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Untangling the primary drivers of pinyon monoterpene production and emissions under predicted drought

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Climate and insect herbivory have important consequences for plant function, atmospheric composition, and the functioning of ecosystems and ecological communities. Within the last decade, pinyon-juniper woodlands throughout the southwestern U.S. have suffered large-scale mortality, especially of pinyon pine, due to drought and associated insect outbreaks. While much research has focused on the primary metabolic mechanisms underlying pinyon's sensitivity to drought, there remains a gap in our knowledge concerning how the resulting shift in carbon allocation toward plant secondary compounds, particularly monoterpenes, affects atmospheric process and ecological interactions.

Monoterpenes are the principal constituents of pinyon resin. Because of their large global emission rates and effect on atmospheric chemistry, particularly ozone creation, identifying controls over emissions and sensitivities to environmental change is critical for global emission models. Furthermore, monoterpenes are known to impact insect behavior and act as defense compounds against herbivores, contributing to insect population fluctuations either directly through toxicity, or indirectly by influencing parasitism susceptibility. Pinyon mortality events are thought to be exacerbated by their susceptibility to herbivores resulting from weakened secondary chemical defenses, but the impact of current and predicted drought on the chemical defense status of pinyons and subsequent atmospheric and ecological consequences remain unknown.

A field study was developed to examine the impact of seasonality and climate, particularly drought, on pinyon pine physiology and chemistry in the context of tiger moth (Lophocampa ingens) herbivory in pinyon-juniper woodlands. We demonstrate the importance of geography and seasonality, particularly mid-summer drought and late summer monsoons, in driving physiology and monoterpene concentrations and emissions. Emission rates significantly decreased throughout the summer and increased with a release from drought stress. Pinyons with past herbivore damage emitted significantly higher levels of monoterepenes ($P<0.05$), suggesting an interactive effect between herbivory and drought. Furthermore, neither temperature nor foliar monoterpene concentrations predicted emission rates, a result most likely due to the composite physiological response to both drought and insect herbivory.

To tease apart the primary drivers of monoterpene emissions under drought stress, we developed a manipulative study by transplanting pinyons into a desert environment and increasing mean annual temperature by $\sim$4 ºC. We then measured pinyon physiology and monoterpene composition and emissions under different water and temperature regimes. Similar to our previous study, we saw that monoterpene emissions decreased with water availability across our treatments ($P<0.05$), with a 60% decrease in emissions from well-watered to drought stressed trees. While monoterpene emission rates early in the growing season in the native habitat were correlated with foliar concentrations and temperature, they were more constrained by water availability in transplanted trees as the growing season progressed. A possible explanation for these results could be that, unlike temperate species, semi-arid trees are physiologically more sensitive to water availability; therefore, we determined specific drought stress level and water potential thresholds at which this decoupling of temperature-dependent monoterpene emissions occurs. These results have led to the development of hypotheses about the consequences of future shifts in monoterpene concentrations and emissions due to drought affecting herbivore species interactions, outbreaks, and atmospheric processes.