

How is Nitrogen acquired and transported?

AM fungi - active uptake as NH_4^+ and NO_3^- , synthesis of amino acid (AA) (arginine), transport to intraradical mycelium (possibly on polyphosphates), breakdown of amino acid, and transport of NH_4 to plant via active transport (Govindarajulu, Pfeffer et al. 2005).

EM fungi (from Smith and Read, chap.8)- active uptake of NH_4^+ (NO_3^-), AA, small peptides, (maybe other sources? chitin monomers), source varies with species involved "protein and non-protein fungi" Shifts in species occur with N deposition (European sites, and Alaska, plus natural)

Transport through mycelium as AA (mostly glutamine), active transport to plant as AA. Some carbon moves back to plant as amino acids, when Nitrogen is transferred. This can be a significant amount (8% of total seedling C)

Some evidence of spatial differences in gene expression of major N acquisition enzyme systems in extraradial mycelium and root tip (Martin figure, from Smith and Read)

How is Phosphorus acquired and transported?

AM fungi have repeatedly been shown to increase [P] in plants. (from Smith and Read, chap.5) This may be caused by 1) the size advantage of hyphae in spatial foraging in soil due to size; 2) ability of hyphae to proliferate rapidly in rich patches of P; 3) Higher affinity (lower K_m) for P; 4) access to pools of P not available to plants

1&2 well documented and may be sufficient to explain all available data; 3) does not appear to be true (both plants and fungi have high and low affinity transport systems with similar K_m) 4) remains unclear.

synergism between P-solubilizing bacteria and AM, but no direct evidence of additional AM-produced chelators.

AM inoculated plants will respond to forms of P (rock phosphate, Fe and Al phosphates, and Phytates) that non-mycorrhizal plants do not access - but this could be due to increased spatial foraging and not specific enzymology (fig 5.6 from Smith and Read)

PO_4 acquired by H^+ ATPase pumps, accumulated in vacuoles probably as short chain polyphosphates (common in other fungi)

Ecto fungi also increase P to plant, but they store P in the mantle and do it out the host over time. (from Smith and Read, chap.9)

Rapid movement via rhizomorphs (4 day autoradiogram photo)

Amount of root colonization and extraradical mycelium correlates with P uptake, but only if compared with a single fungal species, different species can be very different.

Ectos very capable of retrieving P from inorganic sources like rock phosphate and aluminum phosphate – thought to be due to organic acids and chelators.

Multiple Phosphatases present and expression inversely correlate to availability of PO_4

Organic forms inositol penta and hexaphosphate (“phytate”) and phosphodiester (nucleic acids, phospholipids) are also accessible to ectos

How is Carbon transferred?

In AM systems

Main forms of metabolizable carbon in the fungus are lipid (triacylglycerol), glycerol, glycogen, trehalose, manitol.

Following plant labeling the first labeled carbon compounds in the fungus are Trehalose and glycogen. While germinating spores have high concentration of manitol.

AM fungi synthesize most of the carbon into lipids in the intraradical mycelium and transport these to the extraradical mycelium, but Glycogen is also a significant storage molecule. (Bago, Zipfel et al. 2002; Bago, Pfeffer et al. 2003)

In Arum-type most of the C transfer appears to take place in the intracellular hyphae, **not in the arbuscules**. Site of transfer in Paris type unknown.

In ecto systems - (from Smith and Read, chap.7)

Most ectos can not use sucrose in culture - presumed to be dependent on plant invertases to convert sucrose to glucose and fructose. Invertase activity is pH dependent and this may be manipulated by the fungus. Glucose is converted to Trehalose and Glycogen, which don't diffuse back to the plant.

Much is not understood: If excess glucose exists it should inhibit importation of fructose, and if fructose accumulates it should inhibit plant invertases.

45% of the label ends up in Trehalose, 1-22% in manitol,

Carbon budget estimates and methods to get them (Leake, Johnson et al. 2004)

Early estimates came from turnover rates of observable structures (colonized roots), spores, sclerotia, and fruiting bodies

Vogt et al 1982 (cited 128 times) – counted up root tips, sclerotia, fruiting bodies, in a Washington fir forest and estimated 14-15% of NPP (net primary productivity) goes into mycorrhizal fungi, and a total of 45% (young forest) - 75% (mature forest) of NPP is EM fungi + fine root mass; sclerotial production by one fungus (*Cenococcum*) was estimated to be 2700 kg/ha/yr.

Isotopic Labeling followed by quantifying of label in structures.

If ecto plants are labeled with ^{14}C - 15-18X more of the label goes to colonized root tips than to uncolonized; this ratio decreases as mycorrhizal tips age.

In AM plants 4-20% more goes to colonized compared to uncolonized roots. Amount found to vary with fungal species involved.

Estimates based on microcosm labeling with C^{14} and real-time quantification
Carbon allocated to **ER mycelial peak in 24-30 hrs** after plant is labeled and most is respired away.

Estimates based on root-free chambers and disrupting ER mycelial connection and comparing it to non-disrupted

Cutting hyphal connections to tree causes rapid drop in respiration
Carbon received is increased when NH_4^+ or NO_3^- is added into a hyphal compartment – different fungal species (or strains?) have different carbon demands under these settings.

Do Ectomycorrhizal fungi acquire carbon saprophytically?

There is evidence that they have and use cellulases, but they are apparently are not as good as saprobes

Gadgil hypothesis (Gadgil and Gadgil 1971) – EM fungi use host C to mine N and P from detritus at a net carbon loss. – Based on observation that removal of EM fungi actually accelerates decomposition. (Gadgil and Gadgil 1971; Koide and Wu 2003)

Does carbon flow between plants via common mycorrhizal networks?

Early labeling evidence from multiple systems from both EM and AM says it does - But the question of whether there was net flow was unanswered (Figure from Read showing donor and recipient root)

Simard et al (Simard, Perry et al. 1997) did bi-directional labeling ^{14}C and ^{13}C , and claimed to show net flow that was influenced by "sink strength" of host.

Robinson and Fitter (Robinson and Fitter 1999)- carbon moves between roots, but stays in the fungal compartment; other transfers not significant (except with epiparasites).

In AM systems the question of whether the apparently transferred carbon remained in the fungus or was actually transferred to the plant is also an issue. Compound specific isotope work seems to favor the idea that it stays in the fungus. (Pfeffer, Doude et al. 2004)

Epiparasites are found in both AM and Ecto systems. Do they exploit normal pathways to obtain C or did they all invent novel ways to do it?

Is the significance of common mycorrhizal networks dependent on Carbon transfer? - Differential investment by plants may still result in biased outcomes.

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