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Research article

Fungal endophytes associated with roots of nurse cushion species have positive effects on native and invasive beneficiary plants in an alpine ecosystem

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ABSTRACT

Facilitation has been proposed to be a fundamental mechanism for plant coexistence, being particularly important in highly stressful environments such as alpine environments. In this type of environment, species called "cushion plants" can ameliorate the stressful conditions, acting as nurses for other plants. Of the several mechanisms proposed in the positive-interactions framework, plant–microorganism interaction may be one of the most common, but least documented. Here we show that the presence of endophytes isolated from the roots of cushion plants *Laretia acaulis* can play a fundamental role in the establishment, performance and survival of both native and exotic plant seedlings that are known to be facilitated by the cushion species.

To test this, we measured survival and growth of two native and one invasive species at 3200 m in the Andes of Central Chile. Plants were grown inside artificial cushions filled with native soil, with or without sterilization, and with or without fungal endophytic inoculation to evaluate the role of fungal endophytes on survival and growth. In addition, we conducted a second experiment in a greenhouse with the invasive species to evaluate the effect of fungal endophytic infection/association on plant ecophysiological performance, dry biomass and seed output.

Overall, our results showed a strong positive effect of fungal endophytes on the survival and growth of both native and invasive species. Moreover, maximum quantum efficiency (Fv/Fm), biomass accumulation and seed production were enhanced in the invasive species when soils were inoculated with endophytes. Thus, facilitation by root endophytic fungi on native and invasive alpine plants could determine survival and establishment in this harsh environment.

Several studies have shown that direct facilitation by cushion plants in alpine environments improves the performance and fitness of both native and exotic plants. Our results suggest that there are indirect effects, mediated by microorganism associations that may also help to explain the successful establishment of native and invasive species in these environments. If indirect plant–plant facilitation through root fungal endophytes proves to be a widespread phenomenon in alpine ecosystems, it could be a key component in the structuring of plant communities in those stressful environments.

Introduction

Positive interactions have been proposed to be a fundamental mechanism for plant coexistence (Bruno et al., 2003; Callaway, 2007). These positive interactions are especially important in environments where abiotic stress is high, such as alpine environments

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(Callaway et al., 2002; Cavieres et al., 2006, 2013; Anthelme and Dangles, 2012). There is ample evidence that plants in these environments, particularly those with cushion type morphologies, help other species. Cushion plants have been shown to act as nurses for other plants (Callaway et al., 2002; Badano et al., 2002; Cavieres et al., 2008; Reid et al., 2010; Butterfield et al., 2013; Schöb, 2014), having a positive impact on the diversity and productivity of alpine communities (Cavieres and Badano, 2009; Cavieres et al., 2013). Several mechanisms have been proposed to explain the facilitative effect of cushions on the establishment and growth of other plants. Alpine cushion plants can reduce water stress and increase water availability for other plants (Núñez et al., 2009a; Molina-Montenegro et al., 2006; Schöb, 2013), increase nutrient availability (Anthelme and Dangles, 2012; Schöb, 2014), buffer extreme temperatures (Molina-Montenegro et al., 2006; Cavieres et al., 2008) and stabilize otherwise dynamic substrates (Körner, 2003). In general, cushion plants improve the physiological performance of the individuals growing inside of them by developing microsites with better abiotic conditions compared to open areas (Cavieres et al., 2005, 2008; Schöb et al., 2012). However, although these direct mechanisms behind alpine cushion facilitation are well documented, other biotic actors may have powerful effects mediating facilitation in these extreme environments, including ubiquitous soil microorganisms and their interactions with plant species. Soil microorganisms can influence plant performance either positively, e.g., through mycorrhizal associations (van der Heijden and Horton, 2009; Smith and Read, 2010) or root fungal endophyte infection (Rodríguez et al., 2009), or negatively, e.g., through the accumulation of soil pathogens that impair plant establishment (Van der Putten and Peters, 1997; Bever, 2003). Overall, soil biota has a strong influence on plant performance (Rodriguez et al., 2009; Bever et al., 2010), plant community diversity (Wardle et al., 2004; van der Heijden et al., 2008), succession (Kardol et al., 2006; Lozano et al., 2014), plant invasions (Callaway et al., 2008; Meisner et al., 2013) and ecosystem function (Loreau, 2001; van der Heijden et al., 2008; Wagg et al., 2014). This impact of soil biota on plants at different scales strongly suggests that plant–soil interactions may also have an impact on plant competitive abilities and on the outcome of these plant–plant interactions (Bever, 2003; Callaway, 2007; Bever et al., 2010; Van der Putten, 2009; Martínez-García and Pugnaire, 2011; Montesinos-Navarro et al., 2012). Actually, it is well recognized that neighboring plants commonly tend to share mycorrhizal networks (van der Heijden and Horton, 2009). These mycorrhizal networks may have either positive or negative effects on individual plants, and, for example, can play an important role in nurse-seedling facilitation processes, although there are also negative impacts documented (Selosse, 2006; Booth and Hoeksema, 2010; and see review by van der Heijden and Horton, 2009). Moreover, recent studies have shown that soil microbial communities may have an effect on the outcome of plant–plant competitive interactions (Selosse, 2006; Kardol et al., 2007; Pendergast et al., 2013) and may even have an effect on plant–plant facilitation processes (Rodríguez-Echeverría et al., 2013). Overall, evidence of the impacts of soil microorganisms on plant–plant interactions is growing but is still low, particularly under field conditions in alpine environments.

Plants provide a unique ecological niche for diverse communities of belowground mutualistic microorganisms which in turn often provide multiple benefits to plants such as enhanced photosynthesis, higher resource use efficiency, and tolerance to abiotic and biotic stress (Harley and Smith, 1983; Smith and Read, 2010). These symbiotic relationships are common and fundamental for plants in nature (Sapp, 2004). Particularly, the symbiosis between a plant host and the fungal endophytes residing in plant internal tissues is one of the most documented in harsh environments (Harley and Smith, 1983; Rodríguez et al., 2009, 2010; Redman et al., 2011). Root-colonizing endophytic fungi are a highly diverse group (Vandenkoornhuyse et al., 2002) that can exert a wide range of plant host effects, i.e., they have different degrees of virulence or even positive effects (Schulz and Boyle, 2005; Rillig et al., 2014). The endophyte–host relationship is thus described as a continuum ranging from mutualism through commensalism to parasitism (Lewis, 1985; Aly et al., 2011; Rillig et al., 2014). The presence of endophytes in plants can alter food webs, community composition, ecosystem processes, and are important to the structure, function, and health of plant communities (Clay and Holah, 1999; Read, 1999; Aschehoug et al., 2014). Endophytic fungi have also been reported to have direct positive effects on a number of plant species (e.g., Read, 1987; Rodríguez et al., 2009; Vos et al., 2012; Johnson et al., 2012; Aschehoug et al., 2014). They can reduce water stress of the host plant (Ortega et al., 2004; Smith and Read, 2010; Harris-Valle et al., 2009; Atala et al., 2012), contribute to the overall plant nutrition (Kipfer et al., 2011), and have been suggested to help some plants to deal with environmental stresses (Clay and Holah, 1999; Redman et al., 2002). Nevertheless, some carbon is exported from the plant to the fungi (Read, 1987; Harris-Valle et al., 2009), reducing the resources available for plant growth and reproduction. By enhancing or impairing their host plant fitness, endophytic plant symbionts may have profound effects on the ability of host plants to interact with other organisms like pathogens, other plant species and consumers and on its competitive ability (Aschehoug et al., 2014), but analysis of the possible impact of root fungal endophytes on facilitative plant–plant interactions is lacking.

In an alpine ecosystem, Casanova-Katny et al. (2011) showed previously that the abundance of root colonizing fungi was higher in plants growing within cushion species than in open areas. These findings were evidence of a particular spatial distribution of alpine microorganisms, however, they did not disentangle the role of these endophytes in the ecophysiological performance and fitness of alpine species facilitated by cushion species. Overall, there is a paucity of studies analyzing the role of soil biota in explaining the observed positive effects of alpine cushions on other species (but see, Casanova-Katny et al., 2011; Gibert et al., 2012). Thus, our aim in this study was to analyze the effect of local soil endophytical fungi associated with the roots of a cushion nurse species, *Laretia acaulis*, on the establishment and performance of three species known to be facilitated by *L. acaulis*: two native (*Phacelia secunda* and *Hordeum comosum*) and one exotic (*Taraxacum officinale*) species. We hypothesized that the presence of the endophytes found preferentially in cushion plant patches of *L. acaulis* would play a fundamental role in the establishment, performance and survival of both native and exotic seedlings. With this purpose we combined a series of greenhouse and field experiments in an alpine community where we analyzed the survival and biomass of beneficiary species planted within artificial cushions with different soil inocula. We also measured the effect of endophytes associated with roots of the cushion species on the physiological and reproductive response of the exotic beneficiary species.

Methods

Study site

Our study site is located at 3200 m above sea level (a.s.l.) in the Andes mountains in Central Chile (33° S) and close to the Valle Nevado ski complex (33°20′ S 70°16′ W). Central Chile region possesses a Mediterranean-type climate (di Castri and Hajek, 1976), which is characterized by cool rainy winters and long dry summers. During the growing season (November to March) the mean