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Root exudation rate increases, and composition changes in a mature temperate forest under elevated carbon dioxide

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The carbon fertilization effect under increasing atmospheric carbon dioxide (CO_2) may contribute to removing 30% of anthropogenic CO_2, with mature forests central to this. However, the ability of mature forests to continue to act as a long-term sink of carbon (C) is dependent on the availability of essential nutrients; nitrogen, and phosphorus. It has been suggested root exudates may increase under elevated CO_2 (eCO_2) as a mechanism to acquire these nutrients from soil, via priming of the soil microbial community to increase nutrient turnover, or abiotic release. However, this is yet to be tested in a mature forest. Furthermore, it is unknown if root exudate composition also changes in response to eCO_2, as has been observed for drought. Given the role of root exudates in nutrient acquisition, their response to elevated CO_2 in a mature temperate forest may be a key mechanism for nutrient acquisition, supporting their ability to act as a long-term sink of CO_2.

We used the unique Birmingham Institute of Forest Research (BIFoR) free air carbon enrichment experiment (FACE), where a mature temperate deciduous forest dominated by English Oaks (*Q. robur*) is fumigated with eCO_2 at +150 ppm above the ambient atmospheric CO_2 concentration during the growing season, since 2017. Root exudates were collected quarterly from summer 2020 to summer 2021 from in-situ fine (<2 mm) oak roots in the O horizon, accessed via root boxes, into a soil-free bead-filled static cuvette system over 24 hours. Root exudates were analyzed for total dissolved carbon and nitrogen content, and roots and exudates from Summer 2020 underwent metabolomic analysis to investigate changes in composition. Root exudation rates were normalized to root surface area.

Carbon exuded by fine roots was 40% higher under elevated CO_2 across the year, with a clear seasonal trend whereas nitrogen exudation rate did not significantly differ between elevated CO_2 and control plots with no seasonal trend. Enhancement of C exudation resulted in a trend of a

relatively larger C:N ratio, indicating a compositional change under eCO_2, despite no differences in root C:N. Untargeted metabolomic analysis of root exudates collected in Summer 2020 confirmed significant changes in composition of root exudates. Compounds associated with the metabolism of amino acids, carbohydrates and cofactors and vitamins, and biosynthesis of secondary metabolites were upregulated under eCO_2, and this was also reflected in the metabolome of the roots.

The increased carbon exudation rates reflected higher photosynthetic rates observed in oaks leaves under eCO_2, and compositional changes indicated by lower nitrogen exudation rates, relative to carbon. Furthermore, compositional changes investigated via metabolomics revealed significant changes in the metabolome, pointing to potential eCO_2 cascading impacts on nutrient acquisition strategies of mature oaks. These must be accounted for to be able to fully account for nutrient constraints of C uptake by forests under future climates, including within CNP-coupled and ESM models.