Mycorrhiza
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ORIGINAL PAPER

Arbuscular mycorrhiza increase artemisinin accumulation in *Artemisia annua* by higher expression of key biosynthesis genes via enhanced jasmonic acid levels

Shantanu Mandal · Shivangi Upadhyay · Saima Wajid · Mauji Ram · Dharam Chand Jain · Ved Pal Singh · Malik Zainul Abdin · Rupam Kapoor

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Abstract It is becoming increasingly evident that the formation of arbuscular mycorrhiza (AM) enhances secondary metabolite production in shoots. Despite mounting evidence, relatively little is known about the underlying mechanisms. This study suggests that increase in artemisinin concentration in *Artemisia annua* colonized by *Rhizophagus intraradices* is due to altered trichome density as well as transcriptional patterns that are mediated via enhanced jasmonic acid (JA) levels. Mycorrhizal (M) plants had higher JA levels in leaf tissue that may be due to induction of an allene oxidase synthase gene (*AOS*), encoding one of the key enzymes for JA production. Non-mycorrhizal (NM) plants were exogenously supplied with a range of methyl jasmonic acid concentrations. When leaves of NM and M plants with similar levels of endogenous JA were compared, these matched closely in terms of shoot trichome density, artemisinin concentration, and transcript profile of artemisinin biosynthesis genes. Mycorrhization increased artemisinin levels by increasing glandular trichome density and transcriptional activation of artemisinin biosynthesis genes. Transcriptional analysis of some rate-limiting enzymes of mevalonate and methyl erythritol phosphate (MEP) pathways revealed that AM increases isoprenoids by induction of the MEP pathway. A decline in artemisinin concentration in shoots of NM and M plants treated with ibuprofen (an inhibitor of JA biosynthesis) further confirmed the implication of JA in the mechanism of artemisinin production.

Keywords Arbuscular mycorrhizal fungi · Jasmonic acid · Trichome density · Artemisinin biosynthesis genes · Methyl erythritol phosphate pathway · Mevalonate pathway

Introduction

There is extensive evidence implying that secondary compounds have a paramount role in various interactions occurring between plants and their natural environment (Bennett and Wallsgrove 1994; Morandi 1996; Dixon 2001; Verpoorte and Memelink 2002; Treutter 2006). The symbiotic interaction between plants and arbuscular mycorrhizal (AM) fungi is influenced by terpenoids (Strack and Fester 2006), especially strigolactones (sesquiterpenoid lactones) derived from apocarotenoids (Akiyama et al. 2005). In the last two decades, quantitative and qualitative changes in terpenoids in the above-ground parts of mycorrhizal (M) plants have been increasingly reported (Kapoor et al. 2002a, b; Copetta et al. 2006; Khaosaad et al. 2006; Rapparini et al. 2008; Mandal et al. 2013). These alterations have usually been associated with higher plant biomass yields and nutritional benefits of mycorrhization (Gupta et al. 2002; Kapoor et al. 2004; Copetta et al. 2006; Khaosaad et al. 2006; Toussaint et al. 2007). There are also studies correlating enhanced terpenoid levels in M plants with greater glandular trichome density and altered hormonal balance (Torelli et al. 2000; Copetta et al. 2006; Kapoor et al. 2007; Moreno-Fortunato and Avato 2008). However, molecular interactions between host plants

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S. Mandal · S. Upadhyay · V. P. Singh · R. Kapoor (✉)
Department of Botany, University of Delhi, Delhi 110007, India
e-mail: kapoor_rupam@yahoo.com

S. Wajid · M. Z. Abdin
Department of Biotechnology, Centre for Transgenic Plant Development, Jamia Hamdard, New Delhi 110062, India

M. Ram · D. C. Jain
Department of Green Technology, Ipca Laboratories Ltd., Ratlam 457002, Madhya Pradesh, India

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Shantanu Mandal
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