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Differential responses of BVOC emissions in *Pinus massoniana* to drought stress and rehydration: Implications for climate change and air quality

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Abstract: Drought has been demonstrated to exert a substantial influence on the growth of plants and the chemical emissions thereof. The present study aims to examine the alterations in biogenic volatile organic compound (BVOC) emissions and chemical compounds in *Pinus massoniana* seedlings under the conditions of drought stress and subsequent rehydration. The findings revealed that drought stress and rehydration significantly altered the emission of total BVOCs, monoterpenes, and sesquiterpenes, with isoprene emission showing only a marginal decrease. Under conditions of drought stress, the emission of total BVOCs, monoterpenes and sesquiterpenes increased significantly, while the emission of isoprene decreased slightly. Following rehydration, the discharge of each chemical compound essentially recovered to the level prior to drought stress. Given the inconsistent response of different plant BVOCs to drought stress, it is imperative to closely monitor the effects of drought stress and global change on plant BVOC emissions in future research.

Keywords: biogenic volatile organic compounds; plants; rehydration; terpenes

Biogenic volatile organic compounds (BVOCs) – including isoprene, terpenes, aldehydes, and alcohols – are volatile metabolites emitted by vegetation (Peñuelas, Llusià 2003). Globally, plant-derived VOC emissions far exceed those from anthropogenic sources (Monson et al. 2013), with total BVOC fluxes estimated at 1–1.5 Pg carbon per year. This magnitude represents approximately 10% of the net carbon fixed via photosynthesis annually (Guenther 2002), underscoring their pivotal role in the global carbon cycle. Isoprene and monoterpenes constitute the majority of these emissions (Guenther et al. 2012).

Beyond their ecological functions in plant defence against oxidative stress and herbivory, BVOCs exert a significant influence on atmospheric chemistry. Once emitted, these reactive compounds participate in photochemical reactions, serving as key precursors for tropospheric ozone (O_3) and secondary organic aerosols (SOA) (Atkinson, Arey 2003; Yang et al. 2023; Xu et al. 2026). Consequently, fluctuations in BVOC emissions directly impact regional air quality and radiative forcing. The magnitude and composition of BVOC emissions are highly sensitive to environmental perturbations. Key drivers

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include elevated temperatures (Khan et al. 2025), drought stress (Riches et al. 2022), and light intensity (Dubuisson et al. 2022), as well as other abiotic factors (e.g. ozone exposure) and biotic stressors (e.g. herbivory) (Zeng et al. 2023).

As a dominant afforestation species in subtropical China, *Pinus massoniana* is a particularly strong emitter of BVOCs. Its monoterpene emissions alone are estimated to contribute approximately 16% of China's total annual monoterpene emissions (Li, Xie 2014), marking it as a high-emission species critical for regional atmospheric chemistry modelling. Under global climate change, the frequency and severity of drought events are increasing, with China among the most vulnerable countries globally (Zhang et al. 2016; Su et al. 2021). Consequently, understanding the response of BVOC emissions from this specific species to water stress is of paramount importance.

Previous studies have investigated the impact of drought on BVOC emissions across various species. For instance, Huang et al. (2023) reported a trade-off in the emission balance between isoprene and other BVOC constituents in *Pinus massoniana* under drought stress. Trowbridge et al. (2019) suggested that drought stress significantly affects monoterpene emissions, often surpassing the effect of temperature. Furthermore, investigations in European forests have revealed substantial uncertainties in isoprene emission inventories under drought-heatwave synergies, with variations reaching up to 40% (Otu-Larbi et al. 2019; Ferracci et al. 2020). However, while these studies focus on the drought response, the resilience of BVOC emissions during post-drought rehydration remains insufficiently explored, particularly regarding compositional shifts among specific terpenoids. Given that precipitation patterns are becoming increasingly erratic, understanding the recovery trajectory of BVOC emissions is crucial for accurate modelling.

Therefore, this study investigated the variations in major BVOC emissions from *Pinus massoniana* saplings under different drought severities, and subsequent rehydration. By quantifying the changes in emission rates and chemical composition, this work aims to provide fundamental data to support the development of more precise BVOC prediction models (e.g. MEGAN) and to assess the implications of soil moisture fluctuations for regional air quality in China.

MATERIAL AND METHODS

Experimental materials. Nine 2-3-year-old *Pinus massoniana* (tree height 85~98 cm, trunk diameter 9.2~9.8 mm) were selected as the research objects for the pot experiment, and they were randomly divided into three groups. These plants were grown in a greenhouse in Huzhou City (Zhejiang Province, China; 20°52'N, 120°04'E), where the temperature was kept in the range of 22~27 °C and the relative humidity of the air was maintained at 50~70% by a humidifier.

At the commencement of the experiment, the potted plants were subjected to a standard watering schedule for a period of five consecutive days, during which the soil moisture content was meticulously recorded to establish a baseline. Subsequently, the collected BVOC emission samples served as the control group (CG). The drought stress phase was initiated by gradually reducing the watering schedule, resulting in a 20% to 40% decrease in soil moisture content relative to the baseline, which was designated as the light drought (LD) condition. A 60% to 80% decrease represented the severe drought (SD) state. During the rehydration phase (RH), the soil moisture content was restored to the baseline level through augmented watering. Soil moisture content was determined using the gravimetric method (heat loss): A certain mass of soil sample is taken, dried in an oven until constant weight, the mass of the dried soil is weighed, and the soil moisture content is calculated based on the change in the mass of the soil before and after drying. To ensure emission stability, a minimum interval of five days was observed between each phase transition. Subsequently, a systematic collection of BVOC samples was conducted from each phase for subsequent analysis.

Sample collection and analysis. Needle dimensions were measured using a digital calliper. BVOCs emitted by plants were collected using the dynamic headspace adsorption method. Specifically, the plant was covered with a transparent polytetrafluoroethylene (PTFE) bag and connected to the sampling device using a Teflon tube. Throughout the experiment, the sampling bag was employed to envelop the entire plant, thereby minimising any disruption to the plant's ecosystem. During the sealing process, the sampling bag was continuously filled with clean air at a constant flow rate of 2.5 $L \cdot min^{-1}$ following the removal of VOCs by activated carbon adsorp-

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tion. Concurrently, the gas inside the bag flowed out through the gas outlet at the same flow rate, thereby ensuring that the gas inside the bag was in a circulating state. Subsequent to the closure and equilibration of the sampling bag for a period of 2–3 hours, the gas contained within the bag was collected by a Tenax adsorption column (Markes International Ltd., United Kingdom) (2,6-dibenzofuran porous polymer). The parameters of this process included a sampling flow rate of 300 mL·min^{-1}, a duration of 20 min, and a volume of 6 L. A total of three parallel samples and one blank sample were set up for each tree species. The collected samples were stored in a refrigerator at 4 °C prior to detection.

After desorption using a thermal desorber (Turbo Matrix 350, USA), the samples were analysed with a gas chromatography-mass spectrometry system (Agilent 7890A-5977C, USA). The chromatography column used was an HP-5MS capillary column (Agilent 30 m × 0.25 mm, USA). The experimental conditions were set as follows: thermal desorption temperature of 260 °C, cold trap collection temperature of –20 °C, carrier gas of helium with a flow rate of 1 mL·min^{-1}, and an initial column oven temperature of 40 °C with a maximum temperature of 280 °C. The rate of temperature increase is 5 °C per minute.

In this study, calibration curves for isoprene, monoterpenes, and sesquiterpenes were established using mixed solutions of authentic standard compounds (purchased as commercially available analytical-grade products) prepared at different concentrations (repeated three times to ensure their accuracy). Quantitative analysis was conducted using the external standard method.

The emission rate of BVOCs was calculated using Equation (1):

$$ER = \frac{F \times \left(C_{\text{outlet}} - C_{\text{inlet}}\right)}{m} \quad (1)$$

where:

ER – emission rate (μg·m^{-2}·h^{-1});

F – zero air flow rate (L·min^{-1});

C_{outlet},C_{inlet} – mass concentrations of VOCs in outlet and inlet sample bags (μg·m^{-3});

m – leaf area (m^2), calculated by measuring the length and width of needles.

Statistical analysis. Data are presented as mean ± standard deviation (SD). Significant differences in BVOC emission rates among the control (CG), light drought (LD), severe drought (SD), and rehydration (RH) groups were assessed using one-way analysis of variance (ANOVA) followed by Tukey's honest significant difference (HSD) post-hoc test. Statistical significance was defined as $P < 0.05$.

RESULTS AND DISCUSSION

Changes in BVOC emissions under drought stress. Drought has been demonstrated to exert a substantial influence on plant growth and BVOC emission. According to Li et al. (2020), the BVOC emissions of *Pinus massoniana* under mild drought stress increased by 1.84 times. As demonstrated in Figure 1 and Table S1 in the Electronic Supplementary Material (ESM), the BVOCs chemical composition of *Pinus massoniana* under various environmental conditions in this study displays a comparable trend. The findings reveal that drought stress significantly alters BVOC emission profiles, with the emission increased to 1.35 times and 1.69 times under mild and severe drought conditions, respectively, aligning with established research trends. Following rehydration, BVOC emission returned to pre-stress levels.

As demonstrated in Table S1 in the ESM, drought stress exerts a significant influence on the emission rates of isoprene, total monoterpenes, and total sesquiterpenes from *Pinus massoniana*, exhibiting a discernible response pattern. In this study, the emission of isoprene continuously decreased under drought stress, with a reduction of 14.88% and 12.16% under mild and severe drought conditions, respectively. Conversely, the emissions of total monoterpenes and sesquiterpenes exhibited a consistent increase under drought stress, with an increase of 39.57% and 37.68% for total monoterpenes, and 14.28% and 18.58% for sesquiterpenes, under mild and severe drought conditions, respectively. Fitzky et al. (2023) found that isoprene and monoterpenes are synthesised in the same metabolic pathway (MEP), while sesquiterpenes are synthesised by the mevalonic acid (MVA) pathway. Harrison's research showed that there was a competition of isoprene and monoterpene for substrates and enzymes (Harrison et al. 2013). Differences in synthetic pathways and competition for nutrients and enzymes may lead to different changes in these components under drought stress.

The way in which BVOCs are stored after synthesis also affects their emissions. Previous stud-

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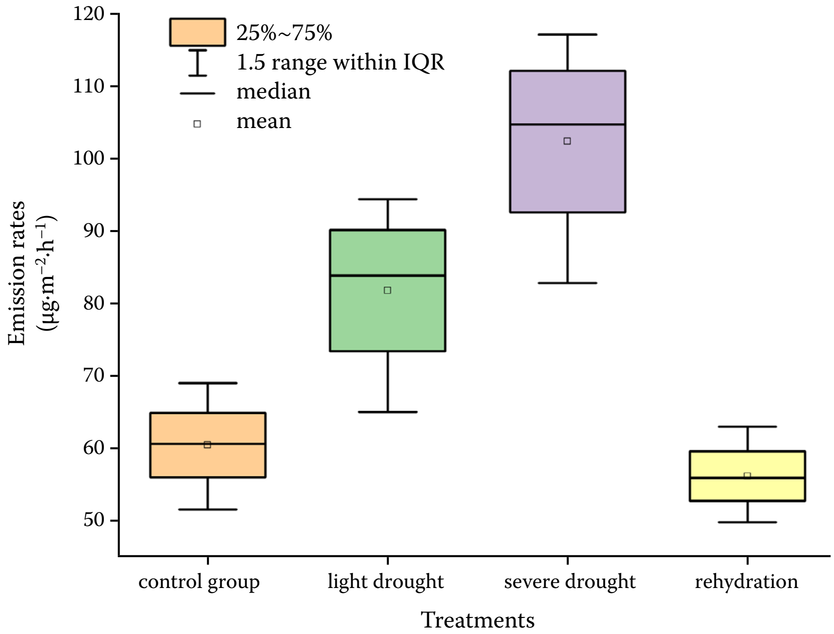

Figure 1. Change of BVOC emissions under different conditions

IQR – interquartile range

ies have shown that isoprene is released directly into the environment after synthesis in plants (Liu et al. 2025). Consequently, the emission of isoprene is significantly influenced by the stomatal conductance of plants. Under conditions of drought stress, a decrease in stomatal conductance is observed, leading to a rapid response in isoprene emission, which subsequently declines. However, it is noteworthy that total monoterpenes and total sesquiterpenes are initially stored in specific plant tissues and organs after their synthesis, and their release is only observed under favourable conditions or when the plant is under stress. Consequently, a decrease in stomatal conductance can lead to an increase in their emissions. The contrasting responses of isoprene and monoterpenes align with their divergent metabolic pathways (MEP vs MVA), where drought-induced stomatal closure preferentially suppresses isoprene emission while stored monoterpenes accumulate.

Responses of different BVOC compounds to drought stress. As demonstrated in Figure 2, the chemical composition of BVOC emissions varies significantly under different environmental conditions. It is evident that, while the composition of the various BVOCs emitted by *Pinus massoniana* remained consistent across diverse environmental contexts, there was a substantial alteration in the emission volumes. The analysis indicates that monoterpenes constituted the predominant chemical category in *Pinus massoniana* emissions, with a percentage ranging from 88.30% to 92.46%. Conversely, sesquiterpenes exhibited a decline in emission, ranging from 7.04% to 5.53% as the drought intensity intensified. As the drought intensity escalated, the emission of various BVOCs chemical compounds increased (e.g. α-pinene, β-pinene, and D-limonene), decreased (e.g. isoprene) or remained largely unchanged (e.g. β-caryophyllene and α-cedrene). The varied responses of these chemical compounds to drought stress may be ascribed to their distinct metabolic synthesis pathways within the plant (Zhou et al. 2020).

Among the total monoterpenes, D-limonene had the highest emission, with its proportion in total monoterpenes decreasing from 28.86% to 25.23% under different drought intensities and then increasing to 29.98%. Other monoterpenes with relatively high emission proportions include α-pinene, β-myrcene, and β-pinene, all of which account for approximately 20% to 22%. Among the total sesquiterpenes, α-caryophyllene exhibited the highest emission proportion, with its proportion in total sesquiterpenes increasing from 67.25% to 70.15% under different drought intensities and then decreasing to 68.53%. Among the various BVOC compounds, β-pinene exhibited a favourable response relationship with drought stress, with its

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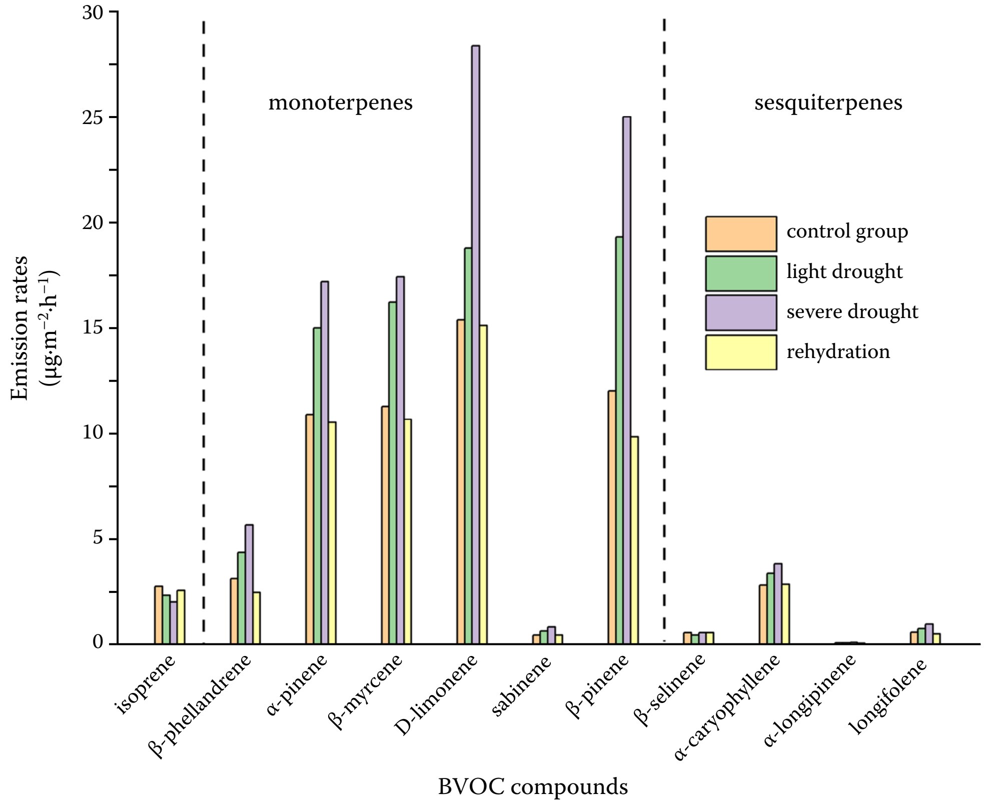

Figure 2. Emission changes of chemical compounds under different conditions

emission increasing as drought intensity increased and returning to its original level after water recovery. This selective response of β-pinene may be attributed to its role in plant stress signalling or its synthesis pathway's lower sensitivity to stomatal closure. Furthermore, its emission accounted for a relatively high proportion (approximately 20%) of the total BVOCs, indicating its significant role. In summary, β-pinene may be used as a marker chemical compound in future studies on the impact of drought stress on BVOC emission from *Pinus massoniana*.

The study by Li et al. (2020) posited that the relative content of α-pinene and α-caryophyllene were highest in the BVOCs emitted by *Pinus massoniana*. However, the results of the present study indicate that limonene and caryophyllene have the highest content. This discrepancy may be attributed to the inconsistencies in the measurement methods used. The preceding study amalgamated empirical measurements with model estimations to ascertain emission amounts, and these findings were considerably influenced by the configuration of model parameters. In contrast, the present study used empirical measurements to calculate the concentration of each chemical constituent, a technique that has been shown to be more effective in demonstrating the concentration of different chemical constituents.

The average value of the initial state BVOC components was used as a benchmark to normalise the content of the BVOC components under different conditions, and the results are presented in Table 1. This makes it more obvious how the different BVOC compounds change under drought and rehydration conditions.

Impact of drought stress on air quality. Research has indicated that China's BVOC emission totalled 33.6 million tons in 2018, with isoprene, monoterpenes and sesquiterpenes accounting for 64.21%, 10.58% and 2.12% of these emissions, respectively (Cao et al. 2022). Furthermore, the terpene emissions from *Pinus massoniana* in China have been determined to be 0.92 million tons per year (Yang et al. 2021; Luo et al. 2025). When considered in conjunction with the extent of changes in terpene emissions in response to drought stress as determined in this study (see Table 1), it is possible to make a preliminary estimate of possible changes in terpene emissions in *Pinus massoniana*

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Table 1. Normalisation results of BVOC compounds under different conditions*

Compound	CG	LD (%)	SD (%)	RH (%)
Isoprene	1	85.12	72.96	93.21
Monoterpenes	1	139.57	177.25	92.37
β-Phellandrene	1	139.54	180.60	80.06
α-Pinene	1	137.46	157.41	96.62
β-Myrcene	1	143.59	154.32	94.67
D-Limonene	1	122.01	184.10	98.23
Sabinene	1	137.17	173.65	97.89
β-Pinene	1	160.26	207.25	81.87
Sesquiterpenes	1	114.28	132.86	98.92
β-Selinene	1	82.92	99.25	98.98
α-Caryophyllene	1	119.21	135.38	101.69
α-Longipinene	1	105.58	114.32	94.93
Longifolene	1	124.24	157.84	87.32
Total	1	135.26	169.27	92.87

*Normalised to the control group (CG = 1); LD – light drought; SD – severe drought; RH – rehydration

under drought stress conditions. The assumption was made that the emission of plant BVOC components is related to their emission rates and that they vary proportionally under ideal conditions. Under this assumption, we may consider the example of 2018, when under mild and severe drought conditions, the emissions of isoprene from *Pinus massoniana* may have decreased from 10 200 t to 8 700 t and further to 7 400 t, while the emissions of total monoterpenes and total sesquiterpenes increased from 808 200 t and 106 600 t to 1 128 000 t and 121 800 t, and further to 1 432 500 t and 141 600 t (the magnitude of change for each BVOC component was based on the values in Table 1). It has been observed that, in the presence of mild and severe drought stress, *Pinus massoniana* continues to exhibit an increase in total BVOC emission, resulting in an approximate increase of 35.26% and 69.27%, respectively.

It is noteworthy that the atmospheric impact of BVOC emissions depends not only on total mass but also on chemical reactivity. Compounds such as D-limonene and β-pinene exhibit significantly higher ozone formation potentials (OFP) and secondary organic aerosol (SOA) yields than other terpenes (Atkinson, Arey 2003). Our data (Table 1) show these highly reactive compounds increased by 84.1% and 107.3% under severe drought, respectively. This compositional shift suggests that drought events could disproportionately enhance atmospheric oxidative capacity and particulate pollution in forested regions, posing a greater risk to regional air quality than total flux measurements alone would indicate.

This study highlights the potential for drought-induced enhancement of BVOC emissions in China under global climate change. Specifically, our findings indicate that severe drought conditions could increase BVOC emission fluxes by up to 69% (relative to baseline levels), posing a significant risk to regional atmospheric chemistry and air quality. These results underscore the need for incorporating drought-BVOC feedback mechanisms into regional air pollution management strategies.

CONCLUSION

(*i*) Drought stress significantly affects the emission of BVOCs from *Pinus massoniana*, with a significant increase in total monoterpenes and total sesquiterpenes.

(*ii*) Under different experimental conditions, the types of BVOC chemical compounds remain consistent, with D-limonene and α-caryophyllene being the dominant chemical compounds in total monoterpenes and total sesquiterpenes, respectively.

(*iii*) The response of each BVOC chemical compound to drought stress varies, among which β-pinene demonstrates a good response rela-

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tionship with drought stress in terms of both emission quantity and proportion.

(*iv*) Severe drought conditions may elevate total BVOC emissions from *Pinus massoniana* by up to 69.27% compared to baseline levels in China (assuming proportional scaling of emission rates), significantly affecting the regional atmospheric environment.

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