could not be resolved.

Growth of Q. cerris and Q. look at the edge of their distribution

Among the four oak species studied here, *Q. cerris* is the only wide-range species. Therefore, we initially assumed that its low representation on Mt Hermon is related to the fact that this is its southernmost limit. However, in Lebanon, among its seven oak species, *Qercus cerris* has the narrowest elevational range (1200–1400 m, identical to Mt Hermon) (Stephan et al. 2016). Intriguingly, despite its wide distribution, *Q. cerris* has only slight adaptation advantage over its relative species. *Q. cerris* seedlings performed better than two other oak species in well-watered conditions but were less drought-resistant (Manes et al. 2006). In that experiment, minimum LWP was −5.0 MPa, lower than the −3.3 MPa measured here, which was similar to that measured in mature trees in the Eastern Balkan (Wolkerstorfer et al. 2011), and again lower than the −4.0 MPa measured in mature trees in Tuscany (Tognetti et al. 2007). The seasonal gas exchange behavior of *Q. cerris* measured on Mt Hermon was similar to that reported in those European sites, showing an early summer peak, followed by a midsummer minimum, and recovery in fall. The slightly lower photosynthesis rates measured on Mt Hermon ($2–12$ μmol m^{-2} s^{-1}), compared with those measured in Tuscany ($4–17$ μmol m^{-2} s^{-1}; Tognetti et al. 2007), may indicate a somewhat lower performance of *Q. cerris* at its range edge vs its range core. Little was known of *Q. look*, except for its restriction to high elevations in Lebanon (Stephan et al. 2016). Gas exchange data were available only for its relative, *Q. libani*, from the Zagros Mountains of Iran. In a seedling experiment, *Q. libani* had photosynthesis and transpiration rates of 11.7 μmol m^{-2} s^{-1} and 4.7 mmol m^{-2} s^{-1}, respectively (Moradi et al. 2017). Interestingly, while these transpiration rates are higher than measured here for *Q. look*, photosynthesis rates were similar, indicating higher water-use efficiency in Mt Hermon.

Study implications for montane species conservation under climate change

Our unique mountain site in the Eastern Mediterranean introduces a new factor to the formation of treelines, involving a drought limitation on GSL. This site presents the elevation edge for each of the species, as well as the southern distribution edge for both the endemic *Q. look* and the broad-range *Q. cerris*. In this sense, we expand on recent observations in conifers from the Swiss Alps, where temperature and water potential were shown to co-limit stem growth (Cabon et al. 2020). We presented evidence that the treeline is slowly moving up, probably a form of warming-induced expansion, considering that tree populations

below the treeline did not show the same response (Figure 10; Figure S6 available as Supplementary data at *Tree Physiology* Online). This is in agreement with observations in other treelines (Peñuelas and Boada 2003, Harsch et al. 2009). Based on our analysis, we speculate that the mechanism behind this upward expansion is an earlier growth initiation in spring. In parallel, forests below the treeline might shrink and lose woody species, as seen in other Mediterranean mountains (Pauli et al. 2012), sooner in the south- than north-facing slopes (Salzer et al. 2014). Considering our results, the drought-sensitive *Q. cerris* is at the highest risk, and will probably be replaced by *Q. calliprinos* as warming intensifies, as predicted in the Western Mediterranean for *Q. pyrenaica* and *Q. coccifera*, respectively (Gea-Izquierdo et al. 2013, Al-Qaddi et al. 2017).

Authors' contributions

I.K. and T.K. initiated the research project, managed by P.B.-O. IK established the research plots. IK, P.B.-O. and T.K. installed the monitoring instruments. P.B.-O. and A.Y. led the measurement campaigns. P.B.-O. analyzed the data under the supervision of T.K. O.R. consulted on the remote sensing analysis. P.B.-O., T.K. and U.M. wrote the paper, with contributions from all authors.

Conflict of interest

The authors declare no conflict of interest in preparing this manuscript.

Data availability statement

Data used in analyses in this paper will be uploaded to a public archive (Figshare.com) following acceptance for publication.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

Acknowledgments

The authors wish to thank all helpers in field campaigns; Ella Pozner, Roni Mualem; Nitsan Birnbaum, Stav Livne-Luzon (Weizmann Institute of Science) for assistance in statistical analysis; Yuval Reuveni for 2100 m a.s.l. meterological data; and Rachid Cheddadi (University of Montpellier) for help in deciphering the history of the Mt Hermon forest in the pollen record. The work has been facilitated by the Israel Nature and Parks Authority.

Funding

The project was funded by the Israel Ministry of Science and Technology.

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