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Decomposition of beech (*Fagus sylvatica*) and pine (*Pinus nigra*) litter along an Alpine elevation gradient: Decay and nutrient release

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ABSTRACT

Litter decomposition is an important process for cycling of nutrients in terrestrial ecosystems. The objective of this study was to evaluate direct and indirect effects of climate on litter decomposition along an altitudinal gradient in a temperate Alpine region. Foliar litter of European beech (*Fagus sylvatica*) and Black pine (*Pinus nigra*) was incubated in litterbags during two years in the Hochschwab massif of the Northern Limestone Alps of Austria. Eight incubation sites were selected following an altitudinal/climatic transect from 1900 to 900 m asl. The average remaining mass after two years of decomposition amounted to 54% (beech) and 50% (pine). Net release of N, P, Na, Al, Fe and Mn was higher in pine than in beech litter due to high immobilization (retention) rates of beech litter. However, pine litter retained more Ca than beech litter. Altitude retarded decay (mass loss and associated C release) in beech litter during the first year only but had a longer lasting effect on decaying pine litter. Altitude comprises a suite of highly auto-correlated characteristics (climate, vegetation, litter, soil chemistry, soil microbiology, snow cover) that influence litter decomposition. Hence, decay and nutrient release of incubated litter is difficult to predict by altitude, except during the early stage of decomposition, which seemed to be controlled by climate. Reciprocal litter transplant along the elevation gradient yielded even relatively higher decay of pine litter on beech forest sites after a two-year adaptation period of the microbial community.

1. Introduction

High-mountain ecosystems are especially vulnerable to climate change, since these areas will experience stronger temperature fluctuations than the global climate (Schröter et al., 2005). Mountain regions cover about one fifth of the earth's continental area but their ecological and economical importance, e.g. regarding water cycle regulation, reaches far beyond their boundaries (Beniston et al., 1997), and their soil organic carbon stocks are among the highest in terrestrial biomes (Djukic et al., 2010b; Ward et al., 2014).

Hence, research on decomposition processes, their relation to soil properties and their regulating factors in alpine ecosystems is important. Decomposition processes are important for cycling of nutrients in terrestrial ecosystems and are influenced by macro- and microclimate, litter quality, activity of decomposing organisms and soil nutrient status (Berger and Berger, 2012, 2014; Berger et al., 2010; Coûteaux et al., 1995; Gavazov, 2010; Prescott, 2010; Vesterdal, 1999). Manipulation experiments such as soil warming (Melillo et al., 2002; Schindlbacher et al., 2011) have provided useful information on short-term soil responses to changed climatic conditions. However, such experiments offer little insight into responses that occur over longer periods, such as migration of vegetation zones. Climate-gradient studies help filling this gap via "space-for-climate" substitution. Along such gradients (climosequences), the combined effects of several factors that change with climate, can be studied, since climate change is not a mere change in temperature. Direct and indirect effects of climate may change i) soil water regimes, i.e. waterlogging or surface drying (Davidson and Janssens, 2006; Gavazov, 2010; Sjögersten and Wookey, 2004), ii) soil insulation through snow cover (Hobbie et al., 2000; Williams et al., 1998), and iii) climate driven shifts in species composition and associated litter quality (Cornelissen et al., 2007; Cornwell et al., 2008; Theurillat and Guisan, 2001). It is the combination of all these factors that will govern litter decomposition under changing climatic conditions.

Increasing elevation can select for plant species and functional groups possessing functional traits that are better adapted to nutrient limitation (Vitousek et al., 1988). The relative biomass or abundance of dominant functional groups of soil organisms can be highly responsive to elevation. For instance, the ratio of fungal to bacterial biomass can increase with elevation (Sundqvist et al., 2013; Wagai et al.,

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2011). Belowground consumers are intrinsically linked to aboveground communities (Wardle, 2002). Hence, changes in vegetation can shape the responses of soil communities to elevation. In a recent comprehensive review Sundqvist et al. (2013) concluded that decomposer organism densities and community composition often respond to elevation, but only few studies have explicitly tested the consequence of this fact for litter decomposition rates.

That is why, we performed a study on litter decomposition, based on a climosequence approach in the Hochschwab massif of the Northern Limestone Alps. Foliar litter of European beech (*Fagus sylvatica*) and Black pine (*Pinus nigra*) was incubated at eight sites along an elevation gradient of 1000 m (6 different altitudes at 200 m intervals) over a two-year period. Vegetation changed from alpine grassland (1900 m asl) over shrubland with mountain pine (*Pinus mugo*) bushes towards spruce (*Picea abies*) stands and finally montane beech (*F. sylvatica*) forests (900 m asl), characterized by specific climatic conditions and microbial community compositions. Previous work along this elevational gradient by Djukic et al. (2010a,b, 2012) and Duboc et al. (2012) demonstrated that differences in soil organic matter stocks and characteristics were more closely related to vegetation composition, their C input and litter quality than to variations in climatic conditions along the elevation gradient. The highest amounts of soil microbial biomass were found at sites with high soil pHs and low C/N ratios and the bacterial to fungal biomass ratio increased significantly from forest sites to shrubland and grassland sites.

The overall objective of this study was to evaluate direct and indirect effects of climate on decomposition of beech and pine litters. Below we have developed our objectives into four specific research questions accompanied by corresponding hypotheses.

1) How do beech and pine litter differ in mass loss and nutrient release during the first two years of decomposition? We used litter of beech (low-elevation sites) and pine (high-elevation sites) to test differences between these species, since it is commonly believed, that broadleaf litter decomposes faster than needle litter (Prescott et al., 2004). We hypothesized that mass loss and nutrient release are higher for beech than for pine litter.
2) Are mass loss and nutrient release more closely related to the litter type or the site of incubation (forest type), and do litter of beech and pine decay faster in their respective home environments? Using relatively (so-called) high (beech) and low (pine) quality litter enabled testing home-field advantages (HFAs) via reciprocal litter transplants at the pine and beech sites: Decomposer communities are often adapted to degrade the type of leaf litter that they encounter, which typically comes from the plant species above them, resulting in litter decomposing more rapidly in its “home” environment than in an “away” environment (Ayres et al., 2009; Veen et al., 2015; Wallenstein et al., 2013). However, several studies do not support the idea of increased decomposition of litter in its home environment, as outlined in a recent review on plant litter–decomposer affinity effects by Austin et al. (2014). Recent analyses suggest that the innate ability, or functional breadth, of the microbial community may overestimate or obscure HFA effects (Keiser et al., 2013). If litter quality is the sole driver, then more recalcitrant litter (e.g., pine; higher C/N ratio and lignin content) will decompose more slowly with any soil microbial community, regardless of its origin. On the other hand, soil microbial community may modify litter decomposition, whereby low-nutrient ecosystems have high microbial functional breadth in response to the diversity of compounds found in chemically-complex litter (the opposite is true for nutrient-rich ecosystems). Hence, in accordance with Keiser et al. (2013) we hypothesized that the soil microbial community at the pine sites (higher elevation, nutrient poor) will decompose high- (beech) and low quality (pine) litter at similar rates and the microbial community at the beech sites (lower elevation, nutrient rich) will decompose pine litter at slower rates.
3) Does altitude affect mass loss and nutrient release? Temperature is a well-known direct driver of litter decomposition, and litter mass loss and nutrient release are often greater at lower elevations due to warmer conditions (Sundqvist et al., 2013). Hence, we hypothesized that mass loss and nutrient release of decomposing litter will decline with increasing altitude, though indirect effects of climate changes along an elevation gradient (e.g., shifts in species composition and associated litter quality; see above) may obscure direct climate effects.
4) Which altitudinal changes in the environment (climate, vegetation, litter, soil, microbial community) are most closely associated with the observed decomposition patterns? Berg and McClaugherty (2008) concluded that climate is important during early stages but the later phase of litter decomposition appears to be strongly influenced by litter chemistry. We must be cautious when generalizing such statements, since responses to elevation are commonly driven by changes in temperature, and many community- and ecosystem-level variables (Sundqvist et al., 2013). Hence, given this complexity, our capacity to predict responses to elevational gradients is often limited. Nevertheless, we hypothesized that the use of simple regression techniques will contribute to disentangling direct and indirect effects of climate on litter decomposition.

2. Material and methods

2.1. Study sites

The study area is located in the Hochschwab massif of the Northern Limestone Alps. Eight sites were selected for this study along an elevation gradient from 1900 to 900 m (6 different altitudes at 200 m intervals). Site characteristics are given in Table 1. There are two sites at 1300 m (sites 1302 and 1301) and at 900 m (sites 902 and 901), in all other cases one site per altitude (sites 1900, 1700, 1500, 1100). The elevation gradient represents a climosequence from the alpine to the subalpine and montane climate/vegetation zones. Mean annual temperature ranges from 2.1 to 6.2 °C, mean annual precipitation from 1725 to 1178 mm and mean annual snow cover from 221 to 123 days between the altitudes 1900 to 900 m asl. The vegetation along the transect changes from alpine grasses and mountain pine (*P. mugo*) bushes above the timberline over spruce (*P. abies*) – and mixed spruce–beech – to beech (*F. sylvatica*) forests. All study sites are on calcareous parent material and exhibit similar soil type (Leptic Histosol, IUSS, 2006) and soil depth (between 20 and 30 cm).

2.2. Soils

Five replicate soil monoliths (area 20 × 20 cm) were collected from each of the eight sites and divided into the soil depths 0–5 and 5–10 cm. The forest litter layer (at the forested sites only) above the 0–5 cm soil depth layer was not part of this study. Fine soil, separated by sieving <2 mm, was analyzed for total C and N contents by dry combustion and carbonate was measured gas-volumetrically. Organic C was calculated as the difference of total and carbonate C. For simplicity, organic C is abbreviated C throughout the paper. Soil pH was measured in deionized H_2O at a soil:solution ratio of 1:10. More detailed methods of soil sampling and chemical analyses are given by Djukic et al. (2010b).

2.3. Litterbag experiment

We used a litterbag approach to measure decay and nutrient release. Details are given by Duboc et al. (2012), who used the identical litterbags at 6 sites within their study on molecular characteristics of litter materials during different decompositional stages. Shed leaves of European beech (*F. sylvatica*) and needles of Black pine (*P. nigra*) were collected in November 2006. The litter was dried at 50 °C for 24 h whereby only whole, intact leaves/needles were used, and subsequently stored at room temperature. The litterbags were made of polyethylene