Vertical gradients of potential enzyme activities in soil profiles of European beech, Norway spruce and Scots pine dominated forest sites

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ABSTRACT

Management of forest sites has the potential to modulate soil organic matter decomposition by changing the catalytic properties of soil microorganisms within a soil profile. In this study we examined the impact of forest management intensity and soil physico-chemical properties on the variation of enzyme activities (β-glucosidase, β-xylosidase, α-glucosidase, phenol oxidase, N-acetyl-glucosaminidase, L-leucine aminopeptidase, phosphatase) in the topsoil and two subsoil horizons in three German regions (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb). The sandy soils in the Schorfheide-Chorin (SCH) showed lower ratios of the activity of carbon (C) acquiring enzymes (β-glucosidase) relative to nitrogen (N) acquiring enzymes (N-acetyl-glucosaminidase + L-leucine aminopeptidase), and activity of C acquiring enzymes relative to phosphorous (P) acquiring enzymes (phosphatase) than the finer textured soils in the Hainich-Dün (HAI) and Schwäbische Alb (ALB), indicating a shift in investment to N and P acquisition in the SCH. All enzyme activities, except phenol oxidase activity, decreased in deeper soil horizons as concentrations of organic C and total N did, while the decrease was much stronger from the topsoil to the first subsoil horizon than from the first subsoil to the second subsoil horizon. In contrast, phenol oxidase activity showed no significant decrease towards deeper soil horizons. Additionally, enzyme activities responsible for the degradation of more recalcitrant C relative to labile C compounds increased in the two subsoil horizons. Subsoil horizons in all regions also indicate a shift to higher N acquisition, while the strength of the shift depended on the soil type. Further, our results clearly showed that soil properties explained most of the total variance of enzyme activities in all soil horizons followed by study region, while forest management intensity had no significant impact on enzyme activities. Among all included soil properties, the clay content was the variable that explained the highest proportion of variance in enzyme activities with higher enzyme activities in clay rich soils. Our results highlight the need for large scale studies including different regions and their environmental conditions in order to derive general conclusions on which factors (anthropogenic or environmental) are most influential on enzyme activities in the whole soil profile in the long term at the regional scale.

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Introduction

Forest soils play an important role in the global C cycle (Jobággy and Jackson, 2000). In the context of the global nutrient cycles, extracellular enzymes mediate the decomposition of soil organic matter (OM) and mineralize soil organic carbon (OC), nitrogen (N) and phosphorus (P) (Bandick and Dick, 1999; Finzi et al., 2006). In addition to environmental changes, human activities influence the nutrient cycling in forests through different forest management practices including the selection of tree species, harvesting and thinning. The type of forest management determines the amount and quality of plant and root litter input entering the soil, and thus enzyme activity patterns. Weand et al. (2010) found that different tree species have distinct enzyme activity patterns due to varying litter quality. Harvesting often resulted in a decline of enzyme activities due to reduced microbial biomass as a result of smaller litter input and changes in soil microclimate (Hassett and Zak, 2005). Thinning of a 62-year-old pine stand, however, had no notable effect on enzyme activities (Maassen et al., 2006). While the previous studies mostly determined short-term responses (<10

years) of different harvesting intensities on enzyme activities, the question remains, whether long-term forest management practices (>20 years) also have effects on enzyme activities at the stand level. When forest management on soil enzyme activity is studied over a larger spatial scale, inherent climatic and edaphic differences among study regions need to be considered. Usually, results obtained within one soil type can often not be generalized and transferred to other soil types (Gianfreda et al., 2005). Thus, it is necessary to perform enzymatic studies in several regions with their specific soil types and properties to identify patterns shared among different regions.

Surface soil horizons – often less than 10 cm thick – are rich in fresh-C inputs that enter the soil as leaf litter and root exudates. These organic compounds serve as an important energy source for microorganisms and enable the production of extracellular enzymes. However, a considerable amount of the soil C within the soil profile is also stored in subsoil horizons despite low C concentrations (Batjes, 1996; Wang et al., 2010). This can be explained by the higher thickness of subsoil horizons which are in total often more than 50 cm thick. In subsoil horizons, where fresh-C inputs are smaller in comparison to surface soil horizons and a large proportion of soil OC is stabilized by interaction with mineral surfaces, only small amounts of OC are easily accessible for microorganisms (Schöning and Kögel-Knabner, 2006; Fontaine et al., 2007; Kögel-Knabner et al., 2008). This is reflected in the microbial biomass, which typically declines with soil depth (Taylor et al., 2002). To date, most studies on enzyme activities have been conducted with surface soils (Kandeler et al., 1999; Andersson et al., 2004; DeForest et al., 2004), whereas respective studies in subsoils are rare (Taylor et al., 2002; Zhang et al., 2005; Sotomayor-Ramírez et al., 2009).

The ratios between energy and nutrient acquiring activities of extracellular enzymes (e.g. ratio of β-glucosidase activity: phosphatase activity, an indicator of potential C:P acquisition activity) can be used to follow shifts in nutrient or energy supply and demand (Sinsabaugh et al., 2008, 2009; McDaniel et al., 2013). Enzyme activity ratios have been used to study ecoenzymatic stoichiometry of terrestrial soils and freshwater sediments (Sinsabaugh et al., 2009, 2012), the recalcitrance of OM across different forests, prairies, scrublands and deserts (Sinsabaugh and Follstad Shah, 2011), and effects of climate and soil properties across ecosystems (Sinsabaugh et al., 2008; McDaniel et al., 2013). To the best of our knowledge, no study has followed the vertical gradient of enzyme activity ratios in forested soil profiles.

In this study we determined soil enzyme activities mediating the degradation of cellulose, hemicellulose, starch, lignin, chitin, proteins and organic phosphorous at 25 forest plots. The forest plots were distributed over three German regions. Further, enzyme activities were studied in topsoil and subsoil horizons allowing us to compare the latitudinal and vertical variation of enzyme activities. The study sites included coniferous and deciduous forests that were managed as forests under age class management, deciduous forest under selection cutting, and unmanaged deciduous forests. Enzyme activity ratios were used to identify shifts in supply and demand for soil C, N and P between study regions and within the soil profile.

Materials and methods

Study sites

This study was carried out at 25 forest plots located in the Schorfheide-Chorin (SCH) in northern Germany, Hainich-Dün (HAI) in central Germany, and Schwäbische Alb (ALB) in southern Germany (Fischer et al., 2010), and constitute a latitudinal gradient of 800 km (Supplementary Table 1). Mean annual temperature ranges from 6 to 7 °C in the ALB, 6.5 to 8.0 °C in the HAI, and 8.0 to 8.5 °C in the SCH. Mean annual precipitation increased in the order SCH (500–600 mm), HAI (500–800 mm) and ALB (700–1000 mm). In the SCH glacial till was the dominant parent material, which was often covered by aeolian and fluvial sand. The parent material of the HAI was loess over Triassic shell lime stone. ALB soils were developed on Jurassic lime stone. Soils in the SCH were Arenosols, Luvisols in the HAI, and Cambisols in the ALB (IUSS Working Group WRB, 2006). The plots in each region covered three forest management types: coniferous and deciduous forests under age-class management, and unmanaged deciduous forests (Supplementary Table 1). Forests under age-class management were even-aged regenerations after a clear cut with harvesting intervals of 80–120 years. Unmanaged deciduous forests are uneven-aged forests with trees of different sizes and ages. In the SCH no trees have been harvested since 1990 in the unmanaged deciduous forests (Biosphere Reserve "Schorfheide-Chorin"). In the unmanaged deciduous forests of the HAI no trees have been harvested since 1997 (National park), and from 1965 to 1997 under the use of a military training ground, only small amounts of wood were extracted. Plots of the unmanaged deciduous forest in the ALB experienced restricted timber harvesting under nature conservation aspects (e.g. removal of spruce trees to protect old beech trees), or were not managed at all for the last 80 years. In the HAI beech forest under selection cutting was studied as an additional forest management type. These forests are uneven-aged forests with trees of different sizes and ages, and trees are harvested selectively. Number of replicates per management type differed (Supplementary Table 1), because only plots with the main soil group in the respective region were considered. Plots of the managed and unmanaged deciduous forests are dominated by European beech (*Fagus sylvatica* L.) in all regions, while in the managed coniferous forest plots the dominant tree species is Scots pine *(Pinus sylvestris* L.) in the SCH, and Norway spruce *(Picea abies* L.) in the HAI and ALB. The silvicultural management intensity indicator (SMI) proposed by Schall and Ammer (2013) was used to quantify silvicultural management intensity of each forest plot. The SMI is calculated as the average of two components, the risk of stand loss and the stand density. The risk component of the SMI reflects the species-related survival probabilities and rotation periods, while the stand density component quantifies removal effects and the regeneration method using biomass related to a reference.

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.pedobi.2014.03.003.

Soil sampling

Soil samples were collected in April 2008 just before foliation started. At each plot (20 m × 20 m) the aeromorphic organic layer was sampled with a metal frame at five sampling points (20 cm × 20 cm in SCH and ALB, 40 cm × 40 cm in HAI). The mineral soil was then sampled down to the bedrock using a motor driven auger (diameter of 8.3 cm). Arenosols in the SCH and Luvisols in the HAI comprised three mineral soil horizons, while the Cambisols in the ALB had two mineral soil horizons. The first mineral soil horizon, the AEh horizon in the SCH, and the Ah horizon in the HAI and the ALB was termed as A horizon. The second soil horizon, ABhw in the SCH, BEw/BEg in the HAI and Btw in the ALB were designated as B1 horizon (first subsoil horizon). The third soil horizon, Bw in the SCH and Btg in the HAI were termed as B2 horizon (second subsoil horizon). Samples were taken from each soil horizon, stored in ice boxes and transported to the field lab. The samples from the organic layers were oven-dried at 70 °C for 1 week. Mineral soil samples were split up into two sub-samples after removal of coarse roots and stones >2 mm. One sub-sample was air-dried