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Isoprene is more affected by climate drivers than monoterpenes: A meta-analytic review on plant isoprenoid emissions

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Abstract

Isoprene and monoterpenes (MTs) are among the most abundant and reactive volatile organic compounds produced by plants (biogenic volatile organic compounds). We conducted a meta-analysis to quantify the mean effect of environmental factors associated to climate change (warming, drought, elevated CO_2, and O_3) on the emission of isoprene and MTs. Results indicated that all single factors except warming inhibited isoprene emission. When subsets of data collected in experiments run under similar change of a given environmental factor were compared, isoprene and photosynthesis responded negatively to elevated O_3 (−8% and −10%, respectively) and drought (−15% and −42%), and in opposite ways to elevated CO_2 (−23% and +55%) and warming (+53% and −23%, respectively). Effects on MTs emission were usually not significant, with the exceptions of a significant stimulation caused by warming (+39%) and by elevated O_3 (limited to O_3-insensitive plants, and evergreen species with storage organs). Our results clearly highlight individual effects of environmental factors on isoprene and MT emissions, and an overall uncoupling between these secondary metabolites produced by the same methylerythritol 4-phosphate pathway. Future results from manipulative experiments and long-term observations may help untangling the interactive effects of these factors and filling gaps featured in the current meta-analysis.

KEYWORDS

BVOC, climatic change, drought, elevated carbon dioxide, elevated temperature, isoprene, meta-analysis, monoterpenes, ozone pollution, warming

1 | INTRODUCTION

Many vascular plants produce and emit biogenic volatile organic compounds (BVOCs) to the atmosphere (Loreto & Schnitzler, 2010) at an estimated rate of 1–1.5 Pg C per year on a global scale (Guenther et al., 2006). BVOCs are precursors of tropospheric O_3 and atmospheric aerosols, accounting for the majority of secondary organic aerosol in the atmosphere (Goldstein, Koven, Heald, & Fung, 2009). Volatile isoprenoids (isoprene, monoterpenes [MTs], and sesquiterpenes) are among the most abundant and reactive BVOCs produced by plants. In particular, isoprene (the simplest 5-carbon isoprenoid, C_5H_8) is the dominant BVOC emitted to the atmosphere, representing about half of the total global BVOCs (Guenther et al., 2012). The emission of isoprene is light and temperature dependent because it is formed through the methylerythritol 4-phosphate (MEP) pathway in the leaf chloroplasts by photosynthesis intermediates and is released immediately after production (Loreto & Schnitzler, 2010). MTs are 10-carbon isoprenoids that also come from the MEP pathway (Loreto & Schnitzler, 2010). MTs contribute about 15% of the global BVOCs emission (Guenther et al., 2012) and may have a different dependency on light and temperature compared with isoprene. This is due to higher solubility of some MTs (e.g., oxygenated MTs such as linalool, Loreto et al., 1996) or to their storage in specialized structures (Loreto & Schnitzler, 2010). Emission of stored MTs is essentially temperature-dependent only, whereas those MTs that are not stored are light and temperature dependent. Sesquiterpenes are 15-carbon compounds, synthesized in the cytosol by the mevalonic acid pathway (Loreto & Schnitzler, 2010), and are emitted primarily in response to temperature. Sesquiterpenes are very reactive, and ecologically important in allowing plant communication with other organisms (Dicke & Baldwin, 2010), but only represent 3% of the global BVOC emissions (Guenther et al., 2006, 2012).

BVOCs may be emitted constitutively or in response to biotic and abiotic stresses (Loreto & Schnitzler, 2010). Isoprene was suggested to stabilize membranes and protect plants from oxidative stress, for example, caused by O_3 (Loreto & Fares, 2007) or high temperature (Velikova et al., 2011). BVOCs can react inside the leaf with reactive oxygen species (ROS) and reactive nitrogen species (Velikova, Fares, & Loreto, 2008) and directly reduce oxidative damage (Jardine et al., 2012), although appearance of oxidation products of isoprene reaction with ROS could not be recently proved (Cappellin, Loreto, Biasioli, Pastore, & McKinney, 2018). Isoprenoids (MTs and sesquiterpenes in particular) can also help removing O_3 in the canopy and subcanopy regions due to their high reactivity (Fares et al., 2012). BVOCs emissions are widely modelled as inputs to large-scale atmospheric chemistry simulations (Guenther et al., 2012; Kulmala et al., 2013). A comprehensive and reliable integration of BVOCs in modelling requires knowledge on the quantitative effects of co-occurring stressors, as the model sensitivity to variations in BVOCs emission is high (Fares et al., 2013).

Changing climate (e.g., rising CO_2 and temperatures) may lead to significant changes in BVOC emissions (Karl et al., 2010; Loreto & Schnitzler, 2010; Rosenstiel, Potosnak, Griffin, Fall, & Monson, 2003;

Sharkey & Monson, 2014). However, the quantitative effects of climate change on BVOCs are still difficult to predict, due to the likely onset of complex feedback and feedforward biochemical mechanisms (Sharkey & Monson, 2017) and interactive effects. To review present knowledge about the complex impact of climate change on BVOC emissions, we performed a meta-analysis of available information. In detail, we aimed to address the following questions: (a) How much elevated temperature, drought, CO_2, and O_3 will impact on isoprene and total/individual MT emissions from plants? (b) Are direction and magnitude of these impacts consistent with impacts on plant gas exchange responses across climate-change drivers? (c) Are these impacts modified by other factors, namely, rooting environment, type of O_3 exposure (acute vs. chronic), O_3 sensitivity of plant species, plant types, presence of specialized storage structures for MTs, and combination of stressors?

2 | MATERIALS AND METHODS

2.1 | Database collection

A survey of all peer-reviewed literature published between 1980 and 2017 was made using the keywords "isoprene" or "monoterpene" on Thompson ISI Web of Science. Studies under natural environmental conditions and manipulative experiments were considered. The literature was also cross-checked through the list of references included in review papers. Articles and measurements were included in this meta-analysis and divided into subgroups on the basis of the following criteria: (a) The treatments were elevated CO_2, elevated O_3, drought, and warming. (b) The compounds were isoprene, total MTs, and the following most represented nonoxygenated individual MTs (α-pinene, β-pinene, camphene, carene, cymene [or isopropiltoluene], limonene, myrcene, ocimene, phellandrene, sabinene, terpinene, thujene, and tricyclene [or cyclene]). (c) Measurements were carried out at leaf level. (d) Results were expressed as a flux per leaf (either area or mass) and time unit. (e) Exact measurements of either actual or standardized emission rates were available, together with their standard deviations (SD) or standard errors (SE) and replication number. (f) Measurements carried out after a recovery period (e.g., following rewatering after a drought treatment) were not included in this analysis. (g) The treatment duration was more than 7 days. An exception was acute O_3 stress. (h) The concentration of CO_2 in the elevated CO_2 treatment did not exceed 800 ppm. (i) Water availability was quantified in both control and drought treatments. (j) A clear description of the rooting environment (either pots or ground rooting) was available.

Out of over 1,000 articles analysed, only 74 (Appendix S1) met the criteria that were given above and were therefore used for meta-analysis. Data were available for 48 species (Table S1). The majority of species (85%) and corresponding data (75%) were angiosperms. The majority of observations were for species native from Europe (42%), Asia (40%), Africa (25%), and North America (21%). Notably, some species are native in both continents. Observations on

cultivated species (including crops, and also the trees hybrid larch and hybrid poplar) were 19% of the total.

Besides isoprene and MTs, photosynthesis (Pn) and stomatal conductance (g_s) were included when present in the selected articles. Mean values, SD, and number of replications in control and treatments were recorded. Data from figures were digitized using data extraction software (GRAFULA 3 v.2.10, Wesik SoftHaus, St. Petersburg, Russia). For each climate change driver, a distinct database was compiled. Meta-analytic methods require individual observations to be statistically independent. Following previous meta-analyses (Curtis & Wang, 1998; Feng, Kobayashi, & Ainsworth, 2008), parameter values were considered independent if they were obtained from (a) different cultivars/clones within a plant species, O_3 concentrations, CO_2 concentrations, temperatures, or water stress treatments; and (b) combined treatments of two climate change drivers, for example, warming and drought. Factors were included in this analysis if there were at least both eight observations and three independent articles.

To analyse climate change drivers, in the case of O_3 and CO_2, we simply compared treatments with elevated concentrations of the two gases with control concentrations that were always close to ambient levels in clean air, that is, 0–35 ppb O_3 and 350–430 ppm CO_2.

When dealing with warming and drought, we expressed the values as a differential value between elevated treatment (e) and control treatment (c). In the case of warming, this was a simple difference of temperature (T), that is, $\Delta T = T_e - T_c$. In the case of drought, water availability (W) was quantified in both control (W_c = well-watered plants or precipitation-inclusion experiments under natural field conditions) and drought (W_e) treatments. The variable used to measure the relative drought stress (RW = $W_e/W_c \times 100$) was either soil water content or the fraction of transpirable soil water.

2.2 | Sources of variation

To explain the variation in the response of isoprenoids to climate change factors, the following additional six categorizations were made: (a) O_3 fumigation type (chronic O_3 treatments [O_3 concentrations lower than 150 ppb for more than 10 days] vs. acute O_3 treatments [O_3 concentrations higher than 150 ppb for less than 10 days, typically a few hours]); (b) O_3 sensitivity (sensitive species [poplar and birch] vs. nonsensitive species [including the tolerant species *Brassica oleracea*, *Quercus ilex*, *Phragmites australis*, and *Sphagnum papillosum* as well as the intermediate-sensitivity species *Ginkgo biloba*, *Picea abies*, and *Quercus pubescens*]). Attribution to a class of O_3 sensitivity was based on the literature (e.g., Jøndrup, Barnes, & Port, 2002; Manes et al., 2008; Wittig, Ainsworth, & Long, 2007); (c) rooting environment (pot vs. ground); (d) additional treatments (single factor treatments vs. combined treatments). In the case of combined treatments, the control is the secondary-factor treatment, for example, when comparing the effect of drought as main factor and warming as secondary factor, the control is single warming at control water availability; (e) plant foliar life span (deciduous vs. evergreen); (f) presence of storage structures of MTs (storage vs.

nonstorage), because accumulation into storage organs makes MT pools much larger and slower to respond to environmental stimuli (Niinemets, Loreto, & Reichstein, 2004). When comparing categories, subdatasets at similar intensity of each factor were extracted to avoid artefacts due to differences in exposure, for example, data from deciduous and evergreen species were compared only for those experiments at similar O_3 concentrations.

2.3 | Data analysis

The meta-analysis was carried out using a meta-analytical software package (MetaWin2.1.3.4, Sinauer Associates, Inc. Sunderland, MA, USA; Rosenberg, Adams, & Gurevitch, 2000). To estimate the treatment effect, a mixed-effect model was used, assuming random variation in effect size, which was calculated by the natural log of the response ratio (r = variable in treatment/variable in control; Hedges, Gurevitch, & Curtis, 1999; Rosenberg et al., 2000). The variance of the effect size was calculated using resampling techniques after 9,999 iterations (Feng et al., 2008; Li et al., 2017). The overall response was reported as the percentage change from control as $(r - 1) \times 100$ (Curtis & Wang, 1998; Feng et al., 2008). Negative percentage changes indicate a decrease in the variable in response to the treatment, whereas positive values indicate an increase. Confidence limits around the effect size were calculated using a bootstrap method (Rosenberg et al., 2000). Estimates of the effect size were assumed to be significant if the 95% confidence intervals (CI) did not overlap zero (Curtis & Wang, 1998). Furthermore, the categorical analysis proceeded by partitioning the total heterogeneity (Q_T) into the between-group heterogeneity (Q_B) and within-group heterogeneity (Q_W). Differences among categories were assumed to be significant when the randomized P value generated by resampling techniques was less than 0.05.

The natural log of the response ratio for isoprene and MTs was also correlated to the natural log of the climate-driver ratio (E/A = factor in treatment/factor in control, where factor is the absolute value of O_3 concentration, CO_2 concentration, air temperature, and soil water content or fraction of transpirable soil water). Basically, E is factor intensity in the treatment (e.g., 700 ppm CO_2) and A is factor intensity in the control (e.g., 380 ppm CO_2). To have all factors increasing with increasing E/A, drought was expressed as 1-RW. To weight for different availability of data, the isoprene and MTs response data were divided into 10 classes with the following step-wise increases for each environmental factor: in the case of isoprene, 0.20 of Ln(E/A) for O_3, 0.05 of Ln(E/A) for CO_2, 0.32 of Ln(E/A) for drought, and 0.04 of Ln(E/A) for warming; in the case of MTs, 0.26 of Ln(E/A) for O_3, 0.02 of Ln(E/A) for CO_2, 0.24 of Ln(E/A) for drought, and 0.04 of Ln(E/A) for warming. In each class, we calculated a mean value, weighted by sample size, and then applied a simple linear regression model by using the weighted means. When all regressions were statistically significant, an analysis of covariance was applied to compare the slopes of the regressions. Results were considered significant at $P < 0.05$.

3 | RESULTS

3.1 | Elevated O_3

Elevated O_3 significantly decreased Pn (−27% at 118 ppb O_3 on average) and g_s (−10% at 130 ppb O_3 on average) relative to controls exposed to 0–35 ppb (Figure 1a). Elevated O_3 (91 ppb on average) significantly reduced isoprene emission by 21%, while it did not significantly affect total and selected MTs, with the exception of camphene (+102%, but with a 95% CI ranging from 29% to 209%) and β-pinene (+36% with a 95% CI ranging from 7.6% to 72.5%; Figure 1a). When subsets of similarly high chronic O_3 concentrations (on average 45 ppb) were compared, Pn (−10%) and isoprene (−8%)
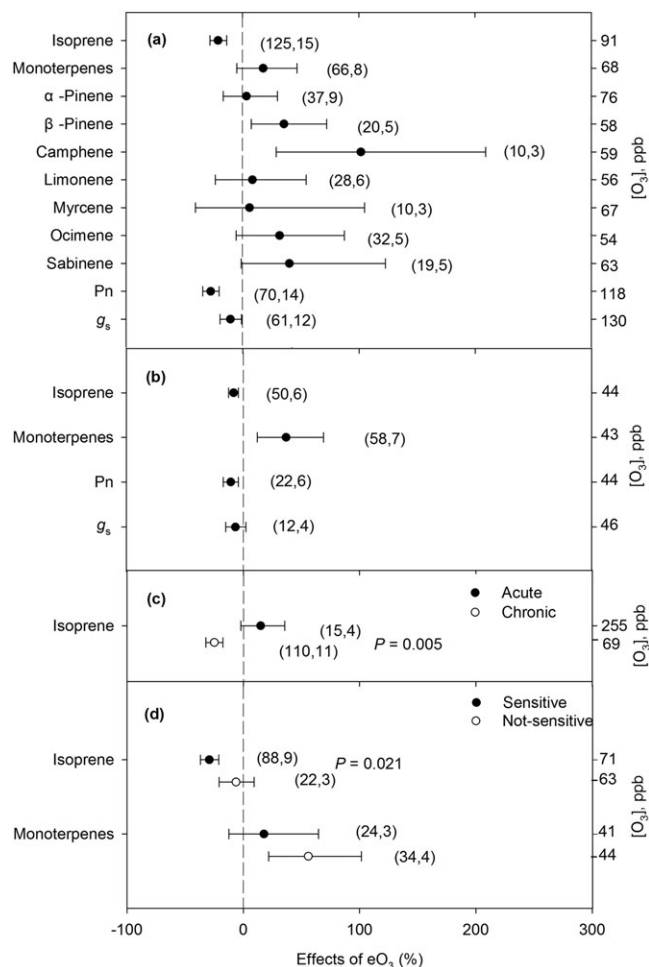

FIGURE 1 Percent change (±95% CIs) in the emission of isoprene, total and individual monoterpenes, photosynthesis (Pn), and stomatal conductance (g_s) for plants grown in elevated ozone (eO_3) relative to nonfiltered air or ambient air (0–35 ppb O_3): (a) all database; (b) plants exposed to similar eO_3 of around 43–46 ppb; (c) plants exposed to acute (>150 ppb for <10 days) versus chronic (<150 ppb for >10 days) eO_3. (d) O_3-sensitive versus nonsensitive plant species exposed to chronic eO_3. Numbers in parentheses show samples and articles, respectively. Average eO_3 concentrations are given on the right y-axis. For each categorical comparison, only P value less than 0.05 was shown

declined similarly, whereas MTs significantly increased (+37%; Figure 1b).

By further categorizing O_3 fumigation, chronic O_3 exposure (69 ppb on average) significantly reduced isoprene emission (−25%, similar to results given above), whereas acute exposure to very high O_3 concentrations (about 250 ppb) for a few hours or days did not significantly affect isoprene (Figure 1c). When results are not shown, as for MTs in Figure 1c, data were insufficient for the analysis. When the species were categorized into sensitive and insensitive to O_3, only data for chronic O_3 were sufficient (Figure 1d). A decrease of isoprene emission (−29% at 71 ppb) was observed in the sensitive species only, whereas an increase of MTs emission (+56% at 44 ppb) occurred in insensitive species only. The decrease in the O_3-sensitive species was the same as in the entire database (Figure 1a) because 80% of the database was represented by those sensitive species. The effect of O_3 on MTs was significantly different from the controls in evergreen species (+62%, Figure S1a) and in species with storage organs (+56%, Figure S2), although the differences between evergreen and deciduous species or between storage and nonstorage species were not significant.

3.2 | Elevated CO_2

Elevated CO_2 (730 ppm on average) significantly stimulated Pn (+48%), but slightly (not significantly) decreased g_s (Figure 2a). An average CO_2 concentration of 649 ppm significantly decreased isoprene emission by −22%. When subsets at similar elevated CO_2 (~760 ppm) were compared, Pn significantly increased by 55%, and isoprene emission significantly declined by −23% with respect to ambient CO_2 (Figure 2b). Insufficient data were available to test the combined effects of elevated CO_2 and other treatments. The rooting environment significantly inhibited isoprene emission in potted plants (−38%) but not in field-rooted plants that were exposed to elevated CO_2 (Figure 2c). Total MTs emission was not affected by elevated CO_2 (Figure 2a), independent of the presence of storage organs (Figure S2).

3.3 | Drought

Drought (51–57% RW, where the lower the RW, the higher the stress relative to the control) significantly reduced Pn (−53%), g_s (−55%) and —to a lower, yet significant, extent—also isoprene emission (−23%; Figure 3a). When subsets at similar drought level (~52%) were analysed, drought significantly reduced Pn (−42%), g_s (−49%), and isoprene emission (−15%) but did not affect MTs emission (Figure 3b). When the effect of drought (50–60% RW) was combined with those of other treatments (only warming available for this analysis), a negative impact on isoprene, similar to that observed under drought only, was observed (Figure 3c). The response of isoprene and MTs emission to drought was similar in potted and ground plants (Figure 3d) or in deciduous and evergreen plants (Figure S1b) or in species with and without storage organs (Figure S2).
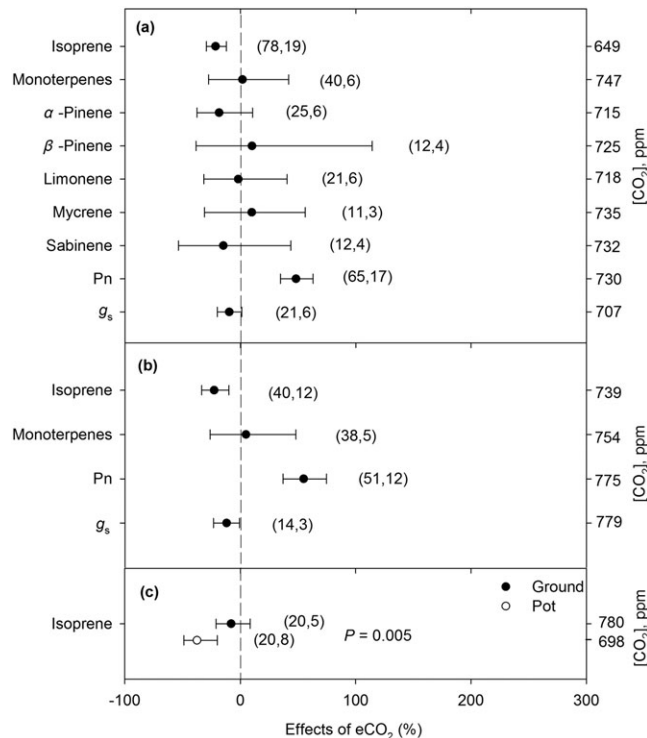
FIGURE 2 Percent change (±95% CI) in the emission of isoprene, total and individual monoterpenes, photosynthesis (Pn), and stomatal conductance (g_s) for plants grown in elevated carbon dioxide (eCO$_2$) relative to ambient CO$_2$ (380 ppm on average): (a) all database; (b) plants exposed to similar eCO$_2$ levels of 739 to 779 ppm; (c) effects of rooting environment (pot vs. ground) on the response to similar eCO$_2$ concentrations. Numbers in parentheses show samples and articles, respectively. Average eCO$_2$ concentrations are given on the right y-axis. For each categorical comparison, only P value less than 0.05 was shown

3.4 | Warming

Pn and g_s were significantly reduced (−17% and −20%, respectively) by a 5.7°C and 7.4°C increase of temperature, respectively (Figure 4a). Warming (+6.6°C and +1.7°C, respectively) significantly increased the emission of isoprene (+22%) and MTs (+39%; Figure 4a). When subsets at similar T between warming treatments and controls (~10.8°C) were compared, isoprene emission was increased by 53% and Pn decreased by 23% (Figure 4b) although there were not enough data for MTs. Based on the available dataset, there were no significant differences in MTs emission when warming combined with elevated O$_3$ was compared with single warming (Figure 4c). Responses of MTs to warming did not differ when separating species with storage and nonstorage structures (Figure S2).

3.5 | Comparing the effects of the four climate-change drivers

The linear regressions of isoprene response intensity (r) versus factor intensity (E/A) were significant for all four climate-change factors
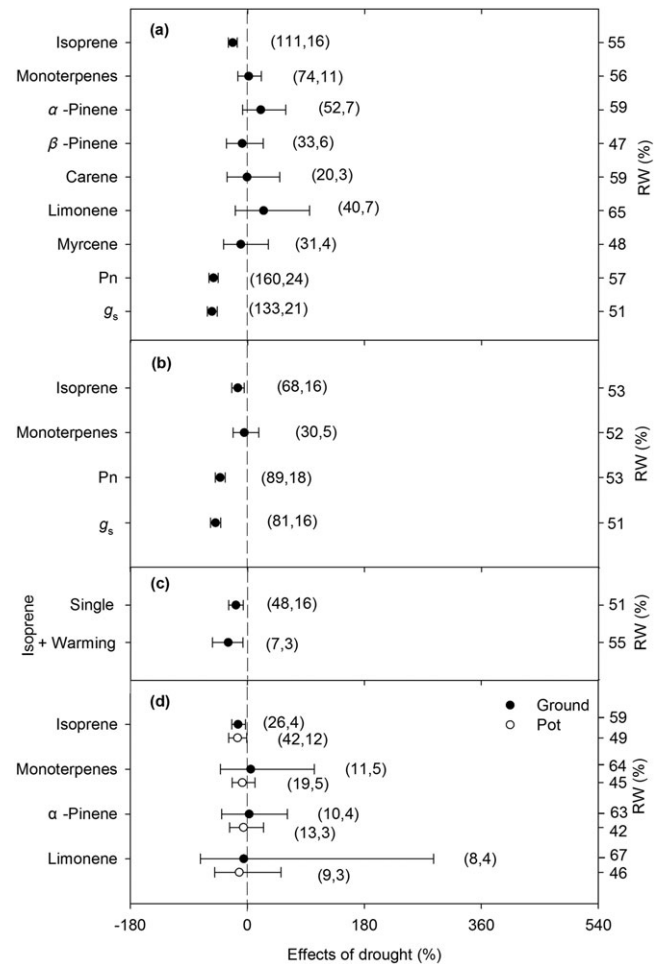

FIGURE 3 Percent change (±95% CI) in the emission of isoprene, total and individual monoterpenes, photosynthesis (Pn) and stomatal conductance (g_s) for plants grown under drought stress: (a) all database; (b) plants exposed to similar drought stress (about 52% RW); (c) single drought treatments versus treatments where drought was combined with another factor (only studies with similar RW levels were selected and only warming available for this analysis); (d) effects of rooting environment (pot vs. ground) on the response to similar drought levels. Numbers in parentheses show samples and articles, respectively. Water availability relative to control (RW) is given on the right y-axis. For each categorical comparison, only P value less than 0.05 was shown

(Figure 5). It should be noted that significance was achieved when integrating data across the whole range of log-transformed responses, including intense treatments that resulted in large variations of isoprene response. This adds further information to the single point analysis shown in Figures 1–4. Furthermore, significant response to any factor mostly occurred at high intensity. By comparing the slopes of the regressions, we found that the strongest decline in isoprene emission was due to exposure to increasing CO$_2$ concentrations. The decline due to increasing O$_3$ concentrations did not differ from that due to increasing drought levels. Increasing warming levels stimulated isoprene emission, and thus, this slope was clearly different from those of the other regressions. None of the linear regressions of the MTs response intensity r versus the factor intensity E/A was significant.
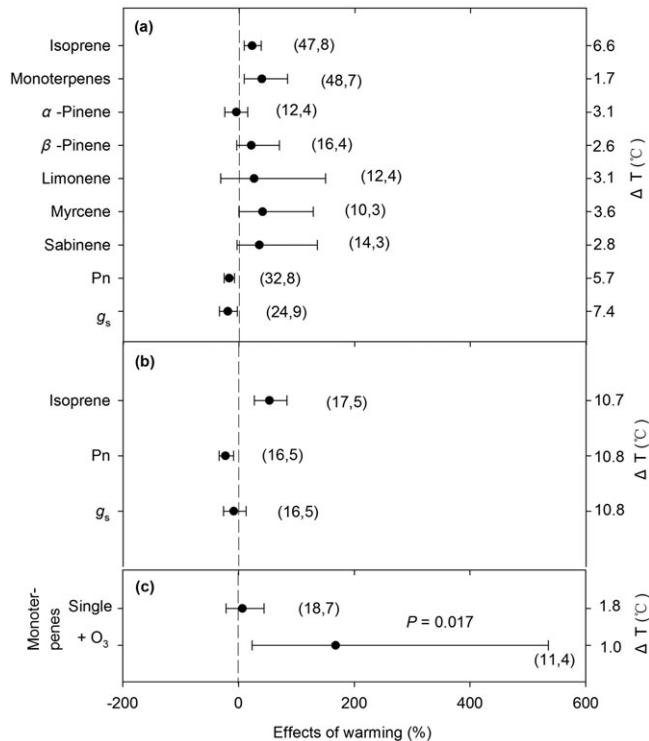
FIGURE 4 Percent change (±95% CI) in the emission of isoprene, total and individual monoterpenes, photosynthesis (Pn), and stomatal conductance (g_s) for plants grown under warming stress: (a) all database; (b) plants exposed to similar warming (10–13°C, with an average of 10.8°C); (c) single warming treatments versus treatments where warming was combined with another factor (only studies with similar ΔT levels were selected and only eO_3 available for this analysis). Numbers in parentheses show samples and articles, respectively. Temperature difference between treatment and control (ΔT) is given on the right y-axis. For each categorical comparison, only P value less than 0.05 was shown
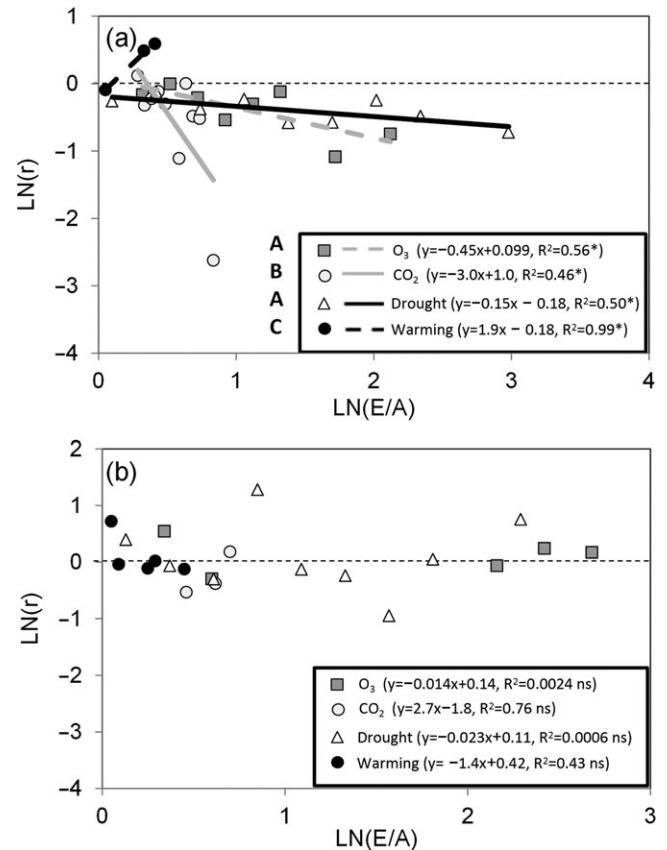

FIGURE 5 Relationships between the log-transformed response ratio (LN(r)) of isoprenoid (isoprene (a) or monoterpenes (b)) and the relative intensity of climate change factors (LN(E/A)), where E is intensity in the treatment (e.g., 700 ppm CO_2) and A is intensity in the control (e.g., 380 ppm CO_2). To express all factors as increasing with increasing E/A, drought was expressed as 1-RW. Each point is a sample-size weighted average. Simple regression analysis was used. * means $P < 0.05$, and ns is not significant ($P \geq 0.05$). Because all regressions were statistically significant in the case of isoprene, an analysis of covariance (ANCOVA) was applied to compare the slopes of the regressions. Different capital letters denote significant differences of the slopes ($P < 0.05$)

4 | DISCUSSION

4.1 | General considerations

An analysis of the database that met the requirements for this meta-analysis suggests the following general considerations:

1. The majority of the 1,082 observations on isoprenoid emission collected here were for species native of temperate climates (81%) and from Europe (42%). However, the percentage of iso-prene emitters is equally spread over the globe—as found by Loreto and Fineschi (2015) by comparing tropical and temperate perennial species—which suggests that more research is needed on species from tropical climates, especially native to the most under-represented continents, namely, South America and Ocea-nia. Because isoprene emission is absent in annual plants (Loreto & Fineschi, 2015), interest has converged around perennial plants. Out of the woody plants, 57% were deciduous and 43% were evergreen in our dataset. Three quarter of these deciduous species

emitted isoprene, which is consistent with the fact that isoprene emission is more common in deciduous than in evergreen peren-nial plants (Loreto & Fineschi, 2015). Excluding crops (5.5%) and grasses (1.5%), 52% and 48% of our database were about broad-leaf and needle-leaf species, respectively. Broadleaf species are more investigated because isoprene emission is more common in fast-growing plants that do not endure long periods of environ-mental stress (Loreto & Fineschi, 2015). The majority of data available for this meta-analysis was from species that are high isoprenoid emitters, such as poplars (29%), pines (26%), and oaks (14%). The most investigated species was Scots pine, *Pinus sylvestris* (17% of data). When we selected subdatasets where both deciduous and evergreen species were subject to similar-level factors (i.e., 43 ppb in the case of eO_3 and 53% RW), data were insufficient for a comprehensive analysis, and insignificant differences between the two plant types were found.

2. Since the seminal paper by Arp (1991), there is scientific consensus that the rooting environment considerably affects plant physiological performances. In particular, restricted rooting volume induces a less carbon fixation, which may affect isoprenoid biosynthesis. Several studies, therefore, have raised concerns about experiments on isoprenoids in potted plants (Pegoraro et al., 2004). Data for this kind of analysis were sufficient only in the case of elevated CO_2 and drought. Significant differences were found only for isoprene emission at elevated CO_2, which declined more in potted than in grounded plants. However, more than 60% of field data (Figure 2c) were investigated under combined CO_2 and drought treatments, whereas data from pots were only from single CO_2 treatments. When we further analysed single CO_2 treatments, no significant differences in isoprene emission were observed in plants rooted in pots and field ($P = 0.398$). Different isoprene emission in plants grown under different rooting environment and elevated CO_2 might be attributed to a drought-induced stomatal closure and consequent reduction of Ci, in turn decreasing the magnitude of the inhibitory effect of elevated CO_2 on isoprene emission (Guidolotti, Calfapietra, & Loreto, 2011). A confirmative conclusion still needs more experiments data, which can be designed in the future.

3. We confirm that the MEP pathway is resistant to drought stress, probably because alternative carbon sources contribute to BVOC biosynthesis when Pn is progressively constrained by drought (Brilli et al., 2007). Our data show that halving the water availability in the soil reduced Pn (−42%) much more than isoprene emission (−15%). Interestingly, MTs are far more insensitive to drought and other environmental factors (elevated O_3 or CO_2) than isoprene, suggesting that sensitivity to environmental factors is at the level of the enzymatic reactions producing isoprene from MEP substrate dimethylallyl diphosphate rather than at the level of the whole MEP pathway.

4. There were too few observations of the interactive effects of combined stress factors to conclusively project how the interaction between climate change drivers alters isoprenoid emission under real-world conditions.

4.2 | Main effects of the single factor

4.2.1 | Ozone

Exposure to chronic O_3 pollution (91 ppb) significantly reduced isoprene emission by 21% relative to controls (0–35 ppb). Such elevated O_3 levels are realistic and occur in many forest ecosystems around the world (Fares, McKay, Holzinger, & Goldstein, 2010; Feng, Hu, Wang, Jiang, & Liu, 2015; Moura & Alves, 2014; Paoletti, 2006; Yuan et al., 2015). Surprisingly, acute O_3 exposure (255 ppb on average) did not significantly affect isoprene emission, but this result may be biased by the fact that only insensitive species were exposed to the acute treatment. However, O_3 levels exceeding 100 ppb are unlikely to occur under present ambient conditions, with very few exceptions, for example, in China and California central valley (Fares et al., 2012; Feng et al., 2015).

A short-term O_3-stimulation of isoprenoid emissions has been observed (Carriero et al., 2016; Loreto, Pinelli, Manes, & Kollist, 2004). Isoprene is known to protect the photosynthetic machinery of fast-growing plants such as poplars during active plant growth in the warm season (Behnke et al., 2007) or under acute oxidative stress (Loreto & Velikova, 2001). It is well established that isoprene stabilizes plant membranes (Singsaas, Lerdau, Winter, & Sharkey, 1997) and scavenges ROS (Loreto et al., 2001; Velikova et al., 2011). However, more recent reports suggest that isoprene and MTs act indirectly on stress resistance, perhaps priming antioxidant responses and systemic acquired resistance (Harvey & Sharkey, 2016; Riedlmeier et al., 2017). These protective mechanisms, however, may not ensure tolerance in the long term. Our meta-analysis suggests that a chronic exposure to O_3 may impair the production of photosynthates that feed carbon for isoprene biosynthesis, thus reducing the positive effect of isoprene. A hormetic O_3 dose–response effect was postulated by Calfapietra, Fares, and Loreto (2009) and confirmed by Agathokleous, Kitao, Harayama, and Calabrese (2018), with a positive effect at moderate O_3 doses replaced by a negative impact on isoprene when the O_3 dose is high enough to inhibit photosynthesis. Perhaps, this is why plant species inhabiting the more stressful environments did not evolve high isoprene emission as a competitive mechanism for survival and colonization (Loreto & Fineschi, 2015; Monson, Jones, Rosenstiel, & Schnitzler, 2013; Rinnan, Steinke, McGenity, & Loreto, 2014; with exceptions, see, e.g., isoprene emission by resurrection plants reported by Beckett et al., 2012). Interestingly, MTs emission was often associated to O_3 resistance in our meta-analysis, as resistant (or insensitive) plants were often evergreen species where MTs are stored in specific organs.

4.2.2 | Carbon dioxide

Exposure to elevated CO_2 (649 ppm) significantly reduced isoprene emission (−22%) relative to the controls in ambient CO_2 (380 ppm). Under the current rate of CO_2 increase, such high concentration is predicted for the year 2065 according to the most pessimistic RCP8.5 scenario (Meinshausen et al., 2011), whereas 400 ppm were reached in the year 2015 (Blunden & Arndt, 2016). Such a dramatic CO_2-driven reduction of isoprene emission from plants might have relevant effects on tropospheric chemistry because isoprene has been shown to significantly affect the concentration of tropospheric ozone and other oxidants (Jiang et al., 2018), and perhaps also the capacity to adapt to climate change (Lerdau, 2007; Loreto et al., 2014). However, it was shown that most of the negative effect of elevated CO_2 on isoprene is lost under a simultaneous increase of temperature (Sharkey & Monson, 2014). Unfortunately, absence of data about combined high temperature and elevated CO_2 does not allow us to test this in our meta-analysis.

Even though CO_2 fertilization stimulated Pn (+48%), it is not surprising that isoprene emission declined at elevated CO_2. Rosenstiel

et al. (2003) demonstrated that high CO_2 reduces the cellular content of dimethylallyl diphosphate, the substrate for isoprene synthesis, as a result of competition with the carbon assimilation processes for phosphoenolpyruvate. Once again, as for the other environmental factors, MTs were not affected by high CO_2. A reduction of MTs, similar to that observed for isoprene emission was expected, at least where de-novo synthesis is uncoupled from emission from large internal pools (Ghirardo et al., 2010). MT insensitivity to elevated CO_2 was first observed by Loreto et al. (1996, 2001) and again indicates that isoprene response to most environmental factors do not reflect changes of the entire MEP pathway, as discussed above.

4.2.3 | Drought

Reduced water availability (55% relative to 100% in the controls) had a negative effect on isoprene emission (−23%), whereas MTs were not significantly affected. The overall response of isoprene to drought in this meta-analysis contrasts with previous studies reporting a stimulation of isoprene emission, possibly as a result of stomatal closure and internal CO_2 (Ci) reduction (Blanch, Peñuelas, Sardans, & Llusià, 2009; Delfine, Loreto, Pinelli, Tognetti, & Alvino, 2005; Pegoraro et al., 2004; Yuan et al., 2016). Indeed, reduction of Ci stimulates isoprene emission (Guidolotti et al., 2011) by an effect opposite to the inhibition caused by elevated CO_2. As isoprenoid formation depends on metabolites, which are primarily formed by photosynthesis, a decrease in emissions is expected to occur when a severe drought stress inhibits primary metabolism (Brilli, Tricoli, Fares, Centritto, & Loreto, 2008; Fortunati et al., 2008; Ormeño et al., 2007; Wu et al., 2015), and this may appear even days after stomatal closure and photosynthesis down-regulation had begun (Beckett et al., 2012; Tattini et al., 2015). Clearly, most of the meta-analysed studies fell into this group of responses, as also suggested by the large average reduction of soil water content in the examined papers. It is also worth noting that rewatering experiments, where emission of isoprene is consistently reported to increase after recovering from drought (Brilli et al., 2007; Sharkey & Loreto, 1993), were excluded from our database.

4.2.4 | Warming

An increase of 1.7°C and 6.6°C stimulated MTs and isoprene emissions by 39% and 22%, respectively, relative to the controls. Such temperature increases are within the range of global average warming predicted for a doubling of atmospheric CO_2 concentrations (Sherwood, Bony, & Dufresne, 2014). Light and temperature are known to exert the main control on isoprenoid biosynthesis and emission (Loreto & Sharkey, 1990). Our findings confirm that temperature-driven increased emissions of both isoprene and MTs are well described by empirical algorithms (Guenther, Zimmerman, Harley, Monson, & Fall, 1993; Tingey, Manning, Grothaus, & Burns, 1980). Current results showed that MTs were more affected by warming than isoprene. However, we should observe that almost all data (96%) for MTs were investigated in potted environment, whereas 55% of the isoprene data were collected in the field. Results from field

experiments do not always match laboratory studies (Peñuelas & Staudt, 2010). As noted above, we did not collect enough data to address this point in our meta-analysis. Also, notably, MT emission responded to warming similarly between species with and without storage organs.

4.3 | Comparing the effects of the single factor on isoprene and MT emission

By relating the intensity E of the four environmental factors in treated plants to the level A of the same factors in controls, we were able to compare the relative impacts on the intensity of the BVOC response (r). As expected, warming strongly stimulated isoprene emission (Guenther et al., 1993). Elevated CO_2 was the factor inducing the strongest decline of isoprene emission, in line with the well-known inhibitory action of CO_2 (Rosenstiel et al., 2003). The two oxidative stressors, namely, elevated O_3 and drought, induce convergent and slightly decline in isoprene emission. In contrast, MT emissions were not significantly affected by climate-change factors in this analysis. Even the stimulatory effects of warming and O_3 on MT emission discussed above were not significant in this analysis where all categories (plant type, with/without storage structures) were put together. We tested the hypothesis that MTs not stored in reservoirs were more sensitive to the factors affecting the availability of photosynthetic intermediates than stored MTs but did not find a significant difference across the different environmental factors.

5 | CONCLUSIONS

It is often assumed that plants respond to stress by releasing BVOCs (Ameye et al., 2018). However, in our meta-analysis, all single environmental factors except warming (causing the well-known temperature-driven isoprene increase) inhibited isoprene emission. The same factors did not significantly affect MTs, again with the exception of warming. Isoprene emission and photosynthesis declined similarly when plants were exposed to either elevated O_3 or drought, whereas the responses were uncoupled in plants exposed to elevated CO_2 (isoprene decreased and photosynthesis increased) or warming (isoprene increased and photosynthesis decreased). There were too few observations on the interactive effects of such factors to conclusively project how they will jointly impact on the emissions. Our meta-analysis includes studies focusing on 48 species with poplars representing 29%. This is the same bias of previous experiments where Salicaceae were mainly investigated (e.g., Loreto et al., 2014). Too few species have been investigated so far, and more research is needed, particularly in MT-emitting species and in plants from South America and Oceania, to fill gaps in the taxonomic and geographical distribution of the sampled plants that emerged from our analysis.

Climate change effects on other reactive isoprenoids such as sesquiterpenes or oxygenated BVOCs have been poorly investigated in the past years due to minute emissions and technological limitations. However, these compounds also have important functions in

biosphere and biosphere-atmosphere interactions. Recent research mainly carried out on crop species suggests that sesquiterpenes may respond to environmental stress in a similar way of MTs (Acton et al., 2018; Ormeño et al., 2010), which may be tested meta-analytically when more data will become available.

CONFLICT OF INTEREST

The authors declare no competing financial interests.

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SUPPORTING INFORMATION

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