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Canopy gaps accelerate soil organic carbon retention by soil microbial biomass in the organic horizon in a subalpine fir forest

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ABSTRACT

Canopy gaps are a key component of the disturbance regime and old-growth character in subalpine coniferous forests. Despite the importance of canopy gaps in the dynamics and management of subalpine forests, limited information is available on the temporal dynamics of microbial pools and their roles in the responses of soil organic matter and nutrient flux to canopy gaps. This study tests the hypothesis that gap creation facilitates soil organic carbon (C) retention by soil microbial biomass in the organic horizon. Based on the degree of decomposition, the organic horizon can be divided into fresh litter layer (LL), fragmented litter layer (FL) and humified litter layer (HL) components; these layers represent different stages of litter decomposition. We examined the microbial biomass carbon (MBC), microbial biomass nitrogen (MBN) and microbial biomass phosphorus (MBP) from the gap center to closed canopy in a subalpine Minjiang fir (*Abies faxoniana*) forest during different seasons. Gap creation promoted soil organic C retention by soil microbial biomass in the organic horizon. Storage of total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP) accumulated in the HL. Moreover, gap creation accelerated C, nitrogen (N) and phosphorus (P) releases from the LL but inhibited C, N and P outputs from the HL. Microbial biomass in the LL responded rapidly and sensitively to canopy gaps. The most important factors affecting microbial biomass in the organic horizon were soil temperature and snow cover, which are governed by the canopy gap. Microbial pools and their stoichiometry were significantly and positively correlated with TOC. A thorough comprehension of the spatio-temporal traits of microbial biomass pools in the organic horizon under gap creation could aid the regeneration of protected subalpine fir forest on the eastern Tibetan Plateau.

1. Introduction

Canopy gaps are small openings that form in the canopy of various forest types following the injury or death of one or more canopy trees; they generally occupy < 0.1 ha in area (Yamamoto, 2000). Canopy gaps are a key component of the disturbance regime and old-growth character of subalpine coniferous forest in the upper reaches of Yangtze River (Taylor and Zisheng, 1988). According to gap dynamics theory (Yamamoto, 2000), mature forest communities are composed of a "mosaic" of patches at different stages of successional and compositional maturity. By increasing environmental heterogeneity and altering the distributions of abiotic and biotic resources, canopy gaps affect not only aboveground ecological process but also forest floor and belowground processes (Zhang and Zak, 1995; Bach et al., 2010; Wu et al., 2014). Consequently, gaps must be considered when examining ecological processes in old-growth forests.

The organic horizon is recognised as an important source of carbon (C) and nutrients for plants and plays an important role in maintaining forest productivity (Grayston and Prescott, 2005). According to the degree of litter decomposition (Takeda, 1988; Feng et al., 2006), the organic horizon can be divided into different components: of a fresh litter layer (LL), a fragmented litter layer (FL), and a humified litter layer (HL). The decomposition of leaf litter always starts with a high concentration of organic C, which decreases as the leaf material is incorporated into the FL and HL as well as the mineral soil layer (Grüneberg et al., 2013; Xu et al., 2014). The organic horizon plays

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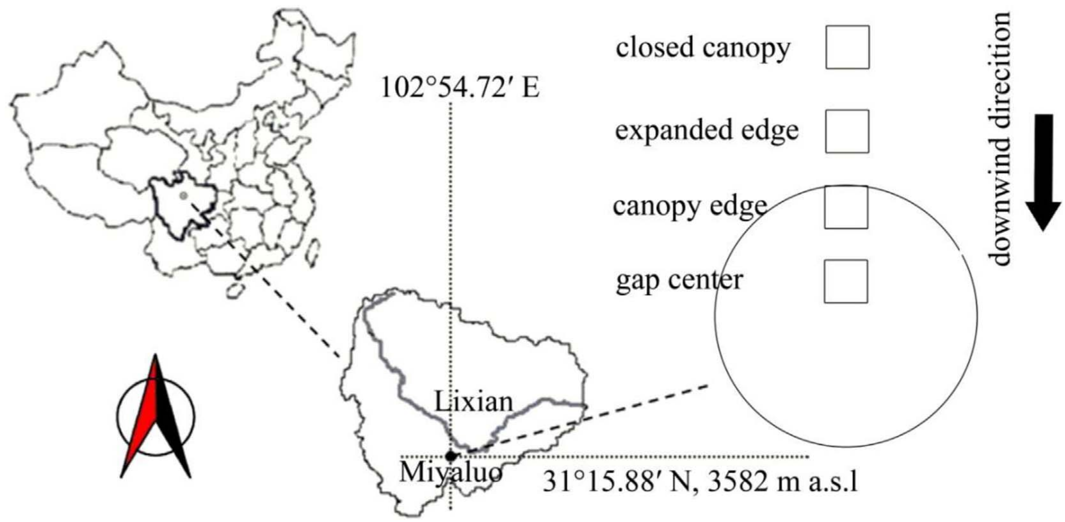

Fig. 1. Location and sampling positions of the selected gaps in the eastern Tibet Plateau. The depicted circle (25 m diameter) is an example of a forest gap, and the squares (4 × 4 m) represent the different gap positions selected for sampling.

crucial roles in nursing invertebrate and microbial biodiversity and conserving soil and water (Yang et al., 2007; Grüneberg et al., 2013). Soil microbial biomass, as a sensitive indicator of forest management practices (Bauhus and Barthel, 1995b), can be susceptible to microclimate variation such as thinning and canopy removal. Therefore, an understanding of biological and biochemical properties in the organic horizon is fundamental to understanding nutrient cycling in conjunction with associated microclimate variation.

Canopy gaps facilitate dramatic top-down trophic interactions between vegetation and soil microbe-mediated processes (Bauhus and Barthel, 1995a; Schmidt et al., 2007). Many studies of canopy gaps have concentrated on aboveground processes (Wu et al., 2013), whereas relatively few studies have addressed the belowground effects of canopy gaps, such as the influences of tree species (Kanerva and Smolander, 2007), treefall gap size or soil properties on soil microbial biomass (Arunachalam et al., 1996). However, whether gap creation alters microbial nutrient pools in surface organic horizons and how these pools relate to the total organic carbon (TOC), total nitrogen (TN) and total phosphorus (TP) are unknown. We hypothesized that gap creation will alter microbial nutrient pools and accelerate soil organic C retention by soil microbial biomass in the organic horizon. Limited information is presently available on the spatial and temporal dynamics of microbial pools and their influences on the responses of soil organic matter and nutrient flux to canopy gaps in subalpine fir forests. This study was designed (1) to determine the effects of canopy gaps on microbial C, microbial nitrogen (N) and microbial phosphorus (P) and their stoichiometric relationships in the organic horizon and (2) to investigate the microbial pools for TOC, TN and TP and the responses of stored TOC, TN and TP to canopy gaps.

2. Materials and methods

2.1. Site description

The study site is located at the long-term subalpine forest ecosystem research station, Miyaluo Nature Reserve (31°14′–31°19′N, 102°53′–102°57′E, 2458–4619 m above sea level (a.s.l.)), Li County, Sichuan, Southwest China. The subalpine forest is located along the upper reaches of the Yangtze River on the eastern Tibetan Plateau, which is characterised by seasonal snow cover for half the year (Wu et al., 2010) and freeze–thaw cycles in the autumn and spring (Yang et al., 2007). The annual precipitation varies with elevation and ranges from 680 mm at 2458 m a.s.l. to 1260 mm at 4619 m a.s.l. The mean annual air temperature in this region is 2–4 °C, and the maximum and minimum air temperatures are 23 °C and -18 °C, respectively. The forest soil is an acid-udic cambisol (USDA soil taxonomic system), and the organic horizon is a typical mor type humus. Snow cover lasts from November to April of the following year. The main forest vegetation is *Abies faxoniana* in the primary forest, where *A. faxoniana*, *Betula albo-sinensis*, *Larix mastersiana* and *Sabina saltuaria* are the representative tree species. The understory plants are dominated by *Festuca ovina*, *Berberis sargentiana*, *Carex* spp., *Cystopteris montana* and *Rhododendron delavayi* (Wu et al., 2015). The percent cover of these understory plants is approximately 50%, and the crown density is approximately 0.7. The most common method of natural gap formation in primary coniferous forest is breakage at the base of gap makers. Gap makers mainly consist of trees that have been uprooted, trees with broken trunks, and dead trees that form a gap. Most gap makers die due to both age and their reduced capability to resist adverse surroundings, such as frequent snowstorms (Wu et al., 2013). Gaps can be classified into two types according to Runkle (1981): canopy gaps, defined by the projected area directly under a canopy opening that has appeared due to dead trees or branches, and expanded gaps, defined by the area of the canopy gap plus the adjacent area that extends to the bases of the bordering canopy trees. In our study, the canopy gaps were formed by natural disturbances in the subalpine coniferous forest. The size of most of the canopy gaps was less than 200 m^2, and the average sizes of the canopy gap and expanded gap were 72 m^2 and 154 m^2, respectively (Xian et al., 2004). The average tree age is 130 years. Three canopy gaps that each measured 25 m in diameter (gap circle diameter) and were surrounded by similar canopy densities within a dominant fir forest (31°15′N, 102°54′E, 3582 m a.s.l.) were chosen for measurement. The three gaps were separated by at least 500 m. For each gap, four 4 × 4-m quadrats were established at 6-m intervals from the center to the canopy, representing the gap center, canopy edge, expanded edge and closed canopy, to ensure adequate sampling of the heterogeneous micro-environmental conditions (Fig. 1). There were a few shrubs in the canopy gaps. The organic horizon was characterised as a mor profile and contained a fresh litter layer, a fragmented litter layer and a humified litter layer (Wu et al., 2015). The fresh litter layer consisted of recently fallen needles from the annual litterfall; the fragmented litter layer consisted of large, fragmented needles; and the humified litter layer consisted of small needle fragments mixed with humic particles. Thus, these three layers represented the three stages of plant litter decomposition. We measured the thicknesses of these three layers, which varied with position within the gap locations. Layer thickness increased