



Labile, recalcitrant, microbial carbon and nitrogen and the microbial community composition at two *Abies faxoniana* forest elevations under elevated temperatures



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ABSTRACT

We investigated the interactions of altitude and artificial warming on the soil microbial community structure in a subalpine *Abies faxoniana* forest in southwestern China after four years of warming. Open top chambers (OTCs) at two elevations (3000 m and 3500 m) were established, and their soil microbial characteristics, organic carbon (C) and nitrogen (N) were measured. The microbial community structure was quantified by phospholipid fatty acid (PLFA) analysis. A two-step sulfuric acid hydrolysis was used to quantify the labile and recalcitrant C fractions in the soil organic matter. The results showed that bacterial PLFAs and gram-negative bacterial PLFAs increased and the fungal PLFAs and the fungi/bacteria ratio decreased with warming at the high altitude. By contrast, the warming effects on those parameters at low altitude were small. The higher proportion of labile easily decomposable soil C may explain the different responses of the microbial community composition at the two altitudes. An RDA analysis confirmed that the variations in the soil community structure were significantly associated with soil organic matter properties such as the sizes of the soil labile N pool (LP-N), the recalcitrant N pool (RP-N), and the labile C pool as well as dissolved organic C (DOC) and dissolved organic N concentrations (DON). Our results also showed that labile C and N pools increased with the altitude, but the microbial biomass C as measured with chloroform fumigation techniques decreased. Warming increased only the recalcitrant C pools at the high altitude. Given the longer mean residence time for recalcitrant C and the much greater size of this soil organic carbon pool, the results indicated that a rise in temperature in our case increased soil C pools at higher altitudes, at least during the early stages of experimental soil warming. Warming could also cause changes in the composition of the microbial community and enzyme activities, consequently leading to functional changes in soil ecosystem processes at the high altitude.

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1. Introduction

Mountain forest soils occur under colder climate conditions than lowland soils. Because of the cold climate, highland soils have slower rates of decomposition and consequently longer carbon turnover times than lowland soils. However, even small changes in the soil carbon in subalpine areas might lead to large changes in

CO₂ emissions, because mountain forest soils store large amounts of labile carbon (Belay-Tedla et al., 2009; Sjögersten et al., 2011). The carbon stocks in the mountain areas are important; for example, soil organic carbon storage at the 0–80 cm depth ranges from 163.8 to 256.4 t/ha in our research area, namely the subalpine region of southwestern China dominated by *Abies faxoniana* (Zhang et al., 2013). Moreover, in mountain areas, the temperature decreases with increasing altitude. The dramatic environmental gradients that occur over short distances in mountain regions make altitude a good proxy for understanding both the dynamic and steady-state response of ecosystems to climate change studies. In

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addition, because the soils at the high elevation are exposed to harsher environmental conditions, microbial communities at the high altitude may have a different response to warming when compared with those in low-elevation areas. Although the altitudinal effects on different pools of soil carbon and the microbial community composition have been considered previously (Fierer et al., 2011; Singh et al., 2014), less attention has been paid to the combined effect of warming and altitude on the structure of soil microbial communities and biogeochemical processes.

Soil organic carbon (SOC) can be chemically divided into different pools with different chemical and physical characteristics, but separating the pools is still difficult (Schmidt et al., 2011). The sizes of the pools are often used as measures of soil organic matter quality. Labile carbon pools have a rapid turnover from weeks to years and can be easily mineralized. Labile carbon and nitrogen pools including inorganic nitrogen, microbial biomass carbon and nitrogen (SMB-C and SMB-N) represent an important component in the biogeochemical cycles of ecosystems. Carbon in recalcitrant pools has a lifetime of decades or even centuries and is considered a more stable carbon stock (Rovira and Vallejo, 2002; Cheng et al., 2007). The labile carbon in the soil is reportedly more sensitive to changes in moisture, temperature and plant species than recalcitrant carbon (Neff et al., 2002). Therefore, it is likely that the effects of warming on the relative sizes of the different carbon pools differ.

The soil microbial community and specific microbial processes, such as extracellular enzyme activities, play key roles in nutrient cycling and organic matter degradation (Xu et al., 2010a). Numerous studies have reported that climate change significantly affects microbial composition and microbial biomass (Staddon et al., 2003; He et al., 2009), soil enzyme activities and soil physiological profiles (Zhou et al., 2012). Nevertheless, the responses of the soil microbial community to warming are mixed (Staddon et al., 2003; Biasi et al., 2008). Soil warming may lead to higher (Belay-Tedla et al., 2009), lower (Frey et al., 2008) or unvarying (Biasi et al., 2008) microbial biomass. However, the effect of soil temperatures on microbial community composition is more complex. Decreases in total bacteria or fungi, increases in bacteria or fungi, or no significant changes in the microbial community composition were observed under warming in different experiments (Vanhala et al., 2011; Schindlbacher et al., 2011). We do not have a good understanding of whether the contradictory results are caused by differences in the ecosystem type, temperature or other factors. The different functional groups of microorganisms use different soil substrates (Berg and McLaugherty, 2008). For example, there is a general understanding that bacteria are mostly considered responsible for using easily available substrates (Moore-Kucera and Dick, 2008), and fungi are often able to process recalcitrant carbon as well as nitrogen-poor substrates (Otten et al., 2001). We still lack a clear understanding of how the combined effects of altitude and warming will affect the soil microbial community and in turn, how changes in the community structure will feed back into carbon cycling dynamics (Zhao et al., 2009).

Under climate change, it is predicted that the mountainous areas in the Tibetan Plateau region will experience a higher-than-average increase in surface temperatures in the future (Giorgi et al., 2001). The western slopes of the region are dominated by *A. faxoniana* over a large range of altitudes (Wang, 2004). A relatively simple plant community structure and a long cold season followed by a short growing season are characteristic features of this subalpine coniferous forest ecosystem. Experiments have been performed in this area to examine the impacts of short-term warming on plant growth (Ran et al., 2013), but the influence of warming on soil carbon fractions and the soil microbial community structure has not been well characterized. In the present study, we investigated the warming effects of open top chamber on soil

microbial biomass and microbial community composition in the rhizosphere soil of *A. faxoniana* at two elevations (3000 m and 3500 m) continuously over four years. Moreover, we evaluated the relative contributions of different microbial groups to the decomposition of different substrates on the basis of the causality between these factors. Specifically, we tested the following hypotheses: (1) Warming and altitude decrease the amount of labile SOC and enzyme activity because warmer ecosystems are substrate-limited and cool ecosystems are temperature-limited; (2) Warming and altitude alter the composition of soil microbial communities, and the ratio of fungi/bacteria decreases with warming (Rinnan et al., 2007; Frey et al., 2008) but increases with altitude; (3) the effects of warming on the soil microbial community and soil processes vary between altitudes because of differences in the quantity and quality of litter from changes in the productivity of the ground vegetation as well as differences in microclimatic conditions; and (4) changes in the soil microbial community composition are correlated with the changes in carbon and nitrogen availability that are induced by warming and altitude.

2. Materials and methods

2.1. Experimental site and design

The study area is located in a National Nature Reserve in Pingwu County of western Sichuan, southwestern China (32°49′–33°02′N, 103°55′–104°10′E). The mean annual temperature is 2.5–2.9 °C, the mean yearly maximum and minimum temperatures are 26.2 °C and –17.8 °C, respectively, and the mean annual precipitation is 801–825 mm. Rainfall primarily occurs from May to October. Mountain slopes are dominated by *A. faxoniana*; the stands are composed of 70–90% *A. faxoniana*. The *A. faxoniana* tree heights can reach up to 30 m or more, and they are sparsely distributed without forming a closed canopy. Common species in the shrub layer are *Fargesia denudate*, *Rhododendron lapponicum*, *Lonicera* spp., *Ribes alpestre*, *Rosa* spp. and *Smilax china* L. The shrub layer changes with the altitude. A moss carpet consisting of *Hylocomium splendens* and *Pleurozium* sp. is well developed but varies in its thickness and coverage. From the low altitude at 3000 m to the high altitude at 3500 m, the mean thickness of the soil profile above the unaltered C horizon is approximately 30 cm. The mean topsoil (20 cm depth) total C is 58–67 g kg soil⁻¹, the total N is 4.05–6.18 g kg soil⁻¹, the total P is 0.76–1.06 g kg soil⁻¹, and the total K is 15.93–18.61 g kg soil⁻¹. The average pH is 5.87 ± 0.36, and the soil bulk density is 0.91 g cm⁻³. Initial samples that were taken in 2007 to characterize the plots of the same dimensions before the experimental warming showed that the open top chambers (OTCs) compared with the control locations were not initially different in terms of their soil microbial C, soil microbial N and soil organic C, and N pools (Table 1). Thus, all the treatment differences measured in our study were caused by the OTCs, rather than by preexisting soil heterogeneity. The soil particle size composition was 17% clay (<0.002 mm), 66% silt (0.05–0.002 mm), and 17% sand (0.05–2 mm). The experiment was conducted by employing a comparative trial design at average elevations of 3000 ± 50 and 3500 ± 50 m above sea level with typical spodosol coniferous forest soil (USDA soil taxonomy). The dominant canopy trees for both altitude plots are *A. faxoniana*. The high altitude plots have a stand density of 483 trees ha⁻¹, a canopy density of 0.65, an average height of 3.9 m and an average DBH of 4.5 cm, and the low altitude plots have a stand density of 650 trees ha⁻¹, a canopy density of 0.75, an average height of 18.0 m and an average DBH of 40 cm. OTCs were constructed around naturally established *A. faxoniana* saplings at each altitude with similar forest canopies, and they were established on slopes (30–40° steepness) facing from north to east.

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