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Elevated [CO_2] affects whole-plant gas exchange and primary metabolism during heatwave combined with drought in Aleppo pine seedlings

Benjamin Birami (1), Marielle Gattmann (1), Yakir Preisler (2), Andreas Gast (1), Thomas Nägele (3), Rüdiger Grote (1), Almut Arneth (1), and Nadine Ruehr (1)

(1) Karlsruhe Institute of Technology KIT, Institute of Meteorology and Climate Research – Atmospheric Environmental Research, 82467 Garmisch-Partenkirchen, Germany (benjamin.birami@kit.edu), (2) Weizman Institute of Science, Department of Earth and Planetary Science – Environmental Sciences and Energy Research, 76100 Rehovot, Israel, (3) University of Vienna, Molecular System Biology – Molecular System Dynamics, 1090 Vienna, Austria

Aleppo pine (*Pinus halepensis*), one of the most abundant tree species in the Mediterranean region, has been described as heat and drought tolerant in today's climate. However, with climate change, atmospheric [CO_2] concentrations will increase, which will affect tree metabolism including water use efficiency, photosynthetic capacity and allocation. Up to date, large uncertainty persists on the combined effects of elevated [CO_2], heat and drought on tree metabolism.

The effects of heat, drought and elevated [CO_2] on whole-plant gas exchange and primary metabolism of 1.5-year-old *P. halepensis* seedlings were investigated. Seedlings were grown from seeds (originating from the Yatir forest, Israel) under ambient (400 ppm) or elevated (900 ppm) [CO_2] in a carbon free substrate and daily irrigated to 50% relative water content (RWC). Before placing the seedlings into tree cuvettes that were designed to measure the CO_2 and H_2O exchange of the canopy and root system separately, biomass allocation and photosynthetic capacity was measured and irrigation of the drought treatment was reduced to maintain 10% RWC for a minimum of 45 days.

Seedlings of all four treatments (control-ambient, drought-ambient, control-elevated and drought-elevated) were placed in the cuvettes and subjected to a step-wise increase in daily-averaged air temperature (25˚C, 35˚C, 38˚C to 40˚C) that increased vapor pressure deficit (VPD). Canopy and root gas exchange was measured continuously and needle samples were taken for water potential measurements. For metabolomics, needle and roots were sampled at different temperature intervals and immediately frozen in liquid nitrogen and stored at -80˚C until analysis.

We found that after germinating and growing Aleppo pine seedlings under elevated [CO_2], the seedlings' biomass was strongly increased compared to the ambient CO_2-treatment, while stomatal conductance and photosynthetic capacity decreased. With increasing temperature and VPD, net CO_2 uptake declined steeply independent on [CO_2] and at about 38˚C root respiration exceeded carbon gain of photosynthesis even in high moisture treatment. In the drought treatments the tipping point was reached earlier at lower temperatures. First results of the metabolomics analysis indicate a specific response of primary metabolism to treatment combinations substantially differing between sink and source tissues. Root metabolism showed strong stress-induced reprogramming of the TCA cycle (tricarboxylic acid cycle), which, in contrast, seems to play a minor role in heat or drought response of needle tissue. In needle tissue, sucrose and raffinose levels increased significantly under combined drought, heat and elevated [CO_2] which was not observed under ambient [CO_2].

These findings suggest a role of mesophyll [CO_2] in stress response capacity. Increasing root respiration with both, increased temperature and elevated [CO_2] indicate a higher carbon allocation into roots and eventually lead to an increased carbon turnover but not necessarily to better plant performance.

In summary, we can show that elevated [CO_2] does strongly affect the whole-tree metabolism of Aleppo pine and alters its stress response.