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# Photosynthesis, stomatal conductance and terpene emission response to water availability in dry and mesic Mediterranean forests.

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**Abstract** Water stress results in a reduction of the metabolism of plants and in a reorganization of their use of resources geared to survival. In the Mediterranean region, periods of drought accompanied by high temperatures and high irradiance, occur in summer. Plants have developed various mechanisms to survive in these conditions by resisting, tolerating or preventing stress. We used three typical Mediterranean tree species in Israel, *Pinus halepensis* L., *Quercus calliprinos* and *Quercus ithaburensis* Webb, as models for studying some of these adaptive mechanisms. We measured their photosynthetic rates (A), stomatal conductance (gs), and terpene emission rates during spring and summer in a geophysical gradient from extremely dry to mesic from Yatir (south, arid) to Birya (north, moist) with intermediate conditions in Solelim.

A and gs of *P. halepensis* were three fold higher in Birya than in Yatir where they remained very low both seasons. *Quercus* species presented 2-3 fold higher A and gs but with much more variability between seasons, especially for *Q. ithaburensis* with A and gs that decreased 10-30 fold from spring to summer. Terpene emission rates for pine were not different regionally in spring but they were 5-8 fold higher in

Birya than in Yatir in summer ($P < 0.05$). Higher emissions were also observed in Solelim for the drought resistant *Q. ithaburensis* ($P < 0.001$) but not for *Q. calliprinos*. α-Pinene followed by limonene and 3-carene were the dominant terpenes. Warmer summer conditions result in increased Terpene emission rates except under severe drought, in which case they strongly decrease.

**Keywords** Mediterranean drought conditions, terpene emission rates, gas interchange, *Pinus halepensis*, *Quercus calliprinos*, *Quercus ithaburensis*.

**Author Contribution Statement** The campaigns and measurements were planned and executed jointly by all coauthors, the paper was writen by JL with comments from all co-authors

**Key Message** Warmer summer conditions result in increased terpene emissions except under severe drought, in which case they strongly decrease.

## Introduction

The reduction in water intake by plants results in a slowing down of their metabolism (Hsiao 1973) and a reorganization of their energy resources geared to survival (Dobrota 2006). In the Mediterranean region, periods of drought are accompanied by high temperatures and high irradiance in summer (Aschmann 1973; Gasith and Resh 1999; Tsakiris et al. 2007; Gratani et al. 2013). This leads to stressful conditions for plants that may result in increased mortality. However, plants have developed their own mechanisms to survive in these hydric stress conditions (Chaves et al. 2002; Rubio- Casal et al. 2010; Bai et al. 2008; Letts et al. 2011; Damesin and Rambal 1995; Werner et al. 1999) resisting, tolerating, or preventing stress (David et al. 2007; Mittler 2002; Werner et al. 1999).

One of these mechanisms is the use of volatile organic compounds (VOCs) (Peñuelas and Llusia 1999, 2002, 2003; Munné-Bosch et al. 2004; Peñuelas et al. 2005, 2009; Llusià et al. 2005, 2008; Copolovici et al. 2005; Filella et al. 2007; Porcar-Castell et al. 2009). Volatile organic compounds not only have an important biological role but also environmental effects, affecting atmospheric chemistry (Llusia et al. 2012b; Seco et al. 2013) , the formation of secondary aerosol (Claeys et al. 2004; Cahill et al. 2006; Camredon et al. 2007; Kroll and Seinfeld 2008) and, ultimately, climate (Peñuelas and Llusia 2003; Yuan et al. 2009; Riipinen et al. 2012) .

The production and emission of biogenic volatile organic compounds, such as isoprene and monoterpenes which constitute a majority of the biogenic VOCs, may confer protection against the high temperatures and the drought conditions (Sharkey and Singsaas 1995; Singsaas 2000; Peñuelas and Llusia 2002, 2003; Copolovici et al. 2005; Peñuelas and Staudt 2010).

The rates of plant VOC emissions are altered by water availability (Bertin and Staudt 1996; Peñuelas and Llusia 1997; Llusia and Peñuelas 1998; Hansen and Seufert 1999). While the behavior is complex and may differ among chemical and biological species, it seems that in moderate drought conditions, isoprenoids help plants resist stress (Gershenzon et al. 1978), but isoprenoid emissions strongly decrease under severe drought conditions (Llusia and Peñuelas 1998; Hansen and Seufert 1999). They also respond to temperature (Seufert 1997; Hansen and Seufert 1999; Peñuelas and Llusia 2002, 2003; Llusia and Peñuelas 2000), and seasonality (Yokouchi and Ambe 1984; Lerdau et al. 1995; Llusia and Peñuelas 1998, 2000; Peñuelas and Llusia 1997). Temperature increases production and emission rates of most terpenes exponentially by enhancing enzymatic activities of synthesis, increasing the vapor pressure of the terpene, and decreasing the resistance of the emission pathway (Tingey et al. 1991; Loreto et al. 1996; Peñuelas and Llusia 2001). However, terpene emissions by trees combining temperature and drought comparing drier and milder sites is not known.

Israel presents strong gradient in water availability from semi-arid conditions in the south to Mediterranean/sub-humid in the north. The climatic trend of annual aridity (humidity) index P/PET (P = Precipitation; PET = Potential Evapotranspiration) is ranging between 0.05 in the south to above 0.65 in the north (Kafle and Bruins 2009). The native Mediterranean woody vegetation in Israel is strongly dominated by one species – the evergreen sclerophyllous *Quercus calliprinos* Webb (Kermes oak) which accounts for 80–90% of the tree coverage (Zohary 1973). The Tabor oak, *Quercus ithaburensis* (Decne.) is an East-Mediterranean deciduous oak. *Q. ithaburensis* appears to be more suitable for the restoration/reforestation of dryer environments (Siam et al. 2008). This species dominates in the east and south Mediterranean region (Kaplan and Gutman 1999). This species is considered to be drought-resistant and capable of growing on shallow and poor soils. The Alepo pine, *P. halepensis*, is a major conifer forest tree in the Mediterranean forests with large distribution around this region (Schiller et al. 1986). This tree's characteristics include it being a pioneer species, a fast grower, and a drought tolerant species (Atzmon et al. 2004) with a shallow root system. These advantages made it a favorable tree for plantation in that region, particularly in Israel. Its ability to withstand drought is enabled mainly by reducing growth rate and water loss, as well as by minimizing and shifting the photosynthetic activity to early morning and late afternoon (Maseyk et al. 2008).

In our study we used three Mediterranean tree species that can serve as models for studying the terpene emissions in these particular Mediterranean conditions where warm summer temperatures are accompanied by a gradient of drought conditions ranging from mild to very severe. These species are *Pinus halepensis* L., *Quercus calliprinos* and *Quercus ithaburensis* Webb. In this Mediterranean region these species undergo periods of drought and high temperature frequently (Atzmon et al. 2004; Grünzweig et al. 2008). We measured them in Yatir (in the south, arid) Birya (located north, Mediterranean sub-humid conditions) and Solelim (located north, Mediterranean conditions).

Our aim was to compare the same species, *P. halepensis*, growing in extremely contrasting water availabilities in space and time (Yattir and Birya in spring and summer), and to compare two species of *Quercus sp.* of contrasting seasonal biology in a dry site (Solelim also in spring and summer), in order to test the hypothesis that summer warmer conditions should increase terpene emissions except under severe drought in which case terpene emissions would strongly decrease.

## Materials and Methods

Sites of the study

*Yatir*

Yatir forest is a 45-year-old *P. halepensis* plantation located at the northern edge of the Negev desert, Israel (31°20'N, 35°20'E). The forest covers an area of about 2,800 ha and lies on a predominantly light brown Rendzina soil (79 ± 45.7 cm deep), overlying a chalk and limestone bedrock. The climate is hot (40-year mean annual temperature is 18.2°C) and dry (40-yr average mean annual precipitation is 279 ± 90 mm), and 247mm during the hydrological studying year (October 2012-September 2013) (Fig. 1). Stand density is ca. 300 trees $ha^{-1}$, mean tree height is 10.2 ± 2.49 m and mean diameter at breast height (DBH) is 19.8 ± 5.61 cm.

*Birya*

Birya forest is a ~50–yr-old *P. halepensis* plantation located at the northern part of Israel in the Galilee region (33°00'N, 35°30'E). The forest covers an area of about 2,000 ha and lies on a Rendzina and Terra rossa soil. The climate is Mediterranean sub-humid with average temperature of 16°C, average annual precipitation of 710 mm, and 885mm during the hydrological studying year (October 2012-September 2013) (Fig. 1). Average stand density is 375 trees $ha^{-1}$, mean tree height is 11 m and mean DBH is 20.3 cm.

*Solelim*

Solelim forest is a native oak forest, dominated by two oak species *Q. calliprinos* and *Q. ithaburensis*. Since 1940 no massive human interference was done in this forest, allowing the current native vegetation society to stabilise. The forest is located at the north part of Israel in the Galilee region, 30 km south of Birya forest (32°75'N, 35°23'E). The forest lies on a Rendzina and Terra rossa soil. The climate is Mediterranean with average temperature of 21°C, average annual precipitation of 580 mm, and 743 mm during the hydrological studying year (Fig. 1). The measurement site area is characterised by an average stand density of 280 trees $ha^{-1}$, mean tree height of 8 m and mean DBH of 18.9 cm.

Gas exchange measures and sampling of terpene emissions

Photosynthetic rates (A) and stomatal conductances ($g_s$) were measured between 9:00 a.m. and 6:00 p.m. at a quantum flux density of 1080±19 µmol $m^{-2}$ $s^{-1}$ and a constant air temperature of 30±1.5 °C under a controlled $CO_2$ concentration of 400±2 ppm. One or several leaves were enclosed in a clamp-on gas-exchange cuvette of 6 $cm^2$ and 80 $cm^3$. Air flow through the dynamic cuvette was 732±0.05 ml $min^{-1}$. A Licor-6400XT (4647 Superior Street P.O. Box 4425 Lincoln, Nebraska USA) gas-exchange system was used.

The same gas-exchange system (Licor-6400XT) described above was used for sampling of terpene emissions. Air exiting the cuvette was pumped through a stainless steel tube (89 mm in length and 6.4 mm external diameter) manually filled with adsorbents, 115 mg of Tenax® TA and 230 mg of SulfiCarb®, separated by sorbent-retaining springs fixed using gauze-retaining springs and closed with air-tight caps (Markes International Inc. Wilmington, USA). Air samples were collected using a $Q_{max}$ air-sampling pump (Supelco, Bellefonte, Pennsylvania). The flow was measured with a flowmeter Bios Defender 510 fluxometer (Bios International Corporation, Butler, USA) and controlled with a metallic valve. The hydrophobic properties of activated adsorbents minimized any sample displacement by water. The terpenes were not chemically transformed in these tubes, as determined by reference to trapped standards (α-pinene, β-pinene, camphene, myrcene, *p*-cymene, limonene, sabinene, camphor, α-humulene and dodecane). Prior to terpene sampling, the tubes were conditioned for 35 min at 350 °C with a stream of purified helium. The sampling time was 10 min, and the flow was 315±35 mL $min^{-1}$. The trapping and desorption efficiency of standards such as α-pinene, β-pinene and limonene was 99%. Blank samples of air without plants in the cuvette were collected in the tubes for 10 min immediately before each measurement. The sampled tubes were stored in a portable refrigerator at 4 °C and transported to the laboratory. The terpene content of the blank samples was subtracted from the samples collected from plants for calculating the rates of terpene emission.

Terpene analysis

The terpene emissions trapped in the metallic tubes were released with an automatic sample processor (TD Autosampler, Series 2 Ultra, Markes International Inc. Wilmington, USA) and thermally desorbed using a coupled injector (Unity, Series 2, Markes International Inc. Wilmington, USA) connected to a Gas Chromatograph (7890A, Agilent Technologies, Santa Clara, USA) with a mass spectrometer detector (5975C inert MSD with Triple-Axis Detector, Agilent Technologies). A full-scan (between 25 to 445 m/z) method was used in the chromatographic analyses. The desorbed samples were injected into a capillary column (HP 5MS, 30m x 0.25 μm x 0.25 mm). The initial oven temperature was 35 ºC for the first 2 min, then was increased stepwise at 15 ºC $min^{-1}$ to 150 ºC and maintained for 5 min, at 30 ºC $min^{-1}$ to 250 ºC and maintained for 5 min and finally at 30 ºC $min^{-1}$ to 280 ºC and maintained for 5 min. The flow of helium was 1 ml $min^{-1}$, and the total run time was 29 min.

The identification of terpenes was performed by a comparison of the mass spectra with published spectra (Wiley 7n library) and known standards, while quantification of the peaks was conducted using the fragmentation product with mass 93 (Blanch et al. 2012; Llusia et al. 2012b). Calibration curves for quantification were prepared with commercial standards of some of the most abundant compounds in the samples: four monoterpenes (α-pinene, sabinene, β–pinene and limonene), one sesquiterpene (α-caryophyllene) and one non-terpene internal standard (dodecane), all from Fluka Chemie AG, Buchs, Switzerland. Terpene calibration curves were always highly correlated ($r^2 \geq 0.99$) in the relationship between signal and terpene concentration. The most abundant terpenes had very similar sensitivities (differences were less than 5%). The desorbed sample was retained in a cryo-trap at -25ºC. The split was 1:20. The sample was desorbed again at 300ºC for 10 min and injected into the column with a transfer line at 250ºC. Following sample injection at 35ºC (initial time 1 min), the column temperature was increased stepwise at 15ºC min-1 to 150ºC and maintained for 5 min, at 50ºC $min^{-1}$ to 250ºC and maintained for 5 min and finally at 30ºC $min^{-1}$ to 280ºC and maintained for 5 min. Total run time was 26.7 min, and the helium flow was 1 ml $min^{-1}$. The identification of terpenes was performed as above for the analysis of terpene concentrations. The rates of terpene emission were expressed in μg $g^{-1}$ (dw) $h^{-1}$.

Statistical analysis

Data variables A, gs and emissions of total terpenes were analyzed using the Shapiro-Wilk test ($n > 30$) and followed a normal distribution with $P > 0.05$. Fisher's LSD post-hoc test was used to analyze differences among means when the ANOVAs indicated significant differences ($P < 0.05$), using STATISTICA v.6.0 for Windows (StatSoft, Inc. Tulsa, Oklahoma). SigmaPlot v. 11.0 for Windows (Systat Software, Chicago, USA) was used for graphics.

**Results**

Net photosynthetic rates and stomatal conductances

The net photosynthetic rates (A) and the stomatal conductances (gs) of *P, halepensis* were significantly three fold higher in Birya than in Yatir especially in the spring ($P < 0.05$, Fig. 2). In summer, only A significantly decreased 28 % in Birya ($P < 0.01$, Fig. 2).

The two studied species of *Quercus* showed similar values of both A and gs in both the spring and summer seasons, although in the summer the A levels decreased significantly ($P < 0.001$) in both species but more in *Q. ithaburensis* ($P < 0.001$, 97 %) than in *Q. calliprinos* ($P < 0.01$, 80 %). The gs levels decreased significantly ($P < 0.01$) in both species but more in *Q. ithaburensis* ($P < 0.01$, 89 %) than in *Q. calliprinos* ($P < 0.01$, 67 %).

Terpene emission rates

*P. halepensis*, emitted similar amounts of terpenes in both sites during spring (around 8±3 $\mu g\ g^{-1}\ dw\ h^{-1}$, Fig. 3). In summer, however, the emission rates of *P. halepensis* were 5-8 fold lower in the arid Yatir forest (0.22±0.16 $\mu g\ g^{-1}\ dw\ h^{-1}$) while they increased  ca. 5 fold in the mesic Birya forest (39±26 $\mu g\ g^{-1}\ dw\ h^{-1}$) ($P < 0.01$, Fig. 3).

*Q. ithaburensis* showed significant differences of terpene emissions between seasons ($P < 0.001$, Fig. 3). In summer, emissions increased 9 fold for *Q. ithaburensis* (up to 38.8±18.6 $\mu g\ g^{-1}\ dw\ h^{-1}$) and only 35 % for *Q. calliprinos* (up to 4.42±2.26 $\mu g\ g^{-1}\ dw\ h^{-1}$, $P < 0.05$, Fig. 3).

The terpene emissions response to light studied in Yatir forest show an increase with increasing PAR, reaching a peak between 1000 and 1500 μ mol $m^{-2}$ $s^{-1}$ (33±4 μ g $g^{-1}$ d.m. $h^{-1}$) (Fig. 4). At the same curve inflection point photosynthetic rates reached their maximum value (1.9 μmol $m^{-2}$ $s^{-1}$).

In general, all the individual monoterpenes shown in Fig. 5 (α-pinene, camphene, β-pinene, limonene and 3-carene) followed the same pattern as for the total terpene emissions (Fig. 3).

**Discussion**

Photosynthesis and stomatal conductance

A and gs patterns observed during the spring and summer in this study were consistent with previous studies of the Mediterranean species *P. halepensis* and *Quercus ilex* (Baquedano and Castillo 2007; Peñuelas and Llusià 1999; Llusià and Peñuelas 2000), and *Q. calliprinos* and *Q. ithaburensis* (Klein et al. 2013; Schiller et al. 2010; Grünzweig et al. 2008). A and gs showed the seasonal trend expected in a Mediterranean climate (Llusià and Peñuelas 2000) except under the near-desertic conditions of Yatir forest (Maseyk et al. 2008) where values were extremely low both in spring and summer (Figs. 1 and 2). These low rates of photosynthesis and stomatal conductance in an extreme climatic environment for *P. halepensis* indicate the adaptive success of this species to the severe stress, by presenting low rates of growth and reproduction (Matesanz and Valladares 2014; Gratani 2014; Bussotti et al. 2015).

Terpene emission rates

The individual terpenes detected in *P. halepensis* were similar to those detected in the same species in other Mediterranean regions (Llusia and Peñuelas 2000; Ormeño et al. 2007). The compounds detected in the *Quercus* species studied here are similar to those found in other *Quercus* of other Mediterranean region (Llusia and Peñuelas 2000; Plaza et al. 2005).

*P. halepensis* showed the typical seasonal behavior of plants in the Mediterranean region (Llusia and Peñuelas 1998; Ormeño et al. 2007). In Birya and Solelim, during the summer sampling, *P. halepensis* and *Q. ithaburensis* showed higher terpene emission rates than in spring, as a result of higher temperatures and more mesic conditions than in Yatir forest. Similarly to what has been often described in similar Mediterranean conditions, for example for *Q. suber* and *Q. coccifera* species (Pio et al. 2005; Llusia et al. 2013). *Q. ithaburensis* had higher emissions than those of *Q. calliprinos* during summer sampling. These differences in emissions between these two species could be due to genetic causes (Loreto et al. 2009; Welter et al. 2012). The differences between the two species of *Quercus* may be due to the geographical adaptations and/or genetics (Staudt et al. 2004; Loreto et al. 2009; Welter et al. 2012). Interspecific gene flow is common in oaks. Specifically, in Mediterranean region. This process would have produced geographical differences and new species, which may have contributed to the differences in the production and emission of volatile terpenes in oak species. The mechanisms and driving forces behind this diversification in European oaks are still unknown. In fact, the extent of intraspecific variability in the production and emission of volatile terpenes in *Quercus* sp. has been little studied (Staudt et al. 2001, Loreto et al. 2009). The variability in terpene emissions within and among populations of oaks has only been widely investigated in the species *Quercus ilex* L. (Staudt et al. 2001, 2004) and *Quercus suber* (L.) (Staudt et al. 2004, 2008, Loreto et al. 2009). For both species, inherent differences were seen in emission profiles of individual trees. The chemotypes abundance of these varied between populations, perhaps reflecting the fragmentation paleogeographic range of species in the Mediterranean area and the selective adaptation ecotype to new habitats (Loreto et al. 2009). Another possible source contributing to the diversification of emissions of isoprene and monoterpenes in *Quercus* could be the selection and breeding associated with human activities and ease of miscegenation between sympatric species of oak (Staudt et al., 2004). Oak trees have been tried to classify according to taxonomic data and terpenoid emissions but it was concluded that no clear grouping is possible taking into account the terpenoid emissions and taxonomic classifications and that the different terpenoid emission rates may be due to the different physiological acclimation to the environmental conditions (Csiky and Seufert, 1999). On the other hand, the emission rates form the two *Quercus* studied species, *Q. calliprinos* and *Q. ithaburensis*, were very similar quantitatively and qualitatively to those reported by Csiky and Seufert (1999).

The responses of the terpene emission rates and photosynthetic rates to increasing PAR intensities showed that *P. halepensis* needles reached the maximum terpene emission and photosynthetic rates at lower PARs than usual (Peñuelas and Llusia 1999; Owen et al. 2002; Niinemets et al. 2010) indicating stressful conditions in the arid location of Yatir. The severe decrease in the terpene emissions in summer in Yatir soundly demonstrate decreased emissions under severe drought conditions in contrast with increased emissions with warming under moderate drought (Llusia and Peñuelas 1998; Llusia et al. 2012a).

**Conclusion**

These results thus demonstrate a contrasting seasonal change in the arid and the mesic localities. While in the arid Yatir, the summer terpene emissions almost disappeared, in the mesic site they increased 5-fold. This illustrates the complex interactions between water availability and temperature where temperature can drive increased emissions unless water availability becomes severely limiting.

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**Conflict of Interest** The authors declare that they have no conflict of interest.

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**Figure legends**

**Fig. 1.** Daily average (+SE) of air temperature (ºC) and daily average (+SE) of VDP (Pa) in Yatir (from April to May and from August to September 2013), in Birya (May and September 2013) and Solelim (May and August 2013).

**Fig2.** Net photosynthetic rates and stomatal conductances (+SE) of *Pinus halepensis* (in Yatir and Birya), *Quercus calliprinos* and *Quercus ithaburensis* (in Solelim) in Spring (empty bars) and Summer (black bars). Different letters indicate significant differences ($P < 0 .05$) among sites and among species in the case of *Quercus* sp, and asterisks indicate statistical differences between seasons (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

**Fig3.** Total terpene emission rates (+SE) of *Pinus halepensis* (in Yatir and Birya), *Quercus calliprinos* and *Quercus ithaburensis* (in Solelim) in Spring (empty bars) and Summer (black bars). Different letters indicate significant differences ($P < 0 .05$) among sites, and asterisks indicate statistical differences between seasons (*, $P < 0.05$; **, $P < 0.01$).

**Fig4.** Light responses curves of terpene emission rates (+SE) (black triangles) and net photosynthetic rates (+SE) (black circles) conducted in Yatir forest during the spring campaign.

**Fig5.** Individual terpene emission rates (+SE) of *Pinus halepensis* (in Yatir and Birya), *Quercus calliprinos* and *Quercus ithaburensis* (in Solelim) in Spring (empty bars) and Summer (black bars). Different letters indicate significant differences ($P < 0 .05$) among sites, and asterisks indicate statistical differences between seasons (*, $P < 0.05$; **, $P < 0.01$).

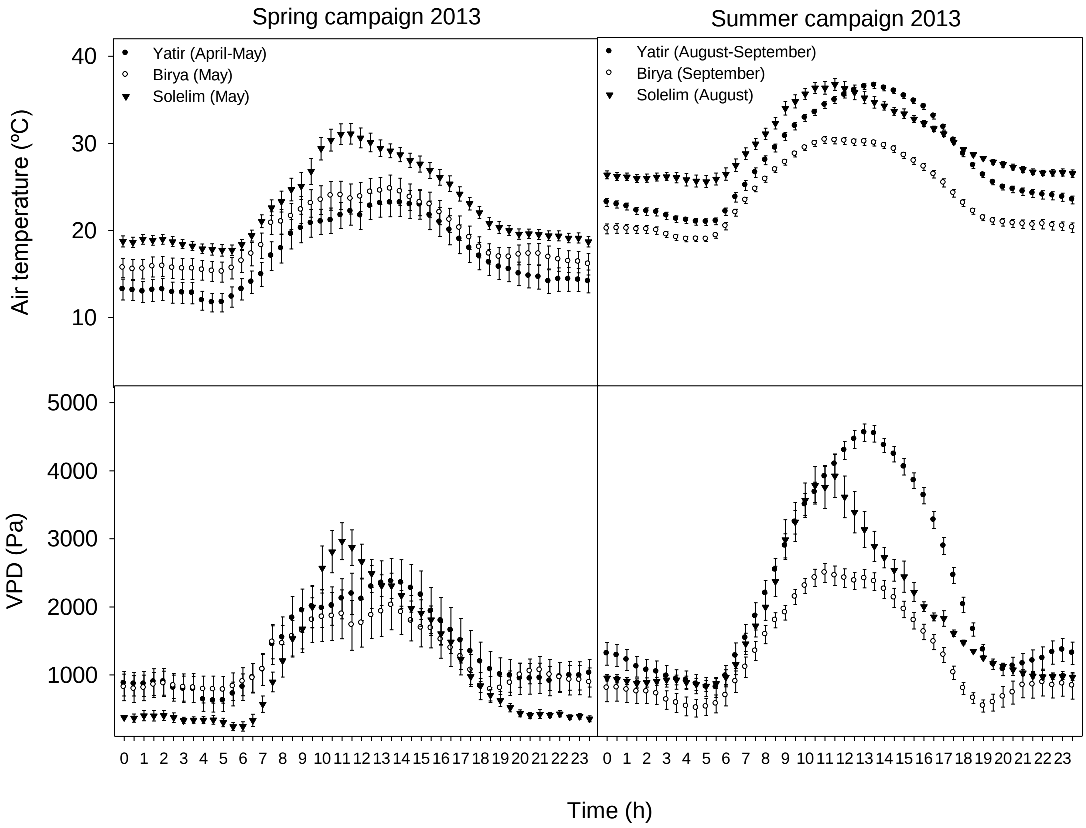

Spring campaign 2013
Summer campaign 2013
Yatir (April-May)
Birya (May)
Solelim (May)
Yatir (August-September)
Birya (September)
Solelim (August)
Air temperature (ºC)
VPD (Pa)
Time (h)
40
30
20
10
5000
4000
3000
2000
1000
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23

**Fig1.**

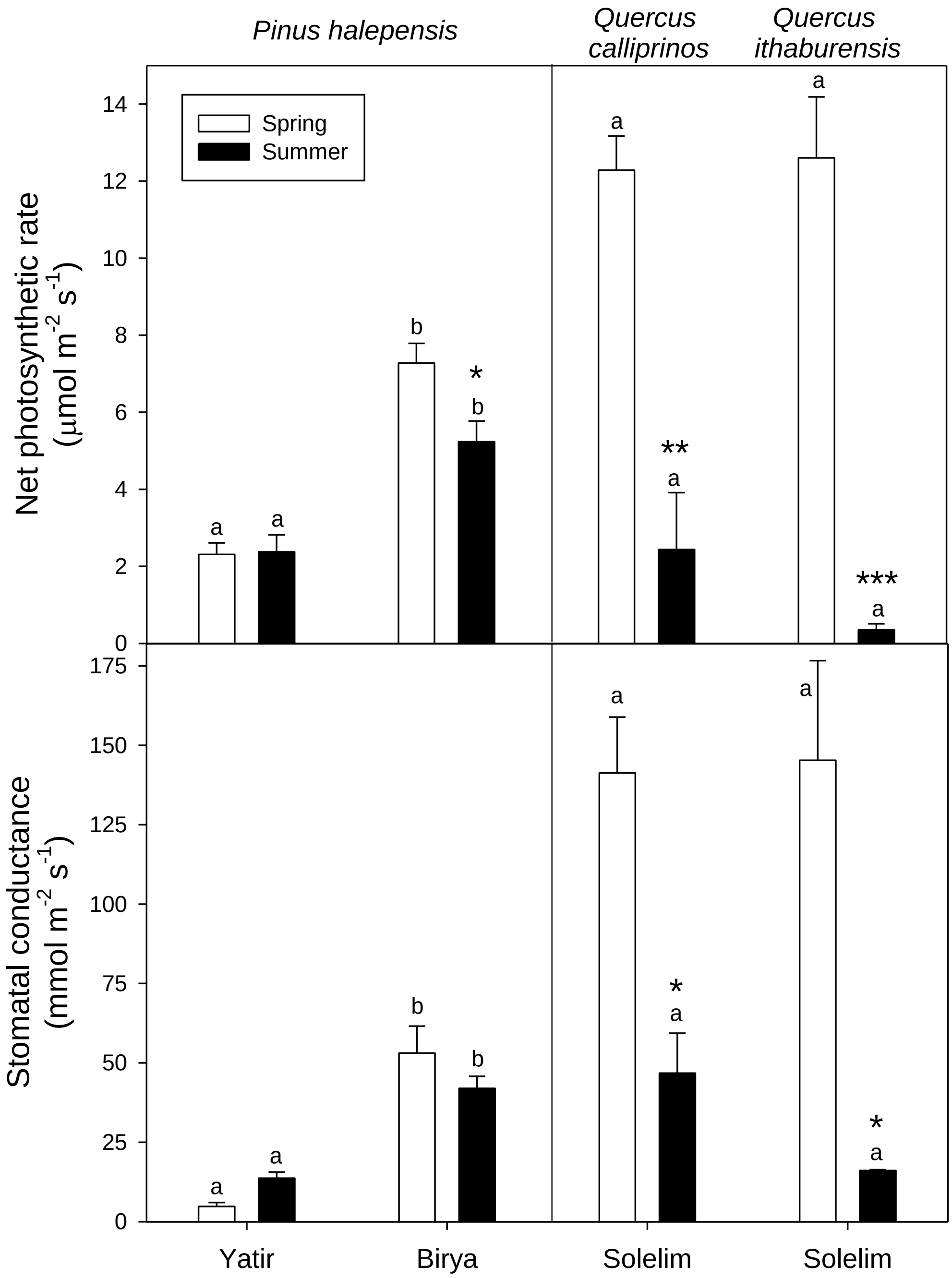
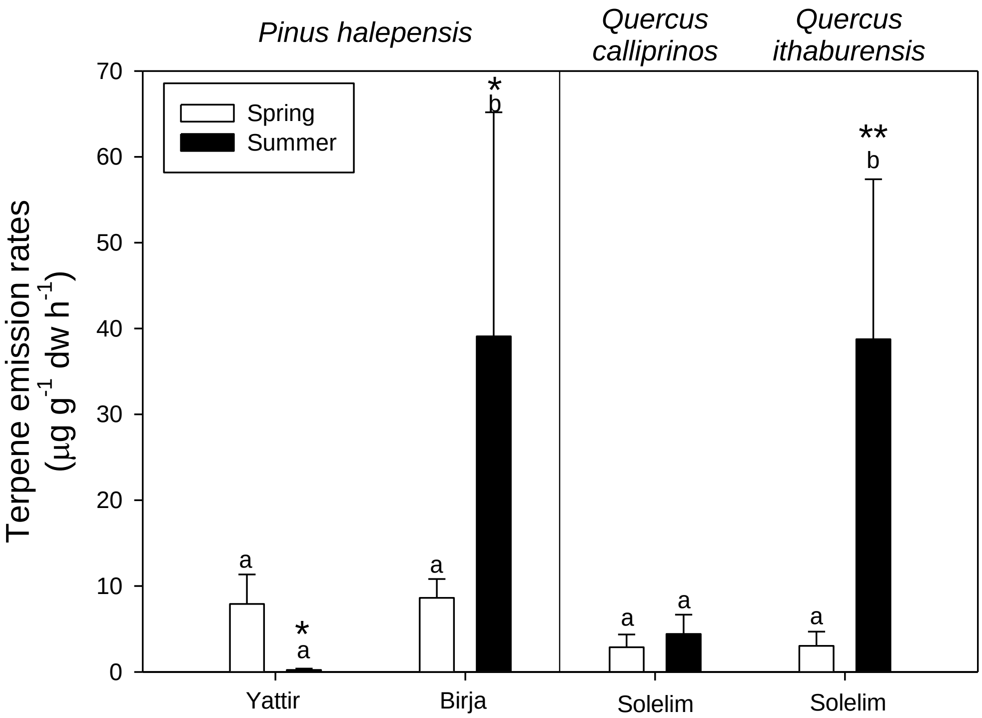
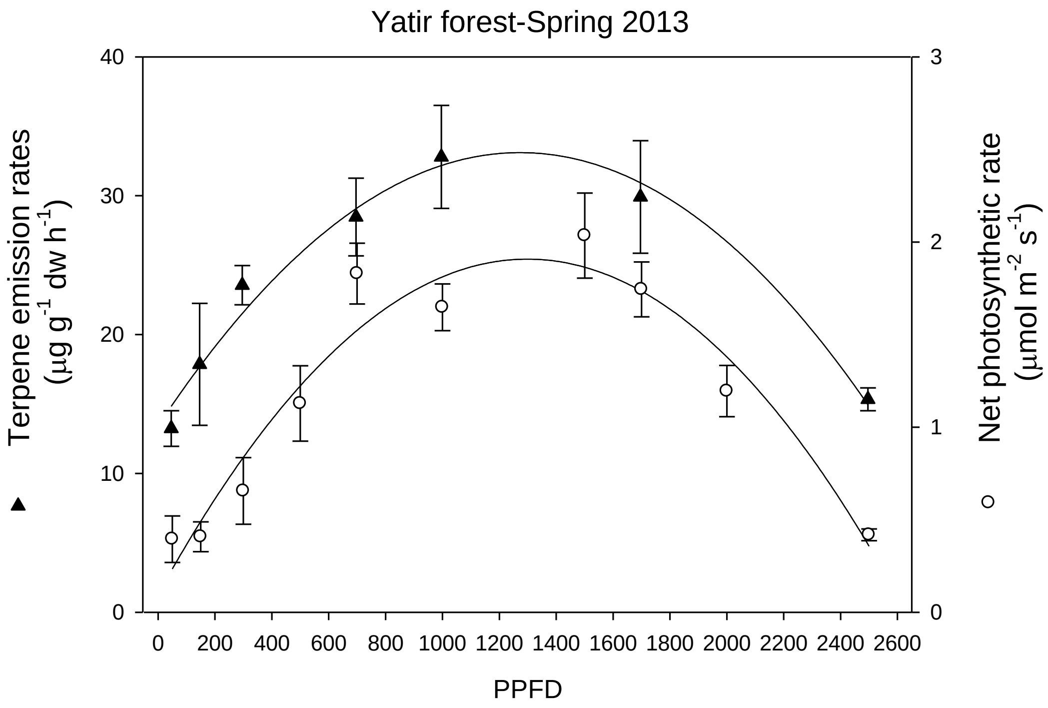

Pinus halepensis
Quercus calliprinos
Quercus ithaburensis
Spring
Summer
Net photosynthetic rate (µmol m-2 s-1)
Stomatal conductance (mmol m-2 s-1)
Yatir
Birya
Solelim
Solelim

**Fig 2.**



Pinus halepensis
Quercus calliprinos
Quercus ithaburensis
Spring
Summer
Terpene emission rates (µg g-1 dw h-1)
70
60
50
40
30
20
10
0
*
b
**
b
a
a
*
a
a
a
a
Yattir
Birja
Solelim
Solelim


**Fig3.**



Yatir forest-Spring 2013
Terpene emission rates (µg g-1 dw h-1)
Net photosynthetic rate (µmol m-2 s-1)
PPFD
0
10
20
30
40
0
1
2
3
0 200 400 600 800 1000 1200 1400 1600 1800 2000 2200 2400 2600


**Fig4.**

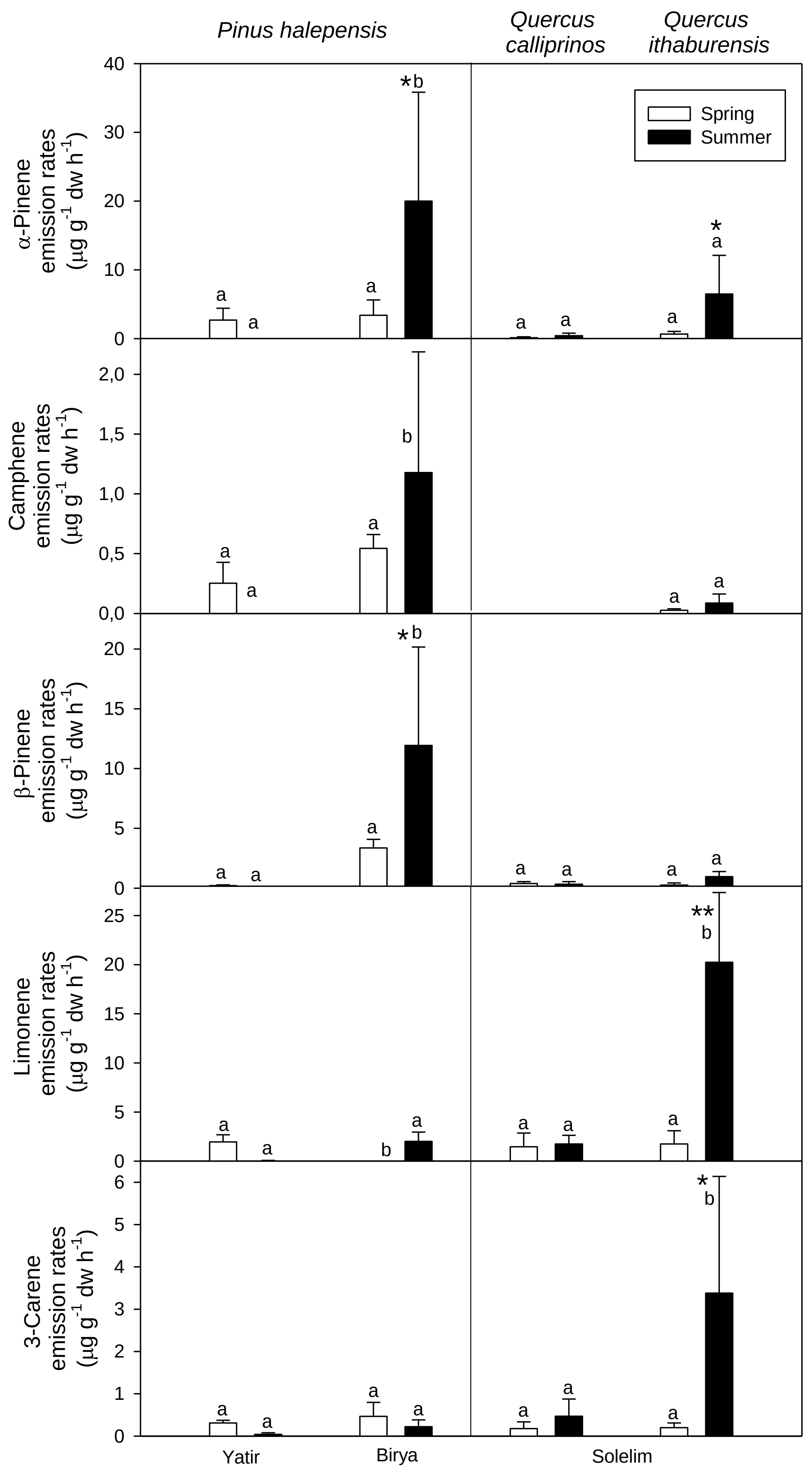

Pinus halepensis
Quercus calliprinos
Quercus ithaburensis
Spring
Summer
α-Pinene emission rates (μg g-1 dw h-1)
Camphene emission rates (μg g-1 dw h-1)
β-Pinene emission rates (μg g-1 dw h-1)
Limonene emission rates (μg g-1 dw h-1)
3-Carene emission rates (μg g-1 dw h-1)
Yatir
Birya
Solelim

**Fig5.**