Tree regeneration retards decomposition in a temperate mountain soil after forest gap disturbance

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ABSTRACT

Disturbances significantly affect the carbon (C) cycle of forest ecosystems. Surviving trees from an understory layer are recognized to play an important role in post-disturbance C dynamics. However, their influence on decomposition of soil organic matter (SOM), an important ecosystem C pool, has yet to be rigorously investigated. Over four consecutive years, we investigated the effects of advance spruce regeneration on decomposition processes in a mountain soil after forest gap disturbance. Gap disturbance was accomplished by clear cut harvest and decomposition was assessed by combining measurements of soil CO_2 efflux, heterotrophic respiration, soil enzymes activity, and mass loss from standardized litter bags. Soil CO_2 efflux showed no response to gap formation, independent of whether regeneration was present or absent, indicating that reduced autotrophic respiration was offset by accelerated heterotrophic respiration from decomposing microbes. Incubation studies revealed no effects of gap disturbance on heterotrophic respiration and its temperature sensitivity under controlled lab conditions. Since potential enzyme activities, at a given temperature, did not respond to gap formation either, it appears that neither C nor other nutrient limitations of the decomposing microbes changed in this SOM-rich mountain forest soil after disturbance. Mass loss of standardized litter was ~5% higher after gap formation in plots without regeneration, while under the regeneration it remained at control stand levels. Our findings indicate that canopy removal by gap disturbance lead to an increase in decomposition, primarily due to warmer soil conditions. However, an established regeneration retards decomposition due to its modulating effect on soil temperature. Our study therefore shows that facilitating regeneration pre-disturbance can reduce post-disturbance soil C losses from decomposition.

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1. Introduction

Forests of the northern hemisphere store large amounts of carbon (C) and thus represent a globally important C sink (Goodale et al., 2002; Luyssaert et al., 2010). Natural and man-made disturbances can, however, significantly alter the C balance and the C sequestration potential of these ecosystems (Kowalski et al., 2004; Kurz et al., 2008; Amiro et al., 2010; Paul-Limoges et al., 2015).

Beside the changes in ecosystem CO_2 fluxes associated with photosynthesis and autotrophic respiration, disturbances can impact heavily on the CO_2 efflux coupled to the decomposition of soil organic matter (SOM). Although disturbance type (e.g. clear cut harvest, bark beetle attack, fire), severity (e.g. single tree mortality, stand replacing mortality), and time since disturbance (e.g. weeks, decades) might influence decomposition differently, recent meta-analyses have shown that disturbances generally cause long-lasting C losses from forest soils (Nave et al., 2010; Thom and Seidl, 2015; Zhang et al., 2015). If, and to what extent a decrease in soil C stocks is actually related to altered decomposition rates and/or changes in C input to soil is, however, still uncertain (Yanai et al., 2003; Spielvogel et al., 2006; Christophel et al., 2015). Furthermore, how the post-disturbance soil C pool is influenced by surviving sub-canopy trees has yet to be addressed in detail.

Live tree legacies are of considerable importance for ecosystem resilience (Seidl et al., 2014). Surviving trees from a sub-canopy layer (e.g. seedlings and saplings from regeneration, sub-

dominant trees) are recognized to influence biomass production and CO_2 uptake of disturbed forest ecosystems (Brown et al., 2010; Bowler et al., 2012; Hicke et al., 2012; Mathys et al., 2013; Emmel et al., 2014). CO_2 uptake from remaining trees and understory vegetation, for example, was assumed to enable bark beetle attacked forests to return to C neutrality by about half a decade faster than forests which were harvested by clear cutting (Brown et al., 2010). However, the return to C neutrality might not only be related to photosynthetic uptake of surviving trees, but also to their effects on decomposition processes and the release of CO_2 from soil. Since decomposition is strongly influenced by temperature and moisture (Davidson and Janssens, 2006), a modulating effect of surviving trees on soil temperature potentially results in retarded decomposition and associated respiration from soil heterotrophs compared to sites without regeneration (Mayer et al., 2017). Alterations of soil moisture by root uptake and crown interception may additionally affect microbial activity. On the other hand, root exudation by surviving trees may have a stimulatory impact on decomposition. It has been shown that a reduced belowground allocation of photosynthates decreases not only root activity (i.e. exudation, respiration) (Högberg et al., 2001; Scott-Denton et al., 2006), but also affects factors influencing litter and SOM decay e.g. extracellular enzyme activity (e.g. glucosidase, xylosidase, phenol oxidase), microbial biomass, and microbial community composition (Weintraub et al., 2007; Kaiser et al., 2010; Koranda et al., 2011; Subke et al., 2011; Stursova et al., 2014; Brzostek et al., 2015). Stursova et al. (2014) for example, reported an overall reduction in fungal biomass together with the decline in root symbionts after a bark-beetle induce tree dieback, despite a relative increase in saprotrophic fungi abundance.

In the present study, we investigated whether and how the presence of advance tree regeneration (i.e. established pre-disturbance in the understory) impacts decomposition processes in a temperate mountain forest soil following gap-scale disturbance. Understanding the role of regeneration in organic matter decomposition is necessary to understand and model ecosystem resilience and post-disturbance C dynamics. For the studied forest soil, we hypothesized that gap formation will increase decomposition primarily due to warmer soil conditions, while the presence of established tree regeneration dampens this respective increase due to its modulating effect on soil climate. We tested our hypothesis by measuring a set of indices for decomposition in the field (soil CO_2 efflux, standardized litter decomposition) and under controlled laboratory conditions (heterotrophic respiration and potential extracellular enzyme activity) over the course of four consecutive years. Disturbance was simulated by experimental gap formation after a pre-treatment period of several months. In contrast to studies along chronosequences (Johnson and Miyanishi, 2008; Paul-Limoges et al., 2015), this approach allowed initial site conditions to be taken into account.

2. Materials and methods

2.1. Study site

The study site is a montane temperate mixed forest stand, located in the Höllengebirge mountain range, Austrian Alps (47°47′19″ N, 13°38′21″ E). Altitude is about 1000 m a.s.l and exposition is south to south-west. Mean annual air temperature and precipitation is 6.6 °C and 1964 mm, respectively (20 year average; data provided by Zentralanstalt für Meteorologie und Geodynamik, ZAMG). The ~220 year old stand is dominated by European beech (*Fagus sylvatica*), Norway spruce (*Picea abies*) and silver fir (*Abies alba*). Advance regeneration, dominated by ca. 15 year old Norway spruce trees, is unevenly distributed in the understory. The uneven

distribution reflects the previous scattered bark-beetle attacks and related small canopy openings, which were subsequently closed again by beech by time the study started. A very sparse ground vegetation layer (<3% cover) is comprised of herbs (*Mycelis muralis, Prenanthes purpurea*) and grasses (*Calamagrostis varia, Carex alba*). The bedrock is limestone in paragenesis with dolomite. Soil types are Chromic Cambisols, Rendzic Leptosols and Folic Histosols (IUSS Working Group WRB, 2006) with the soil texture of the mineral horizons varying between silt and loam (Hollaus, 2012). Humus types are Moder and Tangel (Zanella et al., 2011). Soil organic carbon stocks were estimated at ~70 t ha^{-1} (Mayer et al., 2017).

2.2. Experimental set-up

In spring 2013 four areas (~400–600 m^2) along a contour line were selected for measurements. The selected areas were similar regarding overstory stand structure, topographic features, and soil and humus types. Two areas were dominated by advance regeneration of spruce saplings (Table 1) while in the other two areas regeneration was absent. In August 2013 (after 4 months of pre-treatment measurements) all canopy trees (20 trees) of two areas next to each other (one with-, and one without regeneration) were removed by clear cut harvest, resulting in an experimental gap of ~1000 m^2. Note that advance regeneration was not removed during the harvest operation, and even in the third year after gap formation ground vegetation (grasses and herbs) remained scarce (<3%). All branches and most of the logs were removed from the areas. The harvested areas were designated as "gap" and "gap-regeneration" treatments, respectively. The two remaining areas served as control stands and were accordingly designated as "control" and "control-regeneration" treatments. In May 2013 12 plots (1 × 1 m) were selected within each of the 4 treatments. Control and control-regeneration plots were distributed randomly (note: control plots were established as part of an earlier experiment). To cover the full extent of gap and gap-regeneration treatments, plots were established along two ~30 m north-south (8 plots), and ~15 m east-west transects (4 plots), respectively (Fig. S1). One plot in the control-regeneration treatment was destroyed by a blown-over tree in summer 2013 and was not subsequently replaced. In the centre of each plot one plastic collar (10 cm diameter, 4 cm height) was installed (3 cm soil insertion depth) for soil CO_2 efflux measurements. Collars were installed 1 week prior to the first measurements and kept in place throughout the study.

2.3. Soil CO_2 efflux and soil climate measurements

From spring 2013 (~4 month before gap formation) until autumn 2016 soil CO_2 efflux was measured by means of a portable infrared gas analyser (EGM-4, PP Systems International, Inc., Amesbury, MA, USA) and an attached respiration chamber (SRC-1, PP Systems International, Inc., Amesbury, MA, USA) during snow-free conditions. Efflux measurements were conducted by connecting the chamber to the plastic collars for a maximum of ~2 min. For detailed information on measurement procedure see Mayer et al. (2014). During efflux measurements soil temperature (5 cm depth) and moisture (as volumetric water content (vol%), 0–7 cm depth) were recorded next to each collar. Soil temperature and moisture were measured with a handheld thermometer and a calibrated soil moisture meter (Field Scout, Spectrum Technologies, Inc., Plainfield, IL, USA), respectively. In order to prevent a temporal sampling bias, the measurement order of plots and treatments was changed regularly.

In the centre of the gap and gap-regeneration treatments, soil temperature and moisture (5 cm depth) were also measured continuously (30 min logging interval) by means of combined