

The significance of mannitol metabolism in ectomycorrhizal associations

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In many fungi, both mycorrhizal and non-mycorrhizal, the main soluble carbohydrate found is mannitol (M) (Lewis & Harley 1965, Martin et al. 1987), and several possible roles have been suggested for it, e.g. osmoregulatory functions, carbon storage (Wedding & Harley 1976, Harley & Smith 1983). Lately, the synthesis and degradation of M have received considerable attention and a cyclic pathway for M metabolism in certain fungi has been hypothesized (Hult & Gatenbeck 1978). In mycorrhizal fungi, this enzyme system could be responsible for a continuous turnover of the M pool, a carbohydrate reserve that could reach a cellular concentration of 50–80 mM in actively growing mycelia (Martin et al. 1988). In this sense M would be of importance both as a carbohydrate storage compound, not available to the host, and as a part of a cyclic pathway producing NADPH.

The enzymes involved in the cyclic M metabolism are NADH-specific mannitol 1-phosphate dehydrogenase (M1PDH), mannitol 1-phosphatase (M1P:se), NADPH-specific mannitol dehydrogenase (MDH) and hexokinase, giving the reaction $F6P \rightarrow M1P \rightarrow M \rightarrow \text{Fructose} \rightarrow F6P$. All the enzymes of the cycle have been detected in ascomycetes and Fungi imperfecti, but in basidiomycetes the first enzyme of the pathway, M1PDH, has not been shown (Hult & Gatenbeck 1978, Ramstedt et al. 1987).

The kinetics of the other three enzymes, however, strongly favours a forward direction of the cycle (Ramstedt et al. 1986), which in turn would need conversion of F6P to M1P. The high specificity of M1P:se supports the hypothesis of M production over this phosphorylated compound. Reverse production of M by reduction of fructose by MDH is not very plausible, since the equilibrium of the MDH reaction is strongly in the fructose direction and the high concentration of fructose needed for the reverse reaction is never reached in fungi.

An interesting difference between mycorrhizal and non-mycorrhizal basidiomycetes is the NADP specificity of MDH in the former (Ramstedt et al. 1987). This is necessary for the NADPH-producing M cycle and is not found in the non-mycorrhizal ones, where only NAD was used. Other routes for M production have been considered, but no other likely ways have been confirmed.

For this purpose NMR spectroscopy was used to study the incorporation pattern of labelled glucose in several fungi (Martin et al. 1985, Martin et al. 1987, 1988). These investigations clearly show that M is rapidly formed directly from absorbed glucose without further scrambling of the label, and no other carbohydrates are labelled during the first hours of ^{13}C -glucose feeding. The rate of M accumulation was 50–65 nmol/g fresh weight of the mycelium per min. No significant levels of fructose have been detected that could account for backward operation of the M cycle. The labelling pattern of trehalose, the other important fungal carbohydrate, also indicates continuous and rapid turnover of the M pool, which would be consistent with the M cycle (Martin et al. 1988). Glucose labelled at C1 would normally label only trehalose in the C1 position. The C1/C6 incorporation in trehalose (Martin et al. 1987, 1988) indicates that part of the glucose forming trehalose has first been cycled through the M pool. Evidence of the operation of this cyclic pathway *in vivo* is still lacking, however, and the first step of M synthesis in fungi in which M1PDH has not been detected requires further investigation.

References

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