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Host plant and arbuscular mycorrhizal fungi show contrasting responses to temperature increase: Implications for dioecious plants

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ABSTRACT

Individual plants live in complex environments where they interact with other organisms such as herbivores, pollinators, fungi and pathogens. The influence of rising temperature on biotic interactions has begun to receive attention, and is an important research frontier currently. However, the belowground interactions with organisms such as arbuscular mycorrhizal (AM) fungi have received little attention so far. In this study, we investigated the response of the dioecious plant *Antennaria dioica* and its AM fungi to increased temperature in a controlled environment simulating the period of growth of *A. dioica* in central Finland. Specifically, we evaluated the effect of rising temperature on plant survival, growth, flowering and physiology in plants growing with or without AM fungi. Overall, increased temperature had a positive effect on plant survival, but a negative effect on the growth and flowering compared with the control temperature, while it did not affect the physiological parameters analyzed. Females suffered more of rising temperature in terms of reduced flowering, but a larger proportion of plants survived compared to males. In contrast, the rising temperature had positive effects on the frequency of AM fungal colonization in roots regardless of sex, but sex-specific differences were observed in the amount of extraradical hyphae and the number of spores produced. These findings suggest than the sexes in dioecious species and their associated fungi respond differently to increasing temperature. If rising temperature affects host plants and symbionts in a contrasting way, a potential functional mismatch might appear.

1. Introduction

Global average temperatures have increased 0.2 °C per decade since the 1970s (IPPC, 2007), and the increase is predicted to be most pronounced in cold climate. Global warming has already caused a number of changes in the natural life history of species (reviewed in Walther et al., 2002; Parmesan, 2006). Several studies have quantified the effects of global warming on the phenology and physiology of organisms as well as changes in the abundance and distribution of species (see Parmesan, 2006; Walther, 2010). Thus, direct individual responses to global change have been well characterized. However, species live in complex environments in which they interact with other organisms both above- and belowground, and studies using a more holistic approach are therefore needed. Recently, Gellesch et al. (2013) reviewed the effect of climate change on pairs of interacting organisms. Rising temperature has an effect on interactions independent from the interacting organisms (e.g. plant–plant, plant–herbivore, plant–fungus). Reports document positive (e.g. facilitative neighbor effects on survival, increased growth and reproduction, earlier developing) and negative (e.g. increases in seed predator populations, saprophagous macrofauna, grazing rates) effects (Gellesch et al., 2013). However, few studies deal with belowground interactions even though belowground organisms may alter plant responses to increased temperature (see Kivlin et al., 2013 for a recent review).

Among plant–fungus interactions, arbuscular mycorrhizal (AM) symbioses are the most abundant and widespread. AM fungi are obligate symbionts that colonize the roots of about 74% of angiosperm species and occur in almost all terrestrial ecosystems (Brundrett, 2009). Plants supply their associated AM fungi with carbohydrates that are essential for fungal survival and growth; the fungi may consume up to 30% of plant's carbohydrates (Jakobsen and Rosendahl, 1990; Drigo et al., 2010). In return, AM fungi form extensive networks of hyphae in the soil (extraradical hyphae) that forage for mineral nutrients more efficiently than the roots, and translocate them to their host plant in symbiotic-specific structures that develop inside roots (Smith and Read, 2008). Due

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to the improved nutrient acquisition, mycorrhizal symbiosis often increases plant growth and fitness, and mycorrhizal plants are better able to tolerate abiotic and biotic stresses than non-mycorrhizal plants (Smith and Read, 2008). In general, AM fungi seem to be cost-efficient for the host, and host plant may detect and preferentially reward the "best" fungal partners with more carbohydrates, and in turn, the fungal partners can increase the translocation of soil nutrients to their host plant (Kiers et al., 2011). It has been suggested that the benefit of a plant associating with fungal symbionts depends on the symbiont's identity (Johnson et al., 1997), the fungal colonization frequency (Vannette and Hunter, 2011), and biotic (e.g. herbivory, Gehring and Bennett, 2009) and abiotic (e.g. drought, salinity, Miransari, 2010) factors.

Temperature is a critical ecological factor for most biological processes and understanding the effects of global warming is therefore crucial. Rising temperatures not only directly alter the physiology and performance of plants, but it may also affect plants indirectly via their fungal symbionts (Staddon et al., 2002; Kivlin et al., 2013). Studies addressing AM symbioses have shown that high temperatures (around 15–25 °C) have generally positive effects on both plant and fungal performance, with variation among the hosts and fungal species involved. For example, in plants, greater germination percentage, larger biomass and shoot nitrogen and phosphorus concentration have been documented in response to higher temperatures (e.g. Ruotsalainen and Kytöviita, 2004; Kytöviita and Ruotsalainen, 2007; Gavito and Azcón-Aguilar, 2012). In AM fungi, greater frequency of colonization inside roots (Staddon et al., 2002; Heinemeyer and Fitter, 2004; Kytöviita and Ruotsalainen, 2007; Gavito and Azcón-Aguilar, 2012) and more prolific extraradical hyphae (Heinemeyer and Fitter, 2004; Gavito et al., 2005; Gavito and Azcón-Aguilar, 2012) have been observed at higher temperature. Both plants and fungi usually benefit from rising temperatures even though their benefit may be asymmetric. For instance, Kytöviita and Ruotsalainen (2007) showed that an increase in temperature may benefit the AM fungus an order of magnitude more than the host plants.

In dioecious plants, where the female and male sexual functions are in separate individuals, sexes often allocate different amounts of resources to growth, defense and reproduction (Geber et al., 1999; Obeso, 2002), and females usually show higher proportional investment into reproduction than males (Obeso, 2002). Over evolutionary time, this mode of resource allocation could lead to differences in morphology, physiology, life history traits (Geber et al., 1999), and intensity of biotic interactions (reviewed in Vega-Frutis et al., 2013a) between females and males of the same species. Few studies have evaluated if the relationship between dioecious plants and AM fungi is sex-specific (reviewed in Varga, 2010; Vega-Frutis et al., 2013a), and even fewer studies have examined how abiotic factors shape this relationship (but see Varga and Kytöviita, 2008, 2010 for the effects of drought and soil pH). The limited evidence suggests that females tend to have higher frequency of root AM colonization, and to obtain higher benefit from AM in terms of growth and reproduction compared to males (reviewed in Varga, 2010; Vega-Frutis et al., 2013a). Nevertheless, the opposite pattern in colonization frequency (Gehring and Whitham, 1992), or no differences between sexes have also been reported (Varga and Kytöviita, 2008, 2011, 2012). Given the crucial role of temperature, the next logical step is to evaluate the effect of rising temperature on the sex-specific symbiotic relationship between plants and AM fungi. It has been shown that in dioecious species females are more responsive and suffer more from elevated temperatures than males (Wang, 2007; Xu et al., 2008; Tognetti, 2012), but the effect for the AM fungal partner or dioecious plants in symbiosis with AM fungi has never been examined.

In the present study, we evaluated the performance of the dioecious herb *Antennaria dioica* in response to AM fungal inoculation under three different temperatures simulating the period of growth of *A. dioica* in central Finland. We chose *A. dioica* because it is declining in abundance in Fennoscandia (Öster and Eriksson, 2007), and is red listed in Finland (Kalliovirta et al., 2010), most likely because of the change in land use practices and soil acidification (Öster and Eriksson, 2007; van den Berg et al., 2008). In addition, it is a dioecious species, and global climate change may differently impact the capacity of female and male plants to reproduce successfully, with consequences for demography, evolution and long-term persistence of populations. Our aim was to quantify the effect of temperature on both the plant and the AM fungal performance, focusing on potential differences between females and males. Therefore, we examined plant growth, reproduction, and chlorophyll fluorescence as a proxy of plant photosynthetic capacity in *A. dioica* plants grown with or without AM fungi. We also evaluated the effect of temperature on the intraradical fungal structures (hyphae, vesicles and arbuscules), length of extraradical AM hyphae, and the number of spores produced. Because female plants generally obtain a greater benefit of AM fungi, but also suffer more from abiotic stress than males, our specific research hypotheses were: (1) both plants and AM fungi will have better performance at higher temperatures, but males will benefit more from warmer temperatures than females, (2) both sexes will benefit from AM symbiosis, but the benefit will be different between sexes and larger at higher temperatures, and (3) the performance of the AM fungi will also depend on the sex of the host plant and be greater at warmer temperatures.

2. Materials and methods

2.1. Study species

Antennaria dioica (L.) Gaertn (Asteraceae) is a dioecious, perennial and clonal herb that grows in nutrient-poor habitats such as heaths, dry grassland, sandy or stony places and forest margins. It is widely distributed in temperate to Arctic regions of the northern hemisphere (Tutin et al., 1976). Each individual plant (genet) can produce one to several propagules (ramets) by clonal growth of surface crawling stolons, and generally the ramets produce one flowering shoot when flowering. Female and male plants exhibit secondary sexual dimorphism: males produce more flowering shoots and inflorescences which are also heavier than those of females, even though there is variation among years and populations (Varga and Kytöviita, 2011). In Finland, flowering occurs between June and July and the frequency of reproduction is similar between sexes (Varga and Kytöviita, 2011). *Antennaria dioca* is pollinated by generalist insects (Willis and Burkill, 1903) and produces small seeds that are easily dispersed by wind (Eriksson, 1997). In addition, both sexes have been reported as mycotrophic in the field (Varga and Kytöviita, 2011, 2012; Vega-Frutis et al., 2013b), with female-biased sex ratios and without spatial segregation of the sexes (Öster and Eriksson, 2007; Varga and Kytöviita, 2011).

2.2. Experimental design

2.2.1. Plant and fungal material

In August 2011, 20 female and 20 male plants (i.e. 40 different genotypes) were collected in central Finland (62° 3′ 10″ N, 25° 32′ 48″ E). Each genotype was divided in several clonal fragments (ramets) which were propagated in individual pots filled with sterilized sand under greenhouse conditions at the University of Jyväskylä, Finland. This was done in order to replicate each individual genotype into the six different treatments (see below).