

## Isotopic patterns in caps and stipes in sporocarps reveal patterns of organic nitrogen use by ectomycorrhizal fungi

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Current ecosystem models use inorganic nitrogen as the currency of nitrogen acquisition by plants. However, many trees may gain access to otherwise unavailable soil resources, such as soil organic nitrogen, through their symbioses with ectomycorrhizal fungi, and this pathway of nitrogen acquisition may therefore be important in understanding plant responses to environmental change. Different functional groups of ectomycorrhizal fungi vary in their ability to enzymatically access protein and other soil resources. Such fungal parameters as hyphal hydrophobicity, the presence of rhizomorphs (long-distance transport structures), and exploration strategies (e.g., short-distance versus long-distance, mat formation) correspond with how fungi interact with and explore the environment, and the proportions of different exploration types present will shift along environmental gradients such as nitrogen availability.

Isotopic differences between caps and stipes may provide a means to test for organic nitrogen use, since caps and stipes differ in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  as a result of variable proportions of protein and other classes of compounds, and protein should differ isotopically among *de novo* synthesis, litter sources, and soil sources. Here, we propose that (1) isotopic differences between caps and stipes could be related to organic nitrogen uptake and to the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of different pools of soil-derived or *de novo*-synthesized amino acids; (2) these isotopic differences will reflect greater acquisition of soil-derived organic nitrogen by exploration types of greater enzymatic capabilities to degrade recalcitrant nitrogen forms, specifically long-distance, medium-distance fringe, and medium-distance mat exploration types. To test these hypotheses, we use a dataset of isotopic values, %N, and %C in 208 cap/stipe samples collected from Oregon, western USA.

$\delta^{13}\text{C}$  differences in caps and stipes in a multiple regression model had an adjusted  $r^2$  of 0.292 ( $p < 0.0001$ ), and were explained best by exploration type (45% of explained variance), the interaction of exploration type and %N<sub>cap-stipe</sub> (20%), the interaction of exploration type and %N<sub>cap/stipe</sub> (22%), %C<sub>cap-stipe</sub> (8%), and %N<sub>cap-stipe</sub> (5%).  $\delta^{15}\text{N}$  differences between caps and stipes in a multiple regression model had an adjusted  $r^2$  of 0.486 ( $p < 0.0001$ ), and were explained best by exploration type (47% of explained variance), the interaction of exploration type and %N<sub>cap-stipe</sub> (26%), the interaction of exploration type and %N<sub>cap/stipe</sub> (14%), %N<sub>cap/stipe</sub> (11%), and %C<sub>cap-stipe</sub> (2%).

We argue that these differences in the  $^{13}\text{C}$  and  $^{15}\text{N}$  enrichment of caps relative to stipes reflect not only shifts in the proportions of protein and carbohydrates, but also differences in the extent of fluxes and the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures of soil- and litter-derived organic nitrogen taken up by these fungi. We also propose equations to quantify this uptake. Organic nitrogen from litter (lower  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) may be incorporated by medium-distance mat, short-distance, and contact exploration types of ectomycorrhizal fungi, whereas long-distance and medium-distance fringe exploration types appeared to incorporate deeper soil organic nitrogen.