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Drought and soil amendment effects on monoterpene emission in rosemary plants

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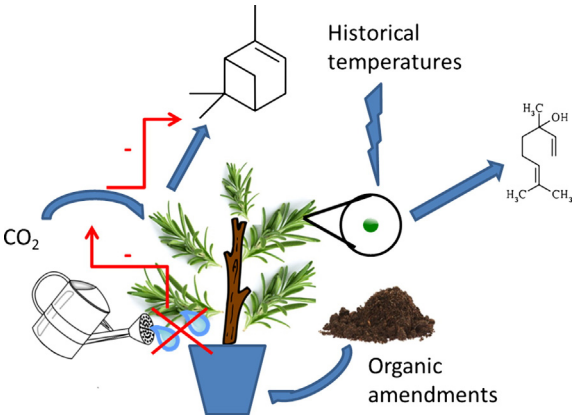
HIGHLIGHTS

- Rosemary isoprenoid emissions under drought and fertilisation were studied.
- Drought reduced photosynthetic rates, stomatal conductance and isoprenoid emissions.
- Non-oxygenated monoterpene emission was dependent on photosynthesis.
- Organic amendment seemed not to induce a significant effect on isoprenoid emission.

GRAPHICAL ABSTRACT



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ABSTRACT

The aim of this work was to study the changes during 15 days in the monoterpene emission rates of the Mediterranean shrub rosemary (*Rosmarinus officinalis* L.), in response to increasing drought stress and fertilisation using two different composts derived from livestock anaerobic digestates (cattle and pig slurry). Drought stress considerably reduced photosynthetic rates, stomatal conductance and isoprenoid emissions and also induced a change in blend composition. In the drought stressed rosemary plants, a positive relationship of non-oxygenated monoterpene emissions and a negative relationship of oxygenated monoterpene with photosynthesis were observed, indicating a different control mechanism over the emissions of the two types of isoprenoids. The emission of non-oxygenated monoterpenes seemed to depend more on photosynthesis and "de novo" synthesis, whereas emission of oxygenate monoterpenes was more dependent on volatilisation from storage, mainly driven by cumulative temperatures. In the short term, the addition of composted organic materials to the soil did not induce a significant effect on isoprenoid emission rates in the rosemary plants. However, the effect of the interaction between fertilisation and seasonality on isoprenoid emission rates was influenced by the amendment origin. Also, we emphasized changes in potential isoprenoid emission factors throughout the experiment, probably indicating changes in the leaf developmental stage.

Abbreviations: A, photosynthesis; g_s, stomatal conductance.

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1. Introduction

Volatile isoprenoids are the most abundant Biogenic Volatile Organic Compounds (BVOCs) synthesized and emitted by plants. These compounds play an important role in tropospheric photochemistry by affecting the ozone budget and by increasing the yield of secondary organic aerosols (Atkinson and Arey, 2003; Carlton et al., 2009). Isoprenoids emission is a main defensive line against abiotic (Loreto and Schnitzler, 2010) and biotic stress conditions (Niinemets et al., 2013) and mediate ecological interactions with the biotic environment (Gershenzon and Dudareva, 2007; Gouinguene and Turlings, 2002; Boege and Marquis, 2005; Niinemets, 2010; Loreto et al., 2014). These compounds also have a role in protecting leaves against oxidative and thermal stresses (Loreto et al., 2004; Grote and Niinemets, 2008) possibly through the enhancement of membrane stability and the scavenging of reactive oxygen species (Vickers et al., 2009).

The main driving variables for the emission of isoprenoids that are not stored in permanent pools are photosynthetically active radiation (PAR) and temperature, which form the basis of all emission models (Arneth et al., 2008; Guenther et al., 2006; Monson et al., 2012). However, other environmental factors, such as seasonality, CO_2 and ozone level, mechanical stresses, and drought, have also been reported to influence isoprenoid emissions (Staudt et al., 2000, 2002; Plaza et al., 2005; Blanch et al., 2007; Curci et al., 2009; Peñuelas and Staudt, 2010; McKinney et al., 2011; Holopainen and Gershenzon, 2010; Loreto and Schnitzler, 2010). In some plant species, monoterpenes are synthesized and stored in secretory organs. This is the case for the glandular trichomes of many *Lamiaceae* (Grote and Niinemets, 2008), e.g. *Rosmarinus officinalis* L. In these cases, emissions seem to be mainly produced by temperature driven diffusion processes of the stored monoterpenes (Schurgers et al., 2009), though there are increasing evidences that "de novo" synthesized monoterpenes also contribute to the total emission of monoterpenes. For instance, several authors have reported an absence of relationship between emitted and stored monoterpenes in *R. officinalis*, suggesting that a fraction of the overall monoterpenes produced by *R. officinalis* leaves could be emitted to the atmosphere directly after synthesis, instead of being stored in storage pools (Peñuelas and Llusià, 1997; Ormeño et al., 2007c, 2009).

Soil water availability represents a major environmental constraint under Mediterranean conditions, and models estimate a further decrease in precipitation in the Mediterranean basin (Gibelin and Deque, 2003). Drought stress caused by low soil water availability does not have a clear impact on isoprenoid emissions. Isoprenoids may decrease, due to restricted carbon acquisition (Hansen and Seufert, 1999; Staudt et al., 2002; Grote et al., 2009; Šimpraga et al., 2011; Burney and Jacobs, 2012), may increase, due to the build-up of intercellular concentration (Sharkey and Loreto, 1993), or may remain unaltered, especially when the stress is prolonged (Peñuelas and Llusià, 1997). Mediterranean soils are also characterised by nutrient deficiencies (Sardans et al., 2006), N and P being the most limiting elements for plant growth and nutrition. Intensive agriculture practices, together with adverse climatic conditions are among the main causes of soil degradation and the loss of soil organic carbon (Bustamante et al., 2011), with negative consequences for plant growth and yield (Turbé et al., 2010).

On the other hand, the intensification of the livestock production implies a potential environmental risk, associated to an inadequate management of the great amounts of organic wastes produced. Anaerobic digestion is an efficient biological method for the energetic valorisation of livestock and agroindustrial wastes, which transforms organic wastes into biogas and the digested material (digestate), the latest being usually composted to improve its properties as organic fertiliser in agriculture (Bustamante et al., 2012, 2013). The application of compost to degraded soils has become a suitable environmental strategy for improving soil physical structure and increasing the amounts of soil organic carbon and other major nutrient such as N and P (Tejada et al., 2006; Bustamante et al., 2012). Compost could affect plant isoprenoid emissions since N and P, which are supplied via compost amendment (Larchevêque et al., 2010), are required for isoprenoid synthesis (Lerdau et al., 1995; Niinemets et al., 2002). However, it has been previously reported that after P and/or N fertilisation isoprenoid emission rates can not only increase (Blanch et al., 2012), but also decrease (Blanch et al., 2007; Fares et al., 2008). Three studies by Ormeño et al. (2009), Olivier et al. (2011a) and Olivier et al. (2011b) on the effects of sewage sludge compost onto isoprenoid emission show variable results, depending on the dose and timing of the treatments (Ormeño et al., 2009). Other previous experiments of fertilisation have also been reported to increase (Lerdau et al., 1995; Possell et al., 2004), decrease (Fares et al., 2008), or not to change (Rosenstiel et al., 2004; Blanch et al., 2007) foliar isoprenoids emissions, depending on plant species, leaf developmental status, type and dose of nutrients, and experimental conditions.

In this work, we aimed to study the changes in monoterpene emission rates of the Mediterranean shrub *R. officinalis* L., in response to increasing drought stress and fertilisation with two different composts derived from livestock anaerobic digestates.

2. Materials and methods

2.1. Characteristics of the soil and of the organic amendments

The soil used in this study was collected from the surface layer (0–20 cm) of a semiarid agricultural area abandoned for ten years in Montelibretti (Rome, Italy, 42° 8′ 7″ N, 12° 44′ 17″ E, 232 m a.s.l). After removal of vegetation, bigger roots and stones, the soil was air-dried and then passed through a 2 mm sieve. The soil at the site was a highly calcareous loam soil, slightly alkaline (pH = 7.6), with low salinity (0.10 dS/m), low concentrations of total N (0.067%) and poor total organic C contents (0.75% C).

The composts were elaborated mainly using the solid fraction of anaerobic digestates of cattle and pig slurry (hereafter named CS and PS, respectively), mixed with vine shoot pruning. On a dry mass basis we used: cattle/pig slurry (75%, CS/PS) + vine shoot pruning (25%). A detailed description of the composting process has been reported elsewhere (Bustamante et al., 2012, 2013). These composts showed high contents of total N (29.0 g kg^{-1} for CS and 30.3 g kg^{-1} for PS) and a suitable degree of maturity to be used as soil amendments (Bustamante et al., 2012, 2013).

2.2. Experimental procedure

The experiment was carried out in a polycarbonate greenhouse placed at the experimental fields of the Istituto di Biologia Agroambientale e Forestale (IBAF-CNR) (42° 06′ 12″ N 12° 38′ 53″ E, elevation 227 m a.s.l., Montelibretti, Rome, Italy), to avoid potential water incomings from rain and to maintain homogeneous Mediterranean-like environmental conditions.

In this study, two factors were applied simultaneously: fertilisation and drought. For the fertilisation treatment, polyethylene pots were filled with 1 kg of soil thoroughly mixed with PS or CS anaerobic digestate based compost at a dose of 60 t compost (fresh weight basis)/ha. These organic amended soils were compared with unamended soil samples (Control). Each treatment was replicated six times, obtaining a total of 18 experimental units. Cuttings of rosemary were planted a week after establishing the fertilisation treatment, in each one of the pots with the corresponding treated soil. To assure genetic identity, the plants used were exclusively propagated by rooted cuttings. Pots were distributed in a randomised complete block design inside a greenhouse. All the pots were well watered and maintained under natural environmental conditions of light and temperature until the beginning of the drought treatment, four months after planting rosemary. Then, the irrigation strategy was diversified to apply the drought factor in two variables: control plants (well-watered, WW),

were watered with 1 L per week and plant (applying 250 mL every 2 days), and plants with drought (drought stressed, DS), where left unwatered during the same period. In this way, the full combination of the two factors was implemented by six treatments replicated three times.

Simultaneous samplings and measurements for this study were carried out every five days in four sampling dates (at days 0, 5, 10 and 15, considering day 0 when the drought treatment was initiated). At the beginning and at the end of the experimental period soil samples were taken to determine soil total N (TN) and total organic C contents (TOC).

2.3. Gas exchange measurements

Net photosynthetic rates (A) and stomatal conductance (g_s) were recorded using an infrared gas analyser (LI-COR 6400) (LI-COR, Lincoln, NE, USA), by enclosing a portion of the branch in a 6 cm^2 cuvette with a transparent upper Teflon window. Parameters such as relative humidity, air temperature and photosynthetically active radiation (PAR) in the leaf chamber were obtained simultaneously with gas exchange measurements. The CO_2 concentration inside the chamber was 385 ± 10 μmol mol^{-1}. Ambient PAR and air temperature ranged between 1270–1390 μmol m^{-2} s^{-1} and 23.8–33.6 °C, respectively. Relative humidity during these measurements ranged from 45 to 55%. Stomatal conductance was calculated using the classic formulation by von Caemmerer and Farquhar (1981). Measurements were taken in branches from three different plants per treatment (soil amendment × water status) between 10.00 and 16.00 h (solar time).

Leaf area was calculated after scanning, using ImageJ software version 1.48 (http://rsb.info.nih.gov/ij/).

2.4. Monoterpene emission

After performing gas exchange measurements, the same branches were used for the collection and measurement of isoprenoid emissions. The air leaving the gas-exchange cuvette was passed through a Teflon-made T connector to a tube (8 cm long and with 0.3 cm internal diameter) filled with 200 mg Tenax particles 35–60 mesh in size (Markes International Limited, Llantrisant, UK). Prior to their use, all the tubes were conditioned for 10 min at 350 °C with a stream of purified helium. A calibrated air sampling pump was used to standardise air flow through the absorption tube. The sampling time was 30 min, and the flow 200 ml min^{-1}. BVOC background was measured every day before starting the measurements by collecting 6 L of air exiting the empty cuvette. After sampling, the glass tubes were stored at 4 °C until analysis (within 24–48 h).

Monoterpenes retained on the adsorption traps were thermally desorbed at 275 °C for 10 min in a Markes Unity 1 thermal desorption unit (Markes International Limited, Llantrisant, UK) under a flow rate of helium, cryofocused in a cold trap containing a 2 mm diameter × 60 mm long bed of Tenax TA backed up by Carbograph 1TDTM separated and supported at each end by quartz wool and kept at −10 °C by a Peltier cell. By rapid heating of the cryogenic trap at 300 °C, BVOCs were injected into a 30 m MS-5HP capillary column with an inner diameter of 0.25 mm (J&W Scientific USA, Agilent Technologies, Palo Alto, CA, USA), connected to a gas chromatographic–mass spectrometric unit (GC–MS–MSD 5975C) supplied by the same company. The column temperature was maintained at 40 °C for 1 min, and then increased up to 210 °C at a rate of 5 °C/min. A final temperature of 250 °C was reached using a rate of 20 °C/min. Helium was used as a carrier gas. The actual emissions were positively quantified by filling the cartridges with 2 L of air in which 70 ppb of gaseous standards (Rivoira, Milan, Italy) of the main monoterpenes (α-pinene, β-pinene, myrcene, limonene) were mixed. For the analysis of the results, monoterpenes were divided in the two components, non-oxygenated monoterpenes (α-pinene, camphene, β-pinene, myrcene, cymene, limonene, terpinene, terpinolene) and oxygenated onoterpenes (cineole, camphor, borneol, linalool, verbenone, terpineol).

The correlation between emission rates and the cumulative temperatures (E/T_n) was also determined (Blanch et al., 2011). The average temperature of the days preceding the measurements (T_n = 1–15) was calculated as:

$$T_n = \sum_{d-1}^{d-n} Td/n$$

where n is the number of days preceding the measurements and Td is the average daily air temperature corresponding to day d.

The algorithm and coefficients of Guenther et al. (1993) were used to calculate potential emission factors (Niinemets et al., 2011) at 30 °C. As *R. officinalis* is a terpene-storing species, the algorithm was the following:

$$E = E_s[\exp[\beta(T - T_s)]]$$

where E is the emission rate (μg g^{-1} DM h^{-1}) at temperature T (in degrees Kelvin, K), E_s is the emission factor in micrograms per gramme dry matter and hour at standard temperature T_s (303 K), and β is an empirically determined coefficient, 0.09 (in degrees Kelvin, K).

2.5. Analytical determinations

Total organic carbon (TOC) and total nitrogen (TN) were determined in the soil samples collected at the beginning and end of the experiment. For this, soil samples were previously air-dried and sieved at 0.5 mm, then acidified with 20 μl 5 M ultrapure HCl and kept at 60 °C for 12 h in order to remove inorganic carbon. Finally, they were analysed using an elemental carbon analyser (Carlo Erba NA 1500 series 2 C/H/N/O/S). TOC and N contents are expressed as percentages (%) of dry weight.

Relative water content (RWC) was determined as an indicator to evaluate plant water status (Saura Mas and Lloret, 2007; Beckett et al., 2012). It was measured in each sampling date, using three to four needles per plant. RWC was determined as 100 × (FW − DW)/(TW − DW), where FW is the fresh weight, TW is the turgid weight after re-hydrating the leaves for 24 h, and DW is the dry weight after oven-drying the leaves at 60 °C for 72 h.

2.6. Statistical analysis

Analyses of variance (ANOVA) were performed using gas exchange and monoterpene emissions as dependent variables, and the factors drought and organic fertilisation as two independent factors. The Fisher post-hoc test was used to investigate the significance of different groups of means, considered significant at a probability level of $P < 0.05$. Correlation analyses were conducted between leaf non-oxygenated monoterpene emission rates (Y variable) and photosynthetic rates (X variable), and between leaf oxygenated monoterpene emission rates (Y variable) and photosynthetic rates (X variable). All statistical analyses were conducted using SIGMASTAT.

3. Results

3.1. Soil total organic C and total N contents in amended and unamended soils

In Fig. 1A and B the concentrations of total organic C (TOC) and total N (TN) in the amended and control soils are shown. In general, the amendments produced an increase in the contents of TOC and TN. Regarding the total organic C, the soils amended with CS showed a greater conservation of the organic matter incorporated. However, the highest total N was observed in the soils amended with the compost PS.

3.2. Environmental conditions and stress indicators

Temperature ranged from 23.8 °C at the beginning of the experiment to 33.6 °C at its end (Fig. 2A), whereas PAR ranged from 1270 to 1390 μmol m^{-2} s^{-1} during the same time span (Fig. 2B).

The leaf RWC water content decreased with the drought treatment from 86.5 ± 1.6 to 43.4 ± 1.6 (Fig. 3). No significant differences were observed in the RWC of plants grown in the different amended soils throughout the 15 days under drought conditions (data not shown).

The net photosynthetic rates did not present differences among the different treatments, being 10.1 + 1.2, 10.5 + 1.2, 8.1 + 0.5 μmol m^{-2} s^{-1} at the beginning of the experiment for plants grown on the soils without amendment, or with PS or CS composts, respectively. However, A was lower in drought-stressed plants than in control plants (Fig. 4A), ($P < 0.001$, ANOVA). In all soil treatments, the effects of seasonality (time) and their interaction with drought stress were significant ($P < 0.001$, ANOVA). Drought also decreased stomatal conductance in all soil treatments (Fig. 4B), ($P < 0.001$, ANOVA). Moreover, drought stress, seasonality and the interaction drought stress x seasonality significantly affected stomatal conductance ($P < 0.001$, ANOVA).

Total monoterpene emission rates were similar in all fertilisation scenarios at the beginning of the experiment, as 2.1 + 0.3, 1.9 + 0.3, 1.7 + 0.2 μg g^{-1} DM h^{-1} were emitted in plants grown in control, PS or CS compost soils, respectively. However, seasonality ($P < 0.001$, ANOVA) and its interaction with fertilisation ($P = 0.045$, ANOVA) significantly affected monoterpene emission (Fig. 5). Emissions of the two components of monoterpenes, oxygenated and non-oxygenated, were significantly affected by seasonality ($P < 0.001$) and its interaction with fertilisation ($P = 0.032$, $P = 0.04$, respectively). Specifically, as a consequence of PS fertilisation, total monoterpene emission rates decreased significantly at the last time point (15 days) ($P = 0.017$).

Also, drought ($P = 0.008$, ANOVA) and its interaction with seasonality ($P < 0.001$, ANOVA) significantly decreased non-oxygenated and total monoterpene emissions (Fig. 6). Emission rates of the last two sampling dates were significantly lower in drought stressed plants than in control ones. As it can be also observed in Fig. 6, both oxygenated and non-oxygenated monoterpene emission rates increased throughout the experiment.

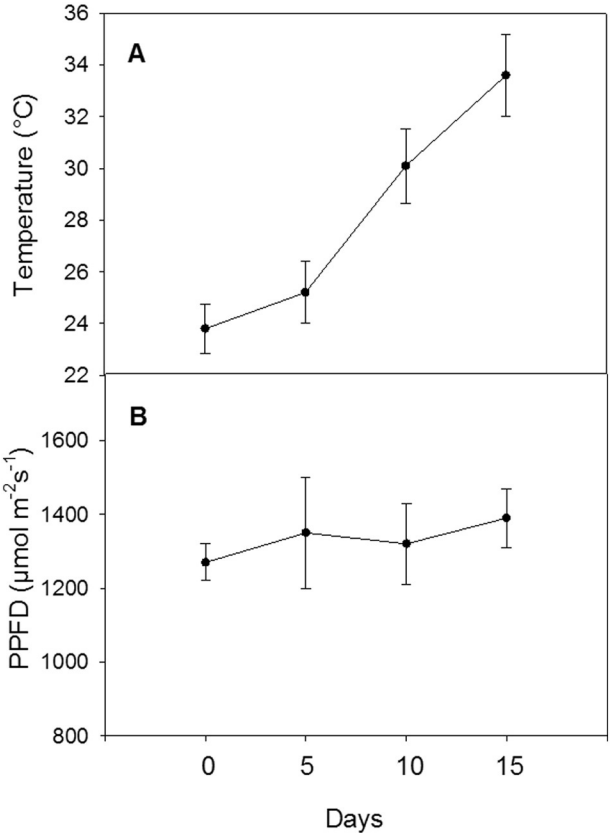

Fig. 2. Ambient variables measured when sampling along the experiment. (A) Temperature and (B) photosynthetically active radiation (PAR) (mean values ± standard error).

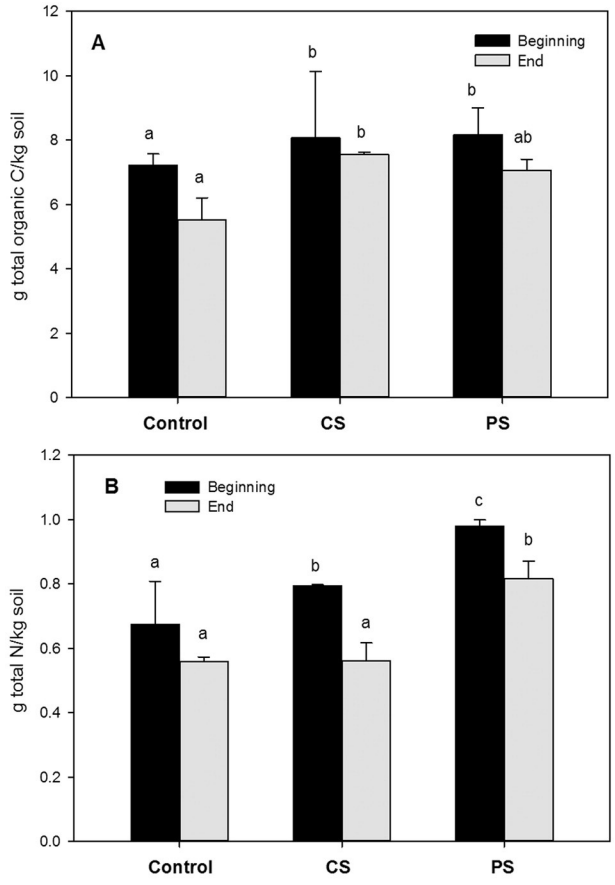

Fig. 1. (A) Soil concentrations of total organic C (g kg^{-1}) and (B) total N (g kg^{-1}) at the beginning and at the end of the experiment for well-watered rosemary plants grown in unamended (control), PS compost-amended (PS) and CS compost-amended (CS) soils. Mean values ± standard error (n = 3). Mean values of each sampling time (beginning and end) followed by the same letter are not significantly different at $P < 0.05$.

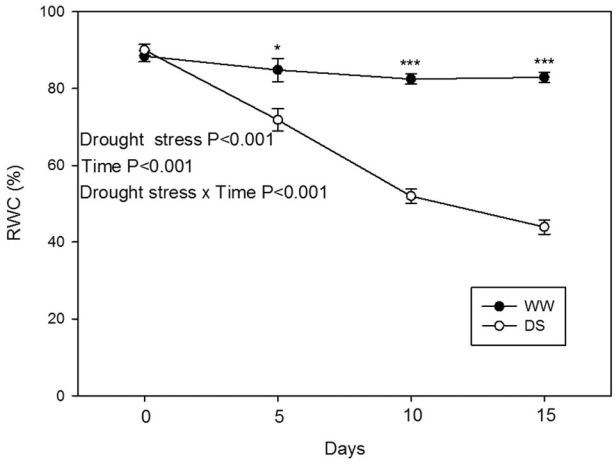

Fig. 3. Relative water content (RWC) during the experiment for drought stressed (DS) and well-watered (WW) rosemary plants. Mean values ± standard error (n = 9). Stars indicate significant differences between the two watering levels (*$P = 0.01$, *** $P < 0.001$).

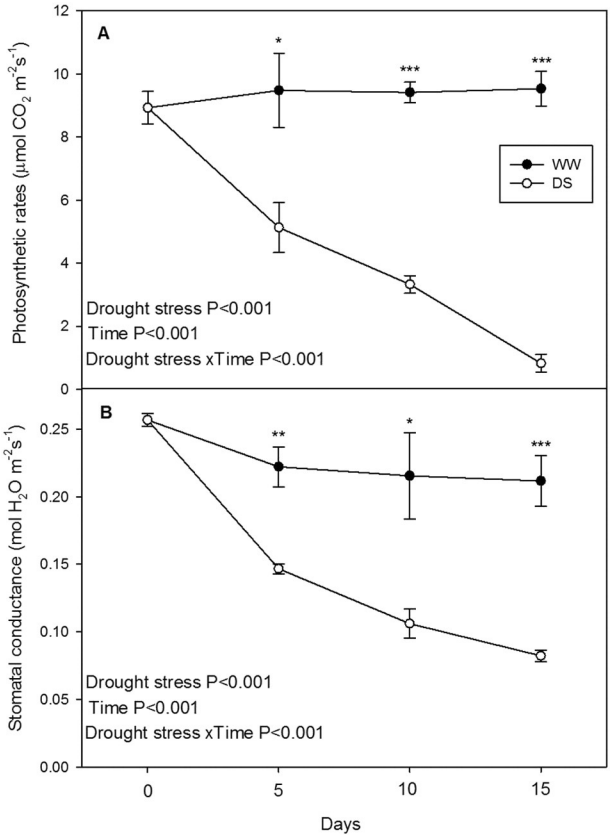

Fig. 4. (A) Net photosynthetic rates (μmol CO_2 m^{-2} s^{-1}) and (B) stomatal conductances (mol H_2O m^{-2} s^{-1}) throughout the experiment for drought stressed (DS) and well-watered (WW) rosemary plants. Mean values ± standard error (n = 9). Stars indicate significant differences between the two watering levels (A;* $P = 0.016$, *** $P < 0.001$, g_s; *$P = 0.02$, ** $P = 0.005$, ***$P < 0.001$).

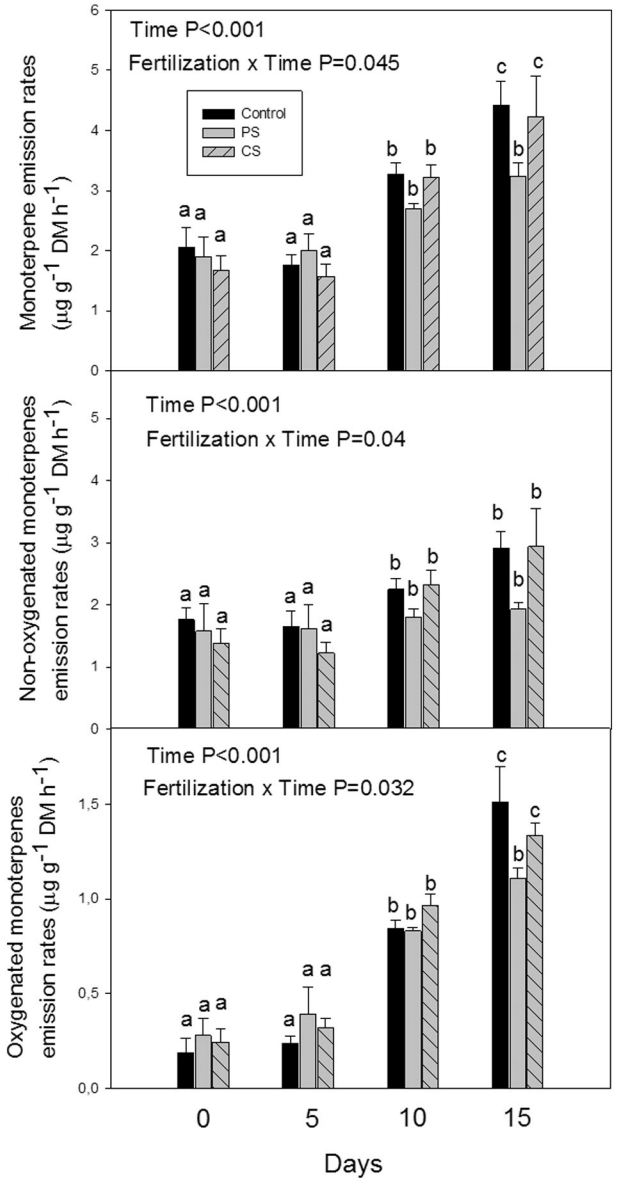

Fig. 5. Total monoterpene, non-oxygenated monoterpene and oxygenated monoterpene emission rates (μg g^{-1} DM h^{-1}) throughout the experiment for well-watered rosemary plants grown in unamended (control), PS compost-amended (PS) and CS compost-amended (CS) soils. Mean values ± standard error (n = 3). Different letters indicate significant statistical differences ($P < 0.05$).

The most abundant monoterpenes were: α-pinene (48 ± 4), camphene (13.8 ± 1), limonene (11.1 ± 1.7) and β-pinene (9.4 ± 0.5) (WW plants grown on unamended soils). Other monoterpene were cymene, myrcene, cineole, terpinene, camphor, borneol, terpinolene, linalool, verbenone, and terpineol. The relative abundance of those compounds is shown in Table 1. The composition of isoprenoid blend changed as a consequence of fertilisation (Table 1). Fertilisation affected the percentage of β-pinene ($P = 0.006$, ANOVA), cineole ($P = 0.042$, ANOVA) and borneol ($P = 0.022$, ANOVA) (Fig. 7). On the other hand, drought stress decreased the percentage of α-pinene ($P = 0.007$, ANOVA) and camphene ($P = 0.034$, ANOVA) and increased the percentage of cineole ($P = 0.003$, ANOVA) and borneol ($P = 0.004$, ANOVA) (Fig. 8).

The correlation between oxygenated emission rates and the cumulative temperatures (E/T_n) in both WW and DS plants ($P < 0.001$) (Tables 2 and 3) increased significantly throughout the experimental period. Seasonality also significantly affected the potential emission factors of several monoterpenes, α-pinene ($P < 0.01$), camphene ($P < 0.05$), myrcene ($P < 0.05$), cymene ($P < 0.05$), cineole ($P < 0.001$), camphor ($P < 0.01$), borneol ($P > 0.001$), linalool ($P < 0.05$), verbenone ($P < 0.01$) (Table 4).

4. Discussion

The main purpose of this study was to evaluate the effects of drought stress and compost fertilisation on monoterpene emission rates. Our results showed a strong drought effect on monoterpene emission rates. Under our experimental conditions, total leaf monoterpene emission rates increased during the first phase of drought, when stress was mild (RWC > 70%) and decreased to 80% and 56% in drought stressed plants in the third and fourth samplings (at 10 and 15 days of drought), respectively. Concomitantly, large reductions of A and gs were observed, confirming previous reports with drought stressed *R. officinalis* plants (Munné-Bosch et al., 1999; Nogués and Baker, 2000). However, as reported by Munné-Bosch et al. (1999), rosemary photosynthesis is unlikely to be permanently damaged even when water deficit, high light and high temperature interact during summer.

Probably, the remaining functionality of photosynthesis is sufficient to drive isoprenoid synthesis in drought stressed rosemary. Increases in the isoprenoid emission rates under mild drought treatments have already been observed in other plants (Brilli et al., 2007; Dani et al., 2014; Tattini et al., in press; Wu et al., 2015). Dani et al. (2014) attributed this fact to the increase in the ratio between electron transport rate (ETR) and net carbon assimilation rate (NAR), as well as to the increased availability of the reducing power to the methylerythritol phosphate (MEP) pathway, leading to isoprenoid synthesis, similarly to that

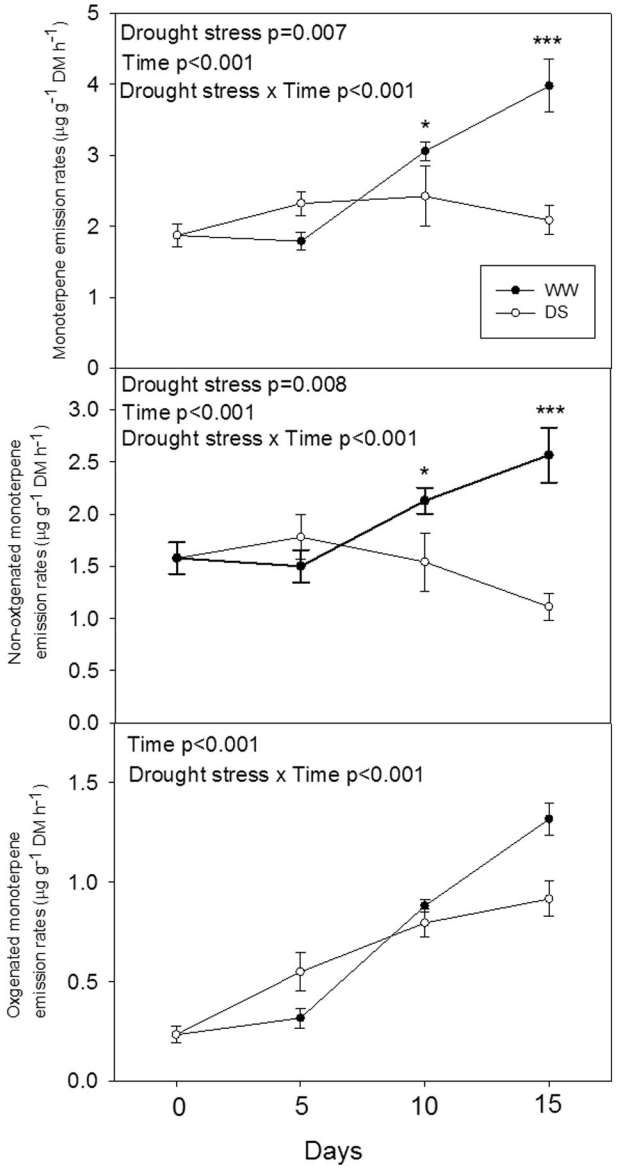

Fig. 6. Total monoterpene, non-oxygenated monoterpene and oxygenated monoterpene emission rates (µg g^{-1} DM h^{-1}) during the experiment for drought stressed (DS) and well-watered (WW) rosemary plants. Mean values ± standard error (n = 9). Stars indicate significant differences among the two watering levels (Total monoterpenes;*P = 0.042, *** P < 0.001, non-oxygenated monoterpenes;* P = 0.045, *** P < 0.001).

observed under other conditions of suboptimal carbon assimilation, such as high-light and/or low-CO_2 (Niinemets et al., 1999).

On the other hand, a reduction of monoterpene emission by terpene-storing species under severe drought conditions could also be expected (Llusià and Peñuelas, 1998). However, Peñuelas and Llusià (1997) and Ormeño et al. (2007d) found no effect of drought stress on *R. officinalis* monoterpene emissions. Peñuelas and Llusià (1997) ascribed this result to resistance to drought of Mediterranean well drought-adapted plants. Consistently, Ormeño et al. (2007d) noted that monoterpene emission by rosemary leaves was not dependent on photosynthesis, and did not reflect photosynthetic inhibition under drought stress conditions (Hansen et al., 1997). A few studies have shown that monoterpene emission from storing species are not only dependent on volatilisation from storage, but may also originate from "de novo" synthesis in the photosynthetic tissue of the leaves (Steinbrecher et al., 1999; Ormeño et al., 2009). A positive relationship of the emission of the non-oxygenated monoterpenes and a negative relationship of oxygenated monoterpene with photosynthesis of drought stressed *R. officinalis* plants was observed (Fig. 9A–B). This may indicate that non-oxygenated monoterpene emission depends more on photosynthesis and "de novo" synthesis, in contrast to oxygenated monoterpene emission.

Also, an increase over the season of the correlation between oxygenated monoterpene emissions and the cumulative temperature in drought stressed plants was observed (Table 2), which constitutes a typical behaviour of emissions from storage (Blanch et al., 2011). The emission from the storage pools, as well as from non-specific storage, is under the control of the specific solubility and consequently, of the gas–liquid phase equilibrium of the different volatile compounds within the leaf (Niinemets and Reichstein, 2003). In some cases, also the stomata can exert control, mainly depending on the rate at which a specific BVOC reaches the equilibrium between the gas and liquid phases within the leaf after any perturbation (Harley, 2013). The faster the equilibrium is established, the less is the control that stomata can exert on emissions (Harley, 2013). Indeed, stomatal control can be different, depending on volatility of terpenes, as in the case of *Pinus pinea* under different drought conditions (Niinemets et al., 2002). Under moderate drought stress, non-oxygenated terpenes are not influenced, while oxygenated ones can be drastically reduced (Harley, 2013). However, in our specific case, oxygenated monoterpenes seemed not to be affected by stomatal conductance. These controversial results may be explained by the initial pool size prior to the changes in the stomatal conductance (Niinemets and Reichstein, 2003). Indeed, a specific monoterpene inside a leaf containing less water (low RWC) will tend to reach faster the gas–liquid phase equilibrium and, consequently stomata will have less opportunity to exert control (Harley, 2013). This is true even for very soluble compounds. This observation may also be related with the increasing monoterpene concentrations that have been observed in many storing species including *R. officinalis*, as a consequence of drought (Kainulainen et al., 1992; Hodges and Lorio, 1975; Llusià and Peñuelas, 1998; Delfine et al., 2005). Thus, the change in the isoprenoid blend emitted by *R. officinalis* under drought mainly depends on the different control of the two types of monoterpenes, oxygenated and non-oxygenated.

Also, for *Cistus albidus*, a different control over emission of different kinds of terpenes, monoterpenes and sesquiterpenes was reported by Ormeño et al. (2007b). The fact that *C. albidus* released monoterpenes that are not previously stored in leaf pools (Ormeño et al., 2007a; Llusià and Peñuelas, 2000), suggests that these compounds are "de novo" synthesized, whereas sesquiterpene emissions are potentially more dependent on storage pools.

In the control treatment, well-watered plants, an increase of both oxygenated and non-oxygenated monoterpene emission rates over the season was observed. In the case of oxygenated monoterpenes, an increase of the correlation E/T_n from T1 to T15 was found (Table 3), indicating that the emission rates depended more on the cumulative temperature of previous days than of the current day. The emission of non-oxygenated monoterpenes, however, seemed to be more dependent on the temperature of the day of sampling than on the mean temperature value of the previous days (Fig. 6), probably reflecting the rapid changes in the activity of specific monoterpene synthases (Fischbach et al., 2000).

Some changes in the potential emission factors throughout the experimental period (from late spring to early summer) were also observed (Table 4). For oxygenated monoterpenes (i.e. borneol, camphor), the emission capacity increased from the beginning to the end of the experiment due to the effect of the cumulative temperature. However, the decreases and increases in the emission capacity of other monoterpenes, such as myrcene, cymene, β-pinene and camphene could be ascribed to other phenological factors, such as growth and leaf development state (Monson et al., 2012). Also, Llusià et al. (2013) found differences in emission factors that could be only attributed to the different ontogenical and phenological characteristics of leaves among seasons (Helmig et al., 2013).

Table 1
Relative amounts of *monoterpenes* (% of the total) in the emission of well-watered (WW) and drought stressed (DS) rosemary plants grown in unamended (control), PS compost-amended (PS) and CS compost-amended (CS) soils. Mean values ± standard error (n = 3).

Treatment	Water regime	a-Pinene	Camphene	b-Pinene	Myrcene	Cymene	Limonene	Cineole	Terpinene	Camphor	Borneol	Terpinolene	Linalool	Verbenone	Terpineol
Control	0 days														
	WW	48.11 ± 4.05	13.99 ± 0.98	9.44 ± 0.49	3.27 ± 1.49	1.69 ± 0.47	10.98 ± 1.74	0.03 ± 0.03	0.28 ± 0.18	3.10 ± 1.28	4.38 ± 1.02	1.28 ± 0.94	1.38 ± 0.81	1.87 ± 1.12	0.72 ± 0.53
	DS	48.11 ± 4.05	13.99 ± 0.98	9.44 ± 0.49	3.27 ± 1.49	1.69 ± 0.47	10.98 ± 1.74	0.03 ± 0.03	0.28 ± 0.18	3.10 ± 1.28	4.38 ± 1.02	1.28 ± 0.94	1.38 ± 0.81	1.87 ± 1.12	0.72 ± 0.53
	5 days														
	WW	50.05 ± 3.62	13.69 ± 1.03	8.51 ± 0.80	3.57 ± 1.75	0.59 ± 0.04	7.23 ± 0.81	4.45 ± 2.10	0.38 ± 0.23	2.59 ± 0.02	4.39 ± 0.43	1.56 ± 0.88	0.96 ± 0.27	1.44 ± 0.72	0.55 ± 0.28
	DS	39.19 ± 0.20	10.26 ± 0.09	7.75 ± 0.57	4.92 ± 0.32	2.53 ± 0.10	9.40 ± 0.36	8.95 ± 0.76	0.36 ± 0.01	3.61 ± 0.39	7.46 ± 0.61	0.69 ± 0.1	2.43 ± 0.44	1.28 ± 0.45	1.15 ± 0.27
	10 days														
	WW	37.25 ± 1.51	10.65 ± 0.79	7.55 ± 0.16	3.15 ± 0.93	2.37 ± 0.13	5.92 ± 0.15	9.52 ± 0.75	0.88 ± 0.28	4.30 ± 0.56	8.99 ± 0.76	2.57 ± 0.60	3.44 ± 0.29	2.21 ± 0.59	1.18 ± 0.24
	DS	20.68 ± 1.07	4.59 ± 0,41	3.72 ± 0.52	5.37 ± 1.63	3.50 ± 0.14	7.35 ± 1.83	32.62 ± 1.98	2.51 ± 1.25	3.17 ± 0.94	12.93 ± 2.31	1.24 ± 0.65	0.00 ± 0.00	1.28 ± 0.75	1.06 ± 0.19
	15 days														
	WW	31.31 ± 1.56	8.45 ± 0.16	6.81 ± 0.46	4,32 ± 0.42	2.37 ± 0.13	6.20 ± 0.50	12.50 ± 1.82	1.14 ± 0.16	4.63 ± 0.16	11.35 ± 0.92	2.01 ± 0.33	4.41 ± 0.67	3.36 ± 0.07	1.12 ± 0.09
	DS	19.63 ± 1.10	4.85 ± 0.47	5.76 ± 1.85	5,73 ± 1.71	3.76 ± 0.22	7.11 ± 2.04	27.93 ± 4.32	2.98 ± 1.41	2.44 ± 0.27	13.41 ± 2.04	1.41 ± 0.70	1.97 ± 1.05	2.02 ± 1.04	1.02 ± 0.19
PS	0 days														
	WW	41.43 ± 4.04	13.90 ± 1.41	7.80 ± 0.89	1.64 ± 0.85	2.09 ± 0.44	13.66 ± 3.89	4.91 ± 3.05	0.36 ± 0.36	2.73 ± 1.08	7.97 ± 2.37	0.36 ± 0.36	0.86 ± 0.60	1.33 ± 0.67	0.96 ± 0.51
	DS	41.43 ± 4.04	13.90 ± 1.41	7.80 ± 0.89	1.64 ± 0.85	2.09 ± 0.44	13.66 ± 3.89	4.91 ± 3.05	0.36 ± 0.36	2.73 ± 1.08	7.97 ± 2.37	0.36 ± 0.36	0.86 ± 0.60	1.33 ± 0.67	0.96 ± 0.51
	5 days														
	WW	39.34 ± 0.64	13.91 ± 0.20	8.66 ± 0.43	1.68 ± 0.86	1.51 ± 0.37	12.97 ± 0.93	7.33 ± 1.33	0.42 ± 0.25	1.66 ± 0.34	6.82 ± 1.47	1.26 ± 0.52	1.29 ± 0.11	1.75 ± 0.54	1,37 ± 0.38
	DS	42.54 ± 0.86	12.94 ± 1.66	7.53 ± 0.68	1.81 ± 0.91	1.84 ± 0.22	5.31 ± 0.56	8.30 ± 0.24	0.53 ± 0.28	3.51 ± 0.75	11.24 ± 1.53	0.44 ± 0.28	1.47 ± 0.45	1.85 ± 0.18	0.68 ± 0.34
	10 days														
	WW	34.65 ± 4.20	10.41 ± 0.80	6.66 ± 0.77	3.79 ± 1.13	2.33 ± 0.41	6.20 ± 1.04	11.65 ± 0.81	0.84 ± 0.42	4.45 ± 0.42	13.01 ± 0.79	1.21 ± 0.36	1.62 ± 0.40	2.24 ± 0.05	0.96 ± 0.29
	DS	32.70 ± 4.35	11.06 ± 1.32	6.82 ± 1.05	3.76 ± 0.85	2.91 ± 0.81	6.06 ± 0.56	14.74 ± 3.13	0.81 ± 0.31	3.64 ± 0.22	12.2 ± 0.70	0.74 ± 0.04	2.60 ± 0.20	1.40 ± 0.71	0.55 ± 0.52
	15 days														
	WW	33.67 ± 4.79	8.63 ± 0.42	5.59 ± 0.30	4.08 ± 0.80	3.01 ± 0.62	5.53 ± 0.58	16.85 ± 1.72	0.89 ± 0.30	3.25 ± 0.85	13.33 ± 1.37	0.74 ± 0.30	2.17 ± 0.44	2.25 ± 0.20	1.27 ± 0.17
	DS	21.52 ± 4.18	9.7 ± 1.26	5.85 ± 0.96	4.68 ± 0.87	3.69 ± 0.40	4.57 ± 1.56	19.53 ± 1.61	1.44 ± 0.35	4.59 ± 1.58	16.34 ± 0.98	0.48 ± 0.19	3.22 ± 0.85	3.18 ± 0.77	1.44 ± 0.27
CS	0 days														
	WW	51.25 ± 3.93	14.34 ± 1.22	7.10 ± 0.34	2.74 ± 1.53	2.43 ± 0.93	8.26 ± 2.11	0.00 ± 0.00	1.53 ± 1.53	2.07 ± 0.34	6.43 ± 1.09	0.10 ± 0.10	2.83 ± 1.70	0.56 ± 0.56	0.70 ± 0.39
	DS	51.25 ± 3.93	14.34 ± 1.22	7.10 ± 0.34	2.74 ± 1.53	2.43 ± 0.93	8.26 ± 2.11	0.00 ± 0.00	1.53 ± 1.53	2.07 ± 0.34	6.43 ± 1.09	0.10 ± 0.10	2.83 ± 1.70	0.56 ± 0.56	0.70 ± 0.39
	5 days														
	WW	42.07 ± 1.65	12.44 ± 0.49	6.26 ± 0.75	2.69 ± 0.86	2.61 ± 0.29	7.40 ± 1.27	10.86 ± 1.88	3.02 ± 1.51	2.27 ± 0.19	6.16 ± 1.14	1. 78 ± 0.56	1.31 ± 0.71	0.87 ± 0.54	0.26 ± 0.26
	DS	41.27 ± 4.31	12.01 ± 0.96	6.62 ± 0.74	4.04 ± 1.05	3.30 ± 0.76	5.25 ± 2.14	5.52 ± 3.05	2.78 ± 1.40	3.76 ± 0.90	10.60 ± 4.49	0.37 ± 0.37	2.69 ± 1.34	1.04 ± 0.53	0.74 ± 0.60
	15 days														
	WW	37.14 ± 1.33	10.70 ± 0.30	6.24 ± 0.40	2.24 ± 1.22	2.12 ± 0.50	7.22 ± 0.63	10.60 ± 1.34	1.90 ± 1.14	3.90 ± 0.93	11.71 ± 1.58	0.95 ± 0.75	2.14 ± 0.10	2.09 ± 0.24	1.05 ± 0.11
	DS	27.05 ± 6.80	8.67 ± 1.74	5.44 ± 1.54	5.09 ± 1.54	9.52 ± 3.57	8.13 ± 0.52	11.93 ± 3.39	3.27 ± 1.73	4.47 ± 0.45	10.10 ± 3.62	2.18 ± 0.96	1.17 ± 0.88	2.27 ± 0.83	0.71 ± 0.71
	20 days														
	WW	33.58 ± 2.30	9.51 ± 0.67	6.60 ± 0.25	4.97 ± 0.40	2.74 ± 0.03	8.24 ± 1.04	11.83 ± 2.56	0.74 ± 0.05	4.64 ± 0.31	9.81 ± 1.16	1.18 ± 0.04	2.83 ± 0.25	2.32 ± 0.23	1.02 ± 0.02
	DS	24.77 ± 1.31	8.61 ± 0.60	5.11 ± 0.41	4.30 ± 2.17	3.15 ± 0.39	3.52 ± 0.19	12.88 ± 0.82	1.28 ± 0.51	8.33 ± 2.07	19.33 ± 0.48	0.78 ± 0.14	1.52 ± 1.30	4.81 ± 0.64	1.55 ± 0.76

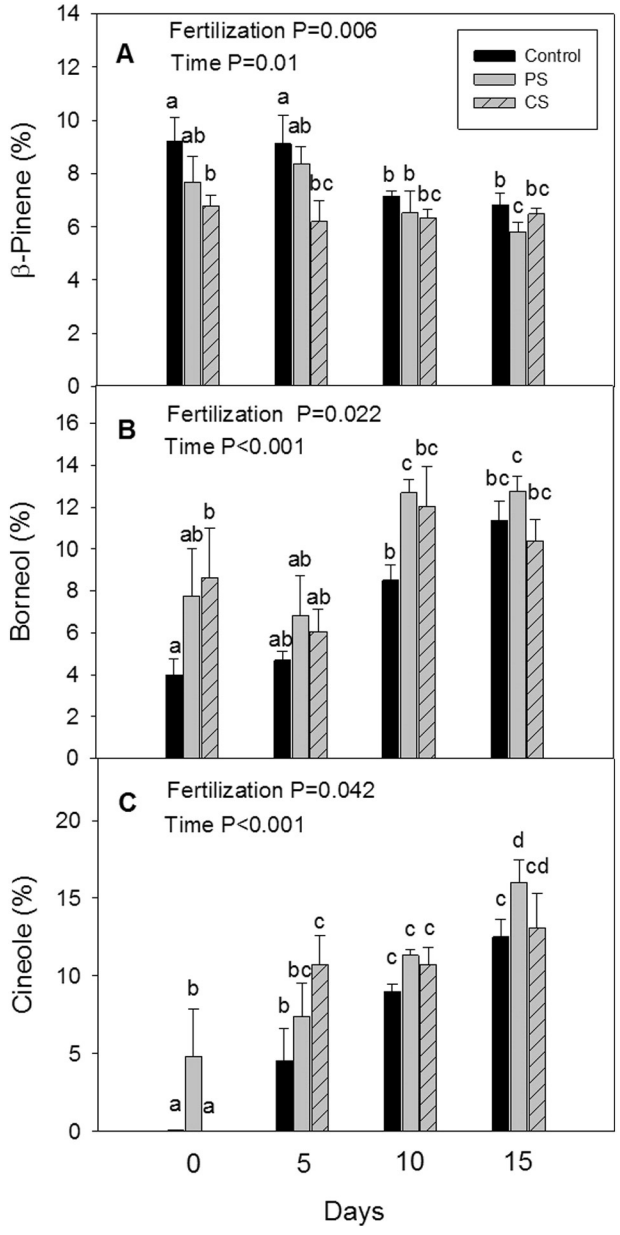

Fig. 7. Percentage of (A) β-Pinene, (B) Borneol and (C) Cineole during the experiment for well-watered rosemary plants grown on unamended, PS compost-amended and CS compost-amended soils. Mean values ± standard error (n = 3). Different letters indicate significant statistical differences (P < 0.05).

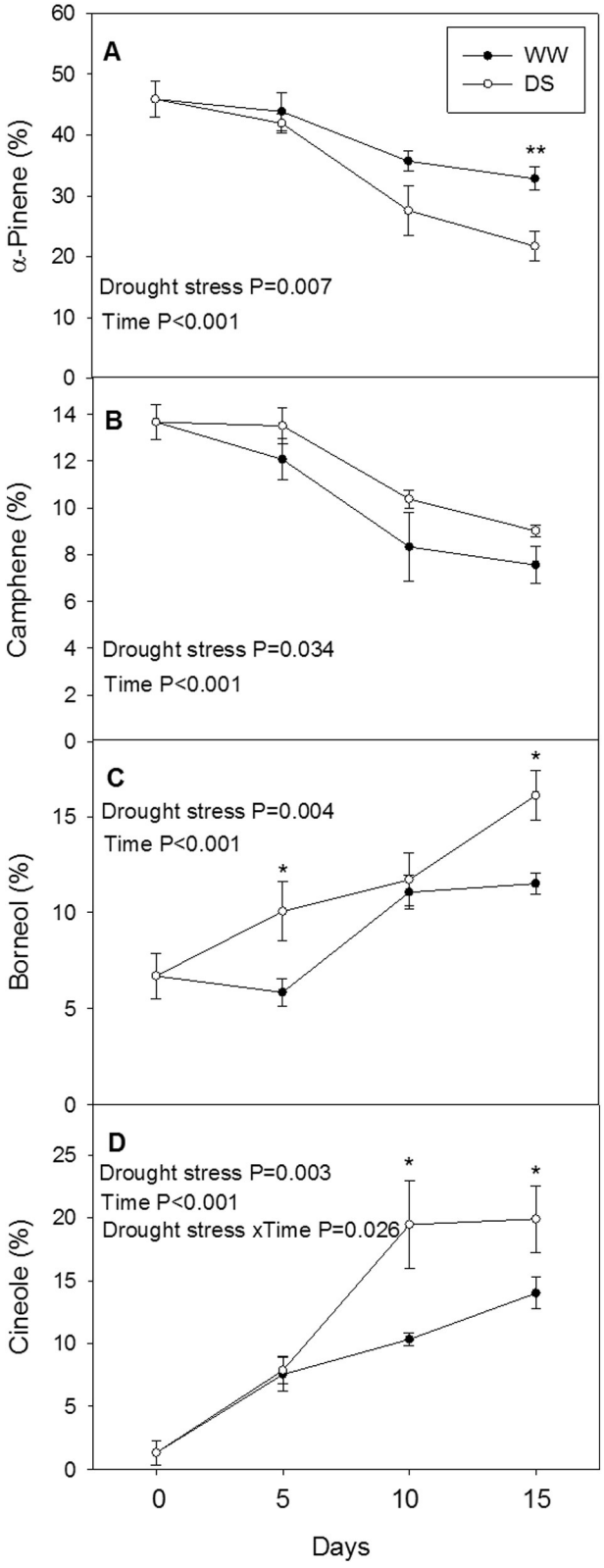

Fig. 8. Percentage of (A) α-Pinene, (B) Camphene, (C) Borneol and (D) Cineole during the experiment for drought stressed (DS) and well-watered (WW) rosemary plants. Mean values ± standard error (n = 9). Stars indicate significant differences between the two watering levels (A; $^{**}P = 0.002$, C; $^{*}P = 0.013$, D; $^{*}P = 0.05$–0.047).

Another objective of this study was to evaluate the impact of the application of two different organic amendments (anaerobic digestate-derived composts) on the terpene emission rates after a short-term exposure to compost. The incorporation of organic materials into soils usually results in an important supply of plant nutrients, such as N, as well as other elements (Bustamante et al., 2011). Indeed, in our case, we observed increased concentrations of total N and organic C in both CS- and PS-amended soils. However, despite the higher nutrient availability, plant growth was not significantly affected (data not shown) by amendment, mainly due to the short duration of the experiment. An increase in nutrient assimilation often promotes terpene emissions (Peñuelas and Staudt, 2010), due to increases in leaf N concentration, though this pattern varies among plant species (Rosenstiel et al., 2004; Blanch et al., 2007), also depending on the plant C/N ratio (Haukioja et al., 1998). Studies about the effect of compost application on terpene emission, however, have not shown to affect greatly leaf terpene content and emission (Olivier et al., 2011a; Ormeño et al., 2009), possibly because compost application failed to improve leaf nutrient concentrations. Our results confirmed previous results regarding

Table 2
Correlation coefficient between non-oxygenated monoterpenes emission rates and oxygenated monoterpene emission rates with the historical average temperature (T_n) for drought stressed rosemary plants. Mean values ± standard error (n = 9) are shown. Different letters indicate significant statistical differences ($P < 0.05$).

Time point	E (μg g^{-1} DM h^{-1})/Tn	
	Non-oxygenated monoterpenes	Oxygenated monoterpenes
0 days	0.066 ± 0.006[a]	0.010 ± 0.002[a]
5 days	0.101 ± 0.031[a]	0.021 ± 0.004[b]
10 days	0.053 ± 0.011[a]	0.031 ± 0.003[bc]
15 days	0.035 ± 0.006[a]	0.033 ± 0.003[c]

the weak effects of organic amendment on terpene emission rates, especially in the short-term. Whereas amendment with CS seemed not to affect monoterpene emission rates, amendment with PS resulted in a 27% reduction in the terpene emission rates in *R. officinalis*, but only at the end of the experiment. The same effect of nutrient availability on the reduction of terpene emissions was also observed by Funk et al. (2006), who reported that fertilisation, and especially N enrichment, did not produce significant increases in emissions from plantation forests of *Eucalyptus saligna*. Blanch et al. (2007), also found that fertilisation with N and P reduced the emissions of terpenes in *Pinus halepensis* by 38%. They indicated that carbon-based secondary compounds, such as terpenoids, can decrease as a result of increased carbon allocation to growth in response to high nutrient availability, in accordance with the carbon nutrient balance hypothesis (Bryant et al., 1983; Koricheva et al., 1998) and the growth differentiation balance (GDB) hypothesis (Loomis and Croteau, 1973). The GDB hypothesis states that any environmental factor that slows growth more than it slows photosynthesis can increase the resource pool available for allocation to differentiation related products (Loomis, 1932), including secondary metabolites. According to this hypothesis, Stamp (2003) stated that the pattern of allocation to secondary metabolites should be curvilinear across a resource gradient, with a peak at intermediate resource levels. Also, sewage sludge compost spreading has been shown to exert variable effects on leaf terpene emissions, depending on the dose of the treatments (Ormeño et al., 2009; Olivier et al., 2011b). Whereas monoterpene emission rates were enhanced with compost doses of 50 t/ha (corresponding to a N leaf content of 0.95% dry matter), they were as low as in control plots with compost rates of 100 t/ha (corresponding to a N leaf content of 1.05%).

5. Conclusions

Our results highlighted two different control mechanisms on emission of non-oxygenated and oxygenated monoterpenes in *R. officinalis* L. plants under drought conditions. On the other hand, while non-oxygenated monoterpene emission seemed to be more dependent on carbon assimilation rates and on the current day temperature, oxygenated monoterpenes were more dependent on the cumulative temperature-induced volatilisation from storage pools. We also found seasonal differences in the potential emission factors of individual monoterpenes, probably following changes in the leaf development stage. Finally, the addition of composted organic materials to the soil

Table 3
Correlation coefficient between non-oxygenated monoterpenes emission rates and oxygenated monoterpene emission rates with the historical average temperature (T_n) for well-watered rosemary plants. Mean values ± standard error (n = 9) are shown. Different letters indicate significant statistical differences ($P < 0.05$).

Time point	E (μg g^{-1} DM h^{-1})/Tn	
	Non-oxygenated monoterpenes	Oxygenated monoterpenes
0 days	0.053 ± 0.005[a]	0.010 ± 0.002[a]
5 days	0.049 ± 0.006[a]	0.012 ± 0.002[a]
10 days	0.061 ± 0.004[a]	0.034 ± 0.001[b]
15 days	0.068 ± 0.007[a]	0.047 ± 0.003[c]

Table 4
Potential emission factors (μg g^{-1} DM h^{-1}) throughout the experiment for well-watered rosemary plants grown in unamended (control), PS compost-amended (PS), and CS compost-amended (CS) soils (n = 3). Mean values for all soil treatments are also shown (n = 9). Different letters indicate significant statistical differences ($P < 0.05$).

Treatment	Time point	a-Pinene	Camphene	b-Pinene	Myrcene	Cymene	Limonene	Cineole	Terpinene	Camphor	Borneol	Terpinolene	Linalool	Verbenone	Terpineol
Control	0 days	1.66 ± 0.24[b]	0.48 ± 0.07[b]	0.32 ± 0.04[a]	0.10 ± 0.04[a]	0.04 ± 0.02[ab]	0.37 ± 0.06[a]	0.00 ± 0.00[a]	0.01 ± 0.01[a]	0.10 ± 0.06[a]	0.15 ± 0.05[a]	0.04 ± 0.03[a]	0.05 ± 0.02[a]	0.06 ± 0.04[a]	0.02 ± 0.02[a]
	5 days	1.57 ± 0.32[b]	0.43 ± 0.09[ab]	0.27 ± 0.05[a]	0.10 ± 0.05[a]	0.02 ± 0.00[a]	0.22 ± 0.01[a]	0.13 ± 0.06[a]	0.01 ± 0.01[a]	0.10 ± 0.01[a]	0.13 ± 0.01[a]	0.04 ± 0.02[a]	0.03 ± 0.01[a]	0.04 ± 0.02[a]	0.02 ± 0.01[a]
	10 days	1.16 ± 0.11[a]	0.33 ± 0.04[a]	0.23 ± 0.01[a]	0.10 ± 0.03[a]	0.07 ± 0.00[b]	0.18 ± 0.01[a]	0.29 ± 0.03[b]	0.03 ± 0.01[a]	0.13 ± 0.01[ab]	0.29 ± 0.01[b]	0.08 ± 0.02[a]	0.11 ± 0.01[b]	0.07 ± 0.02[a]	0.04 ± 0.01[b]
	15 days	1.15 ± 0.09[a]	0.31 ± 0.[02a]	0.25 ± 0.02[a]	0.16 ± 0.02[b]	0.09 ± 0.01[b]	0.23 ± 0.04[a]	0.47 ± 0.10[b]	0.04 ± 0.01[a]	0.17 ± 0.01[b]	0.39 ± 0.05[b]	0.08 ± 0.02[a]	0.16 ± 0.01[b]	0.12 ± 0.01[b]	0.04 ± 0.01[b]
PS	0 days	1.40 ± 0.38[b]	0.47 ± 0.14[b]	0.26 ± 0.07[a]	0.04 ± 0.02[a]	0.06 ± 0.01[a]	0.49 ± 0.23[a]	0.13 ± 0.07[a]	0.01 ± 0.01[a]	0.08 ± 0.03[a]	0.23 ± 0.05[a]	0.01 ± 0.01[a]	0.02 ± 0.02[a]	0.03 ± 0.02[a]	0.03 ± 0.01[a]
	5 days	1.30 ± 0.33[b]	0.46 ± 0.12[b]	0.28 ± 0.06[a]	0.04 ± 0.02[a]	0.05 ± 0.01[a]	0.43 ± 0.11[a]	0.26 ± 0.10[a]	0.02 ± 0.01[a]	0.06 ± 0.03[a]	0.24 ± 0.09[a]	0.03 ± 0.01[a]	0.04 ± 0.01[a]	0.05 ± 0.01[a]	0.04 ± 0.01[a]
	10 days	0.92 ± 0.16[a]	0.27 ± 0.02[a]	0.17 ± 0.02[a]	0.10 ± 0.03[b]	0.06 ± 0.01[a]	0.16 ± 0.02[a]	0.30 ± 0.01[ab]	0.02 ± 0.01[a]	0.12 ± 0.01[b]	0.34 ± 0.03[b]	0.03 ± 0.01[a]	0.04 ± 0.01[a]	0.06 ± 0.04[a]	0.03 ± 0.01[a]
	15 days	0.84 ± 0.13[a]	0.23 ± 0.01[a]	0.14 ± 0.01[a]	0.10 ± 0.02[b]	0.07 ± 0.01[a]	0.14 ± 0.02[a]	0.39 ± 0.06[b]	0.02 ± 0.01[a]	0.10 ± 0.01[ab]	0.31 ± 0.02[b]	0.02 ± 0.01[a]	0.04 ± 0.01[a]	0.05 ± 0.01[a]	0.03 ± 0.00[a]
CS	0 days	1.36 ± 0.22[a]	0.40 ± 0.06[a]	0.19 ± 0.03[a]	0.08 ± 0.04[a]	0.08 ± 0.03[a]	0.25 ± 0.06[a]	0.00 ± 0.00[a]	0.04 ± 0.04[a]	0.08 ± 0.02[a]	0.25 ± 0.08[a]	0.01 ± 0.00[a]	0.08 ± 0.05[ab]	0.02 ± 0.01[a]	0.02 ± 0.01[a]
	5 days	1.07 ± 0.17[a]	0.32 ± 0.05[a]	0.15 ± 0.01[a]	0.07 ± 0.03[a]	0.07 ± 0.02[a]	0.18 ± 0.02[a]	0.26 ± 0.04[b]	0.07 ± 0.04[a]	0.06 ± 0.01[a]	0.15 ± 0.03[a]	0.04 ± 0.01[b]	0.04 ± 0.02[a]	0.02 ± 0.01[a]	0.01 ± 0.01[a]
	10 days	1.21 ± 0.07[a]	0.35 ± 0.02[a]	0.20 ± 0.02[a]	0.08 ± 0.05[a]	0.07 ± 0.02[a]	0.23 ± 0.01[a]	0.34 ± 0.02[b]	0.07 ± 0.04[a]	0.12 ± 0.02[ab]	0.39 ± 0.09[b]	0.04 ± 0.03[b]	0.07 ± 0.00[ab]	0.07 ± 0.01[b]	0.03 ± 0.00[b]
	15 days	1.18 ± 0.24[a]	0.33 ± 0.07[a]	0.23 ± 0.04[a]	0.17 ± 0.04[b]	0.10 ± 0.01[b]	0.28 ± 0.07[a]	0.42 ± 0.01[b]	0.03 ± 0.00[a]	0.16 ± 0.02[b]	0.35 ± 0.02[b]	0.04 ± 0.01[b]	0.10 ± 0.01[b]	0.08 ± 0.01[b]	0.04 ± 0.01[b]
Mean	0 days	2.01 ± 0.26[b]	0.45 ± 0.05[b]	0.26 ± 0.03[a]	0.08 ± 0.02[a]	0.06 ± 0.01[ab]	0.36 ± 0.07[a]	0.03 ± 0.02[a]	0.02 ± 0.01[a]	0.09 ± 0.02[a]	0.21 ± 0.03[a]	0.02 ± 0.01[a]	0.05 ± 0.02[ab]	0.04 ± 0.02[a]	0.04 ± .02[a]
	5 days	1.42 ± 0.25[ab]	0.40 ± 0.05[ab]	0.23 ± 0.03[a]	0.07 ± 0.02[a]	0.04 ± 0.01[a]	0.27 ± 0.05[a]	0.22 ± 0.04[a]	0.03 ± 0.02[a]	0.07 ± 0.01[a]	0.17 ± 0.03[a]	0.04 ± 0.01[a]	0.03 ± 0.01[a]	0.04 ± 0.01[a]	0.04 ± 0.01[a]
	10 days	1.10 ± 0.07[a]	0.32 ± 0.02[a]	0.20 ± 0.01[a]	0.09 ± 0.02[ab]	0.07 ± 0.01[b]	0.19 ± 0.01[a]	0.31 ± 0.13[a]	0.04 ± 0.02[a]	0.12 ± 0.01[b]	0.34 ± 0.03[b]	0.05 ± 0.01[a]	0.07 ± 0.01[b]	0.06 ± 0.01[b]	0.06 ± 0.01[a]
	15 days	0.88 ± 0.11[a]	0.29 ± 0.03[a]	0.20 ± 0.02[a]	0.14 ± 0.02[b]	0.08 ± 0.01[b]	0.22 ± 0.03[a]	0.42 ± 0.03[b]	0.03 ± 0.01[a]	0.14 ± 0.01[b]	0.35 ± 0.02[b]	0.04 ± 0.01[a]	0.10 ± 0.01[b]	0.08 ± 0.01[b]	0.08 ± 0.01[a]

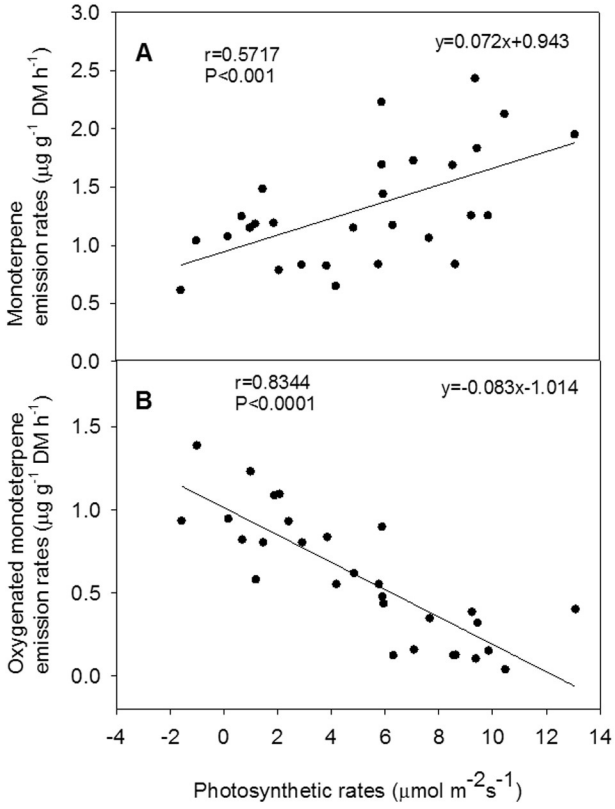

Fig. 9. Correlation of (A) monoterpene emission rates and (B) oxygenated monoterpene emission rates with leaf photosynthetic rates for drought stressed rosemary plants during the experiment.

seemed not to induce in the short-term a significant effect on isoprenoid emission rates in the rosemary plants.

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