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Seasonal and diurnal variations of plant isoprenoid emissions from two dominant species in Mediterranean shrubland and forest submitted to experimental drought

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ABSTRACT

We tested the effect of increasing drought conditions in the Mediterranean Basin on isoprenoid emissions for the coming decades by analyzing their effect experimentally on the dominant Mediterranean species *Erica multiflora* in a Garraf shrubland and *Quercus ilex* in a Prades forest in Catalonia (Spain). Drought was simulated in Garraf using automatically sliding curtains to decrease the amount of soil moisture by 5% and in Prades by partial rainfall exclusion and runoff exclusion for a 25% decrease. We measured photosynthetic rates (A), stomatal conductance (g_s) and rates of isoprenoid emission in the morning and at midday for four seasons and determined the relationship of emission rates with environmental conditions. Terpenes were emitted by both species, but only *E. multiflora* emitted isoprene. α-Pinene and limonene were the most abundant terpenes. Isoprenoid emissions increased with air temperature and generally decreased as the amount of soil moisture increased. The results of this study suggest that higher isoprenoid emissions can be expected in the warmer and drier conditions predicted for the coming decades in the Mediterranean region.

1. Introduction

Mediterranean-type ecosystems provide important ecological services, such as the conservation of biodiversity and nutrient cycling (Peñuelas et al., 2013; Seddon et al., 2016). Precipitation is low for these ecosystems, especially in hot periods, and climate change has contributed to the increasing drought in recent decades (Llusià et al., 2011). Models of global circulation, climate and ecophysiology predict a further reduction in the availability of water in Mediterranean regions around the world (Piñol et al., 1998; IPCC, 2007; Sabaté et al., 2002; Peñuelas and Boada, 2003), which are naturally water-limited (Sardans and Peñuelas, 2007) due to the high temperatures and the consequent high rates of evapotranspiration (Peñuelas and Llusià, 2001). Drought stress can affect numerous physiological and biochemical processes governing plant growth, leading to a reduction in stem elongation, leaf expansion and stomatal conductance (Daie and Patrick, 1988; Alexieva et al., 2001; Liu et al., 2016). Plants, however, can survive these hydropenic stress conditions after long periods of acclimation (Chaves et al., 2002; Bai et al., 2008; Rubio-Casal et al., 2010) by adjusting their metabolism (Hsiao, 1973) and reorganizing their energy resources (Dobrota, 2006), including changes in photosynthetic rate (A) and stomatal conductance (g_s). Biogenic volatile organic compounds (BVOCs) are also an important tool for resisting drought (Peñuelas and Llusià, 2003; Filella et al., 2007; Porcar-Castell et al., 2009).

Approximately half of all plant species growing in Mediterranean-type ecosystems, especially shrubland and forest ecosystems, produce and emit a large variety of BVOCs (Peñuelas and Llusià, 1999). These compounds are formed in various plant organs such as flowers, fruits, leaves, bark and roots (Niederbacher et al., 2015) during diverse physiological processes (Laothawornkitkul et al., 2009), which are then emitted directly or stored in specialized structures (Loreto and Schnitzler, 2010). BVOCs provide protection against high temperatures, high irradiation, oxidative stress and drought stress (Velikova et al., 2005; Holopainen and Gershenzon, 2010; Loreto and Schnitzler, 2010). They can also act as herbivore deterrents, attractants of pollinators and enemies of herbivores (Peñuelas and Munné-Bosch, 2005; Llusià and Peñuelas, 2000) and plant–plant communication signals (Peñuelas and Llusià, 2003). BVOCs are thus a vital and central component of plants due to their significance to the survival of individual plants but in addition they exert a strong influence on atmospheric chemistry (Dicke

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and Loreto, 2010; Seco et al., 2013; Niederbacher et al., 2015). BVOCs play a key role in atmospheric processes that influence the atmospheric burden of pollutants (Kroll and Seinfeld, 2008), which can also interact with climate change in several ways (Peñuelas and Llusià, 2003; Yuan et al., 2009; Riipinen et al., 2012). BVOCs are the main biogenic precursors of ozone and by consuming hydroxyl radical prolong the persistence of other compounds such as the greenhouse gas methane (Di Carlo et al., 2004). Furthermore, the photo-oxidation of BVOCs generates secondary organic aerosols, which have the potential for complex climatic feedbacks (Claeys et al., 2004; Carslaw et al., 2009).

BVOCs are very diverse and consist of various organic classes such as isoprenoids, fatty acid derivatives, alcohols, alkanes, alkenes, esters and acids (Kreuzwieser et al., 1999; Peñuelas and Llusià, 2001). Isoprenoids such as isoprene and monoterpenes, the most common and abundant BVOCs, confer protection against the high temperatures and drought stress under the current trend of climatic warming (Peñuelas and Llusià, 2001; Copolovici et al., 2005).

Several studies have demonstrated the importance of abiotic and biotic factors for the emissions of BVOCs (Peñuelas and Llusià, 2001, 2003; Paris et al., 2010). Among abiotic factors, water availability has a strong effect on BVOC emission, especially under Mediterranean conditions characterized by long dry summers with high solar irradiation and temperatures (Tsakiris et al., 2007; Llusià et al., 2011, 2013). Plant behavior is complex under these integrated environmental influences and may differ among biological species. Rates of isoprenoid emission increase and help plants to resist stress under moderate drought conditions but decrease under severe drought conditions (Gershenzon et al., 1978; Llusià et al., 2011, 2013; Hansen and Seufert, 1999).

The dominant tree species in the Mediterranean Basin have two patterns of terpene emission depending on if they have the ability to store terpenes (Lerdau et al., 1997; Llusià and Peñuelas, 2000). Pool size in resin ducts and internal or external glands in terpene-storing species (Lerdau et al., 1997; Peñuelas and Llusià, 2001; Llusià et al., 2014) affect emission rates, and the short-term response of terpene-emission rates to photosynthetic rates may be stronger and faster in non-storing than storing species (Gershenzon et al., 1978; Staudt and Seufert, 1995). Terpene-emission rates in terpene-storing plants, though, are not necessarily determined by terpene concentration; their response to drought can be involved in the short-term control of emissions, either increasing (Rennenberg et al., 2006) or decreasing (Bertin and Staudt, 1996; Llusià et al., 2006) the emission rates depending on the intensity of the water stress (Llusià and Peñuelas, 2000; Llusià et al., 2011).

Climatic experiments have been widely used on various time scales to predict the potential physiological and phenological changes in plants under simulated future climatic scenarios (Beier et al., 2012; Leuzinger et al., 2011; De Boeck et al., 2015; Ogaya et al., 2014). Numerous field experiments in various ecosystems have demonstrated the effectiveness of identifying the physiological adjustments of plants in response to climate change, despite the variety and complexity of the environmental conditions (Prieto et al., 2009; Limousin et al., 2010; Liu et al., 2016). The short-term diurnal (Peñuelas and Llusià, 1999) and long-term seasonal (Guenther, 1997; Llusià and Peñuelas, 2000) cycles under experimental drought also determine the status of isoprenoid emission (Llusià and Peñuelas, 2000; Llusià et al., 2006). Variations in emissions have been linked to corresponding changes in temperature, radiation, air humidity and water availability (Llusià et al., 2006) but also to leaf development and physiological activity (Llusià and Peñuelas, 2000). These factors are also involved in the variations among isoprenoids due to their diverse physicochemical traits (Llusià and Peñuelas, 2000).

We studied the net photosynthetic rates (A), the stomatal conductance (g_s) and the rates of isoprenoid emissions in the shrub *Erica multiflora* L. and the tree *Quercus ilex* L., which are widely distributed in the western and central Mediterranean Basin and are among the dominant species at our two study sites, Garraf (shrubland) and Prades (forest), respectively (Llusià et al., 2006, 2013; Ogaya et al., 2014). Our aims were to determine the relationship between plant physiology and abiotic factors under Mediterranean field conditions, especially gas exchange and isoprenoid emissions, for predicting the effects of increasing drought stress expected in the coming decades and to improve the algorithms for isoprenoid emission used in models.

2. Material and methods

2.1. Study sites and species descriptions

The study was carried out in the Garraf and Prades Mountains in Catalonia, northeastern Spain. The climate and vegetation at the two sites are typically Mediterranean. Annual rainfalls were 510.2 mm in Garraf and 661.4 mm in Prades during the measurement year.

Garraf Natural Park is a dry shrubland (Rosmarino-Ericion) south of Barcelona (41°18′08″N, 1°49′05″E; 210 m a.s.l.). This site suffered large fires in the summers of 1982 and 1994, the regenerated vegetation has a coverage of 50–60% and a maximum height of 70 cm. The dominant species at the study site are *Erica multiflora* L., *Globularia alypum* L., *Pinus halepensis* L. and *Rosmarinus officinalis* L. (Llusià et al., 2006, 2013). All are common evergreens of the coastal shrubland in the western Mediterranean Basin. We chose one dominant species *Erica multiflora* L. as research object in this site.

The Prades Mountains are in southwestern Catalonia (41°20′42″N, 1°02′04″E; 970 m a.s.l.) and about 30 km from the Mediterranean coast. The Prades sampling site is a holm oak forest with tree heights between 1.5 and 10 m, dominated by *Quercus ilex* (Bolòs and Vigo, 1990; Llusià et al., 2013; Ogaya et al., 2014). The site contains other important evergreen tree and shrub species (*Phillyrea latifolia* L., *Arbutus unedo* L., *Pinus sylvestris* L., *Erica arborea* L. and *Juniperus oxycedrus* L.) and deciduous species such as *Sorbus torminalis* L. and *Acer monspessulanum* L. (Llusià et al., 2013). We chose the dominant species *Quercus ilex* as research object in this site.

2.2. Experimental design

The drought experiments were carried out from 1999 to 2014 (16 years) for both sites. In Garraf, six plots (5 × 4 m) were randomly organized in three blocks for replication, with each block having one drought and one control plot. Transparent and waterproof plastic curtains were activated in the drought treatments by rain sensors to cover the plants and soil during rain for four seasons. Control plots had the same scaffolding but without the curtains. All measurements were conducted in the central 12 m^2 to reduce margin effects. The outer 0.5 m of each plot served as an open buffer zone.

In Prades, four plots (15 × 10 m) were delimited at the same altitude along the slope, two as drought and two as control plots. The drought treatment consisted of partial rain exclusion using PVC strips suspended 0.5–0.8 m above the soil covering approximately 30% of the total plot surface. A ditch 0.8 m deep was excavated along the entire top edge of the drought plots to intercept runoff water.

Emissions were measured in winter 2014 (12, 13 and 14 February in Garraf and 23, 24 and 25 January in Prades), spring 2014 (1, 2 and 3 May in Garraf and 14, 15 and 16 May in Prades), summer 2014 (5, 7 and 9 August in Garraf and 29, 30 and 31 July in Prades) and autumn 2014 (29 and 30 October and 1 November in Garraf and 21, 22 and 23 October in Prades) in the morning (9:00–13:00 solar time) and at midday (13:00–17:00 solar time). Emissions from sunlit and healthy *E. multiflora* needle clusters and *Q. ilex* leaves were measured from three random plants in each plot. Air temperature was measured by an automatic meteorological station, and soil moisture was measured by time domain reflectometry (Tektronix 1502C, Beaverton, United States), both about every 30 min on the day of sampling.