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Reciprocal trade of Carbon and Nitrogen at the root-fungus interface in ectomycorrhizal beech plants

Christina Kaiser (1), Werner Mayerhofer (1), Marlies Dietrich (1), Stefan Gorka (1), Arno Schintlmeister (1), Siegfried Reipert (2), Peter Schweiger (1), Marieluise Weidinger (2), Julia Wiesenbauer (1), Victoria Martin (1), Andreas Richter (1), and Dagmar Woebken (1)

(1) Department of Microbiology and Ecosystem Science, University of Vienna, Vienna, Austria (christina.kaiser@univie.ac.at), (2) Core Facility of Cell Imaging and Ultrastructure Research, University of Vienna, Vienna, Austria

Plants deliver recently assimilated carbon (C) to mycorrhizal fungi, and receive nutrients, such as N and P, in exchange. A reciprocal exchange of C and nutrients between plants and mycorrhizal fungi (i.e., fungi which deliver more nutrients receive more plant C in return and vice versa) has been suggested for arbuscular mycorrhizal symbioses by some studies, but challenged by others. For ectomycorrhizal associations even less is known on how the exchange of C for nutrients is regulated, and whether it is based on reciprocity, or other controls.

The aim of this study was to test the concept of reciprocal rewards between beech (*Fagus sylvatica)* and their associated ectomycorrhizal fungi on different scales, namely (a) across associations between individual root tips of beech and different fungal partners, and (b) at the subcellular scale at the plant-fungus interface. We exposed young beech trees associated with natural mycorrhizal fungal communities to a $^{13}CO_2$ atmosphere and added ^{15}N-labelled amino acids to a 'litter compartment', that mycorrhizal hyphae, but not plant roots could access. Plants were harvested within 2 days after application of ^{15}N and less than one day after applying $^{13}CO_2$. If the trading of C for N was reciprocal, we expect that ^{13}C would be correlated to ^{15}N across individual plant-fungal connections and at the subcellular scale within one mycorrhizal root tip, respectively.

We collected individual mycorrhizal root-tips from 8 plants right after harvest, analyzed their ^{13}C and ^{15}N content by isotope-ratio mass spectrometry (EA-IRMS) and performed ITS sequencing to identify fungal communities associated with individual root tips. Selected mycorrhizal root tips were also prepared for nano-scale secondary ion mass spectrometry (NanoSIMS) to visualize the spatial distribution of ^{13}C and ^{15}N in cross-sections of mycorrhizal root-tips at the subcellular scale.

Our results showed a significant, albeit weak correlation between ^{13}C and ^{15}N across collected mycorrhizal root-tips, the variability of which was seemingly influenced by fungal colonization pattern. Within a cross-section of an individual root-tip, however, NanoSIMS imaging revealed not only a high spatial heterogeneity of ^{13}C and ^{15}N across plant and fungal cells, but also a strong spatial correlation between ^{13}C and ^{15}N in both, plant cells and fungal cells of the Hartig Net, the fungal mantle and external hyphae. Intriguingly, individual 'hotspots' of external fungal hyphae that were highly enriched in ^{15}N (delivering high amounts of the added ^{15}N to the plant), were also always extraordinarily enriched in ^{13}C (receiving more ^{13}C in return).

Our results provide first evidence for a reciprocal exchange of C for N between plants and ectomycorrhizal fungi at the subcellular scale. This indicates that a mechanism at the cellular level exists, that (i) either allows plants to direct their C flow into N-delivering parts of the mycorrhizal hyphal network or (ii) allow the fungus to 'draw' more C from the plant (develop a higher sink strength) when it has access to N. While such a mechanism still remains to be elucidated, our study shows, for the first time, direct evidence for its existence.