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Aspen-associated mycorrhizal fungal production and respiration as a function of changing CO_2, O_3 and climatic variables

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ABSTRACT

The relationships of mycorrhizal fungal respiration and productivity to climate and atmospheric chemistry remain under characterized. We quantified mycorrhizal sporocarp and hyphal respiration, as well as growing season net hyphal production, under ambient and elevated carbon dioxide (CO_2) and ozone (O_3) in relation to natural temperature and moisture variation. Hyphal respiration did not respond significantly to elevated CO_2 and O_3. Sporocarp respiration was affected by temperature and moisture content while hyphal respiratory response to temperature was undetected over the narrower range of soil temperatures captured. Hyphal respiration comprised 31 % of soil respiration, and the ratio of hyphal respiration to soil respiration declined with elevated CO_2. Hyphal biomass was reduced under all treatments though not statistically significant. Given the large fraction of soil respiration represented by mycorrhizal fungi and its sensitivity to climate, a small change in fungal respiration could strongly affect carbon budgets and cycling under climate change.

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Introduction

Understanding the regulators of soil respiration is critical for our ability to model ecosystem carbon (C) cycling within a global change context. Although traditionally not executed, the components of soil respiration should be partitioned into autotrophic and heterotrophic sources, with the latter encompassing organisms directly associated with autotrophs (such as rhizosphere-associated organisms, including mycorrhizal fungi) as well as free-living heterotrophic organisms (such as saprotrophs). Partitioning the heterotrophic and autotrophic components of soil respiration in field studies can be quite challenging (Ekblad et al., 2013; Hanson et al., 2000; Heinemeyer et al., 2011), with the fungal component of soil respiration rarely quantified (but see Heinemeyer et al., 2007; Heinemeyer et al., 2012).

Fungal respiration by different tissue types (e.g., hypha, mycorrhiza and sporocarp) is even less quantified, even though mycorrhizal fungi comprise a significant portion of microbial biomass within forest soils (Cairney, 2012; Ekblad et al., 2013; Högberg and Högberg, 2002; Wallander et al., 2001). Net primary production (NPP) allocated to the fungal components of mycorrhizal fungi ranges from less than 5 % to, more commonly, around 20 % (Hobbie, 2006; Smith and Read, 2008 and references within). Considering that 27–67 % of NPP is partitioned as belowground NPP (BNPP) (Hobbie, 2006), mycorrhizal fungi clearly represent a large fraction of BNPP. Hence, their growth and activities should represent a significant source of CO_2 flux from ecosystems.

Atmospheric change, whether physical or chemical, can affect carbon cycling by altering production, storage, allocation, or respiration (Comstedt et al., 2006; Karnosky, 2003; Karnosky et al., 2005; King et al., 2001; Loya et al., 2003; Miller and Fitzsimmons, 2011; Podila et al., 2011; Pregitzer et al., 2008; Schlesinger and Lichter, 2001). If elevated levels of CO_2 or O_3 influence how primary producers gain and allocate photosynthate to belowground structures, including the supply of carbon to their fungal symbionts, then the end result could be a change in ecosystem C storage. While increased CO_2 typically amplifies NPP, O_3 acts in an opposing manner and will, at least initially, dampen such effects (Karnosky et al., 2003). Studies of enhanced CO_2 and O_3 concentrations within Free-Air Carbon dioxide Enrichment (FACE) systems have already found effects on mycorrhizal fungi, especially at the community level and in the production of sporocarps (Andrew and Lilleskov, 2009; Parrent et al., 2006; Parrent and Vilgalys, 2007; Podila et al., 2011). Consequently, any change in mycelial production and respiration due to altered CO_2 or O_3 concentrations could affect future soil C sequestration (Alberton et al., 2005; Andersen, 2003; Fransson, 2012; Pickles et al., 2012; Rygiewicz and Andersen, 1994; Treseder and Allen, 2000; Schlesinger and Andrews, 2000) as well as the retention of fungal derived C in the soil.

It is important to note that respiration rates are strongly affected by both temperature and moisture (Heinemeyer et al., 2007, 2012; Koch et al., 2007; López-Gutiérrez et al., 2008; Malcolm et al., 2008). While the effect of temperature is broadly captured in Q10 values, reviews of soil respiration literature have indicated that Q10 values are not constant with changing temperature. This limits the conceptual adequacy of a single Q10 for modeling respiration (Davidson et al., 2006; Lloyd and Taylor, 1994). A variety of factors, such as biochemical reaction rates, physiological acclimation, substrate limitation, thermal stress and moisture stress can alter temperature respiration relationships (Davidson et al., 2006). Although much effort has been applied to characterizing temperature–respiration relationships of soils (Boone et al., 1998; Davidson et al., 2006; Kätterer et al., 1998; Lloyd and Taylor, 1994; Winkler et al., 1996), much less has been applied to field studies of fungal temperature–respiration relationships.

Water availability additionally affects soil respiration and can confound estimates of temperature effects (Davidson et al., 2006). Surprisingly, very little is known about moisture impacts on field respiration rates of fungi, although they appear to be physiologically active, albeit at very low rates, at lower water potentials than bacteria (Wilson and Griffin, 1975). It is important to quantify field respiration rates in order to better understand how site variables, such as temperature and moisture, can interact to affect fungal contributions to ecosystem respiration.

The objectives of this study were to: (1) quantify the effects of changes in atmospheric carbon dioxide (CO_2) and ozone (O_3) concentrations on mycorrhizal fungal sporocarp and hyphal respiration *in vivo*; while (2) simultaneously quantifying the effect of natural variation in temperature and water availability on fungal respiration; and to (3) determine treatment effects on net hyphal biomass production. We hypothesized that: (1) fungal respiration would increase under elevated CO_2 and decrease under elevated O_3; (2) fungal respiration would increase under higher temperatures, and decrease as a result of lower water availability; and (3) high CO_2 treatments would increase hyphal biomass production, and elevated O_3 would decrease hyphal biomass production.

Materials and methods

Study area

The Aspen FACE study began in 1997 with the trees planted from seedling stage. It was located on the Harshaw Experimental Farm of the USDA Forest Service, Wisconsin, USA (45° 40′ 48″ N, 89° 37′ 48″ W). The climate is cool continental with summer temperatures averaging 18.3 °C and an average of 106.7 mm of precipitation falling per month from Jul. to Sep.. Prior to the implementation of a forestry research site in the early 1970's, the land was a potato farm. Hybrid poplar and larch trees were grown until development of the FACE study design. Properties of the sandy loam soil graded along a north-south gradient. This was accounted for by incorporating a blocking design (Dickson et al., 2000). Soil carbon content averaged 1.7 % in 2008 (Andrew & Lilleskov, unpublished).

The study had a randomized complete block design with two factors, CO_2 and O_3, at two levels, leading to the following treatment combinations: ambient, elevated CO_2, elevated O_3, and the combination of elevated CO_2 + O_3. These four combinations were replicated in three blocks. Carbon dioxide fumigation levels were fixed at ambient (which increased from 360 to

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