



Short-term utilization of carbon by the soil microbial community under future climatic conditions in a temperate heathland



Sabine Reinsch^{a,*}, Anders Michelsen^b, Zsuzsa Sárossy^a, Helge Egsgaard^a, Inger Kappel Schmidt^c, Iver Jakobsen^a, Per Ambus^a

^a Department of Chemical and Biochemical Engineering, Technical University of Denmark, 2800 Kgs. Lyngby, Denmark

^b Department of Biology, University of Copenhagen, Universitetsparken 15, 2100 Copenhagen Ø, Denmark

^c Department of Geosciences and Natural Resource Management, University of Copenhagen, Rolighedsvej 23, 1958 Frederiksberg, Denmark

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ABSTRACT

An *in-situ* ¹³C pulse-labeling experiment was carried out in a temperate heath/grassland to study the impacts of elevated CO₂ concentration (510 ppm), prolonged summer droughts (annual exclusion of 7.6 ± 0.8%) and increased temperature (~1 °C) on belowground carbon (C) utilization. Recently assimilated C (¹³C from the pulse-label) was traced into roots, soil and microbial biomass 1, 2 and 8 days after pulse-labeling. The importance of the microbial community in C utilization was investigated using ¹³C enrichment patterns in different microbial functional groups on the basis of phospholipid fatty acid (PLFA) biomarker profiles. Climate treatments did not affect microbial abundance in soil or rhizosphere fractions in terms of total PLFA-C concentration. Elevated CO₂ significantly reduced the abundance of gram-negative bacteria (17:0cy), but did not affect the abundance of decomposers (fungi and actinomycetes) in rhizosphere fractions. Drought favored the bacterial community in rhizosphere fractions whereas increased temperature reduced the abundance of gram-negative bacteria (19:0cy) and changed the actinomycetes community (10Me16:0, 10Me18:0). Fastest and highest utilization of recently assimilated C was observed in rhizosphere associated gram-negative bacteria followed by gram-positive bacteria. Utilization of recently assimilated C by rhizosphere associated actinomycetes and fungi was relatively low, but much more pronounced in the soil. The utilization of recently assimilated C by the microbial community was faster under elevated CO₂ conditions compared to ambient. We conclude that changing climatic conditions will affect C utilization by the soil microbial community but might not drastically change the terrestrial C balance.

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1. Introduction

Atmospheric carbon dioxide (CO₂) concentration, temperature and water availability are critical determinants of the terrestrial carbon (C) turnover. Increasing atmospheric CO₂ concentration exerts a positive feedback on CO₂ concentration and global warming (IPCC 2007). Warming often increases soil CO₂ efflux by e.g. extending plant growth periods (Luo, 2007), stimulating microbial activity and can lead to reduced soil C residence times (Amundson, 2001; Heimann and Reichstein, 2008). Temperature increase can turn low productive environments into physiologically active systems (Miller and Smith, 2012), but can also negatively

affect water availability leading to reduced gross primary production and soil C loss (Ciais et al., 2005).

Rising CO₂ concentration has been observed to have pronounced effects on terrestrial C turnover. Plant C uptake can be increased under elevated CO₂ concentration (Ainsworth and Long, 2005; Albert et al., 2011) leading to increased aboveground and belowground biomass and can result in litter increased in lignin content and/or higher C:N ratios (Ball, 1997; Henry et al., 2005). Increased root growth can be stimulated by elevated CO₂ concentration (Arndal et al., 2013) leading to increased rhizodeposition into the soil matrix (Jones et al., 2009). These plant mediated changes in the rhizosphere may change the microbial community towards a decomposer based community: increased lignin content in litter demands lignin degrading enzymes produced by microorganisms (Couteaux et al., 1995) and increased root growth and rhizodeposition potentially increases plant-microbe nutrient competition and induces soil organic matter priming mediated by

* Corresponding author. Tel.: +45 21 32 53 80.

E-mail address: sare@kt.dtu.dk (S. Reinsch).

decomposers (Paterson et al., 2008). However, effects of elevated CO₂ concentration on the soil microbial community differ across ecosystems (Dunbar et al., 2012): increased CO₂ concentration led to a fungal dominated community compared to ambient soils in the Mojave desert (Jin and Evans, 2010). Furthermore, the soil microbial community in a temperate grassland exposed to elevated CO₂ concentration showed increased arbuscular mycorrhizal fungi abundance but an overall decreased fungal activity (Denef et al., 2007). Interestingly, elevated CO₂ stimulated the microbial community in a temperate grassland (Sowerby et al., 2000; Drissner et al., 2007) but the soil C stock remained unchanged (Theis et al., 2007).

Extensive drought periods can reduce overall ecosystem activity, resulting in reduced rhizodeposition and lower microbial activity due to water limitation (Jensen et al., 2003). Low soil water content is a stress factor for soil organisms. However, fungi might be better adapted to limited water availability because their hyphal network facilitates water transport (Augé, 2001). In contrast, warming, if not imposing water limiting conditions, is expected to enhance bacterial abundance, but less fungal appearance (Frey et al., 2008). In general, longer-term effects of increased temperatures and water availability on the composition and activity of microbial communities are sparsely reported and often inconsistent. The fungal-to-bacterial ratio increased under warmed conditions in a tallgrass prairie (Zhang et al., 2005), and 12 years warming of a forest soil reduced fungal abundance, but stimulated gram-positive bacteria (Frey et al., 2008). In contrast, warming did not affect the microbial community composition in a temperate mountain forest (Schindlbacher et al., 2011). The combination of increased temperature with elevated CO₂ concentration and two levels of precipitation in an American old-field grassland revealed the potential of anticipated future temperatures to increase the abundance of gram-positive bacteria, whereas the abundances of gram-negative bacteria, arbuscular mycorrhizal and saprophytic fungi were decreased (Gray et al., 2011). In the same study, precipitation affected the soil microbial community only in combination with a temperature treatment. One year later, however, precipitation was the main predictor for changes in the microbial community (Castro et al., 2010) illustrating the need for detailed investigations of climate change effects on the soil microbial community over time.

Phospholipid fatty acid (PLFA) extraction has frequently been used to assess the microbial community composition in soils and has been proven to be an appropriate method to investigate environmental effects on the soil microbial community (Frostegård et al., 1993, 2011). PLFAs combined with stable C isotope analysis can additionally be used to investigate the metabolic activity of microbial functional groups (Treonis et al., 2004; Denef et al., 2007). Sequential measurements of microbial ¹³C incorporation after a ¹³CO₂ pulse facilitate the tracing of recently assimilated C through the microbial community to evaluate not only the abundance, but also the importance of each microbial functional group in terrestrial short-term C turnover (Jin and Evans, 2010). The microbial activity is important because functional redundancy in microbial communities complicates the investigation of the importance of microbial groups on the basis of community diversity and abundance only (Nannipieri et al., 2003).

In the present study, *in-situ* ¹³CO₂ pulse-labeling was performed in a temperate heath/grassland to investigate climate impacts on the utilization of recently assimilated C by the microbial community. Soil microbial functional groups were identified by phospholipid fatty acid (PLFA) abundances and isotopic PLFA characteristics were related to microbial activity associated with turnover of recently assimilated C. The experiment comprised the climate treatments: ambient and elevated CO₂ concentrations, summer

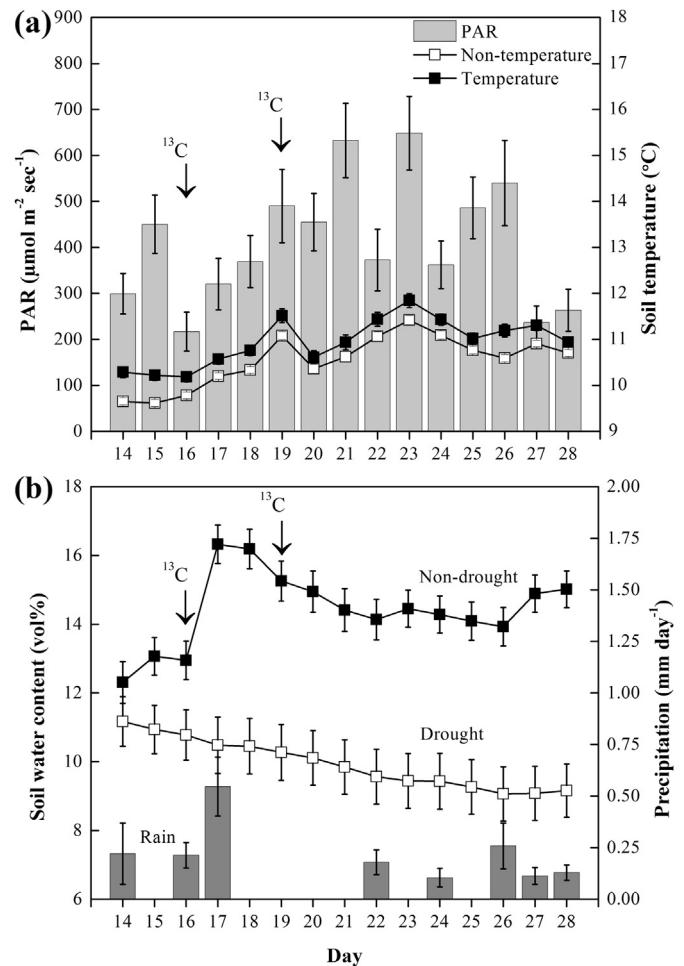


Fig. 1. Soil and environmental conditions during the time of the experiment in May 2011. Arrows indicate the pulse-labeling events. (a) averaged daily photosynthetic active radiation (PAR, bars) and soil temperature at five cm depth in plots with ambient temperature (open symbols) and elevated temperature (solid symbols); (b) daily precipitation (bars) and volumetric soil water contents (0–20 cm depth) in plots without drought treatment (open symbols) and drought-treated plots (solid symbols).

drought and increased temperature. The full factorial treatment reflects the anticipated climatic conditions for Denmark in 2075. We hypothesize that (i) elevated CO₂ favors a fungal-based community, (ii) increased temperature leads to a bacterial-based community, (iii) prolonged drought increases the fungal abundance, (iv) C turnover is faster under elevated than ambient CO₂ concentration and (v) C utilization by the microbial community is similar between ambient and future climatic conditions due to the balance of positively acting (elevated CO₂, temperature) and negatively acting (drought) climate factors.

2. Methods

2.1. Study site

The study site was an unmanaged dry heath/grassland in North Zealand, Denmark (55°53' N, 11°58' E) situated in a hilly area characterized by sandy, nutrient-poor glacial deposits composed of ~70% sand, ~20% coarse sand and minor proportions of silt and clay. The climate is temperate with a mean annual temperature of 8 °C and a mean annual precipitation of ~610 mm. The plant community was co-dominated by the grass *Deschampsia flexuosa* (~70%) and the dwarf shrub *Calluna vulgaris* (~30%), and minor

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