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Opposing effects of nitrogen versus phosphorus additions on mycorrhizal fungal abundance along an elevational gradient in tropical montane forests

Q6 Tessa Camenzind^{a, b, *}, Jürgen Homeier^d, Karla Dietrich^c, Stefan Hempel^{a, b},
 Q5 Dietrich Hertel^d, Andreas Krohn^{a, b}, Christoph Leuschner^d, Yvonne Oelmann^c,
 Pål Axel Olsson^e, Juan Pablo Suárez^f, Matthias C. Rillig^{a, b}

^a Institute of Biology, Freie Universität Berlin, Altensteinstr. 6, 14195 Berlin, Germany

^b Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany

^c Geoecology, University of Tübingen, Rümelinstraße 19-23, 72070 Tübingen, Germany

^d Albrecht von Haller Institute of Plant Sciences, University of Göttingen, Untere Karspüle 2, 37073 Göttingen, Germany

^e Department of Biology, Lund University, Box 118, 22100 Lund, Sweden

^f Departamento de Ciencias Naturales, Universidad Técnica Particular de Loja, Loja, Ecuador

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ABSTRACT

Studies in temperate systems provide evidence that the abundance of arbuscular mycorrhizal fungal (AMF) depends on soil nutrient availability, which is mainly explained in the context of resource stoichiometry and differential plant biomass allocation. We applied this concept to an understudied ecosystem – tropical montane forest – analyzing root and AMF abundance along an elevational gradient with decreasing nutrient availability, combined with responses to nitrogen (N) versus phosphorus (P) additions. At three sites from 1000 to 3000 m above sea-level we analyzed fine root length, AMF root colonization as well as extraradical AMF biomass (neutral lipid fatty acid 16:1 ω 5, hyphal length and spore counts) in a nutrient manipulation experiment. We found a significant increase in root length as well as intra- and extra-radical AMF abundance with elevation. Overall, P additions significantly increased, whereas N additions decreased AMF abundance, with differential though nonsystematic changes along the elevational gradient. Strongest effects were clearly observed at the intermediate site. These findings suggest a general dependency of roots and AMF on nutrient availability, though responses to N and P additions differed from previous studies in temperate systems. In the context of future nutrient depositions, results suggest diverging responses of AMF abundance depending on site characteristics.

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1. Introduction

Arbuscular mycorrhizal fungi (AMF) represent an ancient group of plant symbionts, associated with 80% of land plants (Wang and Qiu, 2006). These monophyletic (Glomeromycota) and obligately biotrophic plant symbionts are regarded as keystone mutualists in terrestrial ecosystems (Rillig, 2004) and distributed worldwide across biomes (Treseder and Cross, 2006; Öpik et al., 2010). Beside pathogen protection, improved water uptake and positive effects

on soil structure, the main function of the symbiosis is improved uptake of soil nutrients in exchange for photosynthetic carbon (Smith and Read, 2008). Intraradical structures like coils and arbuscules allow direct plant-fungus nutrient exchange, and a large extraradical mycelium expanding beyond the root depletion zone enables efficient nutrient uptake (Parniske, 2008). Traditionally, AMF have been associated with plant P nutrition (Koide, 1991; Read, 1991), but a growing amount of studies indicates a similarly important role in the uptake of N (Hodge et al., 2010; Veresoglou et al., 2012) and other nutrients (Marschner and Dell, 1994; Lehmann et al., 2014). Consequently, soil fertility affects AMF abundance and occurrence: if carbon costs at high nutrient levels exceed the mycorrhizal benefits, plants may down-regulate AMF

* Corresponding author. Institute of Biology, Freie Universität Berlin, Altensteinstr. 6, 14195 Berlin, Germany. Tel.: +49 30 838 53145; fax: +49 30 838 53886.
 E-mail address: TessaC@zedat.fu-berlin.de (T. Camenzind).

abundance as has been shown experimentally (Carbonnel and Gutjahr, 2014 and citations therein), whereas infertile soil conditions strengthen the reliance on mycorrhizae (Johnson et al., 2015). In this context, the functional equilibrium model, which assumes that plants invest more into structures associated with the acquisition of a limiting resource, predicts that plant allocation is shifted towards belowground structures like roots and mycorrhizae in low fertility soils (Ericsson, 1995; Johnson, 2010), which has been demonstrated repeatedly: Increases in AMF abundance with declining nutrient availability along fertility gradients have been shown experimentally (Abbott et al., 1984; Bolan et al., 1984; Breuillin et al., 2010), but also along natural gradients comparing different sites (Anderson et al., 1984; Bohrer et al., 2001), successional gradients (Zangaro et al., 2014) and chronosequences (Treseder and Vitousek, 2001; Dickie et al., 2013). In contrast, available studies on altitudinal gradients, which are also characterized by decreasing nutrient availability with elevation due to lower temperatures and slow nutrient cycling (Soethe et al., 2008; Unger et al., 2010), report the opposite trend: AMF abundance decreases towards higher altitudes (Read and Haselwandter, 1981; Wu et al., 2004; Kessler et al., 2014), often associated with increased abundance of dark septate endophytes (DSE) or ericoid mycorrhizae, but also non-mycorrhizal plants (Gardes and Dahlberg, 1996; Schmidt et al., 2008; Urcelay et al., 2011). These findings were explained by decreasing temperature in parallel to declining nutrient availability, negatively influencing nutrient use efficiency and the mutual benefit of both partners (Gardes and Dahlberg, 1996; Ruotsalainen et al., 2002; Averill and Finzi, 2011). However, regarding belowground structures in general, a shift in plant investment towards root biomass was indeed observed along several altitudinal transects (Körner and Renhardt, 1987; Girardin et al., 2010; Hertel and Leuschner, 2010). Additionally, multiple observational studies in altitudes up to 5200 m report high AMF root colonization values in certain areas (Schmidt et al., 2008; Liu et al., 2011; Soteris et al., 2015). Thus, patterns in mycorrhizal abundance along elevational gradients might be far more complex and variable depending on transect characteristics.

Effects of soil fertility on AMF abundance can also be tested in nutrient manipulation experiments. In the light of increased nutrient deposition expected in the future due to anthropogenic activities (Galloway et al., 2008; Mahowald et al., 2008; Wilcke et al., 2013), it is important to understand impacts on this crucial symbiotic association. Field studies in temperate areas have revealed a net negative effect of N and/or P additions on AMF abundance (reviewed in Treseder, 2004) in accordance with the functional equilibrium model (Johnson, 2010), though especially the effects of N but also P additions have been shown to be heterogeneous and context dependent (e.g. Johnson et al., 2003; Blanke et al., 2005; Garcia et al., 2008). This divergence has been mainly explained by potential direct nutrient addition effects on AMF by elimination of nutrient deficiencies of the fungus itself (Abbott et al., 1984; Treseder and Allen, 2002) or changes in soil conditions (Dumbrell et al., 2010). Thus, in very low fertility soils the fungus itself might be nutrient-limited and increase in abundance following nutrient additions (Bolan et al., 1984; Treseder and Allen, 2002; Alguacil et al., 2010). Additional complexity is given by the variation of limiting nutrients among sites – mainly N, P or both in terrestrial ecosystems (Elser et al., 2007; Vitousek et al., 2010) – resulting in potential differences in AMF responses to N versus P additions (Eom et al., 1999; Johnson et al., 2003; Blanke et al., 2012). Furthermore, other factors like plant or microbial community changes may directly or indirectly influence AMF abundance (Johnson et al., 2004; Bradley et al., 2006).

In this study, within the framework of a nutrient manipulation experiment in Southern Ecuador (Homeier et al., 2012, 2013), we

examined the effects of N and P additions on extra- and intraradical AMF abundance along an elevational gradient. In tropical rainforests, AMF are known to represent the dominant mycorrhizal type (Torti et al., 1997; Shi et al., 2006; McGuire et al., 2008; Averill et al., 2014), which is also reported for our study area (Kottke et al., 2004; Camenzind and Rillig, 2013). Nonetheless, most of our knowledge on AMF functionality and ecology is based on studies conducted in temperate areas (Alexander and Selosse, 2009). Available data from another nutrient manipulation experiment in the tropics (Hawaii) partly revealed predictable changes in the response of AMF abundance to N and P additions along the tested soil chronosequence, switching from N- to P-limitation (Vitousek et al., 1995), with additional divergence among the intra- and extraradical phases (Treseder and Vitousek, 2001; Treseder and Allen, 2002). In the case of elevational gradients, besides a decline in overall nutrient availability (Soethe et al., 2008; Unger et al., 2010), theory predicts a shift from P limitation at lower altitudes towards N-limited systems at high altitudes according to soil age: P originates primarily from soil weathering, thus, old systems (at lower altitudes) become depleted in P, whereas N enters the system mainly via fixation from the atmosphere and accumulates over time (Walker and Syers, 1976; Tanner et al., 1998). Though this pattern has been confirmed in general (Vitousek et al., 1995; Meir et al., 2001; Fisher et al., 2013), simple ecosystem limitation of a single nutrient (Liebig's law) was also questioned by findings of N/P co-limitations at low and intermediate altitudes (Kaspari et al., 2008; Fisher et al., 2013), as also reported from our study area (Graefe et al., 2010; Homeier et al., 2012), and the potential concomitant influence of other nutrients (Townsend et al., 2008; Wright et al., 2011; Baribault et al., 2012).

We tested the hypotheses that: (1) mycorrhizal abundance (measured as the percentage of root colonization, colonized root length and extraradical AMF abundance) as well as root length will increase with elevation along the elevational gradient concurrently with decreasing soil fertility, though there might be a shift in mycorrhizal types (e.g. towards ecto- or ericoid mycorrhizae); (2) AMF abundance will generally decrease following nutrient additions, as already short-term effects were visible at least for N additions at one altitudinal level (Camenzind et al., 2014); (3) effects of N versus P additions will shift in relation to the previously described gradient of N/P- towards N-limitation with elevation (Graefe et al., 2010; Moser et al., 2011; Wolf et al., 2011; Homeier, 2013).

2. Materials and methods

2.1. Study area

The study sites are located within or adjacent to the Podocarpus National Park in the Cordillera Real, the eastern range of the South Ecuadorian Andes (Beck et al., 2008; Bendix et al., 2013). This area is part of the "Tropical Andes" hotspot of biodiversity (Myers et al., 2000) and characterized by its high number of plant species (Homeier et al., 2008) as well as other organism groups (Brehm et al., 2005; Orme et al., 2005). Samples were taken at three sites along an altitudinal gradient: (1) the 1000 m site with premontane forest (Bombuscaro; 1000–1140 m, 4°11'S, 78°96'W), (2) the 2000 m site with lower montane forest (Reserva San Francisco, 2050–2150 m, 3°98'S, 79°08'W) and (3) the 3000 m site with upper montane forest (Cajanuma; 2880–2960 m, 4°12'S, 79°17'W). Among these sites there is a complete turnover of tree species, with less than five shared species between the 2000 m site and either of the two other sites (Homeier et al., 2013). For details on plant communities see Homeier et al. (2008). The altitudinal gradient is accompanied by an increase in rainfall (2230, 1950 and

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