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Key Points:

- Isoprene concentrations were monitored for a whole growing season in a temperate forest in the United Kingdom before, during, and after the 2018 heatwave
- Isoprene abundances during the heatwave increased by up to 400%, and stress-related sesquiterpenes were observed during the heatwave
- Higher temperatures in the heatwave cannot account for all the enhanced isoprene abundances, which correlate to drought stress

Supporting Information:

- Supporting Information S1

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Continuous Isoprene Measurements in a UK Temperate Forest for a Whole Growing Season: Effects of Drought Stress During the 2018 Heatwave

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Abstract Isoprene concentrations were measured at four heights below, within, and above the forest canopy in Wytham Woods (United Kingdom) throughout the summer of 2018 using custom-built gas chromatographs (the iDirac). These observations were complemented with selected ancillary variables, including air temperature, photosynthetically active radiation, occasional leaf gas exchange measurements, and satellite retrievals of normalized difference vegetation and water indices. The campaign overlapped with a long and uninterrupted heatwave accompanied by moderate drought. Peak isoprene concentrations during the heatwave-drought were up to a factor of 4 higher than those before or after. Higher temperatures during the heatwave could not account for all the observed isoprene; the enhanced abundances correlated with drought stress. Leaf-level emissions confirmed this and also included compounds associated with ecosystem stress. This work highlights that a more in-depth understanding of the effects of drought stress is required to better characterize isoprene emissions.

Plain Language Summary Plants emit a number of volatile organic compounds into the atmosphere as a response to environmental stimuli such as temperature and incoming sunlight. Once emitted, these compounds undergo chemical processes that can affect local air quality (for instance, contributing to the formation of pollutants such as ground-level ozone) and climate (by contributing to the formation of aerosol particles). Numerical models have been developed to successfully simulate volatile emissions under most environmental conditions. However, one notable exception is during extreme weather events such as heatwaves and droughts, where current models appear inadequate. In this paper, we present a unique data set consisting of continuous measurements of isoprene, the main volatile emission from vegetation, during the summer of 2018 in a UK temperate forest. A prolonged heatwave and drought affected the United Kingdom that summer. We report unusually high levels of isoprene and show that higher temperatures during the heatwave cannot account for all the observed isoprene. Our analysis shows that ecosystem stress brought about by moderate drought correlates with the enhanced isoprene. This work enables an improved description of isoprene emissions under extreme events (droughts) that are predicted to become more frequent in the near future as a consequence of global change.

1. Introduction

Biogenic volatile organic compounds (BVOCs) are emitted into the atmosphere by vegetation in response to a number of environmental stimuli. Among BVOCs, isoprene (2-methyl-1,3-butadiene, C₅H₈) is of particular importance: with global emission rates estimated at ~450–600 TgC year⁻¹, it represents half of all non-methane VOCs emitted into the atmosphere (Guenther et al., 2012, 2006). A dialkene, isoprene is highly reactive and is prone to oxidation by the hydroxyl radical (OH), ozone, and the nitrate radical (e.g. Wennberg et al., 2018), affecting the local production of tropospheric ozone and secondary organic aerosols (SOA) (Carlton et al., 2009).

Isoprene emissions are assumed to be directly coupled to photosynthesis and are mainly driven by incoming photosynthetically active radiation (PAR) and temperature. As a result, they generally follow diurnal and

seasonal cycles, with the highest values in the summer late mornings/early afternoons. Other factors are known to affect isoprene emissions, including leaf age (Baldocchi et al., 1995), herbivory (Visakorpi et al., 2018), oxidative stress (Feng et al., 2019), CO₂ abundance (Arneth et al., 2007; Sharkey & Monson, 2017), and soil moisture (Genard-Zielinski et al., 2018; Guenther et al., 2012, 2006; Jiang et al., 2018; Sindelarova et al., 2014).

A number of isoprene emission models have been developed (Andreani-Aksoyoglu & Keller, 1995; Arneth et al., 2011; Grote & Niinemets, 2008; Guenther et al., 2012, 2006; Müller et al., 2008; Pierce & Waldruff, 1991), with the resulting emission estimates varying by up to a factor of 3 for the same region and season (Guenther et al., 2006; Jiang et al., 2019; Lathièrè et al., 2010). As isoprene emissions are concurrently influenced by many environmental variables, field measurements as well as studies in controlled environments are necessary to validate emission models. This is particularly relevant as global change (e.g., increasing temperatures, higher CO₂ abundances, changes in land use and precipitation) is expected to affect isoprene emissions. However, the magnitude and even sign of projected isoprene emission changes remain uncertain (Bauwens et al., 2018). In the United Kingdom, recent climate projections suggest that prolonged heatwaves (such as those in 1976, 2003, 2006, and 2018) may occur every other year by midcentury, with the average summer rainfall decreasing by ~50% by 2070 (UK Met Office, 2019b). As a consequence, droughts will become an increasingly important environmental stress.

Models have mixed results in reproducing observed isoprene emissions during and after heatwave-drought events (X. Jiang et al., 2018; Kravitz et al., 2016). The effects of drought stress on isoprene emissions have been investigated in several studies, most of which were conducted in laboratories on fully grown plants (Bamberger et al., 2017; Funk et al., 2004; Pegoraro et al., 2004) or saplings (Brilli et al., 2007; Tattini et al., 2015). No unequivocal response of isoprene to drought conditions was identified, with some studies reporting an increase in isoprene emission rates and others observing a decline. Field observations from real-world droughts, though scarce, may offer a potential explanation for the conflicting results from laboratory studies. During the 2011–2012 field campaigns in the Ozarks (United States), isoprene and other BVOCs were monitored for two consecutive growing seasons (Potosnak et al., 2014; Seco et al., 2015). The measurement periods overlapped with two drought periods, one moderate (in 2011) and one severe (in 2012). Higher isoprene emission rates were observed under moderate drought, while lower rates were reported under severe drought conditions, confirming the role of drought severity in determining the sign of the effects on isoprene emissions.

The recent development of the iDirac (Bolas et al., 2020) enables the continuous monitoring of isoprene without needing the scientific infrastructure required by traditional instrumentation (e.g., mains power, frequent maintenance). The iDirac was used during the Wytham Isoprene iDirac Oak Tree Measurements (WISDOM) campaign in 2018 to monitor isoprene concentrations in a temperate forest in the United Kingdom over a full growing season to study seasonal behavior and canopy-atmosphere exchange. A long and uninterrupted heatwave occurred partway through the measurement period. Characterized by unusually high temperatures and little to no rainfall, this allowed us to study the impact of a prolonged heatwave and mild drought on isoprene in a real-world forest.

This paper describes the WISDOM campaign and our analysis of isoprene changes over time. A related paper (Otu-Larbi et al., 2020) describes reconciliation of a canopy exchange model with the observed isoprene abundances.

2. Methods

2.1. Site Description

The WISDOM campaign took place in Wytham Woods, a mixed temperate woodland located 5 km north-west of Oxford (United Kingdom). The site contains ancient seminatural woodland, secondary woodland, and modern plantations (Butt et al., 2009).

During the WISDOM campaign, a tree-top walkway facility, located in the center of the seminatural mature woodland (51°46'24.2"N, 1°20'18.2"W), provided access below, within, and above the forest canopy. The walkway is surrounded by a mix of trees representative of Wytham Woods, including *Quercus robur* (pedunculate oak), *Betula pendula*, *Acer pseudoplatanus*, and *Fraxinus excelsior* (supporting information,

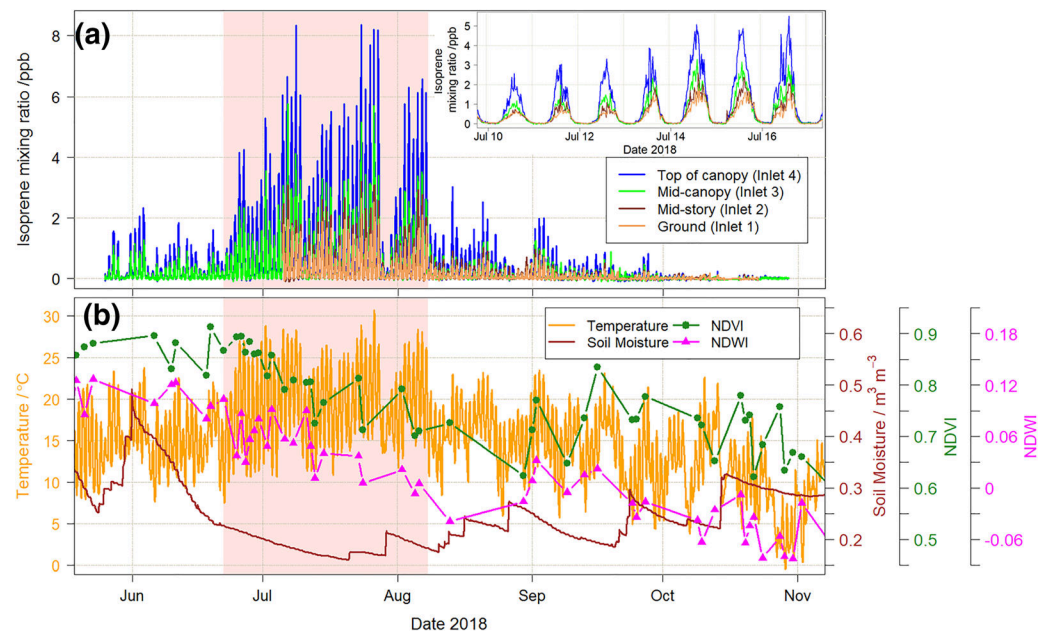


Figure 1. Time series of the WIsDOM measurements. (a) Isoprene concentrations at four heights through the canopy, with detailed diurnal profiles over a 7-day period shown inset. (b) Temperature and soil moisture from the Upper Seeds AWS, along with NDVI and NDWI from satellite retrievals. The pink shaded area indicates the heatwave.

Figure S1a). The *Quercus* genera are the principal isoprene emitters in midlatitude/temperate regions and estimated to emit ~70% of European isoprene emissions (Keenan et al., 2009). Four iDirac inlets were placed at different heights, from ground level to the top of the canopy, each approximately 1.5 m from the trunk of a *Q. robur* (Figure S1b).

The Centre for Ecology and Hydrology (CEH) has maintained a comprehensive automatic weather station (AWS) in Wytham Woods since 1992 as part of their Environmental Change Network (ECN). This weather station collects hourly data of meteorological variables, including solar irradiance, air temperature, rainfall, soil moisture, wind speed, and direction. The weather station is situated ~480 m from the walkway in the Upper Seeds area (51°46'14.2"N, 1°19'57.0"W), an open grassland area surrounded by forest.

2.2. Measurement Description

The WIsDOM campaign took place in 2018. Isoprene mixing ratios, air temperature, and relative humidity were monitored continuously at four heights (0.53, 7.25, 13.17, and 15.55 m) for five months from 25 May to 26 November.

Isoprene abundances were monitored using the iDirac (Bolas et al., 2020), a custom-built portable gas chromatograph with photo-ionization detection (GC-PID). Designed for continuous and autonomous operation, the iDirac has a limit of detection of 40 ppt and 10% precision. The time resolution at each inlet was 20 min. Two iDiracs were deployed (Figure S1b), one sampling alternately from the two highest inlets (top and mid-canopy) and the other from the lowest two (midstory and ground).

Temperature and relative humidity were monitored by four EasyLog probes (EL-USB-2-LCD & EL-USB-2, Lascar Ltd.), each placed next to one of the iDirac inlets. Incoming solar radiation, wind speed, wind direction, and soil moisture (at 20-cm depth) were taken from the Upper Seeds AWS. Jackson et al. (2019) demonstrated good correlation between wind speeds measured at the AWS and those at the canopy walkway. PAR was measured at each sampling inlet at the canopy walkway in September to October 2018. Top-of-canopy PAR for the whole WIsDOM campaign was generated from the AWS solar irradiance data as detailed in the supporting information (Text S1 and Figure S2).

These continuous observations were complemented with occasional leaf gas exchange measurements from the *Q. robur* closest to the iDirac inlets using a portable Li-Cor LI-6400 (Sharkey et al., 1996), made on 11–13

July 2018 (during the heatwave-drought event) and 29–31 August 2018 (after ecosystem recovery). Simultaneously, exhaust gas from the Li-Cor chamber was drawn onto a sorbent tube to adsorb BVOCs emitted from the leaf for subsequent analysis by GC-MS following the technique described by Helmig et al. (1999) and Ruiz-Hernández et al. (2018) (see Text S2 and Table S1 for details).

Normalized difference vegetation index (NDVI), a measure to identify vegetated areas and their condition (Tucker, 1979), and normalized difference water index (NDWI), a measure of moisture content in vegetation and soil (Gao, 1996), were calculated from MODIS data (bands 2 and 1 for NDVI and bands 2 and 5 for NDWI; Vermote & Wolfe, 2015) at 500-m horizontal resolution for the whole period. For each index, the daily value at the four pixels surrounding the target site, containing a majority of woodland vegetation, was averaged. Leaf area index (LAI) measurements overlapping with the WisDOM campaign were available from Brown et al. (2020).

3. Results

The WisDOM campaign overlapped a long uninterrupted heatwave from 22 June to 8 August 2018 inclusive (UK Met Office, 2019a). The isoprene time series for the WisDOM campaign is shown in Figure 1a, with the highest values occurring during the heatwave (shaded area) when mixing ratios above the canopy reached ~8 ppb (or nmol mol^{-1}). Abundances then decrease gradually through September and October as temperatures drop and the canopy thins. An example of the typical isoprene diel cycle observed during WisDOM is shown in the inset panel in Figure 1a.

Figure 1b shows the air temperature and soil moisture from the AWS, along with the NDVI and NDWI retrieved for the site. The mean temperature during the heatwave was 4°C higher than in the 3 weeks before and after and 3°C higher than the 1992–2015 mean over the same period. The mean and maximum daily temperatures during the heatwave exceeded the 1992–2015 climatological averages by as much as 7°C and 8°C, respectively (Figures S3a and S3b). The heatwave was accompanied by exceptionally low rainfall, resulting in a moderate drought as described by the Standardized Precipitation Index (McKee et al., 1993) for the region (Centre for Ecology & Hydrology, 2020). This is consistent with the decrease in soil moisture observed on site (Figure 1b). Similar reductions are seen in NDVI and NDWI, suggesting that the drought was sufficient to affect the ecosystem.

The data presented in Figure 1 can be divided into four time periods: pre-heatwave (25 May to 21 June), heatwave (22 June to 8 August), immediate post-heatwave (9–31 August), and late post-heatwave (1–30 September). By the time measurements began, the leaves of the *Q. robur* were fully emerged with NDVI, suggesting that they had reached maturity (Cole & Sheldon, 2017). NDVI and NDWI were at their lowest in the immediate post-heatwave, indicating that the ecosystem was still under stress despite cooler temperatures and rewetting, but both recovered at the beginning of the late post-heatwave period (September). Canopy thinning commenced later in this period, resulting in increasing variability in isoprene vertical mixing through the canopy (Text S3 and Figure S4). This is evident in the photographic time series of canopy coverage (Figure S5).

We use the four periods defined above to investigate the variation of diel cycle of isoprene and its main drivers (temperature and PAR) throughout the summer, as shown in Figure 2.

Both temperature and PAR are highest during the heatwave, and isoprene mixing ratios during this period are up to a factor of 4 higher than before and after. Temperatures and isoprene abundances are similar during the pre- and immediate post-heatwave, but PAR is generally lower in the immediate post-heatwave. The lowest isoprene concentrations were observed during the late post-heatwave although neither temperature nor PAR differs significantly from other periods.

Isoprene emission rates typically follow an exponential relationship with temperature (at $T < \sim 35^\circ\text{C}$; Guenther et al., 2006, 1993). To compare emission rates with observed concentrations, it is important to assess potential variations in the main isoprene removal pathways: chemical loss (oxidation by OH and ozone, O_3) and dispersion. The lower limit of the chemical lifetime of isoprene is estimated at 30–60 min, with representative $[\text{OH}] = 2.5\text{--}5 \times 10^6 \text{ molecules cm}^{-3}$ (based on modeled OH by Ferracci et al., 2018, and on summer OH measurements at forested sites from Griffith et al., 2013, Kaiser et al., 2016, Mao

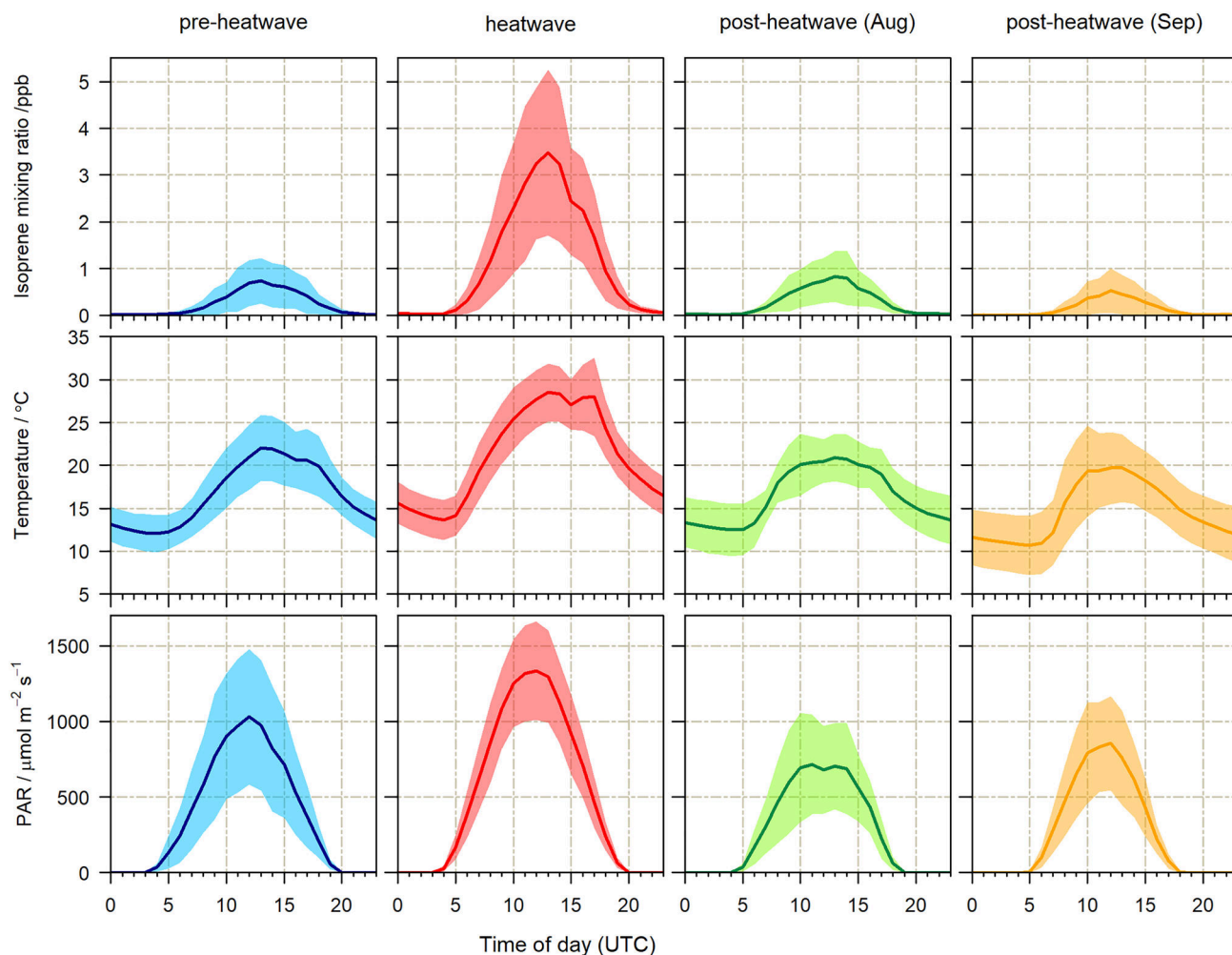


Figure 2. Mean diel cycles of isoprene abundance, temperature, and PAR at the top of the canopy during the four periods of the WISDOM campaign. Shaded areas represent 1 standard deviation above and below each 1-h mean.

et al., 2012, and Ren et al., 2006) and $[O_3] = 60$ ppb (based on measurements from the nearest monitoring stations of the UK Automatic Urban and Rural Network; DEFRA, 2020).

As there are no additional isoprene sources in the immediate surroundings other than the woods itself (Figure S6b), we estimate the emission footprint to be the entirety of Wytham Woods. At the campaign-average daytime wind speed (~ 2 m s⁻¹), isoprene emitted at the edge of the wooded area (~ 500 – $1,000$ m from the canopy walkway; see Figure S6a) would take ~ 4 – 8 min to reach the measurement site. With a mean isoprene chemical lifetime of 30–60 min and a residence time in the upper canopy in the order of seconds to a few minutes (Fuentes et al., 2007; Gerken et al., 2017), we identify dispersion rather than oxidation as the principal removal route for isoprene, with the uncertainty due to chemical loss of 6–25%.

Dispersion is primarily driven by wind, and we show that daytime wind speed and direction do not vary significantly during the different phases of the campaign (Figures S7 and S8, respectively). To ensure that our analyses consider only the observations that are similarly affected by dispersion, data are selected for wind speeds between 1.3 and 2.8 m s⁻¹, corresponding to ± 1 standard deviation from the mean daytime wind speed from May to September 2018 (Figure S7). In addition, to ensure that variation in isoprene source strength (i.e., the oak fraction within the measurement footprint) did not introduce biases, data are further filtered for wind directions between 180° and 270° (corresponding to the prevailing south-westerly winds). Biases introduced by different light intensity (affecting both isoprene emissions and chemical loss) are

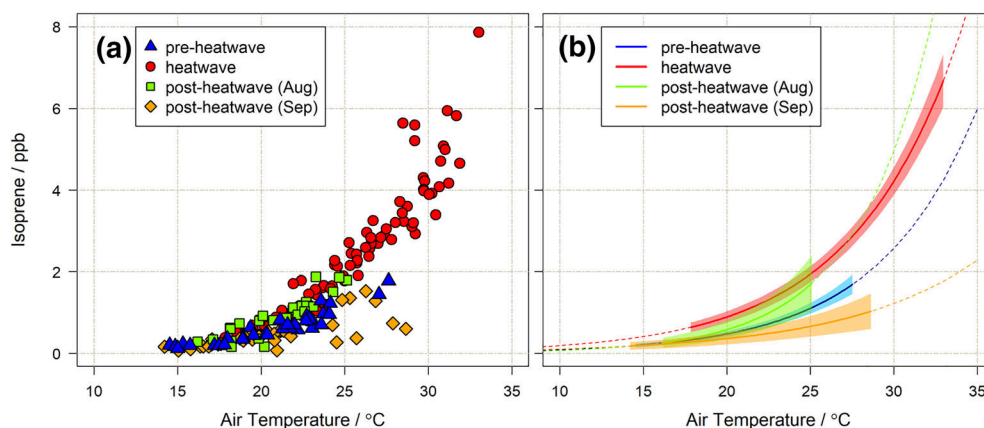


Figure 3. (a) Isoprene mixing ratio against air temperature at the top of canopy filtered by PAR, wind direction, and wind speed. (b) Non-linear least squares (NLS) exponential fits to the data in (a). Solid lines represent the fits over the range of observations while dashed lines represent extrapolations beyond the range of observations. Shaded areas indicate the 95% confidence bands in each exponential fit. Mean normalized root mean square errors for the fits are 0.19, 0.20, 0.22, and 0.52 for pre-heatwave, heatwave, early post-heatwave, and late post-heatwave, respectively.

minimized by selecting data for PAR between 650 and $1,350 \mu\text{mol m}^{-2} \text{s}^{-1}$ (limiting the effects of PAR to within $\sim 10\%$, as calculated using Equation S2). The resulting plots of filtered isoprene mixing ratio against air temperature (Figures 3a and S9) clearly show enhanced isoprene abundances during the heatwave and immediate post-heatwave compared with the pre-heatwave and late post-heatwave periods. Non-linear least squares (NLS) exponential fits to these data (Figure 3b) and t tests (Text S4 and Figure S10) highlight how, for the same temperature, significantly higher isoprene mixing ratios are found during the heatwave and immediate post-heatwave than in the pre- and late post-heatwave periods. Similar results were obtained when different values of the PAR and wind filters were used and also when modeled leaf temperatures (Otu-Larbi et al., 2020) were used.

As our subset of (filtered) data reduces the effects of meteorological variability on isoprene emission and loss processes, we assume that the isoprene mixing ratios observed during the WisDOM campaign are proportional to the isoprene emission rate. We therefore normalize observed isoprene concentrations for temperature and PAR (Text S5). We clearly see increased normalized isoprene concentrations (i.e., emissions) below a threshold value of soil moisture (in this case $\sim 0.25 \text{ m}^3 \text{ m}^{-3}$) as shown in Figure 4. Figure S11 demonstrates that this effect is independent of the normalization algorithm used.

This conclusion is supported by leaf-level volatile samples which showed that not only were isoprene emissions from *Q. robur* higher during the heatwave than early post-heatwave but that this enhancement was greater than would be expected for the increase in average temperature in July compared with August (Table S2). Back-calculated leaf-level emission factors (normalized as described in Text S5) were three times higher during the heatwave than pre-heatwave values (Otu-Larbi et al., 2020; Visakorpi et al., 2018) but only 15% higher than early post-heatwave, suggesting that the system was in recovery during August.

There was also a marked change in composition between leaf-level sampling periods (Table S3) with a clear increase in the proportion of sesquiterpenes present, which have been previously associated with abiotic stress (Holopainen & Gershenzon, 2010). Emissions of bergamotene and α -farnesene increased by as much as 100% in July compared with August. Phytol, an intermediate product of chlorophyll which acts as an antioxidant in leaf chloroplasts, reducing damage from high oxidative stress (Mach, 2015), was also detected during the heatwave but not in August.

4. Discussion

Isoprene emission rates are known to be affected by other environmental factors. For example, phenology drives an apparent seasonality of isoprene emissions (Fuentes & Wang, 1999), and it is important to establish whether the observed temporal pattern of normalized isoprene (Figure S12) is driven by other seasonal

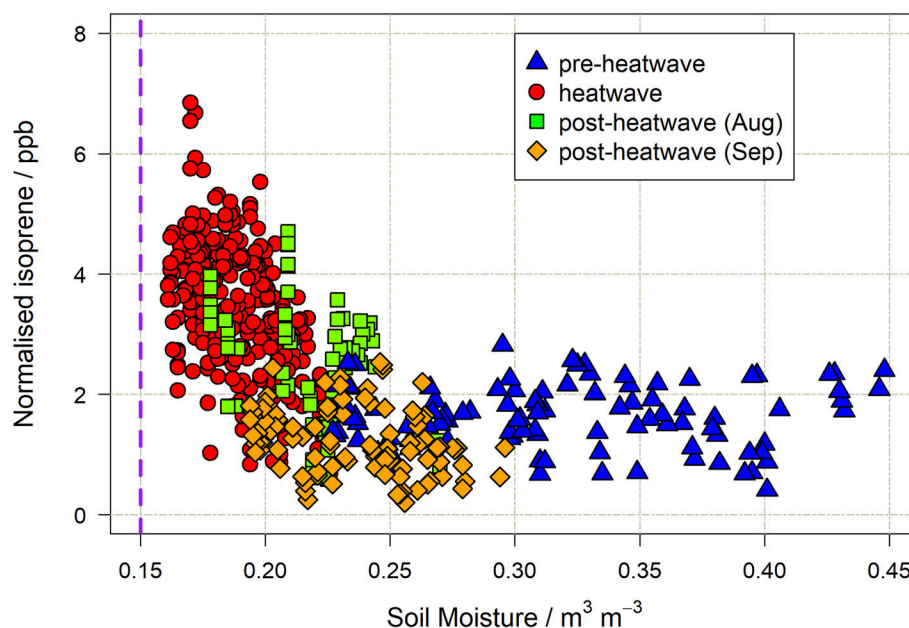


Figure 4. Correlation between normalized isoprene at the top of canopy and soil moisture. Data were filtered by PAR ($>500 \mu\text{mol m}^{-2} \text{s}^{-1}$, to exclude nighttime, dawn, and dusk data) and wind speed (between 1.3 and 2.8 m s^{-1}). The dashed purple line at 0.15 m^{-3} denotes the wilting point for Wytham Woods (X. Jiang et al., 2018). Isoprene mixing ratios were normalized using the G93 algorithm (Text S5 and Figure S11).

behaviors of the canopy. Using values for LAI from the measurement site (Brown et al., 2020; Herbst et al., 2008) and isoprene activity factors from Guenther et al. (2006), we show that the effect of leaf phenology is negligible ($<10\%$) during the main period of the WisDOM campaign (June to September), but becomes increasingly important in October due to leaf senescence (Text S6 and Table S4), which is beyond the measurement period considered in our analysis. The time series in Figure S12 shows that maximum normalized isoprene (hence emissions) corresponds to a marked decrease in NDVI during the heatwave and early post-heatwave as the ecosystem health is affected by moderate drought (also reflected in the NDWI in Figure 1b). As the NDVI (and ecosystem health) recovers in the late post-heatwave, the normalized isoprene returns to values comparable with the pre-heatwave period.

Niinemets (2010) and Potosnak et al. (2014) developed a conceptual framework to describe isoprene emissions during drought stress. This divides droughts into two distinct phases: an initial stage of moderate drought, during which isoprene emission rates are enhanced, and a second stage of severe drought, during which isoprene emission rates fall below non-drought values. The initial response of vegetation to decreasing soil moisture (i.e., at the onset of a moderate drought) is to reduce stomatal conductance to limit water loss by transpiration. This raises leaf temperature, which in turn drives an increase in isoprene emission rates relative to non-drought conditions (Potosnak et al., 2014). Isoprenoids are known to ameliorate heat stress, and studies on the physiological mechanism of isoprene emissions of plants under drought stress (e.g., Tattini et al., 2015) found that this may also complement antioxidant enzymes in quenching reactive oxygen species produced by photo-oxidative stress. However, the reduction in stomatal conductance also reduces the rate of photosynthesis, meaning less carbon is assimilated and therefore available for isoprene synthesis. As soil moisture continues to decrease (i.e., the drought becomes severe), a shortage of substrate leads to a reduction in isoprene synthesis and emissions.

The drought observed in the summer of 2018 during the WisDOM campaign was moderate (Centre for Ecology & Hydrology, 2020), with the minimum soil moisture values observed (0.16 m^{-3}) just above the wilting point for the site (0.15 m^{-3}). Under these conditions, the higher-than-expected isoprene concentrations observed during the heatwave and immediate post-heatwave are consistent with the Niinemets-Potosnak mechanism, that is, induced by increased leaf temperatures resulting from stomatal closure due to the decrease in soil water content. However, as the soil moisture remained above the

wilting point, the complete shutdown of isoprene emissions that would be expected for a severe drought was not observed. This is further corroborated by the modeling work by Otu-Larbi et al. (2020), who used a 1-D canopy model (Ashworth et al., 2015) to reproduce the isoprene concentrations observed during the WISDOM campaign. The model, using standard isoprene emission algorithms (Guenther et al., 1995, 1993), could reproduce the observed mixing ratios before and after the heatwave, but underestimated observations by ~40% during the heatwave-drought period. Inclusion of stress-induced emissions of isoprene based on leaf temperature and soil moisture led to a significantly improved model output.

This work, together with the 2011–2012 field observations from the Ozark site (Potosnak et al., 2014; Seco et al., 2015), corroborates the Niinemets-Potosnak conceptual model. The Ozark site experienced two consecutive years of drought: in 2011, the drought was mild and isoprene emission rates were enhanced (Potosnak et al., 2014), similar to the WISDOM campaign. In 2012 (Seco et al., 2015), the drought was severe and prolonged (~3 months): isoprene emissions rates increased during the first month of the drought (i.e., under moderate drought conditions), in agreement with the results from the WISDOM campaign, but were reduced once the drought became severe.

5. Summary and Conclusions

Isoprene concentrations were measured continuously at four heights below, within, and above the canopy in Wytham Woods, a mixed temperate woodland, during the 2018 growth season. Leaf-level samples were periodically collected from the *Q. robur* adjacent to the sampling platform.

Unexpectedly high mixing ratios and leaf-level emission rates of isoprene were observed during the 2018 heatwave and in the immediate post-heatwave. These observations cannot be accounted for solely by the higher temperatures and PAR in those periods (using the Guenther et al., 2006, 1993 algorithms), and we ascribe this behavior to the effects of low soil moisture (i.e., drought) on plant physiology and ultimately on leaf-level emissions. This is supported by a growing body of work including laboratory (Bamberger et al., 2017; Tattini et al., 2015), field (Genard-Zielinski et al., 2018; Potosnak et al., 2014), and modeling studies (Jiang et al., 2018; Lu et al., 2012; Zimmer et al., 2003).

Wytham Woods is representative of deciduous woodlands in temperate regions that are naturally moist and rarely experience drought. In the summer of 2018, it experienced a prolonged heatwave and drought that, while unusual at present, may be typical of summers in the mid- to late 21st century (UK Met Office, 2019b). This work demonstrates that, at the onset of drought, the physiological response of these ecosystems is to increase isoprene emissions. Taken in conjunction with the Ozarks study (Potosnak et al., 2014; Seco et al., 2015), which observed the same phenomenon in an ecosystem acclimated to virtually annual droughts, this work indicates that all forests are likely to show bursts of isoprene under the initial (mild) stages of a drought. This has significant impacts on the atmospheric composition, local climate, and air quality in forested regions under future scenarios, especially in the light of plans for large-scale reforestation that many governments in midlatitude countries are considering to achieve net-zero carbon emissions. Isoprene emission models that account for the effects of drought will provide improved predictions of regional air quality and of short-lived climate forcers under future scenarios.

Data Availability Statement

The data from the WISDOM campaign are available from the Natural Environment Research Council (NERC) Centre for Environmental Data Analysis (CEDA) archive at <https://catalogue.ceda.ac.uk/uuid/0c39809848ce47bb850d8ca2045e40f2> (last access: 8 April 2020). The meteorological data for Wytham Woods can be downloaded from the UK Environmental Change Network (ECN) website: <http://www.ecn.ac.uk/>.

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